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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 ($<3 \mu\text{M}$) 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 ($<0.4 \text{ nM}$ on average) supported an algal community that was dominated by smaller size algae ($<20 \mu\text{m}$). Deep wind-mixed layers ($>100 \text{ m}$ 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.

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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 $0.3 \mu\text{g l}^{-1}$ (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 antarctica* 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 *Chrysomonadales*. 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

Table 1
Final optimized pigment ratios after CHEMTAX-analyses for the two distinguished bins.

Class	Chl c_2	Chl c_3	Peri	Fuco	19'-Hexfuco	Allo	Chl b
<i>0–50 m</i>							
Prasinophytes	0	0	0	0	0	0	0.706
Dinoflagellates	0	0	0.585	0	0	0	0
Cryptophytes	0.130	0	0	0	0	0.229	0
Haptophytes_P	0.485	0.604	0	0.181	0.383	0	0
Haptophytes_C	0	0	0	0.062	0.646	0	0
Chlorophytes	0	0	0	0	0	0	0.074
Diatoms_1	0.372	0	0	0.259	0	0	0
Diatoms_2	0	0.006	0	0.745	0	0	0
<i>50–100 m</i>							
Prasinophytes	0	0	0	0	0	0	0.706
Dinoflagellates	0	0	0.500	0	0	0	0
Cryptophytes	0.328	0	0	0	0	0.635	0
Haptophytes_P	0.729	0.837	0	0.241	0.266	0	0
Haptophytes_C	0	0	0	0.050	0.610	0	0
Chlorophytes	0	0	0	0	0	0	0.1
Diatoms_1	0.555	0	0	0.457	0	0	0
Diatoms_2	0	0.003	0	0.639	0	0	0

Abbreviations: Chl: chlorophyll; Peri: peridinin; Fuco: fucoxanthin; 19'-Hexfuco: 19'-hexanoyloxyfucoxanthin; Allo: alloxanthin.

by microscopy (single cells and small colonies). Haptophyceae_P did, however, not exclusively refer to *Phaeocystis*. Dinoflagellates were described as a separate class that was defined by peridinin. However, as many dinoflagellates do not carry peridinin, but contain a variety of pigments, this is a very difficult group to identify (see Wright et al., 2010). For distribution patterns of dinoflagellates, only microscopic data were used. Chlorophytes were linked to Chl b . However, this group may also include prasinophytes (Roy et al., 2011). Cryptophytes were based on the presence of alloxanthin. Some accessory pigments were excluded from the initial matrix as the concentrations of these pigments were either too low (e.g. lutein) or too variable (e.g. 19'-butanoyloxyfucoxanthin), to contribute significantly to an accurate outcome of CHEMTAX analysis.

For the determination of cell numbers and species composition, 250 ml seawater samples were taken at 40 m depth, and subsequently preserved in a 0.5% lugol solution for analysis at home. Cell counts and volume estimates were done with an inverted microscope (Olympus IMT-2) with >200 cells counted per sample (see also van Oijen et al., 2003 for an overview of dominant species). Cell volume was converted to carbon following Menden-Deuer and Lessard (2000), using the following carbon-to-volume relationships:

$$\text{Carbon mass (pg C cell}^{-1}\text{)} = 0.444 * \text{cell volume}^{0.864} \text{ (HNF)} \quad (1)$$

$$\text{Carbon mass (pg C cell}^{-1}\text{)} = 0.230 * \text{cell volume}^{0.984} \text{ (HNF)} \quad (2)$$

$$\text{Carbon mass (pg C cell}^{-1}\text{)} = 0.679 * \text{cell volume}^{0.841} \text{ (tintinnids)} \quad (3)$$

$$\text{Carbon mass (pg C cell}^{-1}\text{)} = 0.288 * \text{cell volume}^{0.811} \text{ (diatoms)} \quad (4)$$

$$\text{Carbon mass (pg C cell}^{-1}\text{)} = 0.216 * \text{cell volume}^{0.939} \text{ (all others).} \quad (5)$$

In which HNF stands for heterotrophic nanoflagellates, and cell volume is expressed in μm^3 . The algal carbon data are also incorporated in the extensive databases presented by Leblanc et al. (2012) and Vogt et al. (2012).

3. Results

3.1. Nutrients and algal abundance along the transect

The concentrations of macronutrients changed dramatically over the frontal systems (Fig. 2A). The SAF was marked by strong changes in nitrate and phosphate with concentrations dropping below $10 \mu\text{M}$ and $0.5 \mu\text{M}$, respectively, north of the front. The strongest decrease in silicate was recorded between the APF and the SPF, where concentrations dropped from over $60 \mu\text{M}$ to $<10 \mu\text{M}$. South of the SPF, in the Weddell Gyre and the MIZ, macronutrients were always high.

Concentrations of total dissolved iron (dFe) were also lowest north of the SAF (Fig. 2B) with average values $<0.1 \text{ nM}$. Local enrichment in the PFZ due to atmospheric iron input was associated with increased iron concentrations. Maximum concentrations of ca. 0.5 nM dFe at the APF coincided with elevated biomass. South of the PFZ, concentrations were again lower.

Relatively high chlorophyll a (Chl a) concentrations of ca. $0.5 \mu\text{g l}^{-1}$ were measured at the APF and SPF (Fig. 2B). Maximum values of $>0.6 \mu\text{g Chl } a \text{ l}^{-1}$ were recorded north of the SAF. Unfortunately, no carbon data are available for this area. Chl a was low ($<0.2 \mu\text{g l}^{-1}$) in the Weddell Gyre and the MIZ. Total carbon biomass (phytoplankton plus microzooplankton) was highest at the APF (Fig. 2B). A maximum carbon concentration of $35 \mu\text{g C l}^{-1}$ coincided with an algal bloom at 50°S .

3.2. Vertical profiles of the water column

Vertical profiles of nitrate showed little variation in the upper 100 m (Fig. 3A). Patterns for phosphate and silicate showed a similar distribution, indicating deep mixing of the water column. Also Chl a was generally homogeneously distributed over the water column except for a

Fig. 2. Measurements along the entire transect from north to south. (A) Concentrations of the macronutrients nitrate, phosphate and silicate; (B) trace element iron (Fe), chlorophyll a and carbon biomass. Approximate locations of fronts and the MIZ are indicated.

Fig. 3. Vertical profiles of (A) nitrate concentration (μM) and (B) chlorophyll *a* concentration ($\mu\text{g l}^{-1}$) along the transect. Approximate locations of fronts are indicated.

minor subsurface maximum in the PFZ (Fig. 3B) with concentrations between $0.6\text{--}0.75 \mu\text{g l}^{-1}$ at 80 m depth.

In the PFZ, the ratio of the marker pigments fucoxanthin (Fuco) (Fig. 4A) and 19'-hexanoyloxyfucoxanthin (Hexa) (Fig. 4B) to Chl *a* varied slightly with depth. Fuco/Chl was highest in deep water, whereas Hexa/Chl was more variable. The ratio of the total pool of the photoprotective pigments diatoxanthin plus diadinoxanthin (dt + dd) to Chl *a* was highest in surface waters (Fig. 4C). We cannot explain the distinctively low ratios at 50°S . Like dt + dd/Chl, the photo-protective pigment pool in flagellate algae (VAZ/Chl *a*: viola-, anthera- and zeaxanthin to Chl *a*) was greater at the surface (Fig. 4D). The higher values in deeper waters at 52°S probably are the remnants of a previous algal bloom.

3.3. Phytoplankton and microzooplankton community structure along the transect

Crossing the PFZ, a shift within the algal community was observed (Fig. 5). North of the PFZ, Prasinophytes were most abundant (Fig. 5A). Extrapolation of the CHEMTAX-data unfortunately shows an overestimation of prasinophytes. The SAF was marked by a subsurface maximum of haptophytes (mainly Chrysomonadales) (Fig. 5B). The surface waters between the APF and the SPF were dominated by *Corethron pennatum* and various *Rhizosolenia* species; in the deeper layers a bloom of diatoms_2 (*Pseudonitzschia* sp.) was observed (Fig. 5C). The SPF was marked by a mixed bloom of *Phaeocystis antarctica* (Fig. 5E) and two diatom species (*Rhizosolenia styliformis* and *Tropidoneis* sp.) (Fig. 5C). South of the SPF, a persistent surface community of *Pseudonitzschia* was present (Fig. 5D), along with a mixed community of haptophytes (Chrysomonadales and various other unidentified species of the Chrysophyceae). Near the MIZ, a slight increase in biomass was observed, with Chl *a* between $0.1\text{--}0.15 \mu\text{g l}^{-1}$. The algal community consisted of a mixture of small diatom species ($<20 \mu\text{m}$), haptophytes (a.o. *P. antarctica*) and cryptophytes (Fig. 5E, F). Unfortunately, gridding of the CHEMTAX-data show an overestimation of the contribution of cryptophytes (Fig. 5F). The presence of cryptophytes, was however, confirmed by microscopy. Over the entire transect, chlorophytes were almost absent.

Fig. 4. Vertical profiles of various pigment ratios along the transect. (A) Fuco/Chl *a*, (B) Hexa/Chl *a*, (C) (dt + dd)/Chl *a*, and (D) VAZ/Chl *a*. Abbreviations: Chl: chlorophyll; Fuco: fucoxanthin; Hexa: 19'-hexanoyloxyfucoxanthin; dt: diatoxanthin; dd: diadinoxanthin; VAZ: viola-, anthera- and zeaxanthin. Approximate locations of fronts are indicated.

A significant part of the algal carbon biomass consisted of diatoms. In the $>100 \mu\text{m}$ size class, *Rhizosolenia styliformis* and *R. alata* were found at high biomass (Fig. 6A). In the $50\text{--}100 \mu\text{m}$ size class, *Corethron criophilum* was a major contributor in terms of carbon. *Fragilariopsis kerguelensis* and various other species of *Rhizosolenia* and *Thalassiosira* were prominent species in the middle size class ($20\text{--}50 \mu\text{m}$). South of the PFZ, the bulk of the carbon biomass consisted of small flagellate species ($<10 \mu\text{m}$).

Microzooplankton, mostly tintinnids and heterotrophic dinoflagellates (HNF), contributed significantly to the total carbon biomass (Fig. 6B). The community included predominantly species in the middle size classes ($>20\text{--}50 \mu\text{m}$), mainly various species of *Gymnodinium*, *Protoperdinium*, *Amphidinium* sp. and *Torodinium robustum*. At the southern edge of the PFZ and in the MIZ, microzooplankton made up more than half of the total carbon biomass. Microzooplankton biomass in the APF accounted for $20\text{--}40 \mu\text{g C l}^{-1}$.

Fig. 5. Phytoplankton distribution determined by CHEMTAX-analysis expressed as a percentage of the total algal population along the transect. (A) Prasinophytes, (B) Haptophytes_C, (C) diatoms_2, (D) diatoms_1, (E) Haptophytes_P, and (F) Cryptophytes. For details on species composition see text.

Fig. 6. Contribution of (A) size classes (μm) along the transect expressed as percentage of total algal carbon and of (B) microzooplankton expressed as percentage of total organic carbon.

4. Discussion

Patterns of algal distribution were dictated by the frontal systems. Travelling from north to south, the algal community was subject to a change in growth controlling factors. In the northern waters, silicate was limiting; at the ACC, iron and light governed growth, whereas near the MIZ microzooplankton was highly abundant and the community likely subject to grazer control.

4.1. The Sub-Antarctic Front

The SAF formed the northern margin of the PFZ. This front was marked by a shift in species composition; prasinophytes dominated north of the SAF, and haptophytes were most abundant in the south. The dominance of flagellate species may be a typical end of the season pattern; a similar phytoplankton distribution was previously found in March in the Australian sector of the Southern Ocean (Wright et al., 1996). In the sub-Antarctic waters, silicate concentrations were low and most likely limiting diatom growth. The half saturation constant (K_s) for diatoms can vary widely (1–22 μM ; e.g. Boyd, 2002; Brzezinski et al., 2005; Jacques, 1983). Yet, the low silicate concentrations measured in our study ($<3 \mu\text{M}$), in combination with the absence of diatoms, strongly suggest silicate limitation north of the PFZ. In a previous study, earlier in the season, diatoms were the dominant species in the entire PFZ (Bathmann et al., 1997). At that time, silicate concentrations had not yet dropped to limiting conditions. In autumn 1999, silicate had apparently been consumed by preceding blooms. The southward-travelling of the “silicate-front” has been described in detail

in the Pacific Sector of the Southern Ocean (Hiscock et al., 2003; Nelson et al., 2001). It is characterised by a strong depletion in silicate relative to nitrate. Heavy silicification of diatoms typical for the PFZ may explain this anomaly (Assmy et al., 2013). In addition, an increased Si/N incorporation is observed under iron limitation (Assmy et al., 2013). Low iron concentrations north of the SAF may thus also contribute to the low Si/N signature observed in the seawater (<0.1).

4.2. The Antarctic Polar Front and the Southern Polar Front

The APF and the SPF were characterised as zones of elevated algal biomass, dominated by diatom species. Depth profiles showed little variation in pigment distribution, suggesting only minor variations in species composition in surface waters compared to deeper layers. The importance of the Polar Frontal Zone for diatom growth has been established in several studies (Peeken, 1997; Smetacek et al., 2002; Tremblay et al., 2002; van Leeuwe et al., 1998). The SPF is an area of upwelling, bringing macronutrients to the surface. Silicate was also in ample supply, supporting diatom growth. In addition, the average mixed-layer depth at the PFZ was 40–50 m (Strass and Leach, 2000), providing a favourable light climate for algal growth.

The PFZ between the APF and SPF was also the zone with highest chlorophyll and carbon concentrations. The northward flowing currents create stability of the water column, by which algae are retained near the surface for a prolonged period of time thus allowing the build-up of algal biomass (Strass et al., 2002). The increase in algal biomass was profound when compared to other areas in the ACC, although the autumn biomass was substantially less than in summer. Bloom formation in the APF accounted for 20–30 $\mu\text{g C l}^{-1}$, whereas in the PFZ values of more than 60 $\mu\text{g C l}^{-1}$ were recorded in summer (Smetacek et al., 2002).

The SPF also carries relatively high concentrations of micronutrients that are entrained near the continental zones. Iron enrichment further occurs via lateral transport of nutrient-rich deep waters (de Jong et al., 2012). In autumn, decreasing temperatures and deepening of the wind-mixed layer led to a breakup of the summer stratification thus enhancing upwelling (Strass, pers. communication). This mechanism results in extra input of nutrients. During ANT-XVI/3, local iron enrichment of the surface waters was recorded (Boye et al., 2001) and may have contributed to enhanced algal growth at the PFZ.

In autumn, irradiance is low compared to summer. Yet, photoinhibition may still affect growth, as was previously recorded in the PFZ (Alderkamp et al., 2010). Motions in the water column regularly bring algae to the surface, whilst they may be acclimated to the lower light conditions in deeper layers. Upon exposure to high surface light concentrations, algae will expand their pool of photoprotective pigments, to dissipate excess energy and there with avoid photodamage (Kana et al., 1997; van Leeuwe et al., 2005). During our study, the pool of photoprotective pigments was overall low ($dt + dd/Chl < 0.1$), although elevated pigment ratios reflected some photoacclimation in diatoms. The $dt + dd/Chl$ can measure 0.2–0.4 (e.g. Alderkamp et al., 2010), which indicated that photoinhibition apparently did not play an important role in growth control during ANT-XVI/3.

4.3. The Weddell Gyre

South of the Polar Front, in the Weddell Gyre, small diatom and haptophyte species ($<20 \mu\text{m}$) were present at low biomass. This area is a high nutrient–low chlorophyll (HNLC) area, where light and iron may synergistically control growth (Mitchell and Brody, 1991). In autumn, iron concentrations were generally below 0.2 nM. The low concentrations would explain the absence of big diatoms species: small cells can cope better with iron limitation than larger cells, due to their small surface area to volume ratio (Hudson and Morel, 1990). However, we could not establish growth limitation by iron limitation of the resident algal community. In incubation experiments performed

during the cruise, the addition of iron did not result in enhanced ^{14}C -incorporation by phytoplankton (van Oijen et al., 2004).

Light was a more likely candidate for growth control. Incident irradiance was low, and varied between 1.7–9.9 $\text{MJ m}^{-2} \text{day}^{-1}$ (van Oijen et al., 2003). The incubation experiments performed during the cruise revealed light limitation of the ambient algal community at irradiance of $<20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, which equalled irradiance levels at 20–45 m depth (van Oijen et al., 2003, 2004). In the Weddell Gyre, the wind-mixing depth often extended below 100 m, as was illustrated by the homogeneous nutrient and chlorophyll *a* profiles (see also Strass and Leach, 2000). This implied that phytoplankton was frequently subject to light conditions that were too low to support optimal growth.

4.4. The Marginal Ice Zone

In the MIZ, the algal community consisted of a mixture of haptophytes (including single cells of *P. antarctica*) and cryptophytes. A mixed community appears characteristic for the MIZ (Gibberd et al., 2013; Kopczynska et al., 2007; Spiridonov et al., 1996; Wright et al., 2010), although dominance of *Phaeocystis* colonies in the MIZ has also been observed (Davidson et al., 2010). The form of *Phaeocystis* encountered in Antarctic waters likely depends on its life phase. The flagellate stage that was observed during ANT-XVI/3 may be the initial phase of spore formation, triggered by declining growth conditions in autumn (Davidson and Marchant, 1992).

Biomass at the ice edge was low, with values of less than 10% of what can be observed in summer (Kopczynska et al., 2007). Iron limitation linked with high grazing pressure may have shaped the algal community. Iron concentrations near the MIZ were $<0.2 \text{ nM}$. The MIZ can be a source of iron during the summer melt (Boye et al., 2001). In the course of summer, algal blooms along the ice edge consume probably most of the iron (Wright et al., 2010). Alternatively during our presence in autumn, iron concentrations in the water column decreased even further because of early ice formation, scavenging any remaining iron from the water column (see Boye et al., 2001 for iron data during ANT-XVI/3). At the MIZ, a modest increase in chlorophyll was observed, which may have been the remnants of a summer bloom. In line with potential control by iron limitation, the smaller algae dominated the resident algal community.

The MIZ is likely controlled both by bottom-up as well as top-down control (Banse, 1996). Whereas in absolute values microzooplankton was highest in the PFZ, their relative abundance was most significant in the MIZ. At the southernmost stations, microzooplankton carbon biomass was estimated to be between 20–30 $\mu\text{g C l}^{-1}$, therewith contributing 32–64% to total carbon biomass. The community consisted of HNF, ciliates and tintinnids. A similar microzooplankton community was previously found in marginal ice zone waters (Burkill et al., 1995; Davidson et al., 2010), although the presence of HNF was relatively prominent in our study. Grazing pressure may have exerted significant control on algal biomass. The phytoplankton community was dominated by small cells, which are easily grazed upon. Grazing activity of microzooplankton may consume up to 50% of the primary production (Peloquin et al., 2011). A high grazing impact was previously described near the Antarctic slope during the transition from autumn to winter (Davidson et al., 2010; Krell et al., 2005). Thorium measurements during ANT-XVI/3 indicated high mineralisation rates in the surface waters of the MIZ (Usbeck et al., 2002). These results corroborate the concept of the sea-ice zone as an area with high grazing pressure coinciding with high turnover rates and ultimately low amounts of organic matter being exported into the deep ocean (Usbeck et al., 2002).

4.5. Conclusions

In the transect that extended from subantarctic waters north of the PFZ to the MIZ in the south, a number of different phytoplankton

communities was observed, associated with various growth-controlling factors. In the subantarctic waters in the north the dominance of flagellate algal species was related to low silicate concentrations. With increasing nutrient availability and enhanced stability of the water column due to upwelling of water masses at the southern border of the PFZ, diatoms became the dominant phytoplankton group. In the HNLC waters south of the PFZ, low light and iron availability shaped a community that was dominated by smaller sized algae (<20 µm). At the Marginal Ice Zone (MIZ), the phytoplankton community consisted mainly of low numbers of flagellates and a relatively large contribution of microzooplankton, indicating phytoplankton control by grazing. In a parallel study (Usbeck et al., 2002) it was found that the contribution of the MIZ to carbon export was low. All carbon sequestered by microalgae was likely retained in the water column due to high mineralisation rates. Usbeck et al. (2002) also observed a modest, but apparent, export signal at the PFZ, which matches with the area where we observed the largest-sized diatoms. These findings underline the importance of larger diatom species for the carbon pump in the Southern Ocean. The information on the plankton communities presented here thus provides supplementary insight that help to unravel the mechanisms that control carbon fluxes from the atmosphere into the ocean interior.

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