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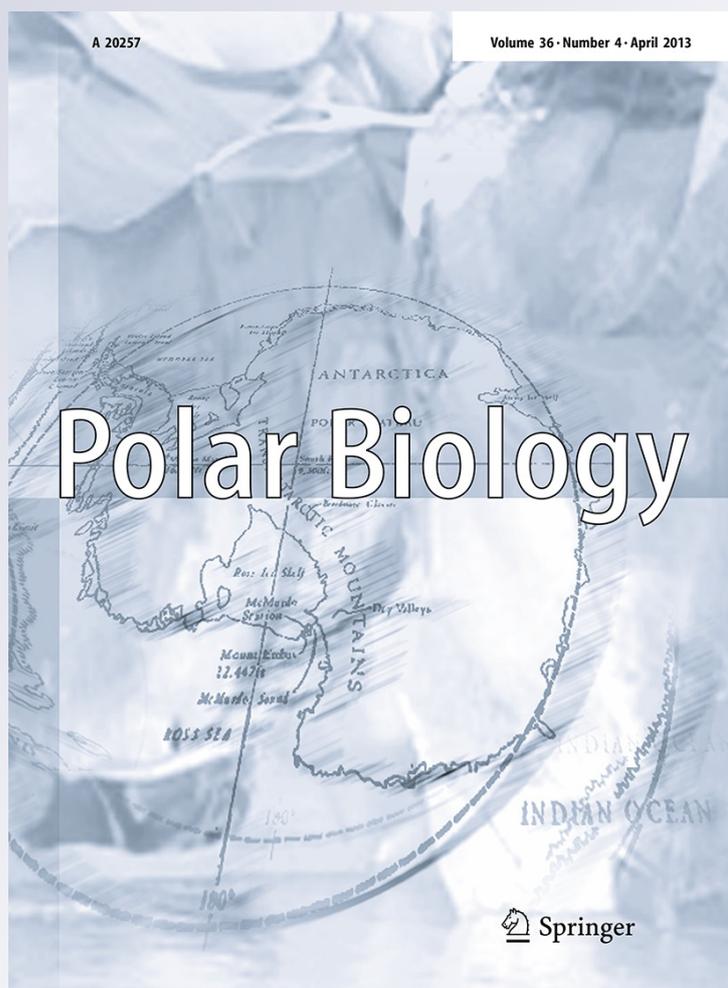
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Shifts in the dominance between diatoms and cryptophytes during three late summers in the Bransfield Strait (Antarctic Peninsula)

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Abstract Recent global warming reduces surface water salinity around the Antarctic Peninsula as a result of the glacial meltwater runoff, which increases the occurrence and abundance of certain phytoplankton groups, such as cryptophytes. The dominance of this particular group over diatoms affects grazers, such as Antarctic krill, which preferentially feed on diatoms. Using three late summer data sets from the Bransfield Strait (2008–2010), we observed variations in the dominant phytoplankton groups determined by HPLC/CHEMTAX pigment analysis and confirmed by microscopy. Results indicate that the dominance of diatoms, particularly in 2008 and 2009, was associated with a deeper upper mixed layer (UML), higher salinity and warmer sea surface temperature. In contrast, cryptophytes, which were dominant in 2010, were associated with a shallower UML, lower salinity and colder sea

surface temperatures. The low diatom biomass observed in the summer of 2010 was associated with high nutrient concentration, particularly silicate, and low chlorophyll *a* (summer monthly average calculated from satellite images). The interannual variability here observed suggests a delayed seasonal succession cycle of phytoplankton in the summer of 2010 associated with a cold summer and a late ice retreat process in the region. This successional delay resulted in a notable decrease of primary producers' biomass, which is likely to have impacted regional food web interactions. This study demonstrates the susceptibility of the Antarctic phytoplankton community structure to air temperature, which directly influences the timing of ice melting and consequently the magnitude of primary production and succession pattern of phytoplankton groups.

Keywords Antarctic Peninsula · Bransfield Strait · Phytoplankton succession · Cryptophytes · Diatoms

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Introduction

The Antarctic Peninsula (AP) is among the world's most susceptible regions to climate change (Turner et al. 2005; Steig et al. 2009); however, the consequences of these changes are not yet fully understood. Regional environmental changes in the AP have been modifying the spatial and temporal patterns of phytoplankton biomass and composition (Garibotti et al. 2005; Ducklow et al. 2007; Montes-Hugo et al. 2009). Furthermore, large spatial and seasonal/interannual variations in physical variables (e.g., air temperature and sea ice coverage) and, consequently, in biological communities are usually observed in the region. However, it is not known whether changes that are currently being observed in such dynamic communities are

natural variations or result from recent climate change. As phytoplankton supports oceanic food webs and plays a key role on the AP marine ecosystem's resilience, changes in the abundance and composition of phytoplankton may have a direct effect on the whole regional ecosystem.

Diatoms, haptophytes (primarily *Phaeocystis antarctica*) and cryptophytes are the three main phytoplankton taxonomic groups in coastal regions of the AP (Rodriguez et al. 2002; Garibotti et al. 2003, 2005; Kozłowski et al. 2011; Mendes et al. 2012). Phytoplankton blooms around the AP are typically associated with the development of a shallow mixed layer, which keeps phytoplankton within adequate light levels and iron availability (e.g., Prézelin et al. 2000). Although blooms are commonly dominated by diatoms and/or *P. antarctica*, some studies have noted the increasing importance of cryptophytes that prevail over diatoms in the AP region, particularly in areas of glacial ice melt (Moline and Prézelin 1996; Moline et al. 2004). As diatoms are more efficiently grazed by Antarctic krill than cryptophytes, the shift from a diatom to a cryptophyte-dominated community may affect food web trophic interactions (Haberman et al. 2003). Changes in the phytoplankton community around the AP have been associated with a recent increase in temperature and a dominance of salps rather than krill as the main consumers (e.g., Moline et al. 2004; Montes-Hugo et al. 2009). Organisms of higher trophic levels, such as penguins and seals, preferably consume krill rather than salps (Loeb et al. 1997). Consequently, shifts in the phytoplankton community composition may have consequences for the ecology of the local marine food web.

A previous work reported the dynamics of phytoplankton communities around the tip of the AP during the late summer of 2008 and 2009, when diatoms dominated the phytoplankton community in the Bransfield Strait region (Mendes et al. 2012). In the present study, we conducted a survey in the same region during the late summer of 2010, when cryptophytes were dominating the coastal sampling stations close to South Shetland Islands (SSI). This work aims to analyze the environmental factors that triggered changes in the phytoplankton communities leading to a dominance of either diatoms or cryptophytes in the Bransfield Strait. In addition, we describe the interannual differences in the phytoplankton community and the environmental factors that may drive the succession of key phytoplankton groups in the region.

Materials and methods

Satellite data

Remote sensing of chlorophyll *a* (CHL-*a*) concentration data was derived from monthly composites of MODIS-

Aqua satellite images. Level 3 (L3) standard mapped image (SMI) images were obtained from the Ocean Color Web (<http://oceancolor.gsfc.nasa.gov> at 4 km resolution). Daily images of sea ice concentration were used for calculating mean monthly images of the study area. The selected period was November to March from 2007 to 2010. Data were collected from the AMSR-E sensor (AQUA platform), with a spatial resolution of approximately 6 × 4 km at 89 GHz. The Artist Sea Ice (ASI) algorithm was applied to retrieve the ice concentration between 0 and 100 % (Spren et al. 2008). Daily maps of hemispherical (6.25 km grid) sea ice concentration (ASI algorithm) were retrieved from the Institute of Environmental Physics, University of Bremen (www.iup.physik.uni-bremen.de).

Sampling and physical measurements

The Bransfield Strait (Fig. 1) was sampled during the late summers of 2008 (21 February to 4 March; 20 stations), 2009 (25 February to 1 March; 20 stations) and 2010 (16–21 February; 16 stations—St. 7 through 10 were not sampled due to ice coverage), as part of the SOS-CLIMATE (Southern Ocean Studies for Understanding Global-CLIMATE Issues) project. Sampling in 2008 and 2009 was part of a broader study covering other regions around the tip of the AP (Mendes et al. 2012).

Both physical data (temperature and salinity) and water samples were collected using a combined Sea-Bird CTD/Carousel 911 + system[®] equipped with 24 five-liter Niskin bottles. Surface water samples were taken in all

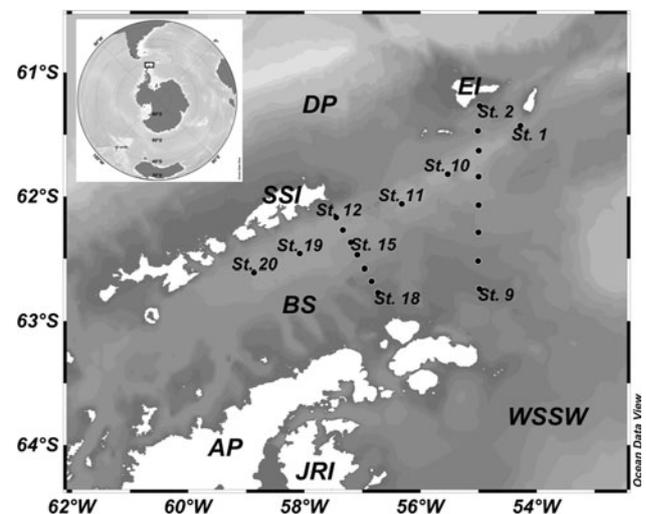


Fig. 1 Study area and station's location during SOS-CLIMATE 2008, 2009 and 2010 summer cruises. Abbreviations are as follows: DP Drake passage, EI Elephant Island, SSI South Shetland Islands, JRI James Ross Island, BS Bransfield Strait, WSSW Weddell Sea Shelf Water, AP Antarctic Peninsula. Inset map includes the South Polar orthographic projection, and the box indicates the magnified region

CTD (conductivity–temperature–depth) stations for nutrient and phytoplankton pigments analyses. In order to investigate differences in phytoplankton composition between different years, three surface sampling stations in a transect crossing the Bransfield Strait were selected for microscope analysis: St. 12 near the SSI; St. 15 at middle of the strait; and St. 18 placed opposite to the SSI (see Fig. 1 for stations' locations). At these stations, water samples for phytoplankton pigment analysis were taken from several depths, which were selected based on fluorescence profiles (WetLabs® profiling fluorometer). Density (kg m^{-3}) was calculated based on temperature, salinity and pressure data in order to evaluate the physical structure of the water column. The upper mixed layer depth (UMLD) was determined as the depth where a change of 0.05 kg m^{-3} occurred over a 5 m depth interval (adapted from Mitchell and Holm-Hansen (1991)). Water column stability (hereafter referred to as stability and represented by the parameter E) was estimated using vertical density variations, as a function of the buoyancy or Brunt-Väisälä frequency (N^2), which is defined by: $N^2 = -\frac{g}{\rho} \frac{\partial \rho}{\partial z}$ ($\text{rad}^2 \text{ s}^{-2}$) leading to $E = \frac{N^2}{g}$ ($10^{-8} \text{ rad}^2 \text{ m}^{-1}$), where g is gravity and ρ is the potential water density. Average stability values (between 0 and 100 m) were used in the statistical analyses.

Nutrient analysis

Surface water samples were filtered through cellulose acetate membrane filters to determine dissolved inorganic nutrients (DIN: nitrate, nitrite and ammonium; phosphate and silicate). Nutrients were analyzed on board, following the recommendations by Aminot and Chaussepied (1983), and absorbance values were measured in a FEMTO® spectrophotometer.

HPLC pigment analysis

Seawater samples (0.5–2 L) were filtered onto Whatman GF/F filters (nominal pore size of $0.7 \mu\text{m}$ and 25 mm in diameter) and immediately stored in liquid nitrogen for HPLC pigment analyses. Pigments were extracted in the dark with 2 mL of 95 % cold-buffered methanol (2 % ammonium acetate) for 30 min at $-20 \text{ }^\circ\text{C}$. Samples were sonicated (Bransonic, model 1210, w: 80, Hz: 47) for 1 min at the beginning of the extraction period and then centrifuged at $1,100g$ for 15 min, at $4 \text{ }^\circ\text{C}$. Extracts were filtered (Fluoropore PTFE membrane filters, $0.2 \mu\text{m}$ pore size) and immediately injected in the Shimadzu HPLC instrument. Method procedures for HPLC analyses (using a monomeric C8 column with a pyridine-containing mobile phase) are fully described in Mendes et al. (2007).

Pigments were identified from both absorbance spectra and retention times and concentrations calculated from the signals in the photodiode array detector (SPD-M10ADVP) or fluorescence detector (RF-10AXL; Ex. 430 nm/Em. 670 nm). The HPLC system was previously calibrated with pigment standards from Sigma (chlorophyll *a*, *b* and β -carotene) and DHI (for other pigments). Three most common marker carotenoids were used for determining distributions of the major phytoplankton taxa: fucoxanthin (FUCO) for diatoms, 19'-hexanoyloxyfucoxanthin (HEX-FUCO) for haptophytes (primarily *P. antarctica*) and alloxanthin (ALLO) for cryptophytes. All pigments detected in this study are listed in Table S1 (see Electronic Supplementary Material).

CHEMTAX analysis of pigment data

The relative contribution of microalgal groups to the overall biomass was calculated using class-specific accessory pigments and total CHL-*a* in the CHEMTAX v1.95 chemical taxonomy software (Mackey et al. 1996). CHEMTAX uses a factor analysis and steepest-descent algorithm to best fit the data on to an initial pigment ratio matrix. The basis for calculations and procedures is fully described in Mendes et al. (2012), where the output results from 2008 and 2009 are shown. Based on the identified diagnostic pigments and confirmation of the higher taxonomic groups by microscopic analysis, six algal groups were loaded on CHEMTAX: diatoms, dinoflagellates-1 (peridinin-containing dinoflagellates), *Phaeocystis antarctica*, cryptophytes, green flagellates (with chlorophyll *b*) and “chemotaxonomic group” (a group including peridinin-lacking autotrophic dinoflagellates and other algal groups such as parmales and chrysophytes). Data from the 2010 cruise were run separately in order to detect potential variations in optimization of CHEMTAX procedures (see output ratios for the 0–50 m in Table S2; Electronic Supplementary Material).

Microscopic analysis

Three sampling stations (St. 12, St. 15 and St. 18) were selected for microscope analysis in order to investigate differences in phytoplankton composition between different years. Samples were immediately preserved with 2 % alkaline Lugol's iodine solution. All methods and procedures for cell counts and carbon biomass estimates are detailed in Mendes et al. (2012). In laboratory, samples were examined in settling chambers under an Axiovert 135 ZEISS inverted microscope (Utermöhl 1958; Sournia 1978). Cell carbon content (carbon biomass) was calculated from biovolume data (V) using different carbon-to-volume ratios. For diatoms and dinoflagellates, cell carbon

was estimated according to Montagnes et al. (1994) applying the formula $\text{pg C cell}^{-1} = 0.109 \times V^{0.991}$. The estimations for all other algae groups were based on Menden-Deuer and Lessard (2000) applying the formula $\text{pg C cell}^{-1} = 0.216 \times V^{0.939}$.

Statistical analysis

As the assumptions for the parametric analysis were not achieved for most variables, a Kruskal–Wallis one-way analysis of variance was used followed by a Dunn's method for pairwise multiple comparison procedures. Relationships between the biomass of phytoplankton groups and environmental variables were explored with a canonical correspondence analysis (CCA; Ter Braak and Prentice 1988). The analysis was carried out in order to determine which environmental factors were mostly associated with the observed phytoplankton community structure. Biotic variables were represented by the CHEMTAX-derived taxonomical groups' biomass (mg m^{-3} of CHL-*a*). Environmental variables included water column stability (Stability), upper mixed layer depth (UMLD), sea surface temperature (T; °C), salinity (Salinity), chlorophyll *a* (CHL-*a*), pheopigments *a*:chlorophyll *a* ratio (PHE-*a*:CHL-*a*), chlorophyllide *a*:chlorophyll *a* ratio (CHLIDE-*a*:CHL-*a*), dissolved inorganic nitrogen (DIN), phosphate and silicate. In order to reduce the influence of the different scales in the data sets, all variables were log-transformed before analysis. In order to evaluate the significance of the CCA, Monte-Carlo tests were run based on 499 permutations under a reduced model ($p < 0.05$).

Results

Air temperature, sea ice and chlorophyll *a* from satellite data

The monthly average air temperatures recorded at Brazil's Antarctic research station, Comandante Ferraz (EACF; 62.08°S, 58.39°W), located in the South Shetland Islands, showed very similar summers in 2008 and 2009 (average air temperatures of 2–3 °C; Fig. S1; Electronic Supplementary Material). An unusually cold summer was observed in 2010, with average air temperatures below 1 °C. Moreover, the summer of 2009 was preceded by a considerably milder winter when compared to the other two summers (2008 and 2010). The air temperature differences were related to distinct sea ice coverage around the tip of AP (see Fig. S2 in Electronic Supplementary Material). The colder 2010 summer showed more extended sea ice coverage when compared to the summer (whole Antarctic warm season) of 2008 and 2009. MODIS CHL-*a* concentration images (Fig. S2; Electronic

Supplementary Material) showed a high CHL-*a* ($>8 \text{ mg m}^{-3}$) belt surrounding the South Shetland Islands (SSI) and in the vicinities of the James Ross Island (JRI), southeast of the AP tip. However, CHL-*a* concentration was relatively lower during the summer of 2010 (values reaching 8 mg m^{-3} only in few spots in January) compared to both previous years.

In situ environmental parameters

The mean surface water temperature showed significant differences ($p < 0.05$) between 2009 ($1.08 \pm 0.87 \text{ °C}$) and 2010 ($0.16 \pm 0.71 \text{ °C}$; Table 1). Intermediate values were observed in 2008 ($0.54 \pm 0.87 \text{ °C}$), and not significantly different from the other 2 years (Table 1). Salinity was very similar in 2008 and 2009 in the upper layer ($<200 \text{ m}$) and notably different from 2010, when the lowest and most variable surface salinity values were observed (see Fig. 2). The salinity pattern observed in 2010 caused a significant degree of stratification, particularly at stations close to the SSI. Excluding the glacial ice-melting effect in 2010 at surface waters, salinity varied between 34.1 and 34.6. Based on data from the T/S diagrams, salinity data suggest that the Weddell Sea water (García et al. 2002) had a significant influence on the region during the three sampling years.

Surface nutrient concentrations recorded high interannual variations (see Table 1). Dissolved inorganic nitrogen (DIN) ranged from 16.6 to 47.8 μM ; the lowest values were recorded in 2008 ($24.1 \pm 4.6 \mu\text{M}$) and highest in 2010 ($41.6 \pm 3.5 \mu\text{M}$). Silicate varied from 23.1 to 79.9 μM , with maximum values observed in 2010 ($69.2 \pm 6.4 \mu\text{M}$). Phosphate varied between 0.3 and 3.4 μM , with minimum values observed in 2008 ($0.8 \pm 0.3 \mu\text{M}$).

Biological data

Significantly lower CHL-*a* values (used as phytoplankton biomass index) were recorded in 2008 (ranging from 0.12 to 1.08 mg m^{-3} ; Fig. 3; Table 1), and the highest value was observed in 2010 (3.78 mg m^{-3} ; St. 12). FUCO, ALLO and HEX-FUCO were the main carotenoids observed in this study, and their concentrations displayed different interannual patterns (Table 1). FUCO was the major carotenoid in the first 2 years, and its concentration reached values higher than 1 mg m^{-3} in 2009. The lowest concentration of FUCO was observed in 2010, whereas ALLO was the main carotenoid in most stations sampled during this year, particularly in the surface layers. The HEX-FUCO concentrations ranged from 0.01 to 0.25 mg m^{-3} , and values were relatively lower in 2009 (see Table 1). Pheopigments *a* (PHE-*a*):CHL-*a* ratio (used as a relative index of grazing) was significantly lower in 2010 ($p < 0.05$) and mostly below 0.05 (Table 1). The maximum values (~ 0.4) were observed in 2008. In

Table 1 Average, standard deviation (in parenthesis), minimum and maximum (in square brackets) values of abiotic variables and pigment data for the three sampling years (2008, 2009 and 2010)

	2008 (<i>n</i> = 20)	2009 (<i>n</i> = 20)	2010 (<i>n</i> = 16)
Abiotic variables			
Temperature (°C)	0.54 (0.87) ^{a,b} [−0.81; 1.54]	1.08 (0.87) ^a [−0.46; 1.88]	0.16 (0.71) ^b [−1.29; 1.14]
Salinity	34.26 (0.08) ^a [34.10; 34.38]	34.26 (0.06) ^a [34.08; 34.36]	33.93 (0.25) ^b [33.20; 34.20]
DIN (μM)	24.05 (4.58) ^a [16.61; 32.68]	32.36 (3.14) ^b [26.10; 36.39]	41.55 (3.52) ^c [37.44; 47.81]
Phosphate (μM)	0.79 (0.33) ^a [0.31; 1.61]	2.67 (0.36) ^b [2.18; 3.40]	1.89 (0.19) ^c [1.56; 2.16]
Silicate (μM)	44.08 (12.62) ^a [6.89; 58.70]	46.93 (3.07) ^a [42.04; 54.61]	69.16 (6.39) ^b [59.00; 79.91]
Pigment data			
Chlorophyll <i>a</i> (mg m ^{−3})	0.52 (0.26) ^a [0.12; 1.08]	0.94 (0.49) ^b [0.35; 1.97]	1.07 (0.80) ^b [0.38; 3.78]
Fucoxanthin (mg m ^{−3})	0.42 (0.25) ^a [0.10; 0.96]	0.61 (0.40) ^a [0.10; 1.42]	0.21 (0.08) ^b [0.08; 0.32]
Alloxanthin (mg m ^{−3})	0.01 (0.02) ^a [0.00; 0.05]	0.01 (0.01) ^a [0.00; 0.03]	0.14 (0.24) ^b [0.00; 0.97]
19'-Hexanoyloxyfucoxanthin (mg m ^{−3})	0.07 (0.03) ^a [0.02; 0.14]	0.02 (0.01) ^b [0.01; 0.06]	0.11 (0.06) ^a [0.03; 0.25]
Chlorophyllide <i>a</i> :Chlorophyll <i>a</i>	0.03 (0.03) ^a [0.00; 0.09]	0.02 (0.03) ^a [0.00; 0.07]	0.01 (0.01) ^a [0.00; 0.04]
Pheopigments <i>a</i> :Chlorophyll <i>a</i>	0.17 (0.1) ^a [0.04; 0.38]	0.13 (0.05) ^a [0.04; 0.23]	0.02 (0.01) ^b [0.01; 0.05]

Different superscript labels (a, b, c) between years indicate significant differences ($p < 0.05$, Dunn's method)

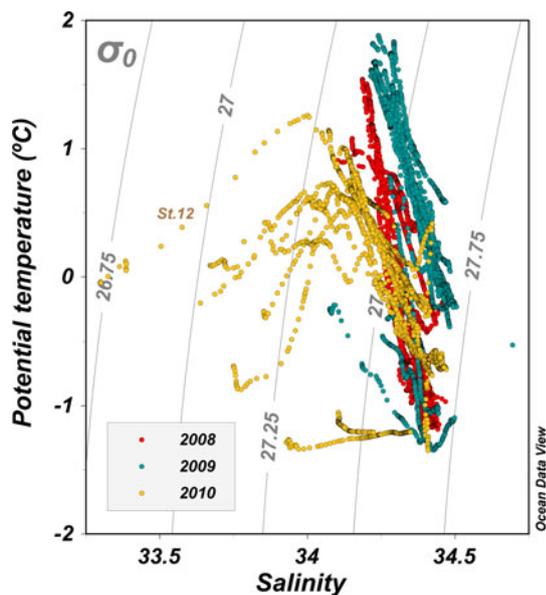


Fig. 2 T/S diagram (temperature and salinity data in the upper 200 m layer) from all stations sampled during late summers in the 3 years (2008, 2009 and 2010). Station near the SSI clearly indicating ice-melting conditions is labeled (St. 12)

contrast, no significant differences among years were observed for chlorophyllide *a* (CHLIDE-*a*):CHL-*a* ratio (used as an index of cells senescence; Table 1).

The relative contributions of the main phytoplankton groups to total CHL-*a* in surface waters, derived from CHEMTAX, are shown in Fig. 4. Diatoms were the dominant group both in 2008 (Fig. 4a) and 2009 (Fig. 4b), with a relatively higher value in 2009 associated with a decrease in the contribution of all nanoplanktonic groups (e.g., *P. antarctica*, cryptophytes and green flagellates). Overall, diatoms were replaced by cryptophytes in 2010 (Fig. 4c). Microscopic observations showed that diatoms were mainly represented by *Actinocyclus/Thalassiosira* spp. and *Corethron pennatum*, particularly in the summer of 2009 (see Table 2). In contrast, cryptophytes were very abundant in the summer of 2010. Fig. 4 also shows the important contribution of the “chemotaxonomic group” for the phytoplankton community in all years. This group was an assemblage consisting of peridinin-lacking autotrophic dinoflagellates (e.g., *Gymnodinium* spp.), other algal groups such as parmales and chrysophytes, and CHL-*c*₃-containing diatoms (e.g., *Pseudonitzschia* spp.).

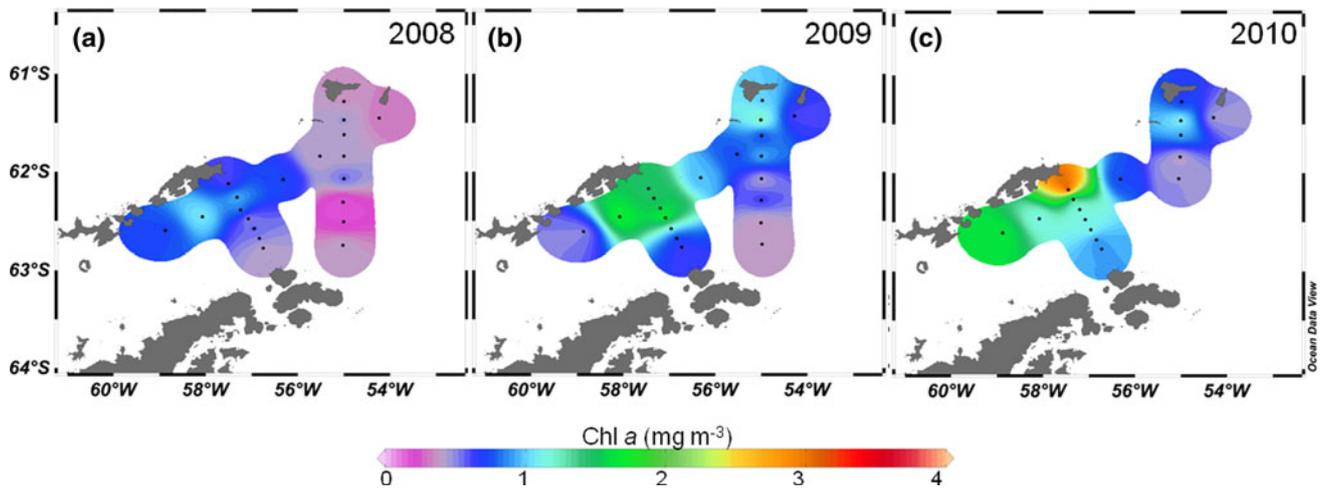


Fig. 3 Surface distribution of total chlorophyll *a* (mg m^{-3}) for 2008 (a), 2009 (b) and 2010 (c) surveys

In 2010, a significant relationship between cryptophytes and salinity was observed (Fig. 5; $r^2 = 0.88, p < 0.001$). The lowest salinity values (<33.7) were observed close to SSI, particularly at St. 12, where cryptophytes were dominant. Off the SSI and toward the tip of AP (St. 12 through St. 18), progressively higher salinity and less cryptophytes contribution were observed. In addition, cryptophytes were almost absent in the northeastern section of our study area (Fig. 5). Overall, cryptophytes were found in the upper layer, above the pycnocline (St. 12 and 15; Fig. 6a, b), whereas diatoms were recorded in deeper mixed layer (St. 18; Fig. 6c).

The multivariate analysis showed a strong association between phytoplankton groups and water physical and chemical properties (Fig. 7). The first axis of the CCA (63.5 % of variation explained) revealed a notable separation between diatoms and cryptophytes, mainly associated with salinity, UMLD, temperature, DIN and silicate. The second axis (29.1 % of variation explained) indicates that most flagellates (e.g., *P. antarctica*) were positively correlated with water column stability and negatively correlated with phosphate concentration (see Fig. 7).

Discussion

Previous works addressed the seasonal succession of phytoplankton communities in the AP region, particularly during the austral summer. Most studies report that the timing of sea ice retreat is critical for the progression of phytoplankton seasonal cycles (e.g., Moline and Prézelin 1996; Garibotti et al. 2005). Diatom blooms are generally observed in early summer, under sea ice retreating process. Later, flagellate blooms, such as cryptophytes, replace diatoms (Ducklow et al. 2007). In a final succession stage, the community is dominated by diatoms and other unidentified phytoflagellates (Moline and Prézelin 1996; Garibotti et al. 2005). In the present study, sampling was always performed during the late summer. Consequently, the observed phytoplankton community was a result of the succession associated with the timing and extent of sea ice melting during the whole summer. In addition to sea ice, another important freshwater input to surface waters is glacial ice melting, which changes the physical environment. Particularly, it decreases salinity and enhances water

Fig. 4 Average relative surface contribution of phytoplankton groups (CHEMTAX-allocated) to total chlorophyll *a* in a 2008, b 2009 and c 2010. Dinoflagellates-1 = peridinin-containing dinoflagellates; Green flagellates = flagellates bearing chlorophyll *b*; *P. antarctica* = *Phaeocystis antarctica*; Chem. group = a group including peridinin-lacking autotrophic dinoflagellates and other algal groups such as parmales and chrysophytes

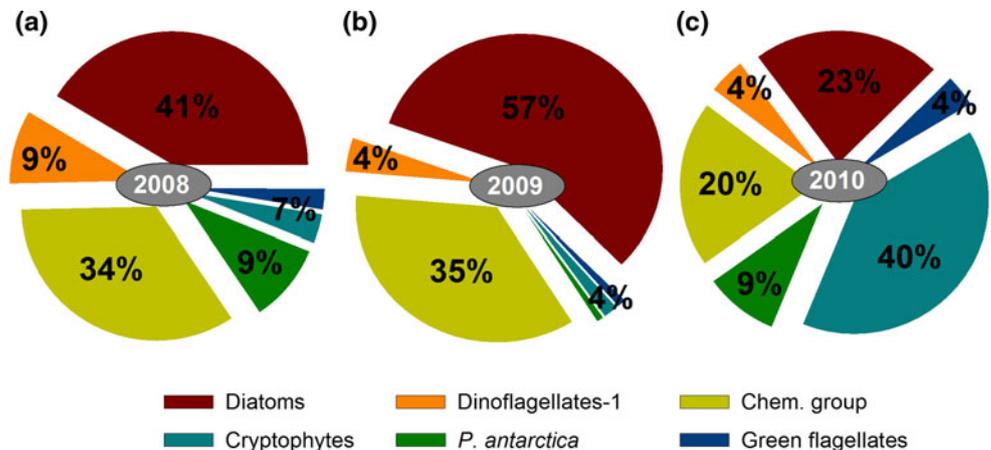


Table 2 Phytoplankton community structure shown as carbon biomass ($\mu\text{g C L}^{-1}$) of dominant phytoplankton taxa

Taxonomical groups	2008			2009			2010		
	St. 12	St. 15	St. 18	St. 12	St. 15	St. 18	St. 12	St. 15	St. 18
Diatoms									
<i>Actinocyclus/Thalassiosira</i> spp. 20–100 μm			0.84	10.75	11.62	1.40			18.44
<i>Chaetoceros</i> spp. <10 μm				1.53	3.69	0.04	0.16	0.31	
<i>Corethron pennatum</i>	1.31	1.87		23.87	44.44	0.98		0.38	2.63
<i>Coscinodiscus/Thalassiosira</i> spp. >100 μm			0.91			1.15			
<i>Odontella weissflogii</i>			1.13	1.14	2.38	2.57			0.46
Pennates 50–100 μm	0.10	0.01		2.64	1.47	0.02		0.25	0.01
<i>Pseudonitzschia</i> spp.	0.09	0.11		0.74	3.72				
<i>Rhizosolenia</i> spp.		0.04	0.03	0.34		0.13			
<i>Thalassiosira gracilis</i>			0.02					0.85	
Other diatoms	0.24	0.06	0.21	19.06	18.23	0.40		1.47	0.23
Sum of diatoms	1.75	2.09	3.13	60.06	85.55	6.69	0.16	3.25	21.77
Dinoflagellates									
<i>Gymnodinium</i> spp. <20 μm	0.79	0.51	0.05	0.34	0.52	0.39	0.67	0.09	0.12
<i>Gymnodinium</i> spp. >20 μm	0.25	0.19	0.11	2.00	0.11	0.10	0.02	0.11	0.02
<i>Prorocentrum minimum</i>	0.10	0.07		0.30	0.66	0.03		0.27	0.03
Other dinoflagellates	0.19	0.31		0.31	0.30	0.06	0.06	0.05	0.01
Sum of dinoflagellates	1.33	1.08	0.16	2.95	1.59	0.58	0.74	0.51	0.18
Flagellates									
Cryptophytes							16.92	6.86	1.30
Other flagellates	1.48	0.87	0.43	1.23	3.45	2.54	0.22	0.50	1.02
Sum of flagellates	1.48	0.87	0.43	1.23	3.45	2.54	17.14	7.36	2.32
Ciliates									
<i>Myrionecta rubra</i>				0.19		0.53		2.67	

The data refer to three selected stations in 2008, 2009 and 2010 summers (see Fig. 1 for stations' location)

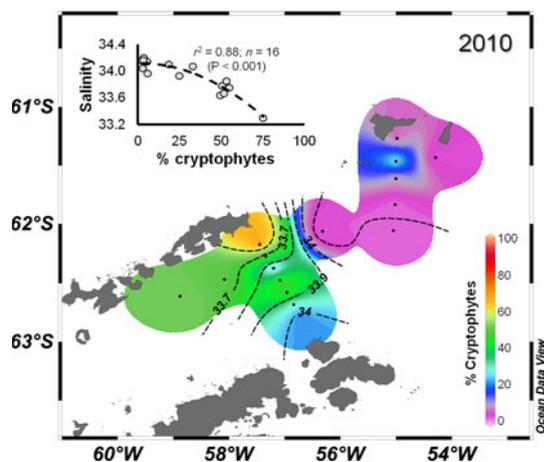


Fig. 5 Relative surface contribution of cryptophytes (CHEMTAX-allocated) to total chlorophyll *a* (color scale) and salinity (dashed lines) in 2010. Inset relationship between relative contribution of cryptophytes and salinity values ($y = -0.0001x^2 + 0.0003x + 34.12$; $r^2 = 0.88$; $n = 16$; $p < 0.001$)

column stratification at nearshore sites (Dierssen et al. 2002) where specific phytoplankton forms may thrive, such as small cryptophytes (Moline et al. 2004). Salinity levels associated with melted glacial ice (average 33.2) are typically lower than salinity associated with melted sea ice (ranging from 33.8 to 34) along the marginal ice zone (Dierssen et al. 2002 and references therein).

In 2010, cryptophytes emerged as the dominant phytoplankton group associated with lower salinity, shallower mixed layer and stronger stratification (see CCA results in Fig. 7), which are typical oceanographic characteristics of glacial ice-melting conditions. Particularly, the highest biomass of cryptophytes in low salinity surface layers was associated with a strong water column stratification, which was observed at some nearshore stations in 2010 (see Fig. 6). As cryptophytes respond to changes in water column salinity (Moline and Prézelin 1996; Moline et al. 2004), taxonomic changes of the phytoplankton community may reflect variations in the timing, duration and

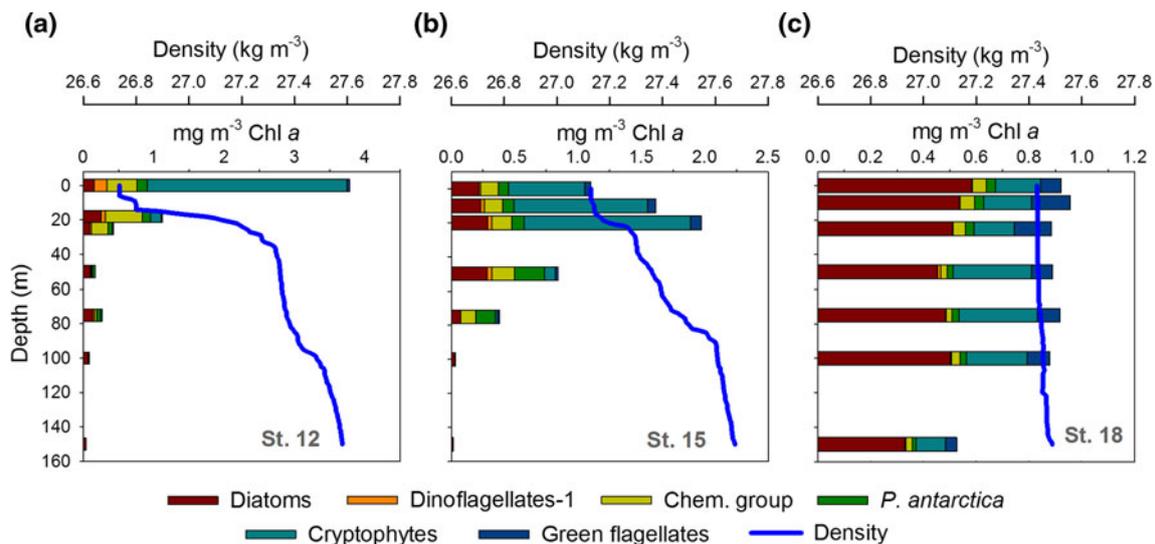


Fig. 6 Depth distribution of phytoplankton groups' biomass (as chlorophyll *a* concentration) calculated by the CHEMTAX program, at the three selected stations in the Bransfield Strait in 2010, and respective density vertical profiles. Dinoflagellates-1 = peridinin-containing dinoflagellates; Green flagellates = flagellates with

chlorophyll *b*; *P. antarctica* = *Phaeocystis antarctica*; Chem. group = a group including peridinin-lacking autotrophic dinoflagellates and other algal groups such as parmales and chrysophytes. See Fig. 1 for stations' locations. Note the different scales in chlorophyll *a* concentration

amount of the annual freshwater input. Water column structure has also been suggested as a possible mechanism triggering the replacement of diatoms by cryptophytes (e.g., Mitchell and Holm-Hansen 1991). A prolonged and strong stratification condition can lead to severe nutrient limitation in surface layers, particularly iron. This probably favors opportunistic small-sized and motile species, such as cryptophytes, which can still grow in very low iron concentrations (Gerringa et al. 2000). In contrast, diatoms require relatively high iron levels (Boyd et al. 2000). Although the association of cryptophytes with stratification/low salinity conditions has already been discussed (Moline and Prézelin 1996; Moline et al. 2004), the association of this group with iron availability is still undefined, partly due to the difficulty of measuring this trace metal in seawater (Lancelot et al. 2009).

In the present work, results from 2010 show cryptophytes' dominance associated with evident glacial ice melting (surface salinity in nearshore waters below 33.8; Dierssen et al. (2002)). Glacial ice melting contributes to stratification but may not be a significant source of iron. According to Klunder et al. (2011), vertical mixing and upwelling are the most important iron supply mechanisms to the upper surface mixed layer in Antarctic regions.

Another factor controlling the phytoplankton community that should also be addressed is grazing pressure (Ross et al. 1998; Anadón et al. 2002). Although data on zooplankton were not collected in this work, the relative concentration of CHL-*a* degradation products can be used as a proxy for grazing pressure and for senescence of phytoplankton cells (Jeffrey 1974). In 2010, when

cryptophytes were the dominant group, very low relative levels of degradation products associated with grazing processes (i.e., PHE-*a*) were observed. This result suggests that grazing activities were less intense in 2010. The dominance of cryptophytes over diatoms in this period may have caused a negative impact on the AP marine ecosystem due to lower efficiency of local grazers, such as krill, on these nanoflagellates (Haberman et al. 2003). The low grazing rates may have also contributed to sustaining the relatively high biomass levels (CHL-*a*) associated with cryptophytes in late summer 2010. Even though the association between PHE-*a*/grazing pressure and cryptophytes' dominance had been observed, the wax and wane of blooms of these nanoflagellates in Antarctic environments need further investigation to clarify the role of microzooplankton grazers on biomass control and energy transfer through the food web.

Based on in situ data results (T/S diagram in Fig. 2), ice melting was more evident in 2010 than in the two previous years. However, the study period (late summer) does not represent the conditions of the whole season. The summer of 2010 was colder than the two previous summers (Fig. S1 in Electronic Supplementary Material), which resulted in a great accumulation of ice around the AP (see Fig. S2 in Electronic Supplementary Material). In contrast to 2008 and 2009, when phytoplankton blooms were more intense during the austral summer, particularly around the South Shetland Islands (see Fig. S2 in Electronic Supplementary Material), the outcome of the cold and icy conditions in 2010 was a lower phytoplankton biomass (CHL-*a* estimated by remote sensing). The higher nutrient

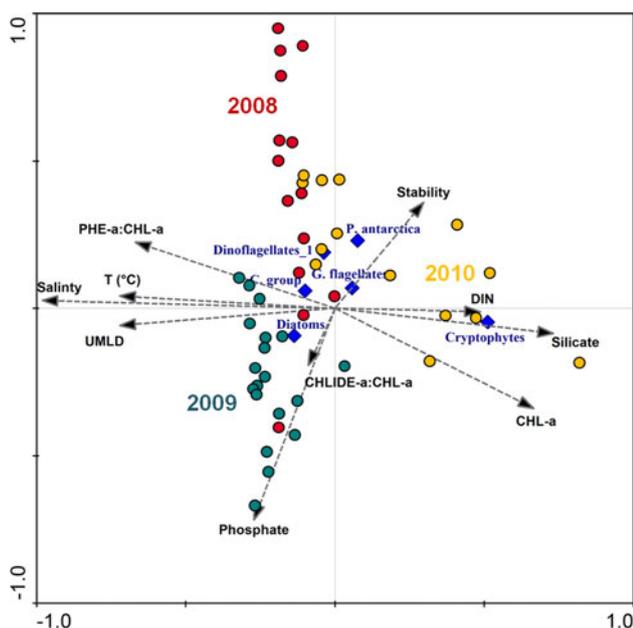


Fig. 7 Canonical correspondence analysis ordination diagram of absolute contributions of different phytoplankton groups at sea surface. The first two ordination axes represent 76.3 % of the total phytoplankton group's variance and 92.6 % of phytoplankton groups-environment relationships. *Arrows* indicate environment variables (water column stability (Stability), upper mixed layer depth (UMLD) and sea surface water values of temperature (T (°C)), salinity (Salinity), chlorophyll *a* (CHL-*a*), pheopigments *a*:chlorophyll *a* ratio (PHE-*a*:CHL-*a*), chlorophyllide *a*:chlorophyll *a* ratio (CHLIDE-*a*:CHL-*a*) and dissolved inorganic nitrogen (DIN), phosphate and silicate). *Blue diamonds* refer to absolute contributions of phytoplankton groups (Diatoms; C_group = chemotaxonomic group; Dinoflagellates_1 = dinoflagellates with peridinin; G. flagellates = Green flagellates; *P. antarctica* = *Phaeocystis antarctica*; Cryptophytes). Stations are separated according to sampling year (*red circles* = 2008; *green circles* = 2009; *yellow circles* = 2010) (color figure online)

concentrations recorded in February 2010 also indicates low consumption rate during the summer of 2010 and, consequently, low biomass accumulation. Silicate, which is mostly taken up by diatoms, was approximately twice the concentration in 2010 when compared with the two previous years. Therefore, the natural diatom bloom that normally precedes cryptophyte development in the early summer (seasonal succession) under sea ice melting (Moline and Prézelin 1996; Garibotti et al. 2005) was likely less intense in 2010.

The results presented in this study suggest that the phytoplankton community sampled in late summer 2010 was in a delayed stage of its seasonal succession cycle during this cold summer. The observed differences in phytoplankton community were not associated with the short temporal disparity of sampling times in different years (sampling in 2010 was performed 1 week earlier than in 2008 and 2009). A possible reason for the delay in the phytoplankton seasonal succession in 2010 may be a lower degree of sea ice melting resulting from relatively lower air

temperatures during the entire summer of 2010 (monthly average air temperatures below 1 °C; see Fig. S1 in Electronic Supplementary Material). These environmental conditions may have hindered the development of the initial diatom bloom in the first stage of the natural succession and delayed the start of the second stage, which is the replacement of diatoms by cryptophytes.

The probable cause of the atypical cold temperatures in late 2009/beginning of 2010 was the moderate-to-strong El Niño episode (source from US National Oceanic and Atmospheric Administration, NOAA). Previous studies have shown direct impacts of the El Niño-Southern Oscillation (ENSO) on Antarctic sea ice variability. For instance, in addition to effects in the Pacific basin (Trenberth and Hoar 1996), the increasing frequency of ENSO events also caused critical disturbances in the timing and intensity of sea ice melting in Antarctica (Yuan 2004; Stammerjohn et al. 2008). As observed in this study, such disturbances can lead to both decrease in phytoplankton biomass levels and changes in the succession of phytoplankton groups, which ultimately may cause cascading effects in the whole ecosystem.

Summary and conclusions

The interannual variation of phytoplankton composition observed during the late summer in the Bransfield Strait was a consequence of a temporal displacement in the seasonal phytoplankton succession, particularly in the summer of 2010. The low temperatures recorded during this particular period, and the associated ice conditions, were not appropriate for the development of phytoplankton blooms of high diatoms biomass, which are typical in this region during the austral summer. Indeed, cryptophytes were the major phytoplankton group in the late summer of 2010. These conditions likely affected all other trophic levels during that particular summer. This study also shows that interannual differences in air temperature and sea ice coverage might affect the regular functioning of the phytoplanktonic primary production and succession in the AP. Future studies should focus on broader spatial and finer temporal scale surveys in order to better understand how the phytoplankton community responds to environmental factors. Such phytoplankton monitoring procedures are vital to fully understand the function of marine food webs, particularly in regions extremely sensitive to global climate change, as the AP region.

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References

- Aminot A, Chaussepied J (1983) Manuel des Analyses Chimiques en Milieu Marin. CNEXO, Brest
- Anadón R, Alvarez-Marques F, Fernandez E, Varela M, Zapata M, Gasol JM, Vaque D (2002) Vertical biogenic particle flux during austral summer in the Antarctic Peninsula area. *Deep-Sea Res II* 49:883–901
- Boyd PW, Watson AJ, Law CS et al (2000) A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature* 407:695–702
- Dierrssen HM, Smith RC, Vernet M (2002) Glacial meltwater dynamics in coastal waters west of the Antarctic Peninsula. *PNAS* 99:1790–1795
- Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC, Stammerjohn SE, Vernet M, Fraser W (2007) Marine pelagic ecosystems: the West Antarctic Peninsula. *Phil Trans R Soc B* 362:67–94
- García MA, Castro CG, Ríos AF, Doval MD, Rosón G, Gomis D, López O (2002) Water masses and distribution of physico-chemical properties in the Western Bransfield Strait and Gerlache Strait during Austral summer 1995/96. *Deep-Sea Res II* 49:585–602
- Garibotti IA, Vernet M, Kozłowski WA, Ferrario ME (2003) Composition and biomass of phytoplankton assemblages in coastal Antarctic waters: a comparison of chemotaxonomic and microscopic analyses. *Mar Ecol Prog Ser* 247:27–42
- Garibotti IA, Vernet M, Ferrario ME (2005) Annually recurrent phytoplanktonic assemblages during summer in the seasonal ice zone west of the Antarctic Peninsula (Southern Ocean). *Deep-Sea Res I* 52:1823–1841
- Gerringa LJA, de Baar HJW, Timmermans KR (2000) A comparison of iron limitation of phytoplankton in natural oceanic waters and laboratory media conditioned with EDTA. *Mar Chem* 68:335–346
- Haberman KL, Ross RM, Quetin LB (2003) Diet of the Antarctic krill (*Euphausia superba* Dana): II selective grazing in mixed phytoplankton assemblages. *J Exp Mar Biol Ecol* 283:97–113
- Jeffrey SW (1974) Profiles of photosynthetic pigments in the ocean using thin-layer chromatography. *Mar Biol* 26:101–110
- Klunder MB, Laan P, Middag R, de Baar HJW, van Ooijen JC (2011) Dissolved iron in the Southern Ocean (Atlantic sector). *Deep-Sea Res I* 58:2678–2694
- Kozłowski WA, Deutschman D, Garibotti I, Trees C, Vernet M (2011) An evaluation of the application of CHEMTAX to Antarctic coastal pigment data. *Deep-Sea Res I* 58:350–364
- Lancelot C, de Montety A, Goosse H, Becquevort S, Pasquer B, Vancoppenolle M (2009) Spatial distribution of the iron supply to phytoplankton in the Southern Ocean: a model study. *Biogeosciences* 6:2861–2878
- Loeb V, Siegel V, Holm-Hansen O, Hewitt R, Fraser W, Trivelpiece W, Trivelpiece S (1997) Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387:897–900
- Mackey MD, Mackey DJ, Higgins HW, Wright SW (1996) CHEMTAX—a program for estimating class abundances from chemical markers: application to HPLC measurements of phytoplankton. *Mar Ecol Prog Ser* 144:265–283
- Menden-Deuer S, Lessard EJ (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnol Oceanogr* 45:569–579
- Mendes CR, Cartaxana P, Brotas V (2007) HPLC determination of phytoplankton and microphytobenthos pigments: comparing resolution and sensitivity of a C18 and a C8 method. *Limnol Oceanogr Methods* 5:363–370
- Mendes CRB, de Souza MS, Garcia VMT, Leal MC, Brotas V, Garcia CAE (2012) Dynamics of phytoplankton communities during late summer around the tip of the Antarctic Peninsula. *Deep-Sea Res I* 65:1–14
- Mitchell BG, Holm-Hansen O (1991) Observations and modeling of the Antarctic phytoplankton crop in relation to mixing depth. *Deep-Sea Res I* 38:981–1007
- Moline MA, Prézelin BB (1996) Palmer LTER 1991–1994: long-term monitoring and analyses of physical factors regulating variability in coastal Antarctic phytoplankton biomass, in situ productivity and taxonomic composition over sub-seasonal, seasonal and interannual time scales. *Mar Ecol Prog Ser* 145:143–160
- Moline MA, Claustre H, Frazer TK, Schofield O, Vernet M (2004) Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. *Glob Change Biol* 10:1973–1980
- Montagnes DJS, Berges JA, Harrison PJ, Taylor FJR (1994) Estimating carbon, nitrogen, protein, and chlorophyll *a* from volume in marine phytoplankton. *Limnol Oceanogr* 39:1044–1060
- Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE, Schofield O (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science* 323:1470–1473
- Prézelin BB, Hofmann EE, Mengelt C, Klinck JM (2000) The linkage between Upper Circumpolar Deep Water (UCDW) and phytoplankton assemblages on the west Antarctic Peninsula continental shelf. *J Mar Res* 58:165–202
- Rodríguez F, Varela M, Zapata M (2002) Phytoplankton assemblages in the Gerlache and Bransfield Straits (Antarctic Peninsula) determined by light microscopy and CHEMTAX analysis of HPLC pigment data. *Deep-Sea Res II* 49:723–747
- Ross RM, Quetin LB, Haberman KL (1998) Interannual and seasonal variability in short-term grazing impact of *Euphausia superba* in nearshore and offshore waters west of the Antarctic Peninsula. *J Mar Syst* 17:261–273
- Sournia A (1978) Phytoplankton manual. Muséum National d’Histoire Naturelle. UNESCO, Paris
- Spren G, Kaleschke L, Heygster G (2008) Sea ice remote sensing using AMSR-E 89-GHz channels. *J Geophys Res* 113:C02S03
- Stammerjohn SE, Martinson DG, Smith RC, Yuan X, Rind D (2008) Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño Southern Oscillation and Southern Annular Mode variability. *J Geophys Res* 113:C03S90
- Steig EJ, Schneider DP, Rutherford SD, Mann ME, Comiso JC, Shindell DT (2009) Warming of the Antarctic ice-sheet surface

- since the 1957 international geophysical year. *Nature* 457:459–463
- Ter Braak CJF, Prentice IC (1988) A theory of gradient analysis. *Adv Ecol Res* 18:271–317
- Trenberth KE, Hoar TJ (1996) The 1990–1995 El Niño–Southern oscillation event: longest on record. *Geophys Res Lett* 23:57–60
- Turner J, Colwell SR, Marshall GJ, Lachlan-Cope TA, Carleton AM, Jones PD, Lagun V, Reid PA, Lagovkina S (2005) Antarctic climate change during the last 50 years. *Int J Climatol* 25:279–294
- Utermöhl H (1958) Zur Vervollkommnung der quantitativen Phytoplankton Methodik. *Mitt Int Ver Theor Angew Limnol* 9:1–38
- Yuan X (2004) ENSO-related impacts on Antarctic sea ice: a synthesis of phenomenon and mechanisms. *Antarct Sci* 16:415–425