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Shifts in microphytoplankton species and cell size at Admiralty Bay, Antarctica

PRISCILA KIENTECA LANGE[1,2], DENISE RIVERA TENENBAUM[2], VIRGÍNIA MARIA TAVANO[1], RODOLFO PARANHOS[2] and LUCIA DE SIQUEIRA CAMPOS[2]

[1]*Instituto de Oceanografia, Universidade Federal do Rio Grande (FURG), Laboratório de Fitoplâncton e Microorganismos Marinhos, Avenue Italia, Km 8, Rio Grand 96201-900, Brazil*
[2]*Instituto de Biologia, Universidade Federal do Rio de Janeiro (UFRJ), Avenue Carlos Chagas, 373, Prédio CCS, Bl. A, Ilha do Fundão, Rio de Janeiro 21949-902, Brazil*
prilange@gmail.com

Abstract: Phytoplankton (> 15 µm) was investigated in three shallow coastal areas at Admiralty Bay (AB) between the summers of 2002–03 and 2008–09. Phytoplankton abundance was low (10^3 cells l^{-1}) and, over time, the prevailing cell size decreased due to a shift in phytoplankton dominant species from diatoms to dinoflagellates. *In situ* and remote sensing data showed that oscillations in sea surface temperature, precipitation, ice formation/melting, irradiance (cloud cover) and bottom circulation (indexed by the Antarctic Oscillation Index; AAO) were shown to govern the structure of the phytoplankton. Under negative AAO, diatoms prevailed, with the dominance of large (> 80 µm) benthic diatoms (e.g. *Corethron pennatum* and *Navicula directa*) in periods of low production (10^2 cells l^{-1} in 2002–03), and medium-sized (31–80 µm) centrics (e.g. *Thalassiosira* spp. and *Stellarima microtrias*) when the abundance was higher (10^4 cells l^{-1} in 2003–04). Conversely, positive AAO led to the co-dominance of dinoflagellates and planktonic diatoms (e.g. *Pseudo-nitzschia* spp.) in the summers of 2007–08 and 2008–09. These results suggest that the AAO can be a good predictor of phytoplankton in coastal areas around the western Antarctic Peninsula, and may help our understanding of changes in other trophic levels of the food web.

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Key words: Antarctic Oscillation Index, diatoms, dinoflagellates, ice melt, temperature rise

Introduction

The Southern Ocean is peculiar for its relatively short food web (Corbisier *et al.* 2004, Cornejo-Donoso & Antezana 2008); therefore, changes in the structure of phytoplankton assemblages may be rapidly reflected in all trophic compartments (Medlin & Priddle 1990, Moline *et al.* 2004, Cornejo-Donoso & Antezana 2008, Ribic *et al.* 2008). Phytoplankton are influenced by chemical (e.g. nutrients, salinity) and physical (e.g. temperature, pH) properties of water masses (Hewes 2009), and by environmental factors such as the wind regime, turbulence and solar radiation. In certain coastal areas of the western Antarctic Peninsula (WAP), winds induce upwellings leading to the resuspension of benthic organisms, such as diatoms, and sediments that carry nutrients to the water column but increase turbidity, reducing light availability for primary production (Brandini & Rebello 1994, Schloss *et al.* 2002). Moreover, light availability regulates primary production rates and the taxonomic composition of phytoplankton assemblages, mainly due to the physiological response of each species when exposed to different light intensities (Mills *et al.* 2010).

Phytoplankton assemblages in surface waters of the WAP are dominated by nanoplankton (2–20 µm) (Montes-Hugo *et al.* 2008). However, microphytoplanktonic (20–200 µm) diatoms contribute significantly to the high biomass in blooms (Moline *et al.* 1997, Schloss *et al.* 2002, Kopczynska 2008). During the last 30 years, warming of the WAP northern waters (including Bransfield Strait) has resulted in increased cloud cover (shading) and wind speed (water column mixing), and decreased ice sheet extent (Montes-Hugo *et al.* 2009). Although the influence of these processes in coastal areas is still under investigation (Schloss *et al.* 2002, Pichlmaier *et al.* 2004, Kopczynska 2008), it has been observed that phytoplankton cell size has decreased in open ocean waters. Typically, the largest microalgae (microplanktonic diatoms) are associated with ice field edges, where light becomes available as the mixed layer shoals (Montes-Hugo *et al.* 2009). However, changes in the wind regime may have favoured advection of the chlorophyll-poor Weddell Sea waters into Bransfield Strait, as opposed to the productive waters from Bellingshausen Sea (Montes-Hugo *et al.* 2009).

In the central waters of Admiralty Bay (AB), King George Island, microphytoplankton generally originates

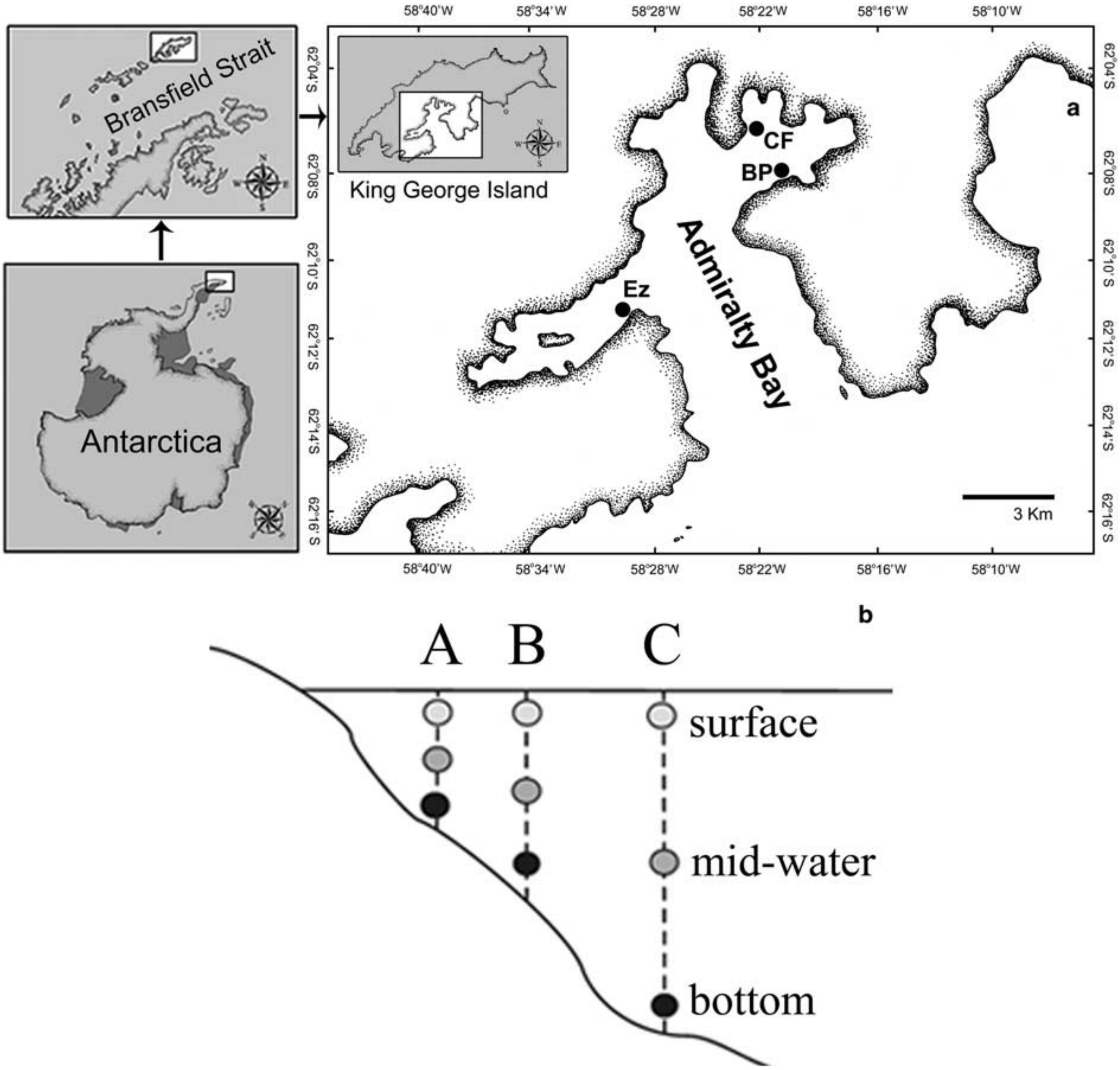


Fig. 1. a. The three sampling sites at Admiralty Bay: Comandante Ferraz (CF; near Comandante Ferraz Station, Brazil), Botany Point (BP) and Ezcurra (EZ; near Arctowski Station, Poland). **b.** Local depths (A 20 m, B 30 m, C 60 m) and approximate sampling depths at each sampling site.

from Bransfield Strait (Kopczynska 2008). In the coastal areas of AB, the microphytobenthos is suspended throughout the water column by coastal upwellings (Brandini & Rebello 1994, Schloss *et al.* 2002) and advection of water bodies caused by continental ice melt (Pichlmaier *et al.* 2004, Nedzarek 2008). Physical processes (i.e. water advection) generated by winds and continental freshwater runoff are also responsible for increased water turbidity (Pichlmaier *et al.* 2004), which decreases light penetration in the water column and, consequently, limits primary production.

It is possible to detect changes in Antarctic coastal ecosystems by monitoring trends in the successional patterns of phytoplankton populations. Interannual variations in phytoplankton composition are more evident than changes in biomass or productivity, as these represent high short-term variability (Moline & Prézelin 1996). At the Antarctic Peninsula, the strong short-term variability of physical processes reflects oscillations in marine primary production (Schloss *et al.* 2002). Consequently, terrestrial biological systems are altered, as marine primary producers are the main energy suppliers for the coastal terrestrial food web (Medlin & Priddle 1990, Ribic *et al.* 2008).

Considering the temporal variability of climate conditions in the WAP and its influence on the phytoplankton structure,

Table I. Sampling seasons, sites sampled (BP = Botany Point, CF = Comandante Ferraz, EZ = Ezcurra), station bathymetry at each site and sampled depths at each station in Admiralty Bay.

Year	November			December			January			February			March			Station bathymetry (at each site)	Sampled depths (at each station)
	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late		
2002–03			CF	EZ						CF						A. 15 m	Surface (1 m)
			BP							BP						B. 30 m	Middle (7, 15 or 25 m)
										EZ						C. 50 m	Bottom (14, 28 or 48 m)
2003–04				EZ	CF				CF							A. 15 m	Surface (1 m)
					BP				BP							B. 30 m	Middle (7, 15 or 25 m)
									EZ							C. 50 m	Bottom (14, 28 or 48 m)
2007–08												CF	EZ			B. 30 m	Surface (1 m)
												BP					Bottom (28 m)
2008–09				CF	EZ											B. 30 m	Surface (1 m)
				BP													Bottom (28 m)

the objective of this study was to associate the temporal and spatial variation in phytoplankton (> 15 μm) size structure and species composition with changes in hydrological variables during four summers (2002–03, 2003–04, 2007–08 and 2008–09) in the shallow (< 30 m) coastal waters of AB.

Material and methods

Study area

Admiralty Bay is a deep embayment located at King George Island (South Shetland Islands, Antarctic Peninsula) at approximately 62°S and 58°W (Fig. 1a). It covers an area of 122 km^2 and the depth exceeds 600 m at the central basin, but at the three inlets (Ezcurra, Mackelar and Martel) does not exceed 150 m (Robakiewicz & Rakusa-Suszczewski 1999). This fjord-like shape reflects a strong glacial influence, subject to freshwater input and high water column turbidity caused by the suspension of soft sediments (Pichlmaier *et al.* 2004). The connection between inner waters and the open ocean (Bransfield Strait) occurs through a wide southward opening. The influence of wind and tidal variations on circulation is more intense in shallow areas, especially at the western side of the bay (Robakiewicz & Rakusa-Suszczewski 1999) where wind plays an important role as a primary production regulator (Brandini & Rebello 1994). Freshwater runoff enriched with guano and fragments of macroalgae are important sources of organic matter and nutrients to the bay (Nedzarek 2008).

Sampling methods and phytoplankton analysis

Admiralty Bay was surveyed during six sampling periods: early and late summer in 2002–03 (27 November–10 December 2002 and 3–10 February 2003), early and mid-summer in 2003–04 (1–12 December 2003 and 16–23 January 2004), late summer in 2007–08 (21 February–5 March 2008) and early summer in 2008–09 (8–14 December 2008) (Table I). Samples were collected near the Brazilian Antarctic Station Comandante Ferraz (CF; 62.082°S, 58.385°W) and at two other sites (Fig. 1a): Botany Point (BP; 62.100°S, 58.353°W) and Ezcurra (EZ; 62.157°S, 58.481°W). Botany Point is distant from any anthropogenic activity. At each site, three sampling stations were established following the bathymetries of 20 m (stn A), 30 m (stn B) and 60 m (stn C) (Fig. 1b). At each station, samples were collected from the surface, mid-water and near the bottom (Table I).

The 164 water samples were collected using 3-l Van-Dorn bottles, stored in 1-l dark polypropylene bottles and mixed with borax-buffered formaldehyde (4%). Phytoplankton was analysed according to the method of Utermöhl (1958), where cells were allowed to settle in 50–100 ml chambers for 48–72 hours depending upon cell concentration. By using an inverted microscope (Olympus® IX70) equipped with phase contrast at a magnification of 200×, organisms > 15 μm were analysed in the whole counting chamber. A higher magnification (400×) was used to identify the smallest taxa. Differential interference contrast (DIC) was also used for the identification of diatoms.

Data from remote sensing (MODIS-Aqua, 4-km resolution) of sea surface temperature (SST) and chlorophyll from an adjacent area at Bransfield Strait located near the entrance of AB (62°S to 62.5°S, 57.5°W to 59°W) were acquired from the Giovanni Online Data System (Ocean Color Project, NASA, accessed 18 January 2012, http://disc.sci.gsfc.nasa.gov/giovanni/overview/index.html). The monthly Antarctic Oscillation Index (AAO) was calculated and provided by the Climate Prediction Center, National Oceanic and Atmospheric Administration (NOAA, http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/aao/aao.shtml2011, accessed 28 December 2011). Data for air temperature, precipitation, solar radiation and wind were acquired from sensors installed at CF, where equipment and datasets are maintained by the Brazilian

Table II. Number of samples or measurements (*n*), mean and standard deviation (SD) of each variable in coastal waters of Admiralty Bay.

	Total		2002–03		2002–03		2003–04		2003–04		2007–08		2008–09	
			Early summer		Late summer		Early summer		Mid-summer		Late summer		Early summer	
	n	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD
Phytoplankton > 15 µm (× 10^3 cells l^{-1})	120	4.2 ± 4.8	27	0.6 ± 0.6	27	1.8 ± 1.6	27	8.6 ± 6.4	27	5.1 ± 2.6	6	4.6 ± 2.7	6	7.7 ± 7.1
Chlorophyll biomass (µg l^{-1})	42	0.35 ± 0.22	9	0.19 ± 0.05	27	0.45 ± 0.22					6	0.13 ± 0.05		
Water temperature (°C)	116	0.5 ± 0.9	27	-0.3 ± 0.3	27	1.6 ± 0.3	27	-0.2 ± 0.3	27	1.0 ± 0.4	6	1.3 ± 0.4	6	1.0 ± 0.5
Salinity	65	34.2 ± 0.6	27	34.6 ± 0.1	26	33.9 ± 0.5					6	33.8 ± 1.0	6	33.8 ± 0.4
$Si(OH)_4$ (µM)	118	51.05 ± 20.52	27	67.39 ± 14.83	25	60.87 ± 24.58	27	40.88 ± 6.14	27	32.07 ± 8.93	6	71.12 ± 12.27	6	47.61 ± 11.10
PO_4^{3-} (µM)	120	2.55 ± 1.77	27	2.52 ± 0.36	27	4.47 ± 2.77	27	2.09 ± 0.95	27	1.54 ± 0.28	6	1.78 ± 0.14	6	1.40 ± 0.18
NH_4^+ (µM)	66	4.01 ± 2.78	27	4.99 ± 3.19	27	4.38 ± 1.94					6	1.05 ± 0.29	6	0.93 ± 0.28
NO_2 (µM)	120	0.22 ± 0.21	27	0.03 ± 0.02	27	0.03 ± 0.01	27	0.34 ± 0.10	27	0.45 ± 0.10	6	0.48 ± 0.24	6	0.13 ± 0.03
NO_3 (µM)	120	23.52 ± 7.45	27	29.55 ± 3.13	27	29.19 ± 4.25	27	22.96 ± 3.83	27	15.73 ± 5.37	6	20.85 ± 5.74	6	11.18 ± 4.92
NO_3:PO_4	120	10.58 ± 4.19	27	12.19 ± 4.07	27	8.57 ± 6.52	27	11.78 ± 2.20	27	9.99 ± 2.27	6	11.65 ± 2.86	6	7.83 ± 2.49
Air temperature of previous winter (°C)				-4.9		-4.9		-3.4		-3.4		-6.3		-2.6
Air temperature during summer (°C)				0.1		0.1		1.0		1.0		0.3		1.5
Mean wind speed (m s^{-1})	120	4.5 ± 2.0	27	5.6 ± 2.9	27	5.2 ± 0.2	27	2.2 ± 0.1	27	4.4 ± 0.9	6	5.0 ± 0.3	6	7.5 ± 1.4
Prevailing wind direction				West		North and west		East and north		West		North and west		South-west and north

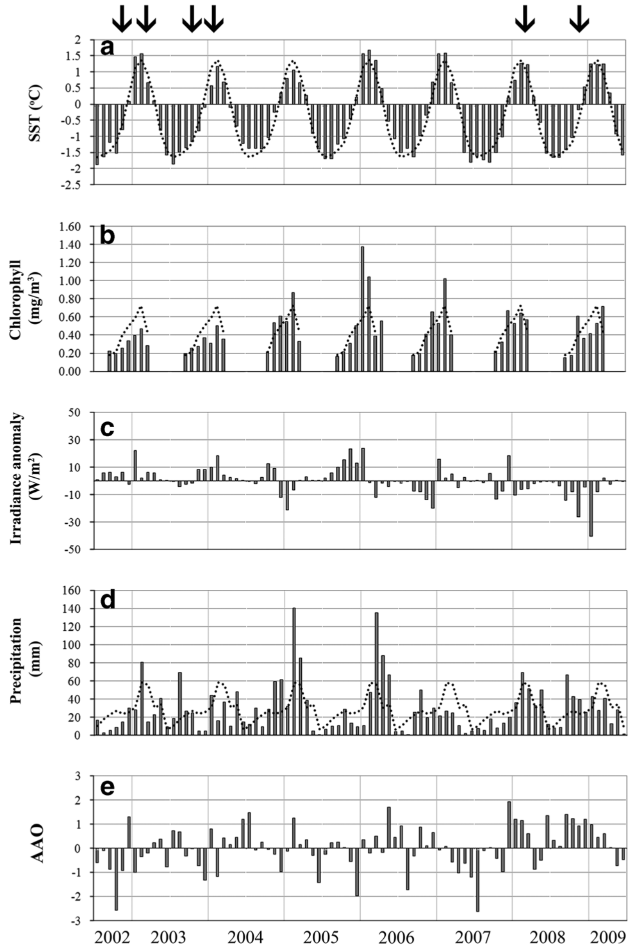


Fig. 2. Climatology from 2002–09 (dashed line) and monthly values. **a.** Sea surface temperature (SST) and **b.** chlorophyll estimated from Aqua-MODIS remote sensors (INPE), **c.** irradiance anomaly and **d.** precipitation measured *in situ*, and **e.** Antarctic Oscillation Index (AAO). Arrows indicate the sampling periods.

National Institute for Space Research (http://www.cptec.inpe.br/antartica/antartica.shtml, accessed 15 December 2009). The average wind speed used in the statistical analyses was calculated for the 24 hours prior to sampling.

In situ temperature measurements were performed using protected reversion thermometers, and salinity was measured using a Beckman inductive salinometer. In 2002–03 and 2003–04, nutrient samples were collected using Go-flo bottles (General Oceanic), filtered through Whatman GF/F filters and stored in polyethylene flasks previously washed with HCl 1:1 and rinsed with distilled water. The filtered water samples were frozen (-20°C) for further analysis. Analyses of nitrate and nitrite were performed using an Auto Analyzer II Bran-Luebbe®. Silicate and phosphate analyses were processed by a spectrophotometric method and measured in a Genesys II spectrophotometer (Bausch & Lomb). All analyses

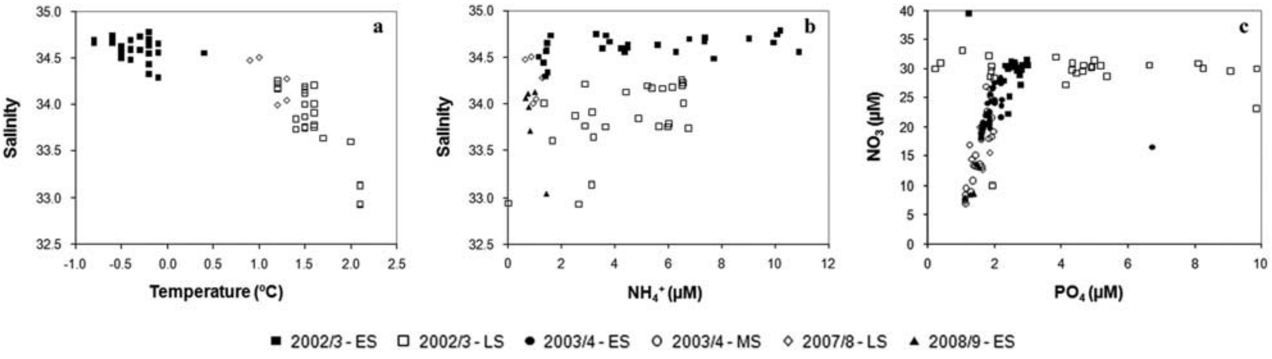


Fig. 3. Relationships between **a.** temperature and salinity, **b.** salinity and ammonium (NH_4^+), **c.** phosphate (PO_4^{3-}) and nitrate (NO_3^-) in coastal waters of Admiralty Bay during the periods when data of both variables were available. ES = early summer, MS = mid-summer, LS = late summer.

followed the recommendations in Grasshoff *et al.* (1999). Chlorophyll *a* was extracted from 1 litre filtered samples (Whatman GF/F filters), frozen (-20°C) and determined by fluorimetry after extraction in 90% acetone, using a Turner Designs TD-700 fluorometer (Parsons *et al.* 1984). In 2007–08 and 2008–09, inorganic nutrients were also analysed using the following methods: ammoniacal nitrogen by indophenols, nitrite by diazotation, nitrate by reduction in Cd-Cu column followed by diazotation, total nitrogen by digestion with potassium persulfate following nitrate determination, orthophosphate by reaction with ascorbic acid, total phosphorous by acid digestion to phosphate, and silicate by reaction with molibdate. Chlorophyll *a* analysis was performed after vacuum filtration (< 25 cm of Hg). The filters (cellulose membrane Millipore HAWP 0.45 µm) were extracted overnight in 90% acetone at -20°C, and analysed with a UV-VIS Perkin Elmer Lambda 20 spectrophotometer (Parsons *et al.* 1984).

Data analysis and statistics

Basic statistics for environmental data (mean, standard deviation, Spearman correlation and cross-correlation *r*, and p-values) were calculated using Microsoft Excel, Statsoft Statistica 6.0 and Past. Principal component analysis (Statistica 6.0) was used to visualize interactions between abiotic components. The influence of abiotic variables on phytoplankton was evaluated through a canonical correspondence analysis (CCA; CANOCO 4.5).

Although microphytoplankton classically comprises cells ranging from 20–200 µm (Sieburth *et al.* 1978), 15–20 µm cells were also included in this study as their abundance and main taxonomic groups (diatoms and dinoflagellates) are similar to conventional microphytoplankton in Antarctica (Medlin & Priddle 1990, Schloss *et al.* 2002, Kopczynska 2008). Therefore, phytoplankton cells > 15 µm were identified and quantified in order to assess variations in the microphytoplankton structure. Phytoplankton cells were

Table III. Correlation (Spearman *r*) between environmental and biological variables in Admiralty Bay, Antarctic Peninsula (only significant *r* values ($P < 0.05$) are displayed.

	T	S	Wind	Rad	PO_4^{3-}	NO_3^-	NO_3:PO_4	NH_4^+	SiO_2	Phyto	Chl	Pheo	AAO	Chl-AMODIS
T	1.00	-0.82	0.57	-0.23			-0.25				0.51	0.54		0.86
S		1.00						0.37	0.31	-0.64	-0.46	-0.64	0.29	-0.69
Wind			1.00				-0.20	-0.37	0.20	-0.29				0.40
Rad				1.00				0.30		-0.25		-0.51		-0.20
PO_4^{3-}					1.00	0.68	-0.29	0.32	0.55	-0.48	0.49		-0.68	
NO_3^-						1.00	0.24	0.62	0.57	-0.64			-0.79	
NO_3:PO_4							1.00				-0.38			-0.27
NH_4^+								1.00		-0.48			-0.41	-0.26
$Si(OH)_4$									1.00	-0.50			-0.44	
Phyto										1.00		0.43	0.58	0.23
Chl											1.00	0.83	-0.79	
Pheo												1.00	-0.75	0.75
AAO													1.00	
Chl-AMODIS														1.00

AAO = Antarctic Oscillation Index, chl = *in situ* chlorophyll biomass, chl-AMODIS = chlorophyll from Aqua-MODIS, NH_4^+ = ammonium, NO_3^- = nitrate, pheo = *in situ* pheophytin, phyto = phytoplankton abundance, PO_4^{3-} = phosphate, rad = solar radiation, S = *in situ* salinity, SiO_2 = silicate, T = *in situ* seawater temperature, wind = wind speed.

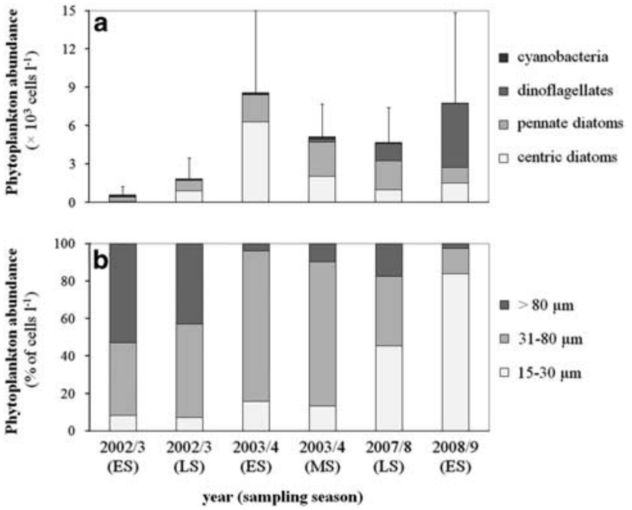


Fig. 4. Phytoplankton (> 15 µm) mean abundance (and standard deviation) showing **a.** the contribution of taxonomic groups and **b.** contribution (%) of cell size classes in coastal waters of Admiralty Bay during early (ES), mid-summer (MS) or late summer (LS) of 2002–03, 2003–04, 2007–08 and 2008–09.

grouped into three size classes: 15–30 µm, 31–80 µm and > 80 µm. These size classes allow a more detailed trophic approach, considering that the food selection by local herbivores depends on the size of particles they can capture with their mouth apparatus (Opalinski *et al.* 1997). Phytoplankton was further divided into four taxonomic groups for statistical analyses: pennate diatoms, centric diatoms, dinoflagellates and cyanobacteria.

In each of the four sampling years, taxa with abundance lower than the mean abundance of all species were considered ‘rare’, and were not included in any species level analyses (cluster analysis and SIMPER routine). In order to normalize distributions and eliminate zero values, phytoplankton abundance data were log-transformed as $\log_{10}(x + 1)$. Percentages were normalized using the square root when proportions were compared. Phytoplankton abundance and environmental data from different sampling years and sites were compared using a one-way ANOVA with a Fisher-LSD test ($P < 0.05$) and Spearman correlation (*r*). Samples were grouped according to the abundance of each species through a cluster analysis using Ward’s Method (Past 1.8). The similarity percentages (SIMPER; Primer 6.0) routine was used to identify the most important species in the groups established by the cluster analysis.

Results

Environmental patterns

Temporal variations of temperature and chlorophyll in surface waters surrounding King George Island show similar patterns to the shallow coastal waters of AB (Table II). According to satellite data (MODIS-Aqua 4-km), the slight increase in SST from 2002 to 2009 was coupled with a small rise in chlorophyll in the surface waters of Bransfield Strait (Fig. 2a & b). The decrease in solar radiation (Fig. 2c) was indicative of denser or more frequent cloud cover and higher precipitation (Fig. 2d). The AAO went from a predominantly negative to a positive phase from 2002 to 2009 (Fig. 2e). The highest surface chlorophyll values in adjacent open waters (Bransfield Strait) were associated with years when the AAO was in a transition between phases, showing values nearest to zero (i.e. summers of 2004–05, 2005–06 and 2006–07). Therefore, the shallow coastal waters of AB were sampled during the least productive summers (e.g. 2002–03, 2003–04, 2007–08 and 2008–09)

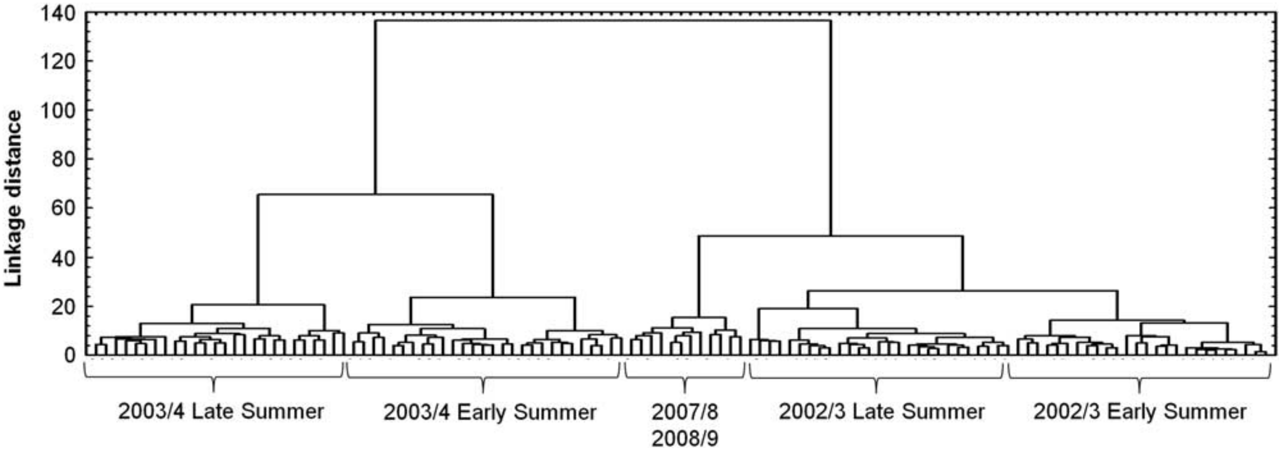


Fig. 5. Cluster analysis of the abundance of each species in water samples from the shallow coastal waters of Admiralty Bay (Ward’s Method, Euclidean Distance).

Table IV. Species that most contributed to the similarity of samples within groups identified by the cluster analysis.

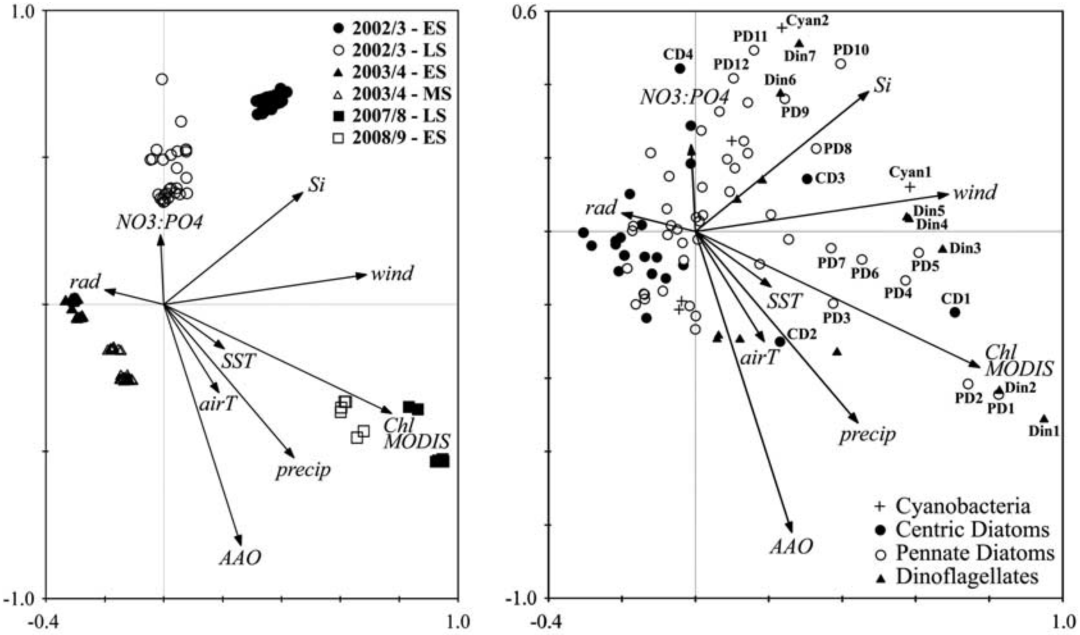
Sampling period	Group	Size class	Species	%
2002–03	CD	> 80 µm	*Corethron pennatum*	14.5
Early summer	DIN	30–80 µm	*Katodinium* sp.	12.4
(AS: 30.2)	PD	> 80 µm	***Gyrosigma* sp.**	11.3
	PD	15–30 µm	***Pseudogomphonema kamtshaticum***	8.6
	PD	> 80 µm	*Cylindrotheca closterium*	6.1
	PD	> 80 µm	***Pleurosigma directum***	5.2
	DIN	30–80 µm	*Gymnodinium* sp.	4.5
2002–03	CD	> 80 µm	*Corethron pennatum*	25.3
Late summer	DIN	15–30 µm	*Katodinium* sp.	12.8
(AS: 43.4)	PD	15–30 µm	***Pseudogomphonema kamtshaticum***	10.8
	CD	30–80 µm	*Thalassiosira ritscheri*	8.5
	PD	30–80 µm	"*Pseudo-nitzschia delicatissima*" complex	7.7
	CD	30–80 µm	*Thalassiosira* sp.3	6.1
	DIN	> 80 µm	*Gyrodinium lachrymal* (Meunier) Kofoid & Swezy	4.5
2003–04	CD	30–80 µm	*Stellarima microtrias*	10.8
Early summer	CD	30–80 µm	*Porosira* sp.	9.2
(AS: 61.0)	CD	30–80 µm	*Thalassiosira* sp.1	7.8
	CD	30–80 µm	*Thalassiosira* sp.3	7.6
	CD	30–80 µm	Unidentified centric diatom	7.6
	PD	15–30 µm	***Pseudogomphonema kamtshaticum***	6.5
	CD	15–30 µm	*Thalassiosira* sp.2	5.6
	CD	30–80 µm	*Charcotia actinochila* (Ehrenberg) Hustedt	4.7
2003–04	CD	30–80 µm	*Porosira* sp.	6.8
Mid-summer	PD	15–30 µm	***Pseudogomphonema kamtshaticum***	6.5
(AS: 64.3)	CD	15–30 µm	*Thalassiosira* sp.2	6.1
	CD	> 80 µm	*Corethron pennatum*	5.9
	DIN	15–30 µm	*Katodinium* sp.	4.8
	CD	30–80 µm	*Thalassiosira ritscheri*	4.6
	CD	30–80 µm	*Stellarima microtrias*	4.3
2007–08	DIN	15–30 µm	*Katodinium* sp.	8.8
Late summer	CD	30–80 µm	*Thalassiosira* sp.3	8.1
	PD	30–80 µm	"*Pseudo-nitzschia delicatissima*" complex	7.8
2008–09	PD	30–80 µm	"*Pseudo-nitzschia seriata*" complex	7.0
Early summer	PD	15–30 µm	***Pseudogomphonema kamtshaticum***	6.9
(AS: 43.8)	CD	30–80 µm	Unidentified centric diatom	6.2
	CD	30–80 µm	*Porosira* sp.	4.8

% = percentage contribution of each species in the group.
AS = average similarity of the sampling groups at each period, CD = centric diatom, DIN = dinoflagellates, PD = pennate diatom.
Benthic species are indicated in bold.

in Bransfield Strait, when chlorophyll concentrations were mostly below the climatological average for each month (Fig. 2b).

In the shallow waters of AB, the temperature rise observed in the last two sampling periods was associated with a slight decrease in salinity and nutrient concentrations (Table II). However, the N:P ratio (NO_3:PO_4 = 11 ± 4) did not vary over time (Table II), being below the Redfield N:P ratio (N:P = 16). The terrestrial inputs of nitrogen (mainly ammonium) and phosphorus (phosphate) are very high and occur in locally-concentrated pulses in these shallow areas. Therefore, it is possible that the high variations in the N:P ratio are caused by these input pulses rather than by variations in uptake rates by phytoplankton, which did not vary in abundance. The summer of 2002–03 was characterized by low water temperature and high salinity early in the season, while temperature increased and salinity decreased during late summer (Table II, Fig. 3a). Concentrations of nutrients (ammonium, nitrate, silicate) were lower at the end of summer (Fig. 3b & c), but phosphate concentrations increased (Table II). The same pattern was observed in the summer of 2003–04 (Table II), most evident at EZ. At BP in late summer 2007–08, high water temperatures occurred simultaneously with low salinity and high levels of silicate, phosphate and nitrate (Table II), in contrast to previous years. In the 2008–09 early summer, the negative correlation between ammonium and salinity (Table III) was more evident at BP, where salinity was low (33.5 ± 0.7) and ammonium was high ($1.245 \pm 0.304\,\mu mol\ l^{-1}$) compared to mean values for this period (Table II).

In summary, the summers of 2002–03 and 2007–08 were characterized by a cold preceding winter (-4.9 and -6.3°C, compared to -3.4 and -2.6°C in 2003–04 and



Environmental variables:

AAO - Antarctic Oscillation Index;
airT - air temperature (*in situ*/INPE);
precip - precipitation (INPE);
SST - sea surface temperature (Aqua-MODIS);
Chl MODIS - chlorophyll concentration (Aqua-MODIS);
wind - wind speed (INPE);
Si - silicate (*in situ*);
NO3:PO4 - dissolved nitrate to phosphate ratio (*in situ*);
rad - solar radiation (*in situ*/INPE).

Phytoplankton species:

Cyan1 - *Leptolyngbya* sp.
Cyan2 - Oscillatoriales spp.
CD1 - *Thalassiosira* sp.
CD2 - *Asteromphalus hookeri*
CD3 - *Thalassiothrix antarctica*
CD4 - Unident. centric diatom (35μm)
PD1 - *Pseudo-nitzschia "delicatissima"* complex Group 1
PD2 - *Navicula glaciei*
PD3 - Unident. pinnate diatom, chain-forming (15μm)
PD4 - *Cocconeis melchioroides*
PD5 - *Plagiotropsis gaussii*
PD6 - Unident. pinnate diatom, chain-forming (45μm)
PD7 - *Nitzschia lanceolata*
PD8 - *Membraneis challengeri*
PD9 - *Amphora* sp.4
PD10 - *Hantzschia* sp.
PD11 - *Navicula algida*
PD12 - *Navicula* cf. *transitrans*
Din1 - *Gonyaulax* sp. 1
Din2 - *Gymnodinium minor*
Din3 - *Prorocentrum* cf. *minimum*
Din4 - Gymnodiniales sp.1
Din5 - Gymnodiniales sp.2
Din6 - *Gymnodinium* sp.1
Din7 - *Protoperidinium* sp.2

Fig. 6. Canonical correspondence analyses of the abundance of phytoplankton species by environmental variables in the shallow coastal waters of Admiralty Bay.

2008–09, respectively) and low AAO indexes (negative values down to -2.5 in 2002 and 2007, compared to predominantly positive values up to 2.1 in 2004 and 2008) (Fig. 2). Consequently, late continental ice melt occurred in 2002–03 and 2007–08, coinciding with high nutrient levels ($r > 0.41$, $P > 0.05$, Table III) (see Table II for nutrient concentrations). In general, water temperature was higher (> 1.0°C) and salinity was lower (< 34) in mid- and late summer when compared to early in the season (< 1.0°C and > 34, respectively) (Table II, Fig. 3a). Ammonium concentrations were associated with high temperatures ($r = 0.37$, $P < 0.05$) and low salinities ($r = -0.37$, $P < 0.05$) (Table III, Fig. 3b).

Phytoplankton changes over time

The average abundance of phytoplankton (> 15 μm) was generally low ($4.2 \times 10^3 \pm 4.8 \times 10^3$ cells l^{-1}), and showed high variability over time, with a shift in the dominant taxonomic groups (Fig. 4a) reflected in a decrease in cell size (Fig. 4b). Large diatoms (> 31 μm) represented more than 90% of the phytoplankton abundance in the 2002–03 and 2003–04 summers, while there was a significant increment of small dinoflagellates in 2007–08 (30%) and 2008–09 (65%). Cyanobacteria were represented more during the 2002–03 summer (5%), and their contribution decreased in the following years (Fig. 4a).

A cluster analysis (Fig. 5) identified five groups, according to the dominant species and their contribution in each period (Table IV). This analysis showed that the spatial variability of phytoplankton populations was negligible when compared to temporal changes. The lowest phytoplankton concentrations occurred in 2002–03 ($1.2 \times 10^3 \pm 1.4 \times 10^3$ cells l^{-1}, $P < 0.01$), when diatoms > 80 µm were the most representative (45%) (Fig. 4b), including species such as *Corethron pennatum* (Grunow) Ostenfeld, *Pleurosigma directum* Grunow, *Gyrosigma* sp., *Fragilariopsis ritscheri* Hustedt, *Navicula directa* (Wm. Smith) Ralfs (see Table IV). In the summer of 2003–04, low wind speeds (2.2 m s^{-1} east in early summer) favoured an increase in phytoplankton abundance ($6.8 \times 10^3 \pm 5.1 \times 10^3$ cells l^{-1}), characterized by the dominance (80%) of mid-sized cells (31–80 µm) (Fig. 4b) represented mainly by centric (*Thalassiosira* spp., *Porosira* sp., *Stellarima microtrias* (Ehrenberg) Hasle & Sims, *Actinocyclus actinochilus* (Ehrenberg) Simonsen) and pennate (*Pseudogomphonema kamtshaticum* (Grunow) Medlin, *Achnanthes* spp., *F. striatula*) diatoms (Fig. 5, Table IV). In contrast, small (15–30 µm) dinoflagellates (e.g. *Katodinium* sp.) became dominant in 2007–08 and 2008–09 (Fig. 4a & b). These dinoflagellates were responsible for the highest abundances in 2008–09 ($7.7 \times 10^3 \pm 7.1 \times 10^3$ cells l^{-1}), associated with the drop in nutrient levels (Table II & III). The contribution of planktonic diatoms (*Thalassiosira* spp., *Pseudo-nitzschia* spp.) and the benthic diatom *Pseudogomphonema kamtshaticum* was also important in later years (Fig. 5, Table IV). The relative abundance of large cells (> 80 µm) was highest in the coldest years (2002–03 and 2007–08) (Table IV, Fig. 4) when continental ice was still present during the summer. However, in 2002–03 these large cells were benthic diatoms, as previously cited, while in 2007–08 these cells were represented by diatoms from the *Pseudo-nitzschia seriata* complex (Cleve) H.Peragallo, mainly *Pseudo-nitzschia* cf. *heimii* Manguin.

Seasonal variations in phytoplankton were distinct in the first two sampling years. In early summer 2002–03 a lower phytoplankton abundance was observed ($0.5 \times 10^3 \pm 0.7 \times 10^3$ cells l^{-1}, Fig. 4a), composed of the centric diatom *C. pennatum*, chain-forming pennate diatoms such as *F.* cf. *ritscheri*, *Navicula* spp. and *F. striatula*, and epiphytic species such as *Pleurosigma directum*, *Gyrosigma* spp., *Pseudogomphonema kamtshaticum* and *Licmophora* spp. (data not shown). During late summer there was a rise in phytoplankton abundance ($1.8 \times 10^3 \pm 1.7 \times 10^3$ cells l^{-1}, Fig. 4a) due to an increase in the abundance of the epontic centric diatom *C. pennatum* (Fig. 4b) and planktonic diatoms like *Thalassiosira* spp. and *Pseudo-nitzschia delicatissima* complex (Fig. 5, Table IV). In 2003–04 phytoplankton abundance was highest during early summer ($8.6 \times 10^3 \pm 6.4 \times 10^3$ cells l^{-1}, Fig. 4a) when compared to mid-summer ($5.1 \times 10^3 \pm 2.6 \times 10^3$ cells l^{-1}, Fig. 4a). High abundances in early summer were driven by planktonic centric diatoms (Fig. 4b) such as *Thalassiosira* spp., *Porosira* sp., *A. actinochilus* and *S. microtrias*. (Fig. 5, Table IV). Conversely, during mid-summer the drop in centric diatom abundance lead to a higher contribution of large diatoms (e.g. *C. pennatum*, *Thalassiosira ritscheri* (Hustedt) Hasle) and the dinoflagellate *Katodinium* sp. (Fig. 5, Table IV).

To summarize the influence of environmental variables driving temporal changes on phytoplankton assemblages, a CCA was performed (Fig. 6), which explained 35.7% of the variation of data. The analysis showed that interannual changes were more evident than the interseasonal variability of phytoplankton populations (Fig. 6a), influenced mainly by the AAO (weight = 0.196, $F = 8.97$, $P < 0.01$). The AAO reflects (and/or co-varies with) changes in the air temperature ($r = 0.63$) and SST ($r = 0.43$), precipitation ($r = 0.86$), winds ($r = 0.24$) and solar radiation ($r = -0.29$). Among those environmental parameters, precipitation showed the largest influence (weight = 0.165, $F = 8.04$, $P < 0.01$) over phytoplankton populations. High precipitation levels (especially in the summers of 2007–08 and 2008–09) coincided with high chlorophyll *a* concentrations, associated with the presence of the diatoms *N. glaciei* Van Heurck, *Pseudo-nitzschia delicatissima* complex (Hasle) and chain-forming *Thalassiosira* spp., and the dinoflagellates *Gonyaulax* sp. and *Gymnodinium minor* Lebour (Fig. 6b). Benthic pennate diatoms (*Hantzschia* sp., *N. algida* Grunow, *N. transitans* Cleve) and cyanobacteria (*Oscillatoriales* spp.), an unidentified centric diatom and the dinoflagellates *Protoperidinium* sp. and *Gymnodinium* sp. were abundant in negative AAO periods, under low precipitation, low SST (weight = 0.165, $F = 8.04$, $P < 0.01$) and low air temperature (weight = 0.148, $F = 8.13$, $P < 0.01$), which occurred in 2002–03 (Fig. 6b). The influence of low wind speeds and high solar radiation over phytoplankton in the summer of 2003–04 is projected on axis I (Fig. 6a & b), highlighting the dominance of planktonic centric diatoms, as opposed to the presence of dinoflagellates (e.g. *Prorocentrum antarcticum* (Hada) Balech/*Prorocentrum minimum* (Pavillard) Schiller) and benthic pennate diatoms (e.g. *Plagiotropis cf. gaussii* (Heiden) Kolbe, *Cocconeis melchioroides* Al-Handal, Riaux-Gobin, Romero & Wulff) under high wind conditions (Fig. 6a).

Spatial variations of phytoplankton populations

Phytoplankton assemblages and environmental variables did not show significant differences ($P > 0.05$) between

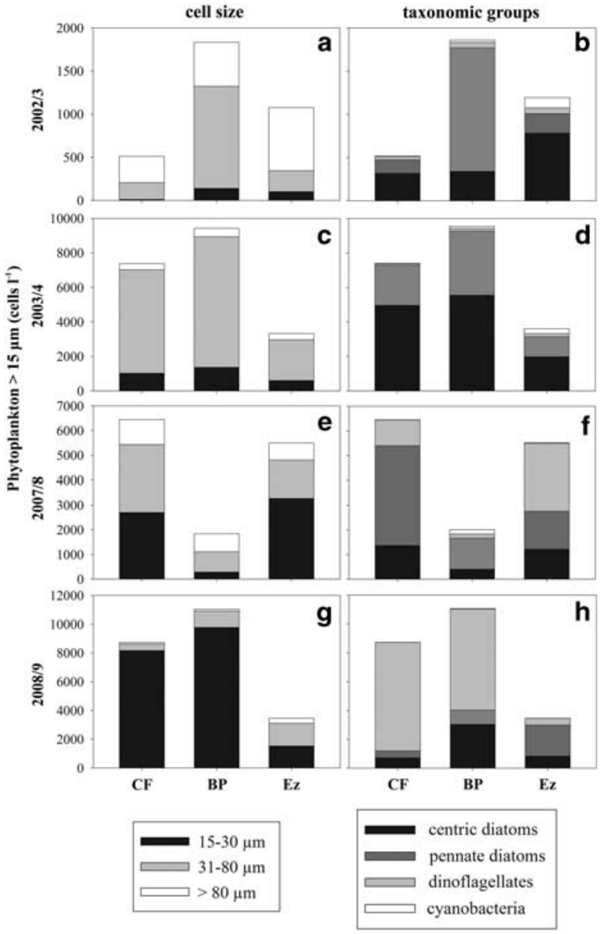


Fig. 7. Abundance (cells l^{-1}) of phytoplankton size classes and taxonomic groups in the four sampling seasons: 2002–03, 2003–04, 2007–08, 2008–09.

sampling depths (surface, mid-water and bottom) at each site, or their local bathymetry (15, 30 and 60 m). Therefore, average values for each site are shown in regard to the spatial variation (comparison between sites) (Fig. 7).

The site BP was always distinct from the other two sites in terms of phytoplankton abundance (highest concentration, except for 2007–08 when it was the lowest) and taxonomic composition (Fig. 7). In the summer of 2002–03, pennate benthic diatoms prevailed at BP, with the large benthic ones (e.g. *Pleurosigma directum*, *Gyrosigma* spp.) during early summer, and the mid-sized (31–80 µm) chain-forming *F. ritscheri* and *F. striatula* in late summer (Fig. 7a & b). At the other sites, the centric diatom *C. pennatum* was dominant, representing most of the large (> 80 µm) cells (Fig. 7a & b). At EZ, filamentous cyanobacteria (e.g. *Oscillatoria* spp., *Leptolyngbya* spp.) were more representative (10%) than at the other sites (1%) (Fig. 7b). In 2003–04, mid-sized (31–80 µm) centric diatoms were dominant at all sites (Fig. 7c & d).

The area where the contribution of cyanobacteria was notable changed from EZ in 2002–03 and 2003–04, where *Oscillatoria* spp., *Leptolyngbya* spp. and others represented more than 5% of the total phytoplankton abundance (Fig. 7b & d), to BP in 2007–08 late summer (Fig. 7f), where large (> 80 µm) benthic diatoms (e.g. *Pleurosigma directum* and *Cylindrotheca closterium* (Ehrenberg) J. Lewin & Reimann) were also abundant (Fig. 7e & f). At the other sites, smaller cells (15–30 µm) showed higher abundances (Fig. 7e). At EZ, dinoflagellates (e.g. *Protoperidinium defectum* Balech) were dominant (50%), contrary to the dominance of diatoms (82%) at the other sites (Fig. 7f). In early summer 2008–09, EZ retained the taxonomic distinction from the previous year as pennate diatoms > 31 µm (*Pseudo-nitzschia* spp.) were the most representative (Fig. 7h), while those > 80 µm (pennate benthic diatom *Cylindrotheca closterium* and planktonic "*Pseudo-nitzschia seriata*" complex) occurred at the other sites where small dinoflagellates (15–30 µm) were dominant (> 89%, Fig. 7h).

Cyanobacteria and large diatoms (except *Cylindrotheca closterium* and *Pseudo-nitzschia* spp., dominant large diatoms in 2008–09) were associated with high-temperature/high-ammonium/low-salinity waters (see Table IV) from terrestrial or marine ice melt, except in 2002–03 when the dominant species *C. pennatum* occurred under these conditions. The genus *Pseudo-nitzschia* was associated with external (Bransfield Strait) waters with high salinity and low temperature/ammonium concentration, most common at EZ. Nevertheless, some species were typical of each site: large (>80 µm) pennate diatoms (*Pleurosigma* spp., *Gyrosigma* spp., *Cylindrotheca closterium*) were typical of BP, the genus *Achnanthes* at CF, and the highest abundance of dinoflagellates (except for 2008–09) was found at EZ. The epiphytic *Pseudogomphonema kamtshaticum* was typically found at CF and EZ (where macroalgae are abundant in the sublittoral).

Discussion

In recent years, interannual changes in environmental conditions at AB's coastal areas, especially hydrological features, have resulted in a decrease of microphytoplankton prevailing cell size, associated with a shift in the dominance of phytoplankton taxonomic groups from diatoms to dinoflagellates. This may be a result of the rise in summer water temperature from 0.5°C during 2002–03 and 2003–04 to 1.2°C during 2007–08 and 2008–09. This temperature rise was also observed in the neighbouring inlet of Potter Cove (King George Island) during a 19 year study (Schloss *et al.* 2012) and confirmed by satellite data (this study). Kopczynska (2008) also reported a reduction in diatom abundance in AB during a 9 year monitoring study. Furthermore, Montes-Hugo *et al.* (2008, 2009) observed similar changes in the phytoplankton assemblages of adjacent areas north of the WAP.

Climate change in this region has led to a rise in the incident radiation and temperature, increasing terrestrial ice melt. Secondary effects of the ice melt (e.g. changes in turbulence leading to changes in suspended inorganic particle concentrations, the turbidity, and therefore in light attenuation) have possibly caused a reduction in diatom abundance. On the other hand, short-term alterations in phytoplankton assemblages are predominantly influenced by changes in the wind pattern and ice cover (Montes-Hugo *et al.* 2009, Schloss *et al.* 2012). The AAO, or Southern Annular Mode (SAM), is a useful tool to predict and track climate change regarding cloud and ice cover, solar radiation, precipitation, atmospheric and water temperatures in the WAP (Liu *et al.* 2004). This index has been directly related to the changes in phytoplankton structure observed in this area (Montes-Hugo *et al.* 2008, Schloss *et al.* 2012). In shallow coastal waters of AB (present study), negative AAO values were related to the dominance of diatoms, whereas positive AAO induced an increase in dinoflagellate abundance. Furthermore, based on remote sensing data, the most productive years (highest chlorophyll concentrations in the summers of 2004–05 and 2005–06), not sampled in this work, coincided with transitional AAO values (negative to neutral, see Fig. 2e), with high precipitation in summer (see Fig. 2d). The effects of AAO fluctuations on the circulation of bottom waters of inlets around King George Island (Schloss *et al.* 2012) are apparently reflected in shallow areas, but do not reach surface waters in the inner AB (Kopczynska 2008, Lange *et al.* unpublished data).

A decrease in phytoplankton size associated with changes in the taxonomic structure in relation to climate change (i.e. warming) has also been reported in other polar regions. In the Arctic Ocean the warming of surface waters led to an increased stratification and consequent decline in nutrient supply from deep waters to the euphotic layer (Li *et al.* 2009). These conditions favoured smaller cells (i.e. picoplankton) due to their larger surface-to-volume ratio (higher ability to absorb nutrients). In the present study a decrease in phytoplankton size was observed, although picoplankton and part of the nanoplankton fraction have not been evaluated. However, it is not clear which was the main factor that triggered the increase of small dinoflagellates ($< 30\,\mu m$) and decline of microplanktonic diatoms in the summers of 2007–08 and 2008–09 (positive AAO), compared to 2002–03 and 2003–04 (mostly negative AAO). As the Antarctic coastal waters are presumably high-nutrient, low-chlorophyll (HNLC; Lange *et al.* 2007, Kopczynska 2008, Nedzarek 2008), it is unlikely that the lack of macronutrients is the cause of low biomass. In fact, high silicate, ammonium and nitrate concentrations (see Table II) were observed in periods when the land was covered by ice (2002–03 and 2007–08, personal observation) compared to periods with more ice-free zones (2003–04 and 2008–09, personal observation). This supports the idea proposed by Nedzarek (2008) that the continental ice melt leads to terrestrial runoff, being the most important nutrient source to shallow coastal zones of AB. Regarding micronutrients, it has been assumed that iron limitation is not severe in the AB (Brandini 1993) since adjacent areas (e.g. Bransfield Strait) have natural levels of iron always above the limiting concentration for primary production (Martin *et al.* 1990). Furthermore, the intense nutrient runoff carried by continental freshwater into the bay possibly contributes to iron input (Nedzarek 2008), although the concentration of this metal has never been measured in AB. Another important consequence of ice melt is the physical environment generated by freshwater flow in acclivitous shores, leading to the suspension of bottom material (Pichlmaier *et al.* 2004). This suspended material causes an increase in turbidity, leading to the decrease of light availability in the water column. High turbidity and low light would theoretically favour smaller cells, which need less light to grow, or motile cells (dinoflagellates) that can be retained at surface, where light is available (Mills *et al.* 2010). Terrestrial ice melt runoff is also indicated by the presence of several tychoplanktonic species (e.g. *Pseudogomphonema kamtshaticum*, *Cocconeis* spp, *Achnanthes brevipes* Agardh, *Pleurosigma* spp.) observed in our study. In general, freshwater input increases water column stability in AB's central basin, further promoting phytoplankton growth, but also causes an increase in turbulence and turbidity in coastal shallow zones, which may reduce primary production (Schloss *et al.* 1997, Kang *et al.* 2002).

The dominance of diatoms amongst the microphytoplankton in the northern region of the WAP has been previously reported (Brandini 1993, Brandini & Rebello 1994, Moline *et al.* 1997, Schloss *et al.* 2002, Lange *et al.* 2007, Kopczynska 2008, Uitz *et al.* 2009). During the earliest sampling years in the present investigation, diatoms were also the dominant taxonomic group in the coastal waters of AB. The frequent contribution of epiphytic diatoms (*Pseudogomphonema kamtshaticum*, *Achnanthes* spp., *Licmophora* spp., *Cocconeis* spp.), especially at CF and EZ, indicate the importance of macroalgae as substrates to microalgae (Al-Handal & Wulff 2008). The epontic centric diatom *C. pennatum* ($> 100\,\mu m$), which normally increases in abundance during ice melting seasons (Kang *et al.* 2002), was the most abundant species in the microphytoplankton during the 2002–03 summer, when fast ice remained until mid-summer (January) at AB. Along with *C. pennatum*, other diatoms were also abundant, such as the benthic pennate *Licmophora* spp., *Pseudogomphonema kamtshaticum*, *F. striatula*, *F.* spp., and *Achnanthes* spp., some of which have been regarded as the main phytoplankton species in the krill diet (Ligowski 2000). However, Opalinski *et al.* (1997) state that krill reject cells > 70 µm (e.g. benthic pennate diatoms such as *N. directa*, *Pleurosigma directum*, *Gyrosigma* sp., also abundant in 2002–03). In the following summer (2003–04), *C. pennatum* was replaced by *Thalassiosira antarctica* Comber, *S. microtrias*, *Porosira* spp. and other centric mid-sized diatoms (30–80 µm). Mid-sized centric diatoms, which are the most palatable species to krill (Opalinski *et al.* 1997, Ligowski 2000), were responsible for the highest abundances (10^4 cells l^{-1}) in the 2003–04 summer, when easterly winds prevailed.

Strong winds on AB drive turbulence in the water column leading to suspension of bottom material along with benthic microalgae in the coastal area (Brandini & Rebello 1994, Schloss *et al.* 2002, Lange *et al.* 2007). When those periods are followed by low speed winds, stability of the water column allows benthic cells to bloom while suspended (Brandini & Rebello 1994, Schloss *et al.* 2002). The wind regime is also responsible for the wide circulation pattern in the bay, along with tide dynamics (Robakiewicz & Rakusa-Suszczewski 1999). Disregarding the role of tide influencing phytoplankton assemblages in these shallow waters, our study indicated that low wind speeds induced high phytoplankton abundance ($8.6 \times 10^3 \pm 6.4 \times 10^3$ cells l^{-1}) in early summer 2003–04, dominated by the planktonic centric diatom species of *Thalassiosira*, *Porosira*, *Stellarima* and others. This condition was earlier reported by Brandini (1993) in the central basin of AB during the summer of 1987, when the same species were important during a low wind speed period. However, the abundance of those centric diatoms (10^3–10^4 cells l^{-1}) does not amount to a bloom condition like the ones previously recorded for this area (10^5 cells l^{-1}), which were mainly composed by pennate chain-forming diatoms (Brandini & Rebello 1994, Kopczynska 2008). Presumably, the relatively low east and north winds in 2003–04 also led to a strong influence from the Bellingshausen Sea waters. It has been reported that *Thalassiosira* spp., and *S. microtrias* can be detected in Bransfield Strait (and AB) under the influence of east wind, as opposed to west wind, which advect waters from Weddell Sea with high abundance of *Rhizosolenia* spp. (Montes-Hugo *et al.* 2009). During late summer 2007–08 and early summer 2008–09, when western winds prevailed, dinoflagellates (*Prorocentrum antarcticum*/*Prorocentrum minimum*, *Protoperidinium defectum*) and planktonic diatoms, such as *Rhizosolenia truncate* G.Karsten, *Proboscia alata* (Brightwell) Sundstrøm, *Chaetoceros socialis* H.S.Lauder, *Pseudo-nitzschia* spp. and *Tropidoneis antarctica* (Grunow) Cleve, became dominant in the shallow coastal waters at AB. Those species are typical from the Weddell Sea (Kang *et al.* 2001) and were also registered in the warmer waters northward at Iles Kerguelen (Armand *et al.* 2008). Moreover, they are usually avoided by the Antarctic krill *Euphausia superba* Dana (Opalinski *et al.* 1997).

The consequences of shifts in phytoplankton size and composition for the food web can be substantial. The diet of *E. superba* consists of 46% benthic diatoms in coastal zones, such as those at AB (Ligowski 2000). The Antarctic krill is an important link in the Antarctic food web (Medlin & Priddle 1990, Pakhomov *et al.* 2002, Corbisier *et al.* 2004). Thus, a reduction in benthic microalgae in the water column would cause a shortage in food availability to krill, as much as to other planktonic herbivores and benthic suspension feeders (Gili *et al.* 1996, Corbisier *et al.* 2004). Small microalgae, which are not palatable to those herbivores, are preferred by salps and other suspension feeders (Moline *et al.* 2004, Montes-Hugo *et al.* 2009). Therefore, a decrease in phytoplankton cell size in coastal zones could lead to a drastic change in the food web at AB. It is possible that the decrease in penguin abundance (Sander *et al.* 2007) and shifts in benthic communities (Montes-Hugo *et al.* 2009) observed in this region result from these shifts in microphytoplankton assemblages. Although the time scale of the present study is small, the results shown here probably signal large environmental and biological changes, such as those detected in longer-term studies (e.g. Montes-Hugo *et al.* 2009, Schloss *et al.* 2012).

In terms of seasonal environmental variations, increases in water temperature and decreases in salinity during late, as compared to the early, summer (as observed in 2002–03 and 2003–04) have been reported in the coastal waters of King George Island (Klöser *et al.* 1993, Lange *et al.* 2007). However, differences in microphytoplankton assemblages were distinct in those two years. In 2002–03 there was an increase in abundance during late summer, and in 2003–04 phytoplankton abundance decreased with increases in temperature, possibly due to the early and rapid ice melt observed in the second year. The structure of phytoplankton assemblages was probably influenced by the spatial variations of environmental variables. The cyanobacteria observed in coastal waters (e.g. *Leptolyngbya* spp., *Oscillatoria* spp.) are typically found in continental drainage channels, lakes and snow (Komarek 2007), which may indicate the influence of continental runoff (Nedzarek 2008) especially at the EZ and BP sites. The highest ammonium concentration is also an indication of freshwater drainage, and was concomitantly found with the highest cyanobacteria contribution. High ammonium concentrations are derived from terrestrial animal faecal matter (Nedzarek 2008), and are possibly related to the adjacent glacial melt, e.g. Wanda Glacier at BP and Ecology Glacier at EZ. Robakiewicz & Rakusa-Suszczewski (1999) and Nedzarek (2008) proposed that nearshore circulation may induce the northward flow of a large portion of the freshwater runoff from Ecology Glacier through the coastal shallow zone, and consequently over the aforementioned sampling sites.

Therefore, the continental ice melt and wind-induced water column mixing are crucial processes that regulate temporal and spatial changes in phytoplankton assemblages in the coastal waters of AB.

Conclusions

Phytoplankton (> 15 μm) assemblages in shallow coastal waters of AB have been reported to be dominated by diatoms. The important contribution of the microphytobenthos, mainly pennate diatoms, to the plankton in coastal waters supports the idea that this compartment may be a significant source of food not only for benthic deposit feeders but also for suspension feeders and planktonic herbivores. The presence of microphytobenthic algae in the water column at the coastal zone in AB is related to weather conditions during the previous winter, indicated by the AAO. Colder winters allow a higher accumulation of continental ice, which melts during summer, causing an intense flow of freshwater runoff and may enhance the suspension of bottom material, including large diatoms from the microphytobenthos and epontic cyanobacteria. Wind speed and direction during summer, which are also related with the AAO phase shift, are associated with the accumulation of biomass of these algae in the water column, and to the intensity of resuspension of bottom material in shallow areas. Summer periods with high terrestrial ice melt and freshwater runoff, indicated by high irradiance and ammonium concentrations, were associated with significant contributions of cyanobacteria and large diatoms (> 80 μm) in the coastal zones. Epiphytic diatoms like *Pseudogomphonema kamtshaticum*, *Achnanthes* spp., *Licmophora* spp. and *Cocconeis* spp. were always present at CF and EZ, where macroalgae are abundant in the sublittoral. Areas most liable to the influence of terrestrial ice melt are EZ and, in more recent years, BP.

The prevailing size of phytoplankton cells decreased and the species composition changed in recent years. Large cells (> 80 μm) were more abundant in the summer 2002–03, and their contribution decreased, as smaller cells (15–30 μm) became more abundant in 2008–09. The cell size change in those coastal waters was associated with a rise in SST and a slight decrease in salinity, probably associated with an increase in precipitation. This may be part of a large-scale change in phytoplankton assemblages in the region. In the present study, phytoplankton composition shifted from large benthic pennate diatoms (*Licmophora* spp., *Achnanthes* spp., *Navicula* spp.) to smaller planktonic diatoms (*Pseudo-nitzschia* spp.) and dinoflagellates. Large centric diatoms (*S. microtrias*, *A. actinochilus*, *Porosira* spp., *T. ritscheri*) were more abundant in 2002–03 and 2003–04, while small *Thalassiosira* spp. and other centric diatoms were most abundant in recent years. Those changes were associated with relatively lower precipitation, greater cloud cover and wind pattern influencing water column processes, and may have trophic consequences due to the food selectivity by Antarctic krill.

We reinforce that the AAO, which is directly correlated with the main physical forcings in the WAP, is a strong indicator of changes in the phytoplankton structure. Large diatoms are dominant in periods of transiting AAO phases (from negative to positive), and small dinoflagellates and the diatom *Pseudo-nitzschia* spp. are more abundant under positive AAO periods. Further studies on the nano- and picophytoplankton structure need to be conducted to understand the importance of microphytoplankton to the primary production in shallow areas of the Antarctic Peninsula.

Author contribution

Priscila K. Lange - water sampling, microscopy analysis of phytoplankton populations, remote sensing data assembly, data processing, statistical analyses, elaboration of manuscript text and figures. Denise R. Tenenbaum - data processing, statistical analyses, elaboration of manuscript text and figures. Virginia M. Tavano - data processing, statistical analyses, elaboration of manuscript text. Rodolfo Paranhos - chlorophyll and nutrients analyses, manuscript review. Lucia S. Campos - sampling strategy design, elaboration of manuscript text.

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