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Picoplankton and nanoplankton variability in an Antarctic shallow coastal zone (Admiralty Bay) during the austral summer of 2010/2011

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Abstract The distribution and variability of picoplankton and nanoplankton in Admiralty Bay (King George Island, South Shetland Islands, Antarctica) were studied by investigation of five sampling sites during the austral summer of 2010/2011. After a relatively warm winter, the water temperature in the early summer (>0.02 °C) was higher than is normal in December. The spatial–temporal variability of salinity was low, whereas water temperature and chlorophyll *a* increased significantly ($p < 0.05$) toward late summer. Nitrite and phosphate concentrations increased whereas nitrate and silicate decreased during the summer. Picoplankton increased by late summer and was dominated by heterotrophs (>96 %), with abundance and biomass tenfold ($\sim 10^9$ cells L^{-1}) and twofold (~ 60 µg C L^{-1}) higher, respectively, than were observed in previous studies. In contrast, nanoplankton was dominated by photoautotrophs (>60 %), and values were highest in the early summer, with cell numbers ($\sim 10^6$ cells L^{-1}) and biomass (~ 90 µg C L^{-1}) a factor of two lower than those found in a previous study. Temperature changes, inputs from ice melting, and grazing relationships between planktonic components seemed to have crucially important effects on the distribution patterns of these pico and nanoplankton communities. We suggest that additional study must be performed to develop a better understanding of abiotic and biotic factors that affect the abundance, biomass, and production of plankton smaller than 20 µm, their place in the microbial food web and the possible consequences of environmental changes on higher trophic levels in such Antarctic coastal environments as Admiralty Bay ASMA.

Keywords Epifluorescence microscopy · King George Island · Plankton biomass · Size-fraction structure · Trophic category · West Antarctic Peninsula

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Introduction

In Antarctic waters, small plankton (picoplankton, 0.2–2.0 µm; and nanoplankton, 2.0–20 µm) dominates the planktonic community (Azam et al. 1991; Hewes 2009). Picophytoplankton generally constitutes approximately 20–30 % of chlorophyll *a* biomass (Chl*a*), whereas nanophytoplankton comprises more than 50 % of this biomass (Hewes 2009; Wright et al. 2009; Tenório et al. 2010). In terms of carbon biomass, photoautotrophic picoplankton and nanoplankton represent ~15 and ~30 % of total phytoplankton carbon (C), respectively. For heterotrophs, 47 % of the carbon is derived from picoplankton, and 20–30 % from nanoplankton (Vosjan and Olańczuk-Neyman 1991; Caron et al. 1995).

Antarctic picophytoplankton is composed primarily of eukaryotic flagellates (Agawin et al. 2002; Rodríguez et al. 2002), and nanophytoplankton is also dominated by eukaryotic flagellates, for example haptophytes (<60 %), cryptophytes (<40 %), and prasinophytes (<17 %), which

are followed by small diatoms (<18 %) and dinoflagellates (<11 %) (Wright et al. 2009).

In the Southern Ocean marine heterotrophic picoplankton is dominated by bacterioplankton (Wynn-Williams 1996; Simon et al. 1999), whereas organisms from the domain Archaea are not usually of substantial importance in surface waters during summer (2 %) and are more common in winter (13–34 %) (DeLong et al. 1994; Murray et al. 1998; Simon et al. 1999; Church et al. 2003). The nanoheterotrophs are composed of flagellate groups (30 % of the nanoplankton biomass), ciliates, and dinoflagellates (Hewes et al. 1990; Azam et al. 1991). The importance of the two small (<20 μm) heterotrophic plankton groups in the structure and function of the ecosystem is associated with their involvement in the microbial loop, because they consume 20–60 % of primary production as dissolved and particulate organic matter (DOM and POM, respectively). The loop recovers energy lost along the classic chain (in which energy and matter are transferred from phytoplankton to top predators via krill) and reincorporates organic carbon at higher trophic levels (Azam et al. 1983; Fenchel 1988; Azam et al. 1991; Moloney 1992; Wynn-Williams 1996).

Planktonic community structures vary in size and composition because of wide variations within each specific size class (Hillebrand et al. 1999). Because larger species with lower abundance can dominate the total biomass, despite the high density of small species (Dennett et al. 1999; Hillebrand et al. 1999), evaluation of carbon biomass can provide more precise estimates of the contribution of different size classes of organisms to biochemical processes (Potapova and Snoeijs 1997) and of carbon fluxes throughout the water column (Rocha and Duncan 1985).

Admiralty Bay is located off the west coast of the Antarctic Peninsula on King George Island. It is a typical polar region that is characterized by wide seasonal oscillations in the composition, biomass, and primary productivity of plankton, with the highest values recorded during summer and associated with shallow areas (Brandini and Rebello 1994; Leakey et al. 1996; Schloss et al. 2014). These variations are driven by physical, chemical, and biological factors, for example light availability, temperature, salinity, wind stress, tides, defrost, turbidity, nutrients, water column stability, and human actions (Brandini and Rebello 1994; Boyd 2002; Hewes 2009).

In the Southern Ocean, marine plankton is believed to be the most important primary producer, whereas productivity originating from terrestrial Antarctic habitats introduced to the ocean is low (Cornejo-Donoso and Antezana 2008). Previous studies have shown that in hypoproductive regions, for example the Antarctic, picoplankton and nanoplankton are responsible for up to 73 % of Chl*a* concentrations, and their rapid turnover enables them to contribute substantially (83 %) to total primary production (Agawin et al. 2002). The production of bacterioplankton may be 22–36 times higher than that of phytoplankton (Azam et al. 1991), which reveals the importance of these components to the food web (Hewes et al. 1983; Ducklow et al. 2011). Both the production of photoautotrophic picoplankton and nanoplankton and the energy recovered by the microbial loop can be transferred to upper trophic levels, which partially explains why Antarctic waters have high productivity at higher trophic levels despite low primary productivity (Azam et al. 1991).

According to Vaughan et al. (2003), the temperature in the western region of the Antarctic Peninsula over the last 50 years has increased by 2.8 °C, which is 4.8 times higher than the global average (0.6 ± 0.2 °C). This has resulted in new environmental conditions and variations in planktonic composition, with microplankton being replaced by smaller organisms (<20 μm) in regions of the Southern Ocean (Montes-Hugo et al. 2009 and references therein). Water temperature variations can also cause changes in the metabolism and rate of growth of planktonic organisms (Zdanowski 1995; Price and Sowers 2004; Doolittle et al. 2008). Temporal variations in environmental conditions during the summer in Admiralty Bay are well documented and are related to the extreme seasonal conditions in Antarctica (Brandini and Rebello 1994; Lange et al. 2007; Tenenbaum et al. 2010; Kejna et al. 2013). Because the climatic conditions on King George Island depend on seawater temperature and the extent of sea ice, variations in air temperature are closely connected to changes in the surrounding marine ecosystem. A significant air temperature increase has been observed at King George Island during the period 1948–2011 (Kejna et al. 2013), reaching 0.19 °C/10 years (increase of 0.11 °C/10 years during summer), and resulting in changes in all environments, for example shrinking of glaciers and melting of terrestrial and sea ice (Becquevort et al. 2009; Kejna et al. 2013; Lannuzel et al. 2013; Mieczan et al. 2013). This rise in air temperature most likely explains the 1.6 % loss of the ice cap on King George Island during the period 2000–2008 (Rückamp et al. 2011). Sea ice dynamics also have an important effect on the entire Antarctic ecosystem in that these processes enrich the surrounding seawater with accumulated components, for example nutrients, dissolved organic matter, and microbial communities (Becquevort et al. 2009; Lannuzel et al. 2013).

Admiralty Bay has been designated an Antarctic Specially Managed Area (ASMA) to control the effects of activities of countries operating in the area. Adequate forecasting and efficient actions to protect and monitor the environment should be implemented in this area (ATCPs 1996; Simões et al. 2001; Montone et al. 2013). Shallow

water monitoring (<30 m deep) was implemented in 2002 in Admiralty Bay under the Brazilian Antarctic Program (PROANTAR) to study marine ecosystem processes and the effects of natural and anthropogenic factors on long-term environmental conditions. In 2009, new measures for monitoring plankton were established; these included analysis of the density and trophic structure of the smallest fractions (Tenenbaum et al. 2010).

In this study we evaluated temporal (early and late summer of 2010/2011) and spatial (sampling sites and depths) variations in cell density, carbon biomass, and trophic categories of the picoplanktonic and nanoplanktonic communities (0.2–20 μm) in the shallow coastal zone of Admiralty Bay (King George Island, Antarctic Peninsula) and identified environmental factors that may affect these variations. To expand on the objective of monitoring the Admiralty Bay ASMA, this research examines local dynamics in respect of the general model of climate change in a sensitive Antarctic coastal environment.

Materials and methods

Study area

Admiralty Bay is located off of the West Antarctic Peninsula along the southern coast of King George Island of the South Shetland Islands (62°03′–12′S, 58°18′–38′W), and covers an area of 122 km^2. The bay has a fjord-like shape with a maximum depth of 150 m at its inlets (i.e., Ezcurra, Mackelar, and Martel) and 500 m at its centre (Rakusa-Suszczewski 1980). An opening to the south connects the bay to the Bransfield Strait and enables exchange of water with the Weddell and Bellingshausen Seas (Rakusa-Suszczewski 1980, 1995). Freshwater inputs occur as a result of melting of local glacial ice, which enriches the bay with nutrients, organic matter, inorganic particles, and iron from the soil and ice (Nedzarek and Rakusa-Suszczewski 2004). Hydrological circulation, especially in shallow areas, is affected by the wind and tides (Brandini and Rebello 1994).

Sampling and analysis

Four surveys were conducted at Admiralty Bay in the shallow coastal zone (<30 m) during early (December 14, 2010, i.e., early summer 1 (ES1); December 23, 2010, i.e., ES2) and late (February 21, 2011, i.e., late summer 1 (LS1); March 1, 2011, i.e., LS2) austral summer. Water samples were collected in Niskin bottles (5 L) at three depths (0, 15, and 29 m) at five sampling sites: the Brazilian Antarctic Station Comandante Ferraz (EACF), Botany Point (BP), the Peruvian Antarctic Station Machu Picchu (MP), Thomas Point (TP), and the Polish Antarctic Station Arctowski (AR) (Fig. 1). The sampling sites were chosen on the basis of the location of research stations or strategic geographical points defined by the objectives of the monitoring program in Admiralty Bay.

A portable digital TAD-500 (Instrutherm, Brazil) thermo anemometer (wind-speed accuracy ±3 % and resolution 0.1 m s^{-1}; temperature accuracy ±2 % and resolution 0.1 °C) was used to monitor in-situ wind speeds and air temperatures during the surveys. Because of logistic limitations, sampling was only conducted in conditions of wind speeds lower than 10 knots. The tidal regime and oscillations of the sea level were obtained from the Directorate of Hydrography and Navigation of Brazilian Navy (DHN 2014). Water temperatures were measured in situ by use of a Seamon Mini (Star Oddi, Iceland) underwater temperature recorder (accuracy ±0.025 °C and resolution 0.001 °C). Samples for analysis of salinity (S) and dissolved inorganic nutrients (nitrite, nitrate, phosphate, and silicate) were collected by use of a Model 900 (Anauger, Brazil) submergible pump (outflow range 750–2300 L h^{-1}) and were stored in the dark at room temperature (salinity) or −20 °C (inorganic dissolved nutrients) until analysis in the laboratory (Cascaes et al. 2012). The samples were analysed by use of the methods described in Grasshoff et al. (1983). Salinity measurements were conducted with an RS-1 (Beckman, USA) induction salinometer (accuracy ±0.001).

For determination of chlorophyll *a* concentration, 500 mL seawater was filtered through GF/F Whatman filters (0.07 μm and Ø 47 mm) and then stored (1.2 mL cryotube at −80 °C) before extraction (90 % acetone at −20 °C over 24 h) of the Chl*a* by use of the procedures described by Tenório et al. (2010). The fluorescence properties of the acetone extracts were measured with a Varian Cary Eclipse (Agilent, USA) spectrofluorimeter (wavelength accuracy ±1.0 nm from 200 to 900 nm). Concentrations of Chl*a* were assessed by use of a modified version of Neveux and Lantoine's (1993) method, described by Tenório et al. (2005). Data acquisition was performed by recording the fluorescence emission spectra for each of 31 excitation wavelengths (3-nm increments from 390 to 480 nm). The emission spectra were recorded at 2-nm intervals from 615 to 715 nm and yielded 51 points for each spectrum. Pigment concentrations were estimated from the resulting 1581 data points. The least-squares approximation technique was constrained to discard negative solutions.

Picoplankton and nanoplankton

Samples (250 mL) were fixed with 0.22-μm-filtered glutaraldehyde (2 % final concentration) and stored in dark

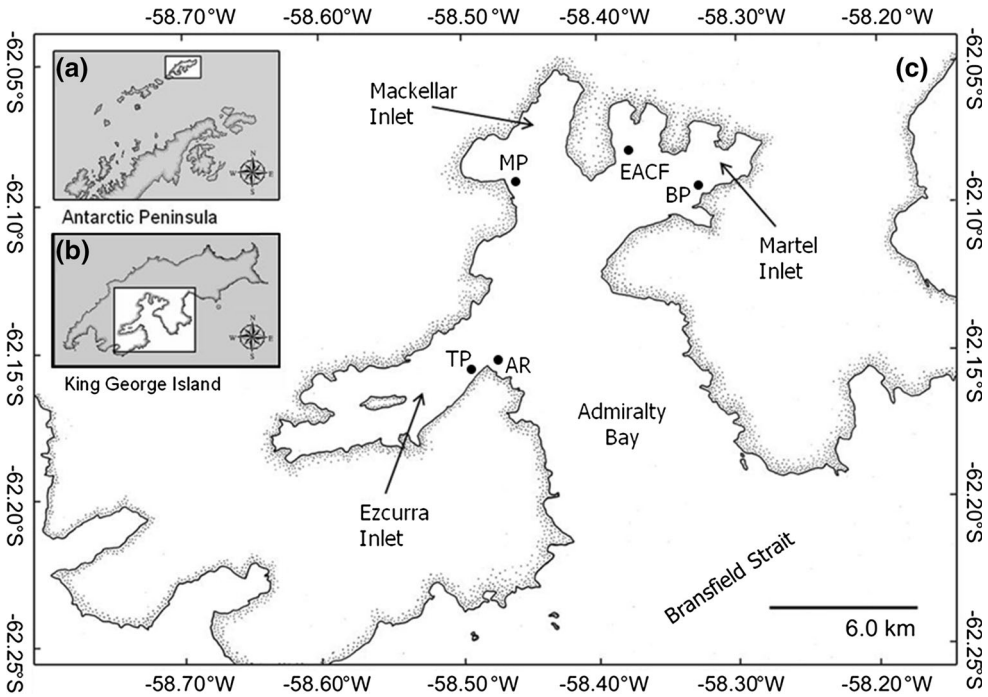

Fig. 1 Study area: **a** Antarctic Peninsula, **b** King George Island, and **c** Admiralty Bay. Locations of the sampling sites are also shown: the Brazilian Antarctic Station Comandante Ferraz (*EACF*), Botany Point (*BP*), the Peruvian Antarctic Station Machu Picchu (*MP*), Thomas Point (*TP*), and the Polish Antarctic Station Arctowski (*AR*)

bottles at 4 °C. After 24 h, 5 mL (picoplankton) or 30 mL (nanoplankton) subsamples were stained for 15 min with DAPI (4′,6-diamidino-2-phenylindole) at a final concentration of 0.01 μg L^{-1} (Thingstad and Martinussen 1991) then filtered through 0.22 and 1.0 μm polycarbonate black membrane filters (Poretics), respectively. The membranes were mounted on microscope slides between layers of non-fluorescing immersion oil (Cargille type A) and kept frozen until examination. Quantitative analysis was performed by epifluorescence microscopy with an Olympus BX51 with 1000-fold magnification. Counts were obtained by use of a combination of UV filters (U-MNUA2), including an excitation filter ($\lambda = 360$–370 nm), emission filter ($\lambda = 420$–460 nm), and dichromatic mirror ($\lambda = 400$ nm) for total number of cells (by use of DAPI) and a combination of blue filters (U-MSWB2), including an excitation filter ($\lambda = 420$–440 nm), emission filter ($\lambda = 475$ nm), and dichromatic mirror ($\lambda = 455$ nm) for photoautotrophic picoplankton and nanoplankton (by use of autofluorescence red for Chl*a*) (Porter and Feig 1980). Counts of heterotrophic organisms were calculated on the basis of the total number of cells minus photoautotrophic cell count, performed separately for picoplankton and nanoplankton. At least 400 picoplankton cells were counted and classified according to trophic category (photoautotrophic or heterotrophic) and morphotype (cocci, rods, or curved). Nanoplankton were counted in 25 random fields and classified according to trophic category, size (<5; 6–10; 11–15 or 16–20 m), and form (sphere, conic sphere, ellipsoid or cylinder).

Fifteen microscope fields were recorded by use of an Olympus XC 50 digital camera during counting. Linear dimensions were measured by use of ImageJ (picoplankton) and or Olympus Celld (nanoplankton) software. Cell volumes were calculated on the basis of the geometric models proposed by Hillebrand et al. (1999). Cell volumes between 0.04 and 0.26 μm^3 (0.12 ± 0.06 μm^3) where regarded as picoplankton whereas cell volumes between 5.59 μm^3 (<5 μm conic sphere) and 1937.53 μm^3 (16–20 μm sphere) were regarded as nanoplankton. For both fractions, biovolumes were calculated by multiplying the mean cell volume for each sample by the total number of organisms. Biovolume was converted to biomass by using the conversion factors 0.25 pg C μm^{-3} for photoautotrophic picoplankton (Fuhrman et al. 1989), 0.4 pg C μm^{-3} for heterotrophic picoplankton (Bjørnsen and Kuparinen 1991), and 0.36, 0.24, and 0.16 pg C μm^{-3} for nanoplankton with cell volumes of 10^1, 10^2, and 10^3 μm^3, respectively (Verity et al. 1992).

Statistical analysis

After checking for normality and homoscedasticity, the distributions were normalised and zero values were eliminated by converting the biological dataset by use of the function $\log_{10}(x + 1)$, which also minimizes excessive effects of outliers. A multivariate analysis test (main effects ANOVA) with a post-hoc test (Tukey's HSD) were performed first to identify the effects of spatial distribution, depth, and survey time on the variability of the dataset.

Spearman correlations and principal-components analysis (PCA; analysis based on correlations) were used to identify patterns within hydrographic data and to evaluate relationships between physical, chemical, and biological variables in a reduced number of variation axes. All statistical analysis was performed by use of Statistica v.7 software.

Results

Meteorological conditions, hydrology, nutrients, and chlorophyll

The ANOVA test results revealed the distributions of biotic variables among the four surveys were significantly different ($p < 0.05$). However, the analysis did not reveal significant differences between depths or sampling sites ($p > 0.05$). Therefore, the correlations and PCA were conducted by using integrated values in the water column and subsequently using the mean values from the sampling sites for each survey. Therefore, the results are represented on a temporal scale.

During the surveys, the ebb tides were predominantly observed except for LS1 (flood tide). Sea level oscillations were between 0.3 and 1.2 m during periods of neap tide (ES1 and LS2, respectively) and 1.7 and 2.0 m during periods of spring tide (ES2 and LS1, respectively) (DHN 2014). Among the four surveys, the in-situ air temperature increased from 1.55 ± 0.29 °C (ES) to 4.34 ± 2.15 °C (LS), with a minimum of 1.2 °C for ES1 and maximum of 6.9 °C for LS2.

Temporal variability of salinity was not generally significant ($p > 0.05$) throughout the study period (average: 34.14 ± 0.17). Nevertheless, salinity values were lower at the surface (34.03 ± 0.25) than at other depths (34.2 ± 0.08) ($p < 0.01$), especially at Botany Point (~33.4 in late summer) because of the proximity of glaciers. However, the water temperature (T) increased ($p < 0.05$) from early summer (0.52 ± 0.10 °C) to late summer (1.62 ± 0.12 °C), although differences between the late summer (LS) surveys were not significant ($p > 0.05$) (Table 1; Fig. 2).

Different trends were observed for dissolved inorganic nutrients during the sampling period. Although mean concentrations of nitrite (NO_2^-) and phosphate (PO_4^{3-}) were higher during late summer, mean concentrations of nitrate (NO_3^-) and silicate (SiO_4^{4-}) decreased throughout the study period (Table 1). Chl*a* concentrations varied from 0.36 to 3.72 μg L^{-1} in the ES and from 0.40 to 6.11 μg L^{-1} in the LS (Table 1). Chl*a,* nitrite, and phosphate were positively correlated ($n = 60$, $p < 0.01$) with temperature, whereas nitrate and silicate correlated negatively with temperature ($n = 60$, $p < 0.01$).

Picoplankton density and biomass

Among picoplankton, heterotrophs accounted for >96 % of density and biomass. Average heterotrophic biomass (HPB) doubled from early (31.19 ± 13.15 μg C L^{-1}) to late (60.78 ± 30.93 μg C L^{-1}) summer, and differences were significant at the end of the study ($p < 0.05$; LS2). In contrast, the density (HPD) was not significantly different between individual surveys ($p > 0.05$) (Table 1; Fig. 3). However, photoautotrophic picoplankton increased substantially from the ES to LS ($p < 0.05$) in both density (PPD) and biomass (PPB). The density averages were three times higher in late summer ($2.73 \pm 1.25 \times 10^7$ cells L^{-1}) than at the beginning of the surveys ($0.87 \pm 0.37 \times 10^7$ cells L^{-1}). Moreover, the biomass varied from 0.39 ± 1.06 μg C L^{-1} in the ES to 1.03 ± 0.63 μg C L^{-1} in the LS (Table 1; Fig. 3). The cell volume of the picoplankton ranged between 0.04 and 0.26 μm^3 (0.12 ± 0.06 μm^3). Cocci dominated (~90 %) the picoplanktonic community.

Nanoplankton density and biomass

In terms of density and biomass, the nanoplanktonic community was dominated by photoautotrophs (>60 %), and their contribution reached a maximum of 94.7 % during the ES2 survey. Compared with the trend observed for the picoplankton, the average abundances of nanophotoautotrophs and nanoheterotrophs were higher during the early summer than during late summer (Table 1). Among the surveys, the ES2 survey yielded the highest density (PND, $4.28 \pm 0.62 \times 10^6$ cells L^{-1}) and biomass (PNB, 48.63 ± 19.80 μg C L^{-1}) of photoautotrophic nanoplankton, whereas the ES1 survey yielded higher densities (HND, $1.34 \pm 0.76 \times 10^6$ cells L^{-1}) and biomass (HNB, 9.96 ± 4.15 μg C L^{-1}) of heterotrophic nanoplankton (Fig. 4). The nanoplankton comprised 82 % of 2–5 μm cells, 15 % of 6–10 μm cells, and 3 % of 11–20 μm cells. Regarding cell forms and the order of the greatest contribution, the nanoplanktonic community was composed of 61.8 % spheres, 17.7 % cylinders, 16.9 % conic spheres, and 3.6 % ellipsoids. The cell volume of nanoplankton varied substantially (5.59–1937.53 μm^3) because of the diversity of shapes and size ranges.

Pico and nanoplankton distribution

When considering both abiotic and biotic variables, the sum of the variability was explained by the first two components of the PCA, which accounted for 74.02 % of the variability in cell density (Fig. 5a) and 75.13 % of the variability in biomass (Fig. 5b), thus confirming the trends observed for the temporal variability in size classes and trophic

Table 1 Hydrological and planktonic variables in Admiralty Bay during the summer of 2010/2011

	T (°C)	*S*	Chl*a* (μg L^{-1})	NO_2 (μmol L^{-1})	NO_3 (μmol L^{-1})	PO_4 (μmol L^{-1})	SiO_4 (μmol L^{-1})	PPICD (10^7 cells L^{-1})
Early Summer 1								
Mean	0.29	34.18	0.41	20.03	1.24	69.35	0.54	0.86
SD	0.17	0.09	0.02	3.87	0.30	10.12	0.12	0.45
Min	0.02	34.01	0.38	13.59	0.64	54.97	0.36	0.40
Max	0.73	34.44	0.44	26.34	1.62	85.45	0.84	2.08
Early Summer 2								
Mean	0.73	34.15	0.42	22.49	1.67	72.82	1.08	0.88
SD	0.08	0.16	0.01	1.47	0.30	10.28	0.77	0.30
Min	0.61	33.70	0.40	20.34	1.28	50.35	0.42	0.49
Max	0.87	34.35	0.45	24.74	2.36	87.63	3.72	1.65
Late Summer 1								
Mean	1.58	34.13	0.74	9.66	1.67	35.50	1.62	2.92
SD	0.18	0.23	0.14	3.52	0.19	6.50	1.04	1.64
Min	1.39	33.41	0.38	4.15	1.42	26.84	0.40	1.47
Max	1.92	34.31	0.94	16.60	2.00	46.15	3.63	6.81
Late Summer 2								
Mean	1.66	34.10	0.79	13.03	1.92	40.18	4.07	2.54
SD	0.06	0.20	0.09	3.29	0.42	9.67	1.37	0.68
Min	1.56	33.40	0.68	7.04	1.41	19.64	1.34	1.72
Max	1.77	34.25	0.95	18.14	2.89	56.60	6.11	4.06

	HPICD (10^9 cells L^{-1})	PNAND (10^6 cells L^{-1})	HNAND (10^6 cells L^{-1})	PPICB (μg C L^{-1})	HPICB (μg C L^{-1})	PNANB (μg C L^{-1})	HNANB (μg C L^{-1})
Early Summer 1							
Mean	1.05	2.00	1.34	0.15	27.69	18.81	9.96
SD	0.24	0.62	0.76	0.13	14.20	7.75	4.15
Min	0.76	0.78	0.29	0.05	14.82	6.23	3.79
Max	1.65	2.90	3.00	0.53	67.28	34.80	17.02
Early Summer 2							
Mean	0.87	4.28	0.23	0.23	35.32	48.63	4.91
SD	0.06	0.82	0.12	0.13	10.57	19.80	3.87
Min	0.78	3.11	0.04	0.11	22.07	26.36	0.57
Max	0.98	5.48	0.40	0.54	58.52	90.59	16.33
Late Summer 1							
Mean	1.09	1.24	0.35	0.80	46.99	12.80	2.44
SD	0.37	0.40	0.32	0.71	31.32	4.56	2.33
Min	0.75	0.55	0.09	0.24	17.06	4.84	0.41
Max	1.93	2.11	1.44	3.09	146.81	21.26	9.02
Late Summer 2							
Mean	0.95	1.29	0.49	1.25	74.57	13.72	3.52
SD	0.18	0.70	0.25	0.47	24.36	9.11	1.95
Min	0.76	0.23	0.12	0.66	38.45	1.64	0.81
Max	1.54	3.05	1.00	2.41	146.25	39.53	6.36

SD standard deviation, *Min* minimum, *Max* maximum, *T* water temperature, *S* salinity, *Chla* chlorophyll *a*, NO_2 nitrite, NO_3 nitrate, PO_4 phosphate, SiO_4 silicate, *PPD–HPD* phototrophic and heterotrophic picoplankton density, *PND–HND* phototrophic and heterotrophic nanoplankton density, *PPB–HPB* phototrophic and heterotrophic picoplankton biomass, *PNB–HNB* phototrophic and heterotrophic nanoplankton biomass

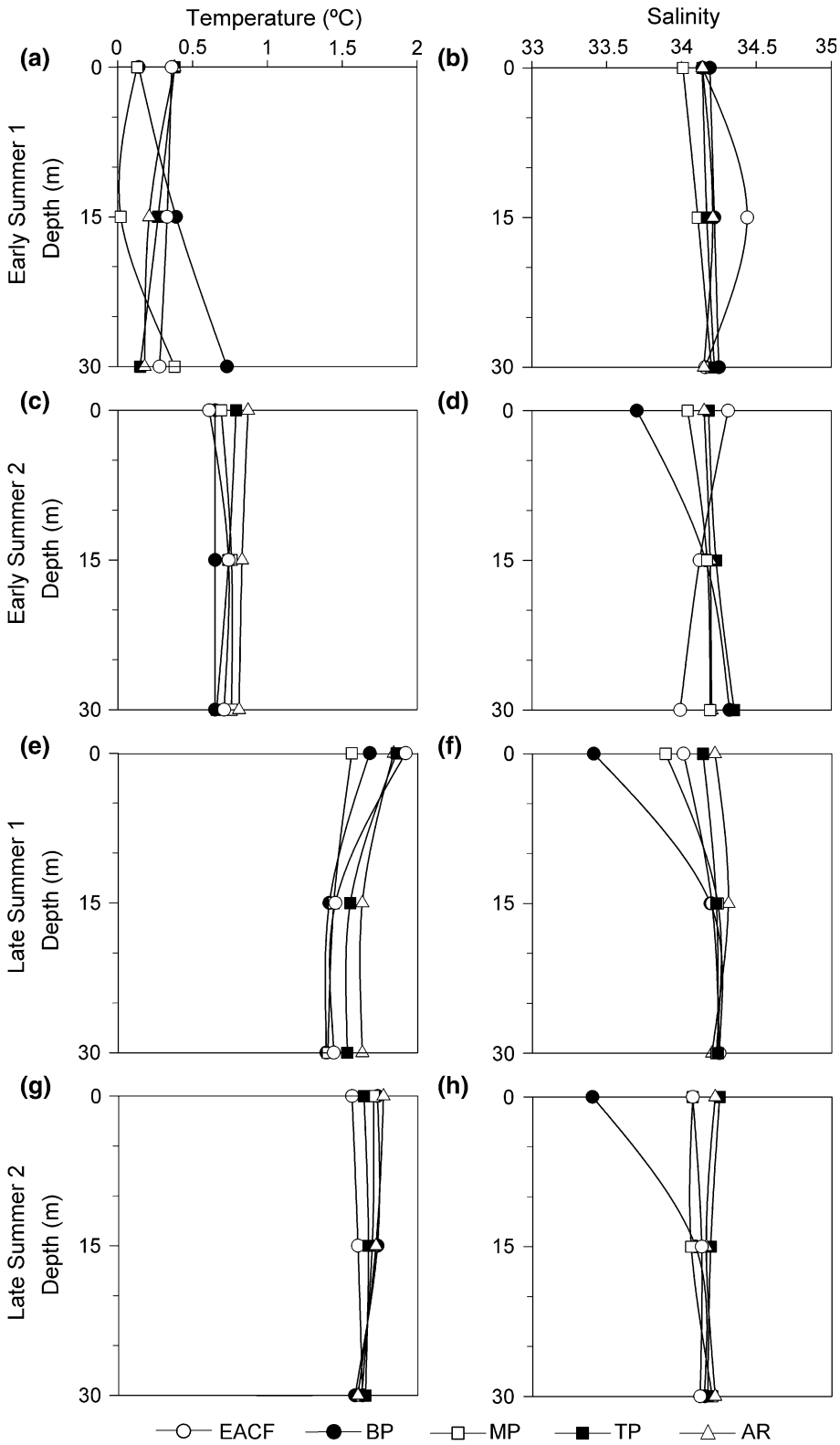

Fig. 2 Vertical profiles of temperature and salinity during the surveys Early Summer 1 (**a**, **b**), Early Summer 2 (**c**, **d**), Late Summer 1 (**e**, **f**), Late Summer 2 (**g**, **h**) in Admiralty Bay during the summer of 2010/2011

differentiation. For both PCAs, Factor 1 explained >54 % of the variance in the data. Samples from early summer, which were characterised by higher concentrations of NO_3^- and SiO_4^{4-}, higher densities, and a greater biomass of nanoplankton, were projected on to the positive portion of the axis. Samples from late summer, which were associated

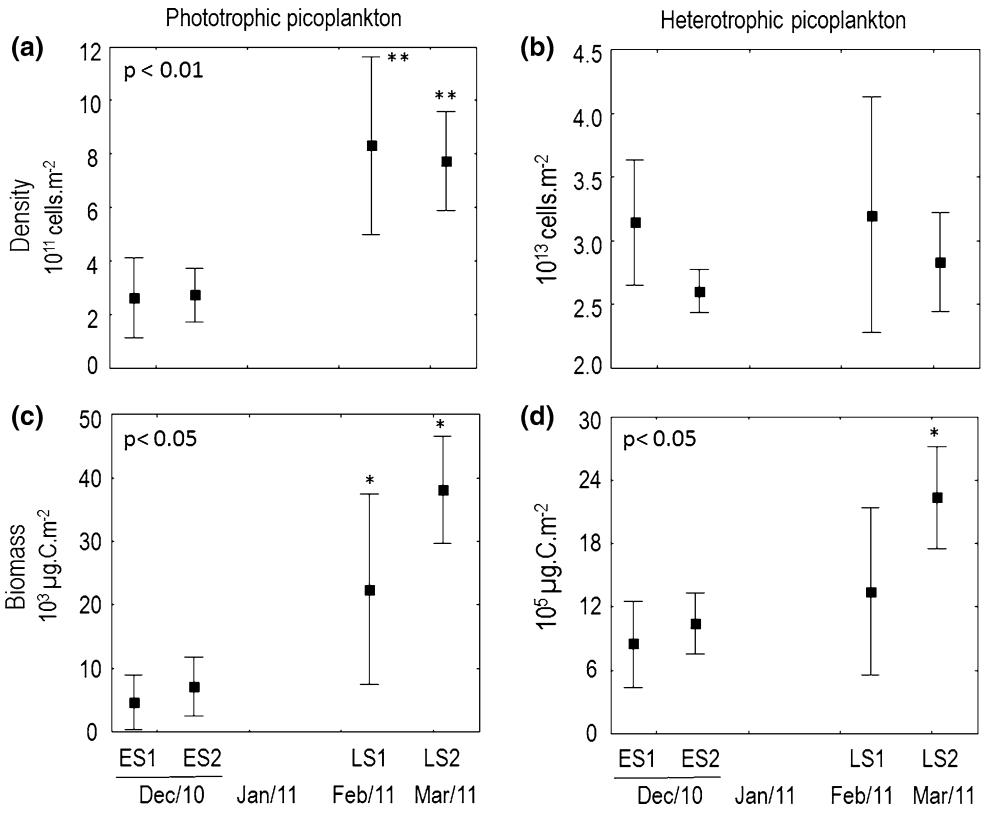

Fig. 3 Integrated values of densities and biomass of phototrophic (**a**, **c**) and heterotrophic (**b**, **d**) picoplankton from different surveys in Admiralty Bay during the summer of 2010/2011. *ES1* Early Summer 1, *ES2* Early Summer 2, *LS1* Late Summer 1, *LS2* Late Summer 2

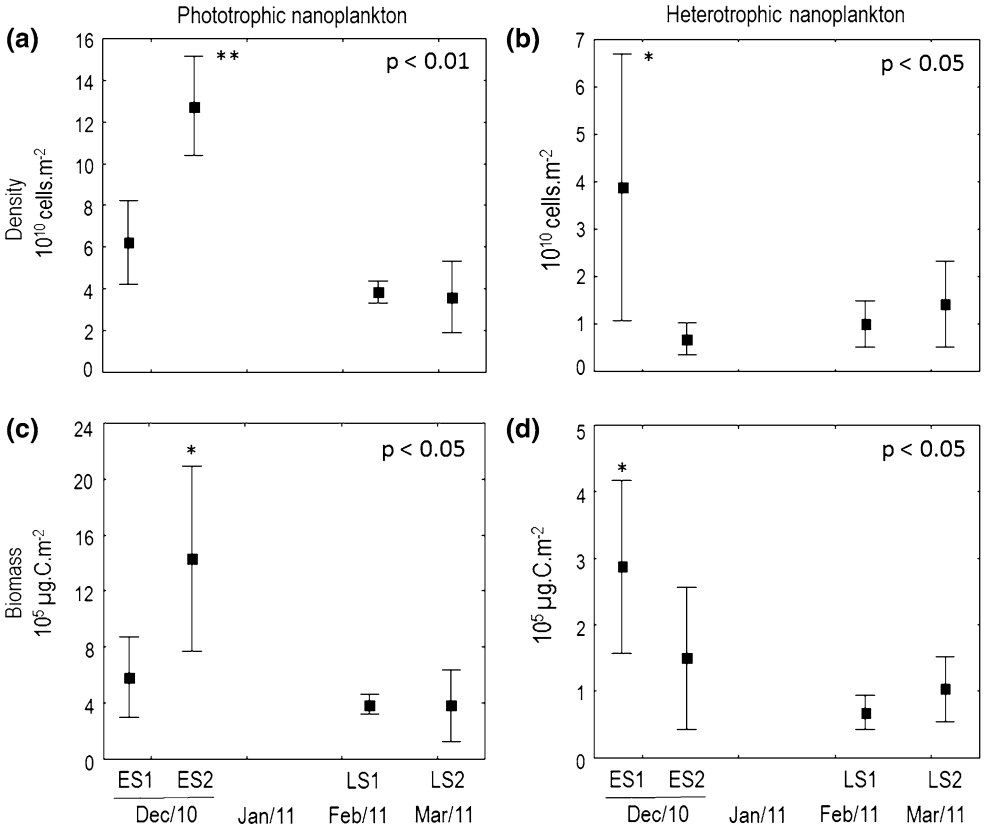

Fig. 4 Integrated values of densities and biomass of phototrophic (**a**, **c**) and heterotrophic (**b**, **d**) nanoplankton in different surveys in Admiralty Bay during the summer of 2010/2011. *ES1* Early Summer 1, *ES2* Early Summer 2, *LS1* Late Summer 1, *LS2* Late Summer 2

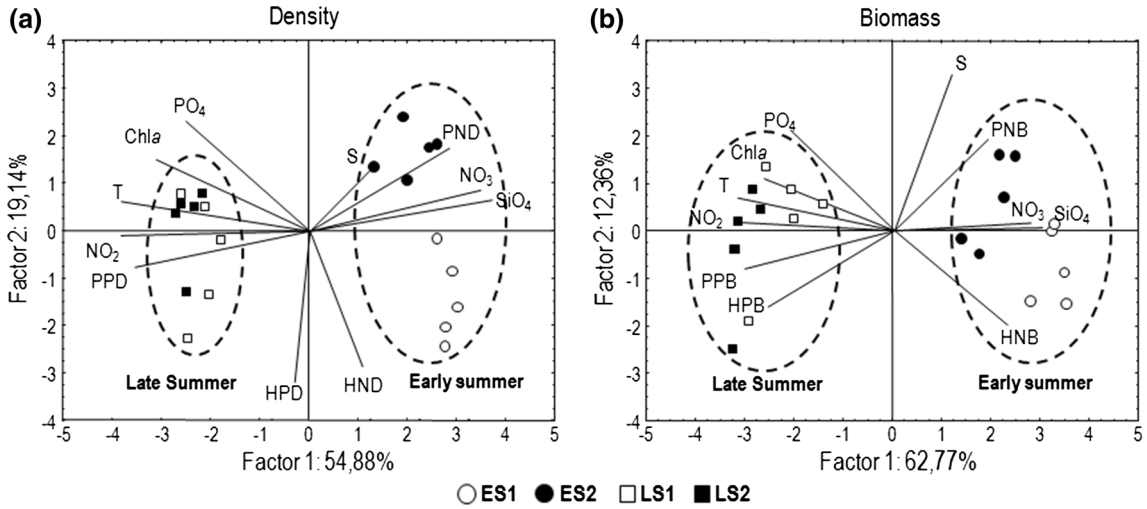

Fig. 5 Principal-components analysis (PCA) of the hydrobiological variables density (**a**) and biomass (**b**) of plankton organisms (0.2–20 μm) and samples from surveys in Admiralty Bay during the summer of 2010/2011. *T* water temperature, *S* salinity, *Chla* chlorophyll *a*, NO_2 nitrite, NO_3 nitrate, PO_4 phosphate, SiO_4 silicate, *PPD–HPD* phototrophic and heterotrophic picoplankton density, *PND–HND* phototrophic and heterotrophic nanoplankton density, *PPB–HPB* phototrophic and heterotrophic picoplankton biomass, *PNB–HNB* phototrophic and heterotrophic nanoplankton biomass, *ES1* Early Summer 1, *ES2* Early Summer 2, *LS1* Late Summer 1, *LS2* Late Summer 2

with higher temperatures, higher concentrations of NO_2^-, PO_4^{3-} and Chl*a*, higher densities, and a greater biomass of photo and heteropicoplankton, were projected on to the negative portion of the axis. Moreover, Chl*a* and PO_4^{3-} correlated positively with *T* ($p < 0.05$) (Fig. 5). Samples with higher abundances of nanophotoautotrophs were located on the positive portion of the axis of Factor 2 (<20 % of the variance). These samples were associated with higher salinity than were those with higher abundances of pico and nanoheterotrophs, which were located on the negative portion of the axis. The early summer surveys were most easily separated according to the abundances of photo and heterotrophic nanoplankton: heterotrophs dominated the ES1 survey whereas photoautotrophs dominated the ES2 survey. In LS, the samples were not clearly separated among the surveys (Fig. 5). As a result of these findings, Factor 1 was related to the importance of the different size classes in the plankton community during the austral summer; Factor 2 was related to differentiation of the trophic community.

Furthermore, total picoplankton was positively correlated with *T* ($p < 0.01$) and Chl*a* ($p < 0.01$). Nanophotoautotrophic densities and nanoheterotrophic biomass were negatively correlated with temperature ($p < 0.01$) and with Chl*a* ($p < 0.05$). Moreover, in terms of density and biomass, the nanoheterotrophs were negatively correlated with picophotoautotrophs ($p < 0.05$). Although the relationship was not significant, nanoheterotrophs were also negatively correlated with picoheterotrophs.

Discussion

Meteorological conditions, hydrology, and nutrients

Mean air temperatures in 2010 were ~1 °C higher than historically, leading to a warmer summer period from November 2010 (1.3 °C) to February 2011 (3.2 °C) (CPTEC, 2015—Brazilian Antarctic Program, http://www.cptec.inpe.br/antartica). This high air temperature during the early summer could explain the positive water temperature anomaly in December 2010 documented in this study, which contrasts with the negative values typically observed during this month (Vosjan and Olańczuk-Neyman 1991; Delille 1993; Rakusa-Suszczewski 1995; Kopczyńska 2008; Tenenbaum et al. 2010). The elevated water temperatures and low salinity values recorded in the surface waters at Botany Point during the summer suggest an increasing effect of melting ice from the glacier near this sampling point. High concentrations of dissolved inorganic nutrients observed in this work are within the range of values reported historically for Admiralty Bay (Lipski 1987; Brandini 1993; Brandini and Rebello 1994; Kopczyńska 2008; Cascaes et al. 2012).

In general, the vertical distribution of the temperature, salinity (except for the cited low salinity in the surface waters at Botany Point during late summer surveys), and nutrients among the surveys in the shallow coastal zone of Admiralty Bay did not vary significantly, which suggests that strong vertical stratification did not occur, as described in previous studies (Brandini 1993; Donachie 1996;

Dennett et al, 2001). This finding can be explained by a combination of:

1 local upwelling, as indicated by the homogeneity of the water column and similar ratios between abiotic variables or planktonic fractions at each depth (Madejski and Rakusa-Suszczewski 1990); and/or
2 the effect of winds and currents, which can create a mixed layer that can extend down to depths of 35 m (Brandini 1993, Rakusa-Suszczewski 1995).

Similarly, no clear horizontal variation in water column properties was observed in Admiralty Bay, except for the salinity at Botany Point. This absence of a horizontal distribution pattern can be explained by the effects of tides and winds in Admiralty Bay, which create homogeneity throughout the shallow coastal zone as a result of circulation of the water (Jażdżewski et al. 1986; Brandini and Rebello 1994). Thus, the dominant ebb tides and large oscillations of the sea level during the sampling periods may have contributed to the homogeneity observed among the sampling points.

Picoplankton distribution

Heterotrophic picoplankton densities, mainly represented by heterotrophic bacterioplankton, observed in this study ($\sim 10^9$ cells L^{-1}) were similar to those recorded in the same region in February 2010 (Table 2). Nevertheless, the values were tenfold higher than those measured in Admiralty Bay and near the West Antarctic Peninsula during austral summers during the 1990s, which typically ranged between 10^7 and 10^8 cells L^{-1} (Table 2). The biomass of heterotrophic picoplankton (max. 146.8 μg C L^{-1}) exceeded values previously reported for the Southern Ocean (<64 μg C L^{-1}) and Admiralty Bay (<37.32 μg C L^{-1}), particularly those recorded in late summer (Table 2). These values were also at least twice as high as values obtained in Antarctic coastal waters by other investigators (Table 2). These differences could partially be explained by the factor used to convert biovolume to biomass. In this study, we used the conversion factor proposed by Bjørnsen and Kuparinen (1991), which depends on cell volume variation. In contrast, most previous studies used a fixed conversion factor of 0.22 pg C μm^{-3} (Bratbak and Dundas 1984). Use of this latter factor in our work resulted in values that were half those obtained by use of the factor of Bjørnsen and Kuparinen (1991). Another important aspect to be considered in studies of the carbon biomass of planktonic communities is the morphology of the picoplanktonic fraction. The literature on this aspect of the Southern Ocean plankton is sparse, includes controversial data, and reports spatial and temporal distributions that are difficult to compare. Similar to the findings in this study, Marchant et al. (1987) and Detmer and Bathmann (1997) reported that cocci were the most abundant fraction of the picoplankton; in contrast, Donachie (1996) noted that the contribution of this morphotype was less than 40 % at depths of less than 50 m in the Southern Ocean. The prevalence of cocci among the heterotrophic picoplankton has been linked alternately to a lack of nutrient limitation, because this shape has the lowest surface/volume ratio, and to nutrient limitations, because most of the small cocci bacterial cells may be inactive (Sigee 2005 apud Teixeira et al. 2011). These inactive cells, however, are difficult to differentiate during the counting process.

Studies of seasonal variations in marine waters of the West Antarctic Peninsula have shown that the abundance of this planktonic fraction is significantly higher in summer than in winter (Donachie 1996; Church et al. 2003) and have suggested a positive correlation between the total picoplankton density and temperature (Marchant et al. 1987; White et al. 1991; Zdanowski 1995; Price and Sowers 2004; Doolittle et al. 2008). Thus, the high water temperature recorded during this study may help to explain the high picoplankton densities, particularly in the surface waters and during late summer. In addition, the positive correlation between HPB and total chlorophyll biomass in our study may have been a response of heterotrophic bacterioplankton to the seasonal growth in phytoplankton biomass during the summer, which generates large amounts of dissolved and particulate organic matter and favours an increase in picoheterotrophic cell volume and biomass (Karl et al. 1991; Leakey et al. 1996; Church et al. 2003; Ducklow et al. 2012). Furthermore, the increased abundance described here may be indicative of enhanced significance of bacterioplankton in the Admiralty Bay trophic web. In addition to the response to temperature changes, seasonal oscillations in the composition and biomass of plankton can be affected by other, related, seasonal factors, for example the length of the day (light availability), melting of pack ice, glacial melt water, and other significant sources (Brandini and Rebello 1994; Boyd 2002; Hewes 2009).

The photoautotrophic picoplankton densities observed in this study were higher than those observed in Admiralty Bay during austral summers from 1994 to 2005 (10^5–10^6 cells L^{-1}); however, our results are similar ($\sim 10^7$ - cells L^{-1}) to those reported for February/March of 2010 and those analysed by use of flow cytometry in the Beaufort Sea, Arctic Ocean (September/October 2002) (Table 2). In terms of biomass, the PPB measured in Admiralty Bay during the summer of 2010/2011 was much higher than that observed in a study during the 1994/1995 summer, when the biomass varied between 0.001 and 0.48 μg C L^{-1} (mean = 0.11 μg C L^{-1}) and decreased from early to late summer (Table 2). In addition to

Table 2 Density and biomass of picoplankton (0.2–2 μm) in different locations and during different sampling periods in Antarctic waters: data from the literature based on different methods of analysis and measurement

Location	Sampling period	Density (cell L^{-1})	Biomass (μg C L^{-1})	Conversion factor (pg C μm^3)	Method of analysis	Measurement	Ref.
Heterotrophs							
Bransfield Strait	December 1986–March 1987	10^8	4–28	0.22	E; DAPI	OM	Karl et al. (1991)
Geologie Archipelago	January 1989–February 1990	10^7–10^8	1–30	0.40	E; AODC	OM	Delille (1993)
Admiralty Bay	April 1990–January 1991	10^7	0.3–37	0.22	E; AODC	OM	Donachie (1996)
	December 1990–January 1991	10^8	8–37	0.22	E	–	Vosjan and Olańczuk-Neyman (1991)
Prydz Bay	December 1993–February 1994	10^8	9–64	0.22	E; DAPI	IA/OM	Leakey et al. (1996)
Antarctic Peninsula	January 1999	10^8	–	–	E; DAPI	–	Church et al. (2003)
Admiralty Bay	February 2010	10^9	–	–	E; DAPI	–	Tenenbaum et al. (2010)
	December 2010–March 2011	10^9	14.8–146.8	0.40	E; DAPI	IA	This study
Autotrophs							
Admiralty Bay	December 1994–February 1995	10^5–10^6	0.001–0.48	$\log_{10}C = 0.94$ $(\log_{10}V)$–0.60	IM	OM	Kopczyńska (1996)
	February 1996–November 1998 January 2003–November 2005	10^5–10^6	–	–	IM	–	Kopczyńska (2008)
Beaufort Sea	September 2002–October 2002	10^7	–	–	FC	–	Schloss et al. (2008)
Admiralty Bay	February 2010	10^7	–	–	E; DAPI	–	Tenenbaum et al. (2010)
	December 2010–March 2011	10^7	0.05–5.96	0.25	E; DAPI	IA	This study

Method of analysis: *E* epifluorescence, *IM* inverted microscopy (Utermöhl 1958), *DAPI* 4′-6-diamidino-2-phenylindole, *AODC* acridine orange direct counts, *FC* flow cytometry

Measurement: *OM* ocular micrometric, *IA* image analysis

Table 3 Density and biomass of nanoplankton (2–20 μm) in different locations and during different sampling periods in Antarctic waters: data from the literature based on different methods of analysis and measurement

Location	Sampling period	Density (cell L^{-1})	Biomass (μg C L^{-1})	Conversion factor (pg C μm^3)	Method of analysis	Measurement	Ref.
Heterotrophs							
Prydz Bay	December 1993–February 1994	10^6	0.0–35.8	0.22	E; DAPI	IA/OM	Leakey et al. (1996)
Ross Sea	Summer 1996/1997	10^4	10^6*	**	E; DAPI	OM	Dennett et al. (2001)
Admiralty Bay	February 2010	10^6	–	–	E; DAPI	–	Tenenbaum et al. (2010)
	December 2010–March 2011	10^6	0.4–17	0.16	E; DAPI	IA	This study
				0.24			
				0.36			
Autotrophs							
Weddell Sea	Summer 1980	10^3–10^6	–	–	IM	–	Detmer and Bathmann (1997)
Atlantic sector/Antarctic	November 1983 –December 1983	10^5	–	–	IM	–	
	October 1988–November 1988	10^5–10^6	–	–	E	–	
Prydz Bay	November 1992–February 1993	10^5–10^7	–	–	E	–	
Ross Sea	Summer 1996/1997	10^4	10^6 (integrated values 60 m)	Strathmann equation	E; DAPI	OM	Dennett et al. (2001)
Beaufort Sea	September 2002–October 2002	10^6	–	–	FC	–	Schloss et al. (2008)
Admiralty Bay	February 1987	10^3–10^5	–	–	IM	–	Brandini (1993)
	February 2010	10^6	–	–	E; DAPI	–	Tenenbaum et al. (2010)
	December 2010–March 2011	10^6	1.6–90.6	0.16	E; DAPI	IA	This study
				0.24			
				0.36			

Method of analysis: *E* epifluorescence, *IM* inverted microscopy (Utermöhl 1958), *DAPI* 4′-6-diamidino-2-phenylindole, *FC* flow cytometry

Measurement: *OM* ocular micrometric, *IA* image analysis

* integrated value on water column (60 m); ** Strathmann's equation (Dennet et al. 2001)

environmental changes, these differences can also be explained by the methodology used in previous studies. In Kopczyńska (1996) and Kopczyńska (2008), the sample preservation (1 % buffered formalin), optical resolution (500× magnification), and the inverted microscope technique (Utermöhl sedimentation technique) used for cell counting may have significantly underestimated picoplankton community numbers (Kopczyńska 2008). In contrast, filtration through a polycarbonate membrane, glutaraldehyde preservation, DAPI staining, and counting by epifluorescence microscopy lead to better retention and more accurate quantification of the abundance of plankton of sizes between 0.2 and 20 μm, and identification of their trophic categories (Leakey et al. 1996). This lack of information regarding the photoautotrophic picoplankton of this region did not enable further conclusions to be drawn.

Nanoplankton distribution

In contrast with total picoplankton, densities of total nanoplankton during the summer of 2010/2011 were of the same order of magnitude as described in previous studies of other Antarctic regions (10^3–10^7 cells L^{-1}); however, densities were a factor of two lower than those observed in Admiralty Bay during the austral summer of 2009/2010 (10^6 cells L^{-1}) (Table 3). The greatest abundances of nanoplankton in our work were associated with cooler water and lower Chl*a* concentrations. Tenenbaum et al. (2010) and Tenório et al. (2010) reached a similar conclusion for a 2009/2010 LS survey; these authors reported elevated nanoplanktonic densities ($8.5 \pm 2.8 \times 10^6$ - cells L^{-1}) despite low water temperatures (<1 °C) and chlorophyll levels (<0.6 μg L^{-1}). Moreover, Leakey et al. (1996) reported a biomass of nanoheterotrophs in Prydz Bay (Antarctic) that was 1.5 times higher at lower temperatures (between −1.4 and −0.4 °C) than those described in this study (Table 3). Furthermore, both Hashihama et al. (2008), at Adélie Land (Antarctica), and Weissenberger (1998), at Rovaniemi (Arctic region), observed increases in the abundances of nanophotoautotrophs and small nanoheterotrophs (4 μm in diameter) in colder waters (<0 °C); the greatest abundances were observed during ice-melt periods. These authors also reported a change in the dominant groups of the plankton community at higher water temperatures, with nanoflagellates (5–20 μm) replaced by diatoms (microplankton) (Weissenberger 1998; Hashihama et al. 2008). In this sense, the decrease in the abundance of nanophotoautotrophs observed in our study was related to an increase in the abundance of microplanktonic diatoms from $0.65 \pm 0.28 \times 10^4$ cells L^{-1} in the ES to $3.16 \pm 1.36 \times 10^4$ cells L^{-1} in the LS (unpublished data, personal communication of Barrera-Alba JJ), suggesting that a similar seasonal development process may occur in the plankton community in Admiralty Bay. As a result, the negative correlation between nanophytoplankton and Chl*a* indicates that other size fractions (for example microplanktonic diatoms) are responsible for the increase in Chl*a* during the LS period, as confirmed by the dominance of the >10 μm fraction of Chl*a* at the end of the 2010/2011 summer (Tenório et al. 2013). An increase in microphytoplankton abundance may also have been responsible for the decrease in nutrient levels, especially nitrate and silicate, recorded from early to late summer of 2010/2011 (Tenório et al. 2013). The same trend was observed by Clarke and Leakey (1996) in the Southern Ocean during the summers of 1988–1994 and by Tenenbaum et al. (2010) in Admiralty Bay in the summer of 2009/2010. Moreover, high primary productivity may also have been responsible for the increase in nitrite concentrations noted in our study as a result of metabolic processes, exudates, and excretion (Treguer and Jacques 1992; Cascaes et al. 2012). The Admiralty Bay region has been reported to be an HNLC (high nutrient, low chlorophyll) region, with large amounts of dissolved inorganic nitrate and nitrite (9.5–46.9 μM), phosphate (0.2–9.9 μM), and silicate (30.15–74.52 μM) and low chlorophyll concentrations (<1.7 μg L^{-1}) (Brandini and Rebello 1994; Lange et al. 2007; Tenório et al. 2010; Cascaes et al. 2012), suggesting that phytoplankton cannot exhaust all of the macronutrients available at the water surface (Blain et al. 2001). Exceptional local blooms can be explained by others factors, for example changes in physical conditions or iron input that may possibly promote high growth and phytoplankton production (Martin et al. 1990; Nedzarek and Rakusa-Suszczewski 2004; Schloss et al. 2014), and could contribute to the observed increase in microphytoplankton through the late summer period cited above.

In terms of biomass, the trend for nanoplankton was similar to that described for its density, with higher values in early summer; in addition, the depth-integrated values ($\sim 10^5$ μg C m^{-2}) were a factor of ten lower than those found in a survey conducted in the Ross Sea ($\sim 10^6$ - μg C m^{-2}), over an integrated depth of 60 m during the summer of 1996/1997 (Table 3). Photoautotrophs accounted for more than 80 % of the biomass of this size-fraction in this study. This dominance in summer was also observed for the continental shelf around the Antarctic (Hewes et al. 1990), the Ross Sea (Antarctic) (Dennett et al. 2001), and Admiralty Bay (Tenenbaum et al. 2010). However, Dennett et al. (2001) found that heterotrophs were dominant during autumn (from April to June). With regard to size fractions, nanoplankton were dominated by organisms smaller than 10 μm, which was also observed in the previous summer at the same sampling sites in Admiralty Bay (Tenenbaum et al. 2010; Tenório et al. 2010).

Picoplankton versus nanoplankton distributions

In the shallow coastal zones of Prydz Bay (Antarctic Peninsula), the effects of grazing by nanoheterotrophs have been reported to be responsible for daily removal of 3–12 % of bacterial biomass (Leakey et al. 1996). Because heterotrophic nanoplankton are typically dominated by small bacterivorous organisms that have a high grazing effect (Leakey et al. 1996; Caron et al. 1999; Dennett et al. 2001), the reduced nanoheterotroph abundance found throughout the summer in this study may also have contributed to the observed increase in total picoplankton abundance during the LS period. However, because nanoplankton can be preyed on, it is still uncertain whether they could control and limit the picoplanktonic community by grazing (Leakey et al. 1996). Control studies in the monitoring program should therefore be improved. Furthermore, terrigenous inputs (Nedzarek and Rakusa-Suszczewski 2004), predation on picoplankton and nanoplankton, and natural mortality may also be responsible for the increase in nutrients, including dissolved and particulate organic matter in the water column, which can serve as additional resources for bacterioplankton production and explain the higher picoplankton biomass observed during the LS surveys.

Positive temperature anomalies observed during December 2010/2011, which induced rapid melting of sea ice, may have enriched the water column with nutrients (Lannuzel et al. 2013), consistent with our findings of high concentrations of dissolved nitrogen, silicate, and phosphate. The input of dissolved organic matter (DOM) by sea-ice melting can be rapidly absorbed by bacterioplankton and thus stimulate bacterial growth (Giesenhagen et al. 1999; Becquevort et al. 2009). The DOM could also be accumulated as a result of lysis of photoauto and heteronanoplankton during grazing (Leakey et al. 1996; Caron et al. 1999; Dennett et al. 2001; Lannuzel et al. 2013). Consequently, the heterotrophic picoplankton may have used this organic matter as a food source, which is likely to have resulted in their greater cell abundances and volumes (Becquevort et al. 2009), as observed in our LS surveys.

However, microorganisms released during melting of sea ice or glaciers may sink as aggregates and feed benthic communities, be rapidly grazed by predators, and/or act as an inoculum for blooms, thereby resulting in a seasonal development pattern that affects the entire planktonic trophic web (Becquevort et al. 2009; Mieczan et al. 2013). Pennate diatoms are the first organisms to detach from ice and settle quickly, thereby dominating the bottom sea ice (Lange et al. 2007, 2014; Lannuzel et al. 2013). On the basis of the atypical temperature in the 2010/2011 summer, we conclude that this process may have occurred before our sampling period. Schloss et al. (2014) also reported a possible early beginning of glacial melting the same summer. In addition, pack ice releases mostly flagellates smaller than 10 μm, which remain in the water column longer and contribute many more autotrophs than heterotrophs (Lange et al. 2007, 2014; Lannuzel et al. 2013), which explains both the predominance of small (2–10 μm) and spherical nanoplanktonic cells and the greater abundance of nanophotoautotrophs in the ES. In the late stage of melting, centric and larger diatoms are released (Lange et al. 2007, 2014), dominating the LS (unpublished data, personal communication of Barrera-Alba JJ).

During seasonal melting, additional groups of microplankton may be incorporated into the water column. These groups may include ciliates and dinoflagellates that exert predation pressure at lower trophic levels and are responsible for significant losses of primary production (Becquevort et al. 2009; Mieczan et al. 2013; Schloss et al. 2014). A study of the melting and retreat of Ecology Glacier (located at Admiralty Bay; Mieczan et al. 2013) indicated a dominance (50–90 %) of medium-sized (50–200 μm) bacterivores, algivores, and ciliate omnivores. Becquevort et al. (2009) reported that both ciliates and dinoflagellates (<40 μm) dominated the biomass in the sea ice of the Southern Ocean and are subject to incorporation into seawater by melting. In addition to grazing pressure, competition for food resources between ice-derived and planktonic organisms in Antarctic waters has also been reported (Becquevort et al. 2009).

During the summer of 2010/2011, the abundance of groups of small (<50 μm) and larger (>50 μm) ciliates and heterotrophic dinoflagellates increased approximately fourfold from early summer to late summer ($\sim 2.5 \times 10^4$ cells L^{-1}), whereas flagellates (10–20 μm; analysed by use of the Utermöhl sedimentation technique) decreased by half (unpublished data, personal communication of Barrera-Alba JJ). Fenchel (1987) suggested that the size of preferred food particles is strictly correlated with the size of the predator, i.e., generally, a ratio of 1:10 between predator and prey size. Accordingly, during the early summer, nanoplankton grazing on picoplankton maintained their population with lower densities, especially during ES2, when a high population of 10–20 μm organisms and the lowest abundance of picoplankton were observed. Toward the summer, high temperatures caused melting and enriched the water column with nutrients, DOM, and protozoan predators (Becquevort et al. 2009; Kejna et al. 2013; Lannuzel et al. 2013; Mieczan et al. 2013; Schloss et al. 2014). The incorporation of heterotrophic ciliates and dinoflagellates that preyed on nanoplankton diminished the abundance of the latter and resulted in less predation pressure on picoplankton, which could then increase in density and biomass because of the DOM released into the water column.

Thus, in recent decades, the proportion of the community that consists of autotrophic and heterotrophic picoplankton has been changing, with the percentage of photoautotrophs decreasing in recent summers (Donachie 1996; Kopczyńska 1996; Leakey et al. 1996, Church et al. 2003; Delille 2004; Kopczyńska 2008; Tenenbaum et al. 2010; Barrera-Alba et al. 2012). In terms of density, total picoplankton, nanoplankton, and microplankton accounted for 99.3, 0.7, and 0.01 % of the global community, respectively, in Admiralty Bay (Barrera-Alba et al. 2012). However, in terms of biomass, autotrophic nanoplankton dominated (~95 %) picoplankton, indicating that larger organisms at lower densities can make a large contribution to the total biomass (Dennett et al. 1999; Hillebrand et al. 1999). These results suggest that it is not only important to estimate the densities but also the cell biovolume to evaluate carbon biomass when attempting to improve studies of trophic dynamics and modelling of ecosystems. Because the biomass measurements include different shapes and sizes of picoplankton and nanoplankton, these measurements reflect the real contribution of each trophic category (or size-fraction) to the carbon fluxes in the water column (Dennett et al. 1999; Hillebrand et al. 1999).

In conclusion, throughout the summer of 2010/2011 the increased picoplankton biomass toward late summer can be explained by:

1 the decreasing abundance of nanoheterotrophs and potential diminishing predation on picoplankton;
2 increasing water temperature, which most likely intensified bacterial growth; and
3 increasing nutrient concentrations (nitrite and phosphate) and dissolved and particulate organic matter, which promoted high bacterioplankton productivity.

In contrast, an inverse response to environmental variability was observed in the nanoplankton community, which decreased in density and biomass into the late summer, also affected by grazing pressure in the summer period and by seasonal development, reflecting the complex relationships between environmental variables and the plankton community. Temperature changes, inputs from ice melting and grazing relationships among planktonic components seemed to be crucially important in determining distribution patterns in the pico and nanoplanktonic communities. We suggest that further research be performed to explain the effects of abiotic and biotic factors on the abundance, biomass, and production of plankton smaller than 20 μm. Such research will help in developing an understanding of their importance in the microbial food web and the possible consequences of environmental changes on higher trophic levels in Antarctic coastal environments, for example the Admiralty Bay ASMA.

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References

Agawin NSR, Agustí S, Duarte CM (2002) Abundance of Antarctic picophytoplankton and their response to light and nutrient manipulation. Aquat Microb Ecol 29:161–172

ATCPs Antarctic Treaty Consultative Parties (1996) A proposal prepared by Brazil and Poland, in coordination with Ecuador and Peru, that Admiralty Bay, King George Island (South Shetland Island) be designated as an Antarctic Specially Managed Area (ASMA). Twentieth Antarctic Treaty Consultative Meeting, Utrecht, Netherlands. May 1996

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water- column microbes in the sea. Mar Ecol Prog Ser 10:257–263

Azam F, Smith DC, Hollibaugh JT (1991) The role of the microbial loop in Antarctic pelagic ecosystems. Polar Res 10:239–243

Barrera-Alba JJ, Vanzan M, Tenório MMB, Tenenbaum DR (2012). Plankton structure of shallow coastal zone at Admiralty Bay, King George Island, West Antarctic Peninsula (WAP) during early summer/2010: pico, ultra and microplankton and chlorophyll biomass. INCT-APA Annual Activity Report. doi:10.4322/apa.2014.071

Becquevort S, Dumont I, Tison JL, Lannuzel D, Sauvée ML, Chou L, Schoemann V (2009) Biogeochemistry and microbial community composition in sea ice and underlying seawater off East Antarctica during early spring. Polar Biol 32:879–895

Bjørnsen PK, Kuparinen J (1991) Determination of bacterioplankton biomass, net production and growth efficiency in the Southern Ocean. Mar Ecol Prog Ser 71:185–194

Blain S, Tréguer P, Belviso S, Bucciarelli E, Denis M, Desabre S, Fiala M, Jézéquel VM, Févre JL, Mayzaud P, Marty JC, Razouls S (2001) A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. Deep Sea Res I 48:163–187

Boyd PW (2002) A review of: environmental factors controlling phytoplankton processes in the Southern Ocean. J Phycol 38:844–861

Brandini FP (1993) Phytoplankton biomass in an Antarctic coastal environment during stable water conditions–implications for the iron limitation theory. Mar Ecol Prog Ser 93:267–275

Brandini FP, Rebello J (1994) Wind field effect on hydrography and Chlorophyll dynamics in the coastal pelagial of Admiralty Bay, King George Island, Antarctica. Antarct Sci 6:433–442

Bratbak G, Dundas I (1984) Bacterial dry matter content and biomass estimations. Appl Environ Microb 48:755–757

Caron DA, Dam HG, Kremer P, Lessard EJ, Madin LP, Malone TC, Napp JM, Peele ER, Roman MR, Youngbluth MJ (1995) The contribution of microorganisms to particulate carbon and nitrogen in surface waters of the Sargasso Sea near Bermuda. Deep Sea Res I 42:943–972

Caron DA, Lonsdale DJ, Dennett MR (1999) Bacterivory and herbivory play key roles in the fate of Ross Sea production. Antarct J US 32:81–83

Cascaes MJ, Barbosa ACRA, Freitas FS, Colabuono FI, Silva J, Patire VF, Senatore DB, Dias PS, Cipro CVZ, Taniguchi S, Bícego MC, Montone RC, Weber RR (2012) Temperature, salinity, pH, dissolved oxygen and nutrient variations at five stations on the surface waters of Admiralty Bay, King George Island, Antarctica, during the summers from 2009 to 2012. INCT-APA Annual Activity Report. doi:10.4322/apa.2014.070

Church MJ, DeLong EF, Ducklow HW, Karner MB, Preston CM, Karl DM (2003) Abundance and distribution of planktonic Archaea and Bacteria in the waters west of the Antarctic Peninsula. Limnol Oceanogr 48:1893–1902

Clarke A, Leakey RJG (1996) The seasonal cycle of phytoplankton, macronutrients, and the microbial community in a nearshore Antarctic marine ecosystem. Limnol Oceanogr 41:1281–1294

Cornejo-Donoso J, Antezana T (2008) Preliminary trophic model of the Antarctic Península Ecosystem (Sub-area CCAMLR 48.1). Ecol Model 218:1–17

CPTEC (2015) Brazilian Antarctic Program. Centro de Previsão de Tempo e Estudos Climáticos. http://www.cptec.inpe.br/antartica. Accessed 03 Feb 2015

Delille D (1993) Seasonal changes in the abundance and composition of marine heterotrophic bacterial communities in an Antarctic coastal area. Polar Biol 13:463–470

Delille D (2004) Abundance and function of bacteria in the Southern Ocean. Cell Mol Biol 50:543–551

DeLong EF, Wu KY, Prézelin BB, Jovine RVM (1994) High abundance of Archaea in Antarctic marine picoplankton. Nature 371:695–697

Dennett MR, Caron DA, Murzov SA, Polikarpov IG, Gavrilova NA, Georgieva LV, Kuzmenko LV (1999) Abundance and biomass of nano- and microplankton during the 1995 Northeast Monsoon and Spring Intermonsoon in the Arabian Sea. Deep Sea Res II 46:1691–1717

Dennett MR, Mathot S, Caron DA, Smith WO Jr, Lonsdale DJ (2001) Abundance and distribution of phototrophic and heterotrophic nano- and microplankton in the southern Ross Sea. Deep Sea Res II 48:4019–4037

Detmer AE, Bathmann UV (1997) Distribution patterns of autotrophic pico- and nanoplankton and their relative contribution to algal biomass during spring in the Atlantic sector of the Southern Ocean. Deep Sea Res II 44:299–320

DHN (2014) Diretoria de Hidrografia e Navegação http://www.mar.mil.br/dhn/chm/box-previsao-mare/tabuas/. Accessed 03 Oct 2014

Donachie SP (1996) A seasonal study of marine bacteria in Admiralty Bay (Antarctica). Proc NIPR Symp Polar Biol 9:1–124

Doolittle DF, Li WKW, Wood AM (2008) Wintertime abundance of picoplankton in the Atlantic sector of the Southern Ocean. Nova Hedwig 133:147–160

Ducklow HW, Myers KMS, Erickson M, Ghiglione JF, Murray AE (2011) Response of a summertime Antarctic marine bacterial community to glucose and ammonium enrichment. Aquat Microb Ecol 64:205–220

Ducklow HW, Schofield O, Vernet M, Stammerjohn S, Erickson M (2012) Multiscale control of bacterial production by phytoplankton dynamics and sea ice along the western Antarctic Peninsula: a regional and decadal investigation. J Marine Syst 98–99:26–39

Fenchel T (1987) Ecology of protozoa: the biology of free-living phagotrophic protests. Springer, Berlin

Fenchel T (1988) Marine plankton food chains. Annu Rev Ecol Syst 19:19–38

Fuhrman JA, Sleeter TD, Carlson CA, Proctor LM (1989) Dominance of bacterial biomass in the Sargasso Sea and its ecological implications. Mar Ecol Prog Ser 57:207–217

Giesenhagen HC, Detmer AE, de Wall J, Weber A, Gradinger RR, Jochem FJ (1999) How are Antarctic planktonic microbial food webs and algal blooms affected by melting of sea ice? Microcosm simulations. Aquat Microb Ecol 20:183–201

Grasshoff K, Ehrhardt M, Kremling K (1983) Methods of seawater analysis. Verlag Chemie, Weinheim

Hashihama F, Hirawake T, Kudoh S, Kanda J, Furuya K, Yamaguchi Y, Ishimaru T (2008) Size fraction and class composition of phytoplankton in the Antarctic marginal ice zone along the 140°E meridian during February/March 2003. Polar Sci 2:109–120

Hewes CD (2009) Cell size of Antarctic phytoplankton as a biogeochemical condition. Antarct Sci 21:457–470

Hewes CD, Holm-Hansen O, Sakshaug E (1983) Nanoplankton and microplankton studies during the circumnavigation cruise. Antarct J US 18:169–171

Hewes CD, Sakshaug E, Reid FMH, Holm-Hansen O (1990) Microbial autotrophic and heterotrophic eucaryotes in Antarctic waters: relationships between biomass and Chlorophyll, adenosine triphosphate and particulate organic carbon. Mar Ecol Prog Ser 63:27–35

Hillebrand H, Dürselen CD, Kirschtel D, Pollingher U, Zohary T (1999) Biovolume calculation for pelagic and benthic microalgae. J Phycol 35:403–424

Jażdżewski K, Jurasz W, Kittel W, Presler E, Presler P, Siciński J (1986) Abundance and biomass estimates of the benthic fauna in Admiralty Bay, King George Island, South Shetland Islands. Polar Biol 6:5–16

Karl DM, Holm-Hansen O, Taylor GT, Tien G, Bird DF (1991) Microbial biomass and productivity in the western Bransfield Strait, Antarctica during the 1986–87 austral summer. Deep Sea Res 38:1029–1055

Kejna M, Araźny A, Sobota I (2013) Climatic change on King George Island in the years 1948–2011. Pol Polar Res 34:213–235

Kopczyńska EE (1996) Annual study of phytoplankton in Admiralty Bay, King George Island, Antarctica. Pol Polar Res 17:151–164

Kopczyńska EE (2008) Phytoplankton variability in Admiralty Bay, King George Island, South Shetland Islands: six years of monitoring. Pol Polar Res 29:117–139

Lange PK, Tenenbaum DR, Braga ESB, Campos LS (2007) Microphytoplankton assemblages in shallow waters at Admiralty Bay (King George Island, Antarctica) during the summer 2002–2003. Polar Biol 30:1483–1492

Lange PK, Tenenbaum DR, Tavano VM, Paranhos R, Campos LS (2014) Shifts in microphytoplankton species and cell size at Admiralty Bay. Antarctic Science, Antarctica. doi:10.1017/S0954102014000571

Lannuzel D, Schoemann V, Dumont I, Content M, Jong J, Tison JL, Delille B, Becquevort S (2013) Effect of melting Antarctic sea ice on the fate of microbial communities studied in microcosms. Polar Biol 36:1483–1497

Leakey RJG, Archer SD, Grey J (1996) Microbial dynamics in coastal waters of East Antarctica: bacterial production and nanoflagellate bacterivory. Mar Ecol Prog Ser 142:3–17

Lipski M (1987) Variations of physical conditions, nutrients and Chlorophyll a contents in Admiralty Bay (King George Island, South Shetlands Islands, 1979). Pol Polar Res 8:307–332

Madejski P, Rakusa-Suszczewski S (1990) Annual observations of iceberg as tracers of water movement in the Bransfield Strait in front of Admiralty Bay (King George, South Shetland Islands). Antarctic Sci 2:259–263

Marchant HJ, Davidson AT, Wright SW (1987) The distribution and abundance of chroococcoid cyanobacteria in the Southern Ocean. Proc NIPR Symp Polar Biology 1:1–9

Martin JH, Gordon RM, Fitzwater SE (1990) Iron in Antarctic waters. Nature 345:156–158

Mieczan T, Górniak D, Swiatecki A, Zdanowski M, Tarkowska-Kukuryk M (2013) The distribution of ciliates on Ecology Glacier (King George Island, Antarctica): relationships between species assemblages and environmental parameters. Polar Biol 36:249–258

Moloney CL (1992) Carbon and the Antarctic marine food web. Science 257:259

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

Montone RC, Alvarez CE, Bícego MC, Braga ES, Brito TAS, Campos LS, Fontes RFC, Castro BM, Corbisier TN, Evangelista H, Francelino M, Gomes V, Ito RG, Lavrado HP, Leme NP, Mahiques MM, Martins CC, Nakayama CR, Ngan PV, Pellizari VH, Pereira AB, Petti MAV, Sander M, Schaefer CEGR, Weber RR (2013) Environmental assessment of Admiralty Bay, King George Island, Antarctica. In: Verde C, Prisco G (eds) Adaptation and evolution in marine environments, 2nd edn. Springer, Berlin, pp 157–175

Murray AE, Preston CM, Massana R, Taylor LT, Blakis A, Wu KY, DeLong EF (1998) Seasonal and spatial variability of Bacterial and Archaeal assemblages in the coastal waters near Anvers Island, Antarctia. Appl Environ Microbiol 64:2585–2595

Nedzarek A, Rakusa-Suszczewski S (2004) Decomposition of macroalgae and the release of nutrients in Admiralty Bay, King George Island, Antarctica. Polar Biosci 17:26–35

Neveux J, Lantoine F (1993) Spectrofluorometric assay of chlorophylls and phaeopigments using the least squares approximation technique. Deep Sea Res I 40:1747–1765

Porter KG, Feig YS (1980) The use of DAPI for identifying and counting aquatic microflora. Limnol Oceanogr 25:943–948

Potapova M, Snoeijs P (1997) The natural life cycle in wild populations of Diatom moniliformis (Bacillariophyceae) and its disruption in an aberrant environment. J Phycol 33:924–937

Price B, Sowers T (2004) Temperature dependence of metabolic rates for microbial growth, maintenance, and survival. PNAS 101:4631–4636

Rakusa-Suszczewski S (1980) Environmental conditions and the functioning of Admiralty Bay (South Shetland Islands) as part of the near shore Antarctic ecosystem. Pol Polar Res 1:11–27

Rakusa-Suszczewski S (1995) The hydrography of Admiralty Bay and its inlets, coves and lagoons (King George Island, Antarctica). Pol Polar Res 16:61–70

Rocha O, Duncan A (1985) The relationship between cell carbon and cell volume in freshwater algal species used in zooplanktonic studies. J Plankton Res 7:279–294

Rodríguez J, Jiménez-Gómez F, Blanco JM, Figueroa FL (2002) Physical gradients and spatial variability of the size structure and composition of phytoplankton in the Gerlache Strait (Antarctica). Deep Sea Res II 49:693–706

Rückamp M, Braun M, Suckro S, Blindow N (2011) Observed glacial changes on the King George Island ice cap, Antarctica, in the last decade. Glob Planet Change 79:99–109

Schloss IR, Nozais C, Mas S, Hardenberg B, Carmack E, Tremblay JE, Brugel S, Demers S (2008) Picophytoplankton and nanophytoplankton abundance and distribution in the southeastern Beaufort Sea (Mackenzie Shelf and Amundsen Gulf) during Fall 2002. J Mar Syst 74:978–993

Schloss IR, Wasilowska A, Dumont D, Almandoz GO, Hernando MP, Michaud-Tremblay CA, Saravia L, Rzepecki M, Monien P, Monien D, Kopczyńska EE, Bers AV, Ferreyra GA (2014) On the phytoplankton bloom in coastal waters of southern King George Island (Antarctica) in January 2010: an exceptional feature? Limnol Oceanogr 59:195–210

Simões JC, Ferron FA, Braun M, Neto JA, Aquino FE (2001) A GIS for the Antarctic specially managed area of Admiralty Bay, King George Island, Antarctica. Geo-Spat Inf Sci 4:8–14

Simon M, Glöckner FO, Amann R (1999) Different community structure and temperature optima of heterotrophic picoplankton in various regions of the Southern Ocean. Aqua Microb Ecol 18:275–284

Teixeira MC, Santana NF, Azevedo JCR, Pagioro TA (2011) Bacterioplankton features and its relations with doc characteristics and other limnological variables in Paraná river floodplain environments (PR/MS-Brazil). Braz J Microbiol 42:897–908

Tenenbaum DR, Barrera-Alba JJ, Duarte RB, Tenório MMB (2010) Plankton Structure of shallow coastal zone at Admiralty Bay, King George Island, West Antarctic Peninsula (WAP): pico, nano and microplankton and Chlorophyll biomass. INCT-APA Annual Activity Report. doi:10.4322/apa.2014.033

Tenório MMB, Le Borgne R, Rodier M, Neveux J (2005) The impact of terrigeneous inputs on the Bay of Ouinné (New Caledonia) phytoplankton communities: a spectrofluorometric and microscopic approach. Estuar Coast Shelf Sci 64:531–545

Tenório MMB, Duarte RB, Barrera-Alba JJ, Tenenbaum DR (2010) Plankton Structure in a shallow coastal zone at Admiralty Bay, King George Island, West Antarctic Peninsula (WAP): chlorophyll biomass and size-fractionated chlorophyll during austral summer 2009/2010. INCT-APA Annual Activity Report. doi:10.4322/apa.2014.034

Tenório MMB, Barrera-Alba JJ, Tenenbaum DR (2013) Plankton Structure of the shallow coastal zone at Admiralty Bay, King George Island, West Antarctic Peninsula (Wap): chlorophyll biomass and size-fractionated chlorophyll during austral summer 2010/2011. INCT-APA Annual Activity Report. doi:10.4322/apa.2014.105

Thingstad TF, Martinussen I (1991) Are bacteria active in the cold pelagic ecosystem of the Barents Sea? Polar Res 10:255–266

Treguer P, Jacques G (1992) Dynamics of nutrients and phytoplankton, and structure of food webs in the different sub-systems of the Antarctic Ocean. Polar Biol 12:149–162

Utermöhl H (1958) Perfeccionamento del metodo cuantitativo del fitoplancton. Commun Assoc Int Limnol Theor Appl 9:1–89

Vaughan DG, Marshall GJ, Connolley WM, Parkinson C, Mulvaney R, Hodgson DA, King JC, Pudsey CJ, Turner J (2003) Recent rapid regional climate warming on the Antarctic Peninsula. Clim Change 60:243–274

Verity PG, Robertson CY, Tronzo CR, Andrews MG, Nelson JR, Sieracki ME (1992) Relationships between cell volume and the carbon and nitrogen content of marine photosynthetic nanoplankton. Limnol Oceanogr 37:1434–1446

Vosjan JH, Olańczuk-Neyman KM (1991) Influence of temperature on respiratory ets-activity of micro-organisms from Admiralty Bay, King George Island, Antarctica. Neth J Sea Res 28:221–225

Weissenberger J (1998) Arctic Sea ice biota: design and evaluation of a mesocosm experiment. Polar Biol 19:151–159

White PA, Kalff J, Rasmussen JB, Gasol JM (1991) The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microb Ecol 21:99–118

Wright SW, Ishikawa A, Marchant HJ, Davidson AT, Enden RL, Nash GV (2009) Composition and significance of picophytoplankton in Antarctic waters. Polar Biol 32:797–808

Wynn-Williams DD (1996) Antarctic microbial diversity: the basis of polar ecosystem processes. Biodivers Conserv 5:1271–1293

Zdanowski MK (1995) Characteristics of bacteria in selected Antarctic marine habitats. In: Rakusa-Suszczewski S, Donachie SP (eds) Microbiology of Antarctic marine environments and Krill intestine, its decomposition and digestive enzymes. Polish Academy of Sciences, Warsaw, pp 5–100