

# Seasonal progression of diatom assemblages in surface waters of Ryder Bay, Antarctica

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**Abstract** Phytoplankton assemblages from seasonally sea-ice covered Ryder Bay (Adelaide Island, Antarctica) were studied over three austral summers (2004–2007), to link sea-ice variability and environmental conditions with algal speciation. Typical of near-shore Antarctic waters, biomass was dominated by large diatoms, although the prymnesiophyte *Phaeocystis antarctica* was numerically dominant. Although there was considerable interannual variability between main diatom species, high biomass of certain species or species groups corresponded consistently to certain phases of seasonal progression. We present the first documentation of an extensive bloom of the late-season diatom *Proboscia inermis* in February 2006, accounting for over 90% of diatom biomass. At this time, water column stratification and nutrient drawdown were high relative to other periods of the study, although carbon export was relatively low. Melt water flux in this region promotes well-stratified surface waters and high chlorophyll levels, but not necessarily concurrent increases in export production relative to seasons with lower freshwater inputs.

**Keywords** Diatoms · Phytoplankton · Seasonality · Sea-ice · Coastal Antarctic · *Proboscia inermis*

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## Introduction

In recent years, the western Antarctic Peninsula (WAP) has been established as one of most rapidly warming regions on the planet (Hansen et al. 1999; Vaughan et al. 2003). Since 1950, July air temperatures have risen 6.5°C (Stammerjohn et al. 2008a, b), while increases of 1° and 0.7°C have been recorded in the surrounding surface waters (Meredith and King 2005) and upper water column (Ducklow et al. 2007), respectively. This warming trend has resulted in important changes in extent and duration of seasonal sea-ice (Meredith and King 2005; Smith and Stammerjohn 2001; Stammerjohn et al. 2008a). Since 1979, monitoring from the Palmer Long Term Ecological Research (Pal-LTER) project have documented a 40% decrease in mean duration of sea-ice cover (Smith and Stammerjohn 2001), and trends of later advance and earlier retreat in the Marguerite Bay area (Stammerjohn et al. 2008a), which strongly influence algal stocks in near-shore Antarctic waters (Clarke et al. 2007; Garibotti et al. 2003a; Smith et al. 1998, 2000).

Ryder Bay, a seasonally ice-covered embayment of Marguerite Bay on the western coast of the WAP, is the site of the Rothera Oceanographic and Biological Time Series (RaTS), one of the longest running year-round oceanographic monitoring stations in coastal Antarctica (Clarke et al. 2008). RaTS data have revealed important regional hydrographic features and local El Niño Southern Oscillation effects (Meredith et al. 2004), effects of polar temperature on benthic invertebrates (e.g. Brockington and Clarke 2001; Peck et al. 2004), and seasonal productivity dynamics from size-fractionated chlorophyll (Clarke et al. 2008).

In Ryder Bay, chlorophyll (chl) *a* levels exhibit typical polar-region dynamics of a summer productivity

event and very low winter levels of photosynthetic biomass, but historically display considerable interannual variability (Clarke et al. 2008). Studies throughout the WAP region have established the importance of small phytoplankton classes (i.e. nanoflagellates) to annual production especially during winter (Clarke et al. 2008; Garibotti et al. 2005; Varela et al. 2002), and that the summer blooms are primarily dominated by larger algae, chiefly diatoms. Throughout this region and the Antarctic marginal sea-ice zone as a whole, many studies have found significant correlations between water column stability (largely resulting from the freshwater lens produced by sea-ice melt and glacial runoff), and overall primary productivity (Garibotti et al. 2003a; Kang and Lee 1995; Smith et al. 2001). This may be a result of the diatom-dominated algal communities in this region, as diatoms are associated with well-stratified conditions (Arrigo et al. 1999).

However, little is known in Ryder Bay regarding the composition of phytoplankton assemblages at the species or class level, especially with regard to temporal evolution during the growing season. Investigations by Garibotti et al. (2003a, 2005) have assessed the contributions of diatoms, cryptophytes and unidentified phytoflagellates in Marguerite Bay, but these assessments cover one time point per year. This study documents seasonal and inter-annual variation in phytoplankton assemblages at the species level, in surface waters of Ryder Bay, covering the austral summers of a 3-year study period. The results presented here, the first of their kind for the Marguerite Bay area, document the temporal variation in phytoplankton classes and species for the 2006–2007 season. Additional samples of diatom assemblages from the two preceding seasons were also available for comparison. These high-resolution biological data, coupled with oceanographic data from RaTS, allow identification of some environmental factors controlling algal succession in Ryder Bay. These processes are relevant to the Marguerite Bay region, where previous studies have demonstrated common water mass sources (Clarke et al. 2008), and the inner shelf of the WAP region where similar coastal influences such as glacial meltwater affect diatom communities containing many of the species listed here (e.g., Garibotti et al. 2005; Varela et al. 2002).

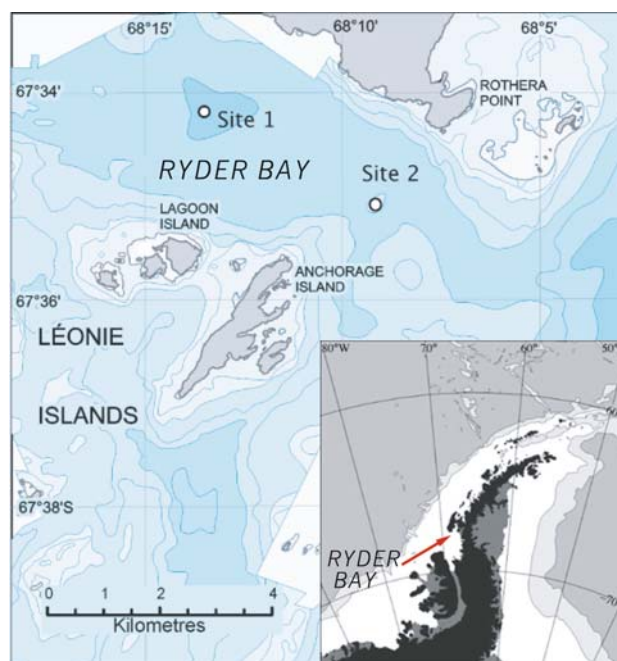
In the region of the WAP, many studies have recently documented changes in seasonal sea-ice cover resulting from current warming (see Stammerjohn et al. 2008a, b). As the coastal regions have the greatest impact on overall WAP primary production (Smith et al. 1996, 1998, 2001), elucidating the interactions between temperature of both air and water, sea-ice coverage, and primary productivity is crucial to understanding future changes in phytoplankton dynamics and the implications that any changes in overall

productivity or species composition may have for higher trophic levels and carbon fluxes in near-shore regions of the WAP.

## Methods

### Study site

Surface water samples were obtained from the RaTS sites 1 and 2 (67°34.02'S, 68°14.02'W and 67°34.850'S, 68°9.340'W, respectively, Clarke et al. 2008; Fig. 1), in Ryder Bay (Adelaide Island, Antarctica) during summer 2006–2007. These sites are ~4 km from shore, over water of 520 and 400 m depth, respectively. Site 2 was used when sea-ice prevented access to Site 1, and both are associated with the same water mass (Clarke et al. 2008). Ryder Bay is located at the northern end of Marguerite Bay, and is thought to be representative of water column conditions throughout Marguerite Bay (Clarke et al. 2008). The circulation in this region is well characterized (Meredith et al. 2004) and is presented in detail elsewhere (Hofmann et al. 1996; Smith et al. 1999).



**Fig. 1** Map of Ryder Bay showing the RaTS sampling sites (dots). Site 1 is situated ~4 km offshore, above the deepest point of Ryder Bay. Site 2, approximately equidistant between Rothera Point and Lagoon Island, was used when sea ice conditions prevented access to Site 1. Map courtesy of the British Antarctic Survey, after Clarke et al. (2007, 2008)

## Sample collection/analysis

All water samples were collected from 15 m depth, the long-term average depth of the chl maximum, usually situated within the most intense bloom, which typically extends from ~8 to ~20 m (Clarke et al. 2008). This was further verified during the study period, where peak chl depth ranged from 8 to 21 m (2006–2007 data) and high chl levels (>50% of the maximum) ranged from  $8 \pm 5$  to  $40 \pm 10$  m (from CTD fluorometer). Thus the 15 m sampling depth consistently captured the high chl signal. Water was collected using a 12 V dolphin pump connected to weighted silicon tubing of 29 mm diameter, and high flow rates ( $\sim 4 \text{ L min}^{-1}$ ) were maintained to avoid size dependent sample biases. Bulk samples for suspended particulate matter (SPM) and nutrients ( $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$ ) were collected in 10 L carboys. Samples for phytoplankton identification were collected from pump outflow and stored in 250 mL amber glass bottles, preserved with 2.5% Lugol's fixative, pre-acidified to  $\sim \text{pH } 7$  to prevent dissolution of silica.

An appropriate volume (2–5 L) of seawater was filtered onto duplicate pre-weighed, pre-combusted ( $400^\circ\text{C}$  for 4 h) 47 mm GF/F filters (pore size  $\sim 0.7 \mu\text{m}$ ), using an acid-washed (10% HCl) Millipore filter housing, and oven dried at  $50^\circ\text{C}$  overnight. Filters were weighed to determine SPM, a rough proxy for biological production as it does not discriminate against non-biological material in the water column. Moistened filters were placed in a glass desiccator overnight with a small amount of HCl to remove carbonates, and then dried. These were run on a Carlo Erba NA 2500 elemental analyzer in-line with a VG PRISM III isotope ratio mass spectrometer to obtain bulk C and N content. The concentration of particulate organic carbon (POC) reflects phytoplankton productivity, balanced by losses due to grazing or sinking of organic matter.

Samples for nutrients were filtered ( $\sim 0.7 \mu\text{m}$ ) and acidified with  $1 \text{ mL L}^{-1}$  of 50% HCl to stop microbial activity. Samples were neutralized with NaOH immediately prior to analysis, which was performed on a Bran + Luebbe Continuous Flow Autoanalyzer 3 in the Crew Laboratories, University of Edinburgh. Surface water nutrient levels reflect inputs (i.e. from deeper waters) and losses such as biological uptake or dilution from meltwater.

Routine CTD cast data and discrete, size-fractionated chl *a* data from 15 m, collected using methods detailed in Clarke et al. (2008), were obtained from the RaTS database (British Antarctic Survey, Cambridge, UK).

## Phytoplankton taxonomy

For counting and identifying phytoplankton, two methods were used: light microscopy (LM) and scanning electron

microscopy (SEM). LM samples were processed by settling 5 mL of Lugol's-preserved seawater in Hydrobios settling chambers for a minimum of 18 h. Counting was performed on a Zeiss, inverted light microscope at  $200\times$  and  $400\times$  magnification. Large cells were counted at  $200\times$ , following the Ütermohl methodology outlined by Hasle (1978), where counts were made of the entire chamber. Identification followed the taxonomic guidelines outlined in Hasle and Syvertsen (1997) for diatoms. Additional references, where needed, were Doucette and Fryxell (1985), Johansen and Fryxell (1985), Jordan et al. (1991) and Scott and Thomas (2005). Dinoflagellates were identified according to McMinn and Scott (2005) and crysophytes according to Konno and Jordan (2007). Small cells (consisting of the diatoms *Fragilariopsis cylindrus*, solitary cells of the *Chaetoceros* subgenus *Hyalochaeta* and their resting spores, small ( $<10 \mu\text{m}$ ) *Thalassiosira* cells, and the prymnesiophyte *Phaeocystis antarctica*), were enumerated at a magnification of  $400\times$  along one transect of the chamber. Large cell counts exceeded 4,500 cells and small cell counts exceeded 1,700 cells. LM analysis was performed on all samples from the third season (2006–2007).

SEM analysis was used to assess phytoplankton assemblages from previous (first (2004–2005) and second (2005–2006)) seasons. For these seasons, preserved water samples were not available. Samples for SEM were collected as for 2006–2007, and an appropriate volume (0.15–0.9 L) of untreated seawater was filtered onto  $0.2 \mu\text{m}$  polycarbonate filters. The filters were dried overnight at  $50^\circ\text{C}$ , and stored in Petri slides until analysis. These were then attached to SEM stubs, and assemblages were imaged on a Philips XL 30 CP microscope using secondary electron imaging with a 20 kV beam and a 10 mm working distance.

As samples for SEM were not fixed prior to filtering, problems with preservation of cells lacking siliceous external structures (i.e. prymnesiophytes) prevents comprehensive analysis of these phytoplankton communities by this method. However, even very delicate siliceous species were present on filters in adequate condition to be identified and counted, therefore, this method was considered an accurate reflection of the siliceous (diatom and silicoflagellate) assemblage.

Species were identified as for the 2006–2007 samples, counting 30 random fields of view at each of two levels of magnification:  $500\times$  and  $1,000\times$  for large and small cells, respectively. Several species were counted at both levels of magnification to ensure consistency and in all cases the cellular abundances calculated for each magnification were within 10%.

For both LM and SEM samples, individual species were grouped in some cases due to ecological preferences,

low abundances or difficulties in distinguishing between species in the light microscope. The *Banquisia* group includes the *Banquisia belgicae*, *Berkeleya* spp, *Entomoneis kjellmanii*, *Haslea trompii*, *Ephemera planamembranacea*, related genera and members of the bottom ice community (Horner 1985), and *Membraneis challengerii*, a related sea-ice species (Scott and Thomas 2005). These species were counted individually, and biomass estimates (below) calculated for each species before being pooled. The *Chaetoceros* subgenus *Hyalochaeta* includes *C. neglectus* Karsten, *C. simplex* Ostefeld and *C. socialis* Lauder. The *Chaetoceros* subgenus *Phaeoceros* includes the larger, less abundant species *C. atlanticus* Cleve, *C. convolutus* Castracane, *C. criophilus* Castracane, *C. dictyota* Ehrenberg and *C. flexuosus* Mangin. Wherever possible, *Chaetoceros* cells were counted at the species level, and biomass estimates calculated for each species before being combined. The *Fragilariopsis curta* group is as defined by Crosta et al. (2005) and includes *F. curta*, *F. cylindrus*, and *F. vanheurkii*; as these species are commonly associated with sea-ice zones. Other *Fragilariopsis* species not associated with sea-ice were relatively rare, and were grouped as *Fragilariopsis* spp. Again, most *Fragilariopsis* cells were identified to species level and grouped after biomass estimates were calculated. The *Proboscia* spp. group consists primarily of *P. inermis*, with negligible (<1%) abundance and biomass contributions from *P. alata* and *P. truncata*. Both *Pseudonitzschia lineola* and *P. turgidula* are included in the *Pseudonitzschia* group, with *P. lineola* being the dominant species (numerically >80%) in all samples.

In SEM samples, identification of discoid, centric diatoms (“Centrics”) was possible to species level. Due to lower magnification, in LM (2006–2007) samples, counts were made on the basis of size (>15 μm, ~20 μm, 20–50 μm, >50 μm, ~100 μm), and the biomass of each size range estimated to calculate total “Centric” biomass. This “Centrics” group includes members of the discoid genera *Actinocyclus*, *Asteromphalus*, *Coscinodiscus*, *Porosira*, *Stellarima* and *Thalassiosira*. Members of these genera, which are generally part of late-summer phytoplankton (Denis et al. 2006; Maddison et al. 2006; Stickley et al. 2005) and have been identified by SEM in samples from the 2004–2005 and 2005–2006 seasons, are assumed to be similarly the main “centric” species present during the 2006–2007 season.

Many of the smaller species (*Chaetoceros Hyalochaeta* spp., *Fragilariopsis curta* group spp.) were easily identified to group level in LM samples as they were present largely in chains. For solitary cells (especially *Minidiscus chilensis* and *F. cylindrus*), while the potential for misidentification was more likely, individual small cells make a relatively small contribution to overall biomass. Thus the emphasis

here is on the community biomass, as this minimizes any biases from difficulty distinguishing individual small cells in LM samples. While it was not possible for all samples, a limited number of samples were analyzed by both methods (LM and SEM) and the estimated relative biomass was consistent between the two methods, generally varying by <5%.

#### Microalgal volume and biomass

Cell volumes were calculated using geometric formulae appropriate to the shape of the cell, following Smayda (1978) and Hillebrand et al. (1999; see Appendix 1), using measurements from electron micrographs of 30 individual cells (where possible) for each species. SEM samples allowed higher precision of cellular measurements, thus these cellular biomass estimates from were used to calculate species biomass from the abundance data in both LM and SEM samples. In all cases, cell sizes estimated from the ocular scale bar on the light microscope were within the size ranges recorded for SEM measurements of the same species. Conversion to biomass was done according to Smayda (1978), and was then converted to cellular carbon (C, in pg C cell<sup>-1</sup>) from the equations of Strathmann (1967), where:

$$\log_{10} C = 0.892(\log_{10} PV) - 0.61$$

for diatoms, where PV denotes plasma volume. A second equation:

$$\log_{10} C = 0.94(\log_{10} V) - 0.60$$

was used for other phytoplankton groups based on total cell volume (V) rather than PV (Eppley et al. 1970, corrected in Smayda 1978).

Cellular C content of *P. antarctica* was calculated separately from the conversion factor of Edler (1979) and the cellular measurements of Rousseau et al. (1990). An average of 13.6 pg C cell<sup>-1</sup> was chosen, as the cells counted here represent a mixture of solitary, colonial, motile and non-motile morphotypes.

#### Sediment trap deployment and analysis

Two time-series sediment traps were deployed from the research ship James Clark Ross on a mooring at RaTS Site 1, situated at 200 m and 512 m, with rotating sediment cups. Each cup contained filtered seawater spiked with 5% NaCl, and a final concentration of 2% (v/v) formaldehyde to prevent bioturbation. The sampling period covered late 2004–2005 (from 29th January, immediately following the second chlorophyll peak), through the 2005–2006 summer season, with sample cups being rotated approximately every 2 weeks.

Diatoms were enumerated in all sediment trap cups where enough material was available. Diatom analysis, sediment treatment and slide preparation followed techniques adapted from those described by Rathburn et al. (1997). Diatom counts followed Schrader and Gersonde (1978) and Laws (1983). Roughly 350 diatom valves were counted in each sample at a magnification of 1,000 $\times$ . Diatoms were identified as for water samples, and the relative abundance of each was calculated as the fraction of diatom species against total diatom abundance in each sample.

## Results

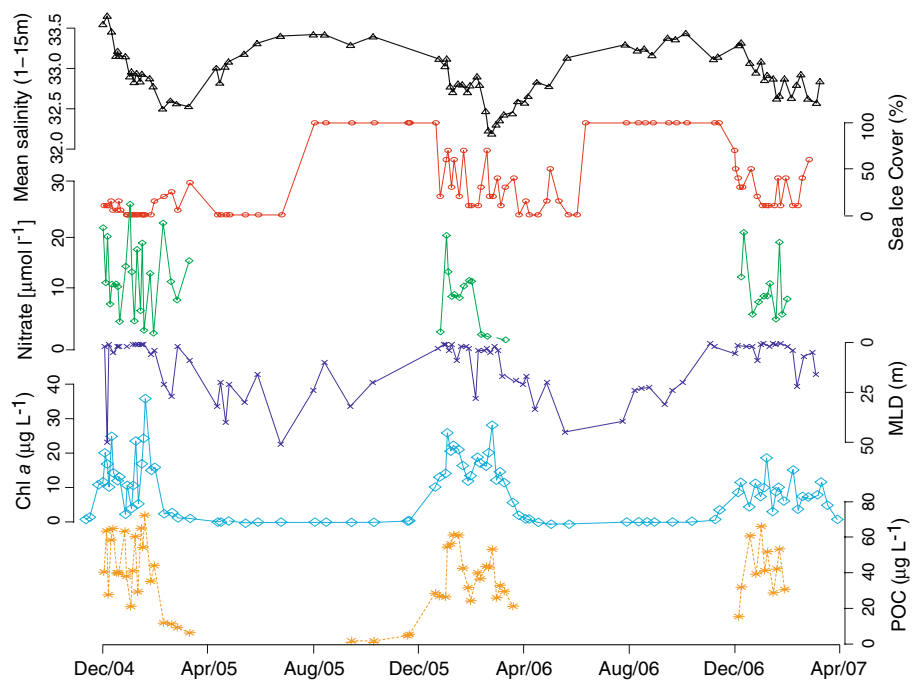
### Hydrography

Sea-ice coverage during the study period was fairly typical of the region, with full winter coverage lasting 4–5 months. Recent warming trends have contributed to  $\sim$ 28 fewer ice days per year in the Ryder Bay area, as well as later sea-ice advance along much of the WAP, relative to the 1980s (Stammerjohn et al. 2008a). However, sea-ice in Ryder Bay displays high interannual variability in both duration and timing (Clarke et al. 2008) which can mask such trends over shorter time scales. In the first (2004–2005) season, sea-ice retreated quickly in November, and Ryder Bay was nearly free of ice by the beginning of December, when our sampling regime commenced (Fig. 2). Full sea-ice conditions persisted until the end of December in 2005–2006, although

the duration of full sea-ice coverage was very similar. Patchy ice coverage ( $\sim$ 50%) within the bay continued through January. Sea-ice in 2006–2007 broke out earlier 17 November, thereafter covering  $>$ 50% of the bay for  $\sim$ 3 weeks, after which the bay was subject to light, patchy coverage (Fig. 2).

The mixed layer depth (MLD) presented here is as defined by Clarke et al. (2008) for the RaTS programme as the depth at which potential density exceeds that of surface (0 m) water by 0.05 kg m $^{-3}$ . During summer when meltwater inputs are greatest, this depth often reflects a very shallow, freshwater lens. During the first season, the MLD was frequently below 20 m, indicating greater wind mixing during this period. Waters had a more persistent, shallow freshwater lens from sea-ice and glacial melt at  $\sim$ 1 m in the second and third seasons (from CTD; Fig. 2), and few mixing events deeper than 15 m during the period of elevated chlorophyll. Salinity, averaged within the top 15 m of the water column, provides an indication of cumulative freshwater input to surface waters and potential for stratification from a melt water lens. This parameter indicates that overall fresh water inputs were greatest in the second season (Fig. 2). The degree of mixing from deeper waters is reflected in nutrient inputs, with the second season having the lowest degree of nutrient injection, consistent with more stratified conditions (Fig. 2). In contrast, the other seasons show multiple nitrate input events in accordance with deeper, more frequent mixing, suggesting that wind-driven mixing is a strong control on nutrient injection from deeper, more nutrient-rich water.

**Fig. 2** Physical properties and biological production across three austral summers. Percent sea-ice cover was estimated from visual observations of the areal extent of sea-ice in Ryder Bay. All other parameters, including mixed layer depth (MLD), were measured at the RaTS Sites. Nitrate concentration was assessed at 15 m. Average salinity was calculated from the top 15 m of the CTD cast and gives an indication of freshwater inputs from melting sea ice and glaciers. Chlorophyll *a*, suspended particulate matter (SPM) and particulate organic carbon (POC), all biological productivity proxies from 15 m depth, show three austral growing seasons separated by typically low winter biomass



## Total algal standing stock

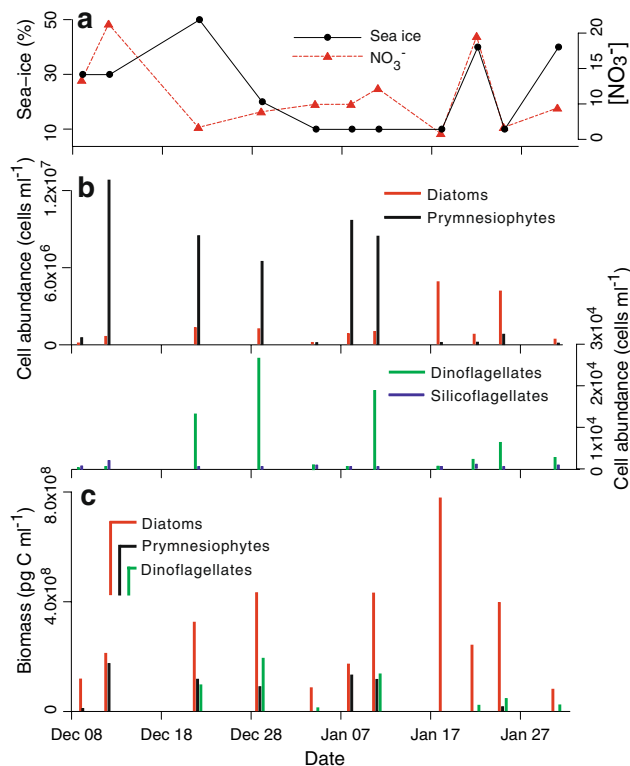
Algal abundances and biomass show a large degree of variability, ranging from  $5.1 \times 10^5$  cells  $L^{-1}$  and  $92 \mu\text{g C L}^{-1}$  in winter, to  $1.4 \times 10^7$  cells  $L^{-1}$  and  $710 \mu\text{g C L}^{-1}$  in summer. These are comparable to cell abundances of  $9.4 \times 10^6$  cells  $L^{-1}$  and biomass of  $603 \mu\text{g C L}^{-1}$  in Marguerite Bay in summer 1997 (Garibotti et al. 2003a), and within the range reported for summer in the entire Pal-LTER area (Garibotti et al. 2005). Seasonal phytoplankton dynamics in Ryder Bay follow a typical coastal polar-region pattern, with elevated productivity defining the “growing season”, compared to low winter productivity during full sea-ice coverage. Chlorophyll *a* in this region often shows two distinct peaks during the growing season (Clarke et al. 2008), which is clearly reflected in our chl *a* data from seasons 1 and 2 (Fig. 2). Biomass concentrations within surface waters remain above winter levels throughout the austral summer, shown clearly by POC and SPM levels (Fig. 2).

## Phytoplankton assemblage composition

Full phytoplankton taxonomic analysis was only possible for the third (2006–2007) season, thus all results and discussion of the entire phytoplankton community are restricted to this period. During our sampling regime, microalgal communities included five classes, and 19 genera or functional groups. Diatoms accounted for 15 of these groups, indicating the relative importance of this class of algae to the region. Chlorophyll *a* was assessed for four different size fractions ( $>20 \mu\text{m}$ ,  $5\text{--}20 \mu\text{m}$ ,  $2\text{--}5 \mu\text{m}$ ,  $0.2\text{--}2 \mu\text{m}$ ) as part of routine RaTS sampling, with the largest fraction, predominantly (70–100% by biomass) diatoms, representing more than 88% of the chl *a* throughout the growing season (Clarke et al. 2008).

*Phaeocystis antarctica* was numerically dominant during most of season 3, showing two large bloom events (12 December and 4 January; Fig. 3) immediately following deepening of the mixed layer below  $\sim 10$  m. The latter half of the season was dominated by diatoms, especially *Chaetoceros (Hyalochaeta) spp.*, which also exhibited two growth events. When converted to biomass, diatoms consistently accounted for the majority of the water column community (Fig. 3).

Dinoflagellate species (*Gyrodinium cf. lachryma*, *Katodinium sp.*, *Podolampas antarctica*, and *Protoperidinium spp.*) were grouped due to low abundances, although their large size and high C content occasionally resulted in a significant contribution to total biomass (up to 27%; Fig. 3).



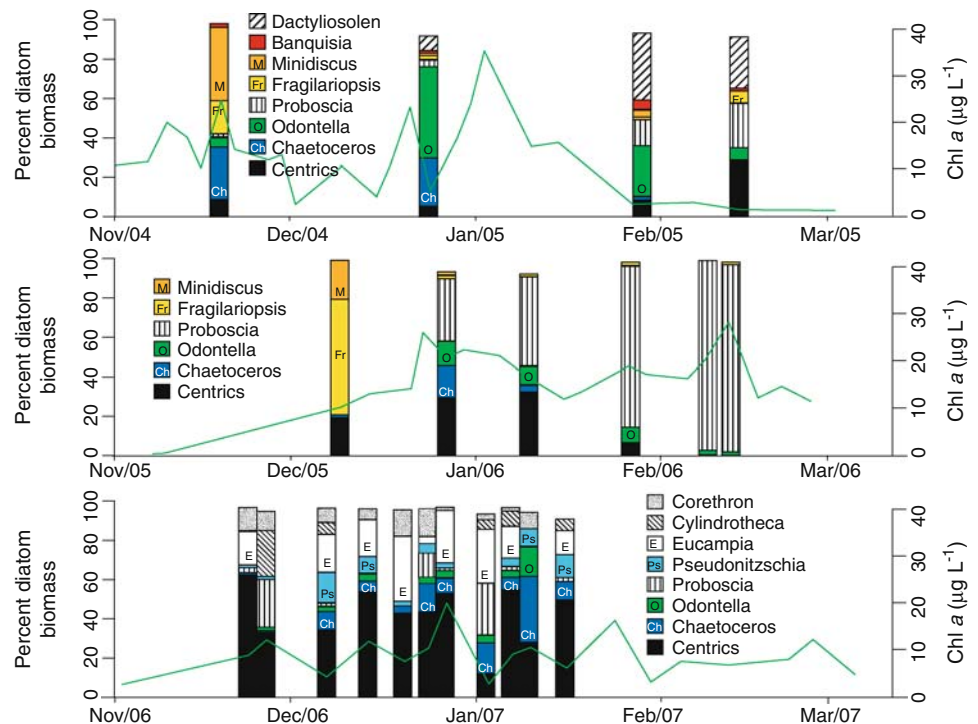
**Fig. 3** Cellular abundances (b) and biomass concentrations (c) of the four main phytoplankton taxa during the 2006–2007 growing season at the RaTS site. Sea-ice coverage and nutrient ( $\text{NO}_3^-$ ) concentrations are indicated at top (a)

## Diatom community composition

Due to uneven preservation between silicified algae (primarily diatoms) and other algal classes (dinoflagellates, prymnesiophytes) on SEM-analyzed samples (see “Methods”), interannual comparisons have only been made for diatoms (Fig. 4), for which the data span all three seasons. Given that even very thinly silicified species (i.e. vegetative form of *Thalassiosira antarctica*) were preserved on filters, and there were no species present in the third season (LM samples) that were not seen in any of the previous, SEM-analyzed samples, the relative abundances (given in Table 1) assessed in SEM samples are considered to be a robust reflection of the diatom assemblage composition. For interannual comparison, data were compiled for diatoms only, and are shown as relative abundance of the diatom community (Table 1) and as percent contribution to estimated diatom community biomass (Fig. 4).

Diatom assemblages show considerable interannual variability (Figs. 4, 5). The relative contributions of species (or species groups) to total diatom biomass, calculated from species specific volume estimates, are shown in Fig. 4. While SEM analysis of 2004–2005 and 2005–2006 samples allowed identification of individual cells to species

**Fig. 4** Diatom community composition from all three sampling seasons. Only species or groups accounting for a minimum of 10% of the estimated diatom biomass on at least one occasion have been shown. Groups are: (discoid) Centrics, *Chaetoceros* (*Hyalochaeta* subgenus), *Odontella* (*weissflogii*), *Proboscia* (*inermis*), *Fragilariopsis* (*curta* group), *Minidiscus* (*chilensis*), *Banquisia* (group), *Dactyliosolen* (*antarcticus*), *Pseudo-nitzschia* (group), *Eucampia* (*antarctica*), *Cylindrotheca* (*closterium*) and *Corethron* (*inermis*)



level in most cases, data are presented in the same groups as the 2006–2007 data, for easier comparison.

First season diatom biomass (Fig. 4a) was initially dominated by *Minidiscus chilensis*, (~38% of the preserved community biomass estimate), then dominance then switched to *Odontella weissflogii* (~43% community biomass). *Dactyliosolen* cf. *antarcticus* then increased in relative biomass to match that of *O. weissflogii* and *M. chilensis* (~20%). The final sample from the first season shows *D. antarcticus*, the centric group and the *Proboscia* group (principally *P. inermis*) all contributed ~20% of the total biomass.

The second season also initially had very high proportions of biomass attributable to *Minidiscus chilensis* and the *Fragilariopsis curta* group, which then both rapidly declined (Fig. 4b). The centric and *Proboscia* groups follow, each contributing ~25%, after which the *Proboscia* group (almost exclusively *P. inermis*) is responsible for >90% of the calculated community biomass. *Odontella weissflogii* also contributed at the end of the second season, with contributions of ~3–6%.

Diatom communities in 2006–2007, (from light microscopy analysis) were more diverse, with biomass contributions rarely exceeding 30% for any one species or species group (Fig. 4c). The early season was characterized by large (>20 µm) members of the “centrics” group (mean 29%) and *Eucampia antarctica* var. *antarctica* (up to 34%), with periodic contributions from *Cylindrotheca closterium*

(up to 22%) and the *Proboscia* group (up to 23%). Mid-season diatom communities were also primarily large centric species (mean 24%) and *E. antarctica* (up to 28%), with increasing amounts of *Chaetoceros* (*Hyalochaeta*) spp. (to 34%) and some *Odontella weissflogii* (~15%) near the end of mid-season.

#### Sediment trap flux and assemblages

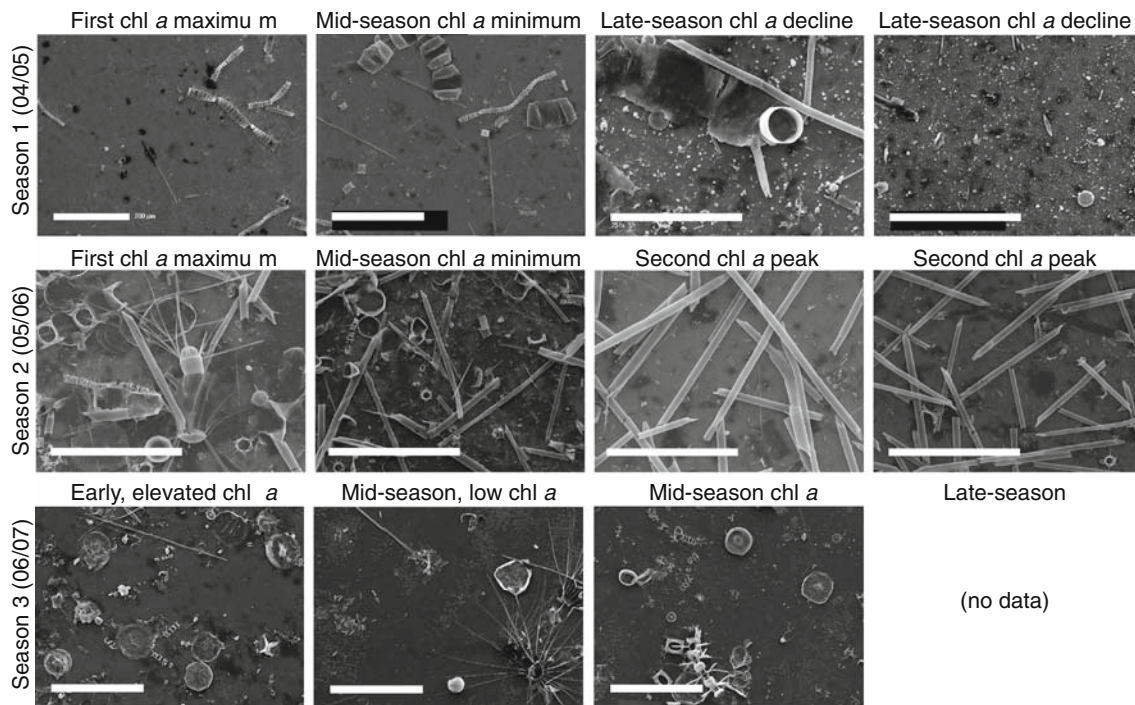
In the 200 m trap on the RaTS mooring, diatom abundances peaked at 325 million valves  $m^{-2} d^{-1}$  during the latter part of the 2004–2005 season and 156 million valves  $m^{-2} d^{-1}$  at the start of the 2005–2006 season (Fig. 6). In the 512 m trap on the RaTS mooring, diatom abundances peaked at 345 million valves  $m^{-2} d^{-1}$  during the latter part of the 2004–2005 season and 35 million valves  $m^{-2} d^{-1}$  at the start of the 2005–2006 season.

In the first season, the 200 m RaTS trap was initially dominated by *Chaetoceros* species (31–60% of valves), while the *Fragilariopsis curta* group accounted for 22–32% (Fig. 6). Other groups such as *Thalassiosira antarctica*, *T. gracilis*, pennate species, and *F. obliquecostata* composed up to ~8% of the assemblage. In the deep (512 m) RaTS trap, the percentage of *Chaetoceros* increased to 60–74%. Conversely, *F. curta* dropped to between 9 and 17% of the assemblage. This reduction in the proportion of *F. curta* in the deep trap is also seen in other small species groups such as *T. gracilis* and the

**Table 1** Relative abundances of main diatom species/groups as a percentage of all diatom cells enumerated

Date	<i>Bq</i> (%)	<i>Chaet</i> (%)	<i>C. Hyal</i> (%)	<i>C. Pha</i> (%)	<i>Cent</i> (%)	<i>Cor</i> (%)	<i>Cylin</i> (%)	<i>Euc</i> (%)	<i>Frag</i> (%)	<i>F. curt</i> (%)
12/13/04	0.0	4.1	4.1	0.0	0.1	0.0%	0.0	0.0	66.5	66.5
1/7/05	0.3	31.4	31.2	0.2	1.1	0.0	0.0	0.0	55.1	54.6
2/12/05	0.4	2.2	1.9	0.0	0.5	0.0	0.0	0.0	91.8	89.8
2/28/05	0.5	1.7	0.0	1.7	7.8	0.0	0.1	0.1	81.3	81.1
12/23/05	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	93.1	93.1
1/10/06	0.2	33.0	32.9	0.0	3.0	0.0	0.0	0.3	47.6	45.1
1/24/06	0.3	6.6	6.4	0.2	4.4	0.0	0.0	0.3	81.1	78.4
2/10/06	0.2	1.6	1.1	0.4	1.7	0.1	0.0	0.2	76.4	73.2
2/23/06	0.8	2.7	0.0	0.6	0.2	0.1	0.0	0.1	49.8	44.1
2/27/06	0.1	0.0	0.0	0.0	0.1	0.1	0.0	0.0	68.6	66.7
12/9/06	2.8	12.4	8.3	3.2	37.2	1.4	0.0	6.2	26.6	16.1
12/12/06	3.3	8.3	5.4	2.1	24.9	0.8	2.1	0.0	38.7	27.0
12/22/06	0.7	36.8	33.2	2.6	13.7	0.7	0.0	3.3	14.3	12.4
12/29/06	0.9	32.7	26.6	3.1	28.1	0.3	0.0	3.8	10.1	5.8
1/4/07	1.3	28.1	22.1	4.0	37.6	1.3	0.0	9.6	11.2	6.6
1/8/07	0.8	48.0	47.5	0.6	25.1	0.6	0.0	0.4	12.3	4.5
1/11/07	1.0	39.1	38.0	0.7	26.8	0.0	0.0	6.5	10.9	5.5
1/18/07	0.7	77.7	51.1	1.8	9.1	0.1	0.2	3.5	2.6	1.6
1/22/07	1.1	70.2	26.2	1.2	14.2	0.1	0.5	4.6	0.5	0.5
1/25/07	0.5	67.0	49.9	0.8	17.6	0.2	0.0	0.0	7.3	7.3
1/31/07	3.2	60.7	26.5	1.1	11.0	0.0	0.2	1.2	5.6	5.4
Date	<i>F.kerg</i> (%)	<i>Mini</i> (%)	<i>Nav</i> (%)	<i>Odont</i> (%)	<i>Prob</i> (%)	<i>Ps-n</i> (%)	<i>Thal</i> (%)	Chl <i>a</i> (%)	SPM (%)	POC (%)
12/13/04	0.1	29.0	0.0	0.0	0.0	0.1	0.0	24.8	15.9	57.9
1/7/05	0.6	4.5	0.2	2.5	0.1	4.6	0.0	10.7	15.5	40.7
2/12/05	0.7	4.2	0.5	0.3	0.0	0.0	0.0	2.58	9.12	11.5
2/28/05	0.2	2.7	1.8	0.4	1.7	1.5	0.0	1.38	7.50	8.89
12/23/05	0.0	6.7	0.0	0.0	0.0	0.0	0.0	10.2	14.2	28.2
1/10/06	2.5	9.3	0.0	0.8	2.7	2.7	0.0	20.5	17.5	55.7
1/24/06	0.5	2.7	0.2	0.6	3.7	0.8	0.0	16.4	12.3	42.1
2/10/06	3.2	0.4	0.1	1.3	17.8	0.2	0.0	18.8	18.0	39.6
2/23/06	0.4	0.0	2.1	0.9	41.4	0.0	0.0	20.1	16.6	42.6
2/27/06	0.0	1.1	1.0	0.5	28.3	0.0	0.0	27.9	16.4	52.7
12/9/06	7.3	0.5	6.9	0.0	0.7	4.6	0.9	8.68	13.0	15.0
12/12/06	0.0	1.7	5.0	0.4	5.8	7.9	1.0	11.6	17.1	31.5
12/22/06	1.6	1.0	0.7	0.3	0.3	26.4	2.0	4.58	13.7	60.3
12/29/06	4.3	0.0	1.8	0.6	0.0	20.2	1.4	11.3	13.0	38.9
1/4/07	4.6	0.0	0.7	0.0	0.0	5.9	4.3	7.51	21.9	65.6
1/8/07	7.8	0.0	0.8	0.3	1.4	8.7	1.5%	10.1	20.4	40.8
1/11/07	1.4	0.7	1.3	0.3	0.3	10.2	2.4	18.6	12.3	51.4
1/18/07	0.8	0.0	1.4	0.3	0.8	3.0	0.5	3.21	9.95	28.4
1/22/07	0.0	0.0	0.4	0.5	0.3	7.4	0.3	8.89	11.7	41.7
1/25/07	0.0	0.0	0.5	0.7	0.0	6.0	0.2	10.2	16.0	52.8
1/31/07	0.2	0.0	2.4	0.0	0.2	15.3	0.2	6.25	9.12	30.2

Groups are as defined in the text: *Bq*, Banquisia group, *Chaet*, all *Chaetoceros* cell, including resting spores, *C. Hyal*, subgenus *Hyalochaeta* spp.; *C. Pha*, subgenus *Phaeoceros* spp., *Cent*, centrics, *Cor*, *Corethron inerme*, *Cylin*, *Cylindrotheca closterium*; *Euc*, *Eucampia antarctica*, *Frag*, all *Fragilariopsis* cells, *F.curt*, *Fragilariopsis (curta* group only), *F.kerg*, *Fragilariopsis (kerguelensis* group only); *Mini*, *Minidiscus chilensis*; *Nav*, *Navicula* spp., *Odont*, *Odontella weissflogii*; *Prob*, *Proboscia inermis*, *Ps-n*, *Pseudonitzschia* spp., *Thal*, *Thalassiothrix antarctica*. Only species groups present at >1% relative abundance on at least one occasion are shown. Also listed are chlorophyll *a* ( $\mu\text{g L}^{-1}$ ), suspended particulate matter (SPM,  $\text{mg L}^{-1}$ ) and bulk particulate organic carbon (POC,  $\mu\text{M}$ ) for sample dates



**Fig. 5** Scanning electron micrographs of preserved phytoplankton communities from three growing seasons. Samples are shown from the first chl *a* maximum in seasons 1 and 2 (13 December 2004, 10 January 2006), and the first period of elevated chl *a* in the 3rd season (11 January 2007) when chl peaks were not well defined. Mid-season, low-chl *a* assemblages are from 7 January 2005 (season 1), 24 January 2006 (season 2), January 22 and 31 2007 (season 3). Late-

season assemblages show the chl *a* decline from the first season (12 and 28 February 2005), and the second chl *a* maximum in the second season (23 and 27 February 2006), where biomass is visibly dominated by *Proboscia inermis*. Sampling concluded before late season assemblages could be collected in 2007. Note that images do not reflect cell concentrations, as different volumes were filtered in each case. White scale bars are 200  $\mu\text{m}$

pennate benthic group. Due to the lack of material in the winter trap bottles at the RaTS site, it was not possible to analyze the winter diatom assemblages.

After retreat of the sea-ice and initiation of the spring bloom during the 2005–2006 growing season, the shallow trap was again dominated by flux of *Chaetoceros* and *F. curta* species (40 and 19% of the assemblage, respectively; Fig. 6). *Thalassiosira antarctica*, *T. gracilis*, pennate species and *Fragilariopsis obliquecostata* again composed up to 8% of valves. In the deep trap, *Chaetoceros* (49%), *F. curta* (21%) and *T. antarctica* (12%) dominated the assemblage. Interestingly, there were high abundances in the deep trap of *T. antarctica*, pennate species (primarily *Pseudonitzschia*), *F. curta* and *F. obliquecostata*, species commonly associated with sea-ice material, while the proportion of *Proboscia* was lower in the deeper trap.

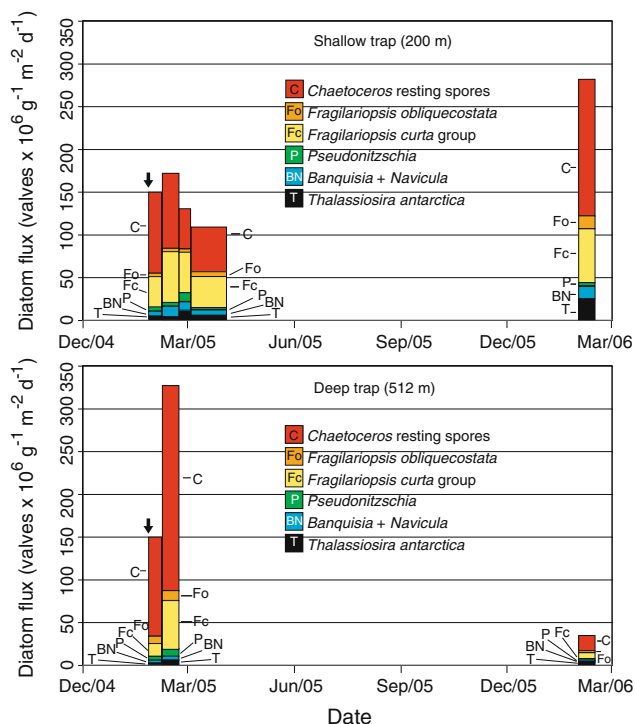
## Discussion

Interannual variation in overall standing stock (POC and SPM) was relatively low ( $\sim 10\%$ ), although chl *a* levels and export production varied considerably. Although

prymnesiophytes were often numerically dominant, surface waters were consistently dominated by diatoms in terms of biomass. This pattern of dominance has been previously observed in the Marguerite Bay region (Garibotti et al. 2003a, b, 2005), in the greater WAP region (Holm-Hansen et al. 1989; Varela et al. 2002), and is common for algal blooms associated with the marginal sea-ice zone (Bianchi et al. 1992; Fiala et al. 1998; Kang and Fryxell 1993). While the species composition of the diatom community varied between seasons, the summer growing period shows strong seasonality, with abundances of several species linked to changes in environmental conditions.

### Total algal standing stock

The Marguerite Bay region typically exhibits very high algal standing stock, relative to most of the western WAP (regionally averaged biomass: 330  $\mu\text{g C L}^{-1}$ , Garibotti et al. 2005). The second season had the highest average chl *a* (17.06 vs. 15.31 and 9.04  $\mu\text{g L}^{-1}$  in seasons 1 and 3, respectively; Table 2), despite very similar duration of the growing seasons. Assuming that lower  $[\text{NO}_3^-]$  was due to biological processes and increases in  $[\text{NO}_3^-]$  resulted from



**Fig. 6** Species composition of diatoms from sediment traps at RaTS site 1. Diatom fluxes (in valves per gram dry sediment  $\text{m}^{-2} \text{d}^{-1}$ ) are shown for (a) the shallow trap at 200 m and (b) the deep trap at 512 m. Resting spores were the overwhelmingly dominant form (>99%) of *Chaetoceros* valves. The *Fragilariopsis curta* group is as defined in the text. The *Pseudonitzschia* group includes the species *P. lineola*, *P. hemii* and *P. turgiduloides*. The *Banquisia* group (see text) and *Navicula* (*N.directa*, *N.gelida* and *N.glaciei*) group have been pooled. The only diatom from the “centrics” group shown here is *Thalassiosira antarctica*, as valves of other species were very rare. Only those groups contributing more than 5% of total valve abundance in at least one sample are shown. The mooring was deployed from 25 January 2005 (arrow) until 17 December 2006 (not shown). Where no species abundance is indicated, sediment accumulation was too low to permit diatom analysis. The latter half of the deployment period is not shown, again due to insufficient sediment accumulation

nutrient input associated with mixing events, estimates of cumulative nutrient drawdown (calculated from the reduction in salinity-normalized  $[\text{NO}_3^-]$  relative to the previous sample concentration) indicate much greater nutrient use in the first season ( $\sim 100 \mu\text{mol L}^{-1}$  vs.  $\sim 12$  and  $\sim 34 \mu\text{mol L}^{-1}$  in the second and third seasons, respectively; Table 2). This likely reflects the high degree of mixing and thus greater nutrient supply to surface waters in the first season. The low average salinity and low nutrient drawdown in the second season coinciding with the highest levels of chl *a* (Fig. 2) suggests that the highest standing stocks occur when stratification is greatest. Limited vertical mixing promotes high biomass by concentrating phytoplankton within the well-lit surface layer and by reducing sedimentation (Garibotti et al. 2003b; Smith and Sakshaug 1990). In situ chl *a* data show high concentrations in the

**Table 2** Average primary production in Ryder Bay evaluated by three proxies, chl *a*, suspended particulate matter (SPM), particulate organic carbon (POC), and carbon export

Primary productivity proxy	2004–2005	2005–2006	2006–2007
Mean chl <i>a</i> ( $\mu\text{g L}^{-1}$ )	15.31	17.06	9.04
Mean SPM ( $\text{mg L}^{-1}$ )	14.1	14.9	14.4
Mean POC ( $\mu\text{mol L}^{-1}$ )	43.7	38.5	41.5
Carbon export ( $\text{g C m}^{-2}$ )	2.1	0.71	No data
Cumulative nutrient use ( $\mu\text{mol N L}^{-1}$ )	100	12	34

upper water column (above  $\sim 60$  m; Clarke et al. 2008), a pattern typical of Antarctic coastal regions (Garibotti et al. 2003b; Holm-Hansen et al. 1989; Smith et al. 1998). However, neither SPM levels nor [POC] were comparatively greater during the second season (Fig. 2, Table 2). On the contrary, mean [POC] in the second season was  $38.5 \mu\text{mol L}^{-1}$ , compared to  $43.7$  and  $41.5 \mu\text{mol L}^{-1}$  during the first and third seasons, respectively (Table 2). Low levels of both SPM and POC during this season (Fig. 2, Table 2), and thus lower C:chl ratios, imply that chl *a* was retained at the surface as a result of stratification, but was accompanied by lower rates of biological productivity than during other study seasons. Sediment trap data indicate considerably less export during the second season compared to the first season ( $0.71$  vs.  $2.1 \text{ g C m}^{-2}$ ; Table 2), in keeping with lower [POC] in the water column, but contrasted by higher peak chl *a* concentrations.

#### Phytoplankton community composition

Both spatial (e.g. Fiala et al. 1998; Garibotti et al. 2005; Varela et al. 2002) and temporal (e.g. Holm-Hansen and Mitchell 1991; Moline and Prezelin 1996; Smith et al. 1998) variability are common features of microalgal assemblages in the Southern Ocean; nevertheless, sea-ice dynamics have been identified as a significant factor governing both photosynthetic biomass and community composition (Garibotti et al. 2003b; Smith et al. 1998, 2000).

This study is in agreement with Kopczynska (1992) and Arrigo et al. (1999) that deep mixing ( $>10$  m in Ryder Bay) promotes growth of *P. antarctica* as a result of the positive buoyancy of its mucilaginous form (Leventer and Dunbar 1996), and an ability to adapt to a large range of irradiance levels (Arrigo et al. 1999). The two large increases in *Phaeocystis* abundance (12 December and 4 January; Fig. 3) immediately followed the two deepest MLD events during the sampling period (9 and 29 December). Conversely, a stratified water column favours diatoms, which are better adapted to higher light levels and would otherwise sink quickly due to their silica frustules,

such that they accumulate preferentially in a stratified water column (Arrigo et al. 1999). In the WAP region, water column stability variations, from sea-ice melting and wind activity, regulate not only phytoplankton standing stock, but also species composition.

Large phytoplankton (>20 µm) are the primary contributors to algal stocks in the Marguerite Bay area (Garibotti et al. 2003b, 2005) and in Ryder Bay (Clarke et al. 2008). As the majority of large cells in this area are diatoms, it follows that greater biomass is found in regions favouring diatom growth. Average diatom contribution to biomass measured here was 78% (±16%, standard deviation), in agreement with previous studies (Garibotti et al. 2005). The dominance of diatoms versus prymnesiophytes along the WAP has particular implications for the ratios of nutrient drawdown and carbon export. Total diatom abundance in sediment traps varies approximately with total C export (data not shown), indicating diatom-dominated C export, although Arrigo et al. (1999) show a greater potential for C export from *Phaeocystis*-dominated regimes in the Ross Sea. Thus, the interaction of sea-ice and glacial melt water input on algal group dynamics and subsequent C export merits further investigation, especially in light of the recent climate change in the WAP region (Clarke et al. 2008). Projections of changing sea-ice regimes (Arrigo et al. 1999; Clarke et al. 2008) and melt water fluxes (Meredith et al. 2008; Torinesi et al. 2003) with continued warming suggest less melt water input to the WAP region, which could favour a shift towards *Phaeocystis*-dominated assemblages and affect the efficiency of the biological pump.

#### Diatom community composition

Diatom assemblages showed progression within each season, although the species associated with the early, middle and late stages of the bloom varied between years. Stages of the growing season are operationally defined here as: up to the first peak in [chl *a*] (early), between [chl *a*] maxima (middle), and from the second [chl *a*] peak through senescence (late). In the third season, chl *a* continued at elevated levels well into March (Fig. 2), but sampling concluded at the end of January. Thus the final season is missing the late stage of seasonal succession, although the time series covers 3 years of both early and middle stages of the growing period. While [chl *a*] began to increase before the initiation of sampling in the first season, the first sample is considered 'early' season, as it corresponds to the first pulse of chl *a* seen in the RaTS data (Fig. 4a).

#### Early season diatoms

In both the first and second seasons, biomass of *Minidiscus chilensis* was initially very high (Fig. 4a). *Minidiscus*

*chilensis* has been observed at very high abundances in open waters of Bransfield Strait where it occurred early in the growing season (Kang et al. 2003). Thus *M. chilensis* is characteristic of the early phase of summer production in WAP waters, although not necessarily present at high abundances in all years.

Other early biomass contributors were *Chaetoceros neglectus* and *Chaetoceros socialis*, species of the subgenus *Hyalochaeta* representing up to 23% of diatom biomass (Fig. 5a). In the second season, the peak in *Hyalochaeta* biomass coincided with the first chl *a* maximum. Relative contributions to diatom biomass dropped to <3%, although the decline was earlier in the second season. In the third season, the *Hyalochaeta* subgenus reached maximum abundance just following the January 11 chl *a* maximum. *Chaetoceros* spp. have been associated with the early phase of production following sea-ice retreat in Marguerite Bay (Garibotti et al. 2005). Farther north in the WAP region, *C. socialis* was the most abundant species present in December and January (Varela et al. 2002). *Chaetoceros neglectus* is a characteristic spring species in the Weddell Sea (Bianchi et al. 1992), indicating that *Hyalochaeta* spp. are indicative of early to mid-season diatom assemblages on both sides of the Antarctic Peninsula.

As an early season group, *Hyalochaeta* spp. would be expected to exhibit very high growth rates, allowing them to quickly build up high biomass in nutrient-rich spring surface waters. The greater extent of nutrient injections in the first and third seasons (Fig. 2) may explain why this group remained abundant in the water column longer in these years. Conversely, low nutrient replenishment (2005–2006) may have led to *Hyalochaeta* spp. being outcompeted by those better adapted to lower nutrient conditions.

In the second season, biomass was initially dominated by the genus *Fragilariopsis* (Fig. 4b). Species from this genus are associated with different environments, but although some of the open ocean *F. kerguelensis* group (as defined by Crosta et al. 2005) were identified, they remained a very small constituent (<1.2%) of diatom biomass. Variation in *Fragilariopsis* abundance and biomass was due to changes in abundance of *F. curta* and *F. cylindrus*, both species indicative of seasonal sea-ice zones (Gersonde and Zielinski 2000). The first sample (23 December 2005) was taken during the initial increase in chl *a* seen in the second season, and at the time of sampling Ryder Bay was still fully ice covered. It is possible that the initial under-ice bloom is routinely dominated by *F. curta* spp., but was not captured by our sampling regime during the first and third seasons, as sea-ice did not persist as late into the spring during those years. This is supported by the percentages of *F. curta* spp. in the RaTS sediment traps, which were very similar between the first and second

seasons, indicating that *F. curta* spp. must have indeed been abundant in surface waters at some point. Unfortunately, SEM does not allow analysis of live versus empty diatom cells, so we are unable to confirm that the high level of *F. curta* spp. biomass in this sample was due to a viable surface community rather than the release of biogenic material accumulated over winter in sea-ice.

The differences in timing of sea-ice break out (much later in 2005–2006) as well as style of breakout (persistent patchy cover in 2005–2006 and 2006–2007 versus a rapid shift to ice-free conditions in 2004–2005) are coupled with high variability in assemblages and seasonal succession. Rapid ice breakout in 2004–2005 was associated with lower proportions of “Centrics” during the early season compared with our other two study years. However, the considerable interannual variability evident in the diatom assemblages presented here (Fig. 4) and in absence of previous data regarding species composition in Ryder Bay, prevents confirmation of any recurrent patterns in response to the style of sea-ice breakout. Additional information is necessary to fully explore the relationship between sea-ice breakout and species assemblages in this region.

#### Mid-season diatoms

*Odontella weissflogii* (Fig. 4) was consistently seen in mid-season assemblages, and has been observed at moderate to high absolute abundances (Froneman et al. 1997; Theriot and Fryxell 1985) and biomass (Garibotti et al. 2005; Varela et al. 2002) throughout the WAP region, often associated with sea-ice (Palmisano and Garrison 1993). Reports of *Odontella weissflogii* in low-salinity waters where sea-ice melt was recent (Gomi et al. 2005) suggest it is well adapted to stratified conditions. Water samples dominated by *O. weissflogii* exhibit low photosynthetic rate versus irradiance, characteristic of species adapted to high-light environments (Sakshaug and Holm-Hansen 1986).

The 2006–2007 season shows a nutrient injection event into well-stratified waters on 22 January, followed by a 7-fold increase in *O. weissflogii* abundance (from 3 to 15% of diatom biomass; Fig. 4c). In all seasons, *O. weissflogii* increases in abundance only after the water column has developed a strong density gradient. The much greater relative contribution to diatom biomass in the first season may reflect the greater degree of nutrient inputs during that season, suggesting that *O. weissflogii* requires both high-light levels from stratification and frequent nutrient replenishment to build up high biomass levels. Previous studies have been unable to establish significant correlations between either salinity/temperature and *O. weissflogii* (Froneman et al. 1997) or nutrients and total phytoplankton assemblages (Priddle et al. 1986; Whitehouse et al. 1993), which may be related to the interaction between these

factors in creating favourable environments for *O. weissflogii* and other bloom-forming Antarctic diatoms.

#### Late-season diatoms

A notable feature of the second season diatom assemblage is the near monospecific community seen at the end of the growing period, where >90% of diatom biomass is attributable to *P. inermis* (Fig. 4b). Aside from its taxonomy (Jordan et al. 1991) and an ability to survive prolonged periods of darkness (Peters and Thomas 1996), relatively little is known regarding this species, particularly its distribution and ecological preferences (Maddison et al. 2006). There have been several studies noting *P. inermis* amongst the diatom assemblage in the Southern Ocean (e.g., Kang et al. 2001; Ligowski et al. 1992; Pike et al. 2008), although at prevalence (<5% relative abundance, up to 11% biomass) than those reported here (41% relative abundance, >90% biomass). One account, from the Weddell Sea, documents an assemblage dominated by a *Proboscia* species, although in this case it was the closely related species *Rhizosolenia* (= *Proboscia*) *alata* Brightwell (Estrada and Delgado 1990), a species typical of the late stage in annual diatom succession (Margalef 1958), with Hart (1942) linking it to the post-bloom period. Brichta and Nothig (2003) report an assemblage dominated by *P. inermis* in the Bellinghousen Sea, but only 21% of phytoplankton C was attributed to this species, far below the ~90% of diatom biomass seen in Ryder Bay.

Sediment records occasionally note high abundances of *Proboscia* spp., which may include *Proboscia alata* or *Proboscia truncata*, but where *P. inermis* specifically has been observed it is reported to co-occur with high abundances of *Rhizosolenia antennata* f. *semispina* (Stickley et al. 2005). Only a single cell from this genus was observed in Ryder Bay, although as a “shade flora” (Kemp et al. 2000) it is possible that this species was present deeper in the water column. This co-occurrence pattern has been suggested to indicate warmer, oligotrophic water conditions (Stickley et al. 2005). Our [NO<sub>3</sub><sup>-</sup>] data strongly support the connection between low nutrient availability and high *P. inermis* biomass, as the highly stable water column with no nutrient injections resulted in an extended period of nutrient depletion unique to the second season. Third season data show a maximum in *P. inermis* abundance occurring on 18 January, coinciding with the nitrate minimum (5.83 μM) observed during that season (Figs. 2 and 4c). Further, Kemp et al. (2000) list *Proboscia* spp. as “shade flora” that may be adapted to low light, or may regulate buoyancy to move between shallow high-light and deeper high-nutrient areas of the water column. However, temperature profiles indicate that the second season was actually 0.2–0.6°C colder than the first and third seasons,

respectively, although these differences were not statistically significant ( $p > 0.05$ , 2-sample  $t$  test), showing that presence of *P. inermis* is not necessarily indicative of warmer temperatures.

Maddison et al. (2006) observed *P. inermis* in sediments from the East Antarctic Margin, where the hypothesized signal of warmer oligotrophic waters (Stickley et al. 2005) was seemingly at odds with observations of other species suggesting the presence of sea-ice (*Fragilariopsis curta* and *cylindrus*). Our record of high *P. inermis* biomass in a seasonally ice-covered environment shows that this species is not necessarily associated with warmer water temperatures, but rather with a period of low nutrient concentration (<15  $\mu\text{M}$  nitrate, for 1–9 weeks in this study). Given this documentation of occurrence in a water column stratified due to sea-ice melt, presence of *P. inermis* in the sedimentary record is consistent with a seasonal sea-ice environment.

#### Sediment diatom assemblages

Diatom species counts in sediment traps show similar species dominating traps and surface waters. The species not observed in traps that were present in surface waters are assumed to not have escaped grazing or remineralization and thus were not exported to depth. The percent contributions of some species to the total valve abundance were lower in the deeper sediment trap (Fig. 6), suggesting that these groups (i.e., *Proboscia* spp., *Pseudonitzschia* spp.) are remineralized more easily. Conversely, *Fragilariopsis kerguelensis* and *Chaetoceros* resting spores which are heavily silicified show increases in relative abundance, consistent with slower dissolution rates and more efficient export of organic matter to deeper waters. This highlights the role of silicification in export production, as larger, thinly silicified species may be more likely to be remineralized in the upper water column.

The presence of several sea-ice indicator species (*Fragilariopsis curta* and *F. cylindrus*, Gersonde and Zielinski 2000; Ligowski et al. 2002; Riaux-Gobin et al. 2003; *Chaetoceros (Hyalochaeta)* spp., Garrison and Buck 1986; Roberts et al. 2007; *Thalassiosira antarctica*, Grossi and Sullivan 1985; Smetacek et al. 1992) at the beginning of the second season imply that sea-ice material may have accumulated in the deeper trap prior to the start of the open water spring bloom. As there was not enough material to conduct winter diatom assemblage analysis, it is unknown if these species are exported during full sea-ice coverage. Export of organic matter in the Southern Ocean generally occurs in short bursts corresponding to sea-ice retreat (Arrigo and Thomas 2004), hence it is likely that the high levels of sea-ice diatoms resulted from build up of biomass

within the sea-ice over winter, which was released after the ice broke out on 25 December 2005.

#### Conclusions

Total phytoplankton abundance and biomass in Ryder Bay are comparable to similar studies from the WAP region, and display a typical growth pattern of two distinct chlorophyll peaks. The prymnesiophyte *P. antarctica* was often numerically dominant, especially after moderate mixing (>10 m). In keeping with most Southern Ocean areas during periods of elevated productivity, large diatoms comprised the largest portion of photosynthetic biomass.

While there was significant variation between diatom assemblages between seasons, some species were seen to correspond to certain stages of seasonal succession. High relative abundance of *Minidiscus chilensis* was limited to the early phase of summer productivity, while increases in *Chaetoceros (Hyalochaeta)* spp. biomass was attributed to nutrient injection events. Abundance of the large biddulphoid diatom *Odontella weissflogii* also varied with nutrient levels, but also required development of a stable, stratified water column.

This study documents an extensive bloom of the rhizosolenioid diatom *P. inermis*, which we believe to be the first report of such an occurrence. This species was responsible for >90% of diatom biomass during the late-summer chlorophyll peak of the 2005–2006 season, and is connected with areas of near-complete nutrient drawdown. *P. inermis* has been associated with incursions of warmer, oligotrophic waters (Stickley et al. 2005), and seasonal sea-ice zones (Maddison et al. 2006). This has implications for the interpretation of sedimentary records, as the bloom event observed here did not coincide with higher temperatures, indicating that warmer surface waters do not always accompany *Proboscia* blooms.

Water column stability is a primary determinant of primary production in this region (Garibotti et al. 2003b; Smith et al. 1998, 2000), and it was noted that the season displaying highest average chlorophyll *a* levels (2005–2006) also exhibited the lowest average salinity above 15 m. Given the current, documented warming trend along the Antarctic Peninsula (Clarke et al. 2007; Meredith and King 2005; Stammerjohn et al. 2008a, b), future work constraining the impact of sea-ice variability on primary production and export is vital to projections of ecosystem and carbon cycle response to predicted climate change.

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## Appendix I

See Table 3.

**Table 3** Mean values of linear measurements ( $\mu\text{m}$ ), surface area (SA;  $\mu\text{m}^2$ ), biovolume (V;  $\mu\text{m}^3$ ), surface area to volume ratio (SA:V;  $\mu\text{m}^2 \mu\text{m}^{-3}$ ) and carbon biomass ( $\text{pg C cell}^{-1}$ ) of phytoplankton species observed in this study

Species	D	P	A	T	Sh	SA	V	SA:V	Biomass
Taxon									
Diatoms									
<i>Actinocyclus actinochilus</i>	36	17			C	4,000	17,000	0.235	883.5
<i>Amphiprora kufferathi</i>		3	58	9	RB	1,400	1,500	0.933	167.1
<i>Asteromphalus hookeri</i>	58	7			C	6,500	18,000	0.361	1032.3
<i>Banquisia belgicae</i>		25	105	10	RB	2,700	6,600	0.409	463.8
<i>Berkeleya</i> spp	13	105			D	3,700	6,700	0.552	433.8
<i>Chaetoceros neglectus</i>		11	9.0	8.7	EP	550	1,300	0.423	111.7
<i>C. simplex</i>		4.7	4.7	2.1	EP	94	75	1.253	11.5
<i>C. socialis</i>		8.7	7.5	16	EP	600	830	0.723	82.9
<i>C.</i> subgenus <i>Hyalochaeta</i> resting spores		5	3	3	EP	59	32	1.844	5.40
<i>C. atlanticus</i>		18	12	11	EP	1,100	3,700	0.297	270.2
<i>C. convolutus</i>		19	12	7	EP	850	2,500	0.340	211.2
<i>C. criophilus</i>		18	13	7	EP	860	2,600	0.331	214.1
<i>C. dictyota</i>		26	13	12	EP	430	560	0.768	61.2
<i>C. flexuosus</i>		6.0	3.2	20	EP	2,000	6,400	0.313	457.7
<i>Corethron pennatum</i>	47	149			C	25,000	250,000	0.100	5477.2
<i>Cylindrotheca closterium</i>		101	51	25	DC	24,000	200,000	0.120	5018.8
<i>C. closterium</i> , small morphotype		67	7	4	DC	630	780	0.808	85.6
<i>Dactylisolen</i> cf. <i>antarcticus</i>	50	*			C	160	2,000	0.080	65.0
<i>Ephemera planamembranacea</i>		3	60	8	EP	930	1,140	0.816	121.0
<i>Eucampia antarctica</i> var. <i>antarctica</i>					Com	9,100	29,000	0.314	1767.1
<i>Fragilariopsis curta</i>		3.8	12	4.1	RRP	190	140	1.357	20.2
<i>F. cylindrus</i>		3.1	10	2.2	RRP	75	20	3.750	3.55
<i>F. kerguelensis</i>		4.2	19	4.8	EP	340	300	1.133	39.8
<i>F. obliquecostata</i>		3.5	21	3.3	RRP	310	250	1.240	33.8
<i>F. ritscheri</i>		4.4	21	4.3	EP	350	310	1.129	41.0
<i>F. sublinearis</i>		3.9	22	3.5	RRP	340	290	1.172	38.6
<i>F. vanheurkii</i>		3.2	53	2.6	RRP	450	220	2.045	30.2
<i>Haslea trompii</i>		12	90	7	EP	3,200	6,200	0.516	384.8
<i>Membraneis challengeri</i>		6	59	17	EP	2,400	4,700	0.511	298.1
<i>Minidiscus chilensis</i>	5.8	4.3			C	120	120	1.000	19.1
<i>Navicula directa</i>		5.9	65	5	EP	1,300	1,500	0.867	162.2
<i>N. gelida</i>		5	16	3	EP	230	190	1.211	26.5
<i>N. glaciei</i>		4	22	3	EP	290	210	1.381	28.9
<i>Odontella weissflogii</i>		66	49	30	EP	10,500	76,000	0.138	2317.8
<i>Porosira glacialis</i>	31		14		C	2,900	10,700	0.271	649.5
<i>P. pseudodenticulata</i>	29		17		C	2,900	10,700	0.271	649.5
<i>Proboscia alata</i>	14	200			C	9,000	29,000	0.310	1752.1
<i>P. inermis</i>	12	248			C	9,700	29,000	0.335	1861.5
<i>P. truncata</i>	25	248			C	20,500	122,000	0.168	4031.9
<i>Pseudogomphonema kamtschaticum</i>		12	28	4	Com	500	450	1.111	57.1

**Table 3** continued

Species	D	P	A	T	Sh	SA	V	SA:V	Biomass
<i>Pseudo-nitzschia lineola</i>		3.4	89.5	3.8	RB	1,400	1,300	1.077	147.1
<i>P. turgidula</i>		3.8	105	4.5	RB	1,700	1,700	1.000	186.9
<i>Pseudostaurosira brevisstrata</i>		8	14	4.3	EP	210	340	0.618	33.1
<i>Stellarima microtrias</i>	52	21			C	7,400	42,000	0.176	1609.3
<i>Thalassiosira ambigua</i>	16	8			C	800	1,600	0.500	153.1
<i>T. antarctica</i>	48	26			C	7,600	47,000	0.162	1677.2
<i>T. dichotomica</i>	12	5.9			C	380	500	0.760	54.8
<i>T. frenguelli</i>	15	7.3			C	650	1,200	0.542	92.2
<i>T. gracilis</i> var. <i>gracilis</i>	17	6.5			C	800	1,500	0.533	111.2
<i>T. gracilis</i> var. <i>expecta</i>	15	6.4			C	680	1,200	0.567	95.4
<i>T. gravida</i>	14	7.8			C	660	1,200	0.550	93.3
<i>T. lentiginosa</i>	72	30			C	14,500	116,000	0.125	3168.1
<i>T. ritscheri</i>	49	24			C	5,600	45,000	0.124	1357.5
<i>Thalassiothrix antarctica</i>		*	6	6	RB	24	36	0.667	4.73
<b>Chrysophytes</b>									
<i>Tetraparma pelagica</i>	2.6				S	21	9.2	2.283	2.02
<i>Triparma columacea</i>	2.7				S	22	9.9	2.222	2.17
<b>Silicoflagellates</b>									
<i>Distephanus speculum</i>	23				S	1,700	6,500	0.262	964.1
<b>Dinoflagellates</b>									
<i>Gyrodinium lachryma</i>	22	13			Com	560	1,200	0.467	197.0
<i>Podolampas antarctica</i>	94	17			Com	2,700	7,600	0.355	1116.8
<i>Polarella glacialis</i> resting spores	9				½ S	200	190	1.053	34.8
<i>Protoperidinium</i> spp.	100	44			Com	21,300	219,000	0.097	26303.7
<i>Protoperidinium</i> , small spp.	40	29			Com	5,300	18,000	0.294	2511.6
<i>Scripsiella troichoidea</i> resting spores	8.6				S	230	330	0.697	58.5
<b>Prymnesiophytes</b>									
<i>Phaeocystis</i> cf. <i>antarctica</i>	5				S	78	65	1.200	13.6

\*Refers to dimensions that were often larger than the field of view, or species that were not found intact. In such cases a measurement was made of each fragment to calculate area and volume in each case, but the mean is not presented here as it does not reflect the average value of that axis  
*D* Diameter, *P* perivalvar axis, *A* apical axis, *T* transapical axis. Shapes (Sh) were used to estimate volume from linear dimensions: *C* cylinder, *DC* double cone, *EP* ellipse based prism, *PB* rectangular box, *RRP* rounded rectangular prism, *S* sphere and *Com* complex

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