

A comparison of epiphytic diatom communities on *Plocamium cartilagineum* (Plocamiales, Florideophyceae) from two Antarctic areas

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Abstract Our understanding of diatoms, one of the most important Antarctic primary producers, is based mostly on investigations of plankton, sea-ice, and sediment samples. Herein, we contribute to the limited research devoted to benthic Antarctic diatoms by presenting a study on epiphytic diatom communities sampled in two remote Antarctic regions: Admiralty Bay (maritime Antarctica, Antarctic Peninsula) and Terra Nova Bay (Ross Sea). Recent studies have demonstrated that the most critical factor for the local epiphytic diatom communities was the nature of the substrate. In order to eliminate this factor so we could evaluate other potential controls, we sampled epiphytic diatoms from only one substrate that is common to both regions: the macroalgae *Plocamium cartilagineum* (L.) Dixon. Thalli of *P. cartilagineum* and their associated microalgal community was collected in January 2011 (Admiralty Bay) and 2012 (Terra Nova Bay) from a water depth of 5–25 m. Dehydrated macroalgal pieces were

placed on stubs and sputter-coated, which allowed observation of diatoms attached to the substrate in their original position using scanning electron microscopy. A total of 72 taxa were observed, of which 31 taxa were common to both regions. Cell abundance and diatom growth form dominance were significantly different in Admiralty Bay and Terra Nova Bay samples. Total diatom abundance was higher in Admiralty Bay samples, dominated by adnate diatoms (*Cocconeis* spp.), but the number of taxa found as well as the values of ecological indices were higher for samples from the Ross Sea, where motile forms were dominant (*Navicula* spp.). Our results suggest that Antarctic shallow-water benthic habitats may present a high degree of microniche heterogeneity and highlight the need of fine-scale analyses in microbial studies. We also suggest grazers as a factor that contributes greatly to the observed differences.

Keywords Antarctic diatoms · Epiphytes · Grazing · Growth form · *Plocamium cartilagineum* · SEM

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Introduction

After decades of extensive research in the Antarctic, it has become clear that throughout much of this region, ecosystem processes are dominated by microscopic organisms (Vincent 2000; Stanish et al. 2013; Wilkins et al. 2013). In the highly productive coastal region of Antarctica they have an important role in biomass and energy flow (Nedwell et al. 1993; Archer et al. 1996; Cattaneo-Vietti et al. 1999; Vincent 2004; Bowman 2013; Wilkins et al. 2013).

Although our current understanding of Southern Ocean diatoms is based mainly on studies of plankton and sea-ice samples, and sediment cores, our knowledge of epiphytic

diatoms on macroalgae, and benthic diatoms in general, is very scarce (Thomas and Jiang 1986; Al-Handal and Wulff 2008a, b; Wulff et al. 2011; Majewska et al. 2013a, b). While diatom analysis of sediments is one of the most important paleoecological techniques for reconstructing past climate and paleoenvironmental changes in Antarctica (Spaulding et al. 2010; Esper and Gersonde 2014; Lyon and Mock 2014), benthic Antarctic species are typically identified only to the genus level, and thus contribute little to paleoclimatic or paleogeographic interpretations (Wulff et al. 2011). The paucity of data on benthic taxa from fossil records not only makes the identification of living species even more challenging, but also limits our ability to deduce patterns of their distribution and dispersal, biodiversity, and identify potential invasive species introduced to Antarctica (Bargagli 2004; Tin et al. 2009; Barbara et al. 2013; Lazarus et al. 2014; Schoefs 2014).

Diatoms are excellent indicators of various oceanographic conditions and environmental stress, including different types of pollution, and climate change (e.g., Palmer and Abbott 1986; Dixit et al. 1992; Sudhakar et al. 1994; Bogaczewicz-Adamczak et al. 2001; Abrantes et al. 2007; Spaulding et al. 2010). It is therefore likely that they could be used effectively for monitoring the changes in Antarctic coastal zones, which may be the most sensitive to human impact (Bargagli 2004). The use of planktonic species, however, creates a serious disadvantage, since these communities are not always truly autochthonous, as their dispersal depends on the water currents and winds, and may be mixed with detached allochthonous cells of benthic origin (Ahn et al. 1997). These handicaps are negligible in case of sessile epiphytic communities, because their composition is a direct result of the combination of environmental factors prevailing at the sampling site. For the same reason, epiphytic diatoms may provide the most reliable information about diatom biogeography, shedding light on their global distributions and habitat preferences.

We present a study on epiphytic diatoms present on the common red alga, *Plocamium cartilagineum* (Linnaeus) Dixon, from two zonally distinct regions of the Antarctic: the maritime Admiralty Bay, King George Island and the continental Terra Nova Bay, Ross Sea. This project sought to address the shortcomings in the scientific literature concerning Antarctic epiphytic diatoms, their relationships, and interactions with the surrounding microenvironment, their identification, consistent with application of taxonomic distinctions, and understanding of their distribution in the modern system that then might be applied to the paleo-records or an efficient environmental monitoring system. Therefore, the main objectives of this paper were to describe in detail the epiphytic diatom community structure and composition, to determine the diatom

distribution patterns and to indicate differences among diatom communities from the two Antarctic areas.

Materials and methods

Study area and samples collection

Thalli of *P. cartilagineum* were collected from December 2010 to February 2011 from Admiralty Bay, King George Island, South Shetland Islands and in January 2012 from Terra Nova Bay in the Ross Sea by SCUBA diving down to 25 m water depths.

Admiralty Bay is a fjord-like bay (ca. 122 km²) with a maximum depth of ca. 535 m (Siciński et al. 2011). Its central basin splits into three inlets (Ezcurra, Mackellar, and Martel Inlet) and opens southwards to Bransfield Strait. Climate here is influenced by intense cyclones moving mainly in an easterly direction and is typical of the maritime Antarctic (Rakusa-Suszczewski 1995a, b; Kuklinski and Balazy 2014). Strong fluctuations characterize both wind and current velocity and directions (Robakiewicz and Rakusa-Suszczewski 1999). Due to the wide connection with Bransfield Strait water of the bay is well mixed and oxygenated (Pruszek 1980). It is influenced by warmer and less saline water originating from the Bellingshausen Sea, especially in summer, and colder and more saline water from the Weddell Sea, in winter (Tokarczyk 1987). Annually, surface water temperature and salinity in the central part of Admiralty Bay vary from −1.77 to 1.76 °C and 33.41 to 33.97 PSU (Lipski 1987; Sarukhanyan and Tokarczyk 1988). Local hydrodynamics are influenced by extreme seafloor heterogeneity that has been altered by local tectonics, geology, and glacial process (Siciński et al. 2011). High concentrations of suspended terrigenous sediment are observed in summer, especially near glacier fronts, and a wide range of sediments sizes, from clay to gravel, cover the seafloor (Rakusa-Suszczewski 1995b; Siciński et al. 2011). Macroalgae cover ca. 30 % of the bottom area of Admiralty Bay (Zieliński 1990; Nedzarek and Rakusa-Suszczewski 2004; Oliveira et al. 2009).

Red alga *P. cartilagineum* was observed at four out of the 16 sites, and these were sampled (see Fig. 1 and supplemental material in Table S1). Water temperature was measured at two sites (3 and 4) every 10 min at 6, 15, and 20-m water depth using HOBO data loggers (Onset Computer Corp UA-002-64) for the month of January; salinity was not measured.

Terra Nova Bay, located between Cape Washington (74°39'S, 165°30'E) and Cape Russell (74°54'S, 163°54'E), has distinctive bio-chemo-physical features, not observed in the other regions of the Ross Sea (Cormaci 1995). Its surface water temperature can reach as high as 2 °C in

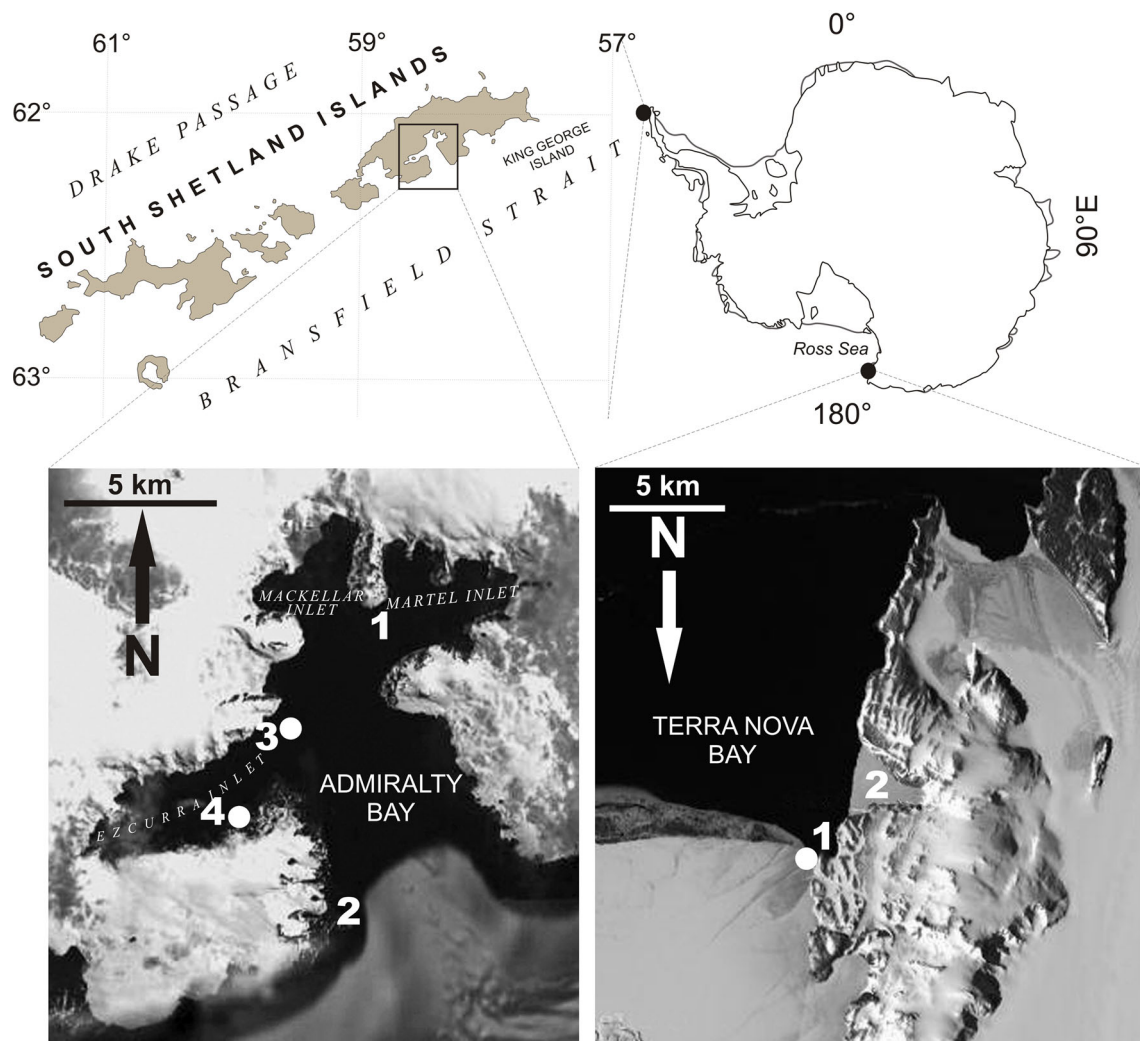


Fig. 1 Map of Antarctica showing sampling sites in Admiralty Bay, King George Island, South Shetland Islands and Terra Nova Bay, Ross Sea, with indication of salinity and temperature measurements (dots)

summer, at times inducing unstable density stratification and phytoplankton blooms (Cattaneo-Vietti et al. 1999; Pane et al. 2004; Baldi et al. 2010; Knuth and Cassano 2011). The seafloor within the bay is composed mainly of granitic rock and coarse sands and gravels. Fine-grained muddy sediment is present near Adelie Cove (Gambi et al. 1994; personal observation). Previous reports noted dense and expansive beds of macroalgae covering the Abbott Granite bottom in shallow regions of Terra Nova Bay (Cormaci et al. 1992; Gambi et al. 1994; Cormaci 1995; Cattaneo-Vietti et al. 1999; Skinner 2011).

In January 2012, 25 sites localized along the coast, from Tethys Bay to Adelie Cove ($74^{\circ}41.331'S$ – $74^{\circ}46.680'S$, $163^{\circ}59.223'E$ – $164^{\circ}09.000'E$), were sampled at various depths (see supplemental material in Table S1). Although two other rhodophytes, *Iridaea cordata* (Turner) Bory and *Phyllophora antarctica* Gepp and Gepp (Gambi et al. 1994;

Majewska et al. 2013a, b)—both well known from this area, were present at every sampling site, *P. cartilagineum* was observed at only two stations (see Fig. 1 and supplemental material in Table S1). Water temperature and salinity were measured at Station 1 three times per month from November 2011 to February 2012 using a CTD logger (Ocean Seven 304 CTD, Idronaut, Brughiero).

Sample preparation

Immediately after collecting, macroalgal samples were fixed in a 4 % formaldehyde solution in sea water. Prior to microscopical examination, replicates of three different specimens collected at each sampling site were chosen. Surface area covered by epiphytic sessile fauna was estimated by direct measurement with light microscopy and a square grid. The epiphytic diatom community growing on

the lower parts of the host plant might have been strongly altered due to mixing with epilithic, epipelic, and epipsammic diatoms from the seafloor surface. In order to avoid bias in the diatom community structure analysis, cauloids and rhizoids were not examined. Remaining parts of the thalli were cut into 1 cm² pieces, dehydrated in a series of aqueous alcohol solutions of increasing concentration (samples were immersed for 1 h in each of the alcohol solutions: 30, 40, 50, 60, 70, 80, 90, 95, and 100 %) and treated in a Critical Point Dryer (K850 EMITECH). Dried material was then mounted on aluminium stubs with adhesive carbon tape and sputter-coated with gold using a DESK V HP TSC Cold Sputter Coater.

SEM observations

Short sections of the red alga thalli with associated epiphytic diatoms were examined by scanning electron microscopy (SEM) using a Zeiss Supra 40. Diatoms were identified to the lowest possible taxonomic level and enumerated on a surface area of ca. 2 mm² of each replicate at magnifications ranging between 400× and 2,000×. Each taxon was divided into growth form groups: erect for cells attached to the alga by stalks, pads or peduncles; adnate for cells strongly adhering to the substrate with a limited motility; motile for cells moving on the alga, tube-dwelling for cells living in mucilage tubes; planktonic for true pelagic species; and plocon for cells loosely associated with the macroalgae. The observed specimens were identified using the following literature: Ehrenberg (1843), Van Heurck (1909), Mangin (1915), Peragallo (1921), Heiden and Kolbe (1928), Manguin (1957, 1960), Frenguelli and Orlando (1958), Hustedt (1958), Frenguelli (1960), Hasle (1965), Poulin et al. (1984a, b, c), Hasle et al. (1994), Romero and Rivera (1996), Cremer et al. (2003), Scott and Thomas (2005), Fernandes et al. (2007), Al-Handal et al. (2008, 2010), Al-Handal and Wulff (2008a, b), Cefarelli et al. (2010), Riaux-Gobin et al. (2011), and others.

Although diatom frustules in our study were not acid-cleaned, some specimens looked quite clean (see Figs. 2, 3), which might suggest that they were dead at the time of sampling. Indeed, in relatively rare cases that was most likely true. As dead (and not preserved) diatom cells detach from the substrate surface, their position on the substrate surface may indicate their physiological condition. On the other hand, many specimens that were alive at the time of sampling appeared to be clean while observing under SEM. We suggest this is because at the time of sample preservation these cells did not excrete any significant amounts of extracellular organic substances like e.g., exopolymeric substances (EPSs). Experience allows one to distinguish between frustules of long dead diatoms and those belonging

to live cells at the time of collection. Clean, empty, often broken frustules (most likely dead at the time of sampling) contributed less than 1 % of the all diatom frustules, and they were excluded from counts.

Statistical analyses

All statistical analyses were carried out using the PRIMER v6 computer program (Clarke and Gorley 2006). The Bray–Curtis similarity index, calculated on square root transformed species abundance (number of cells per 1 mm²) data, was used to create a matrix for cluster analysis. Although cluster analysis is not indispensable in terms of the statistical test, it reduces the dimensionality of the data and is performed to visualize patterns of resemblance among the tested elements. To test for significant differences between diatom communities from different locations, analysis of similarities (ANOSIM) was performed. Being performed on the similarity matrix itself, this non-parametric test does not depend on ordination dimensions or the number of samples. The *R* statistic calculated by ANOSIM lies in the range (−1, 1). *R* is equal to 1 only if all elements within the set are more similar to each other than any elements from any other set, and *R* approximates 0 if similarity between and within sets is the same on average. A value of −1 occurs when the most similar elements are all outside of the sets. The ANOSIM test was conducted on species and growth form abundance data. To determine the main diatom species responsible for major dissimilarities between groups, similarity percentage analysis (SIMPER) was performed. Ecological indices such as the Margalef's species richness *d* [$d = (S - 1) / (\log_e N)$, where *S* = number of species, *N* = number of individuals] and Shannon–Wiener diversity indices *H'* (\log_e) were computed for each of the samples.

Results

Physical parameters

The water temperature of the upper 20-m water column varied from 0.45 to 2.95 °C in Admiralty Bay and from 0.39 to 2.45 °C in Terra Nova Bay in January 2011 and 2012, with slightly warmer temperatures recorded in surface waters (Table 1). The range in water temperature variation was markedly higher at Station AB4 than Station AB3 in Admiralty Bay. Lower temperatures were noted in Terra Nova Bay at 25 m depth (−0.75 to 0.0 °C). Salinity was only measured in Terra Nova Bay in January 2012 and did not vary much through the water column (Table 1).

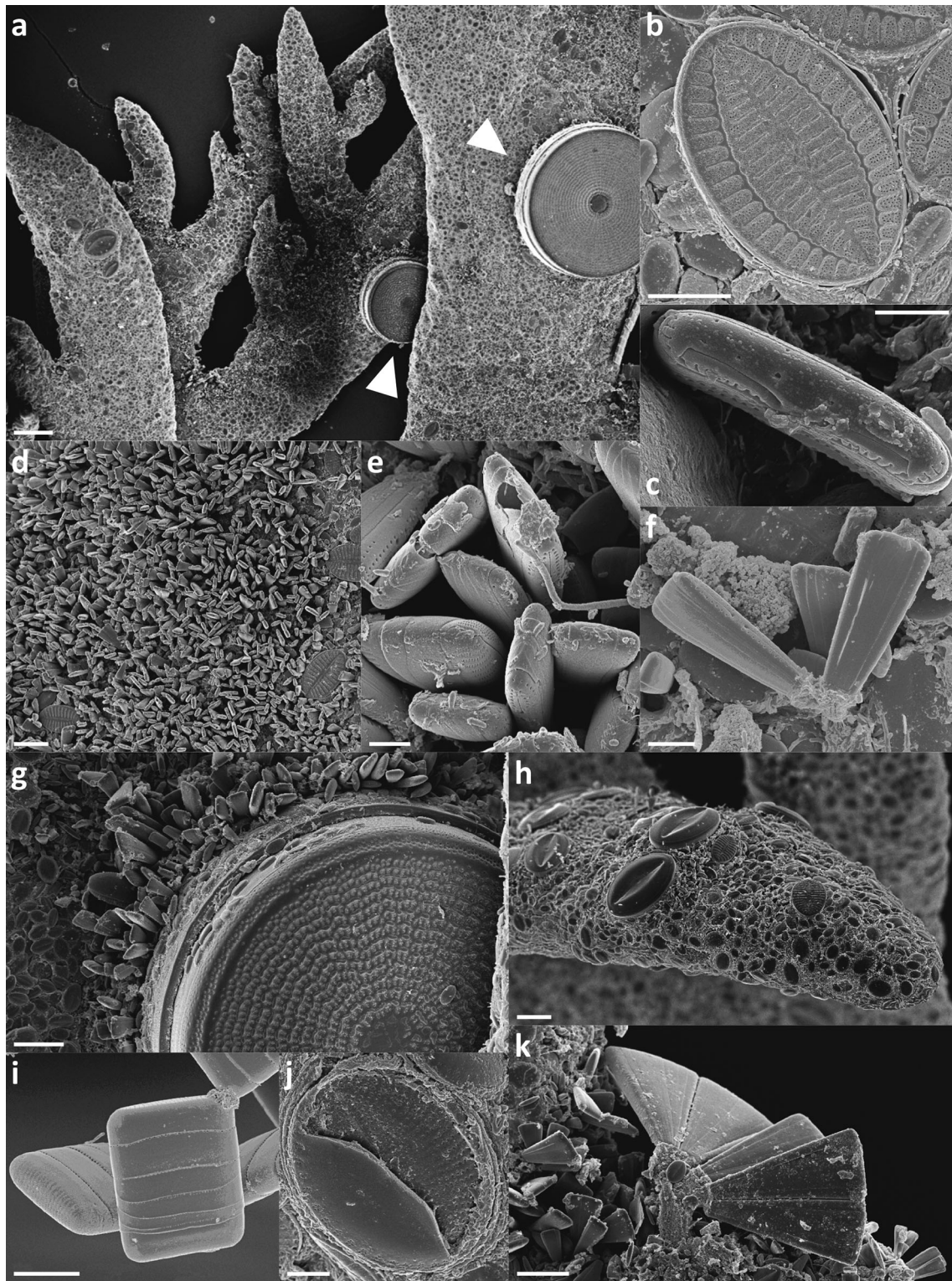


Fig. 2 Epiphytic diatom communities associated with *P. cartilagineum* in Admiralty Bay: **a** *Plocamium* thallus covered by compact crust of *Cocconeis* spp. and erect diatoms on the axes of the branches, with large cells of *Arachnoidiscus japonicus* (arrowheads). **b** External view of a raphless valve of *Cocconeis* sp. 1. **c** Cell of cf. *Amphora*.

d Erect diatoms. **e** Erect diatoms showing *Gomphonemopsis littoralis* and *Pseudogomphonema kamtschaticum*. **f** *Gomphonemopsis littoralis*. **g** Diatoms epiphytic on *A. japonicus*. **h** *Cocconeis* spp. **i** *Grammatophora antarctica*. **j** *Cocconeis dallmannii*. **k** *Licmophora antarctica*. Scale bars **c** 1 μm ; **e**, **f** 2 μm ; **i** 10 μm ; **b**, **d**, **g**, **h**, **k** 20 μm ; **a** 100 μm

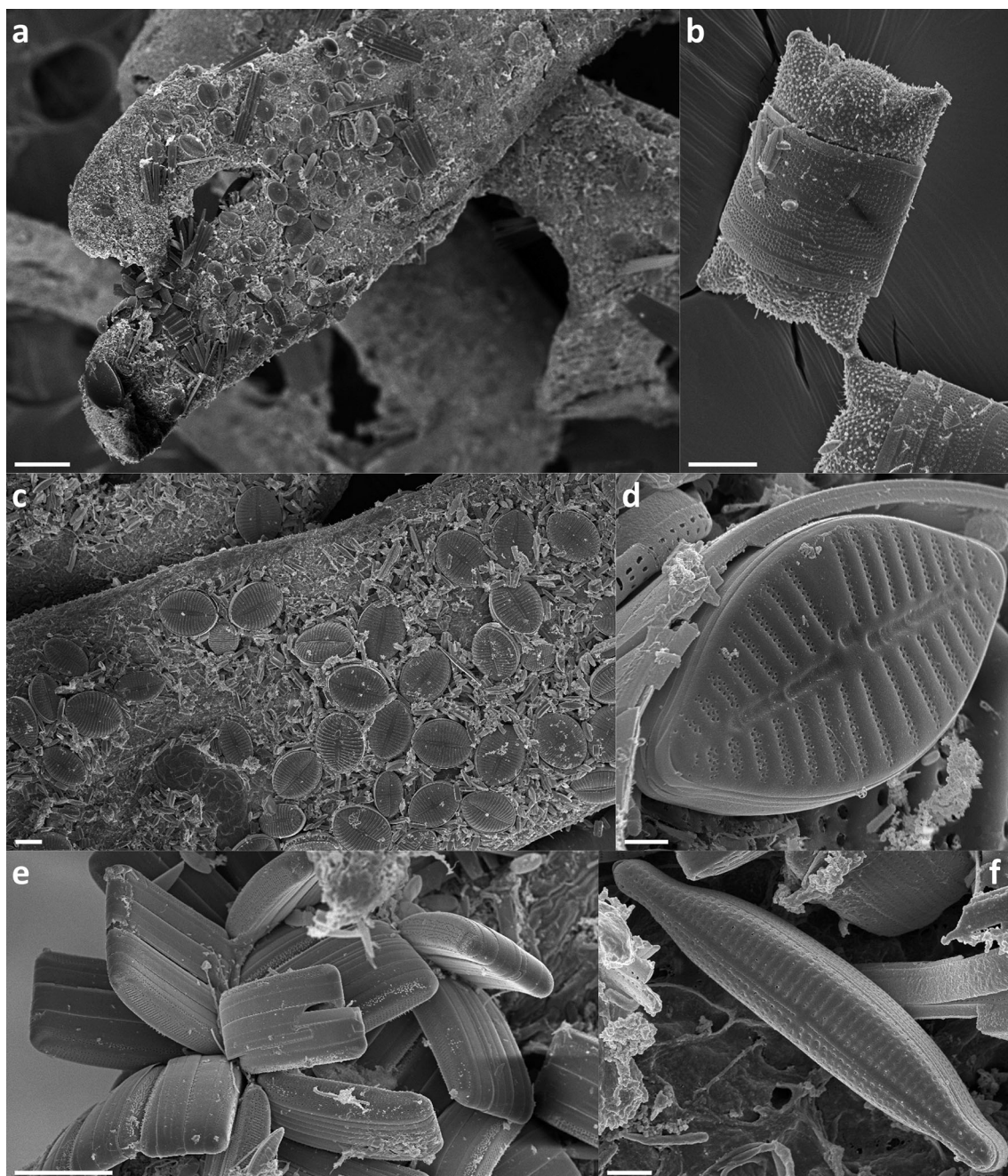


Fig. 3 Epiphytic diatom communities associated with *P. cartilagineum* in Terra Nova Bay: **a** *Plocamium* thallus showing patchy distribution of epiphytic diatoms. **b** *Odontella litigiosa*. **c** *Cocconeis fasciolata* and motile diatoms (*Navicula* spp., *Nitzschia* spp.).

d External view of rapheless valve of *Planothidium* cf. *dubium*. **e** *Grammatophora arcuata*. **f** Cell of cf. *Cymbella*. Scale bars **d**, **f** 1 µm; **b**, **c**, **e** 20 µm; **a** 100 µm

Species composition

A total of 72 diatom taxa (32 genera) were observed associated with the red alga *P. cartilagineum* in Admiralty Bay and Terra Nova Bay in the 2011 and 2012 austral summers (Table 2). Forty-six taxa were present in samples from Admiralty Bay and 57 in those from Terra Nova Bay.

Thirty-one taxa (18 genera) were common to both Antarctic regions, while 15 taxa (3 genera: *Arachnoidiscus*, see Figs. 2a, g, *Gomphonemopsis*, see Figs. 2d–g, and *Rhoicosphenia*) were observed only in Admiralty Bay, and 26 taxa (ten genera) in Terra Nova Bay. Among these, at least 29 taxa could not be assigned definitively to any of the known species (Table 2; Figs. 2b, c, 3f).

Table 1 Water temperature and salinity measured at various water depths at stations 3 and 4 in Admiralty Bay and at station 1 in Terra Nova Bay in January 2011 and 2012, respectively

Depth (m)	Admiralty Bay		Terra Nova Bay	
	Station 3	Station 4	Station 1	
	Temperature (°C)		Temperature (°C)	Salinity (PSU)
6	0.67–1.87	0.67–2.95	0.89–2.45	34.4–34.7
10	nd	nd	0.61–2.24	34.5–34.6
15	0.89–1.87	0.45–2.19	0.45–2.22	34.4–34.6
20	0.78–1.76	0.67–1.98	0.39–1.65	34.4–34.6
25	nd	nd	–0.75 to 0.0	34.4–34.6

nd no data

Among the 46 diatom taxa recorded from Admiralty Bay, only 16 taxa contributed more than 1 % of the cells in any of the examined samples, with cf. *Rhoicosphenia*, *Cocconeis dallmannii* Al-Handal, Riaux-Gobin, Romero and Wulff (Fig. 2j), *C. melchioroides* Al-Handal, Riaux-Gobin, Romero and Wulff, *Gomphonemopsis littoralis* (Hendey) Medlin (Figs. 2d–g), *Navicula perminuta* Grunow, and *Pseudogomphonema kamtschaticum* (Grunow) Medlin (Figs. 2d, e, g) making up >10 % of the total abundance. Eleven taxa exceeding 1 % of total abundance, were reported in every sample, *Achnanthes brevipes* Agardh, cf. *Rhoicosphenia*, *Cocconeis* cf. *californica* sensu Al-Handal and Wulff 2008a, *C. cf. stauroneiformis* (W. Smith) Okuno, *C. fasciolata* (Ehrenberg) Brown (Figs. 2h, 3a, c), *C. melchioroides*, *Cocconeis* sp. 1 (Fig. 2b), *G. littoralis*, *N. perminuta*, *P. kamtschaticum*, and *Synedropsis recta* Hasle, Medlin and Syvertsen, whereas *C. melchioroides* dominated at all four sites (32.5–73.9 %) and was the only species that contributed more than 50 % of total diatom abundance (Table 2).

Twenty-seven out of 57 taxa recorded from Terra Nova Bay accounted for more than 1 % of the total diatom number. Among them, *Achnanthes vicentii* Manguin, *C. cf. californica*, *C. fasciolata*, *C. melchioroides*, *Fragilariopsis nana* (Steemann Nielsen) Paasche, and *N. perminuta* comprised at least 10 % of the total diatom abundance with the latter reaching the highest values (30–59.7 %) and being dominant at every sampling site (Table 2).

Growth form structure and diatom abundance

A well-developed epiphytic diatom community was observed at both locations, however, there were significant differences between Admiralty Bay and Terra Nova Bay samples in both cell abundance (number of cells per mm²) and diatom growth form dominance (global $R = 0.893$, $p = 0.001$, ANOSIM).

In general, samples from Admiralty Bay (AB) had higher diatom abundance compared to Terra Nova Bay (TNB) material (Table 3). The highest abundance was noted for sample AB2 with $10,919 \pm 2,260$ cells mm⁻² and the lowest for TNB1a with $1,140 \pm 390$ cells mm⁻². Higher standard deviation values for samples from Terra Nova Bay reflect a striking difference between the two sample sets evident in SEM micrographs; uniform, compact crust of diatoms covered *Plocamium* thalli from Admiralty Bay (Fig. 2a, b, d, h), whereas Terra Nova Bay epiphytes had a rather patchy distribution (Fig. 3a, c). In addition, epiphytic sessile calcareous bryozoans and hydroids were associated with the red alga in Terra Nova Bay, covering between 2.1 and 7.9 % of the surface algal area examined (Table 3).

Epiphytic diatom communities developed different growth forms on thalli of *P. cartilagineum* (Fig. 4). In Admiralty Bay, diatom communities were dominated by adnate forms (65–87 %; Fig. 2a, b, h, j), followed by erect (8–32 %; Fig. 2d–g, i, k) and motile (4–20 %) forms. Plocon and planktonic forms contributed less than 1 % of the total count. In Terra Nova Bay, motile (40–60 %) and adnate (22–48 %; Fig. 3a, c, d) diatoms dominated, and planktonic diatom abundance was significantly greater than in Admiralty Bay, ranging from 4 to 28 %. A steady decrease in planktonic diatoms with increasing depth was noted. A reverse pattern was observed for erect forms (Fig. 3a, c, e) which accounted for 5–16 % of the diatom community, with the highest percentage recorded at the deepest sampling location (25 m; Fig. 4).

Statistical analyses and ecological indices

Species richness d and species diversity H' indices were calculated for each sampling site. Generally, values of both indices were higher for Terra Nova Bay (1.84–2.18 and 2.72–3.52 for species richness and species diversity, respectively) compared to samples from maritime Antarctica (1.21–2.08 and 1.86–2.24; Table 3).

A dendrogram shows a clear separation of Admiralty Bay and Terra Nova Bay communities (Fig. 5). The distinction among all four Admiralty Bay sampling sites is noted, as is the distinction among Terra Nova Bay stations, with the exception of the two shallowest sites characterized by the highest standard deviation of diatom abundance (Table 3). The ANOSIM test confirmed that these diatom communities differed significantly in composition between the two locations (global $R = 0.974$, $p = 0.001$). The SIMPER analysis allowed determination of characteristic and discriminating taxa of the two regions; *C. melchioroides*, *P. kamtschaticum*, *N. perminuta*, *A. vicentii*, *C. dallmannii*, *G. littoralis*, *F. nana*, and *C. cf. stauroneiformis* contributed the most to the dissimilarity between the

Table 2 Epiphytic diatoms recorded on *P. cartilagineum* at four stations in Admiralty Bay (AB) and two stations (1, 2) in Terra Nova Bay (TNB) in January 2011, 2012, respectively

Taxon	Admiralty Bay		Terra Nova Bay		Location
	A	Av	A	Av	
<i>Achnanthes brevipes</i> Agardh ^a	<1–2	<1	<1	<1	AB: 1, 2, 3, 4; TNB: 1a, 1b, 1c, 1d, 2
<i>Achnanthes</i> sp. 1	np	np	<1	<1	TNB: 1a, 1b, 1c
<i>Achnanthes</i> sp. 2	np	np	<1	<1	TNB: 1b, 1d
<i>Achnanthes vicentii</i> Manguin ^a	<1	<1	5.1–18.1	10.6	AB: 1, 2, 3, 4; TNB: 1a, 1b, 1c, 1d, 2
<i>Amphora</i> cf. <i>terroris</i> Ehrenberg	np	np	<1	<1	TNB: 1a, 1b, 1d, 2
<i>Amphora racovitzae</i> Van Heurck ^a	<1	<1	<1–1.4	<1	AB: 1, 2, 3, 4; TNB: 1a, 1b, 1c, 1d, 2
<i>Amphora</i> sp. 1 sensu Majewska et al. 2012b	np	np	<1	<1	TNB: 1a, 1b, 1c, 1d, 2
<i>Arachnoidiscus japonicus</i> Shadboldt ex Pritchard	<1	<1	np	np	AB: 2
<i>Attheya gaussii</i> (Heiden) Crawford	np	np	<1	<1	TNB: 1c, 1d, 2
<i>Auricula compacta</i> (Hustedt) Medlin	np	Np	<1	<1	TNB: 1a, 1b, 1c
<i>Brandinia mosimanniae</i> Fernandes and Procopiak ^a	<1	<1	<1–1.6	<1	AB: 1, 3 TNB: 1c, 1d, 2
cf. <i>Amphora</i>	2.6–9.5	6.1	np	np	AB: 2
cf. <i>Cymbella</i> ^a	<1	<1	<1–1.7	1.2	AB: 1; TNB: 1a, 1b, 1c, 1d, 2
cf. <i>Rhoicosphenia</i>	<1–12.2	3.3	np	np	AB: 1, 2, 3, 4
<i>Chaetoceros dichæta</i> Ehrenberg	np	np	<1	<1	TNB: 1c
<i>Chaetoceros neglectus</i> Karsten	np	np	<1–7	2	TNB: 1a, 1b, 1c, 1d, 2
<i>Chaetoceros</i> sp. 1 ^a	<1	<1	<1–2.4	<1	AB: 1; TNB: 1a, 1b, 1c, 1d, 2
<i>Cocconeis antiqua</i> Tempère and Brun ^a	<1	<1	<1–4.8	1.4	AB: 2, 3, 4; TNB: 1a, 1b, 1c, 1d, 2
<i>Cocconeis californica</i> var. <i>keruelensis</i> Heiden	<1	<1	np	np	AB: 2, 3
<i>Cocconeis</i> cf. <i>californica</i> sensu Al-Handal and Wulff 2008a ^a	<1–1.4	<1	<1–23.8	2.6	AB: 1, 2, 3, 4; TNB: 1a, 1b, 1d, 2
<i>Cocconeis</i> cf. <i>stauroneiformis</i> (W. Smith) Okuno ^a	<1–8.1	3.6	<1–3	1.3	AB: 1, 2, 3, 4; TNB: 1a, 1b, 1c, 1d, 2
<i>Cocconeis costata</i> var. <i>antarctica</i> Manguin ^a	<1–1.6	<1	<1	<1	AB: 1, 2, 3; TNB: 1b, 1c
<i>Cocconeis dallmannii</i> Al-Handal, Riaux-Gobin, Romero and Wulff	1.3–12.9	6.7	np	np	AB: 1, 2, 3
<i>Cocconeis fasciolata</i> (Ehrenberg) Brown ^a	<1–6	2.7	3.4–20.7	9.6	AB: 1, 2, 3, 4; TNB: 1a, 1b, 1c, 1d, 2
<i>Cocconeis melchioroides</i> Al-Handal, Riaux-Gobin, Romero and Wulff ^a	32.5–73.9	58.4	<1–12.2	2.2	AB: 1, 2, 3, 4 TNB: 1a, 1b, 1c, 1d, 2
<i>Cocconeis</i> sp. 1	<1–6.8	2.2	np	np	AB: 1, 2, 3, 4
<i>Cocconeis</i> sp. 2 sensu Majewska et al. 2012b	np	np	<1–1.6	1	TNB: 1a, 1b, 1d, 2
<i>Cocconeis</i> sp. 3	<1	<1	np	np	AB: 3
<i>Cocconeis</i> sp. 4 ^a	<1	<1	<1	<1	AB: 4; TNB: 1d
<i>Cocconeis</i> sp. 5	<1	<1	np	np	AB: 2
<i>Fallacia marnieri</i> (Manguin) Witkowski, Lange-Bertalot and Metzeltin ^a	<1	<1	<1	<1	AB: 3; TNB: 1a, 1b, 1c
<i>Fragilaria</i> cf. <i>striatula</i> Lyngbye ^a	<1–1.3	<1	<1–4.4	2.3	AB: 3, 4; TNB: 1a, 1b, 1c, 1d, 2
<i>Fragilaria islandica</i> var. <i>adeliae</i> Manguin ^a	<1	<1	<1–1.4	<1	AB: 4; TNB: 1c
<i>Fragilariopsis curta</i> (Van Heurck) Hustedt ^a	<1	<1	<1–1.8	<1	AB: 1; TNB: 1a, 1b, 1c, 1d, 2
<i>Fragilariopsis nana</i> (Steemann Nielsen) Paasche	np	np	<1–24.8	8.9	TNB: 1a, 1b, 1c, 1d, 2
<i>Fragilariopsis ritscheri</i> Hustedt	np	np	<1	<1	TNB: 1d, 2
<i>Fragilariopsis sublinearis</i> (Van Heurck) Heiden	np	np	<1	<1	TNB: 1b, 1c, 1d, 2
<i>Gomphonemopsis littoralis</i> (Hendey) Medlin	<1–16.8	4.6	np	np	AB: 1, 2, 3, 4
<i>Grammatophora angulosa</i> Ehrenberg	<1–3.8	1.6	np	np	AB: 2, 3
<i>Grammatophora arctica</i> Cleve	<1	<1	np	np	AB: 2, 3
<i>Grammatophora arcuata</i> Ehrenberg	np	np	<1–1.5	<1	TNB: 1b, 2
<i>Halamphora</i> cf. <i>acutiuscula</i> (Kützing) Levkov	<1	<1	np	np	AB: 4

Table 2 continued

Taxon	Admiralty Bay		Terra Nova Bay		Location
	A	Av	A	Av	
<i>Hyalodiscus</i> sp.	np	np	<1	<1	TNB: 1c
<i>Licmophora antarctica</i> Carlson	<1	<1	np	np	AB: 2, 4
<i>Licmophora gracilis</i> (Ehrenberg) Grunow ^a	<1	<1	<1	<1	AB: 2, 4; TNB: 1c
<i>Melosira adeliae</i> Manguin ^a	<1	<1	<1	<1	AB: 2, 3, 4; TNB: 1a, 1b, 1c, 1d, 2
<i>Navicula</i> cf. <i>criophila</i> (Castracane) De Toni	np	np	<1	<1	TNB: 1b, 1c, 1d
<i>Navicula</i> cf. <i>directa</i> (W. Smith) Ralfs ^a	<1	<1	<1	<1	AB: 4; TNB: 1a
<i>Navicula</i> cf. <i>jejunoides</i> Van Heurck ^a	<1	<1	<1–3.3	1.2	AB: 2, 3; TNB: 1a, 1b, 1c, 1d
<i>Navicula glaciei</i> Van Heurck ^a	<1	<1	<1–3.6	1.7	AB: 1, 3; TNB: 1a, 1b, 1c, 1d, 2
<i>Navicula perminuta</i> Grunow ^a	1.2–32.2	7.7	30–59.7	42.8	AB: 1, 2, 3, 4; TNB: 1a, 1b, 1c, 1d, 2
<i>Nitzschia acicularis</i> (Kützinger) W. Smith	np	np	<1	<1	TNB: 1c, 1d, 2
<i>Nitzschia</i> cf. <i>australis</i> (M. Peragallo) A. Mann ^a	<1	<1	<1	<1	AB: 3; TNB: 1b
<i>Nitzschia</i> cf. <i>lecoinctei</i> Van Heurck	np	np	<1–2.7	1.2	TNB: 1a, 1b, 1c, 1d, 2
<i>Nitzschia</i> cf. <i>medioconstricta</i> Hustedt ^a	<1	<1	<1–2.5	1.1	AB: 1, 3; TNB: 1a, 1b, 1c, 1d, 2
<i>Nitzschia</i> cf. <i>palea</i> (Kützinger) W. Smith ^a	<1	<1	<1–5.5	1.9	AB: 1; TNB: 1a, 1b, 1c, 1d, 2
<i>Odontella litigiosa</i> (Van Heurck) Hoban	np	np	<1	<1	TNB: 1a, 1b, 2
<i>Paralia sol</i> (Ehrenberg) Crawford	np	np	<1	<1	TNB: 1d
<i>Planothidium</i> cf. <i>dubium</i> (Grunow) Round and Bukhtiyarova	np	np	<1	<1	TNB: 2
<i>Podosira</i> sp.	np	np	<1	<1	TNB: 1a, 1b, 2
<i>Porosira glacialis</i> (Grunow) Jørgensen	np	np	<1	<1	TNB: 1a, 1b, 1d
<i>Pseudogomphonema kamtschaticum</i> (Grunow) Medlin ^a	1.6–16.2	8	<1–7.4	3.1	AB: 1, 2, 3, 4; TNB: 1a, 1b, 1c, 1d, 2
<i>Pseudonitzschia</i> sp. 1 ^a	<1	<1	<1	<1	AB: 3; TNB: 1d
<i>Pseudostaurosira brevistriata</i> (Grunow) D.M. Williams and Round ^a	<1	<1	<1	<1	AB: 1; TNB: 1a, 1b, 2
<i>Rhoicosphenia abbreviata</i> (Agardh) Lange-Bertalot	<1	<1	np	np	AB: 2
<i>Rhoicosphenia genuflexa</i> (Kützinger) Medlin	<1	<1	np	np	AB: 2
<i>Synedropsis fragilis</i> (Manguin) Hasle, Syvertsen and Medlin	np	np	<1	<1	TNB: 1c
<i>Synedropsis recta</i> Hasle, Medlin and Syvertsen ^a	<1–1.9	<1	<1–3.7	<1.5	AB: 1, 2, 3, 4; TNB: 1a, 1b, 1c, 2
<i>Tabularia tabulata</i> (Agardh) Snoeijs ^a	<1	<1	<1–8.6	3.1	AB: 1, 3, 4; TNB: 1a, 1b, 1c, 1d, 2
<i>Thalassiosira</i> sp. 1	np	np	<1	<1	TNB: 1a
<i>Trachyneis aspera</i> (Ehrenberg) Cleve	np	np	<1	<1	TNB: 1d
<i>Trigonium arcticum</i> (Brightwell) Cleve	np	np	<1–1.5	<1	TNB: 1a, 1b, 1c, 1d, 2

A, range of relative abundance (%); Av, mean relative abundance (%)

^a Species found in both locations; 1a: 5 m; 1b: 10 m; 1c: 15 m; 1d: 20 m; np: not present

epiphytic communities, and were responsible for more than 50 % of the observed differences (Table 4).

Discussion

This study revealed interesting differences in marine epiphytic diatom communities associated with the red alga *P. cartilagineum* from two remote and contrasting Antarctic regions. The very few existing reports on Antarctic marine

epiphytic diatoms suggest that the species of host macroalgae and its morphology, as well as the sampling site, season and depth of sampling, are the major factors affecting associated microalgal communities (Thomas and Jiang 1986; Al-Handal and Wulff 2008b; Majewska et al. 2013a, b). In order to limit the factors that might have influenced the microalgal community structure and composition, we sampled one macroalgal species common in two Antarctic zones, within similar depth, during the same season, and using the same methods in both Admiralty Bay

Table 3 Geographic location of sampling stations in Admiralty Bay (AB) and Terra Nova Bay (TNB), with diatom abundance, relative contribution of sessile fauna on *P. cartilagineum*, number of diatom taxa and genera, species richness (d), and species diversity (H')

Station	Location	Depth (m)	Date	Abundance (cells mm ⁻²) \pm SD (%)	Sessile fauna (% of sample surface)	Number of taxa (genera)	d	H'
AB1	S 62°05.652' W 58°23.976'	15	Jan 2011	2,951 \pm 78 (2.7)	np	24 (15)	1.21	2.17
AB2	S 62°12.647' W 58°25.186'	20	Jan 2011	10,919 \pm 2,260 (20)	np	28 (12)	2.08	2.23
AB3	S 62°08.533' W 58°30.472'	15	Jan 2011	4,920 \pm 774 (15.5)	np	30 (16)	1.32	2.24
AB4	S 62°10.021' W 58°32.696'	6	Jan 2011	3717 \pm 536 (14.4)	np	23 (12)	1.36	1.86
TNB1a	S 74°46.470' E 163°59.328'	5	Jan 2012	1,140 \pm 390 (34.1)	7.9	37 (20)	2.18	3.52
TNB1b	S 74°46.470' E 163°59.328'	10	Jan 2012	2,510 \pm 962 (38.3)	6.5	41 (18)	1.84	3.06
TNB1c	S 74°46.470' E 163°59.328'	15	Jan 2012	1,294 \pm 259 (20)	2.9	39 (18)	1.9	3.17
TNB1d	S 74°46.470' E 163°59.328'	20	Jan 2012	1,555 \pm 194 (12.4)	6.2	39 (17)	2.07	2.72
TNB2	S 74°45.104' E 164°04.844'	25	Jan 2012	2,120 \pm 368 (17.3)	2.1	37 (20)	2.04	3.45

np not present

and Terra Nova Bay. Shallow water temperatures were similar for Admiralty Bay and Terra Nova Bay during the study period, as previously recorded (Pruszk 1980; Szafranski and Lipski 1982; Zieliński 1990). Water salinity was measured only in Terra Nova Bay and ranged from 34.4 to 34.7 PSU, which is within the range for a well-mixed water column and were in accordance with previous studies (Rivaro et al. 2011; Olivari and Povero, unpublished data). In Admiralty Bay, small variations in surface water (up to several dozen cm) salinity may occur due to summer fresh-water glacial outflow, though these disturbances do not alter the vertical density gradient (Pruszk 1980; Szafranski and Lipski 1982; Zieliński 1990).

Diatom communities in Admiralty Bay

In Admiralty Bay, 46 diatom taxa were observed on *P. cartilagineum*, with Stations AB3 and AB4 showing the highest and the lowest number of recorded taxa, respectively. The highest cell abundance exceeded 10⁴ in 1 mm² at Station AB2, which was more than three times higher than at Station AB1. This maximum cell abundance was recorded in the vicinity of several large penguin rookeries located on the south-western coast of the bay near its mouth. Previous studies reported the occurrence of large seabird colonies that contributed to large accumulations of guano, as important point sources of nutrient enrichment in

Admiralty Bay (Tatur and Myrcha 1983; Nędzarek and Rakusa-Suszczewski 2007; Siciński et al. 2011; Qin et al. 2014). Zieliński (1990) also considered this part of the bay to be the richest in macroalgal density, biomass and species diversity.

Epiphytic diatom communities were all dominated by adnate forms (*Amphora* spp., *Cocconeis* spp.), presenting a similar pattern of community structure, though observed differences reflected some characteristics particular to each site. Percent contribution of motile diatoms (mainly *Navicula* spp., *Nitzschia* spp.) to the total epiphytic community was slightly higher at Stations AB3 and AB4 compared to AB1 and AB2. This was probably due to the location of Stations AB3 and AB4 near Ezzcura Inlet at the foot of the ice cap, whereas Stations AB1 and AB2 were situated in the vicinity of ice-free rocky and sandy coast. Generally, ice has a great influence on shallow-water benthic communities (Gutt 2001 and references therein), though its role in shifting the benthic community structure may be varied (Powell et al. 1996; Dawber and Powell 1997). In the close proximity to glaciers water transparency decreases, sediment types change to include finer particles, and a high organic matter content and sedimentation, and there is a decrease in number and abundance of faunal species (Rakusa-Suszczewski 1995b; Korsun and Hald 1998). These effects are thought to be more strongly correlated with depth than with distance from the ice cap foot

Fig. 4 Percentage contribution of growth forms to total epiphytic diatom abundance on *P. cartilagineum* at various water depth stations in Admiralty Bay (AB) and Terra Nova Bay (TNB), Antarctica

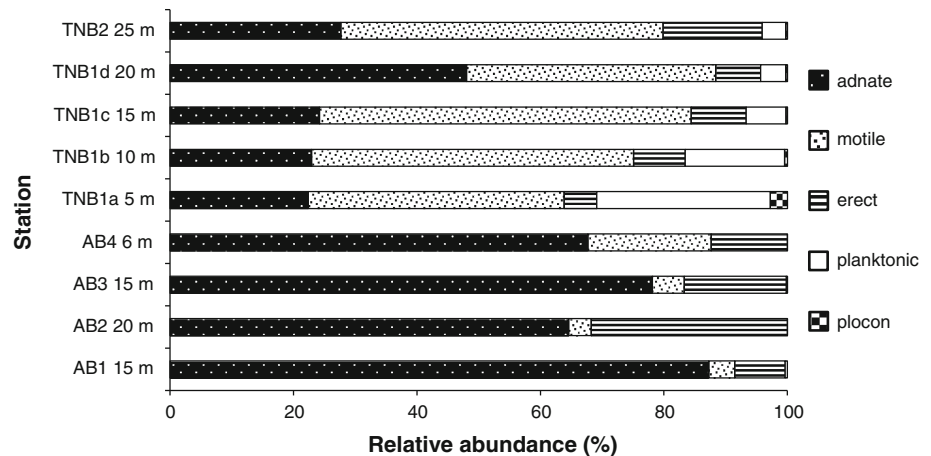
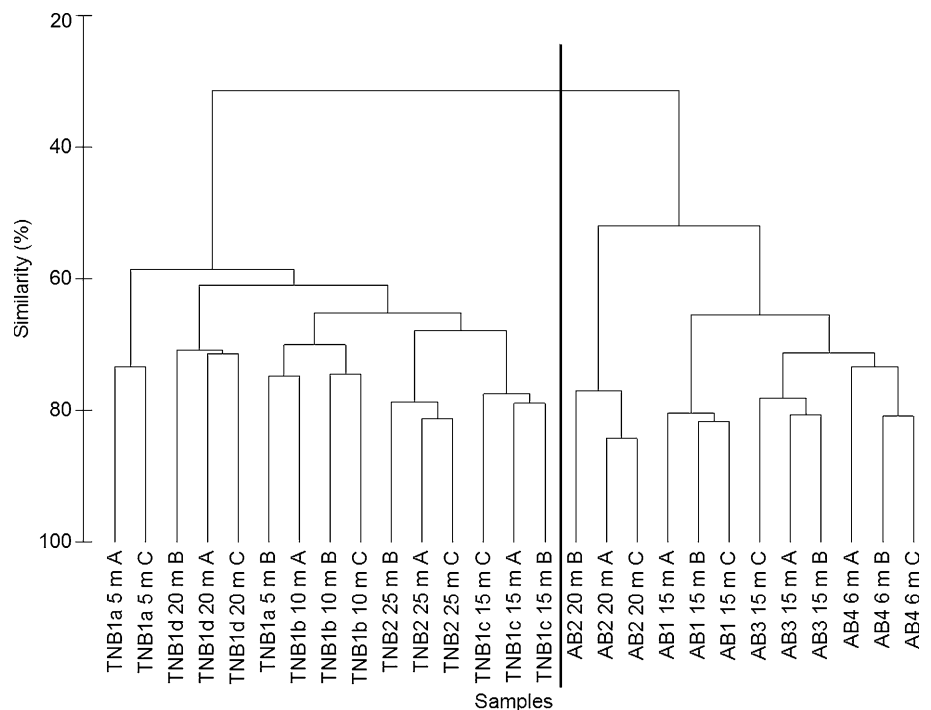


Fig. 5 Dendrogram of 27 diatom samples collected at six stations in Admiralty Bay (AB) and Terra Nova Bay (TNB), Antarctica from a Bray–Curtis similarity matrix using a group-average linkage cluster analysis on square root transformed abundance data



(Włodarska et al. 1996). Benthic communities living near glacier termini are exposed to mechanical damage and highly variable environmental conditions (Rakusa-Suszczewski 1995b; Gutt 2001). Motile diatoms are expected to cope better with these conditions than sessile forms that can neither escape from the disturbing event nor return to their habitats when favorable conditions return. Several biraphid diatom species are possibly related to Antarctic sea ice and glacial ice communities, e.g., *Navicula directa*, *N. glaciei*, small naviculoid species sometimes identified as *N. perminuta*, *Nitzschia lecointei* (e.g., McMinn et al. 2000; Riaux-Gobin et al. 2003; Roberts et al. 2004). Taxa that can survive in the osmotically highly variable brine channels during the winter season are largely benthic

forms. Benthic diatoms evolving in the variable nearshore conditions, are expected to be better adapted to survive in the brine pockets in the ice than oceanic planktonic forms (Everitt and Thomas 1986). Although exchange of substrate between epiphytic and ice-associated diatoms is not common (Al-Handal and Wulff 2008b), most recent studies indicate that in some Antarctic regions ice-associated diatoms may contribute significantly to the epiphytic diatom community at a certain time of the austral summer (Majewska et al. 2013a, b).

The deepest Station AB2 (20 m) was the only one characterized by a greater number of erect forms, which is consistent with previous studies (Majewska et al. 2013a, b); such growth form pattern may be explained by differences

Table 4 Breakdown of average dissimilarity (Av diss) with standard deviation (SD) between Admiralty Bay and Terra Nova Bay samples into contributions (%) from each species

Taxon	Av diss	SD	Contribution (%)	Cumulated (%)
<i>Cocconeis melchioroides</i>	13.67	4.91	19.95	19.95
<i>Pseudogomphonema kamtschaticum</i>	3.54	1.52	5.16	25.11
<i>Navicula perminuta</i>	3.43	1.56	5.01	30.12
<i>Achnanthes vicentii</i>	3.39	2.44	4.94	35.06
<i>Cocconeis dallmannii</i>	3.25	1.22	4.73	39.79
<i>Gomphonemopsis littoralis</i>	3.23	1.40	4.72	44.51
<i>Fragilariopsis nana</i>	3.23	1.95	4.71	49.22
<i>Cocconeis</i> cf. <i>stauroneiformis</i>	2.94	1.78	4.29	53.51
<i>Cocconeis</i> sp. 1	2.74	2.32	3.99	57.51
cf. <i>Rhoicosphenia</i>	2.61	1.23	3.82	61.32
<i>Chaetoceros neglectus</i>	1.47	1.94	2.15	63.47
<i>Tabularia tabulata</i>	1.42	1.57	2.08	65.55
<i>Nitzschia</i> cf. <i>palea</i>	1.40	2.14	2.04	67.59
<i>Cocconeis</i> cf. <i>californica</i>	1.28	1.08	1.87	69.46
cf. <i>Amphora</i>	1.24	0.55	1.81	71.27
<i>Navicula glaciei</i>	1.11	1.48	1.62	72.90
<i>Synedropsis recta</i>	1.03	1.32	1.50	74.40
<i>Cocconeis costata</i> var. <i>antarctica</i>	1.00	1.19	1.46	75.86

Species are ordered in decreasing and cumulated contributions (SIMPER analysis)

in light availability existing between shallow and deeper sampling sites and the erect diatoms' ability to optimize their access to suitable light conditions (e.g., Hudon and Bourget 1983; Gosselain et al. 2005). In Admiralty Bay, surface water circulation in summer depends critically on strong westerly and northerly katabatic winds (Pruszek 1980; Zieliński 1990; Brandini and Rebello 1994). During the study period strong currents were typical for shallow stations, while at deeper sampling sites water movement was reduced (Kuklinski P, pers. obs.). It was demonstrated previously that water flow may dramatically alter a marine epiphytic community directly, by stripping off the macroalgal surface loosely (plocon) or not tightly (erect forms) attached epiphytes (Scoffin 1970), and also indirectly, by reducing the density of grazers and thus enhancing epiphyte growth (Sommer 1996; Schantz et al. 2002).

Al-Handal and Wulff (2008b) reported on epiphytic diatoms from the shallow waters off Potter Cove, King George Island. Macroalgal specimens for their study were collected by SCUBA divers from October to December 2003 from 5 to 7 m depth, as well as from rock pools. The

authors found 50 diatom taxa associated with 19 seaweed species, including green, brown, and red macroalgae. Of the diatom species observed, only 17 were found on *Plocamium* thalli. This number includes 13 diatom taxa also recorded during our study. Species composition of the diatom flora associated with *Plocamium* from Potter Cove is similar to that of Station AB2. In fact, the two locations are separated by ca. 15 km, and both are directly subjected to the Bransfield Strait waters.

Diatom communities in Terra Nova Bay

Fifty-seven diatom taxa were found on five samples of *Plocamium* collected from Terra Nova Bay. Interestingly, this number is more than twice as high as previously reported from the same macroalgae sampled in the region (Majewska et al. 2013b). In that investigation however, the surface area of *Plocamium* thalli examined was only half that used in the present study. Our results here clearly indicate the importance of sample size when assessing microbial diversity. The number of diatom cells per mm² was also higher compared to previous studies, while the differences in cell number between replicates were smaller (Majewska et al. 2013a). As the diatom communities in each sample (at each location and at each depth) were characterized by patchy distribution, this result might also be related to enlarged sample size, which allowed the impact of uneven cell arrangement on the substrate surface to be reduced, which enhanced the reliability of the counts. In every studied case, motile and adnate diatoms dominated. The number of planktonic forms decreased with increasing depth, whereas erect diatoms showed the opposite trend. This is again consistent with earlier studies and supports the conclusion that season and sampling site characteristics greatly influence the diatom communities growth form structure (Majewska et al. 2013a).

Associated fauna and grazer impact

Sessile fauna were associated with *Plocamium* thalli in Terra Nova Bay, while macroalgae sampled off the coasts of King George Island were covered exclusively by microalgae. The presence of epiphytic animals can change the growth form structure and the species composition of the epiphytic diatom community (Majewska et al. 2013a, b). This effect was attributed mainly to a wider range of available microniches introduced into the system by sessile fauna (Bradshaw et al. 2003; Bouma et al. 2009). According to Gili and Hughes (1995) and Gili et al. (2001), epiphytic suspension-feeding colonial and solitary fauna generate small eddies that enhance particle settling in the vicinity of the animal feeding apparatus. This might partially explain the relatively high contribution of small

planktonic and ice-associated diatoms to the total number of microalgae associated with *Plocamium* in Terra Nova Bay. In contrast to Admiralty Bay epiphyton, highly structured diatom communities in Terra Nova Bay were characterized by a high functional diversity, heterogeneity, and patchy distribution with frequent bare areas. The cause of the latter may vary, including grazing pressure and mechanical disturbance such as ice abrasion or anchor ice plucking (McCormick and Stevenson 1991; Klöser et al. 1993). Sea ice formed annually around the continent has already disappeared at the time of this study, though the suspended mineral matter (e.g., from the thawing processes or from the bottom sediments stirred up by waves) might have a similar detrimental effect on epiphytic communities (Elverhøi and Roaldset 1983; Gallardo 1987; Rakusa-Suszczewski 1995b).

Some have proposed that diatom grazers are selective and prefer taxa with certain growth form and size, however the role of herbivores in structuring Antarctic epiphytic communities is poorly known (Giti et al. 2001; Campana et al. 2009; Wulff et al. 2009; Siciński et al. 2011). According to Zacher et al. (2007) and Campana et al. (2008) who investigated diatom communities off King George Island, grazing was the major factor causing biomass reduction and altering diatom community structure and species composition. Zacher et al. (2007) observed that firmly attached diatoms (e.g., *Cocconeis* spp.) were not grazed by amphipods, whereas Campana et al. (2008, 2009) reported that erect and colony-forming species were severely impacted and grazed by herbivorous amphipods and gastropods. According to Siciński et al. (2011), morphology of the macroalgae was the controlling factor for the associated faunal groups. The authors showed that in the shallow waters of Admiralty Bay amphipods were the dominant group associated with branching macroalgae (such as *Plocamium*), while high concentrations of suspended mineral matter was probably a limiting factor for many sessile filter feeders, such as Ascidiaceae or Bryozoa (Rakusa-Suszczewski and Zielinski 1993; Pichlmaier et al. 2004). It was also suggested that the grazers' control on diatom-dominated assemblages might be seasonal; Sundbäck et al. (1996) indicated that the meiofaunal grazing impacted microalgal biomass distribution in spring and autumn but not in summer.

At all stations in Admiralty Bay, the red alga thalli were covered by a uniform compact crust comprised almost exclusively of a few *Cocconeis* species, while other diatom growth forms lived in patches on the axes of *Plocamium* branches or in crevices between larger diatom cells (e.g., *Arachnoidiscus japonicus* Shadboldt ex Pritchard, *C. schuettii*). In Terra Nova Bay, visual patchiness in diatom distribution characterized the entire epiphytic community. Several authors reported on zoobenthic organisms off the

western coasts of the Ross Sea, and it was stated that their abundances are the highest among all known austral sea biotopes (Dayton and Oliver 1977; Arntz et al. 1994, and references therein; Gambi et al. 1994). Gambi et al. (1994) described zoobenthic communities from shallow (up to ca. 20 m) hard bottoms off Terra Nova Bay and found polychaetes, molluscs, and peracarid crustaceans to be dominant. Although in Terra Nova Bay a large number of zoobenthic species are hosted by macroalgal meadows (Gambi MC, personal communication), no information of their feeding strategies and food preferences was presented, but many of them are potential diatom grazers. We hypothesize that observed differences in distribution and growth form and species composition of examined epiphytic communities were due to different types of grazers that dominated the two bays during the study period. Higher density, as well as lower species richness and diversity, which characterized diatom communities from Admiralty Bay, may indicate that dominant grazers were less efficient and more selective compared to those from Terra Nova Bay.

Concluding remarks

Cluster analysis showed dissimilarities between diatom communities from two remote Antarctic locations. Less than 50 % of the observed diatom taxa were common to both regions. Moreover, most of them accounted for less than 1 % of the total diatom number in at least one of the bays. Both the number of taxa and the values of ecological indices were higher for samples from Terra Nova Bay than for Admiralty Bay, which is somewhat in disagreement with generally accepted concept that biodiversity dramatically decreases polewards (e.g., Turner 2004). Here however, other factors (discussed in this paper) must be taken into account.

With this work we would like to emphasize the importance of a proper approach to studying the ecology of microorganisms. Fine-scale objects like diatoms require fine-scale analysis and relevant methodology. It is highly probable that further studies on marine benthic diatoms from the Antarctic will result in many new species being discovered. Yet, ecologists must be aware of the great impact of taxonomic practice on the various theories, hypotheses, and ideas concerning global ecosystem structure and functioning. Trivial errors are common and frequently neglected. All of this becomes even more complicated when taking into consideration contrasting species concepts within diatom taxonomy, as well as a general scarcity of explicit references. Some of the features of diatom specimens observed during this study showed a wide range of intraspecific variability. A considerable number of taxa found could not be satisfactorily identified

on the basis of published literature, much of which concerns temperate regions. Even if some specimens agree with named taxa found in Antarctica, there is always the risk that such identifications are the result of force-fitting using floras developed for other parts of the world. It was hypothesized (e.g., Vincent 2000, and references therein) that benthic microorganisms from the Southern Ocean do not demonstrate local endemism due to minute size and potential ease of dispersal. In addition, relatively constant physical parameters (temperature, salinity, substrate) of benthic habitats would not isolate Antarctic microfloras (Wulff et al. 2009, and references therein). On the other hand, some authors showed that several microbial species have restricted geographical distributions, suggesting that natural selection and local adaptation can generate rapid divergence even when the gene flow exists (Logares 2006, and references therein). At present, our knowledge is far too limited to understand microbial diversification and further studies are obviously needed.

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