

Epiphytic diatom communities of Terra Nova Bay, Ross Sea, Antarctica: structural analysis and relations to algal host

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Abstract: Epiphytic diatoms are important constituents of the Southern Ocean coastal water ecosystem, being a key element in many of the Antarctic trophic chains. However, only limited information exists relating to these microalgal communities. Here we describe our findings of a study on epiphytic diatoms from Terra Nova Bay (Ross Sea, Antarctica) based on material collected during the summer campaigns spanning from 1990–2004. Observations of diatoms associated with three rhodophyte species (*Iridaea cordata* (Turner) Bory, *Phyllophora antarctica* Gepp & Gepp, and *Plocamium cartilagineum* (L.) Dixon) were carried out with the use of a scanning electron microscope. A total of 73 diatom taxa (32 genera) were distinguished, of which 20 taxa exceeded 3% of total abundance. *Cocconeis fasciolata* (Ehrenberg) Brown, *Navicula perminuta* Grunow, and *Fragilariopsis nana* (Steemann Nielsen) Paasche appeared in every sample. The analysis of similarities (ANOSIM) test as well as non-metric multidimensional scaling analysis indicated the nature of host organism as a major factor influencing associated diatom community structure, whereas depth, site, and time of sampling seemed to be less important. The epizooic communities associated with sessile fauna epiphytic on macroalgae differed significantly from those associated with macroalgal surface. A pronounced difference between the communities epiphytic on various host macroalgae species was also observed, although most of the dissimilarities occurred between diatom taxa of the same growth form.

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Introduction

While the structure of Antarctic food webs is relatively well described, many essential interactions remain unknown as basic information on either autecology or synecology of many of the phototrophic organisms from Antarctic seas is missing (Fiala & Oriol 1990, Al-Handal & Wulff 2008a). Up to 75% of the Southern Ocean primary production is contributed by diatoms (Mohan *et al.* 2011). These unicellular microalgae play an essential role in carbon and silicon oceanic cycles, controlling the uptake of atmospheric CO₂ and being a basic element of the so-called silicate pump. The downward flux of silicified diatom cells is a major mechanism of transfer of upper water column elements incorporated into microalgal bodies (C, Si, Ra, Ba, Ge etc; Bargagli 2004 and references therein). Studies on Antarctic diatoms from the southern Ross Sea led by Di Tullio *et al.* (1998) indicated that diatoms may also be responsible for oceanic emission of DMS (dimethylsulphide) and the largest biogenic flux of sulfur to the atmosphere. It is therefore imperative for the sake of the future of Antarctic marine ecosystems to thoroughly investigate and well understand the ecology, taxonomy and biogeography of these microalgae.

Diatoms are reported to be excellent ecological indicators. They have been used for palaeoenvironmental

reconstructions as well as for assessment of recent water bodies' ecological status (Spaulding & McKnight 1999, Mohan *et al.* 2011). In the light of rapid climate change and global warming, Antarctic research has never been more important than it is today and there has been an increasing interest in Antarctic diatoms. While ecological preferences of some common diatom species from lower latitudes are relatively well known, the present state of our knowledge of the autecology of modern Antarctic diatom taxa disables us from using the diatom communities to interpret recent changes or foresee possible anomalies in the Antarctic marine ecosystem (Sabbe *et al.* 2003, Karsten *et al.* 2006). Although microalgae (including diatoms) have been long collected from the Southern Ocean (e.g. Van Heurck 1909, Peragallo 1921, Hustedt 1958, Bargagli 2004 and references therein), many habitats and geographical areas have been at best poorly explored (Webster *et al.* 2004). Moreover, most studies on Antarctic marine diatoms have dealt with planktonic, ice-associated or benthic species found in the sediment cores. Little is known about the epiphytic communities regarding either their ecology or taxonomy, or species relative abundance (Thomas & Jiang 1986, Al-Handal & Wulff 2008a), although existing reports indicate that these microalgae may be the most important primary producers at certain times of the year

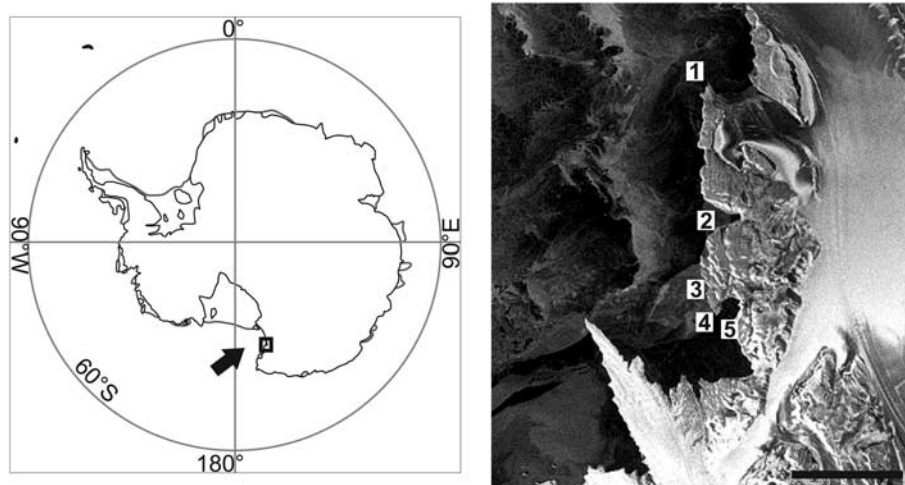


Fig. 1. Study area and sampling sites location: 1 = Cape Russell, 2 = Adélie Cove, 3 = Faraglione, 4 = Molo, 5 = Tethys Bay. Scale bar: 10 km.

(Dayton *et al.* 1986, Gilbert 1991 and references therein, Ahn *et al.* 1997, Karsten *et al.* 2006).

In this paper, we report data on epiphytic diatom communities on different macroalgal species collected from Terra Nova Bay (Ross Sea) during the eight Italian Antarctic campaigns spanning from 1990–2004. Emphasis was placed on understanding the potential effect of the host macroalga on the epiphytic diatom community composition and structure. This study is a complement to previous investigation focused on a structural analysis of diatom growth form distribution in the same area (Majewska *et al.* 2012b).

Materials and methods

Study area

The study area is situated in Terra Nova Bay (74°42'S, 164°46'E), between the Campbell Glacier Tongue and Drygalski Ice Tongue, along northern Victoria Land (Fig. 1). It encompasses the coastal waters between Tethys Bay and Cape Russell, including the waters adjacent to the Italian Mario Zucchelli Station. The shoreline is formed mainly by rocky cliffs, with occasional tracts of gently sloping coast scattered with large boulders (e.g. Adélie Cove). Tides range from 1.5–2 m and sea surface is covered by 2–2.5 m thick pack ice for 9–10 months each year (Stocchino & Lusetti 1990). Most of the sea floor of the area is composed of granitic rocks, with a variable admixture of gravels, coarse sands and muddy sediments (especially in the vicinity of Adélie Cove). Benthic algae exhibit a characteristic pattern of zonation: epilithic cyanobacteria and diatoms colonize the supralittoral hard substrates, green algae *Urospora penicilliformis* (Roth) Areschoug and *Prasiola crispa* (Lightf.) Kütz. dominate sheltered areas of the intertidal zone (1.5–2.0 m wide) (Cormaci *et al.* 1992), while red algae form expanded mats

below a depth of 2–3 m. Amongst them, *Iridaea cordata* (Turner) Bory fully colonizes bottom to a depth of 10–12 m, receding rapidly below this level and yielding to *Phyllophora antarctica* Gepp & Gepp (Gambi *et al.* 1994), often densely covered by sessile organisms such as hydroids, serpulids and bryozoans (*Celleporella antarctica* Moyano & Gordon and *Harpezia spinosissima* (Calvet)) (Rosso & Sanfilippo 2000). Smaller and more delicate *Plocamium cartilagineum* (L.) Dixon seems to be less frequent and have a distribution range overlapping those of the two previously mentioned red macroalgal species. An Adélie penguin rookery (*Pygoscelis adeliae* (Hombron & Jacquinot)) located at Adélie Cove is proven to affect the adjacent marine environment during breeding period by leaving a huge amount of faeces which naturally fertilize shallow coastal waters (Povero *et al.* 2001). Documented human impact within the area is described as “minimal”, although extensive marine research of Terra Nova Bay has been carried out since 1986/87 (Bargagli 2004).

Collection and preparation of samples

Samples of macroalgae were collected during Italian Antarctic campaigns in the summers of 1990–2004 (1989/90, 1993/94, 1994/95, 1997/98, 1999/00, 2000/01, 2002/03 and 2003/04). For the purpose of the study, five locations were selected as sampling sites, each characterized by different coastal features. All sites are typically accessible in summer, as the part of the bay remains ice-free at a certain time of the year, which is rare in this part of Antarctica (Gambi *et al.* 1994, 2000). Thalli of three macroalgal species (*Iridaea cordata*, *Phyllophora antarctica* and *Plocamium cartilagineum*) from various depths (from 0.5–17 m) were collected by SCUBA divers (on fixed 40 x 40 cm quadrats) and immediately preserved with 4% formaldehyde solution in seawater. Relatively small molecules of formaldehyde penetrate deep into

Table I. List of taxa present in the studied samples, percentage of total abundance, percentage of samples in which taxa occurred, and sites where they were present.

Taxa	% of total abundance			host macroalga	locations	% of samples		
	alga	sessile fauna	entire sample*			1	2	3
<i>Achnanthes brevipes</i> Agardh	< 1–13.6	< 1–21.6	< 1–13.6	Ir, Ph, Pl	CR, AC, F, M, TB	97	96	97
<i>Achnanthes vincentii</i> Manguin	< 1–14	< 1–16.1	< 1–11.9	Ir, Ph, Pl	CR, AC, F, M, TB	89	92	89
<i>Actinocyclus actinocilius</i> (Ehrenberg) Simonsen	< 1	-	< 1	Ir	F	3	-	3
<i>Amphiprora kufferathii</i> Manguin	-	< 1–1.4	< 1	Ph	AC, M, F	-	25	16
<i>Amphora</i> cf. <i>racovitzae</i> Van Heurck	< 1	< 1	< 1	Ir, Ph	F, M	11	8	14
<i>Amphora racovitzae</i> Van Heurck	< 1	< 1–4.6	< 1–1.4	Ir, Ph, Pl	CR, AC, F, M, TB	51	58	57
<i>Amphora</i> sp. 1	< 1–4.8	< 1–4.7	< 1–3.2	Ir, Ph, Pl	AC, F, M, TB	57	50	57
<i>Amphora</i> sp. 2	< 1	< 1	< 1	Ir, Ph, Pl	AC, F, M, TB	22	12	24
<i>Amphora</i> type C (<i>sensu</i> Scott & Thomas 2005)	< 1	-	< 1	Ir, Ph	F, M	8	-	8
<i>Asteromphalus hookeri</i> Ehrenberg	-	< 1	< 1	Ph	M	-	4	3
<i>Auricula compacta</i> (Hustedt) Medlin	< 1	< 1	< 1	Ir, Ph	CR, AC, F, M, TB	14	21	22
<i>Brandinia mosimanniae</i> Fernandes & Procopiak	< 1	< 1	< 1	Ir, Ph	AC, F	5	8	11
<i>Chaetoceros gausii</i> Heiden & Kolbe	< 1	< 1	< 1	Ph, Pl	CR, AC, F, M	8	17	14
<i>Cocconeis</i> cf. <i>californica</i> Grunow	< 1	< 1	< 1	Ph	M, F	5	4	5
<i>Cocconeis</i> cf. <i>californica sensu</i> Al-Handal & Wulff (2008a)	< 1–5	< 1–1.4	< 1–5	Ir, Ph, Pl	CR, AC, F, M, TB	16	21	22
<i>Cocconeis</i> cf. <i>costata</i> Gregory	< 1	-	< 1	Ir	F	3	-	3
<i>Cocconeis</i> cf. <i>stauroneiformis</i> (Van Heurck) Okuno	< 1–2.2	< 1	< 1–2.2	Ph, Pl	AC, F, M	8	4	8
<i>Cocconeis costata</i> Gregory var. <i>antarctica</i> Manguin	< 1–42.6	-	< 1–42.6	Ir, Ph, Pl	AC, F, M	16	-	16
<i>Cocconeis fasciolata</i> (Ehrenberg) Brown	< 1–82.1	< 1–38.3	< 1–78.8	Ir, Ph, Pl	CR, AC, F, M, TB	100	96	100
<i>Cocconeis schuettii</i> Van Heurck	< 1–54.5	< 1–2.4	< 1–54.5	Ir, Ph, Pl	CR, AC, F, M	84	29	84
<i>Cocconeis</i> sp. 1 (<i>sensu</i> Al-Handal & Wulff 2008b)	< 1	-	< 1	Ir	M	3	-	3
<i>Cocconeis</i> sp. 2	< 1–7.4	< 1–4.4	< 1–5.2	Ir, Ph	AC, F, M, TB	43	42	49
<i>Coscinodiscus</i> sp.	< 1	-	< 1	Ir	M	3	-	3
<i>Fallacia marnieri</i> (Manguin) Witkowski	< 1–2.4	< 1	< 1–1.5	Ph	CR, AC, F, M, TB	46	17	46
<i>Fragilaria islandica</i> var. <i>adeliae</i> Manguin	< 1	< 1–2.6	< 1	Ir, Ph	TB, M, F	5	17	14
<i>Fragilaria</i> sp.1	< 1–5.9	< 1–15.4	< 1–7.2	Ir, Ph	F, M, TB	22	21	24
<i>Fragilariopsis curta</i> (Van Heurck) Krieger	< 1–6.8	1.5–18	< 1–14.2	Ir, Ph, Pl	CR, AC, F, M, TB	97	100	97
<i>Fragilariopsis cylindrus</i> (Grunow) Krieger	< 1	< 1–2.5	< 1–1.6	Ir, Ph	TB, M, F	8	12	14
<i>Fragilariopsis kerguelensis</i> (O'Meara) Hustedt	< 1	< 1	< 1	Ph	TB, M	3	4	5
<i>Fragilariopsis nana</i> (Stemann Nielsen) Paasche	< 1–28	< 1–43.6	< 1–34.2	Ir, Ph, Pl	CR, AC, F, M, TB	89	100	100
<i>Fragilariopsis obliquecostata</i> (Van Heurck) Heiden	< 1	< 1–2.3	< 1	Ir, Ph, Pl	CR, AC, F, M, TB	11	21	19
<i>Fragilariopsis rhombica</i> (O'Meara) Hustedt	-	< 1	< 1	Ph	CR	-	4	3
<i>Fragilariopsis ritscheri</i> Hustedt	< 1	< 1	< 1	Ir, Ph	F, M	3	4	5
<i>Fragilariopsis sublinearis</i> (Van Heurck) Heiden	< 1	< 1	< 1	Ir, Ph	CR, AC, F, M	5	8	11
<i>Grammatophora arctica</i> Cleve	< 1	-	< 1	Ir	F	5	-	5
<i>Grammatophora arcuata</i> Ehrenberg	< 1	< 1	< 1	Ir, Ph	AC, F, M	3	8	12
<i>Gyrosigma</i> sp.	< 1	-	< 1	Ir, Ph	AC	5	-	5
<i>Haslea</i> sp.	< 1	-	< 1	Ph	AC	3	-	3
<i>Melosira adeliae</i> Manguin	< 1–27.4	< 1–20.8	< 1–27.4	Ir, Ph, Pl	CR, AC, F, M, TB	76	79	81
<i>Melosira</i> cf. <i>moniliformis</i> (Muller) Aghard	< 1	< 1	< 1	Ph, Pl	AC, F	3	4	5
<i>Navicula</i> cf. <i>gelida</i> Grunow	< 1	-	< 1	Ir, Ph	F, M	5	-	5
<i>Navicula</i> cf. <i>incertata</i> Lange-Bertalot & Krammer	< 1–4	< 1–13.4	< 1–6	Ir, Ph	CR, AC, F, M, TB	68	54	68
<i>Navicula</i> cf. <i>jejunoides</i> Van Heurck	< 1–6.7	< 1–23.9	< 1–6.7	Ir, Ph, Pl	CR, AC, F, M, TB	62	67	65
<i>Navicula directa</i> (W Smith) Ralfs	< 1	< 1	< 1	Ir, Ph	F, M, TB	8	12	16
<i>Navicula glaciei</i> Van Heurck	< 1–11.9	< 1–15.7	< 1–11.3	Ir, Ph, Pl	CR, AC, F, M, TB	62	42	62
<i>Navicula perminuta</i> Grunow	5.8–74.5	11.8–81.8	5.8–75.4	Ir, Ph, Pl	CR, AC, F, M, TB	100	100	100
<i>Navicula</i> sp. 1	< 1	< 1–1.4	< 1	Ph	F	3	4	5
<i>Navicula</i> sp. 2	< 1	< 1–1.7	< 1	Ph	F, TB	5	8	5
<i>Nitzschia acicularis</i> W. Smith	< 1	< 1	< 1	Ph	F, M	3	8	5
<i>Nitzschia</i> cf. <i>lecontei</i> Van Heurck	< 1–1.4	< 1–1.5	< 1–1.4	Ir, Ph	F, M, TB	24	17	24
<i>Nitzschia medioconstricta</i> Hustedt	< 1	< 1–8.4	< 1–1.4	Ir, Ph, Pl	AC, F, M, TB	54	62	59
<i>Nitzschia</i> sp. 1	< 1	< 1	< 1	Ir, Ph	CR, AC, F, M	19	12	22
<i>Nitzschia</i> sp. 2	< 1–2.4	< 1–2.2	< 1–2.4	Ir, Ph	CR, AC, F, M, TB	49	29	51
<i>Odontella litigiosa</i> (Van Heurck) Hoban	1.60	-	1.60	Ir	M	3	-	3
<i>Paralia sol</i> (Ehrenberg) Crawford	< 1	< 1–1.4	< 1–1.2	Ir, Ph, Pl	CR, AC, F, M	5	17	14
<i>Parlibellus</i> cf. <i>crucicula</i> (W. Smith) Witkowski <i>et al.</i>	< 1–41.2	< 1–9.9	< 1–41.2	Ir, Ph	AC, F, M, TB	49	67	65
<i>Pleurosigma</i> cf. <i>directum</i> Grunow	< 1	< 1	< 1	Ir, Ph, Pl	CR, AC, F, M, TB	8	25	19
<i>Podosira</i> sp.	< 1	< 1–9.3	< 1–1.3	Ir, Ph, Pl	CR, AC, F, M, TB	19	37	35
<i>Porosira</i> sp.	< 1	< 1	< 1	Ir, Ph	F, M, TB	5	8	11
<i>Pseudogomphonema kamschatcicum</i> (Grunow) Medlin	< 1–32.1	< 1–4.8	< 1–32.1	Ir, Ph, Pl	CR, AC, F, M, TB	95	79	95
<i>Pseudonitzschia</i> sp.	< 1	< 1	< 1	Ph	AC, F, M	3	8	8
<i>Pseudostaurisira brevistriata</i> (Grunow) D.M. Williams & Round	-	< 1	< 1	Ph	AC, F	-	8	5
<i>Synedropsis hyperboreoides</i> Hasle, Medlin & Syvertsen	< 1	< 1	< 1	Ir, Ph	AC, F, M	5	8	11
<i>Synedropsis recta</i> Hasle, Syvertsen & Medlin	< 1–3.5	< 1–7.7	< 1–4.5	Ir, Ph, Pl	CR, AC, F, M, TB	89	79	95
<i>Tabularia tabulata</i> (Agardh) Snoeijs	< 1–1.3	< 1–1.3	< 1–1.2	Ir, Ph	F, M	19	17	24
<i>Thalassiosira antarctica</i> Comber	< 1	< 1	< 1	Ir, Ph	F, M	5	8	11

Table I. Continued

Taxa	% of total abundance			host macroalga	locations	% of samples		
	alga	sessile fauna	entire sample*			1	2	3
<i>Thalassiosira</i> cf. <i>ambigua</i> Kozlova	< 1	-	< 1	Ir	F, M	5	-	5
<i>Thalassiosira gracilis</i> (Karsten) Hustedt	< 1	< 1	< 1	Ph	M, TB	3	12	11
<i>Thalassiosira</i> sp. 1	< 1	-	< 1	Ir	F, M	5	-	5
<i>Thalassiothrix antarctica</i> Schimper ex Karsten	-	< 1	< 1	Ph	CR, M	-	8	5
<i>Thalassiothrix longissima</i> Cleve & Grunow	< 1	-	< 1	Ph	M, TB	5	-	5
<i>Trachyneis aspera</i> (Ehrenberg) Cleve	< 1	< 1–1.6	< 1	Ir, Ph, Pl	CR, AC, F, M, TB	19	46	38
<i>Trigonium arcticum</i> (Brightwell) Cleve	< 1–4.1	< 1–7	< 1–4.1	Ir, Ph, Pl	CR, AC, F, M, TB	22	50	46

Ir = *Iridaea cordata*, Ph = *Phyllophora antarctica*, Pl = *Plocamium cartilagineum*.

CR = Cape Russell, AC = Adélie Cove, F = Faraglione, M = Molo, TB = Tethys Bay.

1 = samples of epiphytic diatom communities, 2 = samples of epizooic communities, 3 = entire samples (including epiphytic and epizooic communities found within a sample).

*entire diatom community found within a sample (including epiphytic and epizooic communities).

diatom adhesive mucilaginous substances and fix well all the elements of complex attachment mechanism, including the simple layer of mucilage interposed between the microalgae and its substrate and morphologically distinct structures (pads, envelopes, stalks, tubes etc.), as well as internal organic components of the diatom cell envelope, making the cells permanently attached to the surface. Once preserved, a diatom cell remains in its original position on the host tissue for years.

For the quantitative study of attached diatoms, macroalgal thalli were cut into small pieces (*c.* 1 cm²), dehydrated by immersion in alcohol solution at increasing gradation, and processed in a critical point drier with four cycles of solvent extraction. After these treatments, macroalgal pieces were mounted on specimen stubs and sputter coated with gold. Three replicates were prepared for each sample. Parallel samples for taxonomic and diagnostic purposes were treated with concentrated nitric and sulfuric acids (in the ratio of 1:3), rinsed thoroughly with several sets of distillate water and subsequently centrifuged. Obtained sediment was placed on stubs, dried, and coated. Observations were carried out with JEOL JSM 60/60 LW and SUPRA 40 (Zeiss) scanning electron microscopes. Diatoms originally settled on the host macroalgae were identified to the lowest taxonomic level possible (species/genus) and counted at a magnification of at least 400 x on the surface of at least 1 mm² of each replicate.

Statistics

All analyses were performed using the PRIMER v6 computer program (Clarke & Gorley 2006), including the add-on package PERMANOVA+ (Anderson *et al.* 2008). Analysis of similarities (ANOSIM) was applied to test for significant differences between the groups of samples due to algal host, sampling site, depth, year, and month of collection, and non-metric multidimensional scaling (nMDS) plots were used to exhibit patterns found. The matrix used for the nMDS was calculated with a Bray-Curtis similarity index based on species abundance (number of cells per mm²) data.

To identify diatom species responsible for the similarity within groups, similarity percentage analysis (SIMPER) was performed. The average contribution of each diatom taxa was compared to the average Bray-Curtis similarity within samples of a cluster. Commonly used community quality indicators 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 calculated for each of the samples.

Results

Seventy-three diatom taxa belonging to 32 genera were distinguished during this study, but more than 87% of the total number of microalgal cells counted was contributed to by only the 20 most abundant taxa (11 genera) in every sample analysed (Table I). Some of the diatom specimens found present problems in their taxonomic identification (in particular forms belonging to *Navicula* and *Nitzschia* genera). In these cases, the dubious taxa are indicated by a "cf." or designated as "sp. 1" and "sp. 2" (if the specimen could not be matched with any described taxon), still each name stands for a single separate species. A more detailed taxonomic analysis of the material is in progress.

Amongst the recorded diatoms, three species exceeded 50% of the total count: *Cocconeis schuettii* (one sample), *C. fasciolata* (six samples), and *Navicula perminuta* (11 samples) (Figs 2 & 3). Another five species (*Cocconeis costata* var. *antarctica*, *Fragilariopsis nana*, *Melosira adeliae*, *Parlibellus* cf. *crucicula*, and *Pseudogomphonema kamtschaticum*) counted for over 25% (in at least one sample), while the most numerous group (43 taxa) were taxa that did not exceed 1% relative abundance in any of the examined samples. Ten taxa were noted relatively frequently (50–90% of samples), and another seven taxa were present in more than 90% of samples, including *Cocconeis fasciolata*, *Fragilariopsis nana*, and *Navicula perminuta* that appeared in every case studied. Fifty taxa were noted in less than 25% of samples.

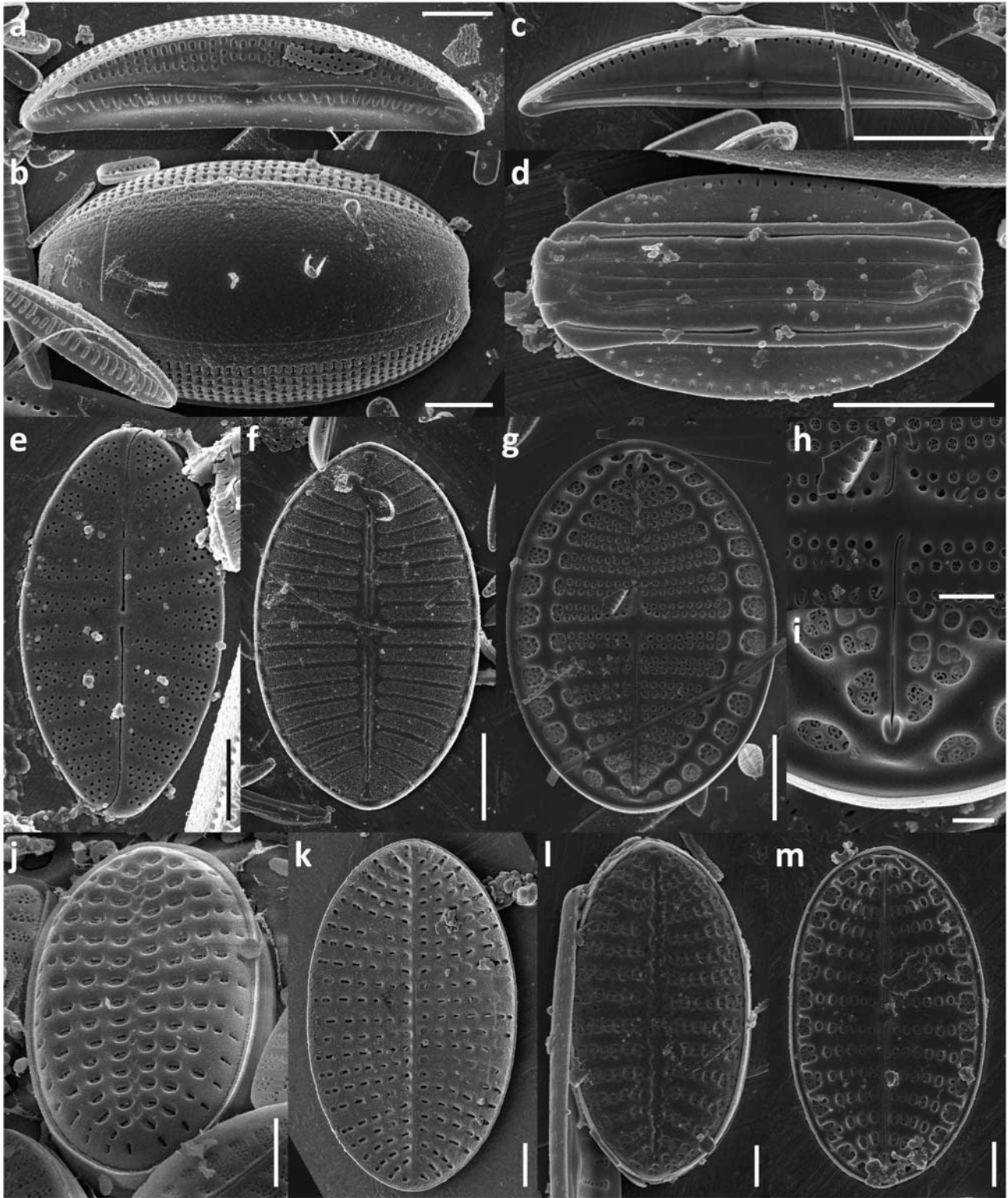


Fig. 2. Epiphytic diatoms from Terra Nova Bay, Antarctica (scanning electron microscopy). **a. & b.** *Amphora racovitzae*, **a.** internal valve view, and **b.** cell in dorsal view. **c. & d.** *Amphora* sp. 1, **c.** internal valve view, and **d.** view of ventral surface. **e.** *Achnanthes vincentii*, external surface of raphe-valve. **f.–i.** *Cocconeis fasciolata*, **f.** rapheless-valve (pseudoraphe-valve), external view, **g.** raphe-valve, internal view, **h.** detail of central raphe endings and central area (internal view), and **i.** internal view of terminal raphe ending. **j. & k.** *Cocconeis* cf. *californica* sensu Al-Handal & Wulff (2008a), **j.** rapheless-valve, external view, and **k.** rapheless-valve, internal view. **l. & m.** *Cocconeis* cf. *stauroneiformis*, **l.** rapheless-valve, external view, and **m.** raphe-valve, internal view. Scale bars: a–d = 5 µm; e, h, & j–m = 2 µm; f & g = 10 µm; i = 1 µm.

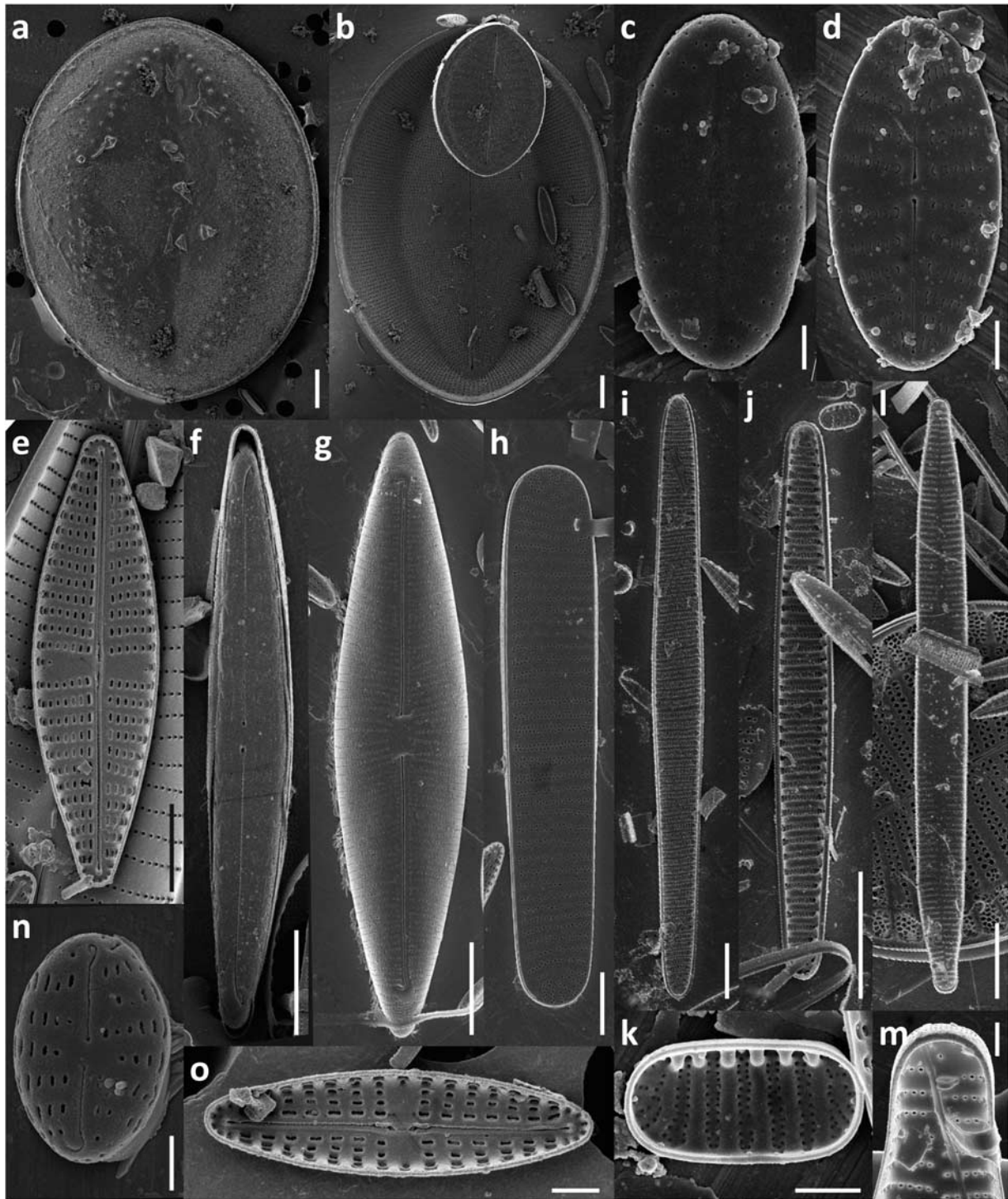


Fig. 3. Epiphytic diatoms from Terra Nova Bay, Antarctica (scanning electron microscopy) **a.** External view of *Cocconeis schuettii* pseudoraphe-valve. **b.** Internal view of *Cocconeis schuettii* and *C. fasciolata* raphe-valves. **c. & d.** *Cocconeis* sp. 2, **c.** external view of rapheless-valve, and **d.** external view of raphe-valve. **e.** Internal view of *Navicula glaciei* valve. **f.** External view of *Navicula* cf. *jejunoides* valve. **g.** *Parlibellus* cf. *crucicula*, external view. **h.** *Fragilariopsis curta*, external view. **i.** *Fragilariopsis obliquecostata*, internal view. **j.** *Fragilariopsis sublinearis*, internal view. **k.** *Fragilariopsis nana*, internal view. **l. & m.** *Brandinia mosimanniae*, **l.** internal valve view, and **m.** internal view of apex with labiate process. **n. & o.** *Navicula perminuta*, **n.** external valve view, and **o.** internal valve view. Scale bars: **a.**, **b.**, **g.**, **i.**, **j.** & **l.** = 10 μm ; **c.**, **d.**, **k.** & **m.**–**o.** = 1 μm ; **e.**, **f.** & **h.** = 5 μm .

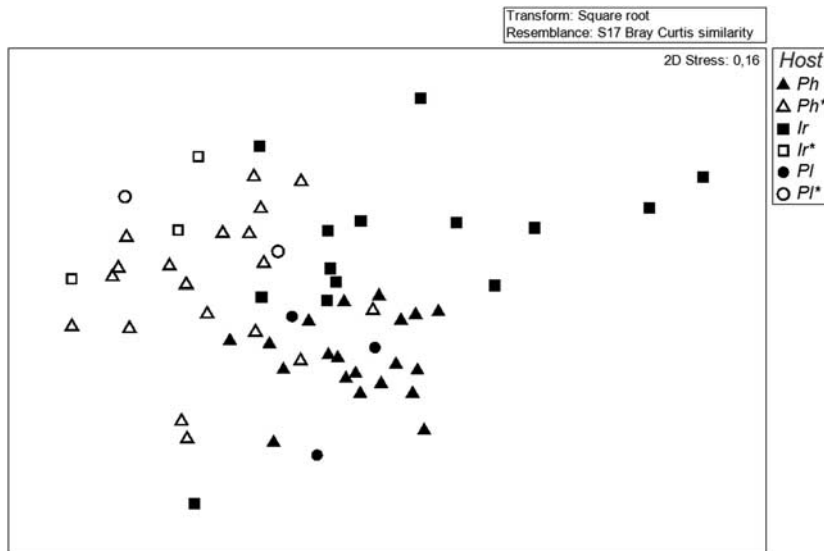


Fig. 4. Non-metric multidimensional scaling (nMDS) graph based on the species abundance data. *Ph* = samples of epiphytic diatom communities associated with *Phyllophora*, *Ph** = samples of epizooic diatom communities associated with sessile fauna found on *Phyllophora*, *Ir* = samples of epiphytic diatom communities associated with *Iridaea*, *Ir** = samples of epizooic diatom communities associated with sessile fauna found on *Iridaea*, *Pl* = samples of epiphytic diatom communities associated with *Plocamium*, *Pl** = samples of epizooic diatom communities associated with sessile fauna found on *Plocamium*.

Twenty-four taxa were found associated with all three host macroalgal species, and 22 were noted at all five sampling sites (Table I).

As more than a half of the samples (especially *Phyllophora antarctica* blades) were densely covered by epiphytic sessile fauna (e.g. calcareous bryozoans and hydroids), and the occurrence of this animal component seemed to strongly influence the diatom community composition and structure, we decided to distinguish between diatom community developed directly on the macroalgal thalli, and epizooic microalgae associated with the animal surface.

The nMDS performed on species abundance data visualized overlapping groups of samples of diatoms recorded on different hosts, however, the general pattern was visible (Fig. 4). Epizooic samples tended to be placed towards one side of the plot and closer to each other than epiphytic ones, which suggested higher floristic heterogeneity of the latter. The ANOSIM test of substrate

(host organism) factor on epibiotic diatom community composition indicated statistically significant differences between host organisms (global $R = 0.484$, $P = 0.001$). Differences between depths, locations and seasons of sampling were less important (global $R < 0.2$, $P > 0.05$), explaining little of the variations.

Comparing the communities, the highest extent of the average dissimilarity occurred between those found on the surface of *Phyllophora antarctica* thalli and the sessile fauna epiphytic on *Iridaea cordata* (63.3%), while the most similar were diatom communities associated with *P. antarctica* and *Plocamium cartilagineum* (42.3%). In general, epizooic communities differed clearly from epiphytic ones. Higher level of similarity was revealed between the communities associated with *P. antarctica* and *P. cartilagineum* than between those found on *I. cordata* and other macroalgal species (Table II).

Navicula perminuta appeared in abundance in epizooic as well as epiphytic communities, but was more numerous on the animal surface, where they dominated together with *Fragilariopsis nana*, and *Fragilariopsis curta*. In epiphytic communities *Fragilariopsis* species were less important and a greater contribution of large-sized *Cocconeis* valves (*C. fasciolata* and *C. schuettii*) was noted. According to the SIMPER analysis, the above-mentioned taxa together with *Melosira adeliae*, *Achnanthes vincentii*, *Achnanthes brevipes*, *Navicula* cf. *jejunoides* and *Parlibellus* cf. *crucicula* were responsible for more than 60% of the dissimilarity between the epibiotic communities (Table III; for more details see Table S1, which will be found at <http://dx.doi.org/10.1017/S0954102012001101>). In the case of epiphytic complexes, *Navicula perminuta*, *Cocconeis fasciolata*, *C. schuettii*, and *C. costata* var. *antarctica* brought about 45% of total input into the average dissimilarity between the communities associated with different macroalgal species. Analyses of the diatom

Table II. Average dissimilarity (%) between diatom communities associated with the investigated hosts organisms.

	<i>Ph*</i>	<i>Ir</i>	<i>Ir*</i>	<i>Pl</i>	<i>Pl*</i>	epiphytic
<i>Ph</i>	54.04	55.84	63.30	42.28	57.18	-
<i>Ph*</i>	-	61.84	51.37	56.06	48.54	-
<i>Ir</i>	-	-	63.15	53.01	60.64	-
<i>Ir*</i>	-	-	-	58.13	44.74	-
<i>Pl</i>	-	-	-	-	51.95	-
epizooic	-	-	-	-	-	58.93

Ph = samples of epiphytic diatom communities associated with *Phyllophora*, *Ph** = samples of epizooic diatom communities associated with sessile fauna found on *Phyllophora*, *Ir* = samples of epiphytic diatom communities associated with *Iridaea*, *Ir** = samples of epizooic diatom communities associated with sessile fauna found on *Iridaea*, *Pl* = samples of epiphytic diatom communities associated with *Plocamium*, *Pl** = samples of epizooic diatom communities associated with sessile fauna found on *Plocamium*.

Table III. Average abundance of diatoms associated with macroalgae and sessile fauna surfaces, and their contribution to the dissimilarity found between the groups.

Taxa	Average abundance		Average dissimilarity	Contribution (%)	Cumulated (%)
	macroalga	sessile fauna			
<i>Navicula perminuta</i>	17.35	24.04	7.12	12.29	12.29
<i>Fragilariopsis nana</i>	5.03	15.49	5.52	9.53	21.83
<i>Cocconeis fasciolata</i>	13.70	7.88	4.66	8.05	29.87
<i>Fragilariopsis curta</i>	2.68	9.21	3.53	6.08	35.96
<i>Melosira adeliae</i>	1.60	6.00	2.57	4.44	40.39
<i>Achnanthes vincentii</i>	3.78	7.72	2.54	4.38	44.77
<i>Achnanthes brevipes</i>	3.18	7.54	2.52	4.35	49.13
<i>Navicula cf. jejunoides</i>	1.54	5.67	2.39	4.12	53.25
<i>Parlibellus cf. crucicula</i>	0.93	4.39	2.09	3.61	56.85

community species composition suggested that the main differences observed between the analysed communities were not caused by presence or absence of some taxa, but rather by the differential dominance of common species changing somewhat with the host organism and substrate type, and thus determining the general structural features of each complex. Based on the obtained results, a general trend could be seen, as average relative abundance of *C. fasciolata* was markedly higher in samples of *Phyllophora* and *Plocamium* than in those of *Iridaea*, while *C. schuettii* presented the opposite pattern (Tables IV–VI; for more details see Tables S2–S4, which will be found at <http://dx.doi.org/10.1017/S0954102012001101>).

Table VII presents values of species-richness (*d*) and Shannon-Wiener diversity (*H'*) indices of the examined microalgal communities. From 12–27 diatom taxa were found in each macroalgal sample (excluding those composing the epizooic community on the sessile fauna). Samples of *Iridaea* tended to have slightly greater species-richness (ranging from 2.06–4, mean value 2.98) as well as diversity (0.88–2.02, mean value 1.55) in comparison with *Phyllophora* (1.68–4.27 (mean value 2.86) and 0.7–2.02 (mean value 1.37), for the species-richness and diversity indices, respectively) and *Plocamium* (1.45–2.92 (mean value 2.07), and 1.22–1.38 (mean value 1.29)) samples. The difference between epiphytic and epizooic communities was more distinct. Although number of recorded epizooic species varied greatly between samples

(9–30), thus controlling substantially the species-richness value that changed in an analogous manner, the diversity index values were higher (often significantly) for communities associated with the animal substrate (ranging from 0.82–2.47, mean value 1.96), compared with those associated with the host macroalgal thalli (mean value 1.45), in every analysed case.

Discussion

The total number of taxa recorded (73) on the three red macroalgal species studied, was higher than that reported from Potter Cove, King George Island (62°14'S, 58°41'W) by Al-Handal & Wulff (2008a). These authors examined diatoms associated with 19 macroalgal species recording 50 diatom taxa. This is somewhat in discordance with the previously reported trend for the Antarctic ecosystems diversity where the species number decreases moving southward. However, the phenomenon of lower biodiversity at higher latitudes has been described and formulated rather in the context of Antarctic inland waters and attributed mostly to the harsh conditions and geographic isolation (Sabbe *et al.* 2003), while Antarctic seas, especially in the vicinity of research stations, are isolated to a considerably lesser degree (Bargagli 2004). In addition, the previously mentioned authors collected their material during three months in a single year, which is a much shorter sampling period than that considered in

Table IV. Average abundance of diatoms associated with *Phyllophora* and *Iridaea* thalli, and their contribution to the dissimilarity found between the groups.

Taxa	Average abundance		Average dissimilarity	Contribution (%)	Cumulated (%)
	<i>Phyllophora</i>	<i>Iridaea</i>			
<i>Cocconeis fasciolata</i>	18.85	5.25	10.68	19.13	19.13
<i>Navicula perminuta</i>	16.90	16.72	9.01	16.13	35.26
<i>Cocconeis schuettii</i>	1.96	5.94	3.43	6.14	41.40
<i>Fragilariopsis nana</i>	5.43	4.63	3.40	6.08	47.48
<i>Achnanthes vincentii</i>	4.38	2.65	2.37	4.25	51.73
<i>Pseudogomphonema kamtschaticum</i>	1.77	4.65	2.21	3.95	55.68
<i>Cocconeis costata</i> var. <i>antarctica</i>	0.06	3.73	1.91	3.41	59.10

Table V. Average abundance of diatoms associated with *Phyllophora* and *Plocamium* thalli, and their contribution to the dissimilarity found between the groups.

Taxa	Average abundance		Average dissimilarity	Contribution (%)	Cumulated (%)
	<i>Phyllophora</i>	<i>Plocamium</i>			
<i>Navicula perminuta</i>	16.90	23.32	7.92	18.74	18.74
<i>Cocconeis fasciolata</i>	18.85	18.86	4.17	9.86	28.60
<i>Cocconeis schuettii</i>	1.96	6.88	3.47	8.22	36.81
<i>Cocconeis costata</i> var. <i>antarctica</i>	0.06	5.03	2.92	6.91	43.72

our study. The number of macroalgal host species examined by them, on the other hand, was much higher, so it is difficult to judge to what extent these two sets of data are comparable. The fact that more than a half of the diatom taxa (including all the species belonging to *Arachnoidiscus*, *Entopyla*, *Isthmia*, *Licmophora*, *Lyrella*, *Petroneis*, *Pinnularia*, *Planothidium*, *Rhabdonema*, and *Rhoicosphenia* genera) recorded at Potter Cove did not occur in the material collected from Terra Nova Bay may suggest that a substantial fraction of epiphytic diatoms from the Southern Ocean do not have a circum-Antarctic distribution. Considering the high number of rare species (< 1% of total abundance) found during our studies (43), we suspect that many other species, less common and abundant, might have been overlooked. Still, this might be the case also for the Potter Cove's samples, as the "very rare" and "rare" (up to ten frustules noted) taxa clearly prevailed (Al-Handal & Wulff 2008a).

In the present study, individuals of the 20 most abundant diatom taxa contributed between 87% and 100% of the total count, which might be indicative of potentially relatively high homogeneity of epiphytic communities. Amongst them, *Cocconeis schuettii*, *C. fasciolata*, and *Navicula perminuta* exceeded 50% of total relative abundance. The two last mentioned species, as well as *Fragilariopsis nana*, were the most common, appearing in every sample. *Cocconeis fasciolata* as well as *Cocconeis schuettii*, are both well known from Antarctic waters (Scott & Thomas 2005 and references therein). Al-Handal & Wulff (2008a) also reported that *C. fasciolata* was one of the most common epiphytic diatom taxa found, although it appeared only on four rhodophyte species, while *C. schuettii* was "rare or frequent" on most rhodophytes and on three

species of phaeophytes. Sutherland (2008) found *C. fasciolata* to be the dominant species on *Phyllophora antarctica* collected under the ice at Cape Evans (McMurdo Sound, Ross Sea) at 10–15 m depth.

A small naviculoid species, preliminarily named *Navicula* cf. *perminuta*, was reported by Al-Handal & Wulff (2008b) to be one of the most common benthic diatom taxa found at Potter Cove (King George Island). As specimens of this taxon exhibited a wide range of valve shape and seemed to not perfectly correspond to the lectotype material, the question has been raised whether the identity of this small species had been established correctly. Most probably, the same taxon was the most frequent one in the ecological studies on grazing and ultraviolet (UV) radiation effects performed on Antarctic intertidal microalgal assemblages by Zacher *et al.* (2007). The authors related *N. perminuta* prevalence to its rapid adaptation and recovery from UV-B induced stress reported previously by Waring *et al.* (2006). Also McLachlan *et al.* (2009) found a strong light-induced response of this diatom and indicated phototaxis of *Navicula perminuta* as an important adaptation to living in benthic environments. Specimens observed in our samples exhibited even wider range of valve length (< 5 µm to > 18 µm) than that reported by Al-Handal & Wulff (2008b). *Navicula perminuta* is often described as a cosmopolitan, brackish/marine, mezotraphentic, mezo- to polisaprobous species with salinity optimum estimated at 10–30‰ (Underwood & Provot 2000, Majewska *et al.* 2012a and references therein). It seems that its morphology changes with stress treatments (e.g. changing temperature or salinity, R. Majewska, personal observation). Therefore, it remains unclear whether Antarctic and European specimens

Table VI. Average abundance of diatoms associated with *Iridaea* and *Plocamium* thalli, and their contribution to the dissimilarity found between the groups.

Taxa	Average abundance		Average dissimilarity	Contribution (%)	Cumulated (%)
	<i>Iridaea</i>	<i>Plocamium</i>			
<i>Navicula perminuta</i>	16.72	23.32	10.31	19.45	19.45
<i>Cocconeis fasciolata</i>	5.25	18.86	10.17	19.18	38.62
<i>Cocconeis costata</i> var. <i>antarctica</i>	3.73	5.03	4.33	8.18	46.80
<i>Fragilariopsis nana</i>	4.63	4.17	3.19	6.02	52.82
<i>Achnanthes vincentii</i>	2.65	5.05	2.46	4.64	57.46
<i>Cocconeis schuettii</i>	5.94	6.88	2.40	4.53	61.99

Table VII. Values of the Shannon-Wiener diversity index (H') and Margalef's species-richness (d) calculated for each of the epiphytic and epizooic (values in brackets) samples. For sampling site locations see Fig. 1.

Sampling station	Macroalgal host	Depth (m)	Sampling date	S	Species diversity (H')	Species-richness (d)
Cape Russell	<i>I. cordata</i>	17	Feb 2004	16	2.02	2.14
Cape Russell	<i>P. antarctica</i>	17	Feb 2004	13 (23)	1.62 (2.27)	2.12 (3.39)
Cape Russell	<i>P. cartilagineum</i>	15	Feb 2004	13 (18)	1.28 (2.00)	1.85 (2.65)
Adélie Cove	<i>I. cordata</i>	8	Feb 1990	16 (18)	1.25 (1.55)	2.11 (1.97)
Adélie Cove	<i>P. antarctica</i>	8	Feb 1990	20 (21)	1.47 (2.15)	2.43 (2.48)
Adélie Cove	<i>P. cartilagineum</i>	8	Feb 1990	21 (16)	1.38 (2.03)	2.92 (1.95)
Adélie Cove	<i>I. cordata</i>	0.5	Jan 1994	14	1.16	2.06
Adélie Cove	<i>P. cartilagineum</i>	0.5	Jan 1994	12	1.22	1.45
Faraglione	<i>I. cordata</i>	2	Jan 1990	18 (17)	1.52 (2.10)	2.61 (2.20)
Faraglione	<i>P. antarctica</i>	12	Jan 1990	19 (30)	1.93 (2.12)	2.73 (3.36)
Faraglione	<i>P. antarctica</i>	16	Jan 1994	21 (18)	1.60 (2.19)	3.46 (2.55)
Faraglione	<i>I. cordata</i>	3	Jan 1995	16	1.66	2.56
Faraglione	<i>I. cordata</i>	5	Jan 1998	20	1.90	2.97
Faraglione	<i>P. antarctica</i>	5	Jan 1998	24 (20)	1.52 (2.24)	3.10 (2.24)
Faraglione	<i>P. antarctica</i>	15	Jan 1998	13 (9)	1.10 (1.62)	1.70 (1.16)
Faraglione	<i>I. cordata</i>	5	Feb 2000	21	0.88	2.27
Faraglione	<i>P. antarctica</i>	15	Feb 2000	16 (20)	1.04 (1.60)	2.45 (2.70)
Faraglione	<i>I. cordata</i>	6	Feb 2001	20	1.80	4.00
Faraglione	<i>I. cordata</i>	8	Feb 2001	15	1.74	3.23
Faraglione	<i>P. antarctica</i>	8	Feb 2001	19 (22)	1.40 (1.92)	2.62 (2.88)
Faraglione	<i>P. antarctica</i>	13	Feb 2001	19 (16)	0.70 (0.82)	2.16 (1.74)
Faraglione	<i>P. antarctica</i>	15	Jan 2001	25 (18)	1.17 (2.01)	3.25 (2.13)
Molo	<i>I. cordata</i>	5	Feb 1994	26 (8)	1.54 (1.60)	3.85 (0.98)
Molo	<i>I. cordata</i>	5	Feb 1998	23	1.44	3.48
Molo	<i>I. cordata</i>	5	Jan 2000	24	1.47	3.94
Molo	<i>I. cordata</i>	6	Feb 2001	13	1.72	3.28
Molo	<i>P. antarctica</i>	6	Feb 2001	19 (21)	0.99 (1.10)	2.63 (2.52)
Molo	<i>P. antarctica</i>	8	Feb 2001	23 (25)	1.51 (1.90)	3.28 (3.39)
Molo	<i>P. antarctica</i>	12	Jan 2001	24 (13)	1.81 (1.90)	4.11 (1.92)
Molo	<i>P. antarctica</i>	15	Feb 2001	18 (23)	1.36 (2.47)	2.58 (3.31)
Molo	<i>P. antarctica</i>	12	Dec 2002	12 (11)	0.73 (1.58)	1.68 (1.66)
Molo	<i>P. antarctica</i>	17	Dec 2002	26	2.02	4.10
Tethys Bay	<i>P. antarctica</i>	6	Jan 1990	27 (29)	1.97 (2.34)	4.27 (3.65)
Tethys Bay	<i>I. cordata</i>	7	Dec 2002	12	1.54	3.21
Tethys Bay	<i>P. antarctica</i>	7	Dec 2002	17 (13)	1.32 (2.23)	2.53 (1.85)
Tethys Bay	<i>P. antarctica</i>	10.5	Dec 2002	21 (24)	0.97 (2.18)	2.91 (3.48)
Tethys Bay	<i>P. antarctica</i>	13.5	Dec 2002	20 (17)	1.23 (2.21)	3.13 (2.18)
mean	<i>I. cordata</i>	-	-	-	1.55	2.98
mean	<i>P. antarctica</i>	-	-	-	1.37	2.86
mean	<i>P. cartilagineum</i>	-	-	-	1.29	2.07
All samples (mean)					1.45 (1.96)	2.71 (2.51)

are two distinct species. A careful morphological analysis of this taxon, including the comparison of material collected from different geographical regions and thorough revision of previous publications, is in progress.

Fragilariopsis nana was another common and abundant specious species found during this study. This taxon was listed by Kawamura & Ichikawa (1984) as occurring in the subsurface waters of the Indian sector of the Southern Ocean. It was pointed out, however, that due to the difficulties in distinction between *Fragilariopsis cylindrus* and *Fragilariopsis pseudonana* Hasle under the light microscope, these two species were combined and expressed as "*Fragilariopsis 'nana'*". The term was used

again by Kang *et al.* (2001), who included under the name "*Fragilariopsis 'nana'*" all *Fragilariopsis* specimens with valve length < 20 µm. While Scott & Thomas (2005) stated that "*Fragilariopsis nana* is now separated into two taxa": the linear-valved *Fragilariopsis nana*, that is a synonym of *Fragilariopsis cylindrus*, and the elliptical-lanceolate-valved *Fragilariopsis pseudonana*, Cefarelli *et al.* (2010) demonstrated that *F. cylindrus* and *F. nana* are in fact two different taxonomic entities. Although the morphological and molecular studies of Lundholm & Hasle (2008) supported the latter thesis, many authors seem to maintain the concept presented by Scott & Thomas (2005) (Leanne Armand & Amy Leventer, personal communication 2011). Subsequently,

we decided to distinguish between *F. cylindrus* and *F. nana*, as the great majority of isopolar, linear-valved *Fragilariopsis* cells found in the studied material were characterized by valve length of 2.5–10 μm and valve width $< 2.4 \mu\text{m}$. Cells longer than 15 μm (identified as *F. cylindrus*) were rare. Moreover, intermediate transitional forms with valve length $> 10 \mu\text{m}$ and $< 15 \mu\text{m}$ were not observed.

The ANOSIM test indicated a clear relationship between the epiphytic diatom community structure and the host organism type, while the nMDS analysis provided a visual representation of the observed similarities/dissimilarities between samples. Although stress function value of the nMDS model (0.16) higher than 0.15 may indicate that some distances in the two-dimensional map are distorted (Kruskal & Wish 1978), analysis allowed organization of data in a useful manner and the “first-glance” conclusions could be drawn. A marked difference between the communities associated with various host macroalgae was evident. In addition, the epiphytic communities differed significantly from epizooic ones. This observation is also confirmed by the fact that the estimated diversity index was always higher for the latter. A similar trend was not observed for species-richness. Here, however, a difference in the surface of examined substrate must be taken into account, as we did not search for sessile fauna, but randomly examined the thallus portion. Thus, the studied surface of the faunistic component observed in certain samples was often lower than the viewed surface of the host macroalgae (3 mm²). Smaller examined-surface most probably negatively influenced the number of diatom taxa found, which, in turn, led to the lower species-richness. As the diversity index does not directly depend on the species number, in this case mentioned discrepancy was negligible. Higher values of diversity index correspond to more even distribution of diatom taxa, which might possibly be due to the higher number of niches provided by sessile fauna with its numerous external surface protuberances (Huston 1979). This effect has already been noticed and more fully discussed in a previous work (Majewska *et al.* 2012b).

Interestingly, contrary to previous studies focused on epiphytic diatom growth forms, the host macroalgal species appeared to be a major factor influencing epiphytic diatom community structure. Depth, site, as well as time of sampling (year and month) seemed to be of secondary importance. Although we cannot exclude that due to the high number of factors that differentiated the examined samples, some relations might have been blurred.

Previously reported growth form analysis showed no overall distinction between communities associated with different macroalgal species (Majewska *et al.* 2012b), largely because most of the differences occurred between diatom species with the same growth form. This tendency was most pronounced for the samples of *Iridaea* and *Phyllophora*: while the latter was densely covered by *Cocconeis fasciolata*,

and a few valves of *C. schuettii* were usually noted, the opposite pattern was found on *Iridaea* blades. Considering a significant difference in size of the observed specimens belonging to two *Cocconeis* species (Figs 2 & 3), we suppose that the relation could be even better expressed by biomass than by abundance. Rather homogenous surface of macroalgal thalli, providing more uniform microenvironment for associated microalgae, favours competitive exclusion of species sharing similar niches. Thus, observed preferences for a specific host macroalga might be an example of adaptation enhancing competitiveness (Huston 1979 and references therein, Martin 1998).

With this study, we hope to contribute to knowledge regarding ecology and biogeography of Antarctic marine diatoms. As the discourse centring on Antarctic diatom species endemism/cosmopolitanism is still very much alive (e.g. Vanormelingen *et al.* 2008), we are fully aware of the profound influence of taxonomic practice on the various theories and perception of not only single taxon distribution patterns but also whole ecosystem structure and functioning. Trivial taxonomic errors, often overlooked and underestimated, create misleading hypotheses and ideas affecting our knowledge within the field of all environmental sciences (Saabe *et al.* 2003, Bortolus 2008). Although modern microscopic techniques (including scanning electron microscopy) provide detailed information on the diatom frustule structure and allow for its more accurate interpretation, recently obtained results are usually not comparable to those reported in old publications (e.g. Mangin 1915, Hustedt 1958). In many cases, the paucity of relevant information in the original descriptions and a lack of adequate illustrations makes identification based on these materials a doubtful procedure (Al-Handal & Wulff 2008a, 2008b, Vanormelingen *et al.* 2008). Therefore, emerging need for supplementation of missing data must be highlighted.

Most of the species listed here have already been found in Antarctica, although not necessarily in the Ross Sea (e.g. Scott & Thomas 2005, Al-Handal & Wulff 2008a, 2008b), and not necessarily as epiphytes. Nevertheless, some of them are probably new records. Relatively high number of uncertain or unidentified species indicates the need for further taxonomic studies. Some of the specimens we have tentatively identified as *Cocconeis* cf. *californica* and *Cocconeis* cf. *costata* presented a very wide range of morphological variability and new species or varieties can be possibly erected from this complex. Moreover, the gradual decrease in cell size and significant differences in valve dimensions within each taxon related to the diatom life cycle, led often to the prominent changes in valve morphology (e.g. *Achnanthes brevipes*, *Pseudogomphonema kamtschaticum*). Forms exhibiting only a few morphological characters useful for identification (e.g. small fragilarioid diatoms, *Nitzschia* genus), were another challenging group. Taking into consideration the “notoriously messy” diatom taxonomy (after Vanormelingen *et al.* 2008), as well as a general

scarcity of explicit references, it was tempting to indicate most of the diatom forms found as “dubious”. We believe that further investigation that is currently being undertaken, will provide reliable information and throw more light on the aforementioned taxonomic problems.

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Supplemental material

Four supplemental tables will be found at <http://dx.doi.org/10.1017/S0954102012001101>.

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