

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/301299752>

# Summer Epiphytic Diatoms from Terra Nova Bay and Cape Evans (Ross Sea, Antarctica) – A Synthesis and Final Conclusions

Article in PLoS ONE · April 2016

DOI: 10.1371/journal.pone.0153254

CITATION

1

READS

138

3 authors:



**Roksana Majewska**

North West University South Africa

25 PUBLICATIONS 63 CITATIONS

[SEE PROFILE](#)



**Peter Convey**

British Antarctic Survey

364 PUBLICATIONS 14,144 CITATIONS

[SEE PROFILE](#)



**Mario De Stefano**

Second University of Naples

115 PUBLICATIONS 1,558 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Endophytic fungi from forest plants at the Astroni Nature Reserve [View project](#)



Biogeography of Antarctic Springtails [View project](#)

All content following this page was uploaded by [Roksana Majewska](#) on 16 April 2016.

The user has requested enhancement of the downloaded file. All in-text references [underlined in blue](#) are added to the original document and are linked to publications on ResearchGate, letting you access and read them immediately.

RESEARCH ARTICLE

# Summer Epiphytic Diatoms from Terra Nova Bay and Cape Evans (Ross Sea, Antarctica) - A Synthesis and Final Conclusions

Roksana Majewska<sup>1,2\*</sup>, Peter Convey<sup>3</sup>, Mario De Stefano<sup>1</sup>

**1** Department of Environmental, Biological and Pharmaceutical Sciences and Technologies, II University of Naples, 81100, Caserta, Italy, **2** BioNEM Laboratory, Department of Experimental and Clinical Medicine, University "Magna Græcia" of Catanzaro, 88100, Catanzaro, Italy, **3** British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, CB3 0ET, United Kingdom

\* [roksana.majewska@unina2.it](mailto:roksana.majewska@unina2.it)



**OPEN ACCESS**

**Citation:** Majewska R, Convey P, De Stefano M (2016) Summer Epiphytic Diatoms from Terra Nova Bay and Cape Evans (Ross Sea, Antarctica) - A Synthesis and Final Conclusions. PLoS ONE 11(4): e0153254. doi:10.1371/journal.pone.0153254

**Editor:** Judi Hewitt, University of Waikato (National Institute of Water and Atmospheric Research), NEW ZEALAND

**Received:** December 31, 2015

**Accepted:** March 26, 2016

**Published:** April 14, 2016

**Copyright:** © 2016 Majewska et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Data Availability Statement:** All relevant data are within the paper and its Supporting Information files.

**Funding:** This work was supported by the Second University of Naples ([www.unina2.it](http://www.unina2.it)) and the Italian National Program of Research in Antarctica (PNRA) co-ordinated by the Italian National Research Council ([www.cnr.it/sitocnr/home.html](http://www.cnr.it/sitocnr/home.html)) [grant ID: 2010/A1.02, MD]. PC is supported by the Natural Environment Research Council ([www.nerc.ac.uk](http://www.nerc.ac.uk)) core funding to the British Antarctic Survey ([www.bas.ac.uk](http://www.bas.ac.uk)) Biodiversity, Evolution and Adaptation Team. The funders had no role in study design, data collection

## Abstract

Despite recent advances in polar marine biology and related fields, many aspects of the ecological interactions that are crucial for the functioning of Antarctic shallow water habitats remain poorly understood. Although epiphytic diatoms play an essential role in the Antarctic marine food web, basic information regarding their ecology, biodiversity and biogeography is largely unavailable. Here, we synthesise studies on Ross Sea epiphytic diatoms collected during 11 summer Antarctic expeditions between the years 1989/90 and 2011/12, presenting a full list of diatom taxa associated with three macroalgal species (*Iridaea cordata*, *Phyllophora antarctica*, and *Plocamium cartilagineum*) and their epiphytic sessile fauna. Diatom communities found during the three summer months at various depths and sampling stations differed significantly in terms of species composition, growth form structure and abundances. Densities ranged from 21 to >8000 cells mm<sup>-2</sup>, and were significantly higher on the surface of epiphytic micro-fauna than on any of the macroalgal species examined. Generally, host organisms characterized by higher morphological heterogeneity (sessile micro-fauna, ramified *Plocamium*) supported richer diatom communities than those with more uniform surfaces (*Iridaea*). Differences between epiphytic communities associated with different macroalgae were reflected better in species composition than in growth form structure. The latter changed significantly with season, which was related strongly to the changing ice conditions. A general trend towards an increasing number of erect forms in deeper waters and tube-dwelling diatoms in the shallowest sites (2–5 m) was also observed. This study explores further important and largely previously unknown aspects of relationships and interactions between Antarctic epiphytic diatoms and their micro- and macro-environments.

and analysis, decision to publish, or preparation of the manuscript.

**Competing Interests:** The authors have declared that no competing interests exist.

## Introduction

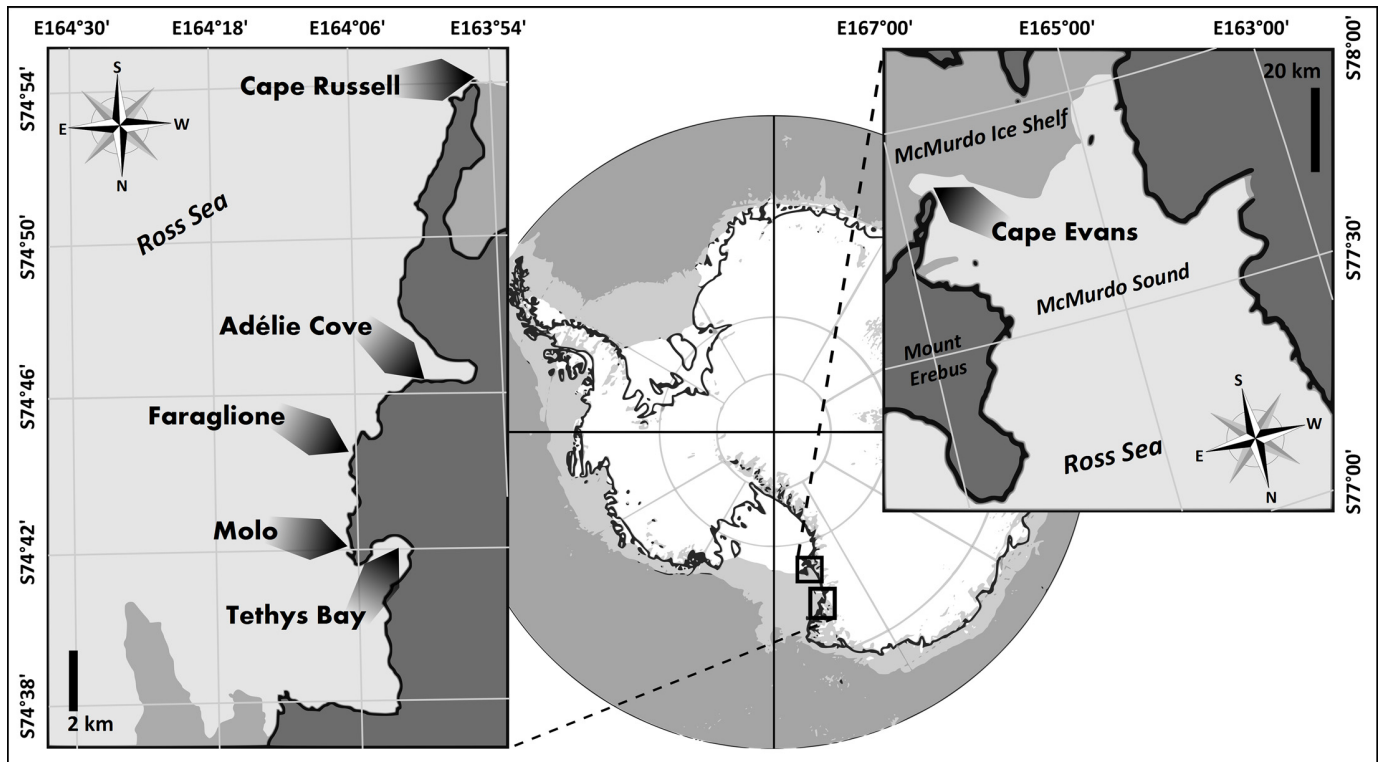
Macroalgae are an important element of the shallow-water ecosystems of the Ross Sea. They provide refuge and habitats for micro- and macrofaunal communities and comprise a large biomass. Undoubtedly they constitute a significant food source for Antarctic marine organisms, but with most of this flowing through detritus-based food chains [1, 2, 3, 4, 5]. By this means, mineral nutrients are released into the water and sediments and can be assimilated by aquatic primary producers and incorporated again into the trophic system [6, 7]. Many herbivorous species also find both shelter and appropriate food source within the dense macroalgal beds, taking advantage of the rich diatom communities that often cover all submerged surfaces, including various parts of macroalgal thalli. There is growing evidence that a large proportion of the Antarctic herbivorous fauna feed mainly on benthic diatoms, which constitute a high quality and readily available food source [8, 9, 10, 11, 12, 13, 14, 15, 16]. However, although epiphytic diatom communities clearly must play a particularly important role in the functioning of Antarctic shallow water ecosystems, many aspects of their ecology, taxonomy, distribution and biodiversity remain understudied and poorly understood.

Epiphytic diatom species are rarely reported in paleoenvironmental studies although they are often found in Antarctic marine sediments [17, 18, 19, 20, 21]. There is currently a pressing need for taxonomic and ecological characterization of polar diatoms for application in both paleoenvironmental and monitoring studies [22, 23, 24, 25]. However, for the generally unknown and unidentified Antarctic benthic species, environmental roles and significance cannot yet be established and, thus, the utility of benthic diatoms in paleoecological studies is currently limited [26, 27]. Therefore, detailed investigation of the contemporary distribution and diversity of Ross Sea epiphytic diatom communities and the factors controlling these is important to the understanding and proper interpretation of modern and past variations in the benthic diatom flora of this region.

This study builds on the results of a recent survey of marine epiphytic diatoms from the Ross Sea [28, 29, 30, 31]. We focus on epiphytic diatoms from Terra Nova Bay and Cape Evans (McMurdo Sound; Fig 1) examining material obtained during 11 summer Antarctic expeditions to these locations in the seasons 1989/90–2011/12. No comparable studies of epiphytes from other locations in the Ross Sea are available. We present qualitative and quantitative assessments of various components of the marine epiphytic diatom communities in order to derive better understanding of the multiple interactions that occur between them and the local environment. Biological, physical and chemical factors may regulate abundance, distribution and species composition of diatom communities associated with marine macroalgae. Amongst these, host macroalgal morphology, sampling site location and depth, grazing pressure, stage of season and ice formation and thaw have been identified as important factors influencing the shallow water communities [28, 29, 30, 31, 32, 33]. Reliable description of basibiont-epibiont-environment interactions is difficult as some of the factors involved are as yet unknown, while the environmental parameters likely to control Antarctic diatom development are strongly and dynamically interrelated. Thus, assessing the influence of each of the selected environmental factors, we considered both their direct effect on the diatom communities and the more ambiguous and complex interactions occurring among all of the elements in the investigated system.

## Materials and Methods

All samples were obtained during different Italian Antarctic Expeditions organized in the framework of the Italian National Antarctic Program (it. PNRA) coordinated by the Ministry of Education, University and Research (MIUR) through three national bodies: the National Scientific Committee for Antarctica (CSNA), the National Research Council (CNR), and the



**Fig 1. Study area and sampling sites.**

doi:10.1371/journal.pone.0153254.g001

National Agency for New Technologies, Energy and Sustainable Economic Development (ENEA). Through the Antarctic Treaty System (ATS), the countries active in Antarctica, including Italy, consult on the uses of a whole continent and comply fully with the ATS's regulatory requirements. Thus, all aspects related to material collection during the Italian Antarctic expeditions are regulated by the Antarctic Treaty and international rules of Antarctic environmental protection. In the present studies, samples collected within Antarctic Specially Protected Area No 161 (ASPA 161) were used. Permits for access and sampling in this area were issued by the Italian Ministry of Foreign Affairs upon a thorough evaluation of the research project. Our study did not involve endangered or protected species.

### Sampling stations

Thalli of three common macroalgal species (*Iridaea cordata*, *Phyllophora antarctica*, *Placodium cartilagineum*) were collected by SCUBA divers from regularly used sampling locations: Tethys Bay (74°41.923'S, 164°01.670'E), Molo (74°54.187'S, 163°55.185'E), Faraglione (74°43.048'S; 164°06.425'E), Adélie Cove (74°46.470'S, 163°59.328'E), Cape Russell (74°41.393'S, 164°6.946'E) [29, 30, 31], and Cape Evans (77°38.066'S, 166°24.847'E; Fig 1; Table 1).

### Sampling procedures

At Cape Evans samples were collected through holes made in the sea ice with a Reed drill [28] (for list of samples see S1 Table). Healthy thalli of similar size were carefully scraped off the rocks and placed in individual plastic bags. Immediately after collection, the material was fixed with 4% formaldehyde solution in filtered sea water. As we were interested in the entire

**Table 1. Description of sampling effort: number of samples, replicates and macroalgal surface examined in different months and at various sites within the Ross Sea.** In addition, a proportional value of macroalgal surface covered by epiphytic sessile fauna is given.

	Number of taxa found (genera)	Number of samples (replicates)	Total surface examined (mm <sup>2</sup> )	Months	Associated fauna (% of surface)	Sampling sites*	Locations**
<i>Iridea cordata</i>	55 (26)	14 (42)	42	Dec, Jan, Feb	3.1	CR, AC, F, M, TB	TNB
<i>Phyllophora antarctica</i>	95 (39)	24 (100)	140	Dec, Jan, Feb	9.5	CR, AC, F, M, TB, CE	TNB, MS
<i>Plocamium cartilagineum</i>	60 (29)	8 (24)	39	Jan, Feb	6.8	CR, AC, F	TNB
In total	109 (44)	46 (166)	221	Dec, Jan, Feb	7.8	CR, AC, F, M, TB, CE	TNB, MS

\*CR—Cape Russell, AD—Adélie Cove, F—Faraglione, M—Molo, TB—Tethys Bay, CE—Cape Evans

\*\*TNB—Terra Nova Bay, MS—McMurdo Sound

doi:10.1371/journal.pone.0153254.t001

surface-associated community (including both metaphytic and true epiphytic taxa), no additional cleaning procedures were applied before the fixation in formalin [29, 30].

### Microscopic analyses

For diatom counting and growth form analysis, ca. 1 cm<sup>2</sup> subsamples were cut from each of the thalli collected. Macroalgal pieces were then dehydrated through a 25, 50, 60, 70, 80, 90, 95, 100% alcohol series, treated with a Critical Point Dryer (K850 EMITECH), placed on aluminium stubs and sputter-coated with gold-palladium or platinum using a DESK V HP TSC Cold Sputter Coater. For taxonomic examination, small sections (ca. 2 cm<sup>2</sup>) of macroalgal thalli were digested with boiling concentrated acid (64% nitric acid and 97% sulphuric acid in a 1:3 volume ratio), rinsed thoroughly with distilled water, centrifuged and decanted. Prior to SEM observations, clean material was mounted on aluminium stubs and sputter-coated with platinum. Diatoms were identified and enumerated on a surface area of ca. 1–2 mm<sup>2</sup> of each of the 166 collected macroalgal individuals at magnifications ranging between 400x to 60000x using JEOL JSM 60/60 LW and Zeiss Supra 40 scanning electron microscopes. In addition, for the epizooic community analyses, 0.5 mm<sup>2</sup> (or larger) samples of epiphytic sessile microfauna were examined for each *Phyllophora* and *Plocamium* thallus.

### Species classification

For structural and functional analysis of the communities, identified taxa were divided into growth form groups: erect (epiphytic cells attached to the substrate by stalks, pads or peduncles), adnate (cells strongly adhering to macroalgal surface), motile (biraphid cells moving on the substrate surface), tube-dwelling (cells producing mucilage tubes), planktonic (true pelagic species), and plocon (metaphytic cells loosely associated with the algal surface). The following literature was used to identify the diatom specimens: Ehrenberg [34], Van Heurck [35], Mangin [36], Peragallo [37], Heiden and Kolbe [38], Manguin [39, 40], Frenguelli and Orlando [41], Hustedt [42], Frenguelli [43], Hasle [44], Poulin *et al.* [45, 46, 47], Hasle *et al.* [48], Romero and Rivera [49], Cremer *et al.* [50], Scott and Thomas [51], Fernandes *et al.* [52], Al-Handal *et al.* [53, 54], Al-Handal and Wulff [55, 56], Cefarelli *et al.* [57], and Riaux-Gobin *et al.* [58].

## Statistical analyses

Statistical analyses were performed using Canoco v5 [59], EstimateS v9.1 [60] and Primer v6 [61] software. Analysis of similarities (ANOSIM) was used to determine whether significant differences in diatom community growth form structure and species composition occurred among the selected macroalgal species, sampling seasons, sites, and depths. Nonmetric multidimensional scaling (nMDS) ordination was used to display differences in communities associated with different macroalgal hosts. To estimate the similarity within groups and dissimilarity among them, and to indicate the percentage contribution of the most important species to the average inter-group dissimilarity, a similarity percentage analysis (SIMPER) was applied. To visualize the effects of selected factors on diatom communities, a redundancy analysis (RDA) and partial RDA were performed on log-transformed abundance data and biplot diagrams were drawn. A Monte Carlo permutation test was used to test the significance of the axes (4999 permutations,  $p < 0.05$ ). In addition, taxa accumulation curves and estimated total species richness were computed using sample-based rarefaction and functional extrapolation methods proposed by Colwell *et al.* [60, 62].

## Results

### Diatom species composition

A total of 109 diatom species (44 genera) was found during the survey (Table 2). Three species, *Cocconeis fasciolata*, *Fragilariopsis nana* and *Navicula perminuta* occurred in all 46 samples (166 macroalgal replicates) analysed, and *Achnanthes brevipes*, *A. vicentii*, *C. antiqua*, *F. curta*, *Melosira adeliae*, *Pseudogomphonema kamtschaticum* and *Synedropsis recta* were present in more than 75% of the samples. Eight species (*Cocconeis antiqua*, *C. costata*, *C. fasciolata*, *F. nana*, *Melosira adeliae*, *Navicula perminuta*, *Parlibellus delognei*, *Pseudogomphonema kamtschaticum*) contributed 25% of total diatom abundance. Of these, *Cocconeis antiqua* comprised over 50% of diatoms counted in at least one of the samples and *C. fasciolata* and *Navicula perminuta* contributed 75% of the total diatom numbers. Twenty-six taxa were found in only a single sample, and 65 species contributed less than 1% of the total diatom abundance across all samples (Table 2).

### Diatom communities and environmental factors

ANOSIM indicated that the diatom communities differed significantly among different sampling seasons, sites, and depths in terms of both species composition and growth form structure. The highest Global R (0.485) value was obtained in the analysis of similarity among diatom communities associated with different macroalgal species when growth form was considered, indicating a high separation between the groups. However, the same test performed on species data indicated that the difference between communities on different macroalgal hosts was not significant ( $p > 0.05$ ; Table 3). Growth form structure appeared to be a parameter that better reflected differences among communities when testing the influence of season and depth, but not that of sampling site (Table 3).

### Host macroalga

The nMDS performed on species abundance data revealed differences among diatom communities associated with different macroalgal hosts (Fig 2). A relatively low stress value (0.15) indicated that the 2-dimensional solution was sufficient to obtain a reliable result. As indicated by SIMPER analysis, average similarity within groups was 41%, 47%, and 57.8% for *Iridaea*, *Phyllophora*, and *Plocamium* epiphytes, respectively. The level of dissimilarity between groups



**Table 2. Epiphytic diatoms recorded on three macroalgal host species (*Iridaea cordata*, *Phyllophora antarctica*, *Plocamium cartilagineum*) at six sampling sites during 11 Antarctic expeditions.**

TAXA	% of total abundance	host macroalga*	Locations**	% of samples***			
				<i>Iridaea cordata</i>	<i>Phyllophora antarctica</i>	<i>Plocamium cartilagineum</i>	All samples
<i>Achnanthes brevipes</i> Agardh	<1–13.6	Ir, Ph, PI	CR, AC, F, M, TB, CE	93	100	100	97.8
<i>Achnanthes</i> sp. 1	<1	PI	F	0	0	37.5	6.5
<i>Achnanthes</i> sp. 2	<1	Ph, PI	F	0	4.2	25	6.5
<i>Achnanthes</i> sp. 3	<1–13.7	Ph	AC, TB, CE	0	12.5	0	6.5
<i>Achnanthes vicentii</i> Manguin	<1–18.1	Ir, Ph, PI	CR, AC, F, M, TB, CE	71.5	100	100	91.3
<i>Actinocyclus actinochilus</i> (Ehrenberg) Simonsen	<1	Ir	F	7.1	0	0	2.2
<i>Amphiprora kufferathii</i> Manguin	<1	Ph	AC, M, F	0	25	0	13
<i>Amphora</i> cf. <i>cymbelloides</i> Grunow	<1–2.6	Ph	TB, CE	0	8.3	0	4.3
<i>Amphora</i> cf. <i>racovitzae</i> Van Heurck	<1	Ir, Ph	F, M, CE	14.3	29.2	0	19.6
<i>Amphora</i> cf. <i>terroris</i> Ehrenberg	<1	Ph, PI	AC, F, TB, CE	0	50	12.5	15.2
<i>Amphora racovitzae</i> Van Heurck	<1–1.4	Ir, Ph, PI	CR, AC, F, M, TB	28.6	66.7	87.5	58.7
<i>Amphora</i> sp. 1	<1–10	Ir, Ph, PI	AC, F, M, TB, CE	50	66.7	87.5	65.2
<i>Amphora</i> sp. 2	<1	Ir, Ph, PI	AC, F, M, TB	14.3	29.2	12.5	21.7
<i>Amphora</i> type C (sensu Scott & Marchant, 2005)	<1	Ir, Ph	F, M	7.1	8.3	0	6.5
<i>Asteromphalus hookeri</i> Ehrenberg	<1	Ph	M	0	4.2	0	2.2
<i>Attheya gaussii</i> (Heiden) Crawford	<1	Ph, PI	CR, AC, F, M	0	16.75	62.5	19.6
<i>Auricula compacta</i> (Hustedt) Medlin	<1	Ir, Ph, PI	CR, AC, F, M, TB	28.6	29.2	37.5	30.4
<i>Brandinia mosimanniae</i> Fernandes & Procopiak	<1–1.6	Ir, Ph	AC, F	7.1	12.5	37.5	15.2
<i>Chaetoceros dictaeta</i> Ehrenberg	<1	PI	F	0	0	12.5	2.2
<i>Chaetoceros neglectus</i> Karsten	<1–7	PI	AC, F	0	0	62.5	20.8
<i>Chaetoceros</i> sp. 1	<1–2.4	Ph, PI	AC, F	0	8.3	62.5	15.2
<i>Chaetoceros</i> sp. 2	<1–1.2	Ph	AC, F, TB	0	12.5	0	6.5
<i>Cocconeis antiqua</i> Tempère & Brun	<1–54.5	Ir, Ph, PI	CR, AC, F, M	100	70.8	87.5	82.6
<i>Cocconeis californica</i> var. <i>kerquelenensis</i> Heiden	<1	Ph	TB	0	4.2	0	2.2
<i>Cocconeis</i> cf. <i>californica</i> Grunow	<1	Ph	AC, F, M, TB	0	16.7	0	8.7
<i>Cocconeis</i> cf. <i>californica</i> sensu Al-Handal & Wulff [55]	<1–23.8	Ir, Ph, PI	CR, AC, F, M, TB	14.3	16.7	75	26.1
<i>Cocconeis</i> cf. <i>costata</i> Gregory	<1	Ir	F	7.1	0	0	2.2
<i>Cocconeis</i> cf. <i>neothumensis</i> Krammer	<1	Ph	CE	0	4.2	0	2.2
<i>Cocconeis</i> cf. <i>stauroneiformis</i> (W. Smith) Okuno	<1–11.3	Ph, PI	AC, F, M, TB, CE	0	25	75	26.1
<i>Cocconeis costata</i> Gregory var. <i>antarctica</i> Manguin	<1–42.6	Ir, Ph, PI	AC, F, M	7.1	12.5	50	21.7
<i>Cocconeis fasciolata</i> (Ehrenberg) Brown	<1–78.8	Ir, Ph, PI	CR, AC, F, M, TB, CE	100	100	100	100

(Continued)

Table 2. (Continued)

TAXA	% of total abundance	host macroalga*	Locations**	% of samples***			
				<i>Iridae cordata</i>	<i>Phyllophra antarctica</i>	<i>Plocamium cartulagineum</i>	All samples
<i>Cocconeis melchioroides</i> Al-Handal, Riaux-Gobin, Romero & Wulff	<1–12.2	Ph, PI	F, AC	0	4.2	62.5	13
<i>Cocconeis</i> sp. 1 (sensu Al-Handal and Wulff [56])	<1	Ir, Ph	AC, M, CE	7.1	8.3	0	6.5
<i>Cocconeis</i> sp. 2 (sensu Majewska et al. [29])	<1–5.2	Ir, Ph, PI	AC, F, M, TB	50	62.5	50	56.5
<i>Cocconeis</i> sp. 3 (sensu Majewska & De Stefano [28])	<1–2.6	Ph	TB, CE	0	8.3	0	4.3
<i>Cocconeis</i> sp. 4 (sensu Majewska et al. [31])	<1	PI	F	0	0	12.5	2.2
<i>Coscinodiscus</i> sp.	<1	Ir	M	7.1	0	0	2.2
<i>Entomoneis</i> sp.	<1	Ph	F	0	8.3	0	4.3
Eunotioid	<1	Ph	CE	0	4.2	0	2.2
<i>Eunotogramma marginopunctatum</i> Long, Fuge & Smith	<1	Ph	CE	0	4.2	0	2.2
<i>Fallacia marnieri</i> (Manguin) Witkowski, Lange-Bertalot & Metzeltin	<1–1.5	Ph, PI	CR, AC, F, M, TB, CE	0	87.5	37.5	52.2
<i>Fragilaria</i> cf. <i>striatula</i> Lyngbye	<1–4.4	Ph, PI	AC, F, TB	0	8.3	62.5	15.2
<i>Fragilaria islandica</i> var. <i>adeliae</i> Manguin	<1–1.4	Ir, Ph, PI	AC, F, M, TB, CE	7.1	33.3	12.5	21.7
<i>Fragilaria</i> sp.1	<1–7.2	Ir, Ph	F, M, TB	14.3	29.2	0	19.6
<i>Fragilaria</i> sp.2	<1	Ph	CE	0	4.2	0	2.2
<i>Fragilariopsis curta</i> (Van Heurck) Krieger	<1–14.2	Ir, Ph, PI	CR, AC, F, M, TB, CE	92.9	100	100	97.8
<i>Fragilariopsis cylindrus</i> (Grunow) Krieger	<1–1.6	Ir, Ph	TB, M, F	14.3	12.5	0	10.9
<i>Fragilariopsis kergulensis</i> (O'Meara) Hustedt	<1	Ph	TB, M	0	8.3	0	4.3
<i>Fragilariopsis nana</i> (Steemann Nielsen) Paasche	<1–34.2	Ir, Ph, PI	CR, AC, F, M, TB, CE	100	100	100	100
<i>Fragilariopsis obliquocostata</i> (Van Heurck) Heiden	<1	Ir, Ph, PI	CR, AC, F, M, TB	21.4	20.8	12.5	19.6
<i>Fragilariopsis rhombica</i> (O'Meara) Hustedt	<1	Ph	CR	0	4.2	0	2.2
<i>Fragilariopsis ritscheri</i> Hustedt	<1	Ir, Ph, PI	AC, F, M, TB	7.1	12.5	25	13
<i>Fragilariopsis sublinearis</i> (Van Heurck) Heiden	<1	Ir, Ph, PI	CR, AC, F, M, TB, CE	7.1	20.8	50	21.7
<i>Gomphonemopsis littoralis</i> (Hendey) Medlin	<1	Ph	CE	0	4.2	0	2.2
<i>Grammatophora arctica</i> Cleve	<1	Ir, Ph	F, CE	14.3	4.2	0	6.5
<i>Grammatophora arcuata</i> Ehrenberg	<1–1.5	Ir, Ph, PI	AC, F, M, CE	7.1	20.8	25	17.4
<i>Gyrosigma</i> sp.	<1	Ir, Ph	AC	7.1	4.2	0	4.3
<i>Haslea trompii</i> (Cleve) Simonsen	<1	Ph	AC	0	4.2	0	2.2
<i>Hyalodiscus</i> sp.	<1	PI	F	0	0	12.5	2.2
<i>Licmophora gracilis</i> (Ehrenberg) Grunow	<1	PI	F	0	0	12.5	2.2

(Continued)



Table 2. (Continued)

TAXA	% of total abundance	host macroalga*	Locations**	% of samples***			
				<i>Iridae cordata</i>	<i>Phyllophra antarctica</i>	<i>Plocamium cartulagineum</i>	All samples
<i>Melosira adeliae</i> Manguin	<1–27.4	Ir, Ph, PI	CR, AC, F, M, TB, CE	92.9	79.2	87.5	84.8
<i>Melosira moniliformis</i> var. <i>australis</i> (Peragallo) Manguin	<1	Ph, PI	AC, F	0	4.2	12.5	4.3
<i>Melosira</i> sp.	<1	Ph	CE	0	4.2	0	2.2
<i>Navicula</i> cf. <i>criophila</i> (Castracane) De Toni	<1	Ph, PI	F, CE	0	4.2	37.5	8.7
<i>Navicula</i> cf. <i>gelida</i> Grunow	<1	Ir, Ph	F, M	7.1	4.2	0	4.3
<i>Navicula</i> cf. <i>incertata</i> Lange-Bertalot & Krammer	<1–6	Ir, Ph	CR, AC, F, M, TB	50	75	0	54.3
<i>Navicula</i> cf. <i>jejunoides</i> Van Heurck	<1–6.7	Ir, Ph, PI	CR, AC, F, M, TB, CE	42.9	83.3	75	69.6
<i>Navicula directa</i> (W Smith) Ralfs	<1	Ir, Ph, PI	F, M, TB, CE	14.3	25	12.5	19.6
<i>Navicula glaciei</i> Van Heurck	<1–11.3	Ir, Ph, PI	CR, AC, F, M, TB, CE	50	79.2	75	69.6
<i>Navicula perminuta</i> Grunow	5.8–75.4	Ir, Ph, PI	CR, AC, F, M, TB, CE	100	100	100	100
<i>Navicula</i> sp. 1	<1	Ph	F, CE	0	8.3	12.5	6.5
<i>Navicula</i> sp. 2	<1	Ph	CE	0	4.2	0	2.2
<i>Navicymbula</i> sp.	<1–1.7	PI	AC, F	0	8.3	62.5	15.2
<i>Nitzschia acicularis</i> (Kützing) W. Smith	<1	Ph, PI	AC, F, M	0	12.5	37.5	13
<i>Nitzschia</i> cf. <i>australis</i> (M. Peragallo) A. Mann	<1	PI	F	0	0	12.5	2.2
<i>Nitzschia</i> cf. <i>lecointei</i> Van Heurck	<1–2.7	Ir, Ph, PI	AC, F, M, TB, CE	14.3	45.8	62.5	39.1
<i>Nitzschia</i> cf. <i>palea</i> (Kützing) W. Smith	<1–5.5	PI	AC, F	0	0	62.5	10.9
<i>Nitzschia medioconstricta</i> Hustedt	<1–2.5	Ir, Ph, PI	AC, F, M, TB	42.9	75	75	65.2
<i>Nitzschia</i> sp. 1	<1	Ir, Ph	CR, AC, F, M, CE	21.4	25	0	19.6
<i>Nitzschia</i> sp. 2	<1	Ph	CE	0	4.2	0	2.2
<i>Nitzschia stellata</i>	<1–2.4	Ir, Ph	CR, AC, F, M, TB, CE	42.9	70.8	0	50
<i>Odontella litigiosa</i> (Van Heurck) Hoban	<1–1.6	Ir, Ph, PI	AC, F, M, TB, CE	7.1	12.5	37.5	15.2
<i>Paralia sol</i> (Ehrenberg) Crawford	<1–1.2	Ir, Ph, PI	CR, AC, F, M	7.1	16.7	25	15.2
<i>Parlibellus delognei</i> (Van Heurck) Cox	<1–41.2	Ir, Ph	AC, F, M, TB	57.1	75	0	56.2
<i>Pinnularia quadratarea</i> (Schmidt) Cleve	<1	Ph	AC, F, TB	0	12.5	0	6.5
<i>Planothidium</i> cf. <i>dubium</i> (Grunow) Round & Bukhtiyarova	<1	PI	AC	0	0	12.5	2.2
<i>Planothidium</i> sp.	<1	Ph	TB	0	4.2	0	2.2
<i>Pleurosigma directum</i> Grunow	<1	Ir, Ph, PI	CR, AC, F, M, TB	14.3	16.7	12.5	15.2
<i>Pleurosigma</i> sp.	<1	Ph	CE	0	4.2	0	2.2
<i>Podosira</i> sp.	<1–1.3	Ir, Ph, PI	CR, AC, F, M, TB	14.3	33.3	35	4.3

(Continued)

Table 2. (Continued)

TAXA	% of total abundance	host macroalga*	Locations**	% of samples***			
				<i>Iridaea cordata</i>	<i>Phyllophora antarctica</i>	<i>Plocamium cartilagineum</i>	All samples
<i>Porosira glacialis</i> (Grunow) Jørgensen	<1	Ir, Ph, PI	F, M, TB, CE	7.1	37.5	62.5	32.6
<i>Porosira pseudodenticulata</i> (Hustedt) Jousé	<1	Ph	AC, F, TB	0	12.5	0	6.5
<i>Pseudogomphonema kantschaticum</i> (Grunow) Medlin	<1–32.1	Ir, Ph, PI	CR, AC, F, M, TB, CE	100	95.8	87.5	95.7
<i>Pseudonitzschia</i> sp.	<1	Ph, PI	AC, F, M	0	12.5	12.5	8.7
<i>Pseudostaurosira brevistriata</i> (Grunow) DM Williams & Round	<1	Ph, PI	AC, F, TB, CE	0	25	37.5	17.4
<i>Rhizosolenia</i> sp.	<1	Ph	TB	0	4.2	0	2.2
<i>Synedropsis fragilis</i> (Manguin) Hasle, Syvertsen & Medlin	<1	PI	F	0	0	12.5	2.2
<i>Synedropsis hyperboreoides</i> Hasle, Medlin & Syvertsen	<1	Ir, Ph	AC, F, M	7.1	8.3	0	6.5
<i>Synedropsis leavis</i> (Heiden) Hasle, Medlin & Syvertsen	<1	Ph	AC	0	4.2	0	2.2
<i>Synedropsis recta</i> Hasle, Syvertsen & Medlin	<1–4.5	Ir, Ph, PI	CR, AC, F, M, TB, CE	92.9	100	75	93.5
<i>Tabularia tabulata</i> (Agardh) Snoeijjs	<1–8.6	Ir, Ph, PI	AC, F, M, TB, CE	14.3	45.8	62.5	39.1
<i>Thalassiosira antarctica</i> Comber	<1	Ir, Ph	F, M	7.1	8.3	0	6.5
<i>Thalassiosira</i> cf. <i>ambigua</i> Kozlova	<1	Ir, Ph	AC, F, M	14.3	8.3	0	8.7
<i>Thalassiosira gracilis</i> (Karsten) Hustedt	<1	Ph	M, TB	0	16.7	0	8.7
<i>Thalassiosira</i> sp. 1	<1	Ir, Ph, PI	AC, F, M	14.3	8.3	12.5	10.9
<i>Thalassiothrix antarctica</i> Schimper ex Karsten	<1	Ph	CR, M	0	8.3	0	4.3
<i>Thalassiothrix longissima</i> Cleve & Grunow	<1	Ph	M, TB	0	8.3	0	4.3
<i>Trachyneis aspera</i> (Ehrenberg) Cleve	<1	Ir, Ph, PI	CR, AC, F, M, TB, CE	14.3	58.3	37.5	41.3
<i>Trigonium arcticum</i> (Brightwell) Cleve	<1–4.1	Ir, Ph, PI	CR, AC, F, M, TB	42.9	29.2	100	45.7

\*Ir—*Iridaea cordata*, Ph—*Phyllophora antarctica*, PI—*Plocamium cartilagineum*

\*\*CR—Cape Russell, AD—Adélie Cove, F—Faraglione, M—Molo, TB—Tethys Bay, CE—Cape Evans

\*\*\*% of samples in which the taxon was found

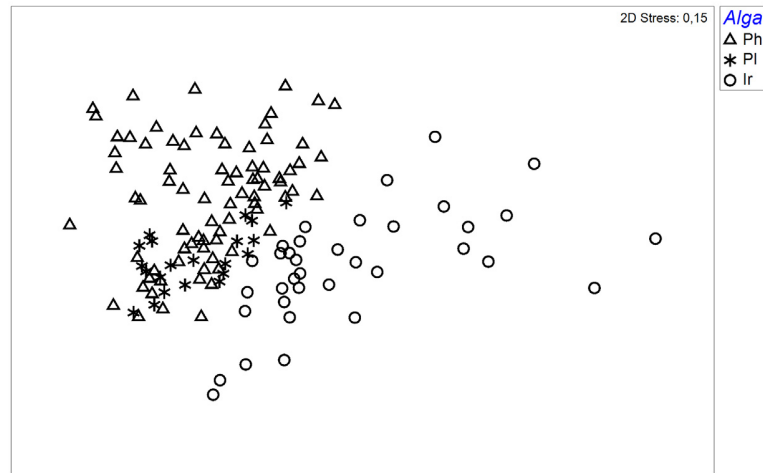
doi:10.1371/journal.pone.0153254.t002

Table 3. Results of ANOSIM test performed on species and growth form abundance data.

	Host alga		Season		Sampling site		Depth	
	GF	S	GF	S	GF	S	GF	S
<i>p</i>	>0.05	0.01	0.005	0.01	0.01	0.005	0.005	0.01
Global R	0.098	0.485	0.389	0.317	0.231	0.319	0.309	0.215

GF—growth form, S—species

doi:10.1371/journal.pone.0153254.t003

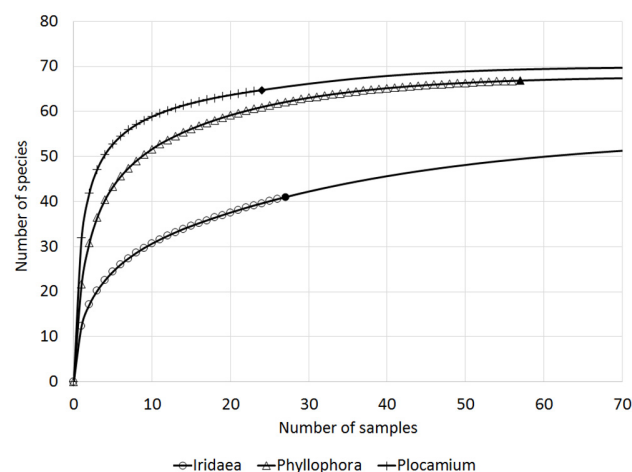


**Fig 2. Nonmetric multidimensional scaling (nMDS) graph based on the species abundance data.** Ph—samples of epiphytic diatom communities associated with *Phyllophora antarctica*, Pl—samples of epiphytic diatom communities associated with *Plocamium cartilagineum*, Ir—samples of epiphytic diatom communities associated with *Iridaea cordata*.

doi:10.1371/journal.pone.0153254.g002

ranged from 53.7% (*Phyllophora* vs *Plocamium*) to 67% (*Phyllophora* vs *Iridaea*). Seven species: *Achnanthes vincentii*, *Coconeis antiqua*, *C. fasciolata*, *Fragilariopsis nana*, *Navicula perminuta*, *Pseudogomphonema kamtschaticum*, and *Tabularia tabulata* were essential for the group differentiation (S2–S4 Tables).

The highest number of diatom taxa was found associated with thalli of *Phyllophora* (95), followed by *Plocamium* (60) and *Iridaea* (55). It should be noted, however, that the numbers of samples examined, replicates and the examined macroalgal surface, as well as the period of study and study locations, differed for different host species (Table 1). Therefore, to equalize the information content of each of the sample sets, rarefaction and extrapolation curves were computed (Fig 3). The analyses indicated that *Plocamium* may be the host algal species that supports the richest diatom community.

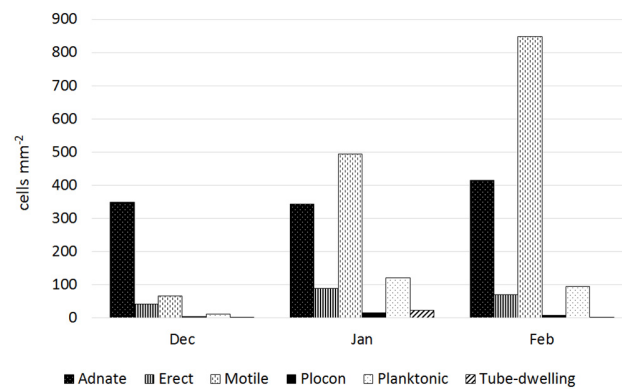


**Fig 3. Extrapolation (plain lines) of rarefaction curves (lines with symbols) based on samples from locations where all three algal species were found (Cape Russell, Adélie Cove, Faraglione).**

doi:10.1371/journal.pone.0153254.g003

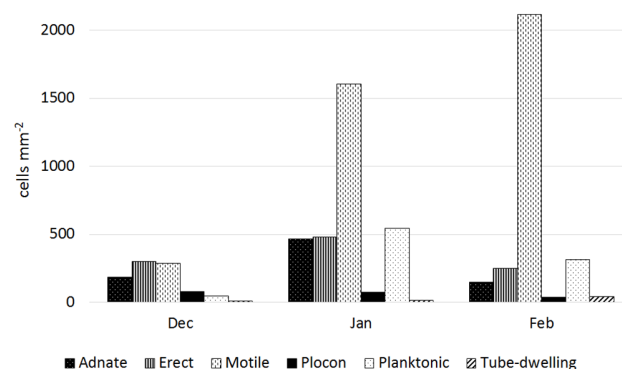
### Seasons

Seasonal change was evident in case of both epiphytic and epizooic communities (Figs 4 and 5, S1 and S2 Figs). Epiphytic communities developed in December contained a high number of adnate forms (e.g. *Achnanthes vicentii*, *Amphora* spp., *Cocconeis* spp; Fig 6a–6d) and low number of planktonic ones (Fig 4, S1 Fig). In January, a substantial change was observed: the number of adnate forms remained almost constant while other groups doubled (erect), tripled (plocon), or increased their number by seven- (motile) or eleven-fold (planktonic; Fig 4), which affected significantly the community growth form structure (S1 Fig). Planktonic species such as *Fragilariopsis curta* and *F. nana* contributed up to 14.2 and 34.2% (Table 2), respectively, of the total diatom community developed on the seaweed thallus surface in January. In February, motile diatom (*Navicula* spp., *Nitzschia* spp.) numbers continued to grow. A slight increase was also noted in the case of adnate forms, while abundances of all other diatom groups decreased (Fig 4). Although adnate forms were the most important group in December, motile diatoms gained dominance as the summer advanced (S1 Fig). A similar seasonal shift in growth form structure was observed for epizooic communities, which, however, contained a much lower percentage of adnate forms and higher of erect ones than found in epiphytic samples (Fig 5, S2 Fig).



**Fig 4. Average abundances of diatom growth forms found on macroalgal surface in different months (based on all macroalgal replicates collected in Terra Nova Bay).**

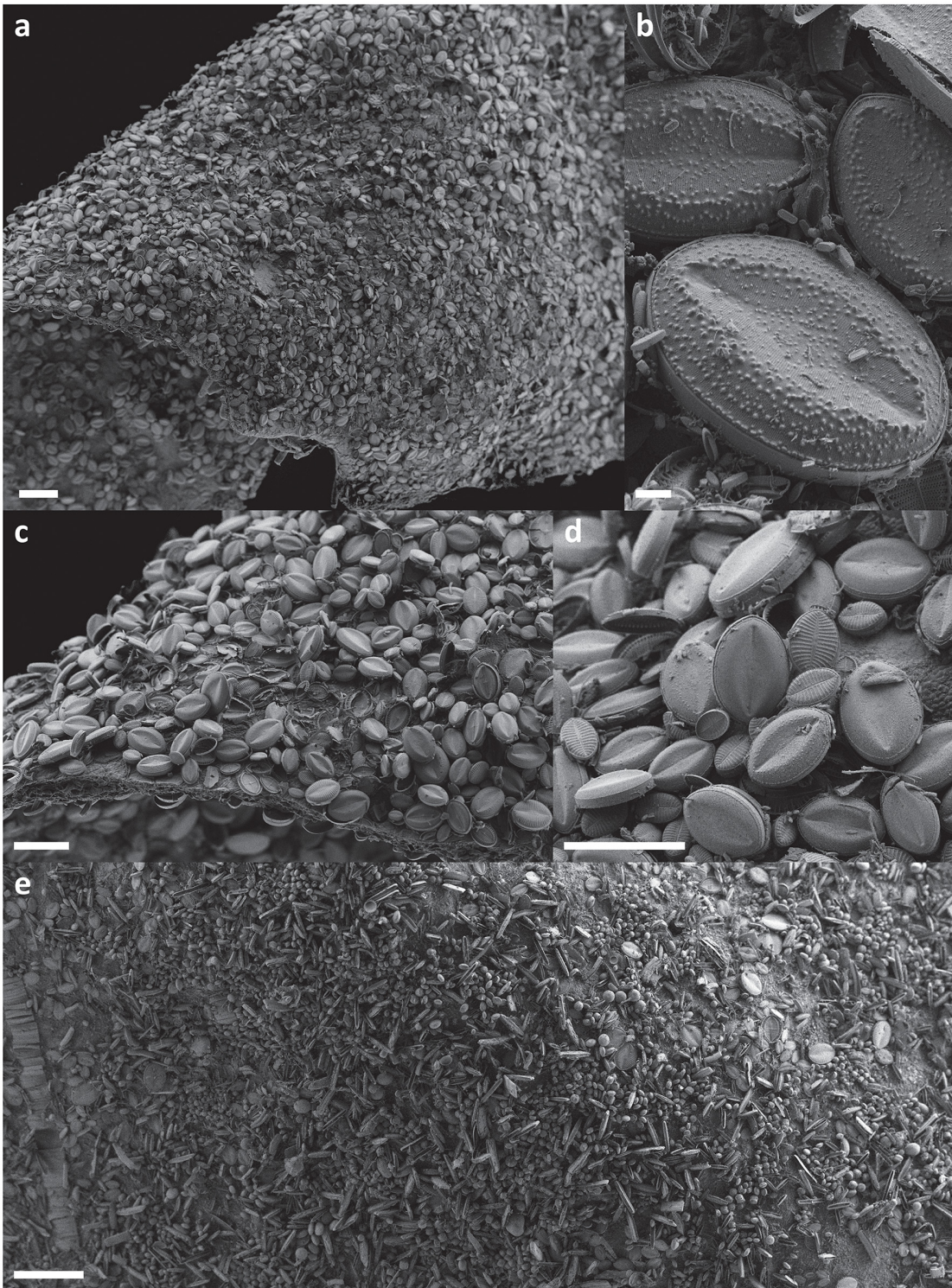
doi:10.1371/journal.pone.0153254.g004



**Fig 5. Average abundances of diatom growth forms found on the surface of epiphytic sessile microfauna in different months (based on all replicates collected in Terra Nova Bay).**

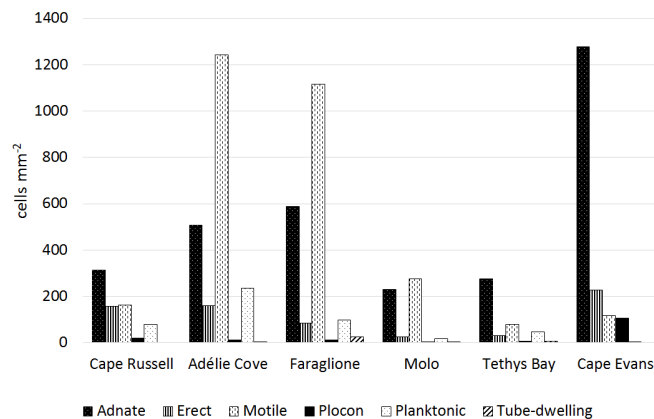
doi:10.1371/journal.pone.0153254.g005





**Fig 6. Scanning electron micrographs of epiphytic diatoms from the Ross Sea. a.-d.** *Iridaea cordata* covered by dominating *Cocconeis antiqua* (Adélie Cove, Terra Nova Bay). **e.** surface of *Phyllophora antarctica* (Cape Evans, McMurdo Sound). Scale bars: a. & e. = 200  $\mu\text{m}$ ; b. = 10  $\mu\text{m}$ ; c. & d. = 100  $\mu\text{m}$ .

doi:10.1371/journal.pone.0153254.g006



**Fig 7. Average abundances of diatom growth forms found on macroalgal surface at selected sampling sites.**

doi:10.1371/journal.pone.0153254.g007

### Sampling site

Differences in growth form structure among sampling sites are presented in Fig 7 (see also S3 Fig). Adnate forms dominated at Cape Russell, Tethys Bay, and Cape Evans, while the other three stations (Adélie Cove, Faraglione, Molo) were characterized by higher percentage of motile forms. The highest average total diatom number was found at Adélie Cove (2155 cells mm<sup>-2</sup>) and Faraglione (1925 cells mm<sup>-2</sup>), and the lowest at Tethys Bay (444 cells mm<sup>-2</sup>; Fig 7). It must be noted, however, that unequal number of samples collected at each of the sampling sites may have had some influence on the results obtained, as factors such as sampling season and depth also affected the communities.

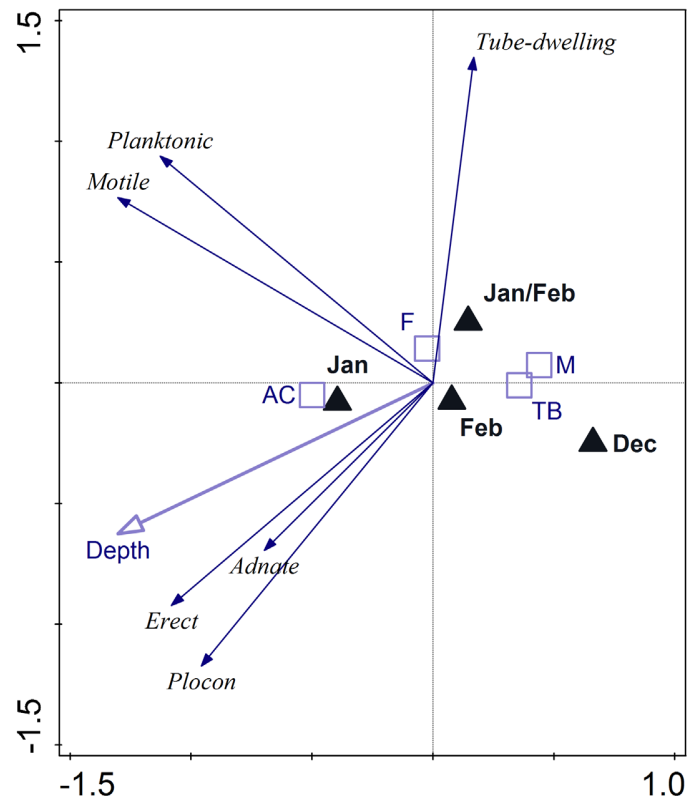
### Depth

Fig 8 visualizes the effect of depth on different diatom growth forms. Supplemental environmental variables (sampling site, season) were added as dummy variables. The adjusted explained variation accounted for 10.3% and the Monte Carlo permutation test ( $p < 0.001$ ) confirmed that the observed effect was significant. Erect and adnate diatoms as well as plocon appeared to be positively correlated with depth, while tube-dwelling forms exhibited a negative correlation. For motile and planktonic species, the correlation was weak or almost non-existent. December was clearly indicated as the season in which the conditions were the least favourable for diatom community development. All of the diatom groups responded positively to the conditions of Adélie Cove and/or Faraglione.

### Epiphytic microfauna

A partial RDA summarized the variation in diatom species composition explained by the host organism (macroalga or microfauna), after removal of the effect of sampling site, season and depth of sampling. Diatoms found in *Phyllophora* and *Plocamium* samples were classified into two groups according to the host organisms (as indicated above). The polygons in Fig 9 were plotted in the space of the first RDA axes. Score scaling was focused on diatom taxa scores (standardized). The explained adjusted variation accounted for 27% of the total variance in diatom compositional data. According to the Monte Carlo permutation test ( $p < 0.001$ ) this effect was significant. Epiphytic and epizooic samples formed two distinct clusters, indicating a substantial difference between the communities (Fig 9). Only *Cocconeis antiqua* and *C. fasciolata*





**Fig 8. Biplot diagram from RDA (redundancy analysis) visualizing the effect of depth on different diatom growth forms.** Supplemental environmental variables (sampling site, season), are added. Analyses is based on 166 subsamples. Due to the relatively low number of samples, results for Cape Evans and Cape Russell sampling sites are not shown. Score scaling is focused on growth form scores (standardized). Eigenvalues: 0.1225, 0.0309, 0.0092;  $p = 0.005$ . Adjusted explained variation = 10.3%. CR—Cape Russell, AD—Adélie Cove, F—Faraglione, M—Molo, TB—Tethys Bay.

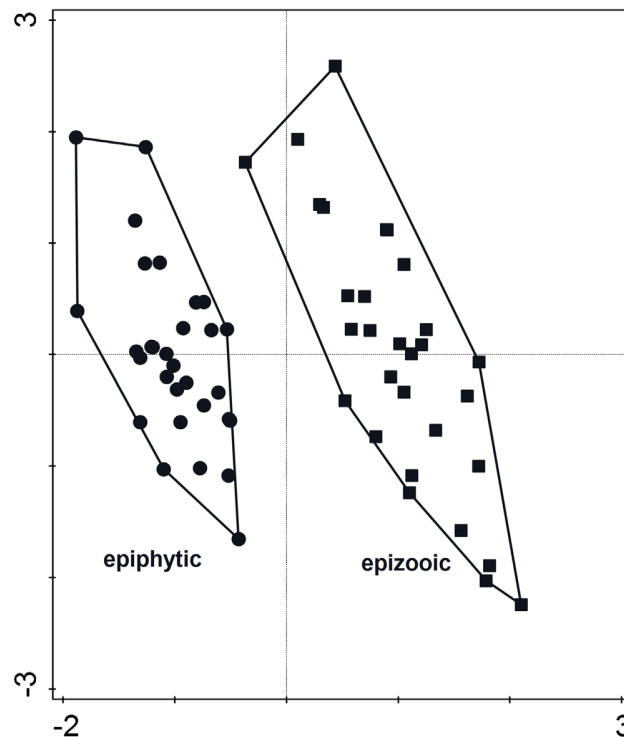
doi:10.1371/journal.pone.0153254.g008

preferred clearly the specific ecological conditions created by host macroalga. Other *Cocconeis* species gave either slightly positive (*C. stauroneiformis*) or slightly negative (*C. californica*) responses to macroalgal substrate, while all other taxa preferred a micro-faunal surface (Fig 10). A partial RDA performed on growth form abundance data confirmed these observations and revealed even stronger influence of host organism type on diatom communities (adjusted explained variation = 47%,  $p < 0.001$ ; Fig 11). Planktonic species showed very high affinity for microfaunal substrate, while adnate diatoms were the only group that preferred macroalgal over microfaunal substrate. The estimated species richness appeared to be higher for epizooic than epiphytic samples in the case of communities associated with both *Phyllophora* and *Plocamium* (Figs 12 and 13). Moreover, epizooic communities were usually characterized by significantly higher total diatom number than epiphytic ones (S4 and S5 Figs, Figs 4 and 5).

## Discussion

The number of diatom taxa found in this synthesis (109) is high in comparison with earlier studies of Antarctic epiphytes [32, 56, 63] and epiphytic diatoms in general [64, 65, 66, 67, 68]. Al-Handal and Wulff [56] reported 50 diatom taxa epiphytic on 19 different host species, including red, brown, and green macroalgae from Potter Cove (King George Island, South Shetland Islands) sampled between October and December 2003. Sutherland [63] observed 31





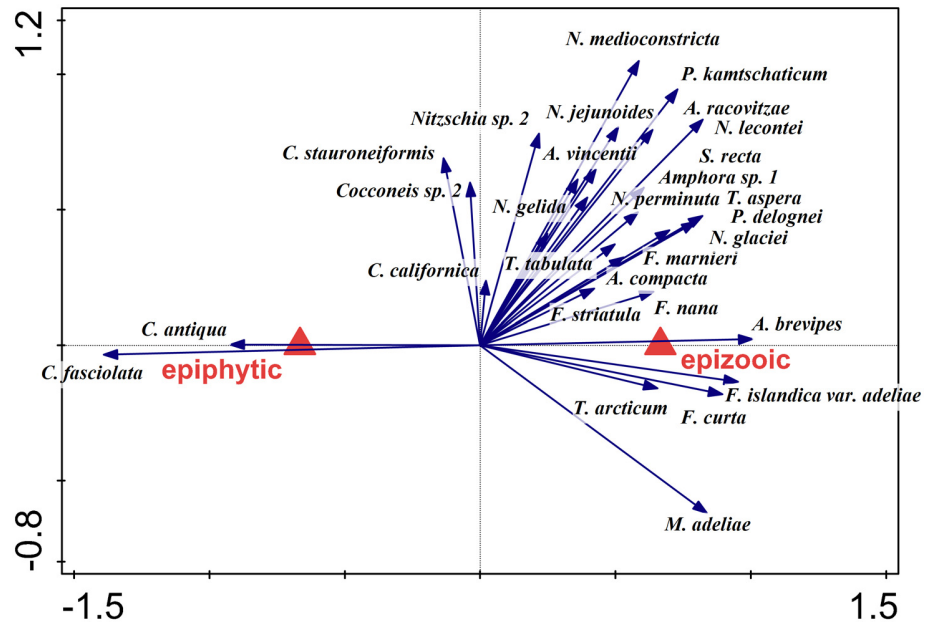
**Fig 9. *Phyllophora* and *Plocamium* samples classified into two groups according to the host organisms: macroalga (epiphytic) or microfauna (epizoic).** The polygons are plotted in the space of the first RDA axes. Score scaling is focused on diatom taxa scores (standardized). Eigenvalues: 0.1967, 0.0994, 0.0706;  $p = 0.0002$ . Adjusted explained variation = 27.0%.

doi:10.1371/journal.pone.0153254.g009

diatom species associated with *Phyllophora antarctica* in material collected from Cape Evans in November 2001. Thomas and Jiang [32] examined surface-associated diatoms near Davis Station (Prydz Bay) in a year-round study including 15 macroalgal taxa, but only identified nine diatom taxa. As reported by Majewska *et al.* [29, 30, 31], epiphytic diatom communities from the Southern Ocean may differ substantially between geographic locations and seasons. Nevertheless, we believe that at least some of the differences in the number of diatom taxa detected were underlain by the differences in methodology used. It has been observed that “traditional” methods of sampling and material processing may strongly influence the results obtained [69, 70, 71, 72]. Procedures involving corrosive substances may damage or completely dissolve weakly silicified diatom frustules, whereas taxa that do not cluster and settle to the bottom of the tube or beaker during the cleaning procedure may easily be overlooked and removed when rinsed [29]. Moreover, sampling effort clearly has a strong influence on the probability of species detection. Previous studies have indicated that careful analysis of 10 replicates of a total surface area of 20 mm<sup>2</sup> is sufficient to allow detection of 85–95% of co-existing epiphytic diatom taxa [28], when used in concert with appropriate preparation and observation methods.

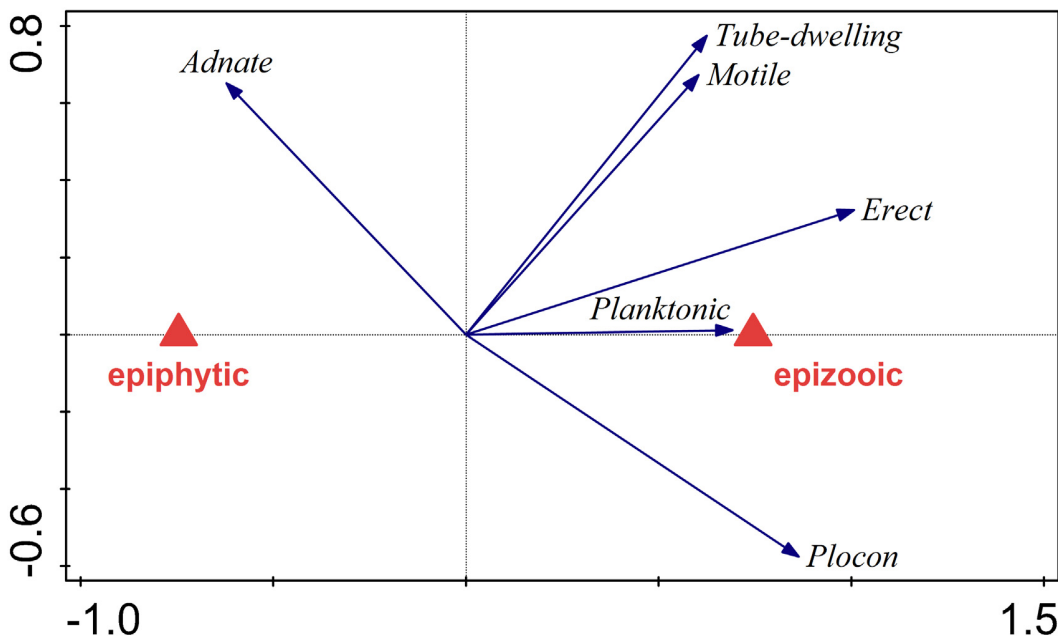
### Host macroalgal species and morphology

Debate continues over the importance of the host macroalgal species for associated microalgal communities. Several studies have suggested that the macroalgal basibiont influences epiphytic communities to a significant degree and indicate that at least some interactions between macroalgae and epiphytes may be species-specific [67, 73, 74]. Investigations worldwide as well



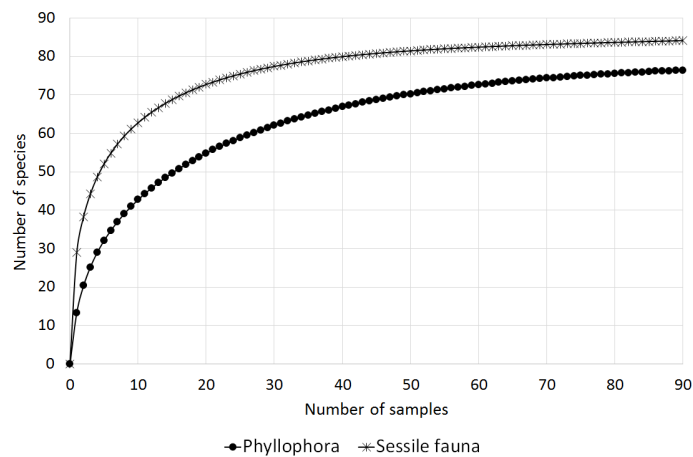
**Fig 10. Biplot diagram from a partial redundancy analysis (RDA) summarizing the variation in diatom species composition explained by the host organism (macroalga or microfauna), after removal of the effect of sampling site, season and depth of sampling.** Score scaling is focused on diatom taxa scores (standardized). Abundance data are log-transformed. Eigenvalues: 0.1967, 0.0994, 0.0706;  $p = 0.0002$ . Adjusted explained variation = 27.0%.

doi:10.1371/journal.pone.0153254.g010



**Fig 11. Biplot diagram from a partial redundancy analysis (RDA) summarizing the variation in diatom growth form explained by the host organism effect (macroalga or microfauna), after removal of the effect of sampling site, season and depth of sampling.** Score scaling is focused on diatom growth form scores (standardized). Abundance data are log-transformed. Eigenvalues: 0.3084, 0.1085, 0.0969;  $p = 0.0002$ . Adjusted explained variation = 47.1%.

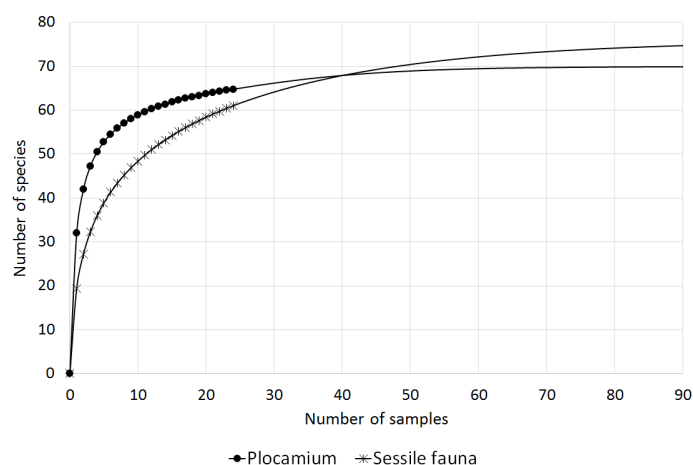
doi:10.1371/journal.pone.0153254.g011



**Fig 12. Extrapolation (plain lines) of rarefaction curves (lines with symbols) based on samples of *Phyllophora* and its associated sessile fauna from locations where both were found (Cape Russell, Adelie Cove, Faraglione, Molo, Tethys Bay).**

doi:10.1371/journal.pone.0153254.g012

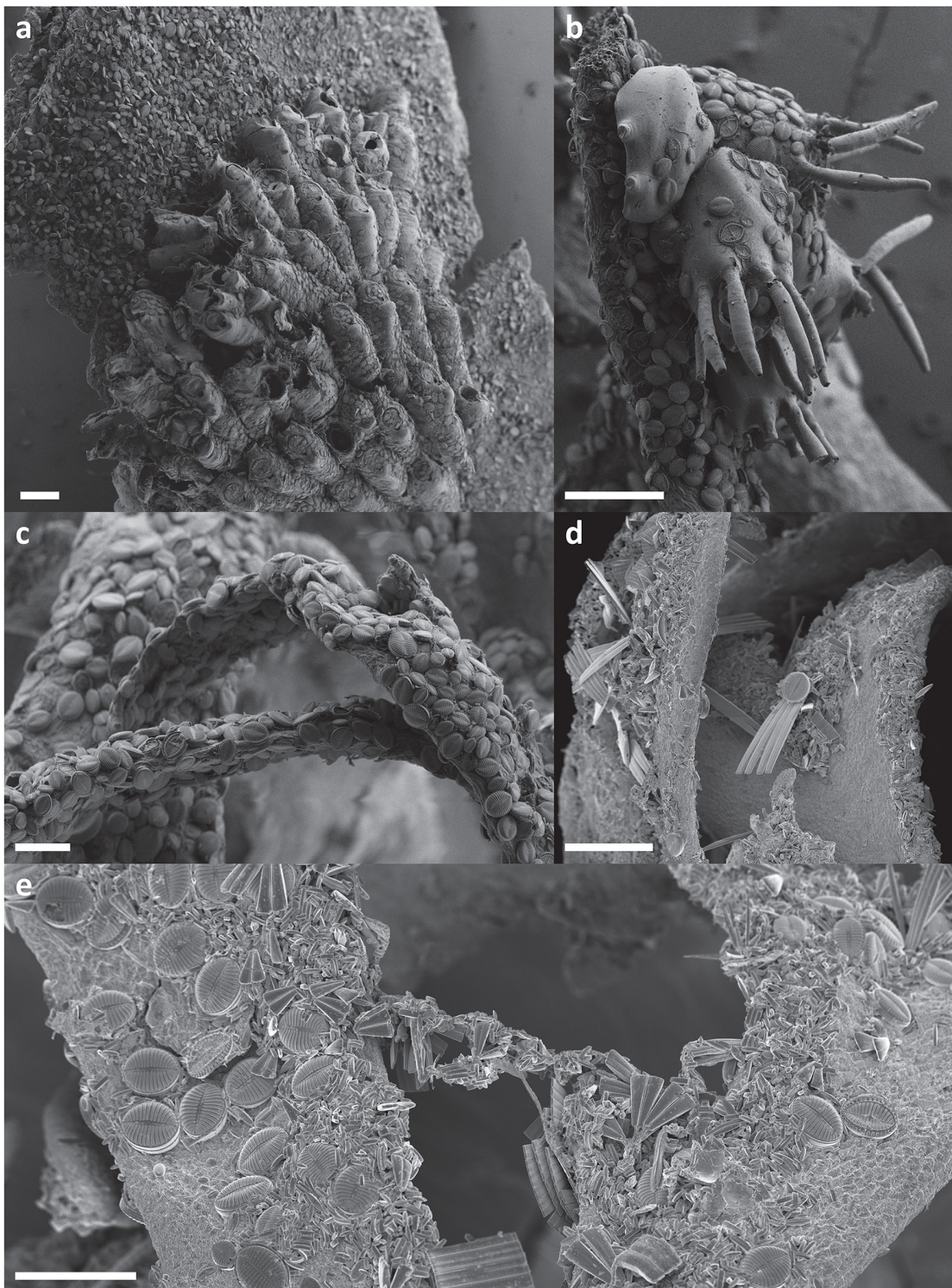
as some studies conducted in the polar regions give contrasting results and interpretations [29, 30, 56, 75, 76]. Thomas and Jiang [32], working in the vicinity of Davis Station (Vestfold Hills, Princess Elizabeth Land), reported that epiphytic diatom community composition depended strongly on macroalgal morphology, with filamentous parts of the macroalgae hosting a different (and usually more diverse) diatom community than broad, folious blades. Our findings are consistent with this observation, with the diatom flora associated with filamentous *Plocamium cartilagineum* differing most clearly from those growing on the other two flat-bladed seaweed species (Figs 6 and 14) [29, 30]. The specific branching pattern of alternating groups of branchlets in pectinate series that is characteristic of *Plocamium* appeared to create an appropriate and sheltered environment for the attachment of many erect (*Fragilaria* spp., *Pseudogomphonema kamtschaticum*), chain-forming (*Grammatophora* spp.), or loosely attached (*Paralia sol*, *Trigonium arcticum*) diatoms (Fig 14c–14e). In the case of diatom communities associated with *Iridaea cordata* and *Phyllophora antarctica*, due to the topographical similarity of



**Fig 13. Extrapolation (plain lines) of rarefaction curves (lines with symbols) based on samples of *Plocamium* and its associated sessile fauna.**

doi:10.1371/journal.pone.0153254.g013





**Fig 14. Scanning electron micrographs of epiphytic diatoms from Terra Nova Bay. a. & b.** examples of epiphytic sessile fauna. **c.–e.** diatoms on *Plocamium cartilagineum*. Scale bars: a. & b. = 200  $\mu\text{m}$ ; c.–e. = 100  $\mu\text{m}$ .

doi:10.1371/journal.pone.0153254.g014

substrate provided by relatively broad macroalgal blades, significant differences in diatom growth form and structure were not found. However, the diatom communities hosted by these latter two macroalgae differed greatly in the dominance of particular diatom species. Most strikingly, of the two dominant *Cocconeis* species, *C. antiqua* was always the most numerous among adnate diatoms on *Iridaea*, while *C. fasciolata* covered all *Phyllophora* samples densely [29, 30]. Both *Iridaea* and *Phyllophora* belong to Rhodophyta, both possess flat-bladed thalli and often occurred at the same sampling site. Host selection by the different diatom species is clearly effective. Dominating *Cocconeis* species have the same growth form and occupy apparently similar niches. While the homogenous microhabitat provided by macroalgal thalli might appear to favour competitive ability amongst coexisting species, preferences for a host macroalga would diminish the strength of interactions between diatom taxa and ensure their long-term ecological success [77, 78].

### Seasonality and ice

Although the data obtained focus on diatom communities developing during the three summer months, a strong seasonal influence was apparent. This is consistent with well-established understanding of Southern Ocean primary productivity, which is characterised by extreme seasonality [79, 80]. In the shallow coastal zone, sea ice has a very strong influence on coastal communities, altering local environmental characteristics and giving rise to distinct microbial assemblages [81, 82, 83]. Several marine microalgal species use different types of sea ice as temporary winter habitat [84, 85, 86]. During the warmer summer season, diatoms melt out of the ice seeding the water column [81] and other available habitats, including seaweed surfaces [28, 29, 30]. Studies have shown that in various Antarctic locations and times of the year, unique ice conditions support blooms of different diatom taxa [80, 87, 88, 89, 90, 91]. Several studies have reported blooms of *F. curta* and *F. cylindrus* seeded by melt-out of either sea ice or the marginal ice-edge [84, 86, 92]. Leventer and Dunbar [93] suggested that more diverse summer diatom assemblages are typical of regions influenced strongly by wind, while Arrigo and McClain [94] and Cunningham and Leventer [81] reported that summer diatom-dominated blooms in Terra Nova Bay are directly linked to the ice edge recession.

Macroalgal thalli collected from Terra Nova Bay in December and the first week of January, as well as those collected in January from Cape Evans (i.e. samples collected from under the ice or directly after ice break-up forced by wind and wave action) contained a high number of adnate forms (e.g. *Achnanthes vicentii*, *Amphora* spp., *Cocconeis* spp; Fig 6a–6d). Epontic, loosely-attached species, sometimes described as “plocon” [95], were present (e.g. *Melosira* spp., *Trigonium arcticum*), but planktonic species were almost absent. However, as the summer season advanced, species with other growth forms increased in abundance relative to sessile adnate diatoms. In January, a high number of planktonic and ice-associated diatoms such as *Fragilariopsis curta* and *F. nana* were present in samples collected in Terra Nova Bay [28, 29, 30]. Other *Fragilariopsis* species (*F. cylindrus*, *F. kergulensis*, *F. obliquecostata*, *F. rhombica*, *F. ritscheri*, *F. sublinearis*) were also present but in much lower numbers. Many samples contained *Chaetoceros* spp. resting spores. Several studies have indicated that *Thalassiosira antarctica* is another diatom closely associated with the coastal sea ice [89, 96, 97], but its environmental role is not fully understood [81]. In epiphytic samples, *T. antarctica* appeared only sporadically and was poorly represented, which may support a previous observation that this species rarely blooms in the coastal zone of Terra Nova Bay [81]. Simultaneously, numbers of small motile *Navicula* spp. and *Nitzschia* spp. began to increase, suggesting that these taxa also belong to the ice-associated group and are released into the water column as the ice melts. The contribution of ice-seeded *Fragilariopsis* species to the total diatom number decreased as



the season progressed further (mid-February), but numbers of *Navicula* spp. and *Nitzschia* spp. increased rapidly and continued to increase until the end of February when the observations were terminated [29, 30].

Adnate taxa are often described as early colonizers that initiate algal succession on newly available substrates [98, 99]. It has been suggested that horizontally-growing epibiotic diatoms, staying in close contact with the host organism tissues, may benefit from the exchange of biogenic substances with the basibiont [100, 101]. Furthermore, adnate forms are highly resistant to both physical disturbance and grazing by various unspecialised herbivores [102]. Many function well in low-light conditions, for instance in relatively deep water, under ice-cover, or overshadowed by apically attached, stalked, or loosely-associated diatoms or settled planktonic forms [102, 101]. In our studies, after ice break-up the average number of adnate forms did not decrease substantially, but small motile diatoms achieved dominance when the *Fragilariopsis* spp. bloom began to decline [29, 30]. In Terra Nova Bay summer diatom blooms and high uptake of biogenic substances may result in significant nutrient depletion [103, 104, 105]. In such conditions, small-celled diatoms, as opposed to large-celled *Cocconeis* (*C. antiqua*, *C. fasciolata*) and bulky *Amphora* species, have an advantage because of their high surface area to volume ratio, which allows them to more easily satisfy their nutrient demand [106]. Sunda and Huntsman [107] suggested that small algae have lower iron requirement than larger taxa, while their growth rates are much higher. In addition, highly motile *Navicula* and *Nitzschia* species are able to migrate in response to various environmental factors, including nutrient gradients and irradiance [108]. They are thus excellent colonizers or re-colonizers of newly-exposed surfaces, and can dominate in habitats where low levels of nutrients inhibit or moderate the growth of less tolerant diatoms. Their populations can recover rapidly from disturbances such as grazing or mechanical removal by physical forces [12, 100, 109] in comparison with large-celled species.

A gradual decrease of *Fragilariopsis* spp. percentage contribution in epiphytic samples from Terra Nova Bay [29, 30] may indicate that diatoms belonging to this genus are less resistant to the sudden nutrient depletion that occurs after the phytoplankton summer peak than are *Navicula* or *Nitzschia* spp, or that these araphid diatoms are not competitive in the new (epiphytic) habitat. Ice-associated diatoms such as *Amphiprora* spp., *Entomoneis* spp., *Nitzschia stellata* and other biraphid, motile taxa are truly benthic, being dependent on the sea ice as an “inverted benthos”, and do not survive and thrive once released into the water column, unlike many *Fragilariopsis* spp. (Amy Leventer, personal communication). Therefore, biraphid diatoms may find adequate habitat on solid surfaces such as macroalgal thalli, while *Fragilariopsis* spp., able to persist in the water column, require lower competitive abilities. In other words, there may be less pressure on *Fragilariopsis* spp. to colonize macroalgae rapidly, as the availability of solid surfaces is not a limiting factor.

The exchange of substrate between ice-associated diatoms and epiphytic forms has been suggested to have only marginal significance [56, 63, 110]. However, our data demonstrate that this depends largely on the season and ice conditions in the investigated area [28, 29, 30, 31]. Benthic or epontic forms constitute a substantial proportion of the diatoms that are able to survive in brine pockets in the winter ice. In contrast with oceanic planktonic taxa, benthic diatoms evolved in highly variable shallow water conditions and are likely to cope better with the high osmotic pressure fluctuations typical of ice-occluded microhabitats [111, 112]. Several studies have indicated that sea ice algae serve as an inoculum for the phytoplankton blooms associated with ice melt in the spring [111, 113, 114]. We suggest that a similar scenario is applicable to many of the ice-related forms of benthic origin, whose ice-associated mode of existence represents a stage of their natural life cycle.

Similar patterns were apparent in samples collected across 11 different years between 1989/1990 and 2012/13. Thus, we suggest that the seasonal effect is stronger than natural variability, and that the changes described are associated directly with local ice conditions [28, 29, 30, 31]. Cunningham and Leventer [81] stressed the importance of the Terra Nova Bay polynya in establishing the algal communities in this zone. However, in terms of both species composition and growth form structure, diatom communities from Tethys Bay observed in the current study collected immediately after ice break-up were more similar to those collected from under the ice at remote Cape Evans than to samples from nearby stations located along the coast of Terra Nova Bay. As the Tethys Bay samples were collected ca. 12–48h after the ice break-up, the diatom communities observed in those samples were still similar to the under-ice, “winter” assemblages and differed significantly from the nearby stations (Molo, Faraglione, Adélie Cove) where the ice broke up several weeks earlier. This supports the hypothesis that ice cover (and ice-associated drivers in general) has a profound influence on epiphytic diatoms and is one of the most important controls affecting polar marine microalgal communities.

### Sampling location

During the survey, amongst the six sampling sites located within Terra Nova Bay and at Cape Evans, the highest values of total diatom abundance were obtained in samples collected in the vicinity of Adélie Cove and Faraglione ( $> 8000$  cells  $\text{mm}^{-2}$ ; Majewska *et al.* 2013b). The nearby penguin rookery and associated large influx of nutrients into the adjacent waters was proposed as a major factor influencing diatom number in this area [29,30]. Adélie Cove is a small, rather deep V-shaped bay, separated from the open sea by a ca. 15 m deep sill [115]. Povero *et al.* [115] described complex interactions among physical, chemical, and biological processes that influence local benthic and pelagic habitats, sustaining a particularly rich (in terms of both species diversity and biomass) benthic fauna. Adélie Cove and Faraglione are under strong terrestrial influences, including not only the nearby Adélie penguin (*Pygoscelis adeliae*) rookery, but also intense katabatic winds which strongly influence the local water mass circulation. The underwater sill and other morphological features of the coast favour nutrient entrapment within the cove [115]. The amount of organic matter found in sediments at 50 m depth was 3–4 times higher than the quantities measured at other sampling stations within the bay [115, 116]. Intense *Phaeocystis* blooms, followed by summer (January–February) diatom blooms are observed regularly in the vicinity of the cove [115] (Maria Cristina Gambi, personal communication; Majewska, personal observation) and the high organic matter content is thought to support development of particularly abundant communities of detritus-feeding and suspension-feeding benthic organisms [115, 117]. However, as noted by Povero *et al.* [115], due to wind action and water circulation pattern the influence of the penguin colony may be even stronger in the vicinity of Faraglione. The observations of Andreoli *et al.* [118] of unusually high densities of planktonic microalgae in this area, may support these inferences.

The least abundant epiphytic diatom communities (from 21 to 1312 cells  $\text{mm}^{-2}$ ) [28, 30] were found in Tethys Bay, a station characterised by particularly unstable summer conditions (strong winds, ice break-up during the study period) and potential mechanical disturbance and damage. Comparing to other sampling sites located within Terra Nova Bay, the macroalgal fauna found in Tethys Bay was relatively poor, which was probably directly related to the longer period of ice cover.

Epiphytic diatom abundances at Cape Evans, located near the southern global limit of macroalgal growth [119], did not differ significantly from those observed at Terra Nova Bay. This suggests that relatively thin (up to 1 m) ice cover and low water temperatures (ca.  $-1.4^{\circ}\text{C}$ ) do not significantly affect diatom growth rates and biomass. Similar conclusions have also been



drawn by Thomas and Jiang [32], who observed that the standing crop of epiphytes from the vicinity of Davis station was high throughout both summer and winter seasons. Miller and Pearse [9] suggested that low temperatures depress respiration rates and thus favour growth and survival in low light conditions.

### Depth and light conditions

Data obtained in the current study indicated that the depth of sampling was of secondary importance for diatom community development [29, 30]. In terms of diatom growth form structure, there was a general trend towards an increasing number of erect forms in deeper waters, presumably owing to the poorer light conditions present at deeper stations. In addition, tube-dwelling diatoms seemed to prefer the shallowest sites (2–5 m). The deepest sampling station, however, did not exceed 25 m and clearly conditions will differ in deeper waters. Sutherland [63] noted a gradual decrease in diatom diversity at Cape Evans as the depth below the sea ice increased, and we suggest that depth can be an important factor limiting species distribution when the incident photosynthetically active radiation (PAR) that penetrates through the water column is just above the lowest values necessary for algal growth. The availability of PAR is a result of complex interactions among factors including water turbidity, suspended particles (organic and mineral), meteorological conditions (clouds), ice cover, substratum slope, or overshadowing by macroalgal beds [120, 121, 122, 123]. An erect position may be an adaptation to conditions where only a small portion of solar radiation is transmitted to the benthic or epiphytic habitats [122]. This may explain the relatively high number of erect diatoms found at Adélie Cove (despite high amounts of suspended particles and dense macroalgal beds) and Cape Evans (ice cover). The formation of mucilaginous tubes, in turn, may provide protection from desiccation, osmotic shock or intense light radiation in upper water layer [124, 125].

### Water currents

A complex, vertical structure of diatom communities may reflect other characteristics of the occupied habitat. As opposed to tightly-attached adnate diatoms, both erect and tube-dwelling diatoms are highly susceptible to physical disturbances such as current-induced shear forces [126]. Therefore, independent of light conditions, loosely attached diatoms find more favourable conditions for their growth at sheltered sites where they are not exposed to strong currents, wind-generated waves or ice scouring. Usually such conditions are typical for sites covered by ice over several months [127]. Ryan *et al.* [110] described the influence of water movement on ice algae at Cape Evans and Cape Hallett, indicating that the currents were negligible at the former location. Moreover they reported that, due to the non-existent or very weak water currents at Cape Evans, ice-associated algae were not present in the water column. Our findings are consistent with these observations, the very weak water currents at Cape Evans prevented exchange between ice-associated and epiphytic communities, resulting in the formation of very distinct assemblages [28].

The specific impact of water currents on epiphytic sessile microfauna, which have a functional significance for epiphytic diatoms, is discussed below. In the case of benthic suspension and deposit feeders, flow regime plays a crucial role in their feeding success. Under low flow conditions, food sources are easily depleted. Therefore, weak water and particle movements may negatively affect growth and survival of sessile invertebrates [128, 129, 130].

### Associated epiphytic microfauna

In contrast with the epiphytic communities of Terra Nova Bay, various growth forms of diatoms at Cape Evans covered the entire macroalgal thalli evenly [28]. All samples from Terra

Nova Bay were also colonised to some degree by sessile microfauna (Fig 14a and 14b), while the Cape Evans macroalgae were free of associated fauna [28]. The associated microfauna has a pronounced influence on the local epiphytic diatom distribution [28, 29, 30, 31]. Generally, more diverse diatom forms tended to cluster on the surface and in the vicinity of sessile microfauna. The number and type of diatoms depended most likely on the microfaunal species or its morphology (e.g. adnate and small motile forms preferred the surface of associated bryozoans, while erect, loosely attached, and large motile forms preferred the vicinity of epiphytic hydroids; Majewska, personal observations), but the presence of a faunal component almost always increased both diatom number and species diversity (S4 Fig) [29, 30]. Topographically uniform macroalgal blades provide a low number of available types of microhabitat, supporting a low number of evenly-distributed epiphytic diatoms. Epiphytic communities clustered in the vicinity of sessile microfauna exhibited a tendency towards increasing biodiversity and more complex community structure, and thus differed substantially from the neighbouring, strictly epiphytic communities. Sessile fauna with their specific morphology, surface roughness and texture offer a wide range of microniches, which attracts high number of surface-associated diatoms [131, 132], while small planktonic forms may become trapped in cavities and depressions of the invertebrate surface [29, 30]. Epiphytic suspension-feeding fauna can also generate micro-eddies and thus increase the rate of particle settling [129, 130, 133], which may explain the high number of small planktonic diatoms (e.g. *Fragilariopsis nana*) concentrated in the vicinity of sessile epiphytic fauna found in our studies of Ross Sea macroalgae [29, 30].

There may also be a trophic relationship between the sessile fauna and their associated diatoms. Planktonic grazers produce microscale nutrient patches that are locally important for pelagic communities [134] and we suggest that similar process may occur in surface-associated communities, and further that epiphytic microalgae may profit from nutrients excreted by associated invertebrates. Such a relationship has been indicated by McCormick and Stevenson [135], who suggested that direct excretion of nutrients by epiphytic snails may increase nutrient availability to associated microalgae. Furthermore, the surface of living sessile animals may provide a favourable substratum for epibiont growth as these areas are usually subjected to weaker grazing pressure [95, 100]. The lack of sessile suspension-feeding organisms at Cape Evans might have been caused by low particle flux (a direct consequence of the absence or very low biomass of phytoplanktonic organisms in the water column beneath the ice) and very weak currents, as mentioned above [129, 136]. The highly patchy distribution of epiphytic diatoms in Terra Nova Bay may also be linked with extensive, non-selective grazing by a wide range of herbivorous organisms [28]. The shallow waters of Terra Nova Bay are especially rich in benthic fauna, many of which may feed on benthic diatoms [115, 129, 137].

## Conclusions

Epiphytic diatom communities investigated at various depths at six sites located in Terra Nova Bay and McMurdo Sound (Ross Sea) proved to be rich, well developed and diverse in terms of both species composition and growth form structure. Generally, the epiphytic diatom flora overlapped that of the sea ice to a relatively small extent, but the contribution of both ice-associated and planktonic diatoms to the epiphytic communities was related strongly to the local ice conditions and increased with progression through the summer season. Spring ice melt or break-up and seeding by ice-associated diatoms are important in determining the composition of epiphytic communities in summer. Although ice cover strongly influenced epiphytic diatom community composition, it neither inhibited their growth nor limited significantly their abundance. A wide range of environmental factors can influence diatom communities, but their effects can only be considered in relation to broader aspects of ecosystem functioning. The host

macroalga influenced the associated diatoms mainly through its morphology and surface texture and roughness, providing a point of attachment and shelter for host-adapted species. However, other interactions (e.g. trophic, chemical) cannot be excluded. In general, less uniform surfaces supported a higher number of epiphytes, and the presence of epiphytic sessile fauna also increased significantly the local biodiversity. Depth affected diatom community growth form structure, which was manifested especially by higher contributions of erect forms to the total diatom number at the deepest stations sampled in this study. Nevertheless, in the generally shallow ice-free marine habitats examined, where water transparency is relatively high, the influence of depth was of only secondary importance for epiphytic communities. Our findings highlight the need for further, long-term and spatially extensive investigations to gather the necessary information about individual species of benthic marine diatoms, in order to permit their use as valid environmental proxies.

## Supporting Information

**S1 Fig. Average percent contribution of diatom growth forms to the total number of diatoms found on the macroalgal surface in different months (based on all macroalgal replicates collected in Terra Nova Bay).**

(TIF)

**S2 Fig. Average percent contribution of diatom growth forms to the total number of diatoms found on the surface of epiphytic sessile microfauna in different months (based on all replicates collected in Terra Nova Bay).**

(TIF)

**S3 Fig. Average percent contribution of diatom growth forms to the total number of diatoms found on the macroalgal surface at selected sampling sites.**

(TIF)

**S4 Fig. Average growth form abundances of diatoms associated with *Phyllophora antarctica* and *Plocamium cartilagineum*. CR—Cape Russell, AD—Adélie Cove, F—Faraglione, M—Molo, TB—Tethys Bay, Dec—December, Jan—January, Feb—February.**

(TIF)

**S5 Fig. Average growth form abundances of diatoms associated with sessile fauna epiphytic on *Phyllophora antarctica* and *Plocamium cartilagineum*. CR—Cape Russell, AD—Adélie Cove, F—Faraglione, M—Molo, TB—Tethys Bay, Dec—December, Jan—January, Feb—February.**

(TIF)

**S1 Table. List of samples.**

(DOCX)

**S2 Table. Average abundance of diatoms associated with *Phyllophora antarctica* and *Plocamium cartilagineum*, and their contribution to the dissimilarity found between the groups.**

(DOCX)

**S3 Table. Average abundance of diatoms associated with *Phyllophora antarctica* and *Iridaea cordata*, and their contribution to the dissimilarity found between the groups.**

(DOCX)

**S4 Table. Average abundance of diatoms associated with *Plocamium cartilagineum* and *Iridaea cordata*, and their contribution to the dissimilarity found between the groups.**

(DOCX)

## Acknowledgments

This work was supported by the Second University of Naples and the Italian National Program of Research in Antarctica (PNRA) co-ordinated by the Italian National Research Council [2010/A1.02]. PC is supported by NERC core funding to the BAS Biodiversity, Evolution and Adaptation Team. We thank Lukasz Polanski, who kindly provided the sampling site map ([Fig 1](#)). This paper also contributes to the SCAR 'State of the Antarctic Ecosystem' (AntEco) research programme.

## Author Contributions

Conceived and designed the experiments: RM PC MD. Performed the experiments: RM. Analyzed the data: RM. Contributed reagents/materials/analysis tools: MD. Wrote the paper: RM. Revised the manuscript: PC MD. Collected samples: RM MD.

## References

1. Montgomery WL, Gerking SD. Marine macroalgae as food for fishes: An evaluation of potential food quality. *Environ Biol Fish* 1980; 5:143–153.
2. Amsler CD, McClintock JB, Baker BJ. Chemical defense against herbivory in the Antarctic marine macroalgae *Iridaea cordata* and *Phyllophora antarctica* (Rhodophyceae). *J Phycol* 1998; 34:53–59.
3. Amsler CD, Iken K, McClintock JB, Amsler MO, Peters KJ, Hubbard JM et al. Comprehensive evaluation of the palatability and chemical defenses of subtidal macroalgae from the Antarctic Peninsula. *Mar Ecol Prog Ser* 2005; 294:141–159.
4. Norkko A, Thrush SF, Cummings VJ, Funnell GA, Schwarz A-M, Andrew NL et al. Ecological role of *Phyllophora antarctica* drift accumulations in coastal soft-sediment communities of McMurdo Sound, Antarctica. *Polar Biol* 2004; 27:482–494.
5. Huang YM, McClintock JB, Amsler CD, Peters KJ. Feeding rates of common Antarctic gammarid amphipods on ecologically important sympatric macroalgae. *J Exp Mar Biol Ecol* 2006; 329:55–65.
6. Reichardt W, Dieckmann G. Kinetics and trophic role of bacterial degradation of macro-algae in Antarctic coastal waters. In: Siegfried WR, Condy RP, Laws RM (eds) *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin, 1985, 115–122.
7. Zielinski K. Bottom macroalgae of the Admiralty Bay (King George Island, South Shetlands, Antarctica). *Pol Polar Res* 1990; 11:95–131.
8. Pearse JS, Giese AC. Food, reproduction and organic constitution of the common Antarctic echinoid *Sterechinus neumayeri* (Meissner). *Biol Bull* 1966; 130:387–401. PMID: 5937189
9. Miller KA, Pearse JS. Ecological studies of seaweeds in McMurdo Sound, Antarctica. *Amer Zool* 1991; 31:35–48.
10. Ligowski R. Benthic feeding by krill, *Euphausia superba* Dana, in coastal waters off West Antarctica and in Admiralty Bay, South Shetland Islands. *Polar Biol* 2000; 23:619–625.
11. Michels J, Schnack-Schiel SB. Feeding in dominant Antarctic copepods—does the morphology of the mandibular gnathobases relate to diet? *Mar Biol* 2005; 146:483–495.
12. Zacher K, Hanelt D, Wiencke C, Wulff A. Grazing and UV radiation effects on an Antarctic intertidal microalgal assemblage: a long-term field study. *Polar Biol* 2007; 30:1203–1212.
13. Campana G, Quartino ML, Yousif A, Wulff A. Impact of UV radiation and grazing on the structure of a subtidal benthic diatom assemblage in Antarctica. *Berichte zur Polar- und Meeresforschung* 2008; 571:302–310.
14. Campana GL, Zacher K, Fricke A, Molis M, Wulff A, Quartino ML et al. Drivers of colonization and succession in polar benthic macro- and microalgal communities. *Bot Mar* 2009; 52:655–667.
15. Schmidt K, Atkinson A, Steigenberger S, Fielding S, Lindsay MCM, Pond DW et al. Seabed foraging by Antarctic krill: Implications for stock assessment, benthic-pelagic coupling, and the vertical transfer of iron. *Limnol Oceanogr* 2011; 56:1411–1428.
16. Siciński J, Jażdżewski K, De Broyer C, Presler P, Ligowski R, Nonato EF et al. Admiralty Bay benthos diversity—a census of a complex polar ecosystem. *Deep Sea Res II—Top Stud Oceanogr* 2011; 58:30–48.
17. Harwood D, McMinn A, Quilty P. Diatom biostratigraphy and age of the Pliocene Sørsdal Formation, Vestfold Hills, East Antarctica. *Ant Sci* 2000; 12:443–462.

18. Taylor F, Whitehead J, Domack E. Holocene paleoclimate change in the Antarctic Peninsula: evidence from the diatom, sedimentary and geochemical record. *Mar Micropaleontol* 2001; 41:25–43.
19. Stickley CE, Pike J, Leventer A, Dunbar R, Domack EW, Brachfeld S et al. Deglacial ocean and climate seasonality in laminated diatom sediments, Mac.Robertson Shelf, Antarctica. *Palaeogeogr Palaeoclimat Palaeoecol* 2005; 227:290–310.
20. Buffen A, Leventer A, Rubin A, Hutchins T. Diatom assemblages in surface sediments of the north-western Weddell Sea, Antarctic Peninsula. *Mar Micropaleontol* 2007; 62:7–30.
21. Michalchuk BR, Anderson JB, Wellner JS, Manley PL, Majewski W, Bohaty S. Holocene climate and glacial history of the northeastern Antarctic Peninsula: the marine sedimentary record from a long SHALDRIL core. *Quat Sci Rev* 2009; 28:3049–3065.
22. Cermeño P, Falkowski PG. Controls on diatom biogeography in the ocean. *Science* 2009; 325:1539–1541. doi: [10.1126/science.1174159](https://doi.org/10.1126/science.1174159) PMID: [19762642](https://pubmed.ncbi.nlm.nih.gov/19762642/)
23. Boyd PW, Rynearson TA, Armstrong EA, Fu F, Hayashi K, Hu Z et al. Marine phytoplankton temperature versus growth responses from polar to tropical waters—outcome of a scientific community-wide study. *PLoS ONE* 2013; 8:e63091. doi: [10.1371/journal.pone.0063091](https://doi.org/10.1371/journal.pone.0063091) PMID: [23704890](https://pubmed.ncbi.nlm.nih.gov/23704890/)
24. Sutton JN, Varela DE, Brzezinski MA, Beucher CP. Species-dependent silicon isotope fractionation by marine diatoms. *Geochimica et Cosmochimica Acta* 2013; 104:300–309.
25. Pančić M, Hansen PJ, Tammilehto A, Lundholm N. Resilience to temperature and pH changes in a future climate change scenario in six strains of the polar diatom *Fragilariopsis cylindrus*. *Biogeosci Discuss* 2015; 12:4627–4654.
26. Kellogg TB, Truesdale RS. Late quaternary paleoecology and paleoclimatology of the Ross Sea: the diatom record. *Mar Micropaleontol* 1979; 4:137–158.
27. Bohaty SM, Scherer RP, Harwood DM. Quaternary diatom biostratigraphy and palaeoenvironments of the CRP-1 drillcore, Ross Sea, Antarctica. *Terra Antarctica* 1998; 5:431–453.
28. Majewska R, De Stefano M. Epiphytic diatom communities on *Phyllophora antarctica* from the Ross Sea. *Ant Sci* 2015; 27:44–56.
29. Majewska R, Gambi MC, Totti CM, De Stefano M. Epiphytic diatom communities of Terra Nova Bay (Ross Sea, Antarctica): structural analysis and relations to algal host. *Ant Sci* 2013a; 25:501–513.
30. Majewska R, Gambi MC, Totti CM, Pennesi C, De Stefano M. Growth form analysis of epiphytic diatom communities of Terra Nova Bay (Ross Sea, Antarctica). *Polar Biol* 2013b; 36:73–86.
31. Majewska R, Kuklinski P, Balazy P, Yokoya NS, Paternostro Martins A, De Stefano M. A comparison of epiphytic diatom communities on *Plocamium cartilagineum* (Plocamiales, Florideophyceae) from two Antarctic areas. *Polar Biol* 2015; 38:189–205.
32. Thomas DP, Jiang J. Epiphytic diatoms of the inshore marine area near Davis Station. *Hydrobiology* 1986; 140:193–198.
33. Clark GF, Stark JS, Perrett LA, Hill NA, Johnston EL. Algal canopy as a proxy for the disturbance history of understory communities in East Antarctica. *Polar Biol* 2011; 34:781–790.
34. Ehrenberg CG. Verbreitung und Einfluss des mikroskopischen Lebens in Süd- und Nord-America. *Abhandlungen der Königlich Akademie der Wissenschaften zu Berlin* 1843; 1:291–445.
35. Van Heurck H. Diatomées. In: *Expédition Antarctique Belge, Résultats du voyage du SY Belgica en 1897–1898–1899 sous de commandement de A de Gerlache de Gomery*. Rapports scientifiques. Botanique. J. E. Bushmann, Anvers, 1909, 1–129.
36. Mangin L. *Phytoplankton de l'Antarctique. Deuxième expédition Antarctique Française 1908–1910, commandée par le Dr Jean Charcot*. Sciences naturelles: documents scientifiques. Masson et Cie, Paris, 1915.
37. Peragallo M. Diatomées d'eau douce et diatomées d'eau salée. In: Joubin L (ed) *Deuxième expédition Antarctique française (1908–1910) commandée par le Dr Jean Charcot*. Sciences naturelles: Documents scientifiques. Botanique, Masson et Cie, Paris, 1921, 1–98.
38. Heiden H, Kolbe RW. Die marinen Diatomeen der Deutschen Süd polar-Expedition 1901–1903. In: von Drygalski E (ed) *Deutsche Südpolar-Expedition 1901–1903, VIII. Band Botanik*. De Gruyter, Berlin, 1928, 447–715.
39. Manguin E. Premier inventaire des diatomées de la Terre Adélie Antarctique. Espèces nouvelles. *Revue Algologique, Nouvelle Série* 1957; 3:111–134.
40. Manguin E. Les diatomées de la Terre Adélie Antarctique. Campagne du “Commandant Charcot” 1949–1950. *Annales des Sciences Naturelles, Botanique, série 12* 1960; 1:223–363.
41. Frenguelli J, Orlando HA. *Diatomeas y Silicoflagelados del sector Antartico Sudamericano*. Publicacion no. 5. Instituto Antartico Argentino, Buenos Aires, 1958.



42. Hustedt F. Diatomeen aus der Antarktis und dem Südatlantik. In: *Deutsche Antarktische Expedition 1938/39* 1958; 2:103–191.
43. Frenguelli J. Diatomeas y Silicoflagelados recogidas en Tierra Adelia durante las Expediciones Polares Francesas de Paul-Emile Victor (1950–1952). *Revue Algologique* 1960; 5:1–47.
44. Hasle GR. *Nitzschia* and *Fragilariopsis* species studied in the light and electron microscopes: III. The genus *Fragilariopsis*. *Skrifter utgitt Norske Videnskaps-Akademi i Oslo* 1965; 21:1–49.
45. Poulin M, Bérard-Therriault L, Cardinal A. Les diatomées benthiques de substrats durs des eaux marines et saumâtres du Québec. 1. *Cocconeioideae* (Achnanthes, Achnantheaceae). *Naturaliste Canadien* 1984a; 111:45–61.
46. Poulin M, Bérard-Therriault L, Cardinal A. Les diatomées benthiques de substrats durs des eaux marines et saumâtres du Québec. 2. *Tabellarioideae* et *Diatomoideae* (Fragilariales, Fragilariaceae). *Naturaliste Canadien* 1984b; 111: 275–295.
47. Poulin M, Bérard-Therriault L, Cardinal A. Les diatomées benthiques de substrats durs des eaux marines et saumâtres du Québec. 3. *Fragilarioideae* (Fragilariales, Fragilariaceae). *Naturaliste Canadien* 1984c; 111:349–367.
48. Hasle GR, Medlin LK, Syvertsen EE. *Synedropsis* gen. nov., a genus of araphid diatoms associated with sea ice. *Phycologia* 1994; 33:248–270.
49. Romero OE, Rivera P. Morphology and taxonomy of three varieties of *Cocconeis costata* and *C. pinnata* (Bacillariophyceae) with consideration of *Pleuroneis*. *Diatom Res* 1996; 11:317–343.
50. Cremer H, Roberts D, McMinn A, Gore D, Melles M. The Holocene diatom flora of marine bays in Windmill Islands, East Antarctica. *Bot Mar* 2003; 46:82–106.
51. Scott FJ, Thomas DP. Diatoms. In: Scott FJ, Marchant HJ (eds). *Antarctic marine protists*. Australian biological resources study. Canberra and Australian Antarctic Division, Hobart, 2005, 13–201.
52. Fernandes LL, Procopiak LK, Portinho D. *Brandinia mosimanniae* gen. nov. et sp. nov., a new marine epiphytic diatom from the Antarctic coasts. *Diatom Res* 2007; 22:45–56.
53. Al-Handal AY, Riaux-Gobin C, Romero OE, Wulff A. Two new marine species of the diatom genus *Cocconeis* Ehrenberg: *C. melchioroides* sp. nov. and *C. dallmannii* sp. nov., from King George Island, Antarctica. *Diatom Res* 2008; 23:269–281.
54. Al-Handal AY, Riaux-Gobin C, Wulff C. *Cocconeis pottercovei* sp. nov. and *Cocconeis pinnata* var. *matsii* var. nov., Two new marine diatom taxa from King George Island, Antarctica. *Diatom Res* 2010; 25:1–11.
55. Al-Handal AY, Wulff A. Marine benthic diatoms from Potter Cove, King George Island, Antarctica. *Bot Mar* 2008a; 51:51–68.
56. Al-Handal AY, Wulff A. Marine epiphytic diatoms from the shallow sublittoral zone in Potter Cove, King George Island, Antarctica. *Bot Mar* 2008b; 51:411–435.
57. Cefarelli AO, Ferrario ME, Almandoz GO, Atencio AG, Akselman R, Vernet M. Diversity of the diatom genus *Fragilariopsis* in the Argentine Sea and Antarctic waters: morphology, distribution and abundance. *Polar Biol* 2010; 33:1463–1484.
58. Riaux-Gobin C, Compère P, Al-Handal AY. Species of the *Cocconeis peltoidea* group with a marginal row of unusual processes (Mascarenes and Kerguelen Islands, Indian Ocean). *Diatom Res* 2011; 26:325–338.
59. ter Braak CJF, Šmilauer P. *Canoco Reference Manual and User's Guide: Software for Ordination (Version 5.0)*. Ithaca: Microcomputer Power, 2012.
60. Colwell RK, Chao A, Gotelli NJ, Lin S-Y, Mao CX, Chazdon RL, Longino JT. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *J Plant Ecol* 2012; 5:3–21.
61. Anderson MJ, Gorley RN, Clarke KR. *PERMANOVA1 for PRIMER: guide to software and statistical methods*. Plymouth: PRIMER-E, 2008.
62. Colwell RK, Mao CX, Chang J. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 2004; 85:2717–2727.
63. Sutherland DL. Surface-associated diatoms from marine habitats at Cape Evans, Antarctica, including the first record of living *Eunotogramma marginopunctatum*. *Polar Biol* 2008; 31:879–888.
64. Carpenter EJ. Diatoms attached to floating Sargassum in the western Sargasso Sea. *Phycologia* 1970; 9:269–274.
65. Sullivan MJ. Epiphytic diatoms of three seagrass species in Mississippi Sound. *Bull Mar Sci* 1979; 29:459–464.
66. Mazella L, Spinoccia L. Epiphytic diatoms of leaf blades of the Mediterranean seagrass *Posidonia oceanica* (L.) Delile. *Giornale Bot Ital* 1992; 126:752–754.

67. Snoeijls P. Distribution of epiphytic diatom species composition, diversity and biomass on different macroalgal hosts along seasonal and salinity gradients in the Baltic Sea. *Diatom Res* 1994; 9:189–211.
68. Chung MH, Lee K-S. Species composition of the epiphytic diatoms on the leaf tissues of three *Zostera* species distributed on the Southern Coast of Korea. *Algae* 2008; 23:75–81.
69. Lewin JC. The dissolution of silica from diatom walls. *Geochimica et Cosmochimica Acta* 1961; 21:182–198.
70. Kamatani A. Dissolution rates of silica from diatoms decomposing at various Temperatures. *Mar Biol* 1982; 68:91–96.
71. Shemesh A, Burckle LH, Froelich PN. Dissolution and preservation of Antarctic diatoms and the effect on sediment thanatocoenoses. *Quat Res* 1989; 31:288–308.
72. Flower RJ. Diatom preservation: experiments and observations on dissolution and breakage in modern and fossil material. *Hydrobiologia* 1993; 269–270:473–484.
73. Eminson D, Moss B. The composition and ecology of periphyton in freshwaters. *British Phycol J* 1980; 15:429–446.
74. Harper JT, Garbary DJ. Host specificity of *Podocystis adriatica* on the red alga *Heterosiphonia crispella* from Senegal. *Diatom Res* 1994; 9:329–333.
75. Millie DF, Lowe RL. Studies on Lake Erie's littoral algae; Host specificity and temporal periodicity of epiphytic diatoms. *Hydrobiologia* 1983; 99:7–18.
76. Orth RJ, Van Montfrans J. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: A review. *Aquatic Botany* 1984; 18:43–69.
77. Huston M. A general hypothesis of species diversity. *Amer Nat* 1979; 113:81–101.
78. Martin T. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* 1998; 79:656–670.
79. Deacon GER. Physical and biological zonation in the Southern Ocean. *Deep Sea Res A* 1982; 29:1–15.
80. Nelson DM, Smith WO Jr. Phytoplankton bloom dynamics of the western Ross Sea ice edge—II. Mesoscale cycling of nitrogen and silicon. *Deep Sea Res* 1986; 33:1389–1412.
81. Cunningham WL, Leventer A. Diatom assemblages in surface sediments of the Ross Sea: relationship to present oceanographic conditions. *Ant Sci* 1998; 10:134–146.
82. Convey P, Chown SL, Clarke A, Barnes DKA, Bokhorst S, Cummings V et al. The spatial structure of Antarctic biodiversity. *Ecol Monogr* 2014; 84:203–244.
83. Rajanahally MA, Sim D, Ryan KG, Convey P. Can bottom ice algae tolerate irradiance and temperature changes? *J Exp Mar Biol Ecol* 2014; 461:516–527.
84. Garrison DL, Buck KR. Sea-ice algal communities in the Weddell Sea: species composition in ice and plankton assemblages. In: Gray JS, Christiansen ME (eds) *Marine biology of polar regions and effects of stress on marine organisms*. John Wiley, New York, 1985, 103–122.
85. Garrison DL, Close R, Reimnitz E. Algae concentrated by frazil ice: evidence from laboratory experiments and field measurements. *Ant Sci* 1989; 1:313–316.
86. Garrison DL, Sullivan CW, Ackley SF. Sea ice microbial communities in Antarctica. *Bioscience* 1986; 36:243–250.
87. El-Sayed SZ. Observations on phytoplankton bloom in the Weddell Sea. *Ant Res Ser* 1971; 17:301–312.
88. Krebs WN. Ecology of neritic marine diatoms, Arthur Harbor, Antarctica. *Micropaleontology* 1983; 29:267–297.
89. Smetacek V, Scharek K, Gordon LI, et al. Early spring phytoplankton blooms in ice platelet layers of the southern Weddell Sea, Antarctica. *Deep Sea Res A* 1992; 39:153–168.
90. Fritsen CH, Lytle VI, Ackley SF, Sullivan CW. Autumn bloom of Antarctic pack-ice algae. *Science* 1994; 266:782–784. PMID: [17730399](#)
91. Lannuzel D, Schoemann V, Dumont I, Content M, de Jong J, Tison J-L et al. Effect of melting Antarctic sea ice on the fate of microbial communities studied in microcosms. *Polar Biol* 2013; 36:1483–1497.
92. Smith WO, Nelson D. Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. *Science* 1985; 227:163–166. PMID: [17843076](#)
93. Leventer A, Dunbar RB. Factors influencing the distribution of diatoms and other algae in the Ross Sea. *J Geophys Res* 1996; 101:18489–18500.



94. Arrigo KR, McClain CR. Spring phytoplankton production in the western Ross Sea. *Science* 1994; 266:261–263. PMID: [17771447](#)
95. Round FE. The ecology of algae. Cambridge University Press, Cambridge, 1981.
96. Hasle GR, Heimdal BR. Morphology and distribution of the marine centric diatom *Thalassiosira antarctica* Comber. *J Royal Microscopical Soc* 1968; 88:357–369.
97. Villareal TA, Fryxell GA. Temperature effects on the valve structure of the bipolar diatoms *Thalassiosira antarctica* and *Porosira glacialis*. *Polar Biol* 1983; 2:163–169.
98. Robinson CT, Rushforth R. Effects of physical disturbance and canopy cover on attached diatom community structure in an Idaho stream. *Hydrobiologia* 1987; 154:49–59.
99. Poff NL, Voelz NJ, Ward JV, Lee RE. Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *J North Amer Benthol Soc* 1990; 9:303–318.
100. Wahl M. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Mar Ecol Prog Ser* 1989; 58:175–189.
101. Totti C, Romagnoli T, De Stefano M, Di Camillo CG, Bavestrello G. The diversity of epizoic diatoms: relationships between diatoms and marine invertebrates. *Cellular Origin, Life in Extreme Habitats and Astrobiology* 2011; 16:323–343.
102. Cardinale BJ, Hillebrand H, Charles DF. Geographic patterns of diversity in streams are predicted by a multivariate model of disturbance and productivity. *J Ecol* 2006; 94:609–618.
103. Catalano G, Povero P, Fabiano M, Benedetti F, Goffart A. Nutrient utilisation and particulate organic matter changes during summer in the upper mixed layer (Ross Sea, Antarctica). *Deep Sea Res I* 1997; 44:97–112.
104. Goffart A, Catalano G, Hecq JH. Factors controlling the distribution of diatoms and Phaeocystis in the Ross Sea. *J Mar Syst* 2000; 27:161–175.
105. Grotti M, Soggia F, Abelmoschi ML, Rivaro P, Magi E, Frache R. Temporal distribution of trace metals in Antarctic coastal waters. *Mar Chem* 2001; 76:189–209.
106. Durbin EG, Krawiec RW, Smayda TJ. Seasonal studies on the relative importance of different size fractions of phytoplankton in Narragansett Bay (USA). *Mar Biol* 1975; 32:271–287.
107. Sunda WG, Huntsman SA. Iron uptake and growth limitation in oceanic and coastal phytoplankton. *Mar Chem* 1995; 50:189–206.
108. McLachlan DH, Brownlee C, Taylor AR, Geider RJ, Underwood GJC. Light-induced motile responses of the estuarine benthic diatoms *Navicula perminuta* and *Cylindrotheca closterium* (Bacillariophyceae). *J Phycol* 2009; 45:592–599. doi: [10.1111/j.1529-8817.2009.00681.x](#) PMID: [27034035](#)
109. Underwood GJC, Paterson DM. Recovery of intertidal benthic diatoms after biocide treatment and associated sediment dynamics. *J Mar Biol Assoc UK* 1993; 73:25–45.
110. Ryan KG, Hegseth EN, Martin A, Davy SK, O'Toole R, Ralph PJ et al. Comparison of the microalgal community within fast ice at two sites along the Ross Sea coast, Antarctica. *Ant Sci* 2006; 18:583–594.
111. Booth JA. The eponitic algal community of the ice edge zone and its significance to the Davis Strait ecosystem. *Arctic* 1984; 37:234–243.
112. Everitt DA, Thomas DP. Observations of seasonal changes in diatoms at inshore localities near Davis Station, East Antarctica. *Hydrobiologia* 1986; 139:3–12.
113. Fukushima H, Meguro H. The plankton in ice as a basic factor of the primary production in the Antarctic Ocean. *Ant Rec* 1966; 27:99–101.
114. Andersen OGN. Primary productivity associated with sea ice at Godhavn, Disko, West Greenland. *Ophelia* 1977; 16:205–220.
115. Povero P, Chiantore M, Mistic C, Budillon G, Cattaneo-Vietti R. Land forcing controls pelagic-benthic coupling in Adélie Cove (Terra Nova Bay, Ross Sea). *Polar Biol* 2001; 24:875–882.
116. Fabiano M, Danovaro R, Chiantore M, Pusceddu A. Bacteria, protozoa and organic matter composition in sediments of Terra Nova Bay (Ross Sea). In: Faranda FM, Guglielmo L, Ianora A (eds) *Ross Sea Ecology: Italian Antarctic Expeditions (1986–1995)*. Springer, Berlin Heidelberg New York, 2000, 503–514.
117. Gambi MC, Buia MC, Mazzella L, Lorenti M, Scipione MB. Spatio-temporal variability in the structure of benthic populations in a physically controlled system off Terra Nova Bay: the shallow hard bottoms. In: Faranda FM, Guglielmo L, Ianora A (eds) *Ross Sea Ecology: Italian Antarctic Expeditions (1986–1995)*. Springer, Berlin Heidelberg New York, 2000, 527–538.
118. Andreoli C, Tolomio C, Moro I, Radice M, Moschin E, Bellato S. Diatoms and dinoflagellates in Terra Nova Bay (Ross Sea—Antarctica) during austral summer 1990. *Polar Biol* 1995; 15:465–475.

119. Schwarz AM, Hawes I, Andrew N, Norkko A, Cummings V, Thrush S. Macroalgal photosynthesis near the southern global limit for growth; Cape Evans, Ross Sea, Antarctica. *Polar Biol* 2003; 26:789–799.
120. Horner R, Schrader GC. Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. *Arctic* 1982; 35:485–503.
121. Petrovich DK. Theoretical estimates of light reflection and transmission by spatially complex and temporally varying sea ice covers. *J Geophys Res: Oceans* 1990; 95:9557–9567.
122. Lotter AF, Bigler C. Do diatoms in the Swiss Alps reflect the length of ice-cover? *Aquat Sci* 2000; 62:125–141.
123. Venables H, Moor CM. Phytoplankton and light limitation in the Southern Ocean: Learning from high-nutrient, high-chlorophyll areas. *J Geophys Res: Oceans* 2010; 115:C02015 doi: [10.1029/2009JC005361](https://doi.org/10.1029/2009JC005361)
124. Sterrenburg FAS. Studies on tube-dwelling *Gyrosigma* populations. *Diatom Res* 1989; 4:143–150.
125. John J. Morphology and ultrastructure of the tubes of *Mastogloia cocconeiformis* (Bacillariophyta) from Shark Bay, Western Australia. *Phycologia* 1993; 32:388394.
126. Liu J, Soininen J, Han B-P. Effects of connectivity, dispersal directionality and functional traits on the metacommunity structure of river benthic diatoms. *J Biogeogr* 2013; 40:2238–2248.
127. Bathmann U, Fisher G, Müller PJ, Gerdes D. Short-term variations in particulate matter sedimentation off Kapp Norvegia, Weddell Sea, Antarctica: relation to water mass advection, ice cover, plankton biomass and feeding activity. *Polar Biol* 1991; 11:185–195.
128. Nowell ARM, Jumars PA. Flow environments of aquatic benthos. *Annu Rev Ecol Systemat* 1984; 15:303–328.
129. Gili JM, Alvà V, Pagès F, Klöser H, Arntz WE. Benthic diatoms as the major food source in the sub-Antarctic marine hydroid *Silicularia rosea*. *Polar Biol* 1996; 16:507–512.
130. Gili JM, Coma R, Orejas C, López\_González PJ, Zabala M. Are Antarctic suspension-feeding communities different from those elsewhere in the world? *Polar Biol* 2001; 24:473–485.
131. Bradshaw C, Collins P, Brand AR. To what extent does upright sessile epifauna affect benthic biodiversity and community structure? *Mar Biol* 2003; 143:783–791.
132. Bouma TJ, Olenin S, Reise K, Ysebaert T. Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. *Helgol Mar Res* 2009; 63:95–106.
133. Gili JM, Hughes RG. The ecology of marine benthic hydroids. *Oceanogr Mar Biol—Annu Rev* 1995; 33:351–426.
134. Blackburn N, Fenchel T, Mitchell J. Microscale nutrient patches in planktonic habitats shown by chemotactic bacteria. *Science* 1998; 282:2254–2256. PMID: [9856947](https://pubmed.ncbi.nlm.nih.gov/9856947/)
135. McCormick PV, Stevenson RJ. Grazer control of nutrient availability in the periphyton. *Oecologia* 1991; 86:287–291.
136. Levinton J. Stability and trophic structure in deposit-feeding and suspension-feeding communities. *Amer Nat* 1977; 106:472–486.
137. Gambi MC, Lorenti M, Russo GF, Scipione MB. Benthic associations of the shallow hard bottoms off Terra Nova Bay, Ross Sea: zonation, biomass and population structure. *Ant Sci* 1994; 6:449–462.