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Diatom communities on an artificial substratum at two contrasting sites at South Bay, Livingston Island

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Abstract: We used an artificial substratum (plexiglass tiles) to compare diatom communities at three different depths at two sites differing in their hydrological conditions and glacier melt-water influence. Samples at 1 m depth were taken during early summer in 2018, whereas samples at 3 m and 6.5 m were obtained in late summer 2020. The tiles were submerged for a period of up to 45 days in 2018, and up to 34 days in 2020. Water temperature, salinity, conductivity, oxygen saturation and concentrations, and Secchi depth were measured multiple times at both sites. During late summer of 2020 Photosynthetically Active Radiation (PAR) was also measured at depths of 3, 6.5 and 10 m at both sites. A total of 50 taxa constituted the diatom communities. Colonization and community development followed the same scheme at both sites and at all depths, with an early establishment of the dominant taxa, and a decline in species richness, diversity and evenness indices over the time towards relatively stable low values. Based on the results of PERMANOVA, ANOSIM and SIMPER analyses, diatom communities were site-specific, with 49% dissimilarity between the sites. Mechanical disturbances, such as wave action and ice scouring, as well as depth (and light availability) seemed to be the main factors driving the differences. The motile *Navicula* aff. *perminuta* dominated under mechanical disturbances at various light conditions, *Navicula glaciei* preferred calm shallow waters, and erect diatom growth forms were present in higher numbers in deeper waters with deteriorated light conditions.

Keywords: Antarctic, Bacillariophyta, marine benthos, colonization.

Introduction

Diatoms (Bacillariophyta) are commonly observed in the coastal Antarctic marine benthic habitats, where they are also main primary producers (McMinn *et al.* 2010) and important food source for many organisms (Gili *et al.* 1996; Błażewicz-Paszkowycz and Ligowski 2002; Daglio *et al.* 2018). With the exclusion of the sedimentary assemblages and sea-ice associated diatoms, which have been a subject of numerous studies in the past half-century, diatoms are also the most neglected organisms in the studies on the Antarctic marine benthos. In the first comprehensive description of the biodiversity and biogeography of intertidal communities in the Antarctic and Subantarctic regions by Griffiths and Waller (2016) diatoms were not considered, even though recent estimates showed that during different seasons benthic microalgae accounted between 40% and up to 90% of the coastal primary production in Antarctica (McMinn *et al.* 2010). In reality, the data we have for marine benthic diatoms from the region are quite "patchy" in terms of study topics, and many uncertainties exist even for species identities (Al-Handal and Wulff 2008a; Majewska *et al.* 2015; Zidarova *et al.* 2022).

Recently, more efforts were put into the characterization of marine epiphythic diatoms and factors influencing their distribution and abundances (Al-Handal and Wulff 2008b, Majewska *et al.* 2013, 2016; Majewska and De Stefano 2015; Burfeid-Castellanos *et al.* 2021). In these studies, a diverse epiphytic diatom flora for the region was reported, and sampling site location, macroalgal host, depth and light availability, and season seemed to influence, to different degrees, taxa composition and abundances. Perhaps also due to the difficulties in sampling, fewer data exist on diatoms living on hard substrata, although rocky and stony shores are typical for the region. Some studies focused on the effects of ultraviolet radiation (UVR) and grazing over the Antarctic diatoms on ceramic tiles placed in marine environment (*e.g.,* Zacher *et al.* 2007; Campana *et al.* 2008). Outside the records in old Antarctic literature (*e.g.,* Peragallo 1921), recent floristic data on Antarctic diatoms on hard substrata were provided in part by Klöser (1998), Ligowski (2002), Al-Handal and Wulff (2008a, ceramic tiles at their site Peñon Uno (PU)) and Daglio *et al.* (2018, ceramic tiles in controlled environment), and more recently by Bae *et al.* (2021). Zidarova *et al.* (2022) studied diatom taxa composition and species distributions of marine benthic diatoms on artificial substrata, cobbles, rocks, sediments, and in tidal pools, at South Bay, Livingston Island. Many of the taxa could not be identified to species level, but they showed distinct distributions across the studied habitat/substratum types related to the disturbing factors at the habitat and ability of the species to resist their combined effect.

Climate change shifts disturbance regimes in the region (Robinson *et al.* 2020), yet the knowledge on how marine benthic diatoms may react to these changes is still limited. Little is also known about the distribution of the different diatom taxa in relation to glacier influence. Bae *et al*. (2021) studied diatom communities from a variety of substrates (sediments, macroalgae, rocks, fauna) at different distances of a retreating glacier inside Marian Cove, King George Island, and observed changes in species composition and abundances in relation to the substrate and depth. Earlier, Zidarova *et al.* (2020) provided preliminary data on diatom colonization and development of marine benthic diatom communities on an artificial substratum at two sites near the coasts of Livingston Island, differing in their exposure to glacier melt-water. These initial results suggested that diatom communities on newly exposed/submerged substrata were fast developing, and differences existed between the communities at the different sites. However, the study was limited to only a single depth of substratum exposure during early summer.

The present study is a continuation of our previous efforts, with main aims to (1) characterize the communities developing during austral summer on a hard artificial substratum at different depths at two contrasting sites by glacier melt-water influence, (2) check whether significant differences exist in communities between the sites and depths over summertime, and possibly to (3) explain what are the reasons for these differences. For comparison with the newly obtained data, part of the data in Zidarova *et al*. (2020) is also included in this study. We used the same artificial substratum, as in Zidarova *et al*. (2020). The substratum used at the two sites had the same nature (same chemistry and surface microtexture) and same orientation in the water column. This reduced the possible variability in diatom communities related to substratum and light conditions depending on its orientation, allowing better comparisons between the sites (Desrosiers *et al.* 2014). In addition, we also compared the diatom valve accumulation (diatom growth) and community development between the two sites on the newly submerged substratum at different depths of its exposure. The study also provides data for the utility of artificial substrata in studies on marine benthic diatoms.

Study area

Livingston Island is the second largest island of the South Shetland Archipelago, located *ca*. 130 km north of the Antarctic Peninsula (Fig. 1). The island has a maritime Antarctic climate, with summer air temperatures above 0°C, high cloud cover and high precipitation (Chipev and Veltchev 1996; Bañon *et al.* 2001). Materials for the study originate from South Bay, a large inlet of the southern side of the island between Hannah Point and Hurd Peninsula, open to south-southwest direction (Fig. 1B). Wave conditions inside the bay are considered moderate with the prevailing southwest winds (Lonin *et al.* 2022), but winds from northeast, the second common wind direction for the area, can create strong katabatic winds over the bay due to the mountainous relief of the island (Navarro *et al.* 2013; Lonin *et al.* 2022). The average wind speed is 4 ms^{-1},

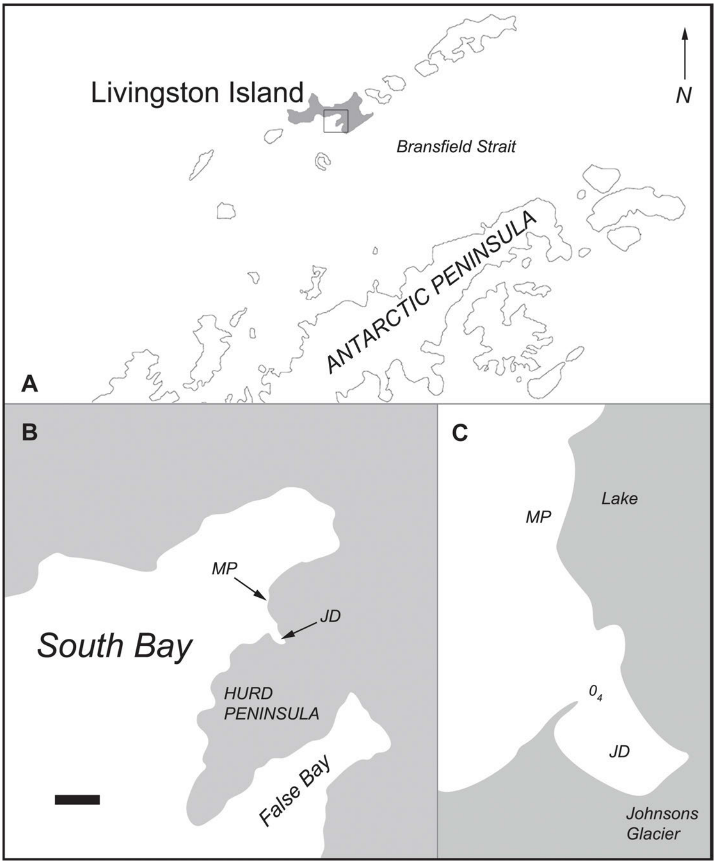

Fig. 1. Map showing the position of (**A**) Livingston Island relative to the archipelago of the South Shetland Islands and Antarctic Peninsula, (**B**) sampling area at South Bay, and (**C**) sampling sites. MP 3–4 Mongolian (Reserve) Port, JD 3–4 Johnsons Dock. Depth at low tide (0.4 m) at the entrance of Johnsons Dock is shown (**C**). Scale bar on B represents 2 km. Map outlines are based on © OpenStreetMap contributors (www.openstreetmap.org), edited and arranged using Adobe Illustrator © and Adobe Photoshop ©.

with frequent gusts above 28 ms^{-1} and peak values above 40 ms^{-1} (Navarro *et al.* 2013). In addition, the northeast winds often bring ice particles of various sizes, detached from the glaciers and floating in a clockwise direction near the eastern shores of the bay. The area experiences mixed, mainly semi-diurnal tidal cycle, with maximum amplitude of *ca*. 2 m during spring tide (López *et al.* 1994). This tidal regimen influences both the salinity and sea water temperature near the coast (Vidal *et al.* 2011).

Two sampling sites were chosen at South Bay, presenting different conditions in terms of glacier melt-water influence over the site. The two sites were also subjected to different levels of wave disturbances. The first site, Mongolian (Reserve) Port (MP), is a very small bay, located just below the “Todorini buzi” (unofficial name) Lake (Fig. 1B-C). In late summer lake’s outflow brings clear (snow-melt) freshwater into the bay. Being entirely open towards South Bay (Fig. 1B), site MP is particularly exposed to waves from the open ocean, and to floating ice particles and small icebergs carried by the currents across the bay. The second site, Johnsons Dock (JD), is located south-southeast of site MP (Fig. 1C), and represents a semi-enclosed bay (cove) below Johnsons Glacier. The glacier melt-water runs into the cove in late summer, giving it a typically milky appearance (Agustí and Duarte 2000). The cove is situated behind a narrow rocky ridge and connected to South Bay with a small entrance, *ca*. 75 m long and only *ca.* 40 cm deep (Isla *et al.* 2001) during low tide. This way it is well protected from waves (Fig. 1C). None of the two sites is directly influenced by bird or mammal colonies on the shores; therefore, no significant external nutrient input can be expected (Zidarova *et al*. 2020).

Methods

Environmental data collection. — In order to better characterize the two sites salinity, conductivity, sea water temperature, oxygen concentrations and saturation were measured multiple times at both sites with a hand-held WTW3410 multiparameter meter. Secchi depth was measured with a Secchi disk repetitively at each site. For both sites, data obtained in November–December 2018 and given in Zidarova *et al.* (2020) are included here for comparison. Additionally, in January–February 2020 multiple measurements of Photosynthetic Active Radiation (PAR) were performed at depths 3 m, 6.5 m and 10 m at each site, using LI-COR® underwater quantum sensors (LI-192SA, 400–700 nm) connected to a data logger, and light attenuation coefficient *Kd* was calculated for each depth and each site.

Diatom sampling and slides preparation. — Samples were obtained from an artificial substratum, submerged into the water column at three different depths (1 m, 3 m and 6.5 m), and kept at place by bruce type anchors in a fleet. More information about the substratum arrangement is given in Zidarova *et al.* (2020). Samples from early summer 2018 were taken at a depth of 1 m at each site (Zidarova *et al.* 2020), whereas in late summer 2020 we sampled substrata placed into the water column at 3 m and 6.5 m at each site. The substratum we used were roughly hand-sanded plexiglass tiles, each with an area of 25 cm^2. Consecutive sampling of the tiles was performed within a period of up to 45 days in December–January 2018 (4 samples at site MP on days 4, 7, 12, 31, and eight samples at site JD on days 7, 10, 14, 18, 22, 25, 38, 45, Zidarova *et al.* 2020). In 2020 the tiles were submerged for a period of up to 34 days at both depths at both sites, and seven consecutive samples were taken from each depth at each site (all on days 6, 10, 15, 20, 24, 28, 34). Each sample contained the biofilm from three randomly selected tiles, collected with a toothbrush into a small vial with filtered water (0.2 µm pore diameter Teknokroma® nylon filters) and preserved in 3%

formaldehyde. Diatom samples were treated following the method of Hasle and Fryxell (1970). Slides were prepared with Naphrax® after air drying a small amount of the treated material onto cover slips. Sampling, treatment and slide preparation were done using equal aliquots, as described in Zidarova *et al.* (2020), in order to obtain quantitatively comparable results.

Diatom valves accumulation on the substratum, taxa identification and community analyses. — Microscopic observations for diatom valves accumulation on the plexiglass tiles were performed at magnification of 1000x with Amplival Carl Zeiss Jena light microscope (LM). Analyses and calculations were done as described in Zidarova *et al.* (2020). Taxa identification and community analyses were performed with a LM Olympus BX51 equipped with Differential Interference Contrast optics at magnification of 1000x (N.A. 1.3). Diatom taxa identification followed Peragallo (1921), Williams (1988), Hasle *et al.* (1994), Cremer *et al.* (2003), Fernandes and Procopiak (2003), Fernandes *et al.* (2007, 2014), Al-Handal and Wulff (2008a, b), Al-Handal *et al.* (2008, 2010), Daglio *et al.* (2018), Zidarova *et al.* (2022), and others. Community analyses were performed with the identification and enumeration of at least 400 valves per sample. Ten slides containing less than 300 valves were excluded from community and subsequent data analyses. For the purposes of this study, data obtained in 2018 by Zidarova *et al.* (2020) at 1 m depth at the same sites and following the same sampling scheme, diatom taxa identification and enumeration are also included.

Data analyses. — Data analyses were performed with Primer v.7 (Anderson *et al.* 2015; Clarke and Gorley 2015). Non-metric multidimensional scaling (nMDS) was used to visualize the samples from the two sampling sites by depth and sampling month, based on the relative abundances of all taxa in the samples. Abundance data were square root transformed and Bray–Curtis similarity matrix was used. Permutational multivariate analysis of variance (PERMANOVA) was further applied in a search for significant differences with the possible combined effect of the site location, sampling depth and month. Two-way crossed Analysis of similarities (ANOSIM) was also used to check whether differences exist between diatom communities at the different studied depths and sites, as well as within each site by depth and sampling moth. Finally, in order to explore the similarity within and dissimilarity between the two sites and the studied depths at each site, and to define the taxa contributing most to the observed similarities and dissimilarities, Similarity percentage analysis (SIMPER) was performed. Shade-plot diagrams visualized the valve accumulation on the tiles over the period of the study, as well as the taxa contribution to the communities in each set of samples by depth and site. Since the data included a set of samples reflecting a colonization process and communities development, for which valve accumulation or species richness (S) alone are not sufficiently informative (Desrosiers *et al.* 2014), Simpson’s (1-D’), Shanon-Wiener’s diversity (H’), and Pielou’s evenness (J’) indices were also calculated for each sample, where sufficient number of valves were present for community analysis. This allowed us to compare the new data with the earlier observations in Zidarova *et al.* (2020).

Results

Environmental parameters. — Values of the measured environmental parameters are given in Tables 1–3. In general, the two sites did not differ considerably in water salinity, conductivity, temperature, and oxygen concentrations and saturation (Tables 1 and 2). However, in early summer (November–December 2018) both salinity and conductivity at site JD were lower, compared to site MP, and salinity was more variable at site JD (Table 2; Zidarova *et al.* 2020). In January–February 2020, and at both sites, salinity, conductivity, and oxygen concentrations and saturation were lower in comparison to the early

Table 1

Environmental parameters values with mean and with standard deviation (SD) measured at site MP at depths of 1 m, 3 m and 6.5 m in early (2018) and late (2020) summer. Date of the measurement is provided.

date	Conductivity (mS/cm)	Salinity (‰)	O_2 (%)	O_2 (mg/L)	Temperature (°C)
		1 m			
09.12.2018	53.5	33.6	101.5	12.4	1.5
12.12.2018	53.1	33.6	98.6	11.4	1.4
15.12.2018	53.5	33.6	105.0	12.7	2.6
20.12.2018	53.0	33.4	99.1	11.8	2.6
mean	53.3	33.6	101.1	12.1	2.0
SD	±0.3	±0.1	±2.9	±0.6	±0.7
		3 m			
23.1.2020	34.9	21.0	94.0	12.6	2.0
25.1.2020	35.1	21.4	94.0	12.0	2.4
27.1.2020	34.5	20.7	91.0	11.9	2.3
29.1.2020	35.7	21.5	93.0	12.3	1.9
31.1.2020	31.2	18.5	89.0	12.2	1.8
02.2.2020	35.9	21.6	94.0	12.2	1.7
05.2.2020	34.6	20.7	77.0	10.1	2.1
09.2.2020	35.4	21.3			2.9
14.2.2020	35.7	21.5			2.9
mean	34.8	20.9	90.3	11.9	2.2
SD	±1.4	±1.0	±6.2	±0.8	±0.4

date	Conductivity (mS/cm)	Salinity (‰)	O_2 (%)	O_2 (mg/L)	Temperature (°C)
6.5 m					
23.1.2020	35.3	21.4	95.0	12.8	2.3
25.1.2020	35.7	21.5	96.0	12.8	2.5
27.1.2020	35.7	21.5	97.0	13.1	2.2
29.1.2020	32.6	19.5	98.0	12.9	1.6
31.1.2020	32.2	19.2	95.0	13.1	1.4
02.2.2020	36.1	21.7	91.0	12.3	1.5
05.2.2020	35.6	21.3			2.2
09.2.2020	32.5	19.4			2.5
14.2.2020					
mean	34.5	20.7	95.3	12.8	2.1
SD	±1.7	±1.1	±2.4	±0.3	±0.5

Table 2

Environmental parameters values with mean and standard deviation (SD) measured at site JD at 1 m, 3 m and 6.5 m depths in early (2018) and late (2020) summer. Date of the measurement is provided.

date	Conductivity (mS/cm)	Salinity (‰)	O_2 (%)	O_2 (mg/L)	Temperature (°C)
1 m					
25.11.2018	43.8	29.9	104.0	13.3	1.8
02.12.2018	47.3	29.4	101.0	12.7	0.8
05.12.2018	52.0	32.6	101.8	12.8	1.4
09.12.2018	48.8	30.2	101.1	12.8	0.4
13.12.2018	51.2	32.3	104.9	12.5	1.4
17.12.2018	51.2	32.1	107.9	12.5	1.4
20.12.2018	52.9	33.2	99.9	12.1	2.1
mean	49.6	31.4	102.9	12.7	1.3
SD	±3.2	±1.5	±2.8	±0.4	±0.6
3 m					
23.1.2020	34.9	20.9	96.0	12.5	2.7
25.1.2020	31.3	18.7	94.0	11.6	2.9
27.1.2020	34.7	20.8	96.0	12.7	2.3
29.1.2020	33.3	20.0	87.0	11.7	1.8
31.1.2020	34.1	20.4	84.0	10.9	2.3
02.2.2020	34.8	20.9	92.0	11.9	2.2

date	Conductivity (mS/cm)	Salinity (‰)	O_2 (%)	O_2 (mg/L)	Temperature (°C)
05.2.2020	35.2	21.1			2.0
09.2.2020	33.9	20.4			2.9
mean	34.0	20.4	91.5	11.9	2.4
SD	±1.3	±0.8	±5.0	±0.7	±0.4
6.5 m					
23.1.2020	35.3	21.2	95.0	12.6	2.5
25.1.2020	35.3	21.1	101.0	13.5	2.5
27.1.2020	35.3	21.2	96.0	13.0	2.0
29.1.2020	34.6	20.7	91.0	12.2	1.8
31.1.2020	34.7	20.8	96.0	13.1	1.9
02.2.2020	35.4	21.2	84.0	11.4	1.7
05.2.2020	35.4	21.2			1.9
09.2.2020	34.7	20.8			2.5
mean	35.1	21.0	93.6	12.6	2.1
SD	±0.4	±0.2	±5.8	±0.8	±0.3

Table 3

Secchi depth (m) with mean values and standard deviation (SD) at the two sites (MP and JD) in early summer 2018 and late summer 2020.

2018			2020		
date	MP	JD	date	MP	JD
25.11.2018		2.00	23.1.2020	2.25	0.70
02.12.2018		1.10	25.1.2020	2.40	0.50
05.12.2018		1.70	27.1.2020	3.00	0.50
09.12.2018	2.70	1.45	29.1.2020	1.85	0.35
12.12.2018	2.75		31.1.2020	1.35	0.35
13.12.2018		1.75	02.2.2020	2.25	0.45
15.12.2018	2.75	0.50	05.2.2020	1.50	0.90
17.12.2018		0.50	09.2.2020	1.50	0.60
20.12.2018	2.10	1.50	14.2.2020	2.25	0.65
			18.2.2020	2.05	0.55
mean	2.58	1.43	mean	2.04	0.56
SD	±0.32	±0.56	SD	±0.50	±0.17

summer of 2018. Especially salinity dropped with more than 10‰, occasionally reaching values of 18.5–18.7‰ in late summer (Tables 1 and 2), in accordance with the freshwater input into the coastal waters with snow and ice melting. Water temperature was slightly higher in late summer but comparable between the sites and different depths. The lowest water temperature was measured at site JD in November–December 2018 (Table 2). Site JD had more stable but lower light conditions when compared to site MP (Figs 2A–C). At 3 m differences in light conditions at the sites were small (Fig. 2A) but became larger with depth

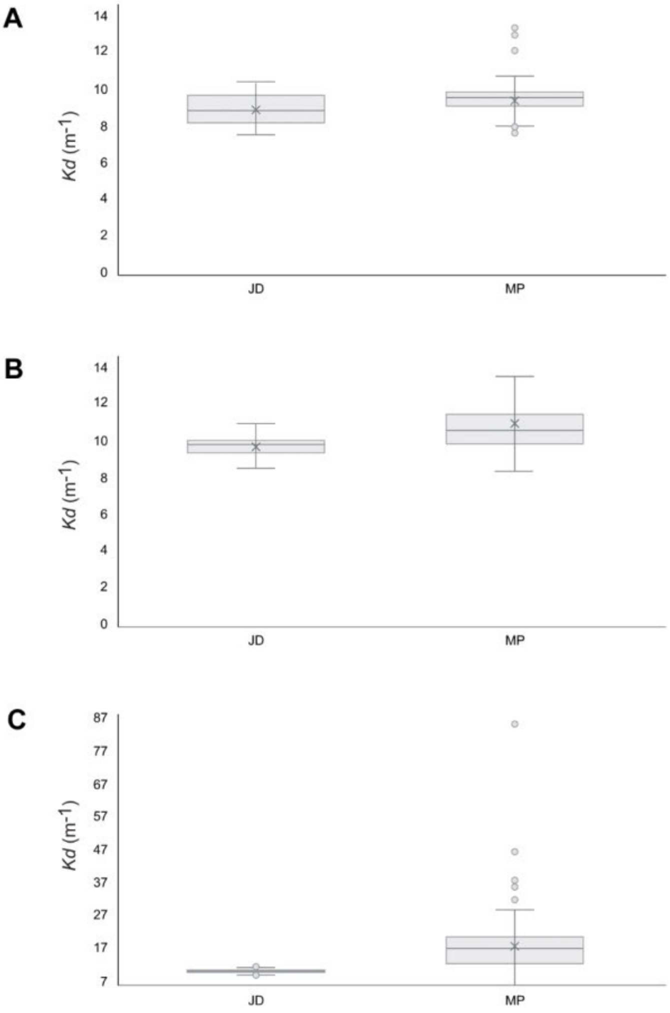

Fig. 2. Box-plots of light attenuation coefficient *Kd* at sites MP and JD at depths (**A**) 3m, (**B**) 6.5 m, and (**C**) 10 m. First and third quartiles are shown by the lower and upper edges of the box, the horizontal line inside the box represents the median, and the average value is shown with x inside the box. Minimal and maximal values are given with whiskers. Circles represent outliers.

(Figs 2A–C). These results are also consistent with the measured Secchi depth (Table 3). At both sites Secchi depth was lower during late summer (January–February 2020, Table 3). At site JD, Secchi depth was always lower than at site MP, even in early summer (Table 3; Zidarova *et al.* 2020). During late summer in January–February 2020 Secchi depth at site JD had a mean of 0.56 (±0.17) m, with the lowest measured value of only 0.35 m (Table 3).

Diatom diversity. — In total, 50 taxa were recorded on the plexiglass tiles during the counts but the number of taxa per site differed (Appendix 1). At site JD 46 taxa were observed while site MP had lower diatom diversity. Only 29 taxa in total were observed during the counts at this site (Appendix 1). The diversity was lowest at a depth of 6.5 m at site MP where only 13 taxa were recorded on the tiles during the entire period of their exposure (versus 20 taxa at depths 1 m and 3 m, each). In contrast, at site JD the overall diatom diversity was highest at the largest studied depth (41 taxa at 6.5 m) (Appendix 1).

The highest number of taxa belonged to *Navicula* and *Cocconeis* (eight, each) but species of the genus *Cocconeis* were always found in very low numbers, usually below 1% of the counted valves in the samples (Appendix 1). Shade-plot diagram (Fig. 3) visualizing the most commonly observed taxa in the samples (relative abundance >1% in at least one sample) shows well that only two taxa were regularly observed, and in high numbers, including *Navicula* aff. *perminuta*

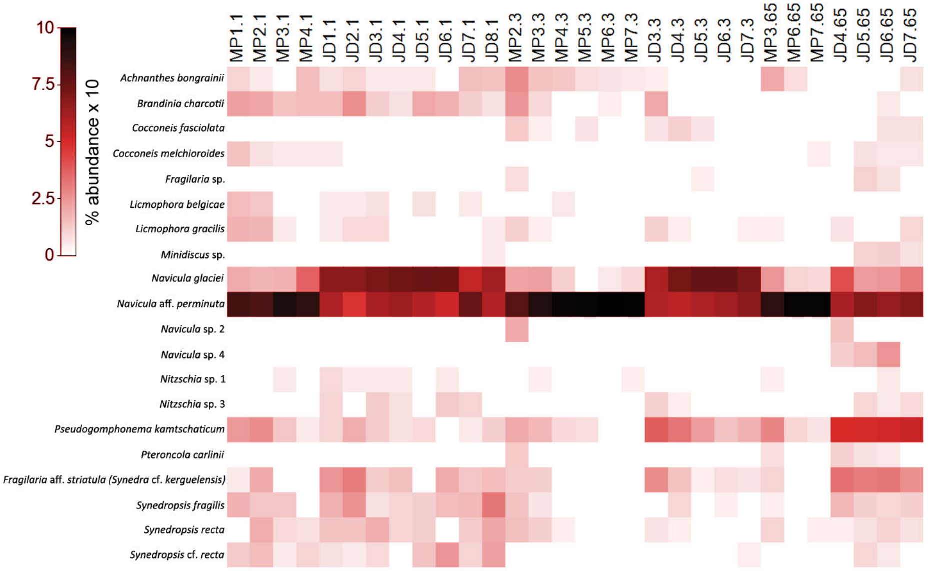

Fig. 3. Shade-plot diagram visualizing the most commonly observed taxa in the samples (relative abundance >1% in at least one sample). Sample labels include the sampling site (MP or JD), the consecutive number of the sample during the study period, and the last one or two digits represent the depth of substrata (*i.e.,* sample JD7.65 is the seventh consecutive sample at 6.5 m at site JD, whereas sample MP1.1 is the first sample taken at 1 m at site MP).

and *Navicula glaciei* (Fig. 3, Appendix 1). Several *Synedropsis* and *Licmophora* taxa, *Brandinia charcotii, Fragilaria* aff. *striatula,* and *Pseudogomphonema kamtschaticum,* were also present in most of the samples, but usually in lower numbers (Fig. 3, Appendix 1).

Diatom valves accumulation on the substratum. — Diatom valve accumulation (or diatom growth) on the newly submerged plexiglass tiles during the period of their exposure is presented on the shade-plot diagram on Fig. 4. Samples used by Zidarova *et al*. (2020) for the same sites at a depth of 1 m are also shown. The highest number of valves on the tiles was observed after 38 days of their exposure at a depth of 1 m at site JD in December 2018 (Zidarova *et al.* 2020). However, in February 2020 at a depth of 6.5 m the lowest number of valves on the tiles was also observed at this site, even after 34 days of their exposure (Fig. 4). It should be noted that at site MP, due to a failure in our equipment, some of the valves at 3 and 6.5 m were lost during the experiment which is visible on the shade-plot diagram on Fig. 4. Nevertheless, the recovery was quite rapid, in only a few days, and only slightly slower at a depth of 6.5 m (see Fig. 4 and compare sample MP4.3 and samples MP4.65 and MP5.65 with the rest of the samples in the same groups). No plateau in the growth was observed at 3 m and 6.5 m at both sites.

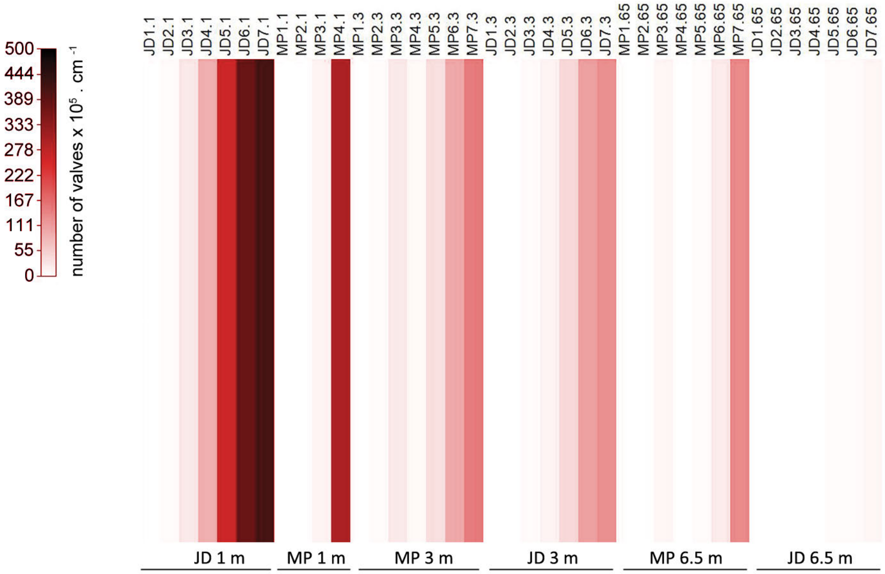

Fig. 4. Shade-plot diagram visualizing the valve accumulation on substrata at all depths and all sites. Sample labels include the sampling site (MP or JD), the consecutive number of the sample during the study period, and the last one or two digits represent the depth of substrata (*i.e*., sample JD7.65 is the seventh consecutive sample at 6.5 m at site JD, whereas sample MP1.1 is the first sample taken from substrata at 1 m at site MP). Groups of samples per site (MP, JD) and depth (m) are indicated.

Community development on the substratum. — Similarly to the previous observations by Zidarova *et al.* (2020) for a depth of exposure of 1 m, at depths of 3 m and 6.5 m and at both sites the dominant taxa established soon after the plexiglass tiles were submerged, and did not change over time (Fig. 3). *Navicula* aff. *perminuta* over-dominated at all depths at site MP (Fig. 3). Both *N. glaciei* and *N.* aff. *perminuta* kept their dominance on the tiles at 1 m and 3 m at site JD, but at 6.5 m at site JD *N. glaciei* decreased in numbers, and the most abundant taxa in communities during the entire period of the study were *N.* aff. *perminuta* and *P. kamtschaticum* (Fig. 3). Species richness (S), and diversity (H', 1-D') and evenness (J') indices, were higher during the early stages of diatom colonization, and gradually decreased in a period of a month, stabilizing around low values after 24 days of substratum exposure at 3 m depth at both site MP and JD (Fig. 5). Species richness at 6.5 m at both sites was, however, more variable, with a decrease at 6.5 m at site JD only on day 34. Similarly, all indices values at 6.5 m at site JD were more stable, with a slight decrease on day 34 (Fig. 5).

Data analyses. — nMDS diagrams with 2D stress of 0.13 visualize the samples from the two sites from the different depths of substratum exposure and different sampling month based on the species present in the samples and their

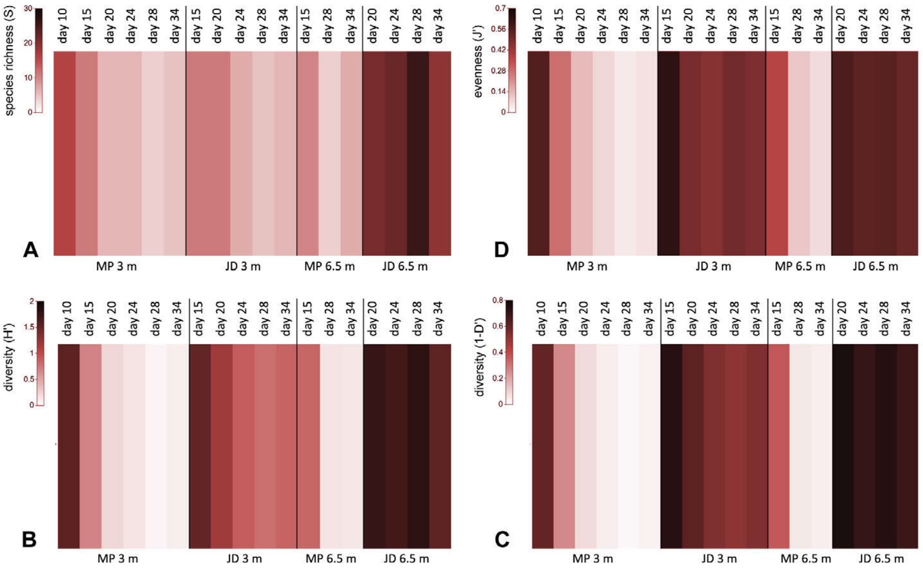

Fig. 5. Shade-plot diagrams visualizing the changes in species richness, diversity and evenness indices of the communities on substrata at depths of 3 m and 6.5 m at both sites during the study period. Sample groups per site (MP, JD) and depth (m) are indicated below each graph, and days of substratum exposure are shown on top. Black lines were added using Adobe Photoshop © to better visualize and separate the different sampling groups on the graphs. **A** - species richness (S), **B** - Shannon-Wiener's diversity index (H'), **C** - Simpson's diversity index (1-D'), **D** - Pielou's evenness index (J').

abundances (Fig. 6). On the diagram showing the samples from the different sampling depths (Fig. 6A), samples from the two sites are separated. Samples from site JD are divided into two groups by the depth of tiles exposure: one group includes samples from 1 m and 3 m depths, and a second group contains the samples taken a depth of 6.5 m. Samples from site MP form several small groups but are not mixed with the samples from site JD on the diagram indicating possible differences in diatom communities between the two sites.

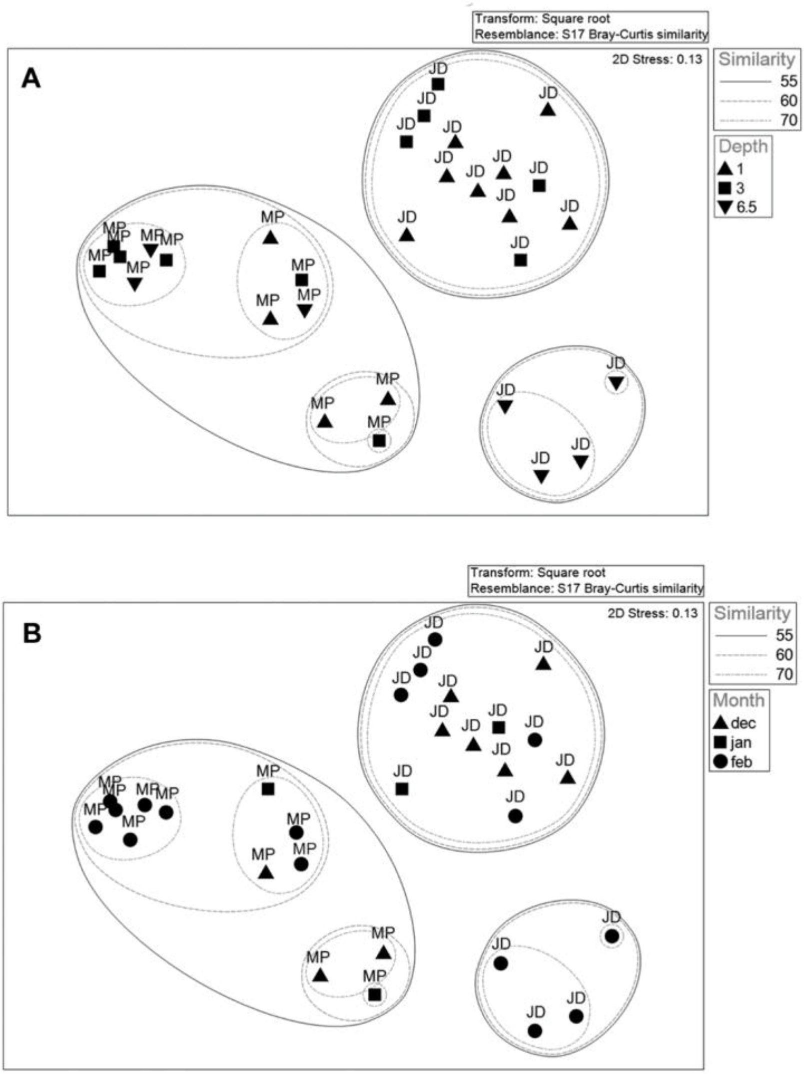

Fig. 6. nMDS graphs of the samples from (**A**) both sites (MP and JD) and depths (1 m, 3 m and 6.5 m) and (**B**) both sites and all months, based on all species abundance data. Sampling months are abbreviated: dec - December, jan - January, feb - February.

When sampling month is taken into account (Fig. 6B), all samples from site JD taken in February and at a depth of 6.5 m are isolated from the rest of the samples. Within site MP, several samples taken in February form a small subgroup (Fig. 6B), all these originating from different depths (Fig. 6A). In overall, however, the samples taken in different sampling months are not separated on the graph.

PERMANOVA (Appendix 2) indicated significant effects of both depth and sampling month, and a combined significant effect of site and sampling month over the communities. However, the test of homogeneity of dispersions (PERMDISP) was also significant for both the sampling month and depth as factors. PERMANOVA with only site as a fixed factor showed a high significance of the site over diatom communities (Pseudo-F = 16.686, P = 0.0001). Since on the nMDS graph separation of the samples based on the depth of the substratum exposure was evident at least for site JD (Fig. 6A), we also performed two-way crossed ANOSIM, with the site and depth included as factors.

Results of ANOSIM analyses are presented in Appendix 3. The site effect (across all sampling depths) was again significant (Global R 0.912, $p<0.01$), and larger than the effect of the sampling depth across all sites (Global R 0.627, $p<0.01$). ANOSIM, performed for each site separately and including depth and month as factors, showed significant differences in diatom communities at site JD in relation to the depth of tiles exposure (Global R 0.981, $p<0.01$) but with low number of permutations. Due to the small and unequal number of replicates for each factor no further conclusions could be made. At site MP, the differences related to the sampling month were significant but at lower p ($p<0.05$) and had very small number of permutations. Negative R value (Global R –0.056) was obtained for the depth factor. Negative R values may occur when variability inside the levels of a studied factor is higher than the variability between the different levels of the same factor (Chapman and Underwood 1999). When R values are 0 or close to 0, we can assume that the factor has no effect (Clarke and Gorley 2015). It is possible that the negative value is a consequence of the inclusion of the entire set of samples at each depth, representing also a colonization process with community development. However, we failed to recognize clear depth related changes in communities at site MP based on the data.

Based on SIMPER analysis (Appendix 4), the similarity between the samples within each site was high, 66% for site JD and 69% for site MP, regardless of the depth and sampling month. At both sites this large percentage of similarity was mostly due to *N.* aff. *perminuta* and *N. glaciei.* These two taxa together were responsible for 82% of the similarity of all samples taken at site MP and 69% of the similarity within site JD. Two other taxa, *Pseudogomphonema kamtschaticum* and *Fragilaria aff. striatula* (as *Synedra* cf. *kerguelensis* in Zidarova *et al.* 2020), contributed additional 15% to the similarity of the samples within site JD.

The dissimilarity between the two sites was 49%. Five taxa contributed almost 60% to this dissimilarity: *N.* aff. *perminuta* and its higher average abundance at site MP, and *N. glaciei, P. kamtschaticum, F.* aff. *striatula* and *Synedropsis fragilis* which were present in larger numbers at site JD (Appendix 4).

Samples taken from the same depth at each site also had a high percentage of similarity (above 70% for each depth at each site). No large changes in taxa composition and abundances were observed at each depth at each site during the colonization of the tiles. However, some differences existed between the communities at the different depths at each site. At site JD, the largest dissimilarity was found between the communities on the tiles at 1 m and 6.5 m (48%, Appendix 4), and between 3 m and 6.5 m (45%, Appendix 4). *Navicula glaciei, P. kamtschaticum* and *F.* aff. *striatula* together contributed 37–38% to the dissimilarity between the larger (6.5 m) and smaller depths (1 m and 3 m). *Pseudogomphonema kamtschaticum* and *F.* aff. *striatula* had higher average abundances at larger depths. Alone, *P. kamtschaticum* was responsible for 16% of the dissimilarity between the communities at 1 m and 6.5 m, and 12% between the communities at 1 m and 3 m, and at 3 and 6.5 m at site JD. *Navicula glaciei* was always a dominant species on the tiles at smaller depths (1 m and 3 m), but its lower abundance at 6.5 m contributed 18% of the dissimilarity between the communities at 3 m and 6.5 m at site JD (Appendix 4).

At site MP differences were smallest between the communities on the tiles at 3 m and 6.5 m (24%), and larger between these two depths and 1 m of substratum exposure (38% and 36%, respectively). *Brandinia charcotii* alone contributed 10% and 13% of the dissimilarity between the communities at depths of 1 m and 3 m and 1 and 6.5 m at site MP, respectively, reaching higher average abundances on the tiles at 1 m in early summer. *Navicula* aff. *perminuta* was abundant on the tiles at all depths (Appendix 4).

Some similar trends between the two sites were observed. *Navicula glaciei* was present in lower numbers on the tiles at larger depths (3 m and 6.5 m) at both sites. *Pseudogomphonema kamtschaticum* had higher average abundances at 6.5 m at site MP as well, contributing 14% of the dissimilarity between the communities on tiles exposed at 3 m and 6.5 m. However, it was also found in larger numbers at a depth of 1 m in early summer during the initial phases of colonization (Appendix 4 and Fig. 3).

Discussion

Diatom diversity. — The number of the taxa found in this study reflects the number of species, which were sufficiently abundant on the plexiglass tiles to be detected during the community analysis. Zidarova *et al.* (2020) reported only 27 taxa on an artificial substratum at 1 m depth. Compared to this study, Zidarova *et al.* (2022) recorded a slightly higher number of species (59 taxa). However, this number included the taxa present on the ropes holding the plexiglass tiles as well, and only six samples from the latest stages on colonization of the tiles were included in their study. The number of taxa recorded in this study is comparable to the number reported by Al-Handal and Wulff (2008a) at site PU near the coast of King George Island. As already discussed by Zidarova *et al.* (2022), Al-Handal and Wulff (2008a) recorded a similar number of taxa (47), but after a much longer period of substratum exposure. The substratum they used were ceramic tiles, exposed for 106 days. *Cocconeis* taxa dominated on their tiles, whereas the most common and abundant species in this study, *Navicula* aff. *perminuta* [as *N.* cf. *perminuta* in Al-Handal and Wulff (2008a)], was reported as frequent. In addition, *Pseudogomphonema kamtschaticum* was not observed on the ceramic tiles. In another experiment on ceramic tiles in Antarctica Daglio *et al.* (2018) found only 21 taxa. The differences between the studies are due to the different substrata, their different positioning in the environment, and the environment itself, which all can bring differences in diatom taxa composition and abundances (Desrosiers *et al.* 2014). When the number of taxa observed on natural hard substrata at South Bay is taken into account, a comparable number of taxa was recorded in the same area (47 taxa on the intertidal cobbles, Zidarova *et al.* 2022). No statistically significant differences were found between the communities on cobbles and artificial substrata (Zidarova *et al.* 2022). In general, the selected artificial substrata seem to mimic well the properties of intertidal cobbles as substratum, and in similar environment diatom communities on both substrata are comparable.

Klöser (1998) concluded that the substratum properties contributed to species abundances and distributions of the Antarctic marine benthic diatoms, but the species did not show the typical distribution associated with a particular substratum type. Similar observations were made by Zidarova *et al.* (2022) and in this study. The taxa that could be identified in this study have been found living on various natural substrata in Antarctica. Although in varying and different abundances, *Achnanthes vicentii,* many of the *Cocconeis* taxa, *Fragilaria* aff. *striatula* and/or *F. islandica* var. *adeliae, Navicula glaciei, N. directa* and *N.* aff. *perminuta,* species of the genera *Licmophora* and *Synedropsis, P. kamtschaticum,* have been reported as epiphytes (Majewska *et al.* 2016; Burfeid-Castellanos *et al.* 2021), epilithically on cobbles (Zidarova *et al.* 2022), on sediments (Al-Handal and Wulff 2008a; Al-Handal *et al.* 2022, Zidarova *et al.* 2022), and some taxa also inhabit sea ice *e.g., N. glaciei, F.* aff. *striatula,* and *Synedropsis* species (Cremer *et al.* 2003 and references therein). Habitat environment seems to be of greater importance for taxa abundances and distribution than the substratum properties.

Patterns in diatom colonization and community development at the different depths and sites. — Unfortunately, there are no studies on diatom colonization in Antarctica, except the previous study at the same sites by Zidarova *et al.* (2020) for a depth of substratum exposure of 1 m. Therefore comparisons could only be made with the latter study. Diatom colonization and communities development on the newly submerged substratum at 3 m and 6.5 m followed the same scheme at both sites and at all depths, with initially higher number of species on the substratum, high diversity and evenness indices, and without changes in dominant taxa over the study period, as observed and discussed by Zidarova *et al.* (2020) for a depth of 1 m of substratum exposure. The initially higher number of taxa on the substratum can only be explained by the presence of a large number of possible colonizers, *i.e.,* benthic diatoms, suspended into the water column (Zidarova *et al.* 2020 and references therein). Once the species settle on a substratum, further development depends on their ability to live and reproduce in the environment of the substratum (Desrosiers *et al.* 2014). The decrease in species richness indicates that conditions were unfavorable for some of the settled species and they soon dropped out of the communities. Other species decreased in abundance over time. This was especially true for the erected forms at a depth of 1 m which were most abundant only during the initial colonization (Zidarova *et al.* 2020). At the same time taxa that could thrive in the environment gained entire dominance. The diminishing number of taxa with the full dominance of a few species resulted in the decrease in diversity and evenness indices over the time of substratum exposure (Zidarova *et al.* 2020). Study of the natural epilithon on cobbles from the same area showed that the natural communities at similar depths are characterized by low number of species, and low diversity and evenness indices (Zidarova *et al.* 2020), *i.e.,* these are disturbed communities typically dominated by a few species which can live and reproduce successfully in this environment. Therefore, the stable decrease in diversity and evenness indices over time in this case, in our opinion, confirms a state of "development" of the communities on the artificial substratum similar to that of the natural epilithon for the area. For a depth of 3 m relatively stable low values of diversity and evenness indices were observed after 24 days of substratum exposure (and after 28 days at 6.5 m at site MP, Fig. 5, but, it should be noted that the process at site MP was disrupted by a failure in our equipment, and therefore the period could be expected to be actually a few days shorter). Nevertheless, this period is comparable to the period observed when substratum is positioned at a depth of 1 m (Zidarova *et al.* 2020). At site JD, at a depth of 6.5 m, we were only able to detect lower values of indices at day 34. Since no further observations are available, here we can only hypothesize that either more time was necessary at site JD due to the deteriorated light conditions at this site or the decrease was less pronounced due to the smaller disturbances by waves at the site. The higher abundances of high-profile guild species (Passy 2007), such as *P. kamtschaticum* and *F.* aff. *striatula,* observed on the plexiglass tiles at 6.5 m at site JD suggests that these communities are at least less disturbed (Hudon and Bourget 1983).

Effect of sampling site, depth and sampling month on diatom communities and their development. — The results of the study indicate that diatom communities on hard artificial substratum off the coasts of Livingston

Island are site-specific. We used the entire set of samples from each depth at each site, from the initial colonization of the substratum to the development of diatom communities over a period of more than a month. Even with this experimental design significant differences between the two sites were found and these differences persisted throughout the entire period of the study. We were able to control some of the factors which may affect the communities and their development including the substratum nature, its chemical composition and surface microstructure, and the depth position and orientation of the substratum in regard to light. However, other factors, such as water chemistry, salinity, turbidity, stresses by waves and currents, and bottom nature, also play a role for the development of diatom communities on newly submerged substrata in marine environment (Desrosiers *et al.* 2014 and references therein). There is only a small number of studies on species composition and abundances of marine benthic diatoms in relation to the sampling site environment, but our results are consistent with other recent reports from both natural or artificial substrata. Off the coasts of South Africa and on an artificial substratum (plexiglass), both diatom species composition and abundances significantly varied between two different studied sites (Cotiyane-Pondo and Bornman 2021). In Antarctica, sampling site environment affected both the growth form structure and cell densities of the epiphytic diatoms (Majewska *et al*. 2013, 2015) and site effect was larger than the effect of the substratum type provided by the macroalgal hosts (Majewska *et al.* 2013). The use of artificial substratum in this study is therefore justified.

Site MP is characterized by its exposure to waves, often combined with ice-scouring when ice pieces detach from the glaciers. Mechanical disturbances seem to be the main factor affecting the diatom communities on the plexiglass tiles at this site. At several locations in Antarctica, strong winds and potential mechanical stresses were possible reasons for the observed reduced abundance of epiphythic diatoms (Majewska *et al.* 2016) or the low number of benthic taxa (Al-Handal and Wulff 2008a). Diatom communities at the disturbed by waves site MP were almost half less diverse compared to the communities at the calmer site JD. When compared to site JD, the number of the valves on the tiles at site MP was also lower at a depth of 1 m (Fig. 4; Zidarova *et al.* 2020). At such small depth a combined and more severe disturbances by waves and ice scouring could be expected. Models on the effect of waves and tidal currents on benthic biofilms have shown that the intensity and frequency of waves and tides (provoking tidal currents) determines benthic biofilm dynamics and the time scale of biofilm growth (Mariotti and Fagerhazzi 2012). Wave forces and turbulence influence the benthic communities to a depth of at least 12 m, causing abrasion of substrata with detachment of the benthic species and their redistribution (Barnes and Conlan 2007 and references therein).

The super-dominant at site MP at all depths and during all sampling months, *N.* aff. *perminuta*, has been found on a variety of substrates in the Maritime Antarctic intertidal zones, including epizoically on the shells of limpets (Bae *et al*. 2021). It was also a super-dominant on intertidal cobbles on the shores of South Bay, sometimes reaching almost 100% of the counted valves in the samples from the natural epilithon (Zidarova *et al.* 2020, 2022). The Antarctic intertidal zone, where this species thrives abundantly, is subjected to intense ice scouring, high UV radiation during summer, and frequent changes in salinity and water temperature (Griffiths and Waller 2016), in addition to the disturbance by waves. The observed fast recovery in the number of the valves on the substratum after the failure of our equipment during the experiment at site MP shows well the great potential of this small-celled *Navicula* species for re-colonization. Such opportunistic taxa are typically found at locations with recurrent unfavorable or catastrophic conditions (Hudon and Bourget 1983; Tuji 2000).

Some similar trends were observed at the second site, JD. Another small-celled *Navicula* species, *N. glaciei,* dominated at small depths together with *N.* aff. *perminuta.* Based on this study, our previous observations (Zidarova *et al.* 2020), and other recent reports from the region (Majewska *et al.* 2015; Bae *et al.* 2021), small-celled species belonging to the motile guild (Passy 2007), such as *Navicula* spp., are excellent colonizers of newly emerged substrates in shallow Antarctic coastal waters. The ability of these species to migrate to more suitable conditions and their fast reproduction give them advantages in the Antarctic coastal benthic habitats, at least in summer months. Majewska and De Stefano (2015) also noted seasonal changes in epiphytic diatom dominance at the Ross Sea: adnate and erect forms were abundant under ice cover, whereas small motile diatoms gained dominance once the ice retreated. Under ice cover, along with the lower light conditions, disturbance by water movement is small.

The second site, site JD, is characterized by a much smaller wave action, but deteriorated light conditions due to the glacier melt-water input in late summer. Valve accumulation at a depth of 1 m was comparatively higher than at site MP (Fig. 4; Zidarova *et al.* 2020), but at this site also the smallest number of valves on the plexiglass tiles was found at a depth of 6.5 m (Fig. 4). According to Mariotti and Fagherazzi (2012), when water turbidity is high, deeper water is unsuitable for biofilm growth, due to the lower light penetration. The stable, but low light conditions are possible explanation for the slower valve accumulation on the plexiglass tiles at 6.5 m at site JD.

When studying the marine epiphytic diatoms in Antarctica, Majewska *et al.* (2016) observed an increase in the number of erect growth forms, such as *Pseudogomphonema kamtschaticum,* in deeper waters. This taxon was observed at all depths and at both sites, but it was most abundant at a depth of 6.5 m at site JD (Fig. 3). Another taxon of the high-profile guild (Passy 2007), *F.* aff. *striatula* (or *Synedra* cf. *kerguelensis,* see Zidrova *et al.* 2022 for this taxon), was also present in larger numbers at larger depth at site JD. Erect growth forms (*i.e., P. kamtschaticum*), and the species from the high-profile guild (Passy 2007) as a whole, are vulnerable to mechanical stresses, including currents and waves, and therefore they usually thrive in sheltered locations (Passy 2007; Liu *et al.* 2013;

Majewska *et al.* 2016). *Pseudogomphonema kamtschaticum* was also observed abundant as an epiphyte on *Plocamium* thalli, which specific branching provides a well sheltered environment (Majewska *et al.* 2016). Bae *et al.* (2021) reported various high profile guild diatoms, including *F. striatula,* as dominant species in the inner part of the deeply indented (*i.e.,* with calmer waters) Marian Cove, King George Island. Erect growth forms, which are part of the high-profile guild, were rarely observed in the natural epilithon on intertidal cobbles (Zidarova *et al.* 2020), but were comparatively better represented on the three-stranded nylon ropes sampled at the same sites of South Bay (Zidarova, unpubl. res.). The ropes had a complex microtexture, which probably provided better opportunities for these taxa to hide from the water movements than the plexiglass tiles at the same locations.

Pseudogomphonema kamtschaticum also tolerates low light conditions (Houdon and Bourget 1983) and the vertical position of the erect growth forms gives them advantage in light absorption over the species growing closer to the substrate (Majewska and De Stefano 2015; Majewska *et al.* 2016 and references therein). However, for the epiphytic diatom communities Majewska *et al.* (2016) concluded that in shallow ice-free habitats with relatively high sea water transparency depth is of only secondary importance. Our results confirm their conclusion. No significant differences existed between the communities at the different depths of substratum exposure at site MP, and on the other hand, *P. kamtschaticum,* although present in relatively large numbers at site MP as well, was never found in abundance, even at larger depths, in contrast to the turbid site JD.

Finally, a dominant species at 6.5 m at site JD, together with *P. kamtschaticum,* was again *N.* aff. *perminuta.* This observation, together with the earlier findings for its resistance to high UVR (Zacher *et al.* 2007), supports the vision that *N.* aff. *perminuta* is a widely tolerant species to changes in light intensities (Majewska and De Stefano 2015).

We failed to recognize a clear influence of the sampling month on diatom communities in this study. Seasonal changes from early to late summer have been documented in summer epiphytic diatom communities in Antarctica (*e.g.,* Majewska *et al.* 2016). However, when studying the distribution of diatoms in several different shallow coastal habitats (macrophytes excluded), Zidarova *et al.* (2022) found that the habitat type with its stress factors had a greater influence over diatom communities than the sampling month during austral summer. At site MP some differences were present between the samples obtained in November–December and those taken in January–February, with the higher abundances of *B. charcotii* on the plexiglass tiles at a depth of 1 m during early summer (Appendix 4, Fig. 3). Little is known about *B. charcotii*. This epilithic species was found most abundant on the sides of large coastal rocks and on the sides and bottom of tidal pools at South Bay (Zidarova *et al.* 2022), but no information is available regarding its seasonal occurrences. It is also a chainforming species (Fernandes *et al.* 2007: fig 7), similarly to *F. striatula,* which has been considered an indicator for cooler temperatures (Cremer *et al.* 2003). Bae *et al.* (2021) found *F. striatula* forming thick carpets on the rocky shores of newly emerged ice-free areas in the inner intertidal zone of Marian Cove, King George Island, and concluded that the species is a rapid colonizer of newly available substrata after sea ice has melted. Further studies will be needed to verify whether this could also apply to *B. charcotii,* which does not seem to be reported from sea ice, unlike *F. striatula* [although due to the morphological similarity between the two taxa (Fernandes *et al.* 2007, Zidarova *et al.* 2022), it is still possible that the species has not been differentiated from *F. striatula,* Zidarova, pers. obs.]. In addition, with regard to the sampling month, dissimilarity of 45% was found between the samples at depths of 3 m and 6.5 m at site JD (Appendix 4), which were all obtained in January–February 2020. Apparently, depth is of greater importance for diatom communities in habitats with turbid calmer waters, but light conditions at different depths can vary depending on the sampling month as well, with the different amount of sediment input from glacier melt-water.

Finally, the overall diversity at site JD was higher compared to site MP despite the lower light conditions. Previous studies (such as Agustí and Duarte 2000; Vaqué *et al*. 2004) report a high inorganic nutrient content, along with low chlorophyll *a* concentration due to the high turbidity limiting the phytoplankton growth in Johnsons Dock (Vaqué *et al.* 2004). Given the limited exchange of the water inside Johnsons Dock with the tidal currents, even with the absence of penguin rookeries on the shores, it is possible that autochthonous organic matter deposits and remains trapped inside the cove, similarly to the case of Adélie Cove (Majewska *et al.* 2016 and references therein), and this favors both the diatom diversity and abundances under lower light, but also under low levels of mechanical disturbance.

Conclusions

The study clearly indicates that marine benthic diatom communities on a hard artificial substratum in Antarctica are site-specific, shaped by the disturbances present at the sites. Some of the stress factors, such as ice scouring, salinity, and light intensity, change during the different months of austral summer. Changes occurring with depth could not be clearly separated from changes with sampling month, and species distributions suggested that mechanical stresses and light intensity together shaped the communities on the artificial substratum at the studied shallow coastal waters. Based on our results so far, we can conclude that at least inside closed bays near glaciers (such as site JD), more variability in diatom communities from early to late summer could be expected in relation to the changing environment. At closed bays and coves, where disturbances from waves are negligible, differences in diatom communities at different depths could become larger in late summer, due to the higher glacier melt-water input, which further reduces the light availability with depth. This also suggests that shifts in disturbances frequency, intensity or duration due to climate change will lead to changes in diatom composition and abundances.

Stress factors in the environment have a greater influence over diatom communities than substrata on which they grow. Most of the species observed in the study have been reported from a variety of other substrates. The most commonly observed marine benthic diatom taxa in Antarctica, *Navicula* aff. *perminuta, N. glaciei* and *Pesudogomphonema kamtschaticum* were well presented during all summer months at the two sites, despite the changes in salinity from early to late summer, and they all apparently thrive under various salinity regimen. The over-dominance of *N.* aff. *perminuta* can indicate strong mechanical disturbances, either from waves or ice. *Navicula glaciei* seems to be more sensitive to mechanical stresses and lower light conditions, given its presence in lower numbers on the tiles in open locations, and on the tiles in deeper waters.

The study also justifies the use of artificial substrata as a tool, especially in areas where sampling natural substrata is difficult, and shows the potential of marine benthic diatoms for monitoring environmental changes in shallow coastal Antarctic benthic habitats. Nevertheless, further knowledge of species ecology will also be required.

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Appendix

Appendix 1.

List of all taxa with their average (av), minimal (min) and maximal (max) abundances per site and depth of substratum exposure. For species found in only one sample abundance is shown as maximal.

	MP									JD								
	1 m			3 m			6.5 m			1 m			3 m			6.5 m		
taxon/abundance	av	max	min	av	max	min	av	max	min	av	max	min	av	max	min	av	max	min
Achnanthes bongrainii M. Peragallo	1.3	2.5	0.3	2.0	7.0	0.3	2.3	6.0	0.4	0.9	2.3	0.3		0.2			0.5	
Achnanthes vicentii Manguin											0.5					0.3	0.4	0.3
Achnanthes sp. 1																0.6	0.7	0.5
Achnanthes sp. 2					0.6												0.5	
Amphora gourdonii M. Peragallo																0.3	0.3	0.2
Amphora lunula var. *parvula* Heiden																	0.2	
Brandinia charcotii (M. Peragallo) Zidarova *et* P. Ivanov	3.4	4.8	2.0	2.3	6.0	0.2				2.5	6.8	0.5		4.0			0.3	
Cocconeis californica Grunow		0.3																
Cocconeis costata W. Gregory s.l.	0.4	0.5	0.3								0.5					0.3	0.3	0.2
Cocconeis dallmannii Al-Handal *et al.*	0.5	0.5	0.5											0.2		0.6	0.7	0.4
Cocconeis fasciolata (C.G. Ehrenberg) N.E. Brown				0.7	1.6	0.2							0.7	1.2	0.4	0.5	0.5	0.5
Cocconeis melchioroides Al-Handal *et al.*	0.8	0.3	2.0					0.2			0.3					0.4	0.5	0.3
Cocconeis matsii (Al-Handal *et al.*) Riaux-Gobin *et al.*					0.2											0.2	0.3	0.2
Cocconeis pottercovei Al-Handal *et al.*					0.2												0.5	
Cocconeis cf. *schmidtii* Heiden														0.2				

	MP									JD								
	1 m			3 m			6.5 m			1 m			3 m			6.5 m		
taxon/abundance	av	max	min	av	max	min	av	max	min	av	max	min	av	max	min	av	max	min
Craspedostauros sp.																	0.3	
Fragilaria islandica var. *adeliae* Manguin											0.3							
	1 m			3 m			6.5 m			1 m			3 m			6.5 m		
taxon/abundance	av	max	min	av	max	min	av	max	min	av	max	min	av	max	min	av	max	min
Fragilaria sp.					0.6									0.2		0.8	1.1	0.5
Gomphonemopsis ligowskii Al-Handal *et* E.W. Thomas																0.3	0.5	0.2
Licmophora antarctica M. Peragallo		0.3						0.2								0.3	0.3	0.3
Licmophora belgicae M. Peragallo	2.1	2.5	1.8		0.3					0.4	1.8	0.5						
Licmophora gracilis (C.G. Ehrenberg) Grunow	2.2	3.3	0.3	0.7	1.2	0.2		0.2		0.5	0.8	0.3	0.5	1.2	0.2	0.7	0.9	0.4
Minisdiscus sp.											0.3					1.0	1.3	0.5
Navicula criophiliforma Witkowski *et al.*														0.4		0.3	0.3	0.2
Navicula directa (W.Smith) Ralfs														0.2			0.2	
Navicula glaciei Van Heurck	5.8	13.3	3.0	2.4	5.0	0.3	2.5	5.8	0.8	47.2	56.3	30.5	51.1	58.2	36.0	9.4	16.8	5.4
Navicula jejunoides Van Heurck																	0.3	
Navicula aff. *perminuta* Grunow	76.4	88.8	66.5	90.0	99.1	62.8	91.5	98.0	79.0	35.8	57.3	22.8	37.4	45.5	31.8	43.5	47.6	36.8
Navicula sp. 1					0.4			0.2			0.3						0.5	
Navicula sp. 2					4.0												2.0	
Navicula sp. 3				0.2	0.2	0.2										0.4	0.5	0.3
Navicula sp. 4																3.3	6.3	1.4
Nitzschia sp. 1		0.3		0.2	0.2	0.2		0.2		0.4	0.8	0.3					0.3	
Nitzschia sp. 2											0.5							

				MP									JD					
		1 m			3 m			6.5 m			1 m			3 m			6.5 m	
taxon/abundance	av	max	min	av	max	min	av	max	min	av	max	min	av	max	min	av	max	min
Nitzschia sp. 3										1.1	1.5	0.5	0.7	1.2	0.2	0.6	0.9	0.3
Nitzschia sp. 4																	0.2	
Petroneis sp.	0.4	0.5	0.3															
Pleurosigma sp.											0.3							
Pinnularia quadratarea (A.W.F. Schmidt) P.T. Cleve																	0.2	
Planothidium sp. 1																0.4	0.5	0.3
		1 m			3 m			6.5 m			1 m			3 m			6.5 m	
taxon/abundance	av	max	min	av	max	min	av	max	min	av	max	min	av	max	min	av	max	min
Pseudogomphonema kamtschaticum (Grunow) Medlin	3.6	7.0	0.3	2.1	4.0	0.6	3.1	8.0	0.4	1.3	3.5	0.3	7.0	14.0	2.0	26.2	28.5	24.8
Pteroncola carlinii Almandoz *et* Ferrario					1.6			0.6								0.7	1.2	0.3
cf. *Pteroncola* sp.																0.4	0.4	0.3
Synedropsis fragilis (Manguin) Hasle *et al.*	2.3	1.8	3.3	1.2	2.0	0.4		0.2		3.5	10.0	0.5	0.6	0.9	0.2	1.6	2.8	0.9
Synedropsis recta Hasle *et al.*	1.5	3.5	0.5	1.2	2.2	0.2	0.6	1.0	0.2	2.2	4.3	1.0	0.3	0.4	0.2	0.6	1.1	0.2
Synedropsis cf. *recta* Hasle *et al.*	1.3	2.5	0.3							2.2	6.0	0.3				0.6	0.9	0.3
Tabulariopsis australis (M. Peragallo) D.M. Williams	0.4	0.5	0.3															
Thalassiosira gracilis (G. Karsten) Hustedt		0.3																
number of taxa	20			20			13			21			16			41		
total number of taxa per site	29									46								

Appendix 2

Results of PERMANOVA analyses.

Factors					
Name	Abbrev.	Type	Levels		
Site	Si	Fixed	2		
Depth	De	Fixed	3		
Month	Mo	Fixed	3		
PERMANOVA table of results					
Source	df	SS	MS	Pseudo-F	P(perm)
Si	0	0		No test	
De	1	1876.7	1876.7	6.8045	0.0001
Mo	1	697.05	697.05	2.5273	0.0462
SixDe	1	1511.4	1511.4	5.4801	0.0018
SixMo	1	388.75	388.75	1.4095	0.2259
DexMo**	0	0		No test	
SixDexMo**	0	0		No test	
Res	21	5792	275.81		
Total	29	27336			
** Term has one or more empty cells					
Factors					
Name	Abbrev.	Type	Levels		
Site	Si	Fixed	2		
PERMANOVA table of results					
Source	df	SS	MS	Pseudo-F	P(perm)
Si	1	10208	10208	16.686	0.0001
Res	28	17129	611.74		
Total	29	27336			
PERMDISP TEST RESULTS					
Factors	P(perm)				
Depth	0.0345				
Month	0.0188				
Site	0.6542				

Appendix 3

ANOSIM tests results. Significant results are given in bold.

	Global R	Signif. Level %	Number of permutations:	Number of permuted statistics ≥ R:	
(SITE x DEPTH)					
Tests for differences between unordered Depth groups					
(across all Site groups)	**0.627**	**0.01%**	9999	0	
Pairwise Tests	R Statistic	Signif. Level %	Possible Perm.	Actual Perm.	Number ≥ Observed
Depth groups					
1 & 3	0.63	0.01	270270	9999	0
1 & 6.5	0.88	0.04	17325	9999	3
3 & 6.5	0.36	2.80	10584	9999	278
	Global R	Signif. Level %	Number of permutations:	Number of permuted statistics ≥ R:	
Tests for differences between unordered Site groups	**0.912**	**0.01%**	9999	0	
(across all Depth groups)					
(DEPTH x MONTH)					
SITE JD	Global R	Signif. Level %	Number of permutations:	Number of permuted statistics ≥ R:	
Tests for differences between unordered Depth groups	0.981	0.8%	126	1	
(across all Month groups)					
Tests for differences between unordered Month groups	0.333	21.4%	26	6	
(across all Depth groups)					
SITE MP					
Tests for differences between unordered Depth groups	-0.056	55.4%	56	31	
(across all Month groups)					
Tests for differences between unordered Month groups	0.801	4.2%	24	1	
(across all Depth groups)					

Appendix 4

Results of SIMPER analyses, with species contributing to the similarity at each site and at each depth at each site, and species contributing to the dissimilarity between the sites and between the different depths at each site. Only taxa contributing more than 4% are included.

JD - Average similarity: 66.30						
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Navicula aff. *perminuta*	6.14	24.16	5.84	36.44	36.44	
Navicula glaciei	6.01	21.87	2.08	32.99	69.42	
Pseudogomphonema kamtschaticum	2.37	5.3	1.3	7.99	77.41	
Fragilaria aff. *striatula* (*Synedra* cf. *kerguelensis*)	1.82	4.75	1.69	7.17	84.58	
MP - Average similarity: 68.66						
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Navicula aff. *perminuta*	9.25	51.26	3.29	74.67	74.67	
Navicula glaciei	1.56	5.28	1.78	7.68	82.35	
MP & JD - Average dissimilarity: 49.29						
	MP	JD				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Navicula glaciei	1.56	6.01	11.42	1.82	23.17	23.17
Navicula aff. *perminuta*	9.25	6.14	7.76	2.43	15.75	38.93
Pseudogomphonema kamtschaticum	1.28	2.37	4.04	1.24	8.19	47.11
Fragilaria aff. *striatula* (*Synedra* cf. *kerguelensis*)	0.45	1.82	3.59	1.61	7.28	54.39
Synedropsis fragilis	0.53	1.17	2.36	1.25	4.80	59.19
Brandinia charcotii	0.85	0.83	2.28	1.23	4.63	63.81

JD - Average similarity: 66.30						
JD 1 m - Average similarity: 78.29						
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Navicula glaciei	6.84	27.14	7.10	34.67	34.67	
Navicula aff. *perminuta*	5.94	23.05	7.22	29.45	64.12	
Synedropsis fragilis	1.70	5.03	3.00	6.42	70.54	
JD 3 m - Average similarity: 79.92						
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Navicula glaciei	7.12	34.87	5.28	43.63	43.63	
Navicula aff. *perminuta*	6.11	30.1	7.68	37.66	81.29	
site JD 6.5 m - Average similarity: 71.78						
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Navicula aff. *perminuta*	6.58	20.48	15.19	28.53	28.53	
Pseudogomphonema kamtschaticum	5.11	16.19	27.64	22.56	51.09	
Fragilaria aff. *striatula* (*Synedra* cf. *kerguelensis*)	3.00	9.07	13.81	12.63	63.72	
Navicula glaciei	2.98	8.02	6.91	11.18	74.90	
JD 1 m & 3 m - Average dissimilarity: 29.60						
	JD 1 m	JD 3 m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Pseudogomphonema kamtschaticum	0.91	2.50	3.63	1.76	12.28	12.28
Synedropsis fragilis	1.70	0.28	3.25	1.77	10.97	23.25
Brandinia charcotii	1.45	0.40	3.03	1.93	10.22	33.47
Synedropsis recta	1.26	0.22	2.54	1.92	8.60	42.06
Synedropsis cf. *recta*	1.15	0.09	2.50	1.34	8.45	50.51
Fragilaria aff. *striatula*	1.63	1.18	2.41	1.63	8.15	58.66

JD - Average similarity: 66.30						
(*Synedra* cf. *kerguelensis*)						
Navicula glaciei	6.84	7.12	1.63	1.22	5.51	64.17
Achnanthes bongrainii	0.77	0.09	1.60	1.43	5.42	69.59
Navicula aff. *perminuta*	5.94	6.11	1.55	1.22	5.25	74.84
JD 1 m & 6.5 m – Average dissimilarity: 47.56						
	JD 1 m	JD 6.5 m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Pseudogomphonema kamtschaticum	0.91	5.11	7.71	5.93	16.2	16.2
Navicula glaciei	6.84	2.98	7.06	3.86	14.85	31.05
Fragilaria aff. *striatula* (*Synedra* cf. *kerguelensis*)	1.63	3.00	2.60	1.61	5.48	36.53
Brandinia charcotii	1.45	0.14	2.40	1.99	5.04	41.57
Navicula sp. 4	0.00	1.3	2.33	1.46	4.89	46.46
JD 3 m & 6.5 m - Average dissimilarity: 44.95						
	JD 3 m	JD 6.5 m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Navicula glaciei	7.12	2.98	8.25	4.00	18.36	18.36
Pseudogomphonema kamtschaticum	2.50	5.11	5.30	2.52	11.78	30.15
Fragilaria aff. *striatula* (*Synedra* cf. *kerguelensis*)	1.18	3.00	3.71	2.07	8.24	38.39
Navicula sp. 4	0.00	1.30	2.52	1.44	5.61	43.99
Synedropsis fragilis	0.28	1.23	1.89	1.96	4.21	48.2
MP 1 m - Average similarity: 71.64						
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Navicula aff. *perminuta*	8.73	36.32	6.06	50.7	50.7	
Navicula glaciei	2.28	7.76	6.73	10.83	61.53	

JD - Average similarity: 66.30						
Brandinia charcotii	1.81	6.75	10.23	9.42	70.95	
MP 3 m - Average similarity: 71.19						
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Navicula aff. *perminuta*	9.46	58.32	3.21	81.92	81.92	
MP 6.5 m - Average similarity: 74.67						
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Navicula aff. *perminuta*	9.55	61.17	4.66	81.93	81.93	
MP 1 m & 3 m - Average dissimilarity: 37.76						
	MP 1 m	MP 3 m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Navicula glaciei	2.28	1.15	3.68	1.18	9.74	9.74
Brandinia charcotii	1.81	0.63	3.66	2.30	9.69	19.43
Pseudogomphonema kamtschaticum	1.70	0.89	2.98	1.54	7.89	27.32
Synedropsis cf. *recta*	1.08	0.00	2.68	3.07	7.11	34.43
Navicula aff. *perminuta*	8.73	9.46	2.57	1.97	6.81	41.24
Synedropsis fragilis	1.11	0.34	2.44	1.40	6.48	47.71
Licmophora gracilis	1.01	0.26	2.24	1.31	5.93	53.64
Achnanthes bongrainii	0.77	1.22	1.98	1.43	5.24	58.88
Synedropsis recta	0.86	0.51	1.97	1.43	5.21	64.09
Cocconeis melchioroides	0.78	0.00	1.94	2.30	5.13	69.22
Fragilaria aff. *striatula* (*Synedra* cf. *kerguelensis*)	0.63	0.39	1.70	0.99	4.51	73.73
MP 1 m & 6.5 m - Average dissimilarity: 35.65						
	MP 1 m	MP 6.5 m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Brandinia charcotii	1.81	0.00	4.67	8.20	13.11	13.11

JD - Average similarity: 66.30						
Navicula glaciei	2.28	1.43	3.19	1.23	8.94	22.06
Synedropsis cf. *recta*	1.08	0.00	2.74	3.18	7.68	29.73
Pseudogomphonema kamtschaticum	1.70	1.49	2.73	1.45	7.66	37.39
Synedropsis fragilis	1.11	0.15	2.63	1.62	7.38	44.77
Navicula aff. *perminuta*	8.73	9.55	2.39	1.72	6.70	51.48
Licmophora gracilis	1.01	0.15	2.27	1.28	6.36	57.83
Achnanthes bongrainii	0.77	0.92	2.19	1.34	6.13	63.96
Synedropsis recta	0.86	0.48	1.76	1.33	4.93	68.89
Fragilaria aff. *striatula* (*Synedra* cf. *kerguelensis*)	0.63	0.33	1.69	0.97	4.75	73.64
MP 3 m & 6.5 m - Average dissimilarity: 24.03						
	MP 3 m	MP 6.5 m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Pseudogomphonema kamtschaticum	0.89	1.49	3.37	1.33	14.04	14.04
Achnanthes bongrainii	1.22	0.92	2.78	1.64	11.58	25.61
Navicula glaciei	1.15	1.43	2.67	1.28	11.12	36.74
Synedropsis recta	0.51	0.48	1.70	1.35	7.09	43.83
Navicula aff. *perminuta*	9.46	9.55	1.66	1.04	6.90	50.73
Brandinia charcotii	0.63	0.00	1.63	0.79	6.78	57.51
Fragilaria aff. *striatula* (*Synedra* cf. *kerguelensis*)	0.39	0.33	1.41	0.91	5.88	63.39
Cocconeis fasciolata	0.39	0.00	1.06	0.89	4.43	67.81
Synedropsis fragilis	0.34	0.15	1.02	0.89	4.26	72.07

References

Agustí S. and Duarte C.M. 2000. Experimental induction of a large phytoplankton bloom in Antarctic coastal waters. *Marine Ecology Progress Series* 206: 73–85. doi: 10.3354/meps206073

Al-Handal A.Y. and Wulff A. 2008a. Marine benthic diatoms from Potter Cove, King George Island, Antarctica. *Botanica Marina* 51: 51–68. doi: 10.1515/BOT.2008.007

Al-Handal A.Y. and Wulff A. 2008b. Marine epiphytic diatoms from the shallow sublittoral zone in Potter Cove, King George Island, Antarctica. *Botanica Marina* 51: 411–435. doi: 10.1515/BOT.2008.053

Al-Handal A.Y., Riaux-Gobin C., Romero O.E. and Wulff A. 2008. 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 Research* 23: 269–281. doi: 10.1080/0269249X.2008.9705758

Al-Handal A.Y., Riaux-Gobin C., Romero O.E. and Wulff A. 2010. *Cocconeis pottercovei* sp. nov. and *Cocconeis pinnata* var. *matsii* var. nov., two new marine diatom taxa from King George Island, Antarctica. *Diatom Research* 25: 1–11. doi: 10.1080/0269249X.2010.9705825

Al-Handal A.Y., Torstensson A. and Wulff A. 2022. Revisiting Potter Cove, King George Island, Antarctica, 12 years later: New observations of marine benthic diatoms. *Botanica Marina* 65: 81–103. doi: 10.1515/bot-2021-0066

Anderson M.J., Gorley R.N. and Clarke K.R. 2015. *PERMANOVA+ for PRIMER: Guide to software and statistical methods.* Primer-E, Plymouth.

Bae H., Ahn I.-Y., Park J., Song S.J., Noh J., Kim H. and Khim J.S. 2021. Shift in polar benthic community structure in a fast retreating glacial area of Marian Cove, West Antarctica. *Scientific Reports* 11: 241. doi: 10.1038/s41598-020-80636-z

Bañon M., Justel A., Velázquez D. and Quesada A. 2001. Regional weather survey on Byers Peninsula, Livingston Island, South Shetland Islands, Antarctica. *Antarctic Science* 25: 146–156. doi: 10.1017/S0954102012001046

Barnes D.K.A. and Conlan K.E. 2007. Disturbance, colonization and development of Antarctic benthic communities. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 362: 11–38. doi: 10.1098/rstb.2006.1951

Błażewicz-Paszkowycz M. and Ligowski R. 2002. Diatoms as food source indicator for some Antarctic Cumacea and Tanaidacea (Crustacea). *Antarctic Science* 14: 11–15. doi: 10.1017/S0954102002000524

Burfeid-Castellanos A.M., Martín-Martín R.P., Kloster M., Angulo-Preckler C., Avila C. and Beszteri B. 2021. Epiphytic diatom community structure and richness is determined by macroalgal host and location in the South Shetland Islands (Antarctica). *PLoS ONE* 16: e0250629. doi: 10.1371/journal.pone.0250629

Campana G.L., Quartino M.L., A. Yousif A. and Wulff A. 2008. Impacts of UV radiation and grazing on the structure of a subtidal benthic diatom assemblage in Antarctica. *Berichte zur Polar- und Meeresforschung* 571: 302–310.

Chapman M.G. and Underwood A.J. 1999. Ecological patterns in multivariate assemblages: Information and interpretation of negative values in ANOSIM tests. *Marine Ecology Progress Series* 180: 257–265. doi: 10.3354/meps180257

Chipev N. and Veltchev K. 1996. Livingston Island: An environment for Antarctic life. *Bulgarian Antarctic Research, Life Sciences:* 1–6.

Clarke K.R. and Gorley R.N. 2015. *Primer v7 user manual/tutorial*. Primer-E, Plymouth.

Cotiyane-Pondo P. and Bornman T.G. 2021. Environmental heterogeneity determines diatom colonisation on artificial substrata: Implications for biomonitoring in coastal marine waters. *Frontiers in Ecology and Evolution* 9: 767960. doi: 10.3389/fevo.2021.767960

Cremer H., Roberts D., McMinn A., Gorec D. and Melles M. 2003. The Holocene diatom flora of marine bays in the Windmill Islands, East Antarctica. *Botanica Marina* 46: 82–106. doi: 10.1515/BOT.2003.010

Daglio Y., Sacristán H., Ansaldo M. and Rodríguez M.C. 2018. Benthic diatoms from Potter Cove, 25 de Mayo (King George) Island, Antarctica: Mucilage and glucan storage as a C-source for limpets. *Polar Science* 15: 39–48. doi: 10.1016/j.polar.2018.01.004

Desrosiers C., Leflaive J., Eulin A. and Ten-Hage L. 2014. Optimal colonization and growth of marine benthic diatoms on artificial substrata: Protocol for a routine use in bioindication. *Journal of Applied Phycology* 26: 1759–1771. doi: 10.1007/s10811-013-0204-3

Fernandes L.F. and Procopiak L.K. 2003. Observations on valve structures of *Navicula directa* (Wm. Smith) Ralfs *in* Pritchard and *Navicula glaciei* V. Heurck from rocky substrates in Antarctic Peninsula. *Hoehnea* 30: 1–10.

Fernandes L.F., Procopiak L.K. and Portinho D. 2007. *Brandinia mosimanniae* gen. nov. et sp. nov., a new marine epilithic diatom from the Antarctic coasts. *Diatom Research* 22: 45–56. doi: 10.1080/0269249X.2007.9705694

Fernandes L.F., Calixto-Feres M., Tenenbaum D.R., Procopiak L.K., Portinho D. and Hinz F. 2014. Fine morphology of four *Licmophora* (Bacillariophyta, Licmophorales) species from Admiralty Bay and Elephant Island, Antarctic Peninsula. *Iheringia, Série Botânica* 69: 465–477.

Gili J.M., Alvà V., Pagès F., Klöser H. and Arntz W.E. 1996. Benthic diatoms as the major food source in the sub-Antarctic marine hydroid *Silicularia rosea*. *Polar Biology* 16: 507–512. doi: 10.1007/BF02329070

Griffiths H.J. and Waller C.L. 2016. The first comprehensive description of the biodiversity and biogeography of Antarctic and Sub-Antarctic intertidal communities. *Journal of Biogeography* 43: 1143–1155. doi: 10.1111/jbi.12708

Hasle G.R. and Fryxell G.A. 1970. Diatoms: cleaning and mounting for light and electron microscopy. *Transactions of the American Microscopical Society* 89: 469–474. doi: 10.2307/3224555

Hasle G.R., Medlin L.K. and Syversten E.E. 1994. *Synedropsis* gen. nov., a genus of araphid diatoms associated with sea ice. *Phycologia* 33: 248–270. doi: 10.2216/i0031-8884-33-4-248.1

Hudon C. and Bourget E. 1983. The effect of light on the vertical structure of epibenthic diatom communities. *Botanica Marina* 26: 317–330. doi: 10.1515/botm.1983.26.7.317

Isla E., Palanques A., Alvà V., Puig P. and Guillén J. 2001. Fluxes and composition of settling particles during summer in an Antarctic shallow bay of Livingston Island, South Shetlands. *Polar Biology* 24: 670–676. doi: 10.1007/s003000100267

Klöser H. 1998. Habitats and distribution patterns of benthic diatoms in Potter Cove (King George Island, Antarctica) and its vicinity. *In*: Wiencke C., Ferreyra G., Arntz W. and Rinaldi C. (eds.) *The Potter Cove coastal ecosystem, Antarctica synopsis of research performed within the frame of the Argentinean- German cooperation at the Dallmann Laboratory and Jubany Station (King George Island, Antarctica, 1991–1997)*. *Berichte zur Polarforschung* 299: 95–105.

Ligowski R. 2002. Diatoms in different habitats of Admiralty Bay, Antarctica. *In*: John J. (ed.) *Proceedings of the 15th International Diatom Symposium, Perth, Australia 28 September–2 October 1998*. A.R.G. Gantner Verlag K.G., Ruggell: 173–191.

Liu J., Soininen J. and Han B.-P. 2013. Effects of connectivity, dispersal directionality and functional traits on the metacommunity structure of river benthic diatoms. *Journal of Biogeography* 40: 2238–2248. doi: 10.1111/jbi.12160

Lonin S., Rios-Angulo W.A. and Coronado J. 2022. Swell conditions at potential sites for the Colombian Antarctic research station. *Sustainability* 14: 2318. doi: 10.3390/su14042318

López O., García M.A. and Sánchez-Arcilla A.S. 1994. Tidal and residual currents in the Bransfield Strait, Antarctica. *Annales Geophysicae* 12: 887–902. doi: 10.1007/s00585-994-0887-5

Majewska R. and De Stefano M. 2015. Epiphytic diatom communities on *Phyllophora antarctica* from the Ross Sea. *Antarctic Science* 27: 44–56. doi: 10.1017/S0954102014000327

Majewska R., Gambi C.M., Totti M.C. and De Stefano M. 2013. Epiphytic diatom communities of Terra Nova Bay, Ross Sea, Antarctica: Structural analysis and relations to algal host. *Antarctic Science* 25: 501–513. doi: 10.1017/S0954102012001101

Majewska R., Kukliński P., Bałazy P., Yokoya N.S., Martins A.P. and De Stefano M. 2015. A comparison of epiphytic diatom communities on *Plocamium cartilagineum* (Plocamiales, Florideophyceae) from two Antarctic areas. *Polar Biology* 38: 189–205. doi: 10.1007/s00300-014-1578-7

Majewska R., Convey P. and 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: e0153254. doi: 10.1371/journal.pone.0153254

Mariotti G. and Fagherazzi S. 2012. Modeling the effect of tides and waves on benthic biofilms. *Journal of Geophysical Research* 117: G04010. doi: 10.1029/2012JG002064

McMinn A., Pankowskii A., Ashworth C., Bhagooli R., Ralph P. and Ryan K. 2010. In situ net primary productivity and photosynthesis of Antarctic sea ice algal, phytoplankton and benthic algal communities. *Marine Biology* 157: 1345–1356. doi: 10.1007/s00227-010-1414-8

Navarro F.J., Jonsell U.Y, Corcuera M.I. and Martín-Español A. 2013. Decelerated mass loss of Hurd and Johnsons Glaciers, Livingston Island, Antarctic Peninsula. *Journal of Glaciology* 59: 115–128. doi: 10.3189/2013JoG12J144

Passy S.I. 2007. Diatom ecological guilds display distinct and predictable behavior along nutrient and disturbance gradients in running waters. *Aquatic Botany* 86: 171–178. doi: 10.1016/j.aquabot.2006.09.018

Peragallo M. 1921. Diatomées d'eau douce et diatomées d'eau salée. In: *Deuxième Expédition Antarctique Française (1908–1910) commandée par le Dr. Jean Charcot.* Sciences Naturelles, Documents Scientifiques, Botanique, Masson et Cie, Paris. doi: 10.5962/bhl.title.64272

Robinson B.J.O., Barnes D.K.A. and Morley S.A. 2020. Disturbance, dispersal and marine assemblage structure: A case study from the nearshore Southern Ocean. *Marine Environmental Research* 160: 105025. doi: 10.1016/j.marenvres.2020.105025

Tuji A. 2000. Observation of developmental processes in loosely attached diatom (Bacillariophyceae) communities. *Phycological Research* 48: 75–84. doi: 10.1046/j.1440-1835.2000.00188.x

Vaqué D., Agustí S. and Duarte C.M. 2004. Response of bacterial grazing rates to experimental manipulation of an Antarctic coastal nanoflagellate community. *Aquatic Microbial Ecology* 36: 41–52. doi: 10.3354/AME036041

Vidal J., Berrocoso M. and Fernández-Ros A. 2011. Study of tides and sea levels at Deception and Livingston islands, Antarctica. *Antarctic Science* 24: 193–201. doi: 10.1017/S095410201100068X

Williams D.M. 1988. *Tabulariopsis*, a new genus of marine araphid diatom, with notes on the taxonomy of *Tabularia* (Kütz.) Williams et Round. *Nova Hedwigia* 47: 247–254.

Zacher K., Hanelt D., Wiencke C. and Wulff A. 2007. Grazing and UV radiation effects on an Antarctic intertidal microalgal assemblage: Along-term field study. *Polar Biology* 30: 1203–1212. doi: 10.1007/s00300-007-0278-y

Zidarova R., Ivanov P. and Dzhembekova N. 2020. Diatom colonization and community development in Antarctic marine waters – a short-term experiment. *Polish Polar Research* 41: 73–98. doi: 10.24425/ppr.2020.133012

Zidarova R., Ivanov P., Hineva E. and Dzhembekova N. 2022. Diversity and habitat preferences of benthic diatoms from South Bay (Livingston Island, Antarctica). *Plant Ecology and Evolution* 155: 70–106. doi: 10.5091/plecevo.84534

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