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Diatom colonization and community development in Antarctic marine waters – a short-term experiment

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Abstract: Main aim of the study was to search for possible differences in diatom colonization and their communities under the influence of glacier meltwater inflow and when unaffected by glacier meltwater, and also to define the time needed for the development of diatom communities on newly submerged substrates at small depths in Antarctica. We used artificial substrates (Plexiglass© tiles), submerged at a depth of 1 m below the sea surface at two locations at the South Bay of Livingston Island: (1) Johnsons Dock – a cove, known to receive glacier meltwater with sediments, and (2) outside the cove, generally unaffected by glacial meltwater. Samples from the natural epilithon at similar depth were also taken as a reference for diatom community structure. Statistical testing the differences between the two sites was not possible this time, but the samples allowed us to compare the sites in terms of diatom growth, species richness, diversity and evenness changes in diatom communities along the time of the experiment at both sites and with the natural epilithon at similar depths. Diatom colonization followed the three-phases scheme (colonization, logarithmic growth and equilibrium) as in other latitudes. Based on the valve density and community indices e.g. species richness, diversity (1-D) and evenness (J'), we consider that at least three weeks might be necessary to obtain sufficiently representative for the environment diatom communities on new substrates at small depths in Antarctica, in conditions similar to those of South Bay. No particular differences between the sites were noted in the colonization scheme, but the diversity (1-D) and evenness (J') were higher at glacier influenced site, as well as the number of the valves on the substrates. Sea ice diatoms prevailed at the glacier influenced site. We suggest that species exchange between the sea ice and other hard substrates do exist, at least for some taxa, and such species might be indicative for variations in both salinity and water transparency, related to glacial meltwater inflow.

Key words: Antarctica, diatoms, colonization, artificial substrates, marine benthos.

Introduction

Marine benthic communities, especially those nearby Antarctic Peninsula, are expected to be largely affected by climate change. It was observed that snow and ice melting in summer lead to variations in salinity in coastal areas (Brandini and Rebello 1994; Moline *et al.* 2004); the sediment inflow of glacier meltwater changes water transparency (Wiencke *et al.* 2007) and/or its chemistry (Dierssen *et al.* 2002). With the temperature rise in the region, an increased mechanical stress on benthic communities caused by ice scouring, is expected (Campana *et al.* 2018). In addition, retreating glaciers open new substrates for colonization (Passoti *et al.* 2015; Smale and Barnes 2008). Diatoms (Bacillariophyceae) are one of the most abundant algal groups in marine coastal waters all around the world (Desrosiers *et al.* 2013), and as primary producers, they have an important ecological role in all, but also in polar oceans (Karsten *et al.* 2011). Diatoms are first colonizers (after bacteria) of newly exposed areas or re-colonizers of denuded habitats, pre-conditioning the substrates for the later development of other organisms (Wahl 1989) or inhibiting their settlement (Zacher and Campana 2008). Benthic diatoms on hard substrates in Antarctica are also found to be adapted to UV stress, and in an ozone depletion scenario they may have a crucial role in marine colonization processes (Campana *et al.* 2008). Considering the importance of diatoms for ecosystem functioning and their role as re-colonizers, it is surprising that no studies addressed the colonization and development of their communities in the Antarctic region. Most of the studies have been focused on macrozoobenthos (reviewed by Barnes and Conlan 2007) or macroalgal succession (Campana *et al.* 2018). Other experiments, which included diatoms, concentrated mostly on the effects of grazing and UV radiation (e.g. Campana *et al.* 2008, review by Campana *et al.* 2009; Zacher *et al.* 2007), or on role of diatoms as food source for other organisms (Daglio *et al.* 2018).

This study, although based on a limited number of samples, provides the first preliminary data for diatom colonization in coastal areas in Antarctica, aiming to compare the development of their communities at two different sites: a glacier influenced site, and a site generally unaffected by glacier meltwater inflow. For the experiments, we used artificial substrates, which allowed to reduce the possible variability in diatom communities due to the substrate nature itself or its microstructure, and to control the sampling depth (Desrosiers *et al.* 2013, 2014). Samples from the natural epilithon at similar depth in the same area were obtained for reference. We also aimed for finding the minimum time needed for development of representative for the environment diatom communities on artificial substrates in Antarctica, which might be useful for other field studies in the region.

Study area

Experiments were carried out between late November 2018 and early January 2019 at the South Bay of Livingston Island, the second largest island of the South Shetland Archipelago (Fig. 1). The South Bay is a large bay (*ca.* 14 km wide), indenting the southern coast of Livingston Island. It is open to the southwest and exposed to the prevailing southwest winds. The northwestern and northern part of the bay are occupied by glaciers, of which parts are breaking and falling into the sea; with the currents and northerly winds ice blocks move later in southwest direction. After observations at field on the usual route of ice blocks across the South Bay, two locations were chosen as safe for the experiment. The first location, Johnsons Dock (JD), is a cove receiving glacier meltwater from Johnsons glacier that leads to a typically milky appearance of the water inside the

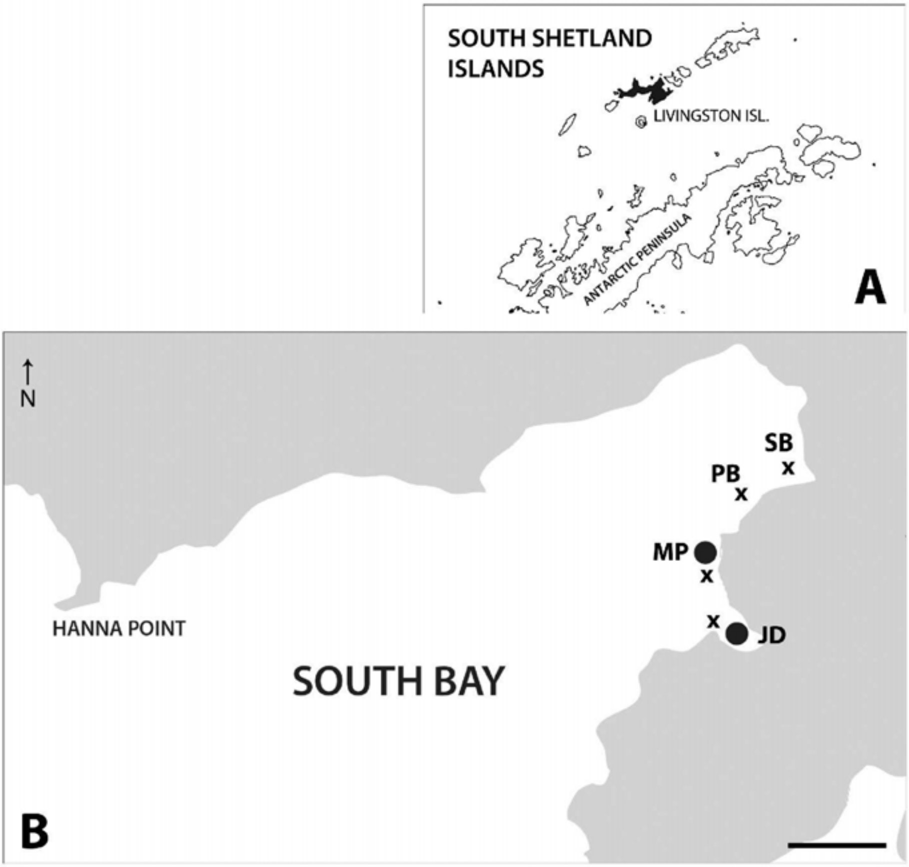

Fig. 1. Map of the region. A. Location of the South Shetland Islands and Livingston Island (shown in black). B. Sampling locations. Dots – experimental sites. X – sampling sites for natural epilithon. MP – Mongolian Port, JD – Johnsons Dock, SB – South Bay, PB – Playa Búlgara. Scale bar represents 1 n. mile.

cove (Agustí and Duarte 2000). The second location, unofficially named "Mongolian port" (MP) is a small opened bay, located to the north/northwest of JD and not affected by glacier meltwater (Fig. 1). In late summer, however, with snow melt, inflow of clear freshwater is available at this site from a lake, located above the bay inland.

As there is no reference for community structure of marine epilithic diatoms in Antarctica, samples were also obtained from the natural epilithon at both sites of the experiment and two adjacent locations (Fig. 1, marked with 'X'). A total of eight samples were taken: thee samples from site JD, two samples from site SB, two samples from site PB, and one sample from site MP (Table 1). Penguin rookeries or seal colonies are absent at each of the sites, thus no strong nutrient input by mammals or birds could be expected.

Material and methods

Colonization experiment design and sampling. — Following Desrosiers et al. (2014 who found that the Plexiglass© was better artificial substrate for such studies than ceramic tiles and glass), roughly hand-sanded Plexiglass© tiles were used as a new substrate for colonization. The tiles (each with an area of 25 cm^2) were mounted to a pane frame. Two panes, each containing 24 tiles, were submerged horizontally at 1 m below the sea surface and anchored at the two sites using a fleet-mooring system (three anchors set at depths of 10–22 m). The panes were held afloat by small marking buoys. In order to trace the colonization process, repetitive sampling was done. We were not able to strictly follow the intended experimental design. The intervals between samplings were determined by both the weather permissions and our logistical abilities. Sampling at site JD was done at days 7, 10, 14, 18, 22, 25, 38 and 45 after the tiles were submerged (n=8). At site MP sampling was done at days 4, 7, 12 and 31 of the experiment (n=4). Despite this irregularity, the collected material still provided good opportunity to trace the main aspects of diatom colonization processes at both sites, and for their comparison in a period of 31 days. For each sample (i.e. colonization day) the biofilm of three randomly selected tiles was collected resulting in a total sampled area of 75 cm^2 per sample. The biofilm was entirely removed using a hard toothbrush and preserved in a known volume of filtered water (0.2 μm pore diameter Teknokroma nylon filters). Material was immediately fixed in a known volume of formaldehyde.

Repetitive measurements of basic environmental parameters at both experimental sites were taken (pH, salinity, conductivity, oxygen concentration and saturation) with WTW 3410 handheld multimeter for a month. As a measure for water transparency Secchi depth was determined with a Secchi disk (Table 1).

Natural epilithon sampling. — For sampling the natural epilithon, the biofilm from 3–5 large cobbles/boulders at each site was scraped with a tooth-

Table 1

Sampling sites with their measured environmental parameters. JD – Johnsons Dock, MP – “Mongolian” Port, SB – South Bay, PB – Playa Búlgara.

site/sample	date	Secchi depth, [m]	pH	salinity, [‰]	conductivity, [µS/cm]	O_2 [%]	O_2 [mg/L]
colonization sites							
JD	25.11.2018	2.00	8.20	29.9	43.8	104.0	13.30
JD	2.12. 2018	1.10	8.20	29.4	47.3	101.0	12.68
JD	5.12. 2018	1.70	8.15	32.6	52.0	101.8	12.78
JD	9.12. 2018	1.45	8.20	30.2	48.8	101.1	12.77
JD	13.12. 2018	1.75	8.12	32.3	51.2	104.9	12.54
JD	17.12. 2018	0.50	8.12	32.1	51.2	107.9	12.48
JD	20.12. 2018	1.50	8.11	33.2	52.9	99.9	12.10
	mean	*1.43*	*8.16*	*31.39*	*49.6*	*102.9*	*12.66*
MP	9.12. 2018	2.70	8.09	33.6	53.5	101.5	12.40
MP	12.12. 2018	2.75	8.05	33.6	53.1	98.6	11.42
MP	15.12. 2018	2.75	8.09	33.6	53.5	105.0	12.70
MP	20.12. 2018	2.10	7.96	33.4	53.0	99.1	11.80
	mean	*2.58*	*8.06*	*33.6*	*53.3*	*101.1*	*12.08*
natural epilithon samples							
JD1	2.12. 2018	1.10	8.20	29.4	47.3	101.0	12.68
JD2	9.12. 2018	1.45	8.20	30.2	48.8	101.1	12.77
JD3	20.12. 2018	1.50	8.11	33.2	52.9	99.9	12.10
MP1	8.12. 2018	n/a	8.09	33.6	53.4	101.5	12.40
SB1	27.11. 2018	2.70	8.10	33.9	54.0	103.6	12.94
SB2	11.12. 2018	3.00	8.05	29.9	47.7	89.4	9.76
PB1	22.11. 2018	n/a	n/a	n/a	n/a	n/a	n/a
PB2	10.12. 2018	2.50	8.05	29.5	47.0	99.2	10.84

List of the taxa in the communities with their abundances (%, in each sample). The number in parenthesis for samples MP and JD shows the colonization day on which the sample was taken, i.e. MP(7) is the sample from site MP at day 7 after the tiles were submerged. Taxa with relative abundances ≥2% in at least one sample are given in bold. The most commonly observed taxa are shown on Fig. 7.

brush and preserved in the same manner as for the artificial substrates. Sampling was done at depths of *ca.* 40 cm at spring low tide only (i.e., mean depth of 1.4 m between tides), assuring the sampled cobbles and boulders were always well submerged, even at the lowest tide.

Diatom sample and slides preparation. — In order to remove the organic material, 10 ml of each sample were treated with H_2SO_4 and $KMnO_4$, following the method of Hasle and Fryxell (1970). The treated sub-samples were then washed several times with distilled water. For each slide, 1 ml of the cleaned material was left to dry overnight on a cover slip (24x32 mm) and after that mounted in Naphrax©. Due to the extremely high number of valves in the samples from the mid and last days of the colonization experiment, cleaned sub-samples were diluted in order to be able to perform microscopic analyses (sometimes up to 1024 times).

Microscopic analyses and growth rate calculation. — In order to get accurate results for the diatom growth on the new substrates along the time of the experiment, we counted the total number of valves (without identifying particular species) in 300 fields of view (FOV) at 1000x magnification at Carl Zeiss Jena Amplival microscope on 3 slides per sample. The diatom growth for each day of the colonization experiment (sample) at each site was expressed as a number of valves x 10^5 per cm^2 of the substrate. Calculations were done with PTC Mathcad software, taking into account the FOV area of the microscope at 1000x magnification, the initial volume of the sample and its final dilution, the amount of cleaned subsample mounted on the slide and the area of the sampled substrate.

Diatom taxa identification and community structure. — Taxa identification analyses were done at 1000x magnification of Olympus BX51 microscope, equipped with DIC (Nomarski) optics. Diatom species were identified based on Al-Handal and Wulff 2008a, b; Al-Handal *et al.* 2008, 2010; Cremer *et al.* 2003; Daglio *et al.* 2018; Fernandes and Procopiak 2003; Fernandes *et al.* 2007, 2014; Hasle *et al.* 1994; Peragallo 1921, among others. For assessing the community structure, a minimum of 400 valves were identified up to species level and counted at random transects on a slide (one per sample). This number is considered sufficient for diatom community analysis in a sample (Karthick *et al.* 2010 and references therein). Taxa present with abundances higher than 10% in the communities were considered dominants; taxa with abundances 4–10% subdominants, and influent taxa those with abundance of 2–4% in the samples. As a measure for species richness the number of taxa constituting the communities was taken (Table 2). For all samples Simpson diversity (1-D) and evenness (J') were calculated (Table 2).

Data analyses. — Kruskal-Wallis test was used to check for differences between sites in their measured environmental parameters. Cluster analysis based on Bray-Curtis similarity on square root transformed species-abundance data of all taxa in the samples from the two experimental sites was done in order to find possible separation in diatom communities in samples from the sites. SIMPER with sites as a factor was further applied to identify the species contributing for dissimilarities. Analyses were done with Primer v6.

Results

Comparison of the colonization sites. — All sampling sites with the values of their measured environmental parameters are presented in Table 1. No significant differences were found between the two experimental sites based on the mean values of the measured parameters. Mean oxygen saturation and oxygen concentrations were similar between sites, as well as pH and salinity. Further analysis of the measured parameters and their values across the different sites and sampling days showed that the sites JD and MP differed in salinity and Secchi depth. At site JD salinity and Secchi depth were always lower, compared to MP, and also variable between the different measurements – Secchi depth ranged from 0.5 m to 2.0 m, and salinity varied with several psu (29.3–33.2‰, Table 1). In contrast, at site MP both Secchi depth and salinity were higher and almost constant over a month: Secchi depth was above 2.0 m, usually *ca*. 2.70 m, whereas salinity was always between 33.4–33.6 ‰ (Table 1).The rest two sites, where only natural epilithon was sampled (SB, PB) always had high Secchi depth values, comparable in values to those at site MP (Table 1).

Diatoms growth on artificial substrates. — Diatoms were clearly present on the tiles at both sites on day 7, but they were found as early as day 4 at site MP (Figs 2C, 3A). At both sites the valve density markedly increased after day 7–10 of the experiment (Fig. 2C1–3, note the differences in the values of the second axis). In general, the valve density at the glacier influenced site (JD) was higher compared to site MP (Fig. 2C). A plateau in the valve density on the new substrates was noted after 25 days at site JD (Fig. 2A).

Diatom communities on artificial and natural substrates. — A total of 30 taxa constituted the communities on artificial and natural substrates at small depths. All taxa with their relative abundances (as % in each sample) are listed in Table 2. Of all taxa only three taxa (*Achnathes* sp. 1, *Cocconeis fasciolata* and *C. pottercovei*) were not found on the Plexiglass© tiles (Table 2). Other seven taxa, which were present on the tiles, were not encountered in the natural epilithon (*F. islandica* var. *adeliae*, *Licmophora antarctica*, *Nitzschia* sp.2, *Petroneis* sp., *Pleurosigma* sp, as well as *Minidiscus* sp. and *Thalassiosira gracilis*, Table 2). All these taxa however had only minor participation in the communities (abundances less than 1.5% in the samples, Table 2).

The cluster analysis showed a separation between the two experimental sites based on their communities ($p<0.01$, Fig. 4). SIMPER revealed however 40.08% dissimilarity in the communities between the sites. Site JD differed with the higher abundances of *Navicula glaciei, Synedra* cf. *kerguelensis* and *Synedropsis*

	site MP				site JD								natural epilithon							
taxon	MP (4)	MP (7)	MP (10)	MP (31)	JD (7)	JD (10)	JD (14)	JD (18)	JD (22)	JD (25)	JD (38)	JD (45)	PB1	PB2	SB1	SB2	MP1	JD1	JD2	JD3
Achnanthes bongrainii M. Peragallo	1.0	0.25		2.5	0.5	1.0	0.25	0.25	0.25		2.25	2.0		1.25	4.0	2.5	0.25	45.0		
Achnanthes vicentii Manguin						0.5												0.75		0.25
Achnanthes sp.1														1.25				0.25		0.25
Brandinia mosimanniae L.F. Fernandes and L.K.Procopiak	4.75	4.25	2.0	2.5	2.5	6.75	1.25	0.5	4.0	3.25	1.25	0.5				0.5		9.25		
Cocconeis californica Grunow		0.25																		
Cocconeis costata Gregory	0.5	0.5	0.25			0.5														0.25
Cocconeis dallmannii Al-Handal, Riaux-Gobin, Romero and Wulff	0.5	0.5																		
Cocconeis fasciolata (Ehrenberg) N.E.Brown														0.5		0.25				
Cocconeis melchioroides Al-Handal, Riaux-Gobin, Romero and Wulff	2.0	0.5	0.25	0.25	0.25												0.25			
Cocconeis pottercovei Al-Handal, Riaux-Gobin and Wulff																				0.25
Fragilaria islandica var. *adeliae* Manguin					0.25							0.75								
Licmophora antarctica M. Peragallo	0.25																			
Licmophora belgicae M. Peragallo	2.5	1.75			0.25	0.25	0.5		0.5		0.25							0.5		
Licmophora gracilis (Ehrenberg) Grunow	3.25	3.0	0.25		0.25	0.75	0.75					0.25						1.25		
Minisdiscus sp.												0.25								
Navicula aff. *perminuta* Grunow	70.5	66.5	88.75	79.75	35.5	22.75	36.5	40.0	33.75	27.25	57.25	33.75	100.0	92.5	90.5	90.5	97.75	18.25	96.0	96.5
Navicula glaciei Van Heurck	3.75	3.0	3.25	13.25	45.5	45.5	51.25	53.75	56.25	55.5	30.5	39.5			1.5	3.5	0.25	14.0	3.0	1.75
Navicula sp. 1											0.25			0.5			0.5			

	site MP				site JD								natural epilithon							
taxon	MP (4)	MP (7)	MP (10)	MP (31)	JD (7)	JD (10)	JD (14)	JD (18)	JD (22)	JD (25)	JD (38)	JD (45)	PB1	PB2	SB1	SB2	MP1	JD1	JD2	JD3
Nitzschia sp. 1			0.25		0.75	0.25	0.25	0.25		0.25					0.25			0.75		
Nitzschia sp. 2					0.5															
Nitzschia. sp. 3					1.0		1.5	0.5		1.5	1.0									
Petroneis sp.		0.25	0.5																	
Pleurosigma sp.						0.25														
Pseudogomphonema kamtschaticum (Grunow) Medlin	5.5	7.0	1.75	0.25	1.0	3.5	1.5	0.5	0.75		0.25	1.25		4.0	0.75	1.5	1.0		1.0	0.75
Synedra cf. *kerguelensis* Heiden	0.25	4.0			6.0	9.25	1.5	2.25		3.75	1.75	2.5						8.5		
Synedropsis fragilis (Manguin) Hasle, Medlin and Syversten	3.25	1.75	1.75		3.25	6.5	0.5	1.0	1.25	2.5	2.75	10			0.25	0.5		0.5		
Synedropsis recta Hasle, Medlin and Syversten		3.5	0.75	0.5	2.0	2.0	3.5	1.0	1.25		1.5	4.25								
Synedropsis cf. *recta* Hasle, Medlin and Syversten	1.5	2.5	0.25	1.0	0.5	0.25	0.75		2.0	6.0	1.0	5.0			2.75	0.75				
Tabulariopsis australis (M. Peragallo) D.M.Williams	0.25	0.5																1.0		
Thalasiosira gracilis (Karsten) Hustedt	0.25																			
number of taxa	**16**	**17**	**12**	**8**	**16**	**15**	**13**	**10**	**9**	**8**	**12**	**12**	**1**	**6**	**7**	**8**	**6**	**12**	**3**	**7**
diveristy (1-D)	*0.49*	*0.55*	*0.21*	*0.35*	*0.66*	*0.72*	*0.60*	*0.55*	*0.48*	*0.61*	*0.58*	*0.72*	*0.00*	*0.14*	*0.18*	*0.18*	*0.05*	*0.73*	*0.08*	*0.07*
evenness (J')	*0.47*	*0.51*	*0.39*	*0.37*	*0.52*	*0.61*	*0.48*	*0.43*	*0.50*	*0.60*	*0.48*	*0.63*	*0.00*	*0.20*	*0.22*	*0.22*	*0.08*	*0.65*	*0.17*	*0.10*

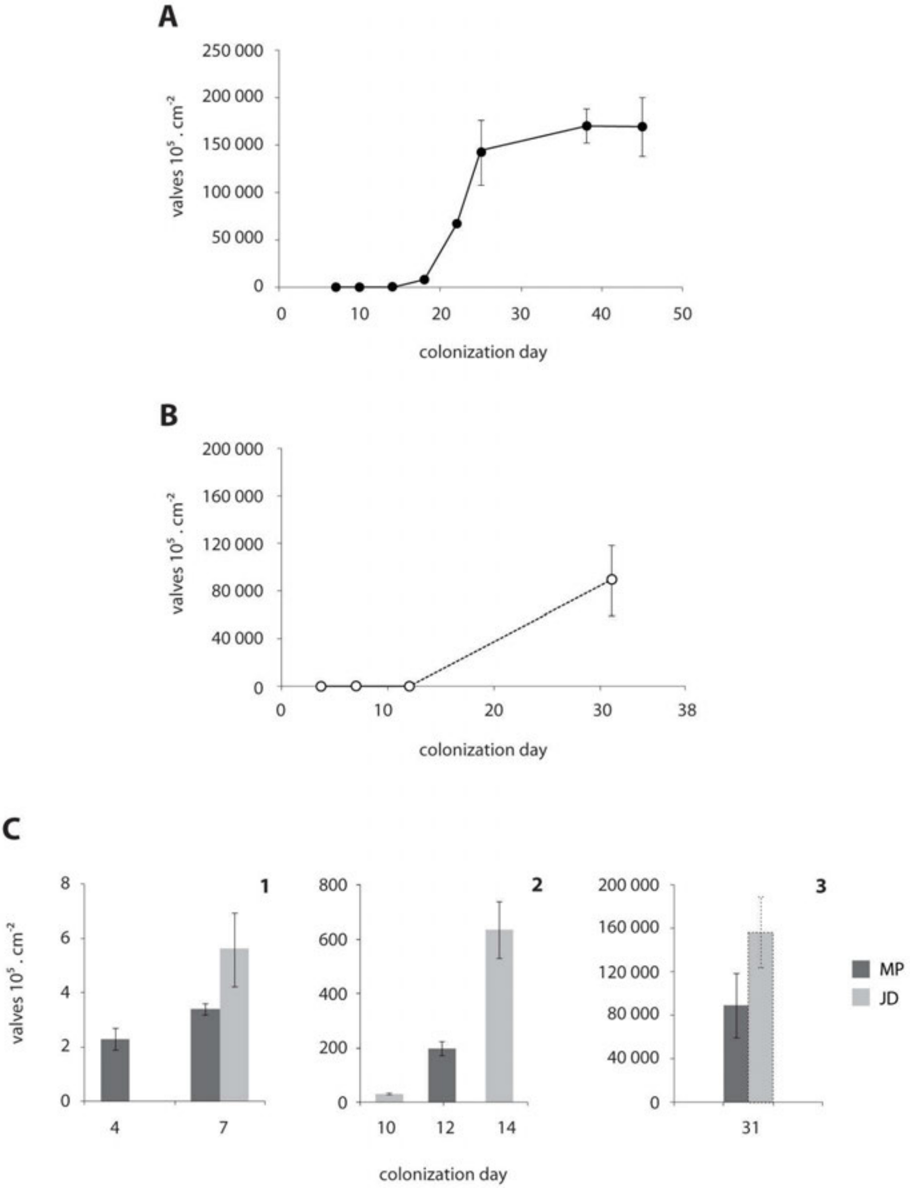

Fig. 2. Diatom valve density on the tiles at the two experimental sites. A. Valve density at site JD for all sampling days. Vertical lines represent SD for each sample (based on the three studied slides per sample, n=3). Due to the small values, compared to the scale of the secondary axis, SD values up to day 25 are not visible on the graph and are listed here: day 7: valve density 10^5.cm^{-2}: 5.6±1.35; day 10: 29.5± 2.9; day 14: 636±103; day 18: 8 517±964; day 22: 68 018±2118. See also Fig. 2C. B. Valve density at site MP for all sampling days. The lack of data between day 12 and day 31 is given with dotted line. Values±SD (n=3) for day 4: 2.3±0.4; day 7: 3.4±0.2; day 12: 198±26. C. Comparison of the valve density between the two sites. Note the differences in the scale of the secondary axes on the graphs: 1. Valve densities during the early colonization (days 4, site MP and 7, site JD). 2. Valve densities during the early logarithmic growth phase (days 10 and 14 for site JD, and 12 for site MP); 3. Valve densities at the last phase (day 31): for site JD data are based on the means for days 25 and 38 (dotted outline). Vertical lines on all graphs represent standard deviations (n=3).

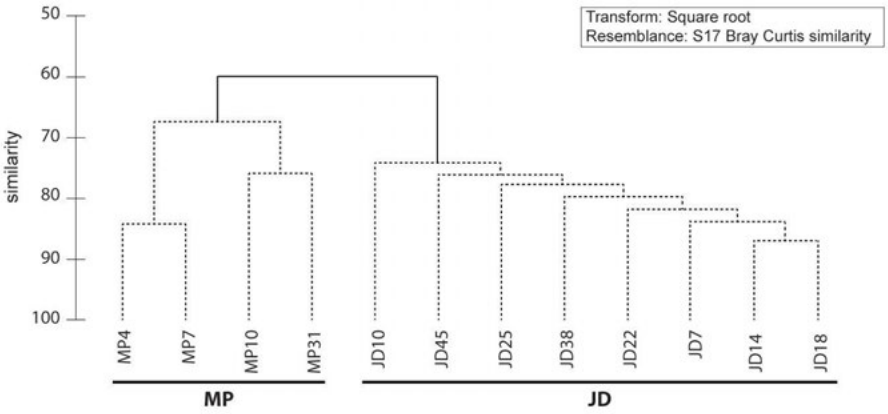

Fig. 4. Cluster dendrogram, showing a separation between the two experimental sites based on their diatom communities (p<0.01).

spp. (Table 3). At site MP *Navicula* aff. *perminuta*, *Pseudogomphonema kamtschaticum* and *Licmophora* spp. were more common (Table 3). Almost full dominant at site MP was *Navicula* aff. *perminuta* (Fig. 3A), whereas at site JD the communities were dominated by *Navicula glaciei,* followed by *Navicula* aff. *perminuta* (Fig. 3B).

At both sites, the main dominant taxa were established since the very early stages of the colonization and no particular changes were noted over the entire period of the experiment (Figs 3A, B). However, on day 38 at site JD there was a temporary prevalence of *N.* aff. *perminuta* over *N. glaciei* (Fig. 5A), and at site MP on day 31 the numbers of *N. glaciei* in the community increased (Fig. 5C). The abundance of *Navicula* aff. *perminuta* as a dominant at site MP increased after day 7 of substrate exposure (Fig. 5C), and for *N. glaciei*- after day 10 of the experiment at site JD, till reaching its maximum abundance on days 22 (Fig. 5A). Other taxa, such as the subdominants *Brandinia mosimanniae, Synedra* cf. *kerguelensis* and *Pseudogomphonema kamtschaticum* (Fig. 3A,B, see also Table 2) at both sites were found in higher numbers only during the early stages of the colonization (Figs 5B, D). Three *Synedropsis* species (*Synedropsis fragilis, S. recta* and *S.* cf. *recta*) followed a similar trend at site MP (Fig. 5D), while at site JD their abundances were more dynamic, and on day 45 markedly increased once again (Fig. 5B).

The natural epilithic diatom communities at small depths were dominated by *Navicula* aff. *perminuta* (sometimes almost as a "monoculture", with up to 100% of the counts, Table 2, sample PB1). Exception is one sample, where *Achnanthes bongrainii* prevailed (Fig. 3C, Table 2, sample JD1). *Pseudogomphonema kamtschaticum* was also observed in the natural epilithon (occasionally as a subdominant, Table 2). *Synedropsis* spp. were present in the natural epilithon, but not abundantly (Table 2).

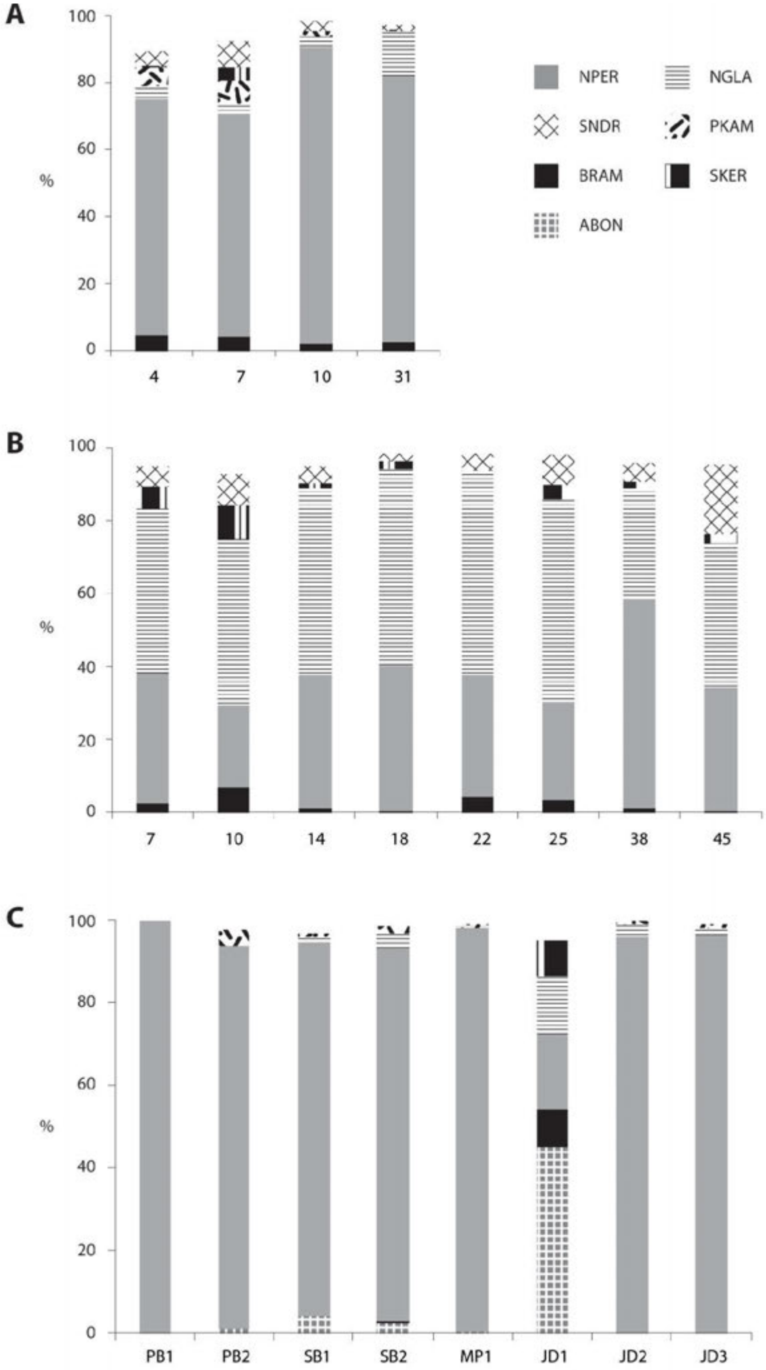

Fig. 3. Relative abundances of dominants and subdominants in diatom communities at the experimental sites and in the natural epilithon. A. At site MP by sampling day (4, 7, 10, 31). B. At site JD by sampling day (7, 10, 14, 18, 22, 25, 38, 45). C. Dominants and subdominants in the samples from the natural epilithon. By sample, see Table 1 for samples and Table 2 for full data. Abbreviations: ABON – *Achnanthes bongrainii,* BRAM – *Brandinia mosimanniae,* NGLA – *Navicula glaciei*, NPER– *Navicula* aff. *perminuta,* PKAM – *Pseudogomphonema kamtschaticum,* SNDR – *Synedropsis* spp., SKER – *Synedra* cf. *kerguelensis.*

Table 3

Contributions of the diatom species to the average dissimilarity (40.08%) between the communities at the two experimental sites (JD and MP)

	site MP	**site JD**				
Species	Av. Abund.	Av. Abund.	Av.Diss.	Diss./SD	Contrib. %	Cum.%
Navicula glaciei	2.28	**6.84**	9.67	4.24	24.13	24.13
Navicula aff. *perminuta*	**8.73**	5.94	6.01	2.67	14.99	39.12
Synedra cf. *kerguelensis*	0.63	**1.63**	2.82	1.55	7.04	46.16
Pseudogomphonema kamtschaticum	**1.70**	0.91	2.17	1.59	5.42	51.59
Synedropsis fragilis	1.11	**1.70**	1.96	1.18	4.90	56.49
Licmophora gracilis	1.01	0.34	1.78	1.40	4.45	60.94
Synedropsis recta	0.86	**1.26**	1.70	1.61	4.25	65.19
S. cf. recta	1.08	1.15	1.55	1.33	3.87	69.06
Cocconeis melchioroides	0.78	0.06	1.49	1.88	3.71	72.77
Licmophora belgicae	0.73	0.36	1.48	1.56	3.68	76.46
Nitzschia sp. 3	0.00	0.64	1.39	1.21	3.47	79.92
Brandinia mosimanniae	1.81	1.45	1.39	1.64	3.46	83.39
Achnanthes bongrainii	0.77	0.77	1.34	1.25	3.34	86.73
Cocconeis costata	0.48	0.09	0.92	1.50	2.30	89.02
Nitzschia sp. 1	0.13	0.36	0.68	1.12	1.71	90.73

Species richness, diversity and evenness on artificial and natural substrates. —The species richness on artificial substrates in the early stages of their colonization was higher compared to the mean for natural epilithon, and later decreased (Fig. 6A). In the natural epilithon of the studied region one to 12 taxa constituted the communities (Table 2), and the mean species richness was only 6.25 species (Fig. 6A, dotted line, the vertical line shows the SD, n=8). In contrast, during the early colonization (day 7) 17 taxa were found on the tiles at site MP, and 16 taxa at site JD (Table 2). The differences between the mean species richness of the natural epilithic communities and those on the tiles decreased over time and became smaller after day 12 at site MP and after day 18 for site JD (Fig. 6A). At site JD, a second peak in species richness was further noted at days 38 and 45 (Fig. 6A). At both sites diversity and evenness were also higher in the early colonization stages, and at site MP they were closer to those of natural epilithic communities (Figs 6B, C). At site JD, during the first stages of

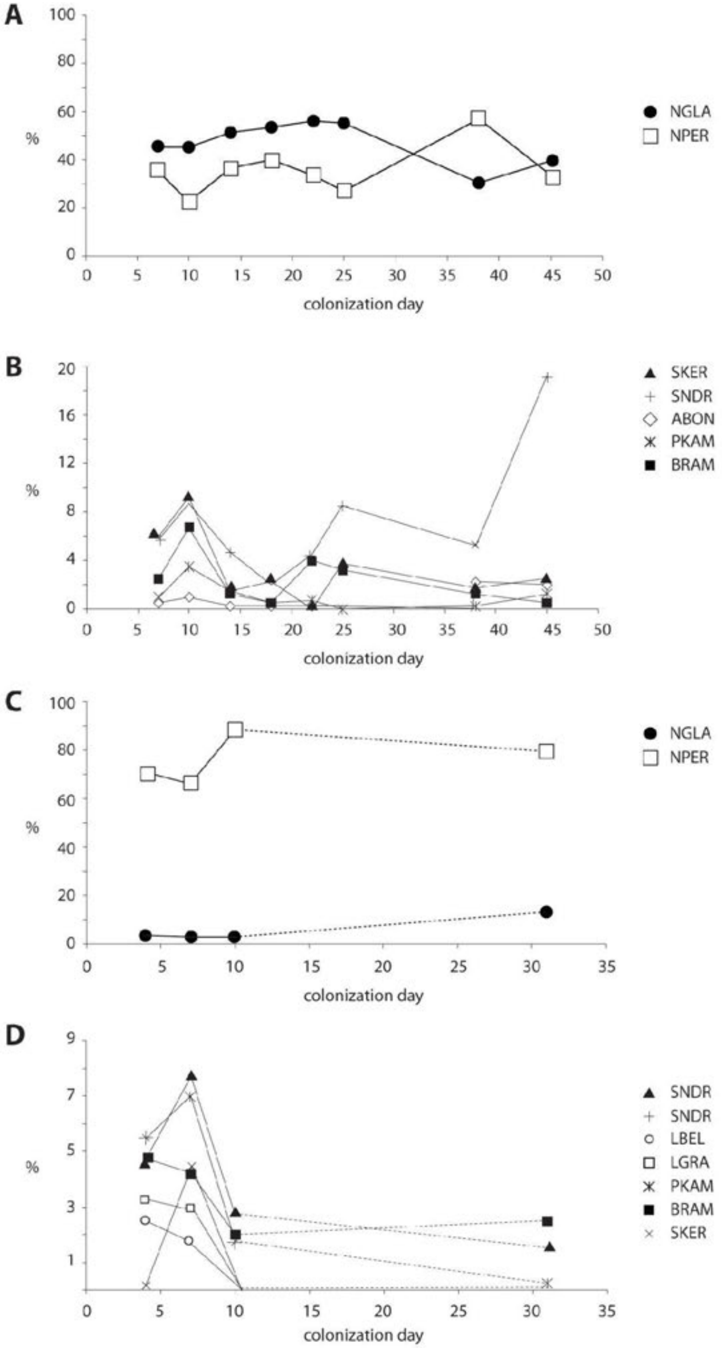

Fig. 5. Dynamics in the relative abundances of the most common taxa in the communities during the experiment. A. Abundances of the dominants at site JD along the time of the substrate exposure. B. Abundances of the subdominants and influent taxa at site JD during the experiment. C. Abundances of the dominants at site MP along the time of the substrate exposure. D. Abundances of the subdominants and influent taxa at site MP during the experiment. Abbreviations: ABON – *Achnanthes bongrainii,* BRAM – *Brandinia mosimanniae,* LBEL — *Licmophora belgicae,* LGRA — *Licmophora gracilis,* NGLA — *Navicula glaciei,* NPER — *Navicula* aff. *perminuta*, PKAM — *Pseudogomphonema kamtschaticum,* SKER — *Synedra* cf. *kerguelensis,* SNDR — *Synedropsis* spp.

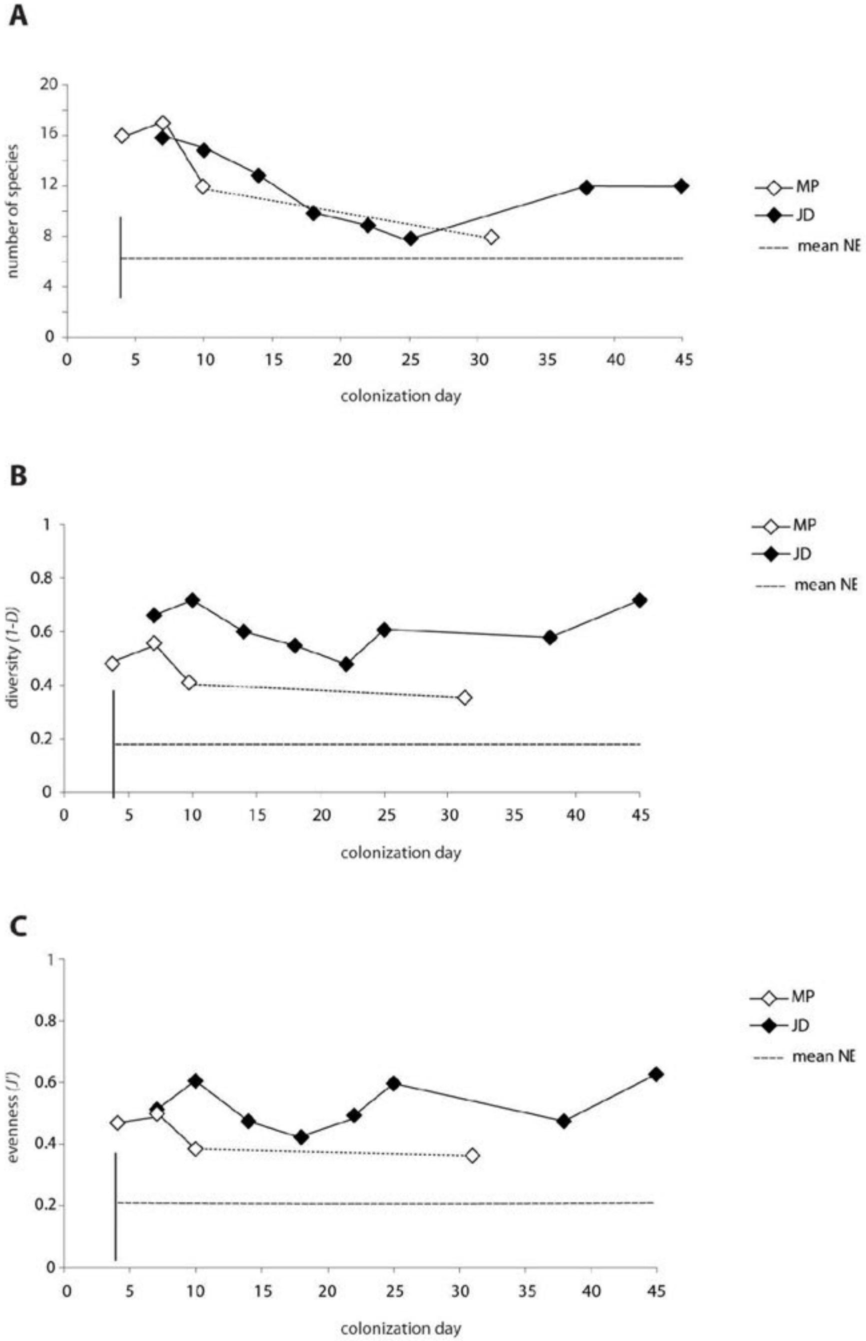

Fig. 6. Species richness, evenness (J’) and diversity (1-D) in diatom communities. A. Species richness at both sites (JD and MP) over the colonization time and compared to the mean for the natural epilithon (mean NE; SD±3.3, n=8). Days 12–31 for site MP, where no samples were possible to take, are given with dotted line. B. Diversity (1-D) at both sites during the experiment compared to the mean values of evenness (mean NE) for natural diatom communities in the area (SD = 0.2, n=8). C. Evenness *(J’)* at both experimental sites compared to the mean of the natural epilithic communities (mean NE, SD=0.2, n=8).

colonization, the evenness was much higher than that of the mean for the natural epilithon and values became closest at day 18, before a second increase on day 22 (Fig. 6C). The same trend was found in diversity (1-D) in the communities (Fig. 6B). In overall, during the entire experiment, the diversity and evenness at site JD were higher compared to the mean of the natural epilithon (mean 1-D of 0.18 and mean J' of 0.21, SD ±0.2 for both, n=8; Figs 6B, C).

Discussion

The lower salinity of Antarctic marine surface waters in summer is a consequence of freshwater inflow, either from melting snow or glaciers (Brandini and Rebello 1994; Rakusa-Suszczewski 1995; Moline *et al.* 2004). The lower Secchi depth (i.e. water transparency) measured in Johnsons dock, and the notable milky appearance of the water inside the cove (Agustí and Duarte 2000) evidence for sediment inflow. In contrast, the second site MP, had almost constant water transparency, and stable salinity values (±0.2‰ between the measurements), the latter also comparable to the mean year-round salinity values for Admiralty Bay, King George Island (summarized by Rakusa-Suszczewski 1995). As a result of the glacial meltwater inflow inside the cove and its exchange with more saline and clear waters from outside the cove, occurring twice daily with the tidal currents (Agustí and Duarte 2000), diatom communities in Johnsons Dock (JD) were subjected to constant variations in both salinity and water transparency.

At present, the colonization of new substrates by diatoms in Antarctica can be compared to the data obtained from the freshwater periphyton and to a few studies so far from marine environment in other regions. The colonization followed the phase scheme of Tilley and Haushild (1975), presented by a curve with three phases — colonization, logarithmic growth and equilibrium (Fig. 2A). The colonization of new substrates depends on the benthic diatom species which are present in the water column. In the Antarctic, a large number of benthic taxa are found resuspended into the water column by the turbulence caused by wind and wave action (Brandini and Rebello 1994), and these serve as a "seed bank" for new substrates colonization. Several studies in the coastal waters of the South Shetland Islands have shown that benthic diatoms constitute a large part of the species, recorded in the coastal plankton (Ahn *et al.* 1997; Kopczyńska 2008; Lange *et al.* 2007). In the study of Tenenbaum *et al.* (2010) 50% of the species found in the phytoplankton in coastal areas of King George Island were benthic. During spring months, sea ice is another potential source of diatoms that are to colonize new substrates. In spring, with the melt of the sea ice various microalgae, including diatoms, are released into the water column (Krebs 1983; Cunningham and Leventer 1998). As benthic species cannot survive in the water column, in first opportunity they attach to any available surface. Apart of a single occurrence of the open water diatom *Thalassiosira gracilis* (Cunningham and Leventer 1998),no other truly planktonic taxa were found on the experimental tiles, and the high diversity on the tiles at the first days of the experiment could only be explain with the high number of potential colonizers available in the water column. The further development of the species on the substrates depends on the particular abilities for attachment of each species and the environmental conditions. Not all the species which initially settled on the tiles managed to attach or to continue their development on the substrates in later stages. Species of the genera *Synedra* and *Licmophora* for instance, which are believed to have very good adhesive properties (Tanaka 1986), are also confirmed here with their appearance on the substrates in the early stages of colonization. Their decrease in numbers in 10 to 14 days after the substrates were submerged (Figs 5B, D) suggests that the conditions offered by the substrates in the environment of small depths, were not suitable for their growth. These species are erect forms (Majewska *et al.* 2015), living attached to the substrate with one of their valve poles only, what makes them vulnerable to mechanical stress such as currents (Liu *et al*. 2013) and less competitive in such conditions. The erect forms are usually abundant in sheltered places, or at larger depths in Antarctica (Majewska *etal.* 2015). In the natural epilithon at small depths the erect forms were also rarely observed (Fig. 3C, Table 2).

The prevalence of motile diatoms, such as *Navicula* spp. (Figs 3A-C, Table 2), is typical for environment with recurrent unfavorable or catastrophic events (Hudon and Bourget 1983, Tuji 2000). The Antarctic benthic communities are subjected to highly variable environmental conditions (Rakusa-Suszczewski 1995; Gutt 2001), including strong mechanical stress from the frequent ice scour, which may even hold the benthic communities (in a broad sense) in early stages of their development (Smale *et al.* 2008 and references therein). Highly motile diatom species (i.e. *Navicula* spp.) are first colonizers and re-colonizers of unstable or denuded habitats, having a fast growth rate and are highly resistant to various stress factors (Morin *et al.* 2008). Their populations can recover rapidly even after mechanical stress (Majewska *et al.* 2016 and references therein). All these features make the small motile diatoms well adapted for the Antarctic marine environment, including habitats at small depths. The inability of most of the species, which initially settled on the tiles to survive and grow on our substrates led to the observed decrease in the diversity at later stages of community development, whereas the increasing dominance of a few, but well adapted species, led to the decrease in evenness in the communities on the tiles. The high number of newly arrived taxa with low abundance on the substrates is a likely reason for the high diversity and evenness during the early stages of the experiment (Figs 6B, C), and such scenario is possible during new colonization or recolonization after disturbing events (Svensson *et al*. 2012).

The optimum community development on new substrates is indicated by both valve density and diversity indices (Desrosiers *at al.* 2014). We were able to compare the communities on the artificial substrates to natural communities at similar depth in the same area. The similarity in species richness, evenness and diversity of the communities on the new substrates to the mean values for the natural epilithon after 14–18 days of the substrates exposure, and the plateau in the valve growth achieved after day 25, suggest that a period of at least three weeks is necessary for development of representative for the environment diatom communities in Antarctic marine waters. At site JD further changes in communities were noted. It is possible however that these changes happened due to a change in the environment or another event, which we were unable to detect. Nevertheless, long periods of exposure are inappropriate due to the high risk of substrate lost (Desrosiers *et al.* 2014), while seasonality is also known to be well pronounced in Antarctica and may lead to changes in the communities during summer months (Majewska and De Stefano 2015, Majewska *et al.* 2016).

Based on our results, the diatom colonization in Antarctic marine waters was not slow, as it was expected (e.g. Zacher *et al*. 2007). Globally, there is a quite limited number of such studies on diatoms in marine environment and these are usually based on a small set of samples from a limited number of sites. Desrosiers *et al.* (2014) studied diatom colonization on a single replicate of three substrates at five sites in the Carribean, whereas Liu *et al.* (2014) based their study on a single type of substrate but at two different depths at two sites at the Yellow Sea. We used three replicates of one substrate at two different sites. Substrate types used, their surface area and depths of their position vary among authors, and there is no adopted methodology for such studies, which makes the comparisons between the reported data more difficult (see the extensive review by Desrosiers *et al.* 2014). Nevertheless, in time frame, the diatom colonization and development processes in the Antarctic marine waters do not seem to differ substantially from the reports from other latitudes, although they are faster compared to the available data. A period of four weeks for development of mature diatom communities on newly submerged substrates was found to be appropriate for the studied conditions at Yellow Sea (Liu *et al.* 2014), but for the oligotrophic Caribbean waters five-week exposure of the substrates was necessary (Desrosiers *et al.* 2014). Compared to these studies, the valve numbers on the substrates at South Bay was remarkably high, reaching values of more than 140000 (x 10^5cm^{-2}) at site JD after 25 days of exposure (Fig. 2A). For instance, Desrosiers *et al*. (2014) reported only 5 (x 10^5 cm^{-2}) valves on their Plexiglass© tiles after six weeks at the Caribbean coast, whereas the maximum diatom abundance on glass substrates positioned at 1 m depth at Yellow Sea was reported to be 10 (x 10^5 cm^{-2}) after four weeks of exposure (Liu *et al.* 2014). Substrate position, bottom nature and silica availability (among other factors) can influence the biofilm development (Desrosiers *et al.* 2014). The extremely high number of valves on our substrates suggests a high growth rate of the Antarctic marine benthic diatoms, undoubtedly also supported by the large amount of dissolved silica available in the water (Tréguer 2014).

There were no differences in the colonization rate between the two experimental sites, but the valve density at the glacier influenced site JD was higher compared to the unaffected site MP (Figs 2C). Campana *et al.* (2018) reported a higher diatom coverage on polyethylene tiles in the glacier influenced site in their experiment. Further, Ha *et al.* (2019) discovered extreme blooms of benthic marine diatoms in glacier influenced areas. These observations suggest that diatoms may play important role in Antarctic coves (and with glacier retreat), but it remains unclear whether there is a connection between the deglaciation and enhanced diatom growths. Different species are also known to have different growth rates (Morin *et al.* 2008), and the prevalence of one or another species (but also in relation to the environmental conditions) can influence the biofilm development on new substrates (Hillebrand and Sommer 2000). However, at present we have no data to confirm that the higher valve density at the glacier influenced site is due to enhanced growth of species in relation to the environmental conditions. There is a big gap in the knowledge of the ecology of marine benthic diatoms in Antarctica, as well as uncertainty in their identities. The (over)dominant *Navicula* aff. *perminuta* for instance has been reported from the Antarctic (as *N. perminuta* or *N.* cf. *perminuta*), either from the plankton (e.g. Kang *et al.* 1999; Lange *et al.* 2018), sea ice (Torstensson *et al.* 2019), or various other substrates (e.g. Zacher *et al.* 2007; Campana *et al.* 2008; Majewska *et al.* 2013, 2016; Majewska and De Stefano 2015; Daglio *et al.* 2018). Across the studies, the species shows morphological variability (Kang *et al.* 1999; Al-Handal and Wulff 2008a,b); its real identity is not well clarified, and its identification across the studies seems to be doubtful. For instance, the depicted valve of *Navicula perminuta* in Al-Handal and Wulff (2008b, fig. 102), is most likely another *Navicula* species but not “*N. perminuta”*as identified in our study (Fig. 7B), in Al-Handal and Wulff (2008a, figs 50–51), and in Majewska *et al.* (2013, fig. 3n–o).

Navicula glaciei is mostly reported as a “cryophilic” diatom from the sea ice (Cremer *et al.* 2003; Withaker and Richardson 1980), released into the water column with ice melt in spring (Krebs 1983; McMinn 1996). Recently both *N. glaciei* and *N.* aff. *perminuta*, as identified in our study and based on the illustrative material provided in other studies were also found to be well represented in the Antarctic epiphyton (Majewska *et al.* 2013). There are fewer reports of these taxa in the Antarctic marine epilithon, which most likely only reflects the low number of studies.

Fernandes and Procopiak (2003) reported *Naviculaglaciei* in high numbers on rock substrates on King George Island and Elephant Island and our data confirm their opinion that hard substrates are another habitat for this species in summer months, and also suggest possible exchange of species between the sea ice and the Antarctic epilithon. Such exchange was supposed for some species found in the Antarctic epiphyton (Majewska *et al.* 2016). Another evidence in support is the presence and growth on the experimental tiles of *Synedropsis* taxa (Table 2, Figs 3A, B), the latter also typically associated with the sea ice (Hasle *et al.* 1994; Cremer *et al.* 2003).

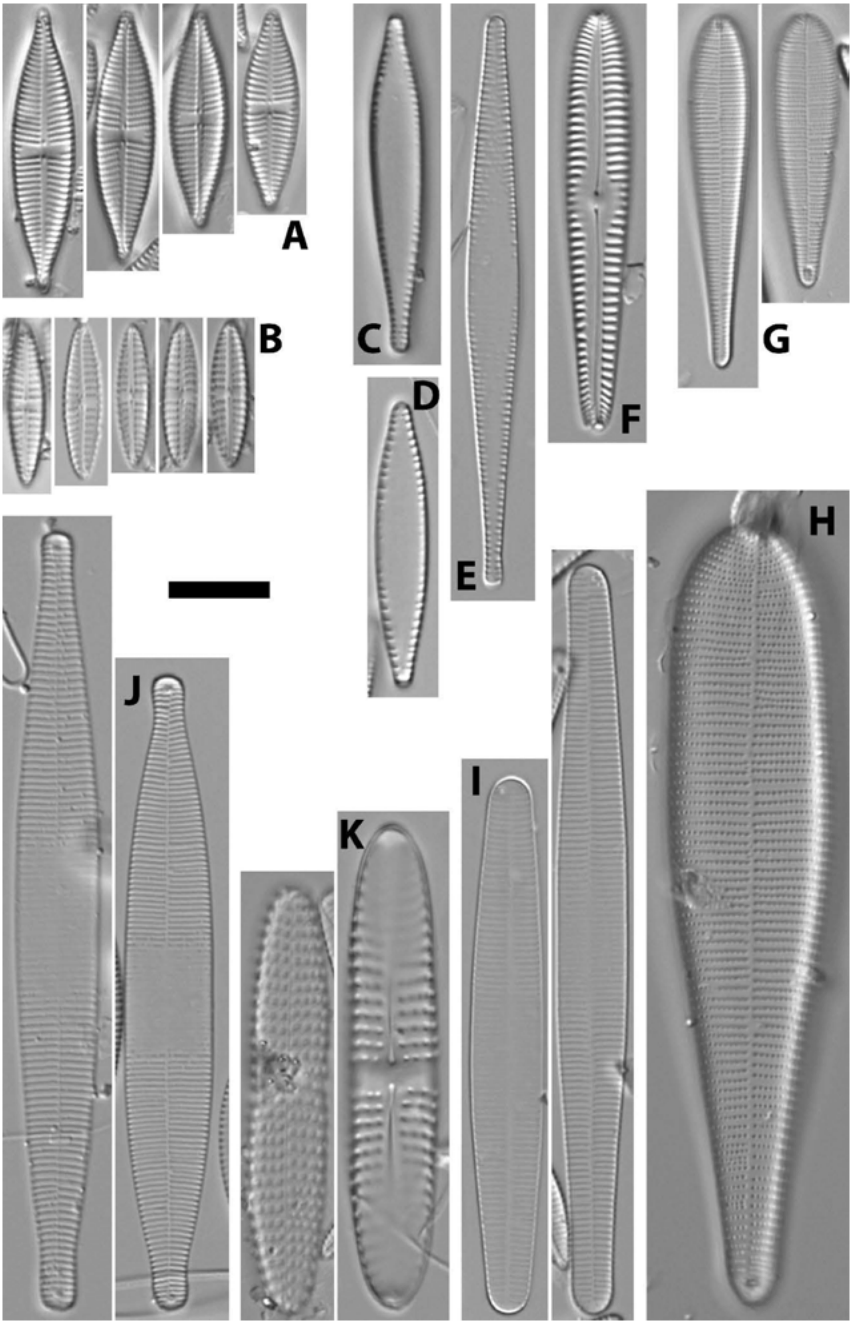

Fig. 7. LM micrographs of the most commonly observed taxa. A. *Navicula glaciei* (JD, tiles). B. *Navicula* aff. *perminuta* (five valves from different populations, the last two valves on the right are from natural epilithic communities). C. *Synedropsis* cf. *recta* (JD, tiles). D. *Synedropsis recta* (JD tiles). E. *Synedropsis fragilis* (JD, tiles). F. *Pseudogomphonema kamtschaticum* (JD, tiles). G. *Licmophora gracilis* MP, tiles). H. *Licmophora belgicae* (MP, tiles). I. *Synedra* cf. *kerguelensis* (JD, tiles). J. *Brandinia mosimanniae* (JD, tiles). K. *Achnanthes bongrainii* (JD, tiles). Scale bar is 10 μm.

Sea ice diatoms were also reported to prevail in benthic diatom communities of recently deglaciated area in the study of Passoti *et al.* (2015). The sea ice is a highly extreme habitat in terms of temperature, salinity and light intensity (Arrigo and Sullivan 1992; Thomas and Dieckmann 2002), and organisms living there should be well adapted to withstand highly variable conditions. Experimental studies on the growth of several sea ice diatom species from both the Arctic and Antarctic have shown that sea ice diatoms grow in a broad range of salinities and are well adapted to salinity changes (Grant and Horner 1976; Schlie and Karsten 2016). Kang *et al.* (1999) suggested that both *Navicula glaciei* and *N. perminuta* are indicative for meltwater inflow, but without making distinction between the two species in their study. Cremer *et al.* (2003) associated the occurrence of *N. glaciei* in high numbers in Holocene sediments with salinity changes in the environment. Based on the prevalence of *Navicula glaciei* and the higher number of *Synedropsis* spp.at the glacier influenced site JD, we suppose that sea ice associated diatoms could be indicative for conditions with variations in both salinity and water transparency. In turn, *Navicula* aff. *perminuta* seems to be a highly resistant species to mechanical stress, such as ice scouring and wave action. In support of this opinion is the overdominance of *Navicula* aff. *perminuta* (more than 90% of the counts, Fig. 3C) in the natural epilithon at small depths, where these two stress factors are most pronounced (Barnes and Conlan 2007). Same species most likely dominated the communities in the grazing experiment by Zacher *etal.* (2007) and was reported as grazer-resistant by Campana *et al.* (2008). *Navicula* aff. *perminuta* is apparently also a typical component of the Antarctic marine benthos during spring and summer months. *Navicula* aff. *perminuta,* as defined in this study (Fig. 7B), was found in high numbers (abundance >70%) living epiphytically on macroalgae in Antarctica (Majewska *et al.* 2013, fig. 3n-o). Of other taxa, which were commonly observed by us, based on the existing iconographic material provided in other studies, *Synedra* cf. *kerguelensis* (Fig. 7I) has either been reported as *Synedra kerguelensis* (e.g. Cremer *et al.* 2003, figs 154–155; Al-Handal and Wulff 2008a, fig.19; Daglio *et al.* 2018, fig. 4I) or *Fragilaria striatula* (e.g. Fernandes *et al*. 2007, figs 8–10). Cremer *et al.* (2003) considered these two taxa might be conspecific, but further research is necessary to confirm that Antarctic populations indeed all belong to *Fragilaria striatula.* The latter species, according to Cremer *et al.* (2003), is also a sea ice associated diatom and an indicator for cooler waters.

Conclusions

The data we have are so far limited to observations in a small region — South Bay of Livingston Island, and still on a small number of samples. Statistical testing was not possible for our study. Based on the observed similarity in the community structure between the natural epilithic diatom communities and the artificial substrates at *ca.* same depths after ~ three weeks of new substrate exposure, and at both sites, we can define this period as the minimum time needed to obtain representative diatom communities on artificial substrates. This time period is most probably similar to the natural processes occurring in the epilithic communities at small depths in environment like the one of the South Bay, if the substrate used is Plexiglass© and positioned at *ca.* 1 m below sea surface.

Between the sea ice and marine epilithon exchange of species exists, and some taxa present in the sea ice also live in the epilithon, at least in summer months. It is possible that once resuspended in the water column, and captured by the forming sea ice in autumn (van Leeuwe *et al.* 2018), the high motility of *Navicula* spp. later allows them to find the most appropriate conditions for life in the sea ice. The prevalence of sea ice associated diatoms at certain location could point for conditions of both salinity and water transparency variations.

The lack of sufficient studies on benthic marine diatoms in Antarctica obscures both their identities, distributions and ecological preferences. This makes impossible to trace changes in their communities, which may be related to changes in the environment. Further studies using both the traditional morphological approach for taxa identification and molecular markers may help in revealing their true identities, while more sampling efforts are definitely necessary to understand their diversity, ecology and distribution in Antarctica.

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