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Microphytobenthic community composition of two sub-Arctic intertidal flats in Huna Bay (Northern Iceland)

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Marine microphytobenthic community composition in relation to habitat characteristics of sub-tidal flats in temperate and Arctic regions is well described. For sub-Arctic areas, especially for northern Icelandic intertidal flats, information is sparse or absent. To investigate sub-Arctic microphytobenthic community composition, surface sediments were collected during neap tide at six stations, along two transects in the Húnaflói in and near Skagaströnd from March to October 2013. Variations in environmental factors were considered as well as microphytobenthic density (abundance and chlorophyll *a*). Overall, 137 species and sub-specific taxa were identified in surface sediment samples (106 bacillariophytes and 31 other taxa). Of these, 53% are considered as marine or brackish water species in the literature. Forty-three per cent of the marine taxa originated from the planktonic realm, suggesting considerable benthic-pelagic coupling in the investigated area. The primary producers in both transects in the Skagaströnd area were mainly Bacillariophyceae (up to 85% of the total communities, with overall mean value of 35.6 and 42.8 × 10² cells cm⁻² in transects I and II, respectively). All communities were characterized by a dominance of epipellic *Navicula* species with temporal successions of secondary species, including several pelagic species (e.g. *Actinocyclus*). The non-diatom taxa at all stations in transects I and II included pelagic species such as *Stichococcus bacillaris* (Prasiolales, Chlorophyta), and cryptophytes, dinophytes, haptophytes and other ochrophytes. Characteristic environmental features such as short growth periods, high glass and basalt fractions in the sediment composition and seasonal fluctuations in terrestrial runoff, as well as strong hydrodynamic forces, influenced the community patterns observed in the present study and further comparative studies with other areas in northern Iceland are required.

Key words: abiotic factors, Bacillariophyta, Chlorophyta, Cyanophyta, Dinophyta, intertidal flats, microphytobenthos, nutrients

INTRODUCTION

Intertidal and shallow subtidal sediments are characterized by dense populations of benthic microalgae, the microphytobenthos (MPB). On sandy and muddy substrates, edaphic communities are often dominated by diatoms (e.g. Admiraal, 1984; de Jonge & Colijn, 1994; Agatz *et al.*, 1999); coccoid and filamentous green algae, euglenophytes, dinophytes and cyanophytes occur only at some stages during the growing season (e.g. Nozaki *et al.*, 2003). MPB diatom populations are usually composed of pennate, prostrate forms, which are either epipsammic or epipellic (e.g. Daehnick *et al.*, 1992; Agatz *et al.*, 1999; Mitbavkar & Anil, 2002).

MPB organisms contribute significantly to primary production in littoral zones (e.g. Pinckney & Zingmark, 1993); they are the major food source for macrozoobenthos and are commercially important for

fish and shellfish stocks as well as for migratory bird populations (e.g. Hillebrand *et al.*, 2002). Seasonal succession in such MPB communities is well described (Admiraal *et al.*, 1984; Oppenheim, 1991; Underwood, 1997; Saburova *et al.*, 1995; Peletier, 1996), and points to correlations between taxon distribution and salinity, physical characteristics of sediments, organic matter and nutrients or temperature (e.g. Admiraal *et al.*, 1984; Underwood, 1994; Underwood *et al.*, 1998; Underwood & Provot, 2000; Thornton *et al.*, 2002; Scholz & Liebezeit, 2012a, 2012b). The importance of production by the microphytobenthic algal community in the Arctic region has also been established (e.g. Glud *et al.*, 2009). The polar coastal areas differ from the better studied temperate regions in being subject to ice-cover and darkness during extensive periods of the year. Furthermore, they experience relatively low temperatures and the seabed is often exposed to ice-mediated erosion and erratic, massive inputs of erosion material

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during spring (Rachold *et al.*, 2004; Zacher *et al.*, 2009).

The coast of Iceland is about 6500 km long (excluding tidal flats). Of this, 560 km consists of exposed, apparently barren, sandy shores. Only about 40% (~ 175 km²) of the intertidal in Iceland comprises relatively wave-protected tidal flats (Ingólfsson, 2006). The lithology of Iceland is predominantly basaltic in composition (80–85%), followed by intermediate and silicic volcanics and minor volcanoclastic sediments (Georg *et al.*, 2007). Regulated by temperature and precipitation, freshwater run-off from the mountains influences the coastal area, leading to fluctuations in salinity and nutrient concentration. There is a rich macroalgal vegetation (e.g. Espinosa & Guerra-García, 2005; Ingólfsson, 2007), and several recent studies conducted on the Icelandic west coast have documented the presence of macrozoobenthic feeders such as *Arenicola marina* (Linnaeus) and *Littorina Féruccac* (e.g. Ingólfsson, 1996, 2002; Bat, 1998; Steinarsdóttir *et al.*, 2009). However, previous studies did not consider the basis of the benthic food web – the microscopic primary producers. In particular, knowledge of marine benthic diatoms from Iceland is scarce and limited to palaeobiological studies of deposited plankton-derived species associated with deep-sea floor soft sediments (Jiang *et al.*, 2001) and epiphytic diatom assemblages on macroalgae collected from the west coast (Totti *et al.*, 2009). Based on the observation of dense consumer populations in the investigated area, especially during the summer months (e.g. shrimps, mussels and migrating birds), it was hypothesized that the microphytobenthos would show a similar biodiversity and comparable cell numbers to those found in previous investigations in the Wadden Sea area (Solthörn tidal flat, southern North Sea; Scholz & Liebezeit, 2012a, 2012b). Hence, the main objectives of the present baseline analysis were: (1) to describe the temporal and spatial distribution of the physical and chemical parameters in the surface sediments and overlying water; (2) to evaluate temporal and spatial variation in MPB biomass, abundance and species composition; (3) to determine which environmental factors most affected MPB species composition; and (4) to discuss, as far as possible, patterns and features in the investigated area in comparison to temperate and polar regions.

MATERIALS AND METHODS

Study area

Huna Bay (Húnaflói) is a large bay between Strandir and Skagaströnd in Northern Iceland (Fig. 1). The study sites were two tidal flats located on the east coast of Húnaflói in and near the small village Skagaströnd (Fig. 2). The flats were studied, in both cases, along a transect characterized by a slight slope down from the shore towards the seabed. The vertical height difference was about 0.15 ± 0.05 m and $0.11 \pm$

0.03 m between stations 1 to 3 and 4 to 5, respectively (Figs 3, 4). Transect I, which included three stations, was located near a stream (Fig. 3) and transect II, comprising two stations, was situated within the sheltered harbour (Fig. 4). The distance between individual stations was about 50 m. While the first tidal flat was characterized by stones functioning as sediment traps and macroalgae which were attached to the stones (Fig. 5), transect II had only sediments showing wave ripples about 2 cm high, without stones or macroalgae (Fig. 6). All chosen stations were dominated macroscopically by faecal strings of *Arenicola marina* (Polychaeta), with higher cluster densities at transect II. Samples were taken monthly at neap tide from March to October 2013. Surface samples were obtained, in triplicate, by inserting 8.5 cm diameter plastic Petri dishes into the sediment to a depth of 1 cm. The distance between the individual samples was 10 ± 2 cm, arranged in a triangle (Fig. 7). Samples of the overlying water, which filled the hole after sediment sampling, were also taken in triplicate at each station with 10 ml disposable plastic vials. All samples were stored at $4 \pm 2^\circ\text{C}$ until further processing in the laboratory.

In situ measurements and analysis of physico-chemical parameters

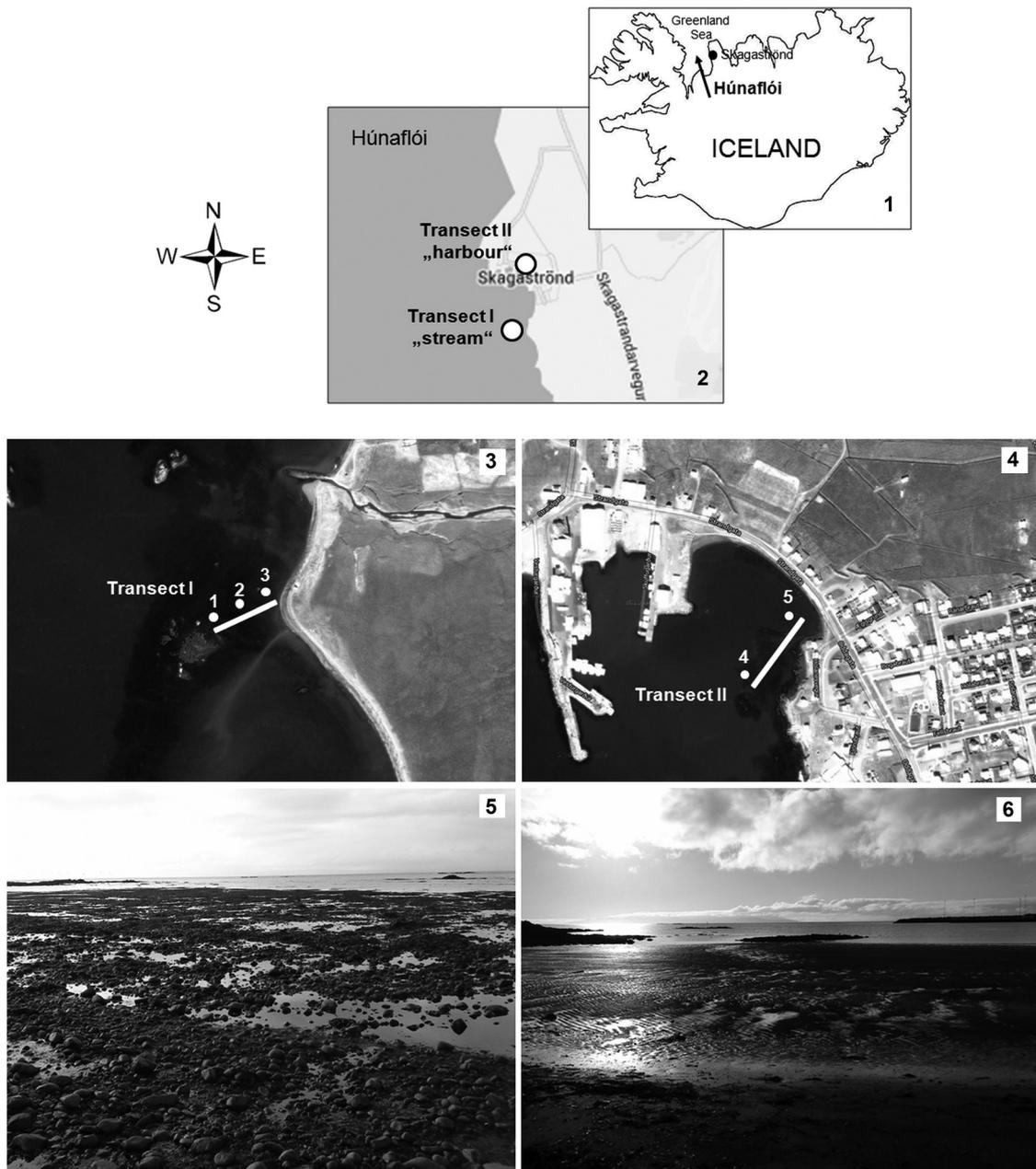
Conductivity, sediment surface temperature, dissolved oxygen and pH were measured *in situ* at the sampling sites, using handheld probes (YK-31SA, YK-200PATC, YK-200PCD and YK-2001PH, SI Model 33, Engineered Systems and Designs-Model 600, Philips W9424). Photosynthetic active radiation (PAR, 400–700 nm) was measured during the sampling period with an underwater spherical quantum sensor LI-193SA connected to a Licor Data Logger LI-250A. Incident ultraviolet-B radiation (280–320 nm) was measured using a broad band 128 ELDONET radiometer (Real Time Computers).

Samples of the overlying water were filtered into 5 ml disposable plastic vials through cellulose acetate filters (pore size 0.45 μm : Sartorius, Göttingen, Germany) and stored frozen until further analysis. Reactive dissolved phosphate (RDP), ammonium, nitrite and nitrate (together comprising dissolved inorganic nitrogen, DIN), and dissolved silica (DSi) in the form of silicic acid were ascertained according to Grasshoff *et al.* (1983, 1999). The nutrient ratios were calculated according to Redfield *et al.* (1963) and Brzezinski (1985).

A total of 10 subsamples from each Petri dish were taken with a shortened syringe (sample volume 1 cm³) and frozen until analysis (-18°C). Two of these were used to determine water content and ash free dry weight (AFDW) by oven drying at 60°C , followed by combustion at 500°C , both for 24 h. Porosity was calculated from the weight loss of a known volume of wet sediment after drying to constant weight at 60°C . For the third sediment sample, median grain size was determined with a Coulter Counter LS particle size analyser (LaserGranulometer, SediGraph). Size ranges were classified according to Wentworth (1922) and the *phi* (ϕ) scale (Krumbein & Sloss, 1963).

Chlorophyll *a*, phaeopigment and phycocyanin analysis

A spectrophotometric method adapted from Parsons *et al.* (1984) using Lorenzen's equations (Lorenzen, 1967) was



Figs 1–6. Location of the two transects in and near Skagaströnd (Huna Bay = Húnaflói, North-Iceland). **Figs 1, 2.** Overview maps. **Fig. 3.** Location of transect I near the stream (stations 1, 2, and 3), **Fig. 4.** Location of transect II in the sheltered harbour of Skagaströnd (stations 4 and 5). **Figs 5, 6.** Pictures of the sampling locations during neap tide.

used to ascertain chl *a* and phaeopigment content in the fourth sediment subsample. Measurements were conducted following the method described by Brito *et al.* (2009). 90% acetone (10% distilled water) buffered with sodium bicarbonate, was added to each sample. The tubes were vortexed, frozen for 6 h at -20°C and centrifuged for 10 min at 3500 rpm (Omnifuge 2.0 RS, Heraeus Sepatch, Osterode, Germany). The supernatants were diluted 1:10 with 90% acetone and measured at 663 and 750 nm (PEQLAB Biotechnology GmbH, Erlangen, Germany). After acidification of the samples using 1.2 M HCl (10%) the reading was repeated for the phaeopigment analysis.

Phycocyanin (PC) content was determined from the fifth sediment subsample according to the method of Oliveira *et al.* (2008). PC extraction after cell disruption by sonification was conducted in 0.1 M phosphate buffer (pH 7.0)

solution. The amount of PC was calculated using the equation: $\text{O.D. at } 615 \text{ nm} - 0.474 (\text{O.D. at } 652 \text{ nm})/5.34$. Chl *a*, phaeopigment and phycocyanin concentrations were calculated in mg m^{-2} .

MPB identification and enumeration

Overall, five out of the 10 subsamples were taken for MPB identification and enumeration from each Petri dish (sample volume 1 cm^3), using three different methods.

For the MPB composition overview counts, conducted in Utermöhl counting chambers (Utermöhl, 1958), the first two sediment subsamples were each initially re-suspended in 40 ml artificial seawater (Tropic Marin[®], GmbH Aquarenttechnik, Wartenberg, dissolved in

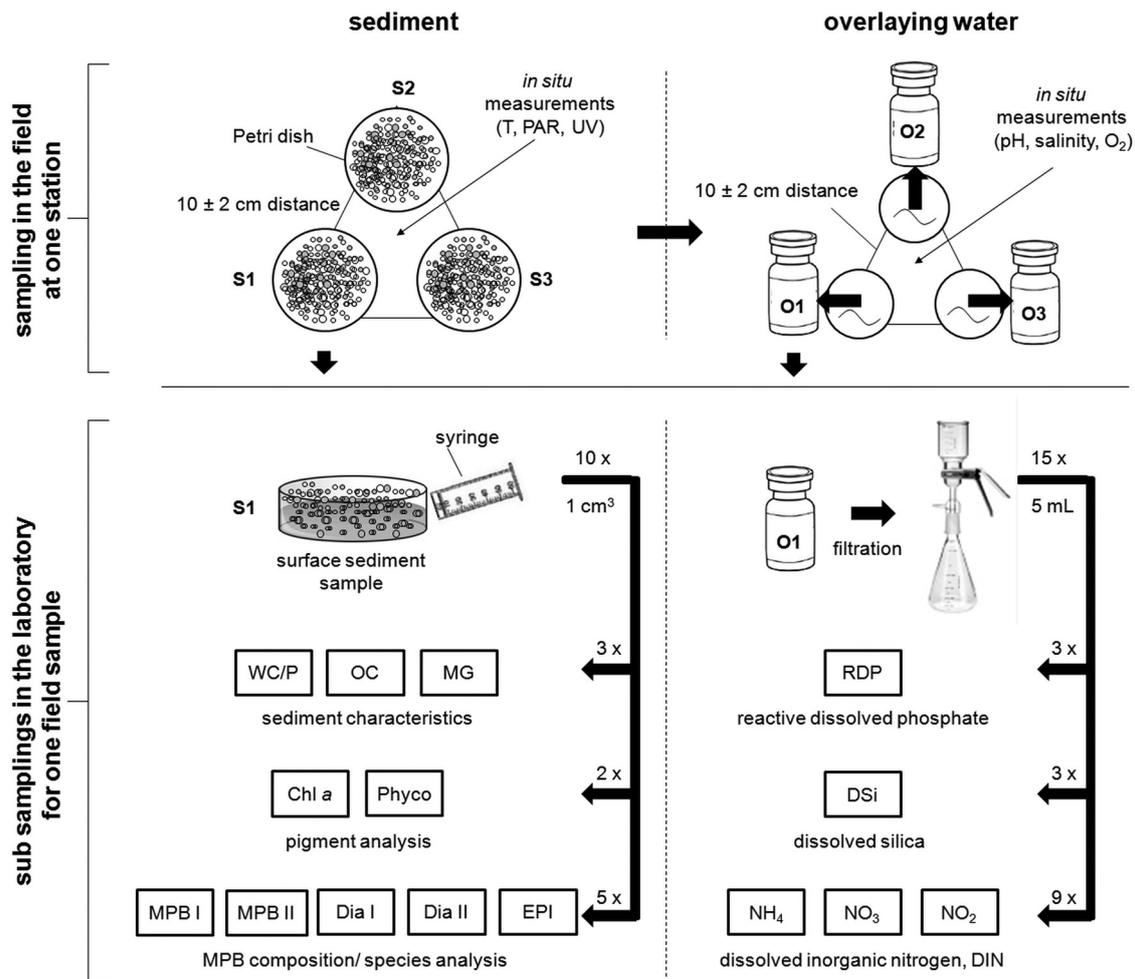


Fig. 7. Scheme of the surface sediment and overlying water sampling at one station in the Húnaflói, North Iceland, including the sub-samplings for each process step in further analysis.

deionized water) and ultrasound treated for 30 s using an ultrasonic processor UP50 (Dr Hielscher GmbH, Tetlow, Germany) with an amplitude of 40% at 0.5 s intervals. Cells were then separated from the sediment grains by gradient centrifugation, using Ludox TM according to the method described by de Jonge (1979). One millilitre of the 70% Ludox TM layer containing the cells was placed in counting chambers and diluted with 2 ml artificial seawater (this was done in triplicate). Control by microscopy of the remained sediments confirmed the complete release of the cells from the sediment grains, using an Olympus BX51 (Hamburg, Germany) equipped with a BX-RFA Reflected Fluorescence system. Up to 400 cells were counted per sample at each station to obtain statistically significant mean values. The chambers were scanned at $400\times$ magnification using an inverted microscope (Olympus IX51, Hamburg, Germany).

Additional microscopic *in situ* analysis with the third sediment subsample was conducted in order to confirm species determination from the counting in the Utermöhl chambers, as well as to quantify numbers of live cells, using epifluorescence. The samples were prepared by initially re-suspending in approximately 40 ml of artificial seawater as described above; 100 μl aliquots of the re-suspended material were drawn off from the slurries under continuous stirring on a vortex and placed on specimen slides. In total, 10–20

subsamples from the re-suspension were taken to minimize scatter from uneven distribution. Up to 1000 cells were counted per sample from each station to obtain statistically significant mean values. The slides were scanned at $400\times$ and $1000\times$ magnification using the equipment described above and only cells fluorescing red under UV light were counted. In both counting methods, cells were identified as far as possible, enumerated and allocated to taxonomic suborders. Taxonomy follows the nomenclature of Pankow (1990), Simons *et al.* (1999), with additional use of Geitler (1985) and Wolowski & Hindák (2005). In this approach the Bacillariophyceae were enumerated without further classification (cf. Fig. 14A, B). Abundance was calculated as the number cm^{-2} sediment surface (cf. Figs 13 and 14) and converted to relative abundances (Fig. 15B, Table 4, Supplementary Table S1).

For diatom identification, two further subsamples were treated with ultrasound and Ludox TM as described previously. Then samples were oxidized with hydrogen peroxide (27%) and acetic acid (99.9%), according to a slightly modified version of the cleaning procedure given by Schrader (1973), described by Sabbe & Vyverman (1991). Cleaned valves were mounted in Naphrax (Brunel Microscopes Ltd, UK) to produce permanent slides in duplicate. Altogether 460 slides were analysed and examined by phase contrast light microscopy. Four to five hundred valves were identified and

counted for each site on each sampling campaign between March and October 2013. Besides the intact cells, frustules which were broken but constituted more than half of the probable original size were also considered. Abundance was calculated as the number cm^{-2} sediment surface (cf. Fig. 14) and converted to relative abundances (Fig. 15 B, Table 4, Supplementary Table S2). For species identification the following literature was used (numbers in square brackets apply to the species references given in Table 4 and in Supplementary Table S2): Cleve (1894 [1], 1895 [2]), Hasle & Syvertsen (1996 [3]), Hendey (1964 [4]), Hoppenrath *et al.* (2009 [5]), Hustedt (1927–1966 [6], 1939 [7]), Krammer & Lange-Bertalot (1986–91 [8]), Kützing (1844 [9], 1849 [10]), Østrub (1916 [11]), Østrub (1918 [12]), Pankow (1990 [13]), Round *et al.* (1990 [14]), Schmidt *et al.* (1874–1959 [15]), Snoeijs (1993 [16]), Snoeijs & Potapova (1995 [17]), Snoeijs & Vilbaste (1994 [18]), Snoeijs & Kasperoviciene (1996 [19]), Snoeijs & Balashova (1998 [20]), Van Heurck (1880–85 [21]), Witkowski (1994 [22]) and Witkowski *et al.* (2000 [23]). Numerical processing of the identified species was done after classification according to taxonomic nomenclature described in Medlin & Kaczmarek (2004).

Statistical analyses

Cluster analysis with unweighted pair-group average hierarchical agglomeration (UPGMA), using Spearman correlation coefficients, was conducted to ascertain similarities between the sampled stations. Fifty-eight marine and brackish water species that occurred on at least three out of the eight sampling dates were chosen and used in the statistical analysis (Tables 3, 4). Canonical Correspondence Analysis (CCA), with a forward selection of variables, was then applied to evaluate the relationship between the abiotic variables and the MPB species composition at both transects. This analysis was done using a covariance matrix with logarithmic transformation [$\log(x + 1)$] for the environmental data and variation range for the biological data. Altogether, 10 environmental variables (temperature, PAR, salinity, median grain size, porosity, water and organic matter content as well as the nutrients DIN, RDP and DSi) and 58 biological variables (14 non-diatoms and 44 diatoms) were used. In order to verify the probability that the eigenvalues of the axes had been attributed by chance, the Monte Carlo Test was applied (999 interactions; $P \leq 0.05$). All tests were performed with the program XLSTAT 2011, Version 2011.2.08 Addinsoft.

RESULTS

Physical and chemical parameters

Each parameter of the *in situ* measurements during the sampling period was characterized by changing weather conditions and biochemical reactions occurring on the sediment surface (Fig. 8). The minimum and maximum sediment surface temperatures were in October and in June 2013 (Fig. 8A) and the overlying water pH alternated between 7.54 and 8.42, respectively (Fig. 8B). Mean sediment surface water salinities averaged 27.5 and 31.8 at transects I and II, respectively, decreasing sharply with the snow melt

from the nearby mountains in April and rain events in July and August (Fig. 8C). The mean oxygen saturation was on average 10.2% lower at transect I than transect II but varied greatly (Fig. 8D). In addition, considerable fluctuations in incident surface light intensities were found during the sampling events, the highest being in June 2013 (Fig. 8E). Relatively low values for UV radiation were found during August, September and October, whereas in June values increased to the maximum (2.07 W m^{-2} , Fig. 8F).

High variability in nutrient concentration was found over the sampling dates and transects (Fig. 9). Mean nitrate concentrations varied from 7.6 ± 1.8 to $27.4 \pm 3.4 \mu\text{M}$ in May and June at transect I and 5.5 ± 0.9 to $12.8 \pm 0.6 \mu\text{M}$ in June and March at transect II, (Fig. 9A, B). Nitrite showed relatively high concentrations in March and October at transect I ($6.3 \pm 1.0 \mu\text{M}$, Fig. 9C) and the lowest values were observed in July at transect II (2.1 ± 0.2 , Fig. 9D). Mean ammonium concentrations varied between 4.3 ± 0.8 and $33.5 \pm 2.9 \mu\text{M}$ (September, March) at transect I, with small peaks in May and July (Fig. 9E). RDP decreased steadily from May to September at transect I (8.6 and $2.3 \mu\text{M}$, respectively, Fig. 9G). In addition, the overall mean RDP concentrations were 29.8% lower at transect II (Fig. 9N). While the overall mean DSi concentrations were similar at both transects (Fig. 9O), individual mean DSi concentrations decreased until June (transect I) and August (transect II; Fig. 9I, J). The DIN: RDP molar ratios averaged $8.7 \pm 23.7 \text{ SD}$ and $7.6 \pm 15.9 \text{ SD}$ at transects I and II, respectively. The values ranged from 2.6 to 20.1, being lowest in June and highest in March (Fig. 10A, B). The DIN: DSi molar ratios ranged from 1.03 to 4.8 at transect I and 0.8 to 1.8 at transect II, respectively. In addition, DIN:DSi molar ratios averaged $1.2 \pm 0.7 \text{ SD}$ and $2.4 \pm 2.5 \text{ SD}$ at transects II and I (Fig. 10C, D).

Sediment grain size displayed no significant temporal variations ($P > 0.05$), while following a gradual pattern from medium to coarser sands at both transects (from station 1 to 3 and 4 to 5, Table 1). While stations 1, 2 and 4 were characterized by medium sands with moderate sorting, stations 3 and 5 had poorly sorted coarse sands. Porosity differences averaged 6.0%, with lowest differences between stations 1 and 2 (3.9%) and highest between stations 4 and 5 (8.4%). The mean interstitial water and organic matter contents did not vary greatly during the sampling time ($P > 0.05$). In the cluster analysis the differentiation of the dendrogram started with a $> 20\%$ similarity index (Fig. 11). Two clusters featuring distinctive sediment characteristics were distinguished as follows: the first cluster contained the seaward stations of the transect (stations 1, 2 and 4), whereas the second cluster included the landward stations (3 and 5).

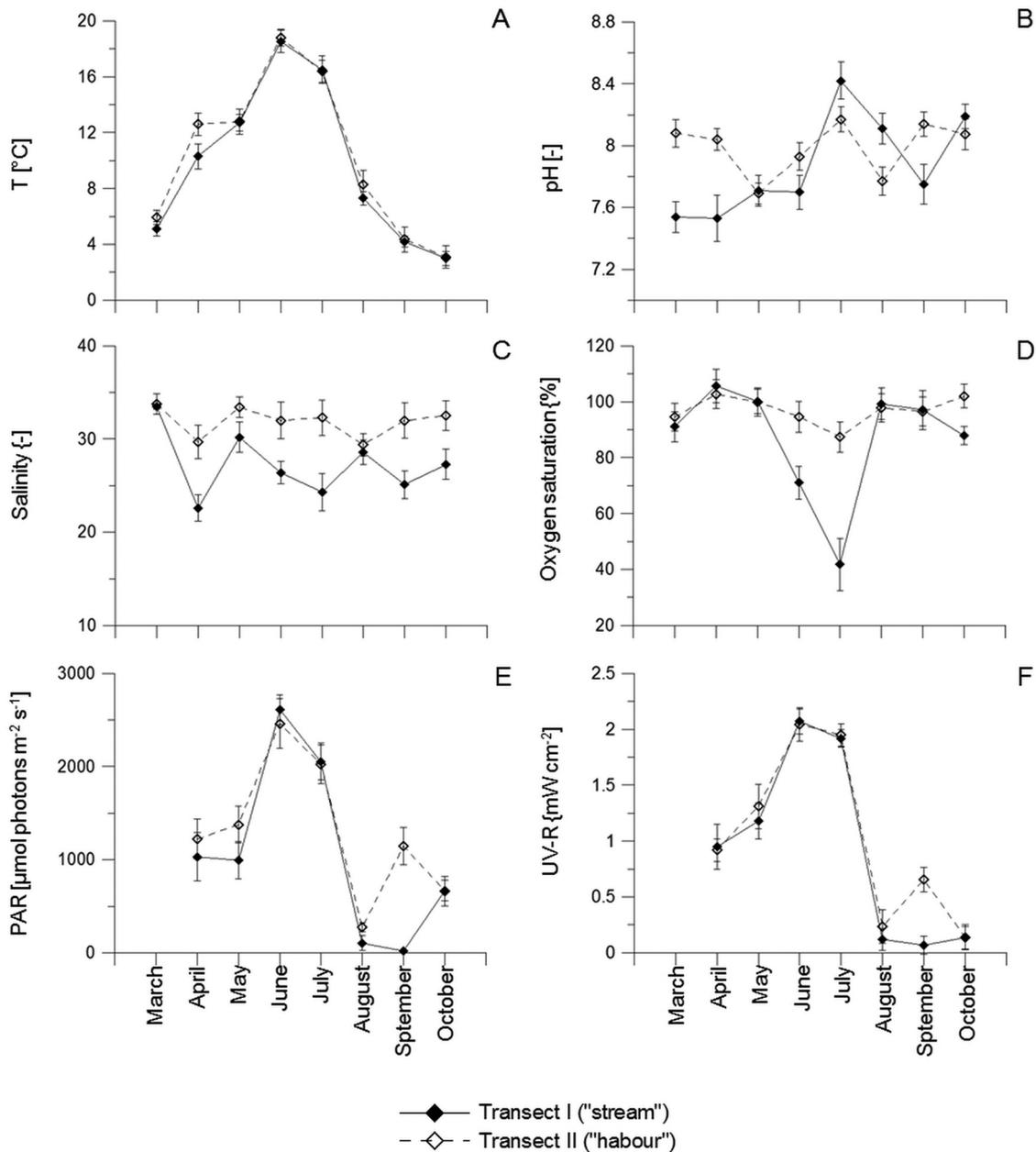


Fig. 8. Variations of *in situ* parameters in the Skagaströnd area from March to October 2013. (A) temperature, (B) pH, (C) salinity, (D) oxygen saturation, (E) photosynthetically active radiation (PAR) and (F) UV radiation. Mean values (\pm SD) for all stations are given.

Temporal and spatial variation in MPB biomass

The chl *a* and phaeopigment concentrations, which represented all the benthic microalgal biomass, varied considerably over the course of sampling events (Fig. 12A). Mean chl *a* concentration ranged from $6.4 \pm 2.2 \text{ mg chl } a \text{ m}^{-2}$ in March to $47.3 \pm 9.9 \text{ mg chl } a \text{ m}^{-2}$ in June 2013. Spatial distribution patterns for pigments showed significant temporal differences (Fig. 12B). In particular, the relative phaeopigment level was highest at station 5 in April (26.8%, Fig. 12C). Phycocyanin concentrations, which represented the overall cyanobacterial biomass, were only detectable once at transect II in August 2013 (Table 2).

Species habitats, lifestyles and occurrence

Overall, 137 species and sub-specific taxa were found in the investigated area. According to the taxonomic literature, the majority of the taxa originated from freshwater and terrestrial realms (48%), representing allochthonous species in the surface sediment samples of the investigated area. Therefore, in order to focus the following species composition analysis on the marine environment, all taxa were subdivided into two groups. The first group comprised the brackish water and marine taxa (group I: 13 and 46 taxa, respectively), but also included one ubiquitous species and 12 taxa reported to have a mixed marine and freshwater habitat description (Tables 3, 4, Figs 13A,

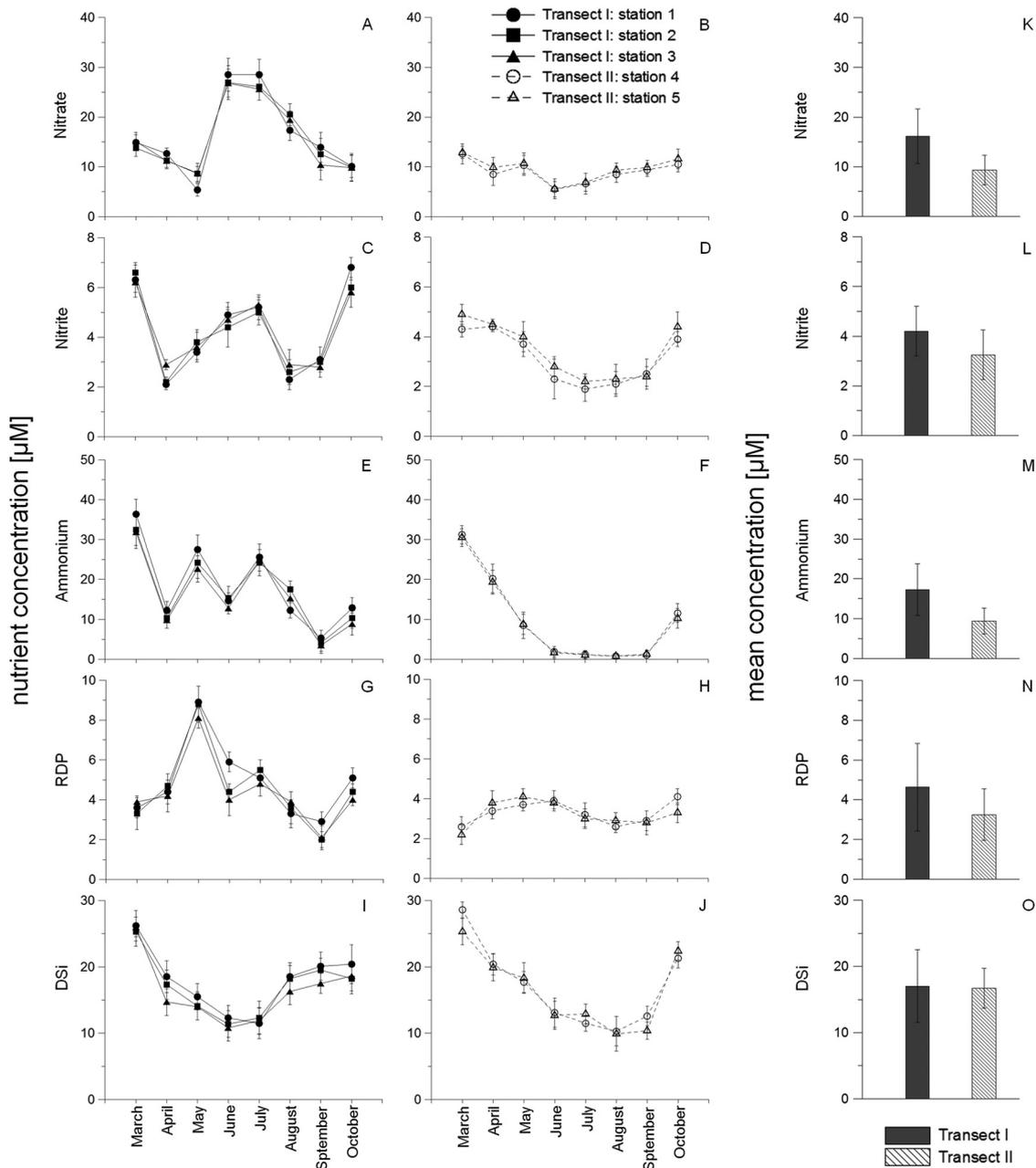


Fig. 9. Left: temporal changes of surface water nitrate (A, B), nitrite (C, D), ammonium (E, F), reactive dissolved phosphate (G, H: RDP) and dissolved silica (I, J: DSi) from March to October 2013 at the both transects, including means (\pm SD) from the triplicates. Right: absolute mean concentrations of nitrate (K), nitrite (L), ammonium (M), RDP (N) and DSi (O) in the two transects: means (\pm SD) calculated for all individual stations and sampling dates in each transect.

B; 14C, D). In contrast, the second group contained 60 freshwater taxa and three terrestrial species along with two species with a mixed habitat (freshwater/terrestrial, group II, cf. Supplementary Tables S1 & S2, Figs 13C, D; 14C, D). Due to the different counting methods used in the present study, secondary differentiation between non-diatoms (including cyanophytes, chlorophytes, charophytes, cryptophytes, dinophytes, haptophytes, ochrophytes and Xanthophyceae; 15 taxa from group I (Table 3) and 16 taxa from group II (Supplementary Table S1)) and diatoms (bacillariophytes; 57 taxa from group I (Table 4) and 49 taxa from group II (Supplementary

Table S2)) was necessary. Thus, the total abundances of all taxa on one sampling date in each individual table were set as 100% and the relative abundances were calculated.

The lowest number of marine/brackish water taxa occurred in October (33), whereas the highest number was observed in August (50; Tables 3 and 4). In contrast, the lowest number of freshwater/terrestrial taxa occurred in March (28) and the highest in June (40; Supplementary Tables S1 & S2). In total, 56 epipelagic, 52 pelagic, 19 epipsammic, six epiphytic and three species with a mixed lifestyle (pelagic/epipelagic) were identified from the taxonomic literature.

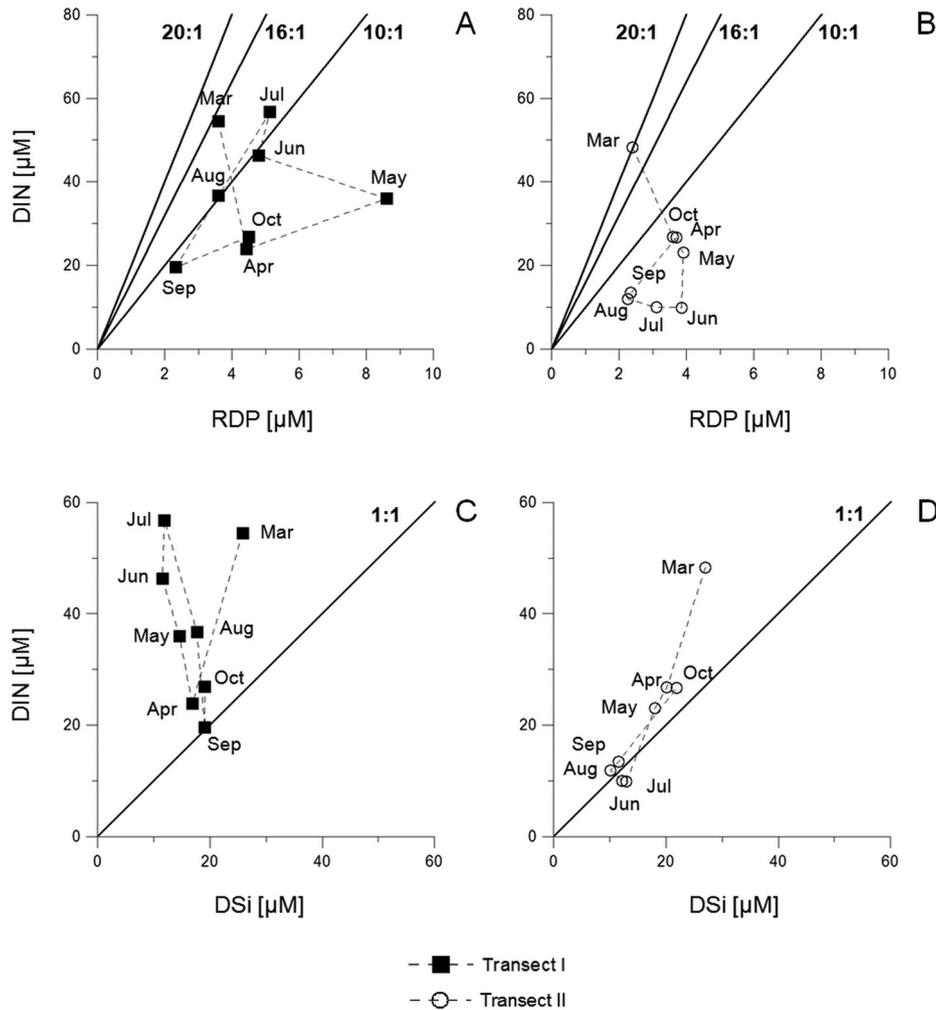


Fig. 10. Dissolved inorganic nitrogen (DIN) versus RDP (A, B) and DIN vs DSi (C, D) for the two transects during the sampling events from March to October 2013.

Table 1. Sediment characteristics (median grain size, ϕ , porosity, water and organic content) of the sampled stations of the two transects in the Skagaströnd area. Mean values for the temporal development including 1 σ standard deviations are given.

Station	Median Grain Size (μm)	ϕ	Porosity [%]	Water content [% DW]	Organic content [% DW]	Sediment colour
Transect I (stream)						
Station 1	294 \pm 11.3	1.7	38.6 \pm 3.3	19.9 \pm 5.3	0.9 \pm 0.3	medium to light grey
Station 2	400 \pm 6.5	1.3	42.5 \pm 4.1	18.2 \pm 2.6	0.8 \pm 0.5	medium grey
Station 3	518 \pm 3.4	0.9	48.3 \pm 5.9	17.3 \pm 1.4	0.5 \pm 0.1	dark grey
Transect II (harbour)						
Station 3	351 \pm 9.9	1.5	40.7 \pm 6.2	19.5 \pm 3.1	0.8 \pm 0.7	medium to dark grey
Station 4	522 \pm 8.8	0.9	49.1 \pm 7.3	18.3 \pm 2.9	0.6 \pm 0.1	black

Out of these, 31 pelagic taxa (all 15 non-diatoms as well as 16 diatom species), 28 epipelagic, 6 epipsammic and 5 epiphytic diatom taxa constituted the ‘marine’ group (group I, Tables 3, 4; pie charts in Figs 13A, B; 14C, D).

The occurrence of the taxa was highly variable over the sampling period from March to October 2013, though 51 species occurred regularly at $\geq 75\%$ (group I: 29 taxa, group II: 22 taxa; Tables 3, 4,

Supplementary Tables S1 & S2). In addition, the majority of species occurred overall $\leq 62.5\%$. In detail, 14 species occurred only once during the sampling period (group I: 8 taxa, group II: 6 taxa), 15 species twice (group I: 6 taxa, group II: 9 taxa) and 23 species three times (group I: 12 taxa, group II: 11 taxa), whereas 16 species were found on four of the eight sampling dates (groups I and II: 8 taxa each). Finally, 18 species were recorded on five out of the

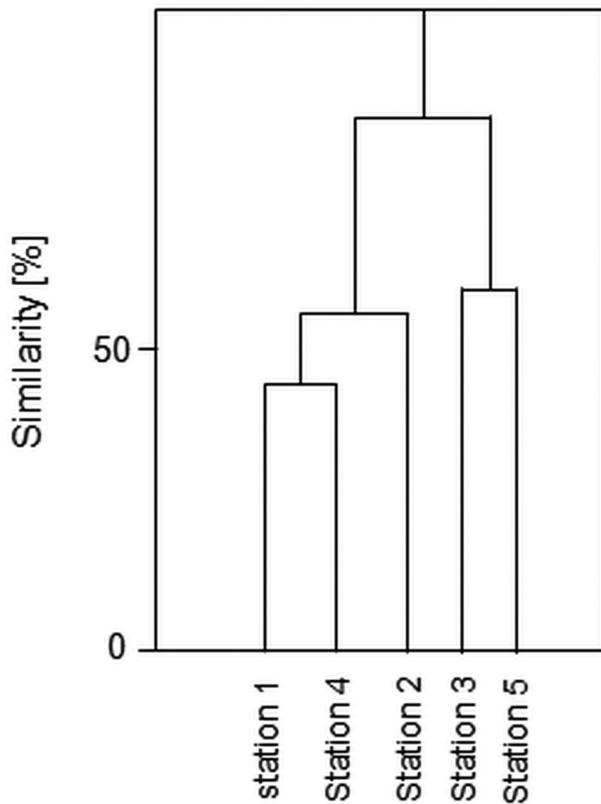


Fig. 11. Results of a cluster similarity analysis, showing the classification of individual stations on the basis of the sediment features listed in Table 1.

eight sampling dates (groups I and II: 9 taxa each). The numbers in square brackets in the following refer to the species lists in Tables 3 and 4.

Temporal and spatial variation in marine non-diatom MPB communities

The marine non-diatom group members were recorded in the sampling campaign from March to October 2013, with total abundances varying from 25.1 to $63.5 \pm 3.2 \text{ cells} \times 10^2 \text{ cm}^{-2}$ at transects I and II, respectively (= 8.1% to 15.7% of the entire marine MPB communities, Figs 13A, B and 14C, B for comparison). The lowest cell numbers were obtained in October at transect I, whereas the highest were recorded in March at transect II (1.31 and $10.1 \text{ cells} \times 10^2 \text{ cm}^{-2}$, respectively; Fig. 13A, B).

The overall abundance of the chlorophytes was 14.2 and $37.1 \pm 1.9 \text{ cells} \times 10^2 \text{ cm}^{-2}$ at transect I and transect II, respectively (Fig. 13A, B), making them the most abundant taxon of the marine non-diatom MPB communities. Chlorophytes were most abundant in March, June and July at transect II (Fig. 13B), while at transect I the highest cell numbers were recorded in June, July and August (Fig. 13A). The non-diatom MPB communities of all stations at transect I and II were mainly represented by *Stichococcus bacillaris* [2] (Prasiolales, up to 36.5% at station 3 in June), whereas *Pyramimonas cyrptofera*

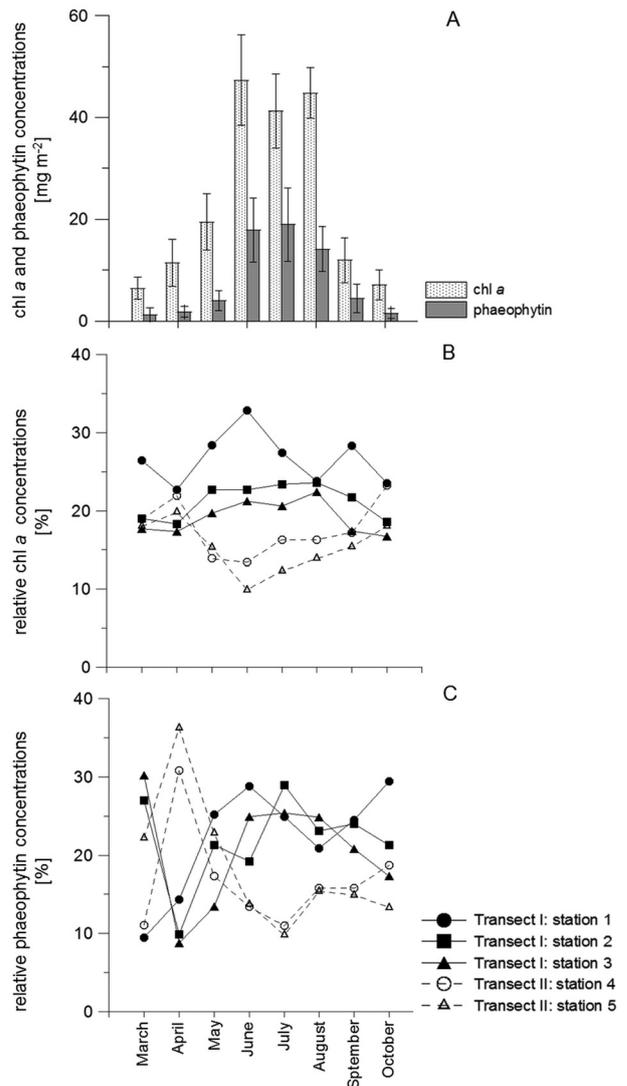


Fig. 12. Temporal (A) and spatial (B, C) variations of chlorophyll *a* and phaeophytin concentrations (mg m^{-2}) from March to October 2013 in the Skagaströnd area. The y axes in Figs B and C are adapted to the relative pigment concentrations. Mean values (\pm SD), based on data for all stations, are given in Fig. A.

Table 2. Spatial variations of phycocyanin concentrations (mg m^{-2}) at transect II in August 2013. Mean values for triplicate measurements including 1σ standard deviations are given.

Month	August
station 4	$0.06 \pm 0.02 \text{ mg m}^{-2}$
station 5	$0.3 \pm 0.05 \text{ mg m}^{-2}$

[3] was only found in lower abundance at transect II (up to 1.1% at station 4; Table 3, Fig. 15A).

The next most abundant non-diatom taxon was the dinophytes (5 species), with total abundances ranging from 3.94 to $7.9 \pm 0.8 \text{ cells} \times 10^2 \text{ cm}^{-2}$ at transect I and transect II, respectively (Fig. 13A, B). Species of Dinotrichales and Peridiniales decreased in abundance

Table 3. Relative abundances of marine and brackish water MPB species (excluding diatoms) obtained from surface sediment samples of two sides in and near Skagaströnd, north-west Iceland from March to October 2013, using Utermöhl chambers and epifluorescence microscopy.

No	Species (Author)	Live form	Location and individual station	Occurrence								Habitat
				Sampling months								
				March 2013	April 2013	Mai 2013	June 2013	July 2013	August 2013	September 2013	October 2013	
CYANOPHYTA (= CYANOBACTERIA)												
<i>Order: SYNECHOCOCCALES</i>												
1	<i>Merismopedia tenuissima</i> Lemmermann	pel.	* ^{4,5}						○		mar/fresh	
CHLOROPHYTA												
<i>Order: PRASIOLALES</i>												
2	<i>Stichococcus bacillaris</i> Nägeli	pel.	+ ^{1,2,3} * ^{4,5}	●	●	●	●	●	●	●	ubi.	
<i>Order: PYRAMIMONADALES</i>												
3	<i>Pyramimonas cyrtoptera</i> Daugbjerg	pel.	* ^{4,5}		○	○	○				mar	
CRYPTOPHYTA												
4	<i>Cryptomonas baltica</i> (G.Karsten) Butcher	pel.	* ^{4,5}	○	○		○	○			mar	
5	<i>Cryptomonas</i> Ehrenberg	pel.	+ ^{1,2,3} * ^{4,5}	○	○	○				●	mar	
6	<i>Hemiselmis amyliifera</i> Butcher	pel.	+ ^{1,2,3} * ^{4,5}			○	●	●	●	●	mar/fresh	
DINOPHYTA												
<i>Order: DINOTRICHALES</i>												
7	<i>Gymnodinium breve</i> C.C.Davis (= <i>Karenia brevis</i> (C.C.Davis) Gert Hansen & Ø.Moestrup)	pel.	+ ¹ * ^{4,5}	○	●	○	○		○	●	●	mar
8	<i>G. catenatum</i> H.W.Graham	pel.	+ ^{1,2,3} * ^{4,5}			●	○		○	○	○	mar
<i>Order: PERIDINIALES</i>												
9	<i>Peridinium pyriforme</i> subsp. <i>breve</i> (Paulsen) E. Balech	pel.	* ^{4,5}					○	○		●	mar
10	<i>Scrippsiella trochoidea</i> (Stein) Balech ex Loeblich	pel.	+ ^{1,2,3}		○	○	●	○	○	●	○	mar
<i>Order: THORACOSPHAERALES</i>												
11	<i>Glenodinium danicum</i> Paulsen	pel.	+ ^{1,2,3} * ⁴		○	●		●		○	○	mar
HAPTOPHYTA												
12	<i>Chrysochromulina</i> Lackey	pel.	+ ^{1,2,3}		○	○	○	○			○	mar
13	<i>Prymnesium parvum</i> N.Carter	pel.	+ ^{1,2,3} * ^{4,5}		○	○	○		○	○	○	brack
OCHROPHYTA												
14	<i>Chattonella marina</i> (Subrahmanyam) Hara & Chihara	pel.	+ ^{1,2,3} * ^{4,5}	●		○	○	○	●	●		mar
15	<i>Dictyocha speculum</i> Ehrenberg	pel.	+ ^{1,2,3} * ^{4,5}	●	●	○	○	○		○	○	mar

Relative abundances: ○ 0.1–5%, ○ 5–10%, ● 10–15%, ● 15–20%, ● 20–30%.

+ 1, 2, 3 = stations in the near of the stream (transect I), *4, 5 = stations in the harbour (transect II).

Abbreviations: pel.: pelagic, ubi.: ubiquitous, mar: marine, brack: brackish water.

Table 4. Benthic marine diatom community compositions obtained from permanent slides prepared according to the method by Schrader (1976) from two sides in and near Skagaströnd, north-west Iceland from March to October 2013.

No	Species (Author)	Ref.	Life form	Location and individual station	Occurrence								Habitat
					Sampling months								
					March 2013	April 2013	Mai 2013	June 2013	July 2013	August 2013	September 2013	October 2013	
Class: COSCINODISCOPHYCEAE													
1	<i>Actinocyclus curvatus</i> Janisch	3	pel.	* ^{4,5}					○	○	○	mar	
2	<i>Paralia sulcata</i> (Ehrenberg) Cleve	20, (9)	epp.	+ ^{1,2,3} * ^{4,5}					○	○	○	○	mar
Class: MEDIOPHYCEAE													
3	<i>Isthmia nervosa</i> Kützing	9	pel.	+ ^{1,2}	○	○	○					mar	
4	<i>Triceratium arcticum</i> Brightwell (= <i>Trigonium arcticum</i> (Brightwell) Cleve)	4	pel.	* ⁵					○	○		mar	
Class: BACILLARIOPHYCEAE													
Order: ACHNANTHALES													
5	<i>Achnanthes borealis</i> A. Cleve	1	pel.	+ ^{1,2} * ⁵	●	○	●	●		○	○	mar	
6	<i>A. cf. brevipes</i> var. <i>parvula</i> (Kützing) Cleve	1	eps.	+ ²		○	○	○				mar	
7	<i>A. pseudogroenlandica</i> Hendey	13	eps.	+ ^{1,2}	○	●	○					mar	
8	<i>Cocconeis costata</i> Gregory	4	pel./ epp.	+ ^{1,2} * ⁵	●	●	●	●	●	●	○	mar	
9	<i>C. fasciolata</i> (Ehrenberg) Brown	13	epp.	+ ^{1,2,3}	○	●	○	○		○		mar	
10	<i>C. molesta</i> var. <i>crucifera</i> Grunow	4	epp.	* ^{4,5}	○	●					○	mar	
11	<i>C. neothumensis</i> var. <i>marina</i> De Stefano, Marino et Mazzella	15	pel	+ ^{1,2}	○	○	○		○	○	○	mar	
12	<i>C. placentula</i> Ehrenberg	6	eph.	* ^{4,5}	○		○	○		○	○	mar	
13	<i>C. scutellum</i> Ehrenberg var. <i>scutellum</i>	8,16	eph.	+ ^{1,2,3} * ^{4,5}	●	●		○	●	●	●	○	mar
14	<i>C. stauroneiformis</i> (Rabenhorst) Okuno	15	eps.	* ⁵	○	○	○	○		○	○	mar	
Order: BACILLARIALES													
15	<i>Cylindrotheca closterium</i> (Ehrenberg) Lewin et Reimann = <i>Ceratoneis closterium</i> Ehrenberg	3, 13	pel/ epp.	+ ^{1,2,3} * ^{4,5}		○	●	●	●	○	○	mar	
16	<i>Denticula neritica</i> Holmes et Croll	14	pel	* ⁴	○	○						mar	
17	<i>Nitzschia distans</i> W. Gregory	7	epp.	+ ¹					○	○	○	○	brack
Order: CYMBELLALES													
18	<i>Gomphoseptatum aestuarii</i> (Cleve) Medlin	1	pel.	+ ^{1,2,3} * ^{4,5}	○	○	○	○	○	○	○	○	mar
19	<i>Rhoicosphenia marina</i> (W. Smith) M. Schmidt	15	pel.	* ^{4,5}	○	○	○	○	○	○	○	○	mar

(continued)

Table 4. Continued.

No	Species (Author)	Ref.	Life form	Location and individual station	Occurrence								Habitat
					Sampling months								
					March 2013	April 2013	Mai 2013	June 2013	July 2013	August 2013	September 2013	October 2013	
<i>Order: FRAGILARIALES</i>													
20	<i>Fragilaria striatula</i> Lyngbye	15	eps.	* ^{4,5}						○		mar	
21	<i>Synedra commutata</i> Grunow	13	pel.	* ⁴	○		○	○			○	mar	
22	<i>Tabularia waernii</i> Snoeijs	17	pel.	+ ^{1,2} * ⁵		○	○	○	○	○		mar	
<i>Order LICMOPHORALES</i>													
23	<i>Licmophora gracilis</i> (Ehrenberg) Grunow Grunow (= <i>Podosphenia gracilis</i> Ehrenberg)	(4)	eps.	+ ¹						○		mar	
<i>Order: NAVICULALES</i>													
24	<i>Amphiptera rutilans</i> (Trentepohl ex Roth) Cleve = <i>Berkeleya rutilans</i> (Trentepohl ex Roth) Grunow	9	epp.	* ^{4,5}			○	○	○	○		brack	
25	<i>Biremis ambigua</i> (Cleve) D.G. Mann	14	epp.	* ^{4,5}						○	○	mar	
26	<i>Craticula halophila</i> (Grunow) D.G. Mann (= <i>Navicula halophila</i> var. <i>subcapitata</i> Østrup)	14	epp.	+ ^{1,2,3}				○	○	○	●	mar/ fresh	
27	<i>Diploneis didyma</i> (Ehrenberg) Ehrenberg	1, 7	epp.	+ ^{1,2} * ⁴	○		○	○	●	●	●	●	mar/ fresh
28	<i>D. elliptica</i> (Kützing) Cleve	1, 15	epp.	+ ^{1,2,3} * ^{4,5}		○	○			○	○	○	mar/ fresh
29	<i>D. ovalis</i> (Hilse) Cleve	2, 15	epp.	+ ^{1,2} * ⁴	○	●	○	●		●	○	○	mar/ fresh
30	<i>Gyrosigma fasciola</i> (Ehrenberg) Griffith et Henfrey	4	pel.	+ ^{1,2,3}					○	●	○	brack	
31	<i>G. tenuissimum</i> (W. Smith) Griffith et Henfrey	15	pel.	* ^{4,5}				○	○	●		mar	
32	<i>Navicula cancellata</i> Donkin	15	epp.	+ ^{1,2,3}	○	○	○	○	○		○	○	brack
33	<i>N. cincta</i> (Ehrenberg) Ralfs	6, 13	epp.	* ⁴				○	●	●	●	○	brack
34	<i>N. cincta</i> (Ehrenberg) var. <i>heufleri</i> Grunow (= <i>Navicula heufleri</i> Grunow)	15	epp.	+ ^{1,2,3}	○	○	○	●	●	○	○	brack	
35	<i>N. clementis</i> Grunow	15	epp.	+ ^{1,2}							○	mar/ fresh	
36	<i>N. cryptocephala</i> Kützing	9, 20	epp.	* ⁴	○		○	●	●	●	●	○	mar/ fresh
37	<i>N. dicephala</i> Ehrenberg	15	epp.	* ^{4,5}							○	mar	
38	<i>N. digito-radiata</i> (Gregory) A. Schmidt var. <i>elliptica</i> (Østrup) M. Moeller	7, 20	epp.	+ ^{1,2,3} * ^{4,5}	●	●	●	●	●	●	●	●	brack
39	<i>N. directa</i> (W. Smith) Ralfs	15	epp.	+ ^{1,2,3}						○		mar	
40	<i>N. hamiltonii</i> Witkowski, Lange-Bertalot et Metzeltin	22	epp.	* ^{4,5}	●	○	○	●	●	●		brack	

(continued)

Table 4. Continued.

No	Species (Author)	Ref.	Life form	Location and individual station	Occurrence								Habitat
					Sampling months								
					March 2013	April 2013	Mai 2013	June 2013	July 2013	August 2013	September 2013	October 2013	
41	<i>N. perminuta</i> Grunow	16	eps.	+ ^{1,2} * ⁴	●	●	●	●	●	●			mar
42	<i>N. pusilla</i> W.Smith (= <i>Cosmioneis pusilla</i> (W.Smith) D.G.Mann & A.J.Stickle)	15	epp.	* ⁴			○	○	●	○	○		mar/fresh
43	<i>N. rhynchocephala</i> Kützing	9	epp.	* ⁴		○	○	○					mar/fresh
44	<i>N. spicula</i> (Dickie) Cleve (= <i>Haslea spicula</i> (Hickie) Lange-Bertalot)	1	epp.	* ⁵						○			mar/fresh
45	<i>Pinnularia gibba</i> Ehrenberg	15	epp.	+ ^{1,2,3} * ^{4,5}	○	○	○	○	○	○	○		brack
46	<i>Pleurosigma elongatum</i> W.Smith	6	epp.	* ^{4,5}	○	○	○	●	●	●	○	○	brack
47	<i>P. kamschaticum</i> (Grunow) Medlin	23	eph.	+ ^{1,2}						○	○		mar
48	<i>Trachyneis aspera</i> (Ehrenberg) Cleve	2	pel.	* ⁴						○	○	○	mar
Order RHABDONEMATALES													
49	<i>Rhabdonema arcuatum</i> (Lyngbye) Kützing	9, 10	eph.	* ^{4,5}						○			mar
Order STRIATELLALES													
50	<i>Grammatophora oceanica</i> var. <i>macilenta</i> (W. Smith) Grunow	8	pel.	* ^{4,5}	○	○		○	○	○	○		mar
51	<i>Hyalosira delicatula</i> Kützing (= <i>Microtabella delicatula</i> (Kützing) Round)	9	pel.	+ ^{1,2}		○	○		○	○	○		mar
Order: SURIRELLALES													
52	<i>Entomoneis gigantea</i> Grunow	15	pel.	* ^{4,5}						○	○	○	mar
53	<i>E. paludosa</i> (W. Smith) Reimer	15	epp.	+ ^{1,2} * ⁴						○	○		mar/fresh
Order: THALASSIOPHYSALES													
54	<i>Amphora abludens</i> Simonsen	15	pel.	* ⁵	○	●		○	○	○	●	○	mar
55	<i>A. acutiuscula</i> Kützing (= <i>Halamphora acutiuscula</i> (Kützing) Levkov)	9	epp.	+ ^{1,2,3} * ⁴	●	○	○	○			○	○	brack
56	<i>A. coffeaeformis</i> (C. Agardh) Kützing	19	epp.	+ ^{1,2,3} * ^{4,5}						○	●	○	brack
57	<i>A. laevis</i> var. <i>laevissima</i> (Gregory) Cleve	1, 15	epp.	* ^{4,5}						○	○		mar

Relative diatom abundances: ○ 0.1–5%, ○ 5–10%, ● 10–15 %, ● 15–20%, ● 20–25%, ● 25–30%.

+ 1, 2, 3 = stations in the near of the stream (transect I), *4, 5 = stations in the harbour (transect II).

Abbreviations: epp.: epipelagic, eps.: epipsammic, eph.: epiphytic, epl.: epilithic, pel.: pelagic, mar: marine, brack: brackish water.

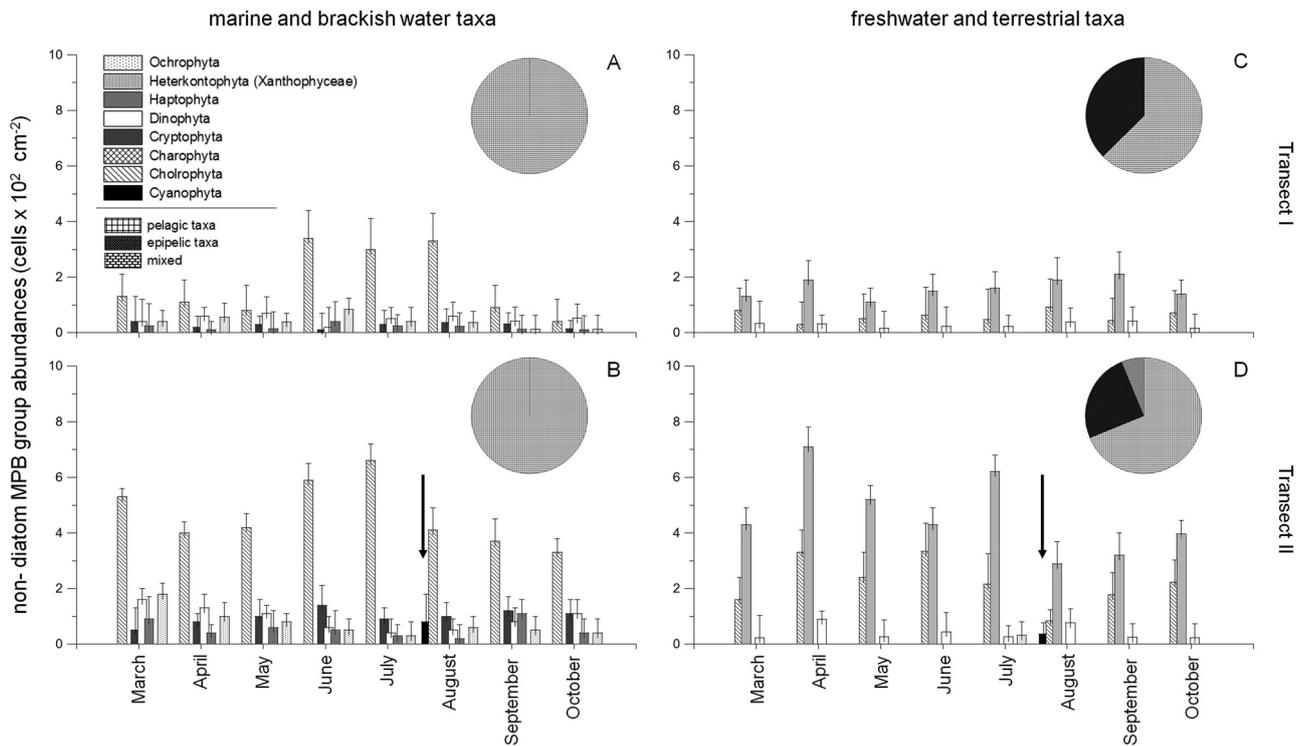


Fig. 13. Temporal and spatial variations of the non-diatom abundances (cells $\times 10^2 \text{ cm}^{-2}$, chloro-, crypto-, ochro-, hapto- and dinophytes) in the Skagaströnd area at transect I and II from March to October 2013, including means (\pm SD) of the individual stations. Displayed are marine and brackish water (A, B) as well as freshwater and terrestrial taxa (C, D). Besides absolute abundances, the percentage values of the live forms such as epipellic, epipsammic and pelagic are displayed in pie charts. For the individual species compositions see Table 3 and Supplementary Table S1.

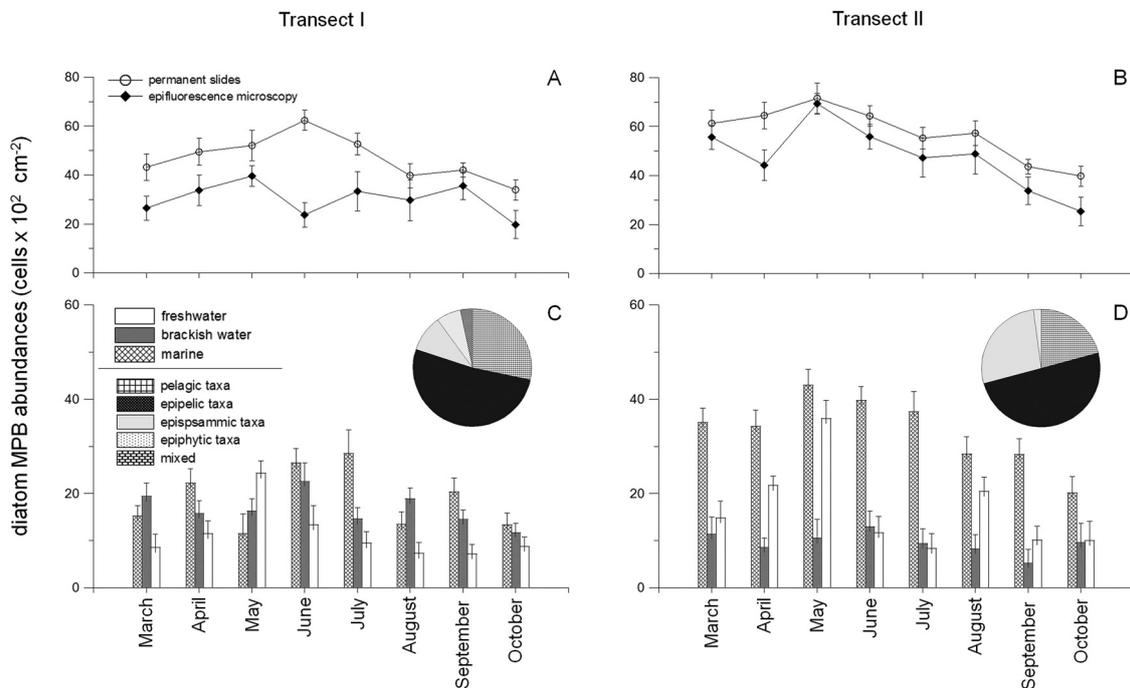


Fig. 14. Temporal and spatial variations of the diatom abundances (cells $\times 10^4 \text{ cm}^{-2}$) in the Skagaströnd area at transect I and II from March to October 2013, including means (\pm SD) of the individual stations. Displayed are results of the overview counts using epifluorescence in comparison to data obtained by analysis of the permanent slides (A, B) and the differentiation in marine, brackish water and freshwater taxa using the latter method (C, D). Besides absolute abundances, the percentage values of the live forms such as epipellic, epipsammic and pelagic are displayed in pie charts. For the individual species compositions see Table 4 and Supplementary Table S2.

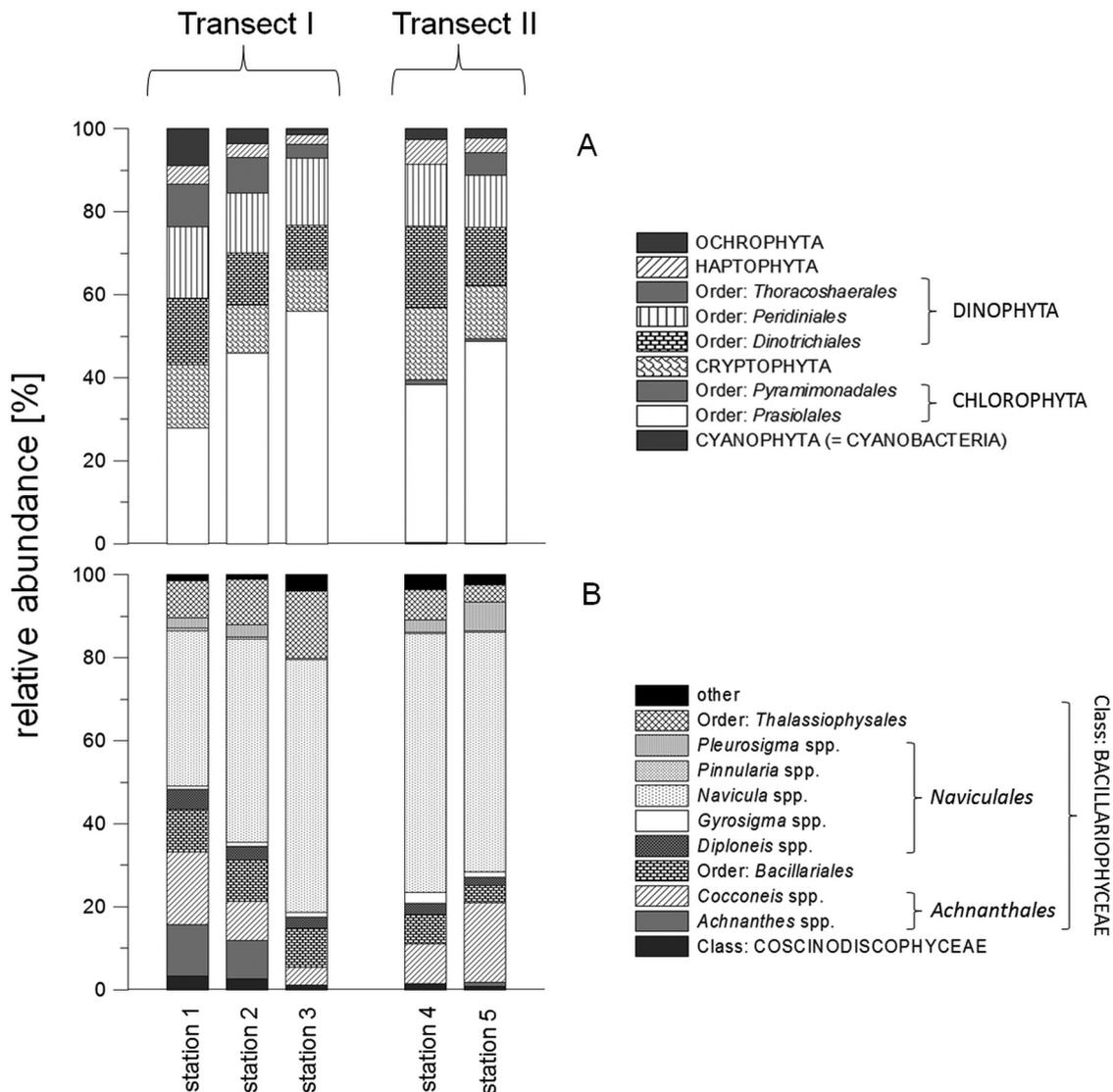


Fig. 15. Spatial composition of MPB assemblages in the Skagaströnd area at transect I (stations 1, 2 and 3) and transect II (stations 4, 5), showing the non-diatom MPB community compositions (A, Cyanophyta, Chlorophyta, Cryptophyta, Dinophyta, Haptophyta and Ochrophyta) and diatoms (B, class: Coscinodiscophyceae, genera: Achnanthes, Bacillariales, Naviculales and Thalassiophysales).

from stations 1 to station 3 and from stations 4 to 5, being the highest at station 1 with 15.9 and 17.3% of the entire non-diatom community, respectively (Fig. 15A). In particular, the dinophyte *Scrippsiella trochoidea* [10] (Peridinales) contributed in higher abundances to the MPB community at station 1 and 2 (up to 17.9% in June), but was not present at transect II (Fig. 15A, Table 3). In contrast, the dinophytes *Peridinium pyriforme* [9] (Peridinales) and *Gymnodinium breve* Davis [7] (Dinotrichales) were most abundant at station 4 (up to 18.3 and 22.6% of the entire non-diatom community in October and September, respectively; Table 3). *Gymnodinium catenatum* Graham [8] (Dinotrichales) was most abundant at station 3 in May (16.5%), and *Glenodinium danicum* [11] (Thoracosphaerales) at stations 1 and 2 in May and July (Table 3).

The third most abundant taxa were the cryptophytes (3 species, total abundances: 2.1 and 7.6 ± 0.3 cells \times

10^2 cm⁻² at transects I and II, respectively; Figs 13A, B; 15A; Table 3). Generally, species such as *Cryptomonas* spp. [5] and *Hemiselmis amyliifera* [6] were recorded at both transects, while *Cryptomonas baltica* [4] were only found at transect II. *Hemiselmis amyliifera* [6] was most abundant at transect II, showing the highest abundances at station 5 from June to September (21.6% in July; Table 3).

The ochrophytes, represented by two species (*Chattonella marina* [14] and *Dictyocha speculum* [15]), were the fourth most abundant non-diatom MPB taxon (total abundances: 3.2 and 5.9 ± 0.5 cells $\times 10^2$ cm⁻² at transect I and transect II, respectively; Fig. 13A, Table 3). *Chattonella marina* [14] was most abundant at transect I in March, while *D. speculum* [15] showed the highest abundances at transect II in April (Table 3). Two species of haptophyte were recorded, with total abundances ranging from 1.61 to 5.4 ± 0.4 cells $\times 10^2$ cm⁻² at transect I and transect II, respectively (Fig. 13A). The

highest abundances, at transect I in June and July, were made up by *Chrysochromulina* spp. [12] and *Prymnesium parvum* [13] (2.5% and 5.3%, respectively). In this context, the lack of *Chrysochromulina* at transect II was noteworthy.

In addition, a small number of cyanophytes were also documented in August at transect II, correlated with the phycocyanin measurements presented above (Tables 2 and 3). Their maximum relative abundance accounted only for 0.1%, placing this taxon in the marginal group of the MPB communities in the investigated area (Figs 13A, 15A).

Temporal and spatial variation in marine diatom MPB communities

The analysis of overall abundances showed a clear dominance of bacillariophytes (diatoms) at transect I and II from March to October 2013 (Fig. 13A, B in comparison to Fig. 14A, B). It must be noted that the diatom cell numbers obtained by different counting/preparation methods (permanent slides vs *in situ* counts using epifluorescence) showed considerable differences between both transects as well as individual sampling dates, being highest at transect I in June (61.9%, Fig. 14A) and transect II in April (36.3%, Fig. 14B). These differences were mainly related to the occurrence of allochthonous freshwater taxa. However, subtracting the number of freshwater taxa obtained by permanent slide counts from the cell numbers achieved by the live counts using epifluorescence did not always account for the difference (diff. up to 9.3%). Although these differences were present, all further analysis of the diatom communities were conducted on data obtained by permanent slide counts in order to distinguish between marine, brackish water and freshwater taxa (Figs 14C, D, 15B, Table 4). Only group I diatoms (marine and brackish water species) were used for the following analysis (Table 4).

With the exception of lower abundances in May at transect I, the MPB showed a dominance of marine bacillariophytes at both transects over all sampled months (transect I: 48.8% and transect II: 65.6% of the entire MPB community of group I; Figs 13A, B and 14C, D for comparison). The highest cell numbers were recorded in May at transect II (43.2 ± 5.2 cells $\times 10^2$ cm⁻², Fig. 14B), whereas at transect I cell numbers were up to 73.2% lower in the same month (Fig. 14A). In addition, brackish water bacillariophytes contributed considerable cell numbers to the entire MPB communities of both transects, varying from 18.7% to 43.1% at transect II and I, respectively (Figs 14C, D).

The diatom MPB communities at both transects were dominated by representatives of the order Naviculales (24 taxa, total abundances from March to October: 138.6 ± 4.9 and 211.2 ± 5.1 cells $\times 10^2$ cm⁻² at transect I and II, respectively). Representatives of the Naviculaceae (13 taxa; Table 4, Fig. 15B), in particular,

Navicula digitoradiata var. *elliptica* [38] were the most abundant taxa at all stations, except in June, July and August 2013. In June, July and August *N. cryptocephala* [36], *N. perminuta* [41] and *N. hamiltonii* [40] contributed in higher abundances to the MPB diatom communities (Table 4). As accompanying taxa, *Diploneis* spp., *Gyrosigma* spp., *Pinnularia* spp. and *Pleurosigma* spp. were recorded, showing strong temporal and also distinct spatial variation. For example, species such as *Diploneis didyma* [27] and *D. ovalis* [29] were only recorded at stations 1, 2 and 4, whereas *Pleurosigma elongatum* [46] was detected in higher relative abundances at transect II with an increase from station 4 to 5 (diff. 3.8%) and only in minor relative abundances at stations 1 and 2 (1.6–2%; Table 4).

The second most abundant order in the marine MPB diatom communities was the Achnanthes (10 species; Table 4). Their total abundances varied from 59.5 and 75.1 ± 4.5 cells $\times 10^2$ cm⁻² at transect II and transect I, respectively. The genera *Cocconeis* and *Achnanthes* (both Achnanthes) were recorded in higher abundances at transect I (up to 12.3% and 17.6%, respectively; Fig. 15B) and showed, as found for most of the non-diatom taxa, a decline in relative abundance from station 1 to station 3. *Cocconeis* spp. consisted of up to 19.3% of the entire diatom community at station 5 (transect II), while *Achnanthes* spp. were only found in traces (0.9%, *Achnanthes borealis* [5]). Species such as *Cocconeis costata* [8] and *Cocconeis scutellum* var. *scutellum* [13] were most abundant at stations 1, 2, 4 and 5 (up to 16.1%; Table 4).

The order Thalassiophysales was recorded as the third most abundant diatom taxon and was represented by four species of the genus *Amphora*. The total abundances varied from 21.9 to 33.4 ± 3.7 cells $\times 10^2$ cm⁻² at transect II and transect I, respectively. The highest proportions were found at transect I (station 3, up to 16.3%; Fig. 10B) and were made up of species such as *Amphora coffeaeformis* [56] and *A. acutiuscula* [55] (Table 4).

The Bacillariales represented the fourth most abundant taxon and included three species; their total abundances ranged from 18.5 to 25.1 ± 2.2 cells $\times 10^2$ cm⁻² at transect II and transect I, respectively. The species *Cylindrotheca closterium* [15], *Denticula neritica* [16] and *Nitzschia distans* [17] contributed to the marine MPB and had distinct differences in their spatial and temporal occurrence. For example, *C. closterium* [15] was very abundant and found at all stations of both transects from April to September (up to 11.3% of the entire diatom communities), whereas *D. neritica* [16] was only detected at station 4 in March and April (0.2–1.1%) and *N. distans* [17] at station 1 from July to October (0.1–1.6%, Table 4).

The Coscinodiscophyceae (2 species) were recorded from July to October (total abundances from March to October: 10.6 to 13.1 ± 1.7 cells \times

10^2 cm^{-2} at transects II and transect I, respectively). *Paralia sulcata* [2] occurred at both transects (up to 6.2% at station 1 in August), whereas *Actinocyclus curvatus* [1] was only found at transect II (Table 4).

The Mediophyceae (2 species), and the orders Cymbellales (2 species), Fragilariales (3 species), Licmophorales (1 species), Rhaphoneidales (1 species), Striatellales (2 species) and Surirellales (2 species) had notably lower total abundances than the five groups already mentioned and can be regarded as marginal groups of the MPB diatom communities of the Skagaströnd area (0.15–2.4%; Table 4, Fig. 15B).

Relationships between environmental parameters and marine MPB species compositions

The canonical correspondence analyses (CCA) of the MPB community composition at transects I and II suggested that several environmental variables were closely correlated with species abundances (Fig. 16). The first two CCA axes explained 70.4 and 76.6% of the variance at transects II and I, respectively. The first CCA axis was positively correlated with dissolved nitrogen (DIN), followed by dissolved phosphate (RDP), temperature of the surface sediment and PAR at transect I (Fig. 16A). In addition, the first CCA axis was negatively associated with salinity, DSi and water and organic matter content of the surface sediments. Temperature, DIN and salinity accounted for 11% of the overall variance among the environmental variables at transect I. At transect II, the first axis was primarily associated with temperature, PAR, dissolved nitrogen (DIN) and the water content of the sediments (Fig. 16D). Furthermore, axis 2 was dominated by the median grain size at both transects (Fig. 16A, D). In general, both CCAs displayed high species/environment Pearson correlations ($r = 0.91$ – 0.93 and $r = 0.95$ – 0.98 at transects I and II for axes 1 and 2, respectively) and approximately 11–19% of the variation in the species matrix was explained by the environmental matrix. Qualitative indication of the environmental optima of selected MPB species is given by their positions relative to the first two canonical axes. In general, the species positioned towards the centre of the diagram, e.g. *Gymnodinium breve* ([7], Table 3, Fig. 16B, E), *Gymnodinium catenatum* ([8], Table 3, Fig. 16B), and *Craticula halophila* ([26], Table 4, Fig. 16C) and *Amphipleura rutilans* ([24], Table 4, Fig. 16E), are either unrelated to the environmental axes or find their optimum there. In contrast, the species arranged towards the borders of the plot, e.g. *Chrysochromulina* ([12], Table 3, Fig. 16F), *Achnanthes pseudogroenlandica* ([7], Table 4, Fig. 16C) and *Cocconeis scutellum* ([13] Table 4, Fig. 16F), showed specializations regarding certain nutrient parameters.

For example, a cluster of non-diatom species including, amongst others, *Scrippsiella trochoidea* [10], *Stichococcus bacillaris* [2], *Glenodinium*

danicum [11] and *Gymnodinium breve* [7] as well as the diatom species *Hyalosira delicatula* [51], *Cocconeis neothumensis* [11], *Paralia sulcata* [2] and *Gomphoseptatum aestuarii* [18], was abundant at high sediment surface temperatures and correlated also with high DIN, RDP and PAR at transect I (Fig. 16B, C; cf. Tables 3 and 4). Another group, containing e.g. *Gymnodinium catenatum* [8], *G. breve* [7], *Glenodinium danicum* [11], *Cocconeis molesta* [10], *C. placentula* [12], *Diploneis elliptica* [28] and *Pleurosigma elongatum* [46], was abundant at high nutrient concentrations in association with lower sediment water content, temperature and irradiance at transect II (Fig. 16E, F; cf. Tables 3 and 4).

DISCUSSION

Methodological aspects and critical remarks

Before discussing the results of the present study, it is necessary to justify some aspects of the methods chosen. Several of the diatom cells were dead and only empty valves were observed during counting in the Utermöhl chambers. This phenomenon was not species-specific. Woelfel *et al.* (2009) made similar observations in their study of the benthic diatom composition in the Arctic Kongsfjorden, Svalbard, but without providing further details. In the present study, comparative counts using epifluorescence were conducted, but the total diatom abundances obtained by the different methods differed considerably. However, the preparation technique used for the determination of diatoms to species level does not distinguish live from dead cells. The area chosen in the present study seemed to be primarily a depositional one, where many dying cells are deposited and accumulate. This applies to transect II, as it was in the sheltered harbour, while it seems to be unlikely for transect I as it faces the open ocean. In addition, more faecal strings of *Arenicola marina* were observed at transect II, whereas at transect I only traces of this species were found. According to Andresen & Kristensen (2002) the carbon budget of this deposit-feeding polychaete, based on rate measures and conversion factors from the literature, shows that bacteria only covered 3–7% of the requirement, while microalgae contributed 42–370%. Thus, the high numbers of empty valves may be explained by the abundance of *Arenicola*, although the samples were not taken in close vicinity of the strings, but tidal currents might have distributed some of the digested cells.

Furthermore, a large number of the taxa found in the present investigation originated from freshwater and terrestrial habitats (48% of the overall 137 taxa, cf. Supplementary Tables S1 and S2) and were also described in an earlier characterization of Icelandic freshwater habitats by Østrub (1918). Thus, a clear differentiation between freshwater and terrestrial taxa

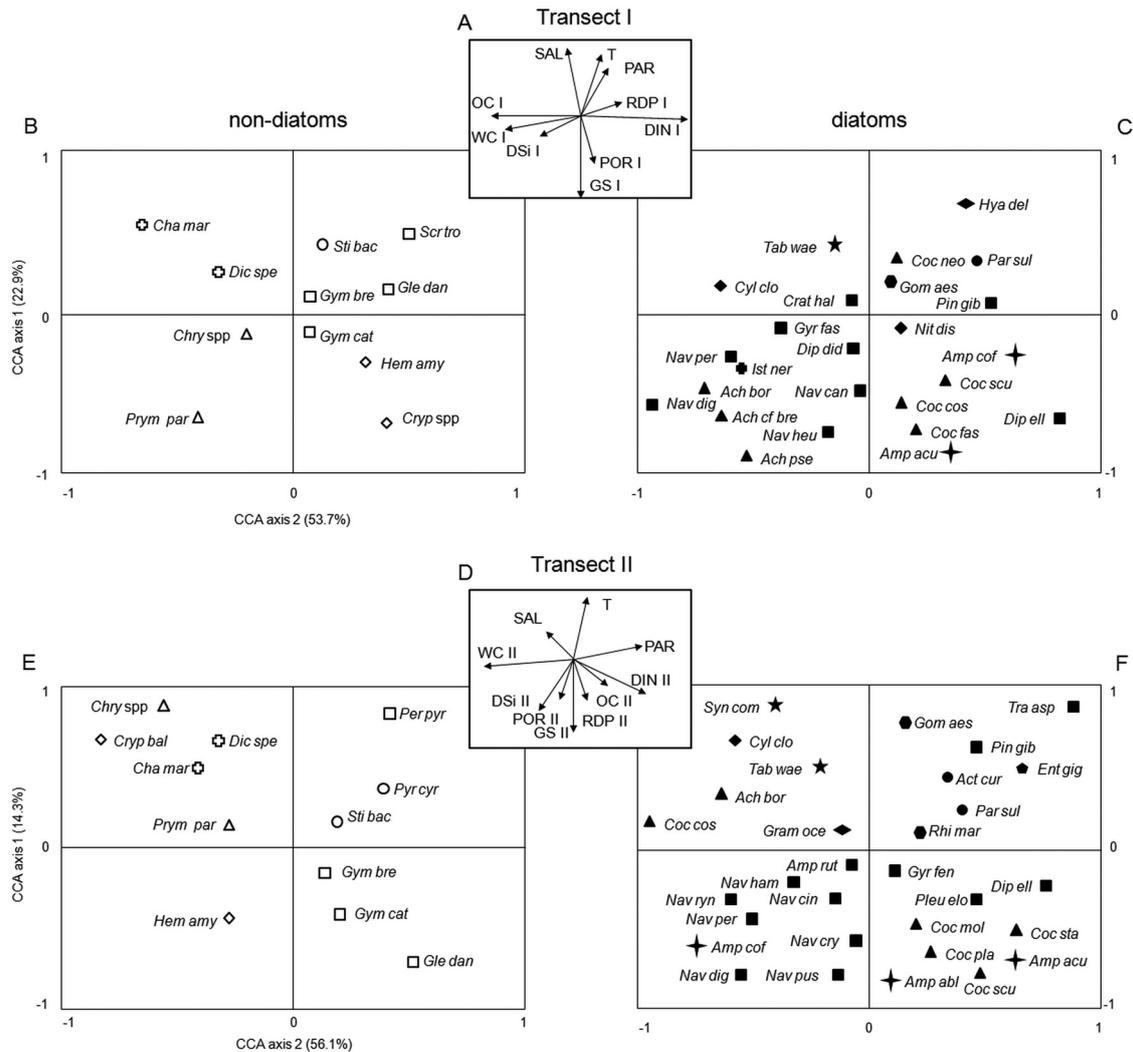


Fig. 16. CCA of 10 environmental variables and 58 MPB species (cf. Tables 3 and 4) for transect I (A, B, C) and II (D, E, F). Legend: non-diatoms (○ Chlorophyta, ◇ Cryptophyta, □ Dinophyta, △ Haptophyta, ⊕ Ochrophyta); diatoms (▲ Achnanthes, ◆ Bacillariales, ● Coscinodiscophyceae, ● Cymbellales, ★ Fragilariiales, ■ Mediophyceae, ■ Naviculales, ◆ Striatellales, ● Surirellales, + Thalassiophysales). Abbreviations: DIN: dissolved inorganic nitrogen, DSI: dissolved silica, GS: median grain size, OC: organic content, PAR: photosynthetic active radiation, POR: sediment porosity, RDP: reactive dissolved phosphate, SAL: salinity, T: sediment surface temperature WC: water content. Species abbreviations: *Ach bor*: *Achnanthes borealis* A. cf. *brevipes*, *Ach pse*: *Achnanthes pseudogroenlandica*, *Act cur*: *Actinocyclus curvatulus*, *Amp rut*: *Amphipleura rutilans*, *Amp abl*: *Amphora abludens*, *Amp acu*: *Amphora acutiuscula*, *Amp cof*: *Amphora coffeaeformis*, *Cha mar*: *Chattonella marina*, *Coc cos*: *Cocconeis costata*, *Coc fas*: *Cocconeis fasciolata*, *Coc mol*: *Cocconeis molesta*, *Coc neo*: *Cocconeis neothumensis*, *Coc pla*: *Cocconeis placentula*, *Coc scu*: *Cocconeis scutellum*, *Coc sta*: *Cocconeis stauroneiformis*, *Cra hal*: *Craticula halophila*, *Cry spp.*: *Cryptomonas* spp., *Cry bal*: *Cryptomonas baltica*, *Chr spp.*: *Chrysochromulina* spp., *Cyl clo*: *Cylindrotheca closterium*, *Dic spe*: *Dictyocha speculum*, *Dip did*: *Diploneis didyma*, *Dip ell*: *Diploneis elliptica*, *Dip ova*: *Diploneis ovalis*, *Ent gig*: *Entomoneis gigantea*, *Gle dan*: *Glenodinium danicum*, *Gom aes*: *Gomphoseptatum aestuarii*, *Gra oce*: *Grammatophora oceanica*, *Gym bre*: *Gymnodinium breve*, *Gym cat*: *Gymnodinium catenatum*, *Gyr fas*: *Gyrosigma fasciola*, *Gyr ten*: *Gyrosigma tenuissimum*, *Hel amy*: *Hemiselmis amyliifera*, *Hya del*: *Hyalosira delicatula*, *Ist ner*: *Isthmia nervosa*, *Nav can*: *Navicula cancellata*, *Nav cin*: *Navicula cincta* var. *heufferi*, *Nav cry*: *Navicula cryptocephala*, *Nav dig*: *Navicula digitoradiata* var. *elliptica*, *Nav ham*: *Navicula hamiltonii*, *Nav per*: *Navicula perminuta*, *Nav pus*: *Navicula pusilla*, *Nav rhy*: *Navicula rhynchocephala*, *Nit dis*: *Nitzschia distans*, *Par sul*: *Paralia sulcata*, *Per pyr*: *Peridinium pyriforme*, *Pin gib*: *Pinnularia pusilla*, *Ple elo*: *Pleurosigma elongatum*, *Pry par*: *Prymnesium parvum*, *Pyr pyr*: *Pyramimonas cyrtoptera*, *Rho mar*: *Rhoicosphenia marina*, *Scr tro*: *Scriptsiella trochoidea*, *Syn com*: *Synedra commutata*, *Sti bac*: *Stichococcus bacillaris*, *Tab wae*: *Tabularia waernii*, *Tra asp*: *Trachyneis aspera*.

as well as marine and brackish water taxa was seen. However, this differentiation was only based on information in the taxonomic literature and several taxa are known to occur simultaneously in different habitats. For example, the morpho-species *Navicula phyllepta* Kützing is often a key species in intertidal mudflats. It

can constitute 60–75% of the biomass of the total MPB community (Thornton *et al.*, 2002; Haubois *et al.*, 2005), and has a widespread biogeographic distribution, suggesting adaptation across a range of environmental conditions such as salinity, emersion time and temperature (e.g. Sabbe *et al.*, 2003).

Evidence from molecular markers indicates that many established diatom morpho-species actually consist of several semi-cryptic or truly cryptic species (e.g. Créach *et al.*, 2006). Furthermore, Vanelslander *et al.* (2009) showed that *Navicula phyllepta sensu lato* comprises different species with specific ecophysiological characteristics rather than a single generalist with a broad physiological plasticity to different environmental conditions. Consequently, the differentiation of the taxa in the present study must be treated with caution.

General community compositions of the marine MPB in the Húnaflói in comparison to temperate areas and the Arctic

The MPB communities of the Skagaströnd transects were highly variable, both temporally and spatially, and only a few species were dominant. The spatial differences were greater than the temporal ones, especially between transects I and II. The MPB primary producers at both transects in the Skagaströnd area were represented by Bacillariophyceae and some phototrophic flagellates (chloro-, crypto-, dino- and haptophytes) as well as one filamentous chlorophyte (*Stichococcus bacillaris*). Marine and brackish water diatoms, obtained from the analysis of permanent slides, had an overall mean value of 35.6 and 42.8×10^2 cells cm^{-2} at transects I and II, respectively. The typical seasonal cycle, as found in some intertidal flats of temperate areas, with blooms in spring and autumn and decreasing cell numbers during summer (Colijn & Dijkema, 1981; Colijn & de Jonge, 1984; Santos *et al.*, 1997; Scholz & Liebezeit, 2012b) was observed to some extent in the investigated area and seemed to be masked by other impacts, such as benthic-pelagic coupling, freshwater inputs and terrestrial run-off as mentioned above. Besides a large number of freshwater and terrestrial species found in the benthic samples, a significant part of the marine MPB in the Skagaströnd area originated from the marine planktonic realm (43% of the 72 taxa; cf. Tables 3 and 4). In temperate areas, it has increasingly been recognized that benthic algae may not be strictly edaphic and that planktonic forms can temporarily dwell on the sediment (De Jong & De Jonge, 1995). In addition, for the Arctic continental shelves it has been suggested that benthic and pelagic systems may be more tightly coupled than in warmer seas (Petersen & Curtis, 1980; Grebmeier & Barry, 1991; Hobson *et al.*, 1995; Renaud *et al.*, 2008).

However, if the pelagic fraction were removed from the total marine abundances, the community compositions of both transects in the present study would be made up of 100% bacillariophytes. Communities on sub-tidal flats in the Arctic consisted of up to 99% diatoms (Woelfel *et al.*, 2009).

Cell numbers in marine intertidal flats in temperate areas, for example for the Solthörn tidal flat (southern North Sea, Germany, e.g. Colijn & Nienhuis, 1977; Scholz & Liebezeit, 2012a) and the Westerschelde estuary (the Netherlands; Peletier, 1996), were up to 84% lower than the abundances obtained in the present study. Similar patterns have been found for individual algal groups, with cell numbers reduced by up to 80% in temperate areas (e.g. Sundbäck *et al.*, 1996; Hoppenrath, 2000; Lee & Patterson, 2002; Scholz & Liebezeit, 2012b).

An additional difference was observed between intertidal flats in temperate regions and the investigated area in the total number of taxa, with approximately 40% lower numbers of taxa contributing to the species diversity in the Skagaströnd area than in, for example, the Solthörn tidal flat (e.g. Colijn & Nienhuis, 1977; Scholz & Liebezeit, 2012a, 2012b).

Beside cell numbers and taxon diversity, considerable differences in chlorophyll *a* (chl *a*) and phaeophytin concentrations emerged during the sampling period, although the typical seasonal cycle of high summer values (e.g. Sundbäck, 1984; de Jong & de Jonge, 1995; Hamels *et al.*, 2001) was also found in the investigated area. The highest mean value in the present study was 47.3 mg chl *a* m^{-2} , which ranks in the lower range for intertidal sediments in temperate areas (Colijn & de Jonge, 1984; MacIntyre *et al.*, 1996) as well as Arctic sub-tidal flats (10–20 m depths, Matheke & Horner, 1974; Woelfel *et al.*, 2009).

Temporal variations of the marine northern Icelandic MPB communities in the Húnaflói in relation to abiotic parameters and environmental conditions

In the statistical analysis several species were significantly associated with salinity, nutrient concentrations, photosynthetic active radiation (PAR) and temperature of the sediment surface ($P < 0.05$). Temperatures were in the range of published data from the region (Gislason & Astthorsson, 1998, 2004) and showed a clear seasonal trend, being 0.9 to 2.9°C higher on the sediment surface than the air and strongly correlated with the incident light intensities (PAR, $P < 0.05$), which also showed a clear seasonal trend. Although the investigated area is close to the Arctic Circle (100 km from Akureyri) it can be only classified as a sub-Arctic habitat, but with several features showing a close relationship to the Arctic environment, such as day lengths of 24 h in summer and a relatively short growing period (usually between late April and early September).

Usually salinity data from northern Iceland show relatively little change and range from 34.7 to 35 psu at a depth of 50 m (Gislason & Astthorsson, 1998, 2004). Data obtained in the present study indicate that both transects in the Skagaströnd area have to be classified as brackish water habitats with strong

temporal variations linked to seasonal snow melt and rain events.

Overall macronutrient concentrations of the overlying water were only slightly higher than in intertidal flats in temperate areas (Admiraal, 1977; Pinckney *et al.*, 1995; Underwood & Provot, 2000). Usually, the ratio of N:P for balanced growth, with equal limitation by N and P, varies between 10:1 and 20:1 (e.g. Hillebrand & Sommer, 1999). The paired DIN and RDP values in the present study showed that this ratio was mostly under the 'standard' ratio of 16:1 at both transects. However, the results of the CCA indicate that the MPB non-diatom and diatom communities in the Skagaströnd area were sensitive to the concentrations of DSi and DIN ($P < 0.05$), whereas RDP was relevant for only a few pelagic species (e.g. *Gomphoseptatum aestuarii*). The seasonal cycle, as found in temperate areas such as the Wadden Sea, with higher DIN, RDP and DSi concentrations in spring and autumn and lower ones during summer (Admiraal, 1977; Pinckney *et al.*, 1995; Underwood & Provot, 2000) was only found at transect II. In particular the unusually high ammonium concentrations suggested an additional impact (e.g. by discharges of waste water in the investigated area during the summer). Previous studies have shown that high concentrations of ammonium can regulate the species composition of benthic diatom populations (e.g. Admiraal & Peletier 1979; Underwood *et al.*, 1998; Sullivan, 1999; Underwood & Provot, 2000). Furthermore, *Nitzschia* spp. was found to be tolerant to high nutrient levels, while *Achnanthes* and *Amphora* typically occur in nutrient-poor regions (Agatz *et al.*, 1999). These observations fit well with our CCA results, suggesting that the distribution of *Achnanthes* spp. was correlated with low macronutrient concentrations, while *Amphora* spp. (e.g. *Amphora coffeaeformis*) were associated with moderate concentrations (cf. Fig. 16C, F). Underwood & Provot (2000) showed that some benthic diatoms had different, though overlapping, ammonium, nitrate and salinity optima, and Cox (1995) has suggested that common species such as *Navicula phyllepta* may contain clones with different, although overlapping, requirements with respect to environmental factors. In addition, a few species such as *Amphipleura rutilans*, *Gyrosigma fasciola* or *Nitzschia distans* were positioned close to the centre of the CCA, suggesting that they are generalists in relation to the environmental variables tested ($r < 0.1$, $P > 0.05$). The Spearman analysis showed weak positive coefficients for DIN or RDP for most of the generalists (e.g. *A. rutilans* for DIN: $r_s < 0.1$, $P < 0.05$), whereas strong positive correlations were found for specialists. For example, *Cylindrotheca closterium* had a weak correlation with DIN in the present study ($r_s < 0.1$, $P > 0.05$) and Staats *et al.* (2000) found that growth of *C. closterium* in batch cultures was not immediately affected by low N

or P concentrations. Generally, the importance of *C. closterium* for intertidal sand- and mudflats has been emphasized by several authors: it is one of the most important EPS producers and thus makes a major contribution to increasing sediment stability (Alcoverro *et al.*, 2000; Staats *et al.*, 2000; Underwood & Provot, 2000). A similar impact of macronutrient concentrations, as recorded for the diatom composition, was also present for the non-diatom fraction in the Skagaströnd area. *Stichococcus bacillaris*, *Hemiselmis amyliifera* and *Chattonella marina* showed strong positive correlations to DIN ($r_s < 0.2$, $P > 0.05$), whereas for several other species no direct relationships were found. Some phytoplankton species are capable of utilizing dissolved organic nitrogen and phosphorus for their growth as well as inorganic forms (e.g. Cembella *et al.*, 1984). This capacity is important to allow their dominance in the surface waters in seasons where inorganic nutrients sometimes become limiting to growth. However, recent work has revealed that dissolved organic nitrogen (DON, including urea and dissolved free amino acids) may also serve as important nitrogen sources for many phytoplankton species (Anderson *et al.*, 2002; Berman & Bronk, 2003) and might be also important for some MPB species.

Other possible temporal impacts on the MPB composition in the Skagaströnd area, which were not further considered in the present study, are for example day length (e.g. Admiraal & Peletier, 1980) and grazing (e.g. Admiraal *et al.*, 1983; Hagerthey *et al.*, 2003). In particular, since *Navicula* species are known to be a preferred food item for several meiofauna (Admiraal *et al.*, 1983), it seems likely that the observed decrease of *Navicula* cells during summer was the result of efficient and highly selective grazing (cf. Table 4).

Spatial variation of marine northern Icelandic MPB communities in the Húnaflói

The main differences along the transects were related to variations in sediment structure, as characterized by median grain size, porosity, water and organic matter contents (cf. Table 1) and several of the species were significantly correlated with the sediment characteristics ($P < 0.05$). Usually mixed sediments are colonized by complex and resilient MPB communities, constituted by small epipsammic life forms that do not form visible biofilms (Hamels *et al.*, 1998). These taxa include monoraphid diatoms, such as *Cocconeis* spp. and *Achnantes* spp., and araphid diatoms, such as *Cymatosira belgica*, that are often observed in mixed intertidal sediments (e.g. Paterson & Hagerthey, 2001). While the monoraphid diatoms such as *Cocconeis* spp. and *Achnantes* spp. were well represented in the present study, several pennate genera such as *Navicula*, *Nitzschia*, *Fragilaria*, *Gyrosigma*

and *Pleurosigma*, which are found both in the ice and on soft bottom sediments in Arctic marine subtidal communities (Horner, 1990; Poulin, 1990; Al-Handal & Wulff, 2008a, 2008b), were found in high abundances in the intertidal communities of the Skagaströnd area. In particular, the diatom communities of both transects were numerically dominated by small species, particularly *Navicula digitoradiata* (almost 15–24% of the total assemblage), and to a lesser extent *N. phyllepta*. The dominance of small *Navicula* species is a common feature of European intertidal mudflats (e.g. Admiraal *et al.*, 1984; Oppenheim, 1988, 1991; Underwood, 1994; Saburova *et al.*, 1995; Sabbe, 1997; Hamels *et al.*, 1998) and it seems likely that better colonization ability gives them an advantage over larger and slower-growing species in intertidal flats, where the MPB has to cope with frequent redistribution of surface sediments. Unfortunately, there are few published studies on the abundance of benthic marine non-diatoms and diatoms using similar counting methodology, which makes it difficult to make further comparisons of the species-specific relative abundance of the different orders and classes with other regions.

The contrasts in spatial distribution can be attributed to the influence of the geomorphological formation of the coastline combined with the strong hydrodynamic forces of the wave actions on the tidal regime, which in turn affect the sediment composition at each station along the transects, particularly at the most landward stations 3 and 5. The coastal area in the Húnaflói is characterized by a very steep slope, which seems to act as an energy barrier (approximately 1–2 km from the coast). The slope increases the normal cross-shore energy gradient and in combination with high wind velocities, which are usual in the Icelandic north (Flatau *et al.*, 2003), the wave action therefore inhibits the deposition of fine material with settling velocities $< 0.5 \text{ cm s}^{-1}$. This material therefore remains suspended in the water column and causes turbidity (Flemming & Nyandwi, 1994; Dellwig *et al.*, 2000). The ‘tidal gradient’ of sediment characteristics remained relatively constant along the transects and did not vary appreciably during the sampling time. The extracellular polymeric substances (EPS) produced by migratory diatoms at stations 3 and 5 were unable to consolidate during the short emersion period (about 2–4 h, depending on wind conditions as well as on spring and neap tides). Consequently, microalgae were readily resuspended, and benthic as well as pelagic diatoms were stripped from the sediment surface by high turbulence. In contrast at the seaward stations 1 and 4, where turbulence was not as strong, pelagic species tended to sink to the bottom and could undergo cycles of suspension and settling through the water column (e.g. Kiørboe, 1993). The higher abundance of pelagic diatoms and higher diversity in

the most seaward part of the transects are thus explainable.

Further characteristics of the northern Icelandic MPB community compositions in the Húnaflói

MPB community compositions in temperate areas show, depending on different environmental factors, a heterogeneous structure with diatoms making up 50–60% of the total MPB followed by other important components such as cyanobacteria and euglenophytes (e.g. Pinckney *et al.*, 1994; Barranguet *et al.*, 1997; Hamels *et al.*, 1998; Cook *et al.*, 2004; Méléder *et al.*, 2005; Brito *et al.*, 2009; Scholz & Liebezeit, 2012b). With the exception of small numbers of cyanobacteria, which were recorded in the present study at transect II in August, both these important components of the MPB in temperate areas were absent during the sampling events from March to October 2013 in the Skagaströnd area. In general, euglenophytes are known to be abundant in eutrophic waters and sediments enriched with organic matter (Round, 1984) and are major components of MPB assemblages on cohesive sediments (Kingston, 1999). Thus, the environmental conditions found in the investigated area may not be favourable for this species group. In contrast, cyanobacteria are known to be able to cope with a broad range of environmental fluctuations such as variations in salinity and nutrient supply using physiological adaptations. It is unlikely that temperature itself is a factor restricting the occurrence of cyanobacteria since cyanobacterial diazotrophs are known to be common in polar terrestrial and freshwater habitats (Jungblut & Neilan, 2010; Harding *et al.*, 2011) and are also described for the northern part of Iceland (Broady, 1978). However, until recently it was assumed that cyanobacteria were absent from polar marine ecosystems (e.g. Vincent, 2000; Vincent *et al.*, 2000). There is no clear cause for the non-occurrence of benthic marine cyanobacteria in the investigated area and further investigations including those of deeper benthic realms in northern Icelandic coastal areas are needed.

Finally, although no petrological investigations of the sediments in the Húnaflói were conducted in the present investigation and there are no studies of the sediment compositions in close vicinity of the coastline in the north of Iceland, comparisons with studies from the southern part of Iceland indicated high fractions of glass (black and grey) as well as basalt as main components of the sediments found in the Skagaströnd area (Guðmundsson, 1977). This is one of the main differences from intertidal flats in temperate areas, which are mainly composed of sand (quartz), clay minerals, feldspars, heavy minerals, carbonates and organic matter (Volkman *et al.*, 2000). It is not known if these peculiar features of the sediments in the Skagaströnd area have an impact

on the settlement of MPB species. Further investigations with species originating from the Wadden Sea are planned in order to study possible effects.

CONCLUSIONS

The present investigation is the first record of microphytobenthic community composition in the northern Icelandic coastal area. Analysis of the species in the community as well as the chemical parameters, such as salinity and nutrients, indicated a high impact of freshwater inputs and terrestrial runoffs. Furthermore, strong hydrodynamic forces, in combination with the geomorphological formation of the coastline as well as the composition of the sediments, which have high glass and basalt fractions, were one of the most important physical features influencing the MPB species compositions at both transects. Due to the community composition and diversity observed in the present study, the intertidal flats in the Skagaströnd area seemed to show a closer relationship to Arctic subtidal communities than to intertidal communities studied in temperate areas.

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SUPPLEMENTARY INFORMATION

The following supplementary material is accessible via the Supplementary Content tab on the article's online page at <http://dx.doi.org/10.1080/09670262.2015.1024286>

Supplementary table S1. Relative abundances of freshwater and terrestrial species obtained from sediment surfaces samples in the Skagaströnd area from March to October 2013, using Utermöhl chambers and epifluorescence microscopy.

Supplementary table S2. Relative abundances of freshwater diatom species obtained from sediment surfaces samples in the Skagaströnd area from March to October 2013, using permanent slides prepared according to the method by Schrader (1976).

AUTHOR CONTRIBUTIONS

B. Scholz: original concept, sampling, reprocessing, measurements, species determination, data analysis, writing of manuscript; H. Einarsson: supported funding acquisition.

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