

Diversity, ecology and community structure of the freshwater littoral diatom flora from Petuniabukta (Spitsbergen)

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Abstract Despite the frequent application of diatoms in palaeoecological research in the High Arctic, our knowledge concerning the diversity, ecology, community associations, community dynamics and survival strategies of High Arctic freshwater littoral diatom floras is still rather limited. In the present study, the diversity, ecological characteristics and community structures of the freshwater littoral diatom flora from ponds and lakes of Petuniabukta (Spitsbergen, Svalbard Archipelago) were studied. In total, 87 samples from the littoral zone of 53 freshwater ponds and lakes were examined using light and scanning electron microscopy. A highly diverse diatom flora dominated by

Achnantheidium and *Nitzschia* was observed. In total, 310 diatom taxa belonging to 59 genera were found, of which about one-third could not be identified beyond the genus level. Based on species composition, four main diatom communities were distinguished. Differences in environmental characteristics, such as habitat type, habitat diversity, habitat stability, streams, water pH and influence of the fjord, biota and human activities, appeared to be important factors in determining the observed diatom communities. The high number of unidentified taxa in this study indicates that a profound revision of the Arctic diatom flora is highly desired, not only to improve our fundamental knowledge concerning the diversity, ecology, community associations and biogeography of Arctic diatoms but also to aid applied (palaeo)environmental sciences.

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Introduction

Diatoms (Bacillariophyta) are the most species-rich group of algae on Earth, with species number estimates varying between 30,000 and 200,000 extant taxa (Mann 1999; Mann and Vanormelingen 2013). They are ecologically widespread, occur in marine, freshwater and (semi)terrestrial habitats worldwide (Mann 1999) and constitute an important part of the polar freshwater algal flora (e.g. Jones 1996). Due to their specific ecological preferences and the long-term preservation of their silica valves in (lake) sediments, diatoms are highly useful as indicators of (palaeo)environmental change (Smol and Stoermer 2010) and are frequently used as such in the High Arctic (e.g.

Jones and Birks 2004; Rühland and Smol 2005; Michelutti et al. 2013a). However, in order to apply diatoms in biomonitoring and palaeoecological studies, detailed information concerning the habitat tolerances and ecological optima of diatom species are needed. In the past, several studies have attempted to shed light on diatom taxa and their ecological preferences in High Arctic regions (e.g. Douglas and Smol 1995; Michelutti et al. 2003; Bouchard et al. 2004; Michelutti et al. 2013b), revealing that diatom communities are influenced by regional conditions such as the climate and geology and a range of local factors including physicochemistry, habitat/substrate type, habitat diversity, inflow, slope steepness and light availability (e.g. Douglas and Smol 1995; Michelutti et al. 2003; Bouchard et al. 2004). Additionally, biological interactions such as grazing pressure might play significant roles (e.g. Douglas and Smol 1995). Furthermore, diatom communities in High Arctic littoral freshwater environments, especially shallow ponds, must withstand various extreme environmental conditions, such as temporary desiccation of their habitats, continuous sunlight and relatively high levels of ultraviolet radiation in the summer season, and complete freezing of their habitats during the winter season, revealing that the occurring species must have developed specific survival strategies to cope in these environments (Douglas and Smol 1995). Survival strategies of diatoms in temperate aquatic and terrestrial environments have already been the subject of various studies, either focusing on attachment strategies and growth forms in natural environments (e.g. Hoagland et al. 1982; Hudon and Legendre 1987; Passy 2007; Wang et al. 2014) or tolerance to extreme conditions such as freezing and desiccation in controlled laboratory experiments (e.g. Souffreau et al. 2010, 2013a). However, our knowledge concerning habitat preferences, ecological tolerances, survival strategies, community associations, community dynamics and geographic distributions of High Arctic littoral diatoms is still rather limited, and it is unclear how past studies focusing on diatom communities have been affected by their taxonomic resolution (see amongst others Pinseel et al. 2015). For example, previous studies clearly pointed out that extensive taxonomic surveys of the High Arctic will yield a higher diversity than observed in most ecological studies (e.g. Foged 1981), and recent re-examinations of the High Arctic diatom flora using a refined morphotaxonomy and modern technologies (e.g. high-resolution scanning electron microscopy) have resulted in the discovery of a high number of taxa new to science (e.g. Van de Vijver et al. 2004; Antoniadou et al. 2008, 2009; Pinseel et al. 2014, 2015) that might have been overlooked or misidentified in past surveys.

In the past, the High Arctic diatom flora of Spitsbergen has been the subject of numerous studies. The first records

of freshwater and terrestrial diatoms in Spitsbergen were provided by Cleve (1867), Lagerstedt (1873), Hustedt (1937) and Krasske (1938). The most extensive study was carried out by Foged (1964) who found 572 taxa in 209 samples of humid soils, terrestrial mosses and freshwater ponds and lakes of Spitsbergen and Prins Karls Forland. However, in more recent decades, only a handful of small floristic and (palaeo)ecological studies have been published from Spitsbergen (e.g. Willén 1980; Picińska-Fałtynowicz 1988; Van de Vijver et al. 1999; Jones and Birks 2004; Guilizzoni et al. 2006; Holmgren et al. 2010; Jiang et al. 2011) or other islands from the Svalbard Archipelago (e.g. Beyens and De Bock 1989; Metzeltin and Witkowski 1996; Beyens and Van de Vijver 2000).

Recently, littoral samples of freshwater lakes and ponds in Petuniabukta (Spitsbergen, Svalbard Archipelago, Arctic region) were taken as part of a Czech education programme of polar ecology organized by the Centre for Polar Ecology of the University of South Bohemia (reports of the Czech research activities can be found on http://polar.prf.jcu.cz/docs_cz.htm). This allowed the study of the freshwater benthic diatom communities of Petuniabukta using a more fine-grained taxonomy in order to provide an ecological and taxonomic revision of the diatom flora present. Due to logistic constraints resulting from the restricted possibilities of working in these remote environments, no detailed physicochemical analysis of the sampled water bodies was performed. Here we aim to provide a first overview of the present-day diatom diversity and community structures in this largely unstudied part of Spitsbergen.

Study area

Petuniabukta (78°40′–78° 44.5′N and 16°26′–16°40′E) is the most northern part of Billefjorden, the inner branch of Isfjorden, situated in central Spitsbergen (Fig. 1). The fjord area is located in the maritime High Arctic climate zone characterized by low precipitation rates of about 200 mm/yr (Birks et al. 2004), relatively cold winters (between –15 °C and –35 °C in 2008–2010) and cool summers (between 0 °C and 15 °C in 2008–2010) (Láska et al. 2012). The fjord is surrounded by steep mountain slopes up to 937 m a.s.l. which are separated from the coast by a lowland area composed of well-preserved marine terraces formed by glacio-isostatic uplift since the end of the Last Ice Age, about 11,200–11,300 years ago (Szczeniński and Rachlewicz 2007; Baeten et al. 2010). The dominating geological layers are composed of Carboniferous–Permian sedimentary rocks such as dolomite and limestone (Dallmann et al. 1999) creating alkaline surface waters in the area. Large parts of Petuniabukta are not or only sparsely vegetated as a result of erosion, extreme climatic

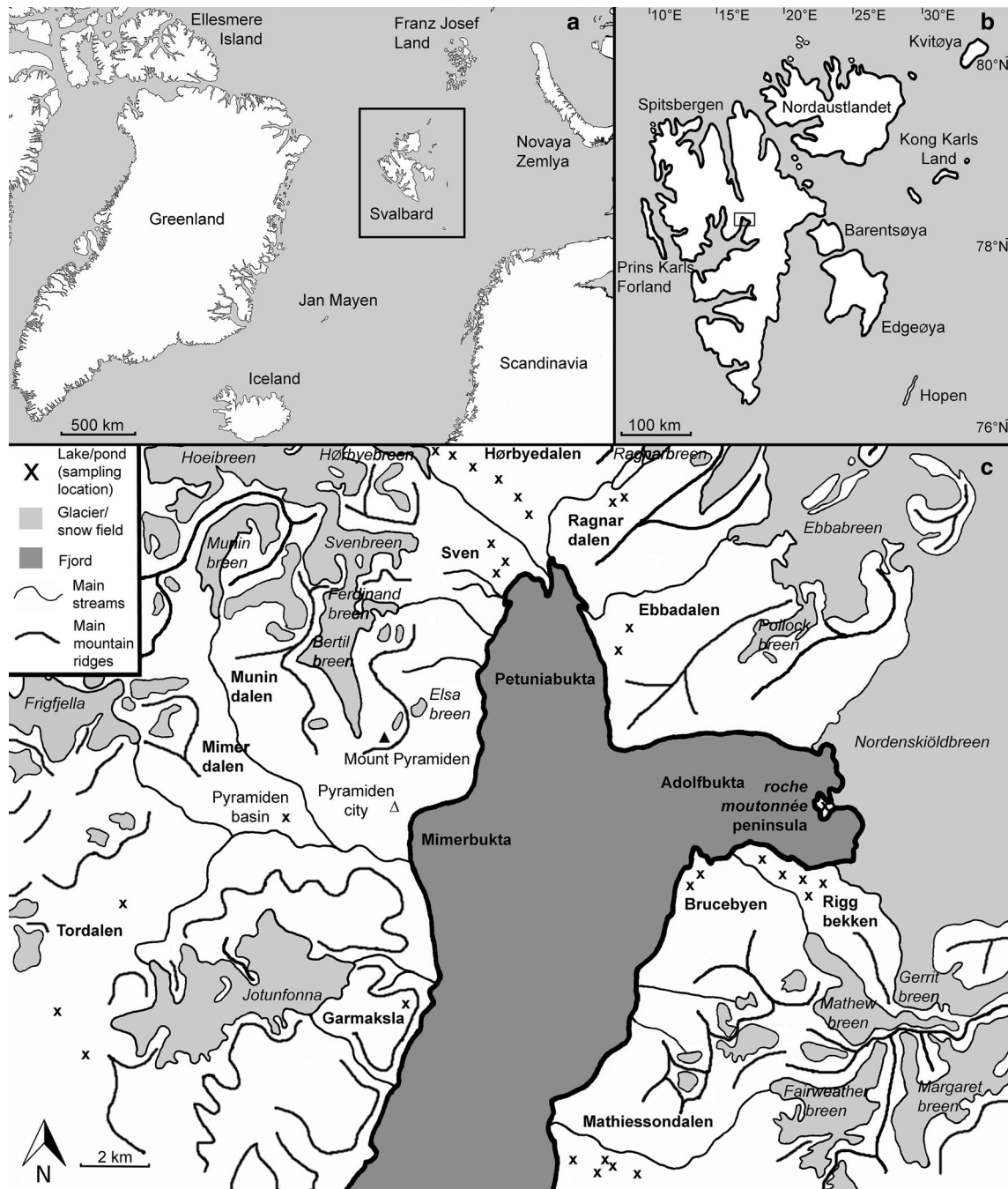


Fig. 1 **a** The Arctic region with Spitsbergen highlighted. **b** Spitsbergen (Bear Island excluded) with the study area highlighted. **c** Detailed map of Petuniabukta in the north of Billefjorden. The main sampled

areas are indicated with an X. Samples were taken from more than one lake/pond at each locality

conditions on exposed sites and recently deglaciated, not yet colonized, areas. Those areas that are vegetated show a rather high plant diversity with mainly mosses and *Carex* L., *Dryas* L. and *Silene* L. taxa (Prach et al. 2012; Prach and Rachlewicz 2012). A certain anthropogenic influence in the area is evidenced by the presence of the Russian mining city Pyramiden that was abandoned in 1998 and is

located near the coast of Petuniabukta. Bird colonies of black-legged kittiwake (*Rissa tridactyla* L.), Arctic tern (*Sterna paradisaea* Pontoppidan) and Atlantic puffin (*Fratercula arctica* L.) occur along the coast and in Pyramiden.

A high number of freshwater lakes and ponds from various origins are present in the area. Several of these

lakes and ponds are located on the raised marine beaches (Mathiessondalen, Brucebyen and Ebbadalen), but some occur in inland valleys (Mimerdalen) and/or on higher altitudes (Mimerdalen, Garmaksla). Most lakes and ponds are, however, found in the moraines of glaciers (Sven, Hørbye, Ragnar and Nordenskiöld) or on a rock formation (i.e. ‘roche moutonnée’ or ‘sheepback’) in front of the tidewater glacier Nordenskiöld which is from now on referred to as ‘peninsula’. These lakes and ponds are recently formed. The end of the Little Ice Age on Spitsbergen at the beginning of the twentieth century and the enhanced greenhouse effect since AD 1920 resulted in a 50–53 % decrease of the extent of Petuniabukta’s glaciers since AD 1900 (Overpeck et al. 1997; Rachlewicz et al. 2007; D’Andrea et al. 2012). Subsequently, large areas where lakes and ponds could develop appeared. And last, several artificial water basins that were used in the past for the water supply of the city of Pyramiden are located nearby the city.

Materials and methods

Field sampling

During the boreal summer seasons of 2011 and 2013, 87 epilithon, epipelon and epiphyton (moss vegetation) samples of the littoral zones from 53 freshwater lakes and ponds in Petuniabukta were collected for diatom analysis. Diatom samples were preserved with 96 % ethanol and stored in 50-mL falcon tubes. All samples and slides used in the present study are listed in Online Resource 1. GPS positions, physicochemical parameters and environmental characteristics of all sampled lakes and ponds are given in Online Resource 2. The pH, temperature and conductivity (for the given ambient temperature) of the field sites were measured using a HANNA Combo pH/EC Tester. Afterwards, the specific conductance was corrected for a standard temperature of 25 °C using linear temperature correction (using a temperature coefficient of two). For all locations, the elevation (m a.s.l.), lake/pond type and the presence of glaciers and streams (seepages not included) were noted. Biotic and human influence, surface area (ha), vegetation coverage in the lakes/ponds and along the shores and lake/pond origin were assessed. Four types of lakes/ponds were defined: permanent lakes/ponds with limited variation in surface area, permanent lakes/ponds with extremely high variation in surface area, semi-permanent/highly variable lakes/ponds due to unstable environment (e.g. certain kettle lakes/ponds) and temporary lakes/ponds (may develop in wetlands at the end of the summer season). The shortest distance to the sea was determined using TopoSvalbard ([\[no/\]\(http://toposvalbard.no/\)\). The maximum ages of the lakes and ponds were estimated based on the geological and glacial history of the landscape, such as the retreat rate of nearby glaciers and the age of the marine terraces.](http://toposvalbard.</p>
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Slide preparation and counting

Small subsamples were prepared for light microscopy (LM) observation following the method described in Van der Werff (1955). Subsamples were cleaned by adding 37 % H₂O₂ and heating to 80 °C for about 1 h. The reaction was completed by addition of KMnO₄. Following digestion and centrifugation (three times 10 min at 3700 ×g), cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom material was dried on microscope cover slides and mounted in Naphrax[®]. For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered through a 1-µm Isopore[™] polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a Gold–Palladium layer of approximately 20 nm and studied in a ZEISS Ultra SEM microscope at 3 kV (Natural History Museum London, UK) or a JEOL-5800LV at 25 kV (Botanic Garden Meise, Belgium). Samples and slides are stored at the Botanic Garden Meise and are available upon request.

In each sample, 400 diatom valves were identified and enumerated on random transects at 100× magnification under oil immersion using an Olympus[®] BX51 microscope equipped with differential interference contrast (Nomarski) optics. After counting, the slides were scanned for diatom taxa not encountered during the counts. Books and articles directly used for identifications are listed in Online Resource 3. Several other recent publications on diatom taxonomy were consulted for comparison. When necessary, scanning electron microscopy (SEM) was used to aid the identifications. Additionally, the type material of several taxa [e.g. *Caloneis thermalis* (Grunow) Krammer, *Cymbopleura angustata* (W.Smith) Krammer] was examined for comparison or verification of identifications. The diatom taxa were identified to species, subspecies, variety or forma level. However, a high number of diatom taxa could not be identified to one of these taxonomic levels due to their unclear taxonomic status. Taxa resembling *Nitzschia perminuta* (Grunow) Perag. were subdivided into five forms based on subtle but clear morphological differences (i.e. valve outline, valve dimensions, structure of the striae and the position of the fibulae). Other taxa with uncertain taxonomic status are indicated with ‘cf.’ (*confer*: it could be this taxon, but it is questionable), ‘aff.’ (*affinis*: it bears some similarity to this taxon, but it is not conspecific) or ‘sp.’ (species). Ongoing morphological and taxonomic research will allow clarifying the identity of these taxa and

will likely result in the formal description of several species new to science. Images of all observed diatoms are available upon request and will be published in future planned taxonomic revisions (Pinseel et al., unpublished results).

Data analysis

In order to assess the extent to which our sampling effort represented the actual species diversity present in the sampled habitats, the mean Chao2 richness estimator (Chao 1984) and the incidence-based species richness estimator ICE (Chao et al. 2000) were calculated using the EstimateS program (version 9.0) (Colwell 2013). The Shannon–Wiener diversity index (ln-based) and Hill’s evenness index were calculated in the statistical package MVSP 3.1 (Kovach Computing Services 2007).

In order to reveal the principal species composition patterns in the samples, a cluster analysis with Bray–Curtis similarity and Hellinger transformation in Primer-E 6.0 (Clarke and Gorley 2006) was run. A similarity profile routine (SIMPROF) in Primer-E 6.0 allowed assessing the significance (999 permutations, $p < 0.05$) of the groups identified in the cluster diagram. To visualize the different clusters, a PCA was run in CANOCO 4.5 (ter Braak and Smilauer 2002). Hellinger-transformed abundance data were used in order to avoid the issue of many zero values typical for these datasets (Legendre and Gallagher 2001). Tilia v2.0b4 (Grimm 1991) allowed visualizing the differences between the diatom communities.

Results

Species composition and diversity

A total of 310 taxa belonging to 59 genera were observed (Online Resource 4). Forty-three of these taxa were only found during scanning of the samples for additional taxa outside the counts. Six samples (SP17, SP24, SP27, SP35, SP43 and SPH6A) did not contain sufficient diatom valves for counting and were therefore removed from all further analysis. Of all observed taxa, 104 could not be identified to species or lower taxonomic level. More in-depth morphological investigations are necessary to clarify the taxonomic status of these taxa. Two of these, *Gomphonema svalbardense* Pinseel et al. and *Achnanthydium petuniabuktianum* Pinseel et al., have recently been described as new to science (Pinseel et al. 2014, 2015), and several other species, belonging to amongst others the genera *Encyonopsis* Krammer, *Stauroneis* Ehrenb., *Navicula* Bory, *Cymbella* C.Agardh, *Cymbopleura* Krammer and

Surirella Turpin, await a formal description (Pinseel 2014; Pinseel et al., unpublished results).

The flattening to the end of the species accumulation curve indicated that a large part of the freshwater littoral diatom flora of Petuniabukta has been collected (Fig. 2). The species richness estimators indicated the theoretical number of taxa in the study area was approximately 367 (CHAO2) or 361 (ICE). Therefore, the sampling effort scored 84 % (CHAO2) or 86 % (ICE) of all present taxa.

The species richness of the samples varied from 8 to 60 taxa with a median value of 29. The 100 least counted taxa together amounted for only 1 % of all counted valves, whereas the 11 most dominant taxa accounted for 50 % of all counted valves. The 10 most dominant genera together represented 78 % of all counted valves. The most taxa-rich genera were *Nitzschia* Hassall (41 taxa), *Navicula* (30 taxa), *Encyonema* Kütz. (17 taxa), *Pinnularia* Ehrenb. (17 taxa) and *Cymbopleura* (15 taxa). Based on abundance, *Nitzschia* (18.9 %) and *Achnanthydium* Kütz. (18.5 %) were dominating. Other important genera included *Denticula* Kütz. (7.1 %), *Navicula* (6.1 %), *Rossithidium* Bukht. and Round (5.8 %) and *Diatoma* Bory (5.1 %). *Achnanthydium* spp was the most dominant reoccurring diatom in this study (18.3 %), followed by *Rossithidium petersenii* (Hust.) Aboal (5.7 %), *Diatoma tenuis* C.Agardh (4.9 %) and *Denticula tenuis* Kütz. (4.3 %). It should, however, be noted that *Achnanthydium* spp actually represented a species complex since molecular analysis of several *Achnanthydium* strains from the study area revealed the presence of three different species closely resembling *A. minutissimum* (Kütz.) Czarn. (Pinseel et al., unpublished results). All three taxa were combined as ‘*Achnanthydium* spp’ since reliable identification in LM during standardized counts was impossible.

Community analysis

Based on a cluster analysis with Bray–Curtis similarity and a SIMPROF significance test, it was possible to divide the samples into seven groups with significantly different diatom compositions (Fig. 3). Three of these were only represented by one to three samples. The cut-off value for separation of these clusters was set on <30 % similarity in order to reveal the main patterns in the diatom communities without excessive detail (Fig. 3). A PCA ordination allowed for the visualization of the samples (Fig. 4). The first two PCA axes (eigenvalues $\lambda_1 = 0.117$, $\lambda_2 = 0.092$) explained in total 20.9 % of the variation of the diatom composition with an additional 14.2 % explained by axes three and four (eigenvalues $\lambda_3 = 0.079$, $\lambda_4 = 0.063$). Figure 5 shows the distribution of the most important taxa in the four major diatom communities. An overview of the

Fig. 2 Species accumulation curve for the total sample set

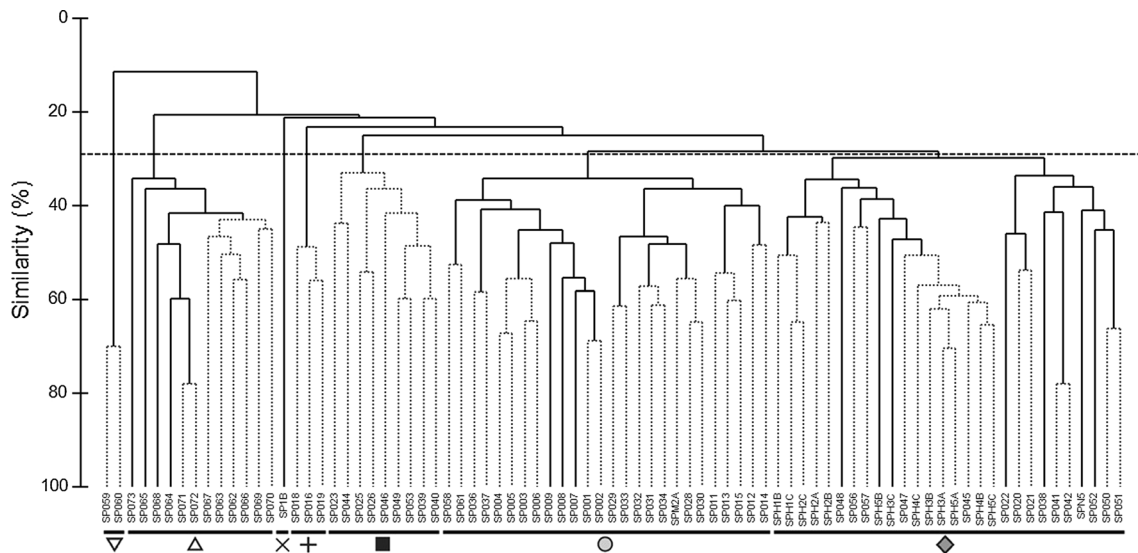
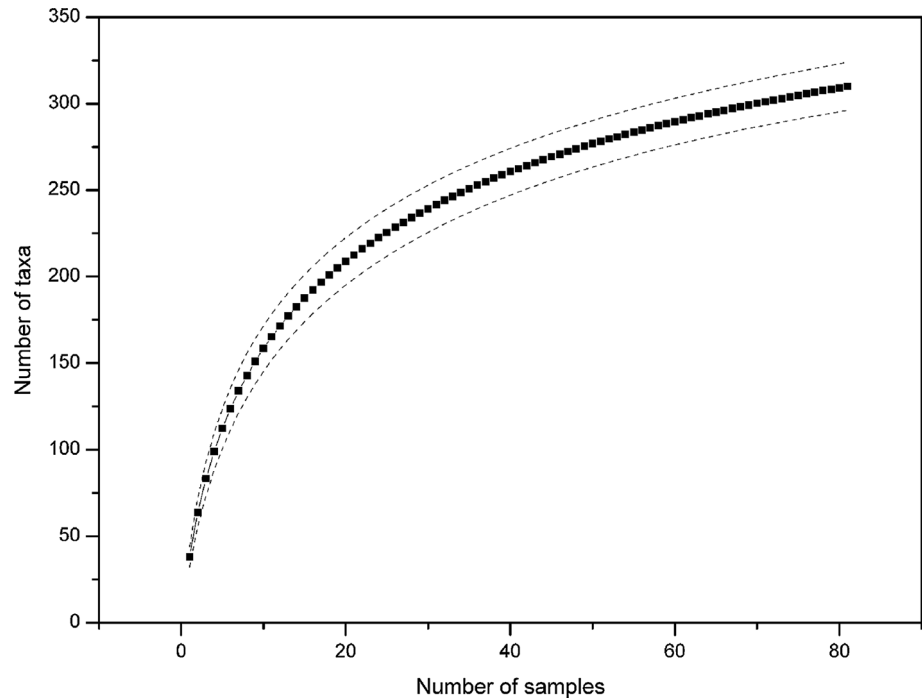


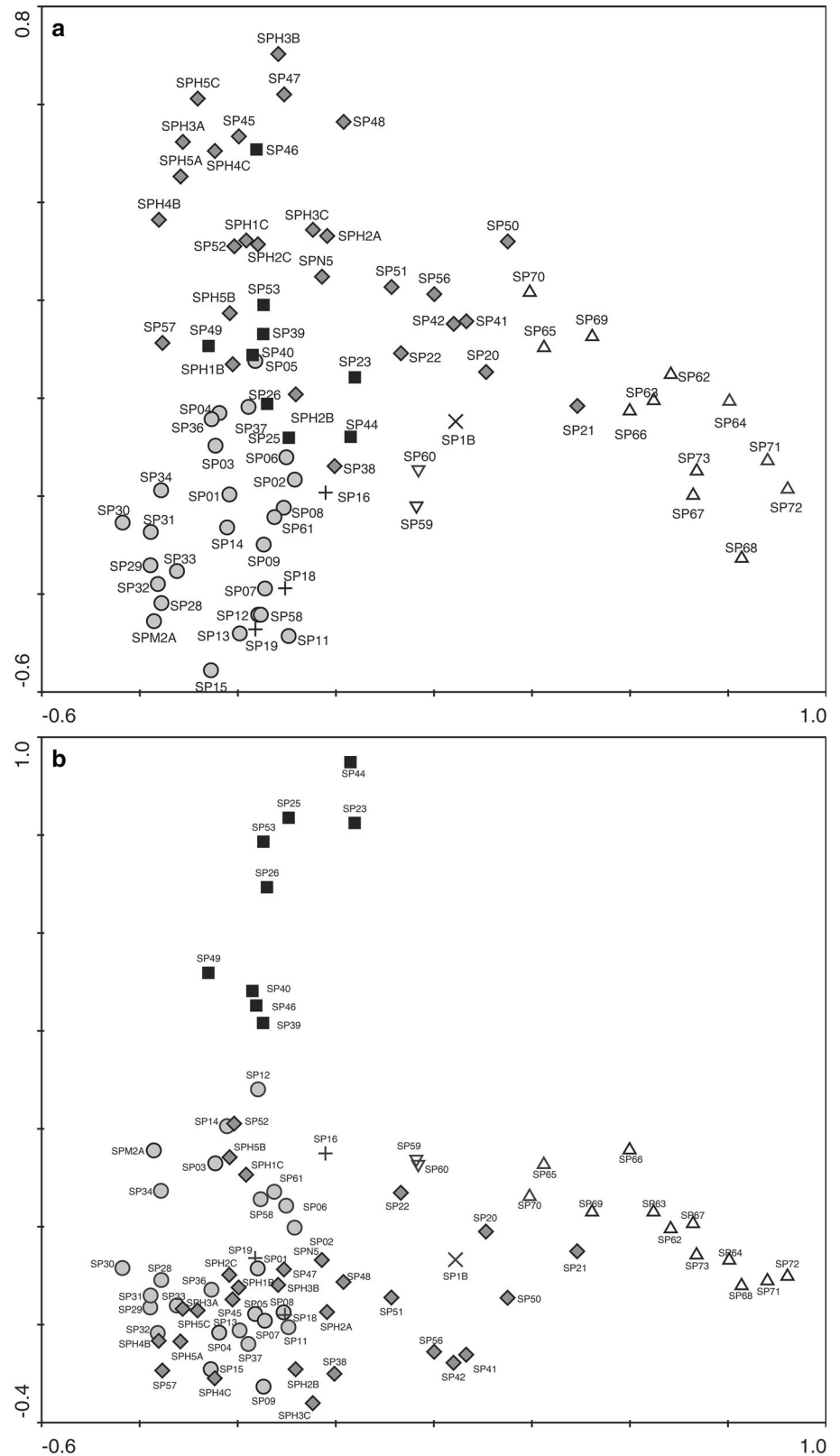
Fig. 3 Cluster diagram (Bray-Curtis similarity using Hellinger transformation of the data) of the total sample set with indication of the seven groups. Solid lines represent significant differences based on the SIMPROF analysis. The horizontal dotted line represents the cut-off value for the different clusters (similarity < 30 %). White down-triangle = samples SP59/60, white up-triangle = *Achnanthydium* spp-

Nitzschia community (group A), cross = sample SP1B, plus sign = samples SP16/18/19, black square = *Achnanthydium* spp-*Diatoma tenuis* community (group B), grey circle = *Achnanthydium* spp-*Rossethidium* community (group C) and grey diamond = *Achnanthydium* spp-*Psammothidium-Encyonopsis* community (group D)

principal characteristics of all communities is given in Table 1. Figures 6–61 and 62–112 show an overview of the most common taxa (>5.0 % abundance in at least one sample) in this study.

Most taxa showed a particular preference for one group. An exception was made by *Achnanthydium* spp which was highly present in almost all groups. As this taxon is a species complex of three different species, it was not clear

Fig. 4 Principal component analysis (PCA) ordination biplots (Fig. 4a: axis 1 and 2, Fig. 4b: axis 1 and 3) of the samples with indication of the seven groups as defined by the cluster analysis. *White down-triangle* = samples SP59/60, *white up-triangle* = *Achnanthydium* spp-*Nitzschia* community (group A), *cross* = sample SP1B, *plus sign* = samples SP16/18/19, *black square* = *Achnanthydium* spp-*Diatoma tenuis* community (group B), *grey circle* = *Achnanthydium* spp-*Rossethidium* community (group C) and *grey diamond* = *Achnanthydium* spp-*Psammothidium-Encyonopsis* community (group D)



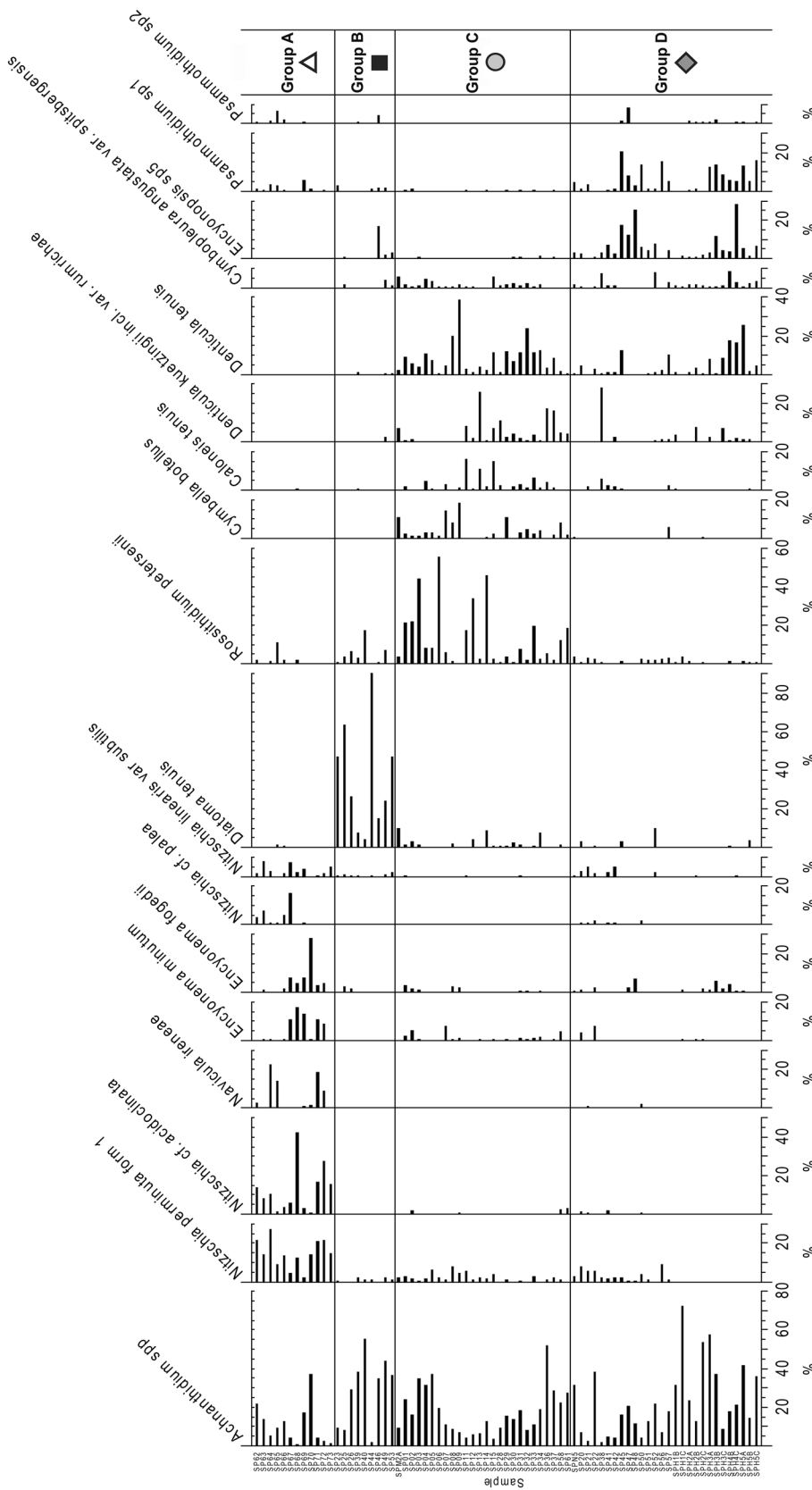


Fig. 5 Relative abundances of more common taxa (explaining at least 30 % of the variation along the four PCA axes and having >7.5 % relative abundance in at least one sample) in the four main diatom groups as defined in this study. The relative abundances of the taxa in each sample are shown. Group A = *Achnanthyidium* spp-*Nitzschia* community, group B = *Achnanthyidium* spp-*Diatoma tenuis* community, group C = *Achnanthyidium* spp-*Rossithidium* community, and group D = *Achnanthyidium* spp-*Pсамmothidium*-*Encyonopsis* community

Table 1 Environmental, sample and community characteristics of the seven groups

	Group A	Group B	Group C	Group D	SP59/60	SP16/18/ 19	SP1B
Number of samples	12	9	26	28	2	3	1
Number of taxa in the counts	12–34 (23)	8–34 (24)	17–59 (41)	14–57 (30)	11–13	19–27	60
Shannon–Wiener index (based on the counts)	1.72–2.89 (2.43)	0.58–2.25 (1.81)	1.52–3.41 (2.68)	1.24–3.42 (2.47)	1.28–1.59	1.32–2.24	3.36
Hill's evenness index (based on the counts)	0.67–0.84 (0.78)	0.21–0.69 (0.61)	0.51–0.85 (0.75)	0.44–0.88 (0.73)	0.54–0.62	0.45–0.68	0.82
pH	8.7–10.9 (9.4)	7.4–9.2 (8.6)	8.1–8.9 (8.5)	8.1–8.7 (8.4)	8.9	8.5–8.7	ND
Conductivity ($\mu\text{S}/\text{cm}$)	133–592 (300)	180–1948 (290)	149–761 (209)	182–1948 (461)	67	420–1222	ND
Specific conductance at 25 °C ($\mu\text{S}/\text{cm}$)	185–876 (442)	269–2938 (431)	221–1148 (313)	273–2938 (690)	99	623–1827	ND
Temperature (°C)	7.4–9.7 (8.5)	3.2–12.7 (8.7)	7.4–10.5 (8.4)	7.0–14.5 (11.3)	4.9	10.1	ND
Altitude (m)	7–28 (20)	5–106 (52)	4–332 (67)	23–275 (50)	434	7–11	70
Distance to sea (m)	19–117 (46)	434–4490 (2480)	236–9470 (633)	469–8820 (2730)	8300	131–184	3400
Min–max estimated lake/pond age (yr)	30–40	5–1000	50–1000+	5–100	1000+	500–1000	± 60
Min–max surface area (ha)	<0.1	<0.1–0.6	<0.1–3.2	<0.1–4.0	<0.1	0.9–2.1	3.5
Number of epilithon samples	12	7	9	24	1	2	1
Number of epipelton samples	0	0	2	3	1	0	0
Number of epiphyton samples	0	2	15	2	0	1	0
Number of samples of lakes/ponds with glacial influence							
0 = no glacial influence	0	2	24	2	2	3	1
1 = glacial moraine	0	7	2	26	0	0	0
1* = peninsula in front of glacier	12	0	0	0	0	0	0
Number of samples of lakes/ponds with stream* influence	0	5	4	2	0	0	0
Number of samples of lakes/ponds with biotic influence	12	0	9	4	0	3	0
Number of samples of lakes/ponds with human influence	0	0	5	0	0	3	1
Number of samples of lakes/ponds with vegetation in lake/pond							
0 = no vegetation	8	9	4	28	2	0	1
1 = few moss patches	4	0	17	0	0	3	0
2 = lake bottom is entirely vegetated	0	0	5	0	0	0	0
Number of samples of lakes/ponds with shore vegetation							
0 = no vegetation	0	7	2	24	2	0	1
1 = few individual plants	10	2	11	0	0	0	0
2 = ca. half of the shore vegetated	2	0	8	4	0	0	0
3 = ca. complete shore vegetated	0	0	5	0	0	3	0
Lake/pond type							
0 = permanent	12	6	19	6	0	3	1
1 = permanent but highly variable	0	0	0	2	2	0	0
2 = highly variable (instable environment)	0	3	2	20	0	0	0
3 = temporal (might develops in wetland)	0	0	5	0	0	0	0

Range (minimum and maximum) and median (between brackets) are presented

ND not determined

* Seepages are not regarded as streams. See Online Resource 2 for more information on the applied vegetation scales

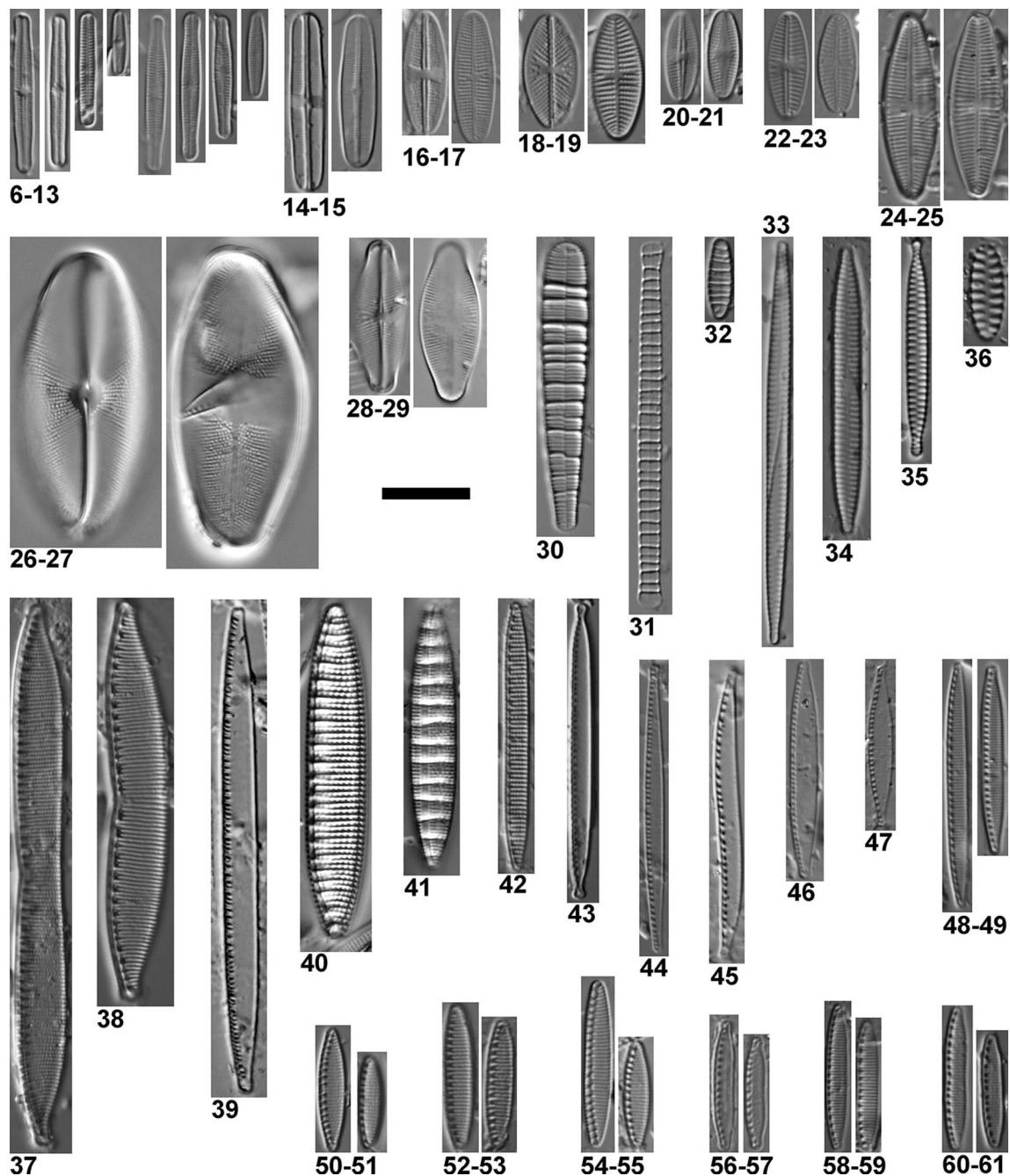


Fig. 6–61 Overview of the most common diatom taxa in the study area (relative abundance >5% in at least one sample). **6–13** *Achnanthydium* spp. **14–15** *Rosseththydium petersenii* **16–17** *Psammothidium* sp1. **18–19** *Psammothidium broenlundense*. **20–21** *Psammothidium marginulatum*. **22–23** *Psammothidium* sp2. **24–25** *Psammothidium kryophilum*. **26–27** *Eucocconeis flexella*. **28–29**. *Eucocconeis laevis* incl. var. *austriaca*. **30** *Meridion circulare* (Grev.) C.Agardh. **31** *Diatoma tenue*. **32** *Diatoma moniliformis*. **33** *Fragilaria gracilis* Østrup. **34** *Fragilaria* sp1. **35** *Fragilaria* sp2. **36** *Staurosirella* aff. *lapponica* (Grunow) D.M.Williams and Round. **37**

Nitzschia subamphioxoides Hust. **38**. *Hantzschia amphioxys*. **39**. *Nitzschia linearis* var. *subtilis*. **40** *Denticula kuetzingii* incl. var. *rumrichae*. **41**. *Denticula tenuis*. **42** *Nitzschia modesta* Hust. **43** *Nitzschia suchlandtii* Hust. **44** *Nitzschia paleaceae* Grunow. **45**. *Nitzschia* cf. *flexoides* Geitler. **46** *Nitzschia* cf. *palea*. **47** *Nitzschia lacuum* Lange-Bert. **48–49** *Nitzschia perminuta* form 4. **50–51**. *Nitzschia* cf. *soratensis*. **52–53**. *Nitzschia* cf. *liebethruthi* Rabenh. **54–55**. *Nitzschia perminuta* form 3. **56–57**. *Nitzschia perminuta* form 2. **58–59**. *Nitzschia perminuta* form 1. **60–61**. *Nitzschia* cf. *acidoclinata*. Scale bar = 10 µm

to what extent this seemingly broad habitat tolerance is real or whether the different species also differ in their preferred environmental conditions. Other rather common taxa

that were not tightly associated with one or more groups include *N. perminuta* form 2, *N. perminuta* form 3, *N. perminuta* form 4, *Eucocconeis laevis* (Østrup) Lange-Bert.

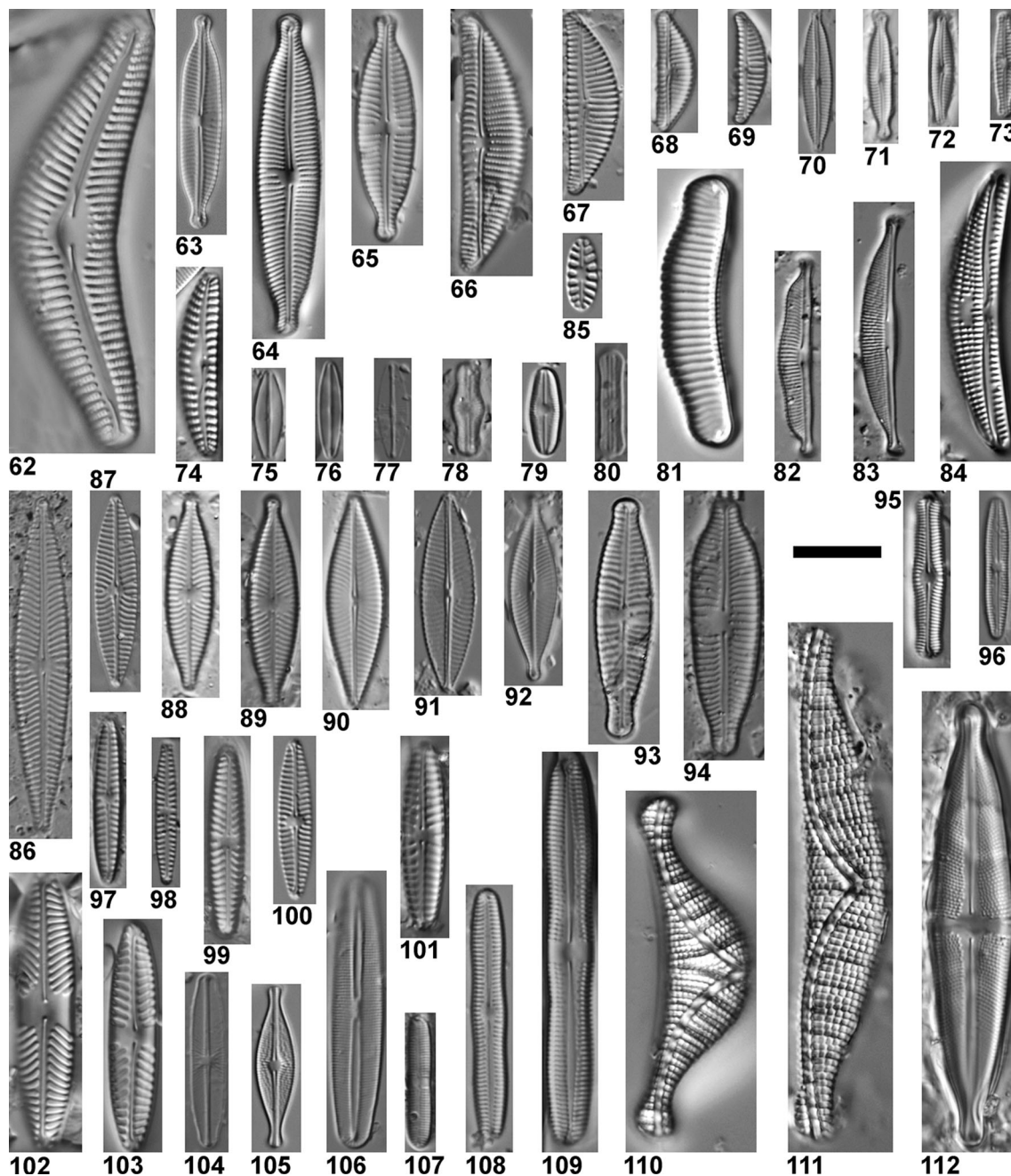


Fig. 62–112 Overview of the most common diatom taxa in the study area (relative abundance >5 % in at least one sample). **62** *Cymbella neocistula*. **63** *Cymbopleura broenlundensis* (Foged) Krammer. **64** *Cymbopleura angustata* var. *spitsbergensis* Krammer. **65** *Cymbopleura* sp1. **66** *Encyonema silesiacum* (Bleisch) Krammer. **67** *Encyonema* aff. *ventricosum* (C.Agardh) Grunow. **68** *Encyonema minutum*. **69** *Encyonema fogedii*. **70** *Encyonopsis subminuta*. **71** *Encyonopsis* sp2. **72** *Encyonopsis* sp3. **73** *Encyonopsis* sp5. **74** *Cymbella botellus*. **75** *Adlafia minuscula* Grunow. **76** *Mayamaea* cf. *aliena*. **77** *Craticula molesta* (Krasske) Lange-Bert. & Willmann. **78** *Humidophila ingaeiformis*. **79** *Humidophila perpusilla*. **80** *Humidophila paracontenta*. **81** *Eunotia* aff. *arcubus* Nörpel & Lange-Bert. **82** *Halamphora dusenii* (Brun) Levkov. **83** *Halamphora oligotrappenta*. **84** *Amphora langebertalotii* var. *tenuis* Levkov & Metzeltin. **85** *Hygropetra balfouriana*. **86** *Navicula* sp5. **87** *Navicula cryptotenella* Lange-Bert. **88** *Navicula*

ireneae. **89** *Navicula* sp6. **90** *Navicula phyllepta*. **91** *Navicula phylleptosoma*. **92** *Navicula* sp7. **93** *Gomphonema micropus* Kütz. **94** *Gomphonema* aff. *nathorstii*. **95** *Chamaepinnularia gandrupii* (J.B.Petersen) Lange-Bert. & Krammer. **96** Diatom sp. (aff. *Caloneis sublinearis* (Grunow) Krammer). **97** *Navicula pseudotenelloides* Krasske. **98** *Navicula bjoermoeyaensis* Metzeltin, Witowski & Lange-Bert. **99** *Navicula doehleri* Lange-Bert. **100** *Navicula arctotenelloides* Lange-Bert. & Metzeltin. **101** *Navicula lacuum* Lange-Bert., L.Hoffm., Werum & Van de Vijver. **102** *Pinnularia brebisonii* var. *acuta* Cleve-Euler. **103** *Pinnularia obscura*. **104** *Kobayasiella* sp. **105** *Brachysira neoexilis* Lange-Bert. **106** *Frustulia amosseana* Lange-Bert. **107** *Caloneis fasciata* (Lagerst.) Cleve. **108** *Caloneis tenuis*. **109** *Caloneis backmanii* Cleve-Euler. **110** *Epithemia* cf. *sorex* Kütz. **111** *Epithemia* cf. *adnata* (Kütz) Bréb. **112** *Stauroneis* aff. *subgracilis* Lange-Bert. & Krammer. Scale bar = 10 µm

incl. var. *austriaca* (Hust.) Lange-Bert. and *Eucoconceis flexella* (Kütz.) Meister.

Group A (white up-triangles) was entirely composed of epilithon samples (Table 1) of the ponds from the peninsula in front of the Nordenskiöld glacier. These ponds were characterized by a relatively young age (30–40 years), were located close to the fjord and were potentially influenced by the Arctic tern colony present on the peninsula (Table 1). All ponds additionally showed the most alkaline pH of all localities (Table 1). *Nitzschia perminuta* form 1 (Grunow) Perag. (14.6 %), *Nitzschia cf. acidoclinata* Lange-Bert. (12.3 %), *Achnanthydium* spp (10.6 %), *Navicula ireneae* Van de Vijver et al. (5.7 %), *Encyonema minutum* (Hilse) D.G.Mann (5.2 %) and *Encyonema fogedii* Krammer (4.8 %) dominated the community (Fig. 5), and several other taxa, e.g. *Nitzschia cf. palea* (Kütz.) W.Smith (2.8 %), *Nitzschia linearis* var. *subtilis* (Grunow) Hust. (2.7 %), *Mayamaea permitis* (Hust.) Bruder and Medlin (0.7 %), *Navicula meniscus* J.Schumann (0.4 %) and *Navicula gregaria* Donkin (0.3 %), were almost entirely restricted to this community. Other *Navicula* taxa reached clearly higher abundances in these ponds compared to the other communities, i.e. *Navicula lacuum* Lange-Bert., L.Hoffm., Werum and Van de Vijver (2.7 %), *Navicula phylleptosoma* Lange-Bert. (1.1 %), *Navicula phyllepta* Kütz. (0.6 %), *Navicula slesvicensis* Grunow (0.1 %) and *Navicula vaneei* Lange-Bert (0.1 %).

Group B (black squares) was dominated by *Diatoma tenuis* (36.0 %) and *Achnanthydium* spp. (28.4 %) (Fig. 5). Other important taxa are *Encyonopsis subminuta* Krammer and E.Reichardt (5.6 %), *E. laevis* incl. var. *austriaca* (4.4 %) and *R. petersenii* (4.3 %). This diatom community was dominant in often rather large lakes and ponds with incoming or outgoing streams (Table 1), often located in moraines (Table 1).

The third group (grey circles) was characterized by *Achnanthydium* spp (17.3 %), *R. petersenii* (13.5 %), *Denticula tenuis* (8.4 %) and *Denticula kuetzingii* Grunow including var. *rumrichae* Krammer (4.6 %). *Cymbella botellus* (Lagerst.) A. Schmidt (4.0 %) and *Caloneis tenuis* (W.Greg.) Krammer (3.0 %) were largely restricted to group C (Fig. 5). Less abundant although typical taxa for group C were amongst others *Fragilaria* Lyngbye sp2 (1.0 %), *Cymbella weslawskii* Krammer (0.8 %), *Cymbella hantzschiana* var. *borealis* Krammer (0.7 %) and *Brachysira zellensis* (Grunow) Round and D.G.Mann (0.4 %). The diatom flora of group C could generally be found in large lakes and ponds located on the raised marine beaches or in inland valleys with extensive vegetation development and, apart from one exception (two samples of a pond in the moraine of Svenbreen), not in moraines (Table 1).

Finally, group D (grey diamonds) was almost entirely restricted to kettle lakes and ponds with the one exception being an inland valley pond with snow fields as main water source and characterized by high water-level fluctuations during the summer season (Table 1). The flora was dominated by *Achnanthydium* spp (22.3 %), *Encyonopsis* sp5 (5.8 %), *N. perminuta* form 4 (5.8 %) and *Psammothidium* Bukhtiyarova and Round sp1 (5.6 %) (Fig. 5). Other important taxa included *Denticula tenuis* (4.4 %), *E. laevis* incl. var. *austriaca* (3.8 %), *N. perminuta* form 3 (3.0 %) and *E. flexella* (2.1 %). *Psammothidium marginulatum* (Grunow) Bukht. and Round (1.6 %), *Psammothidium kryophilum* (J.B.Petersen) E.Reichardt (1.0 %), *Psammothidium broenlundense* (Foged) Hamilton, D.Anton. and Siver (0.8 %) and *Psammothidium* sp2 (0.6 %) reached higher abundances in group D compared to the others.

Six samples could not be attributed to one of the previous groups (Fig. 3). Samples SP59 and SP60 had an entirely different diatom flora dominated by *Humidophila perpusilla* (Grunow) Lowe et al. (40 %), *H. paracontenta* (Lange-Bert. and Werum) Lowe et al. (37.8 %), *Gomphonema* aff. *nathorstii* Foged (7.5 %), *R. petersenii* (4.0 %) and *Cymbella neocistula* Krammer (3.1 %). *Achnanthydium* spp, highly common in the entire study area, was rather rare in this pond (1.3 %). All samples taken from the Brucebyen lakes and ponds (SP16, SP17 and SP18) were predominantly dominated by *Nitzschia cf. serratensis* E.Morales and M.L.Vis (50 %), which is as good as absent in all other localities. Other rather abundant diatom taxa were *D. kuetzingii* incl. var. *rumrichae* (12.9 %), *Achnanthydium* spp (7.4 %) and *Diatoma moniliformis* Kütz. (2.6 %). At last, the artificial basin of Pyramiden (sample SP1B) had the highest number of species of all communities (Table 1). *Fragilaria* sp1 (19 %), *Halumphora oligotraphenta* (Lange-Bert.) Levkov (8 %) and *Pinnularia obscura* Krasske (6 %) were the most common diatoms. *Humidophila ingeaeformis* (Hamilton and D.Anton.) Lowe et al. (5.3 %) and *Stauroneis francisci-josephi* Van de Vijver and Lange-Bert. (0.5 %) were restricted to this basin.

Discussion

Diatom diversity and biogeography

In contrast to many previous ecological studies focusing on Arctic diatom communities, this study used a high number of recent identification guides on diatom taxonomy (Online Resource 3) in combination with detailed SEM observations and investigated type materials in order to distinguish fine detailed differences in populations and species, likely explaining the high number of unidentified valve forms

(morphospecies). This indicates that the diatom flora of Spitsbergen is not well known and that many taxa remain to be discovered and described. Previously, Antoniadès et al. (2008) already argued that the diatom flora of the Canadian Arctic is in need of a thorough taxonomic study and that many taxa belong to species complexes that cannot easily be separated without the use of SEM. The results of this study indicate this is equally true for Spitsbergen, suggesting that the Arctic diatom flora is highly diverse and distinct from other regions, adding additional evidence to previous findings of the existence of distinct diatom biogeographies (Vyverman et al. 2007; Vanormelingen et al. 2008) and confirming the results of Foged (1981) who argued that extensive studies of the High Arctic diatom flora will yield many more new (rare) species. Moreover, it is highly likely that many morphospecies as defined in this study actually comprise (pseudo)cryptic species complexes (e.g. Souffreau et al. 2013b). A first molecular investigation of several *Achnanthisidium* strains already revealed three lineages corresponding to different species that can hardly be identified in LM and that are in need of a more thorough examination in SEM (Pinseel et al., unpublished results). This might equally be the case for morphospecies such as *Hantzschia amphioxys* (Ehrenb.) Grunow, *Hantzschia abundans* Lange-Bert., *D. kuetzingii* and several *Nitzschia* taxa, suggesting that the true diversity is likely to be still underestimated in the present survey. Recent progress in single-cell sequencing (Lang and Kaczmarek 2011; Hamilton et al. 2015; Lefevbre and Hamilton 2015) and environmental next-generation sequencing approaches (e.g. Stoof-Leichsenring et al. 2014) has the potential to shed light on the actual diversity and biogeography of (Arctic) diatoms by undertaking large-scale DNA-based diversity studies.

In general, we found similar diatom floras as other studies from the High Arctic (e.g. Foged 1964; Metzeltin and Witkowski 1996; Antoniadès et al. 2008; Pla-Rabés et al. 2016). However, Foged (1964) reported a much larger number of diatom taxa, which is likely related to the distinctly higher number of samples he studied (209 vs. 87 in this study), the inclusion of samples from humid soils and terrestrial mosses, and the larger study area (about 40,000 km² ranging between 77.5° and 80° N and 10° to 18° E). Although Foged (1964) used a highly refined morphospecies concept, he did not have access to modern-day techniques (i.e. high-resolution SEM) and likely overlooked morphological differences between closely related species or within small-celled taxa, suggesting he might have underestimated the diatom diversity in his samples. For example, Foged (1964) mentioned *Cymbella microcephala* Grunow (currently known as *Encyonopsis microcephala* (Grunow) Krammer) being a common

diatom in Spitsbergen. Krammer (1997b), however, recognized that *C. microcephala* comprises a species complex, and careful examination of valves belonging to the *C. microcephala* complex from our study area revealed at least four morphologically distinct species. More recent surveys from the Svalbard Archipelago might also have underestimated the diversity in their surveys (e.g. Picińska-Fałtynowicz 1988; Beyens and De Bock 1989; Van de Vijver et al. 1999; Beyens and Van de Vijver 2000; Jones and Birks 2004), for example, because they did not had access to modern-day techniques, or because species taxonomy and diversity were not their primary goal.

A direct comparison of this study with the extensive survey of the Canadian Arctic by Antoniadès et al. (2008) revealed that both studies have 127 taxa in common (results based on direct morphological comparison, nomenclatural changes and unidentified but identical taxa taken into account) and several unknown taxa listed in Antoniadès et al. (2008) have also been observed in Petuniabukta, adding additional evidence for the existence of a circumarctic diatom flora (e.g. Pla-Rabés et al. 2016). Moreover, both regions exhibit a large variety of cymbelloid diatoms (mainly *Cymbella*, *Cymbopleura*, *Encyonema* and *Encyonopsis*), *Pinnularia*, *Caloneis* Cleve and *Navicula*. However, Petuniabukta shows a distinctly higher diversity of *Nitzschia*, whereas the Canadian Arctic clearly possesses a larger diversity of *Eunotia* Ehrenb. Genera such as *Berkeleya* Greville and *Nupela* Vyverman and Compère have been observed in the Canadian Arctic but not in the present study, both regions distinctly differ in their species composition of *Stauroneis*, and almost 60 % of the taxa in this study have not been observed by Antoniadès et al. (2008). Such differences can be attributed to environmental and climatological differences of the sampled (micro)habitats and regions. For example, the high diversity of *Nitzschia* in Spitsbergen compared to the Canadian Arctic regions studied by Antoniadès et al. (2008) is likely related to the young and disturbed characteristics of most examined water bodies in this study and not to biogeographical differences, as high abundances of *Nitzschia* have been previously reported from the Canadian Arctic (e.g. Michelutti et al. 2003, 2013b). It can, however, be argued that differences in the diatom floras of both studies are partly related to the presence of (rare) species with restricted regional geographic distributions, confirming the results of Van de Vijver et al. (2005) who found striking dissimilarities in *Stauroneis* diversity and species composition between different Arctic regions. However, it has to be noted that both Antoniadès et al. (2008) and this study examined a very restricted area and more profound large-scale diversity screenings of High Arctic diatom floras are needed to unravel the biogeographies of polar diatoms.

Although generally observed as dominant parts of the High Arctic freshwater diatom flora (e.g. Douglas et al. 1994; Bouchard et al. 2004; Antoniadou et al. 2008; Paull et al. 2008), the tychoplanktonic genera *Staurosira* Ehrenberg and *Staurosirella* Williams and Round (Denys 1991) did not reach high abundances in the samples examined in this study, reaching total abundances of 1.1 and 0.1 %, respectively. Similar observations have been made from Franz Josef Land by Pla-Rabés et al. (2016) who suggested that these genera might show biogeographical patterns in the Arctic region. However, this observation might also (partly) be related to the type of the sampled habitats in this study, as most studies reporting high abundances of *Staurosira* and *Staurosirella* species studied surface sediments from the middle or the deepest point of the water bodies, whereas in this study, the littoral zone was examined. Upon examination of the top layer of a sediment core taken from the deepest zone of one of the lakes in the study area, a relatively high abundance (17 % of all counted valves) of *Staurosira venter* (Ehrenb.) Grunow morphotypes has been observed (Pinseel et al., unpublished results).

It is currently still unclear whether the use of a more fine-grained taxonomy will yield significant benefits when applying diatoms as environmental indicators or to reveal community structures and associations. Whereas it can be argued that distinct differences in growth forms, survival strategies and ecological preferences are largely confined to the generic level, it is becoming increasingly clear that common cosmopolitan morphospecies often constitute of distinct (pseudo)cryptic species that show niche differentiation (e.g. Potapova and Hamilton 2007; Paull et al. 2008; Souffreau et al. 2013b). In this regard, the application of a narrow morphospecies concept theoretically should result in gaining ecological information in (palaeo)environmental studies, but only when the ecological preferences and tolerances of the newly delineated taxa are well known. Currently, little studies exist on the ecology of specific High Arctic diatom taxa, however. Specifically in this study, we found that a refined taxonomy can, but does not necessarily have to, lead to an increase in ecological information. For example, four morphological forms of *N. perminuta* were rather dominantly present in the study area. Whereas *N. perminuta* form 1 reached distinctly higher abundances in group A compared to the other groups and was an important taxon in the ordinations, *N. perminuta* forms 2, 3 and 4 were not confined to one group, occurring in relatively high abundances in all groups. Furthermore, at least three pseudocryptic species of the *A. minutissimum* complex are present in the study area. As these taxa were counted as one, it is up to date not clear whether they differ in their ecological preferences. However, detailed SEM analysis of a selection of samples revealed that the two

most common *A. minutissimum* taxa frequently co-occur, suggesting they overlap in their niche distributions.

Freshwater littoral diatom communities

In general, the diatom flora of Petuniabukta is a typical flora for oligotrophic and alkaline environments and is dominated by *Achnantheidium* and *Nitzschia*. Whereas the former is only represented by a handful of species, the latter is highly diverse. *Nitzschia* seems most diverse and common in young, recently formed, water bodies, suggesting many *Nitzschia* species are successful colonizers of disturbed environments (e.g. Peterson and Hoagland 1990), whereas the dominance of *Achnantheidium* spp in almost all samples likely reflects its ability to immigrate fast in and adapt to a wide range of habitats, including disturbed and instable nutrient-poor environments (e.g. Stevenson et al. 1991; Passy 2007; Wang et al. 2014). Some diatom taxa, such as *Achnantheidium* spp, are generally present in the study area and do not seem confined to a certain habitat type, whereas others do have a specific preference for a certain microhabitat. Examples include taxa that are mainly confined to epiphytic habitats such as *R. petersenii*, *Hygropetra balfouriana* (Grunow) Krammer and Lange-Bert., *Eunotia* and *Epithemia* Kütz., and taxa that are more commonly found in epilithic environments such as *Psammothidium*. This confirms previous studies by Douglas and Smol (1995) and Michelutti et al. (2003).

Four main diatom communities were defined in this study. The PCA analysis did not reveal large differences between the different groups but rather shows one continuum of samples (Fig. 4a, b). This is thought to be logical as all samples were taken from the littoral zones of lakes and ponds in a restricted area, suggesting that (almost) all water bodies will be to some extent subject to an exchange of their diatom floras by vectors such as wind or biota. However, even at this small spatial scale, clear ecological differences exist between the habitat types of the different diatom communities. In this regard, differences in the microhabitat (e.g. the substratum) of the sampled diatom communities are thought to be extremely important in explaining why several different samples of one lake/pond or lakes/ponds of the same locality cluster in different groups.

An unstable environment, often associated with moraines, is suggested as a highly important factor shaping the diatom communities. Both the *Achnantheidium* spp-*Psammothidium-Encyonopsis* (group D) and the *Achnantheidium* spp-*Diatoma tenuis* (group B) communities are tightly associated with the, often unstable and young, kettle lakes and ponds (Table 1). Moreover, a distinct overlap in localities exists between these communities as all samples of the kettle ponds of the glaciers Ragnar and Hørbye

belong to one of them, suggesting that both communities are closely related to each other. First, the *Achnanthydium* spp-*Psammothidium-Encyonopsis* community shows a rather high abundance and diversity of *Psammothidium* spp, which is likely explained by the absence of vegetation and the unstable nature of these water bodies which are susceptible to large water-level fluctuations (Round and Bukhtiyarova 1996; Michelutti et al. 2003; Bouchard et al. 2004; Passy 2007). In contrast, a distinct character of most, but not all, lakes and ponds assigned to the *Achnanthydium* spp-*D. tenuis* community is the presence of water currents due to incoming or outgoing streams with high flow velocity or with environmental signs indicating the presence of temporary streams (Table 1). This suggests that streams are important in separating groups B and D, indicating tolerance of *D. tenuis* for turbulent environments. *Diatoma tenuis* cultures established from single-cell isolates of Petuniabukta formed dense networks of cells that were tightly attached to each other and their substrate, presumably by means of extracellular polysaccharides (Pinseel, own observations). Compared to motile free-living species such as *Navicula*, *D. tenuis* colonies are thus forming multiple rather strong connections with their substrate and are therefore likely to be well adapted to disturbed environments, such as stream-influenced water bodies. This confirms the results of Antoniadou and Douglas (2002) who observed *D. tenuis* in rather high abundances in tidally influenced Arctic streams. Moreover, *D. tenuis* is common in Swedish rivers, north of the Arctic circle (Van de Vijver and Jarlman, unpublished results). Furthermore, similar attachment strategies have been reported for *Achnanthydium* (Wang et al. 2014), the other dominant diatom in group B, and *Hannaea arcus* (Ehrenb.) R.M.Patrick, a taxon typical for streams (Antoniadou and Douglas 2002; Passy 2007; Hoffmann et al. 2011), was found in four out of ten samples of the *D. tenuis* community, in all cases samples taken in lakes and ponds with a distinct current. Therefore, it is hypothesized that the presence of distinct streams or currents separates groups B and D by favouring diatom species with attachment strategies that allow them to withstand stream-created disturbance (e.g. Hoagland et al. 1982), since the localities are similar for all other known aspects (no or few vegetation present, often unstable lakes/ponds and a dominance of epilithon samples). Moreover, incoming streams are expected to profoundly alter the biological and limnological characteristics of the microhabitats by, for example, creating disturbance or supplying the lake with anorganic particulates (e.g. Hay et al. 2000). In this light, differences in microhabitat likely explain why different samples of the same stream influenced locality cluster separately in groups B and D. For example, differences in the intensity of disturbance created by streams in different parts of the water

body will determine whether the diatom communities present are driven by disturbance or competition (Passy 2007). Additionally, it is suggested that localities that did not show in- or outgoing streams at the moment of sampling but that were nevertheless dominated by *D. tenuis* exhibit temporal streams at other times of the year or might be influenced by subsurface run-off which is likely to be present in moraines. It is, however, not to be excluded that other, currently unknown, environmental parameters structure the *Achnanthydium* spp-*D. tenuis* and *Achnanthydium* spp-*Psammothidium-Encyonopsis* communities.

A distinct combination of environmental conditions, including a highly alkaline pH, influence of a nearby fjord and (former) glacial and biotic impact, resulted in the establishment of a relatively unique diatom community (group A) in all ponds of the peninsula. These ponds have a very young age (30–40 years), formed after the Nordenskiöld glacier retreated from the peninsula. Although being located adjacent to the Nordenskiöld glacier, the peninsula is currently hydrologically isolated from the glacier. Additionally, these ponds differ from all other water bodies in the study area by their location in rock cavities, directly associated with the calcareous metamorphic bedrock, which likely causes the highly alkaline pH of these ponds. The presence of several *Navicula* taxa, i.e. *N. gregaria*, *N. meniscus*, *N. phyllepta*, *N. phylleptosoma*, *N. slesvicensis* and *N. vaneii*, typical for brackish conditions suggests an influence of the nearby marine environment, either due to sea spray or by salinity input and/or transport of diatoms from the fjord to the ponds by biotic vectors such as birds. However, the general low abundances of these taxa (0.1–1.1 % of all counted valves) combined with the moderate measured conductivity (Table 1) suggest that the marine influence is limited. The taxonomic status of both prevailing taxa, *N. perminuta* form 1 and *N. cf. acidoclinata*, is unclear, but their dominating presence in group A compared to the other groups suggests they are well adapted to the unique combination of environmental conditions in these young and disturbed ponds and that they are likely highly successful early colonizers of newly available habitats (Peterson and Hoagland 1990). It is thought that the Arctic tern colony has a varying influence on the ponds of the peninsula. Several ponds show rather high abundances of aerophilic *Mayamaea* taxa, such as *Mayamaea cf. aliena* (Krasske) Lange-Bert and *M. permitis*, indicating seasonal water-level changes and/or high levels of organic matter, such as bird's faeces (Lange-Bertalot 1997; Morales and Manoylov 2009). Several other ponds, on the contrary, show rather high abundances of *E. minutum* and *E. fogedii*, which are typically regarded as indicators for oligotrophic waters with moderate electrolyte content (Krammer 1997a; Antoniadou et al. 2008), suggesting that these ponds are less influenced by the bird

colony and confirming the moderate conductivity measurements in most samples of this community. Within-community differences could partially be related to differences in nutrient availability as a result of an unequal influence of the Arctic tern colony.

In contrast to groups A, B and D, group C (the *Achnanthydium* spp-*Rossithydium* community) seemed to be largely associated with (semi)permanent and older, often larger, lakes and ponds with a moderate to very dense developed moss vegetation on the shores, occasionally extending into the lakes and ponds. Furthermore, group C in general seems to have a more diverse diatom community compared to most other groups (Table 1). This might be a reflection of the larger habitat availability in older, larger and ecologically diverse water bodies, which likely explains the higher abundances of larger diatoms such as *Cymbella* in group C (Bouchard et al. 2004). Most moss samples belonged to this community, explaining the high abundances of several typical moss-inhabiting genera such as *Denticula* and the restriction of *Eunotia* and *Epithemia* to this assemblage (e.g. Beyens and De Bock 1989; Douglas and Smol 1995; Van Kerckvoorde et al. 2000) as well as taxa such as *H. balfouriana* (Michelutti et al. 2003, 2013a). Apart from *Achnanthydium* spp, group C is largely dominated by *R. petersenii*. Despite having a similar survival strategy as *Achnanthydium* and *Psammothydium* (Passy 2007; Lange et al. 2011), *R. petersenii* seems mainly confined to epiphytic, often not submerged, habitats, as has been observed earlier by Antoniadou and Douglas (2002) and Michelutti et al. (2003). The former suggested that this finding might be related to the tolerance of *R. petersenii* to periodic desiccation, likely making it a good survivor in littoral zones of Arctic lakes and ponds, which are susceptible to water-level fluctuations during the growing season (Smol and Douglas 2007). *Rossithydium petersenii*-dominated diatom communities have already been reported from the Brøgger peninsula in north-west Spitsbergen (Van de Vijver et al. 1999) and Nunavut, Canada (Van de Vijver et al. 2003), in large shallow pools surrounded by large moss banks and lotic environments, respectively. The *R. petersenii* community from the Brøgger peninsula also showed high abundances of *Achnanthydium minutissimum* s.l. suggesting a high similarity with the *Achnanthydium* spp-*Rossithydium* community of Petuniabukta, both in species composition and in habitat type.

Six samples could not be attributed to one of the previously discussed diatom communities as they represent three distinctly different diatom floras. Samples SP59 and SP60 were both taken from the same pond at a mountain top near Mimerdalen which is characterized by a very short growing season due to prolonged ice cover and extremely high water-level fluctuations during the summer season.

The latter result in temporary desiccation of large parts of the pond and likely explain the dominance of *Humidophila* Lowe et al. taxa, typical for moist subaerial environments (Lowe et al. 2014). The diatom flora of the Brucebyen water bodies (samples SP16, SP18 and SP19) also represents a distinctly different diatom community. Similar to the Ebbadalen ponds of which the diatom flora belongs to the *Achnanthydium* spp-*Rossithydium* community, these water bodies have highly vegetated shores with distinct biotic influence of geese and are located close to the fjord. The presence, however, with low abundance, of *Navicula* taxa typical for brackish conditions, such as *N. vaneei*, *N. luciae* Witowski and Lange-Bert. and *N. hanseatica* ssp. *circumartica* Lange-Bert. and Metzeltin, might suggest a limited influence of the marine environment. Next to both Brucebyen water bodies, two deserted wooden cabins are located which have in the past been used as a base camp of coal miners and whale hunters. It is likely that this former human presence might have influenced the water bodies. The taxonomic status of *N. cf. soratensis*, the dominating diatom, is unclear, but it is suggested that it benefits from eutrophic conditions. Finally, the artificial basin of Pyramiden (sample SP1B), created to supply the Russian mine city Pyramiden with drinking water, is home to one of the most diverse diatom floras in the study area (Table 1) and is characterized by a distinctly different species composition than all other water bodies. It is hypothesized that human activities such as construction works, transportation and disturbance of the water column by pumping up water might have had a distinct influence on the diatom community that is developed in this basin. However, as only one sample of this basin was examined, caution has to be made with any conclusions.

Conclusion

This study revealed a high number of diatom taxa unknown to science that will need formal description in the future, indicating that the diatom flora of Spitsbergen is not well known. In general, a better knowledge of the freshwater diatom flora in Spitsbergen and the Arctic region as a whole is desired in order to improve both our fundamental understanding of the diversity, ecology, community associations and biogeography of Arctic diatoms and to advance future (palaeo)ecological research in the Arctic.

Statistical analysis revealed the presence of four major littoral freshwater diatom communities in Petuniabukta. In general, habitat type, habitat diversity, habitat stability, the presence of streams, pH (related to the bedrock) and marine influence seem to be the major factors determining the diatom communities of Petuniabukta. The *Achnanthydium* spp-*Rossithydium* community is a typical littoral

community found in often rather large lakes and ponds with no or limited flow velocities and, apart from a few exceptions, with a well-developed moss coverage. Both the *Achnantheidium* spp-*Diatoma tenuis* community and the *Achnantheidium* spp-*Psammothidium-Encyonopsis* communities look to be principally associated with unstable kettle lakes and ponds in barren regions, with the former being influenced by distinct streams. In contrast, the *Achnantheidium* spp-*Nitzschia* community is associated with young ponds developed in rock cavities, characterized by variable nutrient conditions, a slight marine influence and a highly alkaline pH caused by the calcareous metamorphic rocks directly underlying these ponds.

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Compliance with ethical standard

Conflict of interest The authors declare that they have no conflict of interest.

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