

Diversity, ecology and biogeography of the freshwater diatom communities from Ulu Peninsula (James Ross Island, NE Antarctic Peninsula)

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Abstract The diversity, ecology and biogeography of diatoms in lakes, seepage areas and streams on the Ulu Peninsula, a large ice-free area in the northern part of James Ross Island (Weddell Sea), were studied. A diverse diatom flora of 123 taxa was observed, dominated by several *Nitzschia* taxa, *Psammothidium papilio*, *Eolimna jamesrossensis*, *Fragilaria capucina* and *Fistulifera saphophila*. The results from the similarity and diversity analysis suggest James Ross Island to be biogeographically positioned within the Maritime Antarctic region, yet with some affinities with the flora of Continental Antarctica, as shown by the presence of *Luticola gaussii* and *Achnanthes taylorensis*. Based on our data, James Ross Island can thus be located close to the boundary of the two main Antarctic biogeographical regions. Diatom communities present in streams and seepage areas could be clearly distinguished from those in lakes, the latter being much more species rich. Based on the multivariate analysis, conductivity and nutrients were selected as the two main environmental factors determining the diatom composition in the Ulu

Peninsula lakes. The revised taxonomy of the Antarctic diatom flora induced the construction of a transfer function for water conductivity in the studied lakes that can be applied in further palaeoecological studies.

Keywords Diatoms · Lakes · Seepages · Streams · Ulu Peninsula · James Ross Island · Community analysis · Antarctic Peninsula

Introduction

The Antarctic Peninsula together with the neighbouring islands and archipelagos is a very dynamic region recently undergoing severe environmental changes, as opposed to the Antarctic Continent (Vaughan et al. 2003). These changes are most likely related to climate change affecting the ecosystems and their biodiversity (Laybourn-Parry and Pearce 1997; Quayle et al. 2002). The analysis and interpretation of the terrestrial and freshwater biodiversity in the Antarctic and sub-Antarctic regions and the environmental factors influencing this diversity are some of the key research topics of the past two decades as demonstrated in the growing

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number of papers dealing with this subject (e.g. Convey 2001; Chown and Convey 2007 and references therein).

Diatoms (Bacillariophyceae) are one of the most abundant algal groups in terrestrial and freshwater ecosystems in the Antarctic and sub-Antarctic regions (Jones 1996; Van de Vijver and Beyens 1999a; Vyverman et al. 2010). Diatom assemblages often serve as valuable bio-indicators, due to the narrow tolerances of most species to site-specific characteristics. Their frustules are composed of long-term resistant silica and are therefore well preserved in sediments. Since the 1990s, diatoms have been widely used in ecological, biogeographical and palaeoecological studies across the entire Antarctic region (e.g. Oppenheim and Greenwood 1990; Jones et al. 1993; Kawecka and Olech 1993; Roberts and McMinn 1996; Van de Vijver and Beyens 1996; Gremmen et al. 2007; Verleyen et al. 2009; Sterken et al. 2012). In contrast to several previously published studies stressing upon the cosmopolitan nature of the Antarctic flora (Toro et al. 2007; Vinocur and Maidana 2010), a highly specific diatom flora has been observed on various islands in the northern Antarctic Peninsula region (e.g. Sabbe et al. 2003; Van de Vijver et al. 2010a, 2011a, 2012; Zidarova et al. 2010; Kopalová et al. 2011).

The construction of the Czech J. G. Mendel research station on the Ulu Peninsula (James Ross Island, NE Antarctic Peninsula) enabled the study of the freshwater habitats and their diatom flora in this area. Until now, only a few non-taxonomic studies focusing on the diatom flora of this island had been published, mostly dealing with palaeoecological issues (Hansson and Håkansson 1992; Burckle and Wasell 1995; Håkansson et al. 1995; Björck et al. 1996). Recently, the diatom diversity of seepage areas and streams has been analysed based on a refined taxonomy (Kopalová et al. 2012). Although a high number of new taxa have recently been described from James Ross Island (Esposito et al. 2008; Kopalová et al. 2009, 2011), the factors influencing the diatom flora in the freshwater habitats of James Ross Island are only poorly known.

The present study is the first focusing on the ecology of diatom communities in freshwater ecosystems on James Ross Island, revealing relationships between site-specific environmental parameters and diatom diversity. As the island is located on the boundary between Maritime and Continental Antarctica (Øvstedal and Lewis-Smith 2001), studying its diatom flora can add valuable information on the biogeographical boundaries of several typical Antarctic taxa.

Study area

The present study has been carried out on the Ulu Peninsula, northern James Ross Island (64°10'S, 57°45'W), a

2,600 km² large island, situated in the north-western part of the Weddell Sea, close to the northern tip of the Antarctic Peninsula (Fig. 1).

Eighty per cent of the island is permanently covered by ice. Only Ulu Peninsula in the northern part of the island deglaciated during the last 12.5 ka (Nývlt et al., pers. observation) forming nowadays a large ice-free area (Davies et al. 2013). Its location in the precipitation shadow of the Antarctic Peninsula, which forms an effective barrier to prevailing westerly winds (Engel et al. 2012), gives the island a more arid outlook compared to islands in the Maritime Antarctic region. Climatic conditions are described in Láska et al. (2011) and in Engel et al. (2012). The terrestrial vegetation of Ulu Peninsula is composed of bryophytes and lichens only (Láska et al. 2011).

In the northern part of the island, a higher number of large open water bodies and fresh water ecosystems can be found, mostly induced by glacial erosion and deposition and formed after ice cap retreat during the Holocene (Nedbalová et al. 2013). More details on the geology of the Ulu Peninsula can be found, for example, in Košler et al. (2009), Svojtka et al. (2009) and Nývlt et al. (2011). Recently, a study of the origin, geomorphological position, hydrological stability, bedrock geology and physical and chemical conditions of the lakes of Ulu Peninsula has been conducted (Nedbalová et al. 2013) defining six different lake types: stable shallow lakes in higher altitudes, semi-stable shallow coastal lakes, stable lakes in old moraines, small unstable lakes in young moraines, less-stable deep cirque lakes and very unstable kettle lakes. Stable lakes are permanent, old lakes and probably already present in the area for several hundreds to thousands of years. Seepages and streams are well developed. Seepage areas are shallow wetlands, representing one of the most characteristic habitats of Maritime Antarctica (Elster 2002). Together with streams, they are fed by melting water from retreating glaciers and snowfields (Engel et al. 2012). Their microflora is mostly composed of cyanobacteria, green algae and diatoms (Komárek and Elster 2008).

Materials and methods

Sampling

A total of 103 samples from streams, seepage areas and lakes were collected from James Ross Island (64°10'S, 57°45'W) during the austral summers of 2004 and 2006–2009 (Fig. 1; Table 1). Due to logistic constraints, no physico-chemical data were collected for stream and seepage area samples. Online Resource 1 summarizes the main physico-chemical parameters of the lake samples.

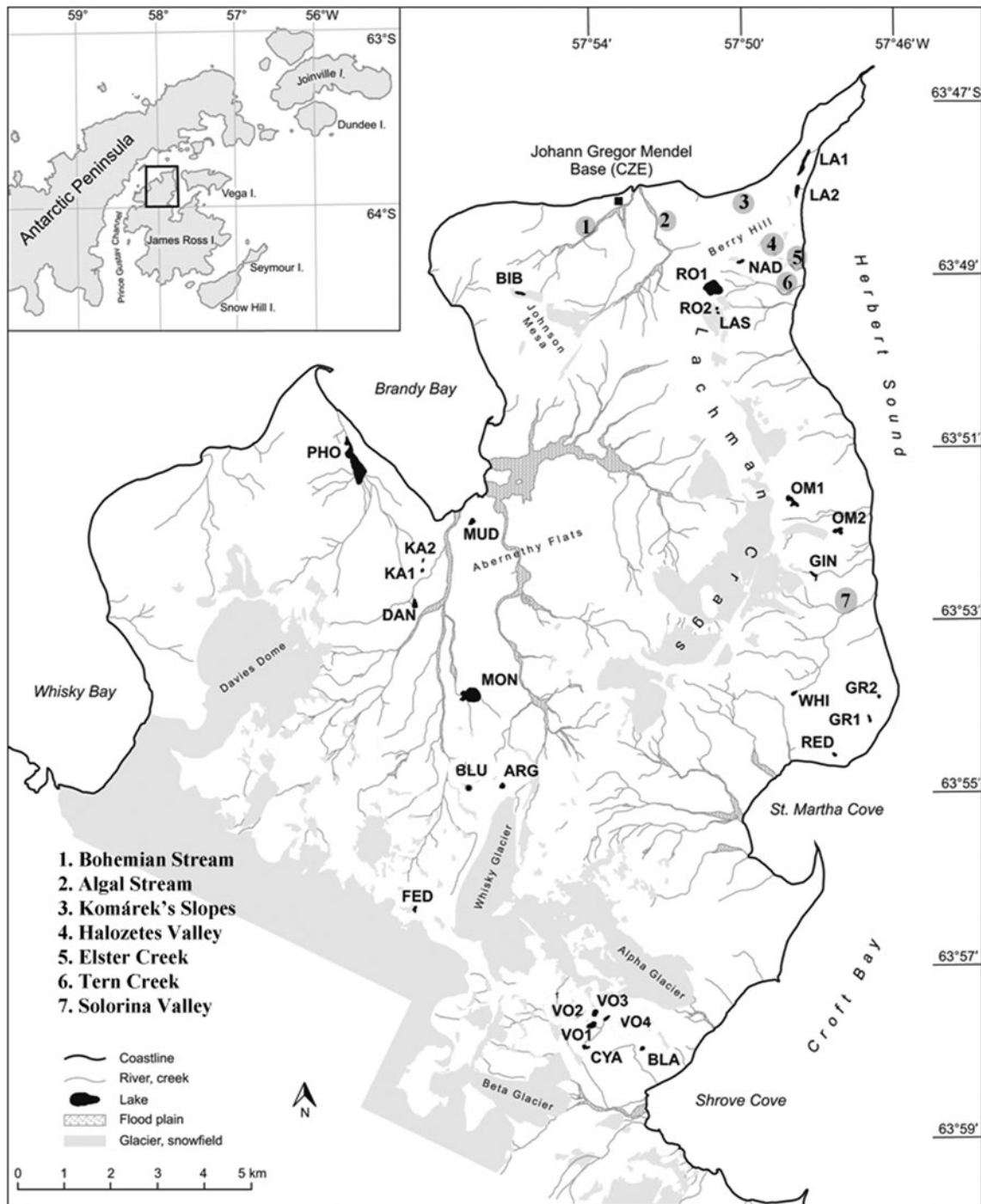


Fig. 1 Location of the sampled streams, seepage areas and lakes on the Ulu Peninsula. The *inset map* shows the position of James Ross Island in the Weddell Sea with the location of the Ulu Peninsula. Topography based on the map by Czech Geological Survey (2009)

When possible, both epilithic and epipellic samples were taken in the littoral zone of the lakes.

Slide preparation

Diatom samples collected in 2004 were kept frozen until analysed, whereas those from 2006 to 2009 were fixed with

formaldehyde (3 % final concentration). Subsamples were cleaned by a modified method described in Van der Werff (1955): small parts of the samples were cleaned by adding 37 % of H₂O₂ and heating to 80 °C for about 1 h, followed by addition of KMnO₄. After digestion and centrifugation (3 times 10 min at 3,700×g), the material was diluted with distilled water to avoid excessive concentrations of diatom

Table 1 List of all samples and sample codes used in this paper

	Sampling location (lake code)	Sample nature
<i>Lake sample</i>		
D1	Lachman 2 (LA2)	Epipelon
D2	Lachman 2 (LA2)	Epilithon
D3	Lachman 1 (LA1)	Epipelon
D4	Lachman 1 (LA1)	Epilithon
D5	Bibby (BIB)	Epipelon
D6	Bibby (BIB)	Epilithon
D8	Phormidium (PHO)	Epipelon
D9	Phormidium (PHO)	Epilithon
D10	Monolith (MON)	Epipelon
D11	Monolith (MON)	Epilithon
D12	Katia 1 (KA1)	Epipelon
D13	Katia 1 (KA1)	Epilithon
D14	Katia 2 (KA2)	Epipelon
D15	Katia 2 (KA2)	Epilithon
D16	Muddy (MUD)	Epipelon
D17	Muddy (MUD)	Epilithon
D19	Dan (DAN)	Epipelon
D20	Dan (DAN)	Epilithon
D21	Rozmberk 1 (RO1)	Epilithon
D22	Laska (LAS)	Epipelon
D23	Laska (LAS)	Epilithon
D24	Nadeje (NAD)	Epilithon
D25	Nadeje (NAD)	Sediment, 6 m depth
D26	Green 1 (GR1)	Epilithon
D27	Red (RED)	Epipelon
D28	Red (RED)	Epilithon
D29	White (WHI)	Epipelon
D30	White (WHI)	Epilithon
D31	Green 2 (GR2)	Epilithon
D32	Green 2 (GR2)	Epipelon
D33	Omega 2 (OM2)	Epilithon
D34	Omega 1 (OM1)	Epilithon
D35	Ginger (GIN)	Epilithon
D36	Ginger (GIN)	Epipelon
D37	Vondra 1 (VO1)	Epilithon
D38	Vondra 1 (VO1)	Epipelon
D39	Vondra 2 (VO2)	Epilithon
D40	Vondra 2 (VO2)	Epipelon
D41	Vondra 3 (VO3)	Epilithon
D42	Vondra 3 (VO3)	Epipelon
D43	Vondra 4 (VO4)	Epilithon
D44	Vondra 4 (VO4)	Epipelon
D45	Cyanobacterial (CYA)	Epilithon
D46	Cyanobacterial (CYA)	Epipelon
D47	Black (BLA)	Epilithon
D48	Black (BLA)	Epipelon
D49	Federico (FED)	Epilithon

Table 1 continued

	Sampling location (lake code)	Sample nature
D50	Argentino (ARG)	Epilithon
D51	Blue-green (BLU)	Epilithon
D52	Blue-green (BLU)	Epipelon
<i>Stream and seepage sample</i>		
S2	Komarek's slopes below Berry Hill	Seepage
S3	Komarek's slopes below Berry Hill	Seepage
ST	Tern creek, upper part, seepages	Seepage
S1A-J	Komarek's slopes below Berry Hill	Seepage
SL1	Seepages near Lachman Lakes	Seepage
SL2	Seepages near Lachman Lakes	Seepage
SB	Seepages, Bohemian stream	Seepage
SS	Seepages in Solorina Valley	Seepage
SP2	Seepages, Halozetes Valley	Seepage
SP3	Seepages, Halozetes Valley	Seepage
T0	Tern Creek	Stream
T1	Tern Creek	Stream
T2	Tern Creek	Stream
T3	Tern Creek	Stream
T4	Tern Creek	Stream
T6	Tern Creek	Stream
T7	Tern Creek	Stream
T8	Tern Creek	Stream
B	Bohemian Stream	Stream
B1	Bohemian Stream	Stream
B2	Bohemian Stream	Stream
B3	Bohemian Stream	Stream
B4	Bohemian Stream	Stream
B5	Bohemian Stream	Stream
B6	Bohemian Stream	Stream
B7	Bohemian Stream	Stream
A1	Algal Stream	Stream
A2	Algal Stream	Stream
A3	Algal Stream	Stream
A4	Algal Stream	Stream
A5	Algal Stream	Stream
A6	Algal Stream	Stream
A7	Algal Stream	Stream
A8	Algal Stream	Stream
A9	Algal Stream	Stream
A10	Algal Stream	Stream
A11	Algal Stream	Stream
A12	Algal Stream	Stream
A13	Algal Stream	Stream
A14	Algal Stream	Stream
A15	Algal Stream	Stream
E1	Elster Creek	Stream
E2	Elster Creek	Stream
E3	Elster Creek	Stream

valves. Cleaned diatom valves were mounted in Naphrax[®]. Samples and slides are stored at the Department of Ecology, Charles University in Prague (Czech Republic), with duplicates at the National Botanic Garden of Belgium (Meise, Belgium).

Sample analysis

In each sample, 400 (lake samples) or 300 (seepage and stream samples) valves were enumerated on random transects at 1,000× magnification under oil immersion using a Olympus BX51 microscope equipped with Differential Interference Contrast optics. Identifications of Antarctic species are based on Van de Vijver et al. (2002a, b, 2004a, 2010a, b, 2011a, b), Sabbe et al. (2003), Ohtsuka et al. (2006), Esposito et al. (2008), Van de Vijver and Mataloni (2008), Kopalová et al. (2009, 2011), Zidarova et al. (2009, 2010, 2012) and Van de Vijver and Zidarova (2011). For several species, identification up to species level was not possible due to their unclear taxonomic situation. Valves belonging to the *Nitzschia perminuta* (Grunow) M. Pergal.-complex were split into *N. perminuta* capitate specimens and *N. perminuta* non-capitate specimens based on the shape of the valve apices.

Further morphological, taxonomic and ecological research will be necessary to establish the correct identity of this species complex in the entire Maritime Antarctic region.

Data analysis

Diversity analysis [Shannon–Wiener diversity index (\log_{10} -based) and evenness index] was performed using the multivariate statistical package MVSP (Shannon and Weaver 1949). To determine the extent to which our sampling efforts represented the freshwater diatom flora of the Ulu Peninsula, the incidence-based species richness estimator (ICE, Chao et al. 2000) and the mean Chao2 richness estimator (Chao 1984), both using the EstimateS program version 8.2 (Colwell 2009), were calculated.

For a pairwise comparison of the diatom flora of James Ross Island with other Antarctic localities such as the Continental Antarctica, South Shetland Islands, Signy Island and the sub-Antarctic region, the community coefficient of Sørensen (1948) was used. This index has the following formula: $2c/(a + b + 2c)$, where ‘*a*’ and ‘*b*’ are the numbers of species exclusively observed in each of the two sites, and ‘*c*’ is the number of species shared by these sites. To enable the comparison with the species composition of the Continental Antarctica, a species list was compiled based on Sabbe et al. (2003), Gibson et al. (2006), Ohtsuka et al. (2006) and Esposito et al. (2008).

For the South Shetland Islands, the comparison is based on the species list of Livingston Island (Kopalová and Van de Vijver 2013) and on the revised list in Zidarova (2008). For Signy Island (South Orkney Islands), unpublished data from Sterken et al. have been used. The species list of Île de la Possession (Crozet Archipelago) in Van de Vijver et al. (2002a), completed with additional data from Kerguelen, Heard Island and the Prince Edward Islands (Van de Vijver et al. 2001, 2004b, 2008), was used as a proxy for the sub-Antarctic region.

Diatom species were expressed as relative abundances (% of total diatom valves per sample). Only those species present at >1 % in any single sample or with more than two occurrences were included in the analysis. All environmental variables except pH were log-transformed [$\log_{10}(x + 1)$] prior to all statistical analyses since they had skewed distributions. All ordinations were performed using CANOCO version 4.5 (ter Braak and Šmilauer 2002) with rare species downweighted in all cases. Acronyms of diatom taxa were generated ad hoc and listed in Online Resource 2. The statistical techniques used in this study are described in full detail in Jongman et al. (1995). Ordination techniques were used to elucidate patterns in species composition. An initial correspondence analysis (CA) was carried out to estimate gradient length, indicating that an unimodal relationship should be used in all further analyses (ter Braak and Prentice 1988).

To discover the principal patterns in the distribution of diatoms and their communities within all freshwater samples from James Ross Island, unconstrained ordination (DCA) was used on the entire data set.

Complete physico-chemical data were only available for the epilithic lake samples and direct multivariate analyses were restricted to samples reducing the initial set to only 27 samples. As not all of the 24 environmental variables influence the diatom distributions independently, canonical correspondence analysis (CCA) with forward selection and unrestricted Monte Carlo permutation tests (999 permutations, $p < 0.05$) was applied. Following Hall and Smol (1992), groups of significantly correlated ($p < 0.05$) environmental variables were identified first by making a Pearson correlation matrix with Bonferroni-adjusted probabilities (Wilkinson 1988) (Online Resource 3). In each group, forward selection was used to select the minimum number of parameters that could explain the largest amount of variation in the species data. The selected variables of each group were then combined together and analysed again by forward selection to obtain a final set of environmental parameters to be used in further analysis.

The significance of each selected variable was assessed using an unrestricted Monte Carlo permutation test (999 permutations). A CCA was performed with the environmental variable of interest as the only explanatory variable.

The ratio of the eigenvalue of the first (constrained) axis to the eigenvalue of the second (unconstrained) CCA axis (λ_1/λ_2) gives a good indication of the explanatory strength of the individual variable. Ratios higher than 0.50 suggest a strong diatom signal for that variable. Values less than 0.50 are less robust and would be of less use in inference models (Dixit et al. 1991; Roberts and McMinn 1996).

To test whether an environmental parameter is of prime importance in determining the diatom composition, the species turnover along the parameter gradient was calculated. The turnover in species composition along a conductivity gradient was determined using Cody's β -diversity (β_c) (Cody 1975): $\beta_c = (G + L)/2$ with G being the number of species gained and L the number of species lost along the conductivity gradient in comparison with the next group of lakes. Low values of β_c indicate low species turnover. Following Verleyen et al. (2003), the conductivity gradient was divided into intervals with the upper limits (UL) determined using the following equation: $UL_x = UL_{x-1} \times 2$.

Weighted averaging (WA) and weighted averaging with tolerance downweighting (WA(tol)) were applied to the 27 epilithon lake samples and the 75 selected diatom taxa in the training set for conductivity reconstruction after removing the outliers. A sample was considered to be an outlier if its WA residual was higher than the standard deviation of the \log_{10} -transformed conductivity (Jones and Juggins 1995). Weighted averaging partial-least-square (WA-PLS) was likewise applied after removing the outliers. Verleyen et al. (2003) discuss the rationale for testing both WA and WA-PLS. WA-PLS often produces calibration models with lower root-mean-squared errors of prediction (RMSEP) than WA (Birks 1998). Since none of the WA-PLS components showed a decrease in RMSEP, only simple WA was used for modelling. In WA reconstructions, averages are taken in both the WA regression and the WA calibration. Therefore, the resulting shrinkage of the inferred environmental parameter is corrected using inverse or classical deshrinking regression (Birks et al. 1990). WA, WA(tol) and WA-PLS were performed using C2 (Juggins 2007).

Results

Species composition and similarity analysis

A total of 123 taxa, including species, varieties and forms, belonging to 37 genera have been found in the analysed samples (Online Resource 2). Samples D8, D21 and D42 contained (almost) no diatoms, even after counting an entire slide. Subsequently, these samples have been removed from the total sample set. Eleven taxa were found

outside the counts, when scanning the slides for additional species. Several, mainly, small-celled naviculoid taxa could not be identified up to the species level, and further morphological investigations were necessary to clarify their taxonomic position. Five of them belonged to the genus *Luticola*, and following detailed light and scanning electron microscopy, they were described as new species such as *Luticola desmetii* Kopalová and Van de Vijver and *L. tomsui* Kopalová (Kopalová et al. 2011). Eleven other taxa were recently described from James Ross Island, such as *Eolimna jamesrossensis* Kopalová and Van de Vijver and *Luticola austroatlantica* Van de Vijver et al., or from the South Shetland Islands, such as *Pinnularia austral-orabenhorstii* Van de Vijver (Esposito et al. 2008; Kopalová et al. 2009; Van de Vijver et al. 2011a, b). A few taxa are reported here with certainty for the first time outside Continental Antarctica, such as *Luticola gaussii* (Heiden) D.G.Mann and *Achnanthes taylorensis* Kellogg et al., whereas *Pinnularia splendida* Hust. is only reported for the second time in the Antarctic region, apart from the type locality on South Georgia (Hustedt in Schmidt et al. 1934).

The flattening towards the end of the species accumulation curve (Fig. 2) indicates that a large part of the freshwater diatom flora was collected. Using species richness estimators, it is possible to evaluate how well the sampling effort reflected the true diatom richness of the area. The expected total number of taxa in all samples is 147 (ICE) or 148 (Chao2) for the James Ross Island freshwater samples, suggesting that our counting scored around 85 % of the (theoretical) total number of taxa present in the samples overall, comparable to the number found in other Antarctic localities where the same taxonomical concepts and sampling strategies have been followed (Van de Vijver et al. 2008; Kopalová and Van de Vijver 2013).

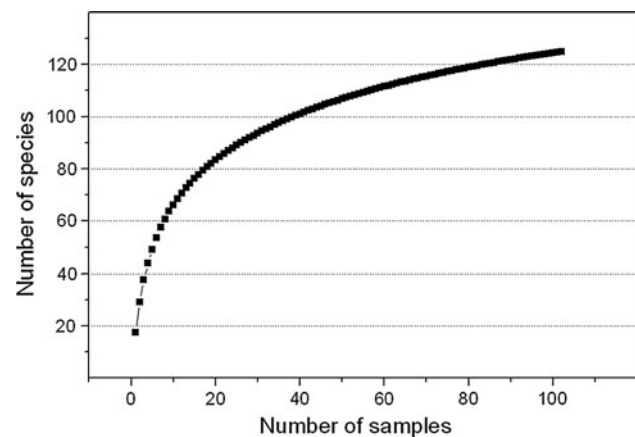


Fig. 2 Species accumulation curve for the Ulu Peninsula sample set

The similarity analysis between the James Ross Island diatom flora and the (revised) floras from several other Antarctic localities revealed a high similarity between James Ross Island and Livingston Island (Sørensen's Index = 0.63) and to a lesser extent Signy Island (0.46). A low affinity was found between James Ross Island and Continental Antarctica (0.25). The lowest similarity was found with the sub-Antarctic Islands (=0.15).

Community analysis

Using DCA (Fig. 3), it was possible to group the samples into two large groups. The first two DCA axes explained 16.4 % of variation in diatom composition. This is low, but not unusual for noisy data sets, that is, data sets containing many blank values (Stevenson et al. 1991). On the right side of the diagram, almost all samples from streams and seepage areas (●) are grouped together, whereas all lake samples (■ and ▼) and a few seepage area samples (SL1, SL2 and SP3) are positioned at the left side of the diagram. Although not entirely separated, it is clear that stream samples from algal (Ax) and Bohemian stream (Bx) are positioned in the lower half of the streams and seepage area group, whereas seepage areas are more in the upper part. Within the lake samples, two subgroups can be distinguished. In the lower half of the diagram, 10 lakes compose the first subgroup (■) grouping White Lake, Dan Lake, Monolith Lake, Lachman Lakes 1 and 2, Katia Lakes 1 and 2, Phormidium Lake, Muddy Lake and the epipellic sample from Laska Lake. All other lakes and the three seepage area samples form the second (▼) subgroup.

The distinction between the two groups is clearly reflected in the species composition. Fifty taxa (40 %) were found in both lake samples and streams and seepage area

samples, whereas 58 (46 %) and 17 (14 %) have been recorded exclusively in the lake samples and stream plus seepage area samples, respectively. Species richness in the samples varied between 7 and 43 taxa for lake samples and between 4 and 28 taxa for stream and seepage area samples with an average \pm SD of 18 ± 8 (Fig. 4). Table 2 shows the most common species in the overall data set and in the two groups. Most taxa, however, belong to the genus *Luticola* (17 taxa) followed by *Nitzschia* (9 taxa), *Didesmias* (7 taxa) and *Pinnularia* (7 taxa). The most abundant taxa in the lake samples are *N. perminuta* capitata form (24.8 % of all counted lake valves), *N. homburgi* Lange-Bertalot (11.8 %), *N. perminuta* non-capitata form (11.2 %) and *N. paleacea* (Grunow) (10.8 %) (Table 2). Stream and seepage area samples are dominated by *Nitzschia gracilis* Hantzsch (18.5 % of all counted stream valves), *E. jamesrossensis* Kopalová and Van de Vijver (15.6 %) and *Fragilaria capucina* Desmazières (12.4 %).

The original set of 24 environmental variables was reduced to 4 following the different selection procedures. Based on a Pearson product-moment correlation matrix, several groups of parameters could be formed. A first group included all parameters related to conductivity (Cond, Ca^{2+} , Na^+ , F^- , K^+ , Cl^- , SO_4^{2-}). A second group is composed of total phosphorus (TP), total carbon (TC), total nitrogen (TN), dissolved nitrogen (DN), dissolved carbon (DC), chlorophyll a (Chla) and dissolved organic carbon (DOC). Forward selection using only each of these groups of variables identified conductivity, TP and DOC as environmental variables explaining significant variation in the diatom data ($p \leq 0.05$). The two variables related to phosphorus [soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP)] showed a correlation of more than 99 % and SRP was selected. The same procedure was

Fig. 3 Detrended correspondence analysis (DCA) of the entire sample set [lakes subdivided into 2 subgroups (square and inverted triangle), streams and seepage areas (circle)]; the first two axes are shown

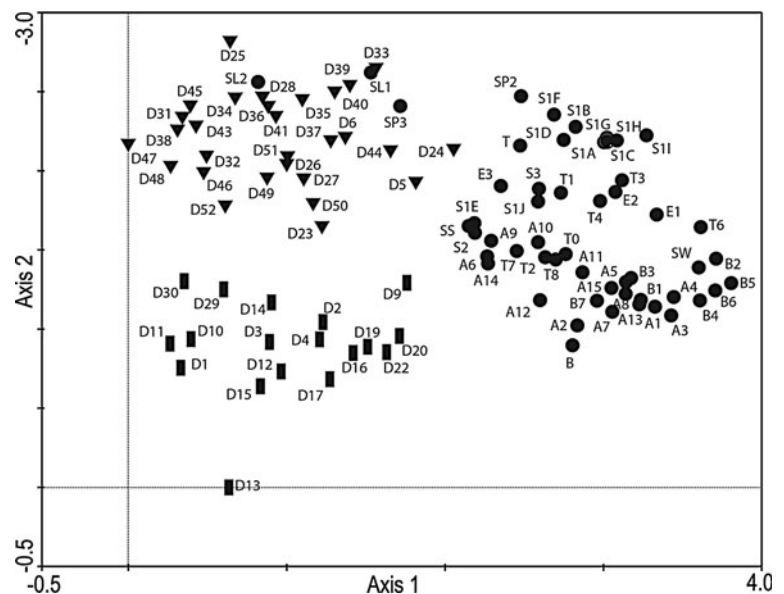


Fig. 4 Distribution of species richness per sample for the two sample categories: streams/seepage areas and lakes

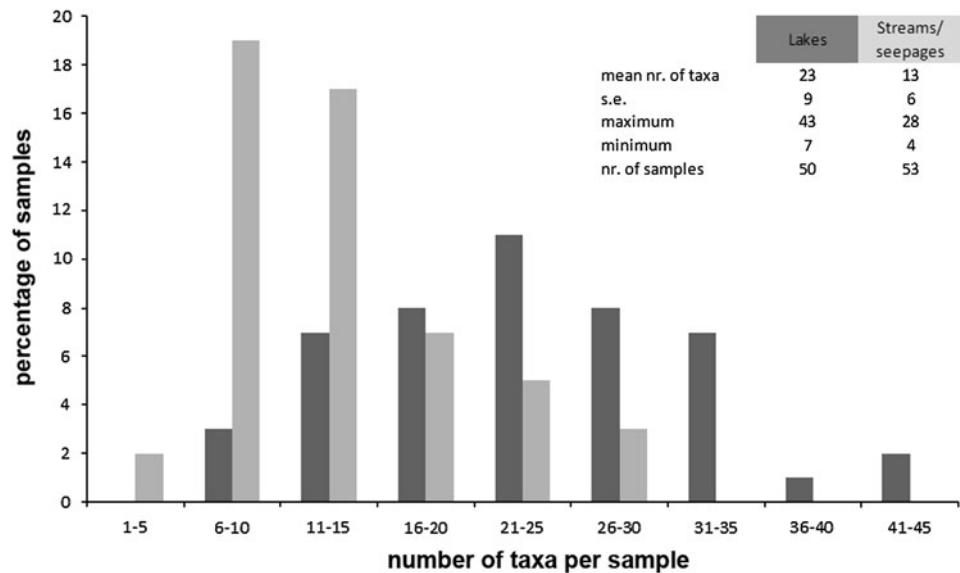


Table 2 Relative abundances of the most commonly encountered species in all samples (overall), lake samples (lakes) and seepage area and stream samples (streams/seepages)

	Overall	Lakes	Streams/ seepages
<i>Nitzschia perminuta</i> capitate forms	16.8	24.8	7.5
<i>N. gracilis</i>	10.3	3.4	18.5
<i>N. hamburgenensis</i>	8.5	11.8	4.5
<i>Eolimna jamesrossensis</i>	7.2	0.1	15.6
<i>Fragilaria capucina</i> -complex	6.4	1.3	12.4
<i>N. perminuta</i> non-capitate forms	6.2	11.4	0.0
<i>N. paleacea</i>	5.8	10.8	0.0
<i>Fistulifera saprophila</i>	5.5	0.4	11.6
<i>Mayamaea atomus permitis</i>	5.0	3.7	6.5
<i>Diademsis australis</i>	2.3	4.2	0.0
<i>Psammothidium papilio</i>	2.1	3.6	0.2
<i>N. inconspicua</i>	1.5	2.7	0.0
<i>Luticola muticopsis</i>	1.4	0.2	2.8
<i>Hantzschia amphioxys</i>	1.3	0.4	2.5
<i>L. austroatlantica</i>	1.3	0.1	2.7
<i>Achnantheidium lailae</i>	1.2	2.3	0.0

The principal species are highlighted

followed for O₂ and sat. O₂ (87 % correlation) selecting O₂ to be included. Finally, the selected variables were combined with pH, alkalinity, R–Si, NO₃–N, NO₂–N and NH₄–N. A second forward selection with only these eleven variables resulted in the selection of pH, conductivity, TP and SRP as explaining variables. The other variables were excluded since they did not significantly contribute in explaining the variation in the diatom data.

A CCA of the 27 samples in the data set constrained to the four selected environmental variables (Fig. 5)

explained only a small proportion of the species variance in the samples. The first two axes ($\lambda_1 = 0.294$, $\lambda_2 = 0.142$) account for only 17.4 % (11.5 and 5.9 %, respectively) of the cumulative variance in the diatom data, which is not surprising for noisy data sets (Stevenson et al. 1991). Forward selection identified four significant ($p < 0.05$) environmental variables (Cond, SRP, TP and pH) explaining 52 % of the total diatom variance that can be explained by the 24 environmental variables initially taken into account in this study. Conductivity ($p > 0.001$) accounted for 17 % of the variance explained, followed by SRP (14 %), pH (11 %) and TP (10.5 %). Monte Carlo unrestricted permutation test (999 permutations) of axes 1 and 2 indicated that both axes were highly significant ($p = 0.001$) (ter Braak and Šmilauer 2002). Axis 1 is relatively strongly correlated with conductivity (inter-set correlation = 0.71) and to a lesser extent with SRP (0.65). The second axis is related to TP (0.74). Consequently, the first gradient from right to left on axis 1 corresponds to a gradient in conductivity. Coastal lakes such as Phormidium Lake (D9), both Lachman Lakes (D2, D4) and Muddy Lake (D17) are separated from the lakes located more southerly on the peninsula (D23–D35). Coastal lakes are dominated by *Nitzschia hamburgenensis*, *Sellaphora seminulum* (Grunow) D.G.Mann, *Stauroneis latistauros* Van de Vijver and Lange-Bert. and *Fistulifera saprophila* (Lange-Bert. and Bonik) Lange-Bert. Typical taxa in the more southern lakes include *Brachysira minor* (Krasske) Lange-Bert., *Psammothidium papilio* (Kellogg et al.) Kopalová and Van de Vijver, *N. perminuta* capitate forms and several *Diademsis* taxa.

The second gradient from bottom to top along axis 2 corresponds with TP concentrations. Most lakes in the southern part of the study area (Lagoons Mesa, D37–D47) with low TP concentrations are separated from the coastal

Fig. 5 Canonical correspondence analysis (CCA) ordination biplot (the first two axes) showing epilithon lake samples black diamonds and species. For sample numbers, see Table 1; for species labels, see Online Resource 1

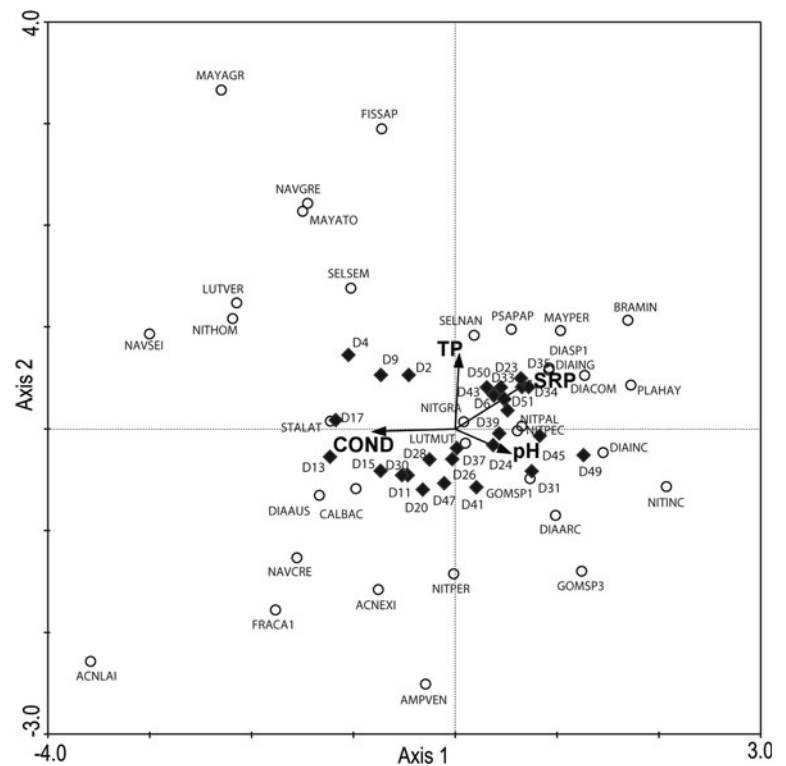


Table 3 Intra-set correlations of selected environmental variables for axes 1 and 2 of the CCA

Variable	Intra-set correlation axis 1	Intra-set correlation axis 2
Conductivity	−0.71	−0.02
SRP	0.65	0.48
TP	0.03	0.74
pH	0.47	−0.24

lakes and the more southerly located lakes showing moderate to higher TP values. The Lagoons Mesa Lakes are dominated by *N. perminuta* non-capitate form, *Navicula cremeri* Van de Vijver and Zidarova, *Amphora* sp1, *F. capucina* s.l. and several *Gomphonema* species. On the other hand, *F. saprophila*, *Navicula gregaria* Donkin, several *Mayamaea* species and *S. seminulum* show a high TP preference.

Transfer function for lake water conductivity

Constrained CCAs using conductivity, SRP, TP and pH individually indicated that conductivity ($\lambda_1/\lambda_2 = 0.76$) and SRP ($\lambda_1/\lambda_2 = 0.71$) had ratios higher than 0.50, suggesting that both may yield significant inference models (Dixit et al. 2002). The degree of species turnover along the conductivity gradient is rather uniform showing similar turnover values in the lower and the upper parts of the

gradient (Table 3). Since this is not the case for SRP, making an inference model for conductivity for the reconstruction of the ion balance in the Ulu Peninsula lakes is more appropriate. Because of the low λ_1/λ_2 ratios, it is not realistic to develop inference models for pH (0.47) and TP (0.39).

Lachman 1 Lake (D4), Katia 1 Lake (D13) and Nadeje Lake (D24) were removed from the model construction since their WA residuals exceeded the standard deviation of \log_{10} -transformed conductivity (0.42).

The WA model shows a strong predicted relationship between observed and diatom-inferred \log_{10} -transformed conductivity values ($r^2 = 0.78$). The predictive abilities for simple and tolerance downweighted WA are almost identical (Table 4). WA(tol) was chosen as it produces a slightly higher predicted correlation between measured and diatom-inferred conductivity (0.84 vs. 0.78) with almost no difference in RMSEP (0.269 and 0.274 vs. 0.275 and 0.272). Both deshrinking techniques produced equal RMSEP values (Table 5). Classical deshrinking showed a slightly higher r^2_{boot} (0.59 vs. 0.57) and had no residual trend compared to inverse deshrinking indicating that classical deshrinking will provide a more reliable estimate of the conductivity, especially at the extremes of the gradient (Jones and Juggins 1995; Roberts and McMinn 1998). Figure 6 shows the plots of observed versus diatom-inferred \log_{10} -transformed conductivity and the observed versus residual \log_{10} -transformed conductivity. Conductivity inferences were calculated from

Table 4 Species turnover along the conductivity gradient

Conductivity range ($\mu\text{S}/\text{cm}$)	Number of lakes	Number of species	Species gained	Species lost	Cody diversity
0–25	1	19	22	6	13
26–50	3	33	40	8	24
51–100	11	65	19	19	19
101–200	7	65	2	47	24.5
201–400	1	20	28	10	19
401–800	3	38	13	15	14
801–1,600	1	36			

Table 5 Summary of the performance of WA and WA_{tol} transfer functions for conductivity using inverse and classical deshrinking

Calibration	Deshrinking	R^2	R^2_{jack}	RMSE	RMSEP
WA	Classical	0.78	0.49	0.18	0.275
WA	Inverse	0.78	0.46	0.16	0.272
WA_{tol}	Classical	0.84	0.59	0.15	0.269
WA_{tol}	Inverse	0.84	0.57	0.13	0.274

the optima and tolerance for the principal diatom taxa in the Ulu Peninsula lake samples. Conductivity optima ranged from 28 to 570 $\mu\text{S cm}^{-1}$. Online Resource 2 lists the calculated conductivity optima and tolerance for all taxa with an occurrence in at least 2 samples. Both taxa with narrow and broad tolerances can be identified along the conductivity gradient.

Discussion

Species composition and biogeography

According to the ubiquity theory proposed by Finlay and Clarke (1999), the level of endemism in the entire Antarctic region is supposed to be low. However, the application of a better defined, narrower species concept (Mann 1999) in combination with more advanced taxonomic-analytical methods reduced the force-fitting of many taxa into similar European or North American relatives (Tyler 1996). Subsequently, a much higher degree of endemism has been demonstrated in the diatom flora on the different islands of the Maritime Antarctic region than previously accepted (Jones 1996; Toro et al. 2007), following major taxonomic revisions and the description of a large number

of new taxa (Van de Vijver et al. 2005, 2010a, 2011a; Van de Vijver and Mataloni 2008; Zidarova et al. 2010; Kopalová et al. 2011).

Based on macro-organism species level, three biogeographical (sub-)regions were defined in the Antarctic region: Sub-Antarctica, Maritime Antarctica and Continental Antarctica, with the latter two separated by the so-called Gressitt Line based on faunal differences between these regions (Chown and Convey 2007). The similarity analysis based on the diatom composition justified the biogeographical position of James Ross Island within the Maritime Antarctic region. A much lower similarity with Continental Antarctica and the sub-Antarctic Islands could be found. The hypothesis of a decreasing trend in diatom diversity with increasing latitude (Jones 1996; Van de Vijver and Beyens 1999a) is confirmed with the data from James Ross Island. The number of observed species decreases rapidly southwards starting at the sub-Antarctic Islands where 200–250 different taxa have been observed (Van de Vijver et al. 2001, 2002a, 2004a, b, 2008) and terminating in Continental Antarctica where only 30–50 taxa could be enumerated (Gibson et al. 2006; Ohtsuka et al. 2006). The Maritime Antarctic region shows an intermediate position, but even within this region, the longitudinal decreasing diversity trend is visible with 125–175 taxa on the South Shetland Islands (Fermani et al. 2007; Zidarova 2008) but only 123 on James Ross Island. Possible causes for this diversity change are multiple and include besides climatic factors, also the availability of microhabitats, oceanic influence and length of time since ice retreat (Jones 1996). This is, however, in clear contrast with biodiversity results in other taxonomic groups such as nematodes for which diversity hotspots were found (Nielsen et al. 2011) in the Maritime Antarctic region, obscuring

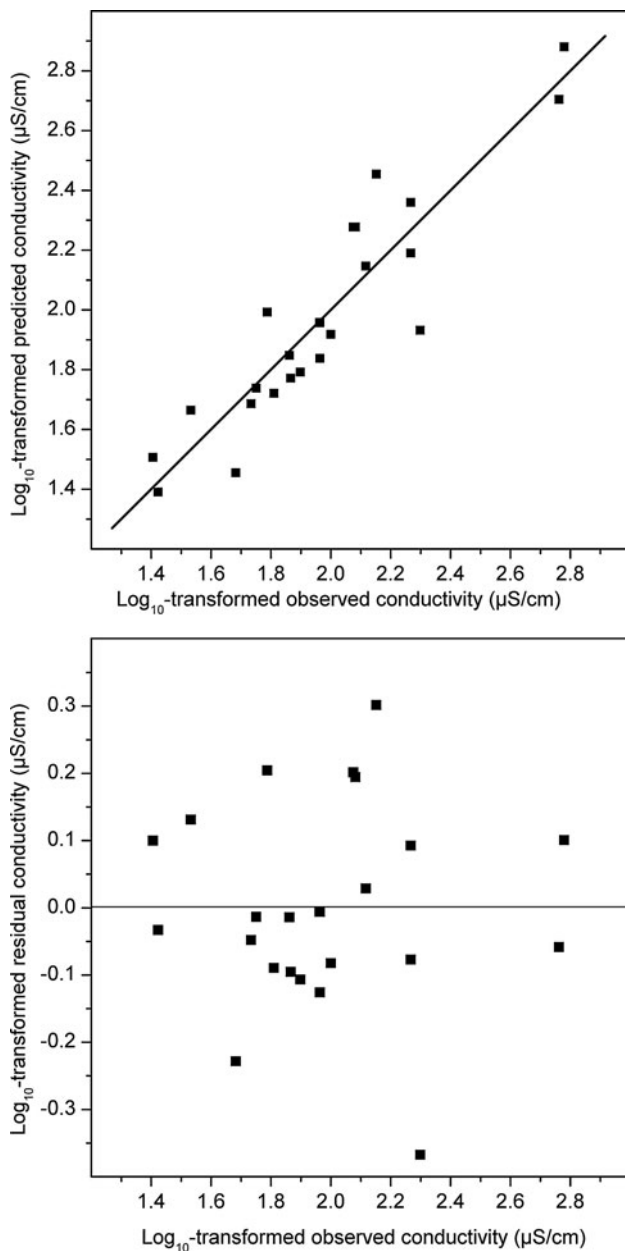


Fig. 6 Plots of observed versus diatom-inferred conductivity for the Ulu Peninsula lake data set and observed versus residual conductivity (observed minus diatom-inferred conductivity) based on weighted averaging regression and calibration model. The *dark squares* represent the different samples

a clear decreasing diversity trend for this taxonomic group when moving southwards.

The transitional position of James Ross Island resulted in a higher similarity with Continental Antarctica than observed between the South Shetland Islands and Continental Antarctica (which was set at 0.19 by Kopalová and Van de Vijver 2013). Several typical continental taxa such as *L. gaussii* (Heiden) D.G.Mann and *A. taylorensis* Kellogg

and Kellogg are present on James Ross Island, but absent from all other Maritime Antarctic localities (Kopalová et al. 2012; Kopalová and Van de Vijver 2013).

The presence of these typical continental diatom taxa might be explained by long-range transport connected to the general sea and air circulation in the Weddell Sea. Algae are known to be dispersed by air (Marshall and Chalmers 1997), making the airborne dispersal of the continental diatoms towards James Ross Island highly likely. Although no verified diatom records exist for the Weddell Sea sector of the Antarctic Continent (Kellogg and Kellogg 2002), all observed continental diatom species on James Ross Island are widely distributed in Continental Antarctica (Kellogg and Kellogg 2002). Persistent low-level counter clockwise katabatic air circulation (Parish and Bromwich 1987) in the Coats and Dronning Maud Lands brings Antarctic continental material towards the western coast of the Weddell Sea. This is predominantly deposited in sea water, but also on snow, sea ice or ice shelves. Ocean circulation in the Weddell Sea area is controlled by the Weddell Gyre (e.g. Diekmann and Kuhn 1999). Surface waters in the Weddell Sea flow as Antarctic Coastal Current (Gill 1973) clockwise along the coast of Coats Land towards the southern Weddell Sea, where it merges with dense and cold ice shelf waters (Foldvik et al. 1985) in front of the Filchner-Ronne Ice Shelf. From the southern Weddell Sea, they follow, similarly to the deep Weddell waters, the Antarctic Peninsula continental shelf towards the north (Hollister and Elder 1969). A similar pattern was found for air circulation on the Weddell Sea. Already in 1970s, Schwerdtfeger brought evidences of strong, cold barrier winds (or low-level jets; Stensrud 1996) flowing from the south or southwest along the eastern coast of the Antarctic Peninsula (Schwerdtfeger 1975). They mostly occur when stable air masses in the central Weddell Sea move westward and are blocked by the ridge of the Antarctic Peninsula. This leads to an increase in pressure, and winds turn north and continue along the Antarctic Peninsula coast to the James Ross Island area. It was shown by different studies (e.g. Swithinbank et al. 1980; Diekmann and Kuhn 1999) that the strong barrier winds along the Antarctic Peninsula eastern coast, together with the Weddell Gyre surface currents, are responsible for the transport of a significant proportion of pack ice into the north-western part of the Weddell Sea. Thus, diatoms may be transported either directly by wind or frozen in packed sea ice or in icebergs from the Coats Land and Dronning Maud Land coast to the James Ross Island archipelago similarly to abiotic material (e.g. Diekmann and Kuhn 1999). Furthermore, the survival of continental Antarctic taxa on the island can be supported by much more arid and also colder climatic conditions on James Ross Island in comparison with the rest of the Maritime Antarctic region

resulting in favourable environmental conditions for continental Antarctic taxa on James Ross Island.

Habitat comparison of diatom communities

Seepage areas, streams and lakes constitute important habitats in Antarctica, and the results of our study show marked differences in diatom communities between these habitats (Fig. 3). Not only the relative abundance of the composing taxa differed between habitats, but Fig. 4 also clearly showed that lakes were far more diverse than seepage areas and streams. The cyanobacterial composition of the different habitats on James Ross Island likewise separates lakes from streams and seepage areas (Komárek et al. 2008). In contrast to diatoms, cyanobacterial communities in lakes seem to have lower species richness than seepage areas and streams.

Streams form a typical habitat of the coastal Polar Regions as a result of the melting of glaciers and snowfields during summer seasons. Although only poorly studied in the past (Jones 1996), stream diatom communities seem to be directly influenced by their habitat features. The relatively low species diversity dominated by only a few taxa is most probably a consequence of the ephemeral nature of these streams. Hawes and Brazier (1991) already pointed out that turbidity was apparently one of the main factors in glacial streams on James Ross Island affecting the abundance and distribution of the microflora. Our results seem to confirm this assumption as a distinct species composition was found in highly turbid streams with high shares of suspended load originating from Cretaceous bedrock. Vincent and James (1996) stated that streams were highly unstable systems, subject to large variations in their chemical and physical properties with sometimes even daily fluctuations. At the beginning and towards the end of the summer, water in streams can freeze (Komárek and Elster 2008) presenting stressful factors for the biota, such as desiccation–rehydration and freeze–thaw cycles. Up to now, diatom strains were not included in laboratory studies testing the tolerance of cyanobacteria and algae to freezing (Elster 2002; Šabacká and Elster 2006). It is clear that the adaptation mechanisms in Antarctic diatoms to these conditions are still poorly. Future studies should therefore focus more on seasonal colonization strategies and dynamics of algal vegetation in these environments. It is, however, clear that only diatom taxa tolerating the combination of these unstable conditions and sometimes high stream velocities are able to survive in this habitat. The genus *Fragilaria*, dominating the stream diatom flora on James Ross Island, is often considered to be a pioneer species linked to rapid changes in water chemistry, mainly trophic status fluctuations (Stabell 1985; Denys 1990), benefiting from short but important nutrient releases after ice and snow melting. The high nutrient status of the

James Ross Island streams is strongly suggested by the co-dominance of *F. saprophila* and *Mayamaea permissis*, both regarded as typically eutrophic species (Lange-Bertalot 2001). Similar results were reported from the sub-Antarctic Islands (Van de Vijver and Beyens 1999a, b; Van de Vijver et al. 2001, 2004b, 2008), Signy Island (Hawes 1989) and Livingston Island (Van de Vijver, pers. observation). Only on King George Island, *Fragilaria* taxa seem to play only a minor role in the stream diatom composition (Kawecka and Olech 1993).

On the other hand, seepage areas are much more diverse than streams. Contradictorily, the main reason is most likely the unstable moisture regime in these areas suggested by the high abundance both in number of taxa and in number of counted valves of typical aerophilic genera such as *Luticola*, *Diademsis*, *Hantzschia* and *Orthoseira* (Van de Vijver et al. 2002b, 2011b; Kopalová et al. 2009; Zidarova et al. 2010). These genera are among the most species rich in the Antarctic region (Zidarova et al. 2010; Kopalová et al. 2011) and are well known to survive extreme environmental conditions (Souffreau et al. 2011) but seem less competitive in aquatic habitats, hence their lower abundance in streams. The high diatom diversity of seepage areas is not unique and is shared by high cyanobacterial diversity (Komárek and Elster 2008). Unfortunately, it is almost impossible to judge the high diversity of seepage areas in Polar Regions as comparable studies are almost entirely lacking in both Arctic and Antarctic conditions. On Deception Island, the soil algal (including diatoms) communities were studied, but only one sample was taken from a seepage area (Fermani et al. 2007). Our results show, however, clearly that seepage areas probably host some of the most diverse terrestrial diatom communities in the entire Antarctic region and that further studies on similar habitats across the Antarctic region need to be undertaken.

Nedbalová et al. (2013) distinguished six lake types on the Ulu Peninsula based on their geomorphological position, stability and physico-chemical characteristics, and it might be expected that the differences in lake characteristics would also influence the diatom communities. Our results show that only two subgroups could be distinguished within the lake diatom communities. However, each of these subgroups contains specific lake types. Two major environmental gradients seem to play the important role in controlling the composition of the James Ross Island lake diatom communities: conductivity and nutrients, regardless of the origin or hydrological stability of the lakes. The same environmental gradients are driving the limnological diversity of the lakes (Nedbalová et al. 2013).

The first subgroup represents lakes found mostly at lower altitudes (shallow coastal lakes and stable lakes in old moraines), situated on calcareous substrates originated

from underlying Cretaceous marine sediments and old glacial sediments. A strong marine influence together with enrichment from the bedrock resulted in a higher conductivity of these lakes. All lakes positioned at higher altitudes and on volcanic substrate were combined in the second subgroup that was characterized by lower conductivity resulting mainly from weaker marine influence. This subgroup includes stable shallow lakes on higher-lying levelled surfaces, small lakes in young moraines, cirque and kettle lakes (Nedbalová et al. 2013). Similar results were obtained on other Maritime Antarctic localities such as the South Shetland Islands (Jones 1996; Kopalová and Van de Vijver 2013), the South Orkney Islands (Oppenheim 1990) and on the Antarctic Continent (Sabbe et al. 2003; Cremer et al. 2004; Ohtsuka et al. 2006). Although more diverse, lakes on Livingston Island (South Shetland Islands) apparently present the same dominant species as on James Ross Island with *N. perminuta*, *P. papilio* and *N. homburgiensis* as dominant taxa (Kopalová and Van de Vijver 2013). This is in clear contrast with the sub-Antarctic Islands where *Nitzschia* species are less dominant in lake ecosystems (Van de Vijver et al. 2008). On the ice-free areas of East Antarctica such as Skarvsnes Foreland or Amery Oasis, on the other hand, only part of the dominant flora is similar, but this is most likely the result of the unique nature of the continental diatom flora. *S. latistauros* and *P. papilio* are markedly present in most lakes, but seem to be replaced as dominant species in lakes with higher conductivity by *Amphora* sp. (Ohtsuka et al. 2006), a species absent in the Maritime Antarctic region. As a conclusion, Antarctic diatom communities seem to be more suitable as bio-indicators for chemical rather than physical changes in their environment.

The construction of transfer functions will greatly improve the use of diatoms in reconstructing these chemical changes. Verleyen et al. (2003) discuss the value of these transfer functions in reconstructing past environmental and climate changes in the entire Antarctic region. The past 15 years, several transfer functions were developed in the entire Antarctic region (Jones and Juggins 1995; Roberts and McMinn 1998; Verleyen et al. 2003), but the combination of a revised (more fine-grained) taxonomy of the Antarctic diatom flora and the unique geographical position of James Ross Island urged the need for a new transfer function for this island in the light of further palaeoecological studies.

The new data greatly improve our knowledge of the environmental preferences of the Antarctic taxa as up to now, usually European data were used. As the species turnover is rather uniform along the entire gradient, the response of the species to conductivity changes for different lake types (oligo- to mesosaline) can be used to reconstruct past conductivity values.

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