Plant Ecology and Evolution 147 (1): 67–84, 2014
http://dx.doi.org/10.5091/plecevo.2014.896

REGULAR PAPER

Moss-inhabiting diatoms from two contrasting Maritime Antarctic islands

Kateřina Kopalová[1,*], Ryszard Ochyra[2], Linda Nedbalová[1] & Bart Van de Vijver[3,4]

[1]Charles University in Prague, Faculty of Science, Department of Ecology, Viničná 7, CZ-128 44 Prague 2, Czech Republic
[2]Wladyslaw Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, PL-31-512 Cracow, Poland
[3]Botanic Garden Meise, Department of Bryophyta & Thallophyta, Nieuwelaan 38, BE-1860 Meise, Belgium
[4]University of Antwerp, Department of Biology, Universiteitsplein 1, BE-2610 Wilrijk, Belgium
*Author for correspondence: k.kopalova@hotmail.com

Background and aims – The Maritime Antarctic vegetation is a poorly developed tundra dominated by lichens and mosses, mostly present in moist environments, providing a favourable habitat for microorganisms. Although, diatoms represent one of the most common algal groups in the Antarctic region, moss-inhabiting diatoms are rarely studied. The moss vegetation on islands in the Maritime Antarctic region forms a favorable habitat for non-marine diatoms. These moss-inhabiting diatom communities are of particular interest as little is known about their species composition, ecological preferences and habitats. The present paper discusses the diversity of moss inhabiting diatoms from Byers Peninsula (Livingston Island) and Ulu Peninsula (James Ross Island), Maritime Antarctic region.

Methods – The composition of the moss inhabiting diatom flora of 84 samples collected from Byers Peninsula, Livingston Island and Lagoons Mesa area, James Ross Island has been studied using light microscopy.

Key results – A total of 130 taxa, belonging to 39 genera has been recorded. Detrended Correspondence Analysis using the entire sample set clearly separates the James Ross Island (JRI) communities from the Livingston Island (LI) communities showing mostly the dominance of taxa preferring terrestrial (JRI) instead of more moist and aquatic conditions (LI). A Principal Component Analysis of only the Livingston Island samples formed three groups clearly separated by their diatom species composition. Although some taxa seem to occur in high abundances in several assemblages, a number of taxa showed a distinct preference for a particular assemblage. Biotic stress caused by marine birds and mammals, expressed in higher nutrient and salinity levels, seems to play a key role in determining the species composition.

Conclusions – Our results showed clearly the presence of a well developed moss-inhabiting diatom flora on both studied localities. The composition of the studied communities is determined by the type of habitat, moisture and biotic influences (salinity and nutrients).

Key words – Diatoms, mosses, Livingston Island, James Ross Island, community analysis, Antarctic Peninsula, Maritime Antarctic region.

INTRODUCTION

The Maritime Antarctic vegetation is strongly affected by its geographical isolation as well as the climatic and environmental conditions prevailing in this region. A classical description made by Holdgate (1970) defined the Maritime Antarctic region as the zone between the southern limit of the extensive, closed phanerogamic vegetation to the southern limit of the extensive cryptogamic (mainly bryophyte) communities. This roughly comprises all landmasses between 70°S northwards to 55°S, including several islands and archipelagos (South Sandwich, South Orkney, South Shetland Islands, Palmer Archipelago), as well as the west coast of the Antarctic Peninsula south to Marguerite Bay. The presence of vascular plants is limited to only two native species reaching their southern limits on north-west Alexander Island in the Maritime Antarctic region: *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl. (Ochyra et al. 2008). The Maritime Antarctic vegetation is therefore restricted to poorly developed tundra, of which lichens and mosses form the dominant component, mostly present on moist, low altitudinal, sheltered (north-facing) coastal habitats. (Ochyra et al. 2008). Habitat seems to play an important role in shaping the diversity of the moss communities that can be dominated by either one or rarely several species. Recently Ochyra et al. (2008) reported the presence of 111 moss species and two varieties belonging to 55 genera in the entire Antarctic region (excluding the sub-Antarctic islands). The most diverse moss flora has been reported from the South Shetland Islands, where 87 species and one variety are present (Li et al. 2009).

Although their occurrence is strongly influenced by their local environment, moss vegetations can sometimes cover up to several hectares in the Maritime Antarctic region providing unique microhabitats for a wide range of microbial epiphytes, such as cyanobacteria, chlorophytes and diatoms. Within Antarctica the more northerly-situated bryophyte communities in the maritime zone, such as the South Orkney Islands, contain a richer algal flora (Broady 1986) than the rest of the region. Habitats with relatively stable conditions tend to have a low moss species diversity compared to more complex habitats, where species diversity significantly increases (Ochyra et al. 2008). Species diversity decreases wherever conditions become colder and drier, for instance in the coastal zones of Continental Antarctica, whereas only a few species are able to survive the extreme conditions of continental inland sites (Jones 1996, Spaulding et al. 2010).

Temperature and extreme aridity are the most important features affecting the suitability of a microbial habitat. Since diatoms tolerate a wide range of environmental conditions, making them suitable bio-indicators (Rimet 2012), they represent one of the most common algal groups in terms of both species richness and number of individuals in the Antarctic region (Jones 1996, Van de Vijver & Beyens 1999, Sabbe et al. 2003). They are present in almost all aquatic and terrestrial habitats, either epiphytically on aquatic and terrestrial moss communities or as epilithon, epipsammon and epipelon biofilms in both lentic and lotic water-bodies (Round et al. 1990). Diatoms are also able to survive in non-submerged or even dry habitats such as terrestrial mosses (Van de Vijver & Beyens 1998). All of these moss-inhabiting diatom communities are of particular interest as little is known about their species composition and ecological and habitat preferences (Van de Vijver et al. 2004, Bertrand et al. 2004).

Over the past decades, there was a growing interest in the use of the Antarctic diatom flora to solve questions about biogeography, palaeoecology and processes related to environmental changes. Despite this increase on diatom research, only a few papers reporting the Antarctic moss-inhabiting diatom flora have been published. Most publications deal with moss-epiphytic diatom communities from the sub-Antarctic region (a.o. Hickman & Vitt 1974, Van de Vijver & Beyens 1998, 1999, Van de Vijver et al. 2001, 2004, 2008 and Gremmen et al. 2007). In Van de Vijver & Beyens (1997a), one moss sample from King George Island (South Shetland Islands) was analysed together with 11 aquatic and one soil sample. Toro et al. (2007) reported on moss communities from Livingston Island, but they only discussed them in relation to the invertebrates living near them and did not mention any diatom communities associated with these mosses. Van de Vijver et al. (2011a) described *Luticola adelae* Van de Vijver & Zidarova from a moss sample taken near White Lake on James Ross Island but apart from the formal description, no further analyses were carried out on the sample. Actually, only one recent paper discusses the Maritime Antarctic moss-inhabiting diatom flora: Vinocur & Maidana (2010) provided the first analysis of the spatial and temporal variations in the diatoms associated with mosses on the South Shetland Islands. Unfortunately, their species list is apparently composed of a large number of cosmopolitan taxa that so far were never found in the Maritime Antarctic region but quite common on more temperate localities reducing the value of the entire analysis.

Recently, a thorough taxonomical and ecological revision of the Livingston and James Ross Island diatom flora started which not only resulted in the description of a large number of new taxa (Kopalová et al. 2011, 2012, Van de Vijver et al. 2010a, 2010b, 2013, Van de Vijver & Zidarova 2011, Zidarova et al. 2009, 2012) but also led to a better ecological characterisation of the aquatic diatom assemblages present on both islands (Kopalová & Van de Vijver 2013, Kopalová et al. 2013).

The present paper completes the ecological analysis of the Livingston and James Ross Island diatom assemblages discussing the terrestrial diatom communities associated with different moss species on the two islands. The main objectives of this study included a floristic analysis of the moss-inhabiting diatom flora of these two islands, a discussion of their biogeographical position within the Maritime Antarctic region and possible similarities and differences between them and with the other communities on the islands in relation to several habitat characteristics.

MATERIAL AND METHODS

Field sampling

During the austral summer of 2009–2010, (Limnopolar Project POL 2006-06635), a total of 68 water-saturated and dry moss samples for diatom analysis were collected from Byers Peninsula (Livingston Island, South Shetland Islands). An additional set of 16 water-saturated and dry moss samples from the Lagoons Mesa from Ulu Peninsula (James Ross Island) was collected during the summer expedition LAGOS 2012 (Picto project 2010–0096). All moss samples were fixed with alcohol and stored in plastic vials. Sampling locations together with GPS co-ordinates are presented in table 1.

Due to the restricted logistic possibilities of working in these extreme conditions, only a limited number of environmental parameters were measured and/or determined. For all samples we noted: elevation (m a.s.l.), biotic influence (0 = none, 1 = heavy manuring and trampling by marine mammals or birds), habitat type (1 = lake, 2 = pond, 3 = stream, 4 = terrestrial) and dominant moss species present. Table 1 lists all samples with their characteristics. Moss species in the samples were identified using Ochyra et al. (2008). Sixteen different moss species, belonging to thirteen genera, were found in the entire sample set. On James Ross Island, only six species were identified, compared to Livingston Island where twelve different species were found. Only two of all moss species were in common between both islands. In order to determine the differences in diatom composition

Table 1 – List of samples with characteristics used in this paper.
Habitat type: 1 = lake; 2 = pond; 3 = stream; 4 = terrestrial. ND = not determined. For more details, see text.

Sample	Sampling date	Site	GPS	F-value	Altitude (m)	Biotic influence	Habitat type	Dominant moss species in the sample
Livingston Island								
BYM001	9/01/2009	Sealer's Hill	6240275/06106560	I	10	1	2	*Warnstorfia fontinaliopsis* (Müll.Hal.) Ochyra
BYM002	9/01/2009	Sealer's Hill	6240275/06106560	IV	10	1	4	*Warnstorfia fontinaliopsis* (Müll.Hal.) Ochyra
BYM003	9/01/2009	Sealer's Hill	6240213/0617259	IV	5	1	4	*Bryum pseudotriquetrum* Gärtner et al.
BYM004	9/01/2009	Sealer's Hill	6240213/0617259	IV	5	1	4	*Brachithecium austrosalebrosum* (C.Muell.) Kindb.
BYM005	9/01/2009	Sealer's Hill	6240102/06107512	V	5	0	4	*Bryum pseudotriquetrum* Gärtner et al.
BYM006	9/01/2009	Sealer's Hill	6240102/06107512	V	5	0	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM007	9/01/2009	Sealer's Hill	6240102/06107512	V	5	0	4	*Brachithecium austrosalebrosum* (C.Muell.) Kindb.
BYM008	9/01/2009	plain before Pinguinera	6240113/06108453	III	5	1	1	*Warnstorfia fontinaliopsis* (Müll.Hal.) Ochyra
BYM009	10/01/2009	Byers Camping Site	ND	VI	5	1	4	*Andreaea gainii* Cardot.
BYM010	10/01/2009	Byers Camping Site	ND	VI	5	1	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM011	10/01/2009	Byers Camping Site	ND	VI	5	1	4	*Andreaea gainii* Cardot.
BYM012	10/01/2009	Byers Camping Site	6239453/06105585	II	11	0	3	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM013	10/01/2009	Byers Camping Site	6239453/06105585	IV	11	0	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM014	10/01/2009	Byers Camping Site	6239453/06105585	VI	11	0	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM015	10/01/2009	Second flag from Camping site	6239357/06106243	II	61	0	2	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM016	10/01/2009	Second flag from Camping site	6239357/06106243	V	61	0	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM017	10/01/2009	rock desert on Central Plateau	6239317/06106480	V	66	0	4	*Bryum pseudotriquetrum* Gärtner et al.
BYM018	10/01/2009	rock desert on Central Plateau	6239317/06106480	II	66	0	2	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM019	10/01/2009	rock desert on Central Plateau	6239241/06106489	II	60	0	1	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM020	10/01/2009	Central Plateau	6239118/06106210	II	59	0	3	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM021	10/01/2009	Central Plateau	6239114/06106194	I	62	0	1	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM022	10/01/2009	Central Plateau	6239114/06106194	V	62	0	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM023	10/01/2009	Central Plateau	6239135/06106045	VI	68	0	4	*Bryum pseudotriquetrum* Gärtner et al.
BYM024	11/01/2009	behind Cerro Smellie	6239041/06107518	II	38	0	1	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM025	11/01/2009	behind Cerro Smellie	6239063/06108039	II	34	0	1	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM026	11/01/2009	behind Cerro Smellie	6239063/06108039	IV	34	0	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM027	11/01/2009	behind Cerro Smellie	6239063/06108039	V	34	0	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM028	11/01/2009	in front of Cerro Smellie	6239115/06108524	VIII	11	1	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM029	11/01/2009	between Cerro Smellie & Pinguinera	6239180/06108237	III	8	0	4	*Brachithecium austrosalebrosum* (C.Muell.) Kindb.

Table 1 (continued) – List of samples with characteristics used in this paper.

Sample	Sampling date	Site	GPS	F-value	Altitude (m)	Biotic influence	Habitat type	Dominant moss species in the sample
Livingston Island								
BYM030	11/01/2009	between Cerro Smellie & Pinguinera	6239180/06108237	V	8	0	4	*Bryum pseudotriquetrum* Gärtner et al.
BYM031	11/01/2009	between Cerro Smellie & Pinguinera	6239232/06107476	II	29	0	2	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM032	11/01/2009	between Cerro Smellie & Pinguinera	6239232/06107476	V	29	0	4	*Bryum pseudotriquetrum* Gärtner et al.
BYM033	11/01/2009	between Cerro Smellie & Pinguinera	6239247/06107460	II	29	0	2	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM034	11/01/2009	between Cerro Smellie & Pinguinera	6239247/06107460	V	29	0	4	*Bryum pseudotriquetrum* Gärtner et al.
BYM035	11/01/2009	Central Plateau	6239248/06107261	II	35	0	1	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM036	12/01/2009	Domo Lake area	6238562/06058459	III	51	0	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM037	12/01/2009	Domo Lake area	6238501/06058246	II	50	0	1	*Sanionia uncinata* (Hedw.) Loeske
BYM038	12/01/2009	Domo Lake area	6238566/06058270	III	61	0	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM039	12/01/2009	Domo Lake area	6238566/06058270	V	61	0	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM040	12/01/2009	near Clarke's Nunatak	6240156/06055255	VII	6	1	4	*Polytrichastrum alpinum* (Hedw.) G.L.Sm.
BYM041	12/01/2009	near Clarke's Nunatak	6240156/06055255	III	6	1	4	*Pohlia nutans* (Hedw.) Lindb.
BYM042	12/01/2009	near Clarke's Nunatak	6240110/06055356	III	5	1	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM043	12/01/2009	near Clarke's Nunatak	6240110/06055356	IV	5	1	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM044	14/01/2009	Central Plateau	6239245/06106055	V	66	0	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM045	14/01/2009	Limnopolar lake area	6238565/06106169	II	60	0	1	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM046	14/01/2009	Limnopolar lake area	6238565/06106169	I	60	0	1	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM047	14/01/2009	Limnopolar lake area	6238549/06106396	III	63	0	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM048	14/01/2009	Limnopolar lake area	6238549/06106396	V	63	0	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM049	14/01/2009	Limnopolar lake area	6238156/06106450	I	63	0	2	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM050	14/01/2009	Limnopolar lake area	6238459/06106159	III	60	0	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM051	15/01/2009	Limnopolar lake - Midge Lake area	6238201/06106442	I	66	0	1	*Drepanocladus longifolius* (Wilson ex Mitt.) Broth. ex Paris
BYM052	15/01/2009	Limnopolar lake - Midge Lake area	6238143/06106393	III	72	0	4	*Bryum pseudotriquetrum* Gärtner et al.
BYM053	15/01/2009	Asa lake	6237524/06106300	II	38	0	1	*Bryum pseudotriquetrum* Gärtner et al.
BYM054	15/01/2009	Asa lake	6237524/06106300	IV	38	0	4	*Bryum pseudotriquetrum* Gärtner et al.
BYM055	15/01/2009	Asa Lake area	6237417/06106304	I	40	0	1	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM056	15/01/2009	Asa Lake area	6237417/06106304	V	40	0	4	*Bryum pseudotriquetrum* Gärtner et al.

Table 1 (continued) – List of samples with characteristics used in this paper.

Sample	Sampling date	Site	GPS	F-value	Altitude (m)	Biotic influence	Habitat type	Dominant moss species in the sample
Livingston Island								
BYM057	15/01/2009	Beach near Camp Site	6239148/06104215	V	20	0	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM058	17/01/2009	Refugio Lake area	6239414/06100264	III	4	1	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM059	17/01/2009	Refugio Lake area	6239414/06100264	V	4	1	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM060	17/01/2009	Cerro Negro	6239217/06100104	V	93	0	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM061	17/01/2009	Cerro Negro area	6238345/06100395	III	80	0	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM062	17/01/2009	Cerro Negro area	6238345/06100395	V	80	0	4	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM063	17/01/2009	Nordic Plain	6238276/06100446	III	40	0	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM064	18/01/2009	Camp site	6239440/06105538	I	11	0	2	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM065	18/01/2009	Camp site	6239440/06105538	IV	11	0	4	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM066	18/01/2009	Camp site	6239344/06105512	II	12	0	2	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
BYM067	18/01/2009	Camp site	6239453/06105482	II	11	0	2	*Sanionia georgicouncinata* (Müll.Hal.) Ochyra
BYM068	18/01/2009	Camp site	6239442/06105493	II	12	0	2	*Warnstorfia sarmentosa* (Wahlenb.) Hedenäs
James Ross Island								
M1	10/02/2012	Lagoons Mesa	6357309/5754179	ND	264	0	4	*Hypnum revolutum* (Mitt.) Lindb.
M2	10/02/2012	Lagoons Mesa	6357264/5754287	ND	274	0	4	*Bryum pseudotriquetrum* Gärtner et al.
M3	10/02/2012	Lagoons Mesa	6357200/5754139	ND	260	0	4	ND
M4	10/02/2012	Lagoons Mesa	6357163/5754112	ND	255	0	4	ND
M21	11/02/2012	Lagoons Mesa	6358391/5753444	ND	22	0	4	ND
M22	11/02/2012	Lagoons Mesa	6358364/5753463	ND	17	0	4	*Bryum pseudotriquetrum* Gärtner et al.
M23	11/02/2012	Lagoons Mesa	6358216/5753581	ND	83	0	4	*Brachithecium austrosalebrosum* (C.Muell.) Kindb.
M24	11/02/2012	Lagoons Mesa	6358157/5754030	ND	111	0	4	*Distichium capillaceum* (Hedw.) Bruch & Schimp.
M25	11/02/2012	Lagoons Mesa	6358097/5754094	ND	154	0	4	ND
M26	12/02/2012	Lagoons Mesa	6358001/5754047	ND	181	0	4	*Syntrichia saxicola* (Cardot) R.H.Zander
M27	11/02/2012	Lagoons Mesa	ND	ND	ND	0	4	ND
V3M1	8/02/2012	Lagoons Mesa	6395931/5790226	ND	247	0	4	*Bryum pseudotriquetrum* Gärtner et al.
V3M2	8/02/2012	Lagoons Mesa	6395873/5790169	ND	247	0	4	ND
V3M3	8/02/2012	Lagoons Mesa	6357305/5754057	ND	245	0	4	*Schistidium antarcticii* (Cardot) L.I.Savicz & Smirnova
M Black lake	12/02/2012	Lagoons Mesa	6357569/5752592	ND	222	0	4	*Bryum pseudotriquetrum* Gärtner et al.
M Anna pool	11/02/2012	Lagoons Mesa	6357543/5754378	ND	194	0	4	ND

due to moisture content, the F-value, referring to the F-classification of Jung (1936) was selected as a representative for moisture and used for each sample of Livingston Island. The F-value was not determined for the James Ross samples. It is a humidity scale based on water content as follows: FI = submerged mosses, FII = free floating mosses, FIII = very wet (water drips from the samples without pressure), FIV = wet (water drips with a slight pressure), FV = quasi-wet (water drips after moderate pressure), FVI = moist (little water produced after high pressure), FVII = quasi-dry (only a few drops of water can be squeezed out), FVIII = dry (contains no water).

Study area – Livingston Island

Livingston Island is the second largest island of the South Shetland Islands, with a total area of about 950 km^2. Based on its ecological and climatological characteristics, this archipelago belongs to the Maritime Antarctic region (Chown & Convey 2007). The island (62°36'S 60°30'W), located 150 km north-west of the Antarctic Peninsula (fig. 1), is almost entirely covered by permanent glaciers and icecaps leaving only 10% of the island ice-free. Byers Peninsula, the largest ice-free area (almost 61 km^2) forming the western tip of the island, is the most important biodiversity area on Livingston Island and is currently included within the list of the Antarctic Specially Protected Areas (ASPA No 126). More information on the climate, geology, hydrology and geomorphology of this area can be found in Chipev & Veltchev (1996) and Toro et al. (2007). Vegetation cover on Livingston Island, as typical for the Antarctic region, is scarce and has a mosaic structure (Toro et al. 2007). It is mainly formed by cryptogams, with lichens and mosses as dominant life forms with only the two above mentioned vascular plants forming small cushions (Toro et al. 2007). Several of the lakes have well developed monospecific stands of the benthic moss *Drepanocladus longifolius* (Wilson ex Mitt.) Broth. ex Paris, which might dominate overall lake productivity because of its large standing stocks (Li et al. 2009).

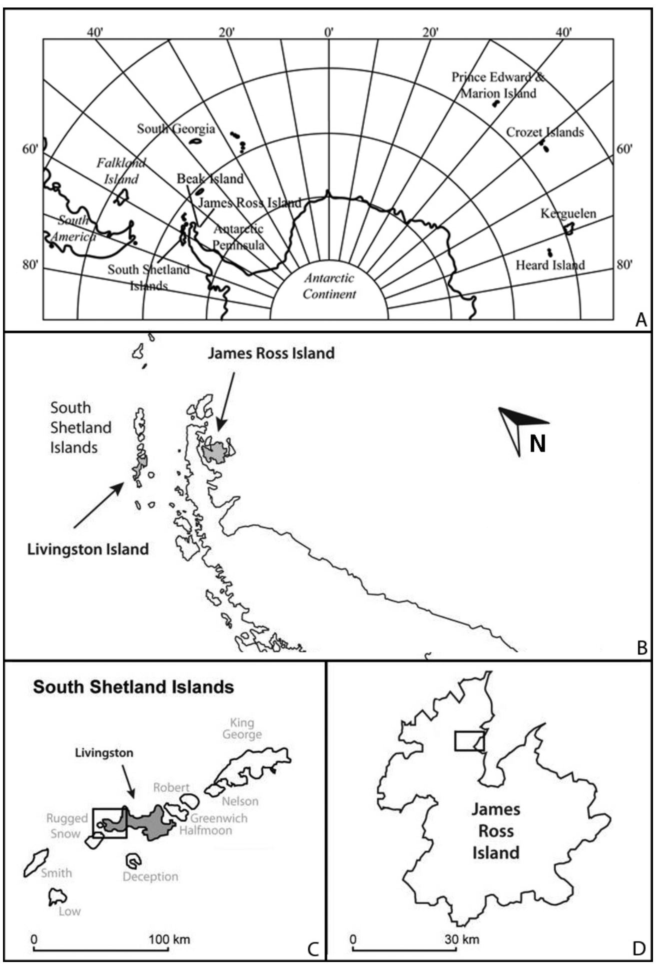

Figure 1 – Geographic location of the studied islands: A, overview of the southern hemisphere with the location of several islands and archipelagos mentioned in the text; B, detailed map of Antarctic Peninsula region showing the position of James Ross Island and Livingston Island; C, the South Shetland Islands. Livingston Island is indicated; D, James Ross Island. The box indicates the locality of the studied area: Lagoons Mesa.

Study area – James Ross Island

James Ross Island is a large island with a total area of ~2600 km^2, in the northern-western part of the Weddell Sea, close to the northern tip of the Antarctic Peninsula. It belongs to the transition zone between the Maritime Antarctic and Continental Antarctic region (Øvstedal & Lewis Smith 2001). More than 80% of the island is covered by an ice cap leaving only the northern part of the island, Ulu Peninsula, ice free (100 km^2). Olivero et al. (2008), Smellie et al. (2008) and Svojtka et al. (2009) discussed the geological history of the island. Ulu Peninsula is characterized by the presence of a large number of streams, seepages and lakes of glacial origin (Nedbalová et al. 2013). The human presence is limited to the Czech scientific base (Johann Gregor Mendel Station) that was constructed on Ulu Peninsula in 2006. The climate of James Ross Island is determined by cold, arid barrier winds from the south and by the location in the precipitation shadow of the Antarctic Peninsula (Engel et al. 2012). In comparison to the South Shetlands Islands, the climate is more arid with low precipitation, estimated to be less than 300 mm/yr. Owing to the dry air and often high wind speeds, evaporation rate is high. Further details on the climatic conditions can be found in Láska et al. (2010, 2011a, 2011b) and in Engel et al. (2012). Inland vegetation, lacking any vascular plants, is restricted to bryophytes and lichens. Their distribution is usually limited due to the deficiency of liquid water (Robinson et al. 2003). Although moss communities are not very frequent on James Ross Island, there are several patches of live or moribund moss (Láska et al. 2011b). On the other hand, the microflora, mostly composed of cyanobacteria, green algae and diatoms, is well developed in freshwater ecosystems such as seepages, lakes and streams (Komárek & Elster 2008, Kopalová et al. 2012, 2013).

Sample treatment and counting

Diatom samples were prepared using the method described in Van der Werff (1955). Subsamples were cleaned by adding 37% H_2O_2 and heating to 80°C for about 1 h. Oxidation

Table 2 – List of all observed species with their acronyms in the investigated moss samples from James Ross Island and Livingston Island.
Distribution: C = Cosmopolitan; MA = Maritime Antarctic Region; A = Antarctic Region; U = Unknown. Marine species are marked with an *.

Taxon name	Acronyms	Distribution
Achnanthes coarctata (Bréb.) Grunow	AchCoa	C
Achnanthes muelleri G.W.F.Carlson	AchMue	A
Achnanthidium exiguum (Grunow) D.B.Czarnecki	AchExg	C
Achnanthidium sp1	AchMin	MA
Achnanthidium sp2	AchMin2	MA
Adlafia submuscora Van de Vijver, Kopalová, Zidarova & E.J.Cox	AdlSms	MA
Brachysira minor (Krasske) Lange-Bert.	BraMin	MA
Caloneis bacillum (Grunow) P.T.Cleve	CalBac	C
Chamaepinnularia antarctica Van de Vijver, Kopalová, Zidarova & E.J.Cox	ChaAnt	MA
Chamaepinnularia australomediocris (Lange-Bert. & Rol.Schmidt) Van de Vijver	ChaAus	A
Chamaepinnularia gerlachei Van de Vijver & Sterken	ChaGer	MA
Chamaepinnularia krookii (Grunow) Lange-Bert. & Krammer	ChaKrk	C
Chamaepinnularia krookiiformis (Krammer) Lange-Bert. & Krammer	ChaKrf	C
Cocconeis spp.	Cocsp	*
Diadesmis arcuata (Heiden) Lange-Bert.	DiaArc	A
Diadesmis australis Van de Vijver & Sabbe	DiaAus	MA
Diadesmis gallica W.Smith	DiaGal	C
Diadesmis inconspicua Kopalová & Van de Vijver	DiaInc	MA
Diadesmis langebertalotii Le Cohu & Van de Vijver	DiaLng	A
Diadesmis tabellariaeformis (Krasske) Lange-Bert. & Wojtal	DiaTab	MA
Diadesmis sp1	Diasp1	MA
Diadesmis sp2	Diasp2	MA
Eolimna jamesrossensis Kopalová & Van de Vijver	EolJrs	MA
Eolimna minima (Grunow) Lange-Bert.	EolMin	C
Eucocconeis sp.	Eucsp	U
Eunotia paludosa Grunow	EunPal	C
Eunotia sp.	Eunsp	MA
Fistulifera saprophila (Lange-Bert. & Bonik) Lange-Bert.	FisSap	C
Fragilaria capucina s.l. Desm.	FraCap	C
Fragilariopsis nana (Steemann Nielsen) Paasche	FrgNan	*
Gomphonema spp.	Gomsp	U
Gomphonemopsis sp.	Gmpsp	*
Halamphora oligotraphenta (Lange-Bert.) Levkov	AmpOlg	C
Halamphora sp1	AmpVen	MA
Hantzschia confusa Van de Vijver & Zidarova	HanCon	MA
Hantzschia hyperaustralis Van de Vijver & Zidarova	HanHyp	MA
Hippodonta hungarica Lange-Bert., Metzeltin & Witkowski	HipHun	C
Licmophora sp.	Licmsp	*
Luticola amoena Van de Vijver, Kopalová, Zidarova & Levkov	LutAmo	MA
Luticola austroatlantica Van de Vijver, Kopalová, S.A.Spaulding & Esposito	LutAat	MA
Luticola cohnii (Hilse) D.G.Mann	LutCoh	C
Luticola doliiformis Kopalová & Van de Vijver	LutDlf	MA
Luticola evkae Kopalová	LutEvk	MA
Luticola gigamuticopsis Van de Vijver	LutGmu	MA
Luticola higleri Van de Vijver, van Dam & Beyens	LutHig	MA
Luticola katkae Van de Vijver & Zidarova	LutKat	MA

Table 2 (continued) – List of all observed species with their acronyms in the investigated moss samples from James Ross Island and Livingston Island.

Taxon name	Acronyms	Distribution
Luticola muticopsis (Van Heurck) D.G.Mann	LutMut	A
Luticola nivalis (Ehrenb.) D.G.Mann	LutNiv	C
Luticola pusilla Van de Vijver, Kopalová, Zidarova & Levkov	LutPus	MA
Luticola tomsui Kopalová	LutTms	MA
Luticola truncata Kopalová & Van de Vijver	LutTru	MA
Luticola vandevijveri Kopalová, Zidarova & Levkov	LutVdv	MA
Luticola vermeulenii Van de Vijver	LutVrm	MA
Luticola sp1	Lutsp1	U
Mayamaea excelsa (Krasske) Lange-Bert.	MayExc	C
Mayamaea josefelsterii Kopalová, Nedbalová & Van de Vijver	MayJos	MA
Mayamaea atomus (Hust.) Bruder & Medlin	MayAtm	C
Mayamaea permitis (Hust.) Bruder & Medlin	MayPer	C
Microcostatus australoshetlandicus Van de Vijver, Kopalová, Zidarova & E.J.Cox	MicAsh	MA
Microcostatus naumannii (Hust.) Lange-Bert.	MicNau	C
Muelleria aequistriata Van de Vijver & S.A.Spaulding	MueAeq	MA
Muelleria algida S.A.Spaulding & Kociolek	MueAlg	MA
Muelleria austroatlantica Van de Vijver & S.A.Spaulding	MueAst	MA
Muelleria kristinae Van de Vijver	MueKrs	MA
Muelleria regigeorgiensis Van de Vijver & S.A.Spaulding	MueRgg	MA
Muelleria sabbei Van de Vijver & Spaulding	MueSab	MA
Muelleria sp1	MueNog	MA
Muelleria sp2	Muesp	U
Navicula australoshetlandica Van de Vijver	NavAsh	MA
Navicula bicephaloides Van de Vijver & Zidarova	NavBic	MA
Navicula cremeri Van de Vijver & Zidarova	NavCre	MA
Naviculadicta sp.	Ndicsp	U
Navicula dobrinatemniskovae Zidarova & Van de Vijver	NavDot	MA
Navicula gregaria Donkin	NavGre	C
Navicula sp.	Navsp	*
Navicula seibigeana (Ehrenb.) Ralfs	NavSbg	C
Nitzschia debilis (Arn.) Grunow	NitDeb	C
Nitzschia gracilis Hantzsch	NitGra	C
Nitzschia homburgensis Lange-Bert.	NitHom	C
Nitzschia inconspicua Grunow	NitInc	C
Nitzschia paleacea Grunow	NitPlc	C
Nitzschia perminuta (Grunow) Peragallo	NItPer	U
Nitzschia cf. *vitrea* G.Norman	NItVit	U
Orthoseira roeseana (Rabenh.) O'Meara	OrtRoe	C
Pinnularia australoborealis Van de Vijver & Zidarova	PinAbo	MA
Pinnularia australodivergens Zidarova, Kopalová & Van de Vijver	PinAdi	MA
Pinnularia australoglobiceps Zidarova, Kopalová & Van de Vijver	PunAglo	MA
Pinnularia australomicrostauron Zidarova, Kopalová & Van de Vijver	PinAmic	MA
Pinnularia australorabenhorstii Van de Vijver	PinArab	MA
Pinnularia australoschoenfelderi Zidarova, Kopalová & Van de Vijver	PinAsch	MA
Pinnularia austroshetlandica (G.W.F.Carlson) Cleve-Euler	PinAsh	A
Pinnularia borealis Ehrenb.	PinBor	C
Pinnularia borealis var. *pseudolanceolata* Van de Vijver & Zidarova	PinBorl	MA
Pinnularia magnifica Zidarova, Kopalová & Van de Vijver	PinMag	MA

Table 2 (continued) – List of all observed species with their acronyms in the investigated moss samples from James Ross Island and Livingston Island.

Taxon name	Acronyms	Distribution
Pinnularia microcarteri Zidarova, Kopalová & Van de Vijver	PinMcr	MA
Pinnularia microstauroides Zidarova, Kopalová & Van de Vijver	PinMcs	MA
Pinnularia obaesa Van de Vijver	PinOba	MA
Pinnularia perlanceolata Van de Vijver & Zidarova	PinPerl	MA
Pinnularia strictissima Manguin	PinStr	C
Pinnularia subaltiplanensis Zidarova, Kopalová & Van de Vijver	PinSlt	MA
Pinnularia subantarctica var. *elongata* (Manguin) Van de Vijver & Le Cohu	PinSub	A
Placoneis australis Van de Vijver & Zidarova	PlaAus	MA
Planothidium australe (Manguin) Le Cohu	PltAus	A
Planothidium frequentissimum (Lange-Bert.) Round & Bukht.	Pltfrq	C
Planothidium haynaldii (Schaarschm.) Lange-Bert.	PltHay	C
Planothidium lanceolatum (Bréb.) Round & Bukht.	PltLan	C
Planothidium renei (Lange-Bert. & Rol.Schmidt) Van de Vijver	PltRen	A
Planothidium rostrolanceolatum Van de Vijver, Kopalová & Zidarova	PltRL	MA
Psammothidium abundans (Manguin) Bukht. & Round	PsmAbu	A
Psammothidium aretasii (Manguin) Le Cohu	PsmArt	A
Psammothidium cf. *germainii* (Manguin) Sabbe	PsmGer	A
Psammothidium incognitum (Krasske) Van de Vijver	PsmIng	A
Psammothidium manguinii (Hust.) Van de Vijver	PsmMng	A
Psammothidium papilio (D.E.Kellogg, Stuiver, T.B.Kellogg & Denton) Kopalová & Van de Vijver	PsmPap	MA
Psamothidium sp.	PsmRG	MA
Psammothidium subatomoides (Hust.) Bukht. & Round	PsmSatm	C
Rhabdonema sp.	Rhasp	*
Sellaphora nana (Hust.) Lange-Bert., Cavacini, Tagliaventi & Alfinito	SelNan	C
Sellaphora seminulum (Grunow) D.G.Mann	SelSem	C
Stauroforma exiguiformis (Lange-Bert.) Flower	StaExg	C
Stauroneis husvikensis Van de Vijver & Lange-Bert.	StrHus	MA
Stauroneis jarensis Lange-Bert., Cavacini, Tagliaventi & Alfinito	StrJar	C
Stauroneis latistauros Van de Vijver & Lange-Bert.	StrLat	A
Stauroneis obtusa Lagerst.	StrObt	C
Stauroneis pseudomuriella Van de Vijver & Lange-Bert.	StrPmu	A
Stauroneis pseudoschimanskii Van de Vijver & Lange-Bert.	StrPsch	MA
Stauroneis subgracilior Lange-Bert., Cavacini, Tagliaventi & Alfinito	StrSgla	C
Staurosira sp.	Strsp	MA
Staurosirella sp.	Strlsp	MA
Thalassiosira sp.	Thasp	*

of organic material was completed by addition of $KMnO_4$. Following digestion and centrifugation (10 min at 3700 x g), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides, dried on microscope cover slips, and mounted in Naphrax®. Samples and slides are stored at the National Botanic Garden of Belgium (Meise, Belgium). In each sample, 400 diatom valves were identified and enumerated on random transects at x1000 magnification under oil immersion using an Olympus® BX51 microscope equipped with Differential Interference Contrast (Nomarski) optics. Identifications of Antarctic species are based on Van de Vijver et al. (2002a, b, 2004, 2010a, 2010b, 2011a, 2011b), Sabbe et al. (2003), Ohtsuka et al. (2006), Esposito et al. (2008), Van de Vijver & Mataloni (2008), Kopalová et al. (2009, 2011, 2012), Zidarova et al. (2009, 2010, 2012), Van de Vijver & Zidarova (2011) and references therein. For several species, identification up to species level was not possible due to their unclear taxonomic situation. All valves belonging to the genus *Gomphonema* were grouped as *Gomphonema* spp. The different taxa with affinity to *Nitzschia perminuta* (Grunow) Perag. were combined as *N. perminuta*-complex. Further morphological and taxonomic research (ongoing) will be necessary to establish their correct identity.

Table 3 – Similarity coefficients of the diatom flora of James Ross Island and Livingston Island compared with sub-Antarctic islands in the southern Indian and Atlantic Ocean.

	Livingston Island	James Ross Island	Livingston + James Ross Island	South Georgia	Heard Island	Prince Edward Islands
Number of taxa	123	57	130	101	188	207
Livingston Island		0.57		0.18	0.19	0.16
James Ross Island	0.57			0.14	0.12	0.11
Livingston + James Ross Island				0.18	0.19	0.17

Data analysis

For a pairwise comparison of the moss-inhabiting diatom flora of Livingston Island and James Ross Island with similar bryophytic communities in 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. The comparison is based on the revised species lists of South Georgia (Van de Vijver & Beyens 1997b), Heard Island (Van de Vijver et al. 2004) and the Prince Edward Islands (Van de Vijver et al. 2008). For the Antarctic Continent, unfortunately, no recent data on moss-inhabiting diatoms are available.

The geographic distribution of the taxa was based on literature data provided with illustrations or descriptions (table 2). When the identity of a taxon could not be determined this was shown using 'cf.' or 'spp.' and its distribution was listed usually as unknown (U). For Antarctic species, the geographic distribution was further subdivided in 'MA' when the species occurred only in the Maritime Antarctic region. Taxa present in the entire Antarctic region are listed as 'A'. Cosmopolitan taxa present as 'C'.

To determine the extent to which our sampling effort represented the total diatom flora of the two islands, 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 9.0 (Colwell 2013) were calculated. Shannon-Wiener diversity index ($\log_{10}$-based) and Hill's evenness index were calculated using the statistical package MVSP 3.2 (Kovach Computing Services 1993).

Ordination was used to elucidate the principal patterns in species composition in the moss samples of Livingston Island. Squareroot-transformed abundance data with downweighting of rare taxa were used in the ordinations. All ordination analyses were performed using the computer program CANOCO version 4.5 (ter Braak & Šmilauer 1998).The statistical and numerical techniques used in this study are described in full detail in Jongman et al. (1995).

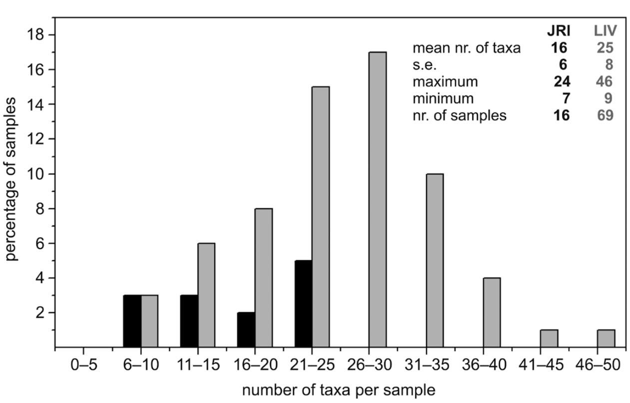

Figure 2 – Distribution of samples for the two sample sets based on species richness. JRI: James Ross Island (black), LIV: Livingston Island (grey).

RESULTS

Species composition and diversity

The microscopic analysis of 84 samples revealed a total of 130 diatom taxa (including species, varieties and forms) belonging to 39 genera. Six samples (V3M3, M1 and M21 from James Ross Island and BYM-9, BYM-10 and BYM-40 from Livingston Island) contained (almost) no diatoms, even after counting an entire slide. Subsequently, these samples have been removed from further analysis. On Livingston Island (68 samples), 123 diatom taxa belonging to 39 genera were found, whereas from James Ross Island (16 samples), only 57 taxa from 23 genera were identified. Table 2 provides an alphabetical list of all observed species together with their biogeographical distribution.

Almost 53% of all observed species have a restricted Antarctic distribution with a majority of these (79%) confined to the Maritime Antarctic region whereas only 43 taxa (32%) have a typical cosmopolitan distribution, such as *Fragilaria capucina* Desm., *Navicula gregaria* Donkin and *Nitzschia gracilis* Hantzsch.

The similarity analysis indicates that the moss diatom flora of Livingston Island and James Ross Island shows a clear difference to the moss-inhabiting diatom flora from South Georgia, and the Prince Edward Islands with Sørensen index values for the complete dataset of both islands together ranging from 0.17–0.19. (table 3). We observed a similarity of only 0.57 between Livingston and James Ross Island. James Ross Island always presented a somewhat lower similarity with the other islands than Livingston Island (0.11–0.14 vs. 0.16–0.19).

Species richness per sample ranged from 9 to 46 for Livingston Island and 7 to 24 for James Ross Island. The distribution of species number per sample clearly differs between both islands. The average number (and standard deviation) of taxa per sample was 25 ± 8 for Livingston Island and 16 ± 6 for James Ross Island (fig. 2). The highest species richness was recorded in several Livingston Island moss samples: BYM-11 (46 taxa), BYM-53 (45 taxa) and BYM-27 (40 taxa) whereas on James Ross Island, the maximum number of counted species was only 24 (sample M22) followed by samples M23 and V3M1 with 23 counted species. The species accumulation curve for Livingston Island (fig. 3) indicates that this sample set contains a large part of the total diatom flora, although it is clear that theoretically not all species have been found. As for James Ross Island only 13 samples were analysed, it is clear that a considerable number of samples still will be needed to obtain a representative dataset for this island. Using species richness estimators, it is possible to evaluate how well the sampling effort reflected the true diatom richness. The expected total number of taxa in all samples is 138 (Chao2) or 142 (ICE) for Livingston, suggesting that our counting scored between 87 and 89% of the (theoretical) total number of taxa present in the samples overall. On the contrary, on James Ross Island, only a counting score of 62% (ICE) – 69% (Chao2) of the (theoretical) total number of taxa was calculated. Based on these differences in species richness, the limited amount of samples from James Ross Island and the species accumulation curve, both datasets will also be treated separately in the following diversity and community analyses.

On Livingston Island, the 51 least abundant species (= 38% of all observed species) together made up only 1% of the total number of valves counted whereas the 7 most dominant species accounted for 50% of all counted valves. As can be seen in fig. 2, a large number of species is restricted to only a few samples and only a few species occur in 50% or more of all samples. The genera *Pinnularia* (sixteen taxa), *Luticola* (thirteen taxa) and *Psammothidium* (nine taxa) were the most species rich genera. Other important genera include *Diadesmis*, *Muelleria*, *Navicula* and *Nitzschia* (seven taxa).

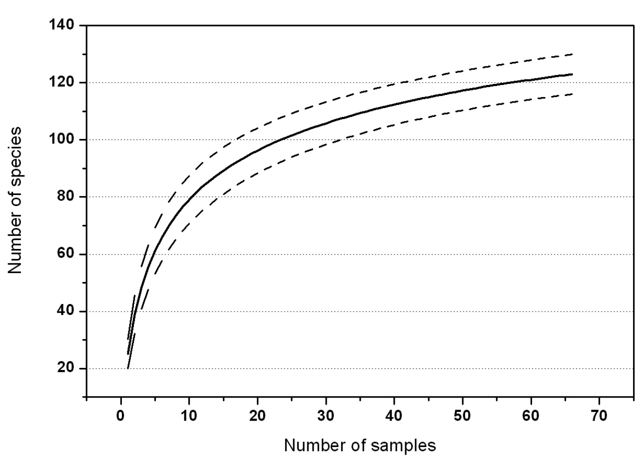

Figure 3 – Expected species accumulation curve (sample based rarefaction curves for the total sample set) for the Livingston Island moss samples. Each time, the 95% confidence interval is given.

The dominant species is *Nitzschia perminuta* with more than 15% of all counted valves followed by *Fragilaria capucina* (9.0%), *Psammothidium incognitum* (Krasske) Van de Vijver (6.6%) and *Gomphonema* spp. (6.3%). It should be noted however that both *N. perminuta* and *Gomphonema* spp. most likely represent complexes of several taxa that need to be split into several independent, most probably new taxa.

The situation is completely different on James Ross Island where the dominant genera include *Luticola* (eleven taxa), *Diadesmis* (six taxa) and *Pinnularia* (five taxa). The flora on this island was dominated by *Pinnularia borealis* Ehrenb. (24.6%), *Hantzschia amphioxys* (Ehrenb.) Grunow (10.7%) and *Nitzschia perminuta* (8.9%).

A considerable number of taxa appeared to be new for science (e.g. *Planothidium rostrolanceolatum* Van de Vijver, Kopalová & Zidarova in Van de Vijver et al.). Several of them have been recently published (Van de Vijver et al. 2013) whereas others (such as *Psammothidium* sp., *Halamphora* sp. or *Diadesmis* sp1 and sp2) await a formal description.

A very small proportion (< 0.1%) of all counted valves belonged to marine species (indicated as '*' in table 2) probably blown in by seaspray or wind or transported on the fur of marine mammals such as elephant seals (*Mirounga leonina* (Linnaeus, 1758) or the feathers of birds such as gentoo penguins (*Pygoscelis papua* Forster, 1781) or southern giant petrels (*Macronectes giganteus* Gmelin, 1789).

Community analysis

An initial detrended correspondence analysis (DCA) using the entire dataset was carried out to estimate gradient length (fig. 4). The results showed that two samples were clear outliers. Sample BYM-02 contained exclusively a very large population of *Eunotia paludosa* Grunow whereas sample BYM-59 was entirely dominated by *Psammothidium germainii* (Manguin) Sabbe. A second DCA with the two outliers omitted showed gradient lengths for the first four axes of 3.322, 2.161, 2.495 and 2.139, suggesting that methods based on unimodal models (Correspondence Analysis) would be appropriate for the ordination of the entire sample set (ter Braak & Prentice 1988). Figure 4 shows clearly that the samples from James Ross Island (JRI) (▲) are entirely separated from the Livingston Island (LI) samples (●). All JRI samples are dominated by *Pinnularia borealis*, *Hantzschia amphioxys* and *H. abundans*, typical terrestrial species that only play a minor role on Livingston Island.

Since the LI sample set was almost five times as large and probably more diverse than the JRI sample set, a new ordination analysis was run, only using the LI samples. The initial DCA showed a maximum gradient length of only 2.0 making linear models (principal component analysis, PCA) more appropriate (ter Braak & Prentice 1988). The PCA analysis divides the LI samples intro three groups (fig. 5). The distinction between these groups is clearly reflected in the species composition. The first two PCA axes (eigenvalues $\lambda_1 = 0.168$, $\lambda_2 = 0.104$) were highly significant ($p = 0.001$) and explained 27.3% of the variation in the diatom composition with an additional 15.7% explained on the next two axes. Table 4 shows the principal characteristics of the different groups including

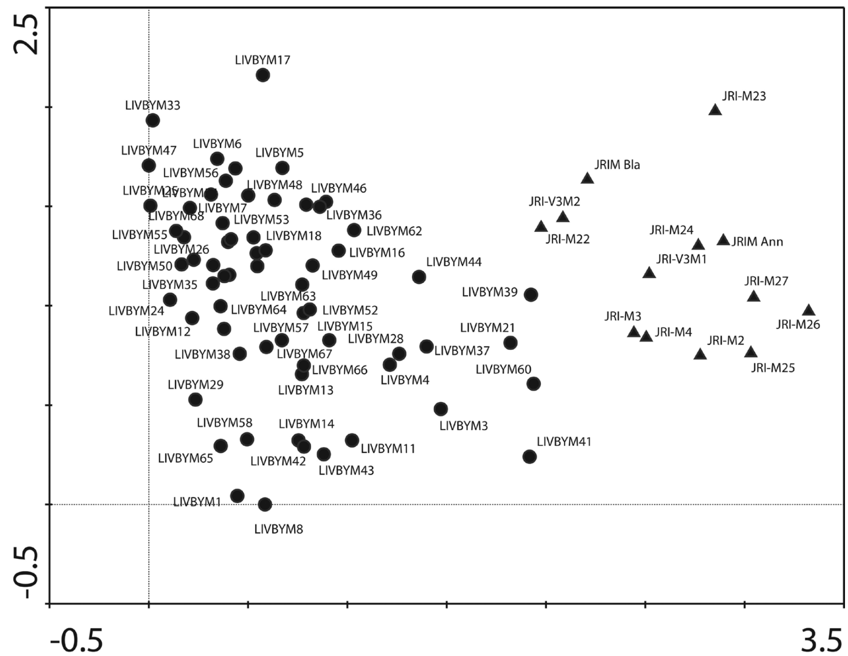

Figure 4 – Detrended Correspondence Analysis (DCA) of the entire sample set. A clear division can be seen between the James Ross Island samples (triangles) and the Livingston Island samples (dots).

the dominant species. The samples on the right side of the diagram (×) form assemblage A. They can be subdivided into two sample groups: assemblage A1 groups coastal localities where the influence of marine mammals and/or birds is very high whereas assemblage A2 contains sites close to the Rotch Dome ice cap, formed after recent glacier retreats. On the left side, two assemblages can be formed within the samples. In the upper half of the diagram, assemblage B (▼) comprises mainly samples from more terrestrial sites at higher elevations, whereas the lower half (assemblage C, ■) is characterized by samples from aquatic habitats (pools and lakes) located at lower altitudes. There are clear differences in diatom species composition between the different assemblages (table 4). Only species with a cumulative fit of > 25% in the PCA diagram are shown (species acronyms are added to table 2). Although some taxa seem to occur in high abundances in several assemblages (such as *Nitzschia perminuta*, *Chamaepinnularia krookiiformis* (Krammer) Lange-Bert. & Krammer or *Fragilaria capucina* sensu lato) it is clear that a number of taxa showed a distinct preference for a particular assemblage. Assemblage A1 is characterized by high frequencies of *Chamaepinnularia krookiiformis*, several *Psammothidium* species (*P. germainii*, *P. papilio* (Kellogg et al.) Kopalová & Van de Vijver, *P.* sp.), *Nitzschia homburgensis* Lange-Bert. and *Pinnularia subantarctica* var. *elongata* (Manguin) Van de Vijver & Le Cohu. Assemblage A2 is characterized by several *Diadesmis* species (mostly *D. arcuata* (Heiden) Lange-Bert. in Moser et al.), *Pinnularia borealis* and *Psammothidium* sp. The second assemblage (B) is dominated by *Nitzschia perminuta*, *Psammothidium incognitum*, *Brachysira minor* (Krasske) Lange-Bert., *Diadesmis inconspicua* Kopalová & Van de Vijver, *D. tabellariaeformis* (Krasske) Lange-Bert. & Wojtal, *Planothidium rostrolanceolatum* and *Gomphonema* spp. Finally, the flora in assemblage C is mostly composed of several *Nitzschia* species (*N. paleacea* (Grunow) Grunow in Van Heurck, *N. gracilis*, *N. perminuta*), *Navicula australoshetlandica* Van de Vijver, *N. dobrinatemniskovae* Zidarova & Van de Vijver and *Fragilaria capucina* sensu lato. No clear separation in the choice for moss species as habitat was observed. Samples associated to *Warnstorfia fontinaliopsis* (Müll.Hal.) Ochyra are only found in assemblage A but both assemblages B and C show a similar number of samples dominated by the three other moss species.

DISCUSSION

Species composition and general biogeography

This study focused on the moss-inhabiting diatoms of two islands located on both sides of the Antarctic Peninsula and therefore undergoing different climatological and ecological influences. Livingston Island is a typical example of the Maritime Antarctic region with relatively high precipitation rates reflected in a higher number of aquatic habitats with more luxuriant wet bryophyte vegetation compared to James Ross Island that has a much drier climate. On the latter island, the extent of aquatic and/or wet terrestrial moss vegetation is rather limited. This is clearly reflected in the observed diatom composition. Whereas the sampled moss-inhabiting communities on James Ross Island are dominated by only typical terrestrial taxa such as *Pinnularia borealis*, *Hantzschia amphioxys* and *Diadesmis arcuata*, known for their preference of drier environments (Petersen 1935, Van de Vijver & Beyens 1997a), dry terrestrial moss vegetations were hardly present and therefore not sampled on Livingston Island resulting in a lower proportion of these terrestrial diatom species in the samples. Based on the differences in sampling effort and habitat types, comparing the species richness

Table 4 – Characteristics of the three groups on Livingston island obtained using PCA analysis.

	Assemblage A1	Assemblage A2	Assemblage B	Assemblage C
Number of samples	13	4	21	26
Mean moisture content range	FIII-FIV	FIII-FIV	FIII-FIV	FII-FIII
Mean altitude of sample	11 ± 13	55 ± 36	50 ± 23	36 ± 21
Number of samples with biotic influence	10	0	0	0
Mean number of taxa	30 ± 8	23 ± 9	21 ± 7	27 ± 8
Mean diversity	2.5 ± 0.3	1.9 ± 1.0	2.0 ± 0.6	2.4 ± 0.4
Mean eveness	0.73 ± 0.07	0.58 ± 0.26	0.65 ± 0.13	0.73 ± 0.07
Number of lake samples	1	1	2	8
Number of pool samples	1	0	3	6
Number of stream samples	1	0	0	1
Number of terrestrial samples	10	3	16	11
Number of samples with dominant:				
Bryum pseudotriquetrum	1	0	4	6
Sanionia georgicouncinata	4	2	6	4
Warnstorfia fontinaliopsis	2	0	0	0
Warnstorfia sarmentosa	3	1	10	12
Other mosses	3	1	1	4
Present in n% of samples # mean Rel. abundance (%) in these samples				
Brachysira minor	75 # 0.7	54 # 1.0	76 # 3.9	58 # 1.3
Chamaepinnularia australomediocris	0 # 0.0	54 # 2.4	14 # 0.2	50 # 0.9
Chamaepinnularia krookiiformis	25 # 1.7	100 # 9.8	86 # 2.1	96 # 4.4
Diadesmis arcuata	75 # 44.1	69 # 1.4	76 # 4.0	88 # 1.3
Diadesmis inconspicua	75 #3.3	30 # 1.3	29 # 3.9	35 # 0.6
Diadesmis sp1	75 # 5.8	30 # 2.3	43 # 0.6	50 # 0.5
Diadesmis sp2	75 # 9.2	54 # 0.6	29 # 0.4	23 # 0.4
Diadesmis tabellariaeformis	25 # 0.4	62 # 1	38 # 3.5	8 # 0.1
Fragilaria capucina s.l.	0 # 0.0	92 # 5	81 # 4.5	88 # 16.2
Gomphonema spp.	75 # 0.9	77 # 1.5	90 # 11.9	100 # 5.0
Navicula australoshetlandica	0 # 0.0	46 # 1	33 # 1.1	73 # 4.4
Navicula dobrinatemniskovae	25 # 0.1	39 # 0.3	14 # 0.4	50 # 2.2
Navicula gregaria	0 # 0.0	8 # 1.6	5 # 0.0	50 # 0.4
Nitzschia gracilis	0 # 0.0	69 # 1.3	67 # 1.3	100 # 7.9
Nitzschia homburgensis	25 # 0.4	100 # 12.8	71 # 1.3	85 # 3.1
Nitzschia paleacea	25 # 0.0	15 # 0.2	38 # 1.6	77 # 4.3
Nitzschia perminuta-complex	50 # 0.9	77 # 1.6	100 # 20.2	100 # 20
Pinnularia borealis	100 # 3.9	62 # 3.3	33 # 0.3	23 # 0.2
Pinnularia subantarctica var. *elongata*	75 # 1.3	92 # 5.8	76 # 2.7	54 # 0.8
Planothidium australe	0 # 0.0	69 # 2.1	24 # 0.4	69 # 1.2
Planothidium rostrolanceolatum	25 # 0.3	62 # 1.8	57 # 5.9	65 # 2.2
Psammothidium germainii	75 # 1.8	77 # 1.3	19 # 0.4	12 # 0.1
Psammothidium incognitum	50 # 0.3	77 # 4.3	90 # 15.6	46 # 1.2
Psammothidium papilio	25 # 0.2	92 #6.0	57 # 2.4	85 # 2.5
Psammothidium sp.	75 # 9.6	69 #10.2	38 # 0.2	27 # 0.2

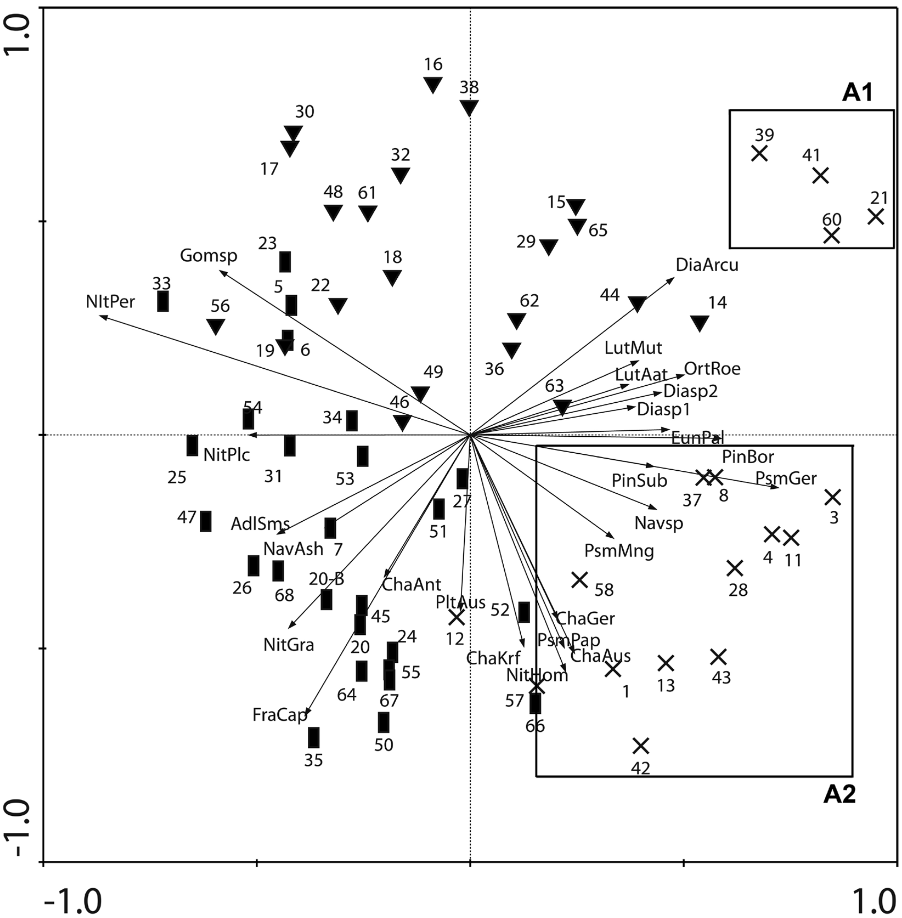

Figure 5 – Principal Components Analysis (PCA) of the Livingston Island sample set. Division into the three groups (group A: ×; group B: ▼; group C: ■) and subdivision of group A is indicated. The first two axes are shown. The acronyms of the species names are given in table 2.

between both islands (57 on JRI vs. 123 on LI) is rather difficult.

It is generally accepted that a decreasing diversity trend when going southwards exists in the Antarctic region (Jones 1996, Van de Vijver & Beyens 1999). This is confirmed by the similarity analysis. The moss-inhabiting diatom communities in the sub-Antarctic region show almost double the species number recorded from Livingston Island (Van de Vijver & Beyens 1997b, Van de Vijver et al. 2004, 2008). The main reason for this decreasing diatom diversity is probably the lower environmental diversity. On the sub-Antarctic islands, the moss vegetation dominates all parts of these islands (Van de Vijver et al. 2002a), forming thick layers in the valleys, on slopes and even fell fields, whereas in the Maritime Antarctic region, mosses are restricted only to the wet areas around lakes, seepage areas and streams. Given the particular dry nature of the James Ross Island samples, it is not entirely sure whether the results in the present study provide a trustful overview of the moss-inhabiting diatom flora of this island. However, the absence of their typical wet moss habitat on James Ross Island is probably one of the main reasons for the lack of epiphytic diatoms on this island. On the nearby Antarctic Continent, the bryophyte flora is restricted to 30 moss species (Lewis Smith 1984), most of them being poikilohydric indicating that they are only wet during periods of snow melts in the summer months (Robinson et al. 2000). Based on the low annual precipitation (Láska et al. 2011a), mosses on James Ross Island apparently undergo a similar desiccation, providing a quite unstable environment for the epiphytic diatoms living on these mosses. Only typical dry-terrestrial diatom taxa are able to overcome these periods of temporal dryness and hence the moss diatom flora on James Ross Island has a lower species richness compared to Livingston Island were mosses remain continuously wet near the numerous lakes and pools on Byers Peninsula.

In the past, Antarctic diatom taxa were force-fitted into European and North-America relatives, which led to the incorrect conclusion that the Antarctic diatom flora is mostly cosmopolitan (Toro et al. 2007, Vinocur & Maidana 2010). However, the recent revisions of the non-marine diatom flora from the entire Antarctic region based on a narrower species concept and a more fine-grained taxonomy (e.g. Van de Vijver et al. 2010a, 2011b, Zidarova et al. 2012) resulted in the description of a large number of typical Antarctic taxa. Many of them were observed in the moss-inhabiting flora. This current revised taxonomy contradicts the Ubiquity Theory developed by Finlay & Clarke (1999) which stated that microorganisms, due to their large population size and small body size can be easily dispersed throughout the world reducing their overall diversity and possible local endemism. Antarctic diatoms clearly show a rather restricted distribution with many endemic taxa. This is confirmed by the results of the similarity analysis. Less than 25% of the taxa found on Livingston Island and James Ross Island are shared with the moss-inhabiting diatoms from the sub-Antarctic islands (on which a similar taxonomic revision was performed), even with localities situated in the southern Atlantic Ocean (South Georgia). Most of the species in common between these islands are mainly cosmopolitan taxa such as *Navicula gregaria* and *Pinnularia borealis*. It is however unclear whether these taxa are truly cosmopolitan since recent studies analysing the genetic similarities and differences between several Antarctic populations of *P. borealis* and *Hantzschia amphioxys* indicate a high degree of cryptic diversity (Souffreau et al. 2013). Together with the rather high number of still unidentified taxa (9–20%) for which further morphological and taxonomic analyses will be necessary to clarify their biogeographical preferences, the proportion of typical Maritime Antarctic taxa will likely increase, confirming the highly specific nature of the Antarctic diatom flora.

Moss-inhabiting diatom communities

The composition of freshwater diatom communities in the Maritime Antarctic region is determined by the amount of nutrients and the conductivity of their habitat (Jones 1993, Kopalová & Van de Vijver 2013, Kopalová et al. 2013) while on the Antarctic Continent lake communities seem to be more influenced by salinity (e.g. Verleyen et al. 2003, Gibson et al. 2006). The moisture availability of the moss habitats presents an additional stress factor for the diatom communities living on these habitats. Moss-inhabiting communities on the sub-Antarctic islands are controlled mainly by moisture of the moss habitat (Van de Vijver & Beyens 1997b, 1999, Van de Vijver et al. 2004, 2008, Vinocur & Maidana 2010). A similar result was found for the moss communities on James Ross and Livingston Island. All moss samples that were collected on James Ross Island were entirely terrestrial and, although not measured, had a rather low moisture content (Kopalová, pers. obs.). This had a clear influence on the moss-inhabiting community that was entirely composed of typical aerophytic species such as *Pinnularia borealis* and several *Hantzschia* taxa. On the sub-Antarctic island of South Georgia, these taxa were only found in the driest mosses (Van de Vijver & Beyens 1997b) and also on other, more distantly located islands, similar communities were observed (see for instance Van de Vijver et al. 2004, 2008). On Livingston on the other hand, dry mosses were almost not sampled which resulted in the observation of totally different communities. The first two axes of the PCA analysis of the Livingston Island samples most likely represent two determining factors: axis one seems to be a biotic axis related to nutrients and salinity whereas axis two represents a moisture axis.

Biotic stress resulting in higher nutrient and salinity input by marine birds and mammals, seems to play a first important role in determining the species composition in the Livingston moss diatom communities separating assemblage A2 from the other assemblages. Marine mammals are frequently found on the shores of this island and show a marked influence on the areas where they often stay for several weeks during their moulting period (Cruwys & Davis 1995). With their excrements, these animals considerably alter the diatom habitat by increasing both the salinity and the nutrient concentrations. Although these parameters were not measured for the moss samples, aquatic samples collected near these moss vegetations show the same trends. Kopalová & Van de Vijver (2013) discuss the environmental factors that determined the diatom composition in the waterbodies of Byers Peninsula and concluded that nutrients and salinity were the controlling factors. Assemblage B clearly represents wet terrestrial moss-inhabiting diatom communities. *Psammothidium incognitum*, originally described from wet mosses on southern Patagonia (Krasske 1939) was found to be one of the dominant terrestrial moss-inhabiting species on South Georgia (Van de Vijver & Beyens 1997b) and also on the sub-Antarctic islands in the southern Indian Ocean, the species was mostly found in wet terrestrial moss vegetations (Van de Vijver et al. 2002a) whereas it is less frequent in aquatic moss vegetations. The assemblage shows also a clear similarity with a South Georgian moss assemblage although some typical sub-Antarctic moss diatoms such as *Psammothidium confusum* (Krasske) Van de Vijver & Beyens are completely missing in the Maritime Antarctic region (Van de Vijver & Beyens 1997b). The aquatic moss assemblage on the other hand shows a large similarity with the epilithic and epipelic aquatic diatom community that was found in lakes on Byers Peninsula. Kopalová & Van de Vijver (2013) reported an almost identical species composition in the lakes. This might indicate that microhabitats in these permanent lakes apparently only play a minor role in the shaping of the diatom composition in these lakes. Most *Nitzschia* and *Navicula* species in the Antarctic region are exclusively aquatic species, hardly found outside permanent waterbodies (Van de Vijver et al. 2011b, Kopalová & Van de Vijver 2013). The results of this study confirm this observation since almost all species of these two genera were found only in the aquatic moss assemblage and not in the terrestrial moss group. Comparison with older data is hardly possible due to the taxonomic revision that started a couple of years ago (Van de Vijver et al. 2011b).

CONCLUSION

In general, a better knowledge of moss-inhabiting diatoms on the Maritime Antarctic islands is important not only from a taxonomical point of view, but also for further ecological and palaeoecological research as some of these moss vegetations present a typical habitat in which diatoms are able to survive, even during more stressful periods. The moss communities on the studied islands are influenced in the first place by the input of nutrients and salinity, most likely due to animal impact and secondly by the moisture content of the habitat.

ACKNOWLEDGEMENTS

This study has been supported by a long-term research development project no. RVO 67985939, the Ministry of Education, Youth and Sports of the Czech Republic and the Picto project nr. 2010–0096. The authors would also like to thank to the members of scientific expedition "Lagos 2012" for their support and help in the field. Samples on Byers Peninsula (Livingston Island) were taken in the framework of the IPY–Limnopolar Project POL2006-06635 (Ministerio de Ciencia y Tecnología, Spain). Mrs. K. Kopalová benefited from an Erasmus grant during her stay in Belgium, GA UK grant nr. 394211 and the Hlávka Foundation for travel funding. The authors would also like to thank the Instituto Antartico Argentino Dirección Nacional del Antarctico for all logistical support. Additional funding was provided by the FWO project G.0533.07 and the BELSPO-CCAMBIO project. Prof. Luc Ector and two anonymous reviewers are thanked for their valuable comments that greatly improved this manuscript.

REFERENCES

Bertrand J., Renon J.P., Monnier O., Ector L. (2004) Relation "diatomées épiphytes-bryophytes" dans les tourbières du Mont Lozère (France). Relationship "epiphytic diatoms-Bryophytes" at Mount Lozère peat bogs (France). Vie et Milieu-Life and Environment 54: 59–70.

Broady P.A. (1986) Ecology and taxonomy of the Vestfold Hills. In: Pickard J. (ed.) Antarctic oasis: terrestrial environments and history of the Vestfold Hills: 165–202. Sydney, Academic Press.

Chao A. (1984) Non-parametric estimation of the number of classes in a population. Scandinavian Journal of Statistics 11: 265–270.

Chao, A., Hwang W.-H., Chen Y.-C., Kuo C.-Y. (2000) Estimating the number of shared species in two communities. Statistica Sinica 10: 227–246.

Chipev N., Veltchev K. (1996) Livingston Island: an environment for Antarctic life. Bulgarian Antarctic Research Life Sciences 1: 1–6.

Chown S.L., Convey P. (2007) Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. Philosophical Transactions of The Royal Society, series B Biological Sciences 362: 2307–2331. http://dx.doi.org/10.1098/rstb.2006.1949

Colwell R.K. (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application available from http://purl.oclc.org/estimates [accessed 16 Jan. 2014].

Cruwys E., Davis P.B. (1995) Moulting juvenile male southern elephant seals Mirounga leonina (L.) at Hannah Point, Walker Bay, Livingston Island, South Shetland Islands. Polar Research 14: 329–334. http://dx.doi.org/10.1111/j.1751-8369.1995.tb00719.x

Engel Z., Nývlt D., Láska K. (2012) Ice thickness, areal and volumetric changes of Davies Dome and Whisky Glacier in 1979–2006 (James Ross Island, Antarctic Peninsula). Journal of Glaciology 58: 904–914. http://dx.doi.org/10.3189/2012JoG11J156

Esposito R.M.M., Spaulding S.A., McKnight D.M., Van de Vijver B., Kopalová K., Lubinski D., Hall B., Whittaker T. (2008) Inland diatoms from the McMurdo Dry Valleys and James Ross Island, Antarctica. Botany 86: 1378–1392. http://dx.doi.org/10.1139/B08-100

Finlay B.J., Clarke K.J. (1999) Ubiquitous dispersal of microbial species. Nature 400: 828. http://dx.doi.org/10.1038/23616

Gibson J.A.E., Roberts D., Van de Vijver B. (2006) Salinity control of the distribution of diatoms in lakes of the Bunger Hills, East Antarctica. Polar Biology 29: 694–704. http://dx.doi.org/10.1007/s00300-006-0107-8

Gremmen N.J.M., Van de Vijver B., Frenot Y., Lebouvier M. (2007) Distribution of moss-inhabiting diatoms along an altitudinal gradient at sub-Antarctic Îles Kerguelen. Antarctic Science 19: 17–24. http://dx.doi.org/ 10.1017/S0954102007000041

Hickman M., Vitt D.H. (1974) The aerial epiphytic diatom flora of moss species from subantarctic Campbell Island. Nova Hedwigia 24: 443–458.

Holdgate M.W. (1970) Antarctic Ecology. London, Academic Press.

Jones V.J. (1993) Use of diatoms in lake sediments to investigate environmental history in the maritime Antarctic: An example from Sombre Lake, Signy Island. In: Heywood R.B. (ed.) Proceedings of the British Antarctic Survey Special Topic Award Scheme Round 2 Symposium: 91–95. Cambridge, British Antarctic Survey.

Jones V.J. (1996) The diversity, distribution and ecology of diatoms from Antarctic inland water. Biodiversity and Conservation 5: 1433–1449. http://dx.doi.org/10.1007/BF00051986

Jongman R.H., ter Braak C.J.F., van Tongeren O.F.R. (1995) Data analysis in community and landscape ecology. Wageningen, Pudoc & Cambridge, Cambridge University Press.

Jung W. (1936) Thecamöben ursprünglicher lebender deutscher Hochmoore. Abhandlungen aus dem Landesmuseum für Naturkunde zu Münster in Westfalen 7: 1–87.

Komárek J., Elster J. (2008) Ecological background of cyanobacterial assemblages of the northern part of James Ross Island, Antarctica. Polish Polar Research 29: 17–32.

Kopalová K., Elster J., Nedbalová L., Van de Vijver B. (2009) Three new terrestrial diatom species from seepage area on James Ross Island (Antarctic Peninsula region). Diatom Research 24: 113–122. http://dx.doi.org/10.1080/0269249X.2009.9705786

Kopalová K., Nedbalová L., de Haan M., Van de Vijver B. (2011) Description of five new species of the diatom genus Luticola (Bacillariophyta, Diadesmidaceae) found in lakes of James Ross Island (Maritime Antarctic region). Phytotaxa 27: 44–60.

Kopalová K., Elster J., Komárek J., Veselá J., Nedbalová L., Van de Vijver B. (2012) Benthic diatoms (Bacillariophyta) from seepages and streams on James Ross Island (NW Weddell Sea, Antarctica). Plant Ecology and Evolution 145: 190–208. http://dx.doi.org/10.5091/plecevo.2012.639

Kopalová K., Van de Vijver B. (2013) Structure and ecology of freshwater benthic diatom communities from Byers Peninsula (Livingston Island, South Shetland Island). Antarctic Science 25: 239–253. http://dx.doi.org/10.1017/S0954102012000764

Kopalová K., Nedbalová L., Nývlt D., Elster J., Van de Vijver B. (2013) Diversity, ecology and biogeography of the freshwater diatom communities from Ulu Peninsula (James Ross Island, NE Antarctic Peninsula). Polar Biology 36: 933–948. http://dx.doi.org/10.1007/s00300-013-1317-5

Kovach Computing Services (1993) Multivariate statistical package version 2.1, users' manual. Pentraeth, Kovach Computing Services.

Krasske G. (1939) Zur Kieselalgenflora Südchiles. Archiv für Hydrobiologie und Planktonkunde 35: 349–468.

Láska K., Prošek P., Budík L. (2010) Seasonal variation of air temperature at the Mendel Station, James Ross Island in the period of 2006–2009. Geophysical Research Abstracts 12: 3880.

Láska K., Nývlt D., Engel Z., Kopačková V. (2011a) Meteorological data and mass balance measurements on Davies Dome and Whisky Glacier in 2006–2010, James Ross Island, Antarctica. Geophysical Research Abstracts 13: 4858.

Láska K., Barták, M., Hájek, J., Prošek, P., Bohuslavová O. (2011b) Climatic and ecological characteristics of deglaciated area of James Ross Island, Antarctica, with a special respect to vegetation cover. Czech Polar Reports 1: 49–62.

Lewis Smith R.I. (1984) Beauchêne Island: a historical account. Polar Record 22: 159–168.

Li S., Ochyra R., Wu P., Seppelt R.D., Cai M., Wang H., Li Ch. (2009) Drepanocladus longifolius (Amblystegiaceae), an addition to the moss flora of King George Island, South Shetland Islands, with a review of Antarctic benthic mosses. Polar Biology 32: 1415–1425. http://dx.doi.org/10.1007/s00300-009-0636-z

Nedbalová L., Nývlt D., Kopáček J., Šobr M., Elster J. (2013) Freshwater lakes of Ulu Peninsula (James Ross Island, NE Antarctic Peninsula): origin, geomorphology and physical and chemical limnology. Antarctic Science 25: 358–372. http://dx.doi.org/10.1017/S0954102012000934

Ochyra R., Lewis Smith R.I., Bednarek H. (2008) The illustrated moss flora of Antarctica. Cambridge, Cambridge University Press.

Ohtsuka T., Kudoh S., Imura S., Ohtani S. (2006) Diatoms composing benthic microbial mats in freshwater lakes of Skarvness ice-free area, East-Antarctica. Polar Bioscience 20: 113–131.

Olivero E.B., Ponce J.J., Martinioni D.R. (2008) Sedimentology and architecture of sharp-based tidal sandstones in the upper Marambio Group, Maastrichtian of Antarctica. Sedimentary Geology 210: 11–26. http://dx.doi.org/ 10.1016/j.sedgeo.2008.07.003

Øvstedal D.O., Lewis Smith R.L. (2001) Lichens of Antarctica and South Georgia. A guide to their identification and ecology. Cambridge, Cambridge University Press.

Petersen J.B. (1935) Studies on the biology and taxonomy of soil algae. Dansk Botanisk Arkiv: 8: 1–183.

Rimet F. (2012) Recent views on river pollution and diatoms. Hydrobiologia 683: 1–24. http://dx.doi.org/10.1007/s10750-011-0949-0

Robinson S.A., Wasley J., Popp M., Lovelock C.E. (2000) Desiccation tolerance of three moss species from continental Antarctica. Australian Journal of Plant Physiology 27: 379–388. http://dx.doi.org/10.1071/PP99133

Robinson S.A., Wasley J., Tobin A.K. (2003) Living on the edge-plants and global change in continental and maritime Antarctica. Global Change Biology 9: 1681–1717. http://dx.doi.org/10.1046/j.1365-2486.2003.00693.x

Round F.E., Crawford R.M., Mann D.G. (1990) The diatoms: biology and morphology of the genera. Cambridge, Cambridge University Press.

Sabbe K., Verleyen E., Hodgson D.A., Vanhoutte K., Vyverman W. (2003) Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East Antarctica. Antarctic Science 15: 227–248. http://dx.doi.org/10.1017/S095410200300124X

Smellie J.L., Johnson J.S., McIntosh W.C., Esser R., Gudmundsson M.T., Hambrey M.J., van Wyk de Vries B. (2008) Six million years of glacial history recorded in the James Ross Island Volcanic Group, Antarctic Peninsula. Palaeogeography, Palaeoclimatology, Palaeoecology 260: 122–148. http://dx.doi.org/doi:10.1016/j.palaeo.2007.08.011

Sørensen T. (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. Det Kongelige Danske Videnskabernes Selskabs Skrifter 54: 1–34.

Souffreau C., Vanormelingen P., Van de Vijver B., Isheva T., Verleyen E., Sabbe K., Vyverman W. (2013) Molecular evidence for distinct Antarctic lineages in the cosmopolitan terrestrial diatoms Pinnularia borealis and Hantzschia amphioxys. Protist 164: 101–115. http://dx.doi.org/10.1016/j.protis.2012.04.001

Spaulding S.A., Van de Vijver B., Hodgson D.A., McKnight D.M., Verleyen E., Stanish L. (2010) Diatoms as indicators of environmental change in Antarctic and subantarctic freshwaters. In: Smol J., Stoermer E. (eds) The diatoms: applications for the environmental & earth sciences: 267–286. Cambridge, Cambridge University Press.

Svojtka M., Nývlt D., Murakami M., Vávrová J., Filip J., Mixa P. (2009) Provenance and post-depositional low-temperature evolution of the James Ross Basin sedimentary rocks (Antarctic Peninsula) based on fission track analysis. Antarctic Science 21: 593–607. http://dx.doi.org/10.1017/S0954102009990241

ter Braak C.J.F., Prentice I.C. (1988) A theory of gradient analysis. Advances in Ecological Research 18: 271–317.

ter Braak C.J.F., Šmilauer P. (1998) CANOCO reference manual and users' guide to CANOCO for Windows. Wageningen, Centre for Biometry.

Toro M., Camacho A., Rochera C., Rico E., Bañón M., Fernández-Valiente E., Marco E., Justel A., Avendaño M.C., Ariosa Y., Vincent W.F., Quesada A. (2007) Limnological characteristics of the freshwater ecosystems of Byers Peninsula, Livingston Island, in Maritime Antarctica. Polar Biology 30: 635–649. http://dx.doi.org/10.1007/s00300-006-0223-5

Van de Vijver B., Beyens L. (1997a) A preliminary study of freshwater diatoms of small islands in the Maritime Antarctic region. Antarctic Science 9: 418–425. http://dx.doi.org/10.1017/S0954102097000540

Van de Vijver B., Beyens L. (1997b) The epiphytic diatom flora of mosses from Strømness Bay area, South Georgia. Polar Biology 17: 492–501. http://dx.doi.org/10.1007/s003000050148

Van de Vijver B., Beyens L. (1998) A preliminary study on the soil diatom assemblages from Ile de la Possession (Crozet, Subantarctica). European Journal of Soil Biology 34: 133–141. http://dx.doi.org/10.1016/S1164-5563(00)88650-1

Van de Vijver B., Beyens L. (1999) Biogeography and ecology of freshwater diatoms in Subantarctica. Journal of Biogeography 26: 993–1000. http://dx.doi.org/10.1046/j.1365-2699.1999.00358.x

Van de Vijver B., Ledeganck P., Beyens L. (2001) Habitat preferences in freshwater diatom communities from sub-Antarctic Iles Kerguelen. Antarctic Science 13: 28–36. http://dx.doi.org/10.1017/S0954102001000050

Van de Vijver B., Frenot Y., Beyens L. (2002a) Freshwater diatoms from Ile de la Possession (Crozet Archipelago, Subantarctica). Bibliotheca Diatomologica 46: 1–412.

Van de Vijver B., Ledeganck P., Lebouvier M. (2002b) Luticola beyensii sp. nov., a new aerophilous diatom from Ile Saint Paul (Indian Ocean, Taaf). Diatom Research 17: 235–241. http://dx.doi.org/10.1080/0269249X.2002.9705541

Van de Vijver B., Beyens L., Vincke S., Gremmen N.J.M. (2004) Moss-inhabiting diatom communities from Heard Island, sub-Antarctic. Polar Biology 27: 532–543. http://dx.doi.org/10.1007/s00300-004-0629-x

Van de Vijver B., Gremmen N.J.M., Smith V. (2008) Diatom communities from the Sub-Antarctic Prince Edward Islands: diversity and distribution patterns. Polar Biology 31: 795–808. http://dx.doi.org/10.1007/s00300-008-0418-z

Van de Vijver B., Mataloni G. (2008) New and interesting species in the genus Luticola D.G. Mann (Bacillariophyta) from Deception Island (South Shetland Islands). Phycologia 47: 451–467. http://dx.doi.org/10.2216/07-67.1

Van de Vijver B., Sterken M., Vyverman W., Mataloni G., Nedbalová L., Kopalová K., Elster J., Verleyen E., Sabbe K. (2010a) Four new non-marine diatom taxa from the sub-Antarctic and Antarctic regions. Diatom Research 25: 431–443. http://dx.doi.org/10.1080/0269249X.2010.9705861

Van de Vijver B., Mataloni G., Stanish L., Spaulding S.A. (2010b) New and interesting species of the genus Muelleria (Bacillariophyta) from the Antarctic region and South Africa. Phycologia 49: 22–41. http://dx.doi.org/10.2216/09-27.1

Van de Vijver B., Zidarova R. (2011) Five new taxa in the genus Pinnularia sectio Distantes (Bacillariophyta) from Livingston Island (South Shetland Islands). Phytotaxa 24: 39–50.

Van de Vijver B., Zidarova R., de Haan M. (2011a) Four new Luticola taxa (Bacillariophyta) from the South Shetland Islands and James Ross Island (Maritime Antarctic region). Nova Hedwigia 92: 137–158. http://dx.doi.org/10.1127/0029-5035/2011/0092-0137

Van de Vijver B., Zidarova R., Sterken M., Verleyen E., de Haan M., Vyverman W., Hintz F., Sabbe K. (2011b) Revision of the genus Navicula s.s. (Bacillariophyceae) in inland waters of the Sub-Antarctic and Antarctic with the description of 5 new species. Phycologia 50: 281–297. http://dx.doi.org/10.2216/10-49.1

Van de Vijver B., Wetzel C., Kopalová K., Zidarova R., Ector L. (2013) Analysis of the type material of Achnanthidium lanceolatum Brébisson ex Kützing (Bacillariophyta) with the description of two new Planothidium species from the Antarctic region. Fottea 13: 105–117.

Van der Werff A. (1955) A new method of concentrating and cleaning diatoms and other organisms. Verhandlungen Internationalen Vereinigung für Theoretische und Angewandte Limnologie 2: 276–277.

Verleyen E., Hodgson D.A., Vyverman W., Roberts D., McMinn A., Vanhoutte K., Sabbe K. (2003) Modelling diatom responses to climate-induced fluctuations in the moisture balance in continental Antarctic lakes. Journal of Paleolimnology 30: 195–215.

Vinocur A., Maidana N.I. (2010) Spatial and temporal variations in moss-inhabiting summer diatom communities from Potter Peninsula (King George Island, Antarctica). Polar Biology 33: 443–455. http://dx.doi.org/10.1007/s00300-009-0719-x

Zidarova R., Van de Vijver B., Mataloni G., Kopalová K., Nedbalová L. (2009) Four new freshwater diatom species (Bacillariophyceae) from Antarctica. Cryptogamie Algologie 30: 295–310.

Zidarova R., Van de Vijver B., Quesada A., de Haan M. (2010) Revision of the genus Hantzschia (Bacillariophyceae) on Livingston Island (South Shetland Islands, Southern Atlantic Ocean). Plant Ecology and Evolution 143: 318–333. http://dx.doi.org/10.5091/plecevo.2010.402

Zidarova R., Kopalová K., Van de Vijver B. (2012) The genus Pinnularia (Bacillariophyta) excluding the section Distantes on Livingston Island (South Shetland Islands) with the description of twelve new taxa. Phytotaxa 44: 11–37.

Manuscript received 10 Jun. 2013; accepted in revised version 16 Jan. 2014.

Communicating Editor: Elmar Robbrecht.