Diatoms composing benthic microbial mats in freshwater lakes of Skarvsnes ice-free area, East Antarctica

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Abstract: Diatoms composing benthic microbial mats in Skarvsnes lakes, East Antarctica, were studied in terms of their taxonomy and relationship to environmental factors. Samples were collected from 13 freshwater lakes in the area. *Amphora* sp. (cf. *veneta*) was dominant in 11 of the 13 samples, while *Craticula* sp. (cf. *molesta*) and *Diadesmis* sp. (cf. *perpusilla*) were respectively dominant in the remaining 2 samples. *Navicula ectoris* Van de Vijver was also reported here for the first time in continental Antarctica. Mosses in the microbial mats did not have a significant effect on the diatom species composition. Redundancy analysis revealed that the main environmental gradient for diatoms was electric conductivity, despite its relatively narrow range (18–390 mS m^{-1}). Our results suggest that *Diadesmis* sp. and *Psammothidium metakryophilum* are halophobes, whereas *Amphora* sp. is a halophile.

key words: benthic microbial mats, diatoms, East Antarctica, electric conductivity, freshwater lakes

Introduction

Benthic diatom assemblages are excellent biological indicators of Antarctic lake environments for the following reasons. Firstly, diatoms are a common component of benthic microbial mats, which are prevalent in Antarctic lakes (*e.g.*, Fumanti *et al*., 1995, 1997; Vincent and James, 1996). Secondly, diatom assemblages clearly reflect environmental factors. For example, Sabbe *et al*. (2004) demonstrated that diatom species composition is strongly related to lake depth and electric conductivity, whereas the distribution of cyanobacterial morphotypes did not show a clear relationship with electric conductivity. Finally, diatoms serve as environmental indicators not only of the present, but also of the past, because their frustules remain in lake-bottom deposits (Spaulding and McKnight, 1999).

Efficient use of diatom assemblages as indicators of past/present environments requires detailed knowledge of their taxonomy, and distribution in relation to habitat types and environmental factors. The taxonomy of Antarctic freshwater diatoms is, however, not fully understood, despite an almost 100-year history of Antarctic diatom studies. Even in the last decade, many species have been newly described (*e.g*., Alfinito and

Cavacini, 2000; Van de Vijver *et al.*, 2004) and the correct taxonomical status of others has been updated (Sabbe *et al.*, 2003). The relationship between diatom assemblages and the environmental factors of Antarctic lakes has been rapidly revealed since the 1990's (*e.g.* Jones *et al.*, 1993; Roberts and McMinn, 1996; Roberts *et al.*, 2001; Sabbe *et al.*, 2004) with the use of canonical correspondence analysis (CCA), a multivariate direct gradient technique developed by Ter Braak (1986). However, because quantitative analyses such as CCA have so far been applied to a restricted number of regions and habitats, further studies are desired.

In the Skarvsnes ice-free area along the central Sôya Coast in East Antarctica, there are many small oligotrophic freshwater lakes without perennial ice cover (Imura *et al.*, 1999). At the bottom of most of these lakes, microbial mats mainly composed of filamentous cyanobacteria, green algae, and diatoms are found. These microbial mats occasionally contain mosses such as *Bryum pseudotriquetrum* (Hedw.) Gaertn., Meyer et Scherb. and *Leptobryum* sp., with *Leptobryum* sp. often taking on a pillar- or column-like growth form known as a "moss pillar" with algae, and sometimes, with *B. pseudotriquetrum* (Imura *et al.*, 1999, 2003; Kudoh *et al.*, 2003a). These conspicuous moss pillars have been studied in terms of their distribution (Imura *et al.*, 2003), chemical composition (Kudoh *et al.*, 2003a), and preferred habitats in connection with water quality and light environment (Kudoh *et al.*, 2003b). However, the algae composing these mats, including diatoms, have yet to be taxonomically examined in detail, although Ohtani and Suyama (2001) and Ohtani *et al.* (2001) published two preliminary reports.

Hirano (1983) reported 71 taxa of diatoms in the Skarvsnes area; however, since the publication of this report, the taxonomy of diatoms has considerably progressed, especially as a result of scanning electron microscopy (SEM) and re-examination of type materials. Consequently, endemism of Antarctic diatoms has once again become a point of focus (*e.g.*, Sabbe *et al.*, 2003; Van de Vijver *et al.*, 2005). Therefore, the diatom flora of Skarvsnes area should also be re-examined in light of this updated taxonomy.

The present paper discusses the diatom species composing benthic microbial mats in Skarvsnes lakes, East Antarctica, in terms of their taxonomy and relationship to environmental factors. We provide both light microscopy (LM) and SEM microphotographs for detailed taxonomic arguments, and statistically analyze the characteristics of the diatom assemblages and their relationship to the environmental factors, especially the presence/absence of mosses.

Materials and methods

Sampling

Microbial mats were sampled from 13 lakes in the Skarvsnes ice-free area (69°19'–32'S, 39°27'–53'E), located along the central Sôya Coast about 60 km south of Syowa Station, East Antarctica (Fig. 1). These lakes are usually ice-free between the end of December and mid-February, but even at these times, ice can remain.

Samples were collected in 19–21 January, 2000 by S. Kudoh. The microbial mats were scraped off the lake bottom using a throw-in type metallic cylinder sampler (*ca.* 10 cm in diameter, 15 cm in length) with an opening mouth containing several picks and a mesh on the other side. The sampler was attached to *ca.* 30 m of nylon rope, and sam-
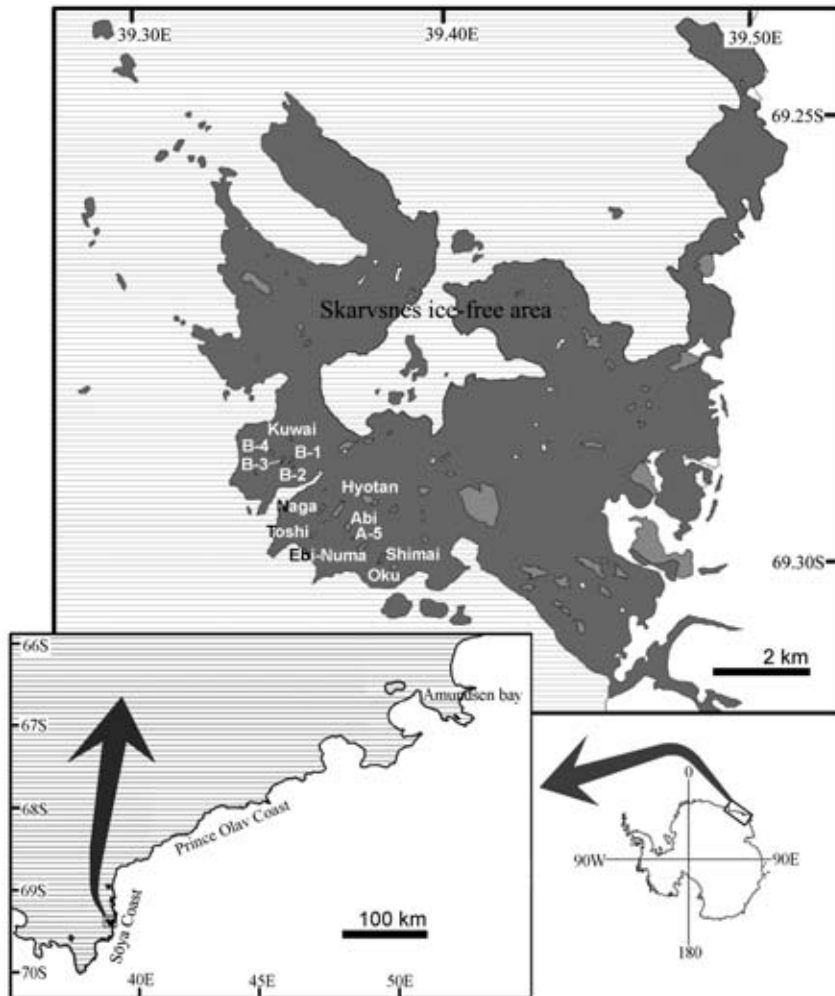
Fig. 1. A map of the study site.

ples were collected from approximately 15 m from the lakeshore. Collected samples were immediately stored in aluminum laminate packages and kept under cool dark conditions until analysis. A total of 22 samples were obtained, 10 from lake B-4 Ike and 12 from the remaining lakes.

Measurement of water characteristics

Water quality was checked at the same time as sampling with a multiple water quality checker (WQC-22A, DKK-TOA Co.) at each lakeshore. Electric conductivity, pH, salinity, dissolved oxygen, turbidity and temperature were recorded.

Anions and cations were analyzed by column chromatography using an ion analyzer (IA-100, Toa Co.). The detection limit for each ion was *ca*. 0.1 mg l^{-1}.

Microscopic observation

Cleaned diatom frustules were observed after the following procedures. Firstly, part of each sample was suspended in 1N-HCl at 60°C then repeatedly rinsed with distilled water to remove calcareous materials. Secondly, they were boiled in 10%-H_2O_2 to oxidize all organic components and again repeatedly rinsed with distilled water.

For LM, part of each cleaned sample was mounted onto slides using Pleurax. Two microscopes, Optiphot (Nikon, Tokyo, Japan) and Ecripse 80i (Nikon, Tokyo, Japan), were then used for observation. Usually normal illumination was used, but for some delicate and less-contrasted valves we also used annular or oblique illumination. A total of 500 frustules were counted on each slide under ×1000 magnification. The relative frequency of each species was evaluated as a percentage. For SEM, the remaining cleaned samples were mounted onto glass slides and coated with palladium. SEM, JSM6301F (JEOL, Tokyo, Japan), was operated at 3.0–5.0 kV.

Species with a relative frequency exceeding 1% in at least one sample were taxonomically examined based on both LM and SEM findings. At least 10 valves for each species were photographed using LM then the length and width of each photographed valve were measured. Stria density was converted from an interval of 10 striae on the valve side, near the center along the apical axis.

Diatom assemblage analysis and their relationship to environmental factors

A total of 13 diatom assemblages from different lakes were analyzed. Species diversity of the diatom assemblages was evaluated based on species numbers within the 500 counted valves and Simpson's (1949) index of diversity, 1-λ. The values of these indices were then compared between samples with and without mosses using Mann-Whitney's U test.

To evaluate the differences in diatom species composition between assemblages, we used modified Matusita's distance, d:

$$d_{12}=\sqrt{1-\sum_{i=1}^{s}\sqrt{p_{i1}\cdot p_{i2}}}\ ,$$

where d_{12} is the modified Matusita's distance between assemblages 1 and 2, S is the number of occurring species, and p_{i1} and p_{i2} are the relative frequencies of ith species in assemblages 1 and 2, respectively (Ohtsuka, 1999). To test whether the presence/absence of mosses significantly influenced species composition, Mantel's (1967) permutation test (999 permutations, $P<0.05$) was performed for the statistic D(between)/D(within), where D(between) is the average d between groups in which mosses are present/absent, and D(within) is the average d within the group.

We also performed redundancy analysis (RDA; Van den Wollenberg, 1977) to analyze the relationship between the diatom assemblages and environmental factors using the computer program CANOCO 4.5 for Windows (Ter Braak and Šmilauer, 2002). The reason for using RDA instead of CCA was that the collected assemblages were similar to each other in species composition and the lengths of the environmental gradients were presumed to be short. In such cases, RDA, which is based on a linear response model, is more feasible than CCA, which is based on a unimodal response model, as has been dis-

cussed by Ter Braak and Prentice (1988). Diatoms with a relative frequency of more than 1% in at least one sample were included in the analysis; the square-rooted relative frequencies of the diatoms were set as objective variables. As tentative explanatory variables, we set the area, maximum depth, surface temperature, electric conductivity (EC), pH, turbidity and SO_4^{2-} concentration of the lakes, and presence/absence (1/0) of *B. pseudotriquetrum* and *Leptobryum* sp. in the microbial mats. Environmental parameters whose distributions were skewed to the right, *i.e.*, area, maximum depth, EC, and SO_4^{2-} concentration, were log-transformed for normal approximation. The concentrations of detected cations and anions other than SO_4^{2-} were not used, because they were highly correlated with conductivity. Forward selection of environmental factors with unrestricted Monte Carlo permutation tests (999 permutations, $P<0.05$) was used to select the minimal number of significant explanatory variables.

Results and discussion

Limnological characteristics of the lakes

The geographic, physical and chemical characteristics of the lakes are presented in Table 1. All the investigated lakes were small and shallow with an area and depth of 4.3–52.9$\times 10^3$ m^2 and 1.0–12.4 m, respectively. Their waters were clear with a turbidity of 3–7 NTU. Nutrients such as nitrate, nitrite, ammonium and phosphate were also measured by ion chromatography, but were all below the detection limit (<0.1 mg l^{-1}), suggesting that the lakes were all oligotrophic. Although they were all classified as freshwater lakes, many had somewhat salty water; the salinity calculated using the EC ranged between 0.009 and 0.20. None of the lakes were frozen over at the time of sampling, although some ice remained in most of them.

Among the microbial mat samples obtained from the 13 lakes, seven contained

Table 1.   Environmental features of the studied lakes, and the presence (+) of mosses in the benthic microbial mats. The names of the lakes are temporary ones.

Lake:	Toshi	Abi	A-5	Ebi-Numa	Shi-mai	Oku	Naga	B-1	B-2	B-3	B-4	Hyo-tan	Ku-wai
Area ($\times 10^3$ m^2)	9	20	2	25	17	17	48	9	5	10	6	53	4
Maximal depth (m)	3.5	4.0	1.0	5.5	6.5	5.0	10.8	4.8	3.1	3.0	3.0	12.4	3.6
Surface temperature (°C)	5.4	7.5	7.6	7.5	7.4	8.8	4.6	7.6	4.8	5.0	3.7	8.8	5.2
EC (mS m^{-1})	121	18	76	174	390	200	116	41	181	65	107	210	32
pH	7.7	7.4	7.8	8.1	7.8	8.0	6.9	7.1	7.5	7.5	7.0	8.0	6.8
Turbidity (NTU)	6	6	5	5	5	6	6	7	5	5	6	6	3
DO (mg l^{-1})	10.5	9.6	9.2	9.4	9.7	10.8	10.8	10.1	11.7	11.2	12.0	11.5	12.2
Na^+ (mg l^{-1})	160	14	99	233	587	283	164	51	263	81	137	334	34
K^+ (mg l^{-1})	6.0	0.8	5.0	9.0	22.0	12.0	5.5	1.8	10.5	2.8	4.4	13.0	1.3
Mg^{2+} (mg l^{-1})	33.5	3.3	21.6	59.0	173.0	70.0	26.5	8.8	50.5	16.2	29.8	63.0	5.3
Ca^{2+} (mg l^{-1})	18.5	5.0	21.6	28.0	30.0	23.0	8.5	9.0	31.5	14.6	19.0	26.0	5.4
Cl^- (mg l^{-1})	290	25	158	440	480	480	292	89	468	156	256	606	61
SO_4^{2-} (mg l^{-1})	21.5	3.5	3.4	47.5	60.0	58.0	16.5	21.5	122.0	29.4	40.6	10.0	11.7
Bryum pseudotriquetrum						+			+		+	+	+
Leptobryum sp.						+		+		+	+		

Table 2.　Diatom species compositions (%) and diversity indices. The species numbers represent the values within 500 counts.　The names of the lakes are temporary ones.

Lake:	Toshi	Abi	A-5	Ebi-Numa	Shi-mai	Oku	Naga	B-1	B-2	B-3	B-4*1	B-4*2	Hyo-tan	Ku-wai
Achnanthes gainii												+		
A. taylorensis					0.2									
Amphora sp. (cf. *veneta*)	96.2	0.8	84.2	89.0	88.0	95.6	39.8	46.0	58.8	83.4	97.6	94.8	95.6	66.2
Cocconeis imperathrix								0.2						
C. sp.												+		
Craticula sp. (cf. *molesta*)	3.4		14.4	9.6	4.0	3.2	45.0	26.8	26.8	7.4	1.8	3.0	4.4	2.6
Cyclotella sp.												+		
Diadesmis sp. (cf. *perpusilla*)		91.0	0.2					12.2		0.8		0.1		
Ellerbeckia arenaria												+		
Hantzschia amphioxys												+		
Luticola murrayi	0.4		0.2		4.6	0.8	14.2	0.2	1.0		0.2	0.3		0.2
L. muticopsis		0.2			0.2			0.4				+		
Navicula ectoris					0.2				9.6		0.4	+		
N. gregaria		0.6	0.4	1.4	2.4	0.2	0.4	5.2	3.8	8.2				29.2
Nitzschia commutata			0.2		0.2	0.2						1.4		1.4
Paralia sp.								0.2				+		
Pinnularia cymatopleura					0.2		0.2							
Psammothidium abundans								0.2						
P. metakryophilum		5.6	0.4				0.2	6.4				+		0.4
P. stauroneioides		1.0						1.0						
Stauroneis latistauros		0.8					0.2	1.2		0.2				
Number of species	3	7	7	3	9	5	7	12	5	5	4		2	6
Simpson's 1-λ	0.074	0.169	0.271	0.199	0.222	0.085	0.620	0.696	0.573	0.293	0.047		0.084	0.477

*1: The ecologically analyzed assemblage first collected from lake B-4 Ike.

*2: Averages of 10 samples collected from lake B-4 Ike. + indicates a relative frequency of less than 0.1%.

mosses and six did not. Among the moss-containing samples, three had only *Leptobryum* sp., two had only *B. pseudotriquetrum* and the remaining two contained both (Table 1).

Taxonomy

　　We found a total of 21 diatom species in the 22 examined samples. Ten diatom species exceeded 1% in relative frequency in at least one sample, indicating that they are probably not rare (Table 2); they were all raphid diatoms. Their taxonomical notes are as follows:

Amphora sp. [cf. *A. veneta* Kütz.] (Figs. 2–8, 46, 47)

　　23.6–60.7 μm long, 5.6–12.8 μm wide, 18–28 striae in 10 μm. Although the size and shape varies largely, there are no discontinuities in valve morphology.

　　This taxon could be identified as *Amphora veneta* Kütz sensu lato, but the valve morphology often deviates from that of typical *A. veneta* (cf. Krammer and Lange-Bertalot, 1986; Kobayasi, 1995). Our specimens were considered conspecific with *A. veneta* sensu Hirano (1983) from Skarvsnes and sensu Cremer *et al*. (2004) from Amery Oasis, East Antarctica. *A. veneta* reported in the saline lakes of Vestfold Hills (Roberts and McMinn, 1999) and Larsemann Hills (Sabbe *et al*., 2003), East Antarctica, are also very similar to our specimens and showed large but continuous morphometric variations.

Although they have coarser striae (14–24 and 14–22 in 10 μm, respectively) than those documented here, this difference probably represents local variation within the same species.

Craticula sp. [cf. *C. molesta* (Krasske) Lange-Bert. et Willmann] (Figs. 9–12, 48, 49)

20.5–27.1 μm long, 5.1–6.0 μm wide, 17–20 striae in 10 μm. Aleorae were often visible in LM, about 35 in 10 μm.

Our specimens are similar to *Craticula molesta* (Krasske) Lange-Bert. et Willmann (=*Navicula molesta* Krasske), the most frequently recorded *Craticula* species from Antarctica (Kellogg and Kellogg, 2002). In addition, they are considered conspecific with *Navicula molesta* sensu Ko-Bayashi (1965) from Ongul Islands, maritime Antarctica, and sensu Hirano (1983) from Skarvsnes, East Antarctica. However, they almost always have larger valves and coarser striae than the type specimen of *C. molesta* (cf. Lange-Bertalot *et al*., 1996).

Our specimens could be identified as *Craticula buderi* (Hust.) Lange-Bert. following the taxonomic concept of Lange-Bertalot (2001). However, we suspended our identification because the type specimens of *C. buderi* originating from culture (Simonsen, 1987) have consistently smaller and blunter valves than our specimens.

Diadesmis sp. [cf *D. perpusilla* (Grunow) D.G.Mann] (Figs. 13–17, 50, 51)

6.6–18.0 μm long, 3.5–5.0 μm wide, 28–34 striae in 10 μm.

Our specimens belong to the same species as *Navicula arcuata* Heiden sensu Hirano (1983) from Skarvsnes, *Diadesmis* cf. *perpusilla* (Grunow) D.G. Mann sensu Sabbe *et al*. (2003) and sensu Cremer *et al*. (2004) from saline lakes in East Antarctica. However, *N. arcuata* reported in Subantarctica (Heiden and Kolbe, 1928; Van de Vijver *et al*., 2002) differs from our taxon by its broader and more rectangular valve (Sabbe *et al*., 2003). We were unable to confidently identify our specimens as *D. perpusilla*, because the morphological variation and ultrastructure of the type specimens have yet to be examined, as discussed by Sabbe *et al*. (2003).

Luticola murrayi (West et G.S.West) D.G.Mann in Round *et al*., The Diatoms 671. 1990. (Figs. 18–21, 52, 53)

Basionym: *Navicula murrayi* West et G.S.West, Br. Antarct. Exped. 1907–9 **1**: 285. *f. 129*. 1911.

Synonyms: *Navicula murrayi* var. *elegans* West et G.S.West, Br. Antarct. Exped. 1907‒9 **1**: 285. *f. 130*. 1911. *Navicula globiceps* var. *amphicephala* F.E.Fritsch, Natl. Antarct. Exped. 1901–4. **6**: 53. *f. 154*. 1912. *Navicula globiceps* var. *elongata* F.E.Fritsch, Natl. Antarct. Exped. 1901–4. **6**: 53. *f. 155*. 1912. *Navicula muticopsis* fo. *murrayi* (West et G.S. West) Ts.Kobay., Antarct. Rec. (Tokyo) **17**: 65. 1963.

12.8–39.8 μm long, 8.5–12.5 μm wide, 12–18 striae in 10 μm. This species exhibits large but continuous variation in valve shape, as discussed by Ko-Bayashi (1963).

L. murrayi has been frequently recorded in the Antarctica and Subantarctica (Kellogg and Kellogg 2002), and is considered endemic to these regions (Sabbe *et al*., 2003). However, a very similar species, *Navicula palaearctica* Hust., has been reported in Franz-Joseph-Land, Arctica (Hustedt, 1961–1966).
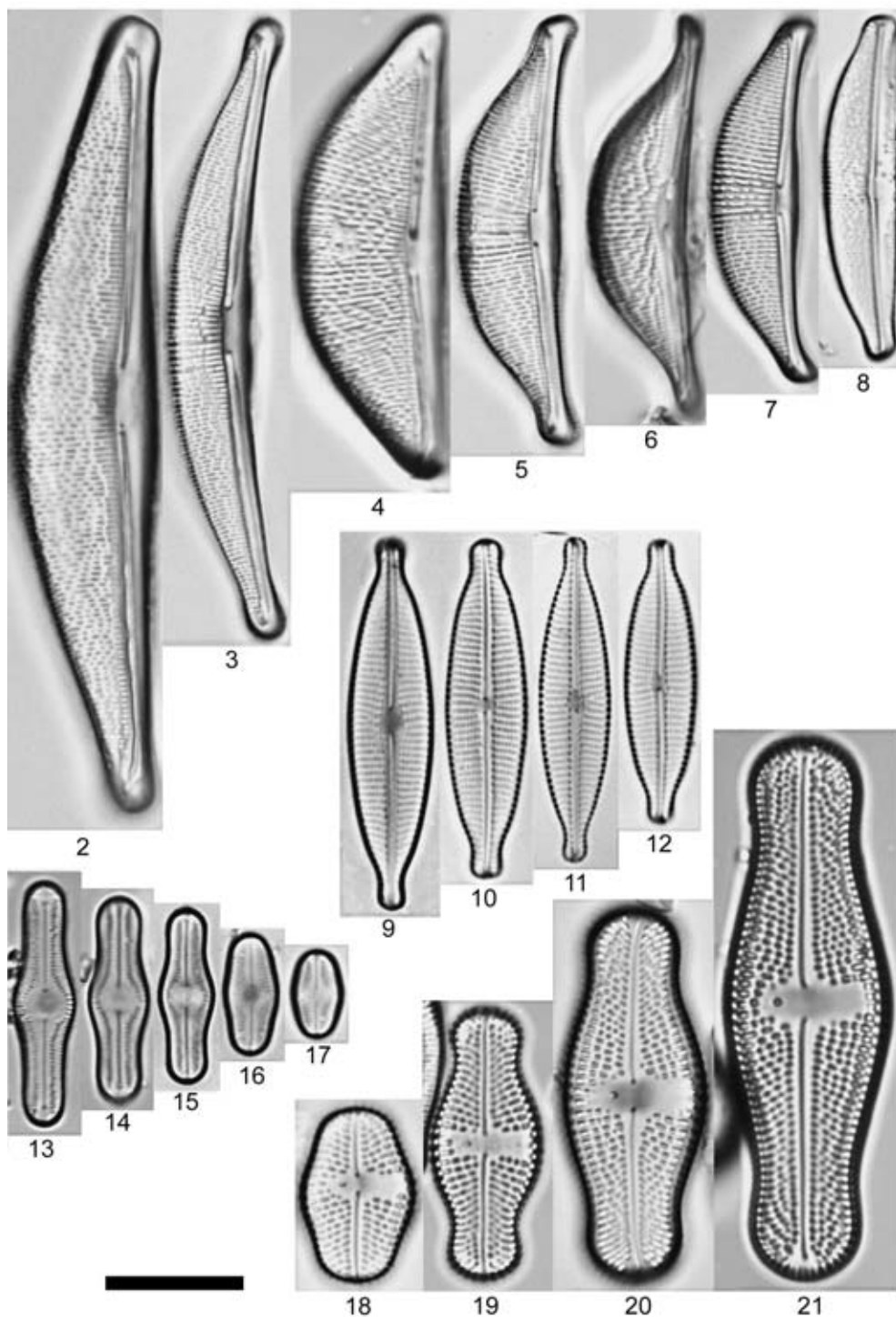
Figs. 2–21. LM photographs of diatom species sampled from the Skarvsnes lakes, all in valve view.
2–8. *Amphora* sp. 9–12. *Craticula* sp. 13–17. *Diadesmis* sp. 18–21. *Luticola murrayi*. Scale bar=10 μm.
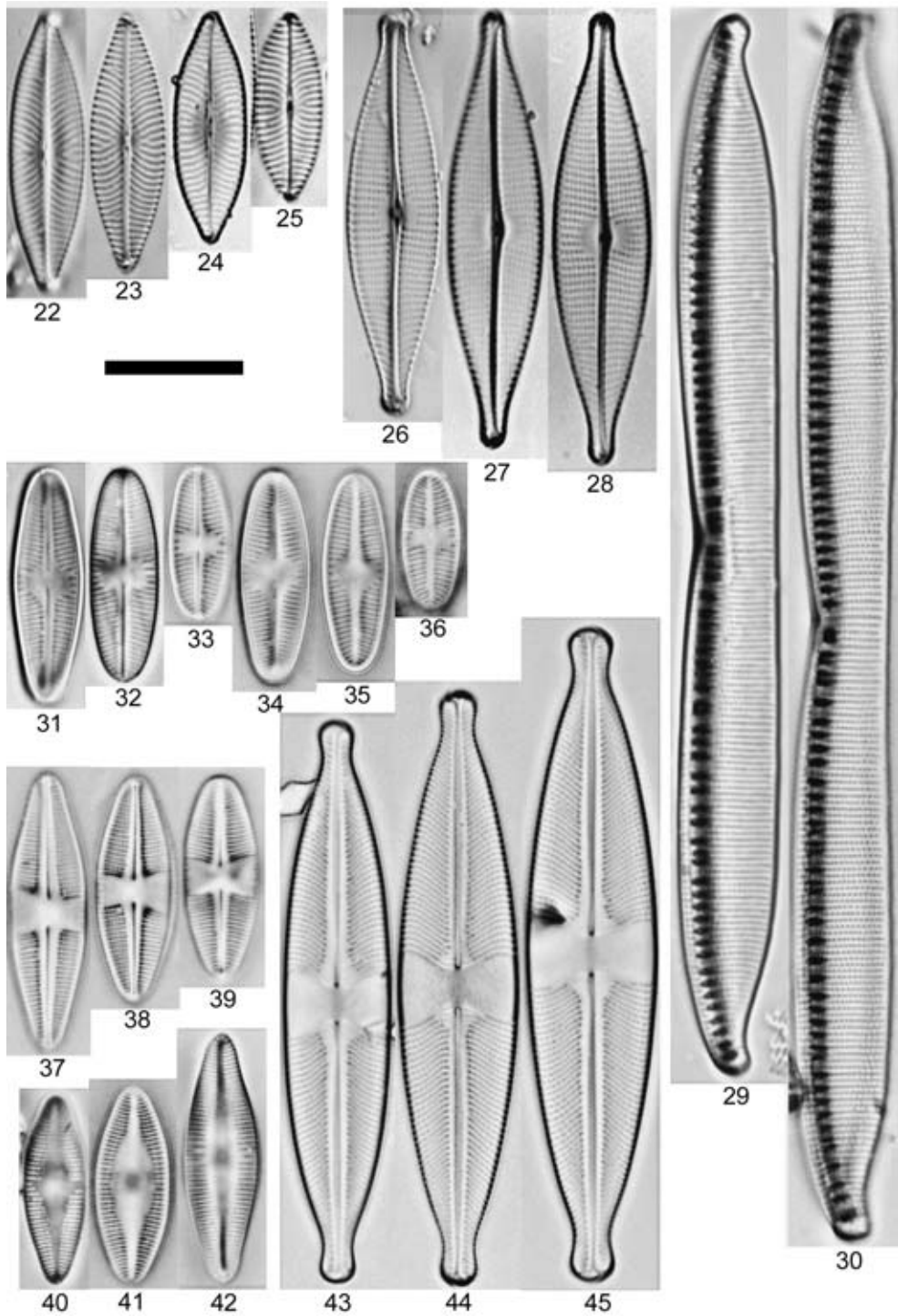
Figs. 22–45.   LM photographs of diatom species sampled from the Skarvsnes lakes, all in valve view. 22–25. *Navicula ectoris.* 26–28. *N. gregaria.* 29–30. *Nitzschia commutata.* 31–36. *Psammothidium metakryophilum.* 37–42. *P. stauroneioides.* 43–45. *Stauroneis latistauros.* Scale bar=10 μm.

Navicula ectoris Van de Vijver in Van de Vijver *et al*., Bilioth. Diatomol. **46**: 63. *pl. 37. f. 1–8*. 2002. (Figs. 22–25, 54, 55)

13.9−20.6 μm long, 5.0–6.0 μm wide, 18–20 striae in 10 μm. Areolae were not visible in LM, but were seen under SEM, about 45 areolae in 10 μm. Although the striae density of the protolog (21–24 in 10 μm) is finer than that of our specimens, the measurements suggest that the type specimens (Van de Vijver *et al*., 2002) have approximately the same stria densities as our specimens.

N. ectoris was originally reported in Ile de la Possession, Crozet Archipelago, Subantarctica (Van de Vijver *et al*., 2002), but this is the first report of this species in continental Antarctica. However, *Navicula cryptocephala* sensu Ko-Bayashi (1965) from Kasumi Iwa, Prince Olav Coast, East Antarctica, is probably *N. ectoris*, although its valve ends tend to be more rostrate.

N. ectoris is possibly a junior synonym of *Navicula phylleptosoma* Lange-Bert. *N. phylleptosoma* sensu Lange-Bertalot (2001) includes specimens that are very similar to *N. ectoris*. The type specimens of *N. phylleptosoma*, however, have more distant central pores and a larger central area than our specimens (cf. Lange-Bertalot and Genkal, 1999). Whether or not the differences are infraspecific variations should be elucidated in future studies.

Navicula gregaria Donkin, Quart. J. Miscroscop. Sci. N. S. **1**: 10. *pl. 1. f. 10*. 1861. (Figs. 26–28, 56, 57)

27.9–33.7 μm long, 6.8–7.3 μm wide, 17–18 striae in 10 μm. Areolae were visible in LM, 27–30 in 10 μm.

Although this species is cosmopolitan and common (Lange-Bertalot, 2001), it is not frequently reported in continental Antarctica (see Kellogg and Kellogg, 2002).

Nitzschia commutata Grunow in Cleve et Grunow, Kongl. Svenska Vetenskapsakad. Handl. **17** (2): 79. 1880. (Figs. 29, 30, 58–61)

77.4–89.4 μm long, 5.7–7.0 μm wide, 19–21 striae in 10 μm, 9–11.5 striae in 10 μm.

This cosmopolitan species (Krammer and Lange-Bertalot, 1988) has also been reported in Antarctica (*e.g*., Pankow *et al*., 1991; Sabbe *et al*., 2003; Cremer *et al*., 2004), where it has also been reported as *Nitzschia dubia* var. *australis* Perag. (*e.g*., Fukushima, 1963; Hirano, 1983), most likely the junior synonym of *N. commutata*.

Psammothidium metakryophilum (Lange-Bert. et Rol.Schmidt) Sabbe, Antarct. Sci. **15**: 242. 2003. (Figs. 31–36, 62–65)
Basionym: *Achnanthes metakryophila* Lange-Bert. et Rol.Schmidt in Rol.Schmidt *et al*., J. Paleolimnol. **3**: 64. *f. 6d–i*. 1990.

Sabbe *et al*. (2003) pointed out that *P. metakryophylum* is perhaps a junior synonym of *Navicula papilio* D.E.Kellogg *et al*., Palaeogeogr. Paleoclimatol. Palaeoecol. **30**: 183. *pl. 1. f. 15; pl. 2. f. 3*. 1980.

10.3–17.1 μm long, 4.5–5.4 μm wide, 25–28 striae in 10 μm (both raphid and araphid valves).

P. metakryophylum is considered an Antarctic endemic (Sabbe *et al*., 2003). Al-

though there are only a few verified reports of this species (Schmidt *et al*., 1990; Sabbe *et al*., 2003; Cremer *et al*., 2004), it is highly likely that it has been reported in the Antarctica under different names (Sabbe *et al*., 2003). Most probably *Stauroneis perminuta* sensu Hirano (1983) from the Skarvsnes area also represents raphid valves of this species.

Psammothidium stauroneioides (Manguin) Buhktiy. in Buhktiy. et Round, Diatom Res. **10**: 23. 1996. (Figs. 37–42, 66–68)
Basionym: *Achnanthes stauroneioides* Manguin in Bourr. et Manguin, Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. **5**: 23. *f. 17a–c*. 1954.

13.8–20.4 μm long, 4.9–5.9 μm wide, 27–31 striae in 10 μm (raphid valves), 25–27 striae in 10 μm (araphid valves).

P. stauroneioides is thought to be restricted to the Antarctic region (Sabbe *et al*., 2003). This species has mainly been recorded in Subantarctica (Kellogg and Kellogg, 2002), but also in maritime Antarctica (Håkansson and Jones, 1994) and continental Antarctica (Sabbe *et al*., 2003; Cremer *et al*., 2004). *Stauroneis perminuta* sensu Fukushima (1966) from Molodezhnaya in East Antarctica most probably represents raphid valves of *P. stauroneioides*.

Stauroneis latistauros Vijver et Lange-Bert. in Vijver *et al*., Biblioth. Diatomol. **51**: 48. *pl. 49. f. 1–13*. 2004. (Figs. 43–45, 69, 70)

40.9–47.6 μm long, 7.9–10.4 μm wide, 20–24 striae in 10 μm. Aleorae were visible in LM, 24–28 in 10 μm.

In comparison with the type specimens (Van de Vijver *et al*., 2004), our specimens tend to have more capitate valve ends and finer striation despite having larger valves. Nevertheless, we identified our specimens as *S. latistauros* because both the type population and our specimens show considerable morphological variations and the ranges of the morphometric parameters overlap; the differences seem to be assigned to local variations within the same species.

Van de Vijver *et al*. (2005) analyzed *Stauroneis* records for continental Antarctica and concluded that only *S. latistauros* has been found in this region. This conclusion seems adequate when taking into account all local variations. *S. latistauros* has usually been reported as *Stauroneis anceps* Ehrenb. (*e.g*., Fukushima, 1962; Kellogg *et al*., 1980; Hirano, 1983; Sabbe *et al*., 2003; Cremer *et al*., 2004). *S. latistauros* is, however, different from the type specimens of *S. anceps* shown by Reichardt (1995) in its fascia, which is broader and strongly widened toward the valve margin. Fumanti *et al*. (1995) reported this species as *Stauroneis agrestis* J.B.Petersen. However, according to Krammer and Lange-Bertalot (1986) *S. agrestis* has smaller valves with finer striae.

Relationship between the diatom assemblages and environmental factors

Amphora sp. was the dominant species in 11 samples, and represented more than 90% in four samples. It was always dominant in the seven moss-containing samples. In the six samples without mosses, *Craticula* sp. and *Diadesmis* sp. were respectively dominant in one sample, while *Amphora* sp. was dominant in the remaining four (Table 2). The diatom assemblages were generally similar to each other in species composition with
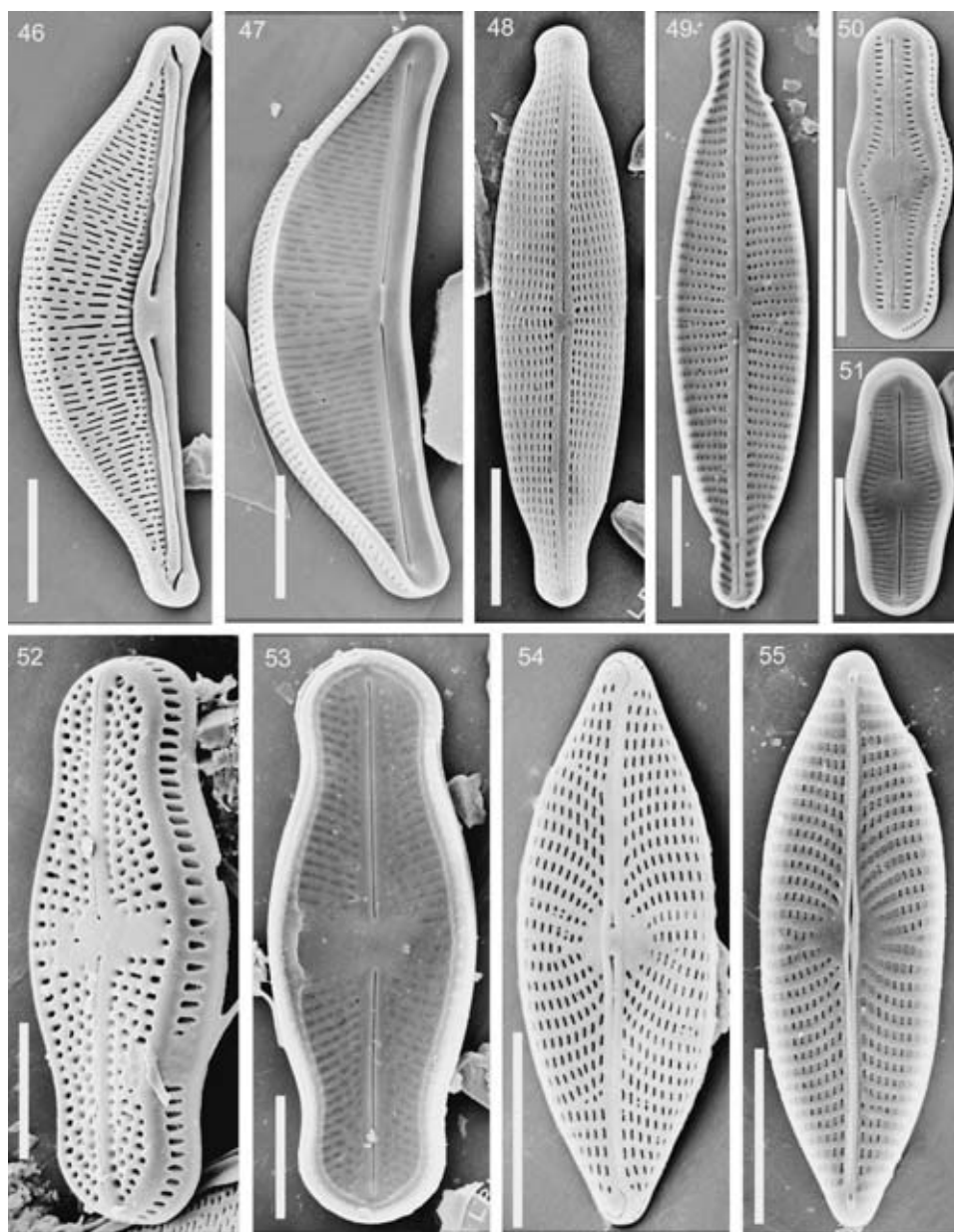
Figs. 46−55.   SEM photographs of diatom species sampled from the Skarvsnes lakes. 46–47. *Amphora* sp. in external (46) and internal (47) views. 48–49. *Craticula* sp. in external (48) and internal (49) views. 50–51. *Diadesmis* sp. in external (50) and internal (51) views. 52–53. *Luticola murrayi* in external (52) and internal (53) views. 54–55. *Navicula ectoris* in external (54) and internal (55) views. Scale bars=5 μm.
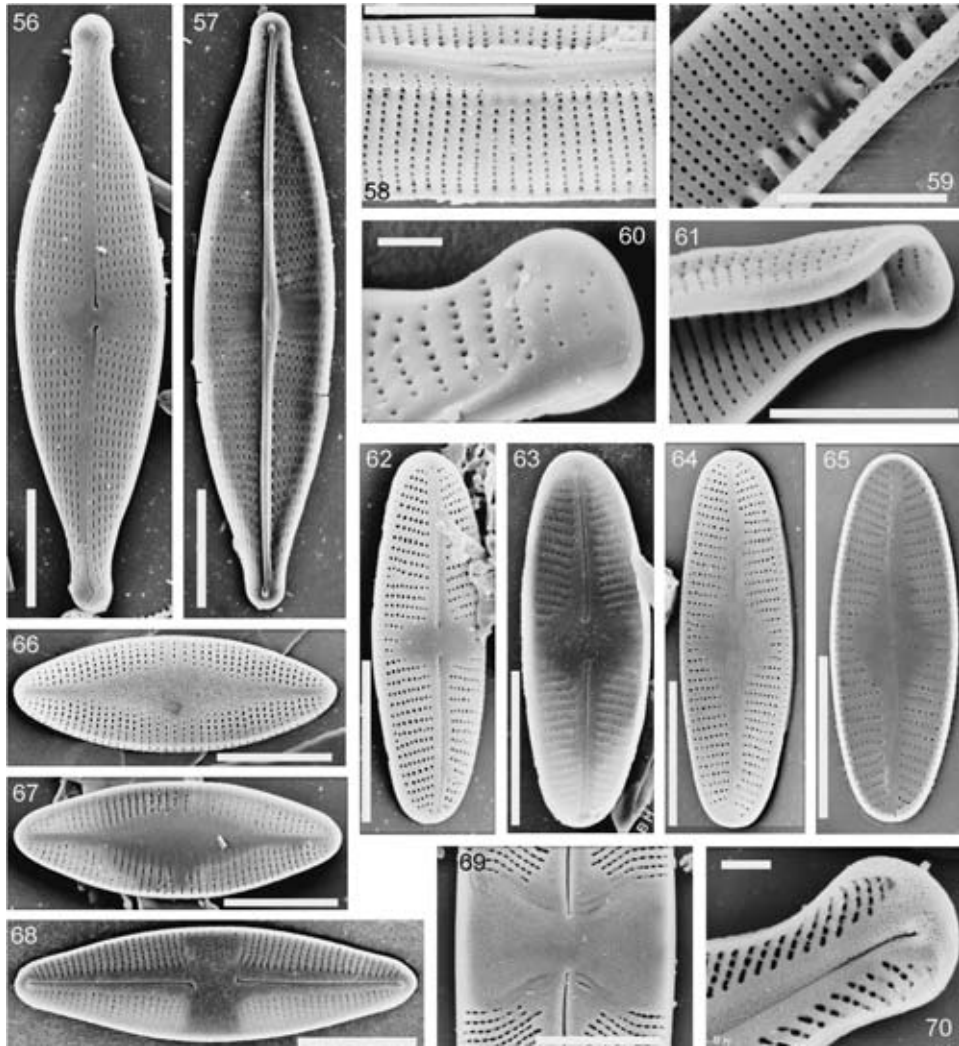
Figs. 56–70. SEM photographs of diatom species sampled from the Skarvsnes lakes. 56–57. *Navicula gregaria* in external (56) and internal (57) views. 58–61. *Nitzschia commutata*, around the valve center in external (58) and internal (59) views, and around the valve ends in external (60) and internal (61) views. 62–65. *Psammothidium metakryophilum*, raphid valves in external (62) and internal (63) views, and araphid valves in external (64) and internal (65) views. 66–68. *P. stauroneioides*, araphid valves in external (66) and internal (67) views, and a raphid valve in an internal view (68). 69–70. *Stauroneis latistauros*, around the valve center (69) and end (70) in an internal view. Scale bars=1 μm for Figs. 60 and 70, and=5 μm for the remainder.
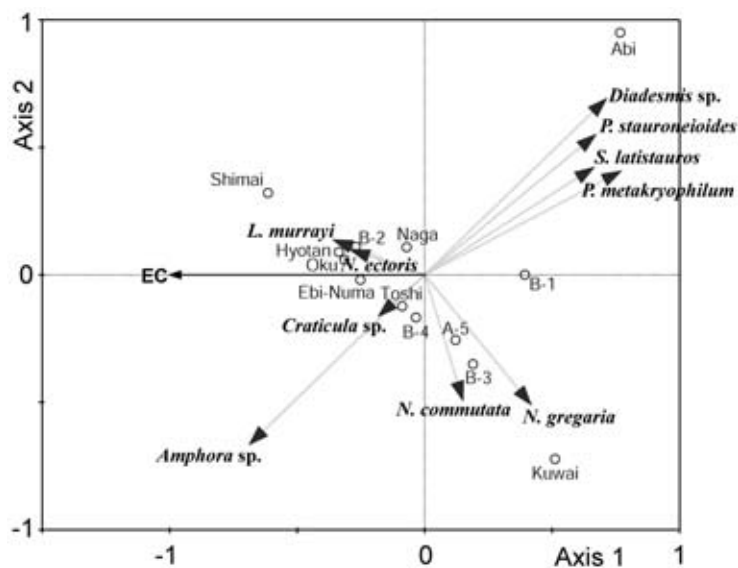
Fig. 71.   Redundancy analysis (RDA) triplots showing the relationships between site (circle), relative frequencies of diatom species (dashed line) and environmental gradients (solid line). Only electric conductivity (EC) was identified as a significant environmental gradient by forward selection. Axes 1 and 2 respectively explained 35% and 32% of the species variance.

the average d=0.40. The ratio of D(between)/D(within)=1.02, with no significant difference between samples with and without mosses (P>0.05).

The diatom assemblages usually showed a markedly low species diversity. Each sample contained only 2–12 species, resulting in a Simpson's 1-λ of 0.047–0.696 (Table 2). Both species number and 1-λ were not significantly different between samples with and without mosses (P>0.05).

From the above results, we concluded that the diatom species composition of the microbial mats was not significantly affected by the presence/absence of mosses. This conclusion was not foreseen before carrying out the observations, because diatom species compositions on macrophytes usually differ from those on abiotic substrata (Goldsborough and Hickman, 1991; Ohtsuka, 1998), or even between different host macrophyte species in infertile lakes (Eminson and Moss, 1980).

Forward selection adopted only EC as a significant explanatory variable for RDA. The first axis of RDA, *i.e.* EC, explained 35% of the variance in the species data. *Amphora* sp. had a large negative score for the first axis, showing an increasing tendency in relative frequency with increasing EC. Conversely, *Diadesmis* sp., *P. metakryophilum*, *P. stauroneioides* and *S. latistauros* had large positive scores, showing decreasing tendencies with increasing EC. The other five species had small absolute value scores, suggesting an indifference to EC or an optimum around the average EC in the data set. Although the second axis explained 32% of the variance in species data, no environmental factors were shown to be related to this axis. *Diadesmis* sp. and *P. stauroneioides* had larger positive scores, whereas *Amphora* sp., *N. gregaria* and *N. commutata* had larger negative scores

(Fig. 71).

The results of RDA indicate that the main environmental gradient for diatoms is EC, despite the relatively narrow range. In the studied lakes, the high EC meant high salinity, because dissolved organic matter was considered low in density. EC and salinity have often been reported as the principal environmental gradients in Antarctic lakes (*e.g.*, Roberts and McMinn, 1996; Sabbe *et al*., 2003).

The marked dominance of *Amphora* sp. in the lakes with a higher EC indicates that this species is a halophile, *i.e.*, a freshwater species that becomes abundant in slightly salty water (Kolbe, 1927). Past reports have also indicated that *Amphora veneta* in Antarctica, which presumably belongs to the same species as our *Amphora* sp., is a halophile. Verleyen *et al*. (2003) determined the salinity optimum of this species to be 2.55‰, while Sabbe *et al*. (2004) reported its dominance in hyposaline lakes with an EC higher than ±150 mS m^{-1}.

In contrast, our results suggest that *Diadesmis* sp., *P. metakryophilum*, *P. stauroneioides* and *S. latistauros* are halophobes, *i.e.*, species unable to survive in saline conditions (Kolbe, 1927). They were most abundant in lakes with an EC of <50 mS m^{-1}, and were not observed in lakes with an EC of >120 mS m^{-1}. *Diadesmis* sp. and *P. metakryophylum* have previously been classified as halophobes (Roberts *et al*., 2001; Verleyen *et al*., 2003; Sabbe *et al*., 2004); however, the halophoby of *P. stauroneioides* and *S. latistauros* remains uncertain, because these species were not common in the present study and past studies do not always support this characteristic (Sabbe *et al*., 2003).

Many of the abundant diatoms in the present study were presumed to be oligotrophic. Although our data do not directly display the diatoms' reaction to nutrients, the fact that no nutrients could be detected by ion chromatography suggests the oligotrophic nature of the studied lakes. Roberts *et al*. (2001) suggested that *Achnanthes metakryophila*, *Amphora veneta* and *Diadesmis perpusilla* have low phosphate optima at 0.5, 0.4 and 0.1 μM, respectively. These species correspond to *P. metakryophilum*, *Amphora* sp. and *Diadesmis* sp., respectively, in the present study.

Acknowledgments

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