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Salinity, depth and the structure and composition of microbial mats in continental Antarctic lakes

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SUMMARY

1. Lakes and ponds in the Larsemann Hills and Bølingen Islands (East-Antarctica) were characterised by cyanobacteria-dominated, benthic microbial mats. A 56-lake dataset representing the limnological diversity among the more than 150 lakes and ponds in the region was developed to identify and quantify the abiotic conditions associated with cyanobacterial and diatom communities.
2. Limnological diversity in the lakes of the Larsemann Hills and Bølingen Islands was associated primarily with conductivity and conductivity-related variables (concentrations of major ions and alkalinity), and variation in lake morphometry (depth, catchment and lake area). Low concentrations of pigments, phosphate, nitrogen, DOC and TOC in the water column of most lakes suggest extremely low water column productivity and hence high water clarity, and may thus contribute to the ecological success of benthic microbial mats in this region.
3. Benthic communities consisted of prostrate and sometimes finely laminated mats, flake mats, epilithic and interstitial microbial mats. Mat physiognomy and carotenoid/chlorophyll ratios were strongly related to lake depth, but not to conductivity.
4. Morphological-taxonomic analyses revealed the presence of 26 diatom morphospecies and 33 cyanobacterial morphotypes. Mats of shallow lakes (interstitial and flake mats) and those of deeper lakes (prostrate mats) were characterised by different dominant cyanobacterial morphotypes. No relationship was found between the distribution of these morphotypes and conductivity. In contrast, variation in diatom species composition was strongly related to both lake depth and conductivity. Shallow ponds were mainly characterised by aerial diatoms (e.g. *Diadesmis* cf. *perpusilla* and *Hantzschia* spp.). In deep lakes, communities were dominated by *Psammothidium abundans* and *Stauroforma inermis*. Lakes with conductivities higher than ±1.5 mS cm^{-1} became susceptible to freezing out of salts and hence pronounced conductivity fluctuations. In these lakes *P. abundans* and *S. inermis* were replaced by *Amphora veneta*. Stomatocysts were important only in shallow freshwater lakes.
5. Ice cover influenced microbial mat structure and composition both directly by physical disturbance in shallow lakes and by influencing light availability in deeper lakes, as well as indirectly by generating conductivity increases and promoting the development of seasonal anoxia.

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6. The relationships between diatom species composition and conductivity, and diatom species composition and depth, were statistically significant. Transfer functions based on these data can therefore be used in paleolimnological reconstruction to infer changes in the precipitation–evaporation balance in continental Antarctic lakes.

Keywords: Antarctica, conductivity, cyanobacteria, diatom, microbial mat

Introduction

Benthic phototrophs are often the most important primary producers in shallow, oligotrophic, clear-water polar and high-altitude lakes (e.g. Vincent *et al*., 1993; Ellis-Evans, 1996; Tang, Tremblay & Vincent, 1997). In polar regions, mat-forming cyanobacteria are generally the major component of these communities (Vincent & Quesada, 1994; James, Pridmore & Cummings, 1995), while diatoms, green algae, and xanthophytes occur as co-dominants (Hamilton & Edlund, 1994; Vezina & Vincent, 1997). The success of cyanobacteria in these extreme environments is generally attributed to their tolerance to desiccation, freeze-thaw cycles, bright, continuous solar radiation (PAR, Tang *et al*., 1997) and defences against UV damage (Vincent & Quesada, 1994; Ehling-Schulz & Scherer, 1999). A variety of macroscopically different mat morphologies have been recognised and their distribution has been related to a suite of environmental factors, including depth, sedimentation of inorganic sediment, light, concentrations of dissolved gases and alkalinity of the lake water (Wharton, Parker & Simmons, 1983; Squyres *et al*., 1991; Ellis-Evans, 1996; Hawes & Schwarz, 1999).

Perennial microbial mats forming deposits several metres thick are widespread in lakes of the Larsemann Hills and Bølingen Islands, two important ice-free oases in continental East-Antarctica (Hodgson *et al*., 2001a; Verleyen *et al*., 2003, 2004). Minimal bioturbation (due to the absence of larger metazoa), limited wind-induced hydrodynamic mixing (most lakes are covered by ice for more than 10 months per year) and slow decomposition are thought to contribute to the strongly laminated, well-preserved nature of these deposits in the deeper lakes (>5 m). Radiocarbon dating has demonstrated that some lakes have existed since the Late Pleistocene (Hodgson *et al*., 2001a), representing the oldest known continuous lacustrine sediment records from Antarctica.

In order to study the history and nature of environmental change in these lakes with the aid of biological proxies, it is critical to understand the factors controlling extant species composition and structure of the microbial communities. To date, however, little is known about the modern distribution of mat-forming cyanobacteria and associated eukaryotic species. The distribution of cyanobacteria and benthic diatoms has been studied in Maritime Antarctic lakes by Oppenheim (1990), Jones & Juggins (1995) and Vinocur & Pizarro (2000). In continental Antarctica, the diatom floras of the Vestfold Hills and Windmill Islands have recently been studied by Roberts & McMinn (1996, 1999) and Roberts *et al*. (2001a), and of the Rauer Islands by Hodgson, Vyverman & Sabbe (2001b). A taxonomic study of the diatom flora of the Larsemann Hills, Bølingen and Rauer Islands can be found in Sabbe *et al*. (2003).

In this paper we describe the composition and distribution of cyanobacterial and diatom morphotaxa and stomatocysts in modern microbial mats in lakes and ponds of the Larsemann Hills and Bølingen Islands, East Antarctica. We examine the nature of their relationships with mat physiognomy, environmental conditions and geomorphological data using multivariate ordination techniques. This study is part of a broader programme on the biodiversity of microbial communities in continental Antarctic lakes and forms the framework for the development of biological proxies based on diatoms, pigment composition and genetic fingerprinting of fossil cyanobacterial assemblages (Squier, Hodgson & Keely, 2002; Verleyen *et al*., 2003, 2004; A. Taton *et al*., unpublished data).

Methods

Study region

The Larsemann Hills (69°23′S, 76°53′E), Prydz Bay, comprise a 50 km^2 ice-free area on the Ingrid Chris-

tensen Coast, Princess Elizabeth Land, located approximately midway between the eastern extremity of the Amery Ice Shelf and the southern boundary of the Vestfold Hills (Fig. 1a). The region consists of two main peninsulas, Stornes to the west and Broknes to the east, together with a number of scattered off-shore islands. Radiocarbon dating of lake sediments, optically stimulated luminescence dating and geomorphological evidence showed that Broknes, and particularly the smaller Mirror Peninsula, has been ice-free for a significantly longer period than Stornes (Hodgson *et al.*, 2001a). The Bølingen Islands form a smaller though significant ice-free archipelago, 25 km to the west-south-west of the Larsemann Hills (Fig. 1b).

Climatic conditions are typical for coastal continental eastern Antarctica. During December, January and February the daily air temperature in the region frequently exceeds +4 °C and has been known to reach +10 °C. Mean monthly winter temperatures are between −15 °C and −18 °C. Precipitation occurs as snow and is unlikely to exceed 250 mm water equivalent annually and strong, katabatic (a cold flow of air blowing downwards) winds blow from the North East quarter most mornings.

More than 150 freshwater lakes are found in the hills (Gillieson *et al.*, 1990) ranging from small ephemeral ponds to large waterbodies such as Progress Lake (10 ha, 38 m deep). They originated from exposure of basins after the retreat of the continental ice cap (proglacial lakes) or after isolation due to isostatic uplift following deglaciation (isolation lakes). Radiocarbon dating of biogenic sediments from these lakes reveals ages between 1500 and >40 000 years old (Hodgson *et al.*, 2001a). Some of these waterbodies are briefly ice-free or partially ice-free in the summer months when their temperatures increase rapidly, with water in some of the shallower ones reaching up to +8 °C. For the remaining 8–10 months of the year they are covered with *c.* 2 m of ice. Some lakes (e.g. LH73 and Sarah Tarn) have evidence of past shorelines up to 2 m above present levels. There is substantial variation in the hydrological balance of these lakes. Some (e.g. Sarah Tarn) have no outflow, whilst the outflows of others (e.g. LH 73) operate for only part of a summer season and indeed may not flow at all in some seasons. Lake systems are connected to the coast by large, steep-sided V-shaped valleys normally around 50–100 m deep and less than 1 km long that dissect the area; a number of streams flow continuously during the summer. Multi-annual snowfields are widespread on Stornes and, together with the relictual ice dome, contribute to cooler microclimatic conditions. In contrast, snow cover is more limited on Broknes during summer and multi-annual snowfields are generally lacking. As a result, solar radiation is absorbed by the bare rock and advected heat maintains a warmer microclimate.

Field work and water chemistry

In the Antarctic summer of 1997–1998, 51 lakes were sampled in the Larsemann Hills and five lakes in the Bølingen Islands (Fig. 1a,b). Lakes were chosen in order to represent the variation in lake morphometry, hydrological characteristics and conductivity in the region (Gillieson *et al.*, 1990; Ellis-Evans *et al.*, 1998). Alkalinity, pH, conductivity, oxygen and turbidity of water samples collected at 3 m depth (or less in shallower lakes) were measured at the sampling location or in the field laboratory on the day of sampling. For field nutrient analysis [NH_4 and dissolved reactive phosporus (DRP)] 2 L of water were filtered through Whatman GF/C filters and analysed within 1 week. The remaining ion and nutrient chemistry was carried out on filtered water samples and frozen in the field. Further nutrient analyses (SiO_2, NO_3, total N and total P) were carried out on an ALPKEM auto analyser following the methods of Eriksen (1997). Analyses of anions (Cl^-, SO_4^{2-}, $CaCO_3$, HCO_3^-) and cations (Ca^{2+}, Mg^{2+}, Na^+, K^+), total organic carbon (TOC) and dissolved organic carbon (DOC) were carried using standard methods (Clesceri, Greenberg & Eaton, 1999). In order to evaluate conductivity changes during summer in the lakes of the Larsemann Hills, data from previously published studies (Gillieson *et al.*, 1990; Ellis-Evans *et al.*, 1998; J. Burgess, pers. comm.) are compared with data from 1997 (this study).

Biological sampling

Samples of benthic microbial mat were collected from the deepest parts of the lakes using a Glew surface sediment corer. This enabled the top 0.5–1 cm of the mats to be sectioned off accurately. The sampled layers thus included several years of mat

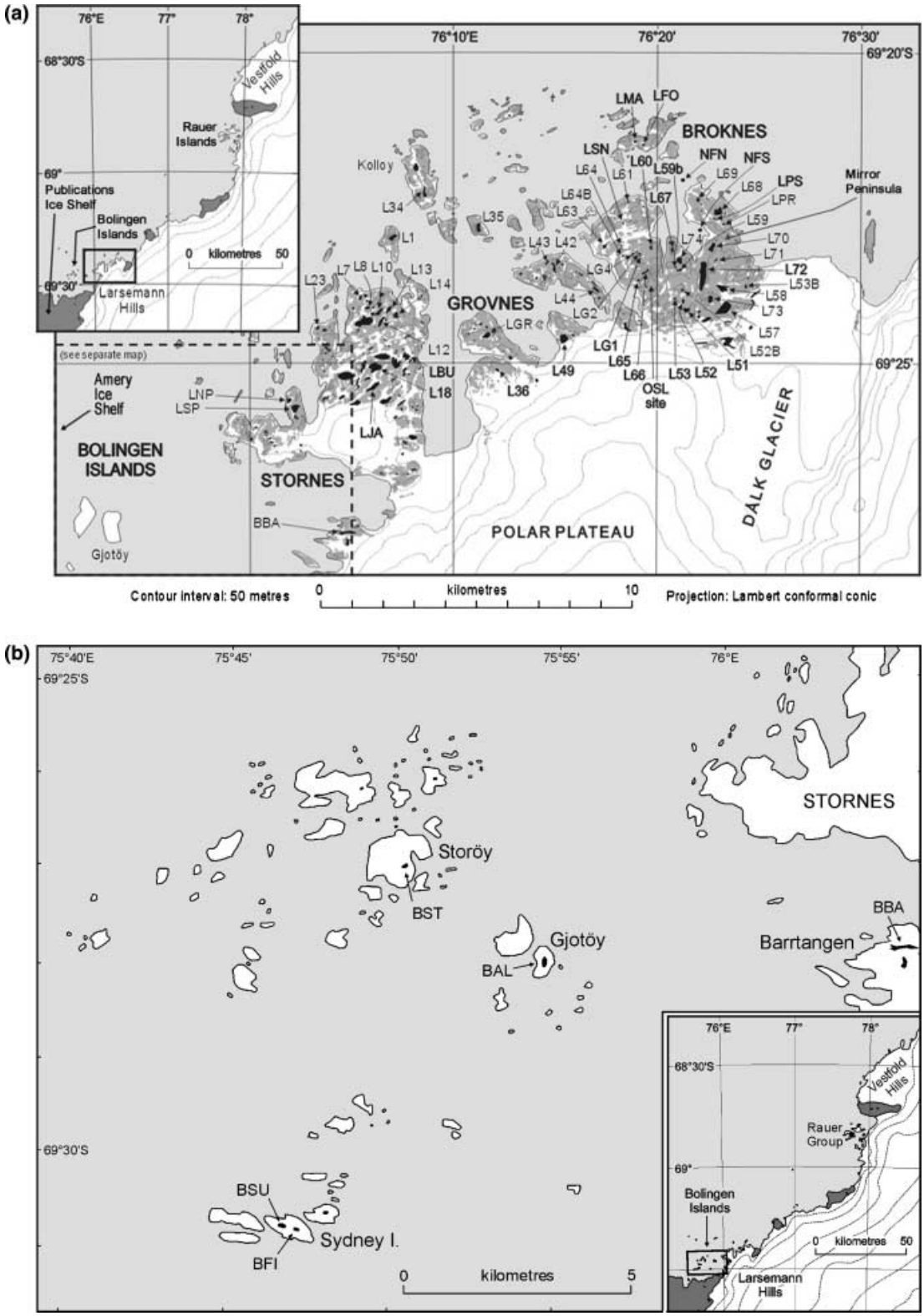

Fig. 1 Location of (a) the Larsemann Hills oasis (inset) and of the sampling sites in the Larsemann Hills and (b) the Bølingen Islands (inset) and of the sampling sites on these islands. Lakes are referred to by label, full names and details are given in Table 1.

growth and accounted (as far as possible) for inter-annual variations in winter ice duration, thickness, transparency and snow cover. When no ice cover was present (lakes <2 m deep), samples were taken between 0.5 and 1 m in the littoral zone. All samples were frozen until analysis and stored in the dark. Benthic pigments were extracted from bulk sediments using repeated additions of acetone, methanol and water (80 : 15 : 5)(Wright *et al.*, 1991) and analysed using HPLC following Leavitt & Hodgson (2001). The main components were a Kromasystem 2000 HPLC with a Kontron pump, auto sampler and diode array detector. Reverse phase columns used were 25 cm × 4.6 mm Spherisorb ODS-2 with a particle size of 5 μm. Pigment detection was at 435, 470 and 665 nm for all chlorophylls and carotenoids, with spectra from 300 to 700 nm being collected continuously. Solvent systems and operating conditions are described in Hodgson, Wright & Davies (1997). The system was calibrated to reference cultures using SCOR protocols (Jeffrey, Mantoura & Wright, 1997) and US Environmental Protection Agency Standards.

Biological analyses

Live and formaldehyde-fixed surface sediments were examined using light microscopy for the distinction and identification of cyanobacteria, usually to genus. In only a few genera was reliable species identification possible, due to the morphological simplicity of many organisms (thin filaments or small unicells) or the difficulty of observation in a complex, thick mat. Morphotypes with a cell width <2.5 μm belonging to the order Oscillatoriales were defined as *Leptolyngbya* spp. Representatives of the genus *Schizothrix* were defined by the presence of several trichomes in one sheath. Morphological diversity (presence/absence) was analysed for 43 of the 56 lakes (Tables 1 and 4). For each locality, three replicate preparations were examined for the presence or absence of cyanobacterial morphotypes. Fifteen fields were examined in detail at two different magnifications (500× and 1260×). In addition, the entirety of each preparation (±25 mm^2) was scanned for the presence of rare taxa.

Acid-cleaned material, following digestion of organic matter by H_2O_2 and mounting in Naphrax, was used for diatom and stomatocyst analysis. When possible *c*. 400 diatom frustules were counted, except in slides prepared from epilithic and interstitial mats in which diatoms were very scarce. However, in all cases at least 100 frustules were counted. A detailed taxonomic treatment of the diatom flora is given in Sabbe *et al.* (2003). Stomatocysts were jointly counted with the diatoms, so only a relative measure of their importance in the benthic mats is available. No distinction was made between different morphological types of stomatocysts.

Data analysis

Prior to multivariate analysis all environmental variables except pH were log-transformed to reduce or remove skewness in the data. Principal component analysis (PCA), with centring and standardisation of the environmental data, was used to explore the major patterns of variation in the environmental dataset. Diatom species data were log-transformed prior to the ordinations; presence–absence data were used for the cyanobacteria. Detrended correspondence analyses (DCA), with detrending by segments, were used to determine the length of the gradient in the species data. The latter is a measure of how unimodal the species responses are along an ordination axis, and therefore allows the best method (unimodal or linear) to be selected for the analyses (ter Braak & Smilauer, 1998). Preliminary DCA's and PCA's were run in order to identify outlying samples, following the criteria summarised in Hall & Smol (1992). Canonical correspondence analysis (CCA), a unimodal direct ordination method, with forward selection of environmental factors and unrestricted Monte Carlo permutation tests (999 permutations, $P \leq 0.05$) was used to select the minimal number of variables explaining the largest amount of variation in the species data. A total of 28 environmental and spatial variables (Table 1) were included in the analyses. The relative contribution of the environmental variables to the ordination axes was evaluated by the canonical coefficients (significance of approximate *t*-tests) and intraset correlations (ter Braak & Smilauer, 1998). Unrestricted Monte Carlo permutation tests (999 permutations, $P \leq 0.05$) were used to test the statistical significance of the first two ordination axes. All ordinations were performed using the computer program CANOCO 4.0 for Windows (ter Braak & Smilauer, 1998).

Table 1 Lake locations, morphometric, physical and chemical characteristics. Lakes have been grouped into five groups based on mat type present (cf. Fig. 3); per group average (AV) and SD of the variables listed is given

Mat type	Lake number	Lake name	Analysed for cyano bacteria	Longitude (E)	Latitude (S)	Altitude (m)	Lake Area (ha)	Catchment area (ha)	Depth (m)	Distance from Plateau (m)	Distance from sea (m)	pH	Alkalinity (meq L^{-1})	NO_3 + NO_2–N (μg L^{-1})	NO_2–N (μg L^{-1})	NH_4–N (μg L^{-1})	Silicate–Si (mg L^{-1})	DRP–P (μg L^{-1})
1	L72	Lake Nella	x	76°22′	69°24′	15	13.0	259.0	18.0	1647	150	6.3	nd	11.2	nd	4.2	0.04	3.1
1	L35	Crater Lake		76°11′	69°23′	30	3.2	9.3	12.0	4250	75	6.9	0.6	9.8	nd	5.6	0.11	6.2
1	L34	Kirisjes Pond	x	76°09′	69°22′	5	12.0	16.5	9.0	5750	225	6.4	0.1	7.0	nd	2.8	0.16	3.1
1	L12	Long Lake		76°07′	69°24′	80	5.0	8.7	11.0	2125	700	6.2	0.1	2.8	nd	1.4	0.03	6.2
1	LBU	Lake Burgess	x	76°07′	69°25′	40	4.0	15.0	16.0	750	225	6.5	0.1	4.2	nd	1.4	0.07	nd
1	L36	–		76°13′	69°25′	60	5.5	17.6	15.0	0	300	6.6	0.4	2.8	nd	1.4	0.32	3.1
1	BBA	–	x	76°05′	69°27′	10	2.8	12.6	15.0	50	50	6.2	0.1	1.4	nd	nd	nd	nd
1	L57	Progress Lake		76°24′	69°24′	65	10.5	39.1	34.0	885	1375	6.7	0.1	2.8	nd	nd	0.42	nd
1	L51	Lake Cameron		76°21′	69°24′	85	2.5	17.3	7.6	610	1425	6.7	0.3	7.0	nd	nd	0.48	nd
AV						43	6.5	43.9	15.3	1785	503	6.5	0.2	5.6	nd	1.4	0.18	3.1
SD						28.7	3.9	76.5	7.3	1867.6	511.9	0.2	0.2	2.8	nd	1.4	0.17	3.1
2	L71	Sarah Tarn	x	76°23′	69°23′	75	1.0	5.7	2.5	1998	550	7.0	13.2	9.8	2.8	215.6	2.58	3.1
2	L59	Moore Lake	x	76°21′	69°24′	20	1.5	48.8	3.8	1845	500	6.4	0.4	8.4	nd	5.6	1.36	nd
2	L67	–	x	76°21′	69°23′	45	4.5	6.3	5.0	2577	175	6.7	0.9	7.0	nd	nd	0.88	nd
2	L74	Discussion Lake	x	76°22′	69°23′	5	2.0	74.8	4.0	2119	150	5.9	0.3	1.4	nd	5.6	0.76	nd
2	L63	–	x	76°18′	69°23′	60	1.0	25.2	3.3	2409	375	6.2	0.1	1.4	nd	2.8	0.08	nd
2	L60	–	x	76°20′	69°23′	45	1.5	23.9	5.4	3035	300	5.5	0.5	14	nd	12.6	0.10	nd
2	L8	–	x	76°05′	69°09′	5	4.8	10.7	4.8	3250	175	6.3	0.2	26.6	15.4	4.2	0.04	nd
2	L7	–		76°05′	69°09′	25	2.5	12.9	4.5	3125	500	6.2	0.1	7.0	nd	5.6	0.01	nd
2	L10	Lake Heidi	x	76°06′	69°24′	60	7.5	12.1	5.0	2500	575	6.3	0.2	4.2	nd	5.6	0.08	3.1
2	L13	–	x	76°07′	69°24′	75	5.0	4.7	4.8	2375	300	6.7	0.8	5.6	nd	11.2	1.20	nd
2	L14	–	x	76°07′	69°24′	60	5.5	7.1	4.7	2250	300	6.7	1.4	2.8	1.4	15.4	2.28	3.1
2	L23	Pup Lagoon	x	76°03	69°25′	5	1.0	7.8	4.6	2250	100	6.4	0.2	15.4	nd	9.8	0.24	3.1
2	LGR	–	x	76°11′	69°24′	50	3.5	7.0	16.0	1000	475	7.7	2.0	2.8	nd	4.2	1.14	nd
2	L49	–	x	76°16′	69°24′	30	2.0	24.3	3.5	0	100	7.0	0.1	1.4	nd	1.4	0.08	nd
2	L44	–	x	76°17′	69°24′	45	3.0	9.6	7.7	1098	175	7.9	4.6	nd	nd	nd	0.57	nd
2	L43	–	x	76°15′	69°23′	10	2.5	9.9	6.5	2745	150	6.7	0.9	15.4	nd	nd	0.90	nd
2	L69	No Worries Lakes		76°23′	69°22′	10	2.5	27.3	3.8	3401	275	6.8	0.5	30.8	nd	2.8	0.17	6.2
2	L70	Lake Reid	x	76°23′	69°23′	30	5.5	19.6	3.8	2455	250	7.1	7.2	9.8	nd	nd	0.75	6.2
2	L68	Heart Lake	x	76°23′	69°23′	5	5.0	57.8	4.5	2623	200	6.3	0.3	14	nd	nd	0.10	nd
2	BAL	Lake Alanna		75°55′	69°28′	20	1.6	7.4	4.0	4800	200	6.9	2.9	7.0	nd	2.8	2.30	nd
2	LJA	Lake Jack	x	76°06′	69°25′	85	4.2	39.0	2.0	2800	1475	6.8	0.1	7.0	nd	nd	0.03	nd
2	L18	Lake Spate	x	76°07′	69°25′	85	9.0	20.7	11.0	3294	1200	7.0	0.3	43.4	nd	nd	0.27	nd
2	L1	Lake Anna	x	76°17′	69°23′	100	2.5	13.5	7.6	6710	100	7.2	3.0	4.2	nd	1.4	0.28	nd
2	L73	–	x	76°23′	69°24′	85	3.5	18.2	4.0	793	1175	6.1	nd	487.2	nd	1.4	0.06	nd

Table 1 (*Continued*)

Mat type	Lake number	Lake name	Analysed for cyano bacteria	Longitude (E)	Latitude (S)	Altitude (m)	Lake Area (ha)	Catchment area (ha)	Depth (m)	Distance from Plateau (m)	Distance from sea (m)	pH	Alkalinity (meq L^{-1})	NO_3 + NO_2–N (μg L^{-1})	NO_2–N (μg L^{-1})	NH_4–N (μg L^{-1})	Silicate–Si (mg L^{-1})	DRP–P (μg L^{-1})
AV						43	3.4	20.6	5.3	2561	407	6.7	1.7	30.8	1.4	12.6	0.68	nd
SD						30.4	2.1	18.0	2.9	1321.0	371.2	0.5	3.0	98.0	2.8	43.4	0.78	nd
3	LSP	–	x	76°02′	69°25′	5	5.0	7.0	8.8	875	75	6.4	0.1	nd	nd	7.0	0.03	nd
3	L42	–	x	76°15′	69°23′	25	4.0	13.5	11.0	2486	250	7.9	4.2	5.6	nd	nd	0.16	nd
3	BST	–		75°50′	69°27′	20	0.8	7.2	2.5	11200	200	6.2	0.0	7.0	nd	nd	0.00	nd
3	LPR	–		76°23′	69°23′	10	0.3	3.3	0.8	3000	200	7.0	0.2	96.6	nd	1.4	0.16	nd
AV						15	2.5	7.8	5.8	4390	181	6.9	1.1	28.0	nd	1.4	0.09	nd
SD						9.1	2.3	4.2	4.9	4629.2	74.7	0.8	2.1	46.2	nd	2.8	0.08	nd
4	BFI	Firelight Lake		75°45′	69°31′	30	0.9	5.6	1.5	3000	200	9.4	1.8	nd	nd	nd	2.48	195.3
4	L53b	–	x	76°23′	69°24′	40	0.5	7.0	0.5	500	1000	6.7	0.1	4.2	nd	nd	0.07	nd
4	LPS	–	x	76°23′	69°23′	10	0.4	5.7	1.0	3250	500	6.5	nd	7.0	1.4	1.4	0.13	nd
4	L52	Lake Bruehwiler	x	76°21′	69°24′	80	1.0	22.8	0.7	1022	1250	6.8	0.1	16.8	nd	1.4	0.43	nd
4	L52b	–	x	76°21′	69°24′	80	0.5	6.3	1.0	1000	925	7.0	0.1	7.0	nd	1.4	0.67	nd
4	L66	–	x	76°20′	69°24′	25	2.5	26.3	2.3	1250	400	7.4	0.6	21.0	nd	nd	0.54	nd
4	L65	–	x	76°19′	69°24′	20	1.0	31.7	0.7	1125	175	7.3	0.3	22.4	nd	nd	0.54	3.1
4	LG2	–	x	76°19′	69°23′	65	0.3	1.5	1.0	1875	750	6.9	0.1	8.4	nd	nd	0.50	nd
4	L64	–	x	76°18′	69°23′	55	0.5	14.4	0.7	2181	775	6.9	0.1	9.8	nd	1.4	0.45	3.1
4	LSN	–	x	76°18′	69°23′	50	0.2	5.1	0.8	3250	550	5.9	nd	2.8	nd	nd	0.04	3.1
4	L61	–	x	76°19′	69°22′	50	0.5	6.2	0.5	3965	150	6.3	nd	7.0	nd	nd	0.05	nd
AV						46	0.7	12.0	1.0	2038	607	7.0	0.3	9.8	nd	nd	0.54	18.6
SD						23.4	0.7	10.2	0.5	1164.2	365.6	0.9	0.5	7.0	nd	nd	0.68	58.9
5	BSU	Sunset Lake	x	75°45′	69°31′	10	1.1	12.6	1.8	3000	160	7.2	0.5	1.4	nd	1.4	0.28	3.1
5	L58	Lake Sibthorpe		76°21′	69°24′	60	12.5	82.0	0.7	1113	1000	6.3	nd	14.0	nd	1.4	0.04	nd
5	LFO	–	x	76°20′	69°21′	30	0.3	2.3	1.0	5500	125	7.2	0.2	8.4	nd	nd	0.64	3.1
5	LMA	–	x	76°19′	69°21′	30	0.4	5.9	1.0	5750	125	6.9	0.1	1.4	nd	1.4	0.03	nd
5	L59b	–	x	76°21′	69°24′	20	0.3	4.9	0.8	2000	375	7.6	0.9	19.6	nd	1.4	0.85	nd
5	LG1	–	x	76°19′	69°23′	65	0.1	0.7	0.8	1750	750	7.6	0.6	200.2	nd	nd	0.24	nd
5	LG4	–		76°19′	69°23′	65	0.4	2.7	1.0	1875	800	7.0	0.2	50.4	nd	5.6	0.45	nd
5	L64b	–	x	76°18′	69°23′	50	0.1	1.5	1.0	1875	750	7.2	0.2	5.6	nd	nd	4.12	3.1
AV						41.3	1.9	14.1	1.0	2858	511	7.1	0.3	37.8	nd	1.4	0.83	nd
SD						21.51	4.299	27.7	0.34	1785.1	353.87	0.42	0.3018	67.62	nd	1.68	1.36	nd

Mat type	Lake number	O_2 (mg L^{-1})	O_2 (%)	Turbidity (NTU)	Conductivity (μS cm^{-1})	Na (mg L^{-1})	K (mg L^{-1})	Ca (mg L^{-1})	Mg (mg L^{-1})	Cl (mg L^{-1})	SO_4 (mg L^{-1})	HCO_3 (mg L^{-1})	TOC (mg L^{-1})	DOC (mg L^{-1})
1	L72	15.6	116.9	−1.0	85.0	12.8	0.7	0.9	1.7	18.8	nd	2.7	nd	nd
1	L35	11.0	98.8	7.7	2780.0	644.0	15.2	23.3	59.0	795.0	75.0	37.0	2.0	2.0
1	L34	12.2	111.4	19.3	405.0	54.0	2.6	3.1	7.2	110.0	14.8	6.5	nd	nd

Table 1 (*Continued*)

Mat type	Lake number	O_2 (mg L^{-1})	O_2 (%)	Turbidity (NTU)	Conductivity (μS cm^{-1})	Na (mg L^{-1})	K (mg L^{-1})	Ca (mg L^{-1})	Mg (mg L^{-1})	Cl (mg L^{-1})	SO_4 (mg L^{-1})	HCO_3 (mg L^{-1})	TOC (mg L^{-1})	DOC (mg L^{-1})
1	L12	12.2	117.9	11.3	173.0	25.0	1.2	0.6	3.3	40.5	4.8	3.6	nd	nd
1	LBU	11.5	106.5	−1.0	182.0	27.8	1.7	2.0	3.0	43.5	5.3	5.2	0.2	nd
1	L36	11.0	103.8	0.0	244.0	38.3	0.9	3.4	3.9	57.0	10.2	25.9	nd	nd
1	BBA	11.6	105.5	0.3	56.0	8.7	nd	0.9	1.4	11.6	nd	3.3	nd	nd
1	L57	11.1	99.6	0.0	320.0	46.7	0.9	3.4	6.0	86.0	8.3	5.0	nd	nd
1	L51	11.4	98.5	−1.0	520.0	95.0	3.6	5.4	11.2	140.0	12.4	21.2	nd	nd
AV		12.0	106.6	4.0	529.4	105.8	3.0	4.8	10.7	144.7	14.5	12.3	0.2	0.2
SD		1.3	7.0	6.8	808.0	191.8	4.4	6.7	17.3	233.3	21.9	11.8	0.6	0.6
2	L71	1.6	11.8	5.0	28000.0	6200.0	160.0	193.0	824.0	10400.0	480.0	804.0	16.9	16.9
2	L59	17.8	125.3	1.8	590.0	81.0	3.2	9.1	13.0	134.0	3.3	26.7	0.2	nd
2	L67	10.3	83.2	2.0	1730.0	310.0	9.8	21.4	32.0	481.0	60.0	56.1	2.7	2.5
2	L74	11.4	84.0	4.7	680.0	119.0	4.3	15.0	14.4	183.0	30.6	17.6	nd	nd
2	L63	12.4	111.5	5.0	375.0	60.0	2.6	4.3	6.2	84.0	13.8	4.4	nd	nd
2	L60	8.1	74.5	8.0	930.0	160.0	8.0	18.4	18.6	257.0	30.0	29.1	nd	nd
2	L8	10.9	99.4	5.3	365.0	48.0	6.5	3.4	6.4	94.0	16.6	14.5	nd	nd
2	L7	10.0	94.4	3.0	362.0	51.0	2.8	3.7	5.9	95.0	nd	7.2	nd	nd
2	L10	12.0	109.9	1.3	345.0	46.2	2.5	3.7	6.4	90.0	12.0	12.4	nd	nd
2	L13	8.1	76.2	4.7	839.0	143.0	5.7	9.7	16.3	234.0	nd	49.0	nd	nd
2	L14	4.8	45.0	7.7	1383.0	210.0	9.0	13.2	27.5	393.0	9.5	86.4	4.8	4.8
2	L23	7.6	70.3	−1.0	1080.0	190.0	10.0	14.5	18.3	277.0	55.0	12.9	2.4	2.5
2	LGR	10.7	103.8	−1.0	3060.0	530.0	18.2	46.6	63.0	860.0	195.0	119.0	0.2	nd
2	L49	10.8	101.9	5.0	86.0	14.9	0.3	2.3	1.6	16.9	nd	4.9	nd	nd
2	L44	8.2	79.7	0.0	4200.0	780.0	24.0	43.3	79.0	1220.0	42.0	280.0	3.4	nd
2	L43	7.5	78.0	0.0	585.0	95.0	3.2	11.4	12.1	140.0	21.2	53.3	3.1	nd
2	L69	6.8	69.9	2.0	976.0	172.0	6.4	9.3	15.9	257.0	44.0	28.4	0.0	nd
2	L70	1.3	12.4	12.0	9160.0	1900.0	58.0	50.0	176.0	2660.0	105.0	440.0	14.6	12.9
2	L68	7.1	74.5	0.7	1620.0	280.0	12.1	26.1	30.4	452.0	80.0	16.7	0.1	nd
2	BAL	4.7	43.1	4.0	2650.0	380.0	21.0	22.6	35.0	773.0	15.0	178.0	8.8	8.7
2	LJA	11.3	104.3	0.0	117.0	19.4	nd	1.1	1.8	25.4	3.8	4.2	nd	nd
2	L18	11.1	97.4	0.0	372.0	51.0	1.3	5.4	5.9	97.0	11.1	18.7	nd	nd
2	L1	6.1	55.6	1.3	4020.0	500.0	23.0	33.3	80.0	1240.0	27.0	182.0	2.4	nd
2	L73	9.0	83.6	−1.0	175.0	24.3	3.5	1.1	3.7	41.5	4.8	1.0	0.3	nd
AV		8.7	78.7	2.9	2654.2	515.2	16.5	23.4	62.2	854.4	52.5	101.9	2.5	2.0
SD		3.6	28.8	3.3	5756.3	1274.1	33.0	38.9	166.7	2116.7	100.9	182.7	4.6	4.5
3	LSP	11.5	117.9	4.8	320.0	46.0	2.2	3.4	5.9	84.0	14.8	4.6	nd	nd
3	L42	8.4	86.9	0.0	2360.0	420.0	14.0	27.8	46.0	599.0	60.0	256.0	1.6	1.5
3	BST	9.7	91.0	2.0	77.0	11.6	0.9	0.6	1.0	15.9	nd	2.9	nd	nd
3	LPR	10.6	103.9	0.0	882.0	161.0	4.7	8.3	16.5	247.0	nd	9.9	0.4	nd
AV		10.1	99.9	1.7	909.8	159.7	5.4	10.0	17.3	236.5	18.7	68.3	0.5	0.4
SD		1.4	14.0	2.2	1023.9	184.9	5.9	12.3	20.2	260.4	28.4	125.1	0.8	0.7

Table 1 (*Continued*)

Mat type	Lake number	O_2 (mg L^{-1})	O_2 (%)	Turbidity (NTU)	Conductivity (μS cm^{-1})	Na (mg L^{-1})	K (mg L^{-1})	Ca (mg L^{-1})	Mg (mg L^{-1})	Cl (mg L^{-1})	SO_4 (mg L^{-1})	HCO_3 (mg L^{-1})	TOC (mg L^{-1})	DOC (mg L^{-1})
4	BFI	9.4	83.4	2.0	4740.0	850.0	25.3	50.0	96.0	1500.0	50.0	110.0	21.5	19.0
4	L53b	10.7	103.4	0.0	138.0	23.2	0.7	1.7	2.2	30.8	3.3	3.6	nd	nd
4	LPS	10.4	101.4	−1.0	623.0	94.0	3.3	5.1	11.8	171.0	27.7	2.6	0.1	nd
4	L52	10.7	99.1	−1.0	231.0	32.7	2.1	1.4	3.5	60.0	8.1	3.8	0.4	nd
4	L52b	10.3	93.9	−0.7	265.0	40.3	1.2	2.9	4.9	67.0	9.2	7.5	nd	nd
4	L66	11.4	96.5	0.0	1032.0	170.0	5.5	18.8	18.3	285.0	29.0	35.0	nd	nd
4	L65	11.6	94.6	0.0	644.0	112.0	3.6	8.0	11.0	173.0	21.0	21.0	nd	nd
4	LG2	10.7	86.5	0.0	217.0	31.1	1.0	2.0	3.4	54.6	8.6	5.6	0.2	nd
4	L64	10.6	86.0	−1.0	327.0	49.2	1.9	3.7	4.6	83.0	7.4	8.9	nd	nd
4	LSN	10.6	83.7	−1.0	124.0	20.1	0.9	0.6	2.0	27.9	6.7	0.4	nd	nd
4	L61	10.9	88.1	−1.0	874.0	148.0	4.4	9.7	17.6	238.0	35.8	2.4	nd	nd
AV		10.7	92.4	−0.3	837.7	142.8	4.5	9.4	15.9	244.6	18.8	18.3	2.0	1.7
SD		0.6	7.2	0.9	1330.1	240.3	7.1	14.4	27.2	425.3	15.1	32.1	6.5	5.7
5	BSU	17.0	156.8	1.0	963.0	161.0	4.3	25.6	19.7	275.0	27.0	31.9	14.2	13.8
5	L58	10.6	103.6	0.0	164.0	25.0	6.2	0.6	2.5	38.0	4.8	1.5	nd	nd
5	LFO	10.4	98.5	−1.0	1088.0	180.0	7.6	7.9	16.5	303.0	34.0	10.1	0.4	nd
5	LMA	10.4	102.4	−1.0	463.0	51.0	2.5	3.7	7.9	108.0	20.3	4.5	3.5	3.5
5	L59b	11.0	91.1	−1.0	1770.0	310.0	13.4	20.0	58.0	498.0	50.0	53.0	3.5	3.7
5	LG1	11.2	93.9	0.0	1215.0	200.0	6.7	16.7	21.5	332.0	42.0	39.4	0.2	nd
5	LG4	11.1	91.2	−1.0	536.0	80.0	3.5	6.0	9.5	122.0	25.8	13.0	2.6	nd
5	L64b	11.5	93.2	1.0	672.0	135.0	5.2	3.8	5.7	183.0	3.8	13.3	nd	nd
AV		11.7	103.8	−0.3	858.9	142.8	6.2	10.5	17.7	232.4	26.0	20.8	3.0	2.6
SD		2.2	21.927	0.89	506.96	92.003	3.3729	9.0497	17.664	148.88	16.352	18.412	4.7653	4.7982

DRP, dissolved reactive phosporus; nd, not detected.

Results

Variation in limnological characteristics

The lakes in the study region were generally small and shallow (Table 1). About one-third of the lakes studied was <2 m deep and only eight lakes were deeper than 10 m. Among the latter, LH57, with a maximum depth of 34 m, was an unusually deep lake for this region. Lake area ranged between 0.1 and 13 ha; catchment areas were equally constrained in size (0.7–259 ha). The hydrology of lakes was primarily determined by meltwater input and basin morphometry. Open lake systems often have multi-annual snowfields in their catchment, have inflow streams from other lakes, or are situated in close proximity to the continental ice sheet (e.g. LH49). During most years, active meltwater streams reduce the evaporative concentration of ionic constituents. In contrast, closed lake systems, fed only by meltwater from annual snowfields and precipitation but with no active outlet, are therefore more susceptible to the concentration of ions (e.g. Sarah Tarn, L. Reid).

Most lakes had low conductivity values (<4200 μS cm^{-1}). Lake Reid and Sarah Tarn, on Broknes, were the most saline lakes (9160 and 28 000 μS cm^{-1}, respectively). The higher the conductivity, the more variable was lake water conductivity over time (Table 2).

PCA of physical, chemical and morphometric data showed that the limnological diversity of the Larsemann Hills lakes was primarily determined by variation in conductivity and lake morphometry (Fig. 2).

Table 2 Historical variation in conductivity in oligo-saline lakes of the Larsemann Hills. Data from 1987 (Gillieson *et al.*, 1990) and 1993 (Ellis-Evans *et al.*, 1998) refer to measurements made before melting of lake ice, data from 1997 include measurements from both before (a) and after (b) melting of ice cover (J. Burgess *et al.*, pers. comm.; this study)

	Conductivity (μS cm^{-1})				
Sampling year	L. Anna	Pup Lagoon	Heart Lake	L. Reid	Sarah Tarn
1987	290	399	987	1730	3340
1993	–	400	570	1370	3320
1997(a)	3810	985	1649	7380	23870
1997(b)	–	–	1640	3760	5520
AV	2050	595	1211	3560	9012
SD	2489	338	528	2755	9959

AV, average, SD, standard deviation, –, no data available.

The first two components captured 52% of the total variance, while the third (8% of the total variance, not shown) mainly reflected variation in dissolved phosphate and latitudinal position. Dissolved oxygen was strongly negatively correlated with conductivity, while DOC, TOC, dissolved silicate and pH were positively correlated with this variable. In most lakes, TOC levels were below detection limits (0.01 mg L^{-1}). However, in the oligosaline lakes BAL, L70, L71 and BFI, and the freshwater lake Sunset (BSU), TOC concentrations ranged between 8.8 and 21.5 mg L^{-1}. Particulate organic matter concentration (calculated as the difference between TOC and DOC) was very low in most lakes; dissolved organic matter contributed more than 97% of TOC (except in Firelight Lake: 88%).

The majority of the lakes were ultra-oligotrophic and had very low concentrations of dissolved nutrients (with a maximum and median for total phosphate and nitrogen of 6.32 and 0.02 μmol L^{-1} and 34 and 0.5 μmol L^{-1}, respectively). Total nitrogen was highest in L71 (mainly ammonia) and L73, LPR and LG1. The hypo-saline Firelight Lake (BFI) in the Bølingen Islands stood out as an outlier because of its high pH (9.38) and phosphate concentration (195.3 μg L^{-1}).

Microbial communities

The very low particulate organic matter concentration (calculated as the difference between TOC and DOC, Table 1) underscored the extreme oligotrophic nature of the lakes and the essential role of benthic microbial communities as the most important primary producers.

A number of macroscopically recognisable mat types (growth forms), which occurred over different parts of the lake depth gradient, were distinguished (Fig. 3). Finely laminated prostrate mats were restricted to deeper lakes (>7 m). Less structured prostrate mats occurred between 2 and 16 m, and parts of these mats sometimes lifted off, due to bubble formation and physical disturbance by wind and ice (Simmons, Vestal & Wharton, 1993). Flake mats, consisting of small (1–2 cm) plate-like growths of cyanobacteria, were confined to shallow lakes up to 2.3 m deep. They consisted of 17–73% inorganic sediment (mean 35.2%). Epipsammic (interstitial) communities consisted of an organic matrix with a high amount of

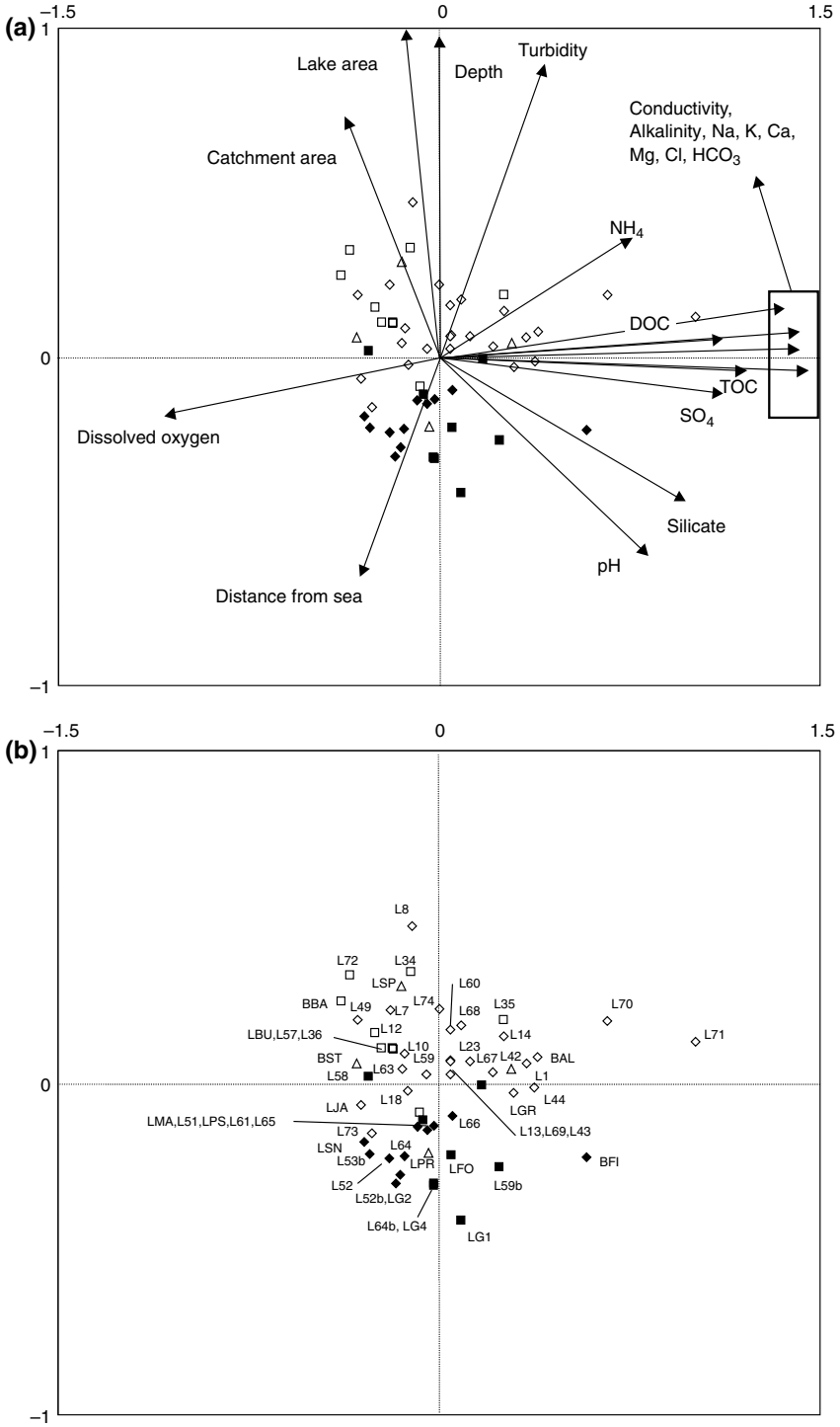

Fig. 2 Principal component analysis (PCA) correlation biplot of physical, chemical, morphometric and geographical variables. Site labels have only been added on Fig. 2b. For lake lables see Table 1. Symbols refer to the type of microbial mats present at the sampling site: □, finely laminated; ◇, prostrate and lift-off; △, epilithic; ◆, flake; ■, epipsammic. The first two principal components account for 41.7% and 10.3% of the total variation, respectively. Firelight Lake (BFI) was identified in a preliminary PCA as an outlier and was omitted from the analysis shown here. Only variables of which more than 20% of the variance is explained along the first and second component are shown.

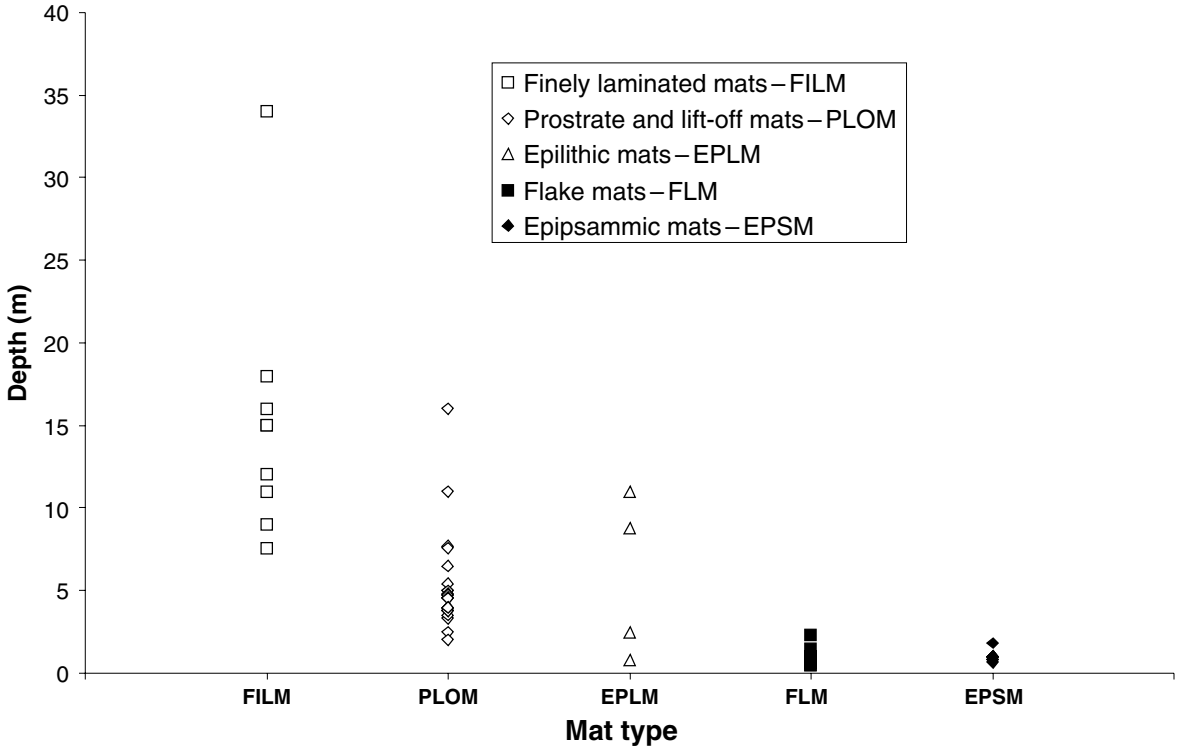

Fig. 3 Depth zonation of microbial mat types in lakes of the Larsemann Hills and Bølingen Islands. The exact names of the lakes in which each mat type was found are given in Table 1.

embedded inorganic sediment (32–99%, mean 78.6%); they were observed in shallow waterbodies only (<1.8 m). In Table 1 lakes are grouped on the basis of the dominant mat type present.

Total chlorophylls did not differ significantly between the different mat types (Fig. 4). Total carotenoids were significantly higher in flake mats than in all other types; epipsammic mats had significantly higher values for carotenoids than finely laminated mats, but not than the other mat types. The ratio carotenoids/chlorophylls was significantly lower in finely laminated and prostrate mats than in flake and epipsammic mats (ANOVA's, $P < 0.05$). In addition, the latter two had higher scytonemin concentrations, an ultraviolet sunscreen pigment known only from the sheaths of cyanobacteria (Proteau *et al*., 1993; Hodgson *et al*., 2001b).

Cyanobacteria. A total of 33 morphotypes was identified, belonging to at least 14 genera (Table 3); some common morphological forms are illustrated in Fig. 5. CCA of presence–absence data showed that the major gradients in species turnover were related to lake depth, pH, calcium and silicate (Fig. 6; Table 4). The environmental factors accounted for only a low proportion (11.7% for the first two axes together) of the total variance in the morphotype data, indicating that the main gradients have not been captured by the variables introduced (ter Braak & Smilauer, 1998). Shallow water communities were characterised by members of the order Nostocales (*Nostoc* spp., *Coleodesmium* cf. *scottianum*, *Calothrix* sp., *Dichothrix* sp. and *Petalonema* cf. *involvens*). *Nostoc* occurred in all studied epipsammic mats. In flake mats morphotypes of the genus *Leptolyngbya* were also regularly observed. The finely laminated, prostrate and lift-off mats of deeper lakes were largely dominated by morphotypes of the genus *Leptolyngbya*. While these filamentous species, embedded in a gelatinous mucilage, determined the mat structure, several other, mainly unicellular, taxa co-occurred. Thirteen of the 33 taxa were observed in only three or less than three lakes (Table 4).

Diatoms and stomatocysts. All 56 lakes were included in the diatom analyses. In total, 26 lacustrine and aerial diatom species were encountered; taxonomic details on all species are given in Sabbe *et al*. (2003). About 40% of the taxa were endemic to Antarctica.

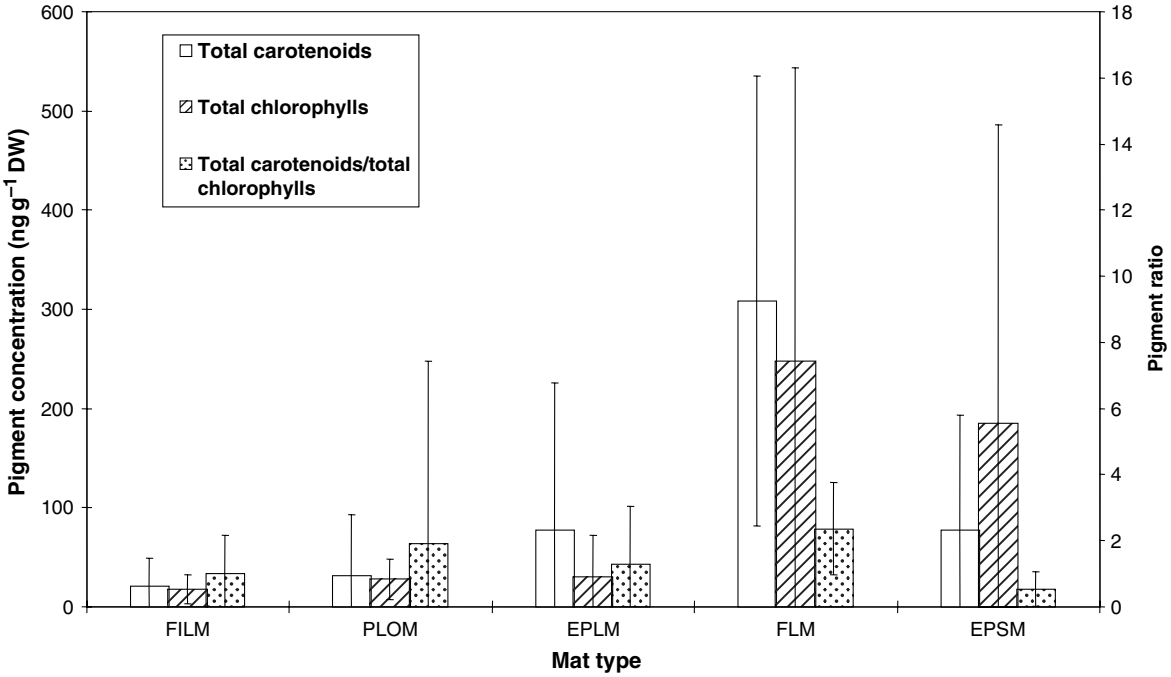

Fig. 4 Mean concentrations of total carotenoids and chlorophylls, and the ratio between them in microbial mats of the Larsemann Hills and Bølingen Islands. For mat type abbreviations, see Fig. 3.

The distribution was poorly known for 23% of the species because of their uncertain taxonomic status. The chemically deviant Firelight Lake (BFI) also had unusual biological characteristics due to the high relative abundance of *Craspedostauros laevissimus* (West & West) Sabbe, a brackish-water species (Sabbe *et al.*, 2003). After removal of this outlier, a CCA analysis of the remaining 55 lakes showed that depth, conductivity, pH, silicate, alkalinity and catchment area could be significantly ($P \leq 0.05$) related to the variation in the diatom species data (Fig. 7).

In contrast to the Cyanobacteria data, the first two CCA axes explained a somewhat higher proportion (about 25%) of the total variation in the species data. The deeper lakes (>2.5 m) with finely laminated and prostrate mats were clearly separated from shallow lakes (<2.5 m), where flake mats or interstitial mats predominated. On average, species richness was slightly higher in shallow than in deep lakes. Shallow water communities were characterised by aerial species such as *Diadesmis* cf. *perpusilla*, *Hantzschia* spp., *Luticola muticopsis*, *Pinnularia microstauron* var. *microstauron* and *P. borealis*. In addition, a morphologically diverse and abundant assemblage of stomatocysts was present in these shallow lakes. In lakes with maximum depths between 2.5 and 3.5 m the araphid diatom *Stauroforma inermis* was the most abundant species, often forming nearly monospecific assemblages. In deeper lakes (3.5–38 m), the attached monoraphid species *Psammothidium abundans* dominated the species-poor diatom community of the finely laminated mats. In deep lakes a further differentiation of the diatom floras was related to conductivity. *Amphora veneta* and *Craticula* cf. *molesta* were abundant in hyposaline lakes but were virtually absent from oligosaline lakes. The relative importance of stomatocysts (with respect to diatoms) was high (>20%, data not shown) only in shallow (<2.5 m) freshwater ponds.

Discussion

The limnological diversity of Larsemann Hills and Bølingen Islands is primarily determined by variation in conductivity and its associated variables (concentrations of major ions and alkalinity) and lake/catchment morphology (depth, catchment and lake area). The majority of the lakes in the Larsemann Hills are oligosaline; no hypersaline lakes were found. This is in contrast to the Vestfold Hills, where 2% of the total surface of the region is occupied by saline and hypersaline lakes (Adamson & Pickard, 1986), which

Table 3 List of cyanobacterial morphotypes and diatom species and labels used in ordination analyses

Cyanobacteria	
Asterocapsa sp.	ASru
Calothrix sp.	CAs1
Chamaesiphon cf. *subglobosus* (Rostaf.) Lemmermann & CMsu	CMsu
Chondrocystis cf. *dermochroea* (Näg.) Komarék & Anagnostidis	CHde
Coleodesmium cf. *scottianum* Welsh	COsc
Dichothrix sp.	DIsp
Gloeocapsa cf. *alpina*Näg. Emend. Brand	GLal
G. cf. *sanguinea* (Agardh) Kützing	GLsa
G. cf. *compacta* Kützing	GLco
Leptolyngbya sp. 1	Lpp01
L. sp.2	Lpp02
L. sp.3	Lpp03
L. sp.4	Lpp04
L. sp.5	Lpp05
L. sp.6	Lpp06
L. sp.7	Lpp07
L. sp.8	Lpp08
Lyngbya sp.	LYs1
Nostoc sp.	Nos
Oscillatoria sp.	OSs1
Petalonema cf. *involvens* (A. Br.) Migula	PEin
Schizothrix sp. 1	SCs1
S. sp. 2	SCs2
S. sp. 3	SCs3
Unicellular sp. 1	U01
Unicellular sp. 2	U02
Unicellular sp. 3	U03
Unicellular sp. 4	U04
Unicellular sp. 5	U05
Unicellular sp. 6	U06
Unicellular sp. 7	U07
Unicellular sp. 8	U08
Unicellular sp. 9	U09
Diatoms	
Achnanthes taylorensis Kellogg, Stuiver, Kellogg & Denton	ACtay
Amphora veneta Kützing	AMven
Craticula cf. *molesta* (Krasske) Lange-Bertalot & Willmann	CAmol
Centric sp. 1	CEsp1
Diadesmis cf. *perpusilla* (Grunow) Mann	DIper
Gomphonema sp.	Gosp1
Hantzschia cf. *amphioxys* (Ehrenberg) Grunow	HAsp1
H. virgata (Roper) Grunow	HAvir
Luticola muticopsis (Van Heurck) Mann	LUmus
Muelleria peraustralis (West & West) Spaulding & Stoermer	MUper
Navicula phyllepta Kützing	NAphy
N. cf. *shackletoni* West & West	NAsha
N. sp. 1	NAsp1
Nitzschia commutata Grunow	NIcom
Pinnularia borealis Ehrenberg	PIbor
P. cymatopleura West & West	PIcym
P. microstauron (Ehrenberg) Cleve	PImic
P. microstauron var. *microstauron* (Ehrenberg) Cleve	PImivc
Planothidium quadripunctatum (Oppenheim) Sabbe	PLqua
Psammothidium abundans (Manguin) Bukhtiyarova & Round	PSabu
Psammothidium germainii (Manguin) Sabbe	PSger
Psammothidium metakryophilum (Lange-Bertalot & Schmidt) Sabbe	PSmet
Psammothidium stauroneioides (Manguin) Bukhtiyarova	PStau
Stauroforma inermis Flower, Jones & Round	STine
Stauroneis anceps Ehrenberg	SAanc

have been the subject of a wide range of studies (e.g. Roberts & McMinn, 1998; Gibson, 1999; Bowman *et al.*, 2000; Labrenz & Hirsch, 2001; Laybourn-Parry, Hofer & Sommaruga, 2001; Laybourn-Parry, Quayle & Henshaw, 2002; Laybourn-Parry, 2002a). Evaporative processes contribute to the salinisation of lakes in the low-precipitation areas of continental Antarctica. Critical in this respect is the balance between the annual input of meltwater and evaporation. The input of melting water is mainly determined by the accumulation and presence of multi-year snowfields in the catchment and the vicinity of the continental ice sheet. None of the studied lakes of the Larsemann Hills and Bølingen islands appears to have been subject to strong salinisation. This is probably due to their generally smaller volume (as compared with the Vestfold Hills lakes, for instance) which results in more rapid dilution of salts even in those lakes which have had known a marine phase during their history (Hodgson *et al.*, 2001a). Exceptions are Lake Reid and Sarah Tarn, which are closed lakes characterised by a long evaporation history associated with the fact that parts of Broknes remained ice-free during the Last Glacial Maximum (Hodgson *et al.*, 2001a).

The negative correlation between conductivity related variables and oxygen in the lakes of the Larsemann Hills, was also discussed by Ellis-Evans *et al.* (1998), who reported anoxia in the benthic microbial mats and oxygen depletion in the water column of the most saline lakes Sarah Tarn and Lake Reid. Concentrations of DOC and TOC in the Larsemann Hills are very low (<0.1 mg L^{-1}), except in the more saline lakes. The higher values in the latter may be caused by organic carbon accumulation in these closed systems. A positive correlation between salinity and DOC has also been observed in saline lakes in the Canadian

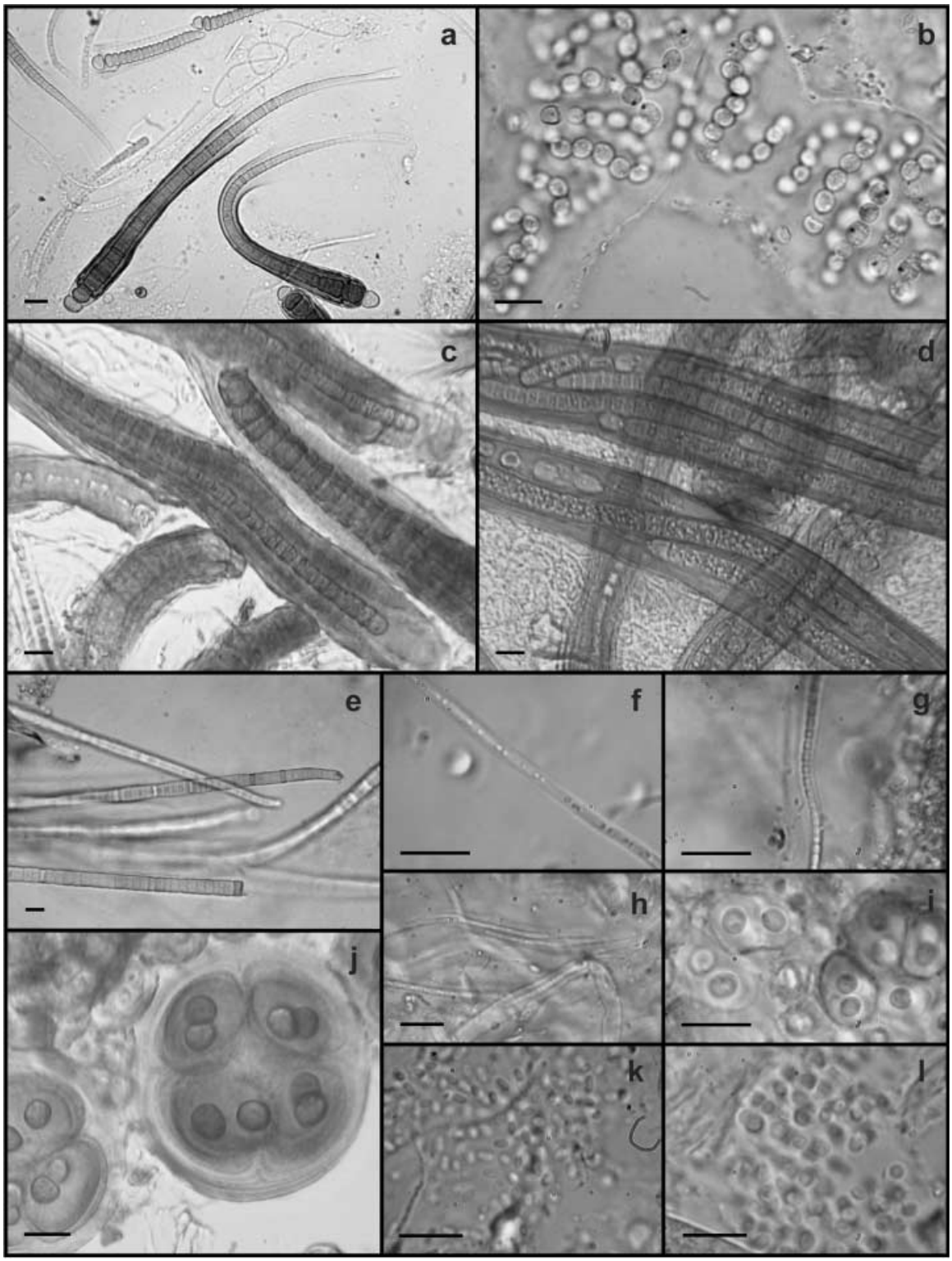

Fig. 5 Common cyanobacterial morphotypes found in the microbial mats of the study lakes. (a) *Calothrix* sp., (b) *Nostoc* sp., (c) *Petalonema* cf. *involvens*, (d) *Coleodesmium* cf. *scottianum*, (e) *Oscillatoria* sp., (f) *Leptolyngbya* sp. 1, (g) *Leptolyngbya* sp. 3, (h) *Schizothrix* sp. 1, (i) *Chondrocystis* cf. *dermochroea*, (j), *Asterocapsa* sp., (k) unicellular 1, (l) unicellular 7. Scale bar = 10 μm in all figs.

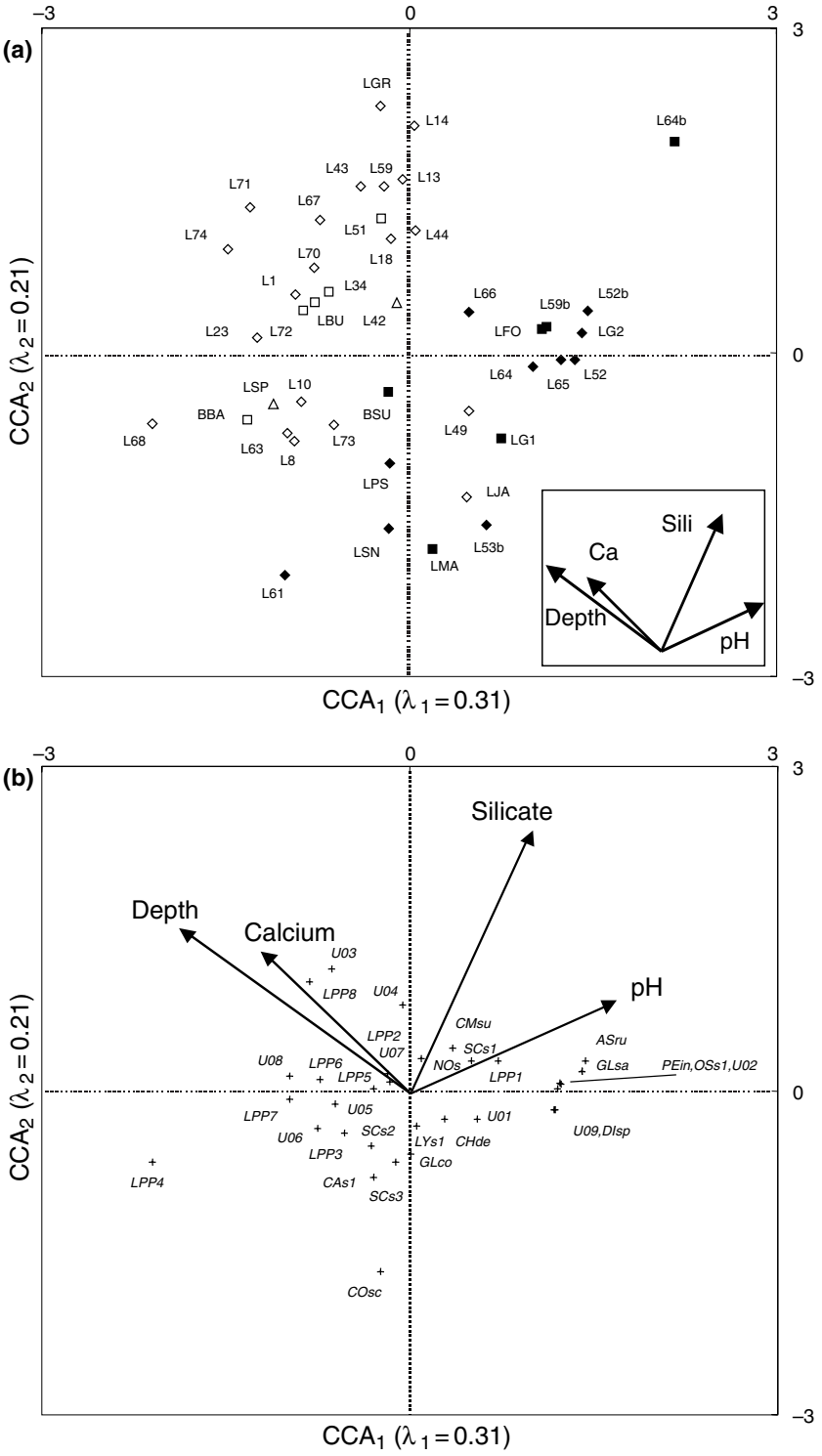

Fig. 6 Canonical correspondence analysis (CCA) biplots showing the relationships between sites, presence–absence of cyanobacteria and environmental gradients [(a) sites and environmental variables (inset), (b) morphotypes and environmental variables]. Only a minimal set of environmental factors identified by forward selection, capturing a maximal amount of variation in the diatom species data, is shown. Symbols correspond to substratum type as in Fig. 2; for species labels see Table 3. λ = eigenvalue of corresponding axis.

Table 4 Presence–absence list of the cyanobacterial morphotypes in selected lakes of the Larsemann Hills and Bølingen Islands. For labels, see Table 3

	U01	U02	U03	U04	U05	U06	U07	U08	U09	CHde	GLco	GLal	GLsa	ASru	CMsu	Lpp01	Lpp02	Lpp03	Lpp04	Lpp05	Lpp06	Lpp07	Lpp08	OSs1	LYs1	SCs1	SCs2	SCs3	Nos	CAs1	DIsp	COsc	PEin
L72							1			1							1												1				
L34							1																										
LBU					1		1														1								1				
BBA							1									1																	
L51			1	1												1			1						1			1					
L71							1	1								1												1					
L59			1													1												1					
L67			1	1			1									1																	
L74			1			1	1	1												1		1					1						
L63						1		1								1	1			1							1	1	1				
L8						1	1														1							1					
L10					1		1				1								1								1		1				
L13			1	1			1								1	1												1					
L14							1																					1					
L23			1	1		1	1												1		1												
LGR							1			1															1			1					
L49							1								1		1								1	1							
L44																1			1														
L43			1	1												1												1					
L70			1				1			1						1								1									
L68						1	1										1	1		1							1	1	1				
LJA							1									1			1									1			1		
L18							1								1					1		1						1					
L1	1					1	1									1									1			1					
L73						1																											
LSP										1	1															1		1					
L42							1												1									1					
L53b	1						1		1	1	1																1	1		1			
LPS	1						1	1		1						1			1								1						
L52						1	1			1														1	1		1	1	1	1			
L52b	1	1					1		1	1				1		1										1		1		1			
L66	1						1			1							1			1							1	1					
L65		1		1			1		1	1						1											1	1					
LG2							1		1	1	1	1	1			1									1		1	1	1	1			1
L64	1	1		1			1			1															1			1					1
LSN										1															1	1	1				1		
L61							1			1						1											1		1		1		
BSU					1		1													1					1			1					
LFO	1						1								1								1		1			1		1			
LMA						1	1			1						1											1	1	1				
L59b									1	1						1									1			1					
LG1	1						1								1	1												1					
L64b																												1					

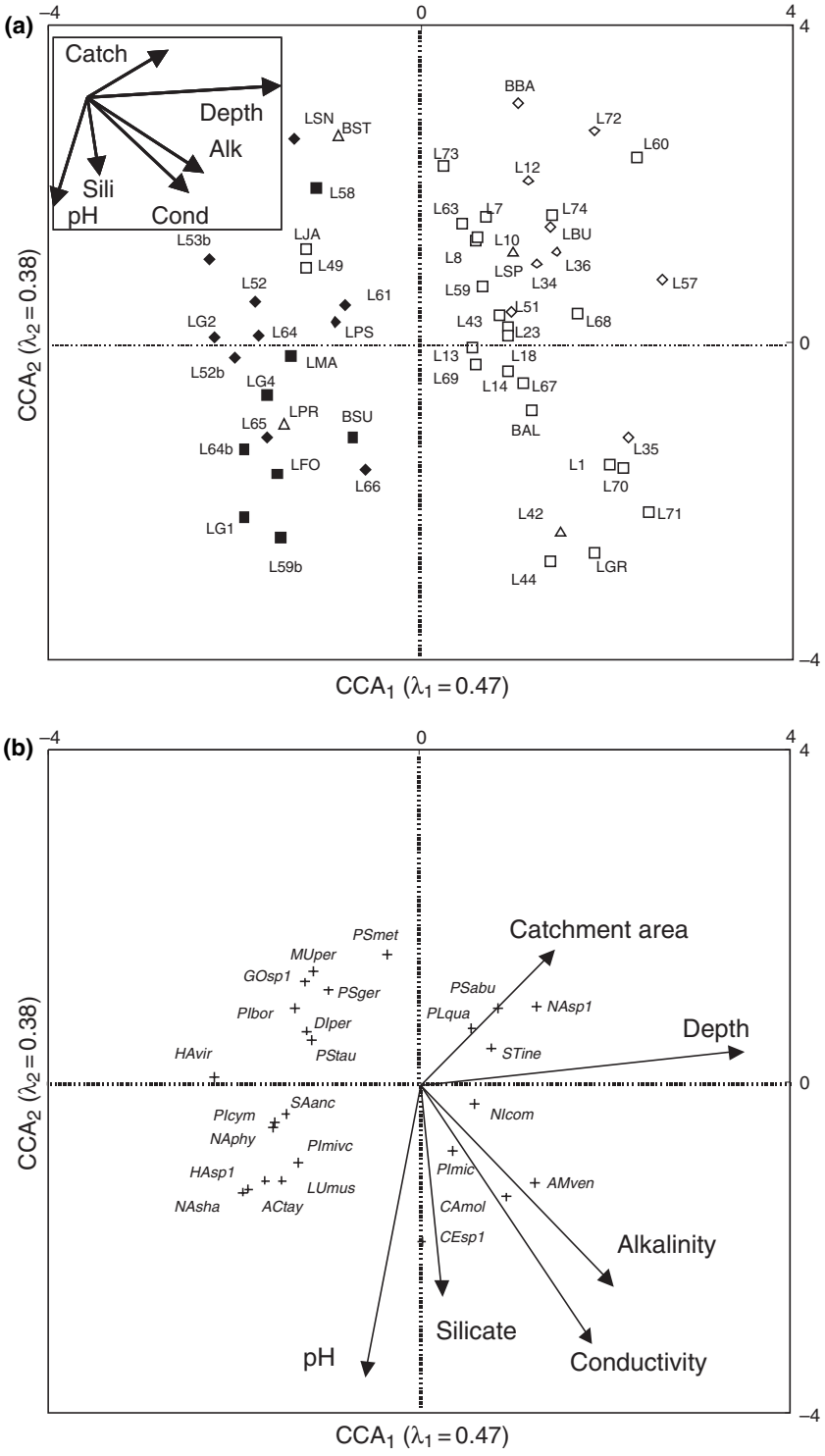

Fig. 7 Canonical correspondence analysis biplots showing the relationships between sites, relative abundance of diatom species and environmental gradients [(a) sites and environmental variables (inset), (b) species and environmental variables]. Only a minimal set of environmental factors identified by forward selection, capturing a maximal amount of variation in the diatom species data, is shown. Symbols correspond to substratum type as in Fig. 2; for species labels see Table 3. λ = eigenvalue of corresponding axis.

Prairie region (Curtis & Adams, 1995), where it was attributed to evaporative concentration of refractory DOC. Whether a similar mechanism is also responsible for the higher DOC values in the more saline Larsemann Hills ponds, is impossible to assess without more detailed data on the composition of the DOC. However, it can be expected that, at these low temperatures, the proportion of refractory to metabolisable DOC is much greater than at higher temperature. Alternatively, communities in these lakes may produce more extracellular carbon. The lack of correlation between primary production and DOC in some lakes from the nearby Vestfold Hills suggest that different plankton communities may exude different amounts of DOC (Laybourn-Parry *et al.*, 2002). The annual freeze-melt cycle in brackish lakes also leads to brine formation and dissolved salt accumulation caused by exclusion during lake ice formation, and depletion of dissolved oxygen (Schmidt *et al.*, 1991; Hawes *et al.*, 1999). This may cause physical and/or osmotic destruction of parts of the mat, and can therefore also lead to higher TOC in the water column. In the most saline lakes, conductivity is more variable than in the slightly saline lakes (Table 2), suggesting that conductivity changes in these lakes (e.g. during freezing and melting of the lake ice) can be marked and a possible stress factor for the microbial mats, leading to cell destruction and carbon enrichment of the lake water. However, pronounced conductivity fluctuations can also occur in low conductivity lakes (e.g. L. Anna, Table 2).

As in other lakes in East Antarctica (e.g. Vestfold Hills, Roberts & McMinn, 1996; Windmill Islands, Roberts *et al.*, 2001a and Rauer Islands, Hodgson *et al.*, 2001b) nitrogen concentrations were low in all lakes. High phosphate is found in Firelight Lake (Bølingen Islands), possibly due to input of nutrients from the excreta of snow petrels (*Pagodroma nivea* Forster), which congregate in the catchment during the breeding season. Furthermore, extensive moss banks are found in the catchment, which may also be a source of nutrients (Ellis-Evans *et al.*, 1998).

Although there have been previous taxonomic and floristic studies on Antarctic lacustrine diatoms and cyanobacteria (Fumanti, Cavacini & Alfinito, 1997; Komárek, 1999; Sabbe *et al.*, 2003 and references in these papers), little is known about the environmental factors associated with their spatial distribution. Previous studies have identified conductivity and lake trophy as the main factors regulating species composition of benthic (mat) communities (Jones, 1996; Vincent & James, 1996; Roberts *et al.*, 2001a). Within-lake spatial variability in mat physiognomy and composition is mainly related to depth (Ellis-Evans *et al.*, 1998; Hawes & Schwarz, 1999 and references therein). Within the Larsemann Hills oasis, mat structure and species turn-over in both diatoms and cyanobacteria are primarily determined by lake depth. In shallow ponds, abrasion by ice and freezing probably act to prevent the development of prostrate mats, which are characteristic of deeper lakes. The higher likelihood of anoxia and freeze-out of salts in shallow lakes may also constitute a stress factor for the benthic communities. Flake mats occur over a slightly greater depth range than epipsammic communities, but are similar in terms of species composition. Both flake and epipsammic mats have high carotenoid/chlorophyll ratios, probably reflecting protective pigmentation against high UV and PAR radiation (Roos & Vincent, 1998; Hodgson *et al.*, 2001b). Accumulation rates differ greatly among lakes (Hodgson *et al.*, 2001a), which may partly reflect annual production, and which is in turn constrained by the light climate of the lakes (length of growing season) and the availability of essential nutrients (by recycling in the microbial mat). In the Larsemann Hills, this tends to favour high accumulation rates in shallow coastal lakes, such as Pup Lagoon, and low accumulation rates in deep inland lakes with multi-annual ice and snow cover, such as Progress Lake. This contrasts with the deep lakes in the McMurdo Dry Valleys, where thick microbial mats occur in some deep lakes (Wharton *et al.*, 1983).

The ecological success of mat forming cyanobacteria in a broad range of Arctic and Antarctic environments is well-established (e.g. Hawes, Howard-Williams & Pridmore, 1993; Tang *et al.*, 1997; Vezina & Vincent, 1997; Nadeau & Castenholz, 2000; Vincent, 2000). In the absence of metazoan grazers and substantial competition from planktonic autotrophs, cyanobacteria are the dominant primary producers in these regions. Filamentous Oscillatoriaceae (*Leptolyngbya* spp., *Schizothrix* spp. and *Lyngbya*), and Nostocales (*Calothrix* spp. and *Nostoc* spp.) are commonly reported from polar benthic habitats (e.g. Wharton *et al.*, 1983; Vincent *et al.*, 1993; Vincent & James, 1996; Broady & Weinstein, 1998). Different cyanobacterial morphotype assemblages are present in deep lakes

and shallow ponds. Deep-water assemblages are dominated by filamentous *Leptolyngbya* morphotypes, while shallow-water assemblages are taxonomically more diverse and, in addition to filamentous Oscillatoriaceae, comprise members of the Nostocales as most characteristic taxa. This may be related to their resilience to desiccation (Mataloni, Tell & Wynn-Williams, 2000) or to the occurrence of UV screening compounds which enables the Nostocales to survive in high UV environments that are harmful to other organisms (Leavitt, Hodgson & Pienitz, 2003).

In contrast to the diatoms (see below), there was no significant relationship between the distribution of the cyanobacterial morphotypes and conductivity, even when conductivity was introduced as the sole explanatory variable in separate CCA analyses. Salinity tolerance has been investigated for a considerable number of cyanobacteria and appears to be quite variable: some taxa are broadly euryhaline (e.g. *Halospirulina*, Nübel *et al*., 1999), while others have much narrower salinity tolerances (e.g. Stal & Krumbein, 1985). The cosmopolitan marine benthic species *Microcoleus chtonoplastes* Thuret occurs across a wide range of salinities (from brackish to hypersaline), but strains from different habitats have distinct and stable growth responses to salinity (Karsten, 1996). It is, as yet, unclear whether these physiological ecotypes can also be distinguished at the pheno- and genotypic level. Garcia-Pichel, Prufert-Bebout & Muyzer (1996) did not find any significant differences in phenotype or 16S rRNA genotype between seven *M. chtonoplastes* strains from different geographic localities and salinity regimes (from marine intertidal to hypersaline). The lack of a clear relationship between the distribution of morphotypes and conductivity may therefore be due to the fact that morphology alone does not allow distinction between strains or taxa with different conductivity preferences.

Compared with cyanobacterial morphotypes, species turnover in diatoms was higher along the conductivity and depth gradients. Multivariate analyses clearly demonstrated that the variation in diatom species composition was significantly related to both lake depth and conductivity. Even on the generic level, differences existed between deep and shallow water assemblages. Genera with many aerial representatives like *Hantzschia*, *Luticola* and *Diadesmis*, which are also commonly reported from terrestrial and stream environments in Antarctica (Kawecka & Olech, 1993; Broady, 1996), occurred in the shallow ponds, while *Psammothidium* and *Stauroforma* were mainly associated with prostrate microbial mats in the deep lakes. The dominant species in the deep lakes were *S. inermis* or *P. abundans*. The latter species lives attached to cyanobacterial sheaths and forms nearly monospecific assemblages in deep lakes with finely laminated mats. *Stauroforma inermis* forms short chain-like colonies and appears to prefer somewhat shallower lakes. This species can become entrained in the water column (Ellis-Evans, 1996), possibly as a result of convective or wind-induced mixing of the water column. It was noticed during sampling that shallow lakes became ice-free before the deeper lakes, presumably because the surface incident radiation flux per unit area takes less time to heat a smaller volume of water column. Further, within the deep lakes the diatom composition was structured by conductivity. The genera *Amphora* and *Craticula* were characteristic of the more saline lakes. The role of conductivity in structuring diatom assemblages is well-documented (e.g. Roberts & McMinn, 1998; Sylvestre, Servant-Vildary & Roux, 2001; Davies *et al*., 2002).

The diatom flora of the Larsemann Hills and Bølingen Islands is less diverse when compared with lower-latitude environments in Maritime Antarctica and the Sub-Antarctic Islands (Jones, 1996; Van de Vijver & Beyens, 1999). However, comparably low species numbers have been reported from other continental Antarctic locations (Jones, 1996 and references therein; Roberts & McMinn, 1999; Sabbe *et al*., 2003), which is in line with the general trend of decreasing diversity with increasing latitude in diatoms and various other groups of aquatic organisms (Jones, 1996; Van de Vijver & Beyens, 1999). Interestingly, species diversity is lower in the Larsemann Hills than in the nearby Vestfold Hills. This is probably associated with the greater range of salinities and the influence of seawater incursions in the Vestfold Hills' lakes, but also with the fact that many of these lakes are meromictic. In meromictic lakes more niches are available for species to occupy (e.g. freshwater diatoms in the oligosaline epilimnion and brackish water diatoms in the mesosaline hypolimnion).

Stomatocysts only became important (with respect to diatoms) in shallow freshwater lakes. These cysts may belong to a wide range of taxonomic groups, including chrysophytes, prymnesiophytes and amoebae. Cyst-forming phytoplankton has been described

from many Antarctic (Beyens *et al*., 1995; Mrozinska, Olech & Massalski, 1998; Van de Vijver & Beyens, 2000) and Arctic lakes and ponds (Douglas & Smol, 1995; Duff, Zeeb & Smol, 1997; Wilkinson *et al*., 1997), but to date there is scant information on their distribution with respect to the environment. It is likely that cysts of marine phytoplankters or sea-ice associated taxa (Stoecker *et al*., 1997) may also be imported into the lakes by sea-spray, given the widespread occurrence of valves belonging to marine diatom taxa in lakes of the Larsemann Hills and Bølingen Islands (cf. also Hodgson *et al*., 2001b).

The use of diatoms as indicators of present and past environmental conditions is well-established. For Antarctic lakes several 'training data sets' have been constructed (Jones, Juggins & Ellis-Evans, 1993; Roberts & McMinn, 1996; Roberts *et al*., 2001a; Hodgson *et al*., 2001b). In these studies, nutrient and conductivity have been identified as strongly determining diatom species composition and distribution. Transfer functions for salinity reconstruction in meso- to hypersaline conditions have been applied to sedimentary records in the nearby Vestfold Hills (Roberts *et al*., 2001b) and Bunger Hills (Roberts, McMinn & Zwartz, 2000). These transfer functions are not readily applicable to the Larsemann Hills. Firstly, the LH lakes cover the lower part of the conductivity spectrum and, secondly, taxonomic inter-calibration is needed. Transfer functions for salinity and depth, based on an intercalibrated dataset from the Larsemann Hills and Bølingen Islands (this study), the Vestfold Hills (Roberts & McMinn, 1996), the Windmill Islands (Roberts *et al*., 2001a) and the Rauer Islands (Hodgson *et al*., 2001b), have therefore recently been constructed by Verleyen *et al*. (2003), and were used to infer past changes in the precipitation–evaporation balance in the lakes of the Larsemann Hills (Verleyen *et al*., in press). Here we have presented detailed ecological data on the structure and composition of benthic microbial mats in which these diatom assemblages reside. Together with the inference models, this will permit ecological data other than those on fossil markers to be incorporated in the reconstruction of past environments spanning the last glacial cycle.

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