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Environmental factors influencing the pigment composition of *in situ* benthic microbial communities in east Antarctic lakes

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ABSTRACT: To compile reference data for palaeolimnological studies using fossil pigments, we examined the extent to which environmental variables, gross morphology and species composition influence the modern pigment content of *in situ* microbial communities in 62 east Antarctic lakes. Pigment contents, measured using HPLC, were compared with 32 environmental variables, gross microbial mat morphology and cyanobacterial species composition in each lake. Results showed low concentrations or an absence of pigments in the water columns of most lakes. For benthic microbial communities, multivariate statistical analyses identified lake depth as the most important factor explaining pigment composition. In deeper lakes the pigment composition was dominated by chlorophylls, in intermediate depth lakes by chlorophylls and carotenoids, and in shallow lakes by scytonemins, ultraviolet-screening pigments found in cyanobacteria. In addition to lake depth, conductivity, turbidity, dissolved oxygen, sulphate and geographical location were all significant ($p \leq 0.05$) in explaining variance in the pigment content. Significant differences in microbial mat gross morphologies occurred at different lake depths ($p \leq 0.01$), and were characterised by significant differences in their pigment content ($p \leq 0.004$). Despite the high abundance of scytonemin in shallow lakes, there were only limited changes in the absolute concentrations of chlorophylls and carotenoids. We conclude that lake depth is the most significant factor influencing both gross mat morphology and pigment content, presumably as a result of its influence on the light climate. In general, the ability of the cyanobacteria to regulate their pigment content, morphology, community composition and motility to best exploit the light environment at different lake depths may explain their dominance in these systems.

KEY WORDS: Microbial communities · Pigments · Antarctic · Lakes · Cyanobacteria · Palaeolimnology · Reference data set

INTRODUCTION

Pigments and their derivatives are now commonly used in palaeolimnological studies, in which the abundance, production and composition of past phototrophic communities are important response variables (Leavitt & Hodgson 2001). In order to interpret pigment stratigraphies in lake sediment cores it is important to compile regional reference data sets. In these data sets, statistical tests are carried out to identify environmental variables that have a significant influence on the modern surface-sediment pigment content. These data are then used to aid the interpretation of the fossil pigment content in sediment cores and infer the environmental conditions at the time of deposition.

Aquatic cyanobacteria and algae use pigments and other compounds to regulate the intensity (photon flux density) and spectral composition of incoming light. This enables them to maximize photosynthetic effi-

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ciency whilst preventing photochemical degradation of cellular components and indirect loss of function mediated by reactive oxygen species (Vincent 2000). Chlorophylls *a* (in algae, cyanobacteria and mosses), *b* (in algae and mosses) and bacteriochlorophylls (in photosynthetic bacteria) are the main photosynthetic pigments in Antarctic aquatic environments (Squier et al. 2002), similar to other geographical areas. These are accompanied by carotenoids, including xanthophylls, which disperse excess heat energy (Demmig-Adams & Adams 2000) and phycobiliproteins that selectively filter incoming light and act as photosynthetic accessory pigments (Hawes & Schwarz 2001). In addition, in cyanobacteria, a variety of compounds including mycosporine-like amino acids (MAAs) and scytonemins occur as extracellular pigments (Garcia-Pichel & Castenholz 1991, Proteau et al. 1993, Cockell & Knowland 1999, Squier et al. 2004) that screen-out harmful ultraviolet radiation (UVR, 280 to 400 nm).

A number of factors may influence the pigment content of aquatic microbial communities, for example, light intensity and spectral composition (mediated by lake depth, water-column transparency and other factors such as the duration and extent of snow and ice cover), species composition and relative abundance, biological productivity, water chemistry and geographical location. However, in communities dominated by cyanobacteria, pigment composition and concentration are often closely related to the light environment. Experiments under both field and laboratory conditions have shown that changes in pigment content can be induced by artificial manipulation of the intensity and spectral composition of light (Quesada & Vincent 1993). For example, in the laboratory, stepwise increases in UVR have been shown to trigger a 'cascade' of physiological responses in *Nostoc commune* (Ehling-Schulz et al. 1997): first, a rapid increase in carotenoids (especially echinenone and myxoxanthophyll), but with no influence on chlorophyll *a*; second, a substantial increase in an extracellular, UVR-absorbing MAA; and finally, synthesis of scytonemin. Such experiments typically measure changes in the pigment content of monospecific cultures in response to manipulation of light and/or a limited suite of environmental variables. This has the advantage of removing or controlling other environmental variables that may influence pigment composition, and eliminates experimental difficulties caused by studying mixed species assemblages. As a consequence, few studies have examined natural species assemblages *in situ* and statistically explored the combined influences of multiple environmental variables on pigment composition.

In this study, we tested the extent to which a combination of environmental variables, gross mat morphology and species composition influence the pigment contents of modern *in situ* benthic microbial communities in 62 shallow lakes and ponds of a coastal east Antarctic oasis and 2 nearby archipelagos. First, we described the physical and chemical environment of the lakes, the gross morphology of microbial mat

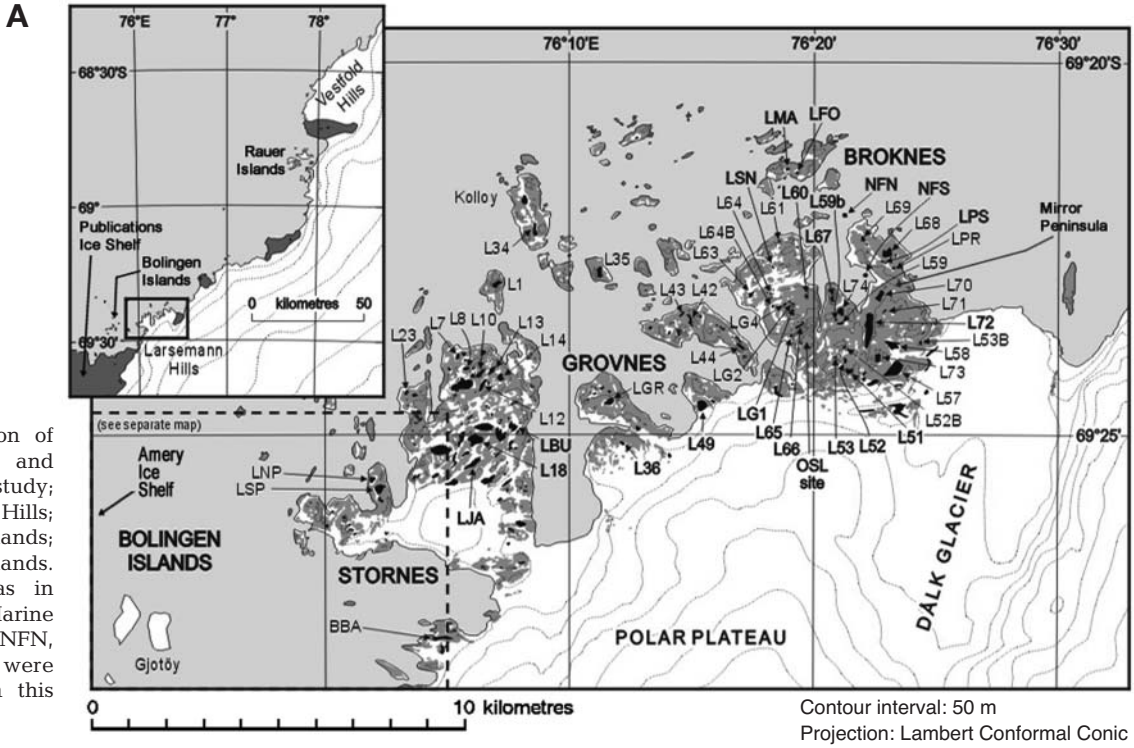

Fig. 1. Location of study regions and lakes in this study; (A) Larsemann Hills; (B) Bølingen Islands; (C) Rauer Islands. Lake codes as in Table 3. Marine sampling sites NFN, NFS and LNP were excluded from this study

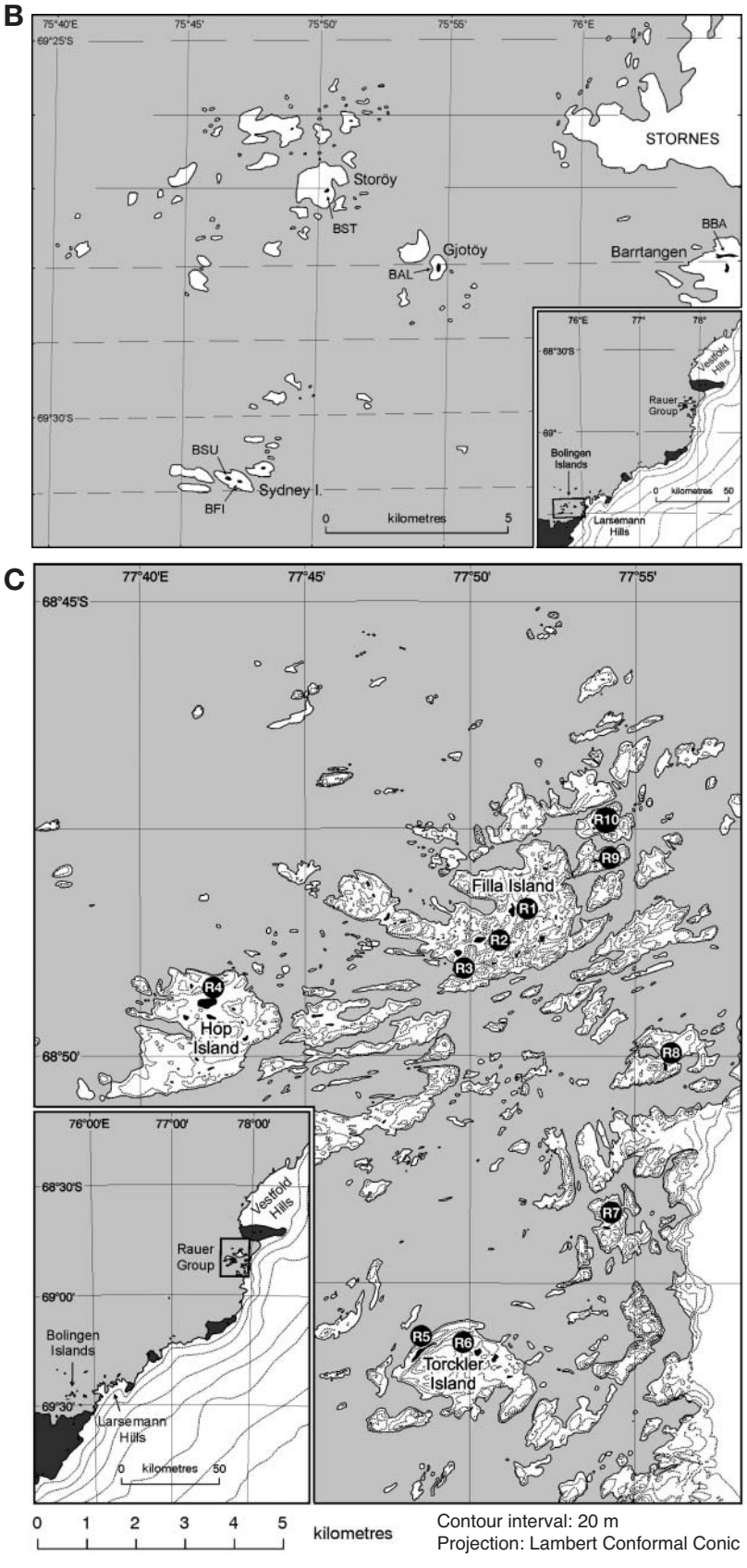

Fig. 1 (continued)

communities and their species composition (by morphological taxonomy). We then carried out statistical tests to explore the relationships between pigment composition and (1) physical and chemical environmental gradients; (2) gross mat morphology, and (3) cyanobacterial morphotypes.

MATERIALS AND METHODS

Study region. The Larsemann Hills (69° 23′ S, 76° 53′ E) is a 50 km^2 ice-free oasis in Prydz Bay, located approximately midway between the eastern extremity of the Amery Ice Shelf and the southern boundary of the Vestfold Hills (Fig. 1A). The Bølingen Islands comprise a small ice-free archipelago, 25 km to the W-SW of the Larsemann Hills (Fig. 1B), and the Rauer Islands an ice-free archipelago 90 km to the NE (Fig. 1C). Climatic conditions are typical for coastal continental eastern Antarctica. During December, January and February the daily air temperature frequently exceeds +4°C and has been known to reach +10°C (Gillieson et al. 1990). Mean monthly winter temperatures are between –15 and –18°C. Precipitation occurs as snow and is unlikely to exceed 250 mm water-equivalent annually.

More than 170 freshwater lakes and ponds occur in the study region, ranging from small ephemeral meltwater ponds to large water bodies such as Progress Lake (10 ha, 38 m deep). Lakes originated either in rock hollows exposed during the postglacial retreat of the continental ice cap (proglacial lakes) or following isolation of lake basins from the sea during postglacial isostatic recovery (isolation lakes) and were typically formed between 1500 and >40 000 radiocarbon yr before present (Hodgson et al. 2001a). For 8 to 10 mo of the year the lakes are covered with ca. 2 m of ice. Some are ice-free or partially ice-free in summer. The hydrology ranges from closed lakes (with no outflow) that accumulate salts through evaporation (Hodgson et al. 2001b), to open lakes (with active summer inflow and outflow streams) where freshwater is recharged during the summer melt. High solar irradiance is experienced in summer. Mini-

mal turbidity and extremely low concentrations of photoprotective dissolved organic matter (DOM) in the lake waters, give rise to low extinction coefficients (Kd) for photosynthetically active (PAR, Kd_{PAR} 0.18 to 0.47 m^{-1}), and ultraviolet, radiation (UVR, $Kd_{UVR\text{-}A}$ 0.21 to 0.28m^{-1}, $Kd_{UVR\text{-}B}$ 0.27 to 0.35 m^{-1}) (Ellis-Evans et al. 1998). Even in the deepest lakes, the presence of chlorophyll *a* in the benthic algae mats indicates sufficient euphotic PAR to support photosynthesis. In recent years, surface irradiance in the UVR wavelengths has increased as a result of depletion of stratospheric ozone by natural and anthropogenic mechanisms (Vincent & Pienitz 1996). Antarctic ozone depletion is most significant during spring and early summer when total atmospheric concentrations can decline by up to 40%. Fluxes of UVR-B (280 to 315 nm) have increased by 6 to 14% since 1980 and this increase is expected to persist until at least 2050 (WMO 2002). At the time of sampling, ozone column depth was 308 Dobson units (data from Total Ozone Mapping Spectrometer [TOMS] satellite over Zhong Shan station, Larsemann Hills, 19 December 1997) and melting was under way at the margins of some of the lakes. This post-dated the 1997 spring ozone column-depth minimum of 148.8 Dobson units on 19 October 1997. The wide range of light intensities experienced between the polar solstices (dark winters, light summers) and the elevated levels of UVR experienced in spring and early summer, resulting from the Antarctic ozone hole, make this an appropriate natural laboratory for examining factors influencing microbial mat pigment composition.

Cyanobacteria and algae are widely distributed in streams and wet seepage areas and occur in every lake (Ellis-Evans et al. 1998, Sabbe et al. 2004). In common with other shallow, oligotrophic, clear-water polar and high-altitude lakes, benthic phototrophs are often the most important primary producers (e.g. Vincent et al. 1993, Tang et al. 1997, Ellis-Evans et al. 1998). Mat-forming cyanobacteria are generally the major component of these communities (Vincent & Quesada 1994, James et al. 1995), while diatoms, green algae and xanthophytes are subdominant (Hamilton & Edlund 1994, Vézina & Vincent 1997). The success of the cyanobacteria is generally attributed to their tolerance to desiccation, freeze-thaw cycles, bright, continuous solar radiation (PAR, Tang et al. 1997) and defences against UVR damage (Vincent & Quesada 1994, Ehling-Schulz & Scherer 1999). Antarctic cyanobacteria occur in a number of macroscopically different mat morphologies and their distribution has been related to a suite of environmental factors, including depth, salinity, inorganic sedimentation, light, dissolved gas levels and alkalinity of the lake water (Wharton et al. 1983, Squyres et al. 1991, Ellis-Evans et al. 1998, Hawes & Schwarz 1999, Sabbe et al. 2004). Zooplankton grazers

Table 1. Environmental variables measured in this study and abbreviations used in ordination analyses. *: variables excluded from ordination analyses. NTU: nephelometer turbidity units

Environmental variable	Abbreviation
Longitude (°E)	East
Latitude (°S)	South
Altitude (m)	Alt
Lake area (ha)	Lake area
Catchment area (ha)	Catchment area
Depth (m)	z-max.
Distance from ice plateau (m)	Plateau
Distance from sea (m)	Sea
pH	pH
Alkalinity (meq l^{-1})	Alkalinity
NO_3+NO_2-N (µg l^{-1})	NO_3.NO_2
NO_2-N (µg l^{-1})	NO_2
NH_4-N (µg l^{-1})	NH_4
Silicate, Si (mg l^{-1})	Silicate
Dissolved reactive phosphorus, P (µg l^{-1})	Phosphate
O_2 (mg l^{-1})	O_2
Total N	*
Total P	*
O_2 (%)	*
Field salinity (ppm)	*
Turbidity (NTU)	Turbidity
Conductivity (µS cm^{-1})	Conductivity
Na (mg l^{-1})	Na
K (mg l^{-1})	K
Ca (mg l^{-1})	Ca
Mg (mg l^{-1})	Mg
Cl (mg l^{-1})	Cl
SO_4 (mg l^{-1})	SO_4
HCO_3 (mg l^{-1})	HCO_3
Total ions (mg l^{-1})	Ion sum
Total organic carbon, TOC (mg l^{-1})	TOC
Dissolved organic carbon, DOC (mg l^{-1})	DOC

Daphniopsis studerii occur in the water column of a few lakes at densities of no more than 1 specimen l^{-1}.

Fieldwork and water chemistry. We selected 62 lakes to represent variations in lake morphometry, hydrological characteristics and chemical gradients in the region (Gillieson et al. 1990, Ellis-Evans et al. 1998, Hodgson et al. 2001b, Sabbe et al. 2004). As part of a reference data set for palaeolimnological studies, a suite of 32 environmental variables was examined at each lake (Table 1). Alkalinity, pH, conductivity, salinity, oxygen and turbidity of water samples were measured on site. For field nutrient analysis (NH_4 and dissolved reactive phosphorus, DRP) 2 l of filtered (Whatman GF/C) water were analysed spectrophotometrically. Additional filtered water samples were frozen for laboratory determination of ion and nutrient chemistry. Nutrients (SiO_2, NO_3, total N and total P) were measured on an ALPKEM autoanalyser at the CSIRO laboratories in Hobart, Australia, following standard methods (Eriksen 1997). The anions chloride (Cl), sulphate (SO_4) and bicarbonate (HCO_3), the cations calcium (Ca), magnesium (Mg), sodium (Na) and potassium (K), total organic carbon (TOC) and dissolved organic

carbon (DOC) were measured at the Water Quality Laboratory, Faculty of Aquatic Science, Deakin University, Warnambool, Australia, using standard methods (Clesceri et al. 1998). Physical properties of the lakes and catchments were measured directly or extracted from GIS (Geographic Information Systems) data.

Biological sampling. Benthic microbial mats were collected from the deepest part of the ice-covered lakes using a Glew surface-sediment corer (Glew 1991), and the top 0.5 cm layer was sectioned-off accurately. In shallow ponds (<2 m deep and often ice-free) microbial mats were collected by wading through the littoral zone to sample the deepest-spot. The sampled layers included several years of mat growth and therefore accounted (as far as possible) for interannual variability. Phytoplankton (plus resuspended material) was collected by filtration (Whatman GF/C) of 2 l of water. Samples were frozen and stored in the dark. Pigments were extracted from thawed mat samples using acetone, methanol and water, 80:15:5 v.v. (Hodgson et al. 1997, Leavitt & Hodgson 2001) although our laboratories now recommend using just acetone to avoid allomerisation (Walker et al. 2002). Separation was achieved using Kromasystem 2000 HPLC with a Kontron pump, autosampler and diode array detector and a Waters Spherisorb ODS2 cartridge column (25 cm × 4.6 mm; 5 µm particle size) protected by a Phenomenex Guard cartridge (ODS2; 3 × 4.6 mm; 3 µm particle size). The 30 min gradient elution programme, using a solvent system comprising methanol, ammonium acetate, acetonitrile and ethyl acetate, has been described elsewhere (Method B: Wright et al. 1991). For complex mixtures of sedimentary pigments we now recommend a new high-resolution method (Airs et al. 2001). Pigments were calibrated to reference cultures following Scientific Committee for Oceanic Research (SCOR) protocols (Jeffrey et al. 1997) and expressed as organic matter-specific concentration (ng g^{-1} TOC) because comparisons of long-term monitoring of lake plankton with the resulting varved fossil record indicates that this metric most accurately captures variations in algal abundance and community composition (Leavitt & Findlay 1994, Leavitt et al. 1997). Pigments resolved by this method are listed in Table 2.

Table 2. Pigments identified in this study, abbreviations used in ordination analyses, HPLC retention times (Tr), and taxonomic affinities. Quantitatively important pigment sources indicated in **bold**. Note: diatoxanthin interconverts with diadinoxanthin; both are elements of xanthophyll cycle in chromophyte algae

Pigment	Abbrev	Tr (min)	Affinity
Chlorophylls			
Chlorophyll *a*	Chl a	20.97–21.57	**All Chlorophyta and Cyanophyta**
Pheophytin *a*	Phytin a	12.99, 20.68, 23–24	
Pheophorbide *a*	Phide a	22.96, 20.31, 6.07, 8.11–8.95	
Chlorophyllide *a*	Chlide a	12.18, 20.07, 24.4	
Chlorophyll *a* derivatives	Chl a der	7.3–7.5, 10.06–10.3, 19.8–21.8	
Chlorophyll *b*	Chl b	18.33	**Chlorophyta, Euglenophyta, higher plants**
Chlorophyllide *b*	Chlide b	7.58–7.69, 24.56	
Chlorophyll *b* derivatives	Chl b der	19.78	
Chlorophyll c1	Chl c1	6.39	Chromophyta algae
Chlorophyll c2	Chl c2	6.71	Chromophyta algae
Bacteriochlorophylls	Bchl	22.8	Anaerobic bacteria, including facultative
Scytonemins			
Scytonemin oxidised	Scyt ox	7.25	**Cyanophyta**
Scytonemin reduced	Scyt red	6.79	
Scytonemin derivatives	Scyt der	7.47	
Scytonemin oxidised derivatives	Scyt ox der	8.32	
Carotenoids			
Fucoxanthin	Fuco	9.87	**Bacillariophyta,** Chrysophyta
Fucoxanthin isomers	Fuco-is	10.56	
Diadinoxanthin	Diadinox	13.86	**Bacillariophyta, Chrysophyta**
Myxoxanthophyll	Myxo	14.33	**Cyanophyta**
Diatoxanthin	Diato	15.17	Bacillariophyta, Dinophyta, Chrysophyta
Antheraxanthin	Anth	15.89, 19.84	Chlorophyta
Lutein	Lut	16.19	**Chlorophyta**
Zeaxanthin	Zea	16.65-17.2	**Cyanophyta,** Chlorophyta
Nostoxanthin	Nostox	16.69	**Cyanophyta**
Echinenone	Echin	16.73	**Cyanophyta**
Canthaxanthin	Cantha	17.43	**Cyanophyta**
α-carotene	a-car	23.18	Chlorophyta
β-carotene	B-car	25.25	**Chlorophyta**, Chromophyta, some phototrophic bacteria, Cyanophyta

Taxonomic assignments. Live and formaldehyde-fixed benthic mats were examined using light microscopy. At each lake, 3 replicate preparations were examined for the presence or absence of cyanobacterial morphotypes. We examined 15 fields in detail at 2 different magnifications (500× and 1260×). In addition, the entirety of each preparation (±25 mm^2) was scanned for the presence of rare taxa. Cyanobacteria were identified to genus level, with reliable species identification only possible in a few genera because of the morphological simplicity of many organisms (thin filaments or small unicells) and/or the difficulty of observation in a complex, thick mat. Morphological diversity (presence/absence) was analysed in 43 of the 62 lakes where cyanobacteria were abundant. Diatom species compositions have been described elsewhere (Hodgson et al. 2001b, Sabbe et al. 2003).

Data analysis. Direct and indirect ordination analyses were carried using CANOCO 4.5 for Windows (ter Braak & Smilauer 2002). Prior to multivariate analyses, pigment data and all environmental variables except pH, latitude and longitude were log-transformed to reduce or remove skewness in the data. All analyses on the pigment data are based on absolute abundances. Major patterns of variation in the environmental data were explored using principal component analysis (PCA), with centring and standardisation of the variables. Detrended correspondence analyses (DCA), with detrending by segments, were used to determine the length of gradients in the pigment 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 further analyses (ter Braak & Smilauer 2002). Outlying samples were identified using PCA and DCA following the criteria of Hall & Smol (1992). Canonical correspondence analysis (CCA) with forward selection, and unrestricted Monte Carlo permutation tests (999 permutations, $p \leq 0.05$), were used to select the minimum number of environmental variables explaining the largest amount of variation in the species data. The relative contribution of individual environmental variables to the ordination axes was evaluated by canonical coefficients (significance of approximate *t*-tests) and intraset correlations (ter Braak & Smilauer 2002). Unrestricted Monte Carlo permutation tests (999 permutations, $p \leq 0.05$) were used to test the statistical significance of the first 2 ordination axes. CCA with forward selection was similarly used to select the cyanobacterial morphotypes significantly explaining the variance in cyanobacterial pigments in the subset of 43 lakes, with cyanobacterial morphotypes represented by presence–absence data. Redundancy analyses (RDAs) were carried out on the individual pigment groups to reveal the minimal set of environmental variables significantly explaining the variation in carotenoid, chlorophyll and scytonemin data. In order to evaluate the specific contribution of each significant variable, RDAs were run with the variables of interest as explanatory variables and the other significant vari-

Table 3. Lake locations and subset of environmental variables that had significant influence on pigment content of the benthic cyanobacterial mats in 1 or more analyses. Lake numbers are those used in ordination analyses; prefixes L, R, B: Larsemann Hills, Rauer Islands and Bølingen Islands respectively. Lakes have been grouped into 5 groups based on their depth. Mat-type definitions follow Sabbe et al. (2004): 1, finely laminated prostrate mats; 2, prostrate and 'lift-off' mats; 3, epilithic mats; 4, mat 'flakes'; 5, epipsammic mats; 6, epipsammic mats, Rauer Islands. Group average (AV) and standard deviation (SD) of each variable are given in **bold**. DRP: dissolved reactive phosporus; nd: not detected; –: no official name; x: taxonomic assignments of cyanobacterial morphotypes determined in these lakes

Lake No.	Lake name	Depth (m)	Mat type	Cyanobacteria analysed	Longitude (E)	Latitude (S)	Altitude (m)	Lake area (ha)	Catchment area (ha)	Alkalinity (meq l^{-1})	DRP - P (µg l^{-1})	O_2 (mg l^{-1})	Turbidity (NTU)	Conductivity (µS cm^{-1})	SO_4 (mg l^{-1})	TOC (mg l^{-1})	DOC (mg l^{-1})
L53b	–	0.5	4	x	76°23′	69°24′	40	0.5	7	0.1	nd	10.7	0	138	3.3	nd	nd
L61	–	0.5	4	x	76°19′	69°22′	50	0.5	6.2	nd	nd	10.9	–1	874	35.8	nd	nd
L52	Lake Bruehwiler	0.7	4	x	76°21′	69°24′	80	1	22.8	0.1	nd	10.7	–1	231	8.1	0.4	nd
L65	–	0.7	4	x	76°19′	69°24′	20	1	31.7	0.3	3.1	11.6	0	644	21	nd	nd
L64	–	0.7	4	x	76°18′	69°23′	55	0.5	14.4	0.1	3.1	10.6	–1	327	7.4	nd	nd
L58	Lake Sibthorpe	0.7	5		76°21′	69°24′	60	12.5	82	nd	nd	10.6	0	164	4.8	nd	nd
LPR	–	0.8	3		76°23′	69°23′	10	0.3	3.3	0.2	nd	10.6	0	882	nd	0.4	nd
LSN	–	0.8	4	x	76°18′	69°23′	50	0.2	5.1	nd	3.1	10.6	–1	124	6.7	nd	nd
L59b	–	0.8	5	x	76°21′	69°24′	20	0.3	4.9	0.9	nd	11	–1	1770	50	3.5	3.7
LG1	–	0.8	5	x	76°19′	69°23′	65	0.1	0.7	0.6	nd	11.2	0	1215	42	0.2	nd
LPS	–	1	4	x	76°23′	69°23′	10	0.4	5.7	nd	nd	10.4	–1	623	27.7	0.1	nd
L52b	–	1	4	x	76°21′	69°24′	80	0.5	6.3	0.1	nd	10.3	–0.7	265	9.2	nd	nd
LG2	–	1	4	x	76°19′	69°23′	65	0.3	1.5	0.1	nd	10.7	0	217	8.6	0.2	nd
LFO	–	1	5	x	76°20′	69°21′	30	0.3	2.3	0.2	3.1	10.4	–1	1088	34	0.4	nd
LMA	–	1	5	x	76°19′	69°21′	30	0.4	5.9	0.1	nd	10.4	–1	463	3.5	3.5	3.5
LG4	–	1	5		76°19′	69°23′	65	0.4	2.7	0.2	nd	11.1	–1	536	25.8	2.6	nd

Table 3 (continued)

Lake No.	Lake name	Depth (m)	Mat type	Cyanobacteria analysed	Longitude (E)	Latitude (S)	Altitude (m)	Lake area (ha)	Catchment area (ha)	Alkalinity (meq l^{-1})	DRP - P (µg l^{-1})	O_2 (mg l^{-1})	Turbidity (NTU)	Conductivity (µS cm^{-1})	SO_4 (mg l^{-1})	TOC (mg l^{-1})	DOC (mg l^{-1})
L64b	–	1	5	x	76°18′	69°23′	50	0.1	1.5	0.2	3.1	11.5	1	672	3.8	nd	nd
R4		1	6		77°42′	68°53′	2	6.64	89.06	3.51	0.62	8.37	3.88	107.7	8630	23.2	8.8
R6		1	6		77°51′	68°53′	15	1.953	65.62	3.59	0.93	8.5	6.34	130.3	15940	nd	nd
R8		1	6	x	77°56′	68°50′	18	1.094	13.67	1.58	0.62	9.11	0.98	6.26	1040	nd	nd
AV		**0.9**					**40.8**	**1.4**	**18.6**	**0.7**	**2.2**	**10.5**	**0.1**	**523.9**	**1363.2**	**3.5**	**6.3**
SD		**0.2**					**24.4**	**3.0**	**27.4**	**1.2**	**1.2**	**0.9**	**1.9**	**457.1**	**4043.8**	**7.1**	**3.6**
BFI	Firelight Lake	1.5	4		75°45′	69°31′	30	0.9	5.6	1.8	195.3	9.4	2	4740	50	21.5	19
R7		1.5	6		77°54′	68°52′	15	1.094	10.547	3.92	2.48	9.4	1.31	28.4	8420	nd	nd
R9		1.5	6		77°54′	68°48′	8	1.016	7.5	1.63	0.93	9.36	2.52	15.3	1780	nd	nd
R10		1.5	6		77°54′	68°47′	30	0.937	10.55	1.15	0.31	9.78	2.55	3.5	280	nd	nd
BSU	Sunset Lake	1.8	5	x	75°45′	69°31′	10	1.1	12.6	0.5	3.1	17	1	963	27	14.2	13.8
LJA	Lake Jack	2	2	x	76°06′	69°25′	85	4.2	39	0.1	nd	11.3	0	117	3.8	nd	nd
AV		**1.6**					**29.7**	**1.5**	**14.3**	**1.5**	**40.4**	**11.0**	**1.6**	**977.9**	**1760.1**	**17.9**	**16.4**
SD		**0.2**					**28.8**	**1.3**	**12.4**	**1.3**	**86.6**	**3.0**	**1.0**	**1880**	**3333.4**	**5.2**	**3.7**
L66	–	2.3	4	x	76°20′	69°24′	25	2.5	26.3	0.6	nd	11.4	0	1032	29	nd	nd
L71	Sarah Tarn	2.5	2	x	76°23′	69°23′	75	1	5.7	13.2	3.1	1.6	5	28000	480	16.9	16.9
BST	–	2.5	3		75°50′	69°27′	20	0.8	7.2	0	nd	9.7	2	77	nd	nd	nd
R3		2.5	6		77°49′	68°49′	3	1.875	16.406	2.79	nd	8.99	2.37	115.2	490	8.82	nd
R2		3	6		77°51′	68°48′	10	2.53	25.39	2.42	0.93	9.68	2.33	131.5	2790	5.19	nd
L63	–	3.3	2	x	76°18′	69°23′	60	1	25.2	0.1	nd	12.4	5	375	13.8	nd	nd
L49	–	3.5	2	x	76°16′	69°24′	30	2	24.3	0.1	nd	10.8	5	86	nd	nd	nd
L59	Moore Lake	3.8	2	x	76°21′	69°24′	20	1.5	48.8	0.4	nd	17.8	1.8	590	3.3	0.2	nd
L69	No Worries Lake[a]	3.8	2		76°23′	69°22′	10	2.5	27.3	0.5	6.2	6.8	2	976	44	0	nd
L70	Lake Reid	3.8	2	x	76°23′	69°23′	30	5.5	19.6	7.2	6.2	1.3	12	9160	105	14.6	12.9
L74	Discussion Lake	4	2	x	76°22′	69°23′	5	2	74.8	0.3	nd	11.4	4.7	680	30.6	nd	nd
BAL	Lake Alanna	4	2		75°55′	69°28′	20	1.6	7.4	2.9	nd	4.7	4	2650	15	8.8	8.7
L73	–	4	2	x	76°23′	69°24′	85	3.5	18.2	nd	nd	9	–1	175	4.8	0.3	nd
R5		4	6		77°49′	68°53′	2	4.297	43.75	4.18	1.24	8.56	1.65	93.6	6650	nd	nd
AV		**3.4**					**28.2**	**2.3**	**26.5**	**2.7**	**3.5**	**8.9**	**3.3**	**3153**	**888.0**	**6.9**	**12.8**
SD		**0.7**					**26.6**	**1.3**	**18.7**	**3.8**	**2.6**	**4.3**	**3.1**	**7538.6**	**1977.8**	**6.6**	**4.1**
L7	–	4.5	2		76°05′	69°09′	25	2.5	12.9	0.1	nd	10	3	362	nd	nd	nd
L68	Heart Lake	4.5	2	x	76°23′	69°23′	5	5	57.8	0.3	nd	7.1	0.7	1620	80	0.1	nd
L23	Pup Lagoon	4.6	2	x	76°03	69°25′	5	1	7.8	0.2	3.1	7.6	–1	1080	55	2.4	2.5
L14	–	4.7	2	x	76°07′	69°24′	60	5.5	7.1	1.4	3.1	4.8	7.7	1383	9.5	4.8	4.8
L8	–	4.8	2	x	76°05′	69°09′	5	4.8	10.7	0.2	nd	10.9	5.3	365	16.6	nd	nd
L13	–	4.8	2	x	76°07′	69°24′	75	5	4.7	0.8	nd	8.1	4.7	839	nd	nd	nd
L67	–	5	2	x	76°21′	69°23′	45	4.5	6.3	0.9	nd	10.3	2	1730	60	2.7	2.5
L10	Lake Heidi	5	2	x	76°06′	69°24′	60	7.5	12.1	0.2	3.1	12	1.3	345	12	nd	nd
L60	–	5.4	2	x	76°20′	69°23′	45	1.5	23.9	0.5	nd	8.1	8	930	30	nd	nd
AV		**4.8**					**36.1**	**4.1**	**15.9**	**0.5**	**3.1**	**8.8**	**3.5**	**961.6**	**37.6**	**2.5**	**3.3**
SD		**0.3**					**27.0**	**2.1**	**16.7**	**0.4**	**0.0**	**2.2**	**3.1**	**539.4**	**27.5**	**1.9**	**1.3**
L43	–	6.5	2	x	76°15′	69°23′	10	2.5	9.9	0.9	nd	7.5	0	585	21.2	3.1	nd
R1		7	6		77°52′	68°48′	10	7.03	33.98	1.79	0.62	9.61	2.18	128.5	1730	nd	nd
L51	Lake Cameron	7.6	1		76°21′	69°24′	85	2.5	17.3	0.3	nd	11.4	–1	520	12.4	nd	nd
L1	Lake Anna	7.6	2	x	76°17′	69°23′	100	2.5	13.5	3	nd	6.1	1.3	4020	27	2.4	nd
L44	–	7.7	2	x	76°17′	69°24′	45	3	9.6	4.6	nd	8.2	0	4200	42	3.4	nd
LSP	–	8.8	3	x	76°02′	69°25′	5	5	7	0.1	nd	11.5	4.8	320	14.8	nd	nd
L34	Kirisjes Pond	9	1	x	76°09′	69°22′	5	12	16.5	0.1	3.1	12.2	19.3	405	14.8	nd	nd
L12	Long Lake	11	1		76°07′	69°24′	80	5	8.7	0.1	6.2	12.2	11.3	173	4.8	nd	nd
L18	Lake Spate	11	2	x	76°07′	69°25′	85	9	20.7	0.3	nd	11.1	0	372	11.1	nd	nd
L42	–	11	3	x	76°15′	69°23′	25	4	13.5	4.2	nd	8.4	0	2360	60	1.6	1.5
L35	Crater Lake	12	1		76°11′	69°23′	30	3.2	9.3	0.6	6.2	11	7.7	2780	75	2	2
L36	–	15	1		76°13′	69°25′	60	5.5	17.6	0.4	3.1	11	0	244	10.2	nd	nd
BBA	–	15	1	x	76°05′	69°27′	10	2.8	12.6	0.1	nd	11.6	0.3	56	nd	nd	nd
LBU	Lake Burgess	16	1	x	76°07′	69°25′	40	4	15	0.1	nd	11.5	–1	182	5.3	0.2	nd
LGR	–	16	2	x	76°11′	69°24′	50	3.5	7	2	nd	10.7	–1	3060	195	0.2	nd
L72	Lake Nella	18	1	x	76°22′	69°24′	15	13	259	nd	3.1	15.6	–1	85	nd	nd	nd
L57	Progress Lake	34	1		76°24′	69°24′	65	10.5	39.1	0.1	nd	11.1	0	320	8.3	nd	nd
AV		**12.5**	**av**				**42.4**	**5.6**	**30.0**	**1.2**	**3.7**	**10.6**	**2.5**	**1165.3**	**148.8**	**1.8**	**1.8**
SD		**7**	**sd**				**32**	**3**	**60**	**2**	**2**	**2**	**6**	**1472**	**440**	**1**	**0**

[a]Unofficial name, but used in other published studies

Table 4. Summary of pigment data (ng g^{-1} TOC) including pigments occurring in more than 2 of the study lakes organised in 5 groups based on lake depth as in Table 3. Bacteriochlorophylls are excluded as they are incompletely resolved by SCOR method. Note: zeaxanthin occurs in both cyanobacteria and green algae. Abbreviations as in Table 2. Group average (AV) and standard deviation (SD) of each variable are given in **bold**. Unkcars: unknown carotenoids

Lake	Chlorophylls		Green algae carotenoids					Cyanobacteria						
No.	Chl *a*	Chl *b*	Diato	Fuco	Lut	Diadinox	Anth	Zea	Echin	Myxo	Cantha	B-car	Unkcars	Scyto
L53b	17.73	0	1.15	8.31	0	0	0	0	7.67	10.95	3.7	16.51	0	255.42
L61	261.77	0	4.66	8.72	4.76	0	0	2.86	63.96	140.89	45.75	2.88	0	673.54
L52	35.31	0	2.62	0.17	0	0	0	0.2	11.64	9.71	10.05	1.44	4.16	24.68
L65	154.69	0	5.06	5.61	0	0	0	8.32	49.05	35.48	37.45	15.45	0	341.34
L64	31.59	0	0	0	0	0	0	0.83	10.92	55.08	24.72	1.09	0	288.02
L58	31.63	0	1.02	1.22	0.21	0	0	1.05	4.38	1.43	4.14	1.67	0	108.78
LPR	127.77	0	0	1.28	0	0	0	0	13.7	0	0	19.33	0	265.67
LSN	69.28	0	0.89	0.95	0.83	0	0	1.03	22.87	8.54	8.35	4.11	16.79	71.07
L59b	2.8	0	0.43	0.1	0	0	0	0.45	2.58	0.88	1.68	0.34	0.39	2.64
LG1	7.42	0	0	0	0	0	0	0	8.69	1.38	5.47	1.93	5.16	0.35
LPS	111.52	4.72	4.4	98.88	0	0	0	3.48	54.41	48.68	12	29.42	0	70.06
L52b	72.12	0	1.39	16.71	0	0	0	0	39.66	1.75	12.79	24.2	0	679.95
LG2	3.18	0	0	0	0	0	0	0	1.38	0	1.18	0.67	0.35	90.21
LFO	38.66	5.24	0.44	2.62	0	0	0	1.03	6.51	8.81	3.2	10.27	0	31.89
LMA	21.28	0	0	3.78	0	0	0	0	15.73	16.23	8.77	12.9	0	6.65
LG4	0.05	0	0	0	0	0	0	0.19	0.09	0	0	0	0	1.09
L64b	0	0	0	0	0	0	0	0	0	0	0	0	0	347.73
R4	272.81	0	6.58	27.31	0	0	0	0	0	0	0	0	0	5667.84
R6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
R8	171.82	0	1.42	9.69	3.74	0	0	4.82	28.78	10.42	13.12	21.65	9.85	22.71
AV	**71.6**	**0.5**	**1.5**	**9.3**	**0.5**	**0.0**	**0.0**	**1.2**	**17.1**	**17.5**	**9.6**	**8.2**	**1.8**	**447.5**
SD	**85.3**	**1.5**	**2.0**	**22.2**	**1.3**	**0.0**	**0.0**	**2.1**	**19.8**	**33.3**	**12.7**	**9.7**	**4.3**	**1246.6**
BFI	48.57	21.26	16.39	4.89	29.11	6.33	2.05	56.6	7.22	0	6.86	7.25	8.67	12.31
R7	36.63	0	1.26	18.01	0.89	5.83	0	0.95	0.53	17.69	0.4	0.4	0	0.58
R9	136	0	5.93	0	1.4	8.99	0	1.23	12.66	0	0	0.73	14.3	324.69
R10	0	0	0	0	0	0	0	0	0	0	0	0	0	132.77
BSU	21.91	11.26	0.48	0.34	4.29	0.87	1.37	2.77	3.41	2.07	0	1.34	1.17	1.09
LJA	22.99	0	0.61	0.03	0.31	1.25	0	0.67	4.3	6.97	0	0.57	2.21	7.04
AV	**44.4**	**5.4**	**4.1**	**3.9**	**6.0**	**3.9**	**0.6**	**10.4**	**4.7**	**4.5**	**1.2**	**1.7**	**4.4**	**79.7**
SD	**47.8**	**9.0**	**6.4**	**7.2**	**11.4**	**3.7**	**0.9**	**22.7**	**4.7**	**7.0**	**2.8**	**2.7**	**5.8**	**130.5**
L66	30.14	0	1.71	4.22	0	0	0	2.09	7.71	10.15	9.13	0.62	0	1.63
L71	11.34	0.78	0.2	2.57	0.5	0	0	0.93	3.05	1.26	0.44	0.47	0.3	0
BST	0	0	0	0	0	0	0	0	0	0	0	0	0	0
R3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
R2	440.65	133.83	0	13.86	0	0	0	0	55.48	0	0	0	0	52.61
L63	42.43	0	0	0.54	4.09	0	0	0	4.63	0	0	0	0.09	0
L49	95.46	0	8.5	5.96	5.67	0	0	9.16	23.89	12.74	10.81	13.39	0	0
L59	9.45	0	0	1.14	0.84	0	0	0.86	3.82	0	0	7.76	0	0.62
L69	424.32	496.9	138.19	13.9	37.55	0	0	3.39	16.7	0	0	96.3	5.31	0
L70	53.69	3.59	0	1.23	4.96	0	0	5.73	9.19	2.3	0	7.3	0	0.99
L74	15.95	0	0	2.35	0.42	0	0	0	1.2	0	0	6.12	0.11	0.56
BAL	20.14	5.36	0.62	0.22	2.23	0	2.19	4.83	2.6	0	0	11.32	1.13	0
L73	19.53	0.82	2.01	1.9	1.08	0	0	0.33	0.43	0.42	0	11.67	0	0
R5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AV	**83.1**	**45.8**	**10.8**	**3.4**	**4.1**	**0.0**	**0.2**	**2.0**	**9.2**	**1.9**	**1.5**	**11.1**	**0.5**	**4.0**
SD	**150.3**	**134.6**	**36.7**	**4.8**	**9.8**	**0.0**	**0.6**	**2.8**	**15.0**	**4.1**	**3.6**	**25.0**	**1.4**	**14.0**
L7	19.01	0	0	0.46	1.38	0	0	0	5.01	2.14	0	7.69	0	0
L68	6.68	0.26	0.35	16.77	0.91	0	0	2.02	0.52	2.74	0	0.17	6.74	2.67
L23	77.52	0.84	6.55	0.82	6.03	0.48	0	2.96	5.41	0	0	32.62	0	0
L14	7.18	0	0.62	0.32	0.32	0	0.72	0.43	0.61	0	0	1.71	0	0
L8	17.06	0	0	0.26	0.12	0	0	0	5.64	0.33	0	7.07	0	0
L13	31.61	0	0.99	2.15	0.22	0	0	1.01	4.05	3.74	0	1.15	1.99	0
L67	15.42	0	0	0.08	1.12	0	0	0.73	3.55	0	0.48	0.23	0.19	0
L10	5.51	9.83	0	2.45	0	0	0	0	0	0	0	1.99	0.67	2.01
L60	35.02	2.41	0.81	0.74	4.42	0	0.73	10.72	1.98	6.68	0	1.25	1.39	0
AV	**23.9**	**1.5**	**1.0**	**2.7**	**1.6**	**0.1**	**0.2**	**2.0**	**3.0**	**1.7**	**0.1**	**6.0**	**1.2**	**0.5**
SD	**22.7**	**3.2**	**2.1**	**5.4**	**2.1**	**0.2**	**0.3**	**3.4**	**2.2**	**2.3**	**0.2**	**10.4**	**2.2**	**1.0**

Table 4 (continued)

Lake No.	Chlorophylls		Green algae carotenoids					Cyanobacteria						
	Chl *a*	Chl *b*	Diato	Fuco	Lut	Diadinox	Anth	Zea	Echin	Myxo	Cantha	B-car	Unk cars	Scyto
L43	26.82	0	0	0.21	0.52	0	0	0.76	9.44	1.39	0	7.84	0	0
R1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L51	19.21	0	0	0	0.21	0	0	0	14.29	0	0	12.32	0	0
L1	3.48	0.1	1.04	5.24	0.69	0	0	0.19	0.24	3.66	0.79	0.11	0	0.23
L44	9.83	0	1.9	0	0.26	0	0	0.14	0.74	0	0	2.15	0	0
LSP	30.41	0	5.64	2.35	0.69	0	0	0	0	0	0	0	0.44	0
L34	127.94	0	0	0.2	23.91	0	0	1.72	13.06	0	0	46.58	0	0
L12	3.93	0	0.27	0	0.09	0	0	0	0	0	0	0	0	0
L18	24.09	0	0	0.06	0.8	0	0	0.66	5.87	0.44	0.77	8.27	0	0
L42	13.59	0	0	0.65	0	0	0	0	0.48	0	0	0.45	0	0
L35	22.26	0	0	0.03	0	0	0	0	0	0	0	0.25	0	0
L36	15.27	0	2.38	0.25	0.47	0	0	0	0	0	0	0.6	0	0
BBA	11.83	7.71	0.1	4.4	0.49	1.16	0	1.87	0.8	1.49	0.32	0.76	5.23	0
LBU	51.27	0	0.18	0.99	5.16	0	0	2.68	9.85	0	0	23.84	0	0
LGR	9.47	0	0	0.83	0.1	1.16	0	0.43	2.7	0	0	3.02	0	0.19
L72	5	0.81	0	0.11	0	0	0	0	0.94	0	0	1.24	0	0.58
L57	35.79	3.47	0	1.21	5.52	0	0	1.4	0	0	0	0	0	0
AV	**24.1**	**0.7**	**0.7**	**1.0**	**2.3**	**0.1**	**0.0**	**0.6**	**3.4**	**0.4**	**0.1**	**6.3**	**0.3**	**0.1**
SD	**29.9**	**2.0**	**1.5**	**1.6**	**5.8**	**0.4**	**0.0**	**0.8**	**5.0**	**1.0**	**0.3**	**12.1**	**1.3**	**0.2**

ables as covariables (Borcard et al. 1992). Correlations were calculated and tested for significance (p-value) using STATISTICA 5.5. Analyses of variance (ANOVA), were carried out in MINITAB 13.1.

RESULTS

Statistical analyses identified a subset of environmental variables that had a significant influence on the pigment content of the benthic cyanobacterial mats (Tables 3 & 4).

Physical and chemical environmental gradients

PCA revealed that the main environmental gradient (first ordination axis) is associated with conductivity, alkalinity, carbon content (DOC/TOC), silicate and phosphate (Fig. 2). The second PCA axis includes

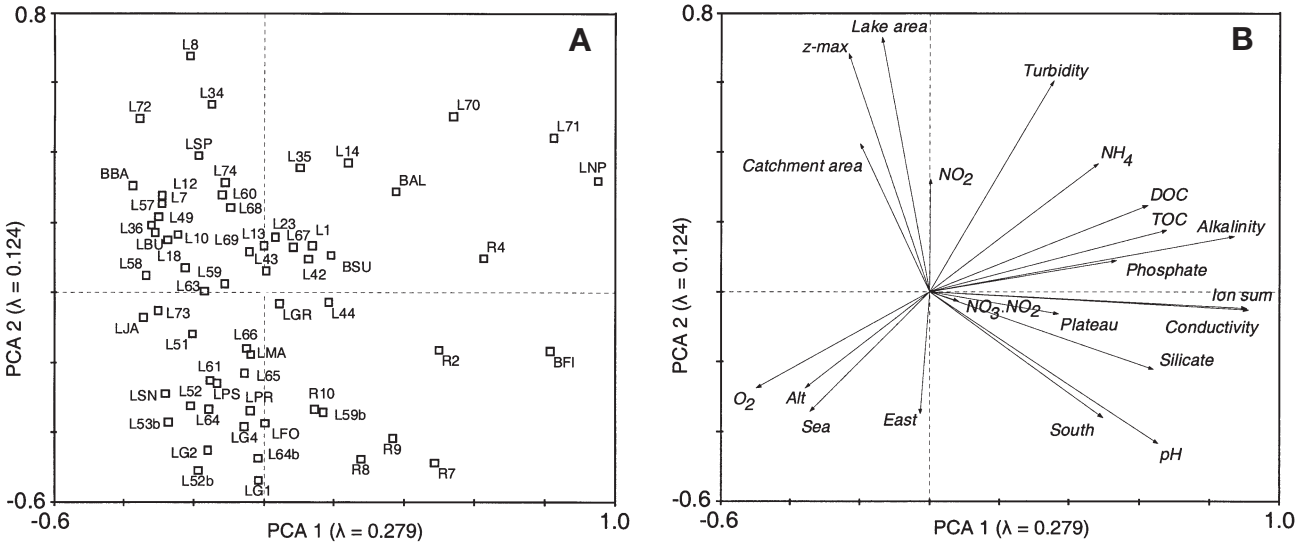

Fig. 2. Principal component analysis (PCA) (with centring and standardisation) of (A) physical and (B) chemical characteristics of lakes. Individual ion concentrations were omitted from analysis as all are significantly intercorrelated with conductivity. Lake codes are given in Table 3, codes for environmental variables in Table 1

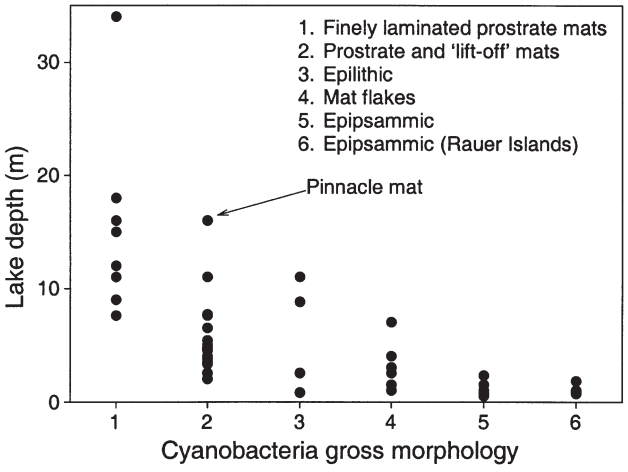

Fig. 3. Distribution of gross morphologies of benthic microbial communities plotted against lake-depth

gradients associated with lake morphometry (depth, area and catchment size) and turbidity. Together, the first 2 axes capture 40.3% of the total variance.

Gross morphology of microbial mat communities

Microscopically the mats consisted of matrices of filamentous cyanobacteria with interstices occupied by colonial cyanobacteria, green algae and diatoms. A number of macroscopically recognisable mat types (growth forms) occurred in lakes of different depths (Fig. 3). These included finely laminated prostrate mats generally restricted to deeper parts of lakes (>7 m), less structured prostrate mats, and 'lift-off' mats, which occurred between 2 and 16 m. The less-structured prostrate mats are a result of individual cyanobacterial colonies competing to occupy the optimum light conditions at the mat surface, thereby breaking the continuous filamentous structures seen in the deeper lakes. These can form concentric colonies, previously described as 'dinner-plate mats' (Ellis-Evans et al. 1998). Cyanobacteria colonies may also 'lift-off', as a result of trapped gases, and colonise the underside of the lake ice in winter. In one lake (LGR), pinnacle mats were observed with a calcite interior, an outer layer dominated by carotenoids and scytonemins and, beneath this, a layer dominated by chlorophylls. Mat flakes, consisting of small, unattached (0.5 to 2 cm) fragments of cyanobacteria mats and colonies, were confined to lakes less than 2.3 m deep. Epipsammic cyanobacteria communities, comprising an organic matrix embedded within an inorganic sediment (mean 78.6% inorganic, range 32 to 99%) were only observed in shallow ponds (<1.8 m) and lakes, including saline ponds in the Rauer Islands. These macroscopically recognisable mat types show a significant relationship with lake depth ($F = 49.15$, $p < 0.005$, 1-way ANOVA generalised linear model, GLM) and significant differences between the depth distributions of mat flakes and finely laminated prostrate mats ($p = 0.0301$, post-hoc Tukey simultaneous test).

Cyanobacterial morphotypes

Morphological and morphometric characteristics were used to define morphotypes of unicellular taxa and the filamentous genera *Leptolyngbya* and *Schizothrix* (listed in Table 5). We defined as *Leptolyngbya* spp., morphotypes belonging to the order Oscillatoriales for which the cell width was smaller than 2.5 µm, except for the genus *Schizothrix* which was characterised by the presence of several trichomes in the same sheath. Representative morphotypes are illustrated and described in Sabbe et al. (2004). Further genotypic characterisation of uncultured cyanobacterial diversity using clone libraries and of representative strains in culture is being undertaken and will be published elsewhere (A. Taton et al. unpubl.).

Table 5. List of cyanobacterial morphotypes and abbreviations used in ordination analyses. Representative morphotypes are illustrated in Sabbe et al. (2004)

Morphotype	Abbrev.	Morphotype	Abbrev.
Asterocapsa sp.	ASru	*Leptolyngbya* sp. 8	Lpp08
Calothrix sp.	CAs1	*Lyngbya* sp.	LYs1
Chamaesiphon cf. *subglobosus* (Rostaf.) Lemmermann	CMsu	*Nostoc* sp.	Nos
Chondrocystis cf. *dermochroea* (Näg.) Komarék & Anagnostidis	CHde	*Oscillatoria* sp.	OSs1
Coleodesmium cf. *scottianum* Welsh	COsc	*Petalonema* cf. *involvens* (A. Br.) Migula	PEin
Dichothrix sp.	DIsp	*Schizothrix* sp. 1	SCs1
Gloeocapsa cf. *alpina* Näg. Emend. Brand	GLal	*Schizothrix* sp. 2	SCs2
G. cf. *sanguinea* (Agardh) Kützing	GLsa	*Schizothrix* sp. 3	SCs3
G. cf. *compacta* Kützing	GLco	Unicellular sp. 1	U01
Leptolyngbya sp. 1	Lpp01	Unicellular sp. 2	U02
Leptolyngbya sp. 2	Lpp02	Unicellular sp. 3	U03
Leptolyngbya sp. 3	Lpp03	Unicellular sp. 4	U04
Leptolyngbya sp. 4	Lpp04	Unicellular sp. 5	U05
Leptolyngbya sp. 5	Lpp05	Unicellular sp. 6	U06
Leptolyngbya sp. 6	Lpp06	Unicellular sp. 7	U07
Leptolyngbya sp. 7	Lpp07	Unicellular sp. 8	U08
		Unicellular sp. 9	U09

Pigment composition of the lakes

Water-column pigments were present in trace quantities, typically lower than 14 ng l^{-1}, representing either a poorly developed planktonic flora and/or resuspended particulates from the benthos. The composition was dominated by chlorophyll *a* and scytonemin, with sporadic occurrences of pigments from green algae and cyanobacteria. The presence of scytonemin in the water column is unusual, as scytonemin-containing cyanobacteria are not typically reported in planktonic environments (Castenholz & Garcia-Pichel 2000). This suggests that resuspension of benthos is taking place, resulting from wind action in those lakes that had melted out or moated (drilling through the lake ice may also have disturbed under-ice communities). In the shallowest lakes, mats are seasonally disturbed by ice-working (freezing of lake ice to the bottom), and are broken up, resulting in benthic material being entrained into the water column. Often the larger particles (mat flakes) are blown onto the leeward side of the lakes during open-water periods or when moats are present. Cyano-

Table 6. Correlation matrix between carotenoid and scytonemin data (excluding non-cyanobacterial pigments) with cyanobacterial morphotypes. Morphotype correlation values underlined significantly explain ($p \leq 0.05$) part of the total variance in pigment data as revealed by CCA. Abbreviations as in Table 5

Morphotype	Scytonemin	Myxoxanthophyll	Canthaxanthin	Zaxanthin isomer 1	Zeaxanthin isomer 2	Echinenone isomer 1	Echinenone isomer 2	Unknown carotenoid derivative 1	Unknown carotenoid derivative 2	Unknown carotenoid derivative 3
Unicellular cyanobacteria										
U01	0.3201 p = 0.036	0.4143 p = 0.006	0.4778 p = 0.001	–	–	–	–	–	–	–
U02	0.4693 p = 0.001	–	–	–	–	–	–	–	–	–
U03	−0.3172 p = 0.038	0.3145	– p = 0.040	–	–	–	–	–	–	–
U05		–	–	–	–	–	–	0.3729 p = 0.014	–	–
U09	0.7079 p ≤ 0.0001	–	–	–	–	–	–	–	–	–
Colonial cyanobacteria										
CHde	0.6497 p ≤ 0.0001	–	0.4476 p = 0.003	–	–	–	–	–	–	–
GLco	0.3135 p = 0.041	–	–	–	–	–	0.5411 p ≤ 0.0001	–	–	–
GLal	0.3721 p = 0.014	–	–	–	–	–	–	–	–	–
GLsa	0.3721 p = 0.014	–	–	–	–	–	–	–	–	–
ASru	0.5089 p ≤ 0.0001	–	–	–	–	–	–	–	–	–
CMsu		–	–	–	–	–	–	–	0.4021 p = 0.008	–
Filamentous cyanobacteria										
Lpp02	–	–	–		–	–	0.3685 p = 0.15	–	–	–
Lpp03	–	–	–	0.3215 p = 0.036	–	–	–	–	–	0.3986 p = 0.008
Lpp04	–	–	–	0.3199 p = 0.037	–	–	–	–	–	0.8537 p ≤ 0.0001
Lpp05	–	–	–	–	–	0.3499 p = 0.21	–	–	–	–
Lpp06	–	–	–	0.3434 p = 0.024	–	–	–	–	–	–
LYs1	–	–	–	–	–	–	–	–	0.3607 p = 0.017	–
SCs1	0.3588 p = 0.018	–	0.3166 p = 0.039	–	–	–	–	–	–	–
SCs3	0.4957 p = 0.001	–	–	–	0.3412 p = 0.025	–	–	–	–	–
DIsp	0.6202 p ≤ 0.0001	–	–	–	–	–	–	–	–	–
COsc	0.3155 p = 0.039	–	–	–	–	0.5634 p ≤ 0.0001	–	–	0.4445 p = 0.003	–
PEin	0.391 p = 0.01	–	–	–	–	–	–	–	–	–

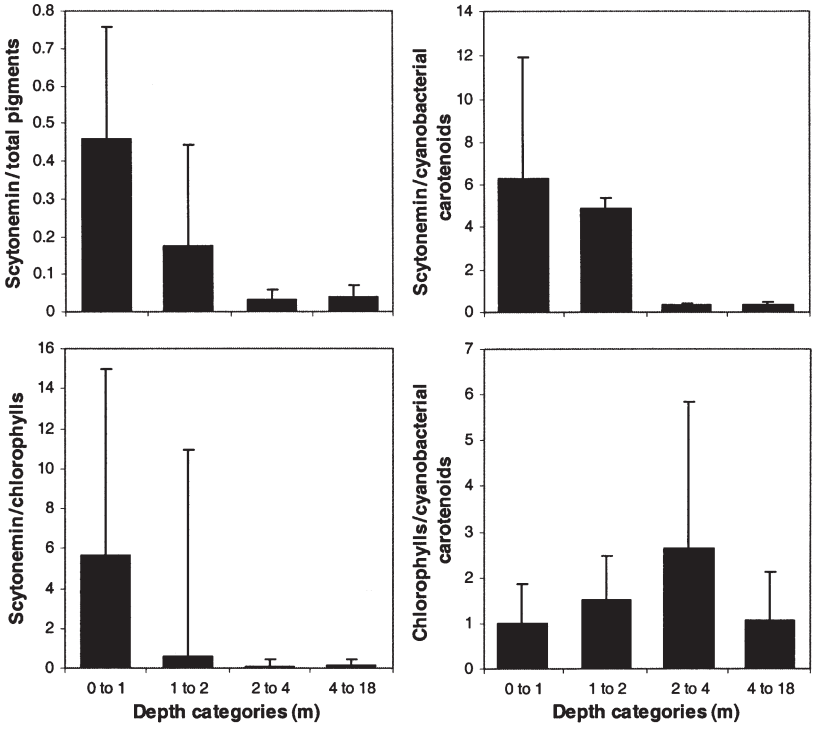

Fig. 4. Mean (+SD) pigment ratios in aggregated lake-depth categories

clude heterotrophic bacteria and dinoflagellates (e.g. *Gonyaulux* spp.), together with resuspended pennate diatoms in the shallower lakes (Ellis-Evans et al. 1998). On account of the low concentrations of pigments in the water column, no further statistical analyses were carried out.

Most benthic microbial mat samples contained a mixture of chlorophylls, carotenoids and scytonemins (Tables 5 & 6). Scytonemin, in both oxidised (yellow-green) and reduced (red) forms, together with some derivatives, was most abundant in lakes between 0 and 2 m depth and was absent or rare in lakes over 4 m depth (Table 4, Fig. 4). Of the 36 samples containing scytonemin, only 4 were at depths of greater than 5 m indicating that the 2 to 4 m threshold, below which the major synthesis of scytonemin occurs, is an important ecological boundary. Cyanobacterial carotenoids were, on average, in slightly higher concentrations in intermediate depth lakes (2 to 10 m depth). Chlorophyll *a* concentrations were relatively high, compared with all other pigments, in the deeper lakes (>4 m depth). Chlorophyll *b* (from the green algae) was less abundant, with the exception of 2 lakes (R2, L69) in the 2 to 4 m category. Ratios of all major pigment groups suggest that pigment content is related to lake depth (Fig. 4).

bacterial pigments may, however, originate from small single-celled planktonic cyanobacteria. Other plankton previously recorded in the Larsemann Hills lakes in-

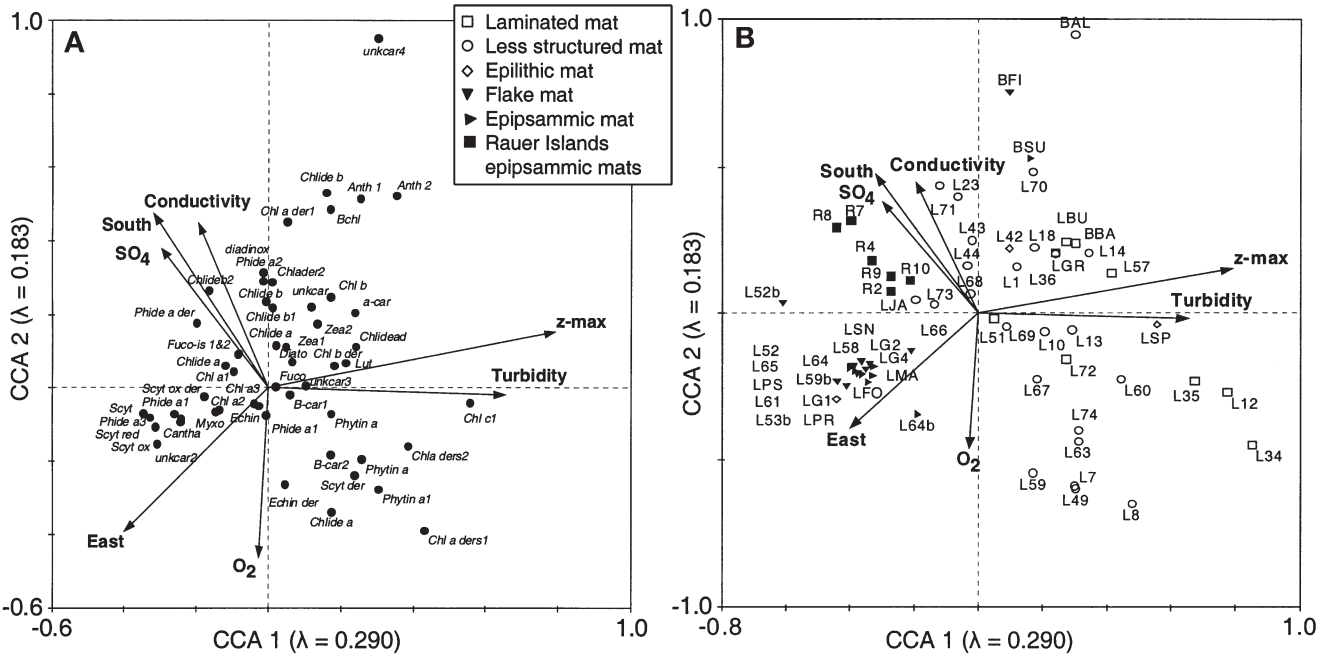

Fig. 5. Canonical correspondence analysis (CCA) of pigment data. (A) Pigments and significant environmental variables and (B) lakes, gross morphologies of mats and significant environmental variables. Gross morphologies of mats in Fig. 3 are indicated by symbols in key. Unkcar: unidentified carotenoid derivatives; other pigment abbreviations as in Table 2; lake codes as in Table 3

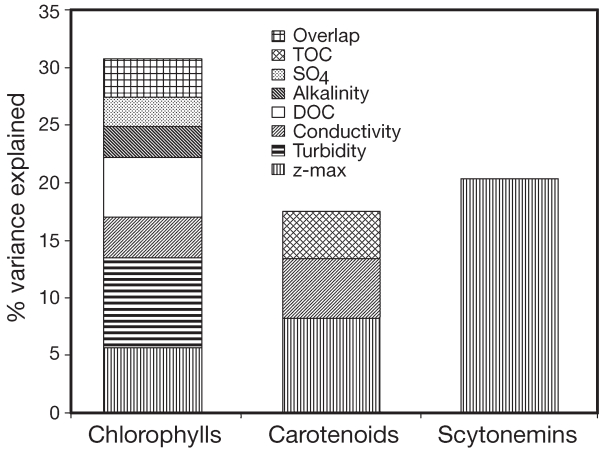

Fig. 6. Summary of redundancy analyses (RDAs) showing environmental variables (see Table 1) that significantly explain chlorophyll, carotenoid and scytonemin content of benthic microbial mats. The % overlap between the environmental variables significantly explaining the chlorophyll data is 3.4 %

Statistical relationships

Physical and chemical gradients versus pigment composition

CCA revealed that lake water depth, turbidity, latitudinal and longitudinal position, dissolved oxygen, conductivity and sulphate significantly ($p \leq 0.05$) explain the variance in pigment data (Fig. 5). Of the total variance, 25 % is explained by these 7 environmental variables. Individual RDAs of the major pigment groups (chlorophylls, carotenoids and scytonemins) showed that variance in the chlorophylls is significantly ($p \leq 0.05$) explained by conductivity, turbidity, DOC, depth, alkalinity and sulphate, in the carotenoid data by depth, conductivity and TOC, and in the scytonemin data by depth only (Fig. 6). More than 20 % of the variance in scytonemin content was explained by depth.

The deeper lakes (situated on the positive side of the first ordination axis in Fig. 5) were clearly differentiated from the shallower lakes (situated on the negative side of the first ordination axis in Fig. 5), as in the latter scytonemins are more abundant. In addition, in the shallower lakes, pigments including scytonemin and the carotenoids (except 1 unknown carotenoid and 1 echinenone derivative) are primarily derived from the cyanobacteria (myxoxanthophyll, canthaxanthin, and echinenone: Fig. 5). The more saline, less-oxygenated lakes (including the saline lakes of the Rauer Islands) were characterised by higher abundances of chlorophyll *b* and its derivatives and by carotenoids present in green algae, compared with the well-oxygenated lakes (negative side of second ordination axis in Fig. 5). The latter were characterised by higher concentrations of cyanobacterial carotenoids (echinenone) and chlorophyll *a* derivatives (chlorophyllide *a* and phaeophytin *a*). Diatom carotenoids (fucoxanthin, diatoxanthin/diadinoxanthin) occured in all lakes, but were relatively less abundant in the shallow freshwater ponds. Phaeophorbides were more abundant in the shallow lakes, whereas phaeophytins were characteristic of the deep freshwater lakes.

Gross mat morphology versus pigment composition

In general, prostrate and laminated mats had the lowest concentration of pigments while shallow-water epipsammic cyanobacteria were the most heavily pigmented. Ratios of total pigments: scytonemin (TP:scyt) and total chlorophyll: scytonemin (Tchl:scyt) showed a significant relationship with mat gross morphologies ($F = 7.74$, $p = 0.001$ and $F = 5.51$, $p = 0.004$ respectively: 1-way ANOVA GLM). Significant differences (post-hoc Tukey simultaneous tests) were found between TP:scyt ratios in epipsammic and prostrate mats ($p = 0.0007$) and prostrate mats and mat flakes ($p = 0.01$) and the depth distributions of mat flakes and finely laminated mats ($p = 0.0301$). Significant differences were also found between the Tchl:scyt ratios in epipsammic and prostrate mats ($p = 0.005$) and prostrate mats and mat flakes ($p = 0.03$).

Cyanobacterial morphotypes versus pigment composition

CCA of the carotenoid and scytonemin data (excluding non-cyanobacterial pigments) with forward selection of cyanobacterial morphotypes as explanatory variables, revealed that 3 morphotypes, CHde; GLco;

Table 7. Canonical correspondence analysis testing significance of relationship between cyanobacterial morphotypes and the carotenoid and scytonemin composition of mats (excluding non-cyanobacteria pigments), with cyanobacterial morphotypes as explanatory variables. Abbreviations as in Table 5

Morphotypes	p (using Monte Carlo permutation tests)	% explained of total variance in pigment data
CHde	0.001	5
U09	0.017	4.5
GLco	0.048	4
LYs1	0.048	3.9
DIsp	0.043	3.8
U01	0.04	3.6

Lys1 explained 12.8% of the total variance in pigment data; 6 morphotypes significantly explained ($p \leq 0.05$) the variance in pigment data when they were incorporated in the analyses as sole explanatory variable (Table 7). Further exploration of the data revealed statistically significant correlations between a number of cyanobacterial morphotypes with carotenoid and scytonemin content (Table 7).

DISCUSSION

This study differs from previous studies by examining the combined influences of environmental variables, gross morphology and species composition on the pigment contents of *in situ* microbial mats and avoiding artificially imposed experimental conditions. Like all multivariate analyses of data from natural systems, only a small amount of the variance is explained by the environmental variables (Birks 1998). However, the advantage of this approach is that it identifies the variables that have an overarching influence on pigment contents and that are environmentally relevant, rather than induced or enhanced by artificial reduction in a laboratory.

The environmental settings of the lakes can be seen as 2 more or less independent gradients. The first gradient is mainly related to conductivity as a result of the wide-ranging lake salinity gradient from oligosaline (salinity ≤2), to hyposaline lakes (salinity 2 to 20, e.g. Lake Reid, Firelight Lake and Sarah Tarn and Rauer 8, 9 and 10), and hypersaline lakes (salinity >20, e.g. Rauer 1 to 7). The second gradient is mainly determined by lake morphology. Both gradients, have previously been shown to exert strong influence on microbial mat structure and composition (in terms of diatoms and cyanobacteria) in the Larsemann Hills region (Sabbe et al. 2004), with lake water depth being the most important variable. Further statistical data on the physical and chemical properties of the lakes in the Larsemann Hills and Bølingen Islands is presented and discussed in Sabbe et al. (2004) and of the lakes from the Rauer Islands in Hodgson et al. (2001b).

As anticipated, the pigment composition of the microbial mats is strongly influenced by the lake water-depth gradient, and turbidity, presumably on account of their impact on the light climate. Other variables (such as conductivity, oxygen and DOC) are also significant, in combined analyses of all pigments, and/or in analyses of separate pigment groups. The influence of conductivity on pigment composition may be related to changes in species composition. The influence of oxygen on pigment composition is likely to be a result of differential preservation. Thus, in deep, less-oxygenated and/or saline lakes, phaeophytins are absent and phaeophorbides, and carotenoids, specific to green algae, are abundant. Aging of microalgal clones in the dark under both oxic and anoxic conditions has shown that oxygen is of paramount importance in determining the products of pigment degradation (Louda et al. 2002). Differential preservation may exert a large influence on apparent species composition. It may, however, also be linked to lake depth (i.e. light) and senescence–death processes (Louda et al. 1998), as in similar Antarctic systems heterotrophic grazing pressure is minimal (Ellis-Evans et al. 1998, Bell & Laybourn-Parry 1999).

The main patterns in the pigment data thus suggest that, in the shallow lakes, the cyanobacteria receive so much PAR and UVR that a major cellular effort is invested in synthesising a range of PAR and UVR screening compounds. Thus, scytonemins and carotenoids are found in higher relative abundance in shallow lakes, although the absolute concentrations of chlorophyll remain largely unchanged. Functionally, the xanthophylls (in higher plants) disperse excess energy (heat) from the cells using the xanthophyll cycle (Demmig-Adams & Adams 2000) and the scytonemins are responsible for UVR protection and stress response (Dillon et al. 2002), preventing the UV-dependent bleaching of chlorophyll and damage to DNA (Garcia-Pichel & Castenholz 1991). Carotenoids have also been implicated in bright-light photoprotection of cyanobacteria (Castenholz & Garcia-Pichel. 2000), and elevated carotenoid content is reported for UVR-resistant cyanobacteria (Buckley & Houghton 1976, Lakatos et al. 2001). Similarly, UVR-screening MAAs have been detected in some of these and similar Antarctic lakes (asterina-330, shinorine, porphyra-334). As the low attenuation values measured for UVR in the lakes allow UVR penetration beyond maximum lake depth in the shallower lakes (Ellis-Evans et al. 1998), cyanobacteria with UVR screening capabilities appear to have an advantage over those phototrophs without UVR screening capabilities.

Scytonemin is most abundant in lakes of less than 2 to 4 m depth. The near ubiquitous presence of scytonemin in these shallow lakes, despite differences in ice cover and UVR attenuation at the time of sampling, implies that although scytonemin is synthesised during periods of high UVR, it is then likely to persist as a permanent extracellular pigment (particularly in mats comprising living, dead and moribund filaments), providing an enduring UVR screening capability. This 'standby-capability' is consistent with some field studies that have found that scytonemin content does not correlate directly with rapid changes in UV irradiance (Pentecost 1993). In contrast, studies of live mats have shown seasonal changes in scytonemin concentration in response to solar irradiance (Karsten et al. 1998) and

also interspecific differences in scytonemin production in response to UVR (Pentecost 1993). Despite this, the overall effect of UVR in this data set appears to be positive for some species in that it selects for UVR-resistant cyanobacteria. Additional members of the community may indirectly benefit by positioning themselves within or below the filaments of protected cyanobacteria (both living and dead) and thereby gain a competitive advantage (Karsten et al. 1998, Sheridan 2001). Other possible UV-protective mechanisms include downward migration of motile species and biochemical adaptations including DNA repair and the production of UV shock proteins (Dillon et al. 2002).

In the intermediate and deeper lakes (>4 m) scytonemin content rapidly declines and carotenoids and then chlorophylls progressively dominate the pigment composition (Fig. 4). These changes in pigment content are consistent with an increasing demand for efficient photosynthesis, as opposed to photoprotection, required to exploit the very small quantities of light available in the deeper lakes, particularly under winter snow and ice cover. In addition, phycobiliproteins have been detected in the deeper pars of these, and similar lakes, where they function as accessory pigments to trap light energy and transfer it to chlorophyll with high efficiency (Hawes & Schwarz 1999).

The high water clarity and substantial levels of both incident PAR and UVR measured in the region's lakes (Ellis-Evans et al. 1998) has a clear impact on the gross mat morphology, species composition (Sabbe et al. 2004) and pigment content of the benthic microbial biological communities. However, the absolute concentrations of chlorophylls remain largely unchanged, even in the shallowest lakes that presumably experience high irradiance and where benthic microbial communities require substantial concentrations of UVR-screening pigments (Fig. 4). This suggests that shallow lakes remain productive despite experiencing the highest levels of PAR and potentially damaging UVR. This apparent maintenance of production, and cell function, even under high UVR, is also found in field measurements of Antarctic bryophytes, which show increased concentrations of UVR-screening pigments and carotenoids under high UVR, but no change in photosynthetic yield (Newsham et al. 2002). Similarly, manipulation studies involving terrestrial cyanobacteria have found no consistent pattern of reduced photosynthetic yield resulting from increased exposure to UV-B (George et al. 2001).

The relationship between pigment composition and cyanobacterial morphotypes is characterised by an abundance of statistically insignificant relationships. However, some significant results are present and provide limited evidence of the species groups associated with higher abundances of specific pigments. In particular these analyses identify those species associated with increased synthesis of scytonemin and confirm that UVR has a structuring function in aquatic environments (Schindler 1998, Wetzel 2001).

This survey of 62 lakes and ponds in eastern Antarctica has revealed that pigment contents and gross microbial mat morphology are primarily related to depth, and presumably its influence on the benthic light environment. The use of carotenoids and screening pigments to survive high intensities of PAR and UVR is well developed in these cyanobacteria and confers a competitive advantage through the preferential inhibition of eukaryotic algae (Vinebrooke & Leavitt 1996). As a result, they are the dominant phototrophs in these lakes. This means that these lakes are unlikely to experience the 10- to 25-fold reductions in lake production (as algae abundance) reported in Arctic ecosystems experiencing elevated UVR as a result of diminishing terrestrial sources of DOM (Leavitt et al. 2003a,b). In contrast, elevated UVR fluxes in the Antarctic may lead to a shift in species composition, towards cyanobacteria that produce UVR-screening compounds.

This and similar studies demonstrate that cyanobacteria have the functional capability to grow under high irradiance in shallow water and terrestrial habitats (Dillon & Castenholz 1999) and to optimally exploit the light environment at different lake depths both through motility and adaptive pigment strategies. It is possible that they have possessed this biochemical advantage from a relatively early stage in their evolution, when neither oxygen nor a protecting ozone layer was present (Achaean atmosphere) and that they were not restricted to deep-water environments to exploit short wavelength radiation absorption by the water column (Häder 1997). This suggests that, for the Antarctic cyanobacteria, any increase in the annual ice-free period (from regional warming) or increase in UVR receipt (as a result of the Antarctic spring ozone hole) represents only a minor challenge, as their adaptive pigment strategy will continue to provide a biochemical advantage over other phototrophs.

CONCLUSION

Under natural conditions, lake depth is the most significant factor influencing gross mat morphology and pigment contents, presumably as a result of its influence on the light climate. Lake conductivity, turbidity, dissolved oxygen, sulphate and geographical location also explain significant ($p \leq 0.05$) variance in the pigment content.

Lake depth is the only significant variable explaining the scytonemin content of benthic biota, accounting for more than 20% of the variance.

Significant differences in microbial mat gross morphologies occur at different lake depths ($p \leq 0.01$), and are characterised by significant differences in their pigment content ($p \leq 0.004$).

In deep lakes, chlorophylls dominate the pigment composition and enable the benthic biota to survive and photosynthesise using the very small quantities of light available, particularly under winter snow and ice cover.

In shallow lakes (<2 to 4 m), high UVR leads to high concentrations of UVR-screening pigments but no corresponding decline in the absolute concentrations of chlorophylls and carotenoids, implying limited, or no, loss of function.

Antarctic cyanobacteria are well-adapted to high-latitude irradiance regimes and the Antarctic ozone hole, and regulate their pigment contents and community composition to provide a competitive advantage that may explain their dominance in these systems.

These reference data will be useful in our interpretation of fossil pigment stratigraphies in regional palaeolimnological studies.

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