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ORIGINAL PAPER

Development and application of sedimentary pigments for assessing effects of climatic and environmental changes on subarctic lakes in northern Sweden

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Abstract A surface-sediment survey of pigments in 100 lakes in the Scandes Mountains, northern Sweden, was combined with a reconstruction of Holocene sedimentary pigments from Lake Seukokjaure to assess the major factors regulating phototrophic communities, and how these controls may have changed during the period from the deglaciation ($\sim$9700 cal. years BP) to the present. The study area covers a pronounced gradient of temperature and precipitation, and encompasses the subarctic tree line, an important ecotonal boundary in this region. Lake Seukokjaure is located in a presently treeless basin close to the modern tree line. The spatial survey of sedimentary pigments was analyzed using principle components analysis (PCA) and redundancy analysis (RDA). PCA explained 73–83% of variance in pigment abundance and composition, whereas RDA explained 22–32% of variation in fossil assemblages. Dissolved organic carbon (DOC) content of lake water, sediment δ^{13}C, maximum lake depth, elevation and lake-water conductivity were all identified as environmental variables with significant association with pigment abundances in the spatial survey, although phototrophic communities of lakes situated in different vegetation zones (alpine, birch, conifer/birch) were incompletely distinguished by the ordinations. In the RDAs, the primary pigment variability occurred along a production gradient that was correlated negatively to water-column DOC content and δ^{13}C signature of sediments. This pattern suggested that the important controls of primary production were light regime and terrestrial supplies of ^{13}C-depleted carbon. In contrast, depth, elevation and conductivity were found to be more important for the differentiation of the phototrophic community composition. Application of these spatial survey results to the Holocene sediment record of Lake Seukokjaure demonstrated the importance of DOC for the temporal development of the lake, from an early state of high production to a period of slight oligotrophication. In general, the algal changes were regulated by the interaction of DOC and conductivity, although transitions in the phototrophic community during the late Holocene were less easily interpreted.

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Terrestrial vegetation development thus appears to be of utmost importance for the regulation of primary production in oligotrophic alpine and subarctic lakes and climate impacts on lakes, whereas other basin-specific factors may control the ontogeny of algal community composition.

Keywords Pigments · Phototrophic community · Climate · DOC · HPLC · Abisko

Introduction

High-latitude lakes are sensitive ecosystems and are expected to react strongly to changes in climate, catchment properties, and nutrient conditions (Battarbee 2000; Douglas et al. 2004; Smol et al. 2005). The phototrophic communities integrate lake responses to changes in climate and environmental conditions (Leavitt and Hodgson 2001). Knowledge of the main regulatory mechanisms of the phototrophic communities is, therefore, important for predicting lake responses to future climatic changes. Contemporary studies have shown that several factors are important regulators of the phototrophic community, including, concentrations of nutrients and dissolved organic carbon (DOC), and climate-related factors such as temperature and precipitation (Battarbee 2000; Karlsson et al. 2005; Brutemark et al. 2006).

Most high-latitude lakes are nutrient limited either by nitrogen (N) or phosphorous (P), or a combination of these elements (Persson et al. 1975; Holmgren 1984; Jansson et al. 1996; O'Brien et al. 2005; Bergstrom et al. 2005; Brutemark et al. 2006). While nutrient additions primarily affect the plankton community, oligotrophic arctic and subarctic lakes are often dominated by benthic communities that can be nutrient-sufficient and limited by other factors such as light and the availability and type of habitats (Björk-Ramberg 1983; Vadeboncoeur et al. 2003; Bonilla et al. 2005). The influence of nutrient addition on the phototrophic community in high-latitude lakes is further complicated by the abundance of mixotrophic or potentially mixotrophic species, not only in turbid lakes (Jansson et al. 1996), but also in clear-water sites (Pålsson et al. 2005; Brutemark et al. 2006). Therefore, nutrient supply represents an important regulatory mechanism of the phototrophic community in some environments while other factors may be more important for primary production and community response of high-latitude lakes.

The quantity and quality of DOC in lakes play important roles in determining the structure and function of biotic communities as well as for the carbon balance of aquatic ecosystems. DOC affects the phototrophic community through its influence on light regime, water column stratification, nutrient availability and competition with the bacterial community (Jones 1992; Schindler 1997; Karlsson et al. 2002; Vinebrooke and Leavitt 2005). Lakes positioned in well-developed forest regions or with abundant peatland in their catchments generally have higher DOC contents compared to lakes above the tree line (Smol and Cumming 2000; Karlsson et al. 2002). Therefore, changes in climate that influence the position of the tree line can exert substantial effects on the DOC content of lakes positioned close to this ecotonal boundary. Newly deglaciated lakes commonly show an increase in DOC with time, but become more dilute in ions due to the succession of terrestrial communities within the catchment area (Engstrom et al. 2000; Fritz et al. 2004; Boyle 2007). DOC content has also been coupled directly to climate and acidification even though the direction of change varies between areas (Schindler 1997; Freeman et al. 2001; Evans et al. 2006).

It is well known that climate affects lakes both directly and indirectly, such as through catchment-mediated changes (Schindler 1997; Battarbee 2000). Biotic communities are affected directly as increased lake-water temperature favors warm-demanding species within organism groups and leads to increased metabolic rates. However, indirect effects on the duration and timing of the ice-free season, stratification, bottom water chemistry, and habitat availability, as well as catchment-mediated changes coupled to hydrology and nutrient cycling, can exert a major impact on the phototrophic and biotic communities in general (Battarbee 2000; Weyhenmeyer 2001; Karlsson et al. 2005; Forsstrom et al. 2005; Blenckner 2005). Similarly, paleolimnological studies have found marked changes in various organism groups (e.g., diatoms, chrysophytes, chironomids) attributed to changes in the ice-free season and water-column stability (Sorvari et al. 2002; Quinlan et al. 2005; Smol et al. 2005). Unfortunately, little is known to date about the precise mechanism of how climate variability (e.g., temperature, precipitation) and DOC varies though time and space to regulate the structure and function of lake ecosystems (Pham et al. 2008; Vincent and Laybourn-Parry 2008).

Paleolimnological studies in remote areas can provide important knowledge about natural variability and long-term trends, and they can increase our knowledge about the responses of biotic communities to changes in climate and ontogenic processes that occur in lakes and their catchments. Recently, considerable research has been conducted on diatoms and chironomids (Sorvari et al. 2002; Bigler et al. 2003; Quinlan et al. 2005; Smol et al. 2005). While fossil pigments in remote high-latitude lake sediments have received less attention (Pienitz et al. 2000; Korhola et al. 2002; McGowan et al. 2008), they hold promise for assessing ecological responses of lake communities to climatic and ecological changes (Leavitt and Hodgson 2001). Sedimentary pigments integrate the response of the entire lake phototrophic community as they are produced by all algae and other photosynthesizing organisms and in some cases are specific to particular groups (Jeffrey et al. 1997; Leavitt and Hodgson 2001). Detailed spatial surveys have been conducted on photosynthetic pigments in surficial lake sediments to increase the knowledge of factors influencing the phototrophic community in various ecosystem types (Vinebrooke et al. 1998; Hodgson et al. 2004; Buchaca and Catalan 2007). However, to our knowledge, no such studies have yet been conducted on subarctic lakes.

The objective of this study was to determine the factors that regulate the production and composition of phototrophic communities based on analysis of sedimentary pigments in lakes situated along steep climatic and environmental gradients in the Scandes Mountains of northern Sweden. A spatial survey of surface sediments from 100 lakes was performed to investigate relationships between environmental gradients and sedimentary pigment abundance. The knowledge gained from the spatial survey was then used to interpret paleolimnological records of sedimentary pigment changes in a Holocene sediment sequence from Lake Seukokjaure (unofficial name) to assess phototrophic response and regulating factors in a time perspective. The lake has experienced a transition from a forested to an alpine catchment during recent millennia (Rosén et al. 2003). Being on an ecotonal boundary, it is therefore expected to reveal changes in its phototrophic community related to the main environmental changes in the region since the deglaciation (~9700 cal. BP). This study significantly extends the knowledge base of sedimentary pigments as proxies for environmental change assessment, and supplements previous investigations of diatoms and chironomids from the same survey lakes (Larocque et al. 2001; Bigler and Hall 2002).

Description of sites studied

The spatial survey includes 100 lakes (67.07°N–68.48°N latitude, 17.67°E–23.52°E longitude) situated in the boreal, subalpine and alpine zones of northwestern Sweden, extending 100–300 km north of the Arctic Circle (Fig. 1). The lakes are generally small (<20 ha) and oligotrophic headwater lakes with an average maximum depth of 6 m. They are situated along a broad gradient of temperature and precipitation due to the influence of elevation and the Atlantic Ocean, respectively. The lakes span an altitudinal gradient of 169–1183 m a.s.l. with corresponding mean July air temperatures of 7.0–14.7°C, and an annual precipitation gradient from >1000 mm in the west to 500 mm in the east with a local minimum of 304 mm in the Abisko Valley (Alexandersson and Karlström 2001; Bigler and Hall 2002, Table 1). The ice-free season varies in length from less than 2 months at the highest elevations to around 6 months at low elevations. The catchment vegetation of the survey lakes ranges from boreal forest (conifer-dominated, *Pinus sylvestris* L., *Picea abies* L.) through mountain-birch woodland (*Betula pubescens* Ehrh. spp. *tortuosa* (Ledeb.) Nyman) and alpine meadows to alpine tundra (mainly lichens and mosses) or barren ground. The main ecological feature of the area is the tree line (500–800 m a.s.l.) consisting of mountain birch (Barnekow 1999; Bigler and Hall 2002). The sites were classified into three vegetation zones; alpine (above tree line >650 m a.s.l.), birch (mountain birch-forest ~500–650 m a.s.l.), conifer/birch (mixed coniferous-birch forest <500 m a.s.l.) according to Bigler and Hall (2002).

To extend the interpretations from the spatial-survey study to a Holocene perspective, a 9700 year sediment sequence covering the period since deglaciation was retrieved in March 2006 from Lake Seukokjaure (unofficial name, 67°46′N, 17°31′E), a

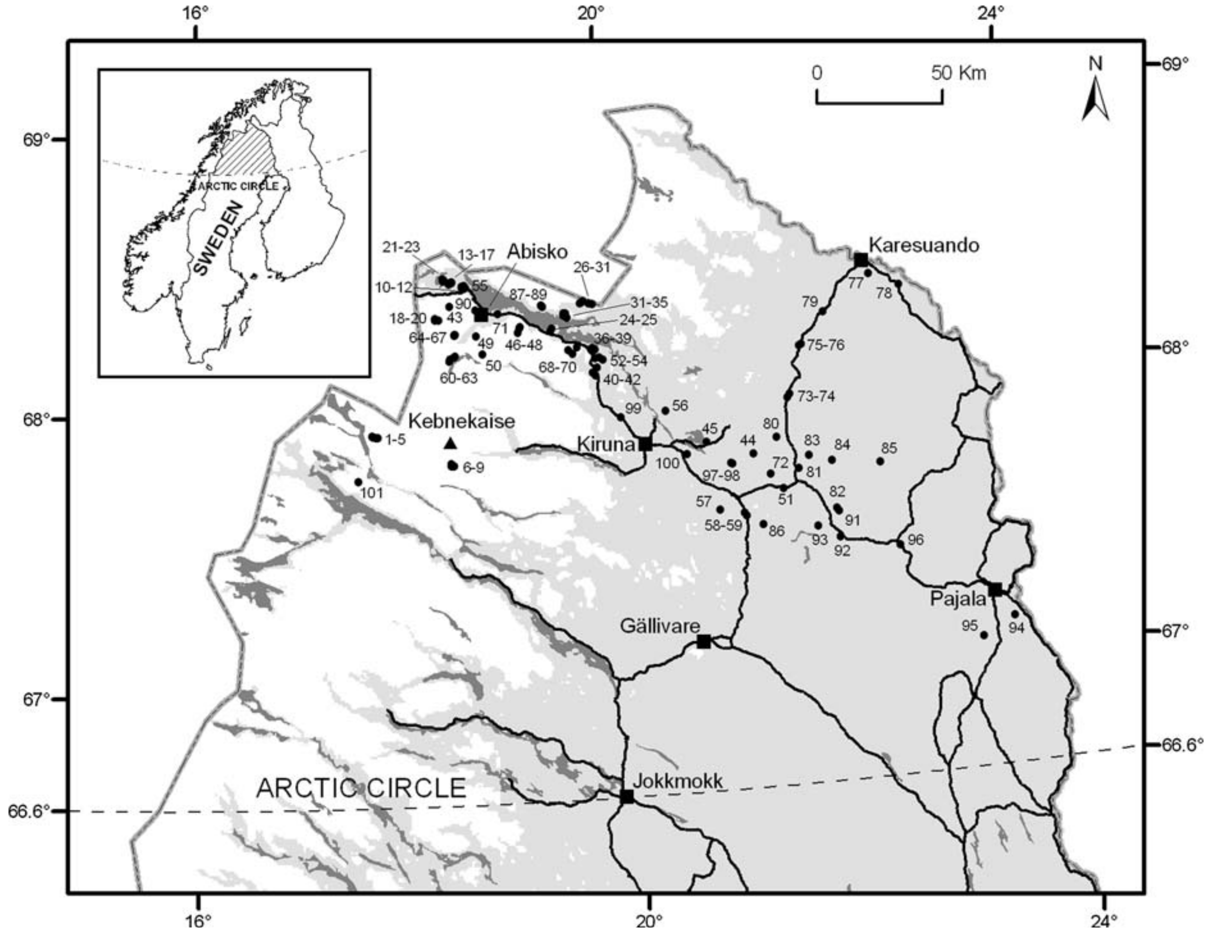

Fig. 1 Map of northern Sweden showing locations of the 100 sampled survey lakes. The boreal zone (grey) is distinguished from sites above the tree line (white). The position of Lake Seukokjaure where the stratigraphic data were collected is indicated as lake number 101

lake close to the village of Ritsem, northern Sweden. The lake is small and shallow (11 ha, max depth 6.1 m) and positioned on a gentle slope close to the local tree line (600–650 m a.s.l.) at an altitude of 670 m a.s.l. The catchment is classified as alpine tundra, dominated by heath communities consisting of dwarf shrubs, willows, grasses, sedges and herbs, in addition to a few scattered tree-sized individuals of mountain birch. The lake is hydrologically open, and small lakes in the area are ice covered from mid-October to late May. At the nearby meteorological station at Ritsem (521 m a.s.l., 4 km south of the site), mean air temperatures for January and July are −11.4 and 11.1°C, respectively, and mean annual air temperature is −0.8°C. Mean annual precipitation is approximately 510 mm, of which 50–60% falls as snow. Meteorological data were collected during the period of 1981–1990 (Alexandersson and Karlström 2001). A sediment sequence retrieved from Lake Seukokjaure in 1996 has previously been analyzed for diatoms, chironomids, pollen and near-infrared spectroscopy (NIRS) (Rosén et al. 2003; Rosén 2005).

Materials and methods

Spatial survey and long-core sampling and chronology

Surface sediments were collected from the deepest part of each of the 100 spatial-survey lakes using a

Table 1 Summary of environmental and sedimentary variables of the 100 survey lakes used in multivariate analyses

Nr	Name	Variable	Max	Min	Mean	Median	SD
		Environmental variables					
	Lat	Latitude	68.48	67.07	68.10	68.20	0.32
*	Long	Longitude	23.52	17.67	19.82	19.57	1.46
*	Veg klas	Vegetation zone (coniferous/birch, birch, alpine)	–	–	–	–	–
1	Mire	Mire (presence/absence)	–	–	–	–	–
2	Elev	Elevation (m a.s.l.)	1,183	169	595	500	260
	Secchi	Secchi depth (m)	11.1	1.0	4.8	4.5	2.2
	Water T	Measured water temperature (°C)	17.5	2.4	10.4	10.5	2.5
*	TaJul	Estimated mean July air temperature (°C)	14.7	7.0	10.8	11.2	1.9
*	TaJan	Estimated mean January air temperature (°C)	−12.9	−16.4	−14.6	−14.5	0.8
3	Depth	Maximum lake depth (m)	17	2	6	5	3
4	pH	pH	8.07	5.79	–	6.72	0.43
5	DOC	DOC (mg/l)	13.4	0.2	3.5	2.8	2.4
6	Si	Si (mg/l)	3.060	0.010	0.789	0.715	0.684
7	Cond	Conductivity (μS/m)	12.800	0.560	2.080	1.640	1.654
*	Ca	Ca (meq/l)	1.030	0.010	0.099	0.066	0.122
8	Mg	Mg (meq/l)	0.175	0.007	0.040	0.027	0.037
9	Na	Na (meq/l)	0.107	0.011	0.036	0.032	0.015
10	K	K (meq/l)	0.050	0.002	0.008	0.006	0.007
*	SO4	SO4 (meq/l)	0.361	0.009	0.041	0.028	0.052
11	Cl	Cl (meq/l)	0.104	0.008	0.025	0.021	0.015
		Sediment variables					
12	d15N	δ15N (‰)	3.20	−3.54	0.79	0.79	1.26
13	d13C	δ13C (‰)	−17.82	−34.52	−26.72	−27.36	3.35
*	C/N	Weight C/N ratio	18.35	7.34	10.76	10.63	1.63
	%C	Weight % C	40.08	0.74	19.14	19.72	8.44
	%N	Weight % N	3.67	0.04	1.78	1.83	0.75
	LOI	Loss on ignition (%)	74.19	2.88	41.89	43.14	16.39
		Pigments (nmol g^{-1} *OM)*					
	Chla	Chlorophyll *a* (undegraded)	346.7	3.1	79.3	53.7	71.3
	Chla1	Chlorophyll *a* derivative	155.0	1.7	37.1	26.5	30.6
#	Pheo_a	Pheophytin *a* (degradation product of chl *a*)	831.4	15.0	382.8	336.4	187.1
#	Pheo_a1	Pyropheophytin *a* (degradation product of chl *a*)	60.7	0.0	20.5	18.5	12.7
	Chlb	Chlorophyll *b*	106.6	0.0	20.1	11.6	20.3
#	Pheo_b	Pheophytin *b* (degradation product of chl *b*)	38.4	0.4	7.9	5.1	7.2
	Chlc1	Chlorophyll *c*1	1,850.0	0.0	252.1	117.4	353.7
	Chlc2	Chlorophyll *c*2	2,298.4	0.0	228.8	102.3	364.5
#	Bcarot	Beta-carotene	163.2	0.7	36.1	27.1	30.3
	Fuco	Fucoxanthin	1145.4	5.8	148.4	96.8	165.0
#	Allox	Alloxanthin	140.9	0.6	24.9	18.4	24.8
	Diadino	Diadinoxanthin	96.7	0.0	13.1	7.9	14.5
#	Diatox	Diatoxanthin	131.9	0.0	19.8	14.4	20.3
#	Lutzea	Lutein + zeaxanthin	237.3	0.4	42.8	31.0	41.0
#	Canth	Canthaxanthin	98.9	0.0	13.8	8.9	14.9

Table 1 continued

Nr	Name	Variable	Max	Min	Mean	Median	SD
#	Echineno	Echinenone	52.3	0.5	12.3	9.8	9.5
	Myxo	Myxoxanthophyll	40.0	0.0	10.9	9.1	8.2
	X1	Unknown carotenoid, possibly from cyanobacteria	53.0	0.0	11.9	8.2	12.4
	X2	Unknown carotenoid, possibly from cyanobacteria	39.5	0.0	5.0	2.2	6.6
	SedA	UV radiation absorbing pigment (not reported)	19.0	0.0	0.7	0.0	2.4
	SedB	UVR pigment, reported as Cb in Leavitt et al. 1999	88.4	0.0	5.6	0.0	14.8
	SedC	UVR pigment, reported as Ca in Leavitt et al. 1999	63.0	0.0	1.5	0.0	6.7

(Modified from Bigler and Hall 2002, values of environmental variables for individual lakes are reported by Larocque et al. 2001)

Numbered variables were included in the redundancy analyses (RDAs). * Supplementary variables in the RDA's. # Pigments included in stable pigment analyses and found in the Lake Seukokjaure sequence

HON gravity corer (Renberg 1991) during summers of 1997 and 1998. Sediment samples were split and sub-samples for pigment analyses were frozen until freeze drying just prior to pigment extraction. Sub-samples for carbon and nitrogen elemental and isotopic analyses were freeze dried and hand ground with a mortar and pestle at a later stage. Water samples were collected at 1 m depth just prior to sediment sampling. Analyses of water chemistry were conducted at the Swedish University of Agricultural Sciences (SLU) in Uppsala. Mean July and January air temperatures were estimated by interpolating records of Climate Normals (1961–1990) from 18 weather stations nearby and applying a lapse rate of 0.57°C per 100 m elevation (Laaksonen 1976). These calculations are identical to the ones used for other studies of climate in the area, as described by Larocque et al. (2001).

The sediment sequence from Lake Seukokjaure was collected at the deepest point of the lake (~6 m) in March 2006. The top 40 cm of flocculent surface sediments were retrieved using a HON gravity core, while deeper sediments were obtained with overlapping 1 m long Russian core sections (dark brown fine-detritus gytja, total core length ~1.8 m). The Russian cores were correlated by magnetic susceptibility at 4-mm increments using a Bartington Instruments MS2E1 surface scanning sensor coupled to a Tamiscan-TS1 automatic logging conveyor. Two core sections covering the entire sequence were chosen for further analyses of pigments, loss on ignition (LOI) and biogenic silica, while additional cores were wet sieved for extraction of macroscopic plant remains for radiocarbon dating.

The gravity core was sectioned into 1-cm intervals in the field and stored frozen in plastic bags at −20°C until freeze drying and extraction of pigments and LOI measurements. The Russian core sections were transferred to rigid supportive PVC trays and wrapped in heavy plastic before storage at +5°C in the dark. The surfaces of the Russian core sections were cleaned under subdued light using a spatula to remove the outer ~2-mm layer, and the core was sectioned in 1-cm intervals. From each sample, a sub-sample for pigment analysis was taken from the interior of the core, excluding the outer 5 mm to ensure that the sediment had experienced minimum exposure to light and oxygen during storage. Sub-samples were stored frozen in glass vials with screw-cap lids until freeze drying and subsequent extraction and analysis of pigments by high performance liquid chromatography (HPLC). Sub-sampling of the cores and pigment analyses were conducted within a month after collection in the field.

Radiocarbon dating by accelerator mass spectrometry (AMS) was conducted on terrestrial macrofossils from four samples along the length of the Russian cores collected in 2006 from Lake Seukokjaure. Samples were analyzed at the Radiocarbon Laboratory, Lund University, Sweden and calibrated to calendar years BP (i.e. pre 1950 AD) expressed as 95.4% probability envelopes using the Intcal04 radiocarbon calibration data set (Reimer et al. 2004).

Sediment analyses

Pigment analyses of the surface samples for the spatial survey were conducted on 0.01–0.25 g freeze-dried sediment, extracted in a mixture of acetone–methanol–water (80:15:5, by volume) for 18 h at 4°C in the dark under N_2. The sediment residue was extracted three times, filtered (0.22 µm Acropore membrane) and evaporated to dryness under N_2 gas and stored at −20°C until analysis. The dried pigments were dissolved in a precise volume of injection solvent containing Sudan II as an internal standard just before analyses with standard reversed-phase HPLC for quantification of the pigments as described by Leavitt and Findlay (1994). HPLC was conducted on an Agilent (Hewlett-Packard) model 1050 HPLC, equipped with a photodiode array detector as detailed in Leavitt and Hodgson (2001).

For pigment analysis of the Lake Seukokjaure sequence, 0.1–0.3 g of freeze-dried sediment were extracted in 100% acetone spiked with Sudan II as an internal standard over night at −20°C. Samples were filtered (0.45 µm, 30 mm, nylon membrane filter) and diluted to 80% acetone (with milli-Q water) before injection on the HPLC to enhance peak resolution. Diluted samples were stored at 4°C in the autosampler for a maximum of 7 h before injection. The run method was a modification of Wright et al. (1991) as described in Reuss and Conley (2005). Quantitative analyses of all pigments were conducted on a Shimadzu HPLC equipped with an on-line photodiode array detector (SPD-M10Avp). A fluorescence detector (RF-10Axl) with excitation set at 440 nm and emission at 660 nm was used for identification purposes only.

The different pigment extraction methods used for the surface and long core samples were due to different laboratory practices and may have caused minor differences in the total amount of pigments and extraction efficiency for more or less polar compounds. The slightly higher polarity caused by addition of methanol and water to the extraction solvent of surface samples will tend to take out more polar compounds compared to the pure acetone extraction solvent used for the long core samples. Triple extraction and evaporation procedure for the surface sediment samples compared to single extraction for the long core samples may also have caused slight differences in the pigment recovery. However, all samples were freeze dried prior to extraction which ensures similar extraction efficiency of sediments with varying water content and this procedure has been shown to significantly increase the amount of pigment recovery from sediment samples (Buffan-Dubau and Carman 2000). A multitude of pigment extraction procedures exists and a few comparative studies have been conducted including various combinations of acetone and methanol extracts (Jeffrey et al. 1997; Buffan-Dubau and Carman 2000; Cartaxana and Brotas 2003). In general, both methods used in the current study have been shown to be efficient for sediment pigment extraction (Buffan-Dubau and Carman 2000; Leavitt and Hodgson 2001; Reuss and Conley 2005) and their inconsistent use in this study is not expected to have had significant influences on the results.

Both HPLC methods ensured good separation of indicator pigments, although they differed slightly in their ability to resolve some pigments, such as bacteriochlorophyll homologues and UVR protection pigments. Tentative identification and quantification of the pigments from both HPLC systems were conducted based on retention time and absorption spectra compared to authentic standards obtained from DHI Water and Environment, Denmark. Pigment concentrations are presented as nmol of pigment per gram of organic matter (nmol g^{-1} OM). Organic matter content was determined as LOI after 1 h at 500°C for surface samples, and 2 h at 550°C for long core samples. Biogenic silica (BSi) content of the Lake Seukokjaure record was measured using the DeMaster (1981) method as modified by Conley and Schelske (2001). Quality control of the BSi measurements was assured by reference samples from an international inter-laboratory comparison (Conley 1998) and 10% duplicate samples.

Sedimentary total carbon and nitrogen elemental content were assessed by combustion in an Eltra Metalyt elemental analyzer system at the Institute for Geography and Geology, University of Copenhagen, followed by carbon and nitrogen stable isotope analysis ($^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively) using a VG-isotope Micromass dual inlet mass spectrometer equipped with a EuroVector elemental analyser and continuous flow inlet at the same laboratory. Carbon/nitrogen ratios (C/N) are expressed as atomic ratios. Carbon and nitrogen isotope compositions are reported in δ-notation; $\delta = [R_{\text{sample}}/R_{\text{std}} - 1] \times 1{,}000$ where R signifies the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in the samples and V-PDB and AIR standards, respectively. Reproducibility measured for ten working standards during each run was better than 0.1‰ for $\delta^{13}C$ and 0.2‰ for and $\delta^{15}N$.

Statistical analyses

To get an overview of differences among the spatial survey lakes, differences in the mean values of environmental variables ($\alpha = 0.05$) among the three vegetation zones (alpine, birch, conifer/birch) were analyzed by one-way analysis of variance (ANOVA) followed by a Tukey post-hoc test with unequal sample size according to Zar (1996). Differences in mean abundance of total pigments among the vegetation zones were also tested by one-way ANOVA.

Variations in sedimentary pigment assemblages along environmental gradients of the 100 spatial survey lakes were explored using multivariate analyses. Detrended correspondence analyses (DCA) was conducted on the $\log(x + 1)$ transformed pigments in the 100-lake spatial survey data set to assess if linear or unimodal based ordination methods were most appropriate for analyses of the data. All gradient lengths were well below 2 SD units, so the linear ordination techniques principal component analysis (PCA) and redundancy analysis (RDA) were chosen for statistical assessment (Birks 1995). PCA was used to assess the distributions of phototrophic pigments among sites. Analyses were conducted for both the full pigment dataset, as well as nine selected stable pigments that are more relevant in combination with stratigraphic data (alloxanthin, diatoxanthin, lutein-zeaxanthin, canthaxanthin, echinenone, β-carotene, pheophytin *b*, pheophytin *a*, and pyropheophytin *a*; Table 1).

Direct gradient ordination by RDA was conducted to determine which linear combination of environmental variables best explain patterns in sedimentary pigments among sites. The environmental variables included vegetation zone, mire presence, longitude (Long), lake depth, elevation (Elev), July and January air temperature estimates (TaJul, TaJan), and modern water chemistry data [pH, and $\ln(x + 1)$ transformed conductivity (Ln_Cond), Ca (Ln_Ca), Mg (Ln_Mg), Na (Ln_Na), K (Ln_K), SO_4 (Ln_SO_4), Cl (Ln_Cl), DOC (Ln_DOC), Si (Ln_Si)], and untransformed surface-sediment variables ($\delta^{15}N$, $\delta^{13}C$, LOI, %C, %N, and C/N) (Table 1). Transformation was conducted to obtain approximately normal distributions of the variables. Bulk organic carbon and nitrogen elemental and isotopic data obtained on the surface-sediment samples were included as additional variables to the environmental dataset of the 100-lake spatial survey of Bigler and Hall (2002). These variables were included to provide information on carbon and nutrient cycling and organic matter supply from the catchment to the survey lakes. C and N data were missing for lake numbers 5, 18, 30, 46, 89, 95, so these six lakes were removed from analyses. LOI was excluded from the redundancy analyses because it was used to standardize pigment concentrations (nmol pigment g^{-1} OM). %C and %N were also excluded because they co-vary with pigments due to similar effects of preservation conditions, and they constitute significant parts of the sediment organic matter (LOI). C/N was retained as a supplementary variable to reveal relationships with the other environmental variables without influencing the results of the ordination. Dissolved organic carbon (DOC) content was selected over total organic carbon (TOC) content as the two parameters were highly correlated and DOC contributed most of the TOC in the lakes. Secchi depth was removed as the Secchi disk was often visible at the lake bottom (Bigler and Hall 2002). Vegetation zone and longitude were excluded from the analyses as they are intimately connected to elevation that was retained in the analyses. Mean January and July air temperature, Ca and SO_4 were excluded because variance inflation factors of >20 indicated they were collinear with the variables elevation and conductivity that were retained in analyses. RDA was performed using forward selection and Monte Carlo tests with 999 permutations to determine a subset of variables that explained significant ($P < 0.1$) and independent amounts of variation in the pigment data. Sample scores, or surface-sediment pigment assemblages, in the ordination diagrams were coded a priori according to the three vegetation zones.

A final RDA, which provided the basis for interpretation of the dataset, was computed with the forward-selected variables as active environmental variables and all other variables as supplementary variables. This latter group did not contribute to the position of sample, species and environmental scores, nor other ordination metrics, but were presented to assess relationships among environmental variables and pigments. The pigment data from the Lake Seukokjaure sequence were plotted passively onto the RDA with the subset of the nine stable pigments and with only the significant explanatory variables included to reveal the trajectory of change of the pigment assemblages in the lake during the Holocene.

All ordinations were performed using CANOCO version 4.5 (ter Braak and Smilauer 2002).

To assist interpretation of the long term development of Lake Seukokjaure, stratigraphic zones of the sediment sequence were defined based on stratigraphically constrained cluster analysis (CONISS, Grimm 1987) using squared Euclidian distances of 12 principal, identified pigments that were log($x + 1$) transformed prior to analysis. The pigments included in the analyses were; chlorophyll *a*, pheophytin *a*, pyro-pheophytin *a*, pheophytin *b*, and bacterial pheophytin *e* (chlorophylls), β-carotene, diatoxanthin, lutein-zeaxantin, alloxanthin, echinenone, cantaxanthin, and fucoxanthin (carotenoids).

Results

Spatial lake survey

The 100 study lakes encompassed a wide gradient in both pigments and environmental variables (Table 1) and were summarized based on similarities and differences among the three contrasting vegetation zones (alpine, birch, conifer/birch). Mean DOC concentration differed significantly among all three vegetation zones, with highest levels in the conifer/birch zone and lowest concentrations in lakes from the alpine zone (Fig. 2). The greatest range of DOC concentration occurred in the conifer/birch zone where also major differences in sediment organic content were found due to very different geological settings (sandy soils to mire areas). Silica (Si) content was significantly higher in the conifer/birch zone than at alpine and birch zones. Mean lake-water pH was highest in the birch zone, but comparable between alpine and birch/conifer zones. Mean lake depth did not differ among vegetation zones. Total pigment concentrations, calculated as the sum of all pigments, was significantly higher in the conifer/birch zone than the birch zone.

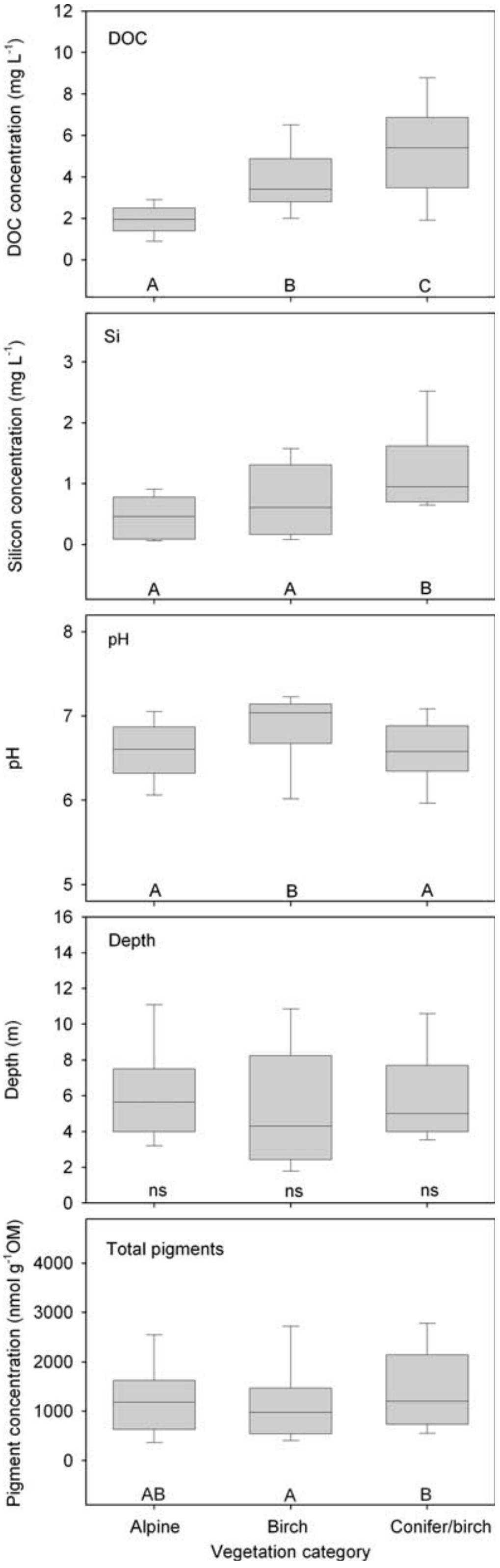

Fig. 2 Comparisons of limnological variables among the three ▶ vegetation zones; alpine, birch, and conifer/birch. The box and whisker plots indicate the median, 10th, 25th, 75th and 90th percentiles. Significant differences between mean values of the tree zones, based on one-way ANOVAs at $\alpha = 0.05$, are indicated by different letters. Similar letters indicate that the zones are not significantly different, ns indicates that none of the three zones are significantly different

The first three axes of the principal component analyses (PCA) of the surface pigment dataset captured 83% of the total variance (47, 19 and 17%, respectively). While there was considerable overlap of sample scores from the three vegetation zones, pigment assemblages from lakes in the birch forest zone tended to be positioned lower on the second PCA axis than those from lakes within the conifer/birch zone, whereas lakes from the alpine zone were spread over the entire plot (Fig. 3a). PCA axis 1 appeared to capture a gradient of pigment abundance with lakes having low abundance of sedimentary pigments plotting to the right and lakes with more abundant pigments to the left. The second axis mainly separated lakes with abundant chromophyte and siliceous algae (diatoms, dinoflagellates, chrysophyceae, haptophyceae) represented by chlorophyll *c*1 and *c*2, fucoxanthin, diadinoxanthin, and diatoxanthin from lakes dominated by green algae, higher plants and cyanobacteria represented by pheophytin *b*, lutein-zeaxanthin, and canthaxanthin. The third axis (not shown) captured differences in UV radiation protective pigments (Sed A, B, C) and two unknown pigments (X1, X2) tentatively identified as cyanobacterial pigments, but this axis did not add to the separation of vegetation zones. The tentative assignment of X1 and X2 to cyanobacteria was based on comparison of sediment samples among several hundreds of lakes where X1 and X2 appear to be associated with abundant cyanobacteria.

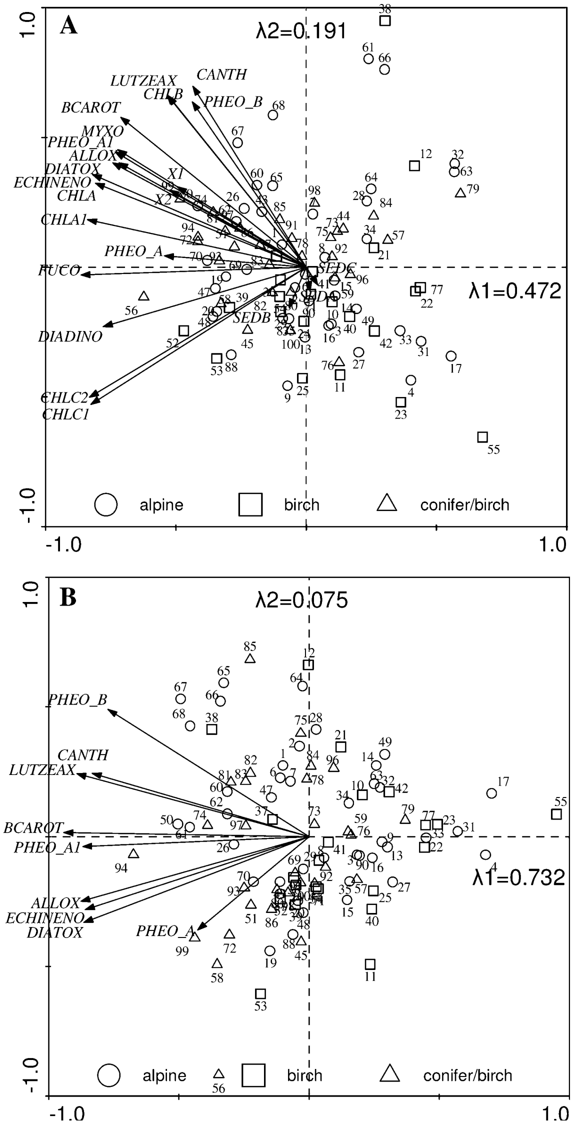

Fig. 3 PCA ordination of surface sediment pigment assemblages from the 100 spatial survey lakes situated along steep eco-climatic gradients in northern Sweden, showing sample scores (pigment assemblages) from alpine (open circles), birch forest (open squares) and conifer/birch forest (open triangles) zones and pigments (as vectors). Sample numbers are as presented in Fig. 1. Panel **a** shows PCA ordination results (axis 1 and 2) that included all pigments, whereas panel **b** shows PCA ordination results that included only the nine stable pigments (see text for details)

Principal component analyses of nine chemically stable pigments (alloxanthin, diatoxanthin, lutein-zeaxanthin, canthaxanthin, echinenone, *β*-carotene, pheophytin *b*, pheophytin *a*, and pyropheophytin *a*, Table 1) was conducted to provide a better background for interpretation of the stratigraphic profiles from Lake Seukokjaure which tend to record only stable pigments. Once again, PCA captured a gradient of pigment abundance along the first axis and explained 73% of the total variance (Fig. 3b). A separation of chromophyte algae versus green algae and cyanobacteria along the second axis explained 7.5% of the variance (Fig. 3b). Sites within the conifer/birch zone tended to be positioned towards the left-hand side of the first PCA axis, whereas sites within the birch zone were generally concentrated towards the right-hand side and no preference was observed for the alpine sites. The third axis only captured 5.6% of the variation and did not add substantially to the separation of vegetation zones or the stable pigments.

Ordination analysis of the surface sediment pigment dataset by RDA identified elevation, depth, conductivity, DOC and δ^{13}C as the subset of variables that explained significant and independent amounts of variation. These five variables explained 24 and 35% of the variance in total and stable pigment assemblages among sites, respectively. RDA axis 1 and all canonical axes were statistically significant ($P < 0.001$).

In the RDA that included all pigments, axis 1 captured a production gradient, indicated by abundance of algal pigments, which was negatively correlated with DOC and δ^{13}C (Fig. 4a). In addition, the production gradient was negatively correlated to the passive variables C/N, δ^{15}N and estimated mean January air temperature (TaJan), and was positively correlated with silica (Ln_Si), longitude and vegetation class (Fig. 4b). Despite the overriding effect of the production gradient on the ordination output, some separation of the various phototrophic groups could be identified. Conductivity was strongly correlated to most water chemistry variables and was positively correlated to labile diatom and other chromophyte pigments (chlorophyll *c*'s, fucoxanthin, diadinoxanthin). Green algal, higher plant and some cyanobacterial indicators (chlorophyll *b*, pheophytin *b*, lutein-zeaxanthin and canthaxanthin) were positively correlated to elevation and negatively correlated to depth. In contrast, the UV radiation protective pigments (Sed A, B, C) were positively correlated to conductivity and depth and inversely related to elevation. The cryptophyte indicator (alloxanthin) and some cyanobacterial indicators (echinenone, myxoxanthophyll) were positioned along the production gradient together with the ubiquitous chlorophyll *a*, chlorophyll *a* degradation products, and β-carotene. Similar to the PCA, visual examination of the site scores in the RDA showed limited separation of sedimentary pigment assemblages according to the vegetation zones (Fig. 4a). In particular, pigment assemblages from the alpine sites were positioned throughout the ordination space. However, sites from the conifer/birch zone were positioned mainly at the right-hand side, while sites from the birch zone tended to occur at the left-hand side. The ordination analysis (RDA) of the nine stable pigments (Fig. 4c, d), showed similar patterns as the ordination that included all pigments and captured both the main gradient of production along the first axis, and a limited separation of lakes from the three vegetation zones.

Lake Seukokjaure

The chronology of the sediment record from Lake Seukokjaure was based on five calibrated radiocarbon dates obtained from macroscopic remains of terrestrial plants (Table 2; Fig. 5). Four of these samples were obtained from the core sequence retrieved in 2006, whereas a fifth date was transferred from a core obtained in 1996 by means of stratigraphic correlation based on LOI. Additional dating control was provided by assuming a maximum age of the basal sediments of ~9700 cal. BP, according to present knowledge of the age of deglaciation in the region (Lundqvist 1998) and by assuming a contemporary age of the sediment surface (−55 cal. BP). Furthermore, the significant decrease in LOI near the top of the sequence (Fig. 6) was assigned an age of −21 cal. BP based on the assumption that this major disturbance of the sedimentary environment reflects the construction of a gravel road 200 m south-west of the lake in 1972 AD. Manual fitting of a smooth line through these eight tie points resulted in a plausible age model giving evidence of maximum post-depositional compaction of the most organic-rich strata (~1.3–0.9 m; Fig. 5). This approach required an assumption of no abrupt changes in sediment accumulation rate within the relatively uniform gyttja succession and a rapid deposition of the silty gyttja at the base. Enhanced compaction of the loose sediments near the top occurred in response to recent deposition of material with elevated mineral matter content. It should be noted that the suggested age model has considerable uncertainty, particularly in the lower part of the record where no terrestrial plant remains for radiocarbon dating could be found. Uncertainty envelopes cannot be statistically defined but a tentative estimate of approximately ±500 years at the base can be assumed, with declining values towards the middle and upper parts of the profile. Two radiocarbon dates from the 1996 sequence (Rosén et al. 2003) were rejected as being too old, presumably because of assimilation of old carbon by aquatic plants. This conclusion was based on our new dates and the regional deglaciation chronology (Lundqvist 1998) and it is consistent with evidence from a similar lake in northern Sweden where bulk-sediment dates yielded anomalous old ages (Barnekow et al. 1998).

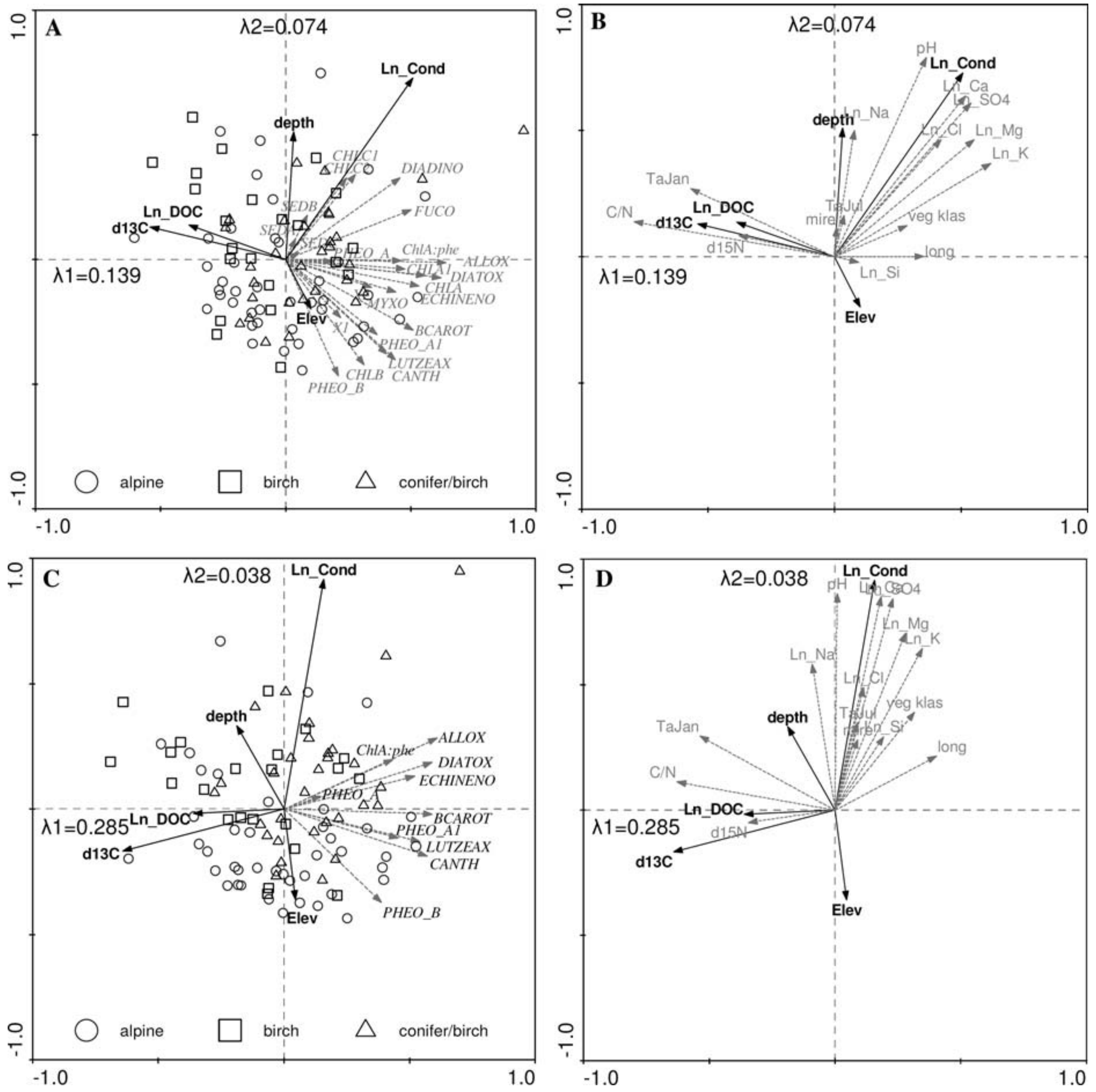

Fig. 4 RDA ordination of surface sediment pigment assemblages from the 100 spatial survey lakes situated along steep eco-climatic gradients in northern Sweden, showing sample scores (pigment assemblages) from alpine (open circles), birch forest (open squares) and conifer/birch forest (open triangles) zones and environmental variables determined by forward selection (vectors). Panels **a** and **b** show RDA ordination results that included all pigments, whereas panels **c** and **d** show RDA ordination results that included only the stable pigments. All panels compare PCA axis 1 and 2. Left hand panels (**a**, **c**) show sample scores and significant environmental variables (black vectors) together with pigments (grey dashed vectors). Right hand panels (**b**, **d**) show significant environmental variables (black arrows) and supplementary environmental variables (grey dashed vectors)

The sedimentary-pigment record from the Lake Seukokjaure sequence revealed that the lake has experienced marked changes in primary production and community composition since the last deglaciation (Fig. 6). The stratigraphic record was divided into six zones based on the CONISS analyses of the main pigments. The six zones were both overall and pairwise significantly different ($P < 0.05$, ANOSIM, Clarke

Table 2 Radiocarbon dates from Lake Seukokjaure

Depth in 1996 core[a] (m)	Depth in 2006 core[a] (m)	Lab. no.	Material analyzed[b]	Weight (mg)	Reported age (^{14}C years BP)	Calibrated age (2σ interval) (cal. years BP)	Calibrated age (mid intercept) (cal. years BP)
	0.375	LuS-7008	*Sal.*	1.9	1555 ± 50	1340–1550	1445
	0.574	LuS-6925	Moss	>20[c]	1925 ± 50	1730–1990	1875
	0.804	LuS-6994	*Bet. Sal.*	2.0	2560 ± 50	2470–2770	2625
0.62	0.822	Ua-11841	Bulk sed.	>100[c]	4030 ± 60	4250–4850	4500[d]
	0.984	LuS-6995	*Bet. Sal.*	2.0	3295 ± 50	3400–3640	3520
1.11	1.472	Hela-344	*Bet.* wood	>100[c]	7260 ± 75	7930–8290	8090
1.32	1.750	Ua-11840	Bulk sed.	>100[c]	9070 ± 75	9900–10,500	10,235[d]

[a] Dates reported by Rosén et al. (2003) and obtained on the sediment sequence collected in 1996 were correlated to the new record obtained in 2006 based on loss-on-ignition. Depths (m) are related to the sediment surface

[b] *Sal.* Leaves, and small twigs of *Salix* spp., *Moss* unidentified aquatic mosses, *Bet.* catkin scales and leaves of *Betula pubescens*, *Bet. Wood* twig of *Betula pubescens*

[c] Exact sample weight not determined

[d] Not included in age model (considered erroneously old)

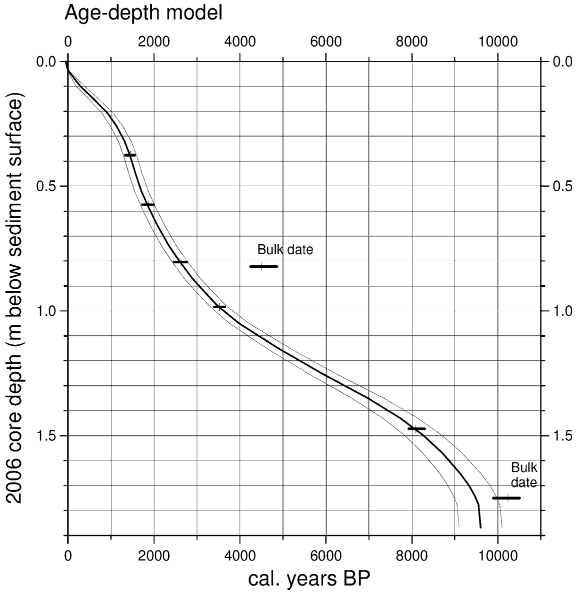

Fig. 5 Age-depth model for the stratigraphic data from Lake Seukokjaure based on five calibrated radiocarbon dates obtained on terrestrial macrofossils (Table 2) and assumptions of the onset and termination of sediment deposition and road construction in 1972 AD, while the two bulk dates were discarded as too old (see text). Estimated uncertainty envelopes are indicated by thin lines

and Green 1988). The ratio of chlorophyll *a*/pheophytin *a* indicated that preservation conditions have been relatively constant throughout the record except in the top ~5 cm of the core, as indicated by incomplete degradation of labile pigments (e.g., chlorophyll *a* and fucoxanthin) in zone VI. High amounts of diatoxanthin and biogenic silica (BSi) indicated dominance of diatoms throughout the sequence, while other common pigments suggested an important influx of green algae, higher plants or cyanobacteria (lutein-zeaxanthin) particularly in the early lake history (zone I) and after ~1750 cal. BP (zone V). Alloxanthin indicated the presence of cryptophytes, while only small amounts of specific cyanobacterial pigments (canthaxanthin, echinenone) and phototrophic bacteria indicators (bacterial pheophytin *e*) were found in the sediments with highest concentrations in the early lake (zone I). Indicators of overall production (particularly β-carotene) showed relatively high concentrations just after the deglaciation (zone I; ~9700–8500 cal. BP) and a relatively stable or slight decline in production since then. This pattern was shown by most of the pigments measured with the primary exceptions of diatoxanthin and lutein-zeaxanthin. Diatoxanthin showed high concentrations in the oldest part of the core (zone I) as well as a distinct increase in concentration in zone IV from ~3200 cal. BP. Lutein-zeaxanthin showed peak concentrations near the base of the sequence (zone I), earlier than any of the other pigments, and relatively high concentrations after ~1750 cal. BP (zone V). The change in pigment assemblages around 1750 cal. BP (zone IV–V) corresponded to the increased presence of phototrophic bacteria (bacterial pheophytin *e*) indicating changes in water column structure and

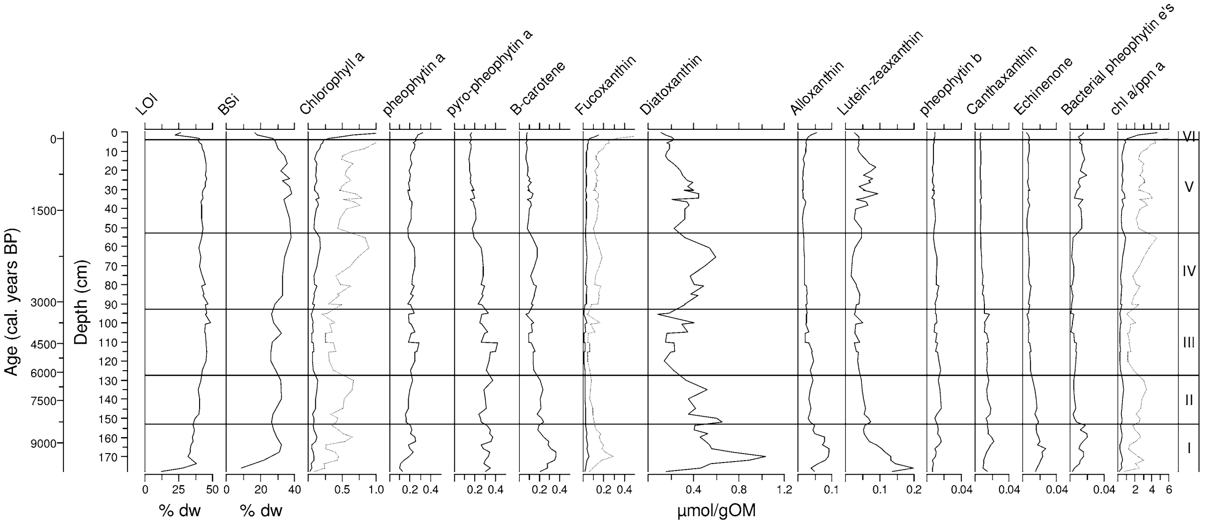

Fig. 6 Sediment pigment content (µmol g^{-1}OM), loss-on-ignition (LOI_{550}, % dry mass), and biogenic silica (BSi; % dry mass) records obtained from the Lake Seukokjaure sediment sequence. Lutein-zeaxanthin = lutein and zeaxanthin not separated, Bacterial pheophytin *e*'s, two continuously identified homologs; chl *a*/ppn *a*, preservation index of chlorophyll *a*/pheophytin *a*; gOM, gram organic matter from LOI. The dotted lines in chlorophyll *a*, fucoxanthin and chl *a*/ppn *a*-ratio represent ×5 exaggerations of the data. Note the different scales on the *x*-axes

development of an anoxic photic zone. Taken together, these patterns suggest a sequence in which a relatively productive initial phase was followed by a slight oligotrophication, and marked changes in the phototrophic community structure towards the present time.

Pigment abundances in the core from Lake Seukokjaure were positioned as passive samples within the RDA ordination of stable pigments from the 100-lake spatial survey (Fig. 7). This revealed that the phototrophic community dynamics of the lake vary along both axis 2, reflecting changes in conductivity and elevation, and axis 1, which reflects changes in DOC and δ^{13}C. Pigment assemblages from Lake Seukokjaure were positioned marginally in the RDA ordination space of the modern survey lakes but were oriented closer to assemblages from conifer/birch sites than to birch sites. Fossil samples could not be related to alpine sites that were scattered throughout the ordination. The most pronounced excursions in the trajectory of Lake Seukokjaure occurred during the first ~2000 years after lake formation. The largest variation in the sequence occurred along the second axis of the RDA, which suggests fluctuations in conductivity and elevation, or more correctly by inference, a fluctuation in temperature. With the exception of two samples from the silty bottom layer, the oldest samples from before ~9000 cal. BP indicated high conductivity, low δ^{13}C, high temperature and high pigment concentrations, all conditions consistent with an ample nutrient supply after deglaciation and prolific algal growth. The excursion along the second axis also implies changes in the importance of different algal taxa, particularly green algae and diatoms. The remainder of the samples group more tightly with variation predominantly along the first axis related to variation of DOC and δ^{13}C and differences in primary production. In general, stratigraphic pigments clustered into two historical groups within the RDA. The first group represents an early Holocene mode before ~6000 cal. BP with relatively high primary production and low DOC and δ^{13}C, and the second group represents a late Holocene mode after ~6000 cal. BP with lower production, and higher DOC and δ^{13}C corresponding to the transition between zone II and III. The community shift observed in the pigment profiles around 1750 cal. BP (zone IV–V) was not observed in the ordination plot.

Discussion

The integrated analyses of sedimentary pigments both in a spatial survey of surface sediments and

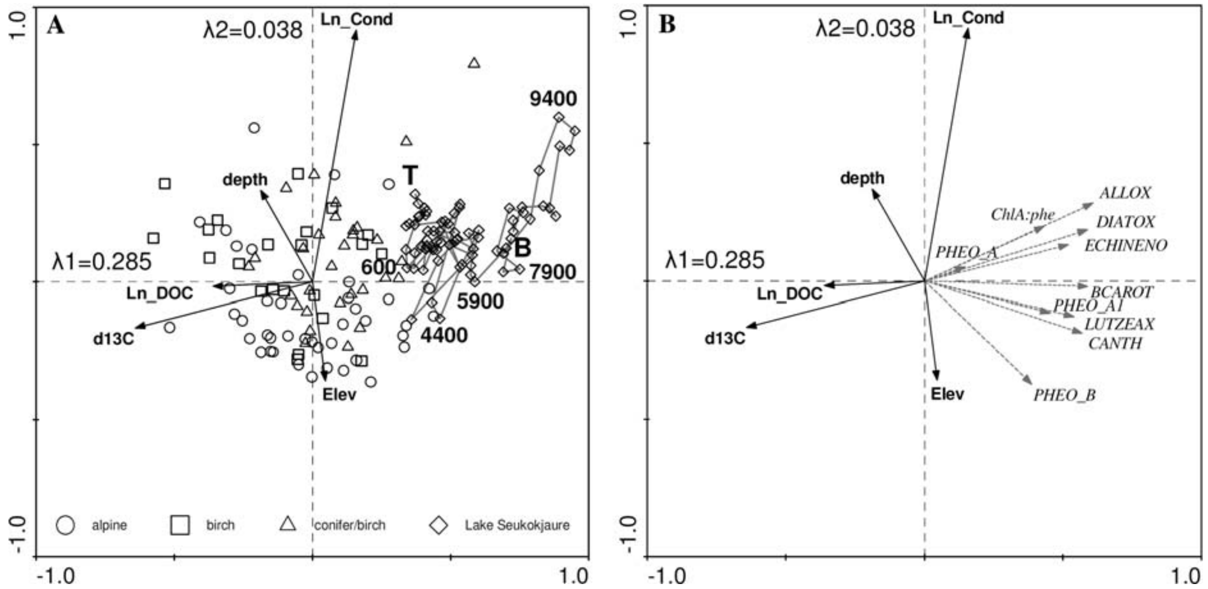

Fig. 7 Fossil pigment data from Lake Seukokjaure (open diamonds) were plotted passively on the ordination of stable pigment assemblages in the surface sediments of the 100 spatial survey lakes situated along steep eco-climatic gradients in northern Sweden, showing sample scores (pigment assemblages) from alpine (open circles), birch forest (open squares) and conifer/birch forest (open triangles) zones, and significant environmental variables determined by forward selection (vectors). Panel **a** shows sample scores and significant environmental variables (black vectors) while the line connects the fossil data sequence, T top sample, B bottom sample, selected dates (cal. years BP) included. Panel **b** shows significant environmental variables (black vectors) and pigments (grey dashed vectors)

throughout a Holocene sequence allowed us to assess the dominant controls on primary production and phototrophic community structure. The analyses revealed that the composition and production of the phototrophic communities of subarctic lakes are governed mainly by carbon cycling (DOC and δ^{13}C), lake water chemistry (conductivity), temperature (elevation), and lake morphometry (depth). The spatial lake survey revealed that algal abundance was inversely correlated to DOC, C/N ratio, δ^{13}C, and δ^{15}N, which suggests that primary production is governed by a delicate balance between the effect of terrestrial organic matter on light availability and the supply of nutrients and ions from the catchment (Leavitt et al. 2003). In general, this pattern is consistent with an expected dominance of the benthic component in the pigment analyses. In addition, the phototrophic community composition appears to be governed primarily by temperature, lake morphometry, and lake water chemistry, likely acting through effects on lake properties such as ice-free duration, habitat availability, light regime, and stratification of the water column. Our findings are consistent with previous regional studies that identified temperature, organic matter content (LOI or TOC), depth and pH as the determining factors of the composition of diatom and chironomid communities (Bigler et al. 2000; Rosén et al. 2000; Larocque et al. 2001; Bigler and Hall 2002). Our findings also are consistent with previous sediment pigment surveys that identified depth and conductivity as some of the main determining factors for the phototrophic community composition (Vinebrooke et al. 1998; Hodgson et al. 2004; Buchaca and Catalan 2007). Analysis of the Lake Seukokjaure core revealed a succession from productive conditions early in lake history to a continued period of slight oligotrophication and dominance by diatoms despite several changes in total amount and relative importance of other phototrophic organisms. This oligotrophication was confirmed by the trajectory of the lake in ordination space of the survey lakes, while shifts in the community composition were not evident. In addition, the ordination analyses of the Lake Seukokjaure data suggest that the effects of conductivity on the phototrophic community of lakes may be most profound during early stages of lake ontogeny when forest and soil development is most pronounced, whereas DOC and other catchment-mediated factors continuously affect the primary production.

Controls of primary production

The most striking feature of the multivariate analyses of surface sedimentary pigments and environmental variables in the 100-lake spatial survey is the negative correlation between primary production (pigment concentrations) and input of terrestrial organic matter (DOC and C/N ratio). This is consistent with reports attributing inverse relations between DOC content and primary production to reduced light, increased competition with bacteria for nutrients and scavenging of nutrients by the DOC (Jackson and Hecky 1980; del Giorgio and Peters 1994; Leavitt et al. 1999; Jansson et al. 2000; Karlsson et al. 2002). However, a previous study of a subset of 15 lakes from the present survey along an altitude gradient showed that high production was coupled not only to the length of the ice-free season but particularly to the input of DOC and inorganic nutrients (Karlsson et al. 2005). This discrepancy could be caused by effects of benthic primary production that was not included in the analyses of the 15 lakes while the current study of surface sedimentary pigments integrates the response of both planktonic and benthic communities. In fact, due to the extensive degradation of pigments in the water column (Leavitt 1993; Cuddington and Leavitt 1999) and the dominance of benthic production in oligotrophic subarctic, arctic and alpine lakes (Vadeboncoeur et al. 2003), the present pigment survey may primarily reflect patterns in benthic algal production. It has been shown that such benthic systems are often more sensitive to fluctuations in light and habitat availability than to nutrient supply (Björk-Ramberg 1983; Bonilla et al. 2005). In addition, indicators of nutrient conditions, such as sedimentary δ^{15}N and silica (Si) content, were not found to be significant predictors of algal change in the ordinations. Instead, we infer that the light regime, as affected by changes in DOC influx, is likely the most important regulating mechanism of the primary production in the survey lakes.

The δ^{13}C and δ^{15}N signatures of sedimentary organic matter provided important insight into the biogeochemistry of the study lakes. For example, the negative correlation between δ^{13}C and primary production suggests a predominant utilization of a ^{13}C-depleted carbon pool by algae, likely arising from a pool of respired CO_2 in lakes or catchment soils. Such general relationships have previously been reported for oligotrophic subarctic and alpine lakes (Wolfe et al. 1999; Hammarlund et al. 2004), as well as for temperate eutrophic lakes (Bunting et al. 2007). The positive correlation between δ^{13}C and DOC on the other hand is consistent with generally higher δ^{13}C values of terrestrial matter relative to lacustrine material (Meyers 1994). Similarly, a negative correlation with production and positive correlation with DOC was found for the δ^{15}N signature of surface sediments suggesting that ^{15}N-depleted dissolved organic nitrogen (DON) may be the main source of N for these lakes. Reduced microbial processing and rapid transport of depleted N to lakes can result in low δ^{15}N values in aquatic ecosystems (Routh et al. 2004). Interestingly, the observed isotopic patterns are in contrast to what is commonly found in more eutrophic and temperate systems, where high production often causes depletion of the dissolved inorganic carbon (DIC) and enrichment in ^{13}C of sedimentary organic matter, while elevated δ^{15}N values are often associated with N pollution from anthropogenic sources (e.g., Leavitt et al. 2006; Bunting et al. 2007; Pham et al. 2008). Taken together, the isotopic evidence indicates that most C and N in the lakes are of terrestrial origin and both are rapidly used by the primary producers in these lakes.

The interpretation of the general decline in production of Lake Seukokjaure was supported by relationships observed within the spatial lake survey, which underlined the importance of DOC for the temporal development of the lake. For example, the trajectory of Lake Seukokjaure in the spatial lake survey ordination shows that high pigment concentrations in the early lake history occurred concomitant with low DOC content and relatively high conductivity, with reciprocal changes in DOC and algal abundance particularly during the mid-Holocene interval. This pattern is consistent with findings from lakes in Alaska where the ionic content declined as DOC levels increased after deglaciation (Engstrom et al. 2000). Similarly, high algal production after deglaciation is a common feature in other high-latitude lakes (Hammarlund et al. 2004; McGowan et al. 2008).

Passive application of lake stratigraphies to surface sediment survey ordinations and inspection of temporal community changes in ordination space have previously been conducted successfully to add information gained from long-term studies (Hall et al. 1999; Bigler et al. 2003). However, degradation is a potential problem in pigment analyses and therefore passive application of the Lake Seukokjaure core samples to the surface sediment dataset was conducted using relatively stable pigments only. It can be expected that the vast majority (>90%) of pigment decomposition has already occurred in both the core and surface sediment samples during settling of algae and algal remains to the lake bottom (Leavitt 1993; Cuddington and Leavitt 1999) while subsequent pigment loss is very slow (Leavitt 1993). In addition, the depth of Lake Seukokjaure is close to the average depth of the surface sediment lakes (6.1 m vs. 6.2 m average), a factor which can have substantial influence on the total sediment pigment concentration (Cuddington and Leavitt 1999). We therefore believe that the use of the passive application of the core samples to the survey dataset is appropriate and the conclusions are valid despite the possible minor biases caused by degradation processes.

Controls of phototrophic community structure

Sedimentary pigment composition was consistent with the presence of algal groups known to be common in other arctic and subarctic lakes. For example, the dominating benthic communities in oligotrophic arctic and subarctic lakes (Vadeboncoeur et al. 2003) often consist of diatoms, cyanobacteria, and green algae (Persson et al. 1975; Björk-Ramberg 1984; Bonilla et al. 2005). Chrysophytes are often the dominating algal group in the phytoplankton of these lakes while green algae, dinoflagellates and cryptophytes are also common (Holmgren 1984; Sheath 1986; Forsström 2006). In addition, many chrysophytes are considered mixotrophic (Jansson et al. 1996) and can also be found in benthic communities.

Variation in composition of phototrophic communities occurred mainly along the second axis in the RDA of the spatial surface-sediment survey, indicating that temperature (elevation), lake morphometry (depth) and lake chemistry (conductivity) were the main control factors. Elevation and depth exert major influence of the phototrophic community through their effects on temperature and length of the ice-free season, water column stability, light conditions at the sediment surface and habitat availability. In contrast, effects of conductivity are likely coupled to a positive correlation with pH and all other chemical measures. The importance of depth as one of the main controlling factors of the phototrophic community is emphasized by previous pigment surveys relating depth to changes in UV radiation protective pigments of cyanobacteria, pelagic/benthic algal ratios and total pigment concentrations in the sediment (Vinebrooke et al. 1998; Hodgson et al. 2004; Buchaca and Catalan 2007). Despite the fact that all lakes in the present study are relatively shallow with light penetration to the bottom, depth seems to exert an important control on the benthic communities. Green algae, cyanobacteria and possibly aquatic mosses appeared to be most abundant in shallow, high-elevation lakes, while chromophyte and pelagic algae appeared more abundant in deep, low-elevation lakes with high conductivity. These results indicate that particularly lake morphometry constitutes an important control of the phototrophic community structure.

The inverse relationship between the UV radiation protective pigments (Sed A, B, C) and lake elevation, as well as the positive relation with depth, was contrary to previous findings that algae in clear shallow lakes at high altitude experience the highest levels of UV radiation and should contain higher amounts of UV radiation protective pigments (Leavitt et al. 1997, 2003; Hodgson et al. 2004). However, the original UV index is based on the ratio of UV radiation protective pigments to the sum of alloxanthin, diatoxanthin and lutein-zeaxanthin and not the absolute value included in our analyses. It has also been suggested that UV impacts on lakes may be strongest for lakes situated at tree line or otherwise experiencing rapid changes in chromophoric dissolved organic matter (CDOM) (Vinebrooke and Leavitt 2005). The two unknown pigments (X1, X2) tentatively identified as cyanobacterial pigments showed good correlation with other cyanobacterial pigments, e.g., zeaxanthin, cantaxanthin and echinenone, but were negatively correlated with the known UV radiation protective pigments. Knowledge of the function of these pigments may help to explain the distribution of specialized pigments in subarctic and alpine lakes.

The ordination approach identified the major transition in Lake Seukokjaure between early and late states in terms of production and community structure. In general, the early Holocene was identified as the period of greatest variability and characterized by the highest conductivity, warmest temperature and lowest DOC with phototrophic community dominated by chromophyte algae. In the period after ~6000 cal. BP fluctuations were more subtle and associated with increasing DOC concentration of lake water and generally declining primary production. Phototrophic community changes during the late Holocene, identified in the pigment stratigraphy (zone IV–V, Fig. 6), were apparently of minor magnitude and were not readily identified by the ordination approach. This lack of sensitivity may reflect the large overlap in fossil pigment composition among lakes from the three vegetation zones, despite the clear differences in lake chemistry (Fig. 2) and fossil diatom communities (Bigler and Hall 2002). Alternatively, the marginal placement of the stratigraphic data within the ordination plots limits the degree to which mechanistic inferences can be drawn from the surface sediment dataset, possibly because the survey may not have included a sufficiently wide gradient of environmental change, relative to Holocene variation. Consistent with this interpretation, we note that PCA explained up to 83% of spatial variation in pigment assemblages, whereas RDA explained less than 35%. This difference suggests that there are large orthogonal gradients of environmental change which were not captured in our spatial survey, and that these unmeasured gradients may have also influenced the pattern of phototrophic community changes during the Holocene. Unfortunately, the additional chemical and physical analyses needed to resolve this issue are beyond the scope of the present paper.

Conclusions

DOC content and its effects on the light regime of subarctic lakes was identified as the main factor influencing the primary production of these high-latitude study sites. The strong influence of terrestrial C and N was further supported by the C/N and stable isotope ratios. Conductivity, depth and elevation were also found to be important factors controlling the phototrophic community structure, particularly the differentiation of relative dominance of chlorophyte and chromophyte algae, likely through their influence on temperature and length of the ice-free season. While catchment properties had a strong effect on the production and composition of the phototrophic communities through their influence on terrestrial and minerogenic input, lakes in different vegetational zones could not be easily differentiated. Instead, spatial variation of pigment composition seemed to be governed by the ratio of terrestrial organic matter and internal lake primary production, factors that varied considerably within each vegetation zone.

Combination of the sediment survey results and the Lake Seukokjaure pigment record supported the recent findings of Engstrom and Fritz (2006) and documented a general oligotrophication of the lake after deglaciation. The subsequent increase in DOC was inferred to be associated with declining production of the lake, while dilution of ions (conductivity) was primarily observed in the initial phase of the lake concurrent with leaching of ions from the newly deglaciated area and rapid soil development. Unfortunately, the surface sediment ordination analyses were not sensitive enough to capture the changes in phototrophic community composition in the late Holocene, and differences in the degree of explanation of the pigment assemblages between the PCA and RDA techniques suggested that important environmental factors were missing from the survey. We conclude that sedimentary pigments are sensitive indicators of changes in phototrophic production in response to external forcing factors, while the pigment composition may also be strongly influenced by the physical setting (morphometry) of subarctic and alpine lakes.

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