Paleohydrology inferred from diatoms in northern latitude regions*

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Abstract

Several recent studies have successfully applied diatom-based paleolimnological techniques to infer past hydrological changes in arctic and subarctic regions. For example, we summarize arctic studies that attempt to determine changes in peat water content, flood frequency, river discharge, effective moisture and ice cover in northern regions. Some of the investigations are still in preliminary stages, but represent innovative approaches to study arctic and subarctic paleohydrology. New data demonstrate that lake depth, which may be related to changing hydrological conditions, is a significant variable influencing the distributions of diatom taxa in lake surface sediment calibration sets from Wood Buffalo National Park (WBNP), on the border of Alberta and the Northwest Territories, Canada, and from Fennoscandia (mainly northwest Finland). Weighted averaging regression and calibration methods were used to develop quantitative inference models for lake depth using diatom assemblages preserved in surface sediments. The predictive abilities of the transfer functions were relatively high (for WBNP $r^2 = 0.70$ and RMSE = 2.6 m, and for Fennoscandia $r^2 = 0.88$ and RMSE = 1.8 m). However, evaluating the transfer functions using jack-knifing procedures indicated lower predictive abilities, possibly reflecting the relatively small sample size and/or short gradients used in these calibration sets. Such transfer functions can be used to track overall *trends* in lake levels, and provide an objective assessment as to *directions* of changing lake levels. Any interpretations of inferred lake levels, especially those related to climate change, must be made cautiously and must include some understanding of the local, present-day hydrological system.

Introduction

It is generally accepted that climate warming, possibly due to increased greenhouse gases, will be amplified in arctic and subarctic regions (Walsh & Crane, 1992; Overpeck et al., 1997). In these regions, climate change will un-

doubtedly be manifested by changes in hydrological factors, including precipitation, evaporation, duration and frequency of ice cover, run-off, lake levels, the amount of permafrost, ocean circulation, etc. (Woo, 1996; Rouse et al., 1997). However, long-term hydrological data from the Arctic and Subarctic are extremely sparse or non-existent, and there is much uncertainty regarding the response of the hydrological system to climate warming in these regions. Paleolimnological techniques may provide one means to study the effects of past climate

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change to northern hydrological systems (Lotter et al., 1999; Douglas & Smol, 1999).

Diatoms are unicellular algae that are characterized by a siliceous cell wall. These microscopic organisms inhabit virtually every aquatic environment where there is sufficient light for photosynthesis. Because environmental variables that can be linked to changing hydrological conditions (e.g., pH, salinity, nutrient availability, lake depth, etc.) often influence diatom community composition, it should be possible to infer past hydrological conditions from fossil diatom assemblages.

A number of innovative approaches have been applied to arctic and subarctic regions to infer past hydrological conditions from diatoms in peatland, fluvial and lacustrine settings. Peatlands are a characteristic feature of northern latitudes, covering approximately 1.4×10^6 km^2 north of 60 °N latitude (Matthews & Fung, 1987). Diatoms, as well as chrysophytes and other paleolimnological indicators, are preserved in peatlands and may be used to reconstruct peatland development (e.g. Foster & Fritz, 1987; Korhola, 1990; 1992; 1995; Brown et al., 1994; Gilbert et al., 1997; Jasinski et al., 1998), which is closely linked to hydrological and climatic conditions (Svensson, 1988; Korhola, 1995). Different stages of peatland development are reflected in the diatom flora by species compositional changes along, for example, habitat and pH gradients. Although this research is still preliminary, marked shifts in diatom, chrysophyte and protozoan assemblage composition have been recorded in fossil peat profiles (e.g. Brown et al., 1994; Gilbert et al., 1997; Jasinski et al., 1998), perhaps reflecting the water content of the peat at the time of development, and therefore past hydrological conditions.

Paleolimnological approaches can also be used to model changes in flooding frequency and watershed hydrology (Hay et al., 1997). Delta lake biogeochemistry is closely linked to the relative amount of river influence and duration of flooding (Lesack et al., 1998). Mackenzie Delta lakes showed separation along a productivity gradient inferred using winter methane. The turbid Mackenzie River reduces macrophyte growth in lakes connected to river channels resulting in decreased winter methane production, whereas limited river input increases macrophyte productivity resulting in increased winter methane production. Ordination of diatom taxa and measured environmental variables in a surface sediment calibration set of delta lakes showed that winter methane levels accounted for a significant amount of variance in the diatom species data (Hay et al., 1997). As the authors recognized, diatoms do not respond directly to winter methane concentrations, but this variable is a useful proxy for summer production levels, which are related to flooding frequency. Because winter methane levels can be related to the degree of connection a floodplain lake has with the river, this new technique may be used to infer past changes in flooding frequency and watershed hydrology (Michelutti, 1999). These approaches can likely be transferred to other arctic delta systems.

Past river discharge can be studied by tracking the abundance of lotic (i.e., taxa characteristic of river environments) diatoms in the sediments of lake basins. For example, Ludlam et al. (1996) identified several diatom taxa that were characteristic of inflowing rivers in a high arctic drainage system on northern Ellesmere Island. They proposed a 'Lotic Index' that compared the ratio of diatom taxa characteristic of the river environment to taxa from the lake environment. The relative abundance of river diatom species present in a varved lake sediment core was then used to track past river discharge into this high arctic lake (Douglas et al., 1996; Ludlam et al., 1996).

Diatoms, which are sensitive to salinity, have been used in athalassic lakes to infer past hydrological conditions. In temperate regions transfer functions have been developed relating diatom assemblages to lakewater salinity and associated variables (e.g. Fritz et al., 1993; Wilson et al., 1996). These transfer functions have been applied to fossil diatoms in athalassic lakes to infer paleosalinity, and therefore, changes in the hydrological balance (e.g. Fritz et al., 1991; Laird et al., 1996). Although athalassic lakes are believed to be rare in arctic and subarctic regions, several have recently been identified (e.g. Pienitz et al., 1992; and unpublished data). Diatom records from these lakes may provide important information regarding past arctic and subarctic hydrological and climatic conditions. For example, diatom-inferred reconstructions of salinity and lake levels revealed that Lake U60, a subarctic athalassic lake, has experienced frequent and rapid fluctuations between less saline and highly saline conditions, probably related to marked hydrological changes associated with rapid climate change (Pienitz et al., in preparation).

Shallow ponds, which characterize the Arctic, may also contain records of hydrological change. Owing to their shallow nature, a slight water lowering can have dramatic influences on diatoms and other biota, making these sites particularly sensitive to past changes in hydrology and/or climate (Douglas & Smol, 1994;

Douglas et al., 1994). For example, past shifts in diatom assemblages appear to track changes in a suite of limnological variables, such as habitat availability for mosses and other substrates (Douglas & Smol, 1995), extent of open-ice conditions, shifts in physical and chemical limnological characteristics, as well as water level changes (see discussions in Douglas & Smol, 1999). Marked changes occurred especially in the nineteenth century, which could be related to other proxy data suggesting warming (Overpeck et al., 1997).

Diatoms have frequently been used in temperate lakes to infer changes in lake level (reviewed in Wolin & Duthie, 1999). The relationship between diatom community composition and lake depth at northern latitudes, however, has not yet been fully explored. In this paper we will present new data from two subarctic sites – one in Wood Buffalo National Park (WBNP), Canada and one in Fennoscandia – in order to evaluate the relationship between diatom community composition and lake depth in northern regions.

Background

Lake levels vary in response to changes in the local hydrological balance (i.e. precipitation and evaporation over the lake and catchment, and groundwater inflows and outflows) (Street-Perrott & Harrison, 1985). Variations of lake levels in closed basins are only dependent on precipitation and evaporation over the lake's surface and catchment, and thus reflect changing climatic conditions (Street-Perrott & Harrison, 1985). The response of overflowing lakes to climatic conditions is obviously more complex, and changes in lake levels may be muted by changes in outflow; however, it has still been possible to derive records of changes in precipitation and evaporation from outflow lakes (e.g. Digerfeldt, 1986; Winkler et al., 1986). Moreover, by compiling lake-level data at a continental scale it has been possible to infer changes in atmospheric circulation (e.g. Street-Perrott & Roberts, 1983; Harrison & Metcalfe, 1985; Harrison & Digerfeldt, 1993; Yu & Harrison, 1995).

Lake levels have long been recognized as an important influence on diatom community composition (reviewed in Wolin & Duthie, 1999). Although some overlap in diatom species' habitats exists, in general, different diatom taxa characterize shallow-water environments than those of deep water environments. Variations in lake depth result in changes in the relative areas of the pelagic and littoral zones, and therefore the ratio of planktonic to benthic diatoms. Because diatoms are well preserved in lake sediments, changes in the planktonic:benthic diatom ratio through time may indicate changing lake levels, and provide insights into past hydrological systems. In many regions, however, this ratio, has been found to be influenced by other factors, such as pH (e.g. Battarbee, 1984; Stokes & Yung, 1986; Anderson & Renberg, 1992). This paper, therefore, examines whether diatom community composition in lakes at northern latitudes reflects lake depth, and whether past lake depth can be inferred from fossil diatom assemblages.

Study areas

Transfer functions to infer lake levels from diatoms were developed from two similar, but geographically distant, subarctic regions. The first transfer function is based on diatom and environmental data collected from 35 lakes located in the region of Wood Buffalo National Park (WBNP), which lies on the border of Alberta and the Northwest Territories, Canada (Figure 1). The second transfer function is based on data from 53 lakes from subarctic northern Fennoscandia (Figure 2).

WBNP lies within the boreal forest, which is characterized by arboreal vegetation, including *Pinus banksiana* (jack pine), *Picea mariana* (black spruce), *Picea glauca* (white spruce), *Larix laricina* (tamarack), *Populus tremuloides* (trembling aspen), *Populus balsamifera* (balsam poplar) and *Betula papyrifera* (paper birch), interspersed with bogs, muskegs and prairies. The climate is characterized by long, cold winters and relatively warm, dry summers (Environment Canada, 1993). The mean annual temperature in Fort Smith (Figure 1) is –3 °C, and mean annual precipitation is 352.9 mm. Discontinuous permafrost underlies this area.

The geology of the WBNP region varies considerably (Research Council of Alberta, 1970). In the eastern portion of the study area, the bedrock is characterized by granite and granitic gneiss exposures, typical of the Canadian Shield. Most of the lakes in this region exist in depressions formed by glacier erosion along pre-existing planes of weakness (Hutchinson, 1957), and will herein be referred to as 'Shield lakes'. West of the Slave River, the bedrock is comprised primarily of Devonian calcareous rocks, including limestone, dolostone and gypsum (Research Council of Alberta, 1970). Sinkholes, formed by solution and/or collapse, are a common feature in this area (Tsui, 1982). These
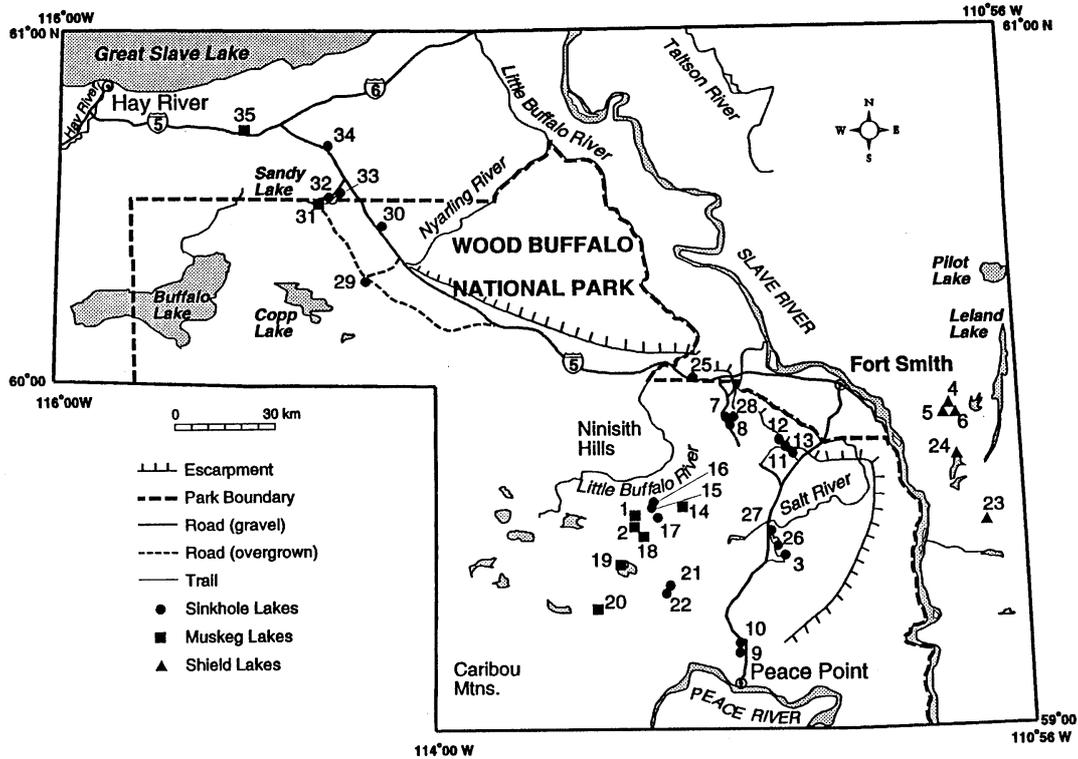
Figure 1. Map showing Wood Buffalo National Park (WBNP) study area and calibration lakes.

sinkholes typically contain lakes, herein referred to as 'sinkhole lakes'. The Hay River Formation, characterized by calcareous shales, outcrops at the western edge of the field area. The relatively impervious nature of the shales and the low-lying topography combine to create poor drainage, leading to the formation of shallow 'muskeg lakes'. The studied lakes are small (most are 0.1–10 ha) in area and have simple morphometries. Maximum depth ranged from 0.5–21.5 m, with a mean of 7.0 m. The sites ranged from ultra-oligotrophic to mesotrophic, and were circumneutral to alkaline (pH range from 7.3–8.9). A complete physical and chemical description of these lakes can be found in Moser et al. (1998) and is summarized in Table 1.

The second calibration lake set is located in northwest Finnish Lapland and spans the boreal coniferous forest zone to the subarctic tundra. The southernmost part of the study area lies in the boreal spruce-pine-birch forest with *Pinus sylvestris* (scots pine) and *Picea abies* (Norway spruce) as dominant tree species. Northwards, the forest gradually changes to pine forest mixed with birch (*Betula pubescens* spp. *tortuosa*), and

further north to birch forest with pine stands. The northernmost corner of the study area consists of mountain birch woodland, and barren grounds. The ground layer of the treeless tundra has a continuous lichen cover and sporadic vascular plants, which consist mainly of dwarf-shrubs, usually *Empetrum nigrum*, *Vaccinium myrtillus* and *Betula nana*. Peatlands are widespread in the northern boreal zone, the majority of them treeless, minerotrophic fens.

Similar to WBNP, the climate is continental, with cold winters and warm summers. The mean annual temperature varies between +0.5 °C in the south and –2 °C in the north. Mean annual precipitation ranges from between 414 and 450 mm in the south and north, respectively, with most of the precipitation occurring in winter in the form of snow and ice. The snow pack often persists until late summer at higher latitudes. Permafrost is discontinuous and sporadic, and is restricted mostly to palsa mounds on peatlands.

The bedrock of the 400 km-long sampling transect consists of Precambrian plutonic (granites and granodiorites) and metamorphic (mica schist, quartzites, phyllites) rocks, except in the northernmost corner of
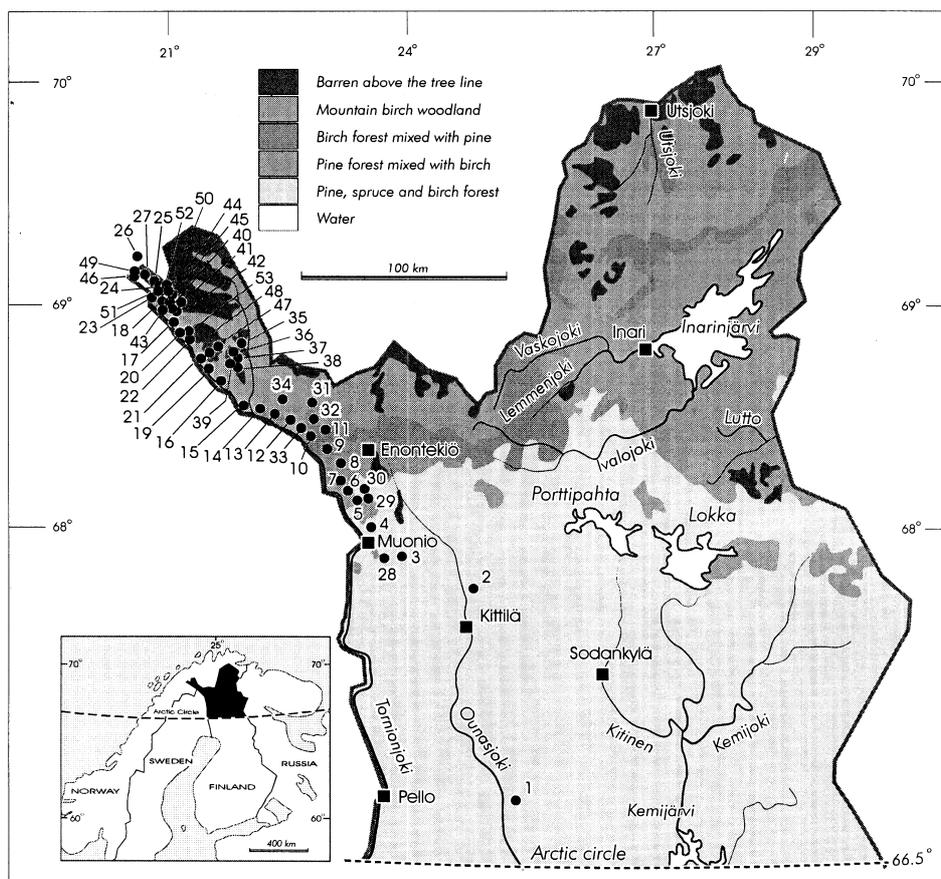
Figure 2. Map showing Fennoscandia study area and calibration lakes.

the study area, where Paleozoic schists and gneisses predominate. The study sites are mostly small, bathymetrically simple, oligotrophic lakes, with a pH range from 5.0–7.7. Maximum depth in the lake data set varied from 0.9–25.0 m, with a mean depth of 6.3 m. A more detailed description of the Fennoscandia lakes can be found in Weckström et al. (1997a, b) and is summarized in Table 1.

Methods

Particulars of the sampling methods and laboratory analyses used for the WBNP and Fennoscandia data sets are available in Moser et al. (1998) and Weckström et al. (1997a, b). Surface lake sediment samples were collected from WBNP between June 28 and July 23, 1993. The upper 1–2 cm of sediment was collected from approximately the centre of the lake, assumed to be the deepest part, using a Glew (1991) corer. Prior to statistical

analysis, the program CALIBRATE (Juggins & ter Braak, 1993) was used to determine the best, if any, transformation necessary to reduce skewness in the distribution of each of the environmental variables. Transformations used in the WBNP data can be found in Moser (1996).

Preparation of diatoms for microscopic identification and enumeration followed standard procedures (Battarbee, 1986). For each of the WBNP samples, a minimum of 600 were enumerated along transects. Identifications were determined using Patrick & Reimer (1966; 1975), Foged (1978; 1981), Germain (1981), Camburn et al. (1984–1986), Krammer & Lange-Bertalot (1986–1991) and Cumming et al. (1995).

Collection and preparation of sediment samples from Fennoscandia were similar to the procedures followed for the WBNP samples with the following exceptions. Surface lake sediment samples were collected from Fennoscandia during the summers of 1994 and 1995 using a LIMNOS®-type gravity corer. For each Fenno-

Table 1. Physical and chemical properties measured in each of the two study areas

Variable	WBNP			Fennoscandia		
	Mean	Max.	Min.	Mean	Max.	Min.
Latitude	59 °48′	60 °43′	59 °15′	68 °26′	69 °11′	66 °55′
Longitude	112 °54′	115 °00′	111 °07′	22 °28′	25 °24′	20 °43′
Altitude (m a.s.l.)	258	305	198	375	931	108
Area (ha)	25.8	338.2	0.1	14.2	115.2	0.9
Perimeter (km)	N/A	N/A	N/A	1.5	7.0	0.4
Catchment area (ha)	N/A	N/A	N/A	211.7	2409.6	4.4
Mire area (% of catchment)	N/A	N/A	N/A	17.3	64.2	0.0
Distance beyond treeline (DBT) (km)	N/A	N/A	N/A	26.45	98.30	−148.40
Maximum depth (m)	7.0	21.5	0.5	5.83	27.00	0.9
Secchi depth (m)	3.7	8.6	0.5	4.1	10.2	0.9
Temperature (°C)	19.8	25.0	16.0	12.6	15.0	16.1
pH	N/A	8.9	7.3	N/A	7.6	5.0
Conductivity ($\mu S\ cm^{-1}$)	261	1030	18	24	45	6
Alkalinity (mg L^{-1} $CaCO_3$)	N/A	N/A	N/A	6.8	15.0	1.0
K (mg L^{-1})	1.9	7.1	0.2	0.4	0.9	0.1
Ca (mg L^{-1})	43.3	193.0	2.3	1.6	3.9	0.3
Na (mg L^{-1})	3.8	26.1	0.5	0.9	1.7	0.2
Mg (mg L^{-1})	17.0	84.4	0.7	0.4	0.1	1.1
Organics (% det. LOI)	N/A	N/A	N/A	47.8	88.0	16.9
Dissolved inorganic carbon (mg L^{-1})	31.4	88.2	1.9	N/A	N/A	N/A
Dissolved organic carbon (mg L^{-1})	14.9	33.7	2.6	N/A	N/A	N/A
Particulate organic carbon ($\mu g\ L^{-1}$)	1006	11000	161	N/A	N/A	N/A
Particulate nitrogen ($\mu g\ L^{-1}$)	103	818	23	N/A	N/A	N/A
Total phosphorus ($\mu g\ L^{-1}$)	12.5	23.6	0.5	N/A	N/A	N/A
Total phosphorus filtered ($\mu g\ L^{-1}$)	5.9	15.7	0.2	N/A	N/A	N/A
Soluble reactive phosphorus ($\mu g\ L^{-1}$)	0.5	2.0	BD*	N/A	N/A	N/A
NH_3 ($\mu g\ L^{-1}$)	20.9	113	BD*	N/A	N/A	N/A
NO_2 ($\mu g\ L^{-1}$)	1.3	5	BD*	N/A	N/A	N/A
SiO_2 (mg L^{-1})	2.14	7.41	0.11	N/A	N/A	N/A
SO_4 (mg L^{-1})	32.9	491.0	0.7	N/A	N/A	N/A
Cl (mg L^{-1})	2.4	21.3	0.4	N/A	N/A	N/A
Al ($\mu g\ L^{-1}$)	6.5	72	BD*	A	N/A	N/A
Zn ($\mu g\ L^{-1}$)	0.9	7	BD*	N/A	N/A	N/A
Cu ($\mu g\ L^{-1}$)	1.6	9	BD*	N/A	N/A	N/A
Ba ($\mu g\ L^{-1}$)	64.2	238.0	7.5	N/A	N/A	N/A
Fe ($\mu g\ L^{-1}$)	54	319	1	190	1200	20
Li ($\mu g\ L^{-1}$)	4.7	21	BD*	N/A	N/A	N/A
Mn ($\mu g\ L^{-1}$)	9.8	61.4	0.6	N/A	N/A	N/A
Sr ($\mu g\ L^{-1}$)	195.7	1670.0	11.8	N/A	N/A	N/A
TOC (mg L^{-1})	N/A	N/A	N/A	8.1	12.6	3.1
Chlorophyll *a* (uncorrected) ($\mu g\ L^{-1}$)	1.4	7.1	0.4	N/A	N/A	N/A
Chlorophyll *a* (corrected) ($\mu g\ L^{-1}$)	0.5	3.5	BD*	N/A	N/A	N/A

*BD = below detection limit.

scandia sample, three separate samples were collected, all from the deepest part of each lake (determined using a Humminbird LCR400 ID portable echo sounder), and homogenized together in the field. For each of the Fennoscandia samples, a minimum of 500 diatom valves were enumerated along transects. The same taxonomic references were used for identification of the Fennoscandia diatoms as were used for the WBNP diatoms, with the addition of Mölder & Tynni (1967–

1973).

A total of 276 and 339 diatom taxa were identified in the WBNP and the Fennoscandia calibration sets, respectively. Diatoms were categorized as planktonic, benthic, tychoplanktonic or unknown based on autecological information found in the references used for diatom taxonomy (see list above), as well as Lowe (1974), Snoeijs (1993–1996) and Round et al. (1990). The dominant planktonic and benthic diatoms are listed

in Table 2. A more complete list of the WBNP and Fennoscandia diatom taxa is available in Moser (1996) and Weckström (1997a, b), respectively. Only those taxa which occurred in a minimum of three lakes, and which attained a relative abundance $\geq 1\%$ in at least one lake, were included in the statistical analyses of both data sets. As a result, 112 and 177 taxa were used in the WBNP and Fennoscandia statistical analyses, respectively. Multivariate statistics, available on the computer program CANOCO version 3.10 (ter Braak, 1988; 1990a), which included detrended correspondence analysis (DCA), canonical correspondence analysis (CCA), detrended canonical correspondence analysis (DCCA) and redundancy analysis (RDA), were used to evaluate the relationship between diatom species' distribution and environmental variables. Transfer functions to infer lake levels from diatom species data were developed from each of the two calibration sets using the program CALIBRATE version 0.3 (Juggins & ter Braak, 1993).

Results and discussion

Does depth influence diatom community composition?

Plots, one for each of the two study areas, show that the percentage of planktonic diatoms generally increases with increasing lake depth (Figure 3). Furthermore, for both lake sets, lakes < 5 m deep never have > 20%

planktonic diatoms. The correlation between these two variables, however, is lower for the WBNP calibration set than the Fennoscandia set ($r^2 = 0.19$ and $r^2 = 0.53$, respectively). The poor correlation between lake depth and the percentage of planktonic taxa in the WBNP lake training set may reflect differences in the way the location of maximum lake depth was determined. For the WBNP data set, maximum depth was assumed to be the centre of the lake, whereas for the Fennoscandia data set maximum lake depth was determined using a Humminbird LCR400 ID portable echo sounder. The poor correlation may also reflect the fact that many of the WBNP sinkhole lakes are extremely clear. As a consequence, lakes that are as deep as 8 m can also have a Secchi depth of ≥ 8 m, and therefore can be dominated by benthic diatoms. It is also possible that the lower correlation is due to limited autecological data for many of the WBNP taxa. Finally, as has been noted by previous workers, the poor correlation between lake depth and the percentage of planktonic species may reflect other factors that affect the distribution of planktonic species, including water quality (Battarbee, 1986), latitude (Allaire, 1997), duration and depth of ice and snow cover (Smol, 1988), wind (Dean et al., 1984) and others.

The above findings, however, do not necessarily negate the use of diatoms to estimate trends in past lake levels at northern latitudes. We used multivariate statistics to further evaluate the relationship between diatom species distribution and depth. Detrended

Table 2. Dominant diatom taxa in each study area

WBNP	Fennoscandia
Planktonic	
Aulacoseira ambigua (Grunow in Van Heurck) Simonsen	several *Aulacoseira* Thwaites species
Cyclotella michiganiana Skvortzow	*Cyclotella rossii* Håkansson
Stephanodiscus minutulus (Kützing) Cleve & Möller	*Cyclotella comensis* Grunow in Van Heurck
Stephanodiscus parvus Stoermer and Håkansson	*Asterionella formosa* Hassall
Asterionella formosa Hassall	*Tabellaria flocculosa* (Roth) Kützing
Fragilaria delicatissima (W. Smith) Lange-Bertalot	
Benthic	
several small *Fragilaria* Lyngbye species	several small *Fragilaria* Lyngbye species
Achnanthes minutissima Kützing	*Achnanthes minutissima* Kützing
Cymbella microcephala Grunow in Van Heurck	*Brachysira brebissonii* R. Ross in Hartley
Navicula cryptotenella Lange-Bertalot	*Brachysira vitrea* (Grunow) R. Ross in Hartley
Navicula pupula Kützing	*Frustulia rhomboides* var. *saxonica* (Rabenhorst) De Toni
Nitzschia cf. *graciliformis* Lange-Bertalot & Simonsen	*Navicula hoeflerii sensu* Ross and Sims
Stauroneis anceps fo. *gracilis* Rabenhorst	*Navicula subtilissima* Cleve
	Pinnularia abaujensis var. *linearis* (Hustedt) Patrick in Patrick & Reimer
	Pinnularia biceps var. *biceps* Gregory
	Pinnularia rupestris Hantzsch in Rabenhorst
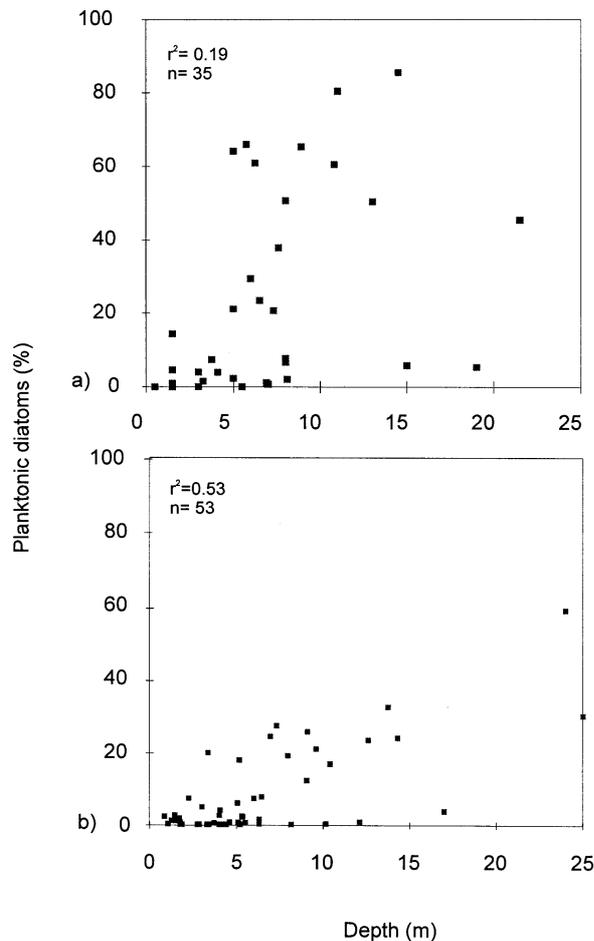
Figure 3. (a) The relationship between maximum lake depth and the proportion of planktonic diatoms in the calibration data-set of 35 WBNP lakes; (b) The relationship between maximum lake depth and the proportion of planktonic diatoms in the calibration data-set of 53 Fennoscandian lakes.

correspondence analysis (DCA) was used to determine the species gradient length (i.e., the maximum amount of variation in species data) (Hill & Gauch, 1980). Because the species gradient was relatively long (i.e. > 2.5) for the WBNP calibration set and relatively short (< 2) for the Fennoscandia data set, canonical correspondence analysis (CCA), a unimodal response model, was used for the WBNP data set and redundancy analysis (RDA), a linear response model, was used for the Fennoscandia data set (ter Braak & Prentice, 1988). However, our analyses showed that results were similar using either CCA or RDA for both data sets. Species data were square-root transformed and rare species were downweighted for all ordination analyses.

Wood Buffalo National Park

CCA was used to identify a subset of environmental variables that explained significant (p ≤ 0.05) and additional amounts of variance in the lake diatom data set. First, variables that were highly collinear with other environmental variables were removed (for details see Moser, 1996). After this deletion step, canonical coefficients and their *t*-test values, as well as intra-set correlations (i.e. the correlation between an environmental variable and a given axis) were evaluated for each of the remaining variables in order to determine which variables were significant in explaining directions of variance in the diatom data (ter Braak, 1988). Fourteen variables, including maximum lake depth, were found to be significant (p ≤ 0.05) in determining axis 1 or 2 of the CCA (Table 3).

Forward selection, with associated Monte Carlo permutation tests, is frequently used to select a subset of variables that explain the species data nearly as well as the full data set for the construction of the CCA biplot. For the WBNP data set, however, the three variables chosen (p ≤ 0.05) using forward selection (i.e. depth, Ca and Fe) only accounted for 22.1% of the total variance explained by all the measured environmental variables. Therefore, all fourteen significant variables, which explained 61.9% of the total variance accounted for by all the measured variables, were used in the construction of the CCA biplot (Figure 4a). The first axis is largely determined by depth (r = 0.65) (Table 3). This relationship is further supported by the significant canonical coefficient of depth with Axis 1 (Table 3). Furthermore, when a constrained CCA was run with depth as the only variable, the eigenvalue of the first axis (λ_1) was significant (p ≤ 0.01) and the ratio of λ_1/λ_2 was large (0.61), indicating that depth explained significant and additional variation in the species data (Table 4). Finally, of the fourteen variables included, depth accounted for 12.8% of the total explained variance.

Fennoscandia

After deleting variables that were highly collinear, forward selection was used to select a subset of environmental variables that explained the species data set nearly as well as the full data set (ter Braak, 1988). Six of the initial 20 variables were selected (p ≤ 0.05), including pH, sediment organic content (LOI), Ca, distance beyond treeline (DBT), Fe, and maximum lake

Table 3. Canonical coefficients, approximate *t*-test values and intraset correlations of the environmental variables for each of the first two CCA axes of the WBNP (35 lake) training set

correlations Variable	Canonical coefficients		*t*-values		Intraset	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Area	−0.10	−0.52	−0.4	−3.3*	0.07	−0.14
Depth	0.69	0.28	2.7*	1.9	0.65	−0.17
pH	−0.16	−0.65	−0.5	−3.6*	−0.25	−0.60
Ca	−0.50	0.32	−2.0	2.2*	−0.39	−0.53
K	0.44	−0.48	2.1	−3.9*	0.05	−0.33
Na	0.00	0.82	0.0	4.4*	0.22	−0.29
Ba	0.29	−0.38	1.1	−2.3*	−0.04	−0.55
SO_4	0.00	−0.44	0.0	−3.3*	−0.32	−0.36
DOC	0.17	0.57	0.7	3.8*	−0.26	0.26
PON	0.26	0.35	1.2	2.7*	−0.37	0.33
NH_3	−0.24	−0.32	−1.3	−3.0*	−0.35	−0.10
TP-F	0.14	0.26	0.05	−3.9*	0.23	−0.08
Mn	−0.55	0.50	−1.8	2.8*	−0.36	0.40
Fe	0.60	−0.49	2.1	−2.8*	0.34	0.44

*Significant at $p \leq 0.05$.

depth (Max depth). These variables captured 68.0% of the total variance explained by all the measured environmental variables. The results of the RDA, with only the six forward-selected and significant variables, are shown in a biplot (Figure 4b). On the basis of this biplot and the summary statistics (Table 5), it is clear that depth is only weakly correlated to axis one ($r = -0.38$). However, calcium ($r = -0.76$), pH ($r = -0.80$), and sediment organic content (LOI) ($r = 0.75$) are strongly correlated with Axis 1, and distance beyond treeline (DBT) ($r = -0.62$) is closely correlated to Axis 2 (Table 5). These results are supported by the canonical coefficients and approximate *t*-tests (Table 5).

A series of constrained RDA's, in which species composition was constrained to only one explanatory variable at a time, were run with the six forward-selected variables to further assess the relative strength of each variable. The results showed that, except for Fe, the remaining five variables all had statistically significant explanatory powers in terms of the variance in the diatom data (Table 6). However, the comparatively low λ_1/λ_2 ratio for depth (0.29), and the relatively small amount of explained variance (5.7%) attributed to depth, indicate that much of the variation in the diatom data is explained by other variables (e.g. pH, Ca, LOI, etc.).

Can diatoms be used to infer trends in subarctic lake levels?

Reliable inference models can potentially be developed for environmental variables having a high ratio of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2) (ter Braak, 1990a,b). Therefore, it should be possible to infer trends in lake depth from diatom species data using either the WBNP or the Fennoscandia data set.

The gradient length of axis 1 (for WBNP is 1.76; for Fennoscandia is 1.71) from detrended canonical correspondence analysis (DCCA), using maximum water depth as the sole independent variable, suggests that either linear or non-linear models could be used. The larger gradient lengths for axes 2–4 (3.23, 2.75 and 2.24 for WBNP and 3.68, 2.11 and 2.03 for Fennoscandia) indicate that there is considerable variation in the diatom data that is not related to maximum depth (Korsman & Birks, 1996).

Therefore, partial least squares (PLS), simple weighted averaging (WA), and weighted averaging partial least squares (WA-PLS) regression and calibration were implemented using the program CALIBRATE version 0.3 (Juggins & ter Braak, 1993). Following the guidelines outlined in Birks (1995) and Korsman & Birks (1996), inverse regression was used to deshrink the data. Diatom data were not transformed for Fennoscandia, but were square root transformed for WBNP. The performance of the predictive ability of the training set in the WA model was estimated by the r^2 between
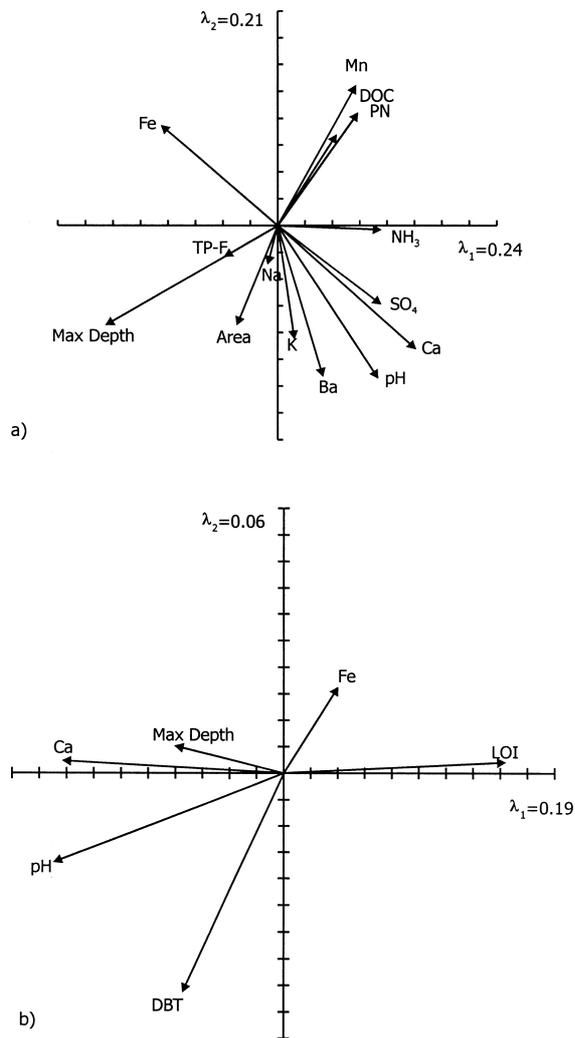
Figure 4. Environmental variables are shown as arrows, such that the length and orientation of the arrows is proportional to their importance and approximate correlation to the CCA axes, respectively (ter Braak, 1988). (a) CCA biplot of WBNP calibration lakes. Both Axis 1 and 2 are significant ($p \leq 0.01$), and eigenvalues are 0.24 and 0.21, respectively. Axis 1 accounted for 10.0% of the variance in the taxa data; whereas, the first two axes together accounted for 18.7% of the variance in the taxa data and 36.9% of the variance in the species-environment relationship; (b) RDA biplot of the Fennoscandia calibration lakes. Both Axis 1 and Axis 2 are significant ($p \leq 0.01$), and eigenvalues are 0.19 and 0.06, respectively. Axis 1 accounted for 18.8% of the variance in the taxa data; whereas, the first two axes together accounted for 24.7% of the variance in the taxa data and 49.6% of the variance in the species-environment relationship.

observed and predicted depth, the standard root mean square error (RMSE), and a root mean square error of prediction (RMSEP). The RMSEP was estimated using

Table 4. Constrained CCA results indicating the contribution of each of the 14 environmental variables, from the WBNP (35 lake) data set, to explaining the variation in diatom assemblages. λ_1 and λ_2 are eigenvalues for axis 1 and axis 2, respectively. p values are based on 99 unrestricted Monte Carlo permutations

Variable	λ_1	λ_1/λ_2	p
Area	0.08	0.26	0.27
Depth	0.15	0.61	0.01
pH	0.14	0.48	0.01
Ca	0.16	0.54	0.01
K	0.09	0.30	0.09
Na	0.08	0.28	0.18
Ba	0.12	0.40	0.01
SO_4	0.11	0.39	0.03
DOC	0.10	0.35	0.03
PON	0.10	0.34	0.04
NH_3	0.08	0.29	0.27
TP-F	0.06	0.22	0.58
Mn	0.11	0.39	0.02
Fe	0.13	0.44	0.01

the 'leave-one-out' jackknife procedure available in CALIBRATE version 0.3 (Juggins & ter Braak, 1993).

For the WBNP calibration set, the lowest RMSEP results were obtained using tolerance down-weighted WA. In general, diatom-inferred values are similar to observed values ($r^2 = 0.70$, RMSE = 2.6 m) (Figure 5a). The predictive ability, however, dropped substantially when the function was evaluated using jack-knifing ($r^2_{jack} = 0.21$, $RMSEP_{jack} = 4.6$ m).

For the Fennoscandia data, a three component weighted averaging partial least squares (WA-PLS) model had the best predictive ability. Similar to the WBNP training set, predicted values of depth are similar to the observed values, and measures of predictive ability ($r^2 = 0.88$, RMSE = 1.8 m) are relatively high (Figure 5b). However, as in the WBNP training set, the predictive ability of the model is reduced with jackknifing

Table 5. Canonical coefficients, approximate t-test values and intraset correlations of the environmental variables for each of the first two CCA axes of the Fennoscandia (53 lake) training set

Variable	Canonical coefficients		t-values		Intraset correlations	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
pH	−0.29	−0.63	−2.6*	−2.6*	−0.80	−0.25
LOI	0.54	−0.49	5.4*	−2.4*	0.75	0.34
DBT	0.16	−0.98	2.0	−5.8	−0.35	−0.62
Ca	−0.45	0.63	−4.6*	3.1*	−0.76	0.39
Fe	0.02	0.00	0.9	−0.7	0.18	0.25
Max depth	0.07	−0.11	0.7	0.4	−0.38	0.08

*Significant at $p \leq 0.05$.

Table 6. Constrained CCA results indicating the contribution of each of the 16 environmental variables, from the Fennoscandia (53 lake) data set, to explaining the variation in diatom assemblages. λ_1 and λ_2 are eigenvalues for axis 1 and axis 2, respectively. p values are based on 99 unrestricted Monte Carlo permutations

Variable	λ_1	λ_1/λ_2	p
pH	0.14	0.97	0.01
LOI	0.13	0.96	0.01
DBT	0.07	0.31	0.01
Ca	0.13	0.99	0.01
Fe	0.04	0.16	0.03
Max depth	0.06	0.29	0.18

$(r^2_{jack} = 0.47, RMSEP_{jack} = 3.9 \text{ m})$. These results indicate that it is possible to estimate trends in depth from our diatom training sets, although our transfer functions are less robust than those developed for inferring, for example, pH (e.g. Birks et al., 1990), nutrients (e.g. Reavie et al., 1995; Bennion et al., 1996), or salinity (e.g. Fritz et al., 1993; Wilson et al., 1996). The low predictive ability determined with jackknifing may, in part, reflect our relatively small sample sizes. Such small data sets are typical for high latitude environments owing to high sampling costs and other logistical difficulties. However, larger data sets should improve our ability to predict changing lake levels in arctic and subarctic regions.

As well, the predictive ability of a training set is largely controlled by the gradient(s) exploited during the sampling campaign. The Fennoscandia lake set was collected following a temperature gradient, whereas the WBNP lake set was collected with the goal of maximizing differences in surrounding vegetation. It is expected, therefore, that if lakes were sampled along depth gradients then the predictive ability of our findings would be greater.

What do changing lake levels mean in subarctic lakes?

In order to accurately interpret changing lake levels inferred from fossil diatoms, it is critical to have knowledge of the lake basin morphometry. It is important to remember that the greatest lake level possible in any given lake is ultimately determined by the morphometry of that lake basin, and therefore it is possible to infer lake depths from transfer functions that are topographically impossible (Birks, 1998). We do, however, believe that diatom-based transfer functions
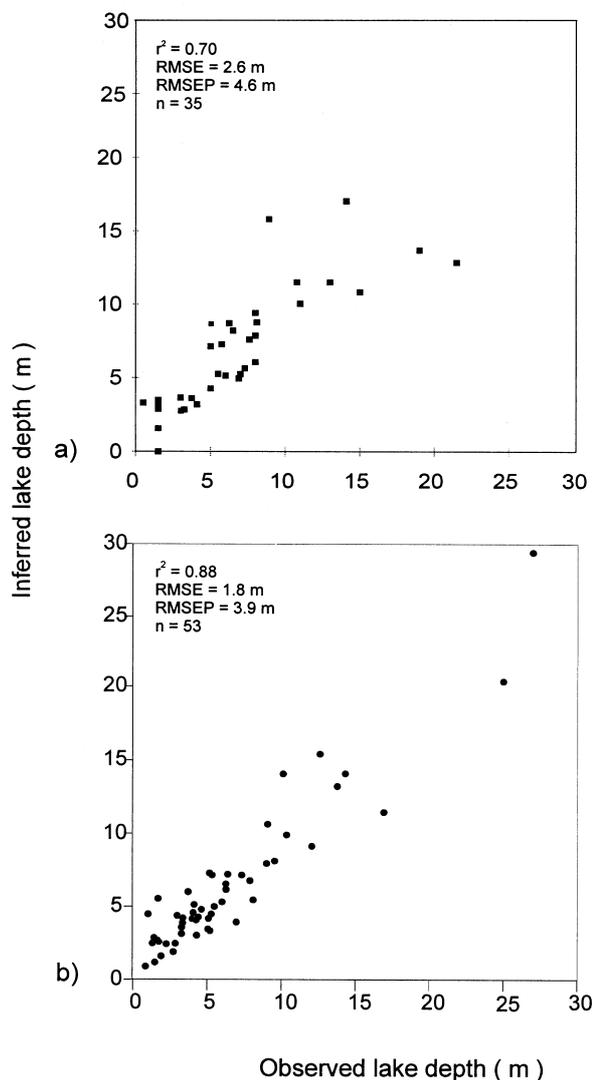
Figure 5. (a) Comparison between actual vs. diatom-inferred lake depth, for WBNP data, using tolerance down-weighted simple weighted averaging (WA); (b) Comparison between actual vs. diatom-inferred lake depth, for Fennoscandia data, using a 3-component weighted-averaging partial least square (WA-PLS) regression technique.

can be used to track overall *trends* in lake levels, and provide an objective assessment as to *directions* of changing lake levels.

Similarly, it is critical to have an understanding of the hydrological balance of the lake being studied in order to interpret the causes of past lake level fluctuations. Many of the Shield lakes in the southern Northwest Territories and Fennoscandia are in impermeable granitic bedrock, with little or no groundwater inflows, and minimal outflows. If there are no

outlets or overflows, then lake levels should primarily reflect changes in effective moisture.

Unfortunately, little information is available on water balances of the WBNP sinkhole lakes, making interpretation of lake level changes difficult. Most of the sinkhole lakes sampled in this study had no input or output streams. Furthermore, Drake (1970) indicates that the WBNP sinkholes are located in the recharge area of the regional groundwater system. Groundwater inflow, therefore, should be minimal. Groundwater outflow, however, could vary considerably from lake to lake, and also over time. If groundwater outflow is relatively small, then the water balance of the WBNP sinkhole lakes would largely depend on precipitation and evaporation. Comprehensive hydrological studies in this area would be necessary, however, before such assumptions could be made.

The muskeg lakes of WBNP, typical of many sub-arctic regions, are so shallow, and the topography of the area so flat, that it is unlikely water levels in these lakes would change considerably, except to possibly dry completely. An increase in the water balance would likely lead to overflow, whereas a decrease in the water balance would likely result in a larger decrease in lake area than in lake depth. Changes in diatom community composition in the peats surrounding the lakes may provide more information on changing hydrological conditions (see above). Interpretation of lake level changes in any of these lake types also requires consideration of other variables, such as forest fires, changes in vegetation, changes in permafrost and human activity.

Summary and conclusions

A variety of approaches can ultimately be used to study past hydrological changes, especially those related to climate change, at northern latitudes. These approaches include inferring, either directly or indirectly from diatoms, water content in peats, flooding frequencies, river discharge, lakewater salinity, ice coverage and lake levels. In this paper we have developed two transfer functions that allow trends in past lakewater depths to be inferred from fossil diatoms. Using these transfer functions, it should be possible to compare trends in changing lake depth to previously documented climate change in order to further our understanding of the links between northern hydrology and future climate warming. Although our statistical analyses suggest that the predictive values of these inference functions are not as strong as those developed to infer pH, nutrients or salinity, we anticipate that larger sample sizes and an increased depth gradient would greatly improve the performance.

Many of our examples are based on recent or preliminary work, and there is great potential for further applications of diatoms and paleolimnological methods to the fields of hydrology and paleohydrology. Furthermore, as discussed in earlier works (e.g. Digerfeldt, 1986), multi-indicator approaches strengthen hydrological inferences. For example, Korhola et al. (see this volume) have demonstrated that Cladocera and Chironomidae can be used to predict hydrological change. We anticipate that in the next decade paleolimnogical methods will provide many new insights into northern paleohydrology.

Acknowledgements

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