Late-Holocene environmental history of two New England ponds: natural dynamics versus human impacts

Dörte Köster[1,2,]* and Reinhard Pienitz[2]

(*[1]Paleolimnology Paleoecology Laboratory, Centre d'études nordiques and Department of Geography, Université Laval, Québec, Québec G1K 7P4, Canada; [2]Department of Biology, University of Waterloo, 200 University Avenue W, Waterloo, Ontario N2L 3G1, Canada)*

Received 10 January 2005; revised manuscript accepted 1 December 2005

A HOLOCENE RESEARCH PAPER

Abstract: Analyses of sedimentary diatoms in two New England ponds reveal limnological changes during the past 2500 years that are related to climatic change, anthropogenic activities and natural disturbance. Deforestation in the lake catchments during the eighteenth and nineteenth centuries temporarily affected diatom assemblages, with subsequent recovery. However, algal communities did not return completely to presettlement conditions as a result of long-term trends in climatic change, small-scale natural disturbances and delayed watershed recovery from acidification. A short-term rise in diatom-inferred dissolved organic carbon (DOC) in Levi Pond was related to partial removal of vegetation by logging in the catchment, and a similar DOC increase at North Round Pond is correlated with a hurricane and increased aquatic productivity. At Levi Pond, increasing diatom-inferred DOC concentrations during the past *c.* 2000 years likely reflect a long-term increase in allochthonous organic matter and peat development in the watershed related to moister conditions, supported by corresponding patterns in the stable-isotope, chironomid and pollen records. These results correspond with moisture patterns in adjacent areas inferred from pollen and sediment analyses, suggesting that diatoms in Levi Pond recorded a larger regional trend in increasing moisture. This is the first study in a temperate region that links diatom-inferred DOC concentration to past changes in moisture balance, suggesting that fossil diatoms may be a promising proxy for future palaeohydrological studies in temperate regions. However, more studies are necessary to separate the effects of peatland growth and allochthonous organic-matter input on lake-DOC concentrations.

Key words: Palaeolimnology, diatoms, forest disturbance, dissolved organic carbon, moisture, New England, late Holocene.

Introduction

Intensive land use by European settlers, such as forest clearance, agriculture, and urban and industrial development, h AD a marked impact on terrestrial and aquatic ecosystems in New England, USA (Davis and Norton, 1978; Engstrom *et al.*, 1985; Foster, 1995; Foster *et al.*, 1998). These impacts are often described in relation to the natural 'baseline conditions', namely the ecosystem state before arrival of Europeans (Foster *et al.*, 1998). However, the presettlement environment and vegetation were highly variable, probably related to climatic change, natural disturbances such as fire and hurricanes, and native people's activities (Gordon, 1953; Russell, 1983; Gajewski, 1987; Rhodes and Davis, 1995; Fuller *et al.*, 1998). Since the interaction between climatic change and human disturbance may produce major changes in ecosystem structure and dynamics, it is essential to understand presettlement ecosystem conditions in order to assess human impact. Insights into past climatic impacts on natural systems and their interaction with human disturbance will also help predict how human-altered ecosystems will respond to future climatic change.

One major concern in studying human impacts on ecosystems is the degree of disturbance and the nature and pace of recovery. Much of the historically deforested areas in the New England uplands were abandoned and reforested in the late nineteenth century because of relocation of US agriculture to mid-western states and of rural populations to urban centres

*Author for correspondence at: Department of Biology, University of Waterloo, 200 University Avenue West, Waterloo, Ontario N2L 3G1, Canada (e-mail: dkoster@sciborg.uwaterloo.ca)

 10.1191/0959683606hl947rp

(Foster, 1995). However, vegetation composition and lake environments have not returned to presettlement conditions, indicating that other disturbances, such as logging, forest diseases, hurricanes and fire suppression continue to influence the watersheds (Fuller *et al*., 1998; Francis and Foster, 2001). Since many palaeolimnological studies in New England have focused on continued effects of human activities on lakes, there is a need for assessments of lake and watershed recovery after disturbance has ceased (Francis and Foster, 2001).

Palaeolimnological studies using fossil diatoms have been applied in a wide range of investigations to infer long-term dynamics of lakes and their watersheds (Smol, 2002; Pienitz and Vincent, 2003). Diatoms, which are often well preserved in lake sediments, are powerful indicators of past environmental change, such as lake trophic status (Hall and Smol, 1999) and lake acidification (Battarbee *et al*., 1999). Applications of diatoms to climatic (Smol and Cumming, 2000) and hydrological studies (Moser *et al*., 2000) are mostly conducted in (sub-) arctic and alpine regions, at ecotonal boundaries, and in semi-arid areas, but seldom in temperate regions. The reason for this may be that palaeoclimatic inferences in temperate, forested lake regions are challenging, because lakes are hydrologically open (Smol and Cumming, 2000), and pH and trophic status often exert a dominant influence on diatom assemblages in the southern, more densely populated areas (Dixit *et al*., 1999). However, diatoms are sensitive to dissolved organic carbon concentrations (DOC) (Kingston and Birks, 1990; Pienitz and Smol, 1993; Korsman *et al*., 1994; Fallu and Pienitz, 1999), which in turn are strongly controlled by precipitation patterns (Schindler *et al*., 1996). They may therefore have some potential for palaeoclimatic inferences in dilute temperate lakes. However, this has not yet been tested, presumably for the reasons discussed above.

The main question we address in this study is: which were the driving natural and anthropogenic factors affecting the past lake environment? More specifically, we investigate the following problems: what changes in the physical and chemical lake characteristics can be identified? How do these changes relate to natural processes and human disturbances in the watershed? How do the lakes respond to recovery of the watershed vegetation? We attempt to answer these questions by reconstructing the environmental history of two New England lakes for the last *c*. 2000 years through fossil diatom analyses in the context of regional vegetation dynamics and disturbance history.

Study sites

The study sites were chosen primarily for susceptibility to climate change and natural disturbances and for their similarity in morphology and human disturbance history. Levi Pond and North Round Pond are small oligotrophic and acidic headwater lakes with similar elevation and watershed:lake area ratio (Table 1). The maximum water depth is 3.4 m in North Round Pond and *c*. 3 m in most of Levi Pond, with only a narrow deep depression in the centre of the lake of 6.8 m. The bedrock mainly consists of Palaeozoic gneiss and schist with some granitic intrusions, which is overlain by Wisconsinan till and humus-rich organic soils (Siccama, 1974). According to historical data, both lakes have undergone anthropogenic disturbance by logging in the watershed after European settlement and subsequent re-establishment of the vegetation. Both lakes are situated within mixed hardwood forest, which is mainly composed of *Fagus grandifolia* Ehrh. (beech), *Quercus borealis* F. Michx. (oak), *Tsuga canadensis* (hemlock), *Betula* spp. (birch), *Pinus strobus* (pine) and *Acer saccharum* Marshall (sugar maple); with additionally *Castanea dentata* (Marshall) Borkh. (chestnut) in the North Round Pond catchment and a belt of *Picea* (spruce) along the edges of Levi Pond.

Table 1 Lake and watershed characteristics of the study sites

	Levi Pond	North Round Pond
Town	Groton	Winchester
State	Vermont	New Hampshire
Latitude	44°15.6′N	42°50.8′N
Longitude	72°13.4′W	72°27.2′W
Elevation (m a.s.l.)	501	317
Lake surface area (ha)	9	4.3
Watershed area (ha)	57	21.3
Watershed:lake area ratio	6:1	5:1
Maximum depth	6.8	3.4
pH	4.9–5.6	5.7–6.1
Alkalinity (μeq/L)	−0.2–1.6	20–44
TP (μg/L)	7–11	10–14
SO_4 (mg/L)	3.9–7.8	3–4
Chl *a* (μg/L)	n.d.	3.9
DOC (mg/L)	4.8	n.d.
Coring date	11 Nov. 1994	20 Feb. 1997

Alkalinity, total phosphorus (TP), sulphate (SO_4) and pH data for North Round Pond represent ranges from two measurements taken in August 1992 and February 1993; whereas chlorophyll a (Chl *a*) was measured in August 1992. Alkalinity, pH and sulphate data for Levi Pond are ranges for several measurements from different seasons taken each year from 1981 to 1989 and in 1999. TP for Levi Pond is the range of six measurements of spring TP taken from 1987–2003. The data for North Round Pond were provided by the Watershed Management Bureau, New Hampshire Department of Environmental Sciences (Robert Estabrook). The data for Levi Pond were provided by the Water Quality Division of the Vermont Department of Environmental Conservation, Waterbury (Neil Kamman).
n.d., no data.

Some differences in location, site characteristics and natural disturbance history are important for interpreting the palaeolimnological record. At Levi Pond, situated in the Green Mountains of Vermont (Figure 1), a forested wetland about 15 m wide covers 40% of the shoreline at the western edge (Neil Kamman, Vermont Department of Environmental Conservation, personal communication, 2004). Levi Pond is more acidic and has lower nutrient concentrations than North Round Pond (Table 1). Major logging around Levi Pond was recorded in the mid-1800s, and the watershed was used briefly for sheep pasture. Afterwards, moderate logging in the watershed continued until *c*. 1950. Near the end of the 1970s, the natural fish fauna was destroyed by application of rotenone, a widely used piscicide and insecticide, in order to subsequently stock lake trout for fishing.

The Pisgah State Park, New Hampshire, where the watershed of North Round Pond is located, experienced episodic logging after AD 1750, but no house construction or farming (Foster, 1988). However, for the watershed of North Round Pond, only minor cutting in the early 1900s is documented (Foster, 1988). In 1938 a hurricane damaged the watershed vegetation. About half of the catchment was moderately affected, and *c*. 25% was severely damaged (Foster, 1988). In the undamaged part, several old-growth forest stands are preserved (Foster, 1988). A lake survey in 1950 stated that the shoreline was 100% forested (Bob Estabrook, New Hampshire Department of Environmental Services, Concord, personal communication, 2004).

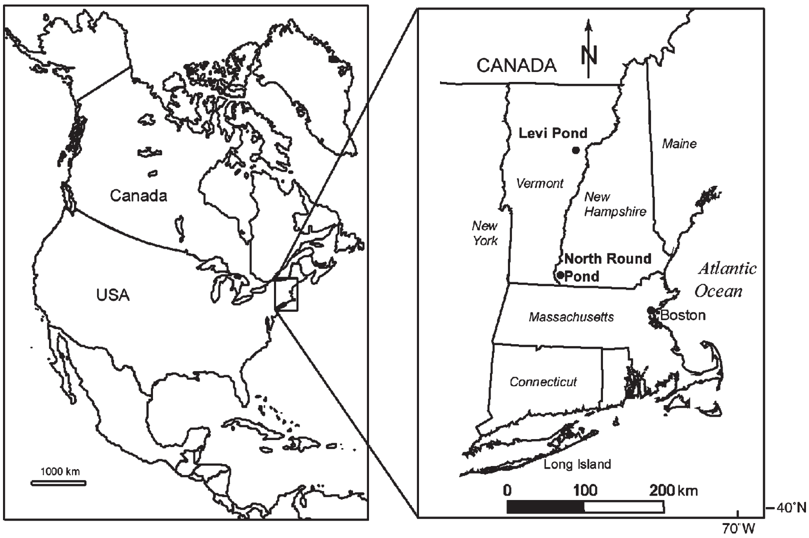

Figure 1 Map of the study region and location of Levi Pond and North Round Pond in New England

Methods

Sediment cores of 1.15 m (North Round Pond) and 1.02 m (Levi Pond) length were taken at the deepest point of the lakes with a clear Lexan coring tube (diameter, 10 cm) fitted with a rubber piston. The sediment cores were subsampled at 1-cm intervals and stored at 4°C.

Bulk-sediment samples of 1 cm (Levi Pond) and 4 cm (North Round Pond) thickness were radiocarbon-dated by accelerated mass spectroscopy at Beta Analytic Laboratories, Miami, Florida. For North Round Pond, four levels were combined, because there was not enough material left after the other analyses. Radiocarbon dates (^{14}C yr BP) were calibrated (cal. yr BP) using the computer program CALIB version 4.3 (Stuiver and Reimer, 1993) and converted to calendar years (yr AD) by adding 50 years in order to permit consistent discussion of palaeolimnological data in the historical context (Table 2). The dates of the other samples were estimated by linear interpolation between ^{14}C dates. The recent chronology was established by the ^{210}Pb technique and ages were calculated with a Constant Rate of Supply (CRS) point transformation model (Binford, 1990). The settlement horizon for North Round Pond was based on the rise of agriculture-indicator pollen, such as *Ambrosia* and *Rumex*, and was assigned to the date of establishment of the town of Winchester in AD 1733. Linear interpolations were made between the ^{14}C dates, the settlement date, and the oldest ^{210}Pb date (Figure 2). The chronology as well as pollen and chironomid stratigraphies of North Round Pond, all analysed on the same core, were previously published by Francis and Foster (2001).

Organic matter was measured at 1-cm intervals by standard loss-on-ignition procedures at 550°C (Heiri *et al.*, 2001).

Diatom extraction followed standard strong-acid-digestion techniques (Pienitz *et al.*, 1995), and a minimum of 500 valves per slide were enumerated under 1000× magnification. Species were identified according to standard and regional taxonomic references (Krammer and Lange-Bertalot, 1986, 1988, 1991a, b; Camburn and Charles, 2000; Fallu *et al.*, 2000). The fossil assemblages were subdivided into diatom zones by optimal partitioning using the computer program ZONE version 1.2 (S. Juggins, unpublished program, 1991), and the number of significant zones was determined by the broken-stick model (Bennett, 1996).

Sediment preparation of subsamples for pollen analysis followed standard procedures (Faegri and Iversen, 1975). Pollen was counted to a total of 500 tree and shrub grains at 400× magnification. Pollen percentages are based on total terrestrial pollen grains, excluding aquatics, but including agricultural grains (ie, herbs). Identification is based on standard taxonomic keys (McAndrews and Boyko-Diakonow, 1989; Moore *et al.*, 1991). The sum of agricultural indicator pollen was calculated by combining Poaceae, *Ambrosia*, *Artemisia*, *Rumex* and *Zea* pollen counts. The pollen data from North Round Pond presented here were previously published by Francis and Foster (2001).

Quantitative reconstructions of environmental variables and calculation of associated sample-specific reconstruction errors were carried out with the computer program C^2 (Juggins,

Table 2 Calibrated radiocarbon dates for Levi Pond and North Round Pond sediments, USA

	Depth (cm)	Lab. number	Age ^{14}C yr BP	Age cal. yr BP	Age yr BC/AD
Levi Pond	29–30	AA 35307	1100	1010±80	1040
	45–46	AA 35308	1740	1640±100	410
	59–60	AA 35309	2150	2090±100	−40
	79–80	AA 35310	2415	2420±50	−370
North Round Pond	44–48	n.a.	570	560±120	1460
	65–69	n.a.	1000	920±240	1130
	91–95	n.a.	1570	1490±200	560
	116–120	n.a.	1650	1530±200	520

Dating was performed on bulk sediment samples at Beta Analytic, Miami, Florida. Dates for North Round Pond were presented previously by Francis and Foster (2001).
n.a., not available.

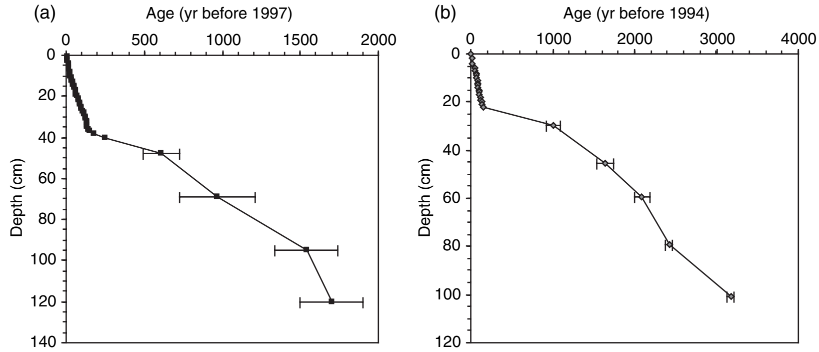

Figure 2 Age–depth curves for (a) Levi Pond, and (b) North Round Pond using (from Francis and Foster, 2001) ^{210}Pb and ^{14}C dating methods, as well as the settlement horizon based on pollen agriculture indicators assigned to AD 1750 yr. Calibrated ^{14}C dates were converted to years AD by adding 50 years in order to fit with ^{210}Pb dates

2003). The diatom-based inference models were based on a calibration set including 82 New England lakes, which were selected from a larger calibration set (Dixit *et al.*, 1999) in order to limit its geographical extent to that of the palaeolimnological study sites. We chose the method of weighted averaging (WA) with inverse de-shrinking for pH and Gaussian logit regression (GLR) for total phosphorus (TP), because these performed best in comparison with the instrumental record in another New England Pond (Köster *et al.*, 2004). DOC did not explain a significant amount of species variation in the model used for TP and pH. Therefore a model encompassing 59 lakes situated along a latitudinal transect from the boreal forest to the tundra in northern Québec was applied (Fallu and Pienitz, 1999) for dissolved organic carbon (DOC) reconstructions. Errors for quantitative inferences were estimated by bootstrapping.

For detecting major trends in the fossil diatom assemblages, principal components analysis (PCA) with intersample distance scaling and covariance matrix was carried out on species percentage data with the computer program CANOCO for Windows, version 4.0 (ter Braak and Šmilauer, 1998). The choice for this linear method was based on the gradient length in fossil species data of 1.6 SD and 1.7 SD in North Round Pond and Levi Pond, respectively, as estimated by detrended correspondence analysis. However, the PCA of Levi Pond diatom data resulted in a severe 'horse-shoe effect', which is a common problem with PCA, if some unimodal species distributions are present (Birks, 1995). Therefore, we used correspondence analysis (CA) instead of PCA on the diatom data of Levi Pond. Correlations between reconstructed variables, ordination axes, and species abundances were estimated using linear regression and *t*-test implemented in the software S-Plus version 4.5.

In order to assess the reliability of quantitative reconstructions, the fit of the fossil samples to the variables of interest was estimated. The squared residual distances of the modern and fossil samples to the first axis in a canonical correspondence analysis (CCA) were compared which was constrained to the respective variable. Fossil samples with a residual distance equal or larger than the residual distance of the extreme 5% (or outside the 95% confidence interval) of the modern training set samples are considered to have 'very poor' fit to the variable. Samples with values equal or larger than the extreme 10% have 'poor fit' and all other samples have a 'good fit' (Birks *et al.*, 1990). In order to assess the reliability of reconstructed values, ANALOG (H.J.B. Birks, unpublished program, 1991, john.birks@bot.uib.no) was carried out based on squared chord distance (Overpeck *et al.*, 1985).

Results

Levi Pond (Vermont)

Four significant zones with different diatom assemblages were identified in the sediment core from Levi Pond (Figure 3). Diatom assemblages in zone I consisted mainly of *Tabellaria flocculosa* (Roth) Kützing str. IIIp sensu Koppen, *Pinnularia mesolepta* (Ehrenberg) W. Smith, *Brachysira brebissonii* Ross in Hartley *Cymbella hebridica* (Grunow) Cleve, *Navicula subtilissima* Cleve, *N. modica* Hustedt and *N. heimansii* Van Dam & Kooyman. These species have been mainly observed in acidic and oligotrophic New England lakes (Davis *et al.*, 1994a; Dixit *et al.*, 1999).

In zone II, from 54 cm (*c.* AD 100) upwards, *Aulacoseira distans* var. *distans* (Ehrenberg) Simonsen increased from around 5% to around 15% relative abundance. At the same time, *Brachysira brebissonii*, *Navicula modica*, *Navicula mediocris* Krasske and *Nitzschia perminuta* (Grunow) M. Peragallo decreased slightly, whereas *Eunotia hemicyclus* (Ehrenberg) Ralfs started to appear more commonly.

With the third diatom zone at 30 cm (*c.* AD 1000), *Aulacoseira distans* var. *distans* increased further to around 20%, simultaneously with an important increase of *Eunotia hemicyclus* by *c.* 10% and a small but abrupt decrease of *Pinnularia interrupta* W. Smith. *Melosira arentii* (Kolbe) Nagumo & Kobayasi temporarily became a dominant part of the assemblage from *c.* AD 1800 to 1959, coincident with the high abundance of agricultural indicators in the pollen profile (Figure 4a). This change is also recorded by the diatom sample scores on PCA axis 2 (Figure 3).

In the most recent sediments, from 7 cm to 0 cm (*c.* AD 1940 to 1997, zone I), *Melosira arentii* and *Eunotia hemicyclus* declined, whereas *Aulacoseira lirata* (Ehrenberg) Ross increased from almost 0 to 10%, and *Aulacoseira distans* var. *distans* reached maximum abundances of 40%.

The small-scale changes throughout zone II and III form together a long-term trend in diatom assemblages starting at *c.* AD 100 and continuing until the early twentieth century, indicated by a gradual increase in fossil diatom sample scores on PCA axis 1 (Figure 3). This long-term trend corresponds both to increasing proportions of planktonic or tychoplanktonic (centric) diatoms (eg, *Melosira arentii*, *Aulacoseira* spp.) at the expense of benthic (pennate) diatoms (eg, *Navicula* spp., *Pinnularia* spp.) and increased diatom-inferred DOC values (Figure 4d, Table 3). This development also coincides with a gradual increase of *Picea* pollen abundances from *c.* AD 100 to 1950 (Figure 4c; Table 3).

The CCA with modern and fossil samples showed that the fossil assemblages have variable fit to the DOC model (Figure 4d). Almost half of the samples (22) have good fit to DOC,

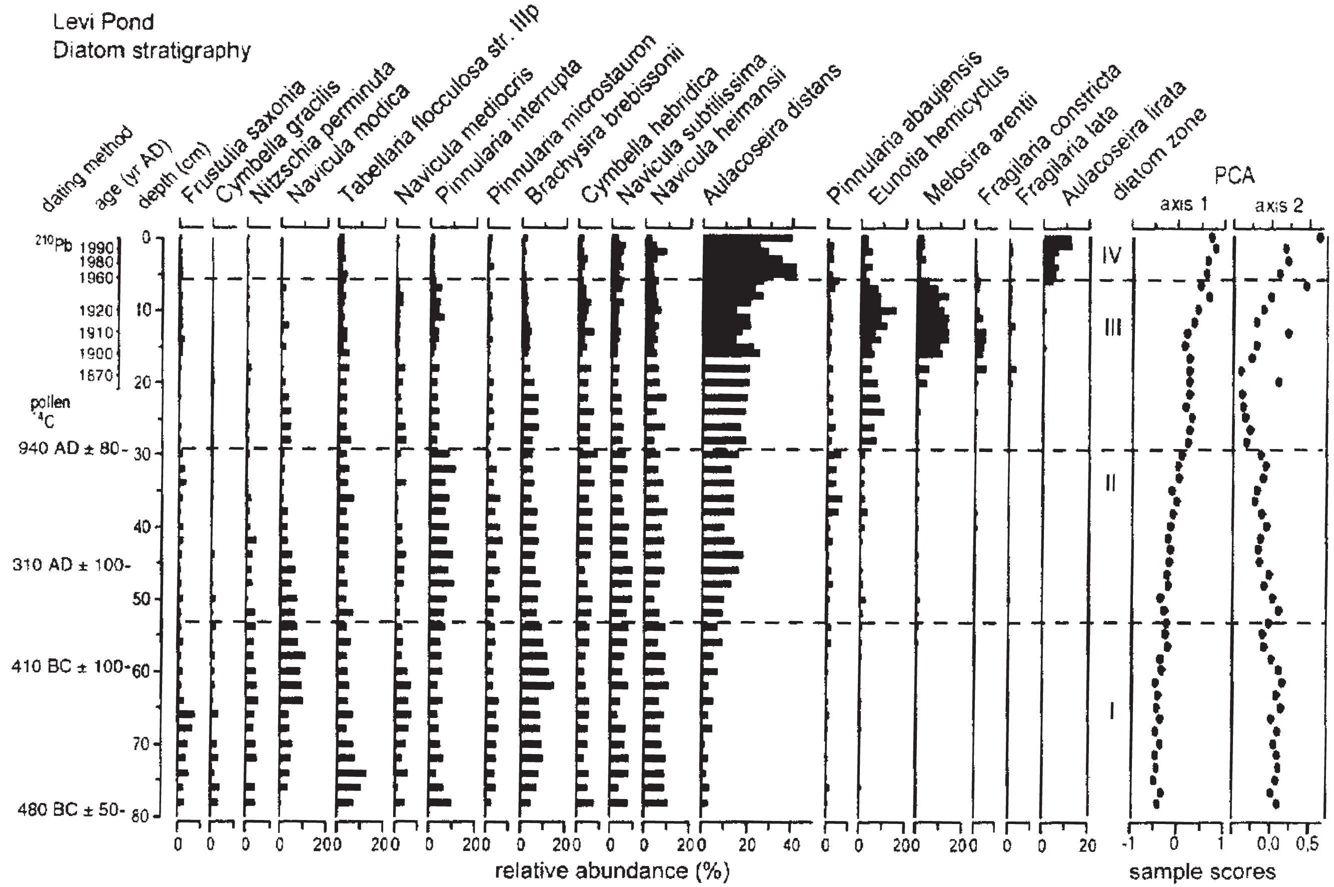

Figure 3 Diatom stratigraphy of Levi Pond with major zonation and fossil sample scores on CA axes 1 and 2. Diatom taxa are arranged according to their chronological appearance in the sediment sequence. Eigenvalues of CA axes 1 and 2 are 0.23 and 0.08, respectively

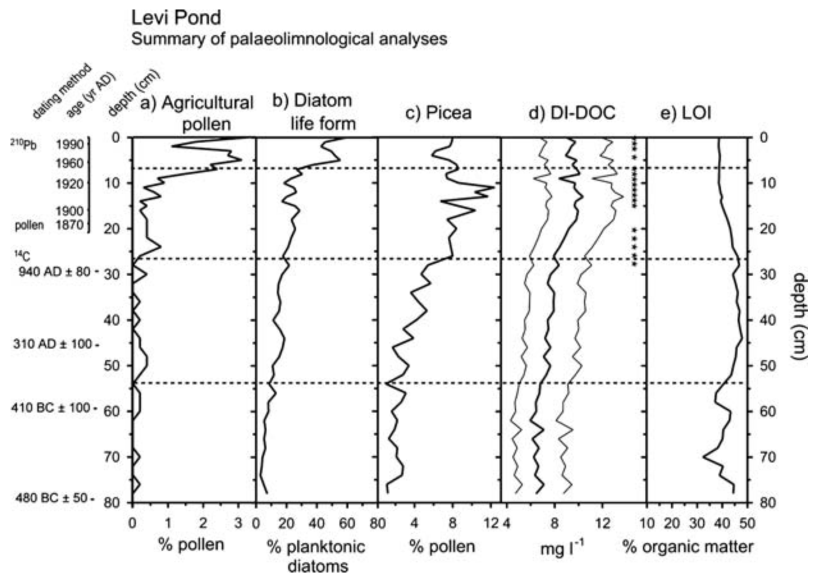

Figure 4 Summary of palaeolimnological analyses for Levi Pond. (a) Percentage of agricultural pollen indicators relative to total upland pollen, (b) percentage of planktonic diatom taxa, (c) relative abundance of *Picea* pollen, (d) diatom-inferred DOC, (DI-DOC), (e) percent organic matter as estimated by loss-on-ignition (LOI). (Asterisks indicate samples with very poor fit to DOC indicating unreliable value)

eight levels have poor fit and 17 samples have very poor fit, indicating that reconstructions for the latter samples are less reliable. However, several samples with good fit were present in each diatom zone, suggesting that the model is appropriate for reconstructing major trends in DOC concentrations of Levi Pond. As almost all fossil samples from Levi Pond show a very poor fit to both the pH and TP model (data not shown), we do not present the inferences derived from these models.

The results of the program ANALOG indicate that all fossil samples have a high dissimilarity compared with the modern samples within the calibration data set. This indicates that the values of the reconstructions are not entirely reliable. The fossil species that are absent in the model have mainly low fossil abundances (only *N. modica* and *Pinnularia abaujensis* h AD a sufficient abundances to be included in Figure 3) and the goodness of fit showed mostly good agreement between the model and the core samples. Therefore we are confident that the reconstructed trends, eg, the direction and timing of changes, are reliable. We still need to note that the poor fit may indicate imprecise values. The latter is confirmed by the comparison of a recent measurement of DOC in Levi Pond in July 1999, which was *c.* 4 mg/l lower than the reconstructed value (4.8 versus 9 mg/l, Vermont Department of Environmental Conservation, Kamman *et al.* 2004).

The LOI profile of Levi Pond showed two minima at the core bottom around 70 cm depth (*c.* 270 BC) with 33% and around 56–58 cm (AD 0) with 38% (Figure 4e). Afterwards, the organic matter in the sediments increased up to 48% at 45 cm (*c.* AD 400), remained stable until 28 cm (*c.* AD 1200), and started to decrease above 28 cm. From 10 cm to the top of the core (AD 1920–1994) it remained quite stable.

Table 3 Correlation matrices of PCA (North Round Pond) and CA (Levi Pond) axes, based on diatom percentage data, diatom-inferred limnological variables, and selected diatom and tree taxa for (a) Levi Pond, and (b) North Round Pond

	Ax1	Ax2
(a)		
MA	0.26**	0.19**
AD	0.82**	0.02
PIC	0.62**	0.14*
DOC	0.78**	0.10*
(b)		
pH	0.09	0.75*
TP	0.87*	0.03
DOC	0.03	0.60*

Numbers marked by * indicate a significant correlation at the 95% confidence limit, and ** indicate a correlation at the 99% confidence limit.

MA, *Melosira arentii*; AD, *Aulacoseira distans.* TP, total phosphorus; DOC, dissolved organic carbon; PIC, *Picea* pollen percentage.

North Round Pond (New Hampshire)

Diatom assemblages in North Round Pond were dominated by oligotrophic to mesotrophic species throughout the last *c.* 1500 years (Figure 5), which is also indicated by the diatom-inferred TP (DI-TP) values that range between 10 and 15 μg/l (Figure 6a). We distinguished three significant changes in the fossil diatom assemblages as detailed below.

In the first zone (95–52 cm; *c.* AD 450–1300), diatom assemblages were dominated by *Tabellaria flocculosa* str. IIIp, *Cyclotella stelligera* CLEVE & GRUNOW, *Fragilaria pinnata* Ehrenberg, and *Navicula heimansii*. With the beginning of zone II at 52 cm (*c.* AD 1300), benthic species, such as *Fragilaria* spp. and *Navicula* spp., increased at the expense of the planktonic species *Cyclotella stelligera* and *Tabellaria flocculosa* str. IIIp (Figure 6e). The diatom-inferred pH (Figure 6b) and TP (Figure 6a) increased slightly. At 32 cm (*c.* AD 1800, Zone III), *Fragilaria* spp. abundance increased further, coincident with a decrease of organic matter (Figure 6c) and the rise of agricultural indicator pollen. During the most recent period (14–0 cm; *c.* AD 1940–1997; Zone IV) several acidophilic taxa (*Eunotia* spp., *Aulacoseira* spp. and *Asterionella ralfsii* W. Smith) appeared or increased in abundance. Diatom-inferred pH decreased (Figure 6b), while diatom-inferred DOC increased (Figure 6d), coincident with the increase of organic matter in the sediments (Figure 6c). Both inferred pH and TP are significantly correlated with PCA axis 1 of the fossil diatom assemblages, while DOC is correlated with PCA axis 2 (Table 3), indicating that the reconstructed values actually reflect main patterns in fossil diatom assemblages.

The good fit of the fossil diatom assemblages at North Round Pond to DOC (except for two levels with poor fit at 0

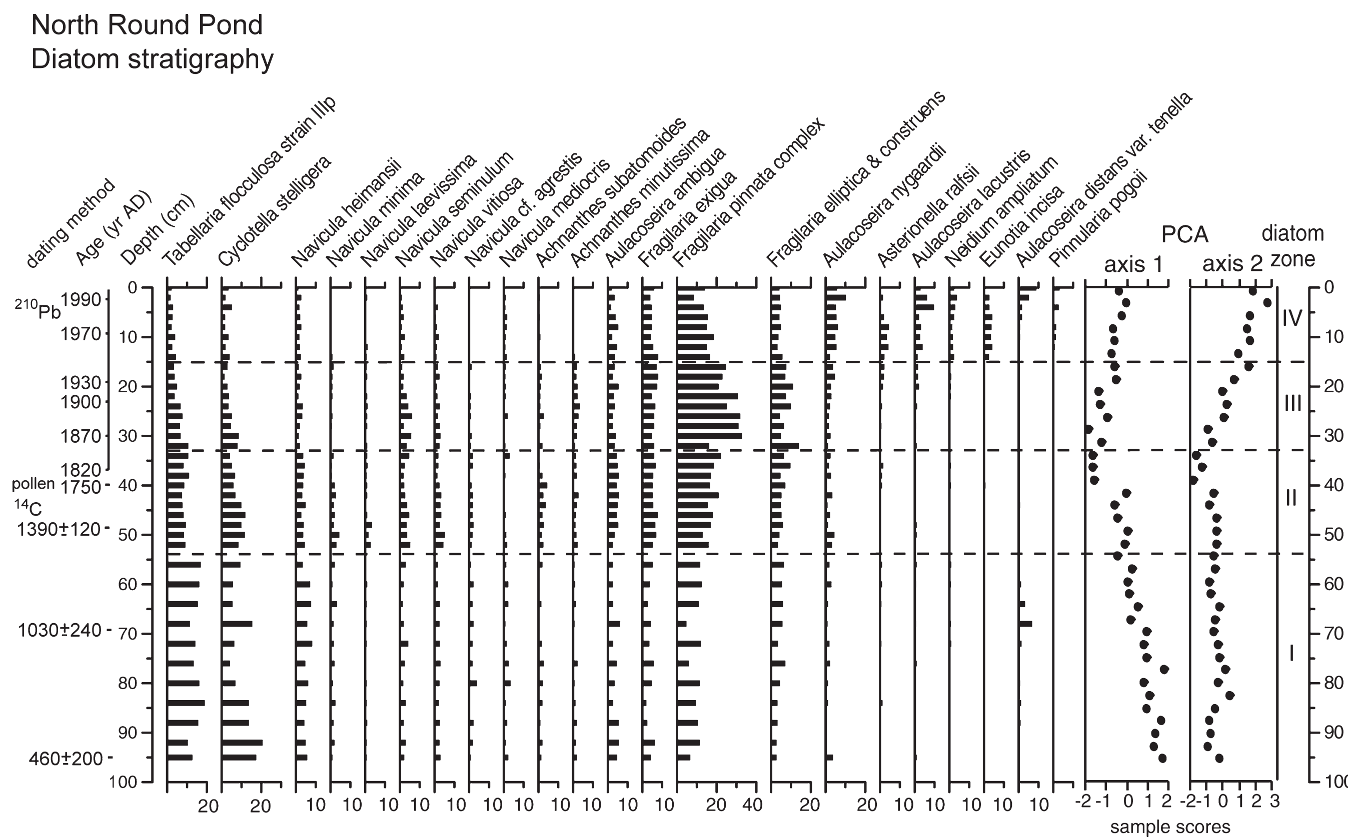

Figure 5 Diatom stratigraphy of North Round Pond with major zonation and fossil sample scores on PCA axes 1 and 2. Diatom taxa are arranged according to their chronological appearance in the sediment sequence. Eigenvalues of PCA axes 1 and 2 are 0.48 and 0.23, respectively

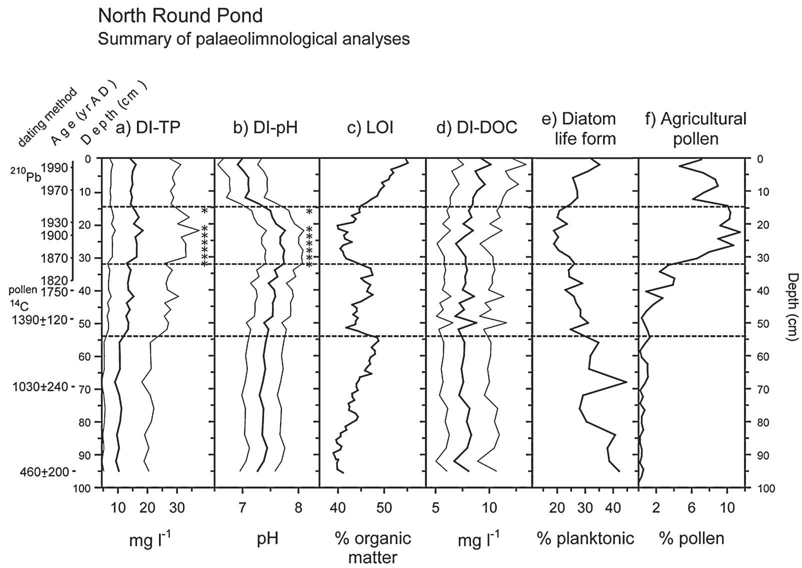

Figure 6 Summary of palaeolimnological analyses for North Round Pond. (a) Diatom-inferred total phosphorus (DI-TP), (b) diatom-inferred pH (DI-pH), (c) percent organic matter as estimated by loss-on-ignition (LOI), (d) diatom-inferred DOC (DI-DOC), (e) percentage of planktonic diatom taxa, (f) percentage of agricultural pollen indicators relative to total upland pollen. Error ranges for quantitative inferences are estimated by bootstrapping. (Asterisks indicate samples with very poor fit to the reconstructed variable indicating unreliable value)

and 2 cm) suggests that the inferred DOC trends are reliable (Figure 6d). Most fossil samples of North Round Pond have good fit to pH and TP. Exceptions are levels 16 to 20 and 34 to 36 cm, which have poor fit (data not shown), as well as the samples 22 to 32 cm, which are outside the 95% confidence interval of the model (Figure 6a, b). Analogues between fossil samples of North Round Pond and the model were poor, because some fossil species were absent in the model. However, the most abundant fossil species, such as shown in Figure 5, were mainly present in the model, except *Asterionella ralfsii*. Thus the range of reconstructed values may be incorrect, while the trends are reliable, as suggested by the general good fit of fossil assemblages to the calibration set.

In contrast to Levi Pond, organic-matter content in North Round Pond sediments increased more steadily from 40% at 80 cm depth (*c*. AD 750) to 50% at 55 cm (AD 1150; Figure 6c). Afterwards, it decreased rapidly to 42% at around AD 1200, and remained low afterwards until a second increase to 50% occurred around 40 cm (AD 1750). At 32 cm, coincident with the start of diatom zone II and rising agricultural pollen, the LOI values fall below 40%. The largest increase from 40% to *c*. 55% occurred in the upper 20 cm (*c*. AD 1920 to the present; Figure 6e).

Discussion

Levi Pond

Although the fossil species composition (Figure 3) indicates that Levi Pond has been slightly acidic and oligotrophic throughout the past 2400 years, significant changes in diatom assemblages suggest that limnological conditions during that time have not been stable.

The overall long-term trend in the diatom assemblages during the last *c*. 2000 years with increased planktonic:benthic species ratios and higher DI-DOC suggests increased relative availability of pelagic habitats and/or increased lake DOC. The planktonic to benthic species ratio mainly reflects the increasing relative abundance of *Aulacoseira distans* var. *distans* and, in the upper levels, *Aulacoseira lirata*. These algae are heavily silicified tychoplanktonic species, which need water turbulence and/or high water levels for suspension in the water column. Therefore, the increased abundance of *Aulacoseira* spp. after AD 0 (52 cm, zone II) may indicate increased mixing intensity or high lake level. Given the continuously closed forest vegetation around the pond before European settlement, as indicated by the dominance of tree species throughout the pollen sequence (David Foster, unpublished data, 2003), the impact of water mixing by wind is unlikely to have changed before AD 1800. However, water levels may have increased because of an increasingly positive water balance, for example as a result of increasing precipitation and/or reduced evaporation. Independent indicators for lake levels, such as macrofossil analyses, would be necessary to test this hypothesis.

The close correlation of the quantitative DOC reconstructions for Levi Pond with the first PCA axis ($r^2 = 0.76$, $p \ll 0.001$, Table 3) and the increase of indicator species for high DOC (eg, *Aulacoseira lacustris* (Grunow) Krammer) suggest that the long-term diatom changes reflect variations in DOC concentrations. Coloured substances contained in DOC are largely responsible for the attenuation of photosynthetically active radiation (PAR) (Wetzel, 2001) and ultraviolet radiation (UV-A and UV-B) in lakes (Morris *et al*., 1995), thereby controlling the light conditions for phytoplankton assemblages (Williamson *et al*., 1996). Therefore, the structure of diatom assemblages may have been altered by changing underwater light conditions due to increased DOC concentrations, as discussed in detail below.

It may be argued that the dominant species *Aulacoseira distans* solely drives the DOC reconstructions and that this was mainly caused by increased pelagic habitat availability. This hypothesis is rejected by parallel increases of several other species with high DOC optima (eg, *Eunotia hemicyclus*, *Pinnularia abaujensis* (PantocŠek) Ross, *Melosira arentii*) and declines of low DOC indicators (*Pinnularia microstauron* (Ehrenberg) Cleve, *Navicula mediocris*, *Nitzschia perminuta*) (Fallu and Pienitz, 1999; Camburn and Charles, 2000). Also, the correlation between DI-DOC and the PCA axis 1 ($r^2 = 0.76$) is stronger than the correlation between DI-DOC and the percentages of *Aulacoseira distans* ($r^2 = 0.61$) alone, indicating that this species explains not all, yet a large part of the reconstructed DOC changes.

As the DOC rise in the second study site (North Round Pond) occurred parallel to a decline in pH, the question arises whether the diatoms in Levi Pond also respond to a change in pH. In the modern calibration set, DOC is not correlated with pH ($r^2 = -0.27$) (Fallu, 1998), indicating an independent response of diatoms to DOC. As in Levi Pond, other studies have shown that diatom-inferred DOC may increase because of catchment vegetation changes without parallel acidification (Korsman *et al*., 1994; Pienitz *et al*., 1999). Measured pH at Levi Pond during the 1980s was around 5.5, and high SO_4 concentrations (maximum 7.8 mg/l in February 1981) suggest that Levi Pond has been heavily impacted by atmospheric pollution (Neil Kamman, Vermont Department of Environmental Conservation, personal communication, 2004). As our diatom-based pH reconstructions were not reliable because of poor fit, another model would be needed to test the hypothesis of recent acidification in Levi Pond.

Within-lake variations in DOC are mainly controlled by climatic processes (Pace and Cole, 2002). Higher DOC concentrations can be produced by late ice-out and higher precipitation (Pace and Cole, 2002), longer residence times (Curtis and Schindler, 1997), and tree or peat development in the catchment (Dillon and Molot, 1997; Pienitz and Vincent, 2000). *Aulacoseira distans* var. *distans* has been associated with higher DOC concentrations because of peatland development in a Minnesota (USA) bog (Brugam and Swain, 2000). A stratigraphic analysis of the bog sediments and their macrofossil remains would help clarify the history of bog development at Levi Pond over the past 2000 years. The timing of ice-out is determined mainly by winter air temperature (Assel and Robertson, 1995), and hence colder winter temperatures might have delayed ice-out and increased DOC in Levi Pond. Climate reconstructions for the northeastern USA using pollen transfer functions indicate a trend to moister and cooler conditions starting at *c*. 2000 years BP (Gajewski, 1988). Additional independent evidence for a cooler and moister climate during the last 2000 years is provided by the pollen, chironomid and stable-isotope data obtained from Levi Pond, as discussed below.

The correlation of the long-term trend in diatoms with increased *Picea* pollen abundances (Table 3) suggests that one factor directly or indirectly influenced both the terrestrial and the aquatic ecosystems. *Picea* immigration to some boreal lake watersheds at the northern tree line led to increased diatom-inferred lake DOC, probably because of increased accumulation of humus derived from decomposing tree matter (Korsman *et al*., 1994; Pienitz *et al*., 1999). Forests always surrounded Levi Pond during the time covered by our core, so vegetation cover has likely not changed in density. In northeastern North America, spruce, particularly *P. mariana* P. Mill, prefers moist and cool habitats (Webb *et al*., 1993). The increase of *Picea* pollen has been related to cooler and wetter conditions in Michigan lakes from the thirteenth century onwards (Bernabo, 1981), in southern Ontario starting at *c*. 600 yr BP (Campbell and McAndrews, 1991) and in Maine starting at *c*. 1000 yr BP (Gajewski, 1987). Stable-isotope analyses of Levi Pond sediments showed coincident decreasing organic $\delta^{13}C$ values and increasing organic $\delta^{15}N$ values (Brent Wolfe, unpublished data, 2004), which may indicate enhanced soil organic-matter decomposition, generation and leaching of organic substances due to moister conditions (Wolfe *et al*., 1999, 2003). The increase in the relative abundance of cold-water chironomid fossils belonging to the genus *Microtendipes* between *c*. AD 200 and 1800 (Donna Francis, personal communication, 2004) suggests that this increased effective humidity likely resulted from a decline in temperature.

A change to moister conditions around 2000 years ago at Levi Pond is consistent with sedimentary and pollen evidence for moister conditions during the last 2000 to 4000 years in New England (Almquist *et al*., 2001; Shuman *et al*., 2001), Ontario (Yu *et al*., 1997) and southern Québec (Lavoie and Richard, 2000). This period corresponds with the onset of the Neoglacial cooling that followed a dry and warm period during the mid-Holocene, the 'Hypsithermal'. The correlation of multiple independent proxies in Levi Pond with regional evidence supports the interpretation that the watershed of Levi Pond has undergone a long-term trend to moister conditions over the last *c*. 2000 years, thereby responding to a larger regional moisture trend.

Increased DOC concentrations and higher lake levels have likely occurred simultaneously at Levi Pond, because they may have the same causes. As discussed above, both trends can result from increased moisture in the watershed. The observed relative increase of planktonic taxa, coincident with increasing diatom-inferred DOC, may be due to higher water levels or lower water transparency caused by increased DOC, which reduces the light required by aquatic macrophytes and thereby limits epiphytic diatoms. In return, higher water levels provide more pelagic habitat and also lead to the augmented decomposition of submerged lake-shore vegetation and eventually to peat development, thereby enhancing the release of organic matter into the lake. On the basis of our analyses, we can conclude that there was an increase in DOC concentrations in Levi Pond, which may have been partly enhanced by higher precipitation and water levels.

The change in assemblage composition between *c*. AD 1800 and 1940 (zone II to III) likely reflects historical logging and agricultural activities in the drainage basin, as it coincides with the historical and pollen-based records of deforestation (Figure 6a). The dominant diatom *Eunotia hemicyclus* is usually found in oligotrophic and dystrophic waters (Krammer and Lange-Bertalot, 1991a; Camburn and Charles, 2000) and *Melosira arentii* lives in dystrophic and mesotrophic environments (Krammer and Lange-Bertalot, 1991a). Thus we conclude that the disturbances were not strong enough to significantly increase the nutrient concentrations of Levi Pond. However, both species are indicators of high DOC concentrations (Fallu and Pienitz, 1999), and the accelerated increase in diatom-inferred DOC (Figure 4 d) indicates that the lake temporarily received higher inputs of organic matter. Logging in the catchment of lakes can result in increased DOC concentrations because of increased erosion of humic soil layers (Carignan *et al*., 2000; France *et al*., 2000). Thus, it is likely that the short-term changes in diatoms reflect additional inputs of DOC to the lake caused by logging in the watershed, which accelerated the long-term, moisture-driven DOC increase.

While the diatom assemblages show signs of recovery from these human disturbances, the overall species composition, diatom-inferred DOC and stable isotopes in Levi Pond sediments suggest that this lake has not returned to predisturbance conditions. *Melosira arentii*, which increased most evidently after logging in the watershed, decreased around AD 1950, indicating rapid recovery of diatom assemblages following reforestation. Conversely, the diatom *Aulacoseira distans*, which had responded to moisture-balance change in presettlement times, continued to dominate the assemblages until 1994. In addition, the stable isotopes of carbon and nitrogen continued to decrease or increase, respectively (Brent Wolfe, unpublished data, 2004), indicating that the lake and watershed continue to be controlled by climatic factors. The forest structure is also different now from the time before European settlement, corresponding to other lake studies in New England and potentially caused by continued forest disturbances, acidification, or climate change (Fuller *et al*., 1998, Francis and Foster, 2001). The reason for the recent appearance of *Aulacoseira lirata* remains unknown, but the reasons cited above as well as continued peat development, rising lake levels and/or a change in food-chain structure due to fish removal in the 1970s may have caused an increase of this taxon.

North Round Pond

The first change in diatom assemblages around AD 1200 (zone I to zone II) to more benthic species (Figure 6e) correlates with changes in pollen and chironomid assemblages (Francis and Foster, 2001), as well as sediment composition. At the same time as the proportion of benthic diatom species increased, *Tsuga* and *Fagus* pollen declined, *Castanea* pollen increased, the charcoal to pollen ratio increased, the chironomid taxon *Microtendipes* (Francis and Foster, 2001) temporary increased and organic matter in the sediment decreased (Figure 6c). The increased charcoal content indicates higher fire frequency or intensity, which is consistent with the increased inorganic matter in the sediments. The same vegetation and charcoal to pollen ratio changes were observed at *c*. AD 1400–1500 in pollen records from several Massachusetts ponds (Fuller *et al*., 1998), but it remains unclear whether these patterns were due to climatic factors, fire frequency and/or Native American activities (Fuller *et al*., 1998). The higher abundance of *Microtendipes* in the chironomid assemblages indicates a slight temperature decrease after *c*. AD 1300 that lasted until *c*. AD 1870. Nevertheless, more independent evidence is needed to test the hypothesis that climatic change has driven the changes at North Round Pond around AD 1300.

The second change in diatom assemblages during the nineteenth century (zone II to zone III) probably reflects logging activities in the watershed, as indicated by the increase in agricultural pollen indicators, but may also be related to natural disturbance such as fire. Although logging was a common activity in the region since settlement in the eighteenth century, historical evidence for logging in the North Round Pond watershed exists only for the early twentieth century. The increase in the proportion of benthic species indicates a higher extent of littoral habitats (Figure 6e). The parallel appearance of aquatic macrophytes in the pollen profile (Francis and Foster, 2001) provides evidence for higher availability of surface substrates on submerged macrophytes for the attachment of benthic diatoms.

As most of the changes in the benthic to planktonic species ratio is represented by increases in small *Fragilaria* species, particularly *F. pinnata*, the explanation for this assemblage change may be found in the ecological preferences of this taxon. As this species is cosmopolitan and an ecological generalist (Krammer and Lange-Bertalot, 1991a), the interpretation of its dominance is challenging. It has been reported to live on sand and under low-light regime in frequently river-flushed lakes (Roland Hall, personal communication, 2004). Material transported to the lake from eroded areas of the watershed following forest disturbance may have supplied that habitat and increased turbidity. The taxon has also been described as a pioneer species that rapidly colonizes newly formed or isolated lake basins, because of high initial supplies of alkalinity from unweathered catchment soils and glacial tills (Stabell, 1985; Marciniak, 1986; Saulnier-Talbot and Pienitz, 2001; Pienitz *et al*., 1991). Increased alkalinity may have resulted from enhanced erosion of catchment soils following disturbance, also indicated by the slight rise of diatom-inferred pH at 34-cm depth (Figure 6c). Similar changes of small *Fragilaria* species have been observed in Ontario lakes following the mid-Holocene hemlock decline in their catchment (Hall and Smol, 1993), indicating that different kinds of forest disturbances may have similar effects on diatom communities. In summary, the increased *Fragilaria* spp. abundances from *c*. AD 1850 to 1940 seem to result from higher macrophyte abundance and/or higher inputs of allochthonous material, resulting in lower water transparency, higher alkalinity and increased epipsammic habitat due to enhanced runoff from deforested catchments. However, the relative importance of these factors remains unknown.

After *c*. AD 1940, the most important shift in diatom assemblages indicates a major disturbance in the watershed. The increase of acidophilic taxa and the resulting decline in diatom-inferred pH suggest that the lake has undergone acidification, accompanied by a small increase in diatom-inferred DOC. One likely cause of lake acidification is atmospheric deposition (‘acid rain’) during industrial development. Deposition of materials associated with fossil fuel combustion started in the late 1800s and early 1900s (Charles, 1990) and acidification of New England lakes began in the early to mid twentieth century (Davis *et al*., 1994b). Numerous studies on diatoms in lake sediments of lakes in the Adirondack Mountains, situated *c*. 200 km northeast of the study region, have demonstrated that atmospheric deposition caused severe lake acidification (Sullivan *et al*., 1990; Cumming *et al*., 1992, 1994; Davis *et al*., 1994b). The limnological changes seen in North Round Pond correspond to this reported regional acidification of surface waters.

Acidification was probably enhanced by the destruction of large parts of the watershed vegetation by a major hurricane event on 20 September 1938 (Foster, 1988). This event is recorded in the sediments by a sudden increase in pollen of agricultural or forest clearance plants, such as Poaceae, Rumex and Ambrosia (Figure 6f; Francis and Foster, 2001). Opening of the forest vegetation may have enhanced leaching of organic and inorganic acids from the soils into the surface waters. As in Levi Pond, the diatom-inferred DOC concentrations also increase following the deforestation. Additionally, an abrupt decrease in $\delta^{18}O$ indicates a flush of precipitation, likely representing enhanced snowmelt inputs during the springs following the hurricane (Brent Wolfe, personal communication, 2004). As snow is naturally acid, rapid input of acidic meltwater may also have favoured acidophilic taxa.

The acidification effects and the increases in DOC concentrations and sedimentary organic matter persist in zone IV up to the core surface, indicating that the lake ecosystem has not fully recovered since human disturbance ended and reforestation occurred after the hurricane. Controls of SO_2 emissions implemented in the USA following the amendments in 1970 to the Clean Air Act have resulted in decreased atmospheric sulphur concentrations, but minimal changes were achieved in NO_x emissions (Driscoll *et al*., 2001). Delayed recovery from acidification due to acidified watersheds has been observed in several regions of eastern North America (Stoddard *et al*., 1999). Delaying processes include decreased acid-neutralizing capacity (ANC) of the soils due to reduced base-cation concentrations (Likens *et al*., 1996) and increased N and S concentrations, which easily leach acids into surface waters (Driscoll *et al*., 1998). These processes may have played a role in delaying the recovery from acidification in North Round Pond.

The reason why DOC and sedimentary organic matter did not return to predisturbance levels, as should be expected from the totally reforested watershed, may be increased aquatic productivity, as suggested by Francis and Foster (2001). They found decreasing C/N ratios, higher macrophyte pollen and spore abundance, as well as the appearance of eutrophication indicators in the chironomid assemblages in the post-settlement period of North Round Pond. Francis and Foster (2001) thus hypothesized that increased nutrient inputs from the watershed, increased sedimentation rates and filling of the lake basin were responsible for the eutrophication. However, the sedimentary and chironomid changes occurred *c*. AD 1930, ie, they showed a delayed response by *c*. 100 years compared with the appearance of macrophytes. This indicates that different factors have driven these changes or that chironomids and sediment chemistry responded with a significant time lag. The diatom assemblages yielded limnological changes at North Round Pond with similar timing but of different nature. Diatoms did reflect a slight trophic change at the time of macrophyte increase but also increased benthic habitat availability, which likely is linked to the rise in aquatic macrophytes. Similar to the results in our study, Francis and Foster (2001) observed most changes in chironomid assemblages after AD 1930, when logging in the watershed was recorded and a severe hurricane affected its vegetation. They interpreted these recent changes to a lack of recovery from the effects of earlier deforestation or as a response to other confounding disturbance factors. These other disturbances (acidification and increased DOC concentrations following a major hurricane) were identified and interpreted in more detail in the present study. Both studies have provided complementary data about the effects of human and natural disturbance on North Round Pond.

Regional versus local factors controlling Levi Pond and North Round Pond

Despite the proximity, comparable elevation, lake morphology, watershed characteristics and land-use history of Levi Pond and North Round Pond, the diatom communities displayed dissimilar trajectories during the past *c*. 2000 years. Differences were observed in patterns of habitat availability, in the response to climatic change, and in the evidence for short-lived natural and anthropogenic disturbance. In Levi Pond, a long-term increase in the relative abundance of planktonic taxa was associated with higher lake DOC, which in turn was coupled with increased moisture. The short-term increase of benthic taxa in North Round Pond, however, was probably related to increased macrophyte abundance and/or increased supply of allochthonous material from deforested areas. These differing patterns in habitat availability indicate that changes in life forms are controlled by diverse local factors and must therefore be interpreted with caution in the context of regional investigations.

It may be surprising that signs of lake acidification were only seen in North Round Pond, since this trend is of great regional and inter-regional importance. However, Levi Pond may have acidified too, but our model was not adequate for pH reconstructions because of poor analogues. It is possible that the massive deforestation caused by the 1937 hurricane enhanced acidification effects in North Round Pond, whereas the watershed of Levi Pond remained mostly forested during the period of acidic deposition (David Foster, unpublished data, 2003).

A climatic signal was only recorded in Levi Pond in the form of a long-term moisture increase over the last *c*. 2000 years. The fact that we did not find this pattern in North Round Pond may simply be explained by the shorter sedimentary record, which did not allow for the comparison of lake histories predating AD 0. Also, the watershed morphology of Levi Pond is such that it may have favoured wetland development and therefore enhanced the moisture signal.

A common pattern observed in both lakes is the response of diatom assemblages to logging in the watershed and their partial subsequent recovery. This correspondence reflects the uniform land-use history across mountainous regions in New England. Another similarity is that algal communities did not completely return to presettlement conditions. This is probably due to a hurricane and delayed recovery from acidification at North Round Pond and continued peat development at Levi Pond. Our results indicate that long-term trends in climatic change and small-scale natural disturbance patterns did not only cause ecosystem variability in presettlement periods, but still influence the dynamics of anthropogenically altered ecosystems and will likely do so in the future. Also, such as noted by Francis and Foster (2001), disturbance events can change the trajectory of lake development, such as in North Round Pond. These factors have therefore to be taken into consideration in management decisions for ecosystem conservation and restoration of the ‘baseline conditions’.

Diatoms, DOC and climate in temperate lakes

Diatom-inferred DOC concentrations appeared to be controlled by climate-driven changes in moisture balance and natural or anthropogenic forest disturbance. In both lakes, rising diatom-inferred DOC is related to partial removal of catchment vegetation by logging or the effects of a hurricane. At Levi Pond, the increasing DOC concentrations and coincident changes in stable-isotope composition and vegetation seem to reflect a long-term increase of allochthonous organic-matter inputs and peat development in the watershed related to moister conditions during the past *c*. 2000 years. As these results correspond to inferred moisture patterns in adjacent areas, fossil diatom assemblages in Levi Pond possibly recorded a larger regional moisture trend associated with Neoglacial cooling. To our knowledge, this is the first study to link diatom-inferred DOC in a temperate lake to past changes in watershed moisture balance. However, the relative role of wetland development versus moisture-driven allochthonous organic-matter input for DOC in lakes remains to be clarified. Therefore, more diatom-based long-core studies in conjunction with stable isotopes and plant-macrofossil analyses, combined with a thorough investigation of climate–lake DOC links, are necessary to test the general usefulness of diatom-based DOC transfer functions as a palaeohydrological proxy. If hydrologically sensitive study sites are carefully chosen to avoid overriding eutrophication or acidification signals, fossil diatoms may be a useful additional proxy for future palaeohydrological studies in temperate regions.

Conclusions

This study of fossil diatom assemblages in two small New England ponds has provided evidence for complex limnological changes related to a multitude of human and natural disturbances in the watershed, as well as climatic change. The regional history of deforestation and subsequent reforestation is reflected in the diatom response and partial recovery of both ponds. Local factors, such as peatland development, macrophyte abundance and hurricane impact are likely responsible for differences in the diatom assemblage patterns between the lakes and the lack of complete recovery. Diatoms and pollen in Levi Pond indicated a change to increased moisture during the past *c*. 2000 years, corresponding to a regional record of increased moisture due to

Neoglacial cooling. This is the first attempt to link diatom-inferred DOC in a temperate lake to past moisture changes, but further investigations are needed to test the applicability of this proxy in palaeohydrological studies. Our study has also shown that diatoms provide independent evidence for natural disturbances and climatic change. Their integration into more palaeolimnological analyses should therefore help generate a more comprehensive picture of factors controlling presettlement ecosystem variability in New England lakes.

Acknowledgements

This research is part of a project funded by NSF (National Science Foundation, USA; grant no. 9903792), that was initiated by J. Fuller and D. Foster. It was also supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) through an operating grant to R. Pienitz. S. Clayden and J. McLaughlin counted the pollen of Levi Pond, and N. Drake the pollen of North Round Pond. We thank D.R. Foster for providing the pollen data. We would like to thank S. Barry, E. Duthie and W. Oswald from Harvard Forest (Petersham, Massachusetts) for laboratory and field assistance and for carrying out the LOI analyses and dating. N. Kamman from the Vermont State Water Department and M.S. Ford kindly provided water-chemistry data for Levi Pond and Robert Estabrook, New Hampshire Department of Environmental Sciences, provided data on North Round Pond. We acknowledge logistic support provided by the Centre d'études nordiques (CEN), Université Laval, Québec and Harvard Forest, Massachusetts. The quality of the manuscript was greatly improved by constructive critics from É. Saulnier-Talbot, S. Hausmann, R. Hall and two anonymous reviewers.

References

Almquist, H., Dieffenbacher-Krall, A.C., Flanagan-Brown, R. and **Sanger, D.** 2001: The Holocene record of lake levels of Mansell Pond, central Maine, USA. *The Holocene* 11, 189–201.

Assel, R.A. and **Robertson, D.M.** 1995: Changes in winter air temperatures near Lake Michigan, 1851–1993, as determined from regional lake-ice records. *Limnology and Oceanography* 40, 165–76.

Battarbee, R.W., Charles, D.F., Dixit, S.S. and **Renberg, I.** 1999: Diatoms as indicators of surface water acidity. In Stoermer, E.F. and Smol, J.P., editors, *The diatoms: applications for the environmental and earth sciences*. Cambridge University Press, 85–127.

Bennett, K.D. 1996: Determination of the number of zones in a biostratigraphical sequence. *New Phytologist* 132, 155–70.

Bernabo, J.C. 1981: Quantitative estimates of temperature changes over the last 2700 years in Michigan based on pollen data. *Quaternary Research* 15, 143–59.

Binford, M.W. 1990: Calculation and uncertainty analysis of 210Pb dates for PIRLA project lake sediment cores. *Journal of Paleolimnology* 3, 253–67.

Birks, H.J.B. 1995: Quantitative paleoenvironmental reconstructions. In Maddy, D. and Brew, J.S., editors, *Statistical modelling of Quaternary science data*. Quaternary Research Association, 161–254.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C. and **ter Braak, C.J.F.** 1990: Diatoms and pH reconstruction. *Philosophical Transactions of the Royal Society of London, Series B* 327, 263–78.

Brugam, R.B. and **Swain, P.** 2000: Diatom indicators of peatland development at Pogonia Bog Pond, Minnesota, USA. *The Holocene* 10, 453–64.

Camburn, K.E. and **Charles, J.C.** 2000: *Diatoms of low-alkalinity lakes in the northeastern United States.* The Academy of Natural Sciences of Philadelphia, 152 pp.

Campbell, I.D. and **McAndrews, J.H.** 1991: Cluster analysis of late Holocene pollen trends in Ontario. *Canadian Journal of Botany* 69, 1719–30.

Carignan, R., D'Arcy, P. and **Lamontagne, S.** 2000: Comparative impacts of fire and forest harvesting on water quality in Boreal Shield lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 105–17.

Charles, D.F. 1990: Effects of acidic deposition on North American lakes: palaeolimnological evidence from diatoms and chrysophytes. *Philosophical Transactions of the Royal Society of London Series B* 327, 403–12.

Cumming, B.F., Smol, J.P., Kingston, J.C., Charles, D.F., Birks, H.J.B., Camburn, K.E., Dixit, S.S., Uutala, A.J. and **Selle, A.R.** 1992: How much acidification has occurred in Adirondack region lakes (New York, USA) since preindustrial times? *Canadian Journal of Fisheries and Aquatic Sciences* 49, 128–41.

Cumming, B.F., Davey, K.A. and **Smol, J.P.** 1994: When did acid-sensitive Adirondack lakes (New York, USA) begin to acidify and are they still acidifying? *Canadian Journal of Fisheries and Aquatic Sciences* 51, 1550–68.

Curtis, P.J. and **Schindler, D.W.** 1997: Hydrologic control of dissolved organic matter in low-order Precambrian Shield Lakes. *Biogeochemistry* 36, 125–38.

Davis, R.B. and **Norton, S.A.** 1978: Paleolimnologic studies of human impact on lakes in the United States, with emphasis on recent research in New England. *Polskie Archiwum Hydrobiologii (Polish Archive of Hydrobiology)* 25, 99–115.

Davis, R.B., Anderson, D.S., Norton, S.A., Ford, J., Sweets, P.R. and **Kahl, J.S.** 1994a: Sedimented diatoms in northern New England lakes and their use as pH and alkalinity indicators. *Canadian Journal of Fisheries and Aquatic Sciences* 51, 1855–76.

Davis, R.B., Anderson, D.S., Norton, S.A. and **Whiting, M.C.** 1994b: Acidity of twelve northern New England (U.S.A.) lakes in recent centuries. *Journal of Paleolimnology* 12, 103–54.

Dillon, P.J. and **Molot, L.A.** 1997: Effect of landscape form on export of dissolved organic carbon, iron, and phosphorus from forested stream catchments. *Water Resources Research* 33, 2591–600.

Dixit, S.S., Smol, J.P., Charles, D.F., Hughes, R.M., Paulsen, S.G. and **Collins, G.B.** 1999: Assessing water quality changes in the lakes of the northeastern United States using sediment diatoms. *Canadian Journal of Fisheries and Aquatic Sciences* 56, 131–52.

Driscoll, C.T., Likens, G.E. and **Church, M.R.** 1998: Recovery of surface waters in the northeastern US, from decreases in atmospheric deposition of sulfur. *Water Air and Soil Pollution* 105, 319–29.

Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L. and **Weathers, K.C.** 2001: Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. *Bioscience* 51, 180–98.

Engstrom, D.R., Swain, E.B. and **Kingston, J.C.** 1985: A paleolimnological record of human disturbance from Harvey's Lake, Vermont: geochemistry, pigments and diatoms. *Freshwater Biology* 15, 261–88.

Faegri, K. and **Iversen, J.** 1975: *Textbook of pollen analysis.* 3rd edition. Hafner Press, 295 pp.

Fallu, M.-A. 1998: Distribution des diatomées d'eau douce en Jamésie-Hudsonie, Québec, et développement d'un modèle de reconstitution paléoclimatique. Masters thesis, Université Laval, Québec, 98 pp.

Fallu, M.A. and **Pienitz, R.** 1999: Lacustrine diatoms in the Hudson Bay and James Bay area of Quebec – reconstruction of dissolved organic carbon concentrations. *Ecoscience* 6, 603–20.

Fallu, M.-A., Allaire, N. and **Pienitz, R.** 2000: *Freshwater diatoms from northern Québec and Labrador (Canada)*. J. Cramer, 200 pp.

Foster, D.R. 1988: Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, southwestern New-Hampshire, USA. *Journal of Ecology* 76, 105–34.

—— 1995: Land-use history and four hundred years of vegetation change in New England. In Turner, B.L., editor, *Global land use change. A perspective from the Columbian Encounter*. Consejo Superior de Investigaciones Cientificas, 253–321.

Foster, D.R., Motzkin, G. and **Slater, B.** 1998: Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems* 1, 96–119.

France, R., Steedman, R., Lehmann, R. and **Peters, R.** 2000: Landscape modification of DOC concentration in boreal lakes: implications for UV-B sensitivity. *Water Air and Soil Pollution* 122, 153–62.

Francis, D.R. and **Foster, D.R.** 2001: Response of small New England ponds to historic land use. *The Holocene* 11, 301–12.

Fuller, J.L., Foster, D.R., McLachlan, J.S. and **Drake, N.** 1998: Impact of human activity on regional forest composition and dynamics in central New England. *Ecosystems* 1, 76–95.

Gajewski, K. 1987: Climatic impacts on the vegetation of eastern North America during the past 2000 years. *Vegetatio* 68, 179–90.

—— 1988: Late Holocene climate change in eastern North America estimated from pollen data. *Quaternary Research* 29, 255–62.

Gordon, M.D. 1953: The Indian as an ecological factor in the northeastern forest. *Ecology* 34, 329–46.

Hall, R.I. and **Smol, J.P.** 1993: The influence of catchment size on lake trophic status during the hemlock decline and recovery (4800 to 3500 BP) in southern Ontario lakes. *Hydrobiologia* 269/270, 371–90.

—— 1999: Diatoms as indicators of lake eutrophication. In Stoermer, E.F. and Smol, J.P., editors, *The diatoms: applications for the environmental and earth sciences.* Cambridge University Press, 128–68.

Heiri, O., Lotter, A.F. and **Lemcke, G.** 2001: Loss-on-ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology* 25, 101–10.

Juggins, S. 2003: *C^2 user guide. Software for ecological and paleoecological data analysis and visualisation*. University of Newcastle, 69 pp.

Kamman, N.C., Lorey, P.M., Driscoll, C.T., Estabrook, R., Major, A., Pientka, B. and **Glassford, E.** 2004: Assessment of mercury in waters, sediments, and biota of New Hampshire and Vermont lakes, USA, sampled using a geographically randomized design. *Environmental Toxicology and Chemistry* 23, 1172–80.

Kingston, J.C. and **Birks, H.J.B.** 1990: Dissolved organic carbon reconstructions from diatom assemblages in PIRLA project lakes, North America. *Philosophical Transactions of the Royal Society London, Series B* 327, 279–88.

Korsman, T., Renberg, I. and **Anderson, N.J.** 1994: A palaeolimnological test of the influence of Norway spruce (*Picea abies*) immigration on lake-water acidity. *The Holocene* 4, 132–40.

Krammer, K. and **Lange-Bertalot, H.** 1986: *Bacillariophyceae, 1. Teil: Naviculaceae.* Gustav Fischer Verlag, 876 pp.

—— 1988: *Bacillariophyceae, 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae.* Gustav Fischer Verlag, 596 pp.

—— 1991a: *Bacillariophyceae, 3. Teil: Centrales, Fragilariaceae, Eunotiaceae.* Gustav Fischer Verlag, 576 pp.

—— 1991b: *Bacillariophyceae, 4. Teil: Achnanthaceae.* Gustav Fischer Verlag, 437 pp.

Lavoie, M. and **Richard, P.J.H.** 2000: Postglacial water-level changes of a small lake in southern Québec, Canada. *The Holocene* 10, 621–34.

Likens, G.E., Driscoll, C.T. and **Buso, D.C.** 1996: Long-term effects of acid rain: response and recovery of a forest ecosystem. *Science* 272, 244–46.

Marciniak, B. 1986: Late glacial *Fragilaria* flora from lake sediments of the Tatra Mts. and the Alps. In Round, F.E., editor, *9th diatom symposium*. Biopress Ltd. and Koeltz Scientific Books, 223–44.

McAndrews, J.H. and **Boyko-Diakonow, M.** 1989: Pollen analysis of varved sediments at Crawford Lake, Ontario: evidence of Indian and European farming. In Fulton, R.J., editor, *Quaternary geology of Canada and Greenland*. Canadian Government Publishing Centre, 528–30.

Moore, P.D., Webb, J.D. and **Collinson, M.E.** 1991: *Pollen analysis.* 2nd edition. Blackwell Scientific Publishers, 216 pp.

Morris, D.P., Zagarese, H., Williamson, C.E., Balseiro, E.G., Hargreaves, B.R., Modenutti, B., Moeller, R. and **Queimalinos, C.** 1995: The attentuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnology and Oceanography* 40, 1381–91.

Moser, K.A., Korhola, A., Weckström, J., Blom, T., Pienitz, R., Smol, J.P., Douglas, M.S.V. and **Hay, M.B.** 2000: Paleohydrology inferred from diatoms in northern latitude regions. *Journal of Paleolimnology* 24, 93–107.

Overpeck, J.T., Webb, T. and **Prentice, I.C.** 1985: Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of Modern Analogs. *Quaternary Research* 23, 87–108.

Pace, M.L. and **Cole, J.J.** 2002: Synchronous variation of dissolved organic carbon and color in lakes. *Limnology and Oceanography* 47, 333–42.

Pienitz, R. and **Smol, J.P.** 1993: Diatom assemblages and their relationship to environmental variables in lakes from the boreal forest-tundra ecotone near Yellowknife, Northwest Territories, Canada. *Hydrobiologia* 269/270, 391–404.

Pienitz, R. and **Vincent, W.F.** 2000: Effect of climate change relative to ozone depletion on UV exposure in subarctic lakes. *Nature* 404, 484–87.

—— 2003: Generic approaches towards water quality monitoring based on paleolimnology. In Kumagai, M. and Vincent, W.F., editors, *Freshwater management: global versus local perspectives.* Springer-Verlag, 61–82.

Pienitz, R., Lortie, G. and **Allard, M.** 1991: Isolation of lacustrine basins and marine regression in the Kuujjuaq Area, northern Quebec, as inferred from diatom analysis. *Geographie Physique et Quaternaire* 45, 155–74.

Pienitz, R., Smol, J.P. and **Birks, H.J.B.** 1995: Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *Journal of Paleolimnology* 13, 21–49.

Pienitz, R., Smol, J.P. and **MacDonald, G.M.** 1999: Paleolimnological reconstruction of Holocene climatic trends from two boreal treeline lakes, Northwest Territories, Canada. *Arctic, Antarctic and Alpine Research* 31, 82–93.

Rhodes, T.E. and **Davis, R.B.** 1995: Effects of late Holocene forest disturbance and vegetation change on acidic Mud Pond, Maine, USA. *Ecology* 76, 734–46.

Russell, E.W. 1983: Indian-set fires in the forests of the northeastern United States. *Ecology* 64, 78–88.

Saulnier-Talbot, É. and **Pienitz, R.** 2001: Isolation au postglaciaire d'un bassin côtier près de Kuujjuaraapik-Whapmagoostui, en Hudsonie (Québec): une analyse biostratigraphique diatomifère. *Géographie physique et Quaternaire* 55, 63–74.

Schindler, D.W., Bayley, S.E., Parker, B.R., Beaty, K.G., Cruikshank, D.R., Fee, E.J., Schindler, E.U. and **Stainton, M.P.** 1996: The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, northwestern Ontario. *Limnology and Oceanography* 41, 1004–17.

Shuman, B., Bravo, J., Kaye, J., Lynch, J.A., Newby, P. and **Webb, T.** 2001: Late Quaternary water-level variations and vegetation history at Crooked Pond, southeastern Massachusetts. *Quaternary Research* 56, 401–10.

Siccama, T.G. 1974: Vegetation, soil, and climate on the Green Mountains of Vermont. *Ecological Monographs* 44, 325–49.

Smol, J.P. 2002: *Pollution of lakes and rivers: a paleoenvironmental perspective.* Arnold, 280 pp.

Smol, J.P. and **Cumming, B.F.** 2000: Tracking long-term changes in climate using algal indicators in lake sediments. *Journal of Phycology* 36, 986–1011.

Stabell, B. 1985: The development and succession of taxa within the diatom genus *Fragilaria* as a response to basin isolation from the sea. *Boreas* 14, 273–86.

Stoddard, J.L., Jeffries, D.S., Lukewille, A., Clair, T.A., Dillon, P.J., Driscoll, C.T., Forsius, M., Johannessen, M., Kahl, J.S., Kellogg, J.H., Kemp, A., Mannio, J., Monteith, D.T., Murdoch, P.S., Patrick, S., Rebsdorf, A., Skjelkvale, B.L., Stainton, M.P., Traaen, T., van Dam, H., Webster, K.E., Wieting, J. and **Wilander, A.** 1999:

Regional trends in aquatic recovery from acidification in North America and Europe. *Nature* 401, 575–78.
Stuiver, M. and **Reimer, P.J.** 1993: Extended C-14 data-base and revised Calib 3.0 C-14 age calibration program. *Radiocarbon* 35, 215–30.
Sullivan, T.J., Charles, D.F., Smol, J.P., Cumming, B.F., Selle, A.R., Thomas, D.R., Bernert, J.A. and **Dixit, S.S.** 1990: Quantification of changes in lakewater chemistry in response to acidic deposition. *Nature* 345, 54–58.
ter Braak, C.J.F. and **Šmilauer, P.** 1998: *CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination (version 4)*. Microcomputer Power, 351 pp.
Webb, R.S., Anderson, K.H. and **Webb, T.** 1993: Pollen response-surface estimates of late-Quaternary changes in the moisture balance of the northeastern United-States. *Quaternary Research* 40, 213–27.
Wetzel, R.G. 2001: *Limnology.* Third edition. Academic Press, 1006 pp.
Williamson, C.E., Stemberger, R.S., Morris, D.P., Frost, T.M. and **Paulsen, S.G.** 1996: Ultraviolet radiation in North American lakes: attenuation estimates from DOC measurements and implications for plankton communities. *Limnology and Oceanography* 41, 1024–34.
Wolfe, B.B., Edwards, T.W.D. and **Aravena, R.** 1999: Changes in carbon and nitrogen cycling during tree-line retreat recorded in the isotopic content of lacustrine organic matter, western Taimyr Peninsula, Russia. *The Holocene* 9, 215–22.
Wolfe, B.B., Edwards, T.W.D., Jiang, H.B., MacDonald, G.M., Gervais, B.R. and **Snyder, J.A.** 2003: Effect of varying oceanicity on early- to mid-Holocene palaeohydrology, Kola Peninsula, Russia: isotopic evidence from treeline lakes. *The Holocene* 13, 153–60.
Yu, Z.C., McAndrews, J.H. and **Eicher, U.** 1997: Middle Holocene dry climate caused by change in atmospheric circulation patterns: Evidence from lake levels and stable isotopes. *Geology* 25, 251–54.