Seasonal diatom variability and paleolimnological inferences – a case study

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Abstract

The seasonality of physical, chemical, and biological water variables is a major characteristic of temperate, dimictic lakes. Yet, few investigations have considered the potential information that is encoded in seasonal dynamics with respect to the paleolimnological record. We used a one-year sequence of diatoms obtained from sediment traps and water samples, as well as the sedimentary diatom record covering the past ca. 1000 years in Bates Pond, Connecticut (USA), to investigate which variables influence the seasonal distribution of diatoms and how this can be used for the interpretation of the fossil record. The seasonal patterns in diatom assemblages were related to stratification and, to a lesser extent, to nitrate, silica, and phosphorus. During mixing periods in spring and autumn, both planktonic and benthic species were collected in the traps, while few lightly silicified, spindle-shaped planktonic diatoms dominated during thermal stratification in summer. Changes in fossil diatom assemblages reflected human activity in the watershed after European settlement and subsequent recovery in the 20th century. A long-term trend in diatom assemblage change initiated before European settlement was probably related to increased length of mixing periods during the Little Ice Age, indicated by the increase of taxa that presently grow during mixing periods and by application of a preliminary seasonal temperature model. We argue that the analysis of seasonal diatom dynamics in temperate lakes may provide important information for the refinement of paleolimnological interpretations. However, investigations of several lakes and years would be desirable in order to establish a more robust seasonal data set for the enhancement of paleolimnological interpretations.

Introduction

In temperate regions, seasonality is a major characteristic of freshwater ecosystem dynamics (Wetzel 2001). The variability of the physical, chemical and biological conditions over the course of a year cause significant changes in the composition, biomass and number of dominant algal species (Sommer et al. 1986; Interlandi et al. 1999;

Wetzel 2001). For example, different diatom species attain peak populations at different times during the annual cycle, thereby growing under different environmental conditions. As these patterns are integrated in surface sediment samples that are used for the development of diatom-based inference models and paleolimnological analyses, they introduce 'noise' into these analyses (Hall and Smol 1999). The seasonally fluctuating parameters

determine what is eventually preserved in the sediments (Anderson 1995). Therefore, knowledge of the responses of the organisms to environmental variability at finer temporal scales is necessary for more refined interpretations of the paleolimnological record (Reynolds 1990). Although Smol (1990) stressed the need for more communication between ecologists and paleoecologists, few researchers have established this link between neo- and paleolimnological studies (Siver and Hamer 1992; Bradbury and Dieterich-Rurup 1993; Bennion and Smith 2000; Lotter and Bigler 2000; Pienitz and Vincent 2000; Bradshaw et al. 2002; Chu et al. 2005).

For the development of robust diatom-based inference models (Tibby 2004; Reid 2005) and for accurate ecological interpretations of the fossil record, the knowledge of the autecological characteristics of individual species is required. As population responses at the seasonal scale are strongly controlled by species-specific physiological integration of smaller-scale, higher frequency stimuli (Reynolds 1990), the study of seasonal dynamics of algal communities and their relation to the environment may be useful for obtaining information on individual ecological preferences of species. To our knowledge, only few such studies of seasonal algal dynamics with regard to their implications for paleolimnological analyses have been completed, for example for chrysophytes in a Connecticut lake (Siver and Hamer 1992) and for diatoms in a Swiss alpine lake (Lotter and Bigler 2000) and a Finnish subarctic lake (Rautio et al. 2000). Studies of parameters controlling the seasonal dynamics of phytoplankton, and particularly diatoms, were mostly conducted in large stratified lakes (Sommer 1986; Sommer et al. 1986; Kilham et al. 1996), whereas data on seasonal diatom succession in small, sometimes well-mixed, North American lakes are rather sparse (Agbeti et al. 1997).

The sediment trap technique has been used successfully for studying seasonal dynamics of algae (Horn and Horn 1990). It can potentially provide more detailed data at finer temporal scales for the calibration of inference models (Smol 1990), as well as yield important information on taphonomic processes (Ryves et al. 2003). With a one-year sediment trap study of diatom succession in Bates Pond combined with analyses of fossil diatoms preserved in the sediments of the same

lake, we attempted to answer the following questions: (1) Is it possible to identify individual species' ecological preferences for environmental variables based on a seasonal sampling strategy and use these data to interpret the fossil record? (2) Do individual diatom species that thrive in particular seasons reliably indicate changes in the relative length of past seasons, if encountered in the fossil record?

Study site

Bates Pond (72°06′ W, 41°39′ N) is situated in southeastern Connecticut, USA, at an elevation of 95 m a.s.l. (Figure 1). Major lake and catchment characteristics are presented in Table 1. Dense

Figure 1. Map of New England (USA) with the location of Bates Pond.

Table 1. Major lake and catchment characteristics of Bates Pond.

Variable	Annual mean	Variable	Annual mean
Surface area (ha)	2.7	SO_4^{2-}	7.9
Watershed area (ha)	68.2	SiO_2	2.7
Maximum depth (m)	3.6	Ca^{2+}	2.6
pH	6	K^+	0.7
TP ($\mu g\ l^{-1}$)	13.5	Mg^{2+}	0.8
SRP ($\mu g\ l^{-1}$)	3.7	Na^+	4.8
TN	0.4	DOC	5.9
NO_2^--N ($\mu g\ l^{-1}$)	3.3	DIC	1.4
NO_3^--N ($\mu g\ l^{-1}$)	17.3	POC	0.5
NH_4^+-N ($\mu g\ l^{-1}$)	44.1	Chl *a* ($\mu g\ l^{-1}$)	2
Cl^-	7.2		

Values for water chemistry are annual means based on 11 measurements from March 2001 to April 2002 (Figure 4c and f). Values are given in mg l^{-1}, if not otherwise indicated. For a complete abbreviation list of limnological parameters see caption of Table 2.

Figure 2. Deployment of the sediment trap. Modified from Horn and Horn (1990).

macrophyte vegetation, composed mainly of *Nymphaea odorata* Ait and *Brasenia schreberi* Gmelin, colonizes the littoral zone. The watershed is at present mostly covered by deciduous forest dominated by *Quercus* spp. (oak), *Betulus* spp. (birch) and *Pinus* spp. (pine), but includes also some grass from lawns. Three houses and a gravel road, situated at the eastern end of the lake, do not contribute to the lake input. Large parts of the watershed were cleared and used for agriculture by European settlers in the 18th and 19th century. In 1935, the Ginetti family acquired the lake and large parts of the watershed. At that time, the watershed was covered with young deciduous forest, which has matured until today.

Methods

Sampling and sample treatment

A sediment trap with three separate black plastic tubes was installed in Bates Pond on March 21st 2001, one day after ice-break-up. It was placed in the deepest part of the lake basin with the bottom of the trap at about 3 m depth, leaving about 2.5 m water column above the trap entry. We used a system with two anchors (Horn and Horn 1990), where one anchor holds the trap with a rope, while the other end of this rope connects diagonally to the buoy located some meters beneath the trap,
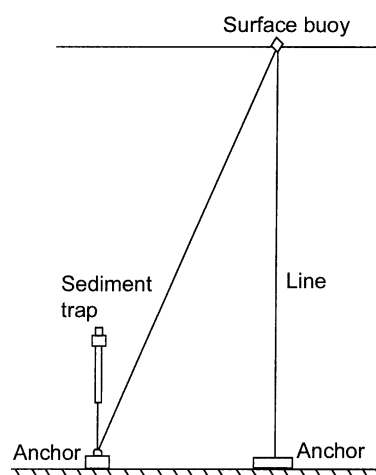
which in turn is kept in place by the second anchor (Figure 2). This assembly precludes contamination by epiphytic algae growing on the rope when the buoy is installed directly above the trap. A preservative agent (Lugol's solution) was added to the bottom of each tube to prevent alteration of diatom assemblages by zooplankton grazing.

Sediment traps and lake water were sampled monthly during the ice-free season, except in January 2002, when the lake was frozen. The contents of the first and second tube were used for replicate diatom analyses. The material from the third tube and the sediment core samples were analyzed for sediment organic matter by loss-on-ignition at 550 °C (Heiri et al. 2001). A 1-l phytoplankton sample was taken at ca. 50 cm depth, preserved with Lugol® and kept in the dark at 4 °C until further processing. For diatom analyses, the trap and phytoplankton samples were cleaned with 30% H_2O_2. A known amount of glass microspheres were added to the sediment trap samples (Battarbee and Kneen 1982), and microscope slides were prepared using Naphrax® mounting medium. A minimum of 300 valves were counted under oil immersion using a Leica DMRB microscope. The mean counts of two replicate trap samples were used for calculating relative abundances and for numerical analyses. For absolute numbers, the mean daily accumulation rate per sampling period was calculated from the total diatom numbers in the sediment trap sample

divided by the number of days of exposure, in order to take into account the different time lags between sampling dates.

Each sampling was accompanied by measurements of vertical temperature, oxygen and specific conductivity profiles (taken around noon at 50 cm intervals) and surface water pH using a Quanta Hydrolab®. Water samples were taken from ca. 50 cm depth at the same location of phytoplankton sampling, water for dissolved nutrient concentrations was filtered the same day and sent to the National Laboratory for Environmental Testing, Burlington, Canada, for analyses of major ions, nutrients, dissolved organic and inorganic carbon (DOC, DIC), and chlorophyll *a* (chl *a*) according to standard procedures (Environment Canada 1994).

In May 2000, a 1.65 m long sediment core was obtained from the deepest part of the lake basin using a clear Lexan coring tube fitted with a rubber piston. Sediment core slices were sub-sampled at 1 cm intervals and stored in plastic bags at 4 °C. Diatom preparation followed standard strong acid digestion techniques (Pienitz et al. 1995), and a minimum of 500 valves per microscope slide were enumerated under 1000× magnification using the same equipment as used for the analyses of sediment trap samples. Species were identified according to several 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 (S. Juggins, unpublished program) and the number of significant zones was determined by the broken-stick model (Bennett 1996).

Chronology

Bulk sediment samples and plant macrofossils were radiocarbon dated by accelerator mass spectrometry at Beta Analytic Laboratories, Miami, FL or at NOSAMS, Woods Hole. Radiocarbon dates (^{14}C yr BP) were converted to calibrated years before present (cal. yr BP) using the computer program CALIB version 4.3 (Stuiver and Reimer 1993) and adjusted to calendar years (yr AD) by adding 50 years in order to permit consistent discussion of paleolimnological data in the historical context (Table 5). Recent sediments were dated by the ^{210}Pb technique and ages were calculated using a constant-rate-of-supply (CRS) point transformation model (Binford 1990). Settlement horizons were based on the rise of agriculture indicator pollen, such as *Ambrosia* and *Rumex*, and were assigned the date 1700 yr AD, based on the foundation of the town of Canterbury.

The age–depth model was established using the ^{210}Pb dates, linear interpolation between the oldest ^{210}Pb date and the settlement date, and a linear interpolation using the settlement date and selected and partly corrected ^{14}C dates (representing the midpoints of the 2 sigma ranges) (Figure 8). The date obtained from bulk sediment of the 51-cm layer, corresponding to the pollen-based settlement horizon, showed a difference of ca. 250 years with regards to the settlement date. As this difference is likely due to an effect of old carbon from weathered limestone in the watershed, we used this value to correct the other dates derived from bulk organic sediment samples by subtracting 250 years from the calibrated dates BP, as has been done in other Connecticut lakes (Deevey and Stuiver 1964; Davis 1969; Brugam 1978). Dates based on plant and insect macrofossils were not corrected, because these organisms have likely lived shortly prior to embedding in the sediment and therefore have incorporated carbon that was contemporaneous to sediment deposition.

Three ^{14}C dates were omitted in the chronology. The 2-sigma range associated with the most recent ^{14}C date from 31 cm was very large (5–420 yr BP) and therefore no useful date could be assigned. Two other ^{14}C dates (170 and 211 cm) were far outside the range of the majority of the dates (Table 5; Figure 8). No major change in sedimentation rate that may justify these dates can be inferred from the LOI data of these levels (data not shown), and were therefore excluded.

Numerical analyses

The environmental data used for numerical analyses were mean values of the measurements of two consecutive sampling dates, i.e., the average of measurements at the corresponding sediment trap sampling date and the measurement taken one month before (2 months before for February

2002). We have chosen this procedure in order to approximate as best as possible the conditions under which the diatoms had grown during the month before trap sampling. Specific conductivity was excluded from the analyses, because data were missing for some sampling dates. The *in situ* measurements of dissolved oxygen and temperature at 0.5 m depth were used for numerical analyses in order to ensure comparability to water chemistry measurements. Dissolved oxygen concentrations were transformed to percent saturation using the temperature-dependent function of oxygen saturation of water (Wetzel 2001). An estimate for strength of stratification was calculated by subtracting the bottom water density from the surface water density, as calculated by the temperature-density function for freshwater atmospheric pressure (Dokulil et al. 2001), and expressed by the density difference ($\Delta\rho$).

Patterns in trap diatom assemblages and relationships between seasonal diatom communities and physical and chemical lake variables were explored using multivariate statistics implemented in the computer program CANOCO (ter Braak and Šmilauer 1998). The total amount of variation in seasonal diatom assemblages was assessed by detrended correspondence analysis (DCA) with detrending by segments. As the variation was relatively low with 1.67 standard deviations (SD), linear relationships of species to environmental gradients were presumed and linear-based methods were applied in subsequent numerical analyses (Birks 1998). Relationships of seasonal diatom assemblages with environmental parameters were explored by redundancy analysis (RDA) in several steps.

In a first step, a combination of variables that were not co-linear and which significantly explained the variation in diatom assemblages was determined by deleting correlated variables and by stepwise backward selection. Correlations between environmental variables were identified using the environmental correlation matrix (Table 3). From groups of correlated variables, one representative variable was chosen based on the fit to species axes and its relevance for paleolimnological inferences. From the highly correlated pH and major ions, pH was selected, and from the correlated group of N-species, NO_3^- was selected. Dissolved oxygen was excluded from the selection because it was

correlated to temperature and stratification and is rather a response variable than a predictor for algal communities. DOC was deleted due to correlation with total phosphorus (TP) and silica (SiO_2) and lower fit to the species axes. The variables that explained the least part of variation in the species data were subsequently removed using the forward selection option in CANOCO, until the variance inflation factors (VIF) of all included variables were less than 20. All subsequent analyses were carried out with the remaining four variables (stratification, total phosphorus, silica, and nitrate) as well as temperature. Temperature was used in the analysis regardless of its high correlation with the variable 'stratification', as it is the more common climatic variable used in paleoecological investigations.

Second, the amount of variance in the species data independently explained by each of these variables was estimated by RDAs with the first axis constrained to one variable (marginal effect) and by partial RDAs (pRDA), where the other variables were set to be co-variables (conditional effect). The significance of these relationships was tested using 199 Monte Carlo permutations adjusted for time series.

Third, the fossil diatom samples were included as passive samples in an RDA with the five variables mentioned above and the trap percentage diatom data. This permits the assessment of similarity of both sample sets and to visualize changes in fossil assemblages.

Diatom model development, quantitative reconstructions of environmental variables and calculation of associated sample-specific reconstruction errors were carried out using the computer program C^2 (Juggins 2003). The pH and TP models were based on a surface sediment diatom calibration set including 82 New England lakes (Köster et al. 2004). These were selected a priori from a larger calibration set (Dixit et al. 1999). The TP was modeled using Gaussian logit regression and the pH model was developed using weighted averaging with inverse deshrinking. Diatom-based inference models based on the modern seasonal data and using the linear method partial least squares regression (Birks 1995) were developed for the variables that explained most of the variation in the seasonal data set. These models were based on the same water chemistry and diatom data as used for ordination.

RDA was also carried out using planktonic diatom samples and the same environmental variables. However, we concentrate on the trap analyses, because these include the monthly integrated diatom assemblages that are relevant for paleolimnological analyses.

Results

Limnology of Bates Pond

Bates Pond was thermally stratified during sampling in April, June, July and August 2001 (Figure 3) and there was a high density difference between epi- and hypolimnion (Figure 4a). During the other months of the ice-free season, there was no difference between surface and bottom water densities, indicating regular mixing of the entire water column. Remarkably, the winter of 2002 was the warmest on record since 1895 (National Climate Data Center; web site: http://www.ncdc.noaa.gov/oa/climate/research/cag3/cag3.html), leading to a one month earlier ice-breakup at Bates Pond in 2002.

The development of major water characteristics over the year is illustrated in Figure 4a–f. Oxygen saturation (data not shown) and inorganic matter

content in the traps were high during the full-circulation periods in spring and autumn, when water column stability was low (Figure 4a). Inorganic matter in the sediment traps was observed at each sampling date, probably originating from suspended particulate inorganic matter and the inorganic parts of organisms, such as siliceous scales, cysts and frustules of chrysophytes and diatoms.

Silicate (SiO_2) was highest in spring 2001, then decreased until October, with a small peak in June, and increased from October 2001 to March 2002 (Figure 4b). Phosphorus was generally low with one peak of soluble reactive phosphorus (SRP; 20 μg l^{-1}) and total phosphorus (TP; 30 μg l^{-1}) in October (Figure 4c). Another peak of TP occurred in June (28 μg l^{-1}), when soluble reactive phosphorus (SRP) was low, indicating that this TP increase was bound in particulate matter. Dissolved total nitrogen (TN) and nitrate (NO_3^-) were low during the spring and summer and increased during late autumn and winter (Figure 4d). The major ions (for the figure exemplified by Cl$^-$, which shows very similar patterns compared to the other major ions) and pH increased steadily from March 2001 to March 2002 (Figure 4e).

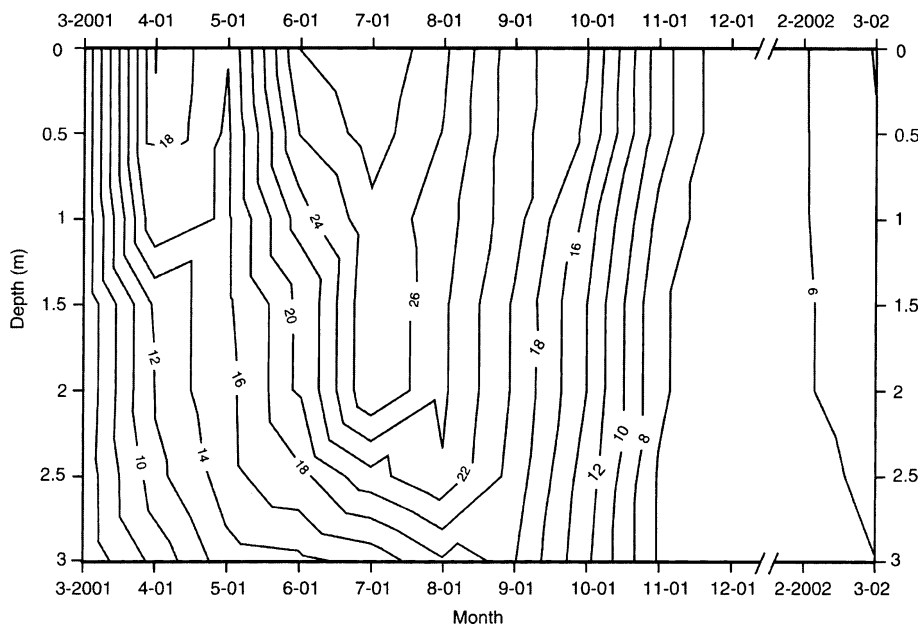Aquatic primary productivity, as indicated by chlorophyll a (chl a; corrected for pheophytins),

Figure 3. Temperature isopleths in °C for Bates Pond from March 2001 to March 2002. Note that data are missing for January 2002 due to the presence of ice cover. Temperature profiles were measured around noon at each sampling date.
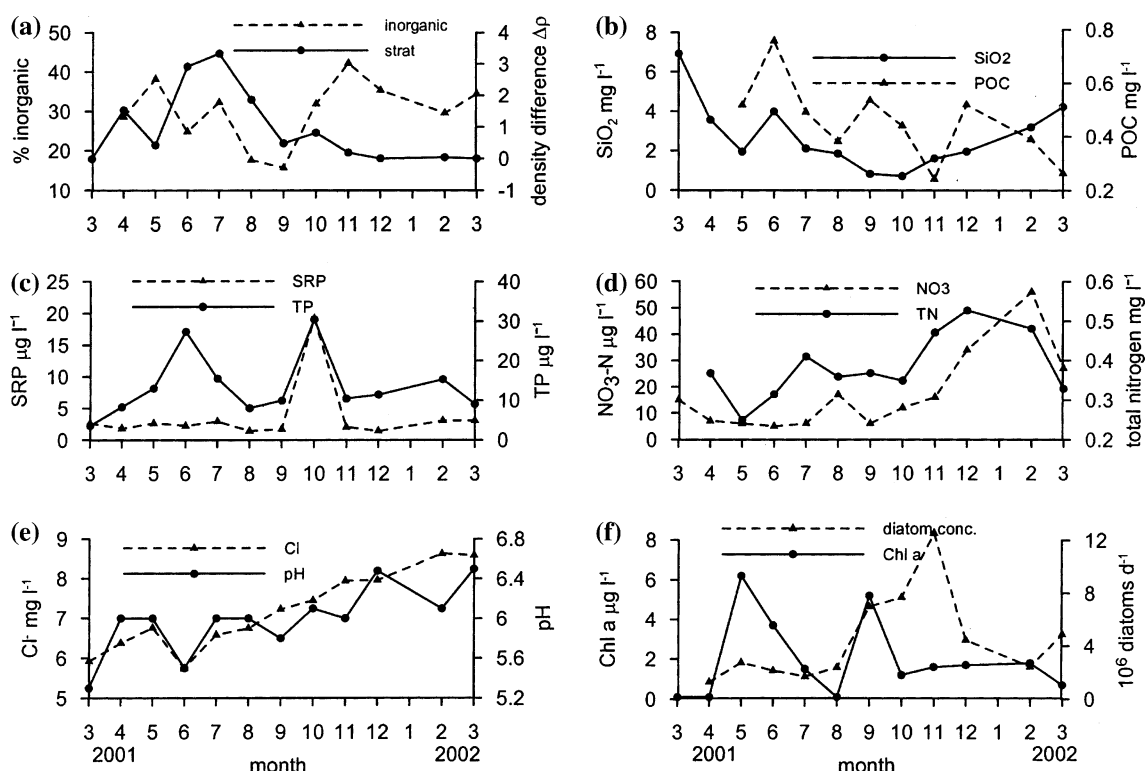
Figure 4. Seasonal variation of limnological parameters at Bates Pond from March 2001 to March 2002. (a) Percentage of inorganic matter in the sediment trap (inorganic) and strength of stratification (strat) expressed as the difference between surface (0 m) and bottom (3 m) water density. (b) Silica (SiO_2) and particulate organic carbon (POC). (c) Soluble reactive phosphorus (SRP) and total phosphorus (TP). (d) Total dissolved nitrogen and nitrate nitrogen (NO_3-N). (e) chloride (Cl^-) and pH. (f) Chlorophyll *a* and monthly mean of daily diatom accumulation rate. Note that no measurement was taken in January 2002.

reached maxima in May, June and September (Figure 4f), whereas diatom productivity peaked from September through November Figure 4f). Chrysophyte scales and cysts were not quantified, but visibly dominated the cleaned sediment trap samples from May through October.

Numerous significant correlations between the measured variables are demonstrated in the environmental correlation matrix (Table 2). The major ions, nitrogen compounds and pH were highly correlated with the physical variables, such as temperature and stratification, whereas the intercorrelated variables DOC, DIC, phosphorus and SiO_2 were less correlated with the other variables.

Seasonal distribution of diatoms

The seasonal distribution of diatoms in the phytoplankton and sediment trap samples from April 2001 to March 2002 was in part similar, in part different (Figure 5). Similarities include the short-term maximum of *Meridion circulare* in April 2001, the dominance of *Tabellaria flocculosa* var. *linearis* and *Eunotia* spp. (see Table 4 for authorities) during spring and early summer, the peak of *Asterionella ralfsii* var. *americana* in July and August, the maximum of *Nitzschia gracilis* in August/September, and the increase of the relative abundances of *Cyclotella stelligera* during autumn. The percentage composition of winter phytoplankton assemblages was dominated by *Eunotia* spp., accompanied in the traps by *C. stelligera* and *Aulacoseira* spp. The peaks of *Tabellaria flocculosa* and *Nitzschia gracilis* were delayed by 1 month from the phytoplankton to the sediment trap samples, indicating that the increase of these species had begun at the phytoplankton sampling date and continued into the following sampling period covered by the sediment traps. Some differences

Table 2. Correlation matrix of environmental variables measured monthly at Bates Pond from March 2001 to March 2002.

	Cl	SO$_4$	SiO$_2$	Ca	Chl a	K	Mg	Na	DOC	DIC	SRP	NO$_2$	NO$_3$	NH$_3$	TP	Temp	DO%	pH	Strat
Cl	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
SO$_4$	**0.85***	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
SiO$_2$	−0.28	0.15	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ca	**0.95***	**0.89***	−0.07	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chl a	−0.3	−0.26	−0.27	−0.32	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
K	**0.81**	**0.91***	0.09	**0.87***	−0.04	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Mg	**0.99***	**0.9***	−0.19	**0.97***	−0.31	**0.83**	1	—	—	—	—	—	—	—	—	—	—	—	—
Na	**1***	**0.88***	−0.24	**0.97***	−0.28	**0.85***	**0.99***	1	—	—	—	—	—	—	—	—	—	—	—
DOC	0.31	−0.17	**−0.68**	0.27	0.08	0.04	0.23	0.28	1	—	—	—	—	—	—	—	—	—	—
DIC	0.22	0.06	−0.59	−0.02	0.26	0.04	0.18	0.18	0.12	1	—	—	—	—	—	—	—	—	—
SRP	0.22	0.01	−0.52	0.05	0.06	−0.04	0.21	0.18	0.21	0.45	1	—	—	—	—	—	—	—	—
NO$_2$	0.55	0.27	−0.28	0.6	0.04	0.55	0.49	0.56	**0.78**	−0.08	−0.05	1	—	—	—	—	—	—	—
NO$_3$	**0.87***	**0.9***	0.12	**0.95***	−0.4	**0.87***	**0.9***	**0.89***	0.12	−0.03	−0.16	0.53	1	—	—	—	—	—	—
NH$_3$	0.48	0.5	0.06	0.42	−0.42	0.54	0.43	0.5	−0.02	0.23	−0.31	0.31	0.6	1	—	—	—	—	—
TP	−0.05	−0.25	−0.41	−0.07	0.53	0.02	−0.08	−0.05	0.53	0.17	0.6	0.44	−0.25	−0.38	1	—	—	—	—
Temp	**−0.74**	**−0.89***	−0.22	**−0.71**	0.35	**−0.82**	**−0.76**	**−0.76**	0.29	−0.24	−0.02	−0.17	**−0.79**	**−0.7**	0.3	1	—	—	—
DO%	−0.28	0.12	0.53	−0.2	0.11	0.17	−0.26	−0.22	**−0.69**	−0.38	−0.29	−0.34	−0.1	0.18	−0.2	−0.17	1	—	—
pH	**0.93***	**0.78***	−0.31	**0.9***	−0.28	**0.8**	**0.89***	**0.94***	0.33	0.08	0.03	0.58	**0.83***	0.59	−0.13	**−0.65**	−0.08	1	—
Strat	**−0.75**	**−0.85***	0.04	**−0.65**	0.21	**−0.69**	**−0.77**	**−0.75**	0.3	−0.46	−0.22	0.03	**−0.65**	−0.49	0.31	**0.9***	−0.04	−0.62	1
	Cl	SO$_4$	SiO$_2$	Ca	Chl a	K	Mg	Na	DOC	DIC	SRP	NO$_2$	NO$_3$	NH$_3$	TP	Temp	DO%	pH	Strat

Cl = chloride, SO$_4$ = sulfate, SiO$_2$ = silicate, Ca = calcium, Chl a = chlorophyll a, K = potassium, Mg = magnesium, Na = sodium, DOC = dissolved organic carbon, DIC = dissolved inorganic carbon, SRP = soluble reactive phosphorus, NO$_2$ = nitrite nitrogen, NO$_3$ = nitrate nitrogen, NH$_4$ = ammonia nitrogen, TP = total phosphorus, Temp = temperature, DO% = dissolved oxygen saturation, Strat = stratification, expressed as density difference between epi- and hypolimnion. Significance levels are marked by bold type ($p < 0.05$) and *($p < 0.001$).
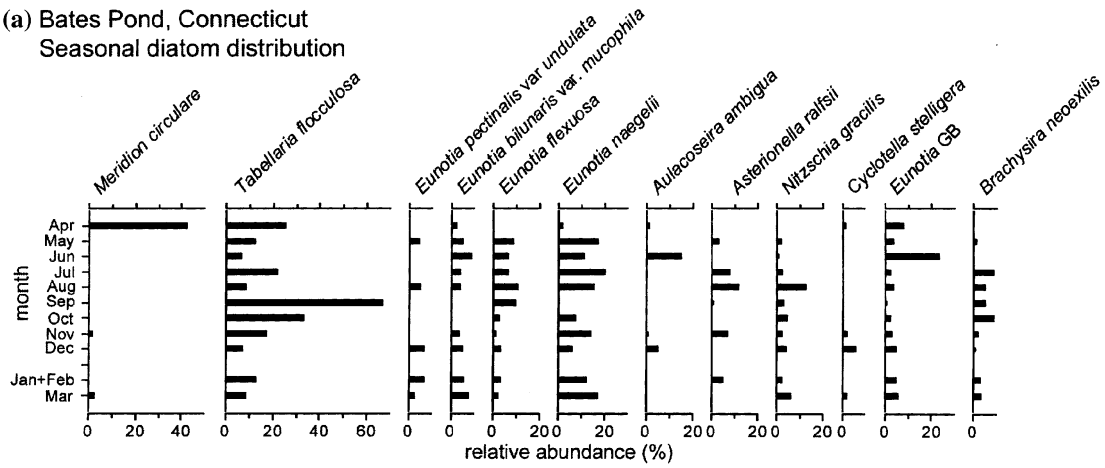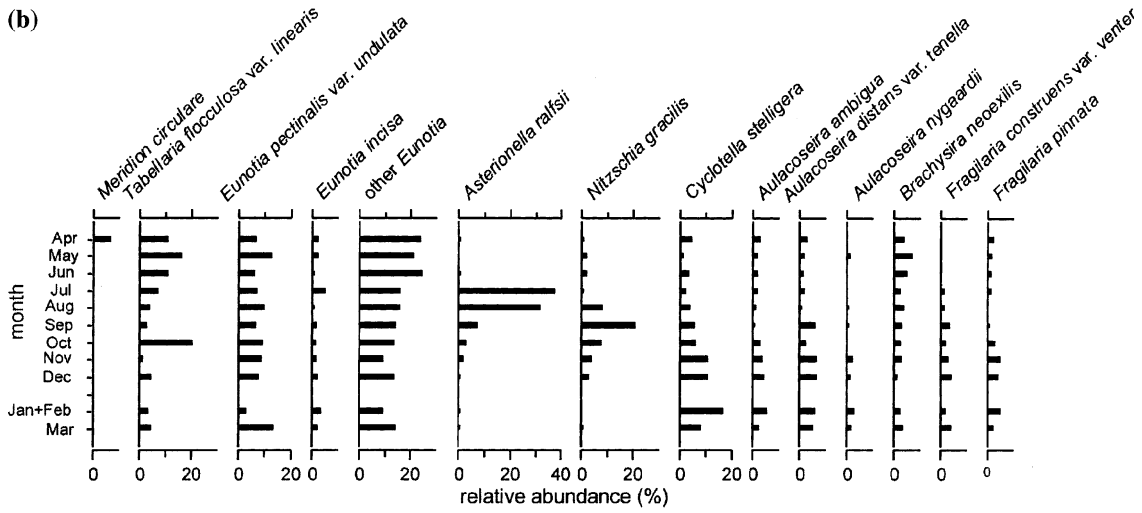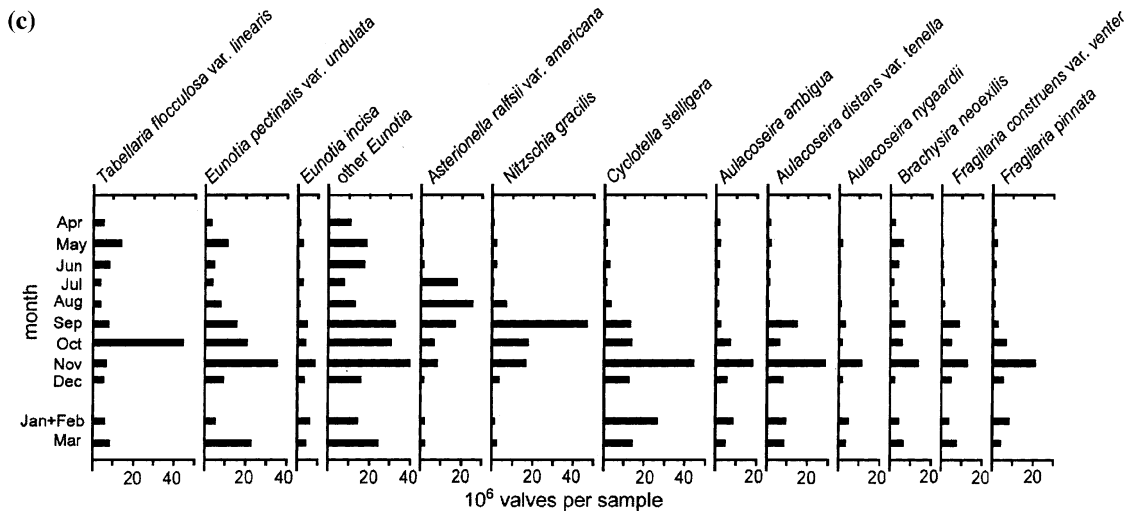
Figure 5. Seasonal distribution of the most abundant diatom taxa collected monthly in (a) phytoplankton, (b) sediment traps, given in relative abundance, and (c) sediment traps, absolute abundances. GB = girdle band view.

between phytoplankton and trap samples were evident in the abundance of *Fragilaria* spp. and *Aulacoseira distans* var. *tenella*, which were only encountered in the sediment traps, a much lower abundance of *Cyclotella stelligera* and *Eunotia pectinalis* in the phytoplankton, and a different distribution of *Brachysira neoexilis*.

Diatom–environment relationships

Stratification, nitrate, silica, and total phosphorus combined explained most of the variance in the seasonal distribution of trap diatom assemblages and were not co-linear. Of these variables, stratification accounted independently for the highest proportion of variance in the species data (15.6%), followed by nitrate (12.4%), silica (7.8%) and total phosphorus (4.8%), as indicated by partial RDAs (Table 3), each representing a group of closely correlated variables, except TP (Table 2). These results are illustrated in the environment–sample biplot (Figure 6), where stratification was strongly correlated with species axis 1 ($r = 0.90$), NO_3^- with species axis 2 ($r = -0.63$), SiO_2 with species axis 3 ($r = -0.53$) and TP with axis 4 ($r = 0.42$). The eigenvalues of the RDA axes 1 and 2 were 0.53 and 0.14, respectively. However, these results have to be viewed with caution, because correlations between stratification and the other variables were detected (Table 2).

The only variables that explained significant portions of the species variance as assessed by Monte Carlo permutations were stratification and temperature (Table 3), with the highest influence shown by stratification. This suggests that these connected variables explained a high amount of variation and that the importance of the other variables (TP, NO_3^-) was at least partly due to correlation with stratification (Table 2). The phytoplankton assemblages were also strongly related to stratification, together with the variable SiO_2 (data not shown).

The individual correlations between the most abundant diatom species in the sediment traps and the environmental variables are illustrated in the species–environment biplot (Figure 7) and in Table 4. Many species were negatively correlated with stratification and temperature, because they grew in autumn and winter, such as *Aulacoseira distans* var. *tenella*, *A. ambigua*, *Fragilaria pinnata*, and *Cyclotella stelligera*. *Asterionella ralfsii* was positively correlated with stratification and temperature, reflecting its appearance in summer. Additionally, *C. stelligera* and *F. pinnata* var. *lancettula* were positively related to NO_3^-, whereas *Tabellaria flocculosa* var. *linearis* was negatively related to NO_3^- (Table 4).

Chronology and lithology

Both the calibrated and assigned dates used for the age–depth model (Figure 8) are given in Table 5. The settlement horizon was assigned to the 54-cm level, where *Rumex* and *Ambrosia* pollen increased significantly, likely reflecting disturbance in the immediate catchment of the lake. However, a slight increase in agricultural indicators at 64-cm core depth indicates that the region and possibly some parts of the watershed vegetation have been cleared earlier and that the town settlement date of 1703 may correspond to some levels below 54 cm.

Organic matter content, as estimated by loss-on-ignition, remained relatively stable at about 40% from 100- to 60-cm depth (Figure 9). It shows a

Table 3. Results of ordination using redundancy analyses and Monte Carlo permutation tests for assessing significance of environment–species relationships.

Variable	RDA one variable		pRDA (4 covariables)	
	% explained	*p*-value	% explained	*p*-value
Stratification	48.6	0.085	15.6	0.04
Temperature	38	0.04	5.2	0.075
NO_3^-	16.8	0.36	12.4	0.33
SiO_2	7	1	7.8	0.21
TP	4.9	0.83	4.8	0.51

% explained: percentage of variance in species data that is explained by this variable, in pRDA after partialling out the effect of the four covariables.
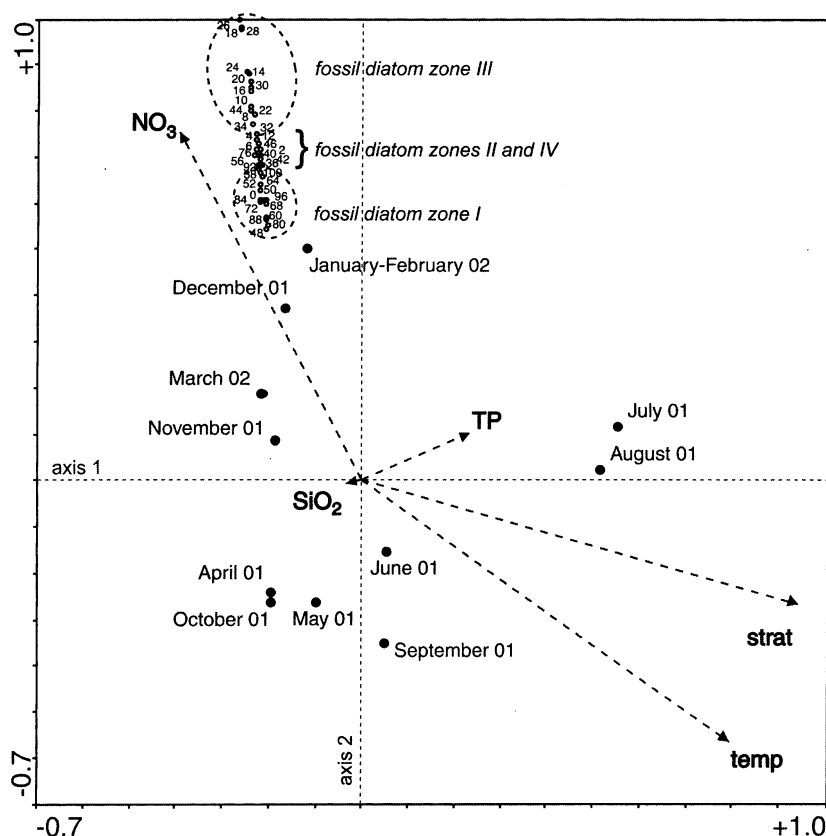
Figure 6. Environment–sample biplot derived from RDA of relative diatom abundances in the trap, fossil diatom samples and monthly environmental variables, with trap-diatom samples set as active samples and fossil diatom samples as passive samples.

small increase around 55 cm, coincident with human settlement, and a gradual increase from ca. 40% at 45 cm (ca. 1750 AD) to ca. 50% at 18 cm (ca. 1885 AD), including a small peak of ca. 48% at 32 cm (ca. 1810 AD). From 18 cm onwards, LOI decreased until it reached pre-settlement values (40%) between 11 cm (ca. 1930 AD) and the surface.

Fossil diatom assemblages and paleolimnological inferences

The fossil diatom samples of Bates Pond have been subdivided into four zones that are based on significant changes in assemblage composition (Figure 9). In Zone I (100–64 cm, ca. 1010–1600 AD), the diatom assemblages were dominated by *Cyclotella stelligera* and *Aulacoseira distans* var.

tenella, while *Fragilaria pinnata*, *Tabellaria* spp., *Brachysira* spp. and *Eunotia* spp. were present in low abundances. In zone II (64–36 cm, ca. 1600–1800 AD), *F. pinnata* and, to a lower extent, *Eunotia zasuminensis* (Cab.) Körner increased, relative to *A. distans* var. *tenella*. Zone III (36–12 cm, ca. 1800–1920 AD) is characterized by temporary increases of *C. stelligera*, *A. ambigua*, and *E. zasuminensis*. In the most recent zone (12–0 cm, ca. 1920–2000 AD), assemblages were similar to those observed in zone I (Figure 9), with decreases of *C. stelligera*, *E. zasuminensis*, *A. ambigua*, and *F. pinnata*, and increases of *E. incisa* and *A. distans* var. *tenella*.

Diatom-inferred total phosphorus (DI-TP) fluctuated between 12 and 18 $\mu g\,l^{-1}$ (Figure 9), indicating that the lake was mesotrophic throughout the last ca. 1500 years. After relatively stable concentrations during the pre-settlement
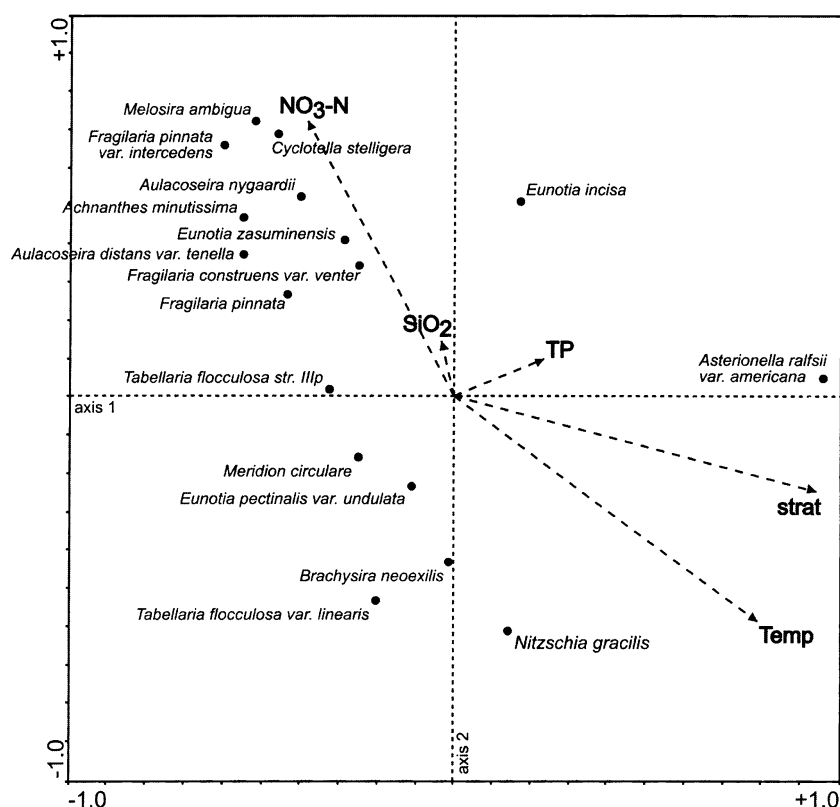
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Figure 7. Environment–species biplot derived from RDA of relative diatom abundances in the trap and monthly measured environmental variables. Species that are plotted close to the arrowhead of an environmental variable are positively correlated with this variable, whereas species plotted at the opposite side of the axes' origin are negatively correlated with the same variable.

period, DI-TP was lower during the 19th century and increased to pre-settlement values after ca. 1920 AD. Diatom-inferred pH is constant with values between 7.2 and 7.5, but showed a slight increase from the bottom to the surface of the core.

Table 4. Correlation coefficients between the most abundant species in the sediment traps and five environmental variables.

Taxon	Strat	Temp	NO$_3^-$	SiO$_2$	TP
Asterionella ralfsii var. *americana* Körner	**0.89***	**0.73**	−0.34	−0.03	0.24
Aulacoseira ambigua (Grun.) Simonsen	**−0.64**	**−0.78**	0.59	−0.08	0.11
Aulacoseira distans var. *tenella* (Nygaard) Florin	**−0.7**	**−0.65**	0.58	−0.3	−0.18
Aulacoseira nygaardii Camburn *in* Camburn and Kingston	−0.6	−0.63	**0.7**	−0.19	−0.1
Brachysira neoexilis Lange-Bertalot	0.16	0.2	−0.36	0.38	−0.2
Cyclotella stelligera (Cleve and Grunow) Van Heurck	**−0.69**	**−0.76**	**0.81**	−0.23	−0.02
Eunotia flexuosa (Brébisson) Kützing	−0.01	0.05	−0.39	0.27	0.09
Eunotia incisa Gregory	0.07	−0.18	0.26	0.29	0.04
Eunotia pectinalis var. *undulata* (Ralfs) Rabenhorst	−0.07	0.03	−0.05	0	−0.1
Fragilaria construens var. *venter* (Ehrenberg) Grunow	−0.45	−0.39	0.56	−0.43	−0.03
Fragilaria pinnata Ehrenberg	−0.39	−0.44	0.06	−0.02	0.12
Fragilaria pinnata var. *lancettula* (Schumann) Hustedt	**−0.76**	**−0.81**	**0.69**	−0.25	0.1
Nitzschia gracile Hantzsch	0.13	0.45	−0.26	−0.56	−0.2
Tabellaria flocculosa (Roth) Kützing str. IIIp sensu Koppen	−0.28	−0.31	0.23	0.44	−0.17
Tabellaria flocculosa var. *linearis* Koppen	0.03	0.2	−0.46	0.05	0.15

The values are derived from a redundancy analysis with centering and standardization by species; Strat = stratification, Temp = temperature. Significance levels are marked by bold type ($p < 0.05$) and * ($p < 0.001$).
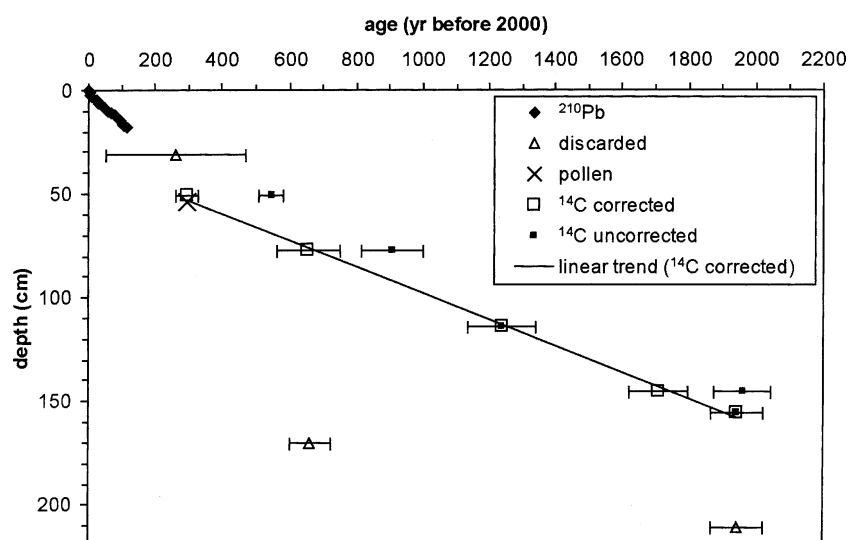
age (yr before 2000)

Figure 8. Age–depth model for the Bates Pond core based on radiocarbon (^{14}C) and ^{210}Pb dates as well as the pollen-based settlement date. Error bars represent the 2-sigma error ranges of ^{14}C dates. The dates from levels 51, 77, and 115 cm were corrected for old carbon based on the difference between the ^{14}C date at 51 cm and the settlement date (see Methods for details).

Table 5. Radiocarbon (^{14}C) dates for the Bates Pond sediment core.

Lab Number	Depth (cm)	Dated material	^{14}C yr BP	2 sigma range with midpoint cal. yr BP	Assigned age cal. yr BP	Yr before 2000 AD	Yr AD
AA-39359[a]	31	Bulk sediment	245 ± 35	5–420 (210)	210	260	1740
AA-41563	51	Bulk sediment	442 ± 35	460–530 (500)	250[b]	300[b]	1700
AA-39360	77	Bulk sediment	957 ± 70	740–950 (860)	610[b]	660[b]	1340
OS-45076	114	Assorted plant fragments[c]	1280 ± 40	1090–1290 (1190)	1190	1240	760
AA-39361	145	Bulk sediment	1970 ± 40	1820–2000 (1910)	1660[b]	1710[b]	290
Beta-189304	155	Plant and insect macrofossils	1930 ± 40	1820–1970 (1890)	1890	1940	60
OS-45077[a]	170	Assorted plant fragments [c]	665 ± 40	550–670 (610)	610	660	1340
Beta-189305[a]	211	Plant macrofossil	1930 ± 40	1820–1970 (1890)	1890	1940	60

[a] Dates discarded for age-depth model. [b] Dates corrected for old carbon by subtracting 250 yrs, based on the difference between the ^{14}C date at 51 cm and the settlement date. See methods for details. [c] Including seeds, wood, leaves, charcoal.

Comparison of trap and sediment samples

In general, most species that were present in the sediment record were also found in the sediment traps, indicating that the lake core provided an accurate assessment of the diatom species in the water column. However, an RDA with trap samples used as active and fossil samples as passive samples, resulted in high squared residual distances of the fossil samples to axes 1–4. These were higher than the maximum distance of the modern samples to the axes (data not shown), indicating

very poor analogs (Birks et al. 1990). These poor analogs resulted from several species being present in different relative abundances in core and trap samples. For example, the taxa that dominated the sediment traps during warm periods in spring (*Tabellaria* spp.) and during summer (*Asterionella ralfsii*, *Nitzschia gracilis*) were rare in the sediments (Figures 5 and 9). On the other hand, *Cyclotella stelligera* and epipelic diatoms, such as *Navicula* spp., were more abundant in the sediments than in the traps. Using ordination, the core samples are situated at the edge of the modern
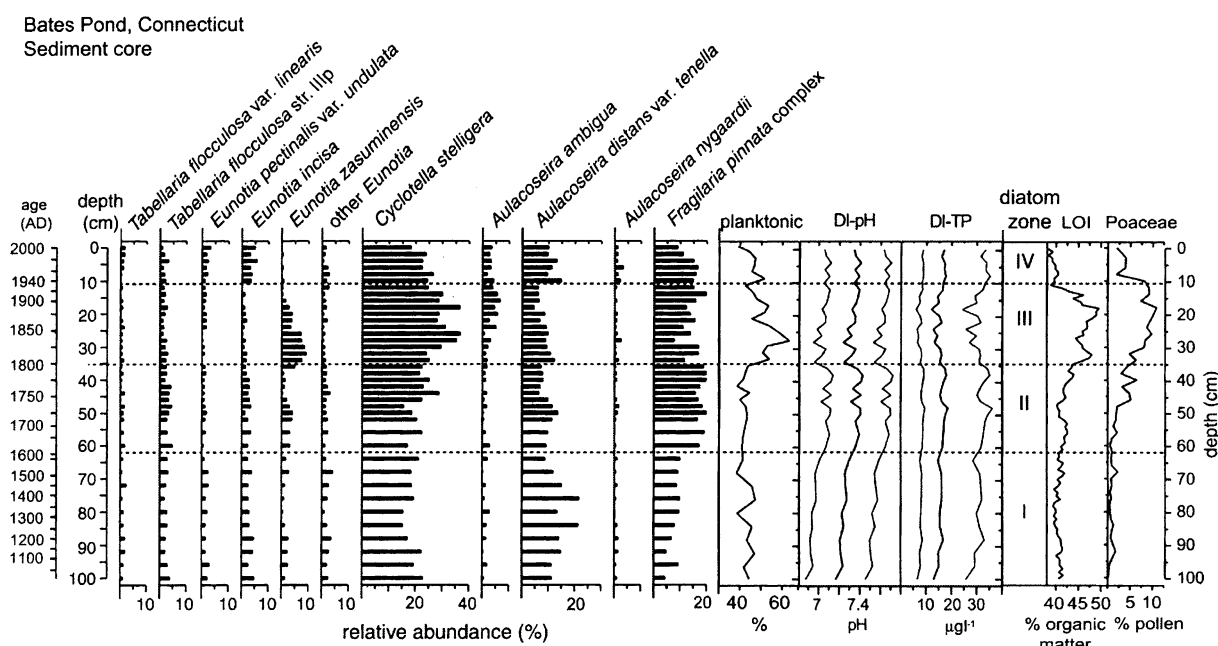
Bates Pond, Connecticut
Sediment core

Figure 9. Fossil diatom assemblages from the surface core of Bates Pond, percentage of planktonic species, diatom-inferred pH (DI-pH) and TP (DI-TP), major diatom zones, organic matter content estimated by loss-on-ignition (LOI), and percentage of Poaceae pollen. Error ranges for DI-pH and DI-TP were estimated by bootstrapping.

environment–sample space, close to the modern autumn and winter samples, indicating that the fossil samples are dominated by diatoms that presently grow during autumn and winter, e.g., *C. stelligera, A. distans,* var. *tenella.* There is a trend in the fossil samples from 72 to 100 cm (diatom zone I) to plot more closely to the axis origin (i.e. corresponding to conditions of stronger stratification, lower NO_3^-). The samples from 10 to 30 cm (diatom zone III) are positioned at the outside of the ordination space (corresponding to weaker stratification, higher NO_3^-).

The best performance of PLS models based on diatom trap and water chemistry data was obtained by those developed for stratification, temperature, and NO_3^- (Table 6), whereas the performance of the TP and SiO_2 models was weaker (data not shown). Cross-validation was not possible because of an insufficient number of samples in the model; therefore only apparent performance statistics are presented. As stratification is not a standard variable, we present only the reconstructions for temperature, which can be used as a surrogate for the water column stability because of its high correlation to stratification. As expected from their high correlation, the reconstructions of temperature and NO_3^- using the respective PLS models resulted in highly correlated

Table 6. Performance of the partial least squares (PLS) models based on monthly diatom samples from April 2001 to March 2002 and associated water parameter measurements.

Variable	Model	RMSE	r^2	Average bias	Maximum bias
stratification	PLS component 1	0.23	0.95	0.00	0.62
	PLS component 2	0.08	0.99	0.00	0.12
Temperature	PLS Component 1	2.61	0.88	0.00	4.16
	PLS component 2	0.68	0.99	0.00	0.48
NO_3	PLS component 1	6.82	0.74	0.01	11.07
	PLS component 2	3.55	0.93	0.00	7.09

RMSE = apparent root mean square error. r^2 = apparent coefficient of determination of the regression of predicted on observed values.

inferences (Figure 9). However, while inferred temperature showed a gradual decreasing trend from 100 to 20 cm depth and then an increase towards the top, nitrate remained stable from 100 to 50 cm and increased later than temperature, from 50 to 28 cm, and then decreased from 28 to 0 cm. The inferred temperature and NO_3^- changes remained within the root mean square error of the model.

Discussion

Patterns and causes of seasonal diatom distribution in Bates Pond

The seasonal distribution of most diatom species during the analyzed year was mainly related to changes in the physical environment (temperature, stratification) and NO_3^- (Figure 7 and Table 4), the latter being correlated to major ion concentrations and pH (Table 2). The strong control of physical factors on diatoms may have resulted from the short duration of ice cover during the studied winter, causing an early onset of full-circulation in 2002. To correct for this, we computed an RDA with the samples from 2001 only (data not shown), which also identified stratification as the most significant variable. During periods of lower water column stability in spring and autumn and short-term storm events in spring or summer, previously deposited diatoms may have been re-suspended into the water column, subsequently multiplying to form rich populations (Smetaéek 1985; Carrick et al. 1993).

Together with temperature, wind patterns may have played a role in the observed distribution of full-mixing periods. Wind data for this site were not available to us, but wind speed data from a station ca. 100 km east from Bate Pond may indicate regional wind patterns. At Buzzard Bay (Massachusetts) average wind speeds were low in April, June, July, and August 2001, corresponding to stabile stratification in Bates Pond (US Dept. of Commerce, National Oceanic and Atmospheric Administration, National Weather Service, National Data Buoy Center; http://www.ndbc.noaa.gov). Higher wind speeds in March, May, and from October 2001 to March 2002 likely enhanced the mixing of the water column. As a closely related variable to stratification, wind is

thus also having an indirect influence on diatom assemblages.

The algae–environment relationships in one of two seasonally sampled oligotrophic Ontario lakes were similar to those observed in Bates Pond, with a high influence of temperature in the shallow and frequently mixed lake (Agbeti et al. 1997). Also, the presence of lightly silicified, spindle-shaped diatoms, such as *Asterionella ralfsii* and *Nitzschia gracilis* during summer in Bates Pond, was related to stratification in that study (Agbeti et al. 1997). A 5-year study of chrysophytes in a nearby lake in Connecticut showed that the seasonal appearances of these algae were also strongly related to temperature (Siver and Hamer 1992). Similarly, in Bates Pond, the water column stability related to temperature and wind patterns appeared to be a major factor determining changes in diatom assemblage composition during the studied year. Still, an important influence of nutrients was indicated for the trap assemblages by nitrate explaining the second most variation in diatom assemblages, by strong relationships between temperature and nutrients, as well as for the phytoplankton assemblages that were strongly related to SiO_2 concentrations (data not shown).

The presence of benthic species in the traps throughout the year, as well as the higher total abundance of diatoms in the traps during autumn suggest that horizontal transport of benthic diatoms has occurred and that re-suspension may have influenced the observed seasonal dynamics. The presence of benthic diatoms in the traps indicates low water column stability and is therefore part of the diatom assemblage response to the physical conditions in the lake. Re-suspension in this sense is therefore not a problem for our interpretations. However, if re-suspended material contained many dead cells, our interpretations become problematic, because dead diatoms had probably lived under different environmental conditions than those measured at the time of trap sampling. Dead cells in relation to living cells would have to be counted and identified in order to estimate the approximate error caused by the portion of trapped diatoms that were non-living material. Such analyses were not carried out in our study. Analyses of the upper 1 cm of sediments in Hagelseewli, Switzerland, showed that the majority of small *Fragilaria* spp. were alive, whereas *Cyclotella comensis* populations consisted of about

50% living and 50% dead cells at depths ranging from 0 to 10 m (C. Bigler, personal communication). These results suggest that important numbers of diatoms that potentially can be resuspended from the sediments may be alive. Unless dead cell portions were estimated, the errors caused by dead cells in general and by dead cells in resuspended material in particular remain unknown.

For comparison with the long-term record of Bates Pond, it would be preferable to know if the one-year pattern observed here is also representative for other years. In the absence of major human or climatic disturbances, seasonal patterns in lake phytoplankton are similar from one year to another (Wetzel 2001). A study of varved sediments in a deep Finnish lake showed similar patterns in diatom assemblages over several consecutive years (Simola 1979), as did algal populations in a shallow, frequently mixed lake in Ontario, Canada (Agbeti et al. 1997). However, other lakes exhibit different seasonal patterns in consecutive years due to inter-annual climatic variations (Rautio et al. 2000). The climatic conditions of the year 2001 were warmer and drier than the 1895 to 2004 normal, but remained within the range of the variability for these years. However, the exceptionally warm winter likely caused unusual patterns in the phytoplankton communities that were sampled in February and March of 2002. Even if the analysis of the 2001 samples also revealed stratification as the most important variable influencing diatom assemblages in Bates Pond, the study of more samples from at least one supplementary year would be necessary to reach solid conclusions regarding the environmental factors controlling recent diatom assemblages.

Fossil diatom assemblages

From 100 cm core depth (ca. 1010 AD) to the present, diatoms indicated relatively stable mesotrophic and circumneutral conditions. However, diatom assemblages responded to human disturbance in the watershed, as discussed below. Sample scores on PCA axis one show an additional increasing trend from 80 cm onwards (data not shown), which continues through zones II and III.

The diatom assemblage change at 60 cm (ca. 1640 AD) and a temporal increase in sedimentary organic matter content (Figure 9) coincide with slight increases of *Rumex*, *Ambrosia*, and Poaceae pollen (Figure 9), which may reflect forest clearing in the catchment. However, a significant increase of agricultural indicators, which is used to prove the presence of disturbance in the immediate catchment (Brugam 1978), occurred only at 54 cm, ca. 60 years later. Therefore, climatic forcing may be an alternative explanation for the species change observed at 60 cm, such as discussed below.

The most evident change in Bates Pond fossil diatom assemblages associated with increased abundances of *Cyclotella stelligera*, *Aulacoseira ambigua*, and *Eunotia zasuminensis* coincided with increased agricultural activities in the watershed. *C. stelligera* increased following logging in Walden Pond, Massachusetts (Köster et al. 2005). *A. ambigua* can thrive in oligo- to mesotrophic waters, and may therefore have been favored by an increase in nutrient availability due to higher inputs of allochthonous matter from deforested and cultivated land. *E. zasuminensis* has a preference for slightly dystrophic waters (Nicholls and Carney 1979; Eloranta 1986) and may therefore indicate higher dissolved organic carbon (DOC) concentrations. Deforestation in the catchment of lakes can cause increases in lake DOC (Carignan et al. 2000), but no independent evidence for such a temporary increase in DOC concentrations at Bates Pond is available.

As all species that increased in zone III are planktonic, they may also have responded to higher availability of open water habitat or higher water turbulence. Increased exposure of the lake to strong winds due to the opening of the landscape may have caused stronger circulation in the water column and thus enhanced proliferation of planktonic algae. In addition, lower water temperatures could have prolonged full circulation periods, as discussed below.

The return to early settlement diatom assemblages during the 20th century suggests an almost complete recovery of the lake following reforestation of the watershed. The current residential use of the lake is limited to one family with a few buildings that are located outside the watershed, and it appears that this low impact is responsible for the present-day dilute character of the lake.

Implications of seasonal diatom patterns for paleolimnological inferences

Presuming that the environment–species relationships described above have not changed over time, the preferences of different diatom species for these variables could be useful for the interpretation of the fossil diatom data in Bates Pond. For example, *Cyclotella stelligera* and *Fragilaria* spp. were most abundant in autumn and winter, when temperature was low, the water column well mixed, and nitrate concentrations high. Therefore, the increased abundance of these species in the fossil record between ca. 60- and 10-cm depth may indicate prolonged circulation periods and therefore generally cooler conditions, stronger winds, and/or higher nitrate concentrations. These taxa are also indicators of human disturbance, as discussed above. Therefore the question to which factor the fossil assemblages mainly respond, arises.

Intuitively, changes in the structure of diatom assemblages of a temperate lake would be interpreted in terms of nutrient availability, light conditions or pH, while temperature has a large effect on growth rates of organisms. Temperature is more likely to influence algal communities in ecosystems at climatic and vegetation boundaries (Smol and Cumming 2000). However, some studies have shown that shifts in fossil diatom assemblages may indicate changes in seasonal mixing patterns induced by climate change (Bradbury 1988; Bradbury and Dieterich-Rurup 1993; Edlund et al. 1995). In Bates Pond, some species that correlated with stratification, but not with the second most important variable NO_3^-, such as *Asterionella ralfsii*. This may suggest that some fossil species also have been controlled by temperature at the time of their deposition.

In order to allow inferences on climate change, e.g. temperature, based on reconstructions of the extent of stratification, both variables have to keep a constant relationship over time. Given that cooler temperatures do not only shorten summer stratification, but also extend winter stratification, very different climatic scenarios may result in the same extent of stratification. Some climate change may be missed this way in the sediment record. An increase in the abundance of stratification indicators can imply seasonally lower temperatures during summer or warmer temperatures during winter, preventing ice cover. Only a change in total energy input could lead to the loss of summer or winter stratification, which would deeply impact the diatom species composition. A solution to this problem may be seasonal transfer functions directly based on temperature, such as presented here. It remains that both variables are closely related in this study and likely in other lakes, so the effect of stratification will be difficult to disentangle from that of temperature. More studies are necessary to explore the temperature preferences of diatoms in temperate lakes.

In Bates Pond, *Fragilaria* spp. entered the sediment traps mainly during autumn and winter (Figure 5), probably indicating a preference for cooler and/or more turbulent conditions. Their abundance increased by 10% at ca. 1640 AD in the fossil record (Figure 9), corresponding to the onset of a period of climatic cooling, the Little Ice Age (Bradley and Jones 1993). A study of diatoms in sediment traps and a sediment core in a Swiss alpine lake showed that *Fragilaria* spp. mainly entered the traps during winter and that higher abundance of these taxa in the sediments corresponded to longer ice cover during the Little Ice Age (Lotter and Bigler 2000). Cooler conditions around 1500 AD (Cronin et al. 2003) and during the 18th century, as well as wetter conditions during the 18th century (Cronin et al. 2000), were recorded in marine cores in Chesapeake Bay (Maryland, USA), which is located ca. 500 km southwest from Bates Pond. perhaps indicating that autumn and/or winter conditions prevailed longer in Bates Pond at that time. Furthermore, the taxon *Aulacoseira distans* var. *tenella*, which was negatively correlated with stratification and temperature in our seasonal study, showed higher abundances in the pre-settlement sediments between 70 and 80 cm (ca. 1350–1500 AD) (Figure 9), possibly indicating increased mixing during this time. Therefore, one explanation for the changes in diatom assemblage composition preceding European settlement may be climate-driven changes in the mixing regime of Bates Pond.

Cyclotella stelligera has often been described as an indicator for warmer temperatures and stronger thermal stratification, mostly in oligotrophic, boreal, subarctic, arctic, and alpine lakes (Rautio et al. 2000; Catalan et al. 2002; Bigler and Hall 2003; Rühland et al. 2003). This is contrary to our finding that it was related to cool conditions and

full circulation in autumn and winter in the mesotrophic Bates Pond. This seemingly opposite behavior of the same species may probably be explained by the different ecoregions and trophic state of the respective study lakes. What is warm in absolute temperatures for northern and alpine lakes may be cold for a temperate lake. Furthermore, *Cyclotella stelligera* may have responded to increasing nutrient concentrations during autumn and winter in Bates Pond caused by mixing of nutrient-rich hypolimnetic waters into the entire water column. More seasonal studies of temperate lakes are needed to obtain more precise ecological information for this in paleoecological records common species. The apparent differences in species responses to environmental variables between regions underline the importance of regional assessment of individual species' ecological preferences for reliable paleolimnological inferences.

One possible factor having triggered the pre-settlement changes in diatom assemblages may be nitrate, as it was also an important variable for the recent diatom assemblages. Nitrogen was important in explaining variation in phytoplankton diatoms in a set of Connecticut lakes (Siver 1999). However, the limiting nutrient in temperate mesotrophic lakes like Bates Pond usually is phosphorus, which was reconstructed from the sediment core and did not exhibit any changes. Also, the inferred NO_3^- shifts, as inferred by the PLS model based on the trap samples, occurred later than the decreasing temperature trend (Figure 10). This may support the hypothesis that natural processes triggered diatom assemblage changes before European settlement, with the effects of human impacts superimposed after European settlement. The comparison of paleolimnological inferences based on the trap models with those derived from classic models shows that the trap models captured supplementary information. Still, both models reconstruct very similar, inverse trends,
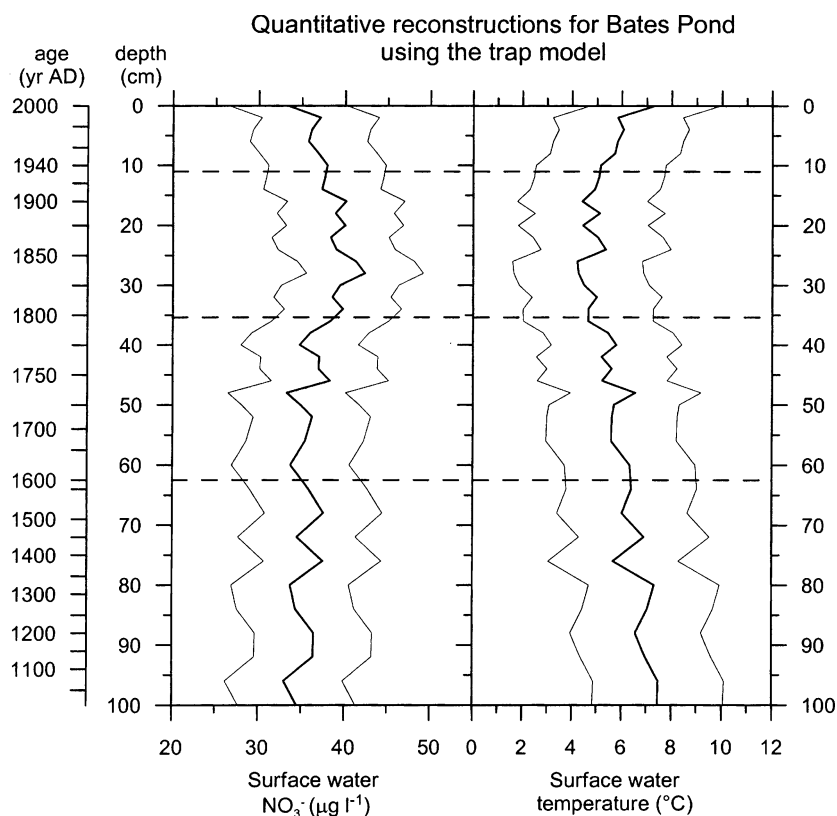

Figure 10. Quantitative reconstructions for surface water nitrate (NO_3^-) and temperature for the fossil samples of Bates Pond, using a PLS model based on 11 sediment trap samples and monthly water analyses. Fine vertical lines indicate the estimated root mean square errors of the models (see Table 6). Horizontal dashed lines indicate major diatom zones as estimated by cluster analysis.

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which is not surprising given the negative correlation of temperature and NO_3^- (Table 2). As the trap model is based on only 11 samples that are not independent at a spatial or temporal scale, it is evident that these results have to be viewed with caution. For developing a statistically more robust model and for reaching conclusive remarks on the temperature/mixing preferences of individual species, investigations in one or more lakes over several years are needed.

Despite the presence of all dominant fossil species in the sediment traps (Figures 5 and 9), different relative abundances of some taxa resulted in a separation between fossil and modern sample sets in ordination (Figure 6). This discrepancy is partly due to the higher proportion of epipelic diatoms (*Navicula* spp.) in the fossil samples, which may be more concentrated in the surface sediments by epipelic and epiphytic growth, sediment focusing, and vertical transport. Vertical transport can also change with altered mixing regimes, but this situation is probably captured by the sediment trap analyses, where increased vertical transport during some periods of the year also resulted in increased valve deposition in the traps. Sediment focusing and epipelic and epiphytic growth were not investigated through this study, and they may potentially influence the interpretation of the sediment record using sediment traps. Therefore, the changing distribution of benthic species in core samples may limit the utility of trap samples for interpreting changes in fossil samples. The only way to avoid these problems is to choose large, deep lakes for a combined sediment-trap/paleolimnological study.

Other differences between trap and sediment samples were the high relative abundances of *Asterionella* spp. and *Nitzschia gracilis* during summer months, which were not reflected in the sediments, as well as higher relative abundances of *Cyclotella stelligera* in the sediments compared to the traps. These differences may be caused by inter-annual variability in the seasonal cycle of the lake, indicating that at least one additional year of observations would be useful for testing the repeatability of our results.

Our study illustrates that ecological information is potentially encoded in the modern seasonal cycle of a lake, which may probably be used in the interpretation of the fossil record of the same lake. This may be particularly relevant for paleoclimatic

studies in temperate regions, where ecotonal and climatic boundaries are difficult to find. Here, climatic changes may result in subtler ecosystem responses, such as changes in the seasonal cycle of organisms. Therefore, if a lake is chosen for a long-term record of environmental change, the knowledge of the current seasonal variability in biological paleoclimatic proxies, such as diatoms, can provide important information for the interpretation of fossil records.

The period of highest diatom abundance in Bates Pond was autumn. This did not completely confirm the generalized pattern of highest diatom abundance during spring and fall overturn in temperate, dimictic lakes (Sommer et al. 1986; Wetzel 2001). While the diatom species with the closest correlation to the major environmental gradient in Bates Pond occurred in autumn (Figures 5 and 7), the spring assemblages responded to similar environmental conditions. This implies that the highest correlation of the measured environmental parameters with the subfossil diatom record likely also exists during spring and autumn. Similar results were obtained in a Connecticut lake, where the surface sediment sample of another siliceous algae group (chrysophytes) showed the closest relationship to chemical data from autumn and winter (Siver and Hamer 1992). For the development of diatom-based inference models using subfossil diatoms, spring and autumn may therefore be the most representative sample seasons. A diatom model based on spring TP in Danish lakes performed slightly better than the model based on mean annual TP (Bradshaw et al. 2002). Autumnal TP was used in the development of robust TP models in Finland (Kauppila et al. 2002) and spring TP was used in Ontario and Switzerland (Hall and Smol 1992; Lotter et al. 1998). However, models based on summer samples (Dixit et al. 1999) or annual means (Bennion 1994; Cameron et al. 1999) do also perform well. As many physical and chemical variables are correlated with season, their past fluctuations are probably evident during all seasons and are thus recorded by all seasonal diatom assemblages. However, some climatic variables, such as temperature, can exhibit long-term trends in certain seasons only. For these cases, seasonal diatom inference models may be useful.

It remains to be tested if seasonal patterns of the periphytic diatoms follow similar timing and

driving factors as the planktonic diatoms. Benthic algal communities can dominate in small and shallow lakes, and their ecology is less well known than that of lake phytoplankton or river epiphyton (Lowe 1996). A study of a lake in England has shown that benthic diatoms reach maximum biomass in the spring (Talling 2002), probably responding to improved light and nutrient availability, like planktonic diatoms. However they are certainly much less influenced by mixing patterns. A better understanding of benthic diatom seasonality and its controlling factors is needed to test if their seasonality can provide information for refinement of paleolimnological interpretations.

The results obtained here are probably relevant for a wide range of small lakes, which are frequently chosen for paleolimnological analyses because of their generally simple morphometry and sedimentation patterns. In the boreal forest regions of North America, small oligotrophic systems represent the large majority of lakes. Temperature is likely an important factor controlling diatom succession in many of these lakes and therefore may be useful for the development of seasonal transfer functions. However, nutrient-rich lakes, which are more widespread in central Europe, are more strongly controlled by the seasonally varying availability of nutrients, which may suggest their suitability for developing seasonal TP transfer functions.

Conclusions

The study of a one-year seasonal sequence of diatoms revealed distinctive seasonal patterns in diatom assemblages that were related to changes in water column stratification and nitrogen. Changes in fossil diatom assemblages reflected human activity in the watershed following European settlement and subsequent recovery during the last century. In addition, a long-term trend in diatom assemblage change initiated before European settlement was possibly related to the extended length of mixing periods during Little Ice Age climate cooling. The study of seasonally varying limnological conditions and diatom succession in more lakes over several years should be encouraged in order to establish more robust seasonal data sets for the improvement of paleolimnological interpretations. This study has provided preliminary evidence that a better understanding of the seasonal diatom dynamics in temperate lakes can provide important insights for the refinement of paleolimnological investigations.

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