

Seasonal climate inferences from high-resolution modern diatom data along a climate gradient: a case study

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Abstract This study represents a step towards developing seasonal climate inferences by using high-resolution modern data sets. The importance of seasonal climate changes is highlighted by the instrumental record of a meteorological station close to our study site (lac du Sommet in the Laurentian Mountains, Québec, Canada): Between 1966 and 2001, May temperatures increased significantly by 3.1°C ($r = 0.41$, $n = 35$, $p < 0.01$) but annual mean temperatures only by 0.6°C ($r = 0.21$, $n = 35$, $p > 0.05$). Comparison of this instrumental record with fossil diatom assemblages in a sediment core from lac du Sommet showed that axis one of a principal component analysis (PCA) of the fossil diatoms was best correlated with wind velocity in June ($r = 0.62$, $n = 19$, $p < 0.005$) and that past diatom production was significantly enhanced in periods with colder July temperatures ($r = -0.77$, $n = 19$, $p < 0.0005$) and higher wind velocity in June ($r = 0.77$, $n = 19$, $p < 0.0005$). The strong impact of the spring and summer conditions on overall

diatom composition and productivity suggests that seasonal lake responses to climate are more important than annual mean temperatures. However, the seasonal dynamics of diatom communities are not well understood, and seasonality is rarely inferred effectively from lake sediment studies. Our research presents a pilot study to answer a twofold question: Is it possible to identify diatom communities which are typical for warmer or colder seasonal climate using sediment traps, and if it is, can this knowledge be used to infer seasonal climate conditions from fossil diatom assemblages? To address these questions, the seasonal dynamics of diatom communities and water chemistry were studied using sediment traps and water samples at biweekly intervals in four lakes distributed along an altitudinal gradient in the Laurentian Mountains from May through October 2002. Date of ice break-up was significantly related to the diatom assemblages taken in spring and uncorrelated to other significant environmental variables. Summer water temperature, circulation of the water column and pH explained a significant part of the biological variance in summer, and total nitrogen (TN) explained most of the biological variance in autumn. To infer these variables, weighted averaging partial least squares models were applied to the seasonal data sets. Inferred ice break-up dates were significantly correlated with number of days below 0°C in April ($r = 0.52$, $n = 19$, $p < 0.025$),

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inferred circulation of the water column was significantly related to measured wind velocity in June ($r = 0.64$, $n = 19$, $p < 0.005$), inferred summer water temperature and inferred pH was significantly related to measured July air temperature ($r = 0.50$, $r = -0.53$, $n = 19$, $p < 0.025$) and inferred TN autumn concentrations had an inverse relationship to August temperatures ($r = -0.53$, $n = 19$, $p < 0.01$). This comparison of the historical record with diatom-inferred seasonal climate signals, based on the comparison of fossil diatom assemblages with modern sediment trap data of high temporal resolution, provides a promising new approach for the reconstruction of seasonal climate aspects in paleolimnological studies.

Keywords Diatoms · Seasonality · Climate · Sediment traps · Multivariate statistics · Paleolimnology · Limnology · Boreal lakes · Shallow lakes

Introduction

The need to understand present day and predict future global climate change greatly enhances the interest in understanding past climate dynamics (Bradley 2000). To obtain climate records that extend beyond instrumental measurements, quantitative reconstruction techniques are needed (Birks 1998), often using diatoms as bioindicators in lake ecosystems. Diatoms possess morphologically diverse silica shells that preserve well in lake sediments and allow identification to the species level. Their short generation cycles allow diatom populations to react rapidly to changes in their environment. Diatoms show strong species-specific responses to changes in their environment (e.g., Reid 2005; Hassan et al. 2006). Direct responses of diatoms to the timing of ice break-up and to the onset of water column stratification, which can be used to detect climate change, have been discussed (Bradbury 1988; Lotter and Bigler 2000; Korhola et al. 2002; Thompson et al. 2005). Climate changes can also be detected indirectly by climate-induced nutrient changes (Douglas and Smol 1999; Anderson 2000).

Inference models based on sets of surface sediment samples constitute a major step forward in paleolimnology. Diatom inference models have been successfully developed for various individual environmental variables (ter Braak et al. 1993). Comparison between inferences and instrumental data have proven the tremendous power in using the surface sediment approach (e.g., Lotter 1998; Hausmann and Kienast 2006).

Surface sediment samples usually encompass several years of diatom deposition. Over the past years, the paleolimnological community has expressed the need for studies on the processes underlying modern community–environment relationships at higher temporal resolution (H.J.B. Birks 2000, Paleolimnology Symposium; Sorvari et al. 2000; T.C. Johnson 2003, 3rd International Limnology Congress). Paleolimnologists recently have made efforts to refine calibration data sets by comparing the performance of models developed for different seasons as well as for different ecological components (planktonic vs. periphytic) of the diatom communities (e.g., Bradshaw et al. 2002; Köster and Pienitz 2006). Bradbury (1988) interpreted the fossil diatom record of Elk Lake (Minnesota, USA), and gained information about seasonally acting climatic factors (e.g., time of ice break-up, circulation) that control diatom assemblages using sediment traps. Köster and Pienitz (2006) inferred temperature by comparing fossil assemblages with samples of monthly resolution from the Bates Pond (Connecticut, USA), where temperature was the most important factor in explaining seasonal changes. The development of a methodology to infer seasonal climate trends from the high-resolution analysis of recent sediments was also an innovative aspect of the EU-project MOLAR (e.g., Sorvari et al. 2000; Lotter and Bigler 2000).

Diatoms undergo a seasonal succession which is driven by seasonal dynamics of environmental conditions (Interlandi et al. 1999). The succession of diatom species and the role of environmental variables were the subject of numerous studies that are of high interest for neo- and paleolimnologists (e.g., Sommer 1986; Anneville et al. 2004). The proposition that lake productivity is influenced directly by climate requires a complete analysis of

paleolimnological productivity proxies, modern limnological observations, model studies, and comparison with other records of regional environmental change. Anderson (2000) suggested that the seasonal succession of diatoms might be driven directly by nutrient availability and only indirectly by temperature changes, as nutrient availability is largely dependent on the melting of ice cover and circulation of the water column (Battarbee 2000; Korhola et al. 2002). To improve the ecological knowledge, Horton (1999) increased sampling frequency in the development of training sets. For a quantitative sea-level inference model based on intertidal foraminifera assemblages, he sampled sediments biweekly at Cowpen Marsh, Tees Estuary (U.K.). Modern samples of high temporal resolution allowed an estimation of the growth period of each species, and helped to understand the influence of environmental conditions on the composition of assemblages. A better knowledge of the seasonality of diatom assemblages and their responses to lake processes related to climate can greatly improve our understanding of how to interpret anomalous results or discrepancies among multiple proxies.

The aim of this study was to observe how diatom assemblages are influenced by seasonal climate and to integrate this information to infer seasonal climate aspects. With the objective that between-lake variability should mainly reflect a temperature gradient, we selected sites that were comparable in terms of trophic state and bedrock geology. Using sediment traps, temperature dataloggers, and water samples, we studied floristic/biotic and limnological changes at bi-weekly intervals in four lakes located along an altitudinal gradient (380–920 m asl) in the Laurentian Mountains, Québec (Canada) from May to October 2002. We tested the statistical relation between environmental variables and diatom assemblages using Monte Carlo permutation tests. The statistically significant impact of the date of ice break-up on spring diatom composition and circulation of the water column on summer diatom composition suggested the potential for the reconstruction of these variables downcore. We assessed the feasibility of this approach through comparisons of our inferences with instrumental records. The results of this

study should provide a solid basis for understanding the output of diatom-based climate models, and allow for far more detailed interpretations of the seasonal climate signals archived in fossil diatom records.

Methods

Coring and dating of sediments

Lac du Sommet (830 m asl; 47°43' N, 70°40' W) is of glacial origin and is located in the boreal zone of a natural reserve near Quebec City (Canada). This reserve is located in the Laurentian Mountains, on granite-gneissic rock of the Canadian Precambrian Shield. In November 2001, a 30-cm long sediment core was taken from the deepest part (4 m) of lac du Sommet with a Kajak-Brinkhurst-type gravity corer (HTH-Teknik, Luleå, Sweden). The sediment samples were extruded at 2.5 mm intervals in the field. An alpha spectrometer was used to measure the radiometric activity of ^{210}Po the daughter product of ^{210}Pb (Flynn 1968). ^{210}Pb activities at the date of coring were used to estimate sedimentation rates (g year^{-1}) using the model of Binford (1990) assuming a constant rate of supply.

Diatom analysis

For diatom analysis, frustules were cleaned with heated 30% H_2O_2 . Afterwards, glass beakers (250 ml) were filled with distilled water and the cleaned diatom frustules were allowed to deposit for at least 12 h at 4°C. In order to calculate fluxes, a known number of microspheres, plastic beads with a diameter of 6 μm ordered from UCL, London, U.K., was added to the diatoms (Battarbee and Kneen 1982). The diatom-microsphere suspensions were applied on ethanol-cleaned cover glasses and, after drying at room temperature, mounted with Naphrax[®] mounting medium on microscope slides. Diatoms were analysed at a magnification of 1000 \times using Leica DMRB microscopes and phase-contrast optics. Between 300 and 500 valves were analysed per sample. The taxonomy followed Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Camburn and Charles (2000) and Fallu et al. (2000).

Statistical analyses of fossil diatom data and instrumental record

The zonation of the diatom stratigraphic data was carried out on percentage data using optimal sum of squares partitioning (Birks and Gordon 1985), as implemented in the program ZONE (Lotter and Juggins 1991). The significant number of diatom assemblage zones was assessed by comparison with a broken-stick model (Bennett 1996).

A principal component analysis (PCA) was applied to describe main changes of fossil diatom assemblages, because the floristic gradient length of the fossil diatom assemblages explored by detrended correspondence analysis (DCA) was 1.6 SD-units (Birks 1995). All ordinations were performed with CANOCO (version 4.0; ter Braak and Šmilauer 1998).

Since 1965, temperatures and wind velocity have been recorded by a meteorological station in Forêt Montmorency (47°20' N; 71°09' W; 670 m asl), located within the study area, operated by Université Laval. Air temperature measurements are taken daily at 8 AM and 6 PM. In order to compare the instrumental record to years encompassed by each fossil sample, the average mean monthly temperature for the years represented by each fossil sample were calculated.

Pearson correlation coefficients were calculated for the relationships between the sample scores of PCA axes one and two for fossil assemblages and the measured mean monthly temperatures, wind velocity in June and the number of days below 0°C in April. In addition, the relative abundances of individual species were compared with mean number of days below 0°C in April, wind velocity in June and with monthly temperatures by Pearson correlation coefficients.

Despite multiple testing, *p*-values of these correlations were not Bonferroni-corrected so that potential confounding variables could be recognized.

Sediment trap study

Site descriptions

In this study, four lakes along an elevational gradient spanning from 380 m to 920 m asl were examined (Table 1). Lakes in geologically similar catchment basins were selected to limit the difference between lakes mainly to climate factors. All lakes are of glacial origin, each has an inflow and an outflow, and the catchments are far from human settlements and have not been altered by agriculture or forestry. However, it was not possible to find lakes of equal conductivity and maximum depth that were distributed equally along an elevational gradient (Table 1). Along the elevational gradient, the vegetation changes from *Betula papyrifera*-dominated mixed forest at lower elevations to *Abies balsamea* conifer-dominated forest at higher elevation which, above 800 m asl, is replaced by *Picea mariana*. In the region, permafrost occurs at an elevation of 960 m asl on Mont du Lac des Cygnes (47°40' N; 70°36' W), which reflects the strong continental character of the regional climate (Payette 1984; Allard and Fortier 1990). Due to the presence of arctic air masses and the absence of Gulf Stream influence, regional seasonality is extreme.

Collection of trap samples

The sediment trap used in this study was designed and built by John Glew (PEARL, Queen's University). It consists of three black thermoplastic

Table 1 Geographical characteristics of the four studied lakes in the Laurentian Mountains, Canada, for May–October 2002

Lake name:	Joachim	Moreau	du Sommet	Elysée
Latitude	47°00' N	47°55' N	47°43' N	47°44' N
Longitude	71°55' W	70°40' W	70°40' W	70°41' W
Date of ice break-up	7 May	22 May	28 May	25 May
Elevation (m)	380	620	830	920
Max. depth (m)	7	16	4	10
Lake surface area (km ²)	0.15	0.27	0.02	0.05
Catchment area (km ²)	3.52	8.13	0.41	0.85

pipes of 52 mm diameter that are 440 mm long (8.5:1 aspect ratio). The lower end of the trap has a threaded collar onto which either an opaque plastic or clear glass receptacle of 110 ml capacity can be attached. Three traps are mounted together on a frame that provides nominal equal centre-to-centre spacing of 520 mm. Submerged vertical stability is provided by an integral central float along with a mooring system similar to that described by Larsson et al. (1986).

In May 2002, Glew sediment traps were installed under the ice of the study lakes, which was up to 80 cm thick. They were placed in the deepest part of each lake where the upper rim was at ca. 1 m above the lake floor. Sediment traps were sampled biweekly from May to the end of October in 2002. At the beginning of the study and on each sampling day, Lugol's solution was added to the empty glass jar in order to prevent grazing of algae by zooplankton. Diatom analysis was performed in the same way as the fossil samples.

Collection of water samples and measurement of physical properties

Each sampling day, water samples were taken at 1 m water depth with a Kemmerer sampler. Water samples were filtered on the day of sampling. For analysis of dissolved organic carbon (DOC), soluble reactive phosphorus (SRP), nitrate (NO_3), nitrite (NO_2), ammonium (NH_4) and silicate ions, lake water was filtered through cellulose acetate filters with a pore size of 45 μm . Samples for DOC analyses were kept in brown glass bottles and those for silicate analyses in polyethylene bottles. Total phosphorus (TP) and total nitrogen (TN) were analysed from unfiltered water. Water samples were stored at 4°C until their chemical analysis by the National Laboratory for Environmental Testing, Environment Canada, Burlington, Toronto. For detailed descriptions of methods consult Environment Canada (1994). For chlorophyll *a* (chl *a*) analysis, 300 ml of water was filtered, on the day of sampling, in dimmed light conditions using Whatman® GF/F filters. These filters were stored in aluminium foil at -15°C until chl *a* fluorescence measurements according to standard procedures

(Nusch 1980). Chl *a* was corrected for phaeopigments using the equations of Jeferey and Wellschmeyer (1997).

Following the collection of water samples, transparency was measured using a Secchi disk (diameter = 20 cm); temperature, pH, conductivity and oxygen profiles were measured in 1 m intervals using a Quanta Hydrolab®. Water temperatures of each study lake were recorded in 1.5 h intervals by two Hobo® dataloggers 10 cm below the lake surface and 50 cm above the lake bottom over the period May to October 2002. A ratio between temperatures measured at the surface of the water column and above the sediment was used to estimate the degree of lake stratification and the inverse was interpreted as lake circulation.

In order to capture the environmental conditions during the time of diatom growth, averages of water chemistry at the beginning and at the end of each bi-weekly exposure period were calculated and average surface water temperatures were calculated, which corresponded to the time of trap exposure. Between May and October 2002, daily means of surface water temperatures of lac du Sommet (Hobo measurements, depth = 10 cm) were compared with daily mean air temperatures of the meteorological station by linear regression.

Statistical analysis of modern data

The relation between standardized environmental variables was explored by PCA. The floristic gradient lengths of seasonal samples were determined by detrended correspondence analysis (DCA), and are discussed elsewhere (Hausmann and Pienitz, in preparation). The seasonal successions of diatom taxa in each lake were tested for auto-correlation assessed by time series analysis implemented in the program S-PLUS (version 4.5).

In order to compare the biological variance between the four lakes during each season, samples were grouped according to their season of deposition. Interactions between climate-related environmental variables and water chemistry and lake morphology were assessed by Pearson correlation coefficients between environmental variables for each seasonal set.

The floristic gradient lengths, as assessed by DCA, of the seasonal sets for the four lakes were large (between 2.6 and 2.9 SD-units), and therefore unimodal methods were used for statistical analysis. The relationships between individual environmental variables and diatom assemblages of each seasonal set were tested for significance by unrestricted Monte Carlo permutation tests (999 permutations), using single-variable CCAs. To select the minimal set of environmental variables which explain most of the biological variance, forward selection as implemented in CANOCO was used.

Comparison of fossil and modern diatoms

The distinct seasonal and spatial distribution of diatoms and the significant relations between climate-related variables and diatoms suggested that the development of seasonal diatom inference models for the date of ice break-up, summer temperature, circulation of the water column, as well as pH and autumn TN concentrations was possible. The robustness of the weighted-averaging partial least squares (WA-PLS) model was evaluated by jack-knifing, using the program CALIBRATE (version 0.82, Juggins and ter Braak 1997) and by comparison with the maximum likelihood method using the program C2 (version 1.3). If the root mean square error of prediction (RMSEP) and the maximum bias decreased and the r^2 increased by more than 5%, the inclusion of an additional component was considered. In order to assess the effectiveness of the models for lac du Sommet, diatom inferences were compared with the instrumental record and diatom flux.

Results

Lac du Sommet sediment core

^{210}Pb dating

An accurate chronology and a high temporal resolution of the fossil record are essential for comparison with instrumental data. The high r^2 (0.99) of the exponential function between ^{210}Pb

activities and cumulative dry mass suggests an undisturbed sediment record (Binford 1990; Fig. 1) and justified the high sampling resolution (2.5 mm). Each sample represented between two to five years of deposition. The investigated 4.75 cm core section therefore represented ca. 36 years of accumulated sediments.

Fossil diatom record

The fossil diatom record (1966–2001) of lac du Sommet can be divided into two statistically significant diatom assemblage zones (DAZ), from 1966 to 1981 (DAZ 1) and from 1981 to 2001 (DAZ 2; Fig. 2). *Fragilaria virescens* var. *exigua* Ralfs was the dominant diatom during the past 30 years in lac du Sommet (Fig. 2). It occurred in DAZ 1 with a relative abundance of 20% and increased to 50% in DAZ 2. In DAZ 1, *Aulacoseira distans* var. *nivalis* (Smith) Haworth increased to 35% towards 1978, and occurred with lower abundance in DAZ 2. *Fragilaria brevistriata* Grunow occurred mainly in DAZ 2 between 1981

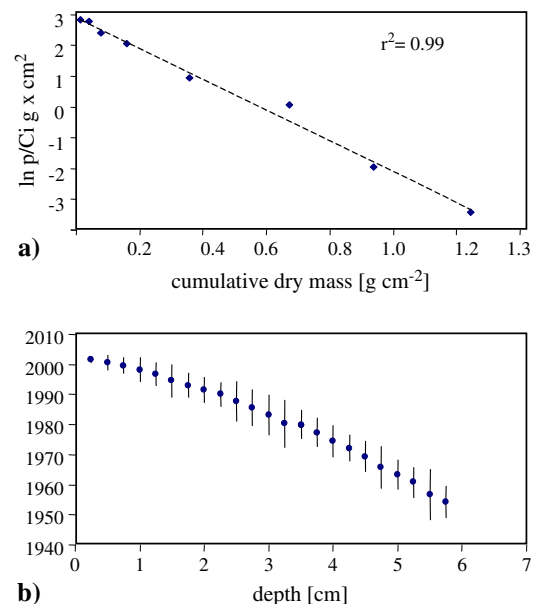


Fig. 1 ^{210}Pb -chronology for lac du Sommet. (a) Relation between unsupported ^{210}Pb activities at the time of coring and cumulative dry mass, and (b) resulting depth-age model of lac du Sommet using the Binford (1990) constant rate of supply model. Error bars indicate SD of the Binford model

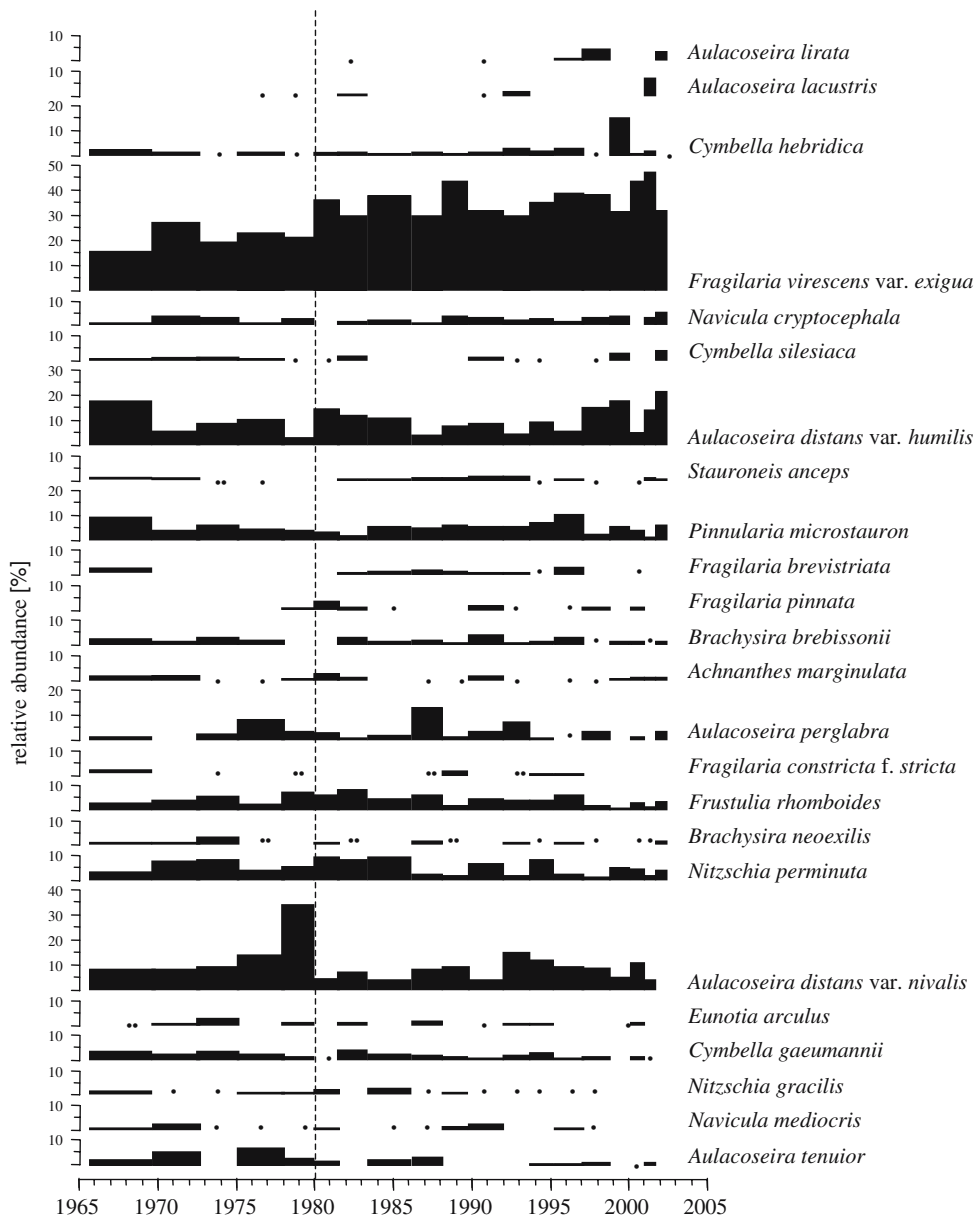


Fig. 2 Diatom biostratigraphic changes in the lac du Sommet sediment core. Relative abundances of selected diatom taxa ($\geq 2\%$) over the past 30 years in lac du

Sommet. Values below 0.5% are depicted as dots. Dashed line indicates the separation of the diatom assemblage zones one and two

and 1995. *Cymbella hebridica* Grunow, *Aulacoseira lacustris* (Grunow) Krammer and *Aulacoseira lirata* (Ehrenberg) Ross increased towards the sediment surface (Fig. 2). Fossil diatom fluxes showed three peaks: in 1981, from 1990 to 1995 and from 1999 to 2001 (Fig. 3).

Comparison of instrumental record with fossil diatoms

PCA axis 1 of the fossil diatom assemblages explained 43% of the biological variance and PCA axis 2 explained an additional 21%. The

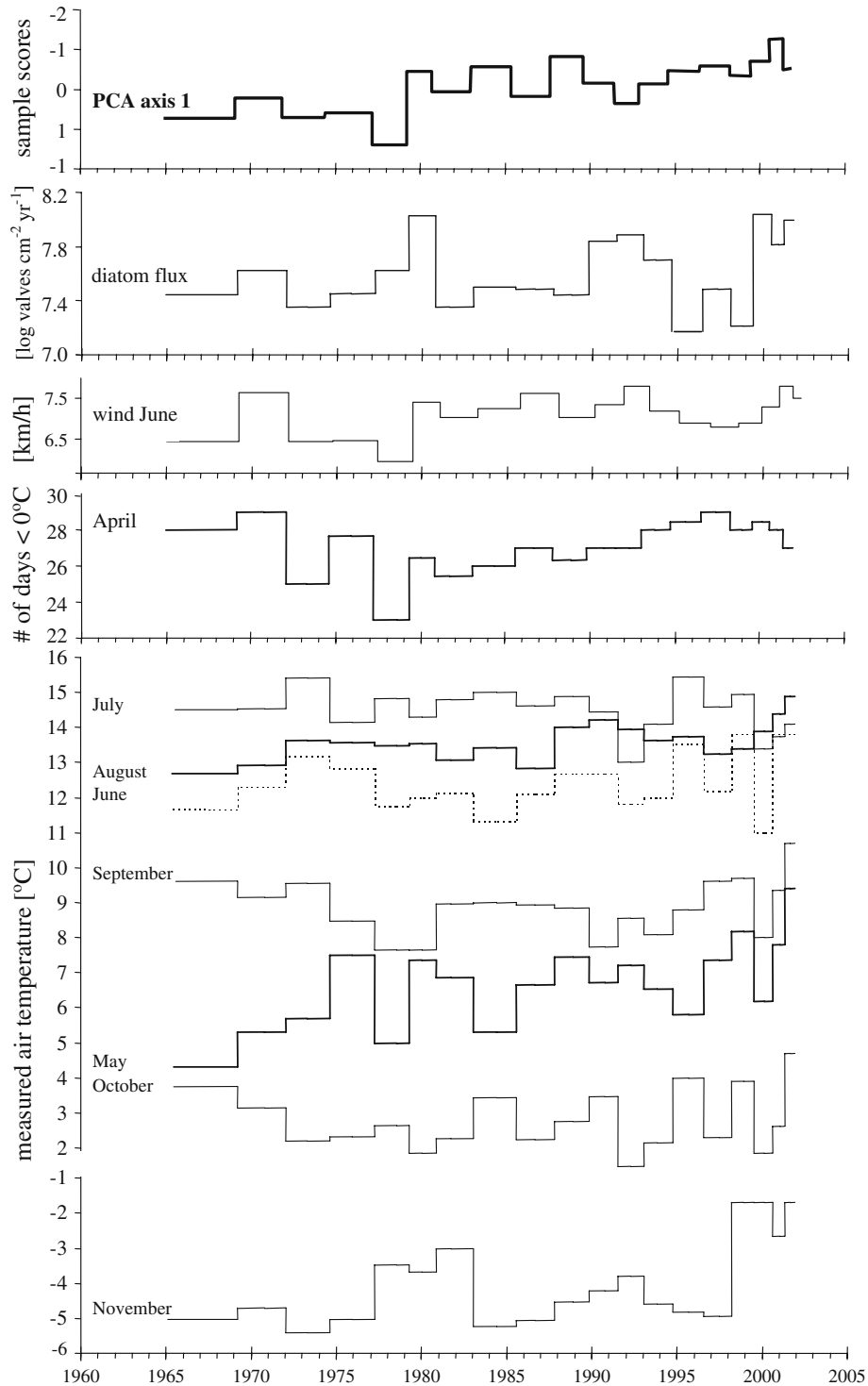


Fig. 3 Comparison of instrumental records and fossil diatoms. Diatom flux over the past 30 years in lac du Sommet, PCA axis one sample scores of fossil diatom

assemblages of lac du Sommet and instrumental record of the meteorological station of Forêt Montmorency (670 m asl) for the period 1966–2001

PCA axis 1 sample scores of fossil assemblages (Fig. 3) were significantly correlated with the wind velocity in June ($r = 0.62$, $n = 19$, $p < 0.005$), the number of days with temperatures below 0°C in April ($r = 0.47$, $n = 19$, $p < 0.025$), and mean May and August temperatures ($r = 0.52$, $n = 19$, $p < 0.01$; $r = 0.48$, $n = 19$, $p < 0.025$). PCA axis 2 was not correlated to the instrumental record. It is remarkable that from 1966 to 2001 only May temperatures increased significantly, on average by 3.1°C (Fig. 3). During DAZ 1 (1966–1981) conditions showed a warming trend and autumn conditions a cooling trend. Past diatom fluxes were significantly enhanced during periods with higher wind velocity in June ($r = 0.77$, $n = 19$, $p < 0.0005$), colder July temperatures ($r = -0.77$, $n = 19$, $p < 0.0005$), and warmer August and November temperatures ($r = 0.52$, $p < 0.0005$; $r = 0.43$, $p < 0.005$, $n = 19$; Table 2, Fig. 4).

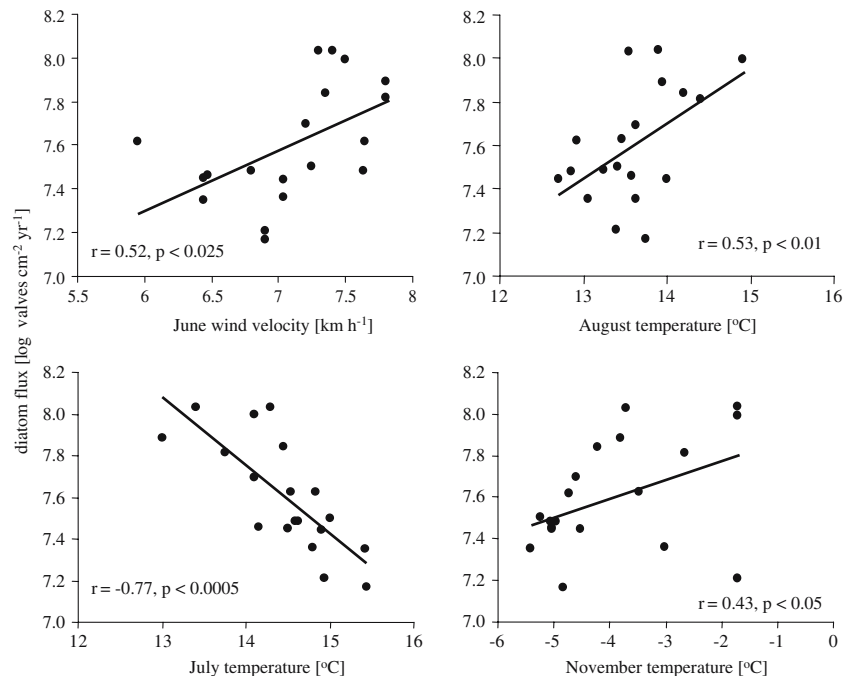
Surface water temperatures of lac du Sommet and air temperatures of the meteorological station were highly correlated ($r^2 = 0.8$). However, differences can be seen in May and June, when air temperature was on average 3.8°C warmer than surface water temperature, whereas from July to October, air temperature was on average 4.7°C cooler than water temperature (Fig. 5b). These differences between water and air temperature are due to the fact that the heat capacity of water is greater than that of air. Higher wind velocity was significantly related to colder air temperatures in June ($r = 0.36$, $n = 36$, $p < 0.025$).

During colder spring periods with a higher number of days below 0°C in April, fossil relative occurrences of *Pinnularia microstauron* Ehrenberg, *Cymbella hebridica* and *Fragilaria brevistriata* were significantly enhanced ($r = 0.48$; $r = 0.45$; $r = 0.44$; $n = 19$, $p < 0.025$, Table 2). During periods of warmer May temperatures, fossil relative occurrences of *Fragilaria virescens* var. *exigua* and *Cymbella silesiaca* Bleisch were significantly higher ($r = 0.42$, $r = 0.48$, $n = 19$, $p < 0.05$, Table 2). The dominant fossil diatom *Fragilaria virescens* var. *exigua* was correlated best to strong winds in June ($r = 0.56$, $n = 19$, $p < 0.01$). During periods when the measured May temperatures were colder, the fossil relative abundances of *Cymbella gaeumannii* Meister and

Table 2 Significant correlations (positive: ↑, negative ↓) between relative abundances of fossil diatoms in lac du Sommet and the instrumental wind and temperature record, and modern occurrences in lakes along an elevation gradient from May to October 2002 (E: lac Elysée, S: lac du Sommet, M: lac Moreau, J: lac Joachim; compare Fig. 9)

	Modern											
	Instrumental record						Modern					
	# of days < 0°C in April											
	April	May	June	July	August	September	October	November	December	January	February	March
<i>Fragilaria brevistriata</i>	↑							→				
<i>Pinnularia microstauron</i>	↑							→				
<i>Cymbella hebridica</i>	↑							→				
<i>Cymbella gaeumannii</i>		→	→	→								
<i>Nitzschia gracilis</i>												
<i>Aulacoseira distans</i> var. <i>navalis</i>					↓							
<i>Aulacoseira perglabra</i>							→	→				
<i>Achnanthes minutissima</i>												
<i>Fragilaria virescens</i> var. <i>exigua</i>				↓								
<i>Cymbella silesiaca</i>			↑	↑								
<i>Navicula subtilissima</i>												
<i>Aulacoseira lacustris</i>												
<i>Navicula cryptocephala</i>												
Past diatom productivity				↓								

Fig. 4 Correlations between fossil diatom flux, observed wind velocity in June and measured air temperatures of July, August and November from 1966 to 2001



Nitzschia gracilis Hantzsch were significantly higher ($r = -0.59$, $r = -0.67$, $n = 19$, $p < 0.005$, Table 2). In 1982, when the highest July temperatures were recorded, abundances of *Navicula subtilissima* Cleve were highest. During episodes with colder July temperatures, abundances of *Achnanthes minutissima* Kützing were significantly higher ($r = -0.60$, $n = 19$, $p < 0.005$, Table 2). During periods of colder temperatures in October, fossil occurrences of *Aulacoseira perglabra* (Oestrup) Haworth were significantly higher ($r = -0.44$, $n = 19$, $p < 0.05$, Table 2). Warmer August temperatures were significantly correlated with fossil occurrences of *F. virescens* var. *exigua* ($r = 0.54$, $n = 18$, $p < 0.02$, Table 2) and *Aulacoseira lacustris*, which increased towards the sediment surface ($r = 0.50$, $n = 19$, $p < 0.025$, Table 2). During periods of warmer October temperatures, occurrences of *Navicula cryptocephala* Kützing were significantly higher ($r = 0.48$, $n = 19$, $p < 0.05$, Table 2). During periods of weaker wind velocity in June, colder September, October and May temperatures ($r = -0.57$; $r = -0.41$; $r = -0.43$; $r = -0.42$; $n = 19$, $p < 0.05$, Table 2) fossil occurrences of *Aulacoseira distans* var. *nivalis* were significantly higher. During periods of warmer November

temperatures, past occurrences of *Fragilaria brevistriata* ($r = -0.43$, $n = 19$, $p < 0.05$), *Pinnularia microstauron* ($r = -0.38$, $n = 19$, $p < 0.05$), *Cymbella gaeumannii* ($r = -0.51$, $n = 19$, $p < 0.025$) and *Nitzschia gracilis* were significantly lower ($r = -0.63$, $n = 19$, $p < 0.005$).

Sediment trap samples

Modern environmental data

All lakes were oligo- to mesotrophic and had annual mean concentrations of DOC of about 4 mg L^{-1} (Table 3, Fig. 6b–g). The pH of all lakes increased towards autumn by 1–3 units (Fig. 6e). Conductivity and silicate concentration of lac Moreau, the deepest lake, were highest (Table 3, Figs. 6, 8). According to PCA (Fig. 8) the conductivity and depth gradient did not seem to be correlated to the elevation gradient. In our study, the date of ice break-up is independent of lake morphology (Table 4).

The ice-free period of the lowermost lake was 36 days longer than that of the highest elevation lake (Fig. 7). The date of ice break-up was statistically significantly correlated to elevation ($r = 0.93$, $n = 4$, $p < 0.05$). In June 2002, there

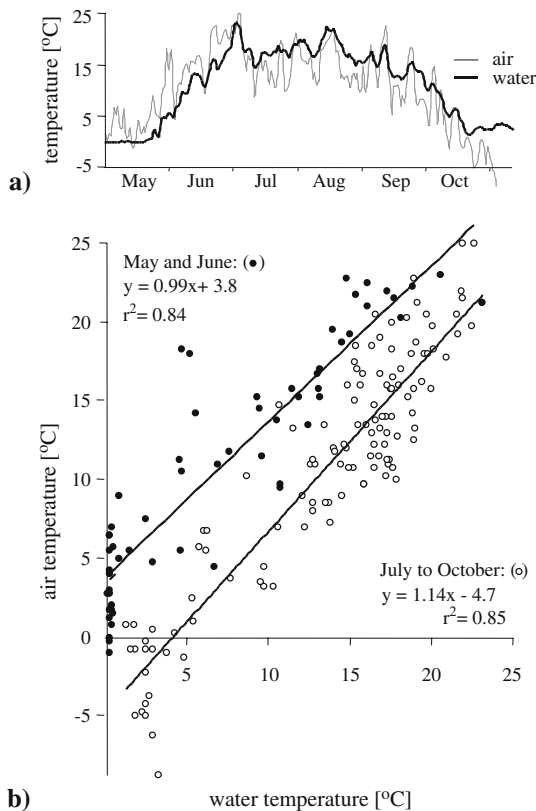


Fig. 5 (a) Surface water temperature measured in lac du Sommet (830 m asl) and air temperature recorded by the meteorological station of Forêt Montmorency (670 m asl) for the period from May to October 2002. (b) Linear regression between water and air temperature for the periods May to June and July to October 2002

were still snow patches present at the shore of lac Elysée. Temperature differences between the lakes varied over the year and were about 7°C (Fig. 6a). According to PCA, circulation of the water column was stronger in the higher elevation lakes (Fig. 8). In summer 2002, a better circulation of the water column corresponded to an increased Si:SRP ratio ($r = 0.46$, $n = 16$, $p < 0.05$; Table 4) and a higher pH ($r = 0.49$, $n = 16$, $p < 0.05$; Table 4). Elevation, TN and DOC were interrelated. In autumn 2002, DOC showed an inverse relationship to elevation ($r = -0.80$, $n = 14$, $p < 0.0005$), and samples with lower DOC concentrations in summer and autumn ($r = -0.45$, $n = 16$, $p < 0.05$; $r = -0.82$, $n = 14$, $p < 0.0005$; Table 4) and lower concentrations of TN in autumn ($r = -0.58$, $n = 14$, $p < 0.01$; Table 4) corresponded with later ice break-up. TN autumn

concentrations were highly correlated to the freeze-over date ($r = 0.77$, $n = 14$, $p < 0.005$). NH_4 concentrations were higher when temperature was lower ($r = -0.57$, $n = 14$, $p < 0.01$; Table 4) and circulation of the water column stronger ($r = 0.44$, $n = 16$, $p < 0.05$; Table 4).

Modern diatom assemblages

The seasonal successions of diatoms were different in each lake and the seasonal species turnover was high in all study sites (Fig. 9), as SD-units of floristic gradients were 1.4 for lac Joachim, 2.1 for lac Moreau and lac Sommet and 2.4 for lac Elysée. Species succession was not auto-correlated. Spring assemblages were different from those in autumn, indicating a strong seasonal species succession. Some diatom taxa were deposited in the trap mainly during one season (Fig. 9).

In lac Joachim, most diatoms were deposited in spring and in autumn and chl *a* concentrations were highest at the end of September (around 2.5 mg L^{-1} , Fig. 7d). The spring diatom bloom was dominated by a small form of *Tabellaria flocculosa* (50%, Fig. 9q) and the autumn bloom by *Frustulia rhomboides* Ehrenberg (40%, Fig. 9s).

Diatoms of lac Moreau showed a spring bloom in June and an autumn bloom in October and chl *a* concentrations were highest in August and September (around 3.5 mg L^{-1} , Fig. 7c), when plankton samples were rich in *Dinobryon* (chrysohyte), *Pediastrum* (chlorophyte) and *Ceratium* (dinophyte). Spring diatom assemblages consisted of *Achnanthes minutissima* (27%, Fig. 9m), *Fragilaria pinnata* (12%, Fig. 9k) and *Meridion circulare* (Greville) Agardh (12%, Fig. 9j). *Cyclotella bodanica* aff. *lemanica* (O. Müller) Bachmann dominated assemblages in summer (40%, Fig. 9n). The dominant diatoms of autumn in Lac Moreau were *Fragilaria virescens* var. *exigua* (20%, Fig. 9i) and *Tabellaria fenestrata* (Lyngbye) Kützing (40%, Fig. 9p).

Diatom deposition in lac du Sommet was highest in June and declined towards the end of the ice-free period. Chl *a* concentrations were highest in July (around 4 mg l^{-1} , Fig. 7b) and

Table 3 Physical and chemical characteristics of the four studied lakes in the Laurentian Mountains, Canada, for May–October 2002

Lake name:	Joachim		Moreau		du Sommet		Elysée	
	Mean min	SD max	Mean min	SD max	Mean min	SD max	Mean min	SD max
NH ₄ ⁺ (μg L ⁻¹)	19.1 7.5	10.0 37.5	18.3 4.0	13.9 40.0	15.2 6.0	7.9 31.0	25.5 5.5	24.1 79.0
NO ₃ ⁻ (μg L ⁻¹)	16.7 5.0	17.7 66.0	22.0 3.00	20.3 59.0	28.0 14.0	10.0 42.5	21.4 3.0	17.1 43.0
NO ₂ ⁻ (μg L ⁻¹)	1.5 1.0	0.3 2.0	1.2 0.5	0.4 1.8	1.3 0.8	0.3 1.8	1.6 1.0	0.5 2.0
TN (μg L ⁻¹)	226 197	25 282	156 128	23 201	208 139	75 411	175 142	22 214
SRP (μg L ⁻¹)	1.6 0.1	1.2 3.3	1.0 0.3	0.5 2.0	1.3 0.2	1.2 3.5	1.8 0.1	2.0 6.9
TP (μg L ⁻¹)	5.1 3.5	1.3 7.9	5.1 3.5	1.7 9.0	9.7 6.3	5.4 24.0	6.6 4.3	2.4 10.4
SiO ₂ (mg L ⁻¹)	2.1 1.0	0.9 3.7	4.7 4.3	0.4 5.4	2.4 1.8	0.5 3.4	2.5 2.4	0.1 2.7
SO ₄ ⁻ (mg L ⁻¹)	13.4 3.0	16.9 46.8	3.9 1.9	1.9 7.3	3.9 2.4	1.2 5.8	3.6 1.6	2.0 7.8
Cl ⁻ (mg L ⁻¹)	0.6 0.2	0.2 0.9	3.0 0.3	2.1 6.8	0.7 0.3	0.5 1.7	0.7 0.3	0.9 3.4
DOC (mg L ⁻¹)	4.7 4.1	0.5 5.8	4.0 3.6	0.4 4.8	4.4 4.0	0.5 5.3	4.3 3.3	1.0 6.7
pH (units)	6.4 5.4	0.8 7.5	7.3 6.8	0.3 7.7	6.7 4.9	0.9 7.6	7.1 5.1	0.9 8.4
Transparency (m)	3.8 3.1	0.3 4.2	3.7 2.5	0.6 4.5	3.3 3.0	0.4 4.0	3.9 2.5	0.8 5.3
Conductivity (μS cm ⁻¹)	14.0 13.0	1.1 16.5	41.7 35.0	4.2 47.0	16.2 14.5	2.7 23.2	14.8 13.0	1.1 16.5

originated from a bloom of *Merismopedia* (cyanobacteria). The dominant diatom of lac du Sommet was *Fragilaria virescens* var. *exigua* (23%, Fig. 9i). In summer, a small form of *Tabellaria flocculosa* (10%, Fig. 9q) appeared, which occurred also in spring in Lac Joachim. In August and September, *Nitzschia gracilis* increased (6%, Fig. 9e).

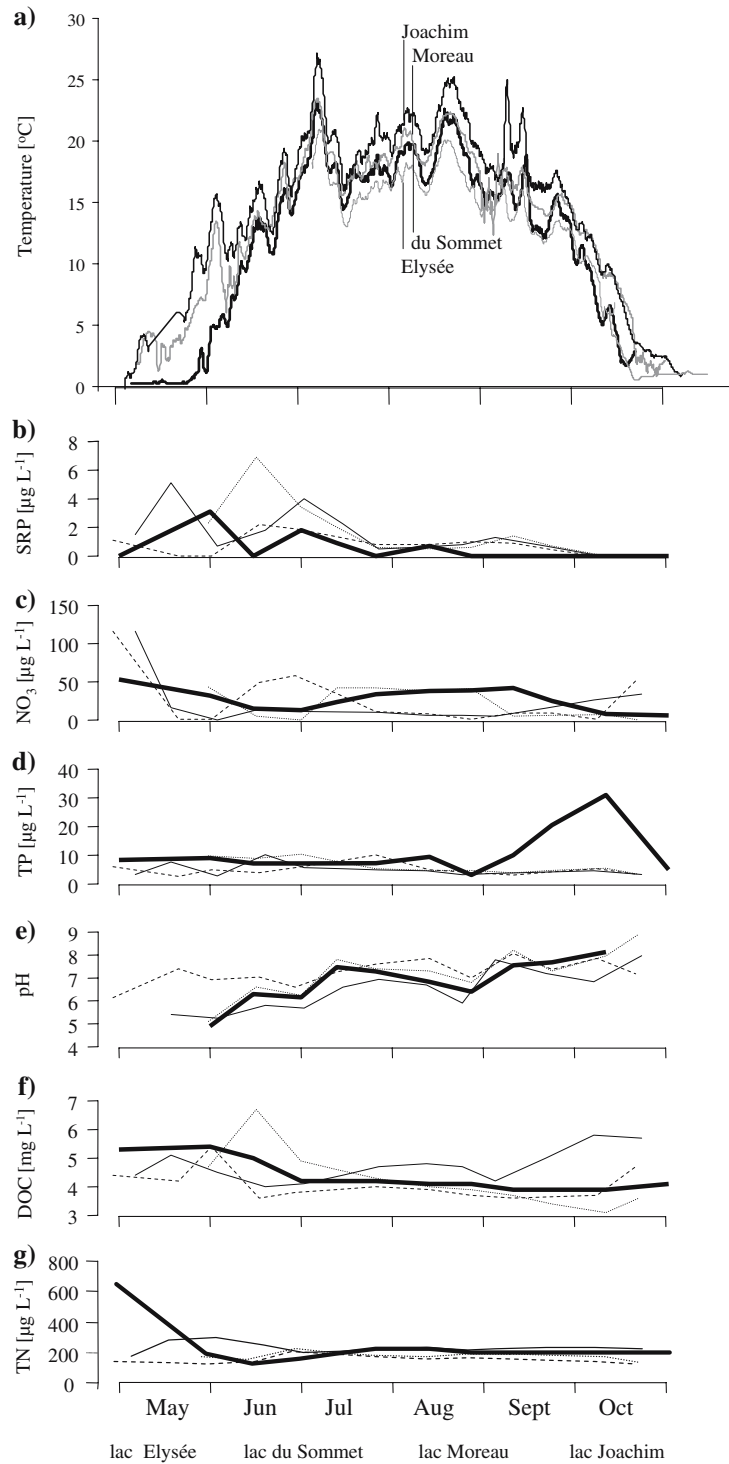
In lac Elysée, most diatoms were deposited in June, July and in October and chl *a* concentrations were highest in August (Fig. 7a). The spring bloom consisted of *Tabellaria flocculosa* (28%) and *Cyclotella bodanica* (43%, Fig. 9q, n). In autumn, *Aulacoseira distans* var. *nivalis* was dominant (30%, Fig. 9g).

Statistical relations between modern diatom assemblages and environmental data

Comparing the spring (May and June, $n = 14$) data from all study lakes depth, date of ice break-

up and elevation explained together 41% of the biological variance. Fifty-nine percent of the biological variance remained unexplained. According to the forward selection option in CANOCO, the inclusion of additional variables did not significantly increase the explained biological variance. Depth was correlated to axis one ($r = 0.91$), date of ice break-up was correlated to axis two ($r = 0.55$), and elevation was best correlated to axis three ($r = 0.87$). As depth and date of ice break-up were not correlated (Table 4), they can be regarded as non-confounding. The significance of depth in spring can be explained by its high correlation with circulation of the water column and many other environmental variables (Table 4). According to Monte Carlo permutation tests, the biological variance had a significant relation to several physical factors and to water chemistry (Table 5). Depth explained most of the variance in the spring and summer (Table 5). In spring (May and June, $n = 14$), the date of ice

Fig. 6 Limnological properties of the study lakes over the period May–October 2002. **(a)** surface water temperatures; **(b)** SRP; **(c)** NO₃; **(d)** TP; **(e)** pH; **(f)** DOC; **(g)** TN



break-up explained a significant proportion of the variance in the diatoms (16%, $n = 14$, $p < 0.002$; Table 5). Differences in diatom communities

were significantly explained also by NO₃, pH, SiO₂, Si:TP ratio, Si:SRP ratio, conductivity and lake morphology (Table 5).

Table 4 Statistically significant correlations (*r*-values) between climate related variables (date of ice break-up, surface water temperature and circulation of the water

column) and depth to water chemistry and lake morphology from May to October 2002 within the seasonal sets

	Spring (<i>n</i> = 14)				Summer (<i>n</i> = 16)				Autumn (<i>n</i> = 14)				
	Depth	Break-up	Temp.	Circ.	Depth	Break-up	Temp.	Circ.	Depth	Break-up	Temp.	Circ.	
NH ₄ ⁺						0.57	-0.65		-0.49			-0.57	0.44
NO ₃ ⁻	-0.47		-0.48		-0.43	0.68			-0.60	0.59			
NO ₂ ⁻		0.53						0.72				-0.43	
TN	-0.51				-0.50				-0.76	-0.58			
pH	0.81				0.51	0.51	-0.69	0.49				-0.58	
SO ₄ ⁻	-0.63			-0.53	0.83	-0.63	0.60	-0.65	-0.56				
SiO ₂	0.77		-0.46	0.67	0.83	0.43			0.88				
TP	-0.63					0.57			-0.53				0.41
SRP	-0.48								0.52			0.61	-0.48
Si:TP	0.80			0.61	0.74				0.86				
Si:SRP	0.71				0.50	0.48		0.46				0.72	
DOC					-0.46	-0.45				-0.82			
Transp.					0.83								
Cl ⁻	0.65				0.49				0.73				
Conductivity	0.83				0.85				0.88				
Depth	1.00			0.50	1.00				1.00				
Surface	0.87				0.83			-0.45	0.81				
Catchment	0.89				0.83				0.82				

In summer (July and August, *n* = 16), tested individually, a significant part of the diatom variance was explained by TN, pH, silicate, Si:TP, Si:SRP, DOC, conductivity, temperature, circulation, elevation, and lake morphology (Table 5). Depth and elevation explained together 29% of the biological variance. The inclusion of additional variables did not significantly increase the

explained biological variance. Depth was correlated to axis one (*r* = 0.94) and elevation was correlated to axis two (*r* = -0.90). As they were not correlated they can be regarded as non-confounding in our data. As in spring, depth was highly correlated with many other environmental variables but not with climate-related variables (Table 4). Yet pH was correlated to depth and to

Fig. 7 Ice cover, water temperatures, productivity of diatoms and chl *a* (line with dots) in (a) lac Elysée (920 m asl); (b) lac du Sommet (830 m asl); (c) lac Moreau (620 m asl); and (d) lac Joachim (380 m asl). Contours of grey shades are in one-degree intervals. Valves per litre are shown for lac Elysée

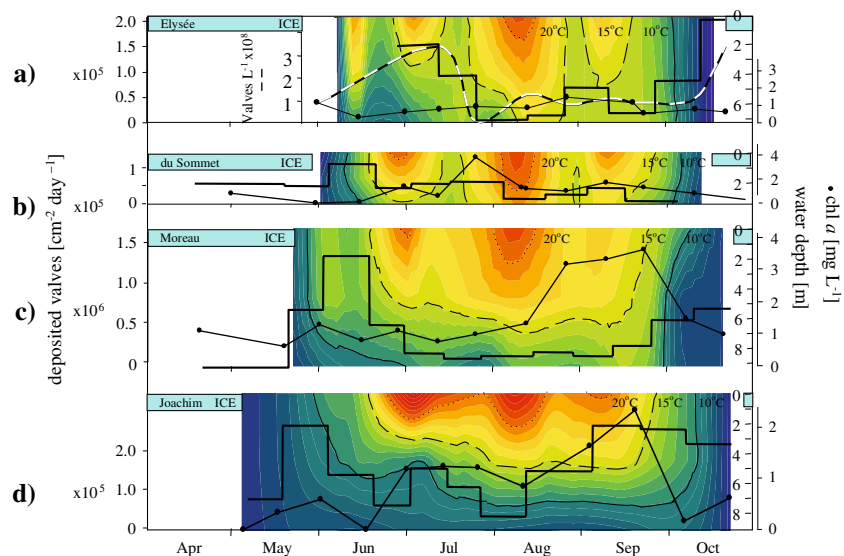
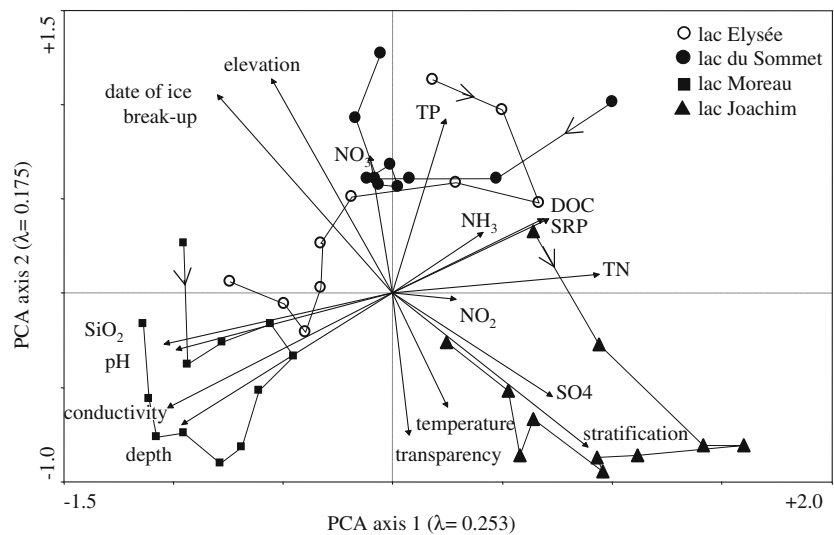


Fig. 8 Variability of environmental variables of four study lakes in the Laurentian Mountains with biweekly time resolution from May to October 2002 as explored by PCA



the circulation of the water column, which to the Si:SRP ratio ($r = 0.46$; $r = 0.49$, $n = 16$, $p < 0.025$; Table 4). Elevation was highly correlated to temperature ($r = -0.83$, $n = 16$, $p < 0.0005$) and to the circulation of the water column ($r = 0.90$, $n = 16$, $p < 0.0005$).

In autumn (September and October, $n = 14$), TN, catchment size, lake depth, elevation and chloride explained 62% of the biological variance. The inclusion of additional variables did not significantly alter the explained biological variance. TN and depth were correlated to axis one ($r = -0.94$, $r = 0.83$, $n = 14$, $p < 0.001$), and elevation, catchment size and Cl were correlated to axis two ($r = -0.81$, $r = 0.79$, $r = 0.64$, $n = 14$, $p < 0.01$). Depth and TN were confounding variables. The high correlation with many other environmental variables (Table 4) explains the importance of depth. Tested individually, lake morphology, TN, NH_4 , SiO_2 , Si:TP ratio, DOC, conductivity, circulation, date of freeze over, and date of ice break-up explained a significant portion of the variance in the diatoms (Table 5).

Interpretation of fossil assemblages using sediment trap samples

The date of ice break-up was reconstructed because it was significantly related to the distribution of diatoms sampled in spring (May and June,

$n = 14$) from lakes along the elevation gradient, and because it was uncorrelated to other significant variables (Tables 4 and 5). WA-PLS with several components can use secondary gradients to update species optima, with the restriction that they are orthogonal and hence uncorrelated to earlier PLS components (ter Braak et al. 1993). The RMSEP for the WA-PLS diatom inference model for day of ice break-up was 3.5 days with one component and 2.9 days with two components. Since the RMSEP and jack-knifed maximum bias improved with the inclusion of a second component by 19% and the r^2 between observed and predicted values by 8% (Table 6), a WA-PLS model with two components was used to reconstruct past dates of ice break-up. Diatom-inferred ice break-up dates were significantly later in periods when the observed number of days below 0°C in April was higher ($r = 0.52$, $n = 19$, $p < 0.025$; Fig. 10a).

In summer (July and August, $n = 16$), surface water temperature, circulation of the water column and pH, all interrelated, explained a significant portion of the variance in the diatoms data. For the reconstruction of summer temperature, circulation and pH, WA-PLS models with one component were used because for temperature the RMSEP was best, for circulation the maximal bias was lowest, and for pH the r^2 was highest (Table 6). Temperature inferences were closely correlated to inferences of circulation and pH

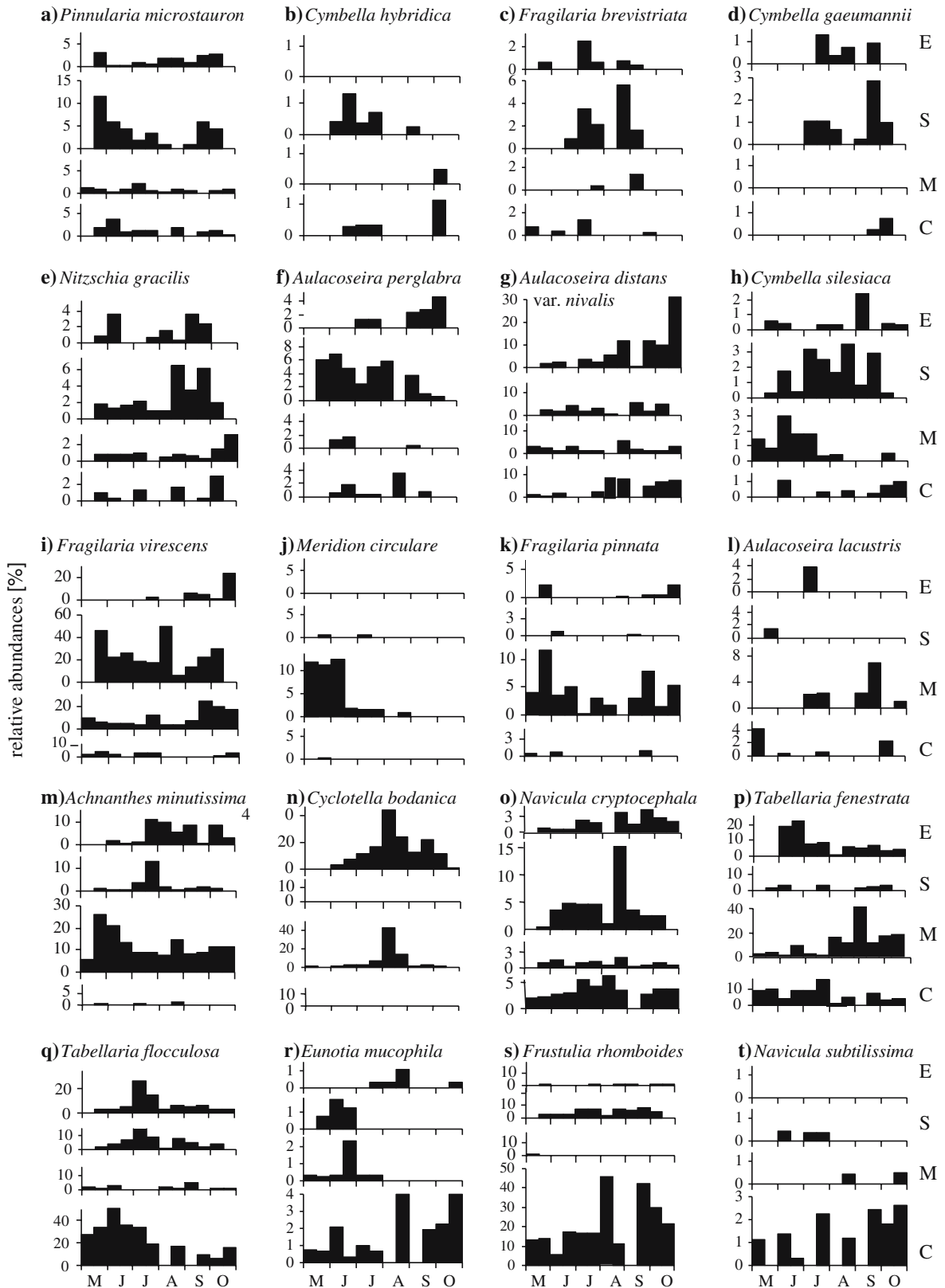


Table 5 *P*-values for the relationships of individual environmental variables to the distribution of diatoms, assessed by Monte Carlo permutation tests (999 permutations) within the monthly sets from May to October 2002. Percentage of variance in the distribution of diatoms explained by individual variables for significant relations (marginal effects)

	Spring (<i>n</i> = 14)		Summer (<i>n</i> = 16)		Autumn (<i>n</i> = 14)	
	<i>p</i> -values	% expl.	<i>p</i> -values	% expl.	<i>p</i> -values	% expl.
NH ₄ ⁺	0.133		0.553		0.045	8.4
NO ₃ ⁻	0.006	14.2	0.110		0.108	
NO ₂ ⁻	0.060		0.608		0.413	
TN	0.300		0.005	12.8	0.001	14.7
pH	0.002	15.7	0.003	13.9	0.064	
SO ₄ ⁻	0.330		0.180		0.240	
SiO ₂	0.008	13.7	0.001	17.3	0.003	11.4
TP	0.059		0.119		0.200	
SRP	0.187		0.463		0.235	
Si:TP	0.020	12.4	0.004	12.8	0.013	10.4
Si:SRP	0.011	13.4	0.008	13.5	0.497	
DOC	0.458		0.011	12.4	0.001	12.7
Transparency	0.075		0.019	12.4	0.085	
Cl ⁻	0.043	12.0	0.012	13.2	0.007	10.7
Conductivity	0.002	16.0	0.001	15.4	0.002	14.0
Depth	0.001	17.4	0.001	18.0	0.001	13.4
Surface	0.017	13.0	0.008	12.4	0.003	11.7
Catchment	0.002	13.4	0.003	12.8	0.003	12.0
Elevation	0.007	14.4	0.038	10.5	0.001	12.0
Temperature	0.294		0.045	8.6	0.517	
Ice break-up	0.002	15.7	0.022	12.0	0.004	12.4
Ice-in	0.001	17.0	0.004	17.3	0.003	14.4
Circulation	0.467		0.044	10.9	0.042	8.0

($r = -0.90$, $n = 19$, $p < 0.0005$; $r = -0.84$, $n = 19$, $p < 0.0005$). Diatom inferences were significantly related to the instrumental record and past diatom flux. For example, summer temperature and pH inferences were significantly correlated with measured July temperatures ($r = 0.50$, $n = 19$, $p < 0.025$; $r = -0.53$, $n = 19$, $p < 0.01$; Fig. 10b). Inferred circulation of the water column was best explained by observed wind velocity in June ($r = 0.64$, $n = 19$, $p < 0.005$), which was also related to inferred pH ($r = 0.44$, $n = 19$, $p < 0.025$). Inferences of lake circulation using WA-PLS and maximum likelihood were highly correlated ($r = 0.84$, $n = 19$, $p < 0.0001$). Past diatom production was higher during periods of enhanced inferred circulation of the water column ($r = 0.77$, $n = 19$, $p < 0.0005$), colder inferred summer temperature ($r = -0.44$, $n = 19$, $p < 0.05$), higher inferred pH ($r = 0.48$, $n = 19$, $p < 0.025$), higher observed wind velocity in June ($r = 0.77$, $n = 19$, $p < 0.0005$) and colder

Table 6 Jack-knifed error statistics for the diatom-inference models for day of ice-out, summer temperature and TN autumn concentrations. RMSEP, r^2 between measured and predicted values and maximum bias of weighted-averaging partial least square models with one and two components

	RMSEP	r^2	max-bias
<i>Date of ice break-up</i>			
one component	3.43	0.85	5.06
two component	2.82	0.91	4.28
<i>Summer temperature</i>			
one component	1.53	0.35	3.60
two component	1.53	0.37	3.90
<i>Summer stratification</i>			
one component	0.50	0.52	1.06
two component	0.54	0.64	1.11
<i>Summer pH</i>			
one component	0.28	0.46	0.50
two component	0.30	0.39	0.49
<i>Autumn TN</i>			
one component	13.36	0.80	26.30
two component	14.18	0.77	27.21

◀ **Fig. 9** Relative abundances of selected diatom taxa in the four lakes located along an elevational gradient from May to October in 2002 (E: lac Elysée, S: lac du Sommet, M: lac Moreau, J: lac Joachim)

observed July temperature ($r = -0.77$, $n = 19$, $p < 0.0005$).

The distribution of modern diatoms in autumn (September and October, $n = 14$) was best ex-

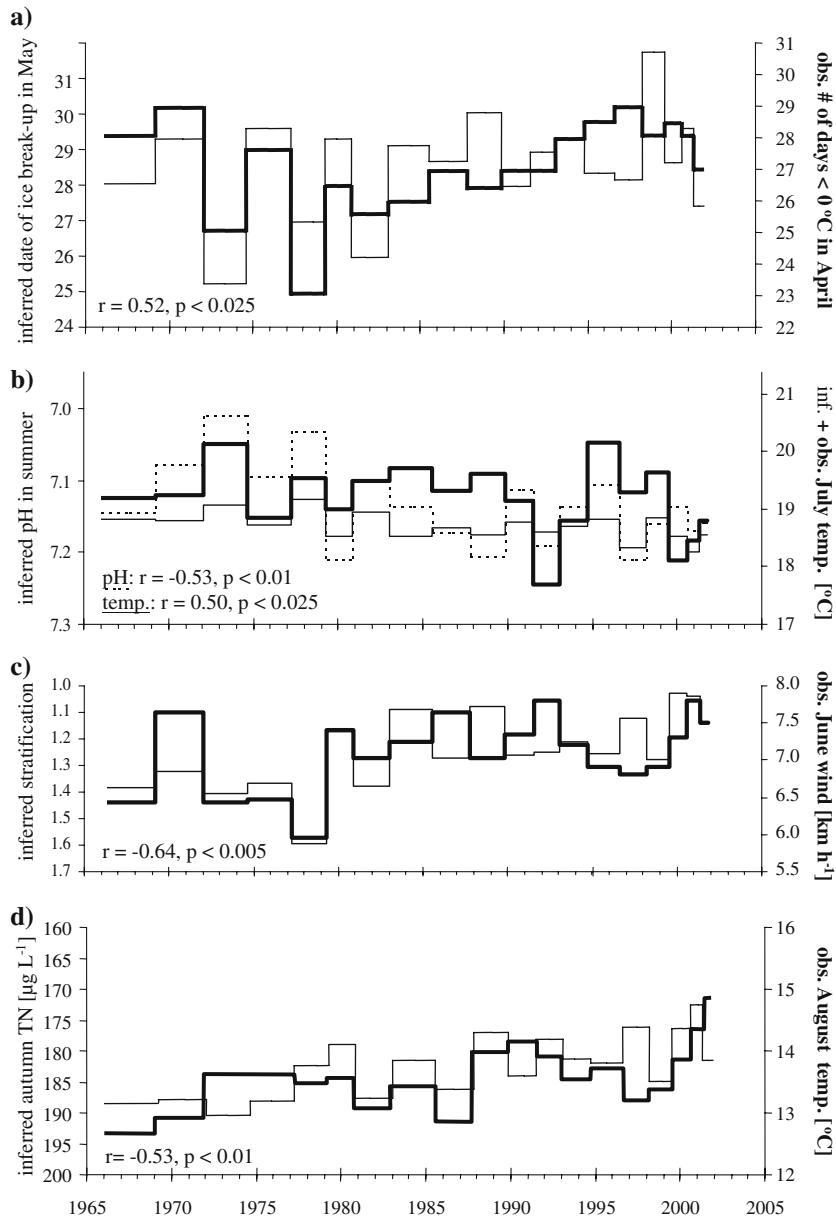


Fig. 10 Comparison of diatom-inferred seasonal climate aspects with the instrumental record (*bold lines*): **(a)** diatom-inferred date of ice break-up in May compared with number of days below 0°C in April; **(b)** diatom-inferred summer temperature (*solid line*) and diatom-inferred summer pH (*dashed line*) compared with

measured air temperatures in July, corrected by the difference of 4.7°C between air and water temperature in July, (compare Fig. 3); **(c)** diatom-inferred stratification of the water column in summer compared with wind velocity in June; and **(d)** diatom-inferred TN concentrations in autumn compared with autumn temperatures

plained by TN autumn concentrations (Table 5), which was correlated to depth (Table 4). Diatom-inferred TN autumn concentrations, using a one component model, were not significantly related

to autumn temperatures, but to August temperatures ($r = 0.53$, $n = 19$, $p < 0.01$; Fig. 10c). TN autumn inferences had an inverse relationship to diatom flux ($r = -0.49$, $n = 19$, $p < 0.025$).

Discussion

Comparison between the instrumental record and fossil diatoms

PCA axis 1 was most strongly correlated with wind velocity in June, and past diatom production was highly correlated with July temperatures, suggesting that spring and summer conditions have a higher influence on the overall diatom composition and production than annual or autumn temperatures. Likewise, in a high-resolution study of fossil diatoms considering historical seasonal temperature patterns, Sorvari et al. (2002) also found that diatom composition was influenced by higher spring temperatures since AD 1800 in Finnish Lapland. The significant correlations between faster wind velocity in June, colder July temperature and diatom production are in agreement with the notion that planktonic diatoms rely on water turbulence for their maintenance in the water column, while other algae groups are more competitive when the water column is stratified. These results are consistent with our sediment trap study, where spring diatom growth occurred in the highest elevation lake in July and in the lowest elevation lake already in May (Fig. 7a, d). The timing of spring circulation is crucial as the light intensity increases towards the summer, thus enhancing primary production.

Importance of environmental variables for the distribution of modern diatoms

Sediment traps are frequently used to sample lake deposits, yet our study depends on the assumption that diatom deposition in the sediment traps reflects their growth cycles. However, it must be noted that there are uncertainties associated with the use of sediment traps in shallow lakes. For example, because we have not estimated the effect of resuspension, it cannot be excluded that turbulence enhanced diatom depositions. A detailed analysis of the proportion of dead cells in relation to living cells could have yielded insights into the importance of resuspended, non-living diatoms which cannot be related to environmental variables. In lac du Sommet, the Secchi disk was always visible at the bottom of the lake,

indicating that light conditions were sufficient for growth of benthic species. Therefore, we must assume that living diatoms could have been resuspended. It is also possible that diatoms were growing on the plastic cylinders, although no biofilm was visible. In addition, in a 4-m deep lake only ca. 75% of the water column was located above the trap, thus the complete water column was not sampled by the trap. Yet, in our study, the marked seasonal diatom succession (Fig. 9), as expressed by the long floristic gradients, suggests that the deposited diatoms do reflect seasonal succession. In addition, the investigation of the diatom succession over two consecutive years confirmed the reproducibility of major species patterns in lac Elysée (Hausmann and Pienitz, in preparation). A sediment trap study by Köster and Pienitz (2006) in a similar shallow lake (3.6 m max. depth) in Connecticut, USA, showed that the sediment trap accurately reflected the seasonal succession of plankton samples.

In the best case (thought unrealistic) scenario, lakes with identical morphometry would have been compared. Lake depth, conductivity, and date of ice break-up explained biological differences in all seasons (Table 5). It is noteworthy that lake depth and conductivity were not correlated to the date of ice break-up, temperature or lake circulation in summer, but lake depth and TN autumn concentrations were correlated (Table 4). Lake depth can influence not only the diatom flux deposited but also the composition of assemblages by horizontal transportation of diatoms from the littoral zone. To accurately calculate the thermal stability of a lake, its depth has to be considered (Wetzel 2001). The ratio of top to bottom temperature is just a rough estimation of water column stratification. The sampling of lakes with different depth and conductivity could not be avoided, because our main goal was to compare climate responses of lakes equally distributed along an elevation gradient.

In the highest elevation lake, ice break-up occurred three weeks later than in the lowest lake (Fig. 7). The duration of ice-cover was very important in explaining the biological differences between the lakes. As soon as a lake is free of ice, the water column can circulate, nutrients can be distributed, and phytoplankton can flourish

(Wetzel 2001; Lotter and Bigler 2000). It seems that duration of ice-cover is not only a strong seasonal signal but also exerts a strong control on the overall dynamics of lakes and their biota, as DOC and TN concentrations in autumn were correlated to date of ice break-up.

All our study lakes were open systems and were influenced by spring snowmelt runoff. *Meridion circulare* and *Fragilaria virescens* var. *exigua* are associated with fresh flowing waters (Patrick and Reimer 1966; Krammer and Lange-Bertalot 1991a), and were probably transported by inflowing streams, which were stronger in spring. Our results are in agreement with previous studies suggesting that diatom growth is strongly influenced by physical factors of the water column. For example Köster and Pienitz (2006) studied the seasonality of diatoms with a monthly resolution in Bates Pond (Connecticut, USA), indicating that temperature and lake circulation explained most of variance within the diatoms. Agbeti et al. (1997) and Elliott et al. (2001) observed a direct impact of vertical mixing on phytoplankton composition, which can be wind-induced at homothermic conditions. Siver and Hamer (1992) studied the seasonality of chrysophytes in Bigelow Pond, a small lake in Connecticut (USA), where water temperature and pH had strong effects on seasonal changes in chrysophytes.

Summer diatom assemblages were significantly related to differences in DOC concentrations, which were lower when ice break-up occurred later. This might be explained by the timing of spring snowmelt runoff, and the onset of terrestrial and aquatic vegetation growth. Possible sources of DOC in oligotrophic lakes are phytoplankton productivity and allochthonous inputs from the drainage basin (Wetzel 2001). Diatom species respond differently to DOC concentration changes (Pienitz and Smol 1993; Pienitz and Vincent 2000), because DOC controls important optical properties in the water column of lakes (Leavitt et al. 2003).

Diatom production is favoured by lake circulation. This relation is reflected in our data by the strong relation between diatom flux and increased observed wind velocity and colder summer temperature (Fig. 4). Diatom production and assimi-

lation of CO₂ leads to enrichment of carbonate and increase of pH, which might explain why pH and lake circulation were correlated in summer (Table 4). The Si:SRP ratio was also correlated with the circulation of the water column. All three variables were important in explaining differences between the samples from the summer (Table 5). According to Kilham et al. (1986), *Fragilaria* prefers a high Si:SRP ratio, in contrast to *Cyclotella*. This relation might be reflected in our study where fossil abundance of *Fragilaria virescens* was highly correlated with measured wind velocity in June, which might have caused an enhanced circulation of the water column in the shallow lac du Sommet. In summer, the nitrate concentrations were significantly higher in the two higher elevation lakes (Fig. 6c), which might be explained by circulation of the water column or sparse vegetation at high elevation. In the study of Köster and Pienitz (2006), low seasonal nitrate concentrations were correlated to lower temperature and weaker circulation. Catalan et al. (2002) described high nitrate levels as a typical feature of mountain lakes, as sparsely developed soils and vegetation in the catchment area take up less atmospheric nitrogen.

Many of the taxa with increased fossil abundance during colder periods occurred in the traps of higher elevation lakes: in our study, *Aulacoseira perglabra* was found in autumn in the highest elevation lake and fossil abundances in lac du Sommet were higher when past October temperatures were colder. Correspondingly, *A. perglabra* is predominantly found in alpine lakes (Krammer and Lange-Bertalot 1986). The dominant fossil diatom *Fragilaria virescens* var. *exigua* is a typical diatom for Nordic lakes (Grönlund and Kauppila 2002). Highest abundances were found in spring and summer in the second highest elevation lake, thus fossil abundances could be as cold spring periods. In our study, past abundances were correlated to observed wind velocity in June, but also to measured May temperatures. *C. hebridica* was correlated to the number of days below 0°C in April. It occurred in spring in lac du Sommet but also in autumn in lac Joachim. Fossil abundance of *C. hebridica* in lake Stuoramohkki, Finnish Lapland, decreased during the spring warming trend since AD 1800 (Sorvari et al.

2002). Fossil occurrences of *Cymbella gaeumanni* and *Aulacoseira distans* var. *nivalis* were significantly higher during periods of cooler May temperature, and both taxa are usually found in northern and alpine lakes (Krammer and Lange-Bertalot 1986, 1991a). *Cymbella silesiaca*, which according to our study is an indicator for warmer spring conditions, was a typical diatom of boreal lakes in a modern training set from northwestern subarctic Canada (Pienitz et al. 1995), whereas *Achnanthes minutissima*, which fossil record in lac du Sommet was significantly correlated with cooler July temperatures, was found by Pienitz et al. (1995) to dominate arctic-alpine lakes.

In lac du Sommet, when the water column became more stratified, diatom growth declined yet chl *a* increased (Fig. 7c). Analysis of live plankton revealed that the chl *a* maximum represented mainly cyanobacteria. Several studies have shown that green algae and cyanobacteria succeed diatoms (e.g., Klee and Schmidt 1987). Often cyanobacteria are associated with highly eutrophic lakes, yet Vinebrooke and Leavitt (1999) found them to be abundant in alpine lakes. Most cyanobacteria can withstand high UVR levels by production of photoprotective pigments (Roy 2000) and a good repair capacity (Quesada and Vincent 1997). It has been shown by several studies that an enhanced thermal stability favors the growth of cyanobacteria (Zohary and Robarts 1989; Bormans et al. 1997; Nakano et al. 2001). In a four-year study of diatom successions in four lakes by Zhang and Prepas (1996), inter-annual statistical analysis revealed that diatom biomass was higher when the temperature was below 15°C, whereas cyanobacteria biomass was higher when the temperature exceeded 15°C. In order to study the relation between diatoms and other algae, an analysis of fossil pigments would be of interest (Vinebrooke et al. 1998).

Seasonal diatom inferences

Inferences of seasonal climate aspects are based on samples with bi-weekly resolution, derived from four lakes, which were grouped into seasonal sets. It might be problematic to mix spatial

and time distributions in one statistical analysis. The comparison of assemblages of lakes from a temperature gradient is more common, but interpretations of downcore assemblages using seasonal succession have also been performed (e.g., Köster and Pienitz 2006). One advantage of the classical modern surface approach is that the modern samples experienced the same taphonomic processes as the fossil samples. Yet in our study modern samples cover different time intervals than the fossil samples. Diatoms that mainly grow during one specific season are more useful for this approach than species that bloom in spring and autumn. Therefore, it might be advantageous to restrict the number of taxa as described in Racca et al. (2003), because some taxa have higher indicator values than others. Instead of using seasonal sets, it might be fruitful to test other statistical techniques that take into account the temporal and spatial structure of the modern data, for example by comparing the seasonal diatom succession in lakes with a three-mode PCA (e.g., Anneville et al. 2004). In addition, the sample number in the present study is rather low and statistical results should be taken with caution.

The seasonal inferences were significantly correlated to the instrumental record (Fig. 10), suggesting that seasonal climate aspects can be reconstructed from fossil diatom assemblages of lac du Sommet. In the modern data summer temperatures, circulation of the water column and pH were interrelated. The resulting corresponding inferences were also significantly correlated to each other. Diatoms are known to be very good pH indicators (Battarbee and Renberg 1990). In a short-term study pH changes might have been the result of algae growth caused by favourite physical conditions. However, during a longer time scale pH changes can also reflect soil development, changes in catchment vegetation or atmospheric pollution. Seasonal diatom inferences from the other three study lakes should produce the same results, which remains to be tested.

Models for ice out and seasonal temperatures based on surface lake sediment samples demonstrated that spring and summer models performed better than the model for autumn temperature

(Thompson et al. 2005). In our study, inferred TN autumn concentrations showed an inverse relationship to measured August temperatures, indicating that summer conditions were more important than autumn conditions. Low TN concentrations are usually associated to low algal productivity. It remains unclear which algal bloom resulted in low diatom-inferred TN concentrations, since diatom flux was positively correlated to measured August air temperature (Fig. 4). Alternatively low TN concentrations can be caused by denitrification or lower solubility of N_2 at warmer temperatures (Wetzel 2001).

It is noteworthy that the reconstructed summer temperature, inferred circulation of the water column and the TN autumn concentration, based on relative abundance of fossil and modern diatoms, are highly correlated to past diatom flux. This result is a strong indication that the reconstruction of seasonal climate aspects using high resolution modern diatom data is feasible.

Conclusions and outlook

We conclude that the study of seasonal patterns of sedimentation from lakes along a climate gradient can notably increase our understanding of the sediment record in relation to climate forcing. We found that the diatom-inferred past ice break-up dates, diatom-inferred circulation of the water column, pH and summer temperature of lac du Sommet were significantly correlated to the instrumental climate record. Seasonal climate change is of importance as increased spring solar insolation may promote earlier ice break-up, whereas decreased summer solar insolation may enhance lake circulation as suggested by Bradbury and Forester (2003). Therefore, it would be interesting to reconstruct seasonal climate lake response to varying degrees of summer insolation (Berger and Loutre 1991) during the Holocene. However, during the Holocene, vegetation changes and soil development might have been more important than direct climatic impact. Hence, an application of the seasonal climate models on fossil diatom assemblages of lac du Sommet from the Holocene should be combined with a multi-proxy study.

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References

- Agbeti MD, Kingston JC, Smol JP, Watters C (1997) Comparison of phytoplankton succession in two lakes of different mixing regimes. *Arch Hydrobiol* 140: 37–69
- Allard M, Fortier R (1990) The thermal regime of a permafrost body at Mont du lac des Cygnes, Québec. *Can J Earth Sci* 27:694–697
- Anderson NJ (2000) Diatoms, temperature and climatic change. *Eur J Phycol* 35:307–314
- Anneville O, Souissi S, Gammeter S, Straile D (2004) Seasonal and inter-annual scales of variability in phytoplankton assemblages: comparison of phytoplankton dynamics in three peri-alpine lakes over a period of 28 years. *Freshwater Biol* 49:98–115
- Battarbee RW (2000) Palaeolimnological approaches to climate change, with special regard to the biological record. *Quatern Sci Rev* 19:107–124
- Battarbee RW, Kneen MJ (1982) The use of electronically counted microspheres in absolute diatom analysis. *Limnol Oceanogr* 27:184–188
- Battarbee RW, Renberg I (1990) The Surface Water Acidification Project (SWAP) paleolimnology programme. *Philos Trans R Soc Lond B* 327:227–232
- Bennett KD (1996) Determination of the number of zones in a biostratigraphical sequence. *New Phytol* 132:155–170
- Berger A, Loutre MF (1991) Insolation values for the climate of the last 10 million years. *Quatern Sci Rev* 10:297–317
- Binford MW (1990) Calculation and uncertainty analysis of ^{210}Pb dates for PIRLA project lake sediment cores. *J Paleolimnol* 3:253–267

- Birks HJB (1995) Quantitative palaeoenvironmental reconstructions. In: Maddy D, Brew JS (eds) *Statistical modelling of quaternary science data*. Technical guide 5. Quaternary Research Association, Cambridge, pp 161–254
- Birks HJB (1998) Numerical tools in palaeolimnology – progress, potentialities, and problems. *J Paleolimnol* 20:307–332
- Birks HJB, Gordon AD (1985) *Numerical methods in quaternary pollen analysis*. Academic Press, London
- Bormans M, Maier H, Burch M, Barker P (1997) Temperature stratification in the lower River Murray, Australia: implication for cyanobacteria bloom development. *Mar Freshwater Res* 48:647–654
- Bradbury JP (1988) A climate-limnologic model of diatom succession for paleolimnological interpretation of varved sediments at Elk Lake, Minnesota. *J Paleolimnol* 1:115–131
- Bradbury JP, Forester RM (2003) Environment and paleolimnology of Owens Lake, California: a record of climate and hydrology for the last 50,000 years. *Smithsonian Contrib Earth Sci* 33:145–173
- Bradley RS (2000) Past global changes and their significance for the future. *Quatern Sci Rev* 19:391–402
- Bradshaw EG, Anderson NJ, Jensen JP, Jeppesen E (2002) Phosphorus dynamics in Danish lakes and the implications for diatom ecology and palaeoecology. *Freshwater Biol* 47:1963–1975
- Camburn KE, Charles JC (2000) Diatoms of low-alkalinity lakes in the northeastern United States. *The Academy of Natural Sciences of Philadelphia, Philadelphia*
- Catalan J, Ventura M, Brancelj A, Granados I, Thies H, Nickus U, Korhola A, Lotter AF, Barbieri A, Stuchlik E, Lien L, Bistusik T, Camaero L, Goudsmit GH, Kopacek J, Lemcke G, Livingston DM, Müller B, Rautio M, Sisko M, Sorvari S, Sporka F, Strunecky O (2002) Seasonal ecosystem variability in remote mountain lakes: implications for detecting climatic signals in sediment records. *J Paleolimnol* 28:25–46
- Douglas M, Smol JP (1999) Freshwater diatoms as indicators of environmental change in the High Arctic. In: Stoermer EF, Smol JP (eds) *The diatoms: applications for the environmental and earth sciences*. Cambridge University Press, Cambridge
- Elliott JA, Irish AE, Reynolds CS (2001) The effects of vertical mixing on a phytoplankton community: a modelling approach to the intermediate disturbance hypothesis. *Freshwater Biol* 46:1291–1297
- Environment Canada (1994) *Manual of analytical methods, vol 1. Major ions and nutrients*. Environmental Conservation Service – ECD. Canadian Communications Group, Toronto
- Fallu M-A, Allaire N, Pienitz R (2000) *Freshwater diatoms from northern Québec and Labrador (Canada)*. Bibliotheca Diatomologica, vol 45. Stuttgart
- Flynn WW (1968) Determination of low levels of polonium-210 in environmental materials. *Anal Chim Acta* 43:221–227
- Grönlund T, Kauppila T (2002) Holocene history of Lake Soldatskoje (Kola Peninsula, Russia) inferred from sedimentary diatom assemblages. *Boreas* 31:273–284
- Hassan G, Espinosa MA, Isla FI (2006) Modern diatom assemblages in surface sediments from estuarine systems in the southeastern Buenos Aires province, Argentina. *J Paleolimnol* 35:39–53
- Hausmann S, Kienast F (2006) Diatom-inference model for nutrients screened to reduce the influence of background variables: application to varved sediments of Greifensee and evaluation with measured data. *Palaeogeogr Palaeoclimatol Palaeoecol* 233:96–112
- Horton BP (1999) The contemporary distribution of intertidal foraminifera of Cowpen Marsh, Tees Estuary, UK: implications for studies of Holocene sea-level changes. *Palaeogeogr Palaeoclimatol Palaeoecol* 149:127–149
- Interlandi SJ, Kilham SS, Theriot EC (1999) Responses of phytoplankton to varied resource availability in large lakes of the Greater Yellowstone Ecosystem. *Limnol Oceanogr* 44:668–682
- Jeferey SW, Welschmeyer NA (1997) Spectrophotometric and fluorimetric equations in common use in oceanography. In: Jeffrey SW, Mantoura RFC, Wright SW (eds) *Phytoplankton pigments in oceanography: guidelines to modern methods*. UNESCO
- Juggins S, ter Braak CJF (1997) CALIBRATE version 0.82. A C++ program for analysing and visualising species environment relationships and for predicting environmental values from species assemblages. User guide Version 1.0. Department of Geography, Newcastle
- Kilham P, Kilham SS, Hecky RE (1986) Hypothesized resource relationships among African planktonic diatoms. *Limnol Oceanogr* 31:1169–1181
- Klee R, Schmidt R (1987) Eutrophication of Mondsee (upper Austria) as indicated by the diatom stratigraphy of a sediment core. *Diatom Res* 2(1):55–76
- Köster D, Pienitz R (2006) Seasonal diatom variability and paleolimnological inferences – a case study. *J Paleolimnol* 35:395–416
- Korhola A, Sorvari S, Rautio M, Appleby RG, Dearing JA, Hu Y, Rose N, Lami A (2002) A multi-proxy analysis of climate impacts on the recent development of subarctic Lake Saanajärvi in Finnish Lapland. *J Paleolimnol* 28:59–77
- Krammer K, Lange-Bertalot H (1986) *Bacillariophyceae*. 1. Teil: Naviculaceae. In: Ettl H, Gerloff J, Heynig H, Mollenhauer D (eds) *Süßwasserflora von Mitteleuropa, Band 2/1*. Gustav Fischer Verlag, Stuttgart, New York
- Krammer K, Lange-Bertalot H (1988) *Bacillariophyceae*. 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. In: Ettl H, Gerloff J, Heynig H, Mollenhauer D (eds) *Süßwasserflora von Mitteleuropa, Band 2/2*. VEB Gustav Fischer Verlag, Jena
- Krammer K, Lange-Bertalot H (1991a) *Bacillariophyceae*. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. In: Ettl H, Gerloff J, Heynig H, Mollenhauer D (eds) *Süßwasserflora von Mitteleuropa, Band 2/3*. Gustav Fischer Verlag, Stuttgart
- Krammer K, Lange-Bertalot H (1991b) *Bacillariophyceae*. 4. Teil: Achnantheaceae, Kritische Ergänzungen zu Navicula (Lineolatae) und Gomphonema, Gesamtliteraturverzeichnis Teil 1–4. In: Ettl H., Gärtner G,

- Gerloff J, Heynig H, Mollenhauer D (eds) Süßwasserflora von Mitteleuropa, Band 2/4. Gustav Fischer Verlag, Stuttgart Jena
- Larsson U, Blomqvist S, Abrahamsson B (1986) A new sediment trap system. *Mar Ecol Prog Ser* 31:205–207
- Leavitt PR, Cumming BF, Smol JP, Reasoner M, Pienitz R, Hodgson DA (2003) Climate control of ultraviolet radiation effects on lakes. *Limnol Oceanogr* 48:2003–2069
- Lotter AF (1998) The recent eutrophication of Baldeggersee (Switzerland) as assessed by fossil diatom assemblages. *Holocene* 8:395–405
- Lotter AF, Bigler C (2000) Do diatoms in the Swiss Alps reflect the length of ice-cover? *Aquat Sci* 62:125–141
- Lotter AF, Juggins S (1991) POLPROF, TRAN and ZONE: programs for plotting, editing and zoning pollen and diatom data. INQUA-Subcommission for the study of the Holocene – working group on data-handling methods. *Newsletter* 6:4–6
- Nakano S, Hayakawa K, Frenette J-J, Nakajima T, Jiao C, Tsujimura S, Kumagai M (2001) Cyanobacterial blooms in a shallow lake: a large-scale enclosure assay to test the importance of diurnal stratification. *Arch Hydrobiol* 150:491–509
- Nusch EA (1980) Comparison of different methods for chlorophyll and phaeopigment determination. *Arch Hydrobiol Ergebnisse Limnol* 14:14–36
- Payette S (1984) Un îlot de pergélisol sur les hauts sommets de Charlevoix, Québec. *Geogr Phys Quatern* 38:305–307
- Patrick R, Reimer CW (1966) The diatoms of the United States, exclusive of Alaska and Hawaii, vol 1 – Fragilariaceae, Eunotiaceae, Achnantheaceae, Naviculaceae. Monograph No. 13. Academy of Natural Sciences of Philadelphia, Philadelphia
- Pienitz R, Smol JP (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, Vincent WF (2000) Effect of climate change relative to ozone depletion on UV exposure in sub-arctic lakes. *Nature* 404:484–487
- Pienitz R, Smol JP, Birks HJB (1995) Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *J Paleolimnol* 13:21–49
- Quesada A, Vincent WF (1997) Strategies of adaptation by Antarctic cyanobacteria to ultraviolet radiation. *Eur J Phycol* 32:335–342
- Racca JMJ, Wild M, Birks HJB, Prairie YT (2003) Separating wheat from chaff: diatom taxon selection using an artificial neural network pruning algorithm. *J Paleolimnol* 29:123–133
- Reid M (2005) Diatom-based models for reconstruction past water quality and productivity in New Zealand lakes. *J Paleolimnol* 33:13–38
- Roy S (2000) Strategies for the minimization of UV-induced damage. In: de Mora S, Demeres S, Vernet M (eds) *The effects of UV radiation in marine ecosystems*. Cambridge University Press, Cambridge
- Siver PA, Hamer JS (1992) Seasonal periodicity of Chrysophyceae and Synurophyceae in a small New England lake: implications for paleolimnological research. *J Phycol* 28:186–198
- Sommer U (1986) The periodicity of phytoplankton in Lake Constance (Bodensee) in comparison to other deep lakes of central Europe. *Hydrobiologia* 138:1–7
- Sorvari S, Rautio M, Korhola A (2000) Seasonal dynamics of the subarctic Lake Saanajärvi in Finnish Lapland. *Verh Int Ver Theor Angew Limnol* 27:507–512
- Sorvari S, Korhola A, Thompson R (2002) Lake diatom response to recent Arctic warming in Finnish Lapland. *Global Change Biol* 8:171–181
- ter Braak CJF, Šmilauer P (1998) CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination (version 4). Microcomputer Power
- ter Braak CJF, Juggins S, Birks HJB, van der Voet H (1993) Weighted averaging partial least squares regression (WA-PLS): definition and comparison with other methods for species-environment calibration. In: Patil GP, Rao CR (eds) *Multivariate environmental statistics*. Elsevier, Amsterdam
- Thompson R, Price D, Cameron N, Jones V, Bigler C, Rosén P, Hall RI, Catalan J, García J, Weckstrom J, Korhola A (2005) Quantitative calibration of remote mountain-lake sediments as climatic recorders of air temperature and ice-cover duration. *Arct Antarct Alp Res* 37:626–635
- Vinebrooke RD, Leavitt RR (1999) Phyto-benthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds: a HPLC-based pigment approach. *J N Am Benthol Soc* 18:14–32
- Vinebrooke RD, Hall RI, Leavitt PR, Cumming BF (1998) Fossil pigments as indicators of phototrophic response to salinity and climatic change in lakes of western Canada. *Can J Fish Aquat Sci* 55:668–681
- Wetzel RG (2001) *Limnology*, 3rd edn. Academic Press, San Diego
- Zhang Y, Prepas EE (1996) Regulation of the dominance of planktonic diatoms and cyanobacteria in four eutrophic hardwater lakes by nutrients, water column stability, and temperature. *Can J Fish Aquat Sci* 53:621–633
- Zohary T, Robarts RD (1989) Diurnal mixed layers and the long-term dominance of *Microcystis aeruginosa*. *J Plankton Res* 11:25–48