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PRIMARY RESEARCH PAPER

Seasonal water chemistry and diatom changes in six boreal lakes of the Laurentian Mountains (Québec, Canada): impacts of climate and timber harvesting

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Abstract The physical and chemical variabilities as well as the distribution of diatoms of six boreal lakes in the Laurentian Mountains (southern Québec, Canada) were studied. The lakes are located along an altitudinal gradient and were sampled at a biweekly resolution from May through October, 2002. In general, we found later onset and weaker lake stratification under colder climates. Lake circulation and SiO_2 are strongly correlated and together significantly explain the distribution of diatoms of the individual lakes. Diatoms that accumulated in the sediment traps were mostly composed of benthic species, suggesting resuspension. However, diatom flux and lake circulation were not significantly correlated, the diatom assemblages in the sediment traps were similar in two consecutive years, and species–environment relationships were comparable among lakes, which indicates that the effects of resuspension were minimal. In addition, we found that one lake was more productive due to forest logging. The forest in the catchment of Lake Maxi was entirely clear-cut shortly prior to our sampling. Mean total phosphorus, dissolved organic carbon, and chlorophyll *a* concentrations were significantly higher when compared to the other five study lakes. This study seeks to improve our understanding of how diatoms in boreal lakes respond to climate change and forest clear-cut.

Keywords Shallow boreal lakes · Water chemistry · Seasonality · Laurentian Mountains · Sediment traps · Diatoms · Multivariate statistics · Climate · Forest clear-cut

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Introduction

Climate warming is having a profound impact on the Earth's environment, including the earlier seasonal ice break-up of rivers and lakes (Smol et al., 2005; Duguay et al., 2006; Intergovernmental Panel on Climate Change, 2007). Many paleoclimate studies have focused on annual climate reconstructions to constrain models of future climate change (Hughes & Ammann, 2009). However, there is a growing interest in higher resolution subannual climate reconstructions (Sorvari et al., 2002; Hausmann & Pienitz, 2007). Siliceous remains of diatoms (class Bacillariophyta) that are archived in lake sediments can provide such high-resolution seasonal quantitative climate records (Stoermer & Smol, 1999; Hausmann & Pienitz, 2007). However, to achieve these high-resolution reconstructions, there must be a greater understanding of modern seasonal processes in lakes. A recent study by Nonaka et al. (2007) found that the spring ice break-up is occurring earlier on boreal lakes and rivers in south-eastern Canada due to climate warming. The changes in lake boundary conditions as a response to climate change should affect lake circulation patterns, nutrient distribution, and diatom assemblages, but need to be quantified (Salonen et al., 1984; Reynolds, 1993). Regularly sampled sediment traps (designed to collect diatoms) deployed in lakes together with water chemistry sampling have the capacity to capture seasonal species–environment relationships under specific climate conditions. Therefore, by monitoring a series of lakes along an altitudinal gradient, seasonal species–environmental relationships as a response to climate change can be quantified. This study explores the impact of altitude on the seasonality of lakes by analyzing diatom-environment responses in southern Québec.

A major requirement for climate reconstructions using lake sediments is that the lake and its biota are sensitive recorders of changes in the lake environment driven by climate (Birks, 1995). A climate gradient can be latitudinal or altitudinal. An altitudinal gradient has the advantage that the insolation among lakes is comparable. At first sight, boreal (taiga) lakes in southern Quebec may appear to be less suited to climate change studies than remote arctic lakes because they have a potentially higher exposure to anthropogenic influences, such as forest harvesting (Desjardins & Monderie, 1999; Pienitz et al., 2004). However, the proximity of these lakes to a population center allows for year-round biweekly sampling, a logistical constraint that often limits high-resolution sampling in the Arctic (Lotter et al., 1999). In addition, diatoms in boreal lakes have been shown to respond sensitively to changes in lake catchment vegetation as a response to climate warming (Pienitz & Smol, 1993; Fallu et al., 2000). In addition, Schindler et al. (1996) found lower SiO_2 concentrations of boreal lakes in the Experimental Lake District Area related to recent climate warming.

This study documents the seasonal changes in the water chemistry and diatom assemblages, which are measured and sampled biweekly using sediment traps in six boreal forest lakes located along a climate gradient in the Laurentian Mountains (southern Québec, Canada). We explored species–environment relationships using multivariate statistics. We also discuss uncertainties related to the use of sediment traps in shallow lakes.

Study sites

The six study lakes (Cyprès, Joachim, Moreau, du Sommet, Elysée, and Maxi) are of glacial origin and are located in a natural reserve in the Laurentian Mountains on granitic–gneissic bedrock of the Canadian Precambrian Shield (Fig. 1). The study lakes are distributed along an elevation gradient (280–950 m asl, Table 1). The maximum lake depth varied between 3 and 16 m, catchment area ranged from 0.41 to 24.67 km^2, and lake surface area ranged from 0.02 to 0.27 km^2 (Table 1). Along the elevation gradient, the lake catchment vegetation changed from *Betula papyrifera* (paper birch) to *Abies balsamea* (balsam fir), which is replaced by *Picea mariana* (black spruce) above 800 m asl. Within the study region, permafrost occurs sporadically at an elevation of 960 m asl, reflecting the strong continental character of the regional climate (Allard & Fortier, 1990). Except for a narrow 20-m-wide zone along the lake perimeter, the catchment of Lake Maxi was completely clear-cut shortly before sampling in 2002, when the soils were still lacking a vegetation cover.

Materials and methods

Collection of water samples and limnological analysis

Over the period May to October 2002, water samples were taken every 2 weeks from each lake at 1 m depth with a Wildco® Kemmerer sampler, and were filtered on the day of sampling through cellulose acetate filters (pore size of 45 μm) for the analysis of dissolved organic carbon (DOC), soluble reactive phosphorus (SRP), nitrate (NO_3), nitrite (NO_2), ammonium (NH_4), chloride (Cl), and silicate ions (SiO_2). Samples for DOC analyses were kept in brown glass bottles and those for SiO_2 analyses in

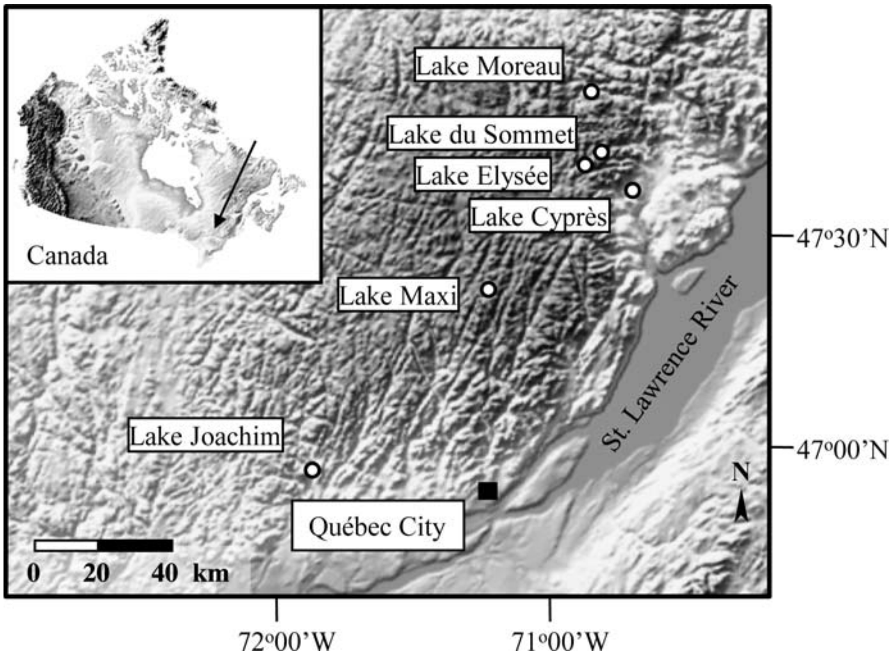

Fig. 1 Location of the study lakes in southern Québec superimposed on a digital elevation map (http://atlas.nrcan.gc.ca)

Table 1 Location, physical characteristics, and day of ice break-up of the six study lakes

	Cyprès	Joachim	Moreau	Sommet	Elysée	Maxi
Latitude	47°37′ N	47°00′ N	47°55′ N	47°43′ N	47° 44′ N	47° 26′ N
Longitude	70°36′ W	71°55′ W	70°40′ W	70°40′ W	70°41′ W	71°07′ W
Maximum depth (m)	3	7	16	4	10	7
Surface (km^2)	0.02	0.15	0.27	0.02	0.05	0.07
Catchment (km^2)	24.67	3.52	8.13	0.41	0.85	1.59
Elevation (m asl)	280	370	619	830	920	950
Day of ice break-up	1-May	7-May	22-May	28-May	25-May	n.d.

polyethylene bottles. Total phosphorus (TP) and total nitrogen (TN) were analyzed from unfiltered water. Water samples were stored at 4°C prior to chemical analysis by Environment Canada laboratories, Aquatic Ecosystem Protection Research Division (Burlington, Ontario). For detailed analytical procedures and methods, consult the Analytical Methods Manual (Environment Canada, 1994).

Subsequent to water sampling, light penetration was measured using a Secchi disk (diameter = 20 cm). Temperature, pH, conductivity, and oxygen profiles were measured using a Quanta Hydrolab®. Water temperatures of each study lake were recorded in 1.5 h intervals by two Hobo® dataloggers circa 10 cm below the lake surface and circa 50 cm above the lake bottom. A ratio calculated between temperatures measured at the bottom and near the surface of the water column was used to estimate the degree of water column stratification and lake circulation (Köster & Pienitz, 2006).

For analysis of chlorophyll *a* (Chl *a*), 300 ml aliquots of water was filtered in dimmed light conditions using Whatman® GF/F glass micro fiber filters. The Chl *a* samples were stored in aluminum foil at −15°C until Chl *a* fluorescence measurements were performed according to standard procedures (Nusch, 1980). Chl *a* was corrected for phaeopigments using the equations of Jeffrey & Welschmeyer (1997). Lake Elysée was also investigated at monthly intervals in 2003.

Sediment trap samples

Glew sediment traps (Paleoecological Environmental Assessment and Research Laboratory, Queen's University, Ontario) were installed in mid-April 2002 under the lake ice cover, which had a maximum thickness of 80 cm. The upper edges of the traps were positioned approximately 1 m above the lake floors. The deposits were collected in removable glass jars of 110-ml capacity at the bottom of each of three black plastic tubes, with an internal diameter of 5.2 cm and a length of 44 cm (8.5:1 aspect ratio). Three traps were mounted together on a frame that provided nominal equal center-to-center spacing of 520 mm. Submerged vertical stability was provided by an integral central float along with a mooring system similar to that described by Larsson et al. (1986). Lugol's solution was added to the jars at the beginning of each sampling interval to prevent grazing of algae by zooplankton. Sediment traps were collected biweekly from May 2002 to the end of October in 2002. In Lake Elysée, sampling continued in 2003 at monthly intervals until October 2003.

For diatom analysis, frustules were cleaned with heated 30% H_2O_2. Afterwards, the glass beakers (250 ml) were filled with distilled water, and the cleaned diatom frustules were allowed to settle for at least 12 h at 4°C. In order to calculate fluxes, a known number of microspheres (plastic beads; University College London) with a diameter of 6 µm were added to the diatom suspension (Battarbee & Kneen, 1982). Aliquots of the diatom-microsphere suspensions were transferred onto ethanol-cleaned cover glasses, and after drying at room temperature, mounted with Naphrax® mounting medium onto microscope slides. Approximately, 400 diatoms per sample were analyzed at a magnification of 1000× using differential interference contrast (DIC) optics. The taxonomy mostly followed Krammer & Lange-Bertalot (1986, 1988, 1991a, b), Camburn and Charles (2000), and Fallu et al. (2000).

Numerical analysis

For each lake, coefficients of correlation between environmental variables (TP, SRP, TN, NO_2, NO_3, NH_4, DOC, SiO_2, Si:TP ratio, Si:SRP ratio, SO_4, DIC, pH, Secchi depth, temperature, circulation, and conductivity) were calculated and tested for statistical significance (Table 2). For each lake, the significance of each environmental variable for the variance in the diatom data during the open water period was tested by Monte Carlo permutation tests (999 permutations) implemented in canonical correspondence analysis and redundancy analysis (CCA and RDA; Table 2; ter Braak, 1986). In order to decide whether unimodal (CCA) or linear (RDA) ordination methods were appropriate, the species turnovers were assessed as lengths of the floristic gradients using a detrended correspondence analysis (DCA). Relative abundances of diatoms were square-root transformed, and the frequencies of rare taxa down-weighted. If the length of the floristic gradient was above two standard deviation (SD) units, a CCA with the focus on inter-sample distance scaling was used (Birks, 1995). If the species turnover was < 2 SD, a RDA, with the focus on inter-sample correlation scaling and centering by species, was applied.

In addition, to determine which environmental variables explained most of the variance among the lakes, a principal component analysis (PCA) was performed. Environmental variables were normalized prior to analysis.

A CCA was performed to determine which environmental variables best explained the distribution of diatom taxa from lakes along the altitudinal gradient. For this purpose, ter Braak & Šmilauer (1998) recommend to remove highly intercorrelated environmental variables, indicated by variance inflation factors (VIF) above 20. After screening for redundant variables, the VIFs of the set of environmental variables of our CCA were between 1.4 and 14.6. CCA was performed, with scaling focused on inter-sample distances, square-root transformation of relative species abundances, down-weighting of rare species, and normalizing environmental variables prior to ordination. All ordinations were performed using the computer program CANOCO (version 4.0; ter Braak and Šmilauer, 1998).

Results

Physical and chemical properties of the six study lakes

Five of six lakes (Lake Cyprès, Lake Joachim, Lake Moreau, Lake du Sommet, and Lake Elysée) were

Table 2 Pearson coefficients of correlation among water chemistry variables of individual lakes and diatom flux, based on biweekly water and sediment trap samples from May through October in 2002. Variables that are significantly related to the diatom assemblages are indicated with an asterisk. Sample size (n) and minimum significant coefficients of correlation (r) with $p < 0.05$ (one-tailed test of significance) are indicated in the columns next to the lake names

		Si/TP	Si/SRP	SRP	TN	TP	NH_4	NO_2	CL	SO_4	SIO_2	DOC	DIC	strati	temp	pH	secchi	cond	d flux		
Cyprès, n = 13, sign.: $r \geq 0.48$			0.71	-0.27	0.43	-0.45	-0.20	0.47	0.13	-0.47	0.94	0.79	0.44	-0.91	-0.85	0.18	-0.02	0.50	0.53	Si/TP	Joachim, n = 10, sign.: $r \geq 0.55$
	Si/SRP	0.24		-0.61	0.00	-0.39	-0.32	0.70	0.46	-0.27	0.65	0.89	0.71	-0.61	-0.47	0.53	0.09	0.89	0.42	Si/SRP	
	SRP	-0.71	-0.37		0.07	0.62	0.74	-0.07	-0.03	0.15	-0.09	-0.58	-0.78	0.16	-0.05	-0.79	0.21	-0.80	-0.36	SRP	
	TN	-0.39	-0.18	0.24		0.16	0.22	0.07	-0.73	0.18	0.30	0.10	-0.30	-0.41	-0.52	-0.42	0.28	-0.25	0.37	TN	
	TP	-0.73	0.06	0.52	0.77		0.90	0.15	-0.16	0.82	-0.39	-0.57	-0.80	0.22	-0.01	-0.80	0.64	-0.64	-0.53	*TP	
	*NH_4	-0.79	-0.44	0.47	0.30	0.47		0.20	-0.02	0.67	-0.16	-0.51	-0.79	-0.01	-0.23	-0.88	0.49	-0.66	-0.43	*NH_4	
	NO_2	0.24	0.40	-0.21	0.16	0.13	-0.64		0.41	-0.03	0.55	0.58	0.20	-0.40	-0.43	0.02	0.62	0.45	0.21	NO_2	
	*CL	-0.94	-0.25	0.57	0.38	0.62	0.77	-0.28		-0.26	0.24	0.27	0.44	-0.11	-0.01	0.38	-0.03	0.49	0.01	CL	
	*SO_4	0.64	0.02	-0.44	-0.50	-0.55	-0.36	-0.29	-0.65		-0.60	-0.56	-0.61	0.27	0.11	-0.54	0.50	-0.44	-0.49	SO_4	
	*SiO_2	0.92	0.47	-0.72	-0.31	-0.54	-0.89	0.56	-0.90	0.48		0.81	0.42	-0.87	-0.83	0.13	0.02	0.46	0.49	SiO_2	
	*DOC	-0.56	-0.37	0.33	0.62	0.51	0.60	-0.53	0.58	-0.21	-0.69		0.78	-0.71	-0.55	0.53	-0.04	0.84	0.53	DOC	
	DIC	0.66	0.49	-0.69	0.04	-0.15	-0.70	0.70	-0.59	0.23	0.84	-0.57		-0.31	-0.05	0.89	-0.35	0.93	0.56	*DIC	
	*strati	-0.60	-0.30	0.30	0.63	0.57	0.54	-0.35	0.57	-0.28	-0.65	0.96	-0.53		0.96	0.05	0.03	-0.35	-0.28	Strati	
	temp	0.58	-0.33	-0.61	-0.21	-0.59	-0.08	-0.23	-0.40	0.57	0.37	-0.21	0.35	-0.34		0.27	-0.17	-0.14	-0.19	temp	
	pH	0.43	0.47	-0.46	-0.45	-0.27	-0.53	0.43	-0.59	0.42	0.62	-0.56	0.45	-0.40	-0.02		-0.33	0.84	0.50	*pH	
	Secchi	0.09	0.25	-0.16	-0.08	-0.01	-0.19	0.27	-0.34	0.04	0.23	-0.06	-0.01	0.15	-0.33	0.68		-0.11	0.06	Secchi	
	cond	0.30	0.21	0.10	-0.66	-0.50	-0.53	0.38	-0.41	0.00	0.38	-0.73	0.04	-0.65	-0.24	0.42	0.31		0.50	cond	
	d flux	-0.21	-0.20	0.09	-0.34	-0.26	0.38	-0.11	0.18	-0.33	-0.24	-0.26	-0.34	-0.23	0.07	-0.07	0.17	0.40		d flux	
Moreau, n = 12, sign.: $r \geq 0.50$	Si/TP		-0.90	0.45	0.15	-0.90	0.23	-0.57	0.41	-0.19	0.49	0.38	-0.79	0.41	0.69	-0.57	0.43	0.26	0.27	Si/TP	Sommet, n = 10, sign.: $r \geq 0.51$
	Si/SRP	0.60		-0.67	-0.10	0.88	-0.43	0.63	-0.56	0.52	-0.69	-0.59	0.86	-0.63	-0.71	0.69	-0.50	-0.36	-0.52	Si/SRP	
	*SRP	-0.54	-0.59		0.33	-0.35	0.85	-0.41	0.95	-0.85	0.90	0.97	-0.69	0.91	0.07	-0.94	0.86	0.77	0.56	*SRP	
	*TN	-0.78	-0.72	0.63		0.01	0.42	0.22	0.38	-0.07	0.52	0.40	-0.17	0.17	-0.45	-0.45	0.52	0.78	-0.11	TN	
	TP	-0.88	-0.41	0.28	0.64		-0.10	0.64	-0.27	0.17	-0.39	-0.28	0.79	-0.32	-0.84	0.42	-0.26	-0.11	-0.41	TP	
	*NH_4	0.10	0.20	0.37	0.06	0.09		-0.43	0.89	-0.88	0.90	0.79	-0.65	0.63	-0.26	-0.72	0.63	0.69	0.47	*NH_4	
	*NO_2	-0.10	-0.54	-0.14	0.24	-0.05	-0.63		-0.49	0.48	-0.45	-0.26	0.84	-0.25	-0.53	0.25	-0.08	0.09	-0.72	NO_2	
	CL	-0.01	-0.27	0.50	0.50	0.01	0.57	-0.05		-0.80	0.88	0.89	-0.69	0.76	-0.06	-0.88	0.79	0.71	0.63	*CL	
	SO_4	-0.84	-0.58	0.33	0.78	0.85	-0.02	0.15	-0.02		-0.84	-0.77	0.61	-0.71	-0.01	0.65	-0.49	-0.48	-0.67	*SO_4	
	SiO_2	0.82	0.69	-0.58	-0.85	-0.56	0.27	-0.42	-0.11	-0.75		0.84	-0.77	0.70	0.03	-0.82	0.69	0.75	0.57	*SiO_2	
	*DOC	0.45	0.81	-0.36	-0.64	-0.17	0.51	-0.76	-0.25	-0.33	0.70		-0.57	0.95	0.00	-0.94	0.92	0.85	0.44	*DOC	
	*DIC	0.15	0.04	-0.40	-0.36	-0.33	-0.90	0.34	-0.60	-0.32	0.06	-0.25		-0.50	-0.46	0.64	-0.45	-0.36	-0.61	DIC	
	strati	-0.77	-0.24	0.47	0.59	0.59	-0.11	-0.21	-0.12	0.64	-0.69	-0.20	0.01		0.18	-0.87	0.88	0.72	0.36	*strati	
	*temp	-0.71	-0.47	0.36	0.76	0.44	-0.42	0.40	0.01	0.65	-0.93	-0.65	0.13	0.76		-0.08	-0.06	-0.30	0.35	temp	
	*pH	-0.11	-0.11	-0.52	-0.05	0.06	-0.93	0.56	-0.53	0.08	-0.18	-0.40	0.81	0.13	0.37		-0.94	-0.84	-0.37	*pH	
	Secchi	-0.47	-0.22	0.01	0.59	0.44	-0.12	0.46	0.06	0.66	-0.68	-0.35	-0.27	0.34	0.71	0.18		0.90	0.16	Secchi	
	*cond	0.09	-0.16	-0.39	-0.11	-0.24	-0.90	0.49	-0.35	-0.16	-0.04	-0.46	0.91	0.01	0.24	0.87	-0.13		0.07	cond	
	d flux	0.21	0.61	0.05	-0.53	-0.33	0.07	-0.62	-0.32	-0.53	0.34	0.53	0.28	0.17	-0.24	-0.18	-0.54	-0.06		d flux	
Elysée, n = 11, sign.: $r \geq 0.52$	*Si/TP		0.77	-0.65	-0.51	-0.94	-0.33	0.50	-0.47	-0.73	0.92	0.68	0.90	-0.80	-0.64	0.43	-0.03	0.42	0.21	*Si/TP	Maxi, n = 8, sign.: $r \geq 0.62$
	Si/SRP	0.60		-0.97	-0.08	-0.85	-0.35	-0.03	-0.85	-0.70	0.81	0.88	0.71	-0.67	-0.39	0.43	-0.10	0.27	-0.21	*Si/SRP	
	*SRP	-0.71	-0.49		-0.02	0.79	0.24	0.16	0.94	0.60	-0.69	-0.91	-0.61	0.52	0.29	-0.41	0.12	-0.14	0.30	*SRP	
	TN	-0.36	-0.51	-0.08		0.46	0.37	-0.87	-0.09	-0.17	-0.28	-0.01	-0.64	0.33	0.87	-0.50	0.65	-0.55	-0.91	TN	
	*TP	-0.96	-0.46	0.73	0.28		0.18	-0.36	0.70	0.62	-0.81	-0.85	-0.85	0.62	0.58	-0.43	0.14	-0.23	-0.16	TP	
	NH_4	-0.74	-0.28	0.36	0.68	0.78		-0.26	-0.05	0.15	-0.47	0.06	-0.46	0.75	0.65	-0.47	0.44	-0.91	-0.26	NH_4	
	NO_2	0.10	0.38	-0.21	0.08	0.10	0.33		0.25	-0.01	0.37	-0.14	0.67	-0.37	-0.78	0.53	-0.34	0.59	0.84	NO_2	
	CL	-0.25	-0.16	0.83	-0.50	0.28	-0.14	-0.31		0.43	-0.47	-0.91	-0.45	0.20	0.11	-0.36	0.13	0.14	0.34	CL	
	SO_4	0.24	-0.23	-0.35	0.36	-0.38	-0.27	-0.50	-0.34		-0.85	-0.61	-0.54	0.73	0.11	-0.07	-0.56	-0.17	0.38	*SO_4	
	SiO_2	-0.36	0.33	0.45	-0.47	0.54	0.29	0.51	0.40	-0.85		0.59	0.87	-0.90	-0.55	0.52	0.09	0.55	-0.01	*SiO_2	
	*DOC	-0.79	-0.56	0.95	-0.05	0.75	0.34	-0.43	0.74	-0.23	0.33		0.53	-0.37	-0.19	0.15	0.03	-0.15	-0.24	DOC	
	DIC	0.68	0.64	-0.49	-0.65	-0.57	-0.65	0.46	-0.11	-0.16	0.24	-0.62		-0.78	-0.84	0.71	-0.28	0.64	0.41	DIC	
	*strati	-0.72	-0.51	0.81	0.26	0.69	0.56	-0.34	0.54	-0.20	0.18	0.84	-0.80		0.65	-0.40	0.01	-0.76	-0.12	strati	
	temp	-0.12	-0.65	0.06	0.66	-0.07	0.15	-0.52	-0.07	0.51	-0.76	0.14	-0.68	0.42		-0.62	0.62	-0.79	-0.77	temp	
	*pH	0.78	0.59	-0.53	-0.14	-0.77	-0.37	0.02	-0.14	0.06	-0.31	-0.58	0.26	-0.40	0.07		-0.54	0.66	0.30	pH	
	Secchi	0.62	0.29	-0.57	0.26	-0.55	-0.07	0.61	-0.43	-0.02	-0.23	-0.77	0.40	-0.48	0.10	0.56		-0.43	-0.63	Secchi	
	*cond	0.90	0.70	-0.76	-0.22	-0.80	-0.47	0.49	-0.41	0.09	-0.15	-0.90	0.77	-0.79	-0.29	0.67	0.79		0.46	cond	
	d flux	0.47	0.87	-0.30	-0.47	-0.28	-0.15	0.32	-0.07	-0.22	0.35	-0.34	0.44	-0.33	-0.65	0.50	0.11	0.51		d flux	

oligotrophic and showed no signs of lake acidification. They had mean TP concentrations of less than 10 μg l^{-1}, Chl *a* concentrations of around 2 μg l^{-1}, mean TN concentrations of at most 200 μg l^{-1}, and Secchi depths between 3 and 4 m (Fig. 2). Lake Maxi had significantly higher TP, Chl *a*, and DOC concentrations, as well as higher turbidity (Secchi depth 3× shallower; Fig. 2).

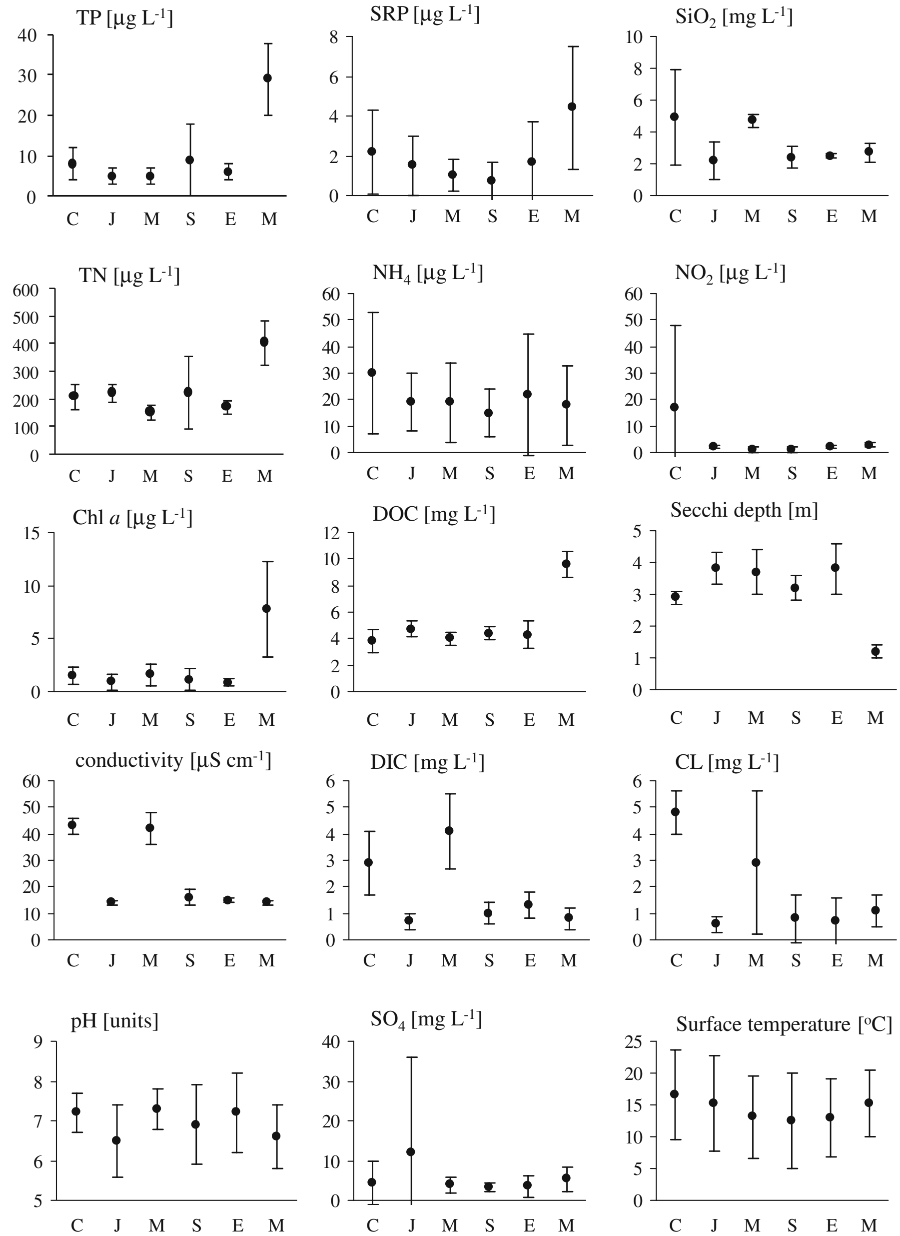

Fig. 2 Mean water chemistry, Secchi depth, and Chl *a* concentrations of the six study lakes in the Laurentian Mountains (*C* Cyprès, *J* Joachim, *M* Moreau, *S* Sommet, *E* Elysée, *M* Maxi). The samples were taken from May through October 2002 at biweekly intervals. The error bars represent the standard deviation. For number of samples, consult Table 2

In all lakes, seasonal SiO_2 fluctuations were significantly correlated with lake circulation or temperature (Table 2). The overall SiO_2 concentrations increased during enhanced lake circulation ($r = 0.39$, $n = 65$, $P < 0.001$; Table 3). In all lakes, except Lake Elysée, SiO_2 and DOC concentrations were positively correlated (Table 2). In four of the six lakes, the Si:TP ratio was highest in autumn; in Lake Moreau, it was highest in spring and in Lake Maxi, it remained low (Fig. 4). Concentrations of NH_4 were highest in June and July, and SO_4 concentrations were highest during late summer.

The onset of thermal stratification was in mid-May in Lake Cyprès (elevation 280 m asl; Fig. 3g). Approximately 2 weeks later in early June, thermal stratification formed in Lake Joachim (370 m asl), Lake Moreau (620 m asl), and Lake du Sommet (830 m asl; Fig. 3d–f). In mid-June, thermal stratification developed in Lake Elysée (920 m asl; Fig. 3c). Lake Maxi (950 m asl) cannot be directly

Table 3 Coefficients of correlation and *P* values between circulation of the water column of six lakes and climate, lake depth, surface, and catchment size of all lakes compared with the removal of the warm polymictic Lake Cyprès and Lake Maxi impacted by forest clear-cut

	Six lakes		Four lakes	
	Circulation	*P*-value	Circulation	*P*-value
SiO_2	0.393	0.001	0.348	0.021
Elevation	0.112	0.375	0.552	0.000
Ice break-up	0.063	0.619	0.597	0.000
Ice in	−0.561	0.0001	0.596	0.000
Ice cover	0.380	0.005	0.602	0.000
Lake depth	0.035	0.787	0.113	0.465
Lake surface	0.196	0.117	0.154	0.319
Catchment size	0.216	0.083	0.101	0.519

compared, as sampling was not possible until mid-July. Lake Cyprès, the lowest elevation lake, was polymictic (Fig. 3g). The two next highest lakes, Lake Joachim and Lake Moreau, had stable thermal stratification of the water column and are considered dimictic (Fig. 3f + e). At higher elevation, Lake du Sommet and Lake Elysée were also polymictic during several periods of uniform water temperature (Fig. 3c + d). Lake Maxi, the highest elevation lake, was stratified during June and July. The autumn water column circulation of the dimictic lakes started in the lower elevation Lake Joachim at the beginning of October, in Lake Moreau in mid-September, and in the highest elevation lake, Lake Maxi, in mid-August (Fig. 3f + e + b).

The duration of ice cover in general increased with lake elevation ($r = 0.83$, $n = 6$, $P < 0.0005$). The ice break-up began in the lowest elevation lake (Lake Cyprès, 280 m asl) at the end of April. Ice-out occurred at Lake Joachim (370 m asl) at the beginning of May, Lake Moreau (619 m asl) and Lake Elysée (920 m asl) during the third week of May, and in Lake du Sommet at the end of May (Table 1; Fig. 3). There is no ice-out data from Lake Maxi. All lakes froze over during the second half of October (Fig. 3).

In general, lakes with longer ice cover had significantly weaker stratification of the water column ($r = 0.380$, $n = 65$, $P = 0.005$; Table 3). However, Lake Cyprès, a shallow lake at the lowest elevation of the altitudinal gradient, behaved in a non-linear fashion (Fig. 3). Lake Cyprès did not stratify for the

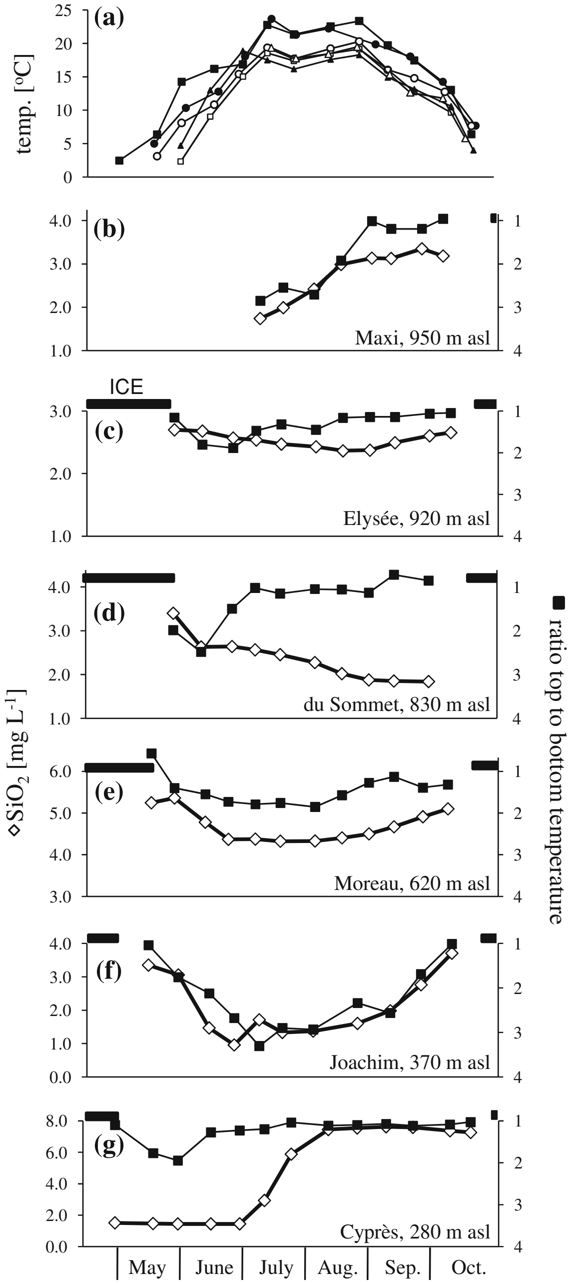

Fig. 3 **a** Surface temperatures of the six boreal lakes during 2002 (Cyprès: *filled square*, Joachim: *filled circles*, Moreau: *empty circles*, du Sommet: *empty squares*, Elysée: *filled triangles*, and Maxi: *empty triangles*). **b**–**g** Ratios of top and bottom temperature (*filled squares*) and SiO_2 concentrations (*empty diamonds*) of the six study lakes during 2002. The *horizontal bars* indicate ice cover. In each lake, and along the climate gradient, the two variables are highly statistically significantly correlated (compare Tables 2 and 3)

Fig. 4 Relative abundance of most abundant diatom taxa with N2 > 10 deposited in sediment traps, diatom flux, water chemistry, and stratification of the water column sampled from May to October in 2002 at biweekly intervals in the six lakes and in Lake Elysée in 2003. The lowest elevation Lake Cyprès is shown at the bottom, starting with samples taken in spring

entire open water period, despite having the shortest duration of ice cover (Fig. 3g). Lake Maxi also had a non-linear response as a result of the forest clear-cut in its catchment. Significantly higher DOC concentrations caused by forest clear-cut darkened the water color and led to surface temperatures similar to those in the lower elevation lakes. In order to determine the driving factors of ice cover on lake stratification and the distribution of diatoms, the non-linear response Lakes Cyprès and Maxi were not included in the CCA (Fig. 5b). As a result, the correlation between the duration of the ice cover and lake circulation increased from 0.380 to 0.602 (Table 3). Stratification of the water column was largely independent of water depth ($r = 0.04$, $n = 65$, $P = 0.79$; Table 3). Elevation and depth were also not significantly correlated ($r = 0.26$, $n = 6$, $P > 0.05$).

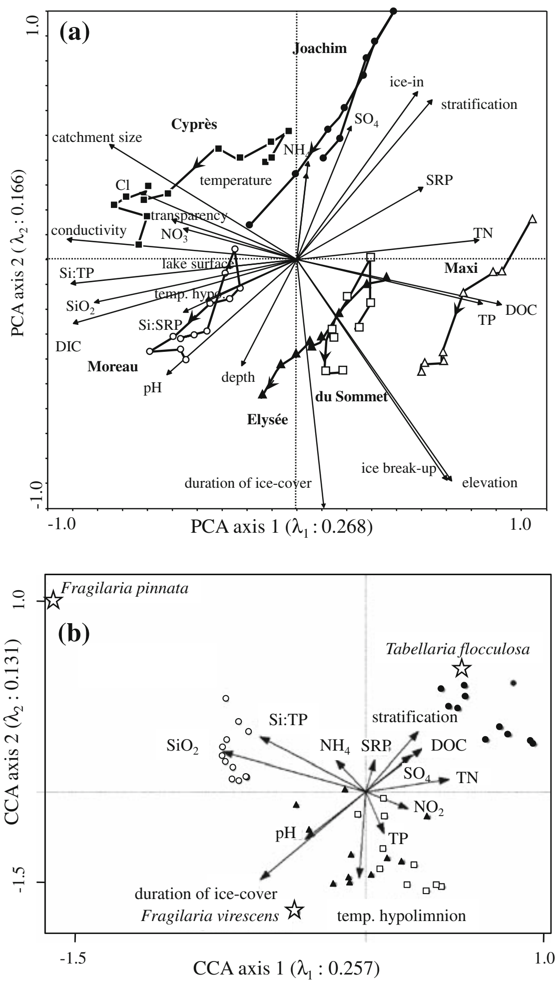

Fig. 5 Indirect and direct ordinations of biweekly samples from six shallow lakes in the Laurentian Mountains from May to October, 2002: **a** Sample–environment biplot of a principal components analysis (PCA), time-series trajectories are shown as *solid lines*, and **b** species–environment biplot of a canonical correspondence analysis (CCA). Symbols for the lakes are the same as in the PCA

Diatoms

Between 61 and 78 diatom taxa were identified in each lake. The relative abundances of the most common taxa (effective number of occurrences (N2) >10) and diatom fluxes are shown in Fig. 4. The seasonal species turnover was >2 SD units in the four higher elevation lakes (Moreau, du Sommet, Elysée, and Maxi) and <2 SD units in the two lower elevation lakes (Cyprès and Joachim). Typically, the highest diatom flux was recorded in spring and/or autumn (Fig. 4). Only the polymictic Lake Cyprès had a third peak in diatom flux during the summer in July (Fig. 4). The diatom taxa were predominantly benthic. Contrary to our expectation, in all study lakes, diatom flux in the traps was uncorrelated to water column circulation (Table 2). Overall diatom flux was highest in lakes with higher SRP ($r = 0.42$, $n = 65$, $P < 0.0005$). As expected, lake circulation was highly correlated to SiO_2, Si:TP, and/or Si:SRP ratios, which significantly explained diatom composition in the individual study lakes (Table 2). A noteworthy observation is that in all but the two lowest elevation lakes, the seasonal diatom distributions were significantly related to SRP.

In spring, during lake circulation, *Fragilaria virescens* var. *exigua* GRUNOW dominated the diatom assemblages (40%) in Lake du Sommet (Fig. 4). *F. virescens* occurred, in spring, also in Lake Cyprès, Lake Joachim, Lake Moreau, and Lake Elysée. In general, it was significantly correlated with lake circulation ($r = 0.24$, $n = 65$, $P < 0.05$, Fig. 5b). From Lake Maxi, no diatom samples during spring are available (Fig. 4).

In Lake Cyprès, the Spring samples consisted mainly of *Fragilaria brevistriata* GRUNOW (35%) and *Fragilaria pinnata* EHRENBERG (20%). Also, *F. pinnata* was present in May, July, October, and November in Lake Cyprès (Fig. 4). In general, *F. pinnata* was significantly more dominant during lake circulation ($r = 0.26$, $n = 72$, $P < 0.025$). In Spring, the lotic diatom *Meridion circulare* (GREVILLE)

C. AGARDH was found in Lake Moreau (10%) and was probably washed in during snowmelt.

In early summer, when the lakes started to stratify, *Tabellaria flocculosa* (ROTH) KÜTZING significantly increased in all lakes with formation of thermal stratification ($r = 0.34$, $n = 72$, $P < 0.005$; Figs. 4 + 5b). In August, *Cyclotella bodanica* aff. *lemanica* MÜLLER EX SCHRÖTER was found during lake stratification in lakes Moreau and Elysée. In August, while the lake was still stratified, *Frustulia rhomboides* EHRENBERG was deposited in the traps of the warmer, low elevation Lake Joachim (Fig. 4). In Lake Joachim, *F. rhomboides* declined with the onset of circulation of the water column (Fig. 4). In general, *F. rhomboides* abundance was significantly higher during lake stratification ($r = 0.43$, $n = 72$, $P < 0.0005$).

In almost all the study lakes, *Achnanthes minutissima* KÜTZING represented approximately 10% of the assemblage during the open water period (Fig. 4). In Lake Cyprès, *Aulacoseira distans* (EHRENB.) SIMONSEN was also prominent, and made up 15% of the diatom assemblage during the entire open water period.

In the mesotrophic Lake Maxi, *Asterionella formosa* HASSALL was the dominant diatom (70%) at the beginning of July and in October at low Si:TP ratios ($r = -0.54$, $n = 7$, $P = 0.029$; Fig. 4). In Lake Maxi, the relative abundance of *A. formosa* increased significantly during periods of elevated sulfate concentrations ($r = 0.86$, $n = 8$, $P < 0.005$; Fig. 4). *A. formosa* occurred also in Lake Cyprès, Lake Joachim, Lake Moreau, Lake Elysée, and Lake Maxi during low Si:TP ratios (Fig. 4). In general, the relative abundance of *A. formosa* was significantly higher at low Si:TP ratios ($r = -0.32$, $n = 72$, $P < 0.005$).

Ordinations of all samples

Principal components analysis axis 1 was correlated most strongly to Si:TP ratio, SiO_2, DOC, TP, TN concentrations, and conductivity, and explained 26.8% of the variance in the physical and chemical variables among all samples (Fig. 5a). PCA axis 2 explained 16.6% of the variance and was negatively correlated to the duration of ice-cover, surface water temperature, SO_4, NH_4, and depth (Fig. 5a). PCA axis 1 was correlated to nutrients and PCA axis 2 to climate.

The selected environmental variables explained 44.3% of the overall diatom distribution, with CCA axis 1 and 2 explaining 13% and 6.6% of the overall diatom variance, respectively. Axis 1 was highly correlated to SiO_2 ($r = 0.84$; Fig. 5b). The CCA results show that *Fragilaria virescens* var. *exigua* and *Fragilaria pinnata* were associated with higher Si:TP ratios and enhanced water column circulation (Fig. 5b), whereas *Tabellaria flocculosa* was related to Si:TP ratio and stronger stratification (Fig. 5b).

Discussion

Climate

Lake circulation was stronger in lakes with longer ice cover (controlled by climate) and led to increase of SiO_2, as seen through significant negative correlations between SiO_2 and thermal stratification, in our boreal study lakes (Table 2). In five out of six study lakes, nutrients and/or SiO_2 concentrations significantly explained the distribution of diatoms. In general, the study lakes had low SiO_2 concentrations. Therefore, any shifts in these nutrient-deprived systems will likely be reflected in diatom assemblage responses (Tilman, 1982). Our observation that *Fragilaria* species were associated with higher Si:TP ratios has been previously reported by Kilham et al. (1986) who demonstrated that *Fragilaria* species have the highest demand of silica among lacustrine diatoms. We conclude that the climatic control on diatoms in our lakes was linked to the redistribution of SiO_2. For a review about indirect climate impact on diatoms, compare Anderson (2000) and references within.

We identified *Fragilaria virescens* as an indicator species for lake circulation and *Tabellaria flocculosa* as indicator species for thermal stratification. In a sediment trap study in Elk Lake conducted in 1979 and 1983, Bradbury (1988) found that during the year with 10 days longer ice cover, *Fragilaria* species dominated as a result of later onset of thermal stratification and higher Si:TP ratios. Our results are also supported by another sediment trap study by Köster & Pienitz (2006) with subannual resolution. *Fragilaria* species were found to be associated with stronger water column circulation. In addition, based on their sediment trap study, Lotter & Bigler (2000) considered the alternation between *Fragilaria pinnata* and *Cyclotella comensis* in a sediment core from Lake Hagelseeli (2,339 m asl; Switzerland) to be in response to changes in the duration of ice cover. These results are in correspondence with Smol (1988) who suggested that, in arctic ponds, the ratio of periphytic to planktonic diatoms is closely related to the duration and extent of ice coverage during summer. In surface sediment samples from subarctic lakes distributed across climate gradients, *Fragilaria* species were usually found at the cold end of the temperature gradient (Pienitz et al., 1995; Lotter et al., 1997; Joynt & Wolfe, 2001). Along an altitudinal gradient, Wunsam and Schmidt (1995) similarly found that *Fragilaria* species are indicative of colder temperature. Sorvari et al. (2002) compared three thermally stratified lakes with two isothermal lakes in Finnish Lapland, determining that isothermal lakes were dominated by *Fragilaria* species.

A comparison of a high-resolution diatom record of Lake du Sommet with the instrumental record of the past 35 years showed that the relative abundance of *Fragilaria virescens* var. *exigua* was significantly higher in samples encompassing years with colder August temperature (Hausmann & Pienitz, 2007). In the subarctic Lake Saanajärvi (Finnish Lapland), Korhola et al. (2002) interpreted a shift in fossil diatom assemblage composition from *Fragilaria* to *Cyclotella* dominance as a response to post-Little Ice Age warming. Solovieva et al. (2008) compared observed June temperatures with a high-resolution diatom record of Lake Vanukty. During recent climate warming, *Fragilaria pinnata* decreased and *Tabellaria flocculosa* increased in this boreal forest lake west of the Ural.

The studies discussed above provide validation for our finding that *Fragilaria pinnata* is an indicator species for lake circulation and *Tabellaria flocculosa* is an indicator species for thermal stratification. The sediment trap deposits from the boreal lakes in this study, situated along an altitudinal gradient, improve the seasonal paleoclimatological interpretation of lacustrine diatom records.

It is likely that the high positive correlation between SiO_2 and lake circulation in four of the six lakes reflects high hypolimnetic SiO_2 concentrations caused by SiO_2 released from sediments (Wetzel, 2001). In order to better understand the links between lake circulation and SiO_2, water samples from different depths should be included in future studies.

Forestry

Water chemistry of Lake Maxi was impacted by forest clear-cut. It had three times higher TP concentrations compared to the other five oligotrophic lakes. According to the lake classification system suggested by Vollenweider (1968), Lake Maxi was mesotrophic. Similarly, Carignan et al. (2000) and Planas et al. (2002) documented significantly increased TP, DOC, and Chl *a* concentrations in their nine study lakes following forest clear-cuts in Haute-Mauricie, Québec. *A. formosa* was the dominant diatom of Lake Maxi with 80% representation. Lund (1950) and Tilman (1982) found that *Asterionella* species can tolerate lower Si:TP ratios. In Lake Maxi, the seasonal distribution of *Asterionella formosa* was significantly increased when the Si:TP ratios were lower and at higher sulfate concentrations. Algae that are dependent on NO_3 and N_2 fixation have a competitive disadvantage at high sulfate concentrations, because NO_3 uptake is inhibited by sulfate (Cole et al., 1986; Marino et al., 1990). However, *A. formosa* has a competitive advantage at high sulfate concentrations, because it can use NH_4 as nitrogen source (Happey, 1970).

There are some studies that show a negligible long-term impact of forest harvesting. Laird et al. (2001) demonstrated that a 90% cumulative forest clear-cut, distributed over a 40-year period, had only negligible long-term impact on diatom assemblages or content of organic matter. However, the impact of Bronze Age forest clear-cut on lake trophy archived in lake sediments has been described by Wick et al. (2003) and Schmidt et al. (1998). At 3,700 cal. BP (Bronze Age), widespread deforestation in the catchment of Lake Sägistalsee, a small lake at 1,935 m asl in the Swiss Alps, is reflected by high erosion activity in the lake's catchment (Wick et al., 2003) which led to reduced chironomid abundance probably due to oxygen depletion caused by eutrophic conditions (Heiri & Lotter, 2003). Köster et al. (2005) discussed a nutrient pulse due to deforestation around AD 1750 in New England as cause for a shift in the diatom assemblages of Walden Pond. The change of a domination of *Aulacoseira* species to *A. formosa* and an associated darkening of the sediment color of the top 5 cm of a gravity core from Lake Maxi followed the forest clear-cut (Hausmann, unpublished data). Paleolimnological studies contribute to better understanding of the long-term impact of catchment disturbances such as forest clear-cuts.

Sediment traps

The use of sediment traps allows for the study of time-integrated diatom growth, but requires caution when interpreting the data (Cameron, 1995). Diatom assemblages in sediment traps are not only affected by chemical and physical conditions of lakes, but also by their settling rate and resuspension. Many diatoms found in our sediment traps, such as taxa belonging to the *Fragilariaceae*, are tychoplanktonics and may indicate resuspension of benthic diatoms (Hustedt, 1923). Resuspension can be problematic when subfossil diatoms bias the modern diatom assemblages collected by the traps. However, in shallow lakes, diatoms can have a benthic life-form, and as a consequence, resuspended modern benthic diatoms deposited in the traps would still be related to water chemistry and allow some insights into species–environment relationships. A distinction between dead and living cells by staining or assessing the ratio of valves with and without chloroplasts was not done in this study, but is highly recommended for future studies (Sawai, 2001).

If the diatoms in our trap samples originated mainly from resuspension, then we would expect a significant correlation between diatom flux and water column circulation, with a seasonal homogeneity of taxa. However, this was not the case in either of our study lakes (Table 2), and most lakes showed a high species turnover from May through October. In addition, the seasonal distribution of diatom taxa in Lake Elysée showed very similar patterns in 2002 and 2003 (Fig. 4).

Another uncertainty is that two of the six lakes were only 3 and 4-m deep; thus, only 60–75% of the water column was located above the trap. The entire water column could not be sampled by the trap. Diatom growth on the trap could have biased the diatom assemblages but black tubes without a funnel were used to minimize this effect. The use of sediment traps for the collection of phytoplankton seems to be more promising in deeper lakes when placed below the euphotic zone. However, Köster & Pienitz (2006) used the same type of traps in a 3-m deep temperate lake from New England, and a comparison of plankton and trap samples showed that the shallow water sediment traps provided realistic reflections of the seasonal succession of planktonic diatoms.

Conclusions

Our study revealed that the onset of thermal stratification was later in lakes with later ice break-up. We demonstrated that lake circulation was significantly stronger in colder lakes with longer ice cover. We showed evidence that lake circulation had a strong impact on SiO_2, nutrients and SO_4 concentrations in boreal lakes, which played a significant role for diatom composition found in the sediment traps. We identified *Tabellaria flocculosa* as indicator of lake stratification and *Fragilaria virescens* and *Fragilaria pinnata* as indicators for lake circulation and elevated Si:TP ratios.

Lake Maxi, the only lake impacted by forest clear-cut, had significantly higher TP, DOC and Chl *a* concentrations.

Our results contribute to a better paleoclimatological interpretation of diatom records from boreal lakes.

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