Limnol. Oceanogr., 48(4), 2003, 1662–1673

Effects of drought-induced acidification on diatom communities in acid-sensitive Ontario lakes

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Abstract

Chemical recovery of many acidified lakes in North America has been delayed or reversed as a result of interactions between climatic variability (alterations between drought and nondrought periods) and previously deposited acids stored in wetlands, but effects of this wetland-mediated reacidification phenomenon on aquatic biota remain unknown. We compare changes in diatom assemblages in 200-yr-long sediment cores from two lakes with similar basin characteristics but different wetland area (4.4% of catchment at Chub Lake, 0% at Blue Chalk Lake) to evaluate the role of wetland-mediated interactions among acid deposition and climatic variability on algal communities in acid-sensitive lakes. Diatom assemblages were significantly more variable in Chub Lake than in Blue Chalk Lake. Variance partitioning analysis of approximately annually resolved sedimentary diatom analyses (1977–1997) identified that unique effects of water chemistry, independent of acid deposition and climatic factors, accounted for the greatest amount of variation (25%) in diatom assemblages at Chub Lake. Acid deposition (24%) and climatic factors (22%) accounted for similar, significant amounts of variation in diatom communities. Complex interactions among all three factors, which are attributable to wetland-mediated drought-induced reacidification, explained an additional 10% of the variation in diatoms at Chub Lake but only 1% at Blue Chalk Lake. Drought-related reacidification effects on water chemistry might thus cause important effects on algal communities in acid-sensitive lakes with modest wetland coverage, but not in lakes without wetlands.

Despite the implementation of sulfur emission control programs in North America and a 60% decrease in bulk sulfate deposition in eastern Ontario since the late 1970s (Clair et al. 1995; Schindler 1998), recent evidence has shown that chemical recovery of acidified lakes has been delayed or reversed as a result of interactions between climatic variability and previously deposited acids stored in wetland(s) (Clair et al. 1995; Schindler et al. 1997; Eimers and Dillon 2002). This delay in recovery has been well documented in several acid-sensitive Precambrian Shield lakes in Ontario, where the anticipated recovery of pH, dissolved organic carbon concentrations ([DOC]), and [sulfate] has not occurred (Dillon et al. 1997; Schindler et al. 1997; Schindler 1998; Dillon and Evans 2001). Schindler (1998), in fact, has reported that only 35% of acidified lakes in eastern Canada are recovering, whereas 11% are still acidifying and 56% show no signs of recovery, despite reduced sulfate emissions in eastern Canada during the last three decades.

Wetlands, specifically their ability to store atmospherically deposited sulfur and then release sulfate following drought periods, appear to play a key role in mediating drought-related reacidification and delayed chemical recovery of acid-sensitive lakes (Dillon and LaZerte 1992; Dillon and Evans 2000; Eimers and Dillon 2002). During relatively cool and moist years, much of the sulfate deposited from the atmosphere is reduced and stored as elemental sulfur (S) in wetlands (Schindler 1998). During drought years, however, this stored sulfur becomes oxidized because of water table drawdown and then is readily exported to lakes and streams as sulfate during subsequent wet periods (LaZerte 1993; Dillon et al. 1997; van Haesebroeck et al. 1997). Drought-related reacidification has been linked with marked chemical changes in acid-sensitive lakes, including declines in pH and increases in [sulfate] (Yan et al. 1996; Dillon et al. 1997; Schindler et al. 1997). This phenomenon has been documented in numerous Precambrian Shield lakes in Ontario (e.g., Swan Lake in 1988 [Yan et al. 1996], Clearwater Lake in 1977, 1988 [Bodo and Dillon 1994], 31 of 38 Sudbury lakes in 1988 [Keller et al. 1992], 56 Algoma-area lakes in 1988 [Kelso et al. 1992], Plastic Lake in 1983, 1987–1989, 1990 [Dillon et al. 1997], and Heney Lake in 1984, 1988, 1994 [Dillon and Evans 2001]). Concern about the ecological effects on acid-sensitive lakes has grown in recent years

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Acknowledgments
This work was supported by NSERC research grants to R.I.H and P.J.D. and by grants from Ontario Power Generation to P.J.D. We thank Adam Jeziorski for assistance with improving the quality of figures. Megan Belore, Suzanne Oudejans, and Derrick Parks assisted with fieldwork. We thank staff at the Ontario Ministry of Environment and Energy's Dorset Research Centre for logistical support and assistance with the field program, particularly Joe Findeis for providing the long-term water chemistry data. The manuscript benefited from comments by Peter Leavitt and two anonymous reviewers.

Table 1. Geographical location, morphometry, and selected chemical properties of Blue Chalk Lake and Chub Lake. Water chemistry variables presented as ice-free means (1977–1997) ± standard deviation (sample size indicated in brackets).

	Blue Chalk Lake	Chub Lake
Latitude (N)	45°11′	45°13′
Longitude (W)	78°56′	78°59′
Lake area (ha)	49.4	32.2
Catchment area (km^2)	128	286
Maximum depth (m)	23	27
Mean depth (m)	8.5	8.9
Lake volume (m^3 × 10^5)	42.1	28.5
Water residence (yr)	5.7	2.2
Wetland area (% of catchment area)	0.0	4.4
Bedrock geology	Gneiss (100%)	Gneiss (100%)
pH	6.6±0.17 (293)	5.6±0.15 (304)
Alkalinity (μeq L^{-1})	119.5±10.88 (276)	57.5±15.07 (271)
Conductivity (μmho cm^{-2})	29.0±1.38 (295)	28.2±2.73 (308)
TP (μg L^{-1})	6.3±1.74 (318)	10.4±2.51 (336)
TKN (μg L^{-1})	184.9±56.32 (293)	270.4±51.22 (304)
DOC (mg L^{-1})	1.8±0.24 (230)	4.8±0.50 (224)
Secchi depth (m)	6.6±1.25 (283)	3.1±0.79 (288)

because of an increased frequency of droughts during the last three decades. Increased drought frequency has been partly attributed to several recent El Niño Southern Oscillation (ENSO) events; specifically, strong ENSO events of 1976–1977, 1982–1983, 1986–1987, 1991–1992, 1993–1994, 1997–1998 (Dillon and Evans 2001).

All previous studies of drought-related reacidification have focused exclusively on patterns of chemical recovery in lakes. Biotic communities are likely to be affected by the chemical changes, but it remains uncertain whether complex interactions between acid deposition and climatic variability exert strong control of biological communities in acid-sensitive lakes. To address this, we analyzed diatom assemblages in sediment cores from a pair of acid-sensitive Precambrian Shield lakes in central Ontario to evaluate the effects of terrestrial wetlands, climatic variability, and acid deposition on one community of aquatic algae. Specifically, the study uses a paired comparison of changes in diatom community composition in highly resolved 200-yr-long sediment cores (i.e., approximately annual resolution during the past 30 yr and subdecadal resolution in older sediments) from two Precambrian Shield lakes in central Ontario that lie only 5 km apart and share very similar bedrock, terrestrial vegetation, soil types, and basin morphometry but which differ in the area of contributing wetlands (Table 1). Catchments in this region have between 0 and 10% wetland coverage, with only a very few with >10% (average = 3.6%, range 0–13.6%; Dillon et al. 1986). For this study, we compare a lake with no wetland effect (Blue Chalk Lake, 0% wetlands) and one with an intermediate role for wetlands (Chub Lake, 4.4% wetlands). The difference in stream and lake chemistry between systems with 0 and 4% wetlands is substantial (Table 1). For example, at Blue Chalk Lake, the inflow draining 0% wetlands has a mean (10 yr) [DOC] of 2.2 mg L^{-1}, compared with >8.1 mg L^{-1} in inflows to Chub Lake, which drain 4% wetlands. Moreover, available evidence indicates that wetlands are a sink for sulfate under normal conditions and that the presence of wetlands in catchments coupled with drought results in the subsequent efflux of previously stored sulfur in acidic form (Dillon et al. 1997; Dillon and Evans 2001; Eimers and Dillon 2002). This output of sulfate represents a substantial extra load of acid to downstream lakes and results in their reacidification (Dillon and Evans 2001). Historical water chemistry records of the past 25 yr show that both lakes were affected by industrial acid deposition (Dillon and LaZerte 1992; Dillon et al. 1997). Blue Chalk Lake has shown signs of chemical recovery from acidification following reductions in sulfate emissions, whereas Chub Lake has exhibited more variable water chemistry, including episodes of reacidification following droughts of the past 20 yr (Dillon and LaZerte 1992; Dillon et al. 1997).

Comparisons of past changes in diatom assemblages were used to assess whether the influence of wetlands around Chub Lake results in more variable conditions in Chub Lake than in Blue Chalk Lake from complex, wetland-mediated interactions among acid deposition and climatic variability. The greater catchment area at Chub Lake results in a more rapid flushing rate than at Blue Chalk Lake (Table 1); consequently, we explore whether water residence time could account for differences in variability among the lakes. Additionally, canonical ordination-based variance partitioning analysis (VPA; sensu Borcard et al. 1992) was used to quantify relationships between approximately annually resolved sedimentary analyses of diatoms and 20-yr records (1977–1997) of acid deposition, climatic factors, and water chemistry changes and their interactions and to test the hypothesis that wetland-mediated reacidification is an important phenomenon regulating diatom communities in acid-sensitive lakes. If this hypothesis is correct, covariation among acid deposition, climatic variability, and water chemistry should account for substantially greater amounts of variation in diatom assemblages at Chub Lake than at Blue Chalk Lake. VPA was performed on entire diatom assemblages as well as separately on planktonic taxa and benthic taxa to assess whether relationships between community composition and these multiple factors differ among major habitat types.

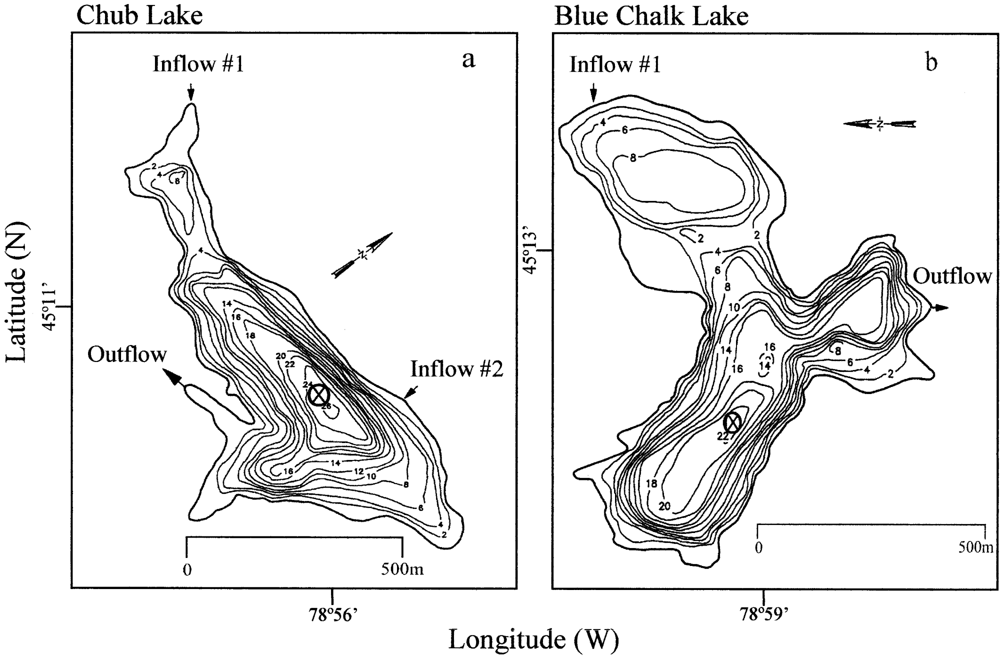

Fig. 1. Bathymetric maps of (a) Chub Lake and (b) Blue Chalk Lake. An "X" denotes an approximate coring location (modified from Nicolls et al. 1983).

Methods

Study sites—The two study lakes, Blue Chalk Lake and Chub Lake, are located in the District of Muskoka in central Ontario, Canada. This area is remote from local point-sources of pollution but receives elevated atmospheric deposition of acids from long-range transport. Both lakes have low acid-neutralizing capacity (ANC) as a result of their geologic setting (Dillon et al. 1997). The local topography consists of a thin layer of soil with scattered deposits of glacial tills, numerous rocky outcrops of granitic Precambrian bedrock, and poorly drained depressions occupied by wetlands. Catchment vegetation is characterized by a mixed deciduous–coniferous forest.

The study lakes were chosen from a set of eight lakes that have been studied for >20 yr. Long-term data sets describing atmospheric deposition, lake and stream water chemistry, and local climate are available. Chub Lake and Blue Chalk Lake were selected from these eight lakes because they appeared to provide an appropriate paired comparison for assessing the effects of wetland-mediated reacidification (Fig. 1). Specifically, the two lakes lie <5 km apart and share similar basin morphometry, bedrock geology, and forest composition but differ in area of contributing wetlands (Table 1). The wetlands located in the Chub Lake catchment are Sphagnum–conifer swamps, with small beaver ponds also evident. These wetlands supply substantial DOC (Dillon and Molot 1997), resulting in the lake being moderately dystrophic, with elevated DOC and color, and lower pH than Blue Chalk Lake. Water residence time is considerably shorter at Chub Lake than at Blue Chalk Lake because of its larger catchment and smaller volume (Table 1). Seasonal water level fluctuations were small (≤0.3 m) in both lakes over the 25-yr period, and there were no changes in storage (i.e., water level) between years (Dillon unpubl. data). As a consequence, terrestrial wetlands (peatlands), and not littoral wetlands or sediments, have been sources of sulfate to the lake.

Field and laboratory methods—A 47-cm sediment core from Chub Lake and a 41-cm core from Blue Chalk Lake were collected on 21 February and 27 June 2000, respectively, from the central deep-water region of each lake using a Glew (1989) gravity corer fitted with a Lucite tube 55 cm long and 7.5 cm internal diameter (Fig. 1). Sediment cores were sectioned immediately after collection using a vertical extruder (Glew 1988), either directly on lake ice (Chub Lake) or at the lakeshore (Blue Chalk Lake). All sediment cores were sectioned into 0.25-cm intervals for the top 10 cm, representing approximately 1 yr of sediment deposition in each lake based on ^{210}Pb analyses (*see below*). Between 10 and 20 cm, the cores were sectioned into 0.5-cm intervals. Sediments below 20 cm were sectioned into 1-cm intervals. Sediment chronology and mass accumulation rates were determined from analysis of ^{210}Pb activity by alpha spectrometry and by the constant rate of supply model (Appleby and Oldfield 1983). Analyses were performed on subsamples from 16 sediment intervals distributed over the entire length of each core by MyCore Scientific Inc. (Dunrobin, Ontario).

Diatom slides were prepared from each core section using standard techniques described by Renberg (1990) and Hall and Smol (1996). For each sample, a minimum of 400 diatoms were enumerated and identified to the lowest taxonomic level possible (usually species or subspecies) along transects using a Zeiss Photomicroscope fitted with phase contrast optics (×100 objective lens, numerical aperture = 1.30). Diatom data were expressed as percent abundance of the total diatom sum in each sample. Diatom taxonomy followed mainly Patrick and Reimer (1966, 1975), Camburn et al. (1984–1986), Krammer and Lange-Bertalot (1986–1991), and Camburn and Charles (2000).

Data analysis—Diatom taxa were included in numerical analyses if they reached $\geq$1% abundance in at least one sediment sample. Principal components analysis (PCA) of fossil diatom assemblages was used to compare patterns of diatom community change in Blue Chalk Lake and Chub Lake over the entire time period included in the sediment cores ($\sim$200 yr) and also during the 20-yr period (1977–1997) of available long-term records. Intersample relationships were relatively simple (i.e., there was one major gradient; *see Results*), indicating that PCA should perform adequately and provide results comparable to other ordination methods (Clarke and Warwick 1994). Nevertheless, multidimensional scaling was performed, using the Bray–Curtis similarity measure, and produced results similar to PCA. Consequently, only PCA results are shown.

Interlake differences in sedimentation rates can confound statistical analysis of differences in temporal variability of diatom assemblages in Chub Lake and Blue Chalk Lake. Consequently, we performed independent samples *t*-tests on PCA sample scores based on a reduced set of sediment samples representing approximately equal (i.e., annual) time intervals during 1977–1997 to test the hypothesis that intersample distances along PCA axes 1 and 2 differed between the two study lakes when controlling for interlake differences in sedimentation rates ($\alpha = 0.05$).

VPA (sensu Borcard et al. 1992) was used to evaluate relationships between three categories of explanatory variables (acid deposition, climatic variability, and water chemistry) and changes in fossil diatom assemblages in the study lakes. VPA uses direct gradient analysis (e.g., canonical correspondence analysis, redundancy analysis) to quantify the proportion of total variation in diatom community composition over time into that which can be explained by unique effects of each explanatory category alone, that which can be explained by covariation among the categories, and that which cannot be explained (i.e., variation that is due to other (unmeasured) factors or noise; Hall et al. 1999).

Our analyses included two-category and three-category VPA. Two-category VPA was used to quantify the unique and interactive effects of acid deposition and climatic variability on diatom community composition during the period of available long-term measurements (1977–1997). Three-category VPA was performed to quantify the additional unique and interactive effects of water chemistry fluctuations on diatom communities in order to assess whether the effects of climatic variability and acid deposition on diatom assemblages are mediated via alterations in water chemistry. Details of the computations required for two- and three-category VPA are presented by Leavitt et al. (1999) and Hall et al. (1999), respectively.

Redundancy analysis (RDA) was used to partition the variance in fossil diatom assemblages because exploratory detrended correspondence analysis suggested that variation in the assemblages over time was best modeled by a linear rather than a unimodal model (ter Braak 1986). The significance of the canonical axes was determined using Monte Carlo permutation tests with 99 random permutations (ter Braak and Šmilauer 1998).

Explanatory categories used in variance partitioning analyses require roughly similar numbers of historical environmental variables to avoid bias in the analyses (Borcard et al. 1992). We used standardized a priori selection criteria developed by Hall et al. (1999) to ensure similar numbers of statistically significant variables per category. Specifically, we selected only variables that accounted for significant amounts of variation in fossil diatom assemblages ($\alpha = 0.05$) based on a series of RDAs constrained to a single explanatory variable at a time, and assigned them to one of the three explanatory categories (acid deposition, climatic variability, water chemistry). Redundancy analysis was then performed on each category, eliminating the variable with the highest variance inflation factor (VIF) until all VIFs were $<$20. This process eliminated collinearity among variables in each category and resulted in roughly similar numbers of variables in each explanatory category.

Variance partitioning analysis of Blue Chalk Lake and Chub Lake diatom data were analyzed using explanatory variables set at 0-, 1-, and 2-yr time lags relative to the response variables in order to determine whether responses of fossil diatom assemblages to external conditions (acid deposition, climatic conditions) were delayed by 1 or 2 yr. Because the study lakes have water residence $>$1 yr, water chemistry and biological community composition might be delayed relative to external conditions of the current year. Additionally, use of time lags might reduce inaccuracies that could be introduced if approximately annually resolved sediment intervals did not correspond exactly with the yearly intervals (i.e., water year) used to estimate mean values of explanatory variables. For all VPAs, environmental variables were time-lagged by 1 and 2 yr for analyses of Chub Lake and Blue Chalk Lake, respectively, because these time lags resulted in the greatest total variation explained by each category.

Two and three-category VPAs were performed on fossil diatom data between 1977 and 1997, the period for which historical data for acid deposition (A), climatic variability (C), and water chemistry (W) were complete. Variables within the acid deposition category included mean annual and monthly deposition of sulfate and nitrate. Climatic factors included mean annual and monthly precipitation and temperature, as well as the mean annual and monthly Southern Oscillation Index (SOI; source: National Oceanic and Atmospheric Administration [NOAA] worldwide web database, www.noaa.gov). Historical climate and acid deposition data were gathered from three observation stations near Huntsville, Ontario (source: Environment Canada, Ontario Climate Centre, Downsview). Water chemistry data used in three-category VPA are mean ice-free season values based on data collected at weekly, biweekly, or monthly intervals over at least 20 yr (Ontario Ministry of Environment). Water chemistry variables included pH, alkalinity, conductivity, Secchi depth, and concentrations of calcium, DOC, sulfate, total phosphorus (TP), and total Kjeldahl nitrogen (TKN).

Comparisons of VPA results between Chub Lake and Blue Chalk Lake are most meaningful if they take into account that sedimentary diatom assemblages in Chub Lake exhibited much greater variability than in Blue Chalk Lake (*see Results below*). Consequently, we expressed the amount of variance explained by the various categories (A, C, A + C, unexplained, etc.) at Blue Chalk Lake as ''relative'' values that account for the relative differences in total variation in diatom assemblages between the two lakes. ''Relative'' VPA values were calculated by multiplying the amount of variance explained in each VPA category at Blue Chalk Lake by the fraction of the total sum of squares (TSS) calculated for each lake based on PCA of the sedimentary diatom assemblages (e.g., relative VPA value = % explained variation at Blue Chalk Lake × [TSS at Blue Chalk Lake/TSS at Chub Lake]).

All ordinations were performed using CANOCO for Windows v.4.02 (ter Braak and Šmilauer 1998). For all PCAs, diatom percent abundance was square root–transformed to equalize variances among taxa. For VPA, data were log transformed ($x + 1$), and rare taxa were downweighted (ter Braak and Šmilauer 1998).

Results

Water chemistry changes (1977–1997)—There were marked differences in temporal water chemistry trends between Chub Lake and Blue Chalk Lake (Fig. 2). Specifically, mean ice-free concentrations of DOC, sulfate, and pH were substantially more variable in Chub Lake than in Blue Chalk Lake. Distinct changes in sulfate concentration and pH occurred after droughts (e.g., 1977–1978, 1981–1982, 1986–1987, 1991–1992, 1993–1994, 1997–1998), corresponding with declines in the SOI (Fig. 2). In Chub Lake, [DOC] fluctuated between ~4.2 and 5.6 mg L^{-1} during 1977–1997 but was lower and less variable (1.9–2.1 mg L^{-1}) in Blue Chalk Lake (Fig. 2c). Mean ice-free pH in Chub Lake was, on average, one pH unit more acidic, and considerably more variable, than in Blue Chalk Lake (Fig. 2b). In fact, Chub Lake experienced a number of marked declines in pH, most of which occurred within 1–2 yr following drought, although not all droughts were followed by pH declines (e.g., 1992). Blue Chalk Lake shows a long-term increase in pH (~0.3 pH units) and a decline in [sulfate] in response to reduced acid deposition (Fig. 2). In contrast, Chub Lake does not show a recovery of pH. Lake water [sulfate] decreased between 1977 and 1997 in both lakes in response to declines in sulfate deposition (Fig. 2a). However, Chub Lake experienced marked increases in [sulfate] following drought periods in 1981–1982 and 1986–1992; in Blue Chalk Lake the changes were much less substantial (Fig. 2a).

Radiometric dating of sediment cores—^{210}Pb activity in sediment cores from Chub Lake and Blue Chalk Lake declined approximately logarithmically with depth (Fig. 3a). The lack of abrupt changes in ^{210}Pb concentrations with depth indicates that sediment accumulation in these lakes was relatively constant and that CRS models were appropriate for estimating the age of sediment at both lakes (Appleby and Oldfield 1983). The ^{210}Pb chronologies from Chub Lake and Blue Chalk Lake showed that the sediment cores captured ~200-yr-long records and included the pre-Industrial era (Fig. 3b). Estimated CRS dates indicated that 0.25-cm sediment intervals deposited during the past 20 yr captured approximately annual time steps.

Changes in diatom community composition—A total of 246 different diatom taxa were identified in the sediment core from Chub Lake. Of these, 69 taxa met our criteria of ≥1% abundance in at least one sample for inclusion in numerical analyses. A total of 244 diatom taxa were identified in the core from Blue Chalk Lake and 43 of these taxa were included in numerical analyses. Diatom assemblages in both lakes were dominated by planktonic taxa. Benthic diatoms, however, contributed a greater proportion of diatom assemblages at Chub Lake (~10–30%) compared with Blue Chalk Lake (~6–12%) (Fig. 4). Diatom assemblages in Chub Lake were dominated by the planktonic diatom, *Tabellaria flocculosa* str. IIIp, which often reached abundances between 20 and 30%, and >50% in some recent samples. Several *Eunotia* species also occurred in every count, with *Eunotia naeglii* and *Eunotia zasuminensis* being the most abundant. Blue Chalk Lake was dominated by one diatom species, *Cyclotella stelligera*, which made up at least 50% of diatom assemblages throughout the entire >200-yr record. Several other planktonic species were abundant in Blue Chalk Lake, including *Asterionella formosa, Asterionella ralfsii* v. *americana,* and *Cyclotella bodanica* v. *lemanica.*

Within a few decades after the turn of the 20th century, diatom assemblages at Blue Chalk Lake and Chub Lake displayed patterns of change consistent with responses to lake acidification (Fig. 4). For example, the relative abundance of circumneutral, acid-sensitive taxa including *Cyclotella kuetzingiana* v. *radiosa* and *C. bodanica* v. *lemanica* decreased in Blue Chalk Lake. Declines of these circumneutral taxa coincided with increased relative abundance of acidophilous *A. ralfsii* v. *americana,* which was virtually absent from this lake previously and which reached its highest abundance during ~1950–1980. Similarly, relative abundance of several acid-sensitive taxa, such as *A. formosa, Aulacoseira distans* v. *distans, C. bodanica* v. *lemanica,* and *Aulacoseira subarctica*, decreased in Chub Lake after ~1940, with concomitant increases of more acid-tolerant taxa (*E. naeglii, Fragilaria* sp. 5 PIRLA).

Comparison of trends in diatom assemblages at the two lakes reveals that diatom assemblages in Chub Lake have been more variable than in Blue Chalk Lake over the past ~200 yr (Fig. 4). Since ~1970, sediments from Chub Lake recorded short-lived fluctuations (1–5 yr) between assemblages consisting of taxa preferring more circumneutral, clear-water conditions (e.g., *A. formosa, Rhizosolenia eriensis, A. distans* v. *distans,* and *C. stelligera*) and assemblages consisting of taxa indicating more acidic conditions and elevated DOC (e.g., *A. ralfsii* v. *americana, T. flocculosa* str. IIIp, *Fragilaria* sp. 5 PIRLA, and *E. naeglii*) (Fig. 4a). Increases in *Fragilaria* sp. 5 PIRLA, which coincided with reduced abundance of *R. eriensis,* tended to occur during years following droughts. Similar short-lived fluctuations were not observed in Blue Chalk Lake (Fig. 4b). Instead, diatom analyses showed a pattern of declining abundance of *A. ralfsii* v. *americana* and increasing *A. formosa,* consistent with recovery from acidification since the late 1970s.

PCA ordinations and independent samples *t*-tests further demonstrated that diatom community composition was significantly more variable in Chub Lake than in Blue Chalk Lake. Using either diatom data from the entire 200-yr sediment record (Fig. 5a) or from samples deposited in 1977–1997 (Fig. 5b), the first PCA axis ($\lambda_{\text{full record}} = 0.62$, $\lambda_{1977\text{–}1997} = 0.68$) separated distinctly different assemblages at each of the two lakes. The second PCA axis ($\lambda_{\text{full record}} = 0.06$, $\lambda_{1977\text{–}1997} = 0.05$) identified the main patterns of community composition change over time within each lake. All samples from Blue Chalk Lake lie close together, indicating that composition of diatom assemblages was relatively constant over the past 200 yr. In contrast, diatom assemblages from Chub Lake were highly variable, as illustrated by the clear separation of sample scores along the second PCA axis. Moreover, PCA axis 2 spanned floristic gradients of 1.5 and 1 units in analyses of the entire >200-yr sediment record and the period 1977–1997, respectively, at Chub Lake, whereas floristic gradients at Blue Chalk Lake spanned only 0.3 and 0.2 units. This pattern occurred despite the slightly higher temporal resolution of sedimentary analyses at Blue Chalk Lake (because of faster sediment accumulation; Fig. 3), which, if all other factors were equal, would have resulted in greater observed variability at Blue Chalk Lake. Additionally, independent samples *t*-tests performed on a reduced dataset of approximately equal (i.e., annual) time intervals during 1977–1997 indicated that intersample distances along PCA axis 1 ($t = 4.41$, $n = 38$, $p = 2.76 \times 10^{-4}$) and axis 2 ($t = 4.54$, $n = 38$, $p = 2.11 \times 10^{-4}$) were significantly greater at Chub Lake than at Blue Chalk Lake.

Variability of diatom assemblages in Chub Lake increased markedly after ~1930, when PCA sample scores displayed considerable movement in ordination space (along PCA axes 1 and 2; Fig. 5a). Greatest variability in diatom community composition, however, occurred since the late 1970s in Chub Lake, as assessed by the wide dispersion of sample scores along PCA axis 2 (Fig. 5). Timing of the observed increases in community variability (post-1930s and post-1970) did not coincide with increased temporal resolution of the sedimentary analyses (which corresponded to post-1965 and post-1988); consequently, changes in temporal resolution of the sedimentary analyses cannot account for the timing of the changes in community variability. Instead, this recent intersample variability coincided with the onset of more frequent ENSO events and droughts of the last three decades (Fig. 2d). Interestingly, sample scores from Chub Lake showed an overall general trend of increasing axis 2 scores since 1977, but reversals of this overall pattern (i.e., periodic downward movements of sample scores on PCA axis 2) tended to occur

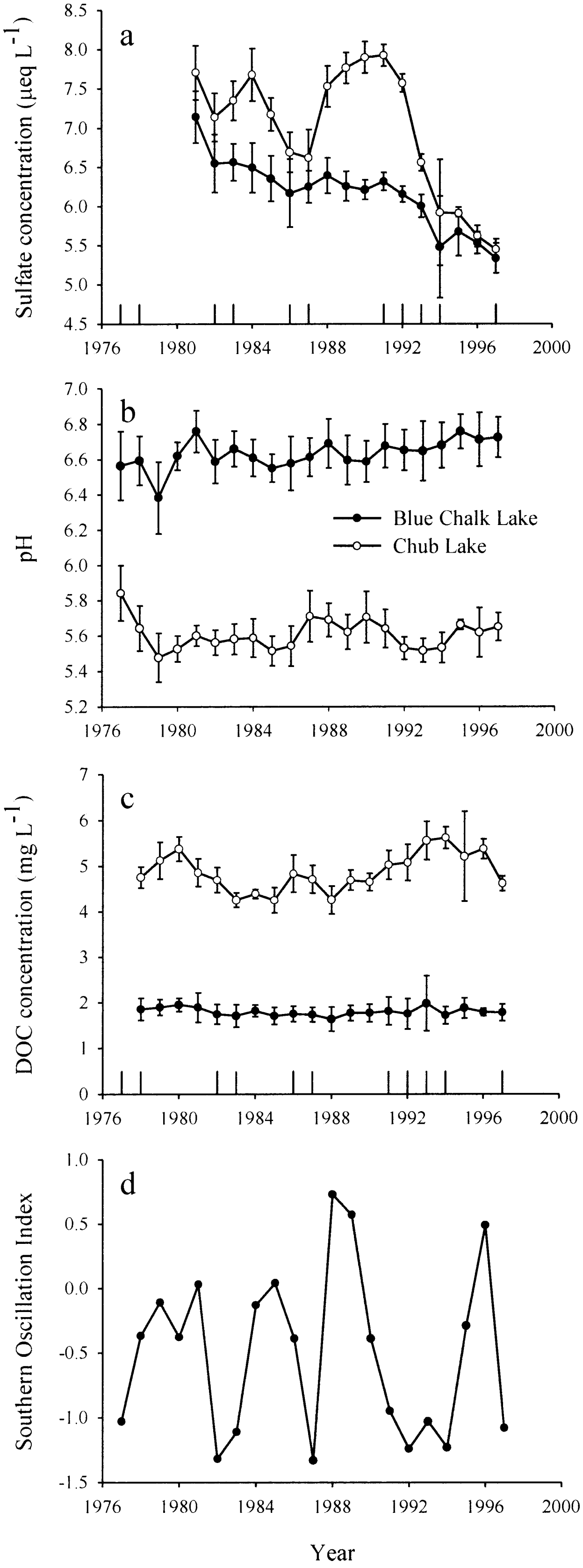

Fig. 2. Mean ice-free season (a) sulfate concentration, (b) pH, and (c) dissolved organic carbon (DOC) concentration measured in

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Chub Lake and Blue Chalk Lake between 1977 and 1997 (data from long-term records maintained at the Dorset Research Centre, Ontario Ministry of Environment). Error bars indicate ±1 standard deviation. (d) The Southern Oscillation Index (SOI) between 1977 and 1997 measured as the sea level pressure anomaly between Tahiti, French Polynesia, and Darwin, Australia (data from NOAA worldwide web database www.noaa.gov, 2000). El Niño years are indicated by vertical lines along the *x*-axis.

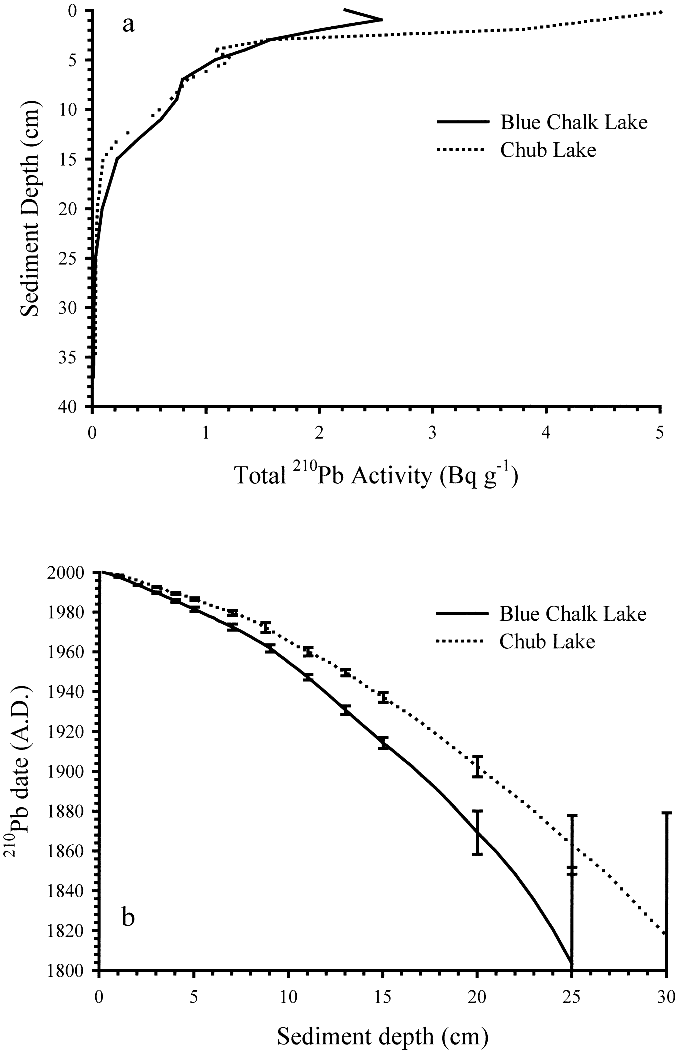

Fig. 3. ^{210}Pb radiometric dating analysis of sediment cores from Chub Lake and Blue Chalk Lake. (a) Sediment depth versus total ^{210}Pb activity (Bq g^{-1} dry weight). (b) Estimated age of sediment (yr A.D.) versus sediment depth. Error bars represent ±1 standard deviation in estimated sediment age.

following drought years, suggesting that the long-term trend of diatom community development was interrupted during ensuing wet years.

Variance partitioning analysis—During the period of available long-term records (1977–1997), changes in acid deposition rates, climatic variability and water chemistry all explained significant ($p < 0.05$) proportions of variation in the composition of fossil diatom assemblages in Chub Lake and Blue Chalk Lake (Fig. 6). Significant amounts of variation in diatom community composition could be explained by a relatively small number of variables (Table 2). The subsets of environmental variables selected for two- and three-category VPAs of diatom assemblages were similar for both lakes. Mean annual sulfate deposition, nitrate deposition, and precipitation during January and August and mean ice-free alkalinity, conductivity, and concentrations of calcium and total phosphorus (TP) were identified as variables explaining significant amounts of variation in diatom assemblages at Chub Lake and Blue Chalk Lake.

Two-category VPA indicated that acid deposition, climatic variability, and interactions among these two factors accounted for relatively greater variability in diatom assemblages at Chub Lake than at Blue Chalk Lake (Fig. 6a). At Chub Lake, the unique effects of acid deposition and climate explained equivalent amounts of variation in diatom assemblages (24.3 and 22.2%, respectively). In contrast, at Blue Chalk Lake, the unique effects of acid deposition accounted for almost twice as much of the variation in diatom assemblages compared with the unique effects of climatic factors (8.3 and 5.0%, respectively). Interestingly, interactive effects of climate and acid deposition did not account for the greatest proportion of explained variability at Chub Lake (8.6%), as would have been expected if wetland-mediated reacidification was a dominant control factor. Almost 45% of the total variation in diatoms at Chub Lake, however, was unexplained by the supplied environmental variables. Consequently, conclusions based on two-category VPA might be misleading because other important variables were not included in the analyses (Borcard et al. 1992).

By adding water chemistry variables to the analyses, three-category VPAs were used to quantify the unique effects of water chemistry on diatom communities and to assess whether the effects of acid deposition and climate on diatom communities were mediated via regulation of water chemistry (Fig. 6b; Table 2). By adding water chemistry data, the explained variation increased to >80% at Chub Lake, indicating that few important variables were missed from this analysis. Water chemistry changes alone, independent of influences from climatic variability and acid deposition (component W in Fig. 6b), explained about a quarter (25.3%) of the total diatom variation at Chub Lake. VPA identified that acid deposition and water chemistry–mediated interactions independent of supplied climatic variables (i.e., the terms A + [A + W] in Fig. 6b) also accounted for a large and statistically significant proportion of variation in diatom assemblages at Chub Lake (24.3%). Similarly, climatic variability and its interaction with water chemistry (C + [C + W]) accounted for a large and statistically significant proportion of variation in diatom assemblages (22.2%). Interestingly, none of the variability in diatom assemblages in Chub Lake was explained by interactive effects of acid deposition and climatic variability that were independent of water chemistry (i.e., A + C = 0%). Complex water chemistry–mediated interactions among climatic factors and acid deposition (A + C + W) explained almost 10% of the variation in diatom assemblages at Chub Lake. This is the VPA component that can be attributed to the wetland-mediated reacidification phenomenon. In the absence of contributing wetlands, water chemistry–mediated effects (A + C + W) explained relatively little variability in diatom assemblages at Blue Chalk Lake (1.1%).

Discussion

Analyses of water chemistry and sedimentary diatom assemblages, including PCA of the diatom data, all indicate

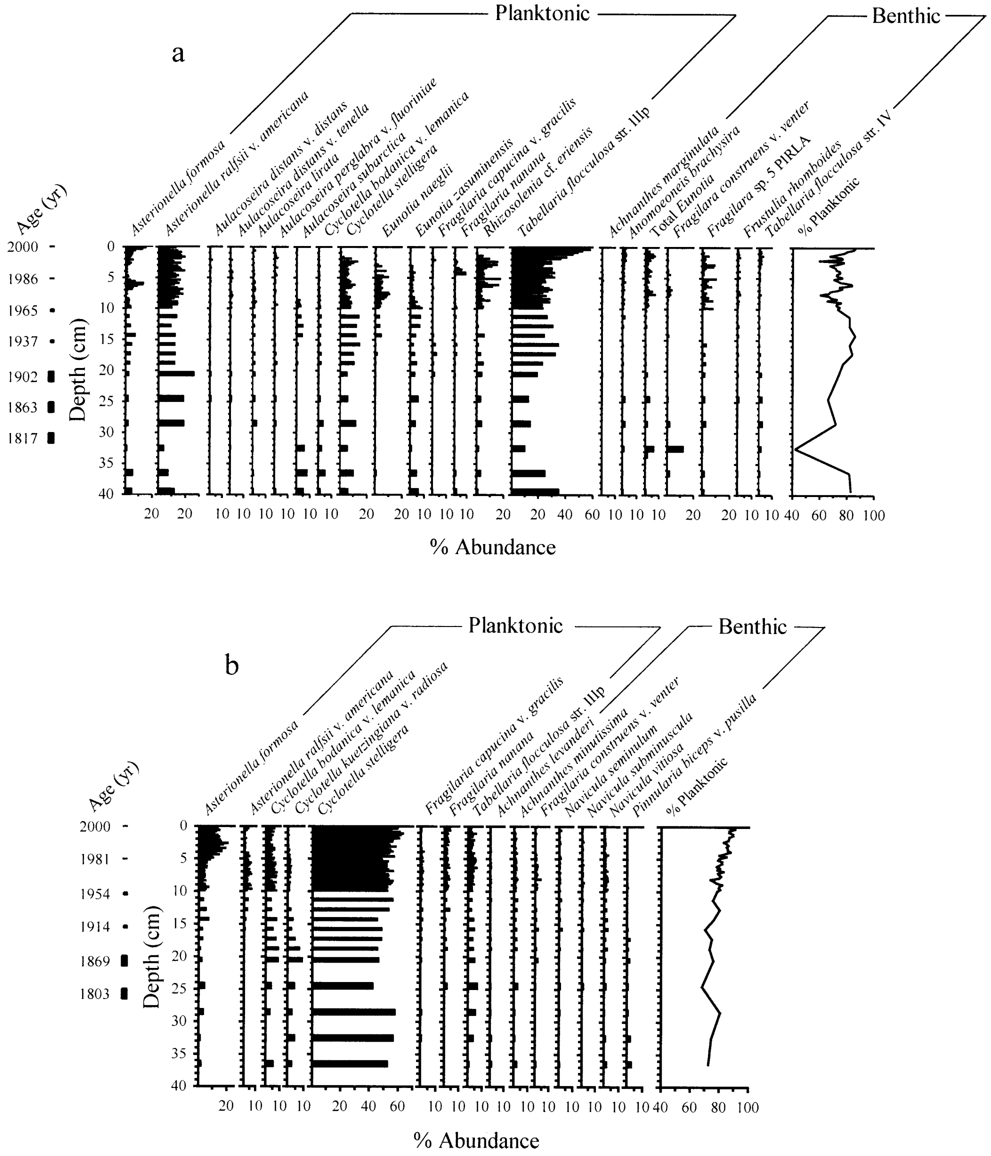

Fig. 4. Changes in percent abundance of the most common planktonic and benthic diatom taxa identified in sediment cores from (a) Chub Lake and (b) Blue Chalk Lake. Relative abundance of planktonic taxa is presented on the right side of each graph. The *y*-axis presents sediment depth (cm) and corresponding ages as estimated by ^{210}Pb analysis.

that chemical conditions and diatom communities are inherently more variable at Chub Lake than at Blue Chalk Lake. Neither basin morphometry nor catchment characteristics of bedrock geology, surficial geology, terrestrial vegetation, or soils can account for the greater variability at Chub Lake because these factors do not differ substantially between the lakes (Nicolls et al. 1983; Dillon et al. 1986). Annual water level fluctuations are small ($<$30 cm yr^{-1} over the past 20 yr), do not differ substantially among the lakes (Dillon unpubl. data), and so cannot account for the observed differences in variability. Additionally, because sediments accumulate more slowly at Chub Lake than at Blue Chalk Lake, differences in temporal resolution of our diatom analyses cannot account for the greater floristic variability observed at Chub Lake.

The study lakes differ substantially in only two main features that could account for greater variability at Chub Lake. First, water residence time at Chub Lake is less than half of that at Blue Chalk Lake (Table 1). Second, fluctuating exports of sulfate and other chemical compounds from wetlands around Chub Lake, but not Blue Chalk Lake, might cause greater variability at Chub Lake. In theory, the shorter water residence time at Chub Lake could provide a mechanism for more rapid responses of water chemistry and biota than at Blue Chalk Lake (e.g., Snucins et al. 2001). However, changes in lake water concentrations of sulfate and base cations at Chub Lake occur coincident with changes at Blue Chalk Lake and other lakes in the Muskoka District (Dillon unpubl. data). Zooplankton populations also tend to be temporally coherent among the lakes despite differences in res-

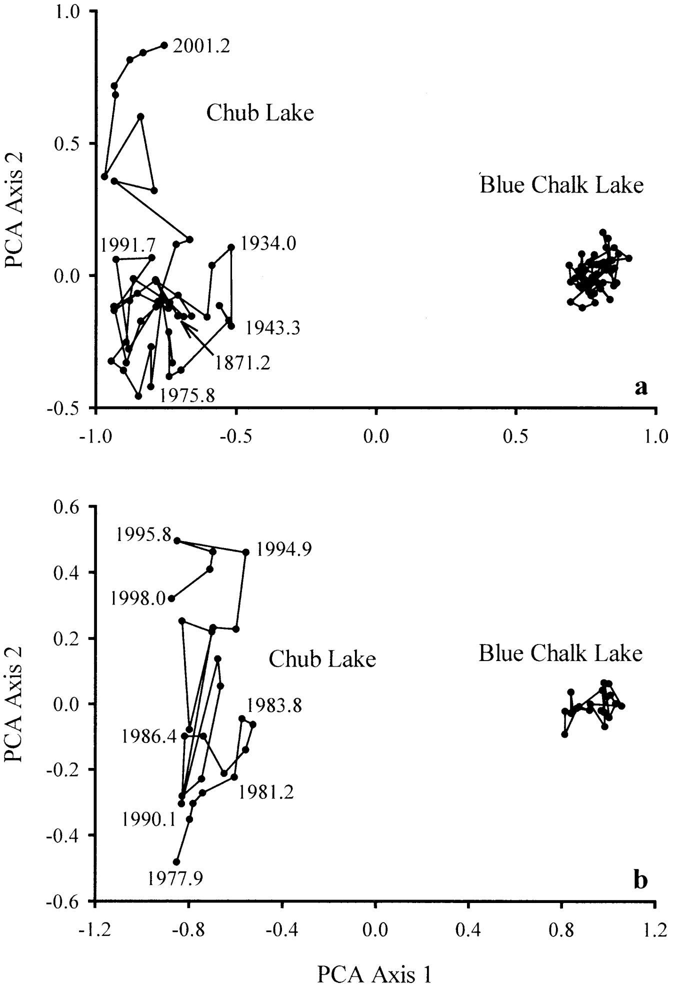

Fig. 5. Principal components analysis (PCA) of changes in sedimentary diatom assemblages (as % abundance) from Chub Lake and Blue Chalk Lake between (a) 1871 and 2000 and (b) 1977 and 1997. For the period 1871–2000, eigenvalues of the first four PCA axes were 0.623, 0.060, 0.034, and 0.028, respectively. For the period 1977–1997, eigenvalues = 0.682, 0.046, 0.039, and 0.030, respectively. Sample scores are presented for the first two PCA axes because they accounted for most of the variation in diatom assemblages. The age of selected samples are shown for Chub Lake to indicate temporal trends and represent the estimated age of the top of each sediment interval based on ^{210}Pb analysis.

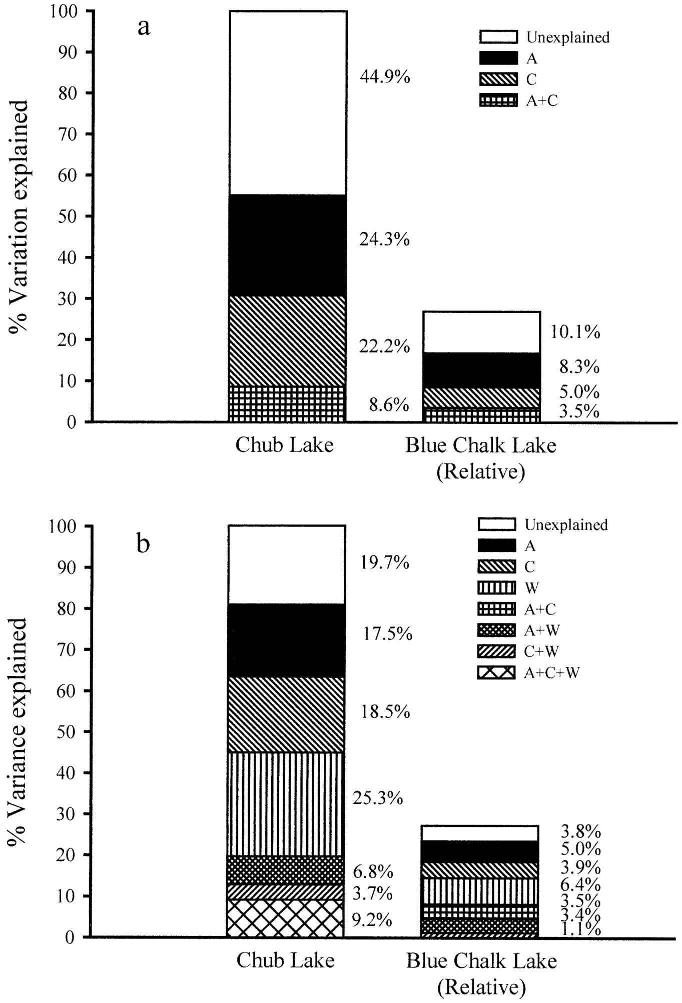

Fig. 6. Results of (a) two-category and (b) three-category variance partitioning analysis (VPA) displaying the amount of variation in sedimentary diatom assemblages explained by the unique and interactive effects of acid deposition (A), climatic factors (C), and water chemistry (W) in Chub Lake and Blue Chalk Lake between 1977 and 1997. Values for Blue Chalk Lake were expressed as the ratio of total diatom variation in Blue Chalk Lake relative to that in Chub Lake (*see Methods*). Variables included in the analyses are listed in Table 2. Values ≤1% are not shown.

idence time (Rusak et al. 1999). Thus, shorter water residence time at Chub Lake does not appear to result in differential response times of water chemistry or biota among lakes. Instead, we conclude that greater variability at Chub Lake is due, at least in part, to the greater area of contributing wetlands (>4% of the catchment area vs. 0%).

Analyses of diatom assemblages in 200-yr-long sediment records, including comparison using PCA ordination, indicate that diatom assemblages have always been inherently more variable in the lake with wetlands (Chub) than in the lake without wetlands (Blue Chalk). Sediments accumulate more slowly at Chub Lake than at Blue Chalk Lake; consequently, differences in temporal resolution of the sediment cores cannot account for the greater floristic variability observed at Chub Lake. Instead, differences in the taxonomic composition of diatom communities among the lakes are consistent with a substantial influence of wetlands on Chub Lake. For example, diatom communities in Chub Lake have been dominated for more than 200 yr by taxa indicative of slightly acidic, brown-water conditions, including *T. flocculosa* str. IIIp, *A. ralfsii* v. *americana, Fragilaria* sp. 5 PIRLA, and *Eunotia* species (Camburn and Charles 2000). Between 10 and 20% of diatom assemblages in Chub Lake consisted of members of the acid-tolerant littoral genus *Eunotia* (Anderson and Renberg 1992; Camburn and Charles 2000), whereas Blue Chalk Lake sediments contained very few members of this genus. In fact, diatom assemblages in Blue Chalk Lake were dominated by taxa indicative of more clear-water, circumneutral conditions. We attribute these differences to the export of natural humic and fulvic acids and

Table 2. Environmental variables selected for two- and three-category variance partitioning analyses of sedimentary diatom assemblages from Chub lake and Blue Chalk Lake.

	Chub Lake	Blue Chalk Lake
Acid deposition (mg m^{-2})	Annual SO_4^{2-} deposition	Annual SO_4^{2-} deposition
	Jan NO_3^- deposition	Jan NO_3^- deposition
	May NO_3^- deposition	Aug NO_3^- deposition
	Aug NO_3^- deposition	Sep NO_3^- deposition
		Dec NO_3^- deposition
Climate (air temperature, °C, precipitation, mm)	Mean Apr temperature	Mean Jan temperature
	Mean May temperature	Mean Jun temperature
	Mean Nov temperature	Jan precipitation
	Jan precipitation	Aug precipitation
	Aug precipitation	
Water chemistry (ice-free mean values)	Alkalinity	Alkalinity
	[Calcium]	[Calcium]
	Conductivity	Conductivity
	[DOC]	pH
	[TP]	[TP]
		[SO_4^{2-}]

DOC from peatlands around Chub Lake, but not around Blue Chalk Lake (Dillon and Molot 1997). Natural climatic variability presumably caused the greater variability in chemical conditions and biological communities in Chub Lake by altering external loads of these substances from wetlands during alternating wet and dry periods, even before onset of industrial acid emission. Close coupling between climate and diatom communities in boreal lakes, mediated by biogeochemical processes in the surrounding catchment vegetation and soils has been demonstrated previously (e.g., Korsman et al. 1994).

Diatom assemblages in both study lakes exhibited taxonomic changes that are consistent with the acidifying effects of industrial emissions after the early 1900s, and especially after the 1950s. The decrease in circumneutral planktonic taxa in both lakes, including *C. stelligera, C. kuetzingiana* v. *radiosa,* and *A. formosa* (Hall and Smol 1996), and the substantial increase in more acid-tolerant taxa like *T. flocculosa* str. IIIp (both lakes) and *E. zasuminensis* and *E. naeglii* (Chub Lake) (Anderson and Renberg 1992; Hall and Smol 1996) since the 1950s indicate that the pH of both lakes was lowered considerably before the onset of limnological monitoring programs.

During 1977–1997, diatom assemblages at Chub Lake were significantly more variable than at Blue Chalk Lake. These recent decades coincide with a high frequency of ENSO events and rapid fluctuations between drought and nondrought years (Dillon et al. 1997). Diatom communities in Chub Lake appear to fluctuate between dominance by taxa indicative of more clear-water (low DOC), circumneutral conditions (*A. formosa, C. stelligera, R. eriensis*) during drought years and increased abundances of taxa indicative of high DOC, acidic conditions (*A. ralfsii* v. *americana, Eunotia* species [mainly *E. naeglii*], *T. flocculosa* str. IIIp; Camburn and Charles 2000) during ensuing wet years (Fig. 4). These patterns of biological change are consistent with the effects of wetland-mediated reacidification on water chemistry that increase external loads of sulfate and DOC and depress pH (Schindler et al. 1996; Yan et al. 1996; Evans et al. 1997; Dillon and Evans 2001). Because similar patterns of change were not observed in Blue Chalk Lake, we conclude that wetlands, specifically their ability to store and then release sulfur during ensuing wet years after drought, exert a discernible effect on diatom communities in at least this one acid-sensitive lake in central Ontario.

The high proportion of explained variation by including water chemistry variables in three-category VPA ($>$80% in Chub Lake) indicates that most of the variation unexplained by two-category VPA ($\sim$45%) could be attributed to unique effects of water chemistry plus water chemistry–mediated interactions with acid deposition and climatic factors on diatoms. Three-category VPA identified that unique effects of water chemistry, independent of acid deposition and climatic factors, accounted for the greatest amount of diatom variation in Chub Lake (25.3%), suggesting that within-lake processes, or external processes unrelated to climatic variability or acidification, exert the strongest control on diatom communities. Although VPA cannot identify the specific causal mechanisms, important factors could include nutrients from cottages, changes in oxygen concentrations in the hypolimnion with concomitant release of nutrients or alkalinity from the sediment, and food-web mediated changes in water chemistry, all of which might act nonlinearly with changes in acid deposition, climatic fluctuations, or their interactions.

Three-category VPA identified that acid deposition (explained variation = 24%) and climatic variability (22%) are important determinants of diatom community composition in Chub Lake and confirm the results of previous studies that have used very different approaches (e.g., whole-lake acidification, mass-balance studies, long-term monitoring, microcosms) to identify the important roles of these factors on chemical conditions in boreal lakes (Dillon et al. 1997; Schindler 2000).

Complex wetland-mediated interactions among acid deposition and climatic variability appear to play a substantial role on diatom communities in Chub Lake. Specifically, the component of three-category VPA that can be attributed to complex wetland-mediated interactions among acid deposition and climatic variability (A + C + W) accounts for almost 10% of variation in diatom communities at Chub Lake (1977–1997) but for almost none of the variation in diatom assemblages at Blue Chalk Lake (1%). We attribute this difference to a substantial effect of peatlands on diatom communities at Chub Lake, but not at Blue Chalk Lake. To place this result in some context, complex wetland-mediated interactions among acid deposition and climate (A + C + W) accounted for almost half as much of the explained variation in diatom communities at Chub Lake (10%) compared with that explained by effects of acid deposition (A + [A + W] = 24%) or climatic fluctuations (C + [C + W] = 22%) that are not mediated by wetlands. Given that acid deposition and climatic variability are recognized as among the most important stressors of aquatic ecosystems in boreal regions of Ontario (Schindler et al. 1996; Yan et al. 1996), our results suggest that wetland-mediated complex interactions of these factors might act as an important additional stressor on diatom communities. Interestingly, three-category VPAs performed separately on subsets of planktonic and benthic diatom taxa resulted in similar decomposition of variation among VPA components (data not shown), indicating that responses of diatom communities to acid deposition, climatic variability, water chemistry, and their interactions do not differ markedly among these major habitat types.

In the absence of accurate estimates of time lags between changes in the external environmental variables and responses of chemical and biotic conditions, this study used constant time lags of 1 and 2 yr in VPAs at Chub Lake and Blue Chalk Lake, respectively, because they resulted in the greatest amount of variation explained. However, there are inherent limitations to the use of a constant time lag in VPA. For example, the direct effects of acid deposition, climatic variability, and water chemistry might not share the same lag effect, and direct effects could have a shorter lag effect than the more complex wetland-mediated interactions among factors (Dillon and Evans 2001). Additionally, true time lags between cause and effect might be variable over time rather than constant during the 20-yr period of our study, with differences depending on whether drought or wet conditions predominated, as well as other factors. These complications, because of our current inability to estimate the actual time lags, will underestimate the true variation explained by explanatory categories in VPA and overestimate the amount of unexplained variation (Hall et al. 1999). Consequently, our estimates of the effects of wetland-mediated interactions among acid deposition and climatic variability on diatom assemblages at Chub Lake are likely conservative.

Overall, the results of this study suggest that wetland-mediated interactions among climatic factors and acid deposition can lead to chemical changes that exert substantial effects on diatom communities at Chub Lake. The effects of drought-related reacidification on water chemistry have been widely observed in acid-sensitive lakes in the region (Dillon and LaZerte 1992; Dillon and Evans 2001). To our knowledge, however, this study presents the first evidence that it might account for important effects on algal communities in a lake. This study is based on a paired comparison of only two lakes, with resulting degrees of freedom equal to 1. The findings, however, demonstrate striking differences in the variability and composition of a community of primary producers over a period of 20–200 yr on a whole-lake scale that can be attributed mainly to differences in the area of contributing wetlands. Given the broad geographic distribution of these multiple stressors and numerous acid-sensitive lakes with contributing wetlands, wetland-mediated complex interactions among acid deposition and climatic variability could be an important, widespread phenomenon affecting algal communities in North America and elsewhere and deserves further study. An important implication of this study is that current estimates of rates of biological recovery in acidified lakes which fail to account for wetland-mediated reacidification events are likely to be erroneous and overoptimistic.

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Received: 8 July 2002
Accepted: 2 March 2003
Amended: 18 March 2003