

Paleolimnological Reconstruction of Holocene Climatic Trends from Two Boreal Treeline Lakes, Northwest Territories, Canada

Reinhard Pienitz,*

John P. Smol,† and

Glen M. MacDonald‡

*Centre d'Études Nordiques (CEN) and Département de Géographie, Université Laval, Québec, Québec, G1K 7P4, Canada.

reinhard.pienitz@cen.ulaval.ca (author to whom correspondence should be sent).

†Paleoecological Environmental Assessment and Research Laboratory (PEARL), Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6, Canada.

‡Department of Geography, University of California at Los Angeles, 405 Hilgard Avenue, Los Angeles, California 90095-1524, U.S.A.

Abstract

Paleolimnological analyses of two lakes located near the northern treeline in the central part of the Canadian Northwest Territories document a history of abrupt postglacial climatic and limnological changes. A diatom-based transfer function, based on weighted-averaging partial least squares regression (WA-PLS) techniques, was used to give quantitative estimates of past trends in lakewater dissolved organic carbon (DOC), a limnological variable strongly aligned with catchment vegetation and soils. The diatom record from the sediment cores provides evidence for profound limnologic change during the mid-Holocene, corresponding to maximum forest-tundra development between 5000 and 3000 ¹⁴C yr BP in both Queen's and Toronto lakes, with a diatom-inferred relative change in lakewater DOC of up to 5.8 mg L⁻¹ between the mid-Holocene and the present-day. Comparison of the diatom-inferred environmental changes with other proxy data (pollen, stable isotopes) from the same lakes provides strong evidence for an episode of climatic amelioration and lake responses to the associated vegetational changes (from tundra to forest-tundra) at sites near the central Canadian treeline. This study illustrates the usefulness of diatoms as quantitative indicators of past climate-related environmental change in northern treeline regions, and implies that aquatic ecosystems at high latitudes might respond with extreme sensitivity to climate warming.

Introduction

Northern treeline vegetation will likely be strongly impacted by future climatic warming (e.g. Houghton et al., 1990; Smith et al., 1992; Monserud et al., 1993), with a poleward displacement of the distribution of tree species being a likely response (Myneni et al., 1997). Because the position of the northern treeline results from and influences the mean position of major atmospheric boundaries (i.e. the Arctic Front; Bryson, 1966; Pielke and Vidale, 1995), it is important to understand the linkages between climate and vegetation along the northern edge of the boreal forests. The sensitivity of arctic treeline to climatic fluctuations makes this ecotone an ideal location for paleoecological studies investigating the effects and timing of past climatic changes. Latitudinal changes in the position of the Arctic Front through time provide important boundary conditions that may be used in testing and evaluating Global Circulation Models.

Several studies have attempted to reconstruct past climatic and vegetational changes at the northern treeline in the Northwest Territories (N.W.T.), Canada, using mainly fossil pollen, conifer stomate, and macrofossil analyses of lake sediments or peat profiles. These studies suggested northward displacements of treeline or increases in the density of tree populations at treeline between 10,000 and 3500 yr BP in the Mackenzie Delta and Tuktoyaktuk Peninsula region of the N.W.T. (e.g., Ritchie and Hare, 1971; Ritchie et al., 1983; Spear, 1983, 1993; Ritchie, 1984), and since 6000 and 4000 yr BP in the western District of Mackenzie and Keewatin District of the N.W.T. (e.g., Sorenson et al., 1971; Nichols, 1975; Kay, 1979; Moser and MacDonald, 1990; MacDonald et al., 1993; Hansen, 1995). A multiple-proxy investigation involving pollen, diatom, stable iso-

tope, and geochemical data in lake sediments suggested a shift of the forest-tundra limit north of its present-day position between 5000 and 4000 yr BP near Great Slave Lake in the central part of the N.W.T. (MacDonald et al., 1993). Many of these studies revealed some important limitations when using pollen analysis alone in reconstructions of past treeline changes (e.g., Payette and Lavoie, 1994; Gajewski et al., 1995; Ritchie, 1995). Paleolimnological approaches using diatom analysis may provide important complementary data, which can be used to strengthen paleoenvironmental interpretations at the northern treeline (Smol et al., 1995).

Natural long-term allogenic influences on lakes are primarily related to climate and vegetation change. These processes in turn alter soil development and hence water chemistry and aquatic biota (e.g., Renberg et al., 1993). The chemical (e.g., nutrient status) and physical properties (e.g., mixing regimes, lakewater transparency) of northern lakes are intimately linked to catchment processes, and changes in climate that affect the water table, soil moisture, mineralization, and run-off processes will in turn influence the aquatic community structure and productivity (Oechel and Vourlitis, 1994). Consequently, any climate-induced changes in the position of the northern treeline will affect the limnology of the mostly dilute and nutrient-poor lakes at this ecotonal boundary. Lakes on opposite sides of northern treeline exhibit striking differences in limnological conditions (Vincent and Pienitz, 1996; Pienitz et al., 1997a, 1997b), which are reflected by abrupt changes in diatom community structure and composition (e.g., Pienitz and Smol, 1993; Pienitz et al., 1995a, 1995b; Rühland, 1996; Allaire, 1997; Weckström et al., 1997; Laing et al., in press). Thus, diatoms (class Bacillariophyceae) should provide valuable insights into limnological changes

across the northern treeline that may be a response to past vegetational and climatic changes.

Considerable progress has been made in the development of inferential statistical techniques to reconstruct past environmental variables from paleoecological data (Birks, 1995). Although the transfer function approach assumes only strong correlation between organisms and inferred variables, and not causality, it nonetheless allows statistically more rigorous paleoclimatic reconstructions. Ecological calibration studies have demonstrated the potential for generating paleoclimate proxy data from diatoms preserved in lake sediments, which should facilitate the reconstruction of past vegetational and climatic changes at the northern treeline (reviewed in Lotter et al., 1998). For example, limnic conditions that are highly correlated with catchment vegetation and soils, such as the concentration of lakewater dissolved organic carbon (DOC) (e.g., Engstrom, 1987; Forsberg, 1992; Wetzel, 1992; Kortelainen, 1993; Kling, 1995; Vincent and Pienitz, 1996), explained significant proportions of the variation in diatom species distribution in calibration sets of lakes from the Yellowknife area (Pienitz and Smol, 1993), Siberia (Laing et al., in press), and from northern Québec (Fallu and Pienitz, in press). Transfer functions generated from these calibration sets can be used to infer past limnological changes related to vegetational changes (e.g., advances and infilling of tree-limit ecotones) at the northern treeline from diatom assemblages preserved in dated sediment cores (Pienitz, 1993). In addition to reconstructing chemical variables (e.g., DOC) associated with treeline movement, several researchers have recently suggested that freshwater diatoms may also provide proxy data on past changes in temperature (e.g., Pienitz et al., 1995a; Vyverman and Sabbe, 1995; Weckström et al., 1997; Lotter et al., 1997) and underwater light conditions (Vincent and Pienitz, 1996). As discussed in Pienitz et al. (1995a) and Anderson et al. (1996), not all of the diatom species responses are directly related to climate, yet the diatom data may yield important information on ecological processes that are intimately linked to climatic and vegetational shifts.

The purpose of the present paper is to demonstrate the potential of diatoms in tracking climatic and vegetational shifts, and to add novel information about the accompanying changes in aquatic conditions. We therefore analyzed the fossil diatoms in lake sediment records from two sites located northeast of Yellowknife (N.W.T.), near the present-day treeline. The high temporal resolution biostratigraphic changes observed in the core sample diatom assemblages were compared with paleoecological data inferred from analyses of fossil pollen (Moser and MacDonald, 1990; MacDonald et al., 1993) and paleohydrologic and paleoclimatic information derived from stable isotope data (Edwards et al., 1996; B. B. Wolfe et al., 1996; B. B. Wolfe, 1997) from the same cores. Based on the fossil diatom data, we compared the performance of transfer functions previously developed for the study region (Pienitz and Smol, 1993) to new inference models in quantitative reconstructions of lakewater DOC concentrations that are closely related to past climatic and vegetational shifts in the study area.

Study Area and Sites

The two lakes, Queen's Lake and Toronto Lake (unofficial names), are located northeast of Yellowknife in the central part of the Northwest Territories (N.W.T.) (Fig. 1), at the extreme limits of spruce krummholz (*Picea mariana*). The relatively sharp ecotonal boundary near northern treeline is characterized by steep climatic gradients, which are related to the mean sum-

mer position of the Arctic Front as well as vegetational patterns (Bryson, 1966; Pielke and Vidale, 1995). Queen's Lake (64°07'N, 110°34'W), located 25 km north of the mapped extent of the forest-tundra zone, has a surface area of approximately 50 ha and a maximum depth of 3.5 m. Toronto Lake (63°43'N, 109°21'W), located at the transition between forest-tundra and tundra zones, is smaller (10 ha) but relatively deep ($z_{max} = 6.75$ m) (B. B. Wolfe et al., 1996). Queen's Lake is a headwater lake and drains a considerably smaller catchment (ca. 200 ha) than Toronto Lake (ca. 2900 ha) which belongs to a fluvial system that is strongly influenced by upstream hydrologic processes (B. B. Wolfe et al., 1996). For more detailed descriptions of the study sites, sediment cores, present-day vegetation, and the Holocene vegetational history of the study area, see Moser and MacDonald (1990) and B. B. Wolfe et al. (1996).

The 22 calibration lakes that were used to develop the transfer function (Pienitz and Smol, 1993) are located between Yellowknife and Contwoyto Lake (Fig. 1), spanning three major ecoclimatic provinces (Boreal, Subarctic, Arctic) (Ecoregions Working Group, 1989). The complete water chemistry data for these lakes are presented in Pienitz et al. (1997a). The majority of these sites are presently shallow, oligotrophic lakes with slightly acidic to alkaline waters (pH 6.2–8.9) and low conductivity ($<100 \mu\text{S cm}^{-1}$). Many of the lakes are slightly colored, with a DOC range of 1.6 to 9.1 mg L⁻¹. Strong color is generally restricted to sites surrounded by peatlands, especially in the forest-tundra and boreal forest zones. Lakes in forested catchments typically showed significantly higher concentrations in DOC and DIC, as well as other nutrients in comparison with lakes in tundra environments. In addition, the pH and calcium (Ca) concentrations of these lakes tended to be higher, probably due to the presence of more alkaline rocks in the Yellowknife area (Pienitz et al., 1997a).

Methodology

Sediment cores were taken from the deepest part of the basin in both Toronto Lake and Queen's Lake, using a 5-cm-diameter modified Livingstone piston corer. Detailed subsampling of the cores for diatom analysis was carried out mostly at 2.5-cm intervals, which were identical to those sampled for pollen and isotopes (MacDonald et al., 1993; B. B. Wolfe et al., 1996). The longer sediment record retrieved from the Toronto Lake basin (170 cm as compared to 110 cm in Queen's Lake) explains the relatively higher temporal resolution achieved in this lake, approximating about 100 yr intervals. Four ¹³C-corrected but uncalibrated AMS ¹⁴C dates provide the Holocene chronology of the Toronto Lake core, whereas five dates determine the chronology of the Queen's Lake core (Table 1). The ¹⁴C age scales shown in Figures 2 and 3 have been determined by linear extrapolation between dated intervals.

Diatom slide preparation involved treating about 1 cm³ of homogenized sediment from each sample with strong acids (potassium dichromate and sulfuric acid, 5% w/v), following the procedures outlined in Pienitz and Smol (1993). An aliquot of the resulting slurry was evaporated onto coverslips and subsequently mounted onto glass slides with Hyrax[®] (R.I. = 1.71). For each sample, between 300 to 500 diatom valves were identified and enumerated along random transects under oil immersion objectives using a Leica DMRB microscope at 1000× magnification. Chrysophyte cysts were enumerated in all samples and expressed as a ratio relative to diatom valves (Smol, 1985), but cyst morphotypes were not distinguished. The taxonomy and identification of diatoms was based mainly on Hustedt (1927–

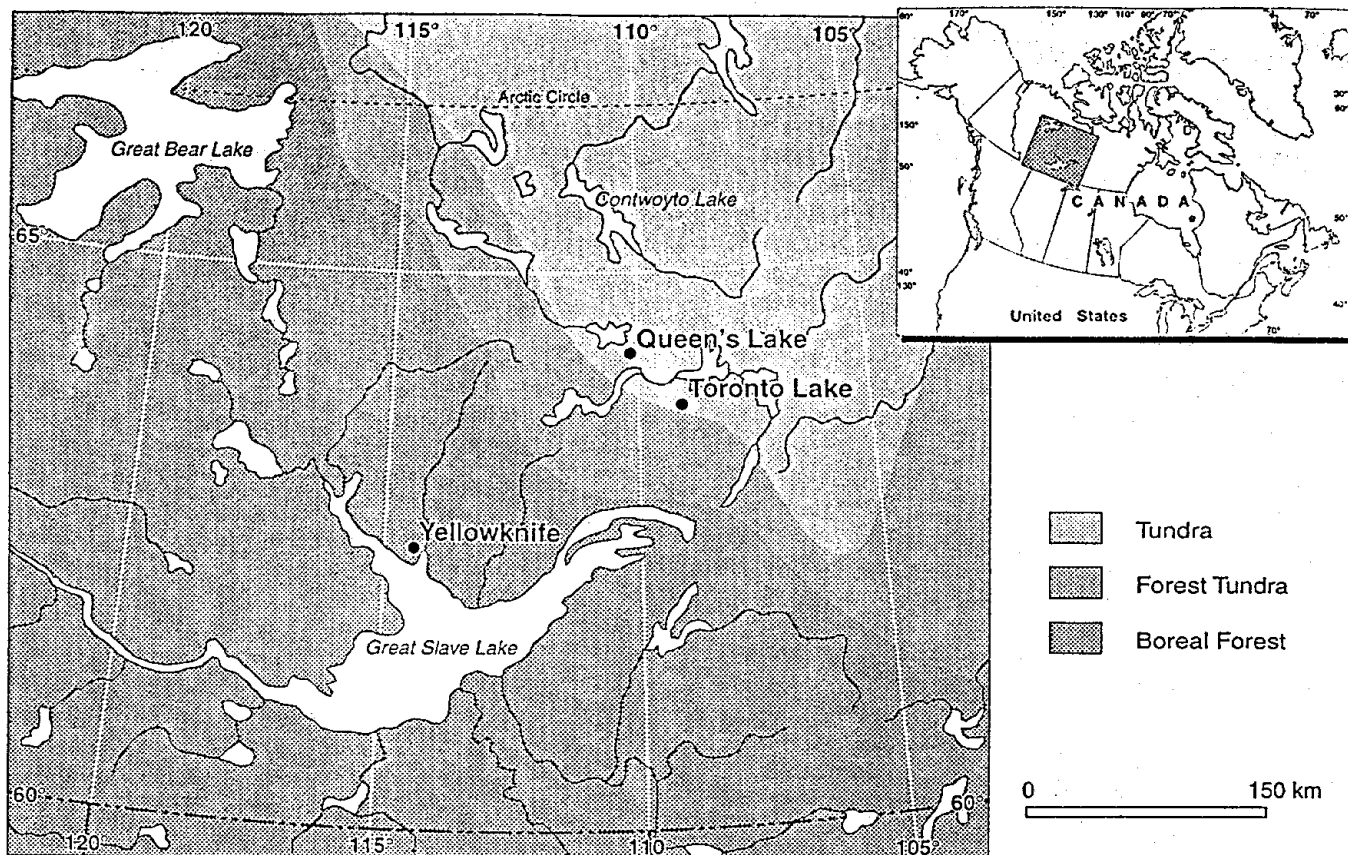


FIGURE 1. Geographical location of study sites Queen's Lake and Toronto Lake northeast of Yellowknife in the Northwest Territories.

1966), Patrick and Reimer (1966, 1975), Mölder and Tynni (1967–1973), Tynni (1975–1980), Foged (1981), Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), and the PIRLA Diatom Iconograph (Camburn et al., 1984–1986). Diatom concentrations in sediment samples from the Queen's Lake core were determined using Battarbee (1973) trays.

DIATOM INFERENCE MODELS

The weighted-averaging (WA) regression and calibration models used for inferring environmental variables were based on

TABLE 1

Radiocarbon dates (^{13}C -corrected) from Queen's and Toronto Lakes (MacDonald et al., 1993)

Depth (cm)	Material	Age (yr BP $\pm 1\sigma$)	Lab number
Queen's Lake			
15–20	Organic sediment	3820 \pm 60	WAT-1770
45–50	Organic sediment	5600 \pm 60	WAT-1771
60–65	Organic sediment	6150 \pm 60	WAT-1772
100–105	Organic sediment	7150 \pm 70	WAT-1773
105	Twig	7470 \pm 80	TO-827
Toronto Lake			
35–40	Organic sediment	1760 \pm 90	Beta-49705
80–85	Organic sediment and moss	4200 \pm 80	Beta-53129
125–130	Organic sediment and moss	5460 \pm 90	Beta-53130
155–160	Organic sediment	7040 \pm 120	Beta-49708

the ecological optima of 76 diatom taxa selected from the calibration set of lakes in the Yellowknife—Contwoyto Lake area (selection and data screening criteria are outlined in Pienitz and Smol, 1993). Though the compositional gradient length in the biological data-set was larger than 2 standard deviation units (3.2) as revealed by detrended correspondence analysis (DCA; Hill and Gauch, 1980), suggesting the use of unimodal-based numerical techniques (ter Braak and Prentice, 1988; Birks, 1995), we nevertheless tested and compared the performance of both linear- and unimodal-based inference models. The comparative tests of partial least squares (PLS), WA-partial least squares (WA-PLS; ter Braak and Juggins, 1993), and WA regression and calibration models (with inverse or classical deshrinking, with or without tolerance downweighting, untransformed or square root-transformed species data) were used to identify the best transfer functions. All model estimates were adjusted by jack-knifing procedures, a cross-validation technique that eliminates the circularity of developing an inference model for species from the same data set (Birks, 1995).

The final model was selected that gave the lowest root mean squared error of prediction (RMSEP) and the highest coefficient of determination (r^2) between observed and predicted values, both assessed by jack-knifing, as well as the lowest mean and maximum biases (ter Braak and Juggins, 1993) in the leave-one-out cross-validations. The model tests and subsequent DOC reconstructions were done by means of the computer programs CALIBRATE version 0.61 and WAPLS version 1.1 (S. Juggins and C. J. F. ter Braak, unpublished programs). All other statistical analyses were done using the program CANOCO version 3.12 (ter Braak, 1988, 1990).

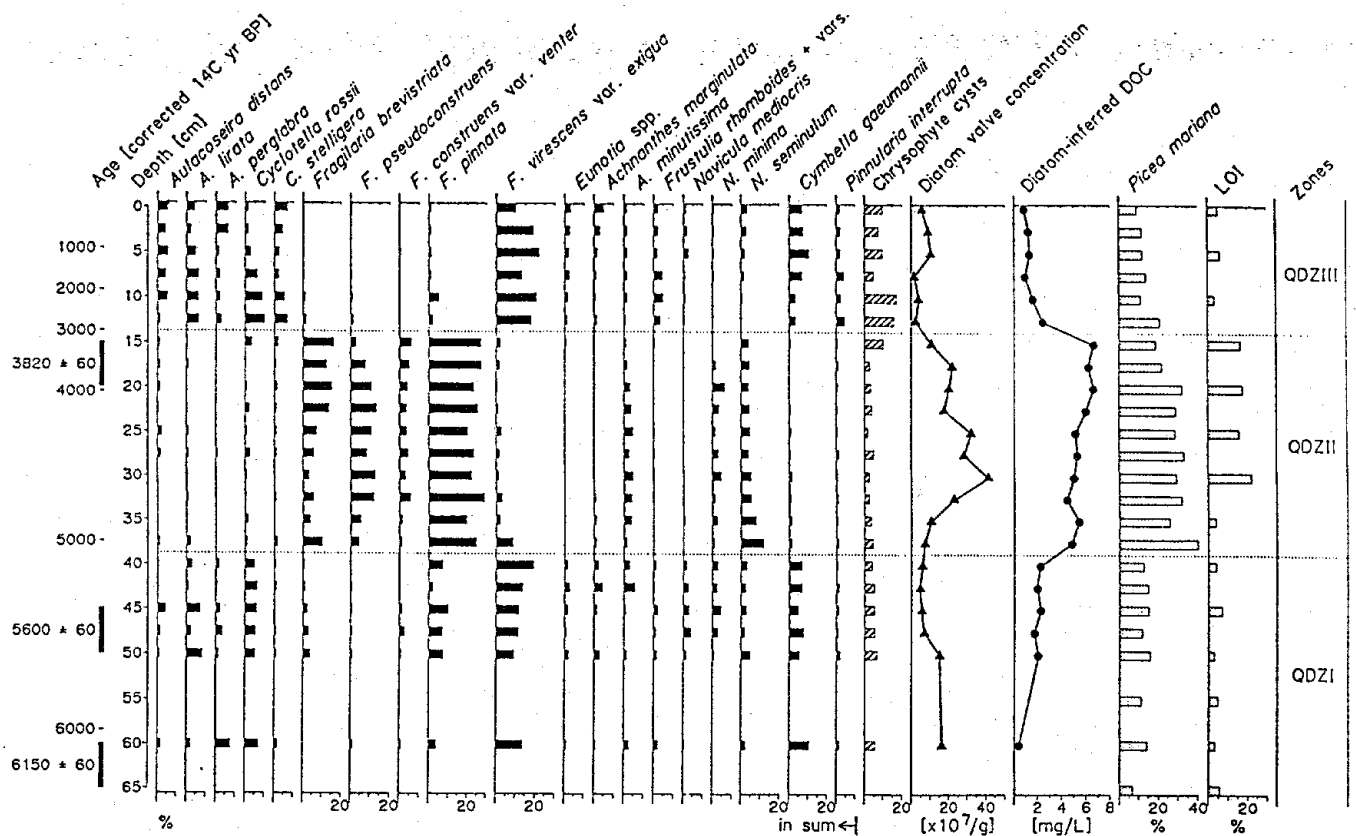


FIGURE 2. Diatom stratigraphy and diatom-inferred profile of dissolved organic carbon (DI-DOC) from Queen's Lake. The loss-on-ignition (LOI) and *Picea mariana* pollen profiles are reproduced from MacDonald et al. (1993).

In order to assess the performance of our final inference model, analog matching, based on a χ^2 dissimilarity index (Prentice, 1980), was used to identify fossil diatom assemblages which lacked modern analogs (Birks et al., 1990). No-analog situations were determined as fossil χ^2 that were more extreme than 95% of χ^2 distributions based on the modern training-set assemblages. Analog matching was performed using the computer program ANALOG version 1.6 (J. M. Line, Cambridge University, and H. J. B. Birks, University of Bergen, unpublished program). The two diatom diagrams shown in Figures 2 and 3 were plotted using TILIA version 2.00 and TILIAGRAPH version 1.25 (Grimm, 1991-1993).

Results

A total of 157 diatom taxa from 19 genera were identified in the Toronto Lake core, whereas 176 diatom taxa from 24 genera were identified in the Queen's Lake core. Only the dominant taxa (i.e. those with at least 2% abundance in at least one sample) were included in the percentage diagrams shown in Figures 2 and 3. The results of the chrysophyte cyst counts are also presented in the diagrams.

The WA-PLS model (3 components) with untransformed diatom percentage data showed the strongest relationship between diatom assemblages and DOC, with a jack-knifed r^2 of 0.61 and a root mean squared error of prediction (RMSEP) of 1.3 mg DOC L⁻¹, a mean bias of -0.051 mg DOC L⁻¹, and a maximum bias of 0.741 mg DOC L⁻¹ (Table 2). The inferred DOC concentrations with the sample-specific error estimates for both lakes are presented in Figures 4 and 5.

Performance measures of the diatom inference models in-

dicated that no-analog situations with modern diatom communities existed in the Toronto Lake core at depths between 167.5 to 165.0, 132.5 to 120.0, and 107.5 to 105.0, and at 97.5 cm, which were mainly due to extreme percentage abundances of fossil *Fragilaria pinnata* Ehrenberg, *Navicula seminulum* Grunow, and *Cyclotella stelligera* Cleve & Grunow, respectively.

HOLOCENE DIATOM STRATIGRAPHIES

Queen's Lake

Three distinct diatom zones (QDZ I-III) are recorded in the sediment core from Queen's Lake (Fig. 2), reflecting three marked successional changes. Diatom assemblages in the uppermost (QDZ III; 12.5-0 cm) and lowermost (QDZ I; 60.0-40.0 cm) zones were similar, separated by a very distinct intermediate zone (QDZ II; 37.5-15.0 cm) (Fig. 2). The early ontogenetic phase of Queen's Lake (110 to 65 cm depth), representing the period from about 7500 to 6200 yr BP, was not analyzed for fossil diatoms. Clearly, a major limnological change occurred during QDZ II, which corresponds to diatom zone II (TDZ II) in the Toronto Lake core and spans the time interval from ca. 5000 to 3000 yr BP. These changes coincide with those inferred from pollen and stable isotope records (Figs. 2, 6), reflecting a rather abrupt climatic change (MacDonald et al., 1993).

QDZ I (60.0 to 40.0 cm) was dominated by the three pennate benthic diatoms *Fragilaria virescens* var. *exigua* Grunow (9.4-19.2%), *Fragilaria pinnata* (2.0-10.0%), and *Cymbella gaeumannii* Meister (5.0-10.5%) (Fig. 2). Both *Fragilaria virescens* var. *exigua* and *Cymbella gaeumannii* are taxa commonly associated with circumneutral to slightly acidic waters (Kram-

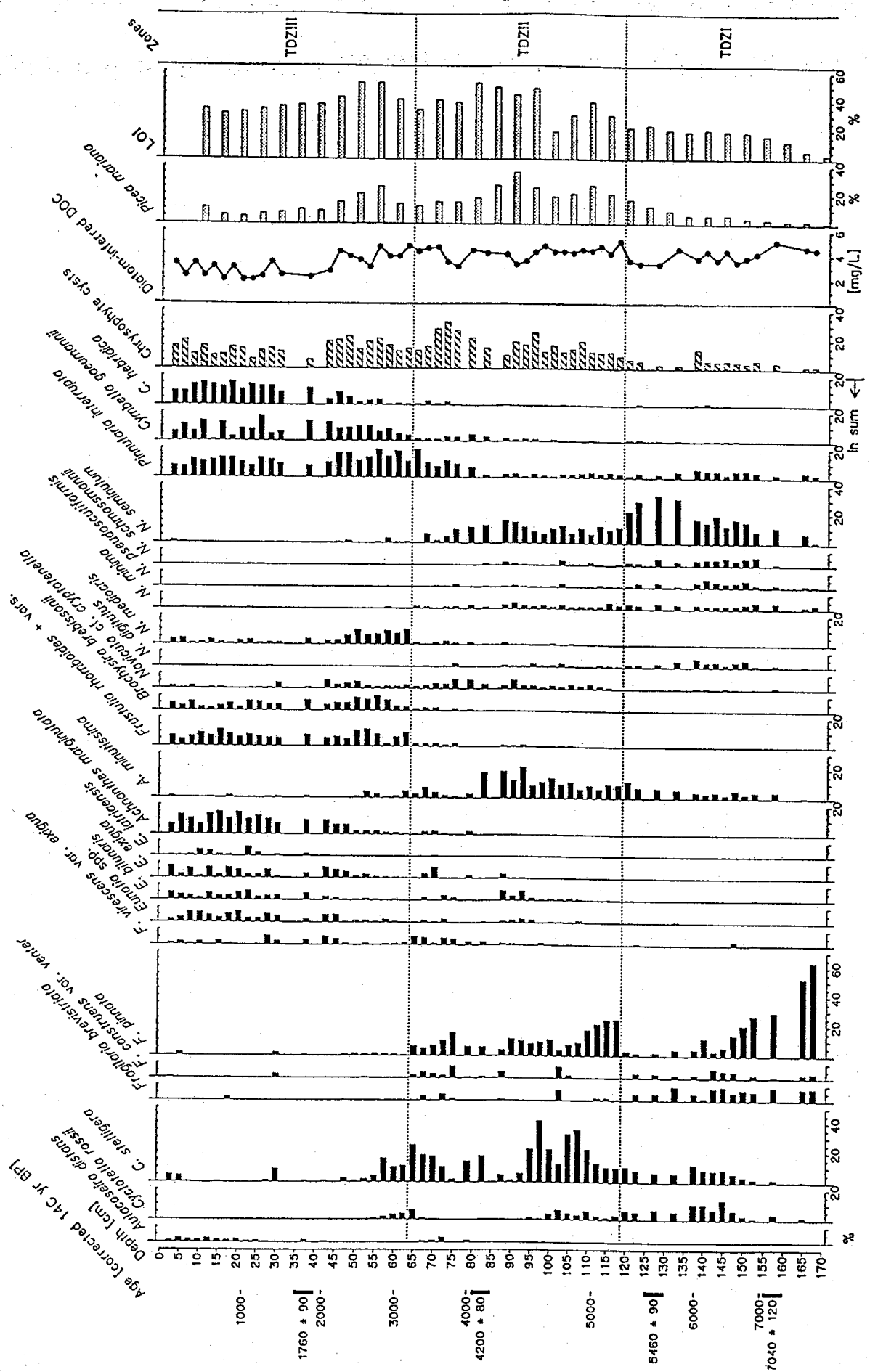


FIGURE 3. Diatom stratigraphy and diatom-inferred profile of dissolved organic carbon (DI-DOC) from Toronto Lake. The loss-on-ignition (LOI) and Picea mariana pollen profiles are reproduced from MacDonald et al. (1993).

TABLE 2

Descriptive statistics for the performance of the WA-PLS, PLS and WA inference models (with classical versus inverse de-shrinking) for dissolved organic carbon (DOC), with and without tolerance down-weighting, as well as with and without square root transformation of species data. Model statistics summarize precision as $r^2_{\text{jack-knifed}}$, root mean squared error of prediction (RMSEP), as well as mean and maximum bias as assessed by jack-knifing.

Prediction model	RMSEP	$r^2_{\text{jack knifed}}$	Mean bias	Maximum bias
Prediction model (untransformed species data)				
WA (inverse)	1.60	0.43	-0.2069	1.036
WA _{tol} (inverse)	1.74	0.32	-0.3306	1.183
WA (classical)	1.51	0.50	-0.2442	0.8259
WA _{tol} (classical)	1.77	0.38	-0.4998	1.044
WA-PLS (3 components)	1.30	0.61	-0.0506	0.7406
PLS	1.53	0.46	-0.0569	0.8579
Prediction model (square-root transformed species data)				
WA (inverse)	1.86	0.22	-0.2088	1.054
WA _{tol} (inverse)	1.88	0.23	-0.4437	1.357
WA (classical)	1.93	0.26	-0.3288	0.8809
WA _{tol} (classical)	2.02	0.27	-0.6971	1.315
WA-PLS (4 components)	1.57	0.44	-0.0363	0.7917
PLS	1.48	0.49	-0.0406	0.868

mer and Lange-Bertalot, 1991a; Pienitz and Smol, 1993). Of the centric diatoms, *Cyclotella rossii* Håkansson (5.0–6.9%) and *Aulacoseira lirata* (Ehrenberg) Ross (0.7–8.0%) were most abundant. Chrysophyte cyst percentages ranged between 4 and 7%, and diatom concentration values did not exceed 17×10^7 valves/g wet sediment. Diatom assemblage composition and the diatom-inferred DOC profile reflect oligotrophic and electrolyte-poor limnic conditions during this period, while fossil pollen data (Moser and MacDonald, 1990; MacDonald et al., 1993) suggest that the region was dominated by tundra (Fig. 2).

The boundary between the basal diatom zone and the overlying QDZ II (between 40.0 and 37.5 cm depth) is marked by a sharp increase in small benthic alkaliphils of the genus *Fragilaria* and an equally abrupt decline in *F. virescens* var. *exigua* and *Cymbella gaeumannii* (Fig. 2). *Fragilaria pinnata* (19.5–28.8%), *F. brevistriata* Grunow (3.0–16.1%), *F. pseudoconstruens* Marciniak (3.0–13.1%), and *F. construens* var. *venter* (Ehrenberg) Hustedt (1.0–5.9%) predominated throughout this zone, whereas previously dominant species (see above) almost entirely disappeared. These *Fragilaria* taxa were accompanied mainly by small pennate diatoms, such as *Navicula seminulum* (3.6–11.7%), *N. minima* Grunow (0.7–6.2%), and *Achnanthes minutissima* Kützing (1.0–4.6%). These taxa reached their highest relative abundance in this zone, which also corresponded to the stratum of lowest chrysophyte cyst numbers (<1.8%). The peaks of *Fragilaria* spp. and total diatom concentrations ($>40 \times 10^7$ valves/g wet sediment), lowest percentages of acidophilic taxa, as well as highest LOI values (Fig. 2), are clear indications of a change towards higher lake productivity and increased pH during QDZ II. These changes are supported by strong diatom-inferred increases in lake DOC concentrations (Figs. 2, 4), and coincide with evidence from the pollen record of establishment of forest-tundra at the site (Moser and MacDonald, 1990; MacDonald et al., 1993), as well as with lake sediment cellulose $\delta^{18}\text{O}$ histories from sites in central Canada that indicate that lake hy-

Queen's Lake

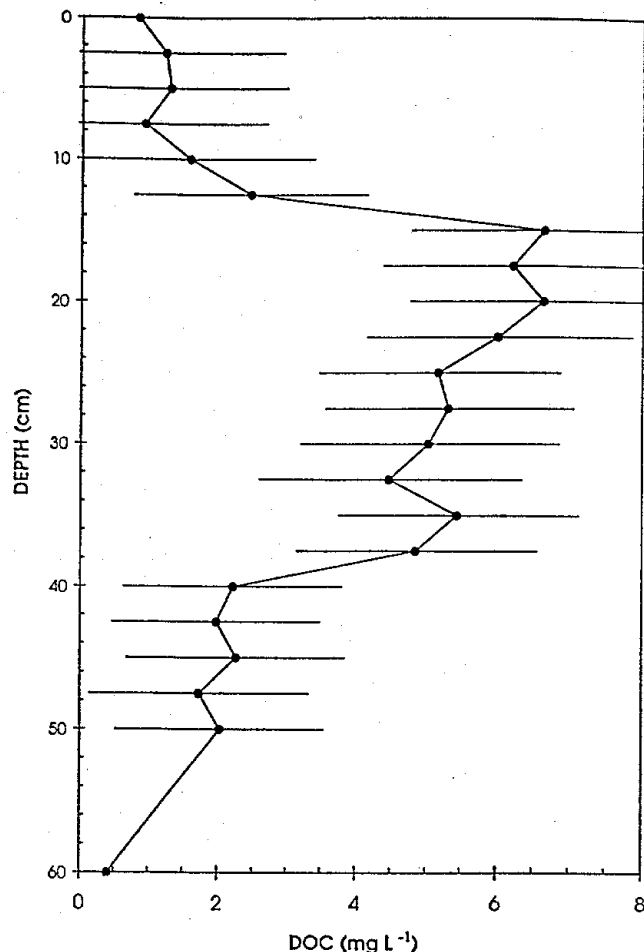


FIGURE 4. Diatom-inferred dissolved organic carbon (DOC) profile for Queen's Lake plotted against sediment depth. Error bars are based on sample-specific error estimates as calculated by Monte Carlo simulation using the initial standard errors of the species regression (beta) coefficients.

drologic balance changed due to increased summer relative humidity during that time (Fig. 6; Edwards et al., 1996; B. B. Wolfe, 1997).

In the uppermost QDZ III (12.5 cm to the top of the core), the sudden and drastic decline in *Fragilaria* spp. and in the diatom valve concentrations ($<10 \times 10^7$ valves/g wet sediment) marks the return to conditions presumably similar to those that prevailed during QDZ I. An equally abrupt decline in lake nutrient status and productivity is indicated by strong decreases in diatom-inferred DOC concentrations, as well as strongly reduced LOI values (Fig. 2). Diatom assemblages became dominated once again by the acidophilic *Fragilaria virescens* var. *exigua* (10.2–22.0%) and *Cymbella gaeumannii* (3.3–10.5%), accompanied by several centric diatom taxa such as *Cyclotella rossii* (1.3–9.9%), *C. stelligera* (2.3–7.0%), *Aulacoseira distans* (Ehrenberg) Simonsen (1.0–5.3%), *A. lirata* (2.3–6.3%), and *A. perglabra* (Oestrup) Haworth (1.3–6.3%). Chrysophyte cysts were most abundant (4.9–17.2%) within this zone. These marked shifts in diatom stratigraphy and the diatom-inferred DOC are again paralleled by abrupt changes in the pollen spectra indicating tundra vegetation, while changes in the coupled $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ records suggest a decrease in the ratio of precipitation to evaporation (MacDonald et al., 1993). Interestingly, the propor-

Toronto Lake

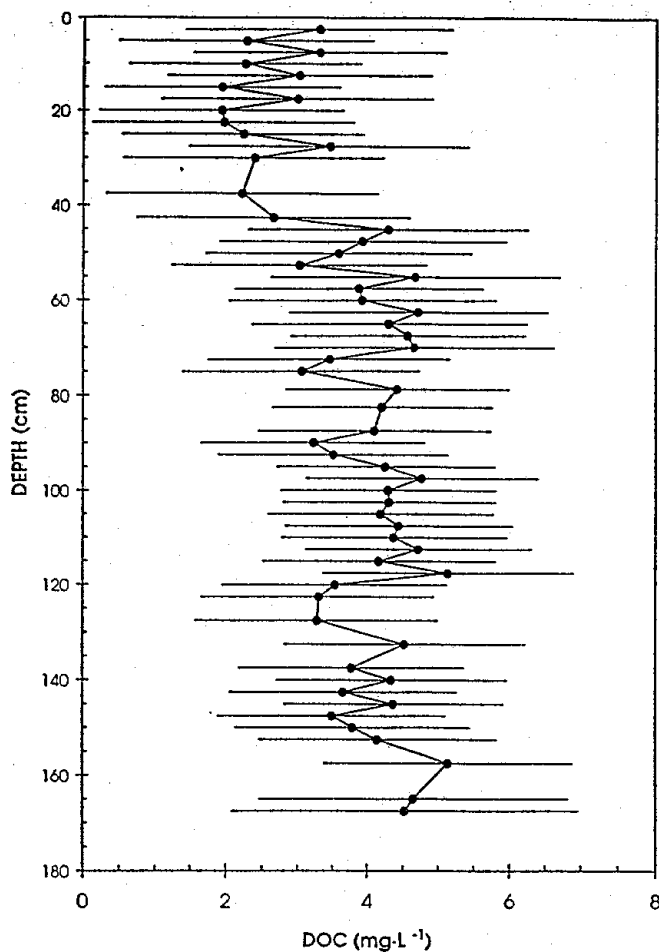


FIGURE 5. Diatom-inferred dissolved organic carbon (DOC) profile for Toronto Lake plotted against sediment depth. Error bars are based on sample-specific error estimates as calculated by Monte Carlo simulation using the initial standard errors of the species regression (β) coefficients.

tion of mero-/tychoplanktonic and benthic diatoms shows two major shifts (from planktonic to benthic to planktonic taxa) at the diatom zone boundaries (40.0/37.5 cm and 15.0/12.5 cm levels). The possible causes for these shifts include changes in water transparency and/or water depth, with subsequent changes in the areal extent of the lake's littoral habitat (MacDonald et al., 1993).

Toronto Lake

We identified three stages (Toronto diatom zones (TDZ) I-III) in the history of Toronto Lake based on major shifts in diatom assemblage composition and the diatom-inferred DOC. Clearly, a major limnological change occurred at the transition between diatom zones I and II (Fig. 3). Most of these changes correspond with (or immediately precede) those recorded in the pollen and stable isotope records (MacDonald et al., 1993; B. B. Wolfe et al., 1996).

The diatom-inferred profiles for DOC attain their highest values at the base of Diatom Zone I (170–120 cm), which represents the time period after glacial retreat. The alkaline character of the lake at this early time in its history (prior to 7040 BP to about 5200 BP) is reflected by the dominance of the small

benthic alkaliphils *Fragilaria pinnata* and *Navicula seminulum*, and the near absence of acidophilic diatom taxa and chrysophyte cysts (Fig. 3). The initial *Fragilaria pinnata* peak (> 60%) remains unparalleled throughout the history of Toronto Lake, and may have developed due to mineral turbidity rather than high DOC. The high abundance of *Fragilaria* spp. at the base of the Toronto Lake core clearly represents a "no-analog" situation, since in the surface calibration set of lakes from the Yellowknife area, *F. pinnata* abundance never exceeded 30%. As a consequence, diatom inferences of DOC are unreliable in this lowermost section of the core, a conclusion reinforced by analog matching tests (see above).

The following time interval (TDZ II (117.5 to 65 cm); approx. 5200 to 3200 yr BP) is characterized by three periods of increased lakewater DOC (corresponding to core depths of 117.5 to 97.5 cm, 87.5 to 80.0 cm, and 70.0 to 65.0 cm; Figs. 3, 5). Each of these short-lived changes at treeline was followed by a return to previous conditions. Stable isotope data indicate that this interval also corresponds to the hydrologically most variable period in the history of Toronto lake (B. B. Wolfe et al., 1996).

The most important shift in limnetic conditions occurred 5200 yr BP between levels 120.0 to 117.5 cm (= boundary between TDZ I and TDZ II), as shown by the most prominent diatom change in the history of Toronto Lake. A very rapid northward advance of treeline and/or infilling of tree cover seems to have affected the area at this time (MacDonald et al., 1993), with diatom-inferred DOC showing significant increases (Figs. 3, 5). These drastic changes suggest a short-lived period of lake overflow and increased lake productivity during the following period encompassing the interval between approximately 117.5 and 97.5 cm depth (= ca. 5200 to 4600 yr BP). The onset of this major change coincides with a sudden increase of *Fragilaria pinnata* at the 117.5-cm level, followed by *Cyclotella stelligera* peaks at the 107.5 and 97.5-cm levels (35.2 and 41.4%, respectively). The small planktonic *C. stelligera* remained the dominant diatom throughout this zone. Other important taxa included the small benthic alkaliphils *Navicula seminulum* (1.9–15.8%) and *Achnanthes minutissima* (1.0–21.2%).

During the subsequent 2000 yr, shifts in fossil diatom assemblages and diatom-inferred DOC may reveal two more minor environmental fluctuations with short-lived increases in lake productivity, possibly associated with local vegetational changes at treeline between about 4300 to 4100 and 3500 to 3200 yr BP (Figs. 3, 5).

The period from about 3200 yr BP until the present-day (TDZ III = 62.5 cm to the top of the sediment core) marks the onset of a period of decreasing concentrations in DOC (Figs. 3, 5), which corresponds to a return to the modern dwarf shrub tundra vegetation (MacDonald et al., 1993). Within this zone, diatom assemblages previously dominated by alkaliphilic taxa in zones TDZ I and II are replaced by assemblages composed of circumneutral to acidophilic species, such as *Frustulia* spp. (*F. rhomboides* (Ehrenberg) De Toni, *F. rhomboides* var. *crassinervia* (Brébisson) Ross, *F. rhomboides* var. *saxonica* (Rabenhorst) De Toni), *Brachysira brebissonii* Ross, *Navicula mediocris* Kraske, *Pinnularia interrupta* W. Smith, *Cymbella gaeumannii*, and *C. hebridica* (Grunow) Cleve. Increasing relative numbers of chrysophyte cysts may also indicate a trend towards long-term natural acidification of Toronto Lake.

The above acidification trend becomes more obvious in the most recent sediments (top 30 cm, corresponding to approx. the last 1500 yr), where increasing numbers of acidophilic epiphytes

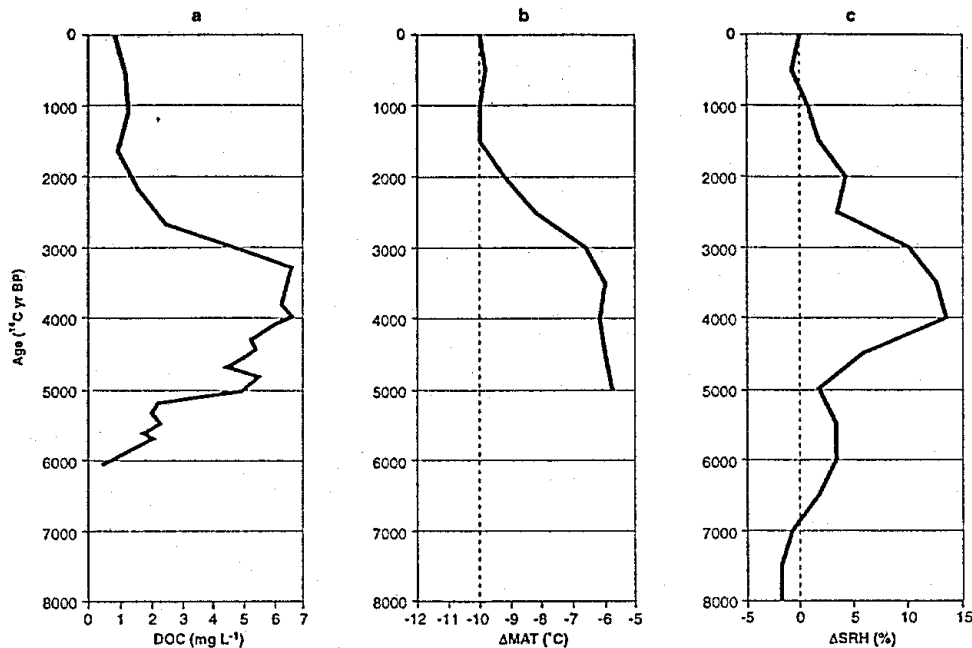


FIGURE 6. Diatom-inferred dissolved organic carbon (DI-DOC) from Queen's Lake as compared to Holocene records of isotope-inferred summer relative humidity (Δ SRH) and mean annual temperature (Δ MAT) change for central Canada based on lake sediment cellulose $\delta^{18}\text{O}$ profiles from Queen's Lake, Toronto Lake and a third site, Whatever Lake, located 600 km to the east (from Edwards et al., 1996 and B.B. Wolfe, 1997). Paleohumidity is estimated using an isotope-mass balance model; paleotemperature is derived from reconstructed precipitation $\delta^{18}\text{O}$ ($\delta^{18}\text{O}_p$) values and the relation, $\delta^{18}\text{O}_p = 0.65 \text{ MAT} - 15.5$. Non-temperature-dependent effects on estimated $\delta^{18}\text{O}_p$ values preclude paleotemperature reconstruction during the early Holocene. Uncertainties are on the order of $\pm 6\%$ and $\pm 2^\circ\text{C}$.

(e.g. *Achnanthes marginulata* Grunow [6.6–15.3%], *Pinnularia interrupta* [7.7–19.1%], *Cymbella gaeumannii* [1.3–17.3%] and *C. hebridica* [9.0–15.8%]) and peat-associated taxa (e.g. *Eunotia bilunaris* (Ehrenberg) Mills, *E. exigua* (Brébisson) Rabenhorst, and *E. iatriaensis* Foged), may reflect progressive paludification of the lake's watershed. The concurrent disappearance of planktonic *Cyclotella* taxa (Fig. 3) is typical of recently acidified lakes (Anderson, 1995).

Discussion

The diatom records from the two study sites show substantial shifts in the diatom assemblages associated with lake water chemistry changes, brought about by catchment-vegetation processes, and hence changed carbon and/or nutrient fluxes. The high sensitivity of these treeline lakes to catchment processes can be attributed to their chemically dilute nature, and their position at a major ecotonal boundary. They also document a history of rapid postglacial climatic, vegetational, and limnologic changes near the northern treeline in the central Canadian Subarctic. The major change occurred about 5000 yr BP, corresponding in both lakes with well defined zones (QDZ II and TDZ II) of sharply increased percentages of *Fragilaria* spp., total organic matter content and *Picea mariana* pollen (Figs. 2, 3; MacDonald et al., 1993). These conditions suggest an abrupt warm and humid interval during the mid-Holocene, accompanied by high levels of lake productivity related to hydrological and vegetational changes in the drainage basin. The paleolimnological evidence of these environmental changes corresponds with fossil pollen, conifer-stomate, and paleosol studies from more easterly sites in central Canada (Sorenson et al., 1971; Kay, 1979; Hansen, 1995), which also indicate major vegetational changes between 4800 and 3700 yr BP in response to shifts in the mean summer position of the Arctic frontal zone. The chronology of this diatom-inferred event is in close agreement with the timing of an episode of wetter and more productive conditions revealed by coupled $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ analyses of organic sediments from the same cores (Fig. 6; B. B. Wolfe et al., 1996; B. B. Wolfe, 1997).

Combined evidence from pollen and isotope analyses suggests treeline advance, high lake productivity, increased summer relative humidity, and open basin hydrologic conditions during the mid-Holocene for northern boreal treeline regions in central Canada (Fig. 6; MacDonald et al., 1993; Edwards et al., 1996; B. B. Wolfe et al., 1996; B. B. Wolfe, 1997). In both lakes, the DOC profiles inferred from diatoms indicate highest concentrations for this warm interval, followed by a decrease in the order of 5.8 mg L^{-1} in Queen's Lake since the return to the modern dwarf shrub tundra vegetation after 3000 yr BP (Fig. 6). Similarly, diatom-based reconstructions of DOC in Swedish boreal forest lakes showed increased concentrations following the natural establishment of spruce (*Picea abies*) in the catchment, with no indication of concurrent lake acidification (Korsman et al., 1994).

The longer paleolimnological record that has emerged from Toronto Lake is likely due to its higher depth-to-area ratio (which favors higher sediment accumulation rates; see Larsen and MacDonald, 1993; Larsen et al., in press), as well as its connection to an extensive headwater catchment (B. B. Wolfe et al., 1996). The more complex vegetation-climate history observed in Toronto Lake corresponds with the "noisier" results obtained from fossil pollen and stable isotope analyses, indicating fundamentally different hydrological settings at these two sites (MacDonald et al., 1993; Edwards et al., 1996; B. B. Wolfe et al., 1996). The extremely low sedimentation rate in the top 20 cm of the closed basin Queen's Lake seems to be the main reason for the relatively subdued record of environmental changes in this section of the core. However, the magnitude of the diatom-inferred mid-Holocene change about 5000 yr BP is greater than that recorded in the Toronto Lake core between 5200 to 5000 yr BP.

The results obtained from the present study suggest that the northernmost position of treeline (or maximum density of forest cover), the highest sustained lakewater DOC and highest lake productivity were reached during the mid-Holocene about 5000 to 3000 yr BP. The timing of this mid-Holocene treeline change

in central Canada does not coincide with early Holocene treeline advance in northwestern Canada, and cannot be attributed to the maximum in high-latitude summer insolation predicted by the Milankovitch theory (Ritchie et al., 1983). MacDonald et al. (1993) argue that the contrasting Holocene environmental changes recorded in central and northwestern Canada reflect regionally asynchronous shifts in the summer position of the Arctic frontal zone. As a consequence, a northward shift of the Arctic frontal zone at 5000 yr BP in central Canada would have produced warmer and moister conditions due to strong Pacific air mass influence in summer. In contrast, a southward movement following 3000 yr BP would have triggered treeline retreat in response to increased influence by cool and dry arctic air masses (MacDonald et al., 1993; Edwards et al., 1996). In addition, regional differences in the climatic history may have been caused by asynchronous fluctuations in ice flow patterns along the retreating Laurentide Ice Sheet margin (e.g., Dyke and Prest, 1987). For example, the melting of inland ice masses in the Keewatin sector to the east of Yellowknife was much delayed, and it is possible that the prolonged proximity to Laurentide Ice, as well as the expansion of glacial lake waters (e.g., glacial Lake McConnell) around its margin, have precluded the expression of earlier warmth in the Great Slave Lake region.

Overall, the diatom-inferred records of DOC imply a southward retreat of treeline (and/or a decrease in forest cover density) and decrease in lake productivity beginning around 3000 yr BP. In Toronto Lake and, to a lesser extent in Queen's Lake, this trend is paralleled by decreasing numbers of alkaliphilic taxa (e.g. *Fragilaria pinnata*, *Achnanthes minutissima*, and *Navicula seminulum*) and their continuous replacement by an increasing number of acidophilic and acidobiontic taxa (e.g. *Eumotia* spp., *Achnanthes marginulata*, *Frustulia* spp., *Brachysira brebissonii*, *Navicula mediocris*, *Pinnularia interrupta*, and *Cymbella* spp.) and chrysophyte cysts over time. The trajectories of the diatom-inferred DOC profiles also seem to indicate a trend towards oligotrophication in the recent history of both lakes. Loss of base cations due to weathering processes, especially during the early limnic history, as well as increasing paludification of the watershed, are likely causes for the long-term natural acidification observed in both lakes.

The coincidence between intervals of increased diatom-inferred DOC and periods of open hydrology, as recorded by analyses of $\delta^{18}\text{O}_{\text{cellulose}}$ (B. B. Wolfe et al., 1996), seems to support the notion of increasing DOC concentrations and water color with decreasing water residence times (cf. Curtis and Schindler, 1997 and references therein). The results obtained from Queen's and Toronto lakes, as well as studies of modern lakes (e.g., Korsman et al., 1994), also suggest that vegetational changes in a lake's catchment, such as invasion by spruce and infilling of forest cover, may promote nutrient enrichment and elevated lake productivity, in contrast to scenarios of lake acidification (Ryan and Kahler, 1987; Whitehead et al., 1989). In this context, the patterns in diatom species trajectories observed in the stratigraphies of the two study sites are very interesting. For example, the small alkaliphilic *Fragilaria* taxa (*F. brevistriata*, *F. construens* var. *venter*, *F. pinnata*) not only show high abundances during the early ontogenetic phase in Toronto Lake (the corresponding phase in Queen's Lake is truncated), but also during the warmer and wetter climatic episodes of the mid-Holocene (see Figs. 2, 3). Early *Fragilaria* spp. peaks are common features of Holocene lake ontogenies, and are most often attributed to strong initial supplies of lake alkalinity resulting from base cation leaching from unweathered catchment soils and tills (e.g., Smol, 1983). Previous studies have related catchment-derived

variations in alkalinity to changes in temperature (Sommaruga-Wögrath et al., 1997; Koinig et al., 1997) and hydrological conditions (Psenner, 1988; Schindler et al., 1990, 1996) that are affecting the physicochemical properties of lakes (e.g. through changes in water residence time, acid-base balance, duration of interaction between runoff and soils, duration of lake ice cover). Explanations for the ensuing smaller mid-Holocene *Fragilaria* spp. peaks in Queen's and Toronto lakes must be sought by implying alkalinity increases due to increased throughflow and replenishment of dissolved CO_2 (as evidenced by the stable isotope data (B. B. Wolfe et al., 1996) and the diatom-inferred DOC profiles), thereby favoring the alkaliphilic *Fragilaria* species. It remains uncertain whether increased reactive organic matter (as reflected by the LOI profiles) has contributed significantly to in-lake alkalinity production via sulfate reduction and denitrification in the sediments (Schindler 1986, 1988). Furthermore, reduced UV (ultraviolet) penetration due to higher DOC concentrations may have resulted in a diminished UV inhibitory effect on periphytic littoral diatoms as suggested by Vinebrooke and Leavitt (1996) for alpine lakes.

The diatom-inferred profiles of DOC suggest that highest concentrations prevailed during the period of a northward advance of treeline and/or infilling of forest cover (Figs. 2, 3). Increases in lake productivity and nutrient enrichment are also reflected in increased diatom concentrations (Fig. 2) and higher total organic matter content (Figs. 2, 3). They are also correlated with higher spruce pollen concentrations, which may indicate a possible additional fertilization effect during these periods through increased atmospheric deposition of macronutrients by pollen (e.g., Doskey and Ugoagwu, 1989; Lee et al., 1996). However, of greater importance for these variations in lake productivity were the vegetational and hydrological changes that accompanied the climatic shifts, resulting in rising external humus inputs from catchment vegetation and soils. Because in northern oligotrophic lakes the pool of DOC, particularly coloured organic matter, is dominated by external inputs to the pelagic zone (Wetzel, 1992), concentrations of DOC, and the staining of water by DOC from terrestrial runoff, are closely correlated with catchment properties, such as the composition and density of terrestrial vegetation (e.g., spruce trees; Pienitz et al., 1997a, 1997b; Vincent and Pienitz, 1996). As a consequence, diatom-based reconstructions of DOC can be used as a proxy for past vegetational shifts (Pienitz, 1993; Pienitz and Smol, 1993). In the present study, the strong linkage between terrestrial and aquatic ecosystems is shown by the highly correlated trajectories of diatom-inferred DOC and *Picea mariana* pollen in the history of both lakes (Figs. 2, 3).

The quantitative reconstructions of DOC illustrated in Figures 4 and 5 are preliminary, so, at this time, these profiles should be interpreted with care. They also revealed some important shortcomings in quantitative environmental reconstructions, especially when dealing with calibration sets that are not sufficiently large enough to capture the diversity of past diatom communities, resulting in "no-analog" situations between modern and fossil samples. For example, the relative abundance of *Fragilaria pinnata* did not exceed 30% in our modern calibration samples (Pienitz and Smol, 1993), whereas core samples showed percentages exceeding 60% (e.g., between 167.5 to 165.0 cm depth in the Toronto Lake core), leading to poor performance of the transfer functions. Similar discrepancies between past and present algal communities have been frequently observed in sediment cores, in particular during early Holocene periods (e.g., Wilson, 1996; A. P. Wolfe, 1996). More accurate quantitative inferences will eventually be achieved by enlarging the size of

the diatom calibration sets (which should increase the number of taxa in the transfer functions), thereby decreasing the likelihood of misleading information in downcore reconstructions.

The present study extends earlier, qualitative approaches by providing the first diatom-based quantitative reconstructions of past lakewater DOC concentrations at the northern treeline in North America. Future scientific efforts should focus on improving these techniques and making them more vigorous in order to refine environmental reconstructions. A better understanding of past variations in water chemistry (e.g., changes in DOC concentrations) will improve interpretations of catchment-lake linkages based on paleolimnological studies, and will allow us to address other important aspects of global change, such as changes in past underwater light environments.

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