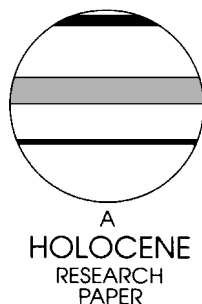


Holocene lake succession and palaeo-optics of a Subarctic lake, northern Québec, Canada

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Abstract: Two diatom-based transfer functions for the reconstruction of past levels of dissolved organic carbon (DOC) and water colour were applied to fossil diatom species assemblages from a coastal isolation basin on the eastern shore of Hudson Bay. Diatom stratigraphic changes and the diatom-inferred patterns of limnological change following the retreat of Holocene marine waters of the Tyrrell Sea revealed a highly variable Holocene lake trajectory associated with successional shifts in lake catchment vegetation and soil development. The main trends observed in the Holocene history of Lake Kachishayoot are: (1) a progressive loss of alkalinity over time; and (2) abrupt increases in DOC and water colour that coincide with the arrival of spruce (*Picea mariana*) in the catchment. Reconstructed DOC allowed the estimation of past depths of ultraviolet (UV) penetration in the water-column of Lake Kachishayoot. Past variations in biological UV exposure were inferred using optical models based on DOC concentrations and the response curves for DNA damage and UV photoinhibition of photosynthesis. The palaeoecological analyses revealed large changes in the underwater photobiological environment over the course of the Holocene period, from extremely high UV exposure after the initial formation of the lake and its isolation from the sea, to an order-of-magnitude lower biological UV exposure under the present conditions of catchment vegetation.

Key words: Diatoms, succession, lake sediments, dissolved organic carbon, DOC, water colour, palaeo-optics, ultraviolet radiation, UVR, Holocene, Subarctic, Québec, Canada.

Introduction

Global climatic change is likely to have wide-ranging effects on high-latitude freshwater ecosystems. One of the primary mechanisms of impact may be through variations in the export of terrestrially derived dissolved organic material (DOM) from their surrounding catchments that would result from changes in catchment hydrology and vegetation (Pienitz and Vincent, 2000). DOM is a 'master' variable that will affect many aspects of lake ecosystem structure and function (Williamson *et al.*, 1999). Lakes located in tundra zones are for the most part clear, shallow, oligotrophic systems, with low nutrient and DOM content directly related to sparse vegetation and poor soil development in their catchments (Engstrom, 1987; Vincent and Pienitz, 1996; Gibson *et al.*, 2001). The predicted possible northward shift of the forest

boundary in certain areas of the northern circumpolar region associated with global warming (Smith *et al.*, 1992) highlights the need to understand the potential response of these northern ecosystems and the magnitude and effects of changes in DOM loading to Subarctic lakes.

In addition to climatic change, the role of ultraviolet radiation (UVR, wavelength 280–400 nm) in marine and freshwater ecosystems has attracted considerable attention since the discovery of the thinning of the ozone layer. UVR is the most photochemically reactive waveband of the solar spectrum and is known to have many damaging effects on aquatic biota (Vincent and Neale, 2000). Prospects of increasing ozone depletion, possibly amplified by climatic warming (Staedin *et al.*, 2001), are raising concerns about the response of northern ecosystems to these environmental disruptions. Over the Arctic, total ozone concentrations have dropped on average from 450 Dobson units (DU) in 1970 to less than 350 DU in 1997 (Newman *et al.*, 1997), causing UVR and

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photosynthetically available radiation (PAR) to be increasingly intense at the Earth's surface. Furthermore, ozone depletion is likely to persist throughout the early decades of this century (Staehelin *et al.*, 2001).

The coloured component of the DOM pool in lakes, referred to as coloured (or chromophoric) dissolved organic matter (CDOM), is largely dependent on the vegetation present in the surrounding catchments (Vincent and Pienitz, 1996). It strongly controls transparency and spectral attenuation in the water-column, thereby acting as a natural screen and protecting freshwater biota from certain harmful effects of UVR (Vincent and Roy, 1993; Morris *et al.*, 1995; Schindler and Curtis, 1997). The vast majority of the lakes located in temperate and boreal zones have relatively high DOC contents and are therefore well protected from the damaging effects of UV penetration. However, high-latitude freshwater ecosystems generally contain low concentrations ($< 4 \text{ mg C l}^{-1}$) of CDOM. Within this range, small variations in CDOM concentrations translate into major fluctuations in underwater UVR (Laurion *et al.*, 1997).

The prospect of accelerated climatic change in the northern environment has underscored the need for the development and application of palaeolimnological techniques to provide information about the causes and effects and the magnitude of change of past environmental variations in northern lakes. Freshwater diatom communities seem to respond directly to changes in DOC concentration and associated changes in water transparency. Previous work has shown that past shifts in catchment vegetation of lakes (associated with changes in climate) located at the treeline have coincided with drastic limnological changes reflected by fossil diatom assemblages in lakes from Arctic and alpine regions (MacDonald *et al.*, 1993; Lotter *et al.* 1999; Pienitz *et al.*, 1999). In light of this, since there is a strong correlation between DOC concentration in a lake and the vegetation in its catchment (Vincent and Pienitz, 1996; Pienitz *et al.*, 1999), DOC can be reliably linked to climate through diatom analyses. However, few studies have focused on the historical variations of DOC and how they have influenced the spectral regime of ecotonal freshwater ecosystems throughout the Holocene.

Quantitative diatom-based models for reconstructing DOC and water colour were developed recently from lakes in northern Québec (Fallu and Pienitz, 1999) and Labrador (Fallu *et al.*, 2002). In the present study, we applied these transfer functions to infer past DOC concentrations and water transparency to the diatom biostratigraphical sequence of a Subarctic lake near the eastern shore of Hudson Bay, Québec. We then applied a model describing the spectral attenuation of UVR and a biological exposure index (T^*) to the inferred DOC values. This approach thus combines the analyses of fossil diatom assemblages preserved in Holocene sedimentary deposits with bio-optical models based on present-day conditions, in order to infer postglacial lake succession and the palaeo-optical regime (past variations in underwater solar radiation) of a Subarctic freshwater ecosystem.

Study site

The eastern coast of Hudson Bay has a continental Subarctic climate, with a mean annual temperature (1968–98) at Kuujuaaraapik-Whapmagostui of -4.5°C (Environment Canada, 1999). Annual precipitation is about 660 mm, 40% of which falls as snow (Bégin *et al.*, 1993). Because of the harshness of the coastal climate, a band of forest-tundra extends along the coast (Figure 1). This biome is characterized by patchy forest and discontinuous permafrost (Payette, 1983; Allard and Séguin, 1987).

Lake Kachishayoot (local Cree name; $55^\circ20.0'N$, $77^\circ37.4'W$) is located *c.* 3 km inland from the eastern shore of Hudson Bay, near the town of Kuujuaaraapik-Whapmagostui in northwestern

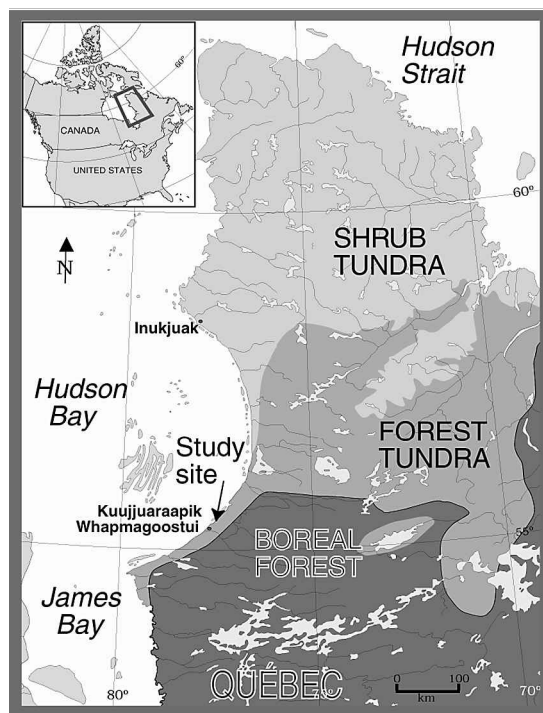


Figure 1 Location of Lake Kachishayoot in northern Québec, Canada.

Québec (Figure 1). It lies on granite-gneiss rocks of the Precambrian Canadian Shield at an altitude of *c.* 100 m above sea level. It is a relatively shallow ($Z_{\text{max}} = 5 \text{ m}$), oligotrophic lake, with a mean water temperature of about 4°C in winter and between 13 and 20°C in summer. Lake basin and catchment areas are 29.5 ha and 210 ha, respectively. The main inflowing stream passes through four other lakes and a wetland zone before entering the lake. Current limnological conditions are summarized in Table 1 and are described in detail by Gibson *et al.* (2001).

In the catchment, organic and mineral soils are restricted to the margins of water bodies and to areas protected from the wind. Peatlands, which comprise about 5% of the catchment, are found

Table 1 Mean values of various limnological variables in Lake Kachishayoot during the summer of 1998 (the number of measurements (N) is included in parentheses following the values)

Temperature ($^\circ\text{C}$)	13–20 (29)
Transparency (Secchi depth) (m)	3.3 (21)
pH	6.7–7.2 (28)
Conductivity ($\mu\text{S cm}^{-1}$)	30–40 (29)
Dissolved O_2 (mg l^{-1})	9.7 (29)
Total carbon (mg C l^{-1})	6.4 (12)
CID (mg C l^{-1})	2.4 (12)
COD (mg C l^{-1})	3.9 (12)
Particulate organic carbon (mg C l^{-1})	0.8 (7)
Soluble reactive phosphorus ($\mu\text{g l}^{-1}$)	1 (16)
SiO_2 (mg l^{-1})	1.1 (16)
Chl <i>a</i> total ($\mu\text{g l}^{-1}$)	0.9 (12)
SO_4 (mg l^{-1})	2.3 (16)
Al (mg l^{-1})	0.04 (12)
Ba (mg l^{-1})	0.05 (12)
Ca (mg l^{-1})	2.6 (12)
Cl (mg l^{-1})	5.3 (16)
Total Fe ($\mu\text{g l}^{-1}$)	41 (12)
K (mg l^{-1})	0.3 (12)
Mg (mg l^{-1})	0.9 (12)
Mn (mg l^{-1})	0.02 (12)
Na (mg l^{-1})	3.3 (16)
Total Sr ($\mu\text{g l}^{-1}$)	18 (12)

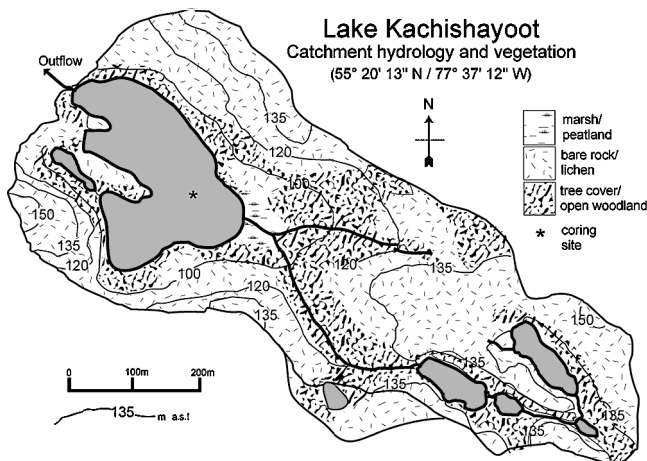


Figure 2 Catchment vegetation and hydrology of Lake Kachishayoot.

in depressions. A thin layer of mosses and lichens (mainly *Cladina stellaris*) growing on bedrock covers most of the catchment (roughly 70%). Areas relatively well protected from the wind support spruce (*Picea mariana*, *P. glauca*), willow (*Salix* spp.), birch (*Betula glandulosa*) and alder (*Alnus crispa*) and an assemblage of low-lying plant species dominated by *Empetrum nigrum* and *Ledum groenlandicum* (Figure 2).

Materials and methods

Field methods

Two sediment cores were taken from the deepest part of the lake in June 1998. A short (36 cm) and long core (80 cm) were collected with a gravity corer (Kajak-Brinkhurst-type) and a piston corer (modified Livingstone; Livingstone, 1955), respectively. Subsampling of the cores into 0.5 cm sections and extraction of macrofossils for AMS dating were performed in the field and in the lab. Sediment subsamples were kept in plastic bags and macrofossils in glass vials (at 4°C) in the dark until treatment.

Radiocarbon dating

Four accelerator mass spectrometry (AMS) ^{14}C dates were performed at Isotracer Laboratory, Toronto, Canada, on plant macrofossils from the long core (Table 2). Dates TO-7591 and TO-7593 provided only 70 μg and 130 μg of datable carbon, respectively, and were therefore analysed at a much reduced precision (R.P. Beukens, personal communication). They were rejected based on their large potential errors (± 500 and ± 150 ^{14}C yr). Dates TO-

Table 2 Calibrated radiocarbon (AMS) dates from the sediment of Lake Kachishayoot, Québec. The calibrated dates in calendar years BP are the midpoint of the probability range of dates calculated using method B in CALIB v. 3.03 (Stuiver and Reimer, 1993); dates in bold were used to infer sedimentation rates

Lab. number	Depth (cm)	Material (mass used in mg)	Age (^{14}C yr BP)	Age (cal. yr BP)
TO-7591	11.0	<i>Picea mariana</i> needle (2.4)	2000 \pm 500	2027 \pm 954
TO-7592	34.0–34.5	Wood fragment (5.5)	1420 \pm 80	1334 \pm 68
TO-7593	50.5	Herbaceous plant fragment (1.6)	4340 \pm 150	4918 \pm 403
TO-7594	79.0	<i>Ledum</i> twig (17.1)	4640 \pm 70	5378 \pm 92

7592 and TO-7594 were used for estimating crude sedimentation rates by dividing the number of cm by the number of years in each of the two intervals.

Laboratory methods

The organic matter content of the sediments (loss-on-ignition, LOI) was determined by drying samples at 65°C for 24 hours and subsequent combustion at 550°C for two hours. Extraction of diatom fossils followed standard acid (nitric/sulphuric) digestion techniques (Pienitz *et al.*, 1995). Diatom counts at 2.5 cm intervals (except within the first 1 cm of the surface and between 37.5 and 38.5 cm, where every 0.5 cm was investigated) were carried out using a Leica DMRB light microscope at a magnification of $\times 1000$ under oil immersion. In total, 38 samples were counted and a minimum of 500 valves per sample was counted in order to characterize each diatom assemblage. Taxonomic identification mainly followed Fallu *et al.* (2000) in order to guarantee taxonomic conformity with quantitative inference models developed for the study region.

The complete sedimentary sequence (short-core and long-core data) was established by identifying and matching the corresponding levels in the diatom stratigraphy, as well as loss-on-ignition (LOI) and water-content data.

Statistical methods

Relative abundances of the most common diatom species (contributing at least 5% of the total valve count in at least one sample) were plotted using TILIA (2.00 version, Grimm, 1991) and TILIAGRAPH (1.25 version, Grimm, 1991–93). A stratigraphically constrained cluster analysis (CONISS, Grimm, 1987) was performed in order to identify zones in the diatom stratigraphy. The Edwards and Cavalli-Sforza chord distance was taken as the dissimilarity coefficient in order to emphasize the weight of subdominant species by downweighting dominant taxa, maximizing the signal-to-noise ratio (Overpeck *et al.*, 1985).

Two different diatom-based inference models were used to reconstruct variations in DOC and water colour in Lake Kachishayoot. These models are based on the distribution of modern diatom assemblages in two separate calibration sets. The first was from northwestern Québec, in which a multivariate relationship was established between DOC and diatom community structure in 59 lakes (Fallu and Pienitz, 1999) spanning boreal forest through Arctic tundra (Figure 1). The second calibration set related water colour to diatom composition and was derived from 63 lakes along a broad range of vegetation types in Labrador. These models show a strong relationship between diatom assemblages and DOC and water colour, respectively, with a jack-knifed r^2 of 0.81 and a root mean squared error (RMSEP_{jack}) of 0.088 $\log(\text{mg C L}^{-1})$ for DOC and a jack-knifed r^2 of 0.85 and a RMSEP_{jack} of 0.18 $\log(\text{Pt-units} + 1)$ for water colour. DOC and water colour are typically related with each other and with CDOM (Rasmussen *et al.*, 1989; Gibson *et al.*, 2000). This approach based on two separate models therefore provided two independent means of reconstructing historical variations in CDOM that in turn affected underwater UV exposure.

The models were not applied to the 6–8 lowermost analysed depth intervals of the core (depending on the model used) because diatom community composition at the bottom of the core was of marine origin and outside the bounds of the training sets (there was no species overlap). For the intervals to which the models were applied, we adopted the same cut-off criteria for diatom species as was used in the models, i.e., at least 1% relative abundance in at least one sample. Quantitative reconstructions were performed using CALIBRATE version 1.0 (Juggins and ter Braak, 1992), which is a program for exploring species-environment relationships and developing transfer functions.

Since reconstructed values for the two environmental variables

(DOC and water colour) are likely to be more reliable if the fossil samples have close analogues within the calibration sets (Birks *et al.*, 1990), we used the computer programs ANALOG (J.M. Line and H.J.B. Birks, unpublished program) and CANOCO 3.12 (ter Braak, 1988; 1990) to evaluate the degree of overlap between the fossil and modern (calibration) sets, and to evaluate how reliably the models could infer DOC and water colour for each core sample (see captions to Figures 4 and 6 for more detail). We followed the screening procedures outlined in Laird *et al.* (1998) and Laing *et al.* (1999b), i.e., we used the squared chord distance as dissimilarity coefficient in ANALOG in order to put emphasis on subdominant species and to lessen the weight of dominant species; fossil samples with dissimilarity coefficients (D.C.) >95% confidence interval were considered to have no analogues in the calibration set and those with D.C. >75% confidence interval to be poor analogues based on the mean minimum D.C. distance within the calibration set (Figures 4 and 6).

Following these statistical screening procedures, the diatom-inferred DOC (DI-DOC) values were used to calculate the attenuation coefficient for UVR at 320 nm (K_d) as well as the underwater biological exposure index (T^*) that integrates the effective exposure to UVR at all wavelengths (Vincent *et al.*, 1998b, Gibson *et al.*, 2000; Pienitz and Vincent, 2000). These two parameters allowed evaluation of the potential effects of changes in the underwater light regime on the aquatic biota throughout the Holocene history of Lake Kachishayoot. The diffuse attenuation coefficient (K_d) was calculated as:

$$K_d(\lambda) = 10^{c+m \cdot \log[\text{DOC}]} \quad (1)$$

where c is the intercept and m the gradient from the graphic representations of K_d as a function of DOC for lakes in the Subarctic region of Québec, and where c and m vary according to wavelength. This model is used to define vertical solar attenuation as a function of wavelength for different bio-optical conditions, so that this information can be combined with measured or inferred UVR data (Laurion *et al.*, 1997).

Several indices were adopted to trace the past underwater optical environment of Lake Kachishayoot, specifically in the time interval since the establishment of a diatom flora dominated by freshwater taxa (i.e., from the time DI-DOC values were positive). First, the percent surface UV radiation (320 nm) at 2 m depth was estimated as:

$$E = 100 e^{-2K_{d320}}$$

where K_{d320} is the diffuse attenuation coefficient at 320 nm.

Then, the underwater biological UV exposure index (T^* ; Vincent *et al.*, 1998b; modified in Gibson *et al.*, 2000) was applied using the weighting function ($\epsilon_{\lambda,r}$) for two types of photobiological damage caused by UVR, photoinhibition of photosynthesis (T^*_{PI}) and photodegradation of DNA (T^*_{DNA}). T^*_{PI} and T^*_{DNA} were calculated as:

$$T^* = \int_{290}^{400} E_{\lambda,r}^0 F_{\lambda,w} \epsilon_{\lambda,r} (1/K_{d,\lambda}) d\lambda \quad (3)$$

where $E_{\lambda,r}^0$ is the relative surface irradiance and $F_{\lambda,w}$ a factor accounting for the effect of ozone depletion on incident UV radiation (details in Gibson *et al.*, 2000). The latter factor was set to 1.0 at all wavelengths to calculate underwater biological exposure (T^*) in the absence of ozone variations. The T^* values are expressed in metres, reflecting the depth of penetration of UVR weighted for its spectral-dependent biological effects.

Results and discussion

Core chronology and sedimentology

Our AMS dates yielded sedimentation rates of $\sim 0.01 \text{ cm yr}^{-1}$ between depths of 79 cm and 34.5 cm and of $\sim 0.025 \text{ cm yr}^{-1}$ between depths of 34.5 cm and 0 cm. The paucity of reliable dates limits our ability to define the exact timing of changes in the lake and surrounding catchment. We therefore place emphasis on the sequence rather than the absolute chronology of events.

The sedimentary sequence recovered from Lake Kachishayoot was made up of 13 cm of silty clay, a relic of the postglacial Tyrrell Sea in the area, overlain by 67 cm of organic mud (gyttja), representing accumulation throughout the subsequent lake phase (see lithology, Figure 3). The two units were separated by a poorly defined isolation interface, showing gradual change and suggesting that the sediment sequence was not interrupted.

Loss-on-ignition (LOI) analysis can be used as a proxy for minerogenic *in situ* production and inwash, but it is a technique most commonly used as a proxy for in-lake production and for the amount of organic matter exported to the lake basin from catchment vegetation and soils. Our LOI analyses (at 550°C) yielded very low values in the clay-rich section (average of 4.4%), gradually increasing throughout the accumulation of gyttja (14.6% average in the lowermost section, between depths of 67 and 63 cm, and 19.3% on average in the uppermost section, between 63 cm and the surface).

Biostratigraphy

The evolution of Lake Kachishayoot is intimately linked to the strong glacial isostatic adjustment of the southeastern Hudson Bay coast and to Holocene recolonization of the emerging landscape by terrestrial vegetation. Information concerning the palaeogeography and isolation of the Lake Kachishayoot basin from marine influence by the postglacial Tyrrell Sea is given in Saulnier-Talbot and Pienitz (2001).

The relative abundances of the most common diatom species, sorted according to three salinity categories (Campeau *et al.*, 1999; Germain, 1981; Hustedt, 1957; Krammer and Lange-Bertalot, 1986–91; Peragallo and Peragallo, 1897–1908), are shown in Figure 3. The main variable affecting the overall changes in the diatom assemblages over the early history of Lake Kachishayoot was salinity, as the basin became gradually isolated from marine influence (Saulnier-Talbot and Pienitz, 2001). However, beyond zone 2b (Figure 3), when the assemblages are dominated by halophobous species, it is unlikely that salinity remained the determining factor in the subsequent assemblage shifts. A gradual loss of alkalinity over time seems to be linked to a corresponding increase in DOC concentrations (as also observed in Alaska by Engstrom *et al.*, 2000). We therefore suggest that DOC became the main variable influencing the diatom assemblages throughout zones 2b and 3.

After 69 cm depth, marine species abruptly disappear, and are replaced by an assemblage dominated by small *Fragilaria* taxa (*F. elliptica*, *F. pseudoconstruens*, *F. brevistriata*, *F. pinnata* and *F. pinnata* var. *intercedens*). These species are considered opportunistic, as they are well adapted to euryhaline conditions and to a very short season of growth, and are also considered to be pioneers, since they are often found during the initial phases of lakes located above sea level (Haworth, 1975; Marciniak, 1986) and during isolation phases of lake basins during periods of retreating marine waters (Stabell, 1985; Pienitz *et al.*, 1991; Zong, 1997; Seppä and Tikkanen, 1998).

The freshwater (halophobous) taxa found in zones 2b and 3 are typical of Subarctic lakes located on either side of the treeline in northern Québec (Fallu *et al.*, 2000; Ponader *et al.*, 2002). The assemblages in these two zones are strongly dominated by *Fragilaria elliptica*, *F. pseudoconstruens*, *F. virescens* var. *exigua* and

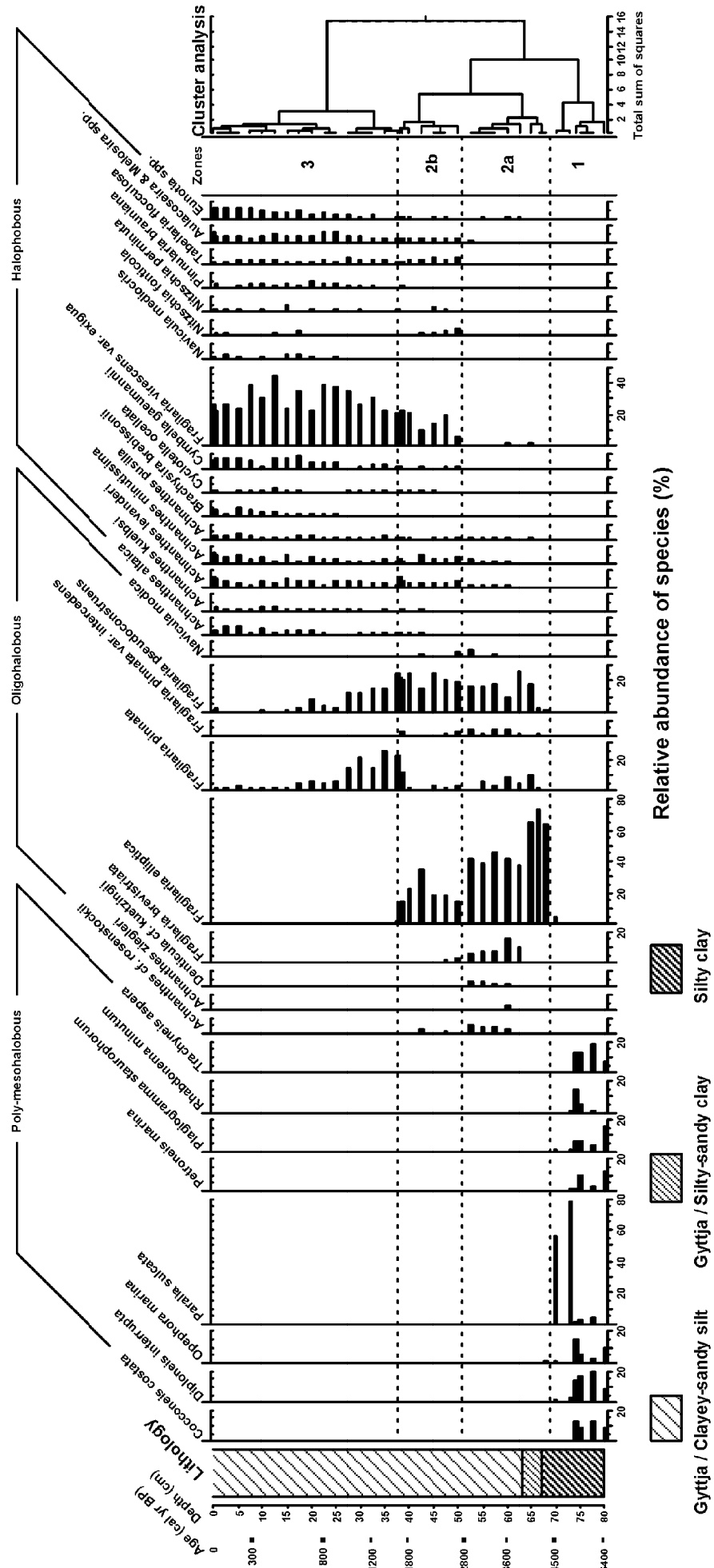


Figure 3 Core lithology and diatom diagram showing relative abundances of most common diatom taxa, and diatom zones as indicated by cluster analysis.

F. pinnata. Various *Achnanthes* species (*A. altaica*, *A. levanderi*, *A. minutissima*, *A. pusilla*) and *Cymbella gaeumannii* are also present in the assemblage of zone 3. These small freshwater taxa are commonly found in circumneutral oligotrophic Subarctic waters. In fact, Laing *et al.* (1999a) report that similar assemblages have been observed in Québec-Labrador (Fallu *et al.*, 2000), the Northwest Territories and the Yukon (Pienitz and Smol, 1993; Pienitz *et al.*, 1995), Alaska (Gregory-Eaves, 1998), Fennoscandia (Pienitz *et al.*, 1995; Weckström *et al.*, 1997) and western Siberia (Laing *et al.*, 1999b). This clearly outlines the circumpolar character of the freshwater diatom flora of Lake Kachishayoot.

Diatom-inferred DOC (DI-DOC)

The reconstructed DOC curve (Figures 4a and 5b) shows that concentrations in Lake Kachishayoot remained at levels below 2 mg C l^{-1} for a long period following basin isolation from the sea, despite high occurrences of *Sphagnum* spp. (Figure 5f) and aquatic plant macrofossils (Figure 5g). At values less than 2 mg C l^{-1} , DOC is considered to be mostly autochthonous (produced by in-lake processes) and therefore having a much lower contribution of CDOM than DOC from allochthonous (catchment) sources (Laurion *et al.*, 1997; Vincent *et al.*, 1998b).

Rising DOC levels coincide with the appearance of spruce (as evidenced by macrofossil analysis) in the catchment of the lake in zone 2b (Figure 5e), thereafter reaching levels of 4 mg C l^{-1} and maximum concentrations of close to 6 mg C l^{-1} in zone 3, with only a slight decrease thereafter. The synchronous increase that can be observed between DI-DOC and the *Picea* needle curve at the beginning of zone 3 lends support to observations of many other authors (e.g., Engstrom, 1987; Pienitz and Smol, 1993; Blom *et al.*, 1998; Seppä and Weckström, 1999) that relate DOC concentrations in small, oligotrophic boreal lakes to organic matter loading from catchment vegetation and soils.

In the most recent part of the sedimentary sequence, there is a substantial drop in the occurrence of *Picea* needles; however, the DI-DOC and DI-water colour curves do not reflect this decrease. We suspect that, despite a reduction in tree cover, the development of the soils and the expansion of a peatland in the catchment

(Miousse, 2001) might have maintained relatively stable DOM inputs into the lake.

The analogues for the fossil diatom assemblages in the modern calibration model from northwestern Québec are generally very good throughout most of the freshwater phase (65.0 cm to 0.0 cm, within the 95% confidence interval), especially in the upper part of the core (38.0 to 0.0 cm), where they are within the 75% confidence interval (Figure 4b). Not surprisingly, due to their marine origin, the diatom species identified in samples between 80.0 and 69.5 cm are not found in the calibration set. For this reason, it was impossible to infer any DOC values at these depths. The first two levels for which DOC values could be inferred (68.0 and 66.0 cm) have diatom assemblages for which good analogues were not available, due to differences in the relative abundance of dominant taxa in the data sets (which explains the occurrence of negative DI-DOC values). At these two levels in the core, the dominant taxon is *F. elliptica* (with relative abundances of 64% and 74%, respectively). Although this species also occurs in the calibration set, its relative abundance never exceeds 1.4%. According to the goodness-of-fit test (Figure 4c), all the assemblages for which DOC was inferred are within the 95% confidence interval, with particularly strong correlations between 38.0 and 0.0 cm. This indicates that the calibration model is capable of inferring DOC variations in the sediment sequence of Lake Kachishayoot. The DI-DOC concentration for the most recent (surface) sediments (4.6 mg C l^{-1}) is close to the mean value measured in the summer of 1998 (3.9 mg C l^{-1} with a range of $0.733 \text{ mg C l}^{-1}$, i.e., 3.7 to 4.4 mg C l^{-1}).

Diatom-inferred water colour (DI-water colour)

Due to more substantial differences between the fossil assemblages in Lake Kachishayoot and modern diatom communities in the calibration model from Labrador, the reconstructed values for water colour should be considered with caution. In spite of this, the goodness-of-fit test (Figure 6c) shows that all the assemblages except one (65.0 cm, the first inferred value) are within the 95% confidence interval, which suggests that overall inferred trends are reliable.

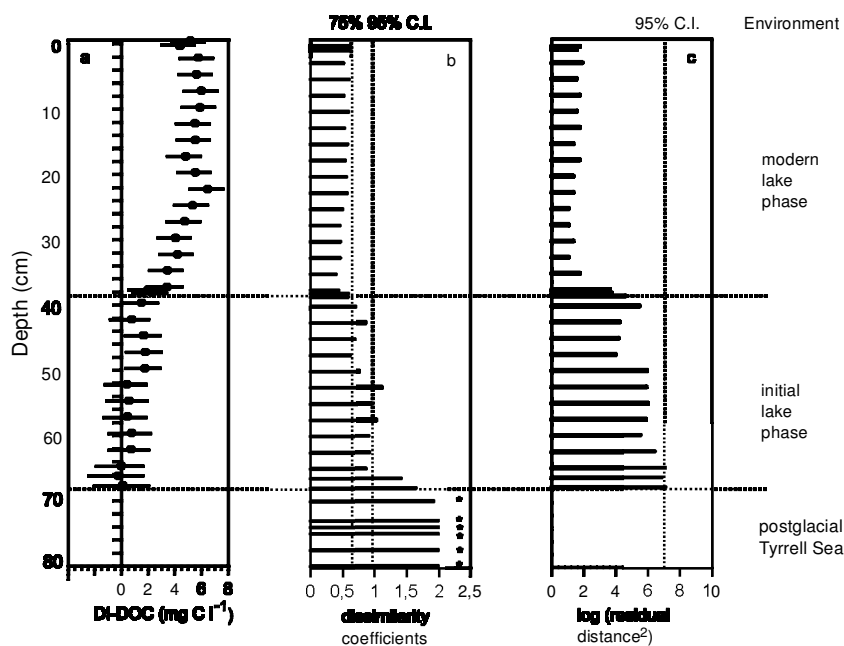


Figure 4 Results of the statistical analysis of fossil diatom assemblages in relation to the DOC model. Asterisks (*) indicate levels where less than 70% of the core diatom assemblages was represented in the calibration model. (a) Reconstructed DOC values (dots) and their errors (lines) in mg C l^{-1} . (b) Analogues between the two data sets (modern + fossil). Core samples above the 95% confidence intervals (CI) were considered to have no analogues in the calibration set, while samples between 75 and 95% were poor analogues. (c) DOC analogues of the fossil diatom assemblages. The samples with residual log distances exceeding the CI are considered poor DOC analogues.

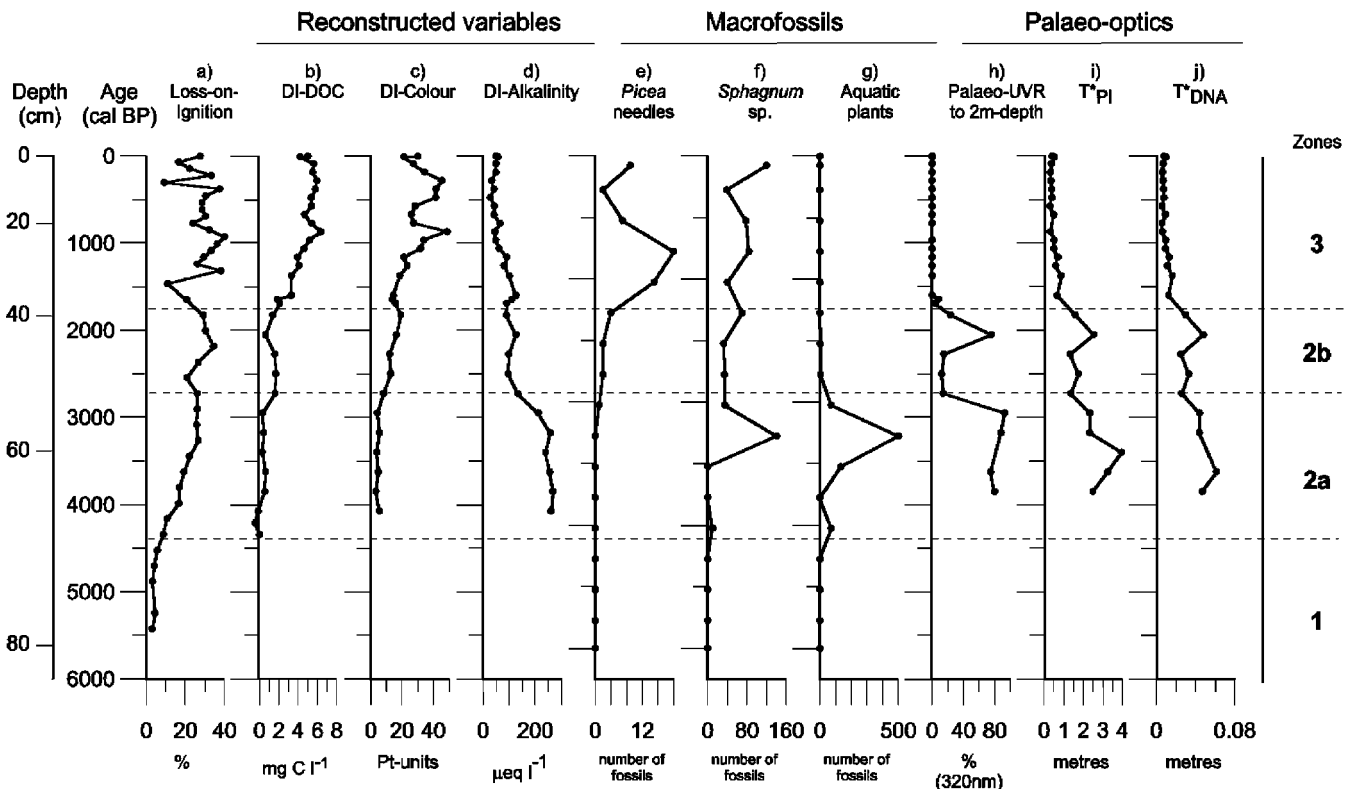


Figure 5 Summary of limnological and palaeo-optical changes in Lake Kachishayoot.

Despite the use of an inference model developed from diatom assemblages from a different region (Labrador), reconstructed water colour trends (Figures 5c and 6a) closely parallel those inferred for DOC. Values remain low (8.1 Pt-units) until the appearance of spruce in the lake catchment and thereafter increase steadily, reaching successive peaks of 47.0 and 43.5 Pt-units during the last millennium.

A similarly close correlation between DI-water colour and DI-total organic carbon reconstructions was also observed by Seppä

and Weckström (1999) in a small, oligotrophic, circumneutral lake in the treeline ecotone of northern Finland. In this case, the increase in these two variables during the Holocene is associated with the expansion of pine and the subsequent development of peatlands in the catchment (and in the region; inferred from pollen and spore analysis). The results of both this study and our study suggest that catchment vegetation in boreal treeline ecotones, which is closely linked to climate, exerts a major control on long-term variations in lake water colour and DOC.

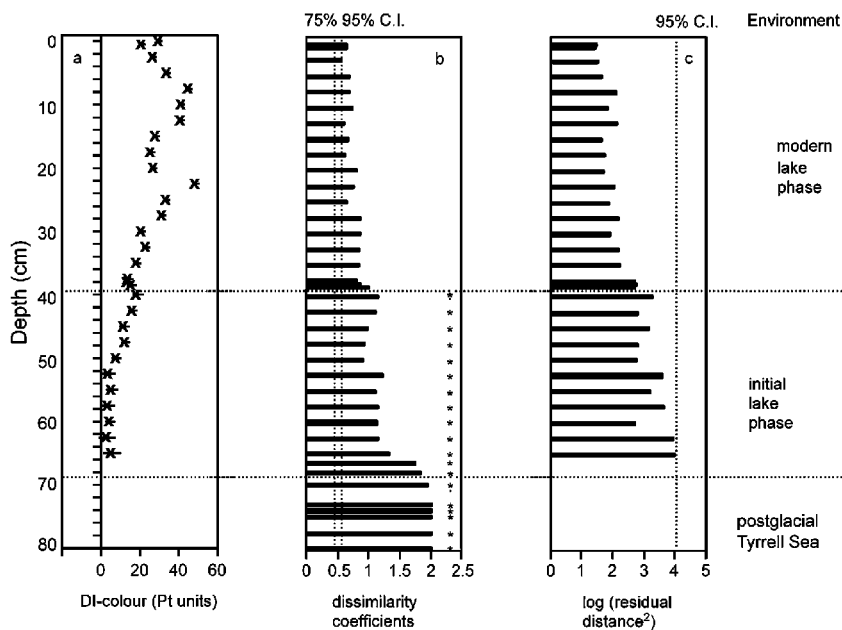


Figure 6 Results of the statistical analysis of fossil diatom assemblages in relation to the water colour model. Asterisks (*) indicate levels where less than 70% of the core diatom assemblages was represented in the calibration model. (a) Reconstructed water colour values (crosses) and their errors (lines) in Pt units. (b) Analogues between the two data sets (modern + fossil). Core samples above the 95% confidence intervals (CI) were considered to have no analogues in the calibration set, while samples between 75 and 95% were poor analogues. (c) Water colour analogues of the fossil diatom assemblages. The samples with residual log distances exceeding the CI are considered poor water colour analogues.

Palaeo-UVR

Lake Kachishayoot presently has a maximal depth of 5 m and an estimated average depth of 2.8 m (Miousse, 2001) and shows DOC concentrations that vary over the summer between 3.7 and 4.4 mg C l⁻¹ (Gibson *et al.*, 2001). This means that 380 nm wavelengths are completely blocked at a depth of about 2 m in the water-column. Figure 5h shows the trend of past UVR penetration in the water-column at 2 m depth based on DI-DOC values calculated using equation (1). In the early stages of the lake's history, extremely low concentrations of DOC (<2 mg C l⁻¹, before significant increases in *Picea*), offered aquatic biota throughout the entire water-column little protection against UVR. Since the invasion of spruce trees in the lake's catchment, DOC has remained at relatively high values (>4 mg C l⁻¹), which would block UVR completely at the lower water depths. Miousse (2001) reports that Lake Kachishayoot probably experienced water-level fluctuations of the order of ± 1 m above and below its present level during its history.

Among a survey of 32 randomly chosen lakes situated along Hudson Bay between 55° and 60° latitude in northern Québec (Fallu, 1998), only two sites combine DOC concentrations ≤ 4 mg C l⁻¹ and a maximum depth inferior to 2 m. However, many sites are only slightly above these thresholds and can therefore be considered very sensitive to climatic and environmental changes.

Like K_{d} , T^* is inversely proportional to the quantity of DOC in the water. Biological UVR exposure as measured by this index was high in zones 2a and 2b, where DI-DOC was low, and negligible in zone 3, where DI-DOC reached concentrations ≥ 4 mg C l⁻¹ (Figure 5i and j). These analyses suggest that UVR exposure was high in the early stages of the lake's history and then declined to the present day order-of-magnitude lower values during the subsequent period of vegetation development.

Our study, similarly to that of Pienitz and Vincent (2000), suggests that aquatic biota in this type of lake experienced greatest UV exposure immediately following Holocene deglaciation and lake formation (prior to the development of CDOM sources in the catchment). Several studies have shown that epilithic diatoms are highly sensitive to UV radiation (e.g., Bothwell *et al.*, 1993; Vinebrooke and Leavitt, 1996) which reflects their inability to avoid, protect or recover from UV radiation damage (Vincent and Roy, 1993; Vinebrooke and Leavitt, 1999). Despite uncertainties concerning the exact ecology of numerous diatom species, those dominating the zones of greater UV exposure in the history of Lake Kachishayoot (zones 2a and 2b) are usually qualified in the literature as being tychoplanktonic, epipellic, epipsammic or epiphytic, suggesting that these species would have strategies for mitigating or integrating the effects of UVR exposure, thereby increasing their competitiveness in such environments. The marked presence of aquatic plant macrofossils during this early period of higher UVR (Figure 5g) suggests that submerged macrophytes may have compensated for the low phytoplankton production as well as provided an additional substrate for epiphytic diatoms in the water-column during this time. It has recently been observed that certain aquatic plants (e.g., *Potamogeton cheesemani*) show no evidence of stress (measured by photosynthesis) when exposed to light with UV (Rae *et al.*, 2001). It is interesting to note that *Potamogeton filiformis* seeds and *Potamogeton* sp. pollen were identified in the early phases of the development of Lake Kachishayoot (Miousse, 2001), consistent with the observation that this plant is indifferent to UVR.

Through the effects of climatic change on catchment vegetation and CDOM loading, freshwater ecosystems presently located in ecotonal regions are likely to experience major shifts in underwater spectral irradiance in the future. Increased levels of UVR would likely favour aquatic species which either have the ability to avoid harmful UVR (such as epipellic and epipsammic diatoms), have the capacity for DNA repair (such as epilithic filamentous

cyanobacteria and planktonic picocyanobacteria) or have photo-protective pigmentation (such as the rotifer *Hesperodiptomus arcticus*) (Vincent and Roy, 1993; Vinebrooke and Leavitt, 1999). On the other hand, CDOM also absorbs PAR within a waveband that is optimal for photosynthesis. The decreased availability of PAR could therefore disadvantage some species (Milot-Roy and Vincent, 1994; Vincent and Belzile, 2003). Such effects have the potential to cause profound changes in the composition of aquatic food webs which may alter the overall structure and functioning of these ecosystems (Vincent and Roy, 1993; Williamson *et al.*, 1996; Pienitz and Vincent, 2000).

Conclusions

By applying two independently derived models, we demonstrate that our reconstructions of DI-DOC and DI-water colour show reliable and consistent trends in the development of in-lake UV exposure over the Holocene, caused mainly by the gradual colonization of the catchment by conifers and the subsequent increase in organic matter inputs to the lake.

The patterns of limnological and environmental change reconstructed from core sedimentology and fossil diatom and macrofossil records in Subarctic Lake Kachishayoot demonstrate the important links between aquatic and terrestrial environments. Our data support observations by Engstrom *et al.* (2000) on the strong external control exerted by landscape evolutionary processes (primary succession; Matthews, 1992) on lake development, especially during the early period of lake evolution in formerly glaciated and inundated landscapes. Our profiles of DI-DOC and DI-water colour reflect aquatic trends associated with vegetational (e.g., revegetation of the newly deglaciated landscape) and edaphic (e.g., soil weathering, humus buildup) succession in the lake catchment.

The importance of CDOM for attenuating UVR in lakes has been widely acknowledged (e.g., Williamson *et al.*, 1996; Laurion *et al.*, 1997). Vincent *et al.* (1998a) have shown that a 20% change in CDOM concentration (as measured by DOC) can have a much greater effect on the biological exposure of phytoplankton to damaging UV radiation than a similar percentage change in stratospheric ozone. Our results show major variations throughout the Holocene in underwater UV exposure and indicate the potentially large impact of climate-induced vegetation change on lakes across the forest-tundra ecotone. We suggest that treeline lakes in northern Québec, similarly to those studied by Pienitz and Vincent (2000) in the central Northwest Territories, are likely to be strongly affected by the predicted future climatic change which would alter existing conditions in DOM exported from their drainage basins. Our analyses show that these ecosystems have survived major fluctuations of this type in the past, but that these palaeo-optical changes were accompanied by shifts in the balance of planktonic versus benthic algal production and probably other lacustrine properties. These major shifts in lake ecosystem structure and function are also likely to accompany future climatic change in the circumpolar forest-tundra environment.

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