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Paleolimnology of a shrub-tundra lake and response of aquatic and terrestrial indicators to climatic change in arctic Québec, Canada

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Abstract

To better understand past aquatic ecosystems and their development, a 99-cm sediment core was extracted from a shrub-tundra lake in northern Québec. Fossil chironomids, diatoms and pollen were analysed at 1.0-cm intervals. Several inference models based on chironomids and diatoms were used to reconstruct lake water conditions (surface water temperature, dissolved organic carbon (DOC), alkalinity, and water colour) for the last 6700 cal. yr. Reconstructed water temperatures varied between 10.3 and 17.6 °C, with a cooling trend since at least 1500 cal. yr BP. DOC concentrations increased with the establishment of terrestrial vegetation in the lake's catchment and decreased with the onset of the late Holocene cooling trend. Lake water alkalinity was higher during the lake's early history and decreased throughout its postglacial development, whereas water colour remained at fairly low levels throughout the entire record. Our results suggest that aquatic organisms directly influenced by temperature (chironomids) reacted most rapidly to climatic changes, whereas terrestrial vegetation (pollen) reacted with a slight lag. The vegetation succession in the catchment had subsequent impacts on the composition of runoff waters, and hence on other aquatic organisms (diatoms).

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1. Introduction

In northern Québec and Labrador, little is known about past aquatic ecosystems and their development through time. Paleolimnology, which is the science of past freshwater environments, uses multiple proxies from lake sediment cores to reconstruct past environmental changes. Several

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paleolimnological studies have recently been carried out in this subarctic region (e.g., Saulnier-Talbot and Pienitz, 2001; Laing et al., 2002; Ponader et al., 2002; Saulnier-Talbot et al., 2003), but more lakes need to be studied to obtain a more complete understanding of the postglacial dynamics of their biota. Furthermore, it has been proposed that aquatic organisms could react more rapidly to climate change than terrestrial biota (e.g., Smol et al., 1991). In order to assess this hypothesis, studies are designed in a way to assess the combined evidence from several aquatic and terrestrial proxy indicators (e.g., Bigler et al., 2002; Seppä et al., 2002; Solovieva and Jones, 2002) at high sediment sampling resolution (e.g., 0.2 cm, Battarbee et al., 2002a; 0.25–2 cm, Solovieva and Jones, 2002). Recently developed statistical inference models provide opportunities for the quantitative reconstruction of environmental variables from northern Québec and Labrador lakes based on the fossil remains of diatoms (algae: Bacillariophyceae) and midges (Insecta: Diptera). The midge-temperature inference model (Walker et al., 1997) has not yet been used in Québec or Labrador, but has been used extensively for late-glacial climatic reconstructions in Atlantic Canada (e.g., Levesque et al., 1997). The diatom-based inference models (Fallu and Pienitz, 1999; Fallu et al., 2002) have been used to reconstruct dissolved organic carbon (DOC) (Ponader et al., 2002; Saulnier-Talbot et al., 2003), water colour (Saulnier-Talbot et al., 2003), and alkalinity (Saulnier-Talbot and Pienitz, 2001) in northwestern Québec.

These models allow us to discern important environmental changes influencing aquatic community composition. When reconstructing surface water temperature from chironomid head capsules, climate changes can be inferred directly. Chironomids are directly affected by temperature throughout their life cycle (e.g., growth, flight, feeding, hatching; Walker and Mathewes, 1989) and indirectly through other processes (e.g., lake stratification patterns, oxygen depletion; Smol et al., 1991; Quinlan et al., 1998; Walker, 2001). Amongst the biological proxies known today, chironomids are considered by Battarbee (2000) to be the most promising tools for reconstructing past temperature. Furthermore, Wooller et al.

(2004) observed a strong correspondence between summer water temperatures inferred from the inference model (Walker et al., 1997) and mean annual temperature based on chironomid $\delta^{18}\text{O}$ in lakes from arctic and temperate regions.

Reconstructions of lake water colour (as Pt units from Pt–Co standard solutions) and DOC concentrations based on diatoms provide an indirect assessment of changes in catchment vegetation. It has been shown that DOC concentrations are correlated with the presence and density of vegetation in the drainage basin (e.g., Pienitz and Smol, 1993; Pienitz et al., 1997a,b; Fallu and Pienitz, 1999). Allochthonous organic matter that resists microbial decomposition in catchment soils represents the major source of dissolved organic matter (DOM) transported to boreal lakes (Wetzel, 2001). Because the concentration of DOC modifies the chemical (availability of certain essential metals or anionic nutrients; Jones, 1998) and the physical properties (water colour and hence underwater light regime; Vincent and Pienitz, 1996; Laurion et al., 1997; Jones, 1998; Gunn et al., 2001) of lake water, it also influences the species composition of aquatic communities (Pienitz and Vincent, 2000).

In recently deglaciated, northern humid regions, lakes tend naturally to become more dilute and acidic with time. This tendency results from the progressive weathering of soluble minerals from immature soils (Engstrom, 1987; Rasmussen et al., 1989; Engstrom et al., 2000) and increasing paludification of the catchment (Battarbee et al., 1999). The use of diatom-alkalinity and/or diatom-pH inference models therefore provides important additional information on the course of lake catchment development since the retreat of the Wisconsin inland ice sheet.

In this first multi-proxy study of a lake in northeasternmost Québec, we employed several inference models to provide detailed reconstructions of Holocene environments in a shrub-tundra setting. The overall objectives were: (1) to reconstruct at high temporal resolution the impact of climatic changes on aquatic and terrestrial organisms, and (2) to assess the degree of synchronicity in these organisms' responses.

2. Study site

As described in Fallu et al. (2004), Lake K2 (informal name; 58°44' 05"N, 65°56' 03"W) was sampled on 17 April 1998. It is a dilute, oligotrophic lake located 6 km northeast of the town of Kangiqsualujuaq (George River), about 11 km southeast of Ungava Bay and at 167 m above present-day sea level

(asl) (Fig. 1). This lake has a surface area of 3.6 ha, a maximum measured depth of 6.7 m (including 1.4 m as ice), and a catchment area of ca. 10 ha. At a depth of 1.8 m the conductivity was 10 μ S while the salinity was below the detection limit for the meter (S-C-T Meter YSI Model 33).

The lake basin is located on Precambrian bedrock on the border of the Central Lake Plateau and the

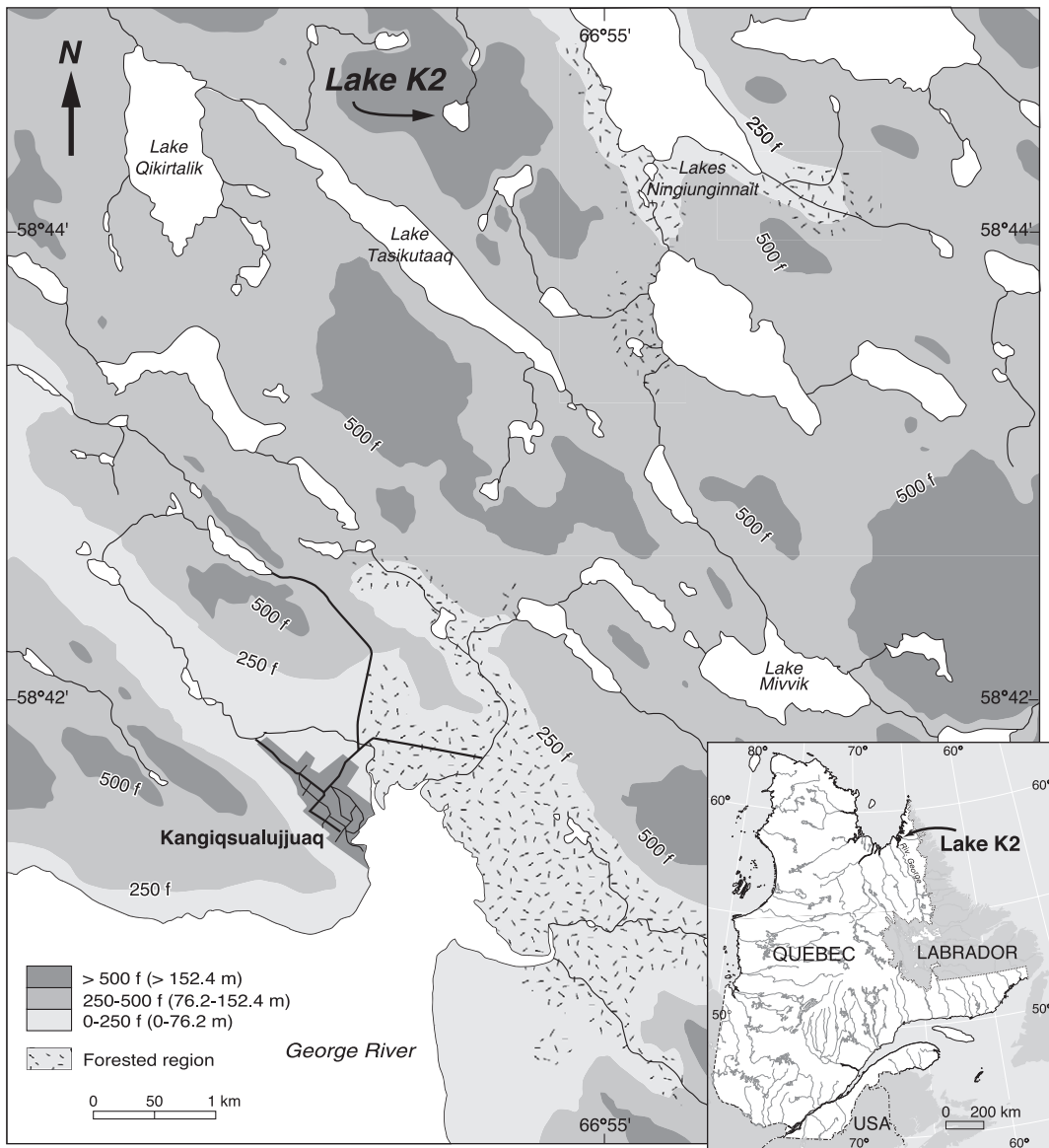


Fig. 1. Location of Lake K2 near the town of Kangiqsualujuaq in northern Québec at the shrub-tundra/forest tundra limit.

George River Plateau of the Churchill geological province (Gouvernement du Québec, 1984). The bedrock is composed of granodioritic and granitic gneiss (Geological Survey of Canada, 1997). The region is believed to have been deglaciated between ca. 8000 (Dyke and Prest, 1987) and 7500 ^{14}C yr BP (Allard et al., 1989; Clark et al., 2000), although Jansson (2003) suggested that deglaciation commenced about 6000 years ago. These dates are maximum ages for lakes located near Ungava Bay. Clark et al. (2000) proposed the fragmentation of the ice sheet into several individual ice caps and glaciers, while Jansson (2003) proposed that a remnant ice sheet persisted over southern Ungava Bay. In this region, the postglacial d'Iberville Sea reached its maximum marine limit at ca. 100 m (± 1 m) asl (Allard et al., 1989). Being located at 167 m asl on an upland plateau, and about 3 km beyond the maximum inland extension of the sea, Lake K2 was not exposed to any direct marine influence since the last deglaciation. In the study region, permafrost is discontinuous and widespread (Allard and Séguin, 1987).

The mean annual temperature at Kangiqsualujuaq is -4 °C while mean annual precipitation is 500 mm, including 40% as snow (Gouvernement du Québec, 1984). The region's harsh climate is characterized by only 40 frost-free days per year. The surrounding vegetation in the lake's drainage basin is a patchy shrub-tundra mainly composed of *Betula glandulosa* Michx., *Alnus* spp., *Picea glauca* (Moench) Voss. (krummholz), *Vaccinium vitis-idaea* L. ssp. *minus* Lodd., *Vaccinium uliginosum* L., *Ledum palustre* L. ssp. *decumbens* Ait., and *Empetrum nigrum* L. ssp. *hermaphroditum* (Hag.) Soer. Today, the regional landscape is composed of lowland forest-tundra (<ca. 80 m asl) and upland tundra (Payette, 1983).

3. Materials and methods

3.1. Sediment sampling and analyses

Lake K2 was sampled from the frozen surface. A 99-cm sediment core was extracted from the centre of the lake using a 5-cm diameter modified Livingstone piston corer (Wright et al., 1984). Clay

was found at the core base (~94–99 cm), suggesting that the record spans the lake's entire history, beginning with its formation following deglaciation. The core was immediately sectioned into 1 cm thick subsamples at the coring site. The sediments in the first few centimetres above the basal clay are composed of organic-rich gyttja containing remains of the aquatic moss *Drepanocladus* in life position.

The dating methods for this sedimentary sequence are described in Fallu et al. (2004). Due to possible contamination by old carbon, both bulk sediment (gyttja) and chironomid remains were dated. Because chironomid remains yielded the most reliable dates, the chronology (linear interpolation) was based on the dating of the latter (Fallu et al., 2004). Table 1 presents the five dates that were calibrated to calendar years BP (cal. yr BP) using the computer program CALIB 4.1 (Stuiver and Reimer, 1993; Stuiver et al., 1998). An apparent age inversion can be seen between the two lowermost dated samples (84–85 and 93–94 cm), but the ages are not significantly different when the error estimates are considered. The age for the 84–85 cm level was removed because it showed the highest error estimate and therefore should be less reliable.

Table 1
AMS ^{14}C dates obtained from chironomid head capsules that were used for establishing the sediment core chronology, as described in Fallu et al. (2004)

Laboratory number ^a	Depth (cm)	Age ^b (yr BP)	Age ^c (cal. yr BP) with range
AA43973	19–21	1230 \pm 53	1052 (1172) 1274
AA43974	46–48	3390 \pm 61	3472 (3636) 3728
AA47358	59–60	4820 \pm 68	5449 (5589) 5661
AA47359	84–85	5880 \pm 170	6376 (6673, 6700, 6720) 7031
AA47360	93–94	5770 \pm 86	6399 (6553, 6563, 6564, 6594, 6594, 6613, 6615) 6753

^a The samples were processed for dating by Accelerator Mass Spectrometry Laboratory, University of Arizona (AA).

^b The ages are corrected for natural and sputtering fractionation to a base of $\delta^{13}\text{C}=-25\%$. The sample ages are quoted as uncalibrated conventional radiocarbon dates using the Libby ^{14}C meanlife of 8033 years. The errors represent a 68.3% confidence limit.

^c The computer program CALIB 4.1 (Stuiver and Reimer, 1993; Stuiver et al., 1998) was used to calibrated the dates (cal. BP).

Organic matter (OM) content (%) was measured by loss on ignition (LOI). Subsamples (0.05–1.93 g) were analysed at 1-cm intervals throughout the core, except between 45 and 48 cm where the sediments were used for radiocarbon dating. The sediments were first dried at 70 °C for 4–5 h, before the organic matter was ignited by heating the samples to 550 °C. Once this temperature was reached, the samples were left in the furnace for 20–30 min (modified from Heiri et al., 2001).

3.2. Microfossil analyses

Chironomid head capsules were processed following Walker et al. (1991). Since it has been shown that a minimum of 50 head capsules is needed to obtain a representative sample (Heiri and Lotter, 2001; Larocque, 2001; Quinlan and Smol, 2001), more than 61 (average of 290 for all samples) head capsules were counted in each of the 99 core subsamples. Each chironomid sample consisted of 0.5–1 cm³ of moist sediment. Magnifications of 400–1000× were used to identify the head capsules. The main references used for identifications were Oliver and Roussel (1983), Wiederholm (1983), and Walker (1988). Chironomid taxonomy is often limited by missing head capsule parts. For example, individual taxa composing the tribe Tanytarsini were only identifiable when all parts needed for their identification were present. In addition to chironomid head capsules, *Chaoborus* mandibles and Acari (mites) were also picked and counted. As recommended by Walker (2001), we use the designations “type” and “group” to indicate our uncertainty with regard to several identifications at the level of genus or species.

Diatom preparation followed standard techniques (Wilson et al., 1996) on ca. 1 cm³ sediment subsamples. A minimum of 500 diatom valves was counted at 1-cm intervals throughout the core. Identifications were made at a magnification of 1000× with reference mainly to Camburn et al. (1984–1986), Krammer and Lange-Bertalot (1986, 1988, 1991a,b), Lange-Bertalot and Metzeltin (1996), and Fallu et al. (2000).

Pollen processing followed standard protocols (Faegri and Iversen, 1989). A sample of 1 cm³ was taken from every subsample, with the exception

of levels 19–23, 45–48, and 83 cm where the available sediment had been used up through other analyses, and the lowermost 7 cm (92–99 cm) where pollen grains were too scarce (clay sediments). A *Eucalyptus globulus* pollen suspension of known volume and concentration was added to each sample before preparation to calculate pollen concentration (grains cm⁻³) (Benninghoff, 1962). A minimum of 500 pollen grains (terrestrial vascular plants) was counted at each level. Pollen counting was done at 400× magnification and at 1000× for critical determinations. Pollen and spore identification followed Richard (1970) and McAndrews et al. (1973).

3.3. Numerical analyses

The computer program Palaeo Data Plotter, Beta test version 1.0 (Juggins, 2002) was used to prepare the microfossil stratigraphies. A stratigraphically constrained incremental sum of square cluster analysis (CONISS) was used to determine zone boundaries within each stratigraphy (Grimm, 1987).

To be consistent with the inference models, our fossil diatom assemblage data were harmonised with the inference model data (i.e., diatom species with a relative abundance 1% and present in at least one sediment level were included). The computer program WAPLS version 1.0 (Juggins and ter Braak, unpublished program) was used to reconstruct past environmental variables from the fossil assemblages and to estimate sample-specific errors of prediction for all inferred values.

We applied the program ANALOG version 1.6 (H.J.B. Birks and J.M. Line, unpublished program) with squared chord distance used as the dissimilarity coefficient (Overpeck et al., 1985) to assess the degree of fit between fossil assemblages and inference model assemblages. Fossil samples were considered to have no analogue in the model if their minimum dissimilarity coefficients exceeded those for 95% of the inference model samples (Laird et al., 1998; Laing et al., 1999). The program CANOCO version 4.0 (ter Braak and Šmilauer, 1998) was used to verify the models' ability to reconstruct the variables of interest at each level (also known as the “goodness-of-fit” test). A canon-

ical correspondence analysis (CCA) was performed on the modern inference model data, with the first axis constrained to represent the variable of interest, and the fossil samples run passively. This procedure measured the squared residual distance (SRD) of each sample from the first axis. Since the SRD was skewed for each of the models tested, the distances were log-transformed to bring them closer to normality. The 95% confidence interval for distances of inference model samples was then calculated. Fossil samples with distances within the 95% confidence interval were considered to have an adequate fit for environmental reconstructions (Birks et al., 1990; Laing et al., 1999).

4. Results

4.1. Performance of inference models

Fig. 5 indicates sediment core levels where no-analogue situations were identified using the two analogue tests (see methods). Lacking no-analogue assemblages entirely, the chironomid-temperature inference model revealed the best results (Fig. 5A). Pioneer diatom assemblages, however, have no analogue in modern assemblages from this region. This situation occurs for the two oldest inferred DOC values, and for the three oldest water colour and alkalinity inferences (Fig. 5B, C, D).

The DOC model from the James Bay/Hudson Bay region (Fallu and Pienitz, 1999) provided a better fit to fossil assemblages than the alkalinity and water colour models from Québec–Labrador (Fallu et al., 2002), even though Lake K2 is located just north of the Québec–Labrador lake training-set region. This may be due to the higher number of species in the James Bay/Hudson Bay model (218 taxa), as compared to the Québec–Labrador model (128 taxa). Also, the Québec–Labrador transect contains some highly alkaline lakes, diversifying the flora towards alkaliphilous taxa. Lake K2 had low water alkalinity, and hence showed less affinity with lakes within the Québec–Labrador training set. Furthermore, the James Bay/Hudson Bay transect extends up to latitude 59°43' N, whereas the Québec–Labrador transect only reaches 57°37' N. Lake K2 (located at a latitude of 58°44' N) could

therefore be more similar to some of the northernmost lakes used in developing the DOC inference model.

Chironomid-based transfer functions often yield sample-specific errors which overlap (e.g., Bigler et al., 2002; Rosenberg et al., 2004). The Holocene temperature changes are much smaller and more difficult to resolve than the late-glacial changes documented in other studies. The Holocene temperature changes may fall within the error range of model predictions (only 1–3 °C in some cases). Fluctuations in other environmental variables (e.g., pH, lake depth, hypolimnetic anoxia; reviewed in Walker, 2001) may also influence chironomid assemblages, and may generate noise that interferes with attempts to infer temperatures with greater precision. To overcome this problem, recent studies have stressed the need to replicate results using multi-site analyses, to ensure that the fossils record regional phenomena (especially climate), and not lake-specific changes in limnological conditions. By averaging the temperature records for several sites in a region it may be possible to filter some of the local noise from the inferences, ultimately improving the precision of midge paleotemperature inferences (Palmer et al., 2002; Kurek et al., 2004; Rosenberg et al., 2004; Velle, 2003).

4.2. Chironomid stratigraphy

4.2.1. Assemblage composition

The chironomid abundance diagram (Fig. 2) shows the stratigraphic distribution of midge taxa ranked in relation to their temperature optima in accordance with the inference model used (Walker et al., 1997) and recent literature (e.g., Brooks, 2000; Brooks and Birks, 2000). A total of 46 taxa was identified and four periods were delineated. Taxa belonging to the subtribe Tanytarsina were abundant throughout the whole sequence (Fig. 2). They are usually most abundant in lakes with cool water temperatures and low productivity (Brooks, 2000), and northern oligotrophic lakes like K2 are most likely to provide favourable conditions for these taxa.

The initial chironomid assemblage (Zone C1; Fig. 2) was composed primarily of *Micropsectra radialis* type and other undifferentiated Tanytarsina.

Micropectra radialis type is often found in cold water lakes (e.g., Porinchu et al., 2002). Tanytarsina reached its maximum abundance in the four oldest levels. Taxa of the cold-stenothermous genus *Heterotrissocladius* (e.g., Walker et al., 1997; Brodersen and Anderson, 2002) briefly dominated, being replaced by the more temperate and acidophilic *Psectrocladius* subgenus *Psectrocladius* (*Psectrocladius sordidellus* and *Psectrocladius semicircularis* groups). This subgenus reached its peak abundance at the lower limit of Zone C2. *Chironomus* was also present at this zone boundary.

Zone C2 (Fig. 2) is characterised by the decline of *Heterotrissocladius* species which coincides with the increase and the peak abundance of *Psectrocladius* subgenus *Psectrocladius*. Within the genus *Psectrocladius*, a shift occurred, with a decrease in the subgenus *Psectrocladius* and a marked increase in *Psectrocladius septentrionalis* and *Psectrocladius* sp. nr. *calcaratus*. The first appearance and increased abundance of many temperate taxa (e.g., *Dicrotendipes* and all Tanytarsina except *Micropectra radialis* type) also characterized this zone. *Dicrotendipes* and *Cladotanytarsus mancus* type reached their greatest abundance in Zone C2. *Chaoborus* mandibles were rare in Zone C1, but relatively common in Zones C2 and C3.

Zone C3 (Fig. 2) is marked by the appearance and/or increased abundance of temperate taxa (e.g., *Psectrocladius septentrionalis* type, *Tanytarsus pallidicornis* type, *Polypedilum*, *Pagastiella*, *Chironomus*). *Sergentia*, a cold stenothermous genus, reached its minimum abundance, whereas *Heterotrissocladius* spp. reappeared.

Zone C4 (Fig. 2) is characterized by slow, but progressive changes. Many temperate taxa (*Pagastiella*, *Polypedilum*, *Dicrotendipes*), *Psectrocladius septentrionalis* type, *Tanytarsus pallidicornis* type and *Chaoborus* decreased, whereas *Heterotrissocladius* spp. became increasingly abundant.

4.2.2. Temperature reconstruction

The surface water temperature reconstruction (Figs. 5 and 6) initially indicates inferred summer surface water temperatures as high as 14.6 °C in Zone 1a (Fig. 6). This is quickly followed by low inferred temperatures, reaching a minimum of 10.3 °C at the boundary between Zones 1a and 1b.

Inferred temperatures then increased to 15.3 °C until ca. 6200 cal. yr BP in Zone 2, and remained relatively stable until 5700 cal. yr BP. The inferred temperature then increased again, attaining a peak of 17.1 °C around 2000 cal. yr BP, in Zone 3. The reconstructed water temperature values for the uppermost sediments were rather unstable. In Zone 3, at 1700 cal. yr BP, the water temperature reached a minimum of 12.5 °C before rising to the highest inferred Holocene temperature (17.6 °C) at ca. 1500 cal. yr BP. The curve then shows oscillating temperatures throughout Zone 4; however, a continuous trend towards lower temperatures (between 12 and 14 °C) is apparent.

4.3. Diatom stratigraphy

4.3.1. Assemblage composition

A total of 243 diatom species from 28 genera was identified. In the diatom stratigraphy (Fig. 3), the dominant species were ranked according to their first occurrence in the sedimentary sequence. The first three levels of Zone D1 were dominated by *Nitzschia fonticola*, *Achnanthes minutissima*, *Pinnularia balfouriana*, *Brachysira neoexilis* Morphotype II, and *Cyclotella ocellata*. *Cyclotella ocellata* and *N. fonticola* are alkaliphilous species which have respective alkalinity optima of 74 and 62 $\mu\text{eq l}^{-1}$ (Fallu et al., 2002). Several taxa (e.g., *B. neoexilis* Morphotype II, *Frustulia rhomboides* var. *crassinervia*, *Cymbella gracilis*, *Navicula pseudoscutiformis*, and *Nitzschia* sp. 3) soon reached their postglacial maxima. At the upper limit of Zone D1, several species declined, whereas *Fragilaria virescens* var. *exigua* increased, to attain its maximum abundance. This taxon dominated the assemblages in all subsequent levels of the core. It is also often dominant in northern Québec lakes (Fallu et al., 2000; Laing et al., 2002; Ponader et al., 2002; Saulnier-Talbot et al., 2003) as well as in other tundra lakes (e.g., Joynt and Wolfe, 2001, Grönlund and Kauppila, 2002; Rühland and Smol, 2002; Rühland et al., 2003).

In Zone D2 (Fig. 3), many species, such as *Nitzschia fonticola*, *Brachysira neoexilis* Morphotype II, *Cymbella gracilis*, *Frustulia rhomboides* var. *crassinervia*, *Pinnularia balfouriana*, and *Cyclotella ocellata* decreased in abundance or

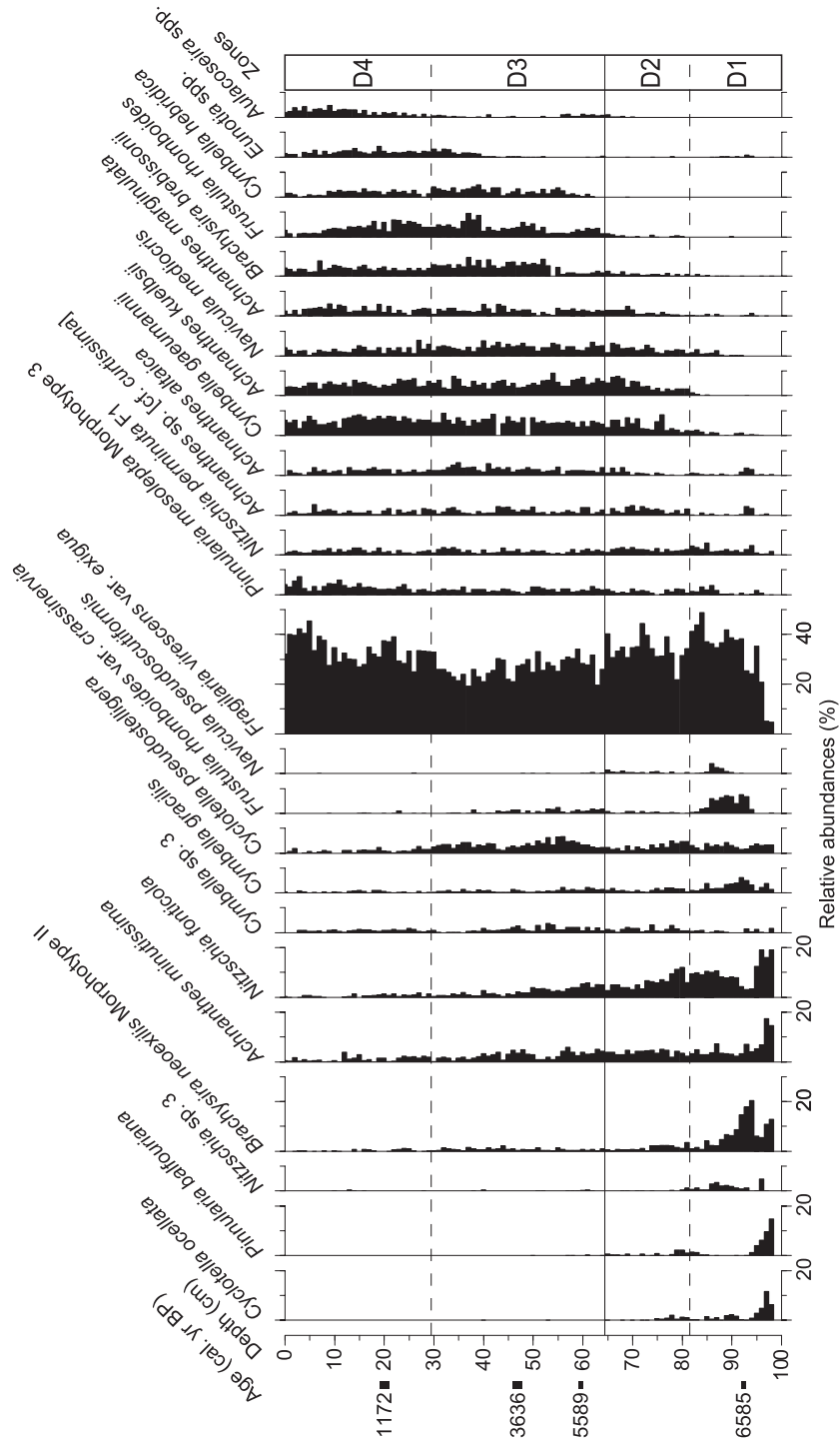


Fig. 3. Relative abundance of common diatom taxa (4% in at least one level and present in at least two levels). Zone boundaries were delimited using CONISS (with all species). The solid line represents the first-order separation and the dotted line, second-order separation. Taxonomy as in Fallu et al. (2000).

disappeared. Many small *Achnanthes* (e.g., *Achnanthes kuelbsii* and *Achnanthes marginulata*) appeared in this zone, along with *Cymbella gaeumannii*, which are circumneutral to slightly acidophilic species.

The transition between Zones D2 and D3 (Fig. 3) is characterized by the decrease and low abundance of many species (e.g., *Achnanthes minutissima* and *Nitzschia fonticola*). The abundance of other species remained relatively constant, although some taxa (e.g., *Navicula mediocris*, *Frustulia rhomboides*, *Brachysira brebissonii*, and *Cymbella hebridica*) that are referred to as benthic acidophiles in several studies (e.g., Rühland and Smol, 2002) reached their post-glacial maximum. Acidophilic taxa belonging to the genus *Eunotia* appeared with relative abundances >1% at 39 cm.

The highest abundance of *Pinnularia mesolepta* Morphotype 3, *Eunotia* spp., and *Aulacoseira* spp. occurred in the uppermost section of Zone D4 (Fig. 3), accompanied by a further decrease in *Cyclotella pseudostelligera*, *Nitzschia fonticola*, and *Brachysira neoexilis* Morphotype II.

4.3.2. DOC reconstruction

Diatom-based DOC inferences (Figs. 5 and 6) for the two lowermost levels were ignored because no analogues were available in the model training set. DOC concentrations were initially low (2.1 mg C l⁻¹) at around 6600 cal. yr BP, followed by an increase to reach 3.8 mg C l⁻¹ at 6550 cal. yr BP (Fig. 6). Between 6550 and 6050 cal. yr BP, DOC remained relatively stable, varying between 2.8 and 3.8 mg C l⁻¹, with the exception of the 6350 cal. yr BP level, where it reached a peak of 4.3 mg C l⁻¹. Between 6050 and 1450 cal. yr BP, DOC concentrations increased gradually from 3.0 to 6.2 mg C l⁻¹. In Zone 3, although some fossil assemblages had poor analogues in the training set assemblages, diatoms yielded results within the amplitude of DOC variations inferred for adjacent levels (Fig. 5). Relatively low values were reached in Zone 3 at 1800 cal. yr BP (4.7 mg C l⁻¹) and in Zone 4 at 1200 cal. yr BP (5.0 mg C l⁻¹). The concentrations then became slightly unstable in the late Holocene (Zone 4; Fig. 6). A gradual increase brought the DOC concentration to its highest value (6.4 mg C l⁻¹) at around 625 cal. yr BP. Since then, DOC

concentrations have been decreasing to about 4.5 mg C l⁻¹ near the present day.

4.3.3. Alkalinity reconstruction

The assemblages from the three lowermost levels had no analogue in the model training set and were ignored (Figs. 5 and 6). It is interesting to note that these levels correspond to those where no-analogue situations were also identified using the DOC training set. This demonstrates the unusual composition of these pioneer diatom assemblages.

Lake alkalinity was initially high (81.2 µeq l⁻¹) at 6630 cal. yr BP (95–96 cm), before sharply decreasing to 52.7 µeq l⁻¹ in Zone 1a (Fig. 6), and increasing again to 72.3 µeq l⁻¹ (Zone 1b) at 6425 cal. yr BP. Throughout Zone 2, alkalinity decreased continuously, reaching its lowest value of 29.2 µeq l⁻¹ at 3350 cal. yr BP (Zone 3). Thereafter, alkalinity remained relatively stable at about 32.0 µeq l⁻¹.

4.3.4. Water colour reconstruction

The diatom-based water colour reconstruction yielded similar trends (Fig. 6), with the same levels as in the alkalinity reconstruction to be ignored for absence of analogues in the model training set. The oldest reconstructed value indicates a peak of 21.4 Pt units at the 6630 cal. yr BP level (Zone 1a). This was followed by an abrupt decrease to 16.0 Pt units in Zone 1b. The highest colour value, 27.2 Pt units, was recorded at 6450 cal. yr BP. A second sharp decrease occurred at 6300 cal. yr BP to 11.9 Pt units, followed by a relatively constant decline in water colour until 5900 cal. yr BP (7.8 Pt units). A short-lived increase to 13.2 Pt units is evident at 5830 cal. yr BP. Thereafter, water colour remained relatively constant, averaging 10.2 Pt units. A slight increase is again noticeable since 2250 cal. yr BP.

4.4. Pollen stratigraphy

Pollen was extremely scarce in the oldest clay sediments, thus the lowermost level analysed was 91–92 cm (6500 cal. yr BP). In Zone P1 (Fig. 4), the most abundant taxa were Cyperaceae, *Alnus*, *Betula* and Poaceae. They remained the dominant pollen types throughout the entire sequence. These lowermost levels in the core were also distinguished

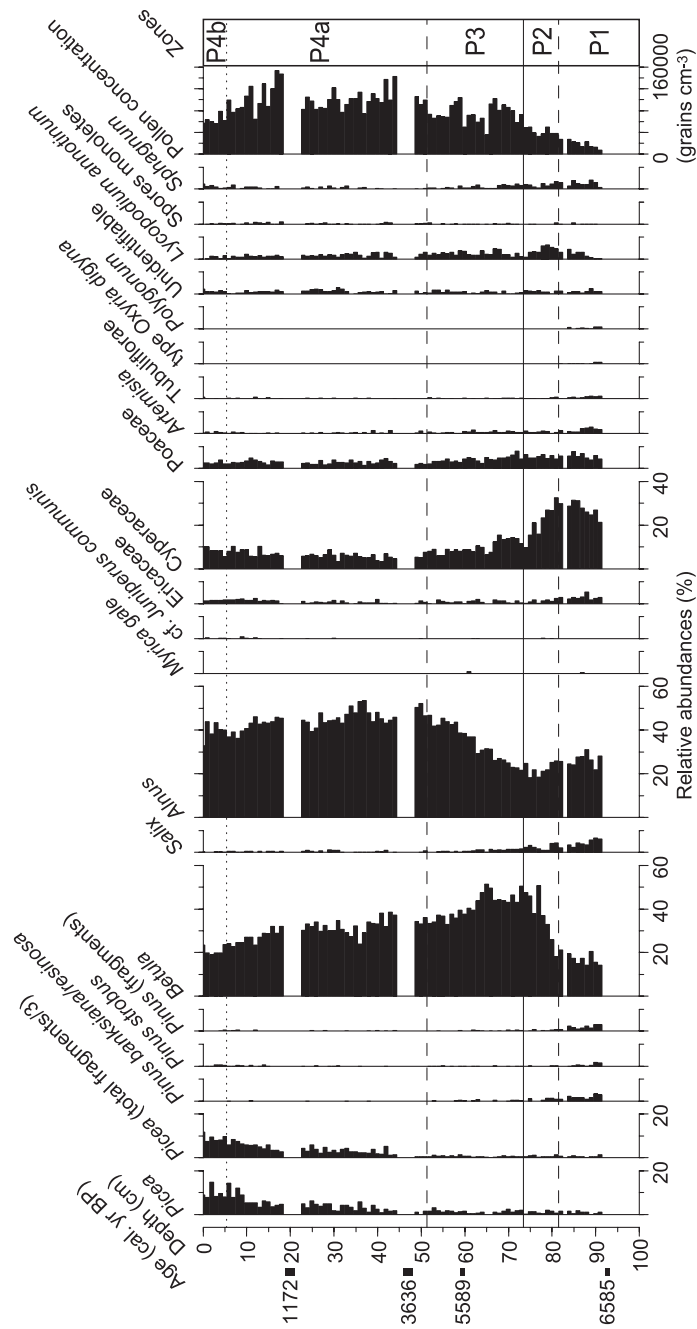


Fig. 4. Pollen relative abundances of common pollen types (1% in at least one level). Zone boundaries were delimited using CONISS (with all taxa). The solid line represents the first-order separation and the dotted line, the second-order separation.

by the highest percentages of pollen belonging to *Salix*, *Sphagnum*, *Artemisia*, *Tubuliflorae*, *Oxyria digyna* type, *Polygonum* and *Ericaceae*.

Zone P2 (6230–6000 cal. yr BP; Fig. 4) is characterized by increased pollen concentrations and by the highest *Cyperaceae* abundance. *Alnus* and

Salix slightly decreased relative to other taxa, whereas *Betula* pollen sharply increased. All the species that peaked in the preceding zone (*Sphagnum*, Ericaceae, *Artemisia*, Tubuliflorae, *Oxyria digyna* type, and *Polygonum*) became less abundant or disappeared.

In the third zone (Zone P3; 6000–4100 cal. yr BP; Fig. 4), *Betula* and *Alnus* clearly dominated. *Betula*, Cyperaceae, Poaceae, and *Salix* decreased slightly, whereas *Alnus* increased. The prominent increase in total pollen concentrations indicates the increasing density of the vegetation cover.

Zone P4 (4100 cal. yr BP to present; Fig. 4) was divided into two sub-zones, the bottom half (Zone P4a) representing the most stable zone in the whole sequence. The only important change is the late Holocene increase of *Picea* spp., which was rare in the preceding zone. In the top half (Zone P4b), *Picea* spp. reached its maximum postglacial abundance and *Betula* decreased slightly. After reaching a maximum at 17–18 cm (1000 cal. yr BP), the total pollen concentrations decreased.

4.5. Loss on ignition (LOI)

Fig. 6 shows the results of the LOI analyses. In the basal clay-rich gyttja (ca. 94–98 cm), the organic matter (OM) concentration was low (1.5%). A sharp increase occurred between the base and the 6500 cal. yr BP level where it reached 14% and later 21% at 3100 cal. yr BP. At around 1175 cal. yr BP, LOI indicates a short-lived peak in OM content (about 40%). In the uppermost 20 cm of the core (1175 cal. yr BP to the present), the OM content was highly unstable, oscillating between 22 and 37%.

5. Discussion

5.1. Holocene history of lake K2

5.1.1. Zone 1: initial lake phase (6700–6400 cal. yr BP)

Zone 1a represents the short-lived period of inferred cool climatic conditions immediately following deglaciation (Fig. 6). Scarcity of pollen grains, together with low inferred DOC and OM

values reflect a barren (early) landscape. Lake alkalinity was high due to the presence of unweathered soils in the catchment that are typical of recently deglaciated terrain (e.g., Engstrom et al., 2000; Saulnier-Talbot et al., 2003). Chironomid assemblages were dominated by cold-stenothermous species and the lowest surface water temperatures were inferred for this zone (Fig. 6). Although warm air temperatures had initiated the ice sheet melting and retreat, low water temperatures could have resulted from cold meltwater discharging into the lake basin.

Fragments of the aquatic bryophyte *Drepanocladus* found in the lowermost sediments possibly indicate an initially low lake level, and high water transparency. The presence of *Pinnularia balfouriana*, an epiphytic (aerophilic) diatom typically associated with arctic mosses (Douglas et al., 1994), supports this interpretation.

Although an alkalinity oscillation is apparent in Zone 1, it occurs within the context of a longer term decrease in alkalinity. Lakes of humid regions are usually most alkaline during the initial stages of their development. The short-term increase in alkalinity evident in the latter part of Zone 1, which creates the apparent oscillation, could be related to the warming following deglaciation. Initially weathering rates, and hence alkalinity and pH values, may have been suppressed by the cold prevailing temperatures and thin active soil layer.

As shown by the pollen diagrams (Fig. 4), a shrub-tundra with widespread herb assemblages (Cyperaceae) was present in the lake's catchment (Zone 1b; Fig. 6). The percentages of tall shrubs (*Alnus* and *Betula*) increased thereby contributing to the DOC supply, while pollen grains of conifer species were likely blown into the site from distant sources. Although not in life position, *Drepanocladus* moss fragments were still found in Zone 1b, until 6300 cal. yr BP. This implies high water transparency and possibly also a relatively shallow water body.

Reconstructed water colour varied markedly in Zone 1b (Fig. 6). There is little correlation with the DOC concentration changes. We propose that either the data are erroneous because of the poor analogue situation, or that changes in water colour were so minimal that species assemblages were influenced by other factors.

In Zone 1b (Fig. 6), the chironomid-inferred water temperature profile indicates rapid warming of lake waters from about 11.5 to 15 °C. The presence of *Chironomus* at the Zone 1a/1b boundary could indicate low oxygen conditions during this phase. These changes were accompanied by lower inferred alkalinity values as shown by increasing abundances of acidophilic diatom taxa (e.g., *Brachysira neoexilis* Morphotype II, *Frustulia rhomboides* var. *crassinervia*, *Cymbella gracilis*, *Achnanthes* sp. [cf. *curtissima*], and *Achnanthes altaica*). Chironomid data also suggest a tendency towards less alkaline conditions, with the increasing abundance of *Psectrocladius* spp. (Walker et al., 1985; Brodin and Gransberg, 1993; Brooks, 1996; Brooks and Birks, 2000; Mousavi, 2002).

5.1.2. Zone 2: initial warming phase (6400 to 4900 cal. yr BP)

After a slight increase between 6430 and 6230 cal. yr BP, the inferred water temperature for Zone 2 remained relatively stable, varying between 12.7 and 16.3 °C (average 14.5 °C; Fig. 6). It suggests a warmer climate as shown by the increased density of the vegetation cover (higher pollen concentration), the appearance of the temperate chironomid *Dicrotendipes*, and the virtual disappearance of *Heterotrissocladius* spp. Even though there are major changes in *Psectrocladius* spp., these changes are not evident in the water temperature reconstruction. Because of taxonomic uncertainties at the time the inference model was developed, all the *Psectrocladius* taxa were amalgamated. Given the potentially important autecological differences among *Psectrocladius* species, we believe a model with a higher taxonomic resolution, especially for the genus *Psectrocladius*, could eventually yield more detailed reconstructions. Although *Psectrocladius* has a temperature optimum estimated at 17.5 °C in the inference model, it is often referred to as a thermally tolerant (eurythermic) taxon (e.g., Palmer et al., 2002).

Not surprisingly, the combined data reveal a trend towards more acidic conditions, as reflected by the alkalinity reconstruction (Figs. 5 and 6). Alkalinity continued to decrease, while OM and DOC increased, and shrubs, mainly *Alnus* and *Betula*, became denser in the catchment. This natural tendency of lakes to acidify has also been

documented in other paleolimnological studies including diatom-based alkalinity reconstructions (Pienitz et al., 1999; Seppä and Weckström, 1999; Saulnier-Talbot and Pienitz, 2001).

In general, lakes receive an increasingly high DOC load (with a higher coloured fraction) as catchment vegetation develops, and organic acids are generated from litter accumulating on the newly exposed soils. As for coloured DOC inputs, the concentrations in shrub-tundra lakes from northern Québec and Labrador are usually low enough such that little or no colour is visible (average of 6 Pt units; Fallu et al., 2002). This may explain the low variability in the colour reconstruction obtained for lake K2. It also illustrates the effectiveness of the DOC inference model in tundra lakes, allowing DOC concentrations to be inferred regardless of their origin, as either autochthonous (transparent DOC) or allochthonous (highly coloured) materials. Diatom-colour inference models have revealed trends parallel to those of TOC and DOC in more strongly coloured European lakes surrounded by mountain birch forest (e.g., Seppä and Weckström, 1999) and forest-tundra lakes of northern Québec (e.g., Saulnier-Talbot et al., 2003).

5.1.3. Zone 3: warm phase (4900 to ca. 1500 cal. yr BP)

The paleolimnological changes as inferred from Zone 3 seem to suggest the most stable paleoclimatic conditions during this period (Fig. 6). The average inferred summer surface water temperature (16.1 °C; range=14.5–17.4 °C) was highest in this zone. *Psectrocladius* was still very abundant, which could be related to further natural acidification of the lake. Acidophilic and/or circumneutral diatom species were also abundant (e.g., *Brachysira brebissonii*, *Frustulia rhomboides*, *Cymbella hebridica*) (Fig. 3). *Eunotia*, a diatom genus typical of low pH waters, appeared with low abundances for the first time. These water chemistry changes were reflected in the alkalinity curve, with particularly low alkalinity values being indicated throughout the rest of the Holocene (Fig. 6).

The relatively warm conditions likely allowed the growth of spruce close enough to lake K2 so that pollen could reach the lake. According to modern pollen spectra near treeline, the 20% spruce isopoll

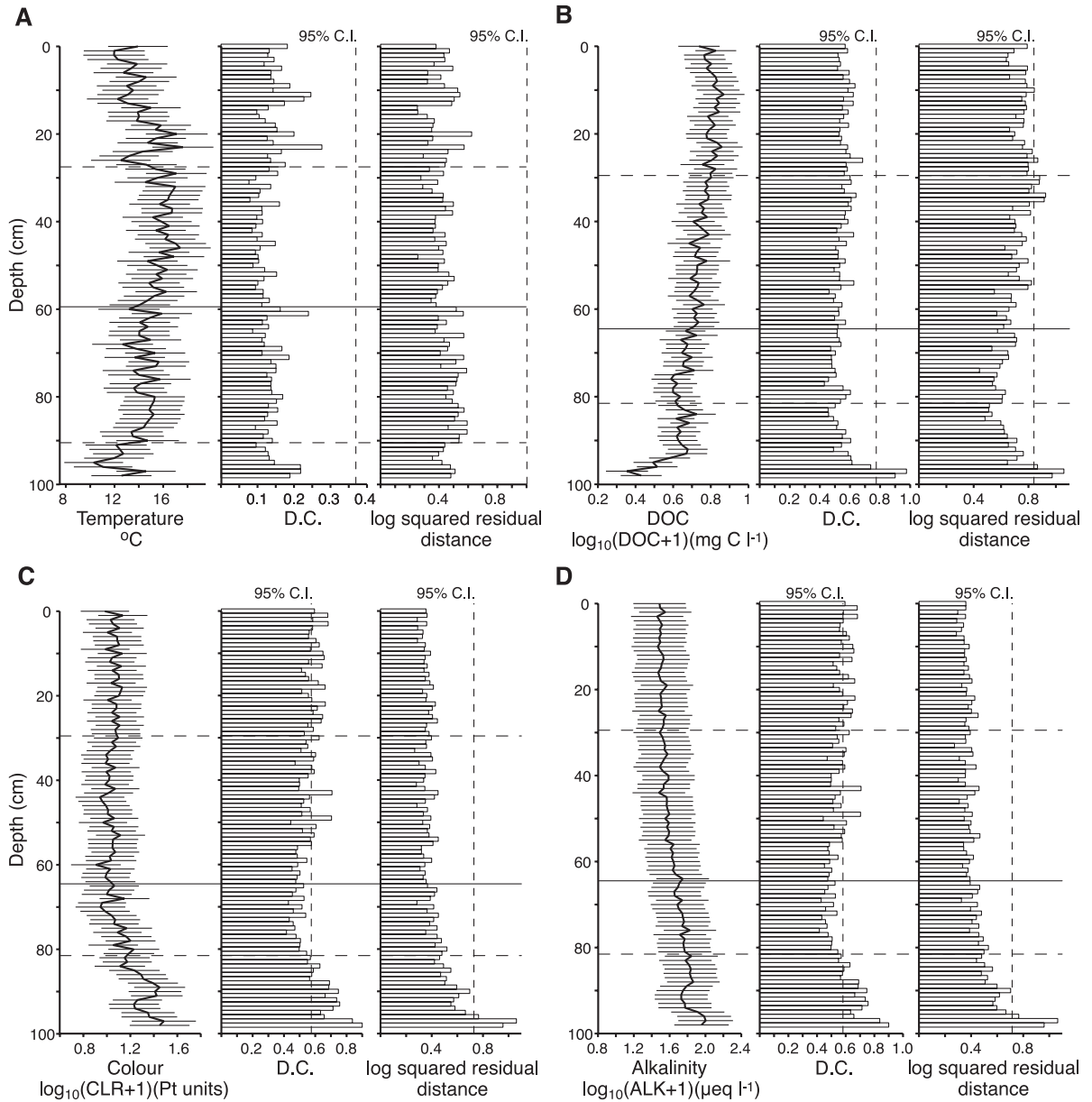


Fig. 5. Temperature, dissolved organic carbon (DOC), colour and alkalinity reconstructions, and analogue assessments for Lake K2. Surface water temperature values, based on chironomids, are presented in (A), while DOC, water colour and alkalinity values, based on diatoms, are presented in panels (B), (C), and (D), respectively. For each reconstruction, dissimilarity coefficient (D.C.) and log squared residual distance are shown at every level. Samples with values exceeding the 95% confidence interval (C.I.) in one of the two tests were considered as having a poor analogue in modern samples, while values greater than the 95% C.I. in both tests were considered to have no analogues. Zone boundaries were delimited using CONISS (as shown on Figs. 2–4). The solid line represents the first-order separation while the dotted lines represent the second-order separations.

corresponds to the spruce limit in northern Québec–Labrador (Gajewski, 1991; King, 1993). The present-day distribution of arborescent spruce is

confined to valleys surrounding the lake K2 plateau. These conifer stands could be the main source of spruce pollen reaching the lake, although it is also

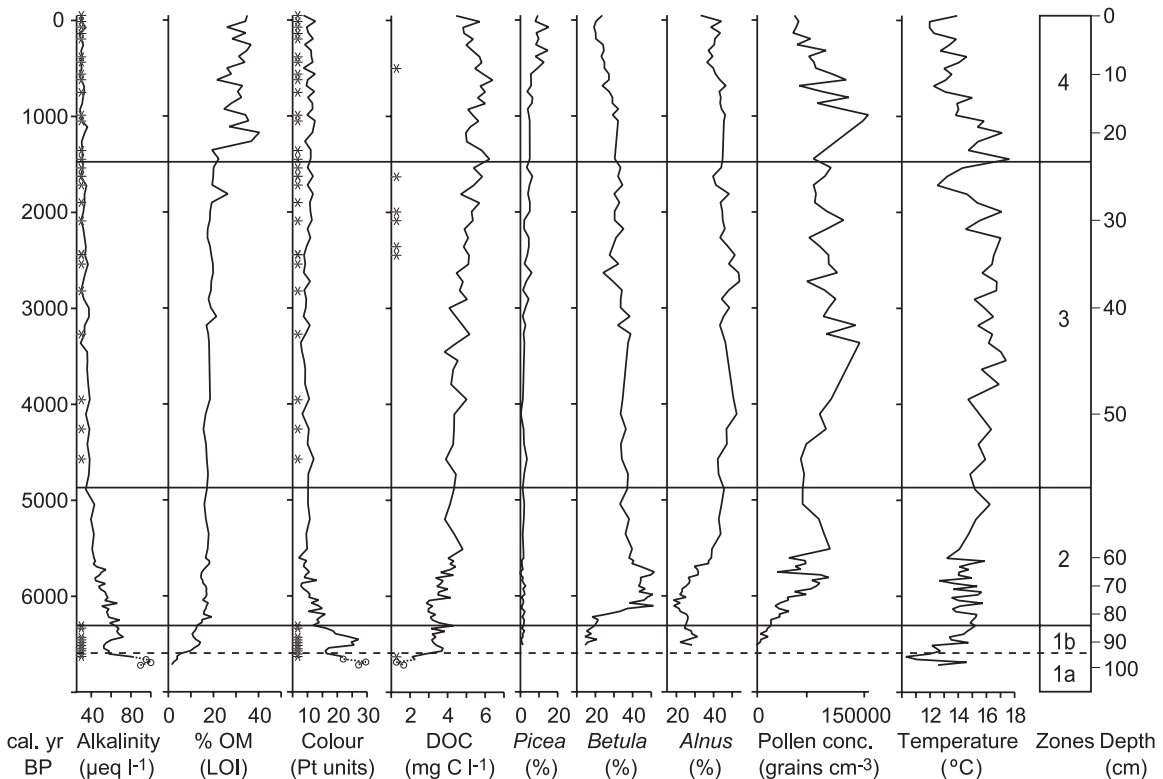


Fig. 6. Synthesis of paleoenvironmental data for Lake K2. Open circles and asterisks respectively indicate no-analogue and poor analogue situations. Zonations were done by visual inspection and by integration of CONISS results from Figs. 2–4. Note that the axis X for alkalinity, colour, DOC, *Betula*, *Alnus*, and temperature does not start at 0.

possible that part of the pollen came from spruce krummholz established in the lake's catchment. Lamb (1985) analysed pollen in Lake Gravel Ridge (475 km southeast of lake K2), and found that *Picea* arrived in the catchment around 5400 yr BP (ca. 6240 cal. yr BP), much earlier than in our study area. Another palynological study by Short and Nichols (1977) of Pyramid Hills Lake (about 75 km southeast from Lake K2) revealed an open spruce woodland around 4500 yr BP (ca. 5120 cal. yr BP). Because conifers are known to produce more acid litter, the arrival of krummholz spruce is likely to have contributed to the natural acidification of Lake K2 and the increased occurrence of acidophilic diatom and chironomid taxa. Unfortunately, the arrival of spruce in the catchment can only be proposed because no macrofossils were found in the lake sediments. The increased input of organic matter from krummholz conifers was likely responsible for the higher OM and DOC concentrations in

the upper part of Zone 3. The water temperature reconstruction suggests a short cooling interval that coincides with the end of Zone 3 (Fig. 6) which likely coincides with the small peak of *Sergentia*, low abundances of *Chaoborus*, and the absence of *Polypedilum* (Fig. 2).

5.1.4. Zone 4: recent cooling (ca. 1500 cal. yr BP to modern time)

Lake water temperature apparently became increasingly unstable in this zone, but with a decreasing trend until today. This trend is reflected by the increased abundance of several *Heterotrissocladius* taxa and the decline of many temperate taxa (Fig. 2), and also coincides with decreasing pollen concentrations (Figs. 4 and 6). Spruce pollen shows higher abundances, but this higher representation could be in part due to a relative decrease in the abundance of other local pollen (e.g., *Betula*). This late Holocene cooling trend has also been reported from other studies conducted in northern

Québec and Labrador. Fossil pollen and diatom records in Square Lake (Clark et al., 1989) revealed a cooling trend since 3000 yr BP (~3190 cal. yr BP), whereas Short and Nichols (1977) proposed that vegetation became sparser after 2800 yr BP (~2900 cal. yr BP) as a consequence of a cooler and drier climate. Furthermore, at Lake Gravel Ridge (central Québec–Labrador), fires became more frequent around 3000 yr BP (~3190 cal. yr BP) and because postfire regeneration is difficult under cold conditions, vegetation cover was considerably reduced (Lamb, 1985).

In our study, diatom-inferred DOC concentrations reached their maximum at 625 cal. yr BP, which was accompanied by a predominance of acidophilic species (*Cymbella gaemannii*, *Pinnularia mesolepta* Morphotype 3, *Brachysira brebissonii*, *Cymbella hebridica*, *Eunotia* spp., and *Aulacoseira* spp.). Organic matter increased early in zone 4 and was unstable until today. Battarbee et al. (2002b) hypothesized that LOI is a good indicator of mean annual temperature when OM is mainly of autochthonous origin. The peak in OM found here (around 1500 cal. yr BP) coincides with the peak in chironomid-inferred temperature, but the OM concentration does not parallel the chironomid-inferred temperature decrease in the uppermost sediments. It is likely that much of the OM at this site has an allochthonous origin, and reflects increased litter or peat accumulation in the catchment and not climate per se.

Although this study was conducted at high sampling resolution, it was impossible to discern any recent warming trend that could be related to anthropogenic activities (Fig. 6). An indication of warmer temperature can be seen in the uppermost level analysed for chironomids, but this short-lived peak is well within the natural variability of the temperature reconstruction (Fig. 6). In lakes with very low sediment accumulation rates, such short-term changes are difficult or impossible to detect. Also, even if the recent cooling trend seems contradictory to the general global warming scenario reported from other arctic regions (e.g., Overpeck et al., 1997), several studies have shown that the northern Québec–Labrador region has remained climatically stable until very recently (e.g., Paterson et al., 2003; Laing et al., 2002; Ponader et al., 2002; Wrona et al., in press). Other studies indicate that the western subpolar region of the North Atlantic

has warmed less than others (IPCC, 2001; Moritz et al., 2002).

5.2. Synchronicity amongst proxies

By examining the degree of synchronicity of the responses among all the analysed biostratigraphic indicators it is possible to assess which proxy indicator(s) responded most sensitively to subtle Holocene environmental changes. To date, few paleolimnological studies have tackled this subject.

Zone 1 (6700–6400 cal. yr BP) represents the lake's formation and phase of initial development. Proxies are unstable in this zone and are not closely correlated. Alkalinity decreased throughout the sequence independent of the other proxies, reflecting a slow and natural lake acidification process. DOC and water colour provide contradictory information, whereas OM, temperature and DOC all increased, but at different times and rates. As previously mentioned, the interpretation of this zone's environmental conditions is problematic because of the poor analogue situation. Initial DOC concentrations could originate mainly from autochthonous sources, while a small proportion of it may result from external inputs, derived from the few herbs and shrubs present in the catchment.

In Zone 2 (6400–4900 cal. yr BP), temperatures inferred from the chironomid-based reconstructions are stable, although a slight increase is evident near Zone 3. Water colour stabilized whereas DOC increased with the establishment of tree vegetation in the region and possibly the lake's catchment. From 6000 to 5500 cal. yr BP, simultaneous increases occurred in DOC, *Betula* and *Alnus* pollen, and pollen concentration.

Little change is evident in Zone 3, and each proxy seems to react independently. The most interesting part of the sequence is the change around 1500 cal. yr BP, at the boundary between Zones 3 and 4. The precise timing of this change was slightly different for each proxy. The first proxy to record the change was the chironomids, with inferred water temperature decreasing in the upper part of Zone 3 followed by a more sustained drop beginning after ca. 1500 cal. yr BP. OM became unstable after 1500 cal. yr BP, but no increasing or decreasing trend is apparent. Pollen concentration and *Betula* pollen declined from about

1000 cal. yr BP until recent time. DOC concentrations started to decrease between 1700 and 1300 cal. yr BP, but more evidently after ca. 700 cal. yr BP, lagging relative to the other proxies. This may be due to the low rate of organic matter decomposition in soils and/or the persistence of *Picea* krummholz in the catchment. Lower temperatures might also have been accompanied by drier conditions; thus, less organic matter would have been delivered to the lake via catchment runoff.

Our proposed interpretations are the starting point for more thorough assessments of synchronicity among proxies' responses to climatic shifts. We originally hoped to be able to evaluate the time lags among each of the proxies in more detail, but this has proven more difficult than anticipated mainly due to extremely low sedimentation rates.

6. Conclusions

The reconstruction of several environmental variables at 1-cm intervals revealed environmental changes in greater detail than previously attained in paleoecological studies from northern Québec–Labrador. Changes observed in the reconstructed variables generally concurred among proxies, and with the results of other paleoenvironmental studies in the Québec–Labrador region. No-analogue diatom assemblages at the base of the sequence may explain the inconsistencies in the early lake record. The most striking similarity among all the reconstructions is evidence for a sustained cooling since around 1500 cal. yr BP. No recent warming trend was detected.

In our study, it was possible to observe a certain degree of asynchronicity amongst proxy responses in the sediments. Changes in chironomids are believed to be directly related to water temperature, and these organisms seemed to react first to climate change. Chironomids, diatoms and vegetation changes generally showed a strong synchronicity in the first part of the lake's sedimentary sequence. In the second part, the vegetation and diatom responses seemed to lag behind the chironomid changes. Diatoms also seemed to show a certain lag to pollen that can be expected since changes in terrestrial vegetation exert a strong control on exports of allochthonous DOC

into lakes and the underwater light conditions. Based on our observations, we argue that aquatic organisms which are directly influenced by water temperature (chironomids) will respond first to climatic changes, followed by the terrestrial vegetation, and subsequently by other aquatic organisms (diatoms) that are indirectly affected through changes in the physical and chemical conditions brought about by shifts in the terrestrial environment. However, the time resolution of the proxy records achieved in Lake K2 is probably insufficient to provide unequivocal information about the exact timing of the proxies' responses. More attempts should be undertaken to assess successional changes in aquatic biota, response times, and aquatic–terrestrial linkages in more detail. Ongoing research in this region will reveal more of the subtle climatic and related environmental changes that have occurred since deglaciation and will build towards a more robust multi-site study of time lags among proxies.

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