

Response of Lacustrine Biota to Late Holocene Climate and Environmental Conditions in Northernmost Ungava (Canada)

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ABSTRACT. Sediment cores from three lakes located in the northernmost region of Ungava, Québec (Canada) were examined to define aquatic community and ecosystem variability during the Late Holocene period. A chironomid-based transfer function was used to reconstruct August air temperature trends, and lacustrine primary production was inferred from sedimentary biogenic silica content and siliceous microfossil abundances. Trends in primary production, sediment organic matter content (estimated through loss on ignition), and chironomid-inferred temperature were compared to explore potential effects of environmental change on biotic assemblage composition at centennial to millennial time scales. Although no direct correlation between chironomid-inferred August air temperature and primary production was observed, we found indications that both chironomid and diatom communities were responding to the same overarching regional climatic and environmental processes. Over the last decade, northern Québec has been undergoing notable, rapid warming that contrasts with the relative inertia of the past few millennia. This study provides a baseline against which recent and future environmental changes in this region can be compared.

Key words: chironomids; diatoms; biogenic silica; climate; northern lakes; Ungava

RÉSUMÉ. Les archives sédimentaires couvrant la période de l'Holocène tardif ont été examinées dans trois lacs situés dans la région du nord de l'Ungava, au Québec (Canada). Un modèle d'inférence basé sur les assemblages de chironomides a été utilisé pour reconstruire la variabilité des températures de l'air du mois d'août, et la production primaire lacustre a été inférée par le contenu sédimentaire en silice biogénique et les abondances des microfossiles siliceux. Les variations historiques de la production primaire, du contenu organique du sédiment (évalué par la perte au feu) et les températures inférées ont été comparées afin d'explorer les effets potentiels des changements environnementaux sur la composition des assemblages à différentes échelles temporelles (centenaires à millénaires). Malgré le fait qu'aucune corrélation directe n'ait été observée entre les températures inférées en août et la productivité primaire, certaines indications suggèrent que les communautés de chironomides et de diatomées répondaient aux mêmes processus climatiques et environnementaux régionaux. Au cours de la dernière décennie, le nord du Québec a connu un réchauffement rapide et marqué, contrastant avec l'inertie relative des derniers millénaires. Cette étude fournit le scénario de référence par rapport auquel les changements environnementaux actuels et futurs pourront être comparés dans cette région.

Mots clés : chironomides; diatomées; silice biogénique; climat, lacs nordiques; Ungava

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INTRODUCTION

Across the Arctic, the biotic assemblages of lakes have shown highly variable rates of change following recent regional climatic warming (e.g., Smol et al., 2005), indicating that shifts in temperature and their effects on aquatic environments have been spatially heterogeneous in northern high latitudes over the last ~150 years. The region of northern Québec and Labrador in eastern Canada, where lakes are a major feature of the landscape, was until recently one of relatively muted ecological change.

The lacustrine ecosystems of this region likely evolved over millennia under stable environmental conditions into highly specialized systems that remained quite unperturbed until the late 20th century (e.g., Saulnier-Talbot and Pienitz, 2001; Laing et al., 2002; Pienitz et al., 2004; Fallu et al., 2005). Recent studies demonstrate that warmer temperatures have reached many parts of this vast region, notably on the eastern coast of Hudson Bay, where air temperatures have increased rapidly since the 1990s (Bhiry et al., 2011). These temperature changes, in turn, have led to important modifications of the landscape, including the

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appearance and development of numerous thermokarst thaw ponds (Bouchard et al., 2014) and the densification of the shrub cover (Ropars and Boudreau, 2012). Moreover, modeled annual temperatures in the region of northernmost Ungava Peninsula are expected to increase by more than 3°C by 2050, with summer arriving 6 to 11 days earlier and driving degree days to increase by 50%–150% (Allard and Lemay, 2013).

As of yet, few long-term environmental data are available for northernmost Ungava's extensive tundra landscape and its abundant lakes. In order to assess the region's sensitivity (its degree of resistance or resilience) to recent and future global environmental change, deeper knowledge of long-term historical variability in the region is needed. In this context, it is more important than ever to monitor these systems to evaluate how the lacustrine biota and water quality will be affected by these changes. In order to assess the current state of the lakes within a longer historical context, it is necessary to establish baseline conditions. Given the rarity or absence of long-term monitoring data sets for most high-latitude regions, investigating the content of lake sediment archives has proven to be a useful method for deriving environmental records of the past in these regions. Chironomids (order Diptera) and diatoms (class Bacillariophyceae) preserved in northern lake sediment records are useful indicators of climatic and environmental change.

Chironomids are a common and widespread group of insects in northern Canada (e.g., Oliver and Dillon, 1997). Their aquatic larvae often dominate benthic faunal assemblages in a wide variety of Arctic and sub-Arctic lakes (e.g., Welch, 1976; Moore, 1979; Danks, 1992). The chironomid larval assemblages, represented by their chitinous head capsules preserved in lake sediments, have become a widely used paleoclimatological indicator group for quantitatively reconstructing past temperatures, especially at high latitudes and altitudes (e.g., Larocque and Bigler, 2004; Fallu et al., 2005; Axford et al., 2009).

Diatoms are major contributors to primary production in dilute high-latitude and high-altitude freshwater ecosystems (Douglas et al., 2004; Lotter et al., 2010). Changes in their abundance (or in the associated amount of biogenic silica; BSi) in Arctic and alpine lakes have been linked to climate at decadal to millennial timescales (e.g., Wolfe, 2003; Schmidt et al., 2004). Historical variations in diatom abundance and in the structure of diatom communities have the potential to serve as reliable proxies for inferring direct or indirect environmental changes in remote high-latitude lakes, where simplified biological processes (e.g., the absence of fish) can permit a more straightforward interpretation of physical processes. Diatoms respond to changes in a variety of variables, both physical (e.g., temperature, light, turbulence and ice-cover) and chemical (e.g., nutrients, pH, dissolved organic carbon content, salinity), variables that are often related to lake catchment dynamics (e.g., Anderson, 2000). Sedimentary diatom remains (their silica shells, called frustules) are routinely used as paleoenvironmental proxies in remote northern regions where long-term

instrumental data are rare or lacking (e.g., Pienitz et al., 2004).

Using this paleolimnological approach, we quantified changes in the chironomid and diatom assemblages preserved in sediment cores from three low-Arctic Ungava lakes to explore patterns of past environmental variability. Our objectives were threefold: 1) to establish baseline characteristics of aquatic microfaunal and microfloral assemblages against which to evaluate recent biotic changes in these freshwater ecosystems, 2) to assess the sensitivity of larval chironomid assemblages to temperature and infer past trends in summer air temperature using a chironomid-based transfer function, and 3) to explore possible connections between variations in diatom assemblages, sedimentological variables, and their relationship to changes in catchment dynamics in this region.

MATERIALS AND METHODS

Study Sites

The three study lakes include two small headwater lakes and one large lake at the bottom of a valley. They are located near the village of Salluit, Nunavik, in northern coastal Ungava, a region at the northernmost tip of the Province of Québec, in eastern Canada (Fig. 1). The region lies 500 km north of the tree line and is characterized by continuous permafrost. Bedrock consists mainly of granitic gneiss of Archean age, overlain by thin Quaternary tills (Fulton, 1995). The catchments of our study lakes are sparsely vegetated by grasses, mosses, and lichens.

Deglaciation in the northern margin of the Ungava Peninsula is estimated to have occurred between 9300 and 8500 BP, although relict glaciers likely occupied valleys and depressions until after 6700 BP (Bruneau and Gray, 1997; Guyard et al., 2011). Glacial retreat occurred from north to south, i.e., from the coast to the interior. Near Salluit, the postglacial d'Iberville Sea reached a maximum marine limit of 150 m above modern sea level (Kasper and Allard, 2001). Glacio-isostatic compensation is more or less complete in northernmost Ungava (Guyard et al., 2011). There is evidence for a climatic optimum in the region around 6000 to 4000 BP, with temperatures likely warmer than today, followed by a general cooling until about 2500 BP and a return to warmer conditions until 500 BP. A colder period subsequently prevailed until the late 20th century (e.g., Williams et al., 1995; Mode, 1996; Saulnier-Talbot and Pienitz, 2010).

The study region is located north of the 10° July isotherm. Climatic data are sparse in Arctic Québec, but temperatures have been measured almost daily at Salluit airport since 1992. Between 1992 and 2004, the mean annual daily temperature was -7.7°C and mean August temperature was 8.3°C. Total annual precipitation for the Ungava Peninsula varies between 350 and 550 mm, of which approximately 50% falls as snow. More details on the climate and hydrology

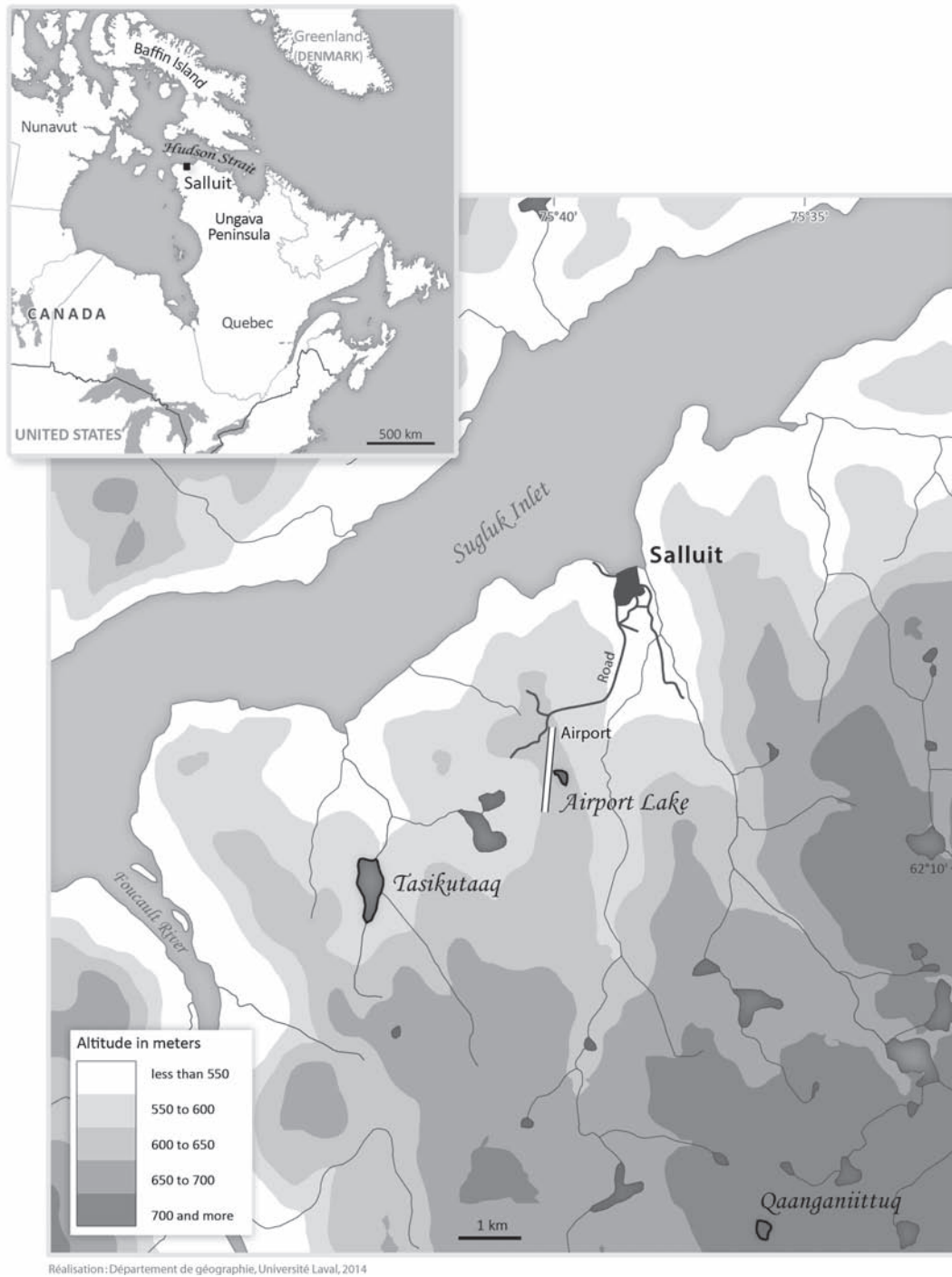


FIG. 1. Location of the study lakes near the village of Salluit, Nunavik (Québec, Canada).

of the region are provided in Saulnier-Talbot et al. (2007). The study lakes remain ice-covered from October to June. They have varied morphologies, but are all highly transparent, ultra-oligotrophic, circumneutral to slightly acidic, and devoid of fish. They vary in their sizes, depths (Table 1) and morphometries: Lac de l'Aéroport (Airport Lake; AER) and Qaanganiittuq (QUA) are small headwater lakes with intermittent inflows, whereas Tasikutaaq (TKQ) is a large lake located in a valley and has a larger catchment area to lake area ratio, with several active inflows during the summer.

High-resolution topographic maps and GoogleEarth[®] were used to determine the coordinates, altitude, and dimensions of the lakes and their catchments and to evaluate the location of the deepest sector in each lake.

Sampling

The three lakes were sampled in April 2001, when they were covered in ice. We used a gravity corer in all three cases, and also a Livingston piston corer in AER, in order

TABLE 1. Geographical attributes and limnological variables of the three study lakes.

Lake name (abbreviation)	Lac de l'Aéroport (AER)	Qaanganiittuq (QUA)	Tasikutaq (TKQ)
Coordinates	62°10'40.69" N 75°39'47.69" W	62°07'22.68" N 75°35'35.91" W	62°09'46.87" N 75°43'14.21" W
Altitude (m asl)	220	470	129
Max depth (m)	8.6	13.9	13.6
Surface area (km ²)	0.039	0.062	0.307
Catchment area (km ²)	0.1	0.4	8.6
C:S ¹	2.5	6.7	27.7
pH	6.8	NA ¹	6.5
Conductivity (μS cm ⁻¹)	0.072	NA ¹	0.023
DO ¹ (mg L ⁻¹) 2004–09	12.3	NA ¹	14
Summer water temperature (°C)	8–12	7.5	6.7
CI-MAAT ¹ in surface sediments (°C)	+6.8	7.7	+7.9

¹ C:S = Catchment to lake surface area ratio; NA = not available; DO = dissolved oxygen; CI-MAAT = Chironomid-inferred mean August air temperature (mean measured August air temperature for 1992–2004 for the region is +8.3°C). Water temperatures were measured in 2003, throughout the summer (10 times in June–August) in AER, once in July in QUA, and three times in July in TKQ. That year, the lake was still 40%–50% ice-covered at the end of June.

to retrieve the older sediments (the other two lakes were too deep for our piston corer). The sediment cores were subsampled vertically in the field at 0.25 to 1.0 cm intervals and kept refrigerated in the dark until lyophilized in the laboratory.

Core Chronologies

Core chronologies were determined using a combination of ²¹⁰Pb and ¹⁴C methods. Since no macrofossils of sufficient mass were found in the sediments, radiocarbon dates were obtained from the humic acid fraction of the sediment using accelerator mass spectrometry. The offset between the ¹⁴C ages of the sediments and their true age was evaluated using ²¹⁰Pb analyses and estimates from previous studies on Baffin Island (Abbott and Stafford, 1996; Miller et al., 1999). The method and site-specific ages established for each core are described in detail elsewhere (Saulnier-Talbot et al., 2009). Unfortunately, because of the difficulties of dating high-latitude sediment cores (see Wolfe et al., 2004), we have only a few dates on them. Therefore, we have opted to be more cautious and have not calculated sedimentation rates or fluxes for different elements. Radiocarbon dates in the text are given in calibrated years before the present (cal. yr BP), with the year 2000 of the Common Era as “present.”

Core Contents

Sedimentary Variables: The organic matter content of the sediment was estimated using the loss-on-ignition method and the equations outlined in Heiri et al. (2001). Briefly, 0.3 ± 0.02 g of freeze-dried sediment was dried at 100°C in a muffle furnace over 24 hours and allowed to cool before being weighed. The remaining fraction was burned at 550°C for four hours, left to cool inside the furnace, and weighed again.

Biogenic silica (BSi) is most often used as an indicator of the amount of siliceous microfossil material in sediments,

which, in most cases, is primarily derived from diatoms (Conley, 1998). BSi content of the core samples was measured at the Amino Acid Geochronology Laboratory, Northern Arizona University, where it was extracted from lyophilized sediments with Na₂CO₃ and the concentration was determined with a spectrophotometer following the procedure outlined in Mortlock and Froelich (1989).

Microfossils: For chironomid analysis, a measured amount of freeze-dried sediment was rehydrated and deflocculated in a warm 5% KOH solution for approximately 20 min, then rinsed through a 74 μm mesh sieve. All chironomid remains present in the subsample were sorted using a Bogorov counting tray at 40× magnification and mounted permanently onto microscope slides using either Entellan® or Clearmount®. Head capsules were identified following Oliver and Roussel (1983), Wiederholm (1983), Walker (1988, 2000), and Larocque and Rolland (2006). A minimum of 50 head capsules was extracted from each level, which represents the minimum established number for quantitative paleoenvironmental inferences (Heiri and Lotter, 2001; Larocque, 2001; Quinlan and Smol, 2001). Head capsules with more than half the mentum were counted as one specimen, halves were counted as such and fragments representing less than one half were discarded.

In preparation for diatom analysis, 40 mg of freeze-dried sediment was digested for 24 hours using 5 ml of 30% H₂O₂ solution. Samples were then heated for two hours until the reaction was complete and the solution had become clear. Then 10 ml of H₂O₂ was added to the solution and left to stand for 24 hours before rinsing. A known number of plastic microsphere markers (diameter ~6.2 μm) were added to the siliceous solutions to estimate diatom concentrations (Battarbee and Kneen, 1982). The slurries were then permanently mounted onto microscope slides using Naphrax® resin. A minimum of 350 diatom valves per sample were counted on random transects, and the number of microspheres and chrysophyte cysts per 350 diatom valves was recorded. Diatom taxonomic identification mainly followed

TABLE 2. Performance statistics of the chironomid mean August air temperature (MAAT) inference model used in this study compared to others from eastern Canada. The Walker et al. (1997) WA-PLS model infers mean summer surface water temperature and the Francis et al. (2006) WA model infers mean July air temperature.

	This study	Walker et al., 1997	Francis et al., 2006
Number of lakes	63	39	68
Number of taxa (or groups)	72	34	44
Temperature range (°C)	4-17	6-27	5-19
RMSEP (°C)	1.54	2.26	1.53
Coefficient of determination (r^2)	0.93	0.88	0.88
Maximum bias (°C)	1.68	2.4	1.24
WA-PLS components	2	2	None

Fallu et al. (2000) and Krammer and Lange-Bertalot (1986, 1988, 1991a, b), and nomenclature was updated to reflect recent taxonomic revisions. The above-mentioned analyses were completed in the Laboratoire de Paléocéologie Aquatique (LPA) at Université Laval, except for BSi (see above) and for chironomid analysis, which was carried out by É. Saulnier-Talbot while on leave at University of KwaZulu-Natal, Pietermaritzburg, South Africa.

Data Analysis and Representation

To summarize the major patterns of compositional variation in the biotic assemblages over time, we conducted ordination analyses of the subfossil assemblage data. In particular, we conducted lake-specific detrended correspondence analyses (DCA) of the square-root transformed chironomid or diatom percentage data using the software package MVSP (Kovach, 2004). The first DCA axis scores from each chironomid sediment core profile were regressed against chironomid-inferred temperature reconstructions in order to evaluate their degree of coherence. We used the software Canoco (ter Braak and Šmilauer, 2002) to conduct canonical correspondence analysis (CCA) on the data from TKQ (with sub-fossil data plotted passively) in order to further explore which variables the chironomids were responding to in this lake. To determine the most likely position of compositional boundaries in each core, we used the software Zone (Juggins, 1992) and determined the number of significant zones by applying the broken-stick model (Bennett, 1996).

Stratigraphical diagrams of the data were plotted using the software C2 (Juggins, 2003). Only taxa representing at least 5% relative abundance in at least one sample were included in the graphic representations. However, all chironomid taxa present with at least 2% relative abundance in at least two samples were included in the reconstructions in order to conform to the cut-off criteria of the inference model. Shifts in biodiversity were evaluated using Hill's N_2 (the reciprocal of Simpson's index), an index that determines the effective occurrence of species in a sample and is sensitive to changes in the abundance of common species (Hill, 1973). We are using this metric with some caution given that changes in sedimentation rate alone could influence biodiversity estimates (Smol, 1981).

Development of the Chironomid-Based Temperature Inference Model

To reconstruct temperature variations in our study lakes, we developed a model based on data previously published by Larocque et al. (2006). This model infers mean August air temperature (MAAT) and is based on meteorological data collected from six stations monitored by Environment Canada over a 12-year period (1993–2005), corrected for altitude. The original training set included modern chironomid assemblages from 52 lakes located along a latitudinal transect between Povungnituk and Matagami, in northwestern Québec, Canada. Here, several more lakes from northernmost Québec, Southampton Island (Nunavut), and the High Arctic (Cape Bounty on Melville Island and northern Ellesmere Island) were added to the original training set, for a new total of 63 lakes. As in the original 2006 model, chironomids in our data set responded most strongly to air (mean August) and surface water (summer) temperature, dissolved organic carbon (DOC), and lake depth.

In a few cases, the taxonomic categories were grouped together; specifically, species of the genus *Zalutschia*, as well as those of the genus *Chironomus* and all *Cricotopus* and *Orthocladius*, were grouped into one category, as well as all the species belonging to the Tribe Pentaneurini. The best resulting model is a two-component weighted-averaging partial least squares regression with leave-one-out cross-validation based on square root-transformed relative abundances of species data. The WA-PLS regression was selected on the basis of the unimodal response of most taxa included in the analysis (Table 2). The new model has a more robust relationship between observed and predicted values ($r^2_{\text{jack}} = 0.86$ instead of 0.67) but a slightly higher measure of random error than the original model (RMSEP_{jack} = 1.54°C instead of 1.17°C), a compromise that nevertheless does not render our model less reliable than the others developed for the region (Table 2). Larger residuals account for temperatures at either end of the gradient (below 5°C and above 20°C), which tend to be over- or underestimated (Larocque, 2008). The model was applied to the downcore microfossil data using the software package C2 (Juggins, 2003).

Goodness-of-Fit

The proportion of sedimentary taxa represented in the modern calibration set can be used as one measure of the robustness of the environmental reconstructions (Birks, 1998). As a result of poor preservation, damage incurred during processing, or taxonomical conservatism on the part of the analyst, some categories that were applied to the sedimentary identifications are not present in the calibration set. These omissions are explained as follows. Many sedimentary head capsules of the abundant Subtribe Tanytarsina could not be identified to a higher taxonomic level because they lacked the antennal tubercles (pedestals) and other distinctive species-specific characteristics (namely the mandibles). These were grouped as category “Subtribe Tanytarsina no ant” (for “no antennal tubercles”), which is not categorized in the MAAT model. Also, when the head capsules of the genus *Heterotrissocladius* could not be identified to the species morphotype level because the necessary characteristics were lacking or unclear, they were treated as “*Heterotrissocladius* indet.” (for “indeterminate”). In the training set, all *Heterotrissocladius* are identified to a species morphotype level. The percentage of the assemblage that consists of taxa not represented in the model data reaches 40% in some cases; therefore, the exclusion of these categories from the inferences might have an impact on the reliability of the reconstructions in terms of the inferred values and also of the trends. Accordingly, we used direct gradient analysis to evaluate the “fit” of each sedimentary assemblage to the environmental variable being reconstructed. In particular, canonical correspondence analysis (CCA) was applied, with modern samples and the variable of interest (MAAT) as active variables and downcore samples run passively. The residual distance (square residual length, SqRL; log-transformed to adjust for skewness) of the modern samples was used as the criterion for fit. Samples with a high residual distance from the environmental variable axis (i.e., exceeding the 95% confidence interval) were deemed to have a “poor” fit to that variable. The fit of a sample does not necessarily determine whether the reconstructed variables accurately reflect past conditions or not, but merely allows for an assessment of how well the composition of the sedimentary assemblages fits into the modern calibration set and indicates a strong or weak relationship between the abundances of the inventoried taxa and the reconstructed variable (Bigler et al., 2002).

RESULTS

We retrieved a 50 cm sequence from Lac de l'Aéroport (AER) and 24 cm cores from lakes Qaanganiituuq (QUA) and Tasikutaaq (TKQ). The basal dates established for the three cores indicate that they cover varying time periods (Fig. 2). The AER core covers the region's entire postglacial history, that is, about the last 8000 years (Saulnier-Talbot and Pienitz, 2010). This dating is also supported by

the lithology (not shown here, but see Saulnier-Talbot et al., 2009), including clay at the bottom of the sequence, followed by a transition to a more organic gyttja. The QUA core covers about half of this period (3800 years), and the TKQ core, only about the last two millennia. The lakes are characterized by slow sedimentation rates, as revealed by the dating of recent sediments indicating that the entire unsupported ^{210}Pb inventory (equivalent to the previous ca. 150 years) occurred in the upper 4 to 5 cm of sediment accumulation (Saulnier-Talbot et al., 2009).

Chironomid Assemblages and Summer Temperature Inferences

Chironomid assemblages differed markedly in the three cores during the late Holocene. The two small lakes (AER, QUA) have a few, very dominant taxa, whereas the large lake (TKQ) has more evenly spread relative abundances of taxa (Fig. 2), likely the result of a more diverse range of habitats in this lake. Chironomid remains were twice as abundant in QUA as in the other two study lakes.

Chironomid succession in the AER core is discussed in length in Saulnier-Talbot and Pienitz (2010). Briefly, the initial development of lake AER's chironomid community in the early postglacial period is characterized by a dominance of the Subtribe Tanytarsina (Fig. 2A). An abrupt and distinct turnover in species composition occurs at 23 cm, corresponding to about 6000 yr BP. This depth in the core is marked by a switch to an Orthoclaadiinae-dominated assemblage. This compositional change is seen in the DCA axis 1 sample scores, which show a twofold decrease. The chironomid-inferred mean August air temperatures (CI-MAAT) suggest a warm initial post-glacial period with a mean of around 10°C, followed by a significant cooling with a mean around 7°C until recent times. Most of the samples in the upper section of the core are within the 95% confidence interval of the goodness-of-fit analysis (vertical line), indicating that the values and trends of the CI-MAATs are reliable.

In Qaanganiituuq (QUA), the Subtribe Tanytarsina is abundant throughout the core, but *Abiskomyia*, an Orthoclad, becomes the dominant genus from 11 cm onwards, accompanied by synchronous, marked increases in the cold-adapted genera *Pseudodiamesa* and *Sergentia* (Fig. 2B). A period of decreased diversity between 11 and 3 cm corresponds roughly with a period of lower CI-MAATs. The reconstructions in the upper portion of the core are strongly driven by the relative abundances of the cold-adapted genera *Abiskomyia*, *Pseudodiamesa*, and *Sergentia*. The high relative abundances of *Abiskomyia* (up to almost 60%) in the upper half of the core have no analogs in the calibration set, which, despite the exact fit between measured temperatures and inferred values in the core top, might constitute a potential source of error in the inferences. The fossil data set is a poor fit with the calibration data set (all samples < 95% confidence). Therefore, the CI-MAAT values in this core should be regarded with some caution. However, the

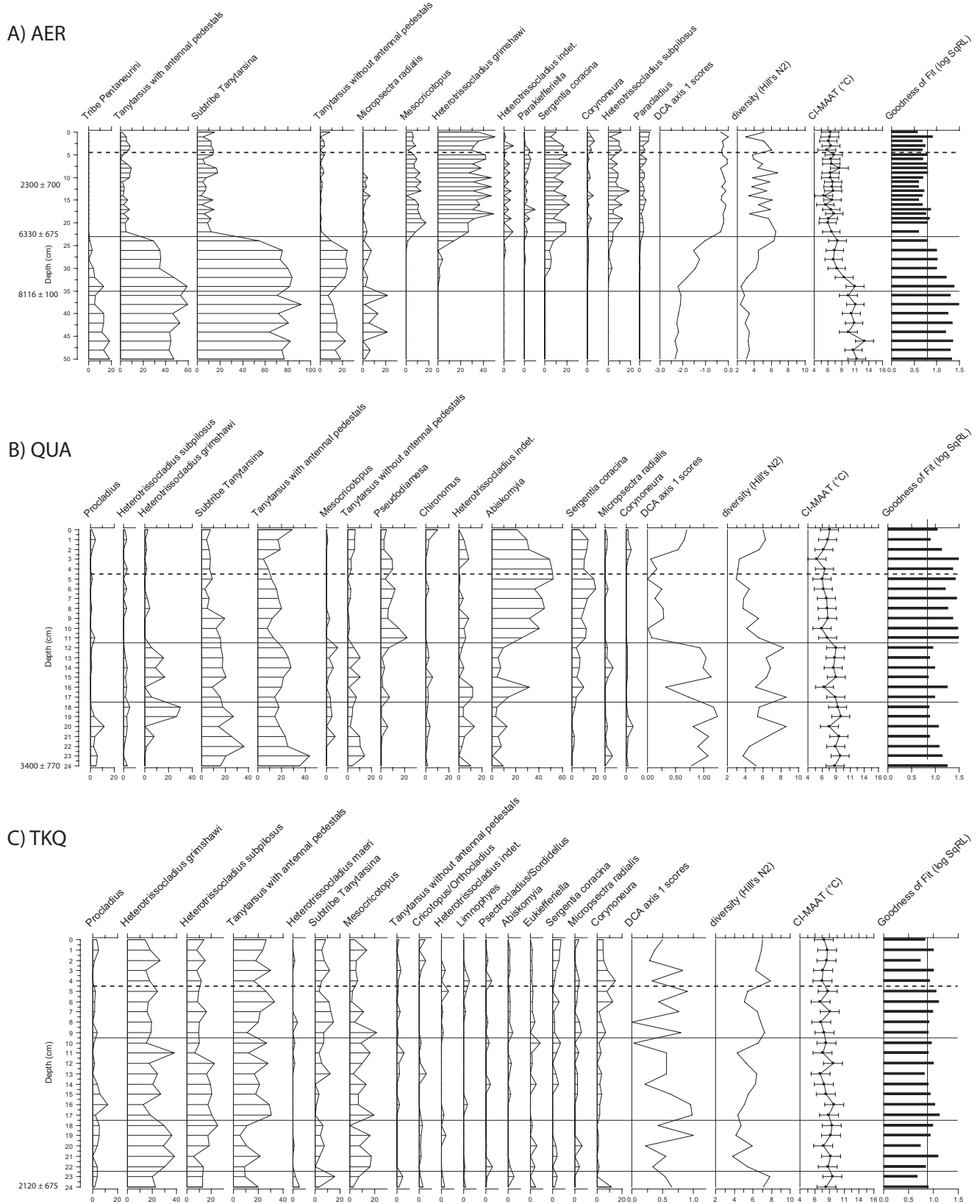


FIG. 2. Relative abundance diagrams (%) of the most abundant (> 5% in at least one sample) chironomid taxa recorded in the sediments of the three study lakes, trends in compositional change (DCA axis 1 scores), diversity (Hill's N2), chironomid-inferred mean August air temperature (CI-MAAT), and related goodness-of-fit for each downcore sample (vertical line indicates 95% confidence interval = 0.8). Taxa are arranged from left to right according to the position of their highest downcore relative frequency. Dashed lines indicate approximate depth corresponding to the period post-1850 (based on ²¹⁰Pb measurements). Solid lines indicate zonal changes in the assemblages.

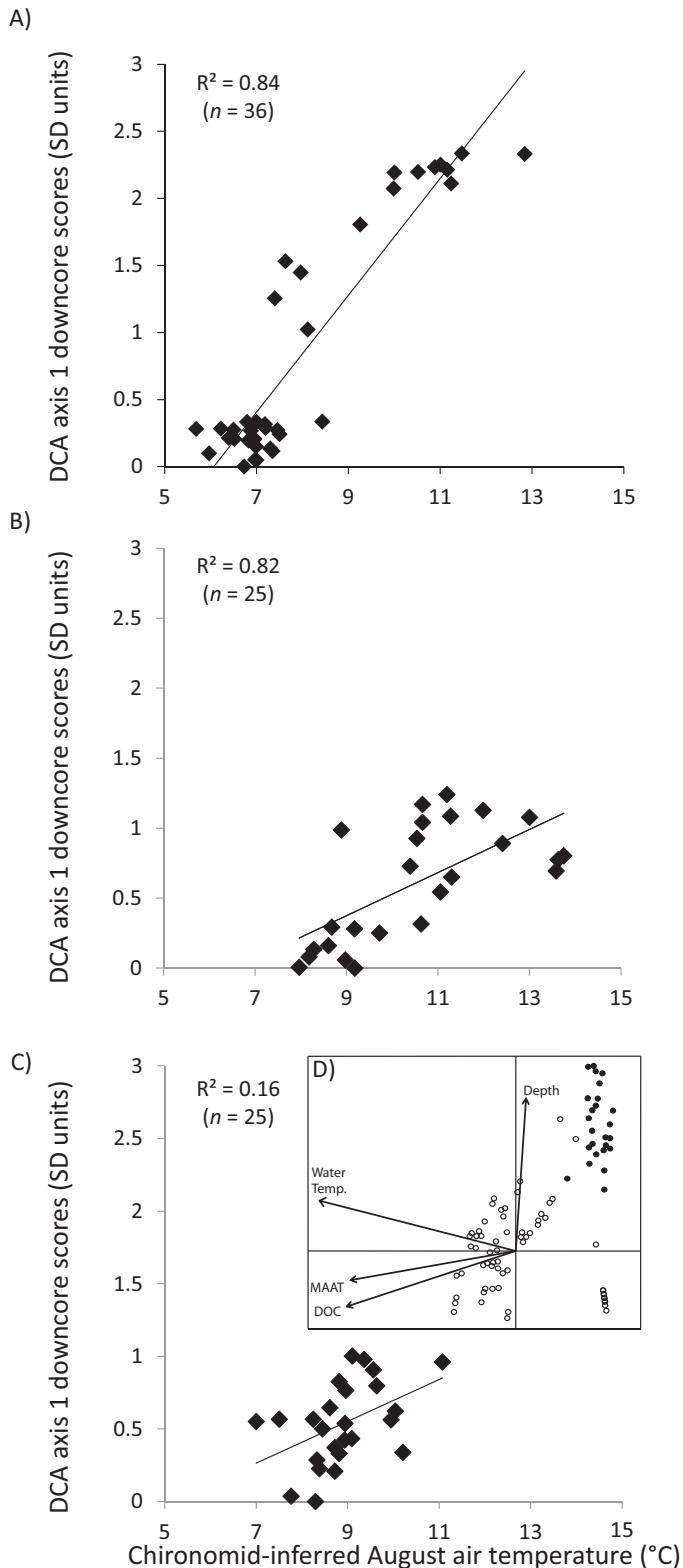


FIG. 3. Relationship between DCA axis 1 scores and chironomid-inferred temperatures in the three cores (A = AER, B = QUA, C = TKQ), and CCA diagram of modern samples (white circles) and environmental variables, with sub-fossil samples (dark circles) plotted passively for lake TKQ (D).

fact that they show an overall trend similar to that of the AER core, with generally cool temperatures throughout the late Holocene, lends support to their plausibility.

The assemblage in the Tasikutaaq (TKQ) core is dominated by the cold-water adapted taxon *Heterotrissocladius* (including *H. grimshawi*, *H. subpilosus*, and *H. maeri*) (Fig. 2C). The Subtribe Tanytarsina (which includes the cold stenotherm *Micropsectra* cf. *radialis* group) is abundant throughout the sequence and *Mesocricotopus* is also well represented. Diversity remains relatively constant throughout the core and CI-MAATs show slightly higher values (around 9°C) in the bottom section of the core until 16 cm depth, when they decrease to an average of about 8°C up to the top of the core. Both the QUA and TKQ cores have poor analogs between the fossil and calibration data sets, and display a similar overall cooling trend. Inferred temperatures in TKQ are the warmest of the three cores and the closest to the measured mean August diurnal air temperature for the locality (see below).

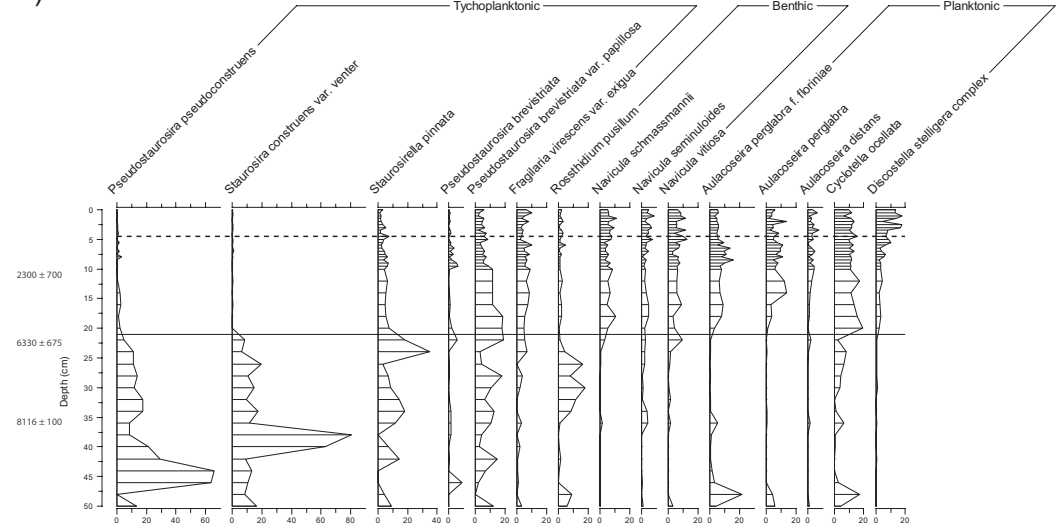
The highly significant correlation between DCA axis 1 scores and CI-MAAT indicates that temperature is an important driver of species composition in lakes AER and QUA (Fig. 3A, B). This is not the case in TKQ (Fig. 3C), where CCA suggests that the chironomid assemblages in this lake are more strongly driven by depth (Fig. 3D). The lakes' morphometry might be an influential factor here; AER and QUA are small headwater lakes with small catchments, whereas TKQ is a much larger lake with a very large catchment and at least two inlets, implying 1) a more diverse set of available habitats and 2) more complex interactions between the lake and its catchment. However, mean August diurnal air temperature at Salluit airport (226 m asl) between 1992 and 2005 was 8.3°C (Government of Canada, 2015), which is very close to our reconstructed values for the late 20th century (Table 1). These values are equal to or within the RMSEP of the model, suggesting reliable inferences, at least for the recent past. Additionally, taking into account the distance from the coast and adiabatic lapse rates, slight differences in temperature between the three lakes are to be expected.

Diatom Assemblages and Sedimentary Indicators

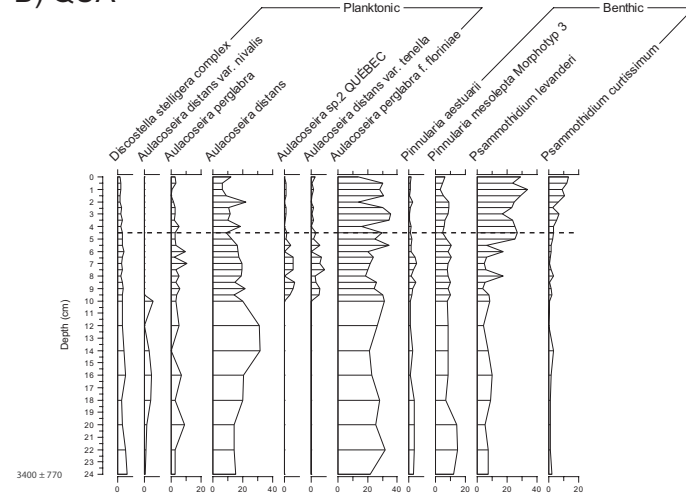
The three lakes are dominated by planktonic diatom assemblages characteristic of oligotrophic northern lakes with high transparency, low DOC, and low alkalinity. Between-lake variability in the taxa (Fig. 4) likely reflects their different depths, morphometries, and available habitats. The magnitude of change in the assemblages over the course of the Late Holocene (following post-glacial stabilization of the lakes, as indicated in Fig. 4A by the full horizontal line at 22 cm corresponding to the only significant zonal change in the cores) is low, with the exception of the recent past in the two smaller lakes.

The sedimentary indicators present in the early portions of the core from Lake AER (Fig. 5A) show typical signs of early lake ontogeny in recently deglaciated terrain, namely the presence of clayey sediments with very low percent loss on ignition (LOI), low BSi concentrations, and generally low diatom and chrysophyte concentrations (Fig. 5).

A) AER



B) QUA



C) TKQ

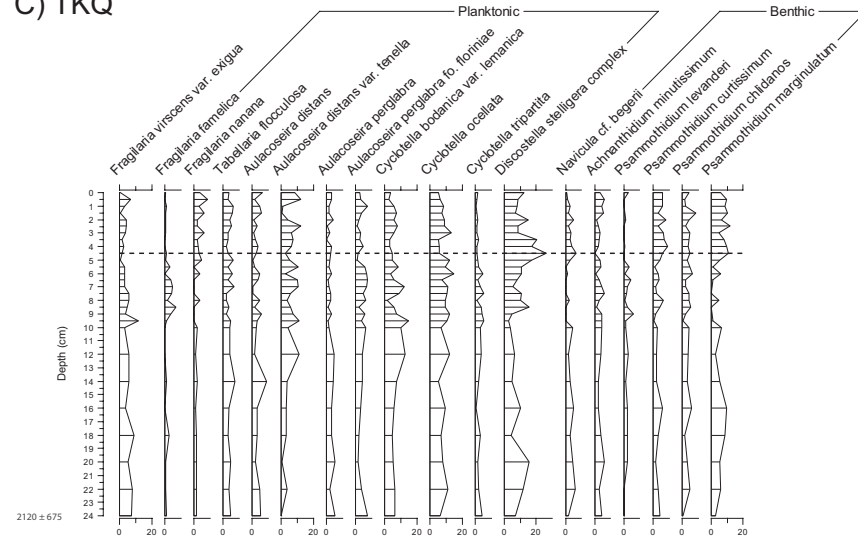


FIG. 4. Relative abundance diagrams (%) of the most abundant (> 5% in at least one sample) diatom taxa recorded in the sediments of the three study lakes. Taxa are grouped according to their life-forms (note that *Fragilaria virescens* var. *exigua* in C is tychoplanktonic). Dashed lines indicate approximate depth corresponding to the period post-1850 (based on ²¹⁰Pb measurements). Solid line indicates zonal change in assemblage (in AER; others have none).

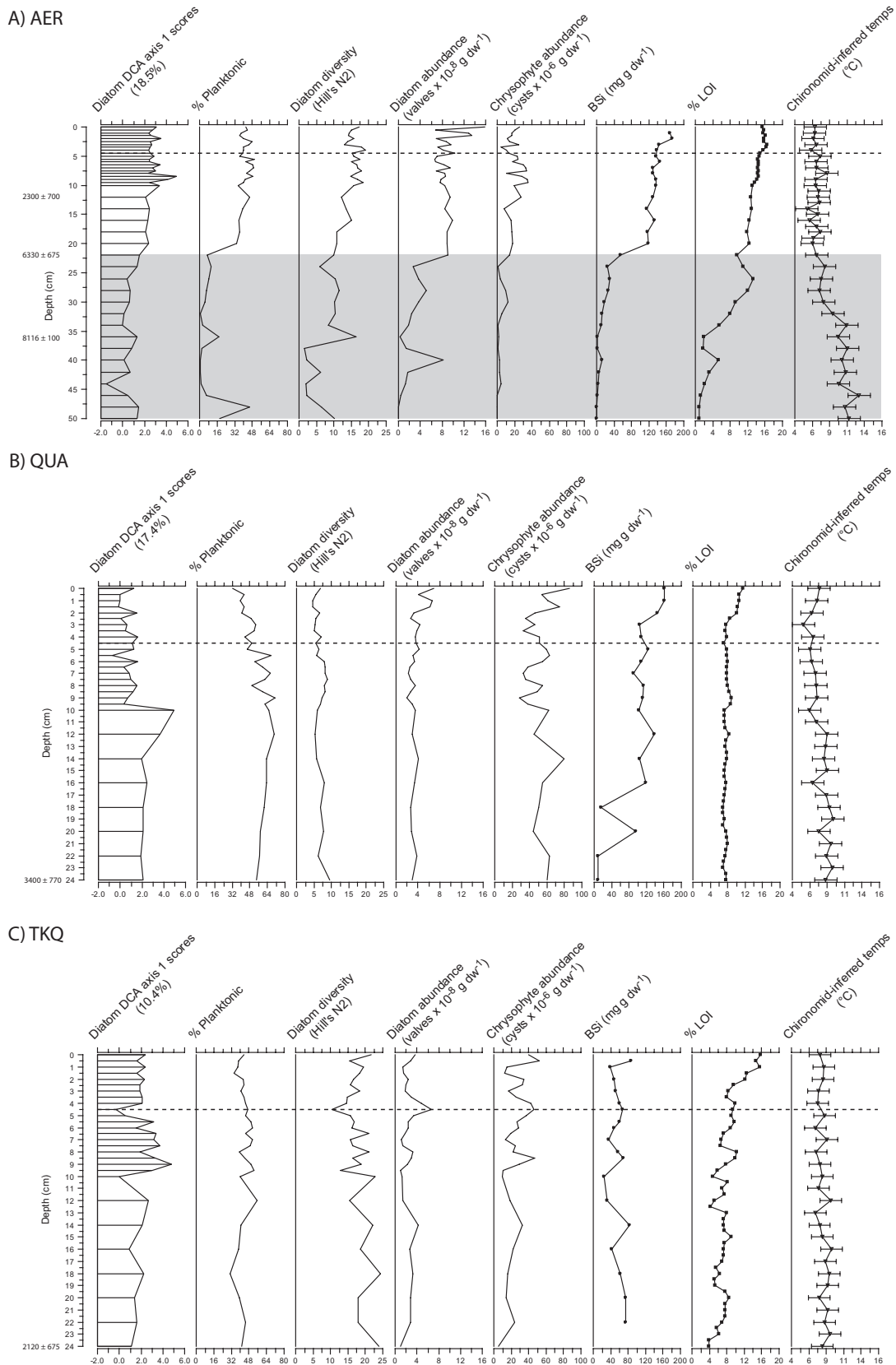


FIG. 5. Trends in diatom compositional change (% variance explained by DCA axis 1 scores), planktonic proportion of the assemblage, species diversity (Hill's N2), diatom and chrysophyte abundances, biogenic silica content of sediments expressed as the deviation from the mean (AER mean calculated from 22 cm core depth to surface to avoid early lake ontogeny effects), and organic matter content (% LOI) in the three study lakes. Dashed lines indicate approximate depths corresponding to the period post-1850 (based on ^{210}Pb measurements). The shaded area in (A) represents the period of early lake ontogeny, dominated by strong deglacial effects. The proxies are presented on the same scales in A, B, and C to facilitate between-lake comparison.

These features are accompanied by a diatom assemblage dominated by small taxa of the genus *Fragilaria sensu lato* (including *Pseudostaurosira brevistriata* var. *papillosa*, *Pseudostaurosira pseudoconstruens*, *Staurosira construens* var. *venter*, *Staurosirella pinnata*) (Fig. 4A), often considered as pioneer species (Saulnier-Talbot and Pienitz, 2001).

The diatoms in AER shift to a more diverse assemblage after 6000 BP, with a marked increase in planktonic species, well represented by the *Aulacoseira* and *Cyclotella* sensu lato genera (Fig. 4A). This change echoes the synchronous transition in the chironomid faunal assemblage from warmer taxa to more cold-tolerant and deep-water taxa. The most notable change in the diatom assemblage in this lake during the Late Holocene period is the recent increase in the relative abundance of the *Discostella stelligera* complex, especially significant in the top 3 cm of the core (corresponding to the 20th century).

The highest abundances of chrysophytes occur between 5 and 10 cm depth, and those of diatoms are found in the core top, corresponding to the most recent accumulation (Fig. 5A). The high BSi content after the mid-19th century suggests that primary production in this lake has been much higher during the most recent period (since the mid-19th century) than it had been since the post-glacial stabilization of the lake catchment system, suggesting more favorable conditions for primary production in the lake in recent times.

The diatom assemblage in the QUA core is indicative of a poorly buffered acidic lake, dominated in abundance and diversity by planktonic *Aulacoseira*, a highly successful freshwater genus that thrives in well-mixed water columns (Fig. 4B). The *Aulacoseira* found in this core have low alkalinity optima (Fallu et al., 2000). The assemblage also includes some species of the genus *Pinnularia*, which is often found in low-conductance, slightly acidic waters, and of *Psammothidium*, which is considered an acidophilic genus (Flower and Jones, 1989; Bukhtiyarova and Round, 1996). The recent increase in the relative abundance of the genus *Psammothidium* (formerly part of genus *Achnanthes*) is responsible for the decrease in the proportion of planktonic taxa in the diatom assemblage. The top 3 cm of the core also shows a synchronous increase (~4%) in % LOI, siliceous algal abundances, and BSi content (Fig. 5B).

The core from the large lake TKQ covers the past ~2000 years, indicating the highest sedimentation rate within this lake set. The presence of two inflows and a large drainage basin likely account for this. LOI values (mean = 8%, n = 50) show a gradual increase throughout the core, culminating at 16% in the top 0.5 cm, almost 12 percentage points higher than the lowest values (< 4%) recorded at the bottom of the core (Fig. 5C). BSi concentrations are lower than in the other two lakes and show variability that is strongly correlated ($r^2 = 0.77$, $p < 0.0005$) to variations in diatom abundance.

In general, little change occurs in diatom assemblage composition throughout the TKQ core, with the first DCA axis accounting for only 10% of the variance. No statistically significant divisions were found in the diatom record, 40% of which is composed of planktonic taxa, as expected in such a

large and relatively deep lake. The most common planktonic genera are *Aulacoseira*, small *Cyclotella* sensu lato and needle-shaped *Fragilaria* (e.g., *F. famelica*, *F. nanana*). The benthic fraction is dominated by small *Achnanthes* (*Psammothidium*), including acidophilic *P. marginulata*. Relative abundances of the *Discostella stelligera* complex are highest between 4 and 8 cm in this core (Fig. 4C), corresponding to the period of highest diatom abundance.

Diatoms are most abundant and BSi values highest in AER, followed by QUA and TKQ (Fig. 5), showing a gradient in primary production among our lake set from the smallest lake (most productive) to the largest (least productive). Diatom abundances and biogenic silica content (BSi) are significantly correlated in AER ($r^2 = 0.86$, $p < 0.0001$) and in TKQ ($r^2 = 0.77$, $p < 0.0001$), and to a lesser degree in QUA ($r^2 = 0.47$, $p < 0.02$) (Fig. 6-I). This correlation is likely due to the higher concentration of other siliceous microfossils (chrysophytes) in the sediments of QUA, which can contribute significantly to the amount of sedimentary BSi. Diatom diversity is highest in TKQ (Fig. 5C), most likely due to the presence of more diverse environments within the larger basin.

LOI and BSi are highest in the uppermost sediments in AER and QUA (Fig. 5), where they are significantly correlated (Fig. 6-II). This fact suggests 1) that BSi is driving LOI values in these two lakes, whereas LOI in TKQ, which is uncorrelated to BSi, is likely driven by external inputs from the catchment, and 2) that recent primary production in the two small lakes is higher than at any other time during the last 4000 years.

DISCUSSION

Our reconstructed history of the three Ungava lakes described here documents ecosystem and climatic stability over the past ~2000–3000 years, with some indication of a recent trend towards change. However, the full post-glacial sequence provided by the longest record (AER) clearly shows that the most pronounced limnological changes of the Holocene, prior to the 21st century, occurred as the effects of deglaciation waned in the surrounding catchment. This period appears to correspond to a time of marked climatic changes, from warmer and drier conditions to cooler and moister climate. This hypothesis is supported by 1) a ~2°C decrease in CI-MAATs and 2) the synchronous shift in chironomid and diatom assemblages, indicating a significant deepening of the water column (dominance of chironomid taxa preferring deeper, cooler waters and a higher proportion of planktonic diatoms). These results agree with comparable lake records from South and Southwest Greenland (Massa et al., 2012; Perren et al., 2012) and with measures of past temperatures from the Greenland Ice Sheet (GIS; Summit and Dye 3 boreholes) (Dahl-Jensen et al., 1998), which show the Holocene climatic optimum from 8000 to 5000 BP, followed by the period of Neoglacial cooling from 5000 to about 2000 BP.

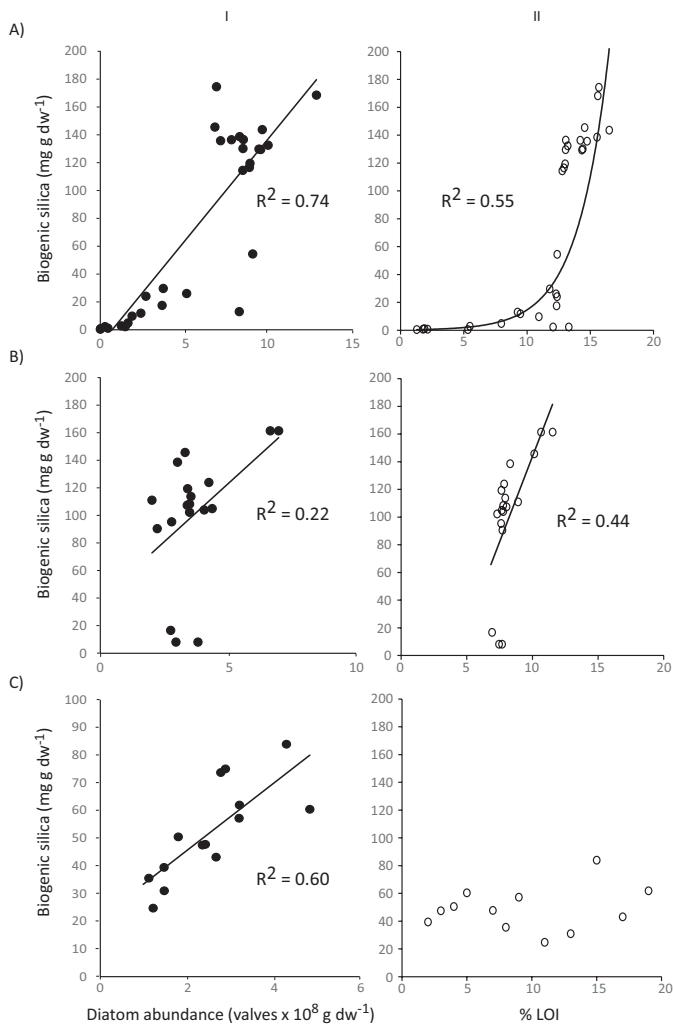


FIG. 6. Correlation between I) downcore diatom abundances and BSi measurements, and II) % LOI and BSi, in the three study lakes (A = AER, B = QUA, C = TKQ).

Overall, we found evidence for reliable chironomid-based inferences of temperature trends for the region, especially from the two headwater lakes. These findings are consistent with the well-established relationships between chironomids and both air and water temperature at high latitudes (Brodersen and Lindegaard, 1999; Luoto et al., 2014). Indeed, many studies have illustrated the accuracy of using chironomids for quantitatively reconstructing air temperature. For example, by comparing meteorological data with chironomid assemblages found in varved Lake Silvaplana, Switzerland, Larocque et al. (2009) obtained more than 80% accurate temperature inferences for the period 1850–2001, demonstrating that chironomids can be a reliable tool for quantitatively reconstructing past air temperatures, at least for the last century. On millennial timescales, a comparison between chironomid-inferred temperatures at different sites showed similarities in the general trends of changes (Larocque-Tobler et al., 2011). Similarities have also been established on longer temporal scales (reviewed in Brooks et al., 2012). Nonetheless, not all lakes are appropriate for temperature reconstructions, as changes in other factors

(such as oxygen and nutrients) might sometimes have an overriding impact on chironomid distribution through time (Velle et al., 2010). Along these lines, a discussion recently re-emerged in which the environmental factor is the most influential in structuring chironomid communities (Velle et al., 2010; Brooks et al., 2012). It is interesting to note that, in this study, the CI-MAATs from the lake TKQ core compare well to the results for the other two lakes, both in values and in trends (or absence thereof), despite indications that they are not statistically robust. This result highlights the need to compare reconstructions with other regional records to assess their reliability. This can be achieved, as exemplified here, by comparing chironomid-inferred records in different lakes or by comparing with reconstructions from other proxies or archives. Even after 30 years of reconstructing past climate with chironomids, the characteristics of lakes where the technique works best, or does not work, have yet to be clearly defined, but advances are being made (Chen et al., 2014). The results of the present study contribute to strengthening the theory that small headwater lakes with small catchments yield clearer and more reliable paleoenvironmental data, not only with regard to chironomids, but for all paleolimnological proxies.

In this study, between-lake differences in ecology appear to be best explained by morphometric and catchment differences. Interestingly, across all lakes we did not find a significant correlation between chironomid-inferred temperatures and primary production as measured by biogenic silica. This discrepancy does not necessarily imply that the CI-temperature reconstructions are erroneous, but could be due to the fact that the primary producers are reacting first and foremost to other environmental variables. Yet, in the context of limited climatic variability (in regard to temperature) at centennial to millennial time scales in this region, it appears that the diatoms nevertheless constitute a sensitive climate proxy. Diatom assemblage composition and siliceous algal production in the cores show variations that, if not linked directly to temperature, might indicate variations in other climate-related environmental variables. Examples are changes in nutrient content in the form of nitrogen (N) inputs, either from soil development or, more recently, from atmospheric N deposition.

The increases observed in the uppermost section of the cores in several of the proxies, including abundance of siliceous fossils, BSi, and LOI, suggest that recent primary production in the smaller lakes is unprecedented over the last ~4000 years. In the absence of evidence for warmer temperatures as inferred from the chironomid data, more favorable conditions for primary production in our study lakes could be attributable to higher nutrient inputs. The marked increase in the diatom *Discostella stelligera* (formerly *Cyclotella stelligera*) observed in the AER core over the last ~200 years is striking. Recent increases of the same nature were documented in a 50-lake study in the central Canadian Arctic tree-line region (Rühland et al., 2003) and in a series of Fennoscandian lakes (Sorvari et al., 2002) and were linked to climatic warming through associated

limnological changes, such as shorter duration of ice cover, longer growing season, and stronger thermal stratification. Additionally, recent experiments by Saros et al. (2014) show that *D. stelligera* responds strongly to nutrient additions and suggest that the growth of small centric diatoms in Arctic lakes is likely to be controlled by processes that alter light availability (water clarity, water column stability) and nutrient concentrations. The absence of a clear trend towards higher temperatures in the study lakes renders significant changes in stratification and mixing unlikely. It appears more likely that the *D. stelligera* complex and increased primary production (indicated by higher BSi values and increased LOI; Fig. 5A), have been responding to increased nutrient loading to the lake. A possible mechanistic explanation could be atmospheric deposition of nitrogen, which has been shown to be increasing even at high latitudes (Galloway et al., 2008) and could easily shift primary production in an ultra-oligotrophic lake such as AER (Hobbs et al., 2010).

Since these lakes were cored in the first year of the 21st century, there have been pronounced changes in climate in the region of Nunavik (northern Québec; Bhiry et al., 2011). Predictions by most models suggest that changes in this region in the near future (mid-21st century) will be felt mostly during the winter, with little change in summer temperatures. Therefore, the composition of chironomid assemblages is unlikely to change much in the near future because of these variations. However, shorter and less harsh winters are predicted to bring about earlier ice-out and longer growing seasons that will likely continue to stimulate primary production, both terrestrial and aquatic. It is therefore likely that shifts in diatom assemblage composition will occur (or might even be occurring at present), especially in the smaller lakes, which are more sensitive to change.

CONCLUSION

This multi-proxy study of three lakes located in northernmost Ungava shows that these ecosystems remained largely stable over the Neoglacial period, which followed a period of pronounced regional change during the mid-Holocene. The comparison of small headwater lakes with a large valley lake shows that the former are more sensitive recorders of environmental change and produced reliable temperature reconstructions. The use of chironomids to infer past temperatures and of diatoms and BSi to infer past primary production allowed us to observe that both proxies were reacting to the same overarching environmental changes, despite the fact that they were not directly correlated with each other. Diatoms in these lakes were more likely to be reacting to changes in nutrient or light availability than to changes related to temperature variations. The recent increase in primary production indicates that climate is likely not the only significant environmental change in this region and that long-distance atmospheric inputs may play a role in shifting limnological dynamics in these ecosystems.

The continued monitoring of these lakes will enable us to better understand their functioning and to compare predictions of climate models with direct field observations. This work will ultimately lead to more refined predictions of climate and related environmental change for the future in northernmost Ungava and the Eastern Canadian Arctic.

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