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Major postglacial summer temperature changes in the central coniferous boreal forest of Quebec (Canada) inferred using chironomid assemblages

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ABSTRACT: Chironomid head capsules preserved in lake sediments were used to reconstruct 8200 years of summer temperatures in the boreal forest of north-eastern Canada. Two training sets were used derived from Canadian and Eastern Canadian transfer functions. Both models reconstructed similar climate patterns, but the Canadian model provided temperatures generally 2–3 °C lower than the Eastern Canadian model. Three main thermal changes inferred by chironomids were: (i) the Holocene Thermal Maximum, which occurred between 8 and 5k cal a BP, with temperatures generally higher than today's, maximum temperatures between 8 and 6.5k cal a BP, and an average of + 0.9 °C; (ii) the Medieval Climate Anomaly around 1.1–1.2k cal a BP with an amplitude of + 0.7 °C; and (iii) a colder period reconstructed between the 14th and 19th centuries, corresponding to the Little Ice Age, with summer temperatures on average −0.5 °C lower than the climate normal. For each of these three climatic events, the timing and the amplitude of changes were similar with other published regional, North American and Northern Hemisphere records. Copyright © 2018 John Wiley & Sons, Ltd.

KEYWORDS: Chironomidae; Holocene Thermal Maximum; Little Ice Age; Medieval Climate Anomaly; transfer functions.

Introduction

Paleoclimatic records covering the Northern Hemisphere are still too sparse to obtain a precise representation of past climate change (Naulier *et al.*, 2015). For example, the amplitude and duration of the Medieval Climate Anomaly (MCA) remain of debate (Mann and Jones, 2003; Viau *et al.*, 2006; Esper and Frank, 2009). The MCA has been characterized by notably higher temperatures between ~950 and 1200 AD over a large part of the North Atlantic, in southern Greenland, the Eurasian Arctic and parts of North America (Lamb, 1965). However, its amplitude, location and extent are still undefined for most parts of the Northern Hemisphere. Another period of concern in North America is the Holocene Thermal Maximum (HTM). In Canada, the HTM seems to have varied between shorter (7–5k cal a BP) and longer (10–3k cal a BP) durations and its amplitude was different depending on the location (Renssen *et al.*, 2012). Thus, it is impossible to strictly define these periods of interest in North America since quantitative long-term data are missing in several regions.

Climate models need quantitative data to be able to accurately predict future ecosystem functioning. Proxy-climate-based reconstructions must be realistic and reliable, and if possible they should be validated by independent climate reconstructions from other proxies (Birks, 2003). Climate (temperature, precipitation) records from biological proxies such as pollen and chironomids preserved in lacustrine deposits allow adequate long-term information to quantify past climatic variability (Larocque-Tobler *et al.*, 2012; Heiri *et al.*, 2015).

Chironomids (Insecta: Diptera: Chironomidae) have been shown to generate high-resolution independent air temperature records due to their capacity to respond rapidly to climatic fluctuation with their short generation time and the ability of winged adults to move readily from site to site (Walker and Mathewes, 1987; Larocque-Tobler *et al.*, 2015). The head capsule of the chironomid larvae is made of chitin, a substance resistant to degradation, thus allowing the larval exoskeletons to be preserved for thousands of years. The distribution of chironomids has been shown to be influenced by air/water temperatures (Walker and Mathewes, 1987). In addition, with the help of transfer functions (Birks and Birks, 1998), they can record low-amplitude summer temperature changes (Brooks, 2006; Larocque-Tobler *et al.*, 2015). For example, when comparing instrumental data to chironomid-inferred temperatures, the differences were on average 0.75 °C in a Polish lake (Larocque-Tobler *et al.*, 2015) and 0.65 °C in a Swiss lake (Larocque *et al.*, 2009).

In the boreal region of north-eastern Canada, Holocene quantitative reconstructions of past climate change are mostly based on pollen analysis using the modern analogue technique (Viau and Gajewski, 2009; Viau *et al.*, 2012). Paleoclimatic data are available but with contradictory information. For instance, according to Viau and Gajewski (2009) and Viau *et al.* (2012), the MCA was cooler than the present day (1961–1990 AD) while warmer conditions were reconstructed in other parts of the country (Naulier *et al.*, 2015). Thus, doubts persist regarding the recording of this climate anomaly in north-eastern Canada, as well as for the other

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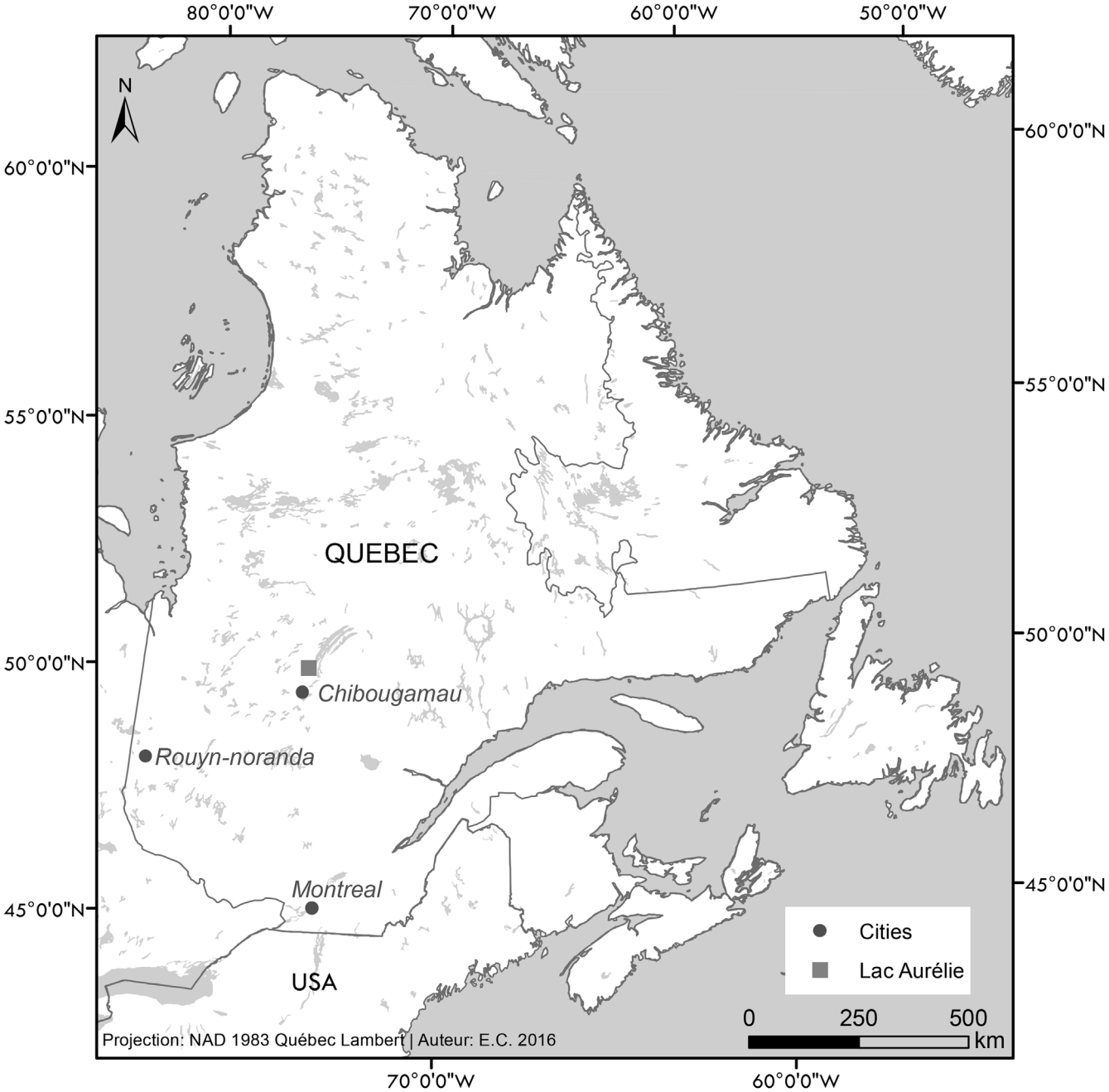

Figure 1. Location map of the study lake 'Lac Aurélie' in central Quebec, Canada.

major climate changes, notably those of weak amplitude, such as the Little Ice Age (LIA). Consequently, it is important to increase our knowledge of millennialscale temperature fluctuations using proxies able to capture low-amplitude climatic fluctuations. In this context, the main goal of this study is to present a new Holocene mean August air temperature reconstruction in the coniferous boreal forest of north-western Quebec (Canada) based on subfossil chironomid assemblages, allowing a discussion of the duration and amplitude of the HTM, MCA and LIA for this region.

Methods

Study area and site

The study site is located in central Quebec (Fig. 1), 66 km north of the town of Chibougamau. 'Lac Aurélie' (unofficial name; 50°25′12″N, 74°13′47″W; 440 m a.s.l.) covers an area of 1 ha and its maximum water depth (10 m) is in the central part of the lake. The lake is located in the black spruce – feather moss bioclimatic domain (Saucier *et al.*, 2009) dominated by black spruce (*Picea mariana* Mill.) and jack pine (*Pinus banksiana* Lamb.). Mean annual temperature from the closest meteorological station [Chapais 2: 1971–2000, 49°47′N, 74°51′W] is 0.0 ± 1.3 °C with an August temperature average of 14.9 ± 1.4 °C. Annual and August precipitation averages are 961 and 105 mm, respectively (Environnement Canada, 2017). Further details about the study site characteristics can be found in El-Guellab *et al.* (2015).

Coring, LOI analysis and chronology

Two overlapping sediment cores (providing a continuous record) were taken in March 2010 on a frozen surface at the center of the lake using a modified Livingstone-type square-rod piston corer (100×5 cm) (Wright *et al.*, 1984). Sediments were covered in polyurethane and aluminum foil for transportation to the laboratory and preserved at

Table 1. Radiocarbon dates at different depths. Dates were obtained from terrestrial plant macroremains. Chronology (not show in this study) was obtained from accelerated mass spectrometry (AMS) and has already been published by El-Guellab *et al.* (2015).

Lab code	Depth (cm)	^{14}C age (a BP)	Calibrated ^{14}C age range (cal a BP; 2σ)	Materials
Poz-35983	43–44	2870 ± 30	3007 (2879–3136)	Plant macroremains
Poz-35984	111–112	3990 ± 35	4443 (4319–4568)	Plant macroremains
Poz-36014	163–164	4750 ± 35	5457 (5329–5586)	Plant macroremains
Poz-36016	220–221	6140 ± 40	7047 (6931–7163)	Plant macroremains
Poz-36017	236–237	6490 ± 40	7396 (7317–7476)	Plant macroremains
Poz-36018	326–327	7460 ± 50	8279 (8185–8373)	Plant macroremains

Poz, Poznań Radiocarbon Laboratory.

4 °C before they were sliced for analyses. The water–sediment interface was collected using a Kajak-Brinkhurst (KB) gravity corer (Glew, 1991). Sub-samples (1 cm^3) were used for measuring the organic matter content by loss-on-ignition (LOI) at 550 °C for 4 h (Heiri *et al.*, 2001). Radiocarbon dates [calibrated at 2 sigma ranges based on the Intcal13.14C data set (Reimer *et al.*, 2013)] and chronology have already been published by El-Guellab *et al.* (2015). A summary is presented in Table 1.

Chironomid analysis

A total of 180 samples were analysed (Supporting Information, Table S1) at a temporal resolution varying between *ca.* 5 and 165 years (ca. 45 years on average). Chironomid head capsules were extracted from 2-cm^3 subsamples by soaking the samples overnight in 10% KOH. The subsamples were then water-rinsed through a sieve of 100 μm. The remnant was poured into a Bogorov tray and observed under a Leica stereomicroscope at a magnification of 20×. Individual subfossil head capsules were picked with fine forceps and mounted on a microscope slide in a drop of Hydromatrix. Previous studies suggested that at least 50 head capsules should be mounted for temperature reconstructions (Larocque *et al.*, 2001; Heiri and Lotter, 2010), but samples larger than 30 head capsules can also provide inferences below the error of the model (root mean square error of prediction, RMSEP) (Larocque *et al.*, 2009; Larocque-Tobler *et al.*, 2016). Taxonomic identification was made using a Motic microscope at a magnification of 400–1000× following the taxonomic keys of Brooks *et al.* (2007), Larocque and Rolland (2006), Oliver and Roussel (1983) and Wiederholm (1983).

Statistical analysis, paleoecological diagrams and constrained zonation

A chironomid percentage diagram was drawn using C2 software (Juggins, 2003). Detrended correspondence analysis (DCA) was performed using ade4 and vegan packages from R v3.2.2 (Borcard *et al.*, 2011) on the *n* (number of samples) by *p* (number of taxa) chironomid matrix of percentages. Data were square root transformed to stabilize the variance. Rare taxa (present in only one sample or with a relative abundance always <2%) were removed from the analysis. The length of the first DCA axis determines whether the distribution of the data set along this axis is linear or unimodal (Borcard *et al.*, 2011). Here, a gradient of 1.95 standard deviation units (SD) was obtained, suggesting linear techniques such as principal components analysis (PCA) were appropriate on our data set.

A PCA was then performed using C2 on the same data matrix used for the DCA. This method was coupled with a constrained sum-of-squares cluster analysis (CONISS) using the program ZONE version 1.2 (Juggins, 1991) to highlight major changes in assemblage composition (Grimm, 1987). The optimal number of significant zones created was determined by a broken stick model (Bennett, 1996). Percentage diagrams of warmer-than-today and colder-than-today taxa were made using the temperature optimum (Table 2) for each taxon obtained using the Eastern Canadian calibration set (see below). Percentages of eutrophic, oligo-mesotrophic, littoral and profundal taxa were calculated using ecological descriptions from Brooks *et al.* (2007). To better understand changes in the lake's conditions, ratios using these percentages were calculated. A > 1 eutrophic/oligo-mesotrophic ratio suggests a tendency towards eutrophic conditions, whereas a ratio < 1 suggests a tendency towards oligo-mesotrophic conditions. A littoral/profundal ratio > 1 indicates a dominance of littoral taxa and a dominance of profundal taxa if it is < 1.

Transfer functions

Two chironomid-based transfer functions were used to reconstruct mean August air temperature and evaluate their reliability in inferring past climate changes. The Eastern Canadian transfer function was first published by Larocque (2008) and was modified. Two lakes were added, and 11 lakes had their temperature measurements changed to mean August air temperature (Lakes A–H) as the earlier version of the calibration possessed only punctual measurements. In the new Eastern Canadian model, mean August temperature varied from 3 to 21 °C (instead of 27 °C) for a temperature gradient of 18 °C. The new data will be available on the NOAA website once the paper is published. The calibration set comprises 75 lakes and 79 taxa. The WAPLS 999-bootstrap transfer function with two components yielded a correlation coefficient (r^2_{boot}) of 0.85, an RMSEP of 1.67 °C and a maximum bias of 3.05 °C.

The second transfer function combined data sets from Canada (Fortin *et al.*, 2015). It comprises 485 lakes and 78 taxa. Mean August temperatures varied from −0.3 to 15.7 °C (gradient = 16 °C). It contains 52 of the 75 lakes in the Eastern Canadian transfer function of Larocque (2008). The correlation coefficient (r^2_{boot}) is 0.73, the RMSEP is 1.8 °C and the maximum bias is 2.9 °C (Fortin *et al.*, 2015).

To verify if the transfer functions could be applied to the fossil assemblages of Lac Aurélie, we estimated if fossil assemblages had modern analogues using the minimum distance to modern assemblages (Overpeck *et al.*, 1985). If the minimum distance was within the 1st–5th percentiles, the assemblages were considered as having 'good analogues'. If the distance was above the 20th percentile, the samples were considered as having no analogues. Furthermore, the goodness-of-Fit was calculated by passively adding downcore samples of Lac Aurélie into a Canonical Correspondence Analysis (CCA) analysis of the Eastern Canadian transfer function samples constrained by temperature (Heiri and

Table 2. Occurrence of taxa in the sediment of Lac Aurélie (total of 179 samples). Comparison of temperature optima obtained with weighted averaging for the three transfer functions: (a) Eastern Canadian transfer function (Larocque, 2008); (b) Canadian transfer function (Fortin *et al.,* 2015) and temperature categories.

Taxa identified in sediment	Occurrence in sediment	Optima		Category	
		(a) Eastern Canada	(b) Canada	Colder than today (15 °C)	Warmer than today (15 °C)
Ablabesmyia spp.	131	14.2	4.5	X	
Allopsectrocladius spp.	33	15.8			X
Brillia spp.	2	14.4	10.4	X	
Chaetocladius spp.	34	13.8	9.2	X	
Chironomus spp.					
Chironomus anthracinus-type	164		9.7		
Chironomus plumosus-type	147	12.1	Merged into *Chironomus* spp.	X	
Cladopelma lateralis-type	75	14.7	Merged into *Chironomus* spp	X	
Cladotanytarsus mancus-type	87	13.5	10.2	X	
Constempellina spp.	34	12.2	9.3	X	
Corynocera oliveri-type	45	14.5	11.2	X	
Corynoneura spp.	43	10.4	8.3	X	
Cricotopus/Orthocladius		7.3	7.9	X	
Cricotopus spp.	96		7.7		
Cryptochironomus spp.	48	11.8	Merged with *Orthocladius*	X	
Dicrotendipes nervosus-type	119	14.9	11.3		
Einfeldia spp.	11	14.5	10.0	X	
Endochironomus tendens-type	54	12.9	11.8	X	
Glyptotendipes pallens-type	36	15.6	11.1		X
Heterotrissocladius spp.		14.7	10.9	X	
H. grimshawi-type	17		7.7		
H. marcidus-type	17	12.4	Merged in *Heterotrissocladius*	X	
H. subpilosus-type	6	12.0	Merged in *Heterotrissocladius*	X	
Labrundinia spp.	2	8.2	Merged in *Heterotrissocladius*	X	
Lauterborniella spp.	60	Not in model	13.9		
Limnophyes spp.	19	22.6	13.4		X
Mesocricotopus spp.	8	17.0	8.6		X
Micropsectra spp.		10.0	8.7	X	
Micropsectra bidentata-type	19		6.2		
Micropsectra insignilobus-type	44	14.7	Merged in *Micropsectra*	X	
Micropsectra radialis-type	47	12.9	Merged in *Micropsectra*	X	
Microtendipes pedellus-type	130	9.4	Merged in *Micropsectra*	X	
Nanocladius spp.	3	13.5	11.0	X	
Orthocladius spp.	39	12.4	10.8	X	
Pagastiella spp.	26	13.5		X	
Parachaetocladius spp.	2	14.5	11.2	X	
Parachironomus varus-type	5	Not in model	Not in model		
Paracladius spp.	1	13.6	10.4	X	
Paracladopelma spp.	2	7.4	4.5	X	
Paracricotopus spp.	1	13.8		X	
Parakiefferiella spp.	40	11.0	9.6	X	
Paratanytarsus spp.	96	10.7	8.4	X	
Paratendipes nudisquama-type	13	12.8	Merged in *Tanytarsina*	X	
Pentaneurini spp.	83	Not in model	11.9		X
Phaenopsectra spp.	9	14.9	9.3		
Polypedilum nubeculosum-type	101	14.9	11.0		
Procladius spp.	168	18.5	11.0		X
Psectrocladius septentrionalis-type	55	14.5	9.5	X	
Psectrocladius sordidellus-type	141	12.2	10.6	X	
Pseudochironomus spp.	63	12.4	10.9	X	
Pseudosmittia spp.	7	Not in model	11.9		
Rheocricotopus spp.	1	15.5	8.5		X
Sergentia coracina-type	20	Not in model	9.1		
Smittia spp.	5	25.8	7.1		X
Stempelinella spp.	21	11.6	Not in model	X	
Stenochironomus spp.	2	14.6	10.6	X	
	)	Not in model	Not in model		
		7.9	7.4	X	

Table 2. (*Continued*)

Taxa identified in sediment	Occurrence in sediment	Optima		Category	
		(a) Eastern Canada	(b) Canada	Colder than today (15 °C)	Warmer than today (15 °C)
Tanytarsus lugens-type	145		8.3		
Tanytarsus mendax-type	145	13.5	Merged in *Tanytarsina*		X
Tanytarsus pallidicornis-type	74	14.1	Merged in *Tanytarsina*		X
Tanytarsus spp.	173	12.9	Merged in *Tanytarsina*	X	
Tanytarsus glabrescens-type	95	12.6	Merged in *Tanytarsina*	X	
Tanytarsus with spur on antenna	44	15.8	Merged in *Tanytarsina*		X
Thiennemaniella spp.	16	15.3	Merged in *Tanytarsina*		X
Thiennemanyia spp.	3	Not in model	9.9		
Xenochironomus spp.	1	11.7	Not in model	X	
Zalutschia mucronata-type	49	Not in model	Not in model		
Number of taxa not included in the training set		8	19		
Maximum temperature (°C)		25.8	13.9		
Minimum temperature (°C)		7.3	4.5		

Lotter, 2010), using the CANOCO 4.5 program. If the distance between downcore and transfer function samples was above the 10th percentile, the downcore sample was characterized as not having a good fit to temperature (Andrén *et al.*, 2015). Thirdly, a percentage of the fossil taxa present in the training set was calculated. A reconstruction should be considered adequate if samples have high percentages of fossil taxa present in the transfer function. Finally, to interpret and compare the chironomid-inferred temperature with other paleoecological climate records, a LOESS regression (span = 0.2) was applied.

Results

Organic matter content

The 335-cm-long core was composed entirely composed of gyttja. At the bottom of the core (326−327 cm), an age of *ca.* 8.2–8.4k cal a BP (2 sigma range) was determined (Table 1).

The uppermost 22 cm of the sediment was used completely for biological analysis, and thus LOI analysis could not be performed for this section of the core. Before *ca.* 7.7k cal a BP, the proportions of organic matter were below 60%. Between *ca.* 7.7 and 7.8k cal a BP, the percentages were very low (<20%) and the sediment was composed of a sandy layer.

Chironomid analysis

Of the 180 samples analyzed, one (48 cm) did not have any head capsules. Fifteen samples with fewer than 30 head capsules were merged for a total of 164 samples. Of those 164, 35 samples had head capsule numbers between 32 and 49.5, and thus 80% of the samples had more than 50 head capsules. In total, 63 taxa were identified to genus or species morphotypes. PCA axes one and two had eigenvalues of 0.25 and 0.11, respectively. The 25 most abundant taxa (percentages reaching at least 10%) are shown in Fig. 2(A).

Five significant zones (Ach-1 to Ach-5) were numerically identified (Fig. 2A). In zone Ach-1 (ca. 8.3–6.7k cal a BP), the PCA axis one scores were positive. This zone was dominated by taxa with temperature optima above 13.5 °C (Fig. 2B) such as *Dicrotendipes nervosus*-type, *Procladius* spp., *Tanytarsus mendax*-type, *Polypedilum nubeculosum*-type and *Endochironomus tendens*-type. Colder-than-today taxa (Fig. 2B) reached 90% at the beginning of the record (8.2–8.0k cal a BP) and many of the cold indicators such as *Corynocera oliveri*-type, *Micropsectra radialis*-type and *Heterotrissocladius marcidus*-type (Fig. 2a) had their highest percentages of the record in the first few samples of this zone. The lake was possibly oligotrophic during this zone, as the ratio of eutrophic/oligo-mesotrophic taxa was below 1 (Fig. 2bB). Littoral taxa dominated after 8.1k cal a BP.

In zone Ach-2 (ca. 6.7–5.5k cal a BP), PCA axis 1 scores were below 0 (Fig. 2B). Warm indicators had percentages generally below average except in one sample at *ca.* 6.2k cal a BP. *Tanytarsus* spp. dominated the assemblages with percentages around 40%. *Chironomus plumosus*-type, *C. anthracinus*-type, *T. lugens*-type and *Procladius* spp. were also well represented in the assemblages. Unstable conditions were identified, with oscillating eutrophic/oligo-mesotrophic and littoral/profundal ratios being recorded (Fig. 2B).

Zone Ach-3 (ca. 5.5–4.9k cal a BP) was characterized by PCA axis 1 scores above 0. The percentages of warm taxa were above average, and the assemblages were dominated by *D. nervosus*-type, *T. mendax*-type, *Procladius* spp., *P. nubeculosum*-type, *C. mancus*-type and *Pseudochironomus* spp. The ratios of eutro/oligo-mesotrophic taxa were slightly below 1, suggesting mesotrophic conditions. Littoral taxa dominated.

In zone Ach-4 (ca. 4.9–0.6k cal a BP), PCA scores were all below 0. This zone was divided into two subzones based on changes in taxa percentages and PCA axis 2 scores, which were above 0 after *ca.* 1.5k cal a BP.

In subzone Ach-4a (ca. 4.9–1.7k cal a BP), the percentages of warm taxa decreased below average, suggesting conditions colder than today. The dominant taxon was *Tanytarsus* spp., a taxon which is considered an indicator of colder-than-today conditions. The lake had a tendency towards oligo-mesotrophy with ratios generally below 1. Littoral taxa dominated.

In subzone Ach-4b (1.7 k cal a BP to 600 cal a BP), changes in PCA axis 2 scores were observed and the number of head capsules was generally between 30 and 70. Both cold and warm taxa were at average values, suggesting a slight climatic amelioration to warmer conditions. The main changes in taxa were the strong decrease in *Tanytarsus* spp.

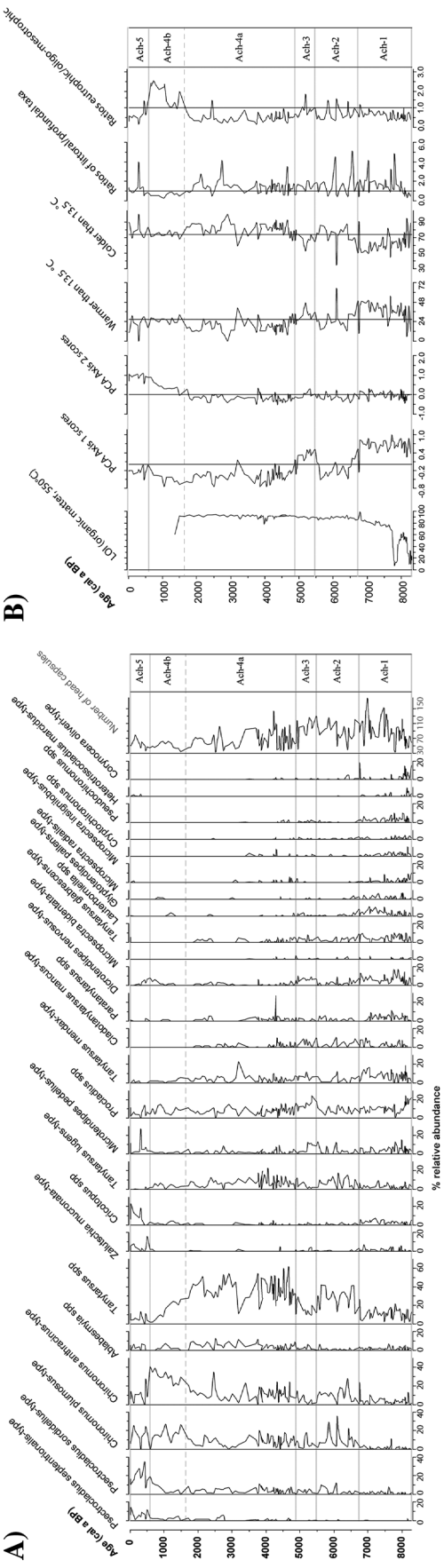

Figure 2. (A) Chironomid stratigraphy of the 26 most abundant taxa (percentages reaching at least 10% in more than four samples) and the number of head capsules identified in each sample. (**B**) Organic matter content (loss-on-ignition at 550 °C). PCA axis 1 and 2 are the sample scores of the first and second axis in a principal components analysis. The vertical line is the PCA 0 score. The warmer- and colder-than-13.5 °C taxa follow their sums of percentages in Table 2. Profundal and littoral taxa were defined using Brooks *et al.* (2007). Littoral/profundal and eutrophic/oligo-mesotrophic taxa ratios were calculated (see Methods), the baselines are 1. Ratios >1 suggest oligo-mesotrophic conditions and a dominance of littoral over profundal taxa.

percentages and the increase in both *Chironomus* types. These increases in *Chironomus* types were linked to sharp increases in eutrophic/oligo-mesotrophic ratios and decreases in littoral/profundal taxa (Fig. 2B); *Chironomus* types are considered as eutrophic and profundal taxa (Brooks *et al.*, 2007).

During zone Ach-5 (ca. 600 cal a BP to present), PCA axis 1 scores remained below 0 and PCA axis 2 scores continued to increase. Cold taxa were above average while warm taxa were below average, suggesting colder conditions. *P. sordidellus*-type, *P. septentrionalis*-type, *Zalutschia mucronata*-type and *Psectrocladius* spp. and *Cricotopus* spp. dominated for the first time. Trophic conditions had a tendency towards oligo-mesotrophy with ratios below 1 and littoral taxa were dominant.

Chironomid-inferred temperature reconstructions

The temperature reconstruction patterns obtained by the two transfer functions are similar (Fig. 3). However, the Canadian transfer function provided estimates which were 2–3 °C lower than those of the Eastern Canadian model. The temperature anomalies obtained from the Canadian model were mostly inferred as lower than today, which does not fit with known climate patterns. The Eastern Canadian reconstruction was thus used to look at details of climate change.

The PCA axis 1 scores and inferred temperatures with the Eastern Canadian model had a significant correlation ($r_{\text{Pearson}} = 0.62$, $p < 0.05$). Low temperatures were recorded before 8k cal a BP with an average anomaly of −0.8 °C (Fig. 3). Temperatures increased to reach a maximum around *ca.* 8k cal a BP and remained high until *ca.* 6.7k cal a BP with an average anomaly of 0.9 °C. During zone Ach-2 (ca. 6.7–5.5k cal a BP), temperatures were generally lower than previously with an average anomaly of −0.5 °C. During zone Ach-3 (ca. 5.5–4.9k cal a BP), the inferred temperatures were similar to today's with average anomaly of −0.2 °C. In zone Ach-4, temperatures were lower than today (−1.4 °C in average). Changes occurred at around 1.2–1.1k cal a BP, with an average anomaly of 0.7 °C, while the zone had lower temperatures than today (−0.8 °C), on average. During zone Ach-5 (ca. 600 cal a BP to present) the average anomaly was −2.1 °C.

Discussion

Ecological interpretation

The first axis of the PCA could be interpreted as a climate gradient probably related to temperature; the correlation (r_{Pearson}) between PCA axis 1 scores and the temperature reconstruction was 0.62. Many taxa had higher temperature optima in the Eastern Canadian model than in the Canadian transfer function (Table 2). Most of the colder-than-today indicators are similarly characterized in Brooks *et al.* (2007).

Changes in PCA axis 2 scores starting at *ca.* 1.5k cal a BP with PCA axis 1 scores remaining below 0 suggest that temperature is not the only factor influencing the changes in chironomid assemblages through time. In our core, PCA axis 2 scores were correlated with the ratios of oligo-meso/eutrophic taxa and with the ratio of littoral/profundal taxa. The effects of nutrients and water depth on chironomids have been previously shown (Lotter *et al.*, 1997; Larocque et al., 2006) and models to reconstruct both parameters were developed (Langdon *et al.*, 2006; Engels *et al.*, 2012). As most members of the *Tanytarsini* tribe are both littoral (except *T. lugens*-type) and eutrophic, their decrease starting at *ca.*

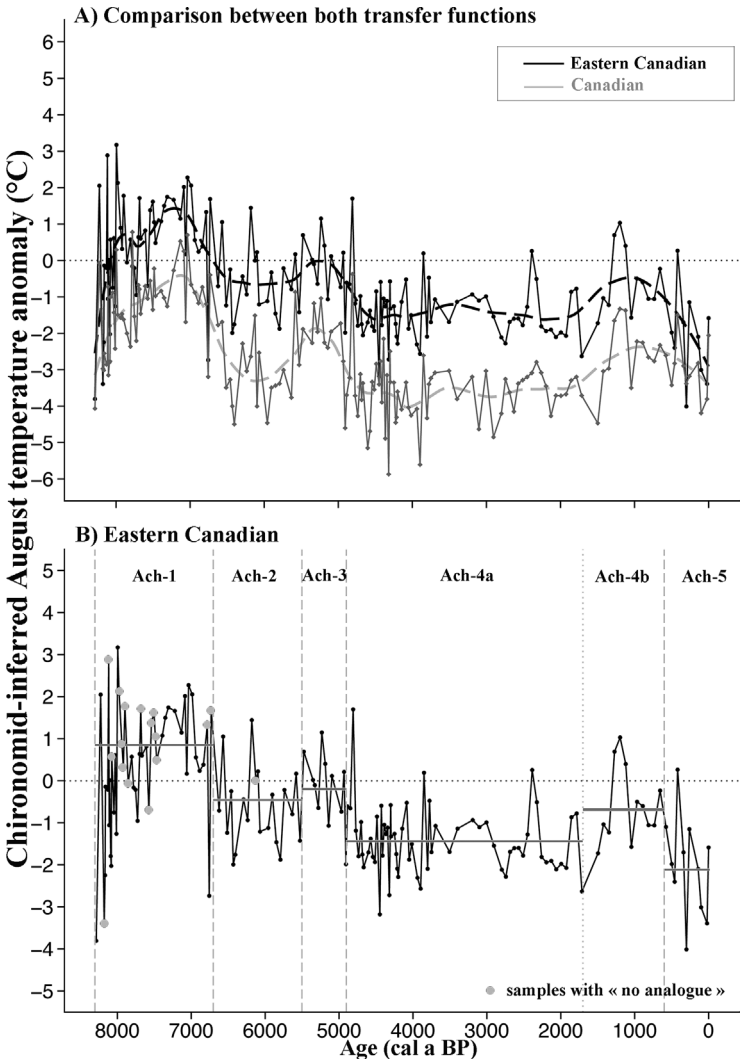

Figure 3. Chironomid-inferred August air temperature anomaly (°C) at Lac Aurélie. (A) Comparison between the Eastern Canadian transfer function and the Canadian transfer function of Fortin *et al.* (2015). The dashed curves indicate the smoothed reconstructions (loess, span 0.2). (B) Details of the Eastern Canadian transfer function, which illustrate a more reliable record. The vertical lines indicate the zonation obtained from the chironomid stratigraphy (Fig. 2A). The horizontal bold lines indicate the average anomaly of the chironomid zones.

1.5k cal a BP identifies trophic levels and water depth as two of the main drivers of the observed ratios. In zone 4b (1.5k cal a BP), profundal taxa dominated (as suggested by ratios above 1), probably due to the increase in both types of *Chironomus*. These taxa have hemoglobin (Walshe, 1950), allowing them to survive short periods of oxygen depletion (Brooks *et al.*, 2007), suggesting that oxygen availability might have changed during this period. Percentages of *Polypedilum nubeculoseum*-type, associated with macrophytes, also increased during this time. The presence of macrophytes has been shown to influence chironomids (Langdon *et al.*, 2008) and lower oxygen levels have been recorded in lakes with a developed macrophyte community (Rose and Crumpton, 1996). In zone 5, represented by a further increase in PCA axis 2 scores, the percentages of both *Psectrocladius* types and *Cricotopus* spp. largely increased with *Pentaneurini* spp. and *Ablabesmyia* spp. *Psectrocladius* is often associated with macrophytes (Brodersen *et al.*, 2001; Langdon *et al.*, 2008) and is acidophilic (Pinder and Morley, 1995), as pH is another factor affecting chironomids (Orendt, 1999). *Cricotopus*, *Ablabesmyia* and *Zalutschia* spp. are associated with vegetation (Brooks *et al.*, 2007), while *Zalutschia* spp. and *Ablabesmyia* occur in acidified lakes (Brooks *et al.*, 2007).

Based on the changes in the chironomid communities, macrophytes, changes in oxygen and pH might have influenced the chironomid assemblages since *ca.* 1.5k cal a BP. However, low-variability climate changes, such as for the LIA, have also been reconstructed from our assemblages (see below), which suggests that, although other factors influenced the assemblages, the pattern of chironomid-inferred temperature changes was still adequately reconstructed. Luoto and Nevalainen (2017) have shown that chironomids can reconstruct climate effectively even under the influence of eutrophication and pollution.

Reliability of the chironomid inferred temperature reconstructions

The Canadian transfer function of Fortin *et al.* (2015) used a very large number of lakes (435) and would, at first, be considered as the most suitable to reconstruct climate in a lake in the boreal forest of Quebec. However, only a few of these lakes have August temperatures above 14 °C and the residuals (fig. 4 in Fortin *et al.*, 2015) suggest that higher temperatures will be underestimated. As Lac Aurélie's current August temperature is 15 °C, which is at the end of the gradient of the Canadian transfer function, its present-day

temperature should possibly be underestimated with the model of Fortin *et al.* (2015). If the temperatures were higher in the past, the inferences would also be lower than expected. Furthermore, because the temperature gradient is relatively small (−0.3 to 15.7 °C) and contains mostly lakes of low temperatures, the optimum for each taxon is relatively low (4.5–13.9 °C; Table 2), which explains why the reconstruction is 2–3 °C lower than the one obtained with the other training set. In addition, Fortin *et al.* (2015) merged certain taxa to a lower taxonomic level, as identified in some of the calibration sets. Consequently, this grouping could induce less realistic inferred temperature reconstructions. However, it should be remembered that the pattern of changes is very similar between each transfer function.

The Eastern Canadian transfer function (Larocque, 2008) is an extended version of the 52 lakes from Larocque et al. (2006) that was used in the Canadian model of Fortin *et al.* (2015). It contains a few lakes north (3 °C) and south (21 °C), thus increasing the temperature gradient (3−21 °C). Although it comprises fewer lakes (75) than the Canadian transfer function, the increased gradient might provide more accurate optima. The temperature optima in the Eastern Canadian model vary between 7.5 and 20.5 °C (Table 2). However, this training set does not include any lakes with August temperatures between 16.8 and 19 °C, temperatures which might have been experienced at Lac Aurélie in the past, so many of the fossil samples did not resemble those found in the training set. To obtain the best coverage (larger gradient and lakes evenly distributed along the gradient) temperatures that may have been experienced, lakes with temperatures between 16 and 19 °C should be added. Unfortunately, such data were not available as lakes were not yet sampled within this range. We assume that the inferences were possibly lower than they should be. However, as weighted average partial least squares (WA-PLS) is based on temperature optima for each taxon found in the fossil record, it is important to include as many fossil taxa as possible in the training set. This is the case in the fossil record of Lac Aurélie, with all samples having more than 83% of their taxa found in the training set lakes, and 133 of 179 samples (74%) having fossil taxa represented in the training set above 95%.

A problem that needs to be considered in evaluating the accuracy of a model is the absence of modern analogues. Seventeen of the 164 samples had no modern analogues (Fig. 3). These samples were mainly in the lower portion of the sedimentary core (<6.7 cal a BP). Nevertheless, WA-PLS methods perform well in non-analogue situations because the estimates are based on modeled taxon temperature optima assuming unimodal responses to temperature (Birks and Birks, 1998). This allows the model to infer temperatures outside the range of the calibration set. In these cases, comparison with other regional paleoclimate records is essential to evaluate the reliability of the temperature reconstruction. The applicability of the Eastern Canadian transfer function to the Lac Aurélie samples was further assessed using goodness-offit to temperature. None of the Lac Aurélie samples was above the 10th percentile, so we assume that all downcore samples had good fit to temperature.

8.2k cal a BP cold event and Holocene Thermal Maximum

After the retreat of the last remnant of the glacier (Dyke, 2004), the chironomid-inferred temperature in Lac Aurélie is 2–3 °C lower than today in three samples around *ca.* 8.2k cal a BP (8282–8175 cal a BP). This might represent the so-called 8.2k cal a BP event (Alley *et al.*, 1997). The Greenland ice core record indicates that temperatures fell by *ca.* 3.3 °C and this period lasted 150 cal years (Kobashi *et al.*, 2007; Thomas *et al.*, 2007). Our results correspond to the ice core record in both timing (ca. 110 years, limited by our sampling technique) and amplitude of change (−3 °C).

The HTM lasted between 11 and 5k cal a BP in the Northern Hemisphere, but with many regional variations (Renssen *et al.*, 2009). Based on pollen data from sites in north-western Quebec, Viau and Gajewski (2009) highlighted high temperatures between 6 and 2k cal a BP. Our results show summer temperatures higher than or similar to today between *ca.* 8.3 and 4.9k cal a BP, but with a sharp decline around *ca.* 6.5k cal a BP. Our reconstruction matches paleoclimate records obtained from the Arctic (GISP2 ice core; Kobashi *et al.*, 2010), from pollen across north-eastern America (Viau *et al.*, 2006) and from a chironomid record on Baffin Island (Axford *et al.*, 2009) (Fig. 4A). The increase in temperature (+2–3 °C in three samples at the beginning of the record) was similarly recorded in the ice core (+3 °C) and from Baffin Island (+4 °C) (Fig. 4a). However, the combined pollen records registered an increase in temperature of about only 1 °C (Viau *et al.*, 2006). This could be due to the merging of various fossil records across north-eastern Canada. Stacking of records of different amplitudes at many locations, as per Viau *et al.* (2006), decreases the average variation. Another reason for differences in amplitude is the use of different models to infer climate. The modern analogue technique generally provides changes of much lower amplitude than the weighted average method used here (Birks, 2003). The amplitude of change has been shown to reach 5 °C at the highest latitudes, between 2.5 and 5 °C in our study region, and smaller amplitudes at lower latitudes (Renssen *et al.*, 2012). Thus, the amplitude of change reconstructed by chironomids at Lac Aurélie seems to be plausible. Furthermore, the decrease in temperature from the late Holocene (4.5–1.5k cal a BP) could be the result of the cold and wet Neoglacial period (Viau and Gajewski, 2009).

Medieval Climate Anomaly

Chironomid assemblages showed an increase in temperature (+0.7 °C) around 1.1–1.2k cal a BP (Figs 3 and 4) probably corresponding to the MCA recorded by various proxies in the Northern Hemisphere (Mann *et al.*, 2009). The pollen data results of Viau *et al.* (2006) recorded across North America agree with ours. Viau and Gajewski (2009) also recorded this warming period in northern Quebec. Rolland *et al.* (2009) inferred a warming period between 1160 and 1360 AD on Southampton Island (Nunavut, Canada) based on chironomid assemblages. In the central Northwest Territories (Canada), chironomid-inferred temperature reconstructions have shown a warming which occurred between 1 and 0.7k cal a BP (Upiter *et al.*, 2014). Arseneault and Payette (1997) also observed a warming trend based on tree rings at the treeline in north-western Quebec. When comparing our record to other proxy records (Fig. 4B), the period around *ca.* 1.5–1k cal a BP is clearly identified as warmer than today with a concomitant timing (PAGES 2k Consortium, 2013). Using chironomids, Millet *et al.* (2009) reconstructed a warming of 1.3 °C in the French Alps. Larocque-Tobler *et al.* (2012) showed increased temperatures (1–2 °C) during the MCA in two Swiss lakes and the composite records composed of tree-rings and diatoms inferred an increase of 0.5 °C (Trachsel *et al.*, 2012), exemplifying that combining different fossil proxies/sites smooths the record.

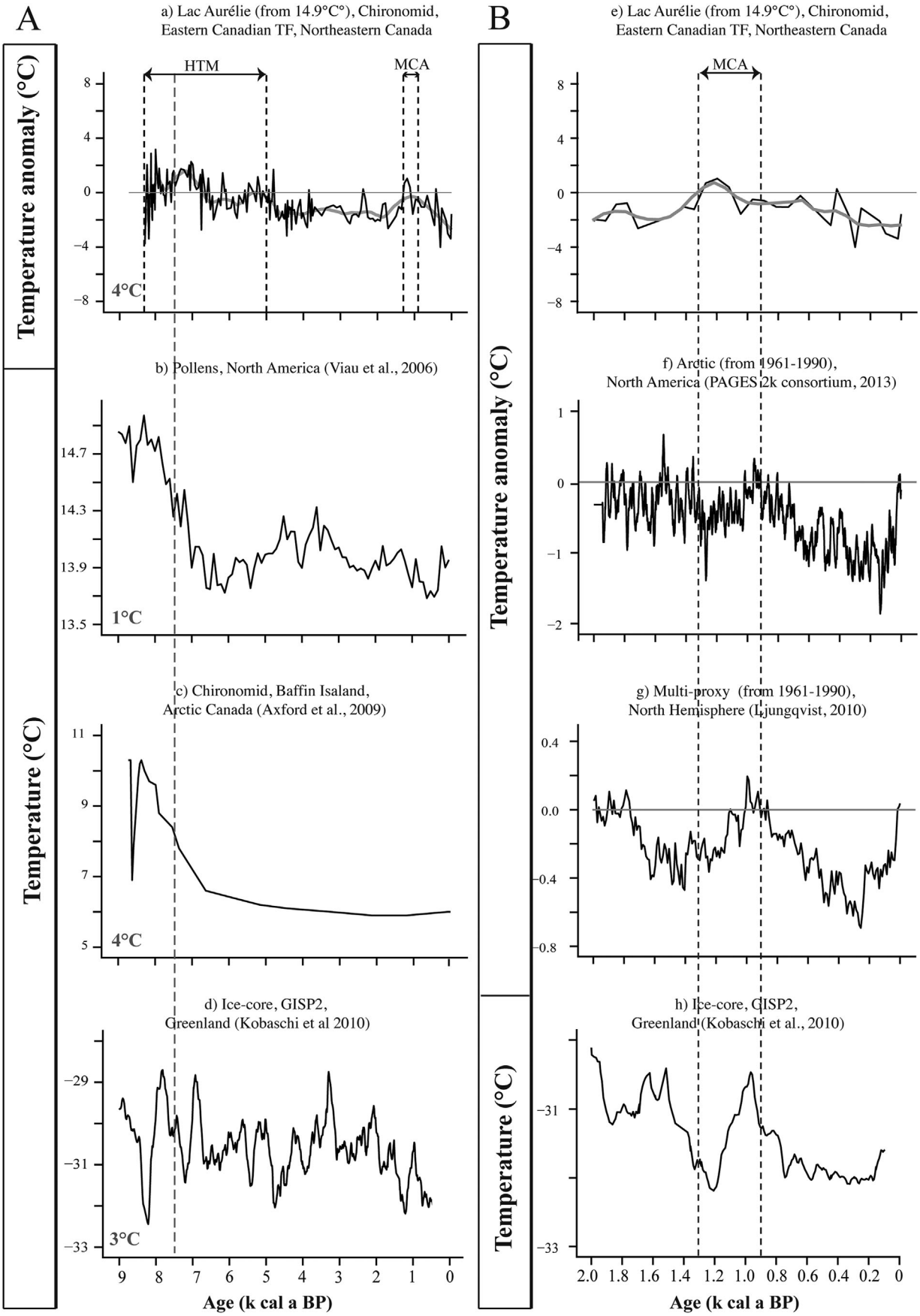

Figure 4. (Continued).

Figure 4. (A) Comparison of various temperature reconstructions during the past 9k cal a BP. The data were obtained from the National Oceanic & Atmospheric Administration (NOAA) World Data Center for Paleoclimatology. (a) Chironomid-inferred August mean temperature anomaly, span of 0.2 (black line) and 95% confidence interval (light grey shading) at Lac Aurélie for the past 8.5k cal a BP related to today's study area temperature (15.0 °C) (this study). (b) Pollen-inferred North American mean July temperatures for the past 9k cal a BP (Viau *et al.*, 2006). (c) Chironomid-inferred July temperatures at Lake CF8 (Baffin Island, Canada) for the past 9k cal a BP (Axford *et al.*, 2009). (d) GISP2 ice-core inferred Greenland temperatures for the past 9k cal a BP (Kobashi *et al.*, 2010). (B) Comparison of different temperature reconstructions during the past 2k cal a BP. (e) Chironomid-inferred August mean temperature anomaly, span of 0.2 (black line) and 95% confidence interval (light grey shading) at Lac Aurélie related to today's temperature of at Chibougamau (15.0 °C) (this study). (f) Northern Hemisphere Arctic temperatures from 1961 to 1990 (PAGES 2k Consortium, 2013). (g) Multi-proxy inferred extra-tropical Northern Hemisphere (90°–30°N) decadal mean temperature anomaly (dark line) related to 1996–1990 with 2 standard deviation error bars (light grey shading) (Ljungqvist, 2010). (h) GISP2, ice-core inferred Greenland temperature (Kobashi *et al.*, 2010).

During this period, PCA axis 2 scores suggested that factors other than climate (macrophytes, oxygen, pH) affected the chironomid assemblages at Lac Aurélie. However, because the MCA seems to have been plausibly reconstructed, it appears that it did not completely affect the relationship with temperature.

Little Ice Age

The LIA is a colder-than-today period which occurred between 1300 and 1850 AD (Matthews and Briffa, 2005) and is defined in north-eastern Canada between the late 1500s to the late 1800s (Payette and Delwaide, 2004). During the LIA, the cooling with the largest amplitude occurred in northern Quebec (Viau and Gajewski, 2009). The temporal resolution of our record decreases during this period (about 40–80 years). The main features of this period are recognized with the start of the cooling being recorded at around 1390 AD and punctuated by a short warming period. Three colder periods are generally seen in high-resolution records at around 1650, 1779 and 1850 AD (Mann and Jones, 2003; Mann *et al.*, 2008). At Lac Aurélie, the two lowest temperatures inferred were temporally close to these high-resolution records at *ca.* 1663 and 1900 AD. However, the colder-than-today temperatures of 1 °C (average 0.5 °C) were inferred in only three samples and should be considered with caution. This amplitude is consistent with high-resolution chironomid records from Switzerland (i.e. Larocque-Tobler *et al.*, 2012), but larger than dendrochronological records in northern Europe (Moberg *et al.*, 2005) and combined proxy records from Switzerland (Trachsel *et al.*, 2010).

In conclusion, despite methodological limits to the transfer function, good correspondences between our climate reconstruction and those obtained at other sites and from diverse proxies suggests that chironomids are useful to detect temperature changes at this site. Main climate events such as the HTM, the Neoglacial period, the MCA and the LIA have been recorded by chironomids at Lac Aurélie. Hence, further high-resolution regional studies, based on chironomid analyses, should be conducted to improve our understanding of past natural climate changes in boreal forest ecosystems.

Supplementary Information

Table S1. Chironomid counts (percentage) for each level Lac Aurélie core.

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Abbreviations. DCA, detrended correspondence analysis; HTM, Holocene Thermal Maximum; LIA, Little Ice Age; LOI, loss-on-ignition; MCA, Medieval Climate Anomaly; PCA, principal component analysis; RMSEP, root mean square error of prediction; WA-PLS, weighted average partial least squares.

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