

Factors influencing the distribution of chironomids in lakes distributed along a latitudinal gradient in northwestern Quebec, Canada

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Abstract: The effect of 33 environmental variables on the distribution of chironomids was studied in 60 lakes of northwestern Quebec (Canada). A detrended canonical correspondence analysis detected linearity in the chironomid assemblages, thus redundancy analysis was used to identify the variables affecting the chironomid communities. Lake depth, dissolved organic carbon (DOC), mean August air temperature, and surface water temperature were the four variables that best explained the distribution of chironomids. Partial least squares analysis was used to develop new inference models. Among models, the one for mean August air temperature had the highest coefficient of determination ($r_{\text{jack}}^2 = 0.67$) and the lowest root mean square error of prediction ($= 1.17$ °C). The results indicated that for downcore temperature reconstructions, it might be hard to dissociate the combined effects of temperature, DOC, and depth. Changes in taxa such as *Heterotrissocladius brundini*-type, *Heterotrissocladius subpilosus*-type, *Heterotrissocladius grimshawi*-type, *Micropsectra radialis*-type, *Tanytarsus lugens*-type, and *Microtendipes* can be attributed to changes in lake depth and (or) temperature. Changes in *Heterotanytarsus*, *Dicrotendipes*, *Cryptotendipes*, and *Cryptochironomus* might be attributed to shifts in temperature and DOC. Relationships among temperature, DOC, and lake depth should be studied in a “neo-ecology” design to better understand their impact on chironomid assemblage composition.

Résumé : L'effet de 33 variables environnementales sur la distribution des chironomides dans 60 lacs du nord-ouest du Québec (Canada) a été étudié. Une relation linéaire dans les assemblages de chironomides a été démontrée par une analyse canonique des correspondances redressée. Une analyse de redondance a donc été utilisée pour identifier les variables influençant les communautés de chironomides. La profondeur du lac, le carbone organique dissous (DOC), la température moyenne de l'air en août et la température de l'eau en surface sont les quatre variables qui expliquent le mieux la distribution. Une analyse partielle des moindres carrés a été utilisée pour développer des modèles d'inférence. Le modèle qui prédit la température moyenne de l'air en août a le plus haut coefficient de détermination ($r_{\text{jack}}^2 = 0,67$) et l'erreur quadratique moyenne de prédiction ($= 1,17$ °C) la plus faible. Les variations de certains taxons (type *Heterotrissocladius brundini*, type *Heterotrissocladius subpilosus*, type *Heterotrissocladius grimshawi*, type *Micropsectra radialis*, type *Tanytarsus lugens* et *Microtendipes*) peuvent être attribuées aux variations de la profondeur du lac et (ou) de la température. Les changements de *Heterotanytarsus*, *Dicrotendipes*, *Cryptotendipes* et *Cryptochironomus* peuvent être associés aux variations de température et de DOC. Les effets combinés de la température, du DOC et de la profondeur du lac sur les assemblages de chironomides devraient être étudiés selon un schéma de « néo-écologie » pour dissocier leurs influences respectives.

Introduction

Numerous chironomid transfer functions have been created since the early 1990s to quantitatively reconstruct air and water temperatures (e.g., Walker et al. 1997; Larocque et al. 2001; Porinchu et al. 2002), oxygen availability (Quinlan et al. 1998), water depth (Korhola et al. 2000), and chlorophyll *a* (Brodersen and Lindegaard 1999) from lake sediment sequences. These training sets are still limited geo-

graphically (Scandinavia, Switzerland, western Canada, eastern Canada, and the USA (Colorado and Maine)), and uncertainties remain regarding the applicability of a training set from one region to reconstruct temperature from lakes located outside of the geographical range of the training set (I. Larocque, unpublished data). Thus, it is still useful to develop new transfer functions that encompass the geographical range of the lakes to be used for paleoclimate (or any other variable) reconstructions. Training sets are useful to

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identify the environmental factors influencing the distribution of chironomids in lakes over a large geographical transect (more than 1000 km), thereby contributing to a better understanding of their ecology and biogeographical distribution.

Northwestern Quebec (from Abitibi–Temiscamingue to northern Nunavik) covers a vast territory where rivers have been dammed and where hydroelectricity plays a key role for the energy supply of industrial centers and communities in southern Quebec. It would be important to determine the effect of climate on future lake water levels and river discharge for the management and regulation of these aquatic ecosystems for the production of hydroelectricity. Although global climate models have shown that a substantial warming will occur in northern environments, regional to local predictions are needed to better manage the northern Quebec facilities. Climate data are thus necessary at regional to local scales. Meteorological data are available only at six locations in northwestern Quebec and data have been recorded only since 1993 (i.e., by Environment Canada). Only paleoarchives can provide longer temporal series of temperature inferences in areas where meteorological data are scarce. Here, we lay the foundations for future climate reconstructions along a south–north transect in northern Quebec by (i) determining those factors that statistically exert the strongest influence on the distribution of chironomids in the surface sediments of 60 lakes in northwestern Quebec and (ii) developing an inference model for the quantitative reconstruction of temperature based on fossil chironomid assemblages.

Materials and methods

Study area

Sixty lakes were sampled in August 1995, which resulted in the development of a dissolved organic carbon (DOC) – diatom transfer function (Fallu and Pienitz 1999). These lakes were located at the northern and southern part of the tree limit in northern Quebec (Fig. 1). The transect covers 1100 km, between 49°48'N to 59°32'N and 75°43'W to 78°78'W. Three eco-climatic zones are covered by this transect: the high boreal, the subarctic, and the low arctic (Environment Canada 1989). The mean annual temperature and precipitation vary from –0.1 °C and 920 mm in Matagami (49°45'N, 77°38'W) to –6.8 °C and 418 mm in Inukjuak (58°27'N, 78°07'W) (Environnement Canada 1993). These three eco-climatic zones are characterized by different vegetation types. The high boreal is composed mainly of spruce trees (*Picea mariana* and *Picea glauca*), with lichen cover (Payette 1983). In this paper, this zone will be referred to as the Boreal Forest. The subarctic has sporadic forest cover (spruce krummholz) and will be referred to as Forest–Tundra. This zone ends with the northern limit of trees. The last ecozone is described as Tundra with no krummholz and low ground vegetation. The southern zone is composed of granites and gneisses while the northern zone (starting at about 55° N) is composed of metamorphic rocks (Landry and Mercier 1992).

Study sites

Most of the 60 lakes had no affluent. The sampling procedures are described in Fallu and Pienitz (1999). Sediment cores were extracted with a modified Kajak–Brinkhurst or Glew gravity corer (Glew 1991) at the deepest part of the lake. The surface sediment (top 1 cm) was extracted and kept in a refrigerator at 4 °C. This centimetre likely represents the last 3–5 years of sedimentation (Richard et al. 1982; Larocque and Hall 2003).

Some physical and limnological parameters were measured on site, while water samples were taken at 40 cm depth and brought back for chemical analysis at the National Water Research Institute in Burlington, Ontario. Salinity, conductivity, and water temperature (WT) were measured in situ with a Yellow Spring Instrument 33 meter at a depth of 50 cm; transparency was measured with a Secchi disk; and pH was measured in the sampled water bottle at the Centre d'Études Nordiques research station in Kuujuaapik–Whapmagoostui. Altitude, area, and distance from the forest were measured on topographic maps (Fallu and Pienitz 1999). All parameters are summarized in Table 1.

Meteorological data were available from Environment Canada at six sites: Matagami (49°45'N, 77°38'W), Radisson (LG2; 53°63'N, 77°07'W), Kuujuaapik (55°28'N, 77°75'W), Umiujak (56°53'N, 76°52'W), and Inukjuak (58°27'N, 78°07'W). Air temperature data at each site were plotted against latitude, and a model was developed to extrapolate temperature at each studied lake. In other training set studies, July air temperature was one of the major factors controlling the distribution of chironomids (e.g., Lotter et al. 1997; Larocque et al. 2001), and in the present study we wanted to test if (i) air temperature was also important in explaining the distribution of chironomids in our training set and (ii) July air temperature (compared with June or August) was the important climate variable explaining the distribution of chironomids.

Chironomid analysis

All the sediment remaining after diatom analysis (Fallu and Pienitz 1999) in the top centimetre was used to extract chironomid head capsules. KOH (10%) was added overnight and the samples were sieved through a 100 µm mesh. The remaining solution was placed in a Bogorov counting tray and examined under a stereomicroscope at × 35 magnification. Head capsules were picked, one by one, and fixed in Hydromatrix mounting medium on a microscope slide. Head capsules were identified using a Van Guard light microscope at × 400 or × 1000. The taxonomy mainly followed Wiederholm (1983) and Oliver and Roussel (1983). Specific keys were used to separate the Tanytarsini subtribe (Brooks et al. 1997; S. Brooks, National History Museum, Cromwell Road, London SW7 5BD, UK, unpublished data). The Tanytarsini who could not be placed into taxonomic groups were separated following the presence (Tanytarsini with) or absence (Tanytarsini without) of a spur on the antenna pedicel. Tanypodinae groups were separated using the position of the setae following Rieradevall and Brooks (2001).

Statistical analysis

We used samples with at least 50 head capsules following the methods outlined in Quinlan and Smol (2000), Heiri and

Fig. 1. Location of the 60 sampled lakes in northern Quebec, Canada. Modified from Fallu and Pienitz (1999).

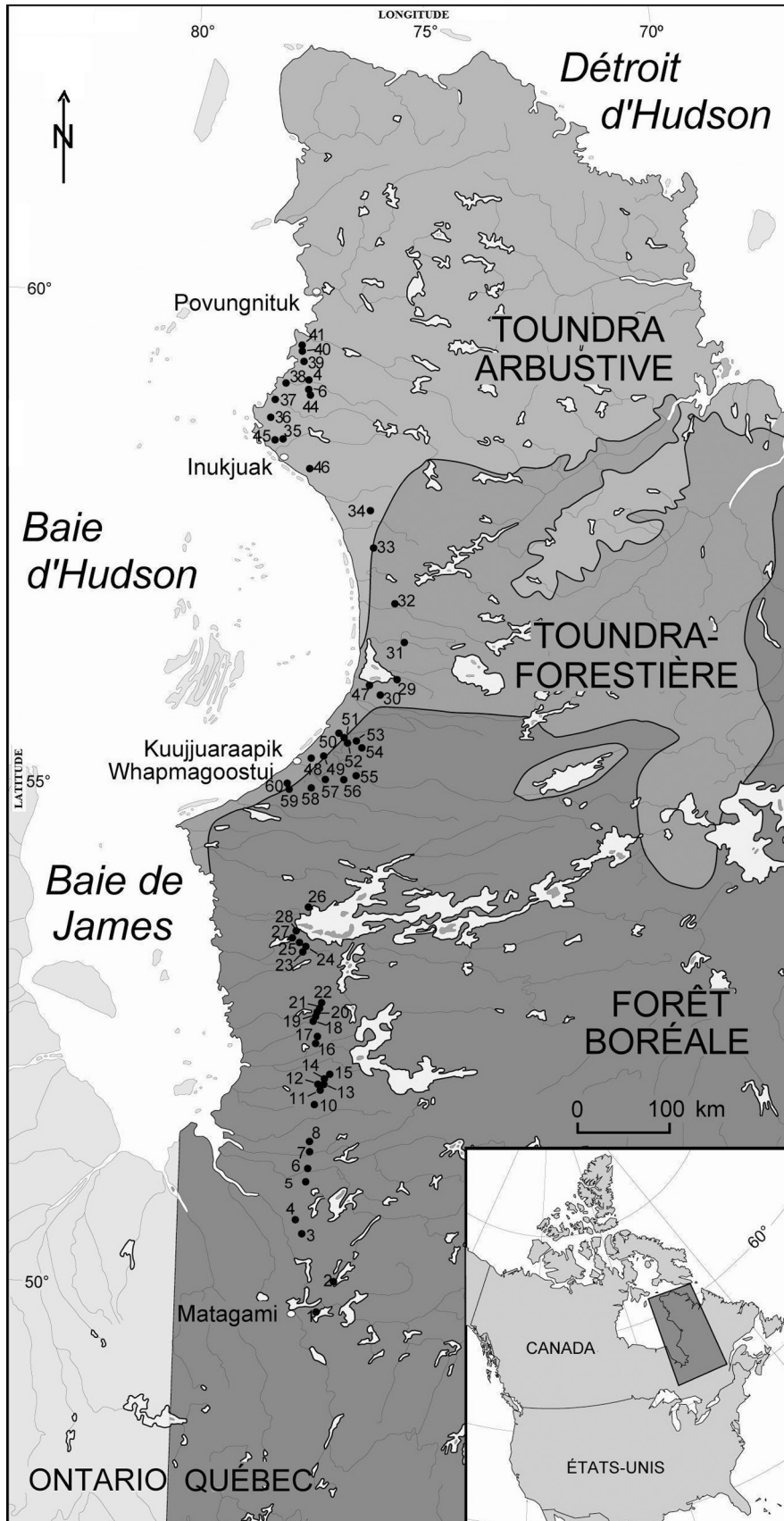


Table 1. Minimum, maximum, mean, and standard deviation (SD) of the environmental characteristics of the 52 studied lakes.

Lake characteristic	Min.	Max.	Mean	SD
TNP ($\mu\text{g}\cdot\text{L}^{-1}$)	1.0	48.9	11.6	7.8
TFP ($\mu\text{g}\cdot\text{L}^{-1}$)	0.6	10.6	3.9	2.3
PRS ($\mu\text{g}\cdot\text{L}^{-1}$)	0.4	7.7	1.9	1.5
TNK ($\mu\text{g}\cdot\text{L}^{-1}$)	32.0	396.0	233.5	83.9
NO ₂ ($\mu\text{g}\cdot\text{L}^{-1}$)	0.0	8.0	2.5	1.8
DIC ($\text{mg}\cdot\text{L}^{-1}$)	0.2	4.8	1.3	1.1
DOC ($\text{mg}\cdot\text{L}^{-1}$)	2.3	19.4	8.1	4.3
Mg ($\text{mg}\cdot\text{L}^{-1}$)	0.2	4.3	0.7	0.6
Ca ($\text{mg}\cdot\text{L}^{-1}$)	0.3	6.2	1.9	1.3
Na ($\text{mg}\cdot\text{L}^{-1}$)	0.6	28.3	3.0	3.9
K ($\text{mg}\cdot\text{L}^{-1}$)	0.0	1.4	0.3	0.2
Cl ($\text{mg}\cdot\text{L}^{-1}$)	1.0	54.6	5.1	7.4
SO ₄ ($\text{mg}\cdot\text{L}^{-1}$)	1.4	8.9	3.5	1.6
SiO ₂ ($\text{mg}\cdot\text{L}^{-1}$)	0.1	5.5	1.5	1.5
CHLaN ($\mu\text{g}\cdot\text{L}^{-1}$)	0.4	17.7	3.7	2.7
CHLaC ($\mu\text{g}\cdot\text{L}^{-1}$)	0.0	13.1	2.6	2.1
POC ($\text{mg}\cdot\text{L}^{-1}$)	0.0	12.7	1.0	1.7
PON ($\text{mg}\cdot\text{L}^{-1}$)	0.0	1.4	0.1	0.2
Al ($\mu\text{g}\cdot\text{L}^{-1}$)	0.0	1000.0	142.8	191.6
Ba ($\mu\text{g}\cdot\text{L}^{-1}$)	0.8	11.1	3.2	2.3
Fe ($\mu\text{g}\cdot\text{L}^{-1}$)	5.0	1100.0	280.3	267.8
Mn ($\mu\text{g}\cdot\text{L}^{-1}$)	1.6	33.0	8.3	6.9
Sr ($\mu\text{g}\cdot\text{L}^{-1}$)	2.9	48.6	12.4	8.5
Altitude (m)	13.0	292.6	167.0	75.9
Area (ha)	4.5	292.6	80.2	162.7
Depth (m)	1.0	18.5	3.9	3.6
Transparency (Secchi)	0.5	6.6	2.2	1.6
Water temperature (°C)	13.0	23.6	18.4	3.2
Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	10.0	170.0	28.7	22.6

Note: TNP, total nonfiltered phosphorus; TFP, total filtered phosphorus; PRS, soluble phosphorus; NKT, total Kjeldahl nitrogen; DIC, dissolved inorganic carbon; DOC, dissolved organic carbon; CHLaN, noncorrected chlorophyll *a*; CHLaC, chlorophyll *a* corrected for pheophytins; POC, particulated organic carbon; PON, particulated organic nitrogen.

Lotter (2001), and Larocque (2001). Taxa with an abundance of at least 2% in two lakes were kept for statistical analyses.

A detrended correspondence analysis (DCA) and a detrended canonical correspondence analysis (DCCA) were used to determine the unimodality or linearity in the chironomid data. A redundancy analysis (RDA) was used to determine those environmental variables that explained most of the variance in the distribution and composition of chironomid assemblages (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003). The CANOCO program (ter Braak and Šmilauer 2002) was used for all ordinations. The chironomid inference models were developed using partial least squares (PLS) methods using the program C2 (Juggins 2003).

Results

Chironomid distribution

Of the 60 lake sediment samples analysed, 52 contained enough chironomid head capsules (>50) to be used for statistical analyses. A total of 97 different chironomid taxa were identified in the surface sediments from the 52 lakes.

Of those taxa, 64 had abundances of 2% and more in two lakes (Table 2) and were therefore used in statistical analyses. *Tanytarsus* without, *Tanytarsus* sp. B., *Procladius*, and the *Psectrocladius sordidellus* group were found in more than 40 of the 52 lakes. The *Heterotrissocladius grimshawi* group had the highest percentage (46%) in one lake (lake 29) followed by *Tanytarsus* without (42%), the *Psectrocladius sordidellus* group (30%), *Zalutschia lingulata pauca* (28%), *Sergentia* (27%), and *Procladius* (26%). Forty-eight of the other taxa had maximum percentages of less than 10%.

The taxa presented in Fig. 2 are those showing the most variations with latitude and vegetation zones. *Cryptochironomus*, *Polypedilum* IIIIC (fig. IIIIC in Wiederholm 1983), and *Zalutschia zalutschicola* were found only in lakes located in the Boreal Forest zone. *Glyptotendipes*, *Chironomus plumosus*-type, *Paracladopelma*, *Heterotanytarsus*, *Pagastiella*, and *Cryptotendipes* were mainly restricted to the boreal zone, with some sporadic (<2) occurrences in lakes located in the two other zones. *Dicrotendipes* had higher percentages in low latitude lakes located in the boreal zone and was absent in the higher latitude lakes. *Tanytarsus lugens*-type and

Cladopelma were absent in lakes located in the Forest–Tundra zone, but were sporadically present in the Boreal Forest and the Tundra zones. *Microtendipes* had higher percentages in the higher latitude lakes in the Boreal Forest zone, but decreased with latitude in the Forest–Tundra zone and disappeared in lakes of the Tundra zone. *Heterotrissocladius grimshawi*-type and *Heterotrissocladius marcidus*-type had higher abundances in the lakes of the Forest–Tundra zone. *Heterotrissocladius subpilosus*-type was found mainly in lakes of the Forest–Tundra and Tundra zones. The *Psectrocladius sordidellus* group percentages were higher in Tundra lakes, although the taxon was present in most lakes. *Corynocera ambigua* was present only in some Tundra lakes, usually at low percentages (<7%).

Relationship with environmental factors

We provide all the meteorological data that were tested in an RDA to determine the ones explaining the best the distribution of chironomids (Table 3). Mean August air temperature in 1993 and 1994 was the air temperature variable that best explained the distribution of chironomids and was added to the 32 other environmental variables for statistical analysis.

Latitude, vegetation zones, and distance from the forest were highly correlated with temperature, so they were removed from statistical analyses. Two types of analyses can determine the unimodality of taxa: a DCA (ter Braak and Šmilauer 2002) or a DCCA (Lepš and Šmilauer 2003). In both cases, the gradient length expressed as standard deviation (SD) units is the measure of unimodality. The gradient length should be higher than 3 to indicate unimodality (Lepš and Šmilauer 2003). In the DCA, the gradient lengths for the first four axes were 2.01, 1.98, 1.44, and 1.99, indicating that chironomids had a linear distribution. The gradient lengths of the DCCA with all variables were 1.97, 1.95, 1.57, and 1.21. In a DCCA with WT as the sole variable, the gradient lengths were 1.139, 2.056, 1.718, and 1.486. Gradient lengths were longer in a DCCA with August temperature (1.537, 2.296, 2.229, and 1.692). Since all gradient lengths were <3, most chironomid taxa showed a linear relationship with surface water and mean August air temperature.

An RDA with 999 Monte Carlo permutations and forward selection of variables was used to determine the relationship between chironomid distributions in the 52 lakes and the 33 environmental data. All variables combined explained 84% of the variance in the chironomid assemblages. The first and second RDA axes explained 38% and 22%, respectively, of the variance. In general, the separation between the chironomid assemblages in Tundra lakes compared with those of the Boreal Forest lakes was clear (Fig. 3a), although 5 of the 37 Forest lakes had chironomid assemblages that resembled those found in Forest–Tundra or Tundra lakes. Seven variables (DOC, depth, area, WT, soluble phosphorus (PRS), dissolved inorganic carbon (DIC), and mean August air temperature) explained 33% of the variance in the distribution of chironomids in the 52 lakes. The variance explained by each environmental variable was estimated in partial RDAs. The variance explained, from highest to lowest, was DOC (9.2%) > depth (9.0%) > mean August air temperature (8.7%) > WT (8.5%) > PRS (6.9%) > DIC (4.4%) > area (3.7%). High λ_1/λ_2 ratios were obtained for depth (0.78),

Fig. 2. Chironomid percentages in the training set lakes. Lakes are listed in order of decreasing latitude (°N). The zones indicate the limit of the three major vegetation types.

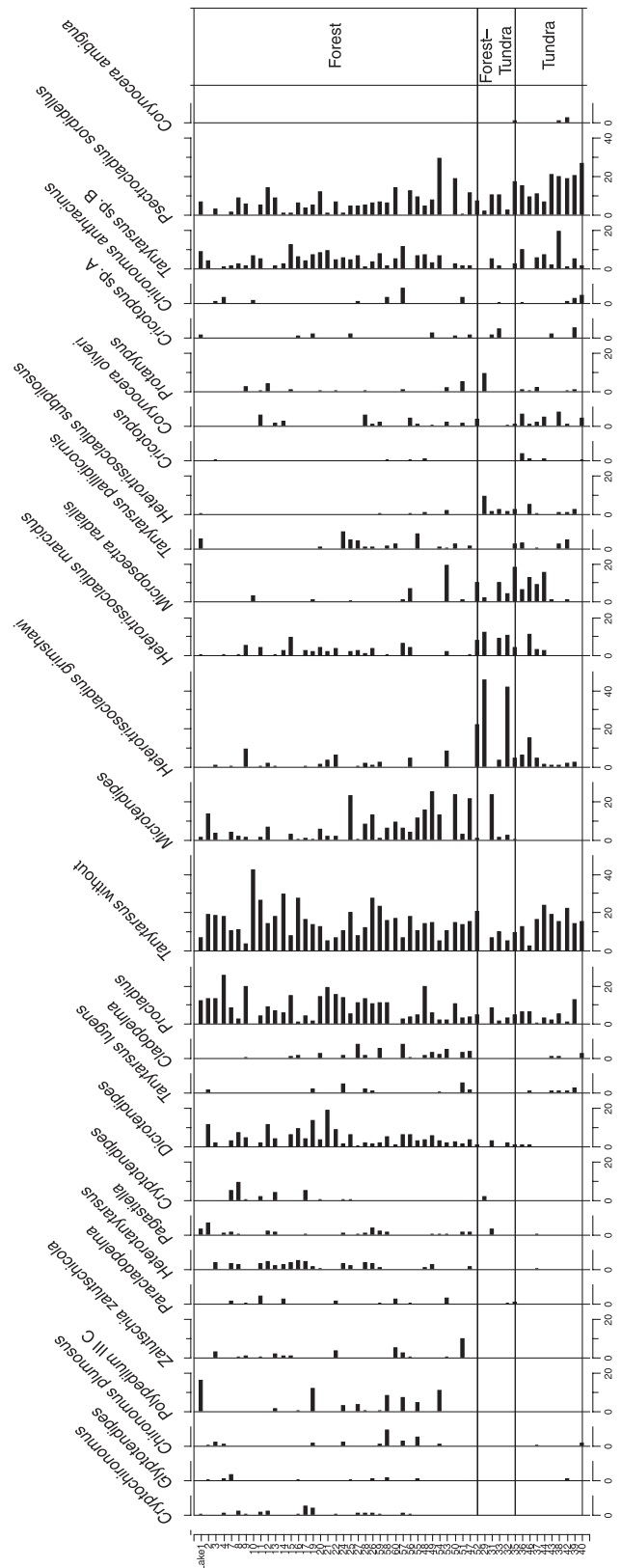


Table 2. Chironomid taxa with percentage of 2% in at least two lakes.

No.	Taxa	No. of lakes	Max. %
1	<i>Chironomus anthracinus</i> -type	14	8.4
2	<i>Chironomus plumosus</i> -type	12	8.7
3	<i>Cladopelma</i>	20	8.1
4	<i>Constempellina brevicosta</i>	21	6.9
5	<i>Cryptochironomus</i>	17	5.4
6	<i>Cryptotendipes</i>	12	10.2
7	<i>Dicrotendipes</i>	39	19.7
8	<i>Einfeldia</i>	8	7.2
9	<i>Endochironomus impar</i> -type	5	9.5
10	<i>Glyptotendipes</i>	10	3.7
11	<i>Microtendipes</i>	38	25.9
12	<i>Omisus</i>	7	4.1
13	<i>Pagastiella</i>	23	7.0
14	<i>Parachironomus</i>	5	2.2
15	<i>Paracladopelma</i>	12	4.6
16	<i>Polypedilum</i>	7	5.7
17	<i>Polypedilum</i> III C	12	16.8
18	<i>Sergentia</i>	19	27.3
19	<i>Stempellinella</i>	24	17.5
20	<i>Micropsectra bidentata</i> -type	12	6.9
21	<i>Micropsectra insignilobus</i> -type	13	13.1
22	<i>Micropsectra radialis</i> -type	19	20.0
23	<i>Cladotanytarsus</i>	18	7.0
24	<i>Paratanytarsus</i>	26	15.3
25	<i>Tanytarsus</i> without	51	43.0
26	<i>Tanytarsus</i> with	13	3.2
27	<i>Tanytarsus chinyensis</i> -type	9	6.9
28	<i>Tanytarsus</i> sp. B	44	19.8
29	<i>Tanytarsus</i> sp. C	6	4.3
30	<i>Tanytarsus lugens</i> -type	14	5.7
31	<i>Tanytarsus pallidicornis</i> -type	19	9.3
32	<i>Allopsectrocladius</i>	15	5.7
33	<i>Corynocera ambigua</i>	3	3.4
34	<i>Corynocera oliveri</i>	24	7.6
35	<i>Corynoneura</i>	5	3.0
36	<i>Cricotopus</i>	8	4.4
37	<i>Cricotopus</i> sp. A	16	6.0
38	<i>Cricotopus</i> sp. B	8	5.6
39	<i>Cricotopus sylvestris</i>	7	3.2
40	<i>Cricotopus cylindricus</i>	6	4.3
41	<i>Georthocladius</i>	2	2.5
42	<i>Heterotrissocladius grimshawi</i> -type	30	46.2
43	<i>Heterotrissocladius marcidus</i> -type	33	12.8
44	<i>Heterotrissocladius brundini</i> -type	7	7.1
45	<i>Heterotrissocladius subpilosus</i>	19	10.3
46	<i>Heterotanytarsus</i>	22	5.1
47	<i>Limnophyes</i>	6	3.0
48	<i>Mesocricotopus</i>	6	9.6
49	<i>Nanocladius</i>	8	3.4
50	<i>Orthocladius</i> sp. A	16	4.3
51	<i>Orthocladius</i> sp. D	7	2.8
52	<i>Paracricotopus</i>	8	3.2
53	<i>Parakiefferiella</i>	9	8.7
54	<i>Paraphaenocladius</i>	4	5.2

Table 2 (concluded).

No.	Taxa	No. of lakes	Max. %
55	<i>Protanytarsus</i>	17	10.3
56	<i>Psectrocladius septentrionalis</i> -group	29	16.8
57	<i>Psectrocladius sordidellus</i> -group	49	30.0
58	<i>Smittia</i>	3	4.3
59	<i>Zalutschia lingulata pauca</i>	35	28.6
60	<i>Zalutschia zalutschicola</i>	15	10.4
61	<i>Ablabesmyia</i>	15	3.7
62	<i>Telopelopia</i>	22	5.6
63	<i>Pentaneurini</i>	34	7.4
64	<i>Procladius</i>	48	26.3

Note: The number of lakes indicates where the taxa was found; Max. % shows the percentage of the lakes where 2% of the taxa are found.

DOC (0.72), WT (0.71), and mean August air temperature (0.63), indicating that inference models could be created for these variables (Fallu and Pienitz 1999; ter Braak and Smilauer 2002).

Heterotrissocladius marcidus-type, *H. grimshawi*-type, *H. subpilosus*-type, *Micropsectra radialis*-type, *Protanytarsus*, and *Heterotrissocladius brundini*-type are taxa that were most influenced by depth (Fig. 3b). *Heterotanytarsus*, *Dicrotendipes*, *Cryptotendipes*, and *Cryptochironomus* seemed to be mostly influenced by WT, mean August air temperature, and DOC.

Transfer functions

Models for WT and mean August air temperature were developed using PLS. The coefficient of determination between mean August air temperature and chironomid percentages was higher ($r^2 = 0.67$) and the root mean square error of prediction (RMSEP) much lower (1.17 °C) than those for WT ($r^2 = 0.59$, RMSEP = 2.24 °C). When inferring WT, lakes with temperature lower than 16 °C were located further away from the 1:1 line of prediction (Fig. 4a), indicating that colder lakes were not so well predicted. In mean August predictions, the temperature in warmer lakes was generally underestimated, and the residuals for these lakes were more important (Fig. 4b).

Although our goal was to create chironomid transfer functions for temperature, models for DOC and depth were also attempted using PLS. While the transfer function for DOC had relatively good statistics ($r^2 = 0.62$, RMSEP = 2.78 mg·L⁻¹), the model for depth had a low coefficient of correlation ($r^2 = 0.40$, RMSEP = 2.84 m).

Discussion

The chironomid distribution in our 52 lakes from north-western Quebec was mainly influenced by four parameters: depth, DOC, WT, and mean August air temperature. The goal of this paper was to create a transfer function for temperature, and the model performance data showed that it was coherent to do so. Although the r^2 (0.67) was lower than that of the Eastern Canadian training set for WT (0.88; Walker et al. 1997), the RMSEP (1.17 °C) was lower (RMSEP Eastern Canadian = 2.26 °C). The better correlation in the Eastern Canadian training set might be explained by the fact that its

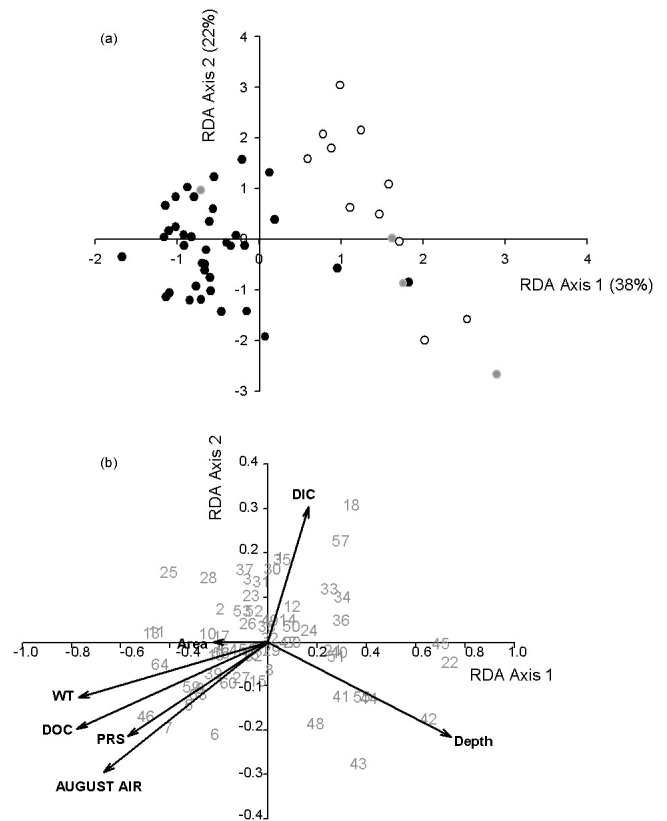
Table 3. Meteorological data analysed in a redundancy analysis.

Variable	Variance explained (%)
All variables	27
June 1993	—
July 1993	4
August 1993	—
Mean summer 1993	—
June 1994	4
July 1994	—
August 1994	—
Mean summer 1994	—
June 1995	—
July 1995	—
August 1995	—
Mean summer 1995	—
June 1993–1994	—
July 1993–1994	—
August 1993–1994	9
Mean summer 1993–1994	—
June 1993–1995	—
July 1993–1995	—
August 1993–1995	—
Mean summer 1993–1995	—

39 lakes were distributed over 3000 km and over a larger temperature gradient (20 °C). Our 52 lakes, however, were located within 1100 km in a temperature gradient of 10 °C. Similar results were obtained in Norway, where the first developed training set comprised only 44 lakes in a temperature gradient of 8.3 °C with $r^2 = 0.69$ (Brooks and Birks 2000), and the second training set comprised 153 lakes in Norway and Svalbard in a temperature gradient of 12.5 °C and an r^2 of 0.90 (S. Brooks, National History Museum, Cromwell Road, London SW7 5BD, UK; and H.J.B. Birks, Botanical Institute, University of Bergen, N-5007 Bergen, Norway, unpublished data). In general, training sets with longer temperature gradients have better r^2 (table 6 in Larocque et al. 2001). These results suggest that to obtain a better r^2 , our training set should be extended, although training sets with lower r^2 also perform in general quite well. For example, inferences based on a Swedish training set with an r^2 of 0.65 were quite similar to meteorological data (Larocque and Hall 2003). It seems evident that the r^2 is not the only statistical parameter that is important for the relevance of the temperature inferences.

The lower RMSEP of our training set might result from higher taxonomic resolution. Here, we separated many of the taxa that were combined in the Eastern Canadian training set (especially the Tanytarsina), and we think we obtained better temperature optima for each taxon, thereby decreasing the error of temperature estimates. Similar results were obtained in Norway; increasing the taxonomic level probably decreased the error of temperature estimates in the 153-lake

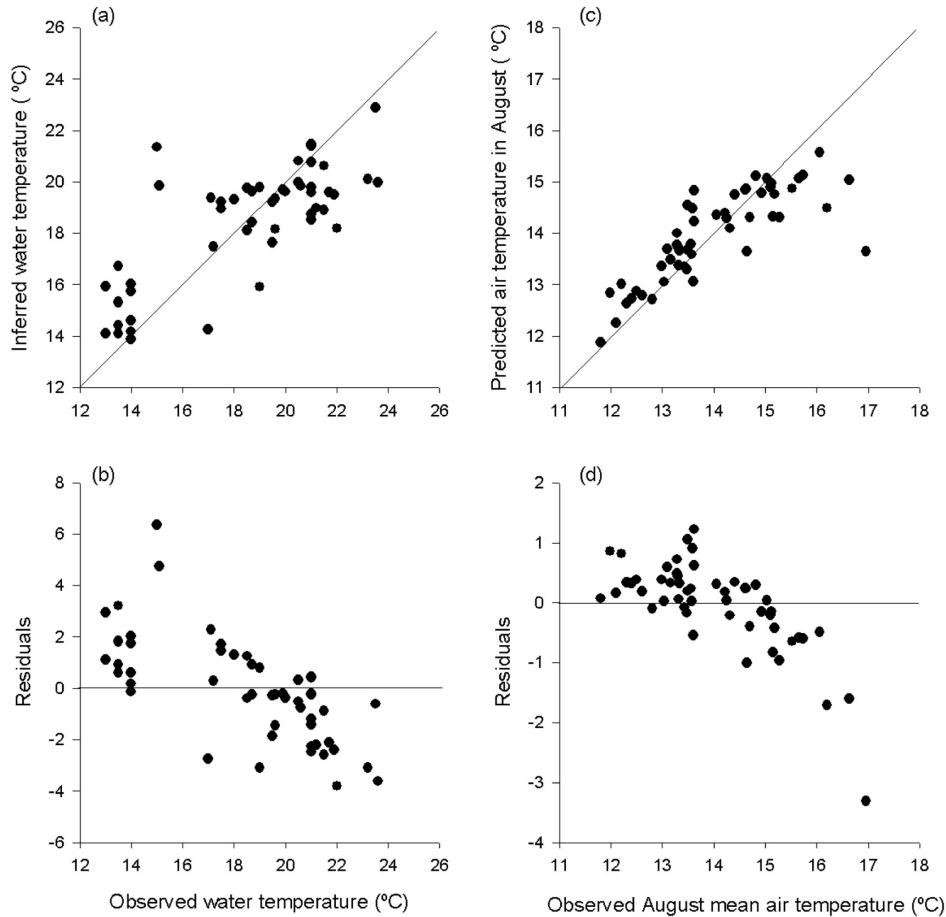
Fig. 3. (a) Redundancy analysis (RDA) of lake data. Solid circles are lakes located in the Boreal Forest zone, shaded circles represent lakes located in the Forest–Tundra ecotone, and open circles represent lakes within the Tundra zone. (b) RDA analysis of taxa. The numbers are associated to taxon names in Table 2. The arrows represent the vectors of the seven environmental data explaining the distribution of chironomids in the 52 lakes. DIC, dissolved inorganic carbon; Area, area of lakes; WT, water temperature; DOC, dissolved organic carbon; PRS, soluble reactive phosphorus; AUGUST AIR, mean August air temperature in 1993 and 1994; Depth, maximum lake depth.



training set (S. Brooks, Natural History Museum, Cromwell Road, London SW7 5BD, UK, personal communication).

The PLS coefficients for each taxa (Table 4) identified the *Psectrocladius sordidellus* group, *Sergentia*, *Micropsectra radialis*-type, *Corynocera oliveri*, and *Heterotrissocladius subpilosus*-type as the coldest indicators. A review of temperature optima from four training sets is presented in Bennike et al. (2004) and is used for comparison with our results. The *Psectrocladius sordidellus* group was not considered as a cold indicator in northern Sweden (optimum = 11.6 °C), but *Psectrocladius* were the most abundant taxon in the cold early Holocene in a shrub–tundra lake in northern Quebec (Fallu et al. 2005). The species name *Psectrocladius sordidellus* is given to a group with similar characteristics of the head capsule but might comprise species with potentially different temperature optima. Here, the *Psectrocladius sordidellus* group is also located along the DIC vector in the RDA analysis and could be influenced by this factor more than by temperature. While *Sergentia* has a cold optimum in eastern Canada (6 °C) and is a cold indicator in our training

Fig. 4. (a) Relationship between observed and inferred water temperature. The solid line represents the 1:1 relationship. (b) Observed water temperature versus residuals. (c) Relationship between observed and inferred mean August air temperature. The solid line represents the 1:1 relationship. (d) Observed water temperature versus residuals.



set, it had higher temperature optima (15 °C) in northern Finland and northern Sweden (Bennike et al. 2004). These contradictory results indicate that the taxa called “*Sergentia*” might not comprise the same species in Canada and in northern Europe. A special taxonomic effort could be given to this taxon to try to separate it into taxonomic groups. *Micropsectra radialis*-type, *Corynocera oliveri*, and *Heterotrissocladius* are cold indicators (optimum <7 °C) in the Canadian and in the North European training sets. *Dicrotendipes*, *Cryptochironomus*, and *Zalutschia* were identified as warm indicators in this training set and in the Eastern Canada and Northern Europe training sets (Bennike et al. 2004). Other taxa have contradictory results. *Cladotanytarsus* and *Cladopelma* were considered here as colder indicators, while they were warm indicators in other training sets; *Heterotanytarsus* is an intermediate taxon in other training sets, while it is a warmer indicator here. These differences might be attributed to the fact that we had linear relationships between the chironomid taxa and the temperature. By increasing the training set north and south, we might get a better distribution of all taxa and be able to calculate optima with unimodal techniques.

Although temperature was an important factor explaining the distribution of chironomids, other parameters obviously

also had an influence on larval distribution. Depth and DOC effects on the chironomid distribution are further discussed below.

Depth

Depth has been identified as an important factor explaining the distribution of chironomids in many other training sets (e.g., Olander et al. 1997; Quinlan et al. 1998; Porinchi et al. 2002). Taxa such as *Micropsectra*, *Heterotrissocladius subpilosus*, and *H. brundini* are restricted to deep lakes or to the profundal zones (Walker 1990; Walker and MacDonald 1995; Simola et al. 1996). These taxa were also found in deeper lakes in our training set. Most *Tanytarsus*, *Tanytarsus lugens*, and *Microtendipes* prefer the littoral zone (Schmäh 1993; Walker and MacDonald 1995; Heiri et al. 2003). In the RDA ordination, these taxa were located at the opposite end of the depth vector, indicating that they prefer shallow lakes. Although an inference model has been built for the reconstruction of depth (Korhola et al. 2000), the low coefficient of determination we obtained here does not indicate that the model would be significant. The importance of depth in explaining the distribution of chironomids should be taken into account when interpreting temperature reconstructions, especially if the community changes involve

Table 4. Partial least square (PLS) coefficients of each taxon.

Taxa	PLS
<i>Psectrocladius sordidellus</i> -group	-0.331
<i>Sergentia</i>	-0.301
<i>Micropsectra radialis</i> -type	-0.177
<i>Corynocera oliveri</i>	-0.163
<i>Heterotrissocladius subpilosus</i> -type	-0.142
<i>Cladopelma</i>	-0.116
<i>Heterotrissocladius grimshawi</i> -type	-0.085
<i>Tanytarsus pallidicornis</i> -type	-0.083
<i>Cladotanytarsus</i>	-0.083
<i>Tanytarsus lugens</i> -type	-0.080
<i>Tanytarsus</i> sp. B	-0.075
<i>Microtendipes</i>	-0.072
<i>Cricotopus</i> sp. A	-0.067
<i>Cricotopus</i>	-0.061
<i>Omisus</i>	-0.058
<i>Paracricotopus</i>	-0.052
<i>Orthocladius</i> sp. A	-0.044
<i>Chironomus anthracinus</i> -type	-0.044
<i>Corynocera ambigua</i>	-0.044
<i>Telopelopia</i>	-0.032
<i>Orthocladius</i> sp. D	-0.029
<i>Parachironomus</i>	-0.026
<i>Cricotopus cylindricus</i>	-0.024
<i>Chironomus plumosus</i> -type	-0.023
<i>Heterotrissocladius brundini</i> -type	-0.020
<i>Ablabesmyia</i>	-0.014
<i>Limnophyes</i>	-0.008
<i>Protanypus</i>	-0.004
<i>Parakiefferiella</i>	-0.004
<i>Paratanytarsus</i>	-0.003
<i>Micropsectra bidentata</i> -type	-0.002
<i>Micropsectra insignilobus</i> -type	0.002
<i>Nanocladius</i>	0.002
<i>Tanytarsus</i> with	0.006
<i>Georthocladius</i>	0.008
<i>Polypedilum</i>	0.011
<i>Einfeldia</i>	0.018
<i>Corynoneura scutellata</i>	0.024
<i>Psectrocladius septentrionalis</i> -group	0.026
<i>Allopectrocladius</i>	0.027
<i>Glyptotendipes</i>	0.029
<i>Constempellina</i>	0.035
<i>Smittia</i>	0.039
<i>Heterotrissocladius marcidus</i> -type	0.042
<i>Tanytarsus</i> without	0.044
<i>Cricotopus</i> sp. B	0.046
<i>Paracladopelma</i>	0.048
<i>Tanytarsus</i> sp. C	0.051
<i>Paraphaenocladius</i>	0.053
<i>Cricotopus laricomalis</i>	0.060
<i>Polypedilum</i> III C	0.069
<i>Mesocricotopus</i>	0.070
<i>Pagastiella</i>	0.074
<i>Zalutschia lingulata pauca</i>	0.086
<i>Zalutschia zalutschicola</i>	0.095

Table 4 (concluded).

Taxa	PLS
<i>Tanytarsus chinensis</i> -type	0.112
<i>Dicrotendipes</i>	0.119
<i>Endochironomus impar</i> -type	0.131
<i>Cryptochironomus</i>	0.132
<i>Cryptotendipes</i>	0.136
<i>Procladius</i>	0.143
<i>Heterotanytarsus</i>	0.150
<i>Stempellinella</i>	0.151
<i>Pentaneurini</i>	0.192

changes in taxa such as *Micropsectra*, *H. subpilosus*-type and *H. brundini*-type, *Tanytarsus*, *Tanytarsus lugens*-type, and *Microtendipes*.

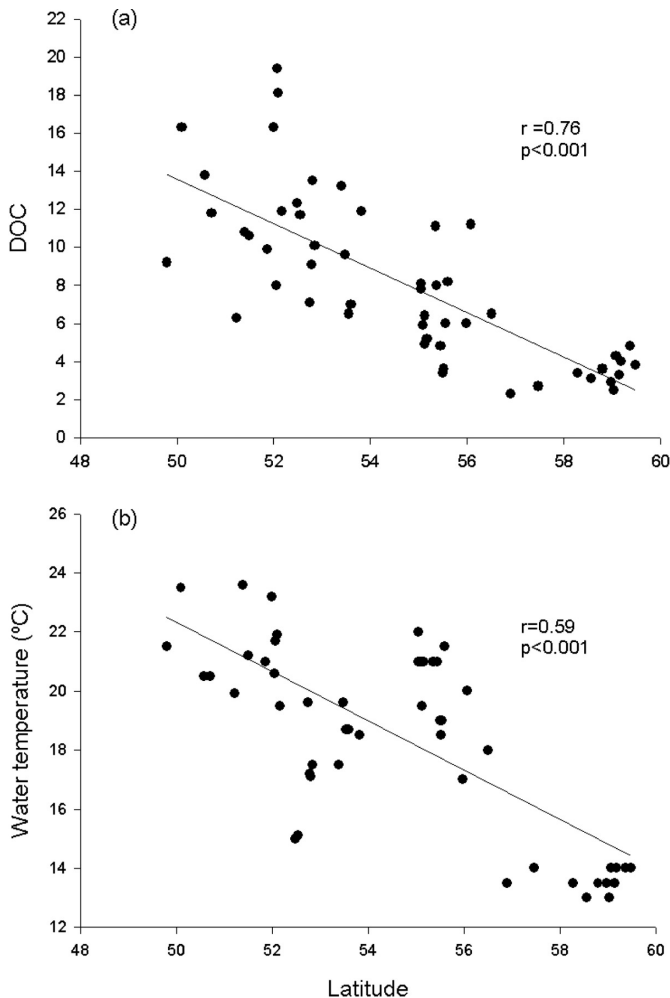
DOC

DOC was not an important parameter explaining the distribution of chironomids in most other training sets either because it was not measured as such (e.g., Walker et al. 1991; Olander et al. 1997 (total organic carbon, (TOC)); Porinchu et al. 2002 (particulate organic carbon) or the DOC gradient along the transect was weak (e.g., Larocque et al. 2001). Lotter et al. (1997) found a relationship between DOC and the chironomid distribution in Swiss lakes, but DOC did not solely explain a high proportion of the variance in the species data. In Finland, TOC was an important factor explaining the distribution of chironomids; high TOC lakes were surrounded by peatlands (Nyman et al. 2005).

In our study sites, DOC derives mainly from allochthonous sources (Fallu and Pienitz 1999). This has been shown also in other high latitude areas (e.g., Labrador, Engstrom 1987; Alaska, Kling et al. 1991; Yukon, Pienitz et al. 1997a; Northwest Territories, Pienitz et al. 1997b; Mackenzie Delta, Ramlal et al. 1994). The relationship between latitude and DOC is relatively important (Fig. 5); DOC is generally higher in lakes located in the Boreal Forest (average 9.8 mg·L⁻¹) and lower in Tundra lakes (average 4.8 mg·L⁻¹) (Fallu and Pienitz 1999). Similar results were obtained in northern Canada (Pienitz et al. 1997a, 1997b), in Siberia (Laing et al. 1999), and in Europe (Kingston and Birks 1990; Stevenson et al. 1991). The feeding habits of chironomid larvae vary, but many are detritivores and (or) filter-feeders, while others graze on bacteria (Walker 2001). These are feeding habits that involve DOC absorption. Binkley et al. (2005) showed that although DOC was thought to come primarily from bacteria degradation, *Chironomus* utilized DOC derived from terrestrial sources. Labile carbon was added to a stream in North Carolina, USA, and lead to a threefold increase in growth rate of chironomid larvae (Wilcox et al. 2005).

DOC can influence aquatic communities by attenuating light penetration (Vincent and Roy 1993) and by changing the thermal stratification of lakes (Scully 1998). In the RDA, DOC and temperature were represented by vectors that pointed in the same direction, indicating that separation of DOC and temperature effects on chironomid distribution

Fig. 5. Relationships between latitude and (a) dissolved organic carbon (DOC) and (b) water temperature. The solid line is the regression line.



might be difficult, although the relationship between WT and DOC was weak (Fig. 5).

The DOC–diatom transfer function elaborated from the same set of lakes seems to be more relevant ($r^2 = 0.90$, RMSEP = $1.23 \text{ mg}\cdot\text{L}^{-1}$) (Fallu and Pienitz 1999), and we therefore do not suggest to use the DOC–chironomid transfer function developed here.

Water, air, and August temperature

Based on other published transfer functions (e.g., Lotter et al. 1997; Brooks and Birks 2000; Larocque et al. 2001), it is not surprising that air temperature is better predicted with chironomids than with WT. This relationship is not entirely due to chironomid ecology and life cycle, although hatching of adults and reproduction might be related to air temperature (Armitage et al. 1995). It is mainly due to the fact that meteorological data have been sampled more frequently than WT. The air temperature data set is thus more representative than the punctual WT measurements.

Mean August air temperature 2 years prior to the sampling year is a better predictor of chironomid distribution

than July air temperature of the sampling year, generally considered in other transfer functions (e.g., Brooks and Birks 2000; Larocque et al. 2001). Chironomid assemblages in surface sediment integrate several years (likely 2–5 years), and larvae might take more than 1 year to become fourth instar, especially in colder lakes (Armitage et al. 1995). August is the month when emergence was highest in temperate zone streams (Pinder 1974), and voltinism (number of annual generations per species in a habitat) decreases with latitude (Armitage et al. 1995). At high latitude sites, one generation per species is generally recorded every 2–3 years, and the adults of certain species (*H. grimshawi*, *Psectrocladius limbatellus*, *Rheocricotopus effusus*, and *Paracladopelma nigritula*) mainly emerge between mid-July and September (Welch 1976). These studies highlight the need for a better understanding of chironomid larval ecology when trying to explain the stronger impact of August (in this case) rather than July, mean June, or mean summer temperatures on the distribution of chironomids.

In conclusion, our results indicate that the northern Quebec lake training set should be extended to (i) get a unimodal response of taxa to better calculate optima of temperature and (ii) to better predict temperature in colder and warmer lakes. By extending the training set, we hope to achieve a better correlation (r^2) between temperature and chironomids. However, statistical analysis should not be the only approach for climate reconstruction. Understanding the relationship between temperature and chironomid larval life strategies (e.g., timing and duration of larval development, emergence) is still a research challenge for paleoecological studies using fossil chironomids. We plan to study more lakes along our transect with weekly sampling intervals to determine which taxa might be better indicators of temperature and to further refine the relationship between chironomids and lake DOC.

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