

The Distribution of Freshwater Chironomidae (Insecta: Diptera) across Treeline near the Lower Lena River, Northeast Siberia, Russia

David F. Porinchu

Department of Geography, University of California, Los Angeles, California 90095-1524, U.S.A.
porinchu@ucla.edu

Les C. Cwynar

Department of Biology, University of New Brunswick, Fredericton, New Brunswick E3B 6E1, Canada.
cwynar@unb.ca

Abstract

Surficial sediment from 31 lakes along a transect spanning treeline in northeast Siberia was analyzed for midge remains in order to assess the modern distribution of midges relative to treeline. Taxa distinct to tundra, forest-tundra, and forest areas were identified. *Abiskomyia*, *Parakiefferiella nigra*, and *Hydrobaenus/Olivieridia* were found predominantly in tundra lakes, whereas *Zalutschia zalutschicola* and *Microtendipes* were restricted to forest-tundra or forest lakes. A sharp delineation exists at the tundra/forest-tundra transition zone with respect to the genus *Corynocera*. *Corynocera oliveri* was found chiefly in tundra lakes whereas *C. ambigua* was found solely in forested areas.

Thirty-two environmental variables describing the physical, chemical, and limnological characteristics of the lakes in the transect were measured. Redundancy analysis (RDA) revealed that statistically significant relationships exist between chironomid distributions and six of the measured environmental variables (particulate organic carbon, particulate organic nitrogen, iron, zinc, lake depth, and Secchi depth), but not surface lake-water temperature. Canonical variate analysis (CVA) demonstrated that chlorophyll *a*, lake depth, pH, and strontium maximized separation of tundra, forest-tundra, and forest lakes from one another. These results illustrate the importance of treeline as an ecological boundary for the distribution of chironomids. The abrupt changes in distribution that occur at treeline for specific chironomid taxa suggest that subfossil chironomid analysis may be used to infer past changes in the position of treeline.

Introduction

Chironomids are nonbiting midges belonging to the order Diptera. They are ubiquitous and frequently the most abundant insects found in freshwater ecosystems (Cranston, 1995). The Chironomidae have three characteristics that are useful in paleoecological studies: relatively short lifecycles, the adults are mobile, and the larvae possess durable chitinous head capsules that are readily preserved in lake sediment (Walker, 1987). Mobility and a short life cycle allow chironomids to respond rapidly to climate change, resulting in distributions that are likely in equilibrium with climate (Walker, 1987; Wilson et al., 1993; Smol et al., 1995; Walker and MacDonald, 1995).

Many climate models predict increases in mean global temperature of between 1 and 4°C by A.D. 2100 (Schlesinger and Mitchell, 1987). The magnitude of warming is expected to be significantly greater in arctic regions, with a projected increase of 5 to 10°C (Schlesinger and Mitchell, 1987). Circumpolar treeline will be greatly affected by global warming and changes in its position may, through feedback mechanisms, further impact global climate (Rizzo and Wiken, 1992). Information relating the response of circumpolar treeline to global warming will improve the ability of investigators to predict and detect the effects of global climate change (MacDonald et al., 1993).

The position of circumpolar treeline in Canada and Eurasia roughly coincides with the mean July position of the Arctic Front and is typified by sharp gradients of decreasing summer temperature and precipitation northward (Bryson, 1966). This relationship between circumpolar treeline and the mean summer

position of the Arctic Front allows researchers to sample large environmental gradients over short geographic distances. Recent papers have illustrated that significant changes in chironomid assemblages occur across latitudinal treeline in central Canada (Walker and MacDonald, 1995), eastern Canada (Walker et al., 1991a), and Fennoscandia (Olander et al., 1997; Olander et al., 1999). However, data regarding the distribution of chironomids across the Eurasian treeline are scant or unavailable.

Earlier work has illustrated the value of using chironomids as a proxy source of paleoclimatic data. It has long been known that chironomids are sensitive to lake water temperature and that individual taxa have differing optima and tolerances. However, the development of chironomid analysis as a tool to quantitatively reconstruct past lake-water temperatures is relatively recent (Walker et al., 1991a; Olander et al., 1997; Walker et al., 1997; Lotter et al., 1997; Olander et al., 1999). Researchers have been able to quantify changes in past temperature in Atlantic Canada and the northeastern United States during the late-glacial, and Western Norway during the late-glacial and the early Holocene (Walker et al., 1991b; Levesque et al., 1993, 1994, 1997; Wilson et al., 1993; Cwynar and Levesque, 1995; Brooks and Birks, 2000).

This study was undertaken as part of a larger project on circumpolar treeline change (PACT) the aim of which is to reconstruct past movements of treeline in relation to climate change. The initial goal of the chironomid analysis was to determine if chironomid assemblages were related to the thermal regime (lake-water temperature) so that a transfer function could be developed in order to provide a quantitative estimate of tem-

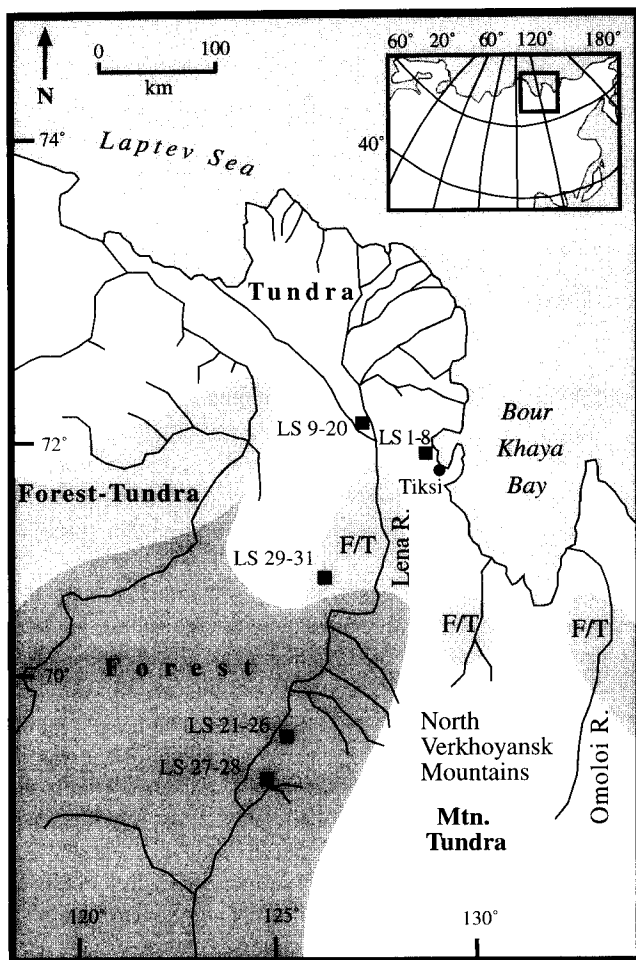


FIGURE 1. Location of study lakes and associated vegetation zones along the Lena River, Siberia. Lakes LS1—LS20 are located in tundra, lakes LS21—LS28 are located in forest, and lakes LS29—LS31 are located in forest-tundra. The location of Dolgoe Ozero (LS9) is also indicated.

perature change independent of the pollen and stomate data used to reconstruct past treeline movements.

In this paper, we describe the modern distribution of chironomids from a transect of 31 lakes spanning treeline near the lower Lena River in north-central Siberia. To examine the relationship that exists between the chironomid assemblages and environmental variables, a calibration or “training set” approach was used. The response of chironomid assemblages to physicochemical environmental variables was evaluated using redundancy analysis (RDA). Canonical variate analysis (CVA) was used to assess whether significant differences in lake water chemistry exist between tundra, forest-tundra, and forest lakes and which environmental variables are most responsible in explaining any difference.

Study Area

The transect is approximately 250 km in length and crosses tundra, forest-tundra, and forest vegetation zones (Fig. 1). The lakes sampled were arranged along a north-south transect, with LS12 being the northernmost site. Lakes LS1 to LS20 are in tundra, LS21 to LS28 are in forest, and LS29 to LS31 are in the forest-tundra transition zone (Fig. 1). Coordinates for the lakes are given in Table 1. Lake depth varied from 0.95 to 10.8 m.

TABLE 1

Coordinates of study lakes and environmental data for study sites

Lake	Date sampled	Latitude (N)	Longitude (E)	Temp (°C)	Depth (m)	Vegetation type ^a
LS-1	23 Jul 94	71°30'64"	128°52'42"	15.0	2.00	T
LS-2	23 Jul 94	71°30'64"	128°52'29"	17.0	1.20	T
LS-3	23 Jul 94	71°30'00"	128°52'36"	16.0	0.95	T
LS-4	23 Jul 94	71°30'96"	128°51'73"	15.0	2.60	T
LS-5	24 Jul 94	71°30'10"	128°53'95"	15.0	2.20	T
LS-6	24 Jul 94	71°29'92"	128°53'66"	14.0	2.20	T
LS-7	24 Jul 94	71°29'92"	128°52'77"	15.0	2.20	T
LS-8	24 Jul 94	71°30'00"	128°51'42"	14.0	2.20	T
LS-9	27 Jul 94	71°52'41"	127°04'39"	11.0	3.95	T
LS-10	28 Jul 94	71°52'65"	127°03'73"	8.5	3.00	T
LS-11	28 Jul 94	71°53'45"	127°02'68"	10.5	3.00	T
LS-12	28 Jul 94	71°54'09"	127°02'15"	10.0	1.70	T
LS-13	28 Jul 94	71°54'09"	127°01'02"	11.0	3.40	T
LS-14	28 Jul 94	71°52'85"	126°58'75"	12.5	3.80	T
LS-15	28 Jul 94	71°52'05"	127°02'35"	11.5	2.00	T
LS-16	29 Jul 94	71°52'01"	127°02'34"	10.5	2.20	T
LS-17	29 Jul 94	71°52'17"	127°03'04"	10.0	1.00	T
LS-18	29 Jul 94	71°52'21"	127°03'91"	11.0	1.50	T
LS-19	29 Jul 94	71°52'44"	127°05'15"	11.0	2.20	T
LS-20	29 Jul 94	71°52'65"	127°04'94"	10.5	3.50	T
LS-21	02 Aug 94	69°23'33"	128°08'37"	14.0	6.30	F
LS-22	03 Aug 94	69°23'31"	125°07'80"	14.0	5.50	F
LS-23	03 Aug 94	69°23'40"	125°07'77"	14.0	10.80	F
LS-24	03 Aug 94	69°23'82"	125°07'26"	14.0	1.90	F
LS-25	03 Aug 94	69°24'04"	125°07'79"	14.0	8.00	F
LS-26	03 Aug 94	69°24'15"	125°07'76"	13.5	1.60	F
LS-27	05 Aug 94	69°02'62"	124°12'50"	15.0	3.10	F
LS-28	05 Aug 94	69°02'57"	124°13'17"	16.0	4.50	F
LS-29	06 Aug 94	70°40'73"	125°52'01"	11.5	2.60	F/T
LS-30	06 Aug 94	70°40'72"	125°52'05"	11.5	2.00	F/T
LS-31	06 Aug 94	70°40'24"	125°52'60"	12.0	3.00	F/T

^a T-tundra, F-forest, F/T-forest-tundra.

The majority of the lakes sampled were not deep enough to undergo thermal stratification.

The vegetation surrounding the tundra lakes is composed primarily of herbaceous taxa, heaths (*Ericaceae*), and cotton-grass (*Eriophorum*). The forest-tundra transition zone is dominated by vegetation common to both the tundra and forest, with tundra vegetation dominating rocky, well-drained sites. The northern limit of treeline in this region is composed of *Larix dahurica*, which also dominates the forest (Pisaric et al., 2000). The bedrock is predominantly Cretaceous sandstone (Markov, 1970). Surficial deposits in the study area are mostly colluvium of Quaternary age. Alluvial deposits of Holocene age also occur (Zarkhidze et al., 1991). The lower Lena River region is typified by a cold, continental climatic regime. Mean annual precipitation is ≤ 300 mm with the majority of precipitation falling during the summer (Pisaric et al., 2000). The mean temperature for January is -34°C and the mean July temperature is 8°C (Miachkova, 1983).

Methods

Surface sediment samples were collected in July and August of 1994. Coordinates for the lakes were obtained using a Magellan Global Positioning System (see Table 1). Sediment was recovered from the approximate center of each lake using

a Glew gravity corer deployed from an inflatable raft (Glew, 1991). Three sets of replicate samples were obtained from each lake. The top 1 cm of sediment was subsampled and stored in Whirl-paks[®] for analysis. Water chemistry measurements were made from epilimnetic samples collected 0.5 m below the water surface at the approximate center of each lake. Measurements of 32 physical, chemical, and biological variables were made for each lake: Cl, SiO₂ (silica), SO₄ (sulfate), DIC (dissolved inorganic carbon), DOC (dissolved organic carbon), SRP-F (soluble reactive phosphorus—filtered), TP-F (total phosphorus—filtered), NO₂-F (nitrite—filtered), NH₃-F (ammonia—filtered), NO₃ (nitrate—filtered) TKN-N-F (total Kjeldahl nitrogen—filtered), Chl *a* (corrected and uncorrected chlorophyll *a*), POC (particulate organic carbon), PON (particulate organic nitrogen), Al, Ba, Ca, Cr, Cu, Fe, K, Mn, Na, Ni, Sr, Zn, pH, conductivity, surface water temperature, maximum depth, and Secchi depth. Physical variables, e.g., temperature, specific conductivity, and Secchi depth were measured 0.5 m below the water surface during lake sediment collection. Measurements of chemical variables (e.g., TP-F, SRP-F, and Chl *a*) were made later in the laboratory. Full details of water chemistry analyses can be found in Duff et al. (1998).

Chironomid analysis followed standard procedures as outlined in Walker (1987). A minimum of 2 ml of sediment was deflocculated in a 5% KOH solution and heated at about 30°C for 30 min. The sediment was then sieved through a screen with 95- μ m meshes. The material retained on the sieve was rinsed with distilled water, backwashed into a beaker and then aliquots were examined in a Bogorov plankton counting tray. Head capsules were handpicked with the aid of a Wild[®] 5 \times dissection microscope at 50 \times . Chironomid head capsules that retained either the entire mentum or greater than half the mentum were counted as one head capsule. Head capsules comprising half of the mentum were enumerated as half a head capsule. Head capsules comprised of less than half the mentum were not enumerated. The specimens were permanently mounted on slides in Entellan[®] and identified at 400 \times , generally to genus. However, in certain cases broader taxonomic groupings were required. For example, the genera *Cricotopus* and *Orthocladius* were combined. In other instances taxa were identified to species, e.g., *Corynocera ambigua* and *C. oliveri*. Identifications were based predominantly on Wiederholm (1983), Walker (1988), and Oliver and Roussel (1983).

A minimum of 100 head capsules were enumerated and identified from each of the lakes with the exception of lake LS14, which was excluded from the calibration set due to low head capsule recovery. Taxa that had a relative abundance of $\geq 2\%$ in two or more lakes were included in the numerical analysis.

Detrended correspondence analysis (DCA) of the chironomid data (square root transformation of species data, rare taxa down-weighted, detrending-by-segments, nonlinear rescaling) was used to identify the length of the environmental gradients sampled. The length of the compositional gradients in the species data-set identified whether a linear or unimodal response model should be used for the constrained ordination. DCA assumes that species respond in a unimodal manner along hypothetical environmental gradients (ter Braak and Prentice, 1988; Pienitz et al., 1995; ter Braak and Verdonschot, 1995). The gradient length of axis 1 from the DCA was 2.16 standard deviations units, which suggested the use of linear-based methods, e.g., RDA for further analyses. Redundancy analysis (RDA) is appropriate in situations where narrow environmental gradients have been sampled, i.e., ≤ 2.0 standard deviation units, which indicates that most taxa

within the calibration set are responding in a linear fashion to changes in the environment (ter Braak, 1995).

Canonical variate analysis (CVA), a linear multivariate technique, was used to identify (1) major patterns of variation in the environmental data, (2) whether significant differences in water chemistry existed between sites grouped by vegetation type (tundra, forest-tundra, and forest), and (3) which environmental variables were significant in explaining the difference (ter Braak, 1995). CVA of the lake vegetation classes with forward selection (999 Monte Carlo permutations and a Bonferroni correction for multiple simultaneous tests) identified the environmental variables that separate the three lake types.

All ordinations were performed using CANOCO version 3.12 (ter Braak, 1988–1991). The chironomid percentage diagram was created using the stratigraphic analysis program TILIA (version 1.12) developed by E. C. Grimm (Illinois State Museum, Springfield).

Results

A total of 57 chironomid taxa and 1 *Chaoborus* mandible were identified in the 30 surface sediment samples. Of the 57 chironomid taxa identified, 28 had a relative abundance of $\geq 2\%$ in two or more lakes and were included in the calibration set. These 28 taxa accounted for between 75.9 and 100% (average 96.6%) of the total chironomid remains enumerated per sample.

The chironomid percentage diagram reveals some interesting patterns with respect to chironomid distribution across tree-line (Fig. 2). Orthoclaadiinae, such as *Paracladius*, *Hydrobaenus/Oliveridia*, *Abiskomyia*, and *Parakiefferiella nigra*, are restricted for the most part, to tundra lakes. Chironominae, such as *Cladoplema* and *Dicrotendipes* are found predominantly and consistently in forest-tundra or forest sites. Other Chironominae, such as *Microtendipes* and *Zalutschia zalutschicola*, are restricted to sites south of tree-line. Tree-line sharply delineates the distribution of *Corynocera* species; *C. ambigua* is found only in lakes south of tree-line, whereas *C. oliveri* is found mostly in tundra lakes. Also of note is the lack of Ceratopogonidae remains in the surficial sediment and the presence of only one *Chaoborus* mandible.

Redundancy analysis (RDA) using each environmental predictor individually and based on the covariance matrix of the square-root transformed species data, with 99 unrestricted Monte Carlo permutation tests identified eight environmental variables that have a significant relationship ($P \leq 0.05$) to the distribution of chironomids along the transect. The eight variables are POC, PON, Fe, Zn, lake depth, Secchi depth, and two vegetation classes, tundra and forest. RDA using these eight variables as the sole environmental variables provided eigenvalues of 0.15 for axis 1 and 0.12 for axis 2. Monte Carlo test (999 unrestricted permutations) indicated that both axes are significant ($P \leq 0.03$). RDA with POC, PON, Fe, Zn, lake depth, and Secchi depth as the environmental variables and with the vegetation classes, tundra and forest, entered passively, provided eigenvalues of 0.14 and 0.09 for axis 1 and axis 2, respectively. This suggests that the explanatory power of the six remaining environmental variables was not greatly reduced by eliminating the tundra and forest classification variables. The species-environment correlations for the first two axes were 0.78 and 0.81, respectively. Axis 1 and axis 2 accounted for 23.2% of the variance in the weighted averages of the chironomid data. RDA axis 1 accounted for approximately 60% of the variance that is explainable on the basis of both axis 1 and axis 2. Monte Carlo unrestricted permutation tests (999 permutations) indicated that both axes were significant

Chironomid Percentage Diagram
 Surface Samples (North-South Transect)
 Lower Lena River Region, Siberia

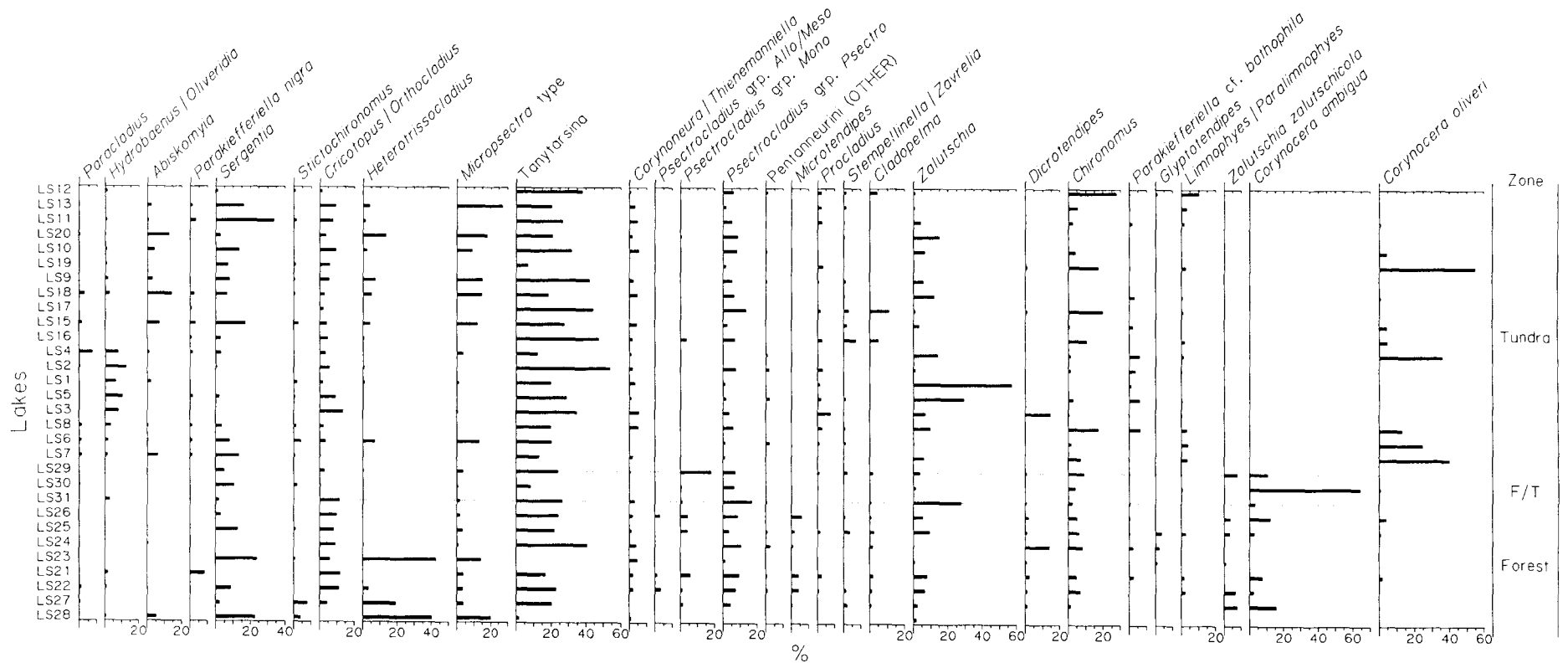


FIGURE 2. Chironomid percentage diagram representing the latitudinal distribution of the 28 chironomid taxa included in the ordination analyses. Northernmost lake at top (LS12), southernmost lake on the bottom (LS28). Psectrocladius is split into three groups: Psectrocladius subgenera *Allopsectrocladius*/*Mesopsectrocladius*, Psectrocladius subgenus *Monopsectrocladius*, and Psectrocladius subgenus *Psectrocladius* which are identified in the diagram as Psectrocladius grp. Allo/Meso, Psectrocladius grp. Mono, and Psectrocladius grp. Psectro, respectively.

TABLE 2

Weighted correlations of environmental variables and environmental ordination axes

	RDA	
	ENV.AX1	ENV.AX2
POC	0.76	0.58
PON	0.71	0.65
Fe	0.70	-0.12
Zn	0.52	0.49
Lake depth	-0.53	0.54
Secchi depth	-0.60	0.19

($P \leq 0.05$). POC is strongly correlated with axis 1, with lake depth and Secchi depth showing a strong negative correlation, and PON is most strongly correlated with axis 2 (Table 2).

The results of the RDA ordination based on 28 chironomid taxa, 6 active environmental variables, and 30 sites are depicted graphically in Figures 3a and 3b. The site-environment biplot suggests that tundra lakes are characterized by relatively low amounts of POC and PON, forest lakes tend to be deeper, and forest-tundra sites are marked by high levels of POC, PON, and Zn (Fig. 3a). Also worth noting is that the ordination clusters the tundra sites together in the lower half of the diagram, which indicates that Axis 1 captures a large proportion of the variation in the chironomid assemblages from tundra lakes. The species-environment biplot identifies three groups of taxa (Fig. 3b). The first group consists of taxa such as *Paracladius*, *Parakiefferiella* cf. *bathophila*, *Corynocera oliveri*, *Hydrobaenus/Oliveridia*, and *Parakiefferiella nigra*. The taxa in this group are found clustered together near the centroid for the tundra vegetation class and are associated with lakes with low levels of POC and PON. The second group consists of taxa that are positioned near the forest/tundra and forest centroids: *Microtendipes*, *Glyptotendipes*, *Psectrocladius* subgenera *Allopsectrocladius/Mesopsectrocladius*, *Psectrocladius* subgenus *Monopsectrocladius*, and *Zalutschia zalutschicola*. These taxa are clustered in the upper half of the diagram and are found in lakes with relatively high levels of POC, PON, and Zn. The third group of taxa appear to be responding to a lake depth gradient. Taxa such as *Heterotrissocladius* and *Micropsectra* tend to be common in deeper lakes, while taxa such as *Dicrotendipes*, *Stictochironomus*, *Limnophyes/Paralimnophyes*, *Procladius*, and *Tanytarsina* are more common in shallower lakes.

CVA of sites grouped on the basis of vegetation type revealed that significant differences in lake water chemistry exist between tundra and forest sites (Fig. 4). A Monte Carlo unrestricted permutation test (999 permutations) of the first axis suggested that it was significant ($P \leq 0.05$). Most of the tundra sites are located in the lower left quadrant of the ordination, while most of the forest sites are positioned in the upper right quadrant. However, it is clear from the large spread of points within the two clusters, i.e. the tundra and forest lakes, that water chemistry differs greatly within both these classes. CVA with forward selection identified four variables as significant ($P \leq 0.01$) in explaining the difference between the sites. In decreasing order of importance the variables are uncorrected chlorophyll *a*, lake depth, pH, and Sr. Tundra sites tend to be shallower and are associated with high concentrations of Sr, whereas forest sites were deeper and had higher pH levels.

Discussion

Earlier work has illustrated that chironomids respond, in part, to the summer temperature of surface lake water (Walker and Mathewes, 1989; Walker et al., 1991a, 1997; Wilson et al., 1993; Olander et al., 1997, 1999; Lotter et al., 1997). Most of the quantitative work relating chironomids to climate has been carried out in Maritime Canada, the northeastern U.S., the Swiss Alps, Fennoscandia, and Scotland. Studies relating the distribution of chironomids to the physical and chemical limnology of lakes in Russia is limited. This is the first attempt at quantifying the modern relationship between chironomids and climate at treeline in Russia.

The chironomid percentage diagram suggests that *Microtendipes*, *Dicrotendipes*, *Zalutschia zalutschicola*, *Psectrocladius* subgenera *Allopsectrocladius/Mesopsectrocladius*, and *Psectrocladius* subgenus *Monopsectrocladius* can be used as forest indicators, since their distribution is limited almost entirely to forested sites. Many littoral taxa, e.g., *Microtendipes* and *Dicrotendipes*, have limited distributions in arctic environments. In Canada, these taxa are found, for the most part, in lakes south of treeline with limited numbers occurring just north of treeline (Oliver and Roussel, 1983). The distribution of these taxa in northeast Siberia is similar to their distribution in Canada, with taxa such as *Dicrotendipes* found predominantly in forested regions and *Microtendipes* restricted entirely to sites south of treeline. This agrees with earlier work identifying *Microtendipes* and *Dicrotendipes* as thermophilous, littoral genera (Walker and Mathewes, 1989; Walker and MacDonald, 1995). The results from this study corroborate Walker and Mathewes's (1989) assertion that the distribution of some littoral chironomid taxa may provide valuable paleoclimate evidence that can be used to distinguish arctic environments from temperate environments. Walker and Mathewes (1989) identified *Psectrocladius* as a common constituent of low-elevation lakes in British Columbia. Our results indicate that *Psectrocladius* subgenera *Allopsectrocladius/Mesopsectrocladius* and *Psectrocladius* subgenus *Monopsectrocladius* are found mainly in forested lakes. This lends support to the suggestion that the distribution of chironomids along an altitudinal gradient is similar to the known distribution of chironomids along a latitudinal gradient (Walker and Mathewes, 1989).

Zalutschia zalutschicola, which is characteristic of acid, humic lakes (Walker and Paterson, 1983; Sæther, 1979; Olander et al., 1997), is found solely at forested sites. A detailed reconstruction of Holocene treeline movement and climate in this region, based on pollen, stomate, diatom, and chironomid evidence from a sediment core taken in this area, suggests that temperatures were higher between 10,000 yr BP and 5500 yr BP, and that *Larix* (larch) and *Picea* (spruce) were present farther north between 8000 and 3500 yr BP (Laing et al., 1999; Pisaric et al., 2000). *Zalutschia zalutschicola* was present only when trees, as indicated by the stomate and macrofossil evidence, were locally present (Pisaric et al., 2000). The appearance of *Z. zalutschicola* during this period may be a function of the changing water chemistry of the lake, which in turn may be attributable to the local presence of trees. This further substantiates the potential use of *Z. zalutschicola* as an indicator of forest.

Also of note in the percentage diagram is the sharp change in the distribution of *Corynocera* that occurs at treeline. Walker and Mathewes (1988) identified *Corynocera* nr. *ambigua* as a common constituent of cold, oligotrophic lakes, and Oliver and Roussel (1983) suggest that *Corynocera* is found predominantly in cold lakes and ponds. Wiederholm (1983) identifies *C. am-*

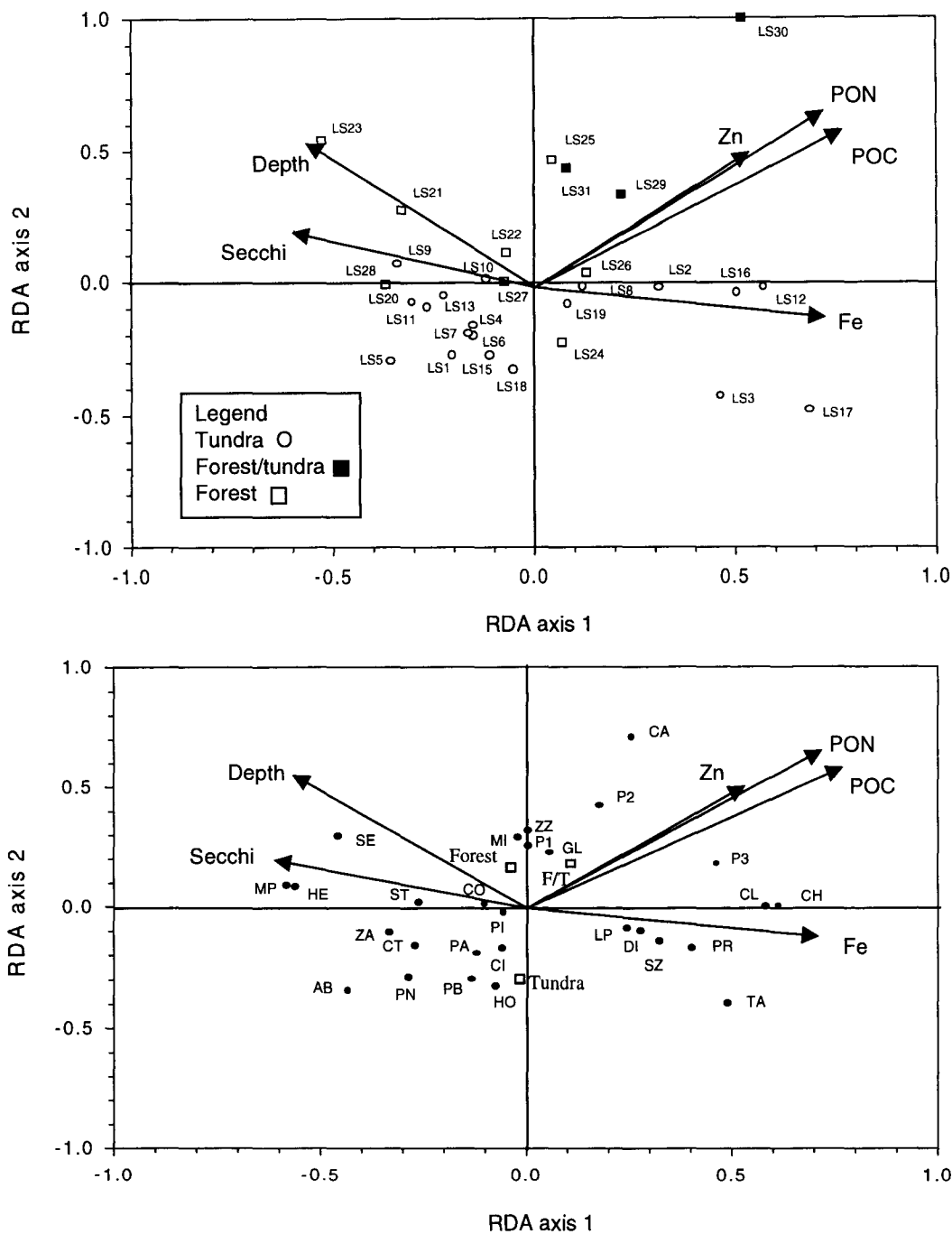


FIGURE 3. Ordination diagram based on redundancy analysis (RDA) of the 30 lake Lena River data set. (A, upper) Relationship between sites and the environmental variables. Sites are represented by symbols. Environmental variables that exert a significant influence on chironomid distribution are illustrated with arrows. (B, lower) Species scores. Quantitative environmental variables that exert significant influence on chironomid distribution are illustrated with arrows. Qualitative variables describing vegetation classes were included passively in the ordination analysis, are positioned based on their centroid value and are represented by open squares. Abbreviations for chironomid taxa: AB—Abiskomyia; CH—Chironomus; CL—Cladopelma; CA—Corynocera ambigua; CI—Corynocera oliveri; CT—Corynoneura/Thienemannella; CO—Cricotopus/Orthocladius; DI—Dicrotendipes; GL—Glyptotendipes; HE—Heterotrissocladius; HO—Hydrobaenus/Oliveridia; LP—Limnophyes/Paralimnophyes; MP—Micropsectra; MI—Microtendipes; PA—Paracletidius; PB—Parakiefferiella cf. bathophila; PN—Parakiefferiella nigra; PI—Pentaneurini (Other); P1—Psectrocladius subgenera Allopsectrocladius/Mesopsectrocladius; P2—Psectrocladius subgenus Monopsectrocladius; P3—Psectrocladius subgenus Psectrocladius; PR—Procladius; SE—Sergentia; SZ—Stempellinella/Zavrelia; ST—Stictochironomus; TA—Tanytarsina; ZA—Zalutschia; ZZ—Zalutschia zalutschicola.

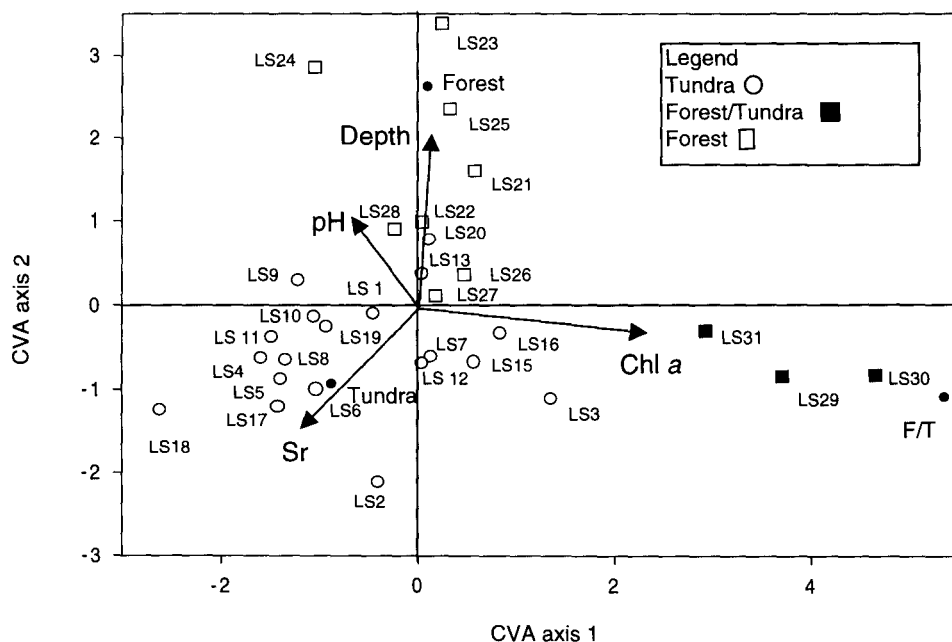


FIGURE 4. Canonical variates analysis (CVA) of the environmental variables in the 30 lake data set. Lakes grouped according to vegetation class. Lakes represented by symbols. Environmental variables with significant variation (Chl a—uncorrected, pH, Sr, Depth) between the lake types are illustrated as solid arrows.

bigua as a constituent of Palearctic and Nearctic lakes. Walker and Mathewes's (1988) *Corynocera* nr. *ambigua* is clearly a different species than the *C. ambigua* recorded in this study (Walker, pers. comm., 1998). The distribution of *C. ambigua* in this region reveals that it is found in warmer, forested sites, whereas *C. oliveri* dominates colder sites north of treeline. The distribution of *Corynocera*, which is clearly delineated by treeline, suggests that it may also provide valuable paleoclimatic information. The distribution of *Parakiefferiella nigra*, which was restricted almost entirely to tundra lakes, agrees with the assessment of Walker et al. (1992), who identified *Parakiefferiella nigra* as most abundant in cold, oligotrophic lakes.

Redundancy analysis (RDA) indicated that six environmental variables (POC, PON, Fe, Zn, lake depth, and Secchi depth) explained a significant proportion of the variation in the chironomid distributions, with POC strongly correlated with axis 1 and PON strongly correlated with axis 2 (Table 2). RDA is a canonical form of principal component analysis (PCA) that represents samples and species relationships in low dimensional space. The ordination axes are constrained to be linear combinations of the measured environmental variables which maximizes the niche separation of the taxa (ter Braak and Verdonschot, 1995; ter Braak and Prentice, 1988). The ordination diagrams (Fig. 3a, 3b) indicate that the tundra sites are shallower and associated with low levels of POC and PON and that the forest-tundra and the forest sites are deeper and have higher levels of POC and PON. Taxa such as *Cladopelma*, *C. ambigua*, *Chironomus*, *Z. zalutschicola*, *Psectrocladius* subgenera *Allopsectrocladius*/*Mesopsectrocladius*, and *Psectrocladius* subgenus *Monopsectrocladius* are found more commonly in forest-tundra and forest lakes. *Parakiefferiella nigra*, *Paracladius*, *Abiskomyia*, and the *Hydrobaenus*/*Oliveridia* group are found more commonly in tundra lakes. The ordination diagram indicates that the chironomids are responding to POC and PON gradients along this transect. This suggests that the chironomids are likely responding to the productivity of lakes, since POC and PON tend to be found at higher levels in productive lakes (Wetzel, 1975). Chironomids have long been used as bio-indicators of lake trophic status (Thienemann, 1921; Brundin, 1958). Brundin (1958) describes classes of temperature-stratified lakes on the basis of the dominant chi-

ronomid taxa present, e.g., *Heterotrissocladius subpilosus* lakes (ultra-oligotrophic) and *Chironomus plumosus* lakes (eutrophic).

Treeline serves as an important biogeographic boundary for the distribution of chironomids, delineating cold water taxa in northern tundra lakes from the temperate taxa found predominantly in lakes south of treeline. Earlier work has shown that summer surface lake water temperature is an important factor in controlling the distribution of chironomids (Walker and Mathewes, 1989; Walker et al., 1991a, 1997; Wilson et al., 1993; Olander et al., 1997; Lotter et al., 1997). However, surface lake-water temperature did not have a statistically significant effect on the distribution of chironomids in this study.

The lack of a significant relationship between chironomid distribution and surface water temperature is attributable, in part, to the direct and indirect effects of sampling a relatively small number of lakes for inclusion in the calibration set. When one is interested in modeling synoptic level differences in the distribution of aquatic organisms, the environmental gradient being studied should be broad enough to capture these differences. The lakes sampled in each vegetation zone were in close proximity of one another and as result did not span a broad environmental gradient. If a larger number of lakes were incorporated in the calibration set, a broader environmental gradient would be sampled and the influence of synoptic scale effects such as climate would be more apparent. Another factor that may have contributed to the negligible importance of surface lake-water temperature involves attempting to relate an environmental variable, measured at a single point in time and space, to species assemblages which represent an integrated sample with respect to time; the uppermost 1 cm of lake sediment represents approximately 5 to 10 yr of deposition. It is possible that unusual environmental conditions at the time of sampling may have skewed the values of important variables, especially physical variables such as surface lake-water temperature. Warmer than usual air temperatures (30°C) accompanied by strong winds resulted in convective mixing of water in the shallow tundra lakes during the field season. Consequently, the relationship between surface lake-water temperature and the cold water taxa found in tundra lakes may have been obscured. A solution to this problem may involve restricting sampling to lakes located near meteorological stations, or

using data loggers to record seasonal fluctuations in the environmental variables of interest.

Conclusion

It is clear from the ordination diagrams and the chironomid percentage diagram that treeline serves as an important biogeographic boundary with respect to the distribution of chironomids in northeast Siberia. Orthoclaadiinae are found more consistently and at higher relative abundances in lakes north of treeline, while Chironominae are more prevalent at sites south of treeline. Contrary to the results of most studies that detail the relationship between chironomids and lake-water temperature, this study found that surface lake-water temperature did not influence the distribution of chironomids in a significant manner. The differences in the chironomid distributions need to be further characterized by expanding the current calibration set. It is apparent that taxa indicative of forest in this region have been identified and, from a paleoecological standpoint, the distribution of these taxa may provide information relating to past movement of treeline.

Acknowledgments

We thank M. Pisaric for kindly sharing his unpublished data and for providing a map of the study area. We also thank various PACT members for help with the field work. We are grateful to Margaret Sharp and Elissa Cabatu for laboratory assistance; M. Hay, T. Laing, and K. Rühlund provided statistical help on an earlier version of this paper. We are especially thankful to H. J. B. Birks for assistance with the statistical analyses. This research was made possible by a NSERC research grant to L. C. C. and PACT funding. This is PACT contribution No. 24.

References Cited

- Brooks, S. J. and Birks, H. J. B., 2000: Chironomid-inferred late-glacial and early-Holocene mean July air temperatures for Kråkenes lake, western Norway. *Journal of Paleolimnology*, 23: 77–89.
- Brundin, L., 1958: The bottom faunistic lake type system and its application to the southern hemisphere. Moreover a theory of glacial erosion as a factor of productivity in lakes and oceans. *Verhandlungen Internationale Vereinigung für Theoretische und angewandte Limnologie*, 13: 288–297.
- Bryson, R. A., 1966: Air masses, streamlines, and the boreal forest. *Geographical Bulletin*, 8: 228–269.
- Cranston, P. S., 1995: Systematics. In Armitage, P. D., Cranston, P. S., and Pinder, L. C. (eds.), *The Chironomidae: The Biology and Ecology of Non-biting Midges*. London: Chapman and Hall, 31–61.
- Cwynar, L. C. and Levesque, A. J., 1995: Chironomid evidence for late-glacial climatic reversals in Maine. *Quaternary Research*, 43: 405–413.
- Duff, K. E., Laing, T. E., Smol, J. P., and Lean, D. R. S., 1998: Limnological characteristics of lakes located across arctic treeline in northern Russia. *Hydrobiologia*, 391: 205–222.
- Glew, J., 1991: Miniature gravity corer for recovering short sediment cores. *Journal of Paleolimnology*, 5: 285–287.
- Laing, T. E., Rühlund, K. M., and Smol, J. P., 1999: Past environmental and climatic changes related to treeline shifts inferred from fossil diatoms from a lake near the Lena River Delta, Siberia. *The Holocene*, 9: 547–557.
- Levesque, A. J., Mayle, F. E., Walker, I. R., and Cwynar, L. C., 1993: A previously unrecognized late-glacial cold event in eastern North America. *Nature*, 361: 623–626.
- Levesque, A. J., Cwynar, L. C., and Walker, I. R., 1994: A multi-proxy investigation of late glacial climate and vegetation change at Pine Ridge Pond, southwest New Brunswick, Canada. *Quaternary Research*, 42: 316–327.
- Levesque, A. J., Cwynar, L. C., and Walker, I. R., 1997: Exceptionally steep north-south gradients in lake temperatures during the last deglaciation. *Nature*, 385: 423–426.
- Lotter, A. F., Birks, H. J. B., Hofmann, W., and Marchetto, A., 1997: Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *Journal of Paleolimnology*, 18: 395–420.
- MacDonald, G. M., Edwards, T. W. D., Moser, K. A., Pienitz, R., and Smol, J. P., 1993: Rapid response of treeline vegetation and lakes to past climate warming. *Nature*, 361: 243–246.
- Markov, F. G. (ed.), 1970: *Geoloyiya SSSR* [Geology of the USSR]. Vol. 18—Western Yakutsk ASSR, Geological description, part 1, book 1. Moscow: Nedra. 535 pp.
- Miachkova, N. A., 1983: *The Climate of the USSR*. Moscow: Moscow University Press. (in Russian.)
- Olander, H., Birks, H. J. B., Korhola, A., and Blom, T., 1999: An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia. *The Holocene*, 9: 279–294.
- Olander, H., Korhola, A., and Blom, T., 1997: Surface sediment Chironomidae (Insecta: Diptera) distributions along an ecotonal transect in sub-arctic Fennoscandia: developing a tool for paleotemperature reconstructions. *Journal of Paleolimnology*, 18: 45–59.
- Oliver, D. R. and Roussel, M. E., 1983: The insects and arachnids of Canada, Part II: The genera of larval midges of Canada—Diptera: Chironomidae. *Agriculture Canada Publication*. 1746. 263 pp.
- Pienitz, R., Smol, J. P., and Birks, H. J. B., 1995: Assessment of freshwater diatoms as quantitative indicators of past climate change in the Yukon and Northwest Territories, Canada. *Journal of Paleolimnology*, 13: 21–49.
- Pisaric, M. F. J., MacDonald, G. M., Velichko, A. A., and Cwynar, L. C., 2000: The late-glacial and post-glacial vegetation history of the northwestern limits of Beringia, from pollen, stomates and tree stump evidence. *Quaternary Science Reviews*, in press.
- Rizzo, B. and Wiken, E., 1992: Assessing the sensitivity of Canada's ecosystems to climate change. *Climate Change*, 21: 37–55.
- Sæther, O. A., 1979: Chironomid communities as water quality indicators. *Holarctic Ecology*, 2: 65–74.
- Schlesinger, M. E. and Mitchell, J. F. B., 1987: Climate model calculations of the equilibrium climate response to increased carbon dioxide. *Review of Geophysics*, 25: 760–798.
- Smol, J. P., Cumming, B. F., Douglas, M. S. V., and Pienitz, R., 1995: Inferring past climatic changes in Canada using paleolimnological techniques. *Geoscience Canada*, 21(3): 113–118.
- ter Braak, C. J. F., 1988–1991: CANOCO—A FORTRAN program for canonical community ordination by [partial][detrended][canonical] correspondence analysis and redundancy analysis. Agricultural Mathematics Group DLO, Box 100, 6700 AC Wageningen, The Netherlands.
- ter Braak, C. J. F., 1995: Ordination. In Jongman, R. H. G., ter Braak, C. J. F., and van Tongeren, O. F. R. (eds.), *Data Analysis in Community and Landscape Ecology*. Cambridge: Cambridge University Press, 91–169.
- ter Braak, C. J. F. and Prentice, I. C., 1988: A theory of gradient analysis. *Advances in Ecological Research*, 18: 271–317.
- ter Braak, C. J. F. and Verdonschot, P. F. M., 1995: Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences*, 57: 255–289.
- Thienemann, A., 1921: Seetypen. *Die Naturwissenschaften*, 18: 643–646.
- Walker, I. R., 1987: Chironomidae (Diptera) in paleoecology. *Quaternary Science Reviews*, 6: 29–40.

- Walker, I. R., 1988: Late-Quaternary paleoecology of Chironomidae (Diptera: Insecta) from lake sediments in British Columbia. Ph.D. dissertation, Simon Fraser University. 204 pp.
- Walker, I. R., 1998: Personal communication. Department of Biology, Okanagan University College, 3333 College Way, Kelowna, British Columbia, Canada V1V 1V7.
- Walker, I. R. and MacDonald, G. M., 1995: Distributions of Chironomidae (Insecta: Diptera) and other freshwater midges with respect to treeline, Northwest Territories, Canada. *Arctic and Alpine Research*, 27: 258–263.
- Walker, I. R. and Mathewes, R. W., 1988: Late-Quaternary fossil Chironomidae (Diptera) from Hippa Lake, Queen Charlotte Islands, British Columbia, with special reference to *Corynocera* Zett. *Canadian Entomologist*, 120: 739–751.
- Walker, I. R. and Mathewes, R. W., 1989: Chironomidae (Diptera) remains in surficial lake sediments from the Canadian Cordillera: analysis of the fauna across an altitudinal gradient. *Journal of Paleolimnology*, 2: 61–80.
- Walker, I. R. and Paterson, C. G., 1983: Post-glacial chironomid succession in two small humic lakes in the New Brunswick–Nova Scotia (Canada) border area. *Freshwater Invertebrate Biology*, 2: 61–73.
- Walker, I. R., Smol, J. P., Engstrom, D. R., and Birks, H. J. B., 1991a: An assessment of Chironomidae as quantitative indicators of past climate change. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 975–987.
- Walker, I. R., Mott, R. J., and Smol, J. P., 1991b: Alleröd–Younger Dryas lake temperatures from midge fossils in Atlantic Canada. *Science*, 253: 1010–1012.
- Walker, I. R., Oliver, D. R., and Dillon, M. E., 1992: The larva and habitat of *Parakiefferiella nigra* Brundin (Diptera: Chironomidae). *Netherlands Journal of Aquatic Ecology*, 26: 527–531.
- Walker, I. R., Levesque, A. F., Cwynar, L. C., and Lotter, A. F., 1997: An expanded surface-water paleotemperature inference model for use with fossil midges in eastern Canada. *Journal of Paleolimnology*, 18: 165–178.
- Wetzel, R. G., 1975: *Limnology*. London: W. B. Saunders. 743 pp.
- Wiederholm, T. (ed.), 1983: Chironomidae of the Holarctic region. Keys and diagnoses. Part I—Larvae. *Entomologica Scandinavica Supplement*, 19: 457 pp.
- Wilson, S. E., Walker, I. R., Mott, R. J., and Smol, J. P., 1993: Climatic and limnological changes associated with the Younger Dryas in Atlantic Canada. *Climate Dynamics*, 8: 177–187.
- Zarkhidze, V. S., Fulton, R. J., Mudie, P. J., Piper, D. J. W., Musatov, E. E., Naryshkin, G. D., and Yashin, D. S. (compilers), 1991: *Circumpolar Map of Quaternary Deposits of the Arctic*. Geological Survey of Canada. Map 1818A, scale 1:6 000 000.

Ms submitted June 1997

Revised ms submitted December 1999

