ORIGINAL PAPER

Chironomid-based inference models for estimating mean July air temperature and water depth from lakes in Yakutia, northeastern Russia

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Abstract We investigated the subfossil chironomid fauna of 150 lakes situated in Yakutia, northeastern Russia. The objective of this study was to assess the relationship between chironomid assemblage composition and the environment and to develop chironomid inference models for quantifying past regional climate and environmental changes in this poorly investigated area of northern Russia. The environmental data and sediment samples for chironomid analysis were collected in 5 consecutive years, 2003–2007, from several regions of Yakutia. The lakes spanned wide latitudinal and longitudinal ranges and were distributed through several environmental zones (arctic tundra, typical tundra, steppe-tundra, boreal coniferous forest), but all were situated within the zone of continuous permafrost. Mean July temperature (T_{July}) varied from 3.4°C in the Laptev Sea region to 18.8°C in central Yakutia near Yakutsk. Water depth (WD) varied from 0.1 to 17.1 m. T_{July} and WD were identified as the strongest predictor variables explaining the chironomid communitiy composition and distribution of the taxa in our data set. Quantitative transfer functions were developed using two unimodal regression calibration techniques: simple weighted averaging (WA) and weighted averaging partial least squares (WA-PLS). The two-component T_{July} WA-PLS model had the best performance. It produced a strong coefficient of determination ($r^2_{boot} = 0.87$), root mean square error of prediction (RMSEP = 1.93), and max bias (max bias$_{boot}$ = 2.17). For WD, the one-component WA-PLS model had the best performance ($r^2_{boot} = 0.62$, RMSEP = 0.35, max bias$_{boot}$ = 0.47).

Introduction

The study of Arctic palaeoenvironmental records enables qualitative and quantitative estimations of past climate changes and provides a basis for prediction of future changes in the region (Andreev et al. 2004). The timing of Holocene climate events in the North Atlantic region is relatively well studied

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(Bond et al. 2001; Solignac et al. 2006). In contrast, there are few quantitative palaeoclimatic data for eastern Siberia, such that hypotheses regarding the timing and spatial coverage of important climate events, like Holocene Thermal Maximum remain untested. In addition, paleolimnological records from northern Eurasia mostly document environmental changes at low temporal resolution and are derived from pollen studies (Anderson et al. 2002; Andreev et al. 2004). Due to the relatively small magnitude of temperature changes throughout the Holocene, reconstructions based on a single variable must be interpreted with caution. Furthermore, current global climate warming can be challenging for the lakes and aquatic fauna of eastern Siberia since this region is among the most sensitive areas affected by extreme changes in climate (Smol et al. 2005).

Many studies have explored the potential of aquatic organisms, including chironomids (Order: Diptera, Family: Chironomidae), as Quaternary palaeoclimate indicators (Porinchu and Cwynar 2002; Dieffenbacher-Krall et al. 2007). Chironomid calibration data sets and inference models for reconstructing mean July temperature (Larocque et al. 2001), lake depth (Korhola et al. 2000), salinity (Eggermont et al. 2007) and lake production (Woodward and Shulmeister 2006), have been developed successfully for Western Europe (Olander et al. 1999; Brooks and Birks 2001), North America (Walker et al. 1997; Barley et al. 2006), Africa (Eggermont et al. 2007), New Zealand (Woodward and Shulmeister 2006) and Tasmania (Rees et al. 2008). But still no calibration data sets and inference models have been established for the Russian high latitudes, including Arctic Siberia.

It is known that most of the models have limited application outside of the regions where they have been developed. Differences in faunal composition between sites included in the calibration set and the studied site make data difficult to interpret and results are sometimes unreliable (Lotter et al. 1999). Attempts to apply a transfer function based on a northern Sweden calibration data set (Larocque et al. 2001) to chironomid records from the northern Russia: Nikolay Lake, northern Yakutia (Andreev et al. 2004) and Lake Lyadhej-To, northern Ural (Andreev et al. 2005), have shown that only 50–59.5% of the taxa from fossil lake sediment assemblages appear in the modern calibration data

set. The application also shows that reconstruction of the mean air temperature of the warmest month (T_{July}) before 10,650 cal. year BP and after 7,000 cal. year BP during the Holocene is problematic because of existing taxonomic incompatibility between the fossil and the training set assemblages (Andreev et al. 2005). Therefore, the necessity of a regional data set containing information on the composition, distribution and ecological preferences of the modern chironomid fauna of Russian north remains very high.

Until now, only two studies of chironomid ecology quantifying the influence of modern environmental conditions on midge distributions in northern Russia are known (Porinchu and Cwynar 2000; Nazarova et al. 2008). Both of them covered only short climatic gradients: $\Delta\ T_{air} = 1.6°C$ and $\Delta\ WD = 10\ m$ in Central Yakutian lakes (Nazarova et al. 2008); $\Delta\ T_{air} = 8.5°C$ and $\Delta\ WD = 9.85\ m$ in lower Lena Delta data set (Porinchu and Cwynar 2000). These were not sufficient for generating inference models for reconstructing temperature or other ecological parameters in Holocene.

We investigated subfossil chironomids from lakes and other periglacial waters of the permafrost zone in Yakutia, northeastern Russia. The region that spreads over 2,500 km from east to west and 2,000 km from north to south over different geographical zones: tundra at the Arctic Ocean coast, mountains in the east and south (up to 2,000–3,000 m a.s.l.) and taiga forests in the west (Tahtadzhan 1978). Nearly the whole territory of Yakutia is underlain by permafrost (Geocriology of USSR 1989). Due to a harsh environment and extreme difficulty in getting access to the lakes, only limited chironomid studies have been undertaken in this region. The existing studies focused on estimation of productivity of benthic communities (Karationis et al. 1956; Streletzkaja 1972; Ogay 1979; Salova 1993; Tjaptirgjanov et al. 1992) or solely on taxonomy or karyotaxonomy of chironomids (Zelentsov and Shilova 1996; Kiknadze et al. 1996; Shobanov et al. 2002).

The objective of this study is to assess the relationship between chironomid assemblage composition and their environment and to develop chironomid inference models for quantifying past regional climate and environmental changes in this poorly investigated area of northern Russia. We intend to address specific research questions such as: When did

temperature begin to increase in Yakutia, signalling the end of the last Ice Age? What is the variation in the timing, magnitude and spatial coverage of the Holocene Thermal Maximum across eastern Siberia? How has the hydrology of this region changed over the past millennium? These models will provide data independent of existing palaeoclimatic inferences, which are largely pollen based, and can be used in testing of hypotheses related to these and other questions.

Study area and study sites

Yakutia is located in the northeastern part of Russia (between 55°29′ and 76°46′ N and 105°32′ and 162°55′ E; Fig. 1). Periglacial landscape is dominated by tundra and taiga vegetation, deep-reaching frozen ground and widespread lake districts (Geocriology of USSR 1989). This part of Eurasia represents one of the Earth's most extreme semi-arid continental settings, whose role in the Arctic climate system so far is poorly understood (Kumke et al. 2007). It is characterized by pronounced seasonal gradients. The amplitude of temperature variations around the year sometimes exceeds 100°C. The coldest month is January, with average temperatures below −40°C and minimum temperatures less than

−60°C. Oymjakon (Region 7, Fig. 1) is the coldest place in the Northern Hemisphere, with the lowest winter temperatures reaching −71.2°C (Gavrilova 1998). Average July temperature varies from about 2–4°C on the New Siberian Islands in the Laptev Sea (Region 9, Fig. 1) to about 18–19°C in Central Yakutia near Yakutsk (Region 2, Fig. 1) with maximum summer temperatures ranging from 38 to 40°C. Annual temperatures in Yakutia average between −10 and −12°C (Gavrilova 1998). Annual precipitation ranges between 141 and 546 mm, which is less than annual evaporation in most areas (Gavrilova 1998). The driest area is the Central Yakutian lowland, where summer evaporation is four times higher than precipitation. Most of the lakes in Yakutia originate by thermokarst processes that cause extensive melting of the underlying permafrost and large, water-filled depressions result. This lakes are rather shallow (1–3 m) and characterized by specific thermal and chemical regimes, making them sensitive to recent climate changes. Other types of periglacial waters in patterned tundra landscapes are polygonal ponds and thaw lakes whose formation is directly connected to permafrost processes like ice wedge growth and initial thermokarst (Wetterich et al. 2008).

More information on regional features of Central Yakutia (Regions 1, 2, 4), northeastern Yakutia

Fig. 1 Location of the regions of investigation: *1* Vilujsk, central Yakutia (CY); *2* Yakutsk, CY; *3* Lena Delta, northern Yakutia (NY); *4* Lena-Amga-interfluve, CY; *5* Moma, northeastern Yakutia (NE); *6* Ust'-Aldansky ulus, CY; *7* Abisky ulus, NE; *8* Anabar, northwestern Yakutia (NW); *9* Bol'shoy Lyakhovsky Island, NY; *10* Yana-Indigirka lowland, NY
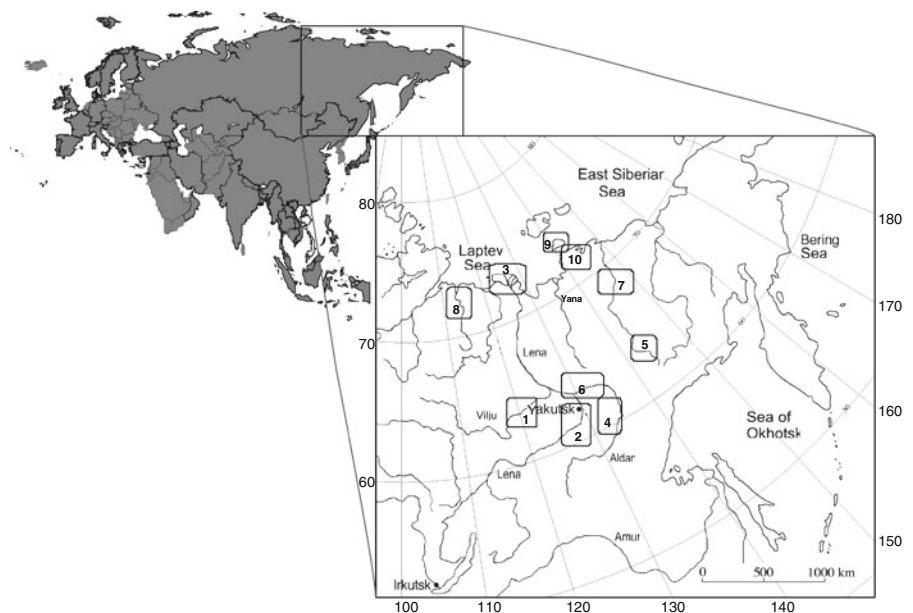
(Region 5) and northern Yakutia (Region 3) can be found in previous publications (Kumke et al. 2007; Nazarova et al. 2008; Wetterich et al. 2008).

Methods

Fieldwork and laboratory analyses

The environmental data and sediment samples for chironomid analysis were collected in 5 consecutive years, 2003–2007, from several regions of Yakutia (Fig. 1). The lakes span wide latitudinal and longitudinal ranges and are distributed through several environmental zones (arctic tundra, typical tundra, steppe-tundra, boreal coniferous forest), but all are situated within the zone of continuous permafrost. Most of the sampled lakes are small and shallow with little or no inflow. Lakes have a simple morphology and a single basin.

From each study lake, we collected water samples for chemical analyses about 50 cm beneath the water surface and surface sediment samples for chironomid analyses. Surface sediment samples were taken using a gravity corer. The water depths (WD) were measured using an echolot. Besides WD, Secchi depths was determined at each sampling site. Total hardness, alkalinity, acidity and oxygen were determined using titrimetric test kits (Aquamerck in 2002, Macherey–Nagel, Visocolor series in 2005 and 2007). Water temperature, pH, and electrical conductivity (EC) were quantified using a handheld multi-parameter instrument (WTW 330i, 340i) equipped with appropriate sensors (pH: SenTix 41; temperature and EC: Tetracon 325).

Water samples for ion analyses were passed through a cellulose-acetate filter (pore size 0.45 μm) in the field. Afterwards, samples for cation analyses were acidified with HNO_3 whereas samples for anion analysis and residue samples were stored in thermoboxes to ensure cool conditions. Upon return to the laboratory, the cation content of the water was analysed by Inductively Coupled Plasma-Optical Emission Spectrometry (ICP-OES, Perkin-Elmer Optima 3000 XL) while the anion content was determined by Ion Chromatography (IC, Dionex DX-320). The bicarbonate concentrations of the water were calculated from the alkalinity measurements in the field and additionally checked by

titration with 0.01 M HCl using an automatic titrator (Metrohm 794 Basic Titrino).

In each lake, 25–30 different chemical and environmental variables were measured. Twenty-two of them were available for all lakes in the present investigation and were included in statistical analyses (Supplementary material ESM 1).

Mean July air temperature (T_{July}) for each site was obtained from a climatic data set compiled by New et al. (2002), measured at 2 m above the ground in standard meteorological screens. Using these data, the mean air temperatures at each lake were estimated by spatial interpolation of elevation and distance from the coast. The New et al. (2002) data set uses climate normals from 1961 to 1990 to create a global climatic grid with a resolution of 10-min latitude/longitude. Some shortfalls are associated with this data set, for example, the relative coarse resolution of the climate data and the climate normals predate the collection of midge data and span a cold phase of the Arctic Oscillation (Overland and Wang 2005). However the global nature of the New et al. (2002) data set, its homogeneity and consistency make it more suitable for our purpose in comparison to the data that were possible to obtain from local meteorological stations. These data have gaps in observations and cover different time spans. As calculated, the Yakutian lakes included in this study are situated within a mean July temperature range between 3.4 and 18.8°C (Supplementary material ESM 1).

Chironomid analysis

Treatment of sediment samples for chironomid analysis followed standard techniques described in Brooks and Birks (2000). Subsamples of wet sediments were deflocculated in 10% KOH, heated to 70°C for up to 10 min, to which boiling water was added, and left to stand for up to another 20 min. Subsequently, the sediment was passed through stacked 125- and 95-μm sieves. Chironomid larval head capsules were picked out of a grooved Bogorov sorting tray using fine forceps under a stereomicroscope at 25–40× magnifications. To capture the maximum diversity of the chironomid population, 47–298 chironomid larval head capsules were extracted from each sample (median 77, mean 93). Several studies have demonstrated that this sample size is adequate for a reliable estimate of inferred temperature (Larocque 2001;

Quinlan and Smol 2001). Larval head capsules were mounted two at a time in Euparal or Hydromatrix, ventral side up, under a 6-mm diameter cover slip, with ten cover slips per microscope slide. In total, 13,948 chironomid head capsules were slide mounted and identified. Chironomids were identified to the highest taxonomic resolution possible with reference to Wiederholm (1983), Makarchenko and Makarchenko (1999) and Brooks et al. (2007).

Data analyses

Only taxa that have abundances of at least 2% in at least two lakes were retained for statistical analyses (Olander et al. 1999; Larocque et al. 2001). All taxon data were transformed to percent abundances, calculated as percentage of total identifiable midges (Brooks and Birks 2001; Barley et al. 2006) and were square root transformed prior to analysis. Environmental variables with skewed distributions (Secchi depth, EC, O_2, Cl^-, SO_4^-, NO_3^-, PO_4^{3-}, Fe^{2+}, Mg^{2+}, Mn^{2+}, Na^+, SiO_2) were transformed using $\ln(x + 1)$, where x was the given environmental variable. Skewness reflects the degree of asymmetry of a distribution around its mean. Normal distributions produce a skewness statistic of about zero. Values that exceeded 2 standard errors of skewness (regardless of sign) were identified as significantly skewed (Sokal and Rohlf 1995). Remaining parameters were left untransformed.

Several ordination techniques were applied to the chironomid and environmental data using CANOCO, version 4.5 (ter Braak and Šmilauer 2002a). Detrended Correspondence Analysis (DCA), detrended by segments, was performed on the chironomid data (rare taxa downweighted) to explore the main pattern of taxonomic variation among sites and to determine the lengths of the sampled environmental gradients, from which we decided whether unimodal or linear statistical techniques would be the most appropriate for the data analysis (Birks 1995). The gradient length of species scores wase relatively long. DCA axes 1 and 2 were 3.72 and 3.10 standard deviation units respectively, indicating that numerical methods based on a unimodal response model were the most appropriate to assess the variation structure of the chironomid assemblages (ter Braak 1995).

Variance inflation factors (VIF) were used to identify intercorrelated variables. Environmental variables with a VIF greater than 20 were eliminated, beginning with the variable with the largest inflation factor, until all remaining variables had values <20 (ter Braak and Šmilauer 2002b). By this process, latitude, longitude and altitude were redundant and subsequently eliminated from the analysis.

Relationships between chironomid distribution and environmental variables were assessed using Canonical Correspondence analysis (CCA). Manual forward selection was used to identify a subset of environmental variables that explained significant variations in the chironomid data. Statistical significance of each forward-selected variable was tested by a Monte Carlo permutation test (999 unrestricted permutation, $p \leq 0.05$) (ter Braak 1990). With the selection of each variable in forward selection, the relative importance of the remaining variables is re-evaluated. A variable will decrease in relative importance if it is correlated with the already selected variables. Thus, a variable that initially appears important might escape selection if it is correlated with already selected variables (Barley et al. 2006). In order to test the robustness of the significant variables identified by forward selection, a further run can be made with the second or third significant variable manually selected as the first. If the order of the remaining variables from this run is consistent with those from the initial run performed with forward selection, then these variables are robust. Significant variables ($p \leq 0.05$) were retained for further analysis.

Model development

Detrended CCA (DCCA), with mean T_{July}, WD as the only constraining variables was used to assess the suitability of these parameters for establishing inference models. The more important an environmental variable is in explaining variance in the species data, the larger the first constrained axis will be in comparison with the second unconstrained axis (ter Braak and Šmilauer 1998). The DCCA showed that T_{july} and WD had larger eigenvalues for DCCA axis 1 that were statistically different ($p \leq 0.05$) from the unconstrained DCA axis. This result suggests that inference models can be established using these data (Birks 1995). A relatively low $\lambda1/\lambda2$ would have indicated that a potential factor affecting the chironomid assemblage besides the explored variables had not been assessed.

Quantitative transfer functions were developed using two unimodal regression calibration techniques: simple weighted averaging (WA) and weighted averaging partial least squares (WA-PLS) (Barley et al. 2006; Woodward and Shulmeister 2006). Statistical performance of each inference model was evaluated by means of the bootstrapped coefficient of determination (r^2_{boot}); root mean squared error of prediction (RMSEP), a measure of random error in the model (Altman and Bland 1983); and mean and max bias$_{boot}$ (the tendency of the model to over- or underestimate along a particular portion of the gradient). Robust transfer functions were those that had the lowest RMSEP, high strong coefficient of determination (r^2_{boot}) and low mean and max bias$_{boot}$. The number of components included in the final model were selected based on reducing the RMSEP by at least 5% (Birks 1998).

Lakes were defined as outliers from the calibration set if absolute residual of the samples exceeded the standard deviation of T_{July} and WD in all trial models (Birks et al. 1990a). Although it is common to delete these outliers from the calibration sets, in our data set they were only deleted if their removal reduced the RMSEP by at least 5% (Quinlan and Smol 2001).

The optimum and tolerance for all chironomid taxa retained in the analyses were estimated by weighted averages and weighted standard deviations (Birks et al. 1990b). Optima of the taxa with N2 values of 5 or more in the modern data are likely to be reliably estimated whereas optima for the taxa with N2 less than 5 are likely to be poorly estimated because these taxa are rare in the modern data (Brooks and Birks 2001). The program C2 version 1.5 (Juggins 2007) was used to develop and assess transfer functions and estimate optima and tolerances. In order to describe the relationship of each taxon to main environmental variables, taxa response models were generated using generalized linear models (GLM), set to a quadratic degree and Poisson distribution, in the CanoDraw component of CANOCO 4.5 (ter Braak and Šmilauer 2002b).

Results

Chironomid taxa

A total of 147 taxa were identified, 105 of them had abundances of at least 2% in at least two lakes and were retained for analyses. The most widespread taxa were *Psectrocladius sordidellus*-type, *Paratanytarsus penicillatus*-type and *Chironomus anthracinus*-type. The complete list of chironomid taxa from Yakutian lakes can be found on the Russian Chironomid homepage (http://www.biosoil.ru/tendipes/catalog.htm).

The subfossil chironomid assemblages displayed a certain faunistic change corresponding to the main environmental parameters (T_{July}, WD Figs. 2 and 3) and revealed a pattern in the distribution of many taxa. The warmer part of the gradient was constituted mainly by different Chironomini taxa. Several taxa were restricted to the warmest part of the gradient: *Einfeldia pagana*-type, *Microchironomus*, *Einfeldia dissidens*-type, *Glyptotendipes pallens*-type, *Psectrocladius barbatipes*-type, *Labrundinia*.

The Yana-Indigirka lowland (Region 10) and Bol'shoy Lyakhovsky Island (Region 9) at the coast of the Dmitry Laptev Strait are the sites with the coldest T_{July} (3–4°C) in our data set. In total, 62 taxa were identified from this region. The most abundant taxa were *Paratanytarsus penicillatus*-type (mean abundance 22.4%; max abundance 45.9%), *Chironomus anthracinus*-type (mean 17.0%; max 34.7%), *Psectrocladius sordidellus* (mean 13.9%; max 35.0%) and cold-stenothermic *Orthocladius I* (mean 10.1%; max 37.37%). *Orthocladius I* was also found in slightly warmer conditions (Fig. 2) but reached its highest abundance in the coastal region of the Dmitry Laptev Strait.

There are several abundant (*Derotanypus, Tanytarsus glabrescens*) and rare (<1%, *Chaetocladius dentiforceps, Tvetenia sp., Chaetocladius B*) cold-stenothermic taxa that are restricted to the shallow lakes of regions 9 and 10. These taxa are correlated to lake depth, likely because most of the lakes in these regions are shallow. *Mesopsectrocladius, Paratendipes, Paracladius, Heterotrissocladius maeri 2* and *Heterotrissocladius grimshawi* are restricted to the deepest lakes in our data set (Fig. 3).

The generalized linear models demonstrate that, among the 104 non-rare taxa, included in both models, only twelve did not have a significant relationship to T_{July} or WD. Fifty three taxa demonstrated a highly significant relationship ($p < 0.001$) to T_{July}. Twenty-nine other taxa demonstrated a significant relationship ($p < 0.05$) to T_{July}. WD was highly significant ($p < 0.001$) for 34 taxa and significant ($p < 0.05$) for 28 taxa. *Ablabesmyia, Chironomus*
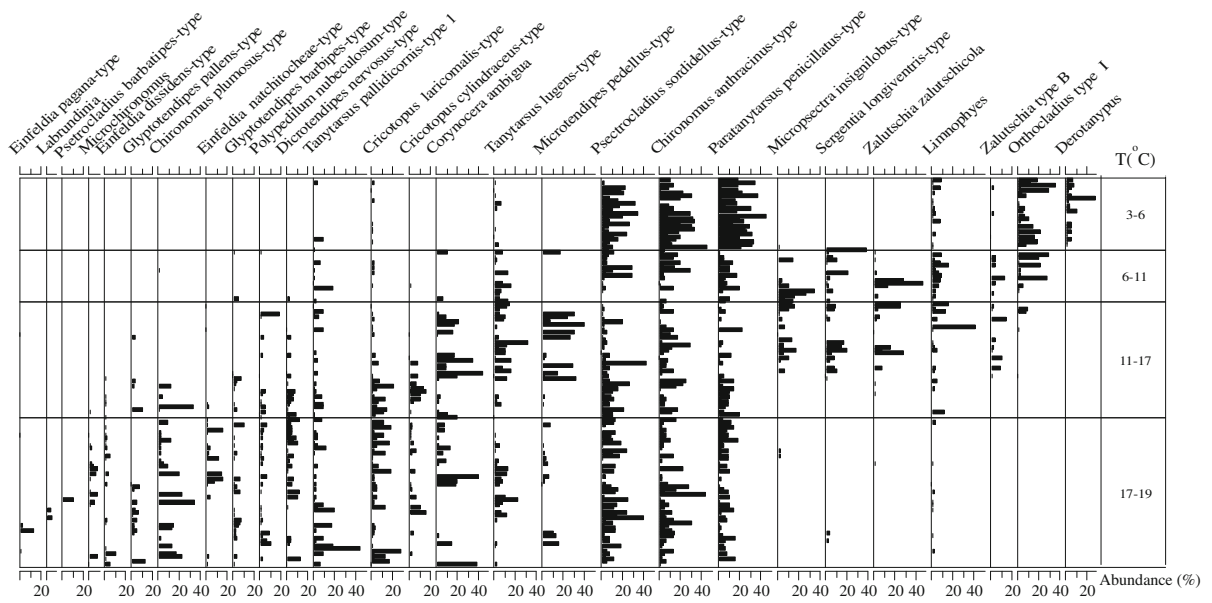
Fig. 2 Stratigraphic diagrams illustrating quantitative distribution of non-rare chironomid taxa in Yakutian lakes. Lakes are sorted by mean July air temperature (T_July; warm to cold). All taxon abundances are presented as % of the total identifiable chironomids. Rare taxa were omitted
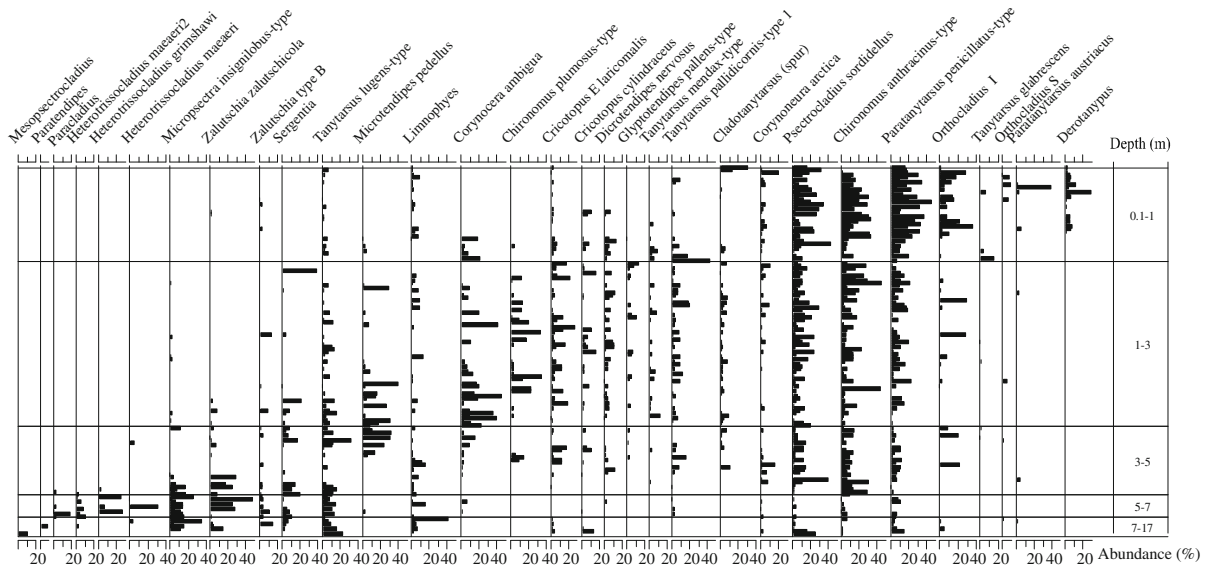

Fig. 3 Stratigraphic diagram illustrating quantitative distribution of non-rare chironomid taxa in Yakutian lakes. Lakes are sorted by water depth (WD; deep to shallow). All taxon abundances are presented as % of the total identifiable chironomids. Rare taxa were omitted

plumosus, Einfeldia pagana, Endochironomus albipennis, Oliveridia and *Procladius* had a highly significant ($p < 0.001$) relationship to T_July and did not respond to WD. For *Corynocera oliveri, Heterotrissocladius maeri 1, Parakiefferiella type A* and *Parakiefferiella nigra,* only WD was statistically highly significant ($p < 0.05$).

Taxon-specific optimum and tolerance estimates were generated using WA (Supplementary material ESM 2). The range of mean T_July optima varied from

3.74°C (*Derotanypus*) to 17.66°C (*Microchironomus*). *Derotanypus* also had the shallowest optimum for WD (0.4 m). *Abiskomyia* had the deepest optimum (5.51 m).

Ordination

The initial CCA with 19 environmental variables shows that the species-environment correlations for CCA axes 1 and 2 are 0.954 and 0.855 respectively. These correlations explain 53.9% of the variance in the chironomid-environmental relationship, suggesting that there is a strong relationship between the environmental variables and the chironomid taxa in the investigated lakes. Forward selection reveals 9 statistically significant ($p \leq 0.05$) explanatory variables: T_{July}, WD, EC, Secchi depth, pH, Mn, Ca, Cl and Fe (Table 1).

In order to see if the selected environmental variables retained their significance, a second CCA run was made with WD manually selected as the first variable. The second run produced the same list of significant explanatory variables in the same order, confirming the robustness of the selected variables. The importance of T_{July} was even higher than in the first run of forward selection (Table 1).

The CCA eigenvalues correspond to axes that are constrained by the nine selected environmental variables (Table 2). These four axes account for 19.2% of taxon variance and 83.9% of the taxon-environment relation. Eigenvalues for axes 1 (0.936) and 2 (0.841) are only slightly lower than those obtained for axis 1 and 2 from the CCA with all 19 environmental variables (0.954 and 0.855), suggesting that the nine selected variables explain the major gradients in the chironomid data.

Relationships between the significant environmental variables and the individual axes are examined through correlation coefficients, *t*-values and interset correlations (Supplementary material 3). Axis 1 of the CCA most strongly correlates with T_{July}, WD, Mn and pH. Their canonical coefficients are the highest in absolute value and their t-values are greater than 2.1, the critical value for a *t*-test at the 5% significance level (ter Braak and Šmilauer 2002b). Axis 2 correlates with WD and EC. Axis 3 correlates with pH and EC, and axis 4 shows correlation with WD and Secchi depths.

A CCA biplot of the sample scores shows that sites are grouped by geographical location (Fig. 4a). The bottom right group are tundra lakes situated in the coldest part of our data set: Bol'shoy Lyakhovsky Island and the Yana-Indigirka lowland (lakes

Table 1 Significant variables as identified by manual forward selection in CCA and the variance they explain. Run 1—CCA with all variables selected in the presented order; Run 2—CCA with WD selected first, and all other variables selected in the presented order

Run 1				Run 2			
Variable	Added with selection	*P* value estimates	*F* value	Variable	Added with selection	*P* value estimates	*F* value
T_{July}	0.26	0.001	12.22	WD	0.17	0.001	7.76
WD	0.18	0.001	9.07	T_{July}	0.27	0.001	13.65
EC	0.08	0.001	4.10	EC	0.08	0.001	4.10
Secchi depth	0.06	0.001	3.06	Secchi depth	0.06	0.001	3.06
pH	0.05	0.001	2.51	pH	0.05	0.001	2.51
Mn	0.04	0.001	2.05	Mn	0.04	0.001	2.05
Ca	0.04	0.001	2.11	Ca	0.04	0.001	2.11
Cl	0.04	0.001	1.85	Cl	0.04	0.001	1.85
Fe	0.03	0.001	1.77	Fe	0.03	0.001	1.77
Total variance explained	0.78				0.78		
Total variance	0.98				0.98		

Table 2 Eigenvalues, taxon environmental correlations, cumulative % variance and significance of the CCA axes

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.305	0.204	0.090	0.055
Taxon -environment correlations	0.936	0.841	0.733	0.728
Cumulative % variance of taxon data	9.0	15.0	17.6	19.2
Cumulative % variance of taxon-environment relation	39.1	65.3	76.8	83.9
Significance (probability) of axis	0.001	0.001	0.001	0.001
Sum of all unconstrained eigenvalues	3.395			
Sum of all canonical eigenvalues	0.728			

121–146, Regions 9, 10; Supplementary material ESM 1). The top right group of sites are lakes situated in northern Yakutia in forest tundra and taiga zones. Central Yakutian lakes that constitute the warmest part of the gradient are grouped in the left part of the biplot.

The distribution of chironomid taxa along the CCA axes reflects their ecological spectra (Fig. 4b). Taxa typical of cold and shallow lakes are located in the bottom right quadrant, with *Derotanypus* (36) as the coldest, stenothermic taxon. Taxa characteristic of cold, deep lakes are located in the top right quadrant. These include *Protanypus* (99), *Zalutschia zalutschicola* (142), *Parakiefferiella nigra* (85) (Supplementary material 2). The two left quadrants include taxa characteristic of warmer conditions of Central Yakutia that are subject to a negative water balance and, therefore, many of the lakes have high ion concentrations and consequently high EC.

Inference models

T_{July} and WD are the strongest predictor variables, explaining the most variance in the chiornomid distributional data (Table 1). The DCCA of T_{July} and chironomid data showed that T_{July} has a higher, statistically significant eigenvalue for DCCA axis 1 relative to the unconstrained DCA axis 2, with a gradient length (SD units) of 1.819, and ratio of $\lambda1/\lambda2$ of 1.273. For WD, the ratio of eigenvalues is high as well (0.824).

Transfer functions were generated using weighted-averaging (WA) with inverse and classical deshrinking techniques (Birks et al. 1990b) and weighted-averaging partial least squares technique (WA-PLS) (ter Braak and Juggins 1993). The results of the models were tested with bootstrapping methods. The model with the best predictive power (i.e. a combination of the lowest RMSEP, highest r^2_{boot}, lowest maximum bias and smallest number of useful components) was identified for each variable (Table 3).

T_{July} models with all 150 lakes yielded high coefficients of prediction ($r^2_{boot} = 0.75$–0.82), root mean squared errors of prediction (RMSEP = 2.3–2.9) and max biases$_{boot}$ (2.5–3.5). On examining the residuals, seven sites were found to be outliers: 34, 105, 107, 132, 133, 142 and were omitted from the training set. All of these lakes were shallow, of a small size, with a lot of macrophytes. In all of the outlying lakes, water temperature (7–22°C) was 2–4 times higher than the air temperature (3.5–11.2°C). The observed chironomid fauna was composed of the taxa which is generally found in enevironments with warmer air temperatures than those recorded at the study site. Therefore the temperature inferred from these assemblages will be warmer than expected. Chironomid assemblages in all of the outlying lakes were dominated by *Limnophyes* which is usually associated with very shallow water depths and littoral to terrestrial conditions (Brooks et al. 2007). The results suggest that these lakes might be ephemeral and undergo periodical drying.

Exclusion of outliers improved the predictive power of the model. The two-component WA-PLS model had the best performance. It produced a strong coefficient of determination ($r^2_{boot} = 0.87$), RMSEP (1.93°C) and max bias$_{boot}$ (2.17°C). The three-component model had a slightly better r^2_{boot} (0.88), but the RMSEP only improved by 1.5% (1.90°C) and the max bias$_{boot}$ increased by 20% (2.6°C). Hence the two-component WA-PLS model was retained as the best (Table 3; Fig. 5a, b).
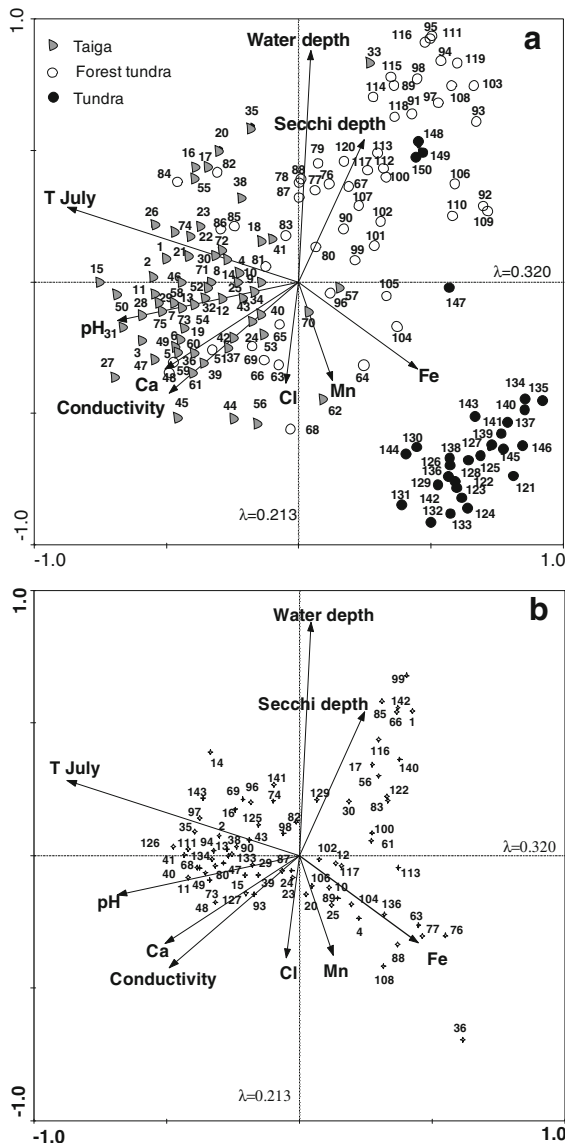
Fig. 4 Canonical correspondence analysis (CCA) illustrating the relationship between the most significant ecological factors and (**a**) chironomid communities of the investigated lakes (sample codes correspond with the sample codes in the model, given in the Supplementary material 1) and (**b**) non-rare chironomid taxa. Taxon codes correspond with full taxon names listed in the Supplementary material 2

Between WD models with all lakes included, the one-component WA-PLS model performed the best, having an r^2_{boot} of 0.53, RMSEP of 0.40 m and max bias$_{boot}$ of 1.77 m (Table 3).Two sites, 33 and 67, had high residuals and were rejected as outliers. These lakes are deep and stratified. Lake 33 is alkaline, with high conductivity, and lake 67 has a low oxygen

concentration. The fauna in both lakes are dominated by *Psectrocladius* taxa (*Psectrocladius sordidellus* and *Psectrocladius barbimanus*-type). Omission of these lakes improved the quality of the models and the one-component WA-PLS model was retained, having the best performance ($r^2_{boot} = 0.62$, RMSEP = 0.35 m, max bias$_{boot} = 0.47$ m) (Table 3; Fig. 5c, d).

Discussion

The extreme climate of the Siberian Arctic, with a short growing season and an extended period of ice-cover, limits the abundance of chironomids. However, our study, as well as previous investigations, has shown that the subfossil chironomid fauna of Yakutian lakes is rich and diverse. Most of the early investigations were from large rivers of the region, such as the Lena, Vilyuy, Amiga and their tributaries (Karationis et al. 1956; Salova 1993; Tjaptirgjanov et al. 1992). There are few examples of hydrobiological studies on Yakutian lakes (Streletzkaja 1972), but some earlier surveys have demonstrated similarities between the chironomid fauna of Yakutia and other parts of Siberia and the Far East (Karationis et al. 1956; Ogay 1979; Salova 1993; Kiknadze et al. 1996).

Investigation of chironomid fauna of the Ust-Lena reserve revealed 125 chironomid species, most of which were identified by imago. Among them, 20 new Russian species and one new genus were described (Zelentsov and Shilova 1996). Different species of the genus *Chironomus* played a dominant role in midge assemblages in most lakes. Early karyological and morphological analyses of the Chironomini tribe from central and southern parts of Yakutia (Kiknadze et al. 1996) have revealed 25 Chironominae species, 17 of which belong to the genus *Chironomus*. Even more *Chironomus* species were identified from latter studies conducted on Yakutian lakes (Kiknadze et al. 2002; Shobanov et al. 2002) and were redescribed from old collections (Sæther 2004). Due to the lack of taxonomically important features on fossilized head capsules, the *Chironomus* genus can only be divided into two taxa: *Chironomus anthracinus*-type and *Chironomus plumosus*-type (Brooks et al. 2007). In our study, these two taxa were found in nearly all Yakutian lakes, but *Chironomus anthracinus*-type had a

Table 3 Comparison of WA and WA-PLS models for reconstructing mean July air temperature (T_{July}) and water depth (WD). The best models are given in bold

	Model		r^2_{boot}	RMSEP (% RMSEP reduced from the previous component)	Max bias$_{boot}$
T_{July}	WA	Inverse	0.77	2.43	2.36
		Classical	0.77	2.56	1.37
	WA-PLS	1 component	0.79	2.38	2.62
		2 component	**0.87**	**1.93 (18.9)**	**2.17**
		3 component	0.88	1.90 (1.5)	2.61
		4 component	0.88	1.97	2.93
		5 component	0.87	2.10	3.19
WD	WA	Inverse	0.64	1.20	2.87
		Classical	0.65	1.29	4.77
	WA-PLS	**1 component**	**0.62**	**0.35**	**0.47**
		2 component	0.61	0.37	0.45
		3 component	0.59	0.39	0.42
		4 component	0.56	0.42	0.42
		5 component	0.55	0.46	0.42

Fig. 5 Plots showing observed versus predicted values, and residuals (inferred-observed) for T_{July} (**a**, **b**); WD (**c**, **d**) inference models
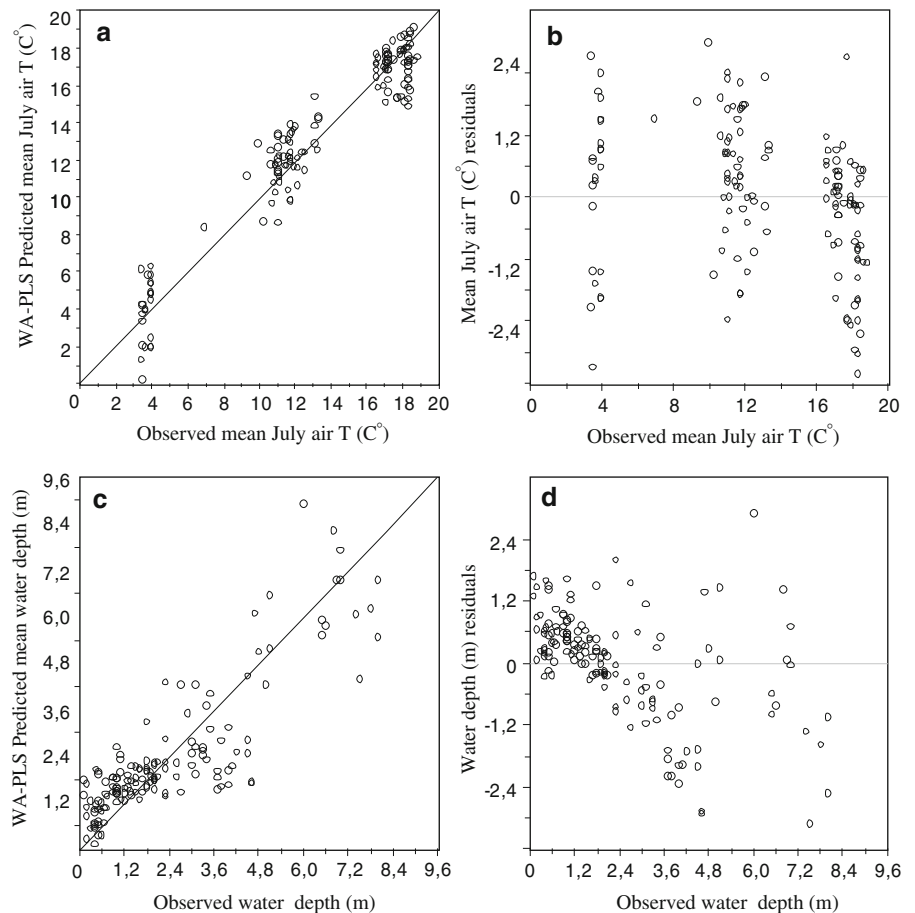
remarkably low T_{July} optimum and demonstrated a high level of ecological plasticity and tolerance within the investigated range of environmental conditions, reaffirming that it might be a taxonomically diverse group of species. *Chironomus plumosus*-type was found mainly in central Yakutia, the region with the highest T_{July} (15–18°C) in the data set and moderate to high EC. Although our study confirms that dividing the *Chironomus* genus into two groups is ecologically meaningful, much still has to be done to distinguish between the taxa within this speciose genus. This is especially important for the regions where *Chironomus* species are as abundant as in Yakutia.

Previous applied and taxonomically advanced studies emphasized the high species richness of chironomid fauna in Yakutia, but still very little is known about the ecology of chironomids in the region. The first quantitative estimations of the modern relationships between chironomid distributions and ecological conditions in Yakutia took place in the Lena Delta, northern Yakutia (Porinchu and Cwynar 2000) and central Yakutia (Nazarova et al. 2008). An investigation of the distribution of chironomids from a transect of 31 lakes spanning the treeline near the lower Lena Delta (north of Yakutia) has shown that chironomids are most likely responding to lake productivity (Porinchu and Cwynar 2000). In two other Yakutian data sets (Nazarova et al. 2008; the present study) lake productivity did not play a significant role in the composition of chironomid assemblages. This is mainly because concentrations of nutrients (i.e. phosphorus and nitrate) were generally low and most of the lakes could be classified as oligotrophic, apart from several lakes in Central Yakutia (Kumke et al. 2007).

The Central Yakutian data set (Nazarova et al. 2008) spanned a broader geographical area than the set of lakes in the study by Porinchu and Cwynar (2000). Many chemical and physical variables of the investigated lakes varied noticeably: Δ WD = 16.4 m, Δ EC = 2,910 μS/cm, Δ T_{water} = 14.6°C. But mean July temperature gradient was still too short to establish a chironomid air temperature inference model. Big differences in variability of mean July air and water temperatures (Δ T_{air} = 1.6°C and Δ T_{water} = 14.6°C in Central Yakutian lakes; Δ T_{air} = 15.4°C and Δ T_{water} = 26.8°C in all Yakutian lakes data set) additionally illustrate low reliability of water temperature as an ecologically important variable if

measurements are not done on a regular basis like, for example, in the investigation of low arctic West Greenland lakes (Brodersen and Anderson 2002).

Lakes sampled in the Lena Delta data set (Porinchu and Cwynar 2000) were in close proximity to one another and did not span a broad climate gradient. As a result, mean July air temperature was not identified as an important variable. If a larger number of lakes spanning a broader environmental gradient were incorporated into the calibration set, the influence of climate would be more apparent. In the Central Yakutian data set (Nazarova et al. 2008), mean July air temperature was among the most important factors driving chironomid distribution.

The present study clearly demonstrates that variable conditions in the physical environment explain significant amounts of variance in the chironomid species data (Table 1; Fig. 4). Among them climate dependant variables (T_{July} and WD) constituted 66% of the explainable variance. Strong correlation is found between concentrations of main ions, pH, EC, and chironomid distribution and is explained by generally negative water balance of Yakutian lakes.

The present data set spans broad environmental gradients for T_{July}, T_{water}, WD, EC, O_2 and other parameters (Supplementary material ESM 1). For T_{July} and WD we established inference models. The T_{July} model has a high r^2_{boot} value (0.87) when compared with other mean July inference models (Supplementary material ESM 4). It has an error estimate (RMSEP = 1.90°C) that constitutes 12.5% of the sampled gradient, which is among the best of all existing chironomid-based air temperature inference models to date. Models developed from midge training sets benefit not only from the number of sampled sites and the length of the gradient, but also from the evenness of the distribution of sampled lakes along that gradient. The last remains a problem in the present study. The majority of sampled lakes (82%) range in T_{July} from 9.3 to 18.8°C and 18% of the lakes range from 3.4 to 3.9°C. Additionally, errors generated by transfer functions are not absolute, they represent errors generated by the model and do not include potential errors in the source data themselves (accuracy of the training set environmental data, or the representativeness of a given midge assemblage in a single sample for the whole lake; Barley et al. 2006).

The significance of WD in the distribution and abundance of chironomid taxa has been found in

other chironomid training sets from different regions (Supplementary material ESM 4). Some studies have generated quantitative lake depth reconstructions using subfossil chironomids (Korhola et al. 2000) although problems do exist in using this approach (Hofmann 1998). Besides T_{July}, WD was the second important variable in our study. The inference model we developed for reconstructing this parameter in Yakutia is of special importance for this region. Lake level fluctuations have direct and indirect influences on the structure and conditions of the littoral and sublittoral habitats, causing changes in sediment composition and the zonation of littoral vegetation. A direct effect of WD on aquatic fauna occurs only in extreme situations, such as aquatic/terrestrial boundary (Hofmann 1998). Chironomid fauna clearly changes in its structure when WD declines. Strongest reaction can be expected from shallow lakes, where the fauna is mainly represented by littoral taxa and is subject to desiccation caused by a negative water balance. As the majority of Yakutian lakes are shallow and have thermokarst origins, the observed faunal response is especially strong and hydrological variation (water level fluctuations) appears to have a crucial role for the dynamics of major ions, nutrients and the ecology of aquatic organisms of Yakutian lakes.

Conclusion

Analysis of the relationships between chironomid distribution and environmental variables from the 150 Yakutian lakes, northeastern Russia, revealed 9 statistically significant explanatory variables: T_{July}, WD, EC, Secchi depth, pH, Mn, Ca, Cl, Fe. T_{July} and WD were identified as the strongest predictor variables in explaining the composition of the chironomid communities and the distribution of the taxa in our data set. Transfer functions were established using weighted-averaging (WA) and weighted-averaging partial least squares (WA-PLS) techniques. The two-component WA-PLS model had the best performance. It produced a strong coefficient of determination ($r^2_{boot} = 0.87$), RMSEP (1.93°C) and max bias$_{boot}$ (2.17°C). For WD the one-component WA-PLS model was retained, having the best performance ($r^2_{boot} = 0.62$, RMSEP = 0.35 m, max bias$_{boot} = 0.47$ m). Performance statistics of these

models suggest that they can be used for reconstructions of T_{July} and WD fluctuations in the area of investigation. However further improvements are still required. In order to strengthen the predictive power of the inference models, we will sample more lakes to fill the current gaps in T_{July} and WD gradients.

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