The distribution and abundance of chironomids in high-latitude Eurasian lakes with respect to temperature and continentality: development and application of new chironomid-based climate-inference models in northern Russia

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ABSTRACT

The large landmass of northern Russia has the potential to influence global climate through amplification of climate change. Reconstructing climate in this region over millennial timescales is crucial for understanding the processes that affect the global climate system. Chironomids, preserved in lake sediments, have the potential to produce high resolution, low error, quantitative summer air temperature reconstructions. Canonical correspondence analysis of modern surface sediments from high-latitude lakes, located in northern European Russia and central Siberia, suggests that mean July air temperature is the most significant variable explaining chironomid distribution and abundance. This strong relationship enabled the development of a chironomid-based mean July air temperature-inference model based on 81 lakes and 89 taxa which has a $r_{jack}^2 = 0.92$ and RMSEP = 0.89 °C. Comparison of taxon responses to July temperature between this Russian and existing Norwegian data-sets shows that the temperature optima of individual taxa were between 1 and 3 °C higher in the Russian data regardless of modelling technique. Reconstructions based on fossil assemblages from a Russian tundra lake core (VORK5) using a Norwegian chironomid-based inference model provide mean July air temperature estimates that are 1.0–2.7 °C colder than from the 81-lake Russian model and are also lower than the instrumental record from a nearby meteorological station. The Norwegian model also did not reconstruct decadal-scale fluctuations in temperature seen in the instrumental record. These observations suggest that chironomid-based inference models should only be applied to sediment cores which have similar climate regimes to the geographic area of the training set. In addition a 149 lake, 120 taxa chironomid-based continentality inference model was also developed from the modern Norwegian and Russian training sets. A 2-component WA-PLS model was the minimal adequate model with $r_{jack}^2 = 0.73$ and RMSEP = 9.9 using the Gorczynski continentality index. Comparison of reconstructed continentality indices from the tundra lake, VORK5, show close agreement with local instrumental records over the past 70 years and suggest that the model is reliable. Recent warming in the Arctic has been spatially and seasonally heterogeneous; in many areas warming is more pronounced in the spring and autumn leading to a lengthening of the summer, while summer temperatures have remained relatively stable. A continentality inference model has the potential to detect these seasonal changes in climate.

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1. Introduction

The Arctic is particularly sensitive to perturbations in climate; average arctic temperatures have increased at almost twice the global average rate over the past 100 years and this trend is predicted to continue over the twenty first century (IPCC, 2007). The

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large landmass of northern Eurasia plays an important role in global climate dynamics and in the amplification of climate change by positive feedbacks. For example, enhanced snow pack and permafrost melting increase freshwater discharge from Eurasian rivers and hence heat advection from low latitudes (Peterson et al., 2002; McClelland et al., 2004). The scarcity of observational and proxy records has meant that northern Russia is often poorly represented in the global perspective of climate trends and their effects on ecosystems (for example Smol et al., 2005). However, given its potential as an important driver of global climates, studies of northern Russia are important for understanding the timing and magnitude of past climate change and the mechanisms underlying those changes.

Instrumental climate records in arctic Russia are sparse, of short duration and often intermittent (Rigor et al., 2000). Meteorological stations are often located in the most benign habitats, for example at lower, warmer elevations, which are unrepresentative of the regional climate (Rawlins and Willmott, 2003). Satellite data have become available over recent decades and suggest mean annual temperatures have increased since AD 1981 in some areas of northern Russia whereas other regions have cooled (Comiso, 2003). In the absence of long-term instrumental or satellite data, palaeolimnological techniques can be used to determine whether these regional responses are a persistent feature of Holocene climate change across northern Russia or a short-term non-equilibrium response to present climate forcing.

Subfossil remains of chironomid midge larvae (Insecta, Diptera, Chironomidae) are abundant and well-preserved in lake sediments (Brooks, 2003). Chironomids are sensitive indicators of environmental conditions (Lindegaard, 1995). Their distribution is influenced by many factors including lake trophic status (Brundin, 1958; Wiederholm, 1983), water depth (Heiri, 2004) and oxygen stress (Quinlan and Smol, 2001b). However, the analysis of training sets of present-day assemblages and associated environmental data from lake surface sediments has shown mean summer temperature to be the dominant factor determining chironomid distribution and abundance over wide geographical regions (for example Walker et al., 1991; Brooks and Birks, 2001; Larocque et al., 2001; Barley et al., 2006). The strength of the relationship has enabled the development of quantitative chironomid-based temperature-inference models which have been used to reconstruct past temperatures in many areas of Western Europe and North America (see reviews in Brooks, 2006a,b; Barley et al., 2006), however relatively little data are available from Russia.

Quantitative chironomid-based reconstructions of palaeotemperature have been derived for northern Russia using European training sets. Solovieva et al. (2005) reconstructed mean July air temperatures in north-east European Russia using a chironomid–July air temperature-inference model based on a modern training set of 153 Norwegian lakes (Brooks and Birks, 2001 and unpublished data) supplemented with data from lakes within the study area. The chironomid–temperature-inference model developed for northern Sweden (Larocque et al., 2001) has also been used for temperature reconstructions in the Lena River Delta (Andreev et al., 2004), the Kola Peninsula (Ilyashuk et al., 2005) and Polar Urals (Andreev et al., 2005). However as more easterly sites are investigated the use of these European-based training sets may not be applicable due to the restricted geographic ranges of certain taxa and potential obstacles to dispersal. A number of important taxa in Russian subfossil assemblages, such as Constempellina and Mesocricotopus (Andreev et al., 2005), are absent or poorly represented in the European data-sets leading to poor analogues and potentially unreliable reconstructions for the Russian sequences. Additionally, the selective pressure resulting

from the extreme continental climate of central Eurasia, where annual temperatures vary from a winter minimum of $-71.2\,°C$ to a summer maximum of $38-40\,°C$ (Nazarova et al., 2008), may elicit physiological or behavioural adaptations in the chironomid fauna or changes in the faunal composition in response to the extreme environment.

The relationship between the distance from the open ocean, climate and vegetation was first recognised by von Humboldt (1827) and the use of continentality indices is well established in agriculture, geography, meteorology and ecology as a means of describing the climate regime, by quantifying the influence of the ocean on the climate. Plant species are often most sensitive to the effects of continentality along their northern limits and Giesecke et al. (2008) used the distribution of temperate tree species in Fennoscandia to develop a pollen-based continentality inference model. Although the influence of continentality has been less well studied in insects than plants a number of studies suggest it may also be important in insect distribution. For example, outbreaks of forest-defoliating insects are more frequent and intense in eastern than western Ukraine (Meshkova, 2002) as the greater continentality of eastern Ukraine results in a more rapid increase in spring air temperature which accelerates larval development. Over the Late Quaternary the climate regime of the Russian Arctic may have changed due to variations in solar radiation, changes in atmospheric circulation around ice sheets or changes in sea level. The latter is particularly important in Siberia where the coastline at the start of the Holocene was approximately 170 km north of its present location (Bauch et al., 2001) resulting in a more continental environment than at the same latitudes today. Increased continentality caused by eustatically lower sea level has been identified as a potential influence on Holocene tree-line dynamics within this region (MacDonald et al., 2000). Therefore the continentality of a location may have changed whilst the summer temperatures remained unaltered. As chironomids are abundant and widespread throughout the Russian arctic the potential for developing a chironomid-based continentality model was investigated in this study.

In this paper, the environmental factors which influence chironomid distribution and abundance in northern Russia are examined with the aim of developing chironomid-based inference models for climate reconstructions in this climatically sensitive region. The faunal composition and species responses are compared with data from Norway; this is a large data-set of modern chironomid distribution and abundance in surface sediments from 157 high-latitude lakes from Svalbard and mainland Norway (Brooks and Birks, 2001 and unpublished data). In theory combining the data-sets would improve the distribution of lakes along the July temperature gradient and the representation of taxa which are uncommon in the Norwegian fauna but is only justifiable if the chironomid assemblages, and responses to environmental variables, are similar.

There are three main aims:

1. To examine the environmental factors which influence chironomid distribution and abundance in northern Russia and assess whether these vary from the factors affecting the distribution and abundance of chironomids in Norway.
2. To determine whether the Norwegian and Russian training sets could be combined to develop a northern Eurasia training set to reconstruct past climates or whether the training sets should be limited to specific geographic areas.
3. To identify climate variables which have the potential for palaeoenvironmental reconstructions and develop chironomid-based inference models for climate reconstructions in north-east Russia.

2. Regional setting

Surface sediments were collected from 100 lakes in arctic and subarctic Russia between 61 and 72°N and 50–132°E (Fig. 1). The study sites span major biomes such as the boundaries between the continuous and the discontinuous permafrost zones and from boreal coniferous forests in the south to tundra vegetation in north. Most of the lakes are shallow (mean water depth 4.1 m) and remote. The lakes represent a range of different climatic conditions and whilst the physical and chemical characteristics, (e.g. pH, conductivity) are similar for the majority of the lakes, the underlying geology varies. Quaternary deposits are widely distributed throughout the Pechora, Lena, and Yenisey river valleys (Nalvikin, 1973). The lakes in the Komi Republic are formed on a sedimentary sequence of Palaeozoic carbonate and deep marine shale (Lindquist, 1999). The remaining lakes from the Putorana Plateau, the southern Lena Delta and near Vilyuysk, in central Yakutia, lie on the Siberian Traps, a large igneous province extruded in the late Permian ca 240–220 Myrs (Zolotukhin and Almukhamedov, 1988). The altitude of the lakes varies from 2 m to 805 m above sea level (a.s.l.). The mean July air temperature ranges from 8.8 to 18.9 °C and the mean annual precipitation from 240 to 640 mm (Table 1, Appendix A).

3. Material and methods

3.1. Site selection and field methods

Surface sediments were collected from 22 lakes in north-east European Russia between AD 1998 and 2001 as part of the EU-funded TUNDRA and SPICE projects as described by Solovieva et al. (2002, 2005) and Sarmaja-Korjonen et al. (2003), 21 lakes from the Lower Lena River as described by Porinchu and Cwynar (2000), and 36 lakes from Central Yakutia by Kumke et al. (2007). Additional surface samples were collected from 10 lakes at Igarka and on the Putorana Plateau in July 2006, 5 lakes near Vorkuta, north-east European Russia in April 2007 and 6 lakes in the Komi Republic, in August 2007. Chironomid assemblage and environmental data from Russia were compared to data from 157 Norwegian lakes from Svalbard and mainland Norway collected between AD 1995 and AD 1999 (Brooks and Birks, 2000, 2001 and unpublished data). The

Table 1
Summary of the environmental data for the 100 Russian lakes (complete data in Appendix A).

	Russian Lakes (100 lakes)				
	Minimum	Mean	Median	Maximum	Std dev
Latitude (N)	61.214	66.4951	67.1167	71.9015	
Longitude (E)	50.5029	99.4822	121.6545	131.2273	
Altitude (m a.s.l)	2	151	111	805	176
Distance to coast (km)	16	485	503	5000	566
pH	5.14	7.7	7.5	9.92	0.89
Conductivity ($\mu S\,cm^{-1}$)	2.4	160.1	58	2980	356.4
Water depth (m)	0.7	3.8	2.2	25	4.3
T_{july} (°C)	8.8	14.5	13.4	19	3.5
T_{jan} (°C)	−39.4	−29.7	−34.4	−15.5	8.8
Continentality Index	31	62	58	91	20
Mean annual precipitation (mm)	239	364	283	640	121
Cl^- ($\mu eq\,l^{-1}$)	2	141	30	5896	621
SO_4^{2-} ($\mu eq\,l^{-1}$)	1	46	25	760	90
Ca^{2+} ($\mu eq\,l^{-1}$)	18	518	344	1921	462
Mg^{2+} ($\mu eq\,l^{-1}$)	15	849	157	17270	2479
Na^+ ($\mu eq\,l^{-1}$)	10	579	84	25141	2666

sampling methods from all the locations are broadly similar to the following method. Sediment cores were collected from the deepest point of each lake using an 80 mm diameter HON-Kajak corer (Renberg, 1991) with a 0.5 m Perspex coring tube. Cores were extruded in the field at 0.25–1.0 cm intervals. For the palaeolimnological study a short core from an unnamed tundra lake, coded VORK5 (67.856972°N, 59.025722°E) (Fig. 1) was sub-sampled at 0.5 cm intervals from 0 to 5 cm depth, then at 1 cm intervals to 19 cm depth. Samples were stored in whirl-pak bags and kept cool and dark in the field prior to storage at 4 °C. The conductivity and pH of the lakes were measured in the field using portable meters.

3.2. Laboratory and desktop methods

3.2.1. Chironomid analyses

Sediment samples for subfossil chironomid analysis were prepared using standard methods. Wet sediments were deflocculated in 10% KOH at 70 °C for 5 min then left to stand in hot water for
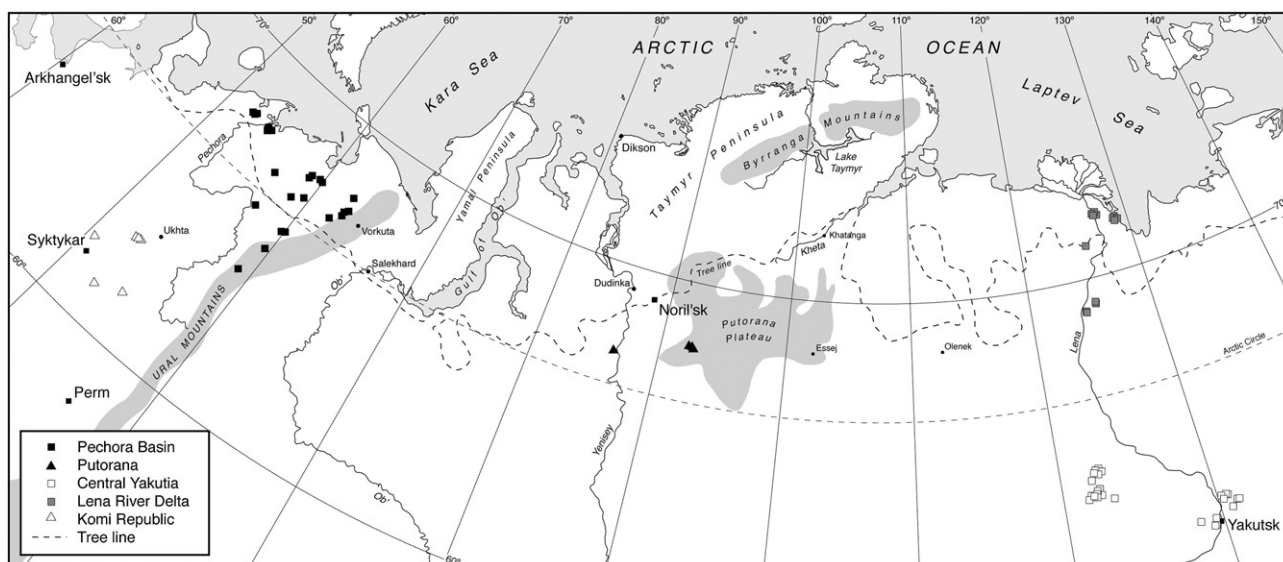
Fig. 1. Map of north-east Russia showing the location of the sampled lakes.

20 min (Brooks and Birks, 2000). Samples were washed through 212 and 90 μm sieves and the re-suspended sediment sorted in a grooved Bogorov tray using a dissecting microscope at ×25 magnification. Head capsules were separated and mounted in Euparal® mounting medium after progressive dehydration in 80% and 100% ethanol. Chironomids were identified with reference to Wiederholm (1983), Schmid (1993), Makarchenko and Makarchenko (1999), Rieradevall and Brooks (2001), Brooks et al. (2007) and the national Chironomidae collection at the Natural History Museum, London, UK. The subfossil assemblage was determined in the uppermost 0–1 cm for the training-set lakes. Between 50 and 560 head capsules were identified from the majority of surface sediments. However only 36–49 head capsules were isolated from seven high-latitude lakes, but the low taxonomic diversity of these assemblages suggests these abundances are acceptable for inclusion in the training set (Quinlan and Smol, 2001a). Between 51 and 194 head capsules were identified from the VORK5 sediment core.

3.2.2. Water chemistry analyses

Water samples from Putorana and north-east European Russia were analysed for major cations and anions at the Komi Science Centre, Syktyvkatr, Russia. Sodium (Na^+) and potassium (K^+) were determined by flame emission and magnesium (Mg^{2+}) and calcium (Ca^{2+}) by atomic absorption spectroscopy. Nitrate (NO_3^-) concentrations were determined colorimetrically by cadmium reduction. Sulphate (SO_4^{2-}) was analysed photomerically and chloride (Cl^-) determined by potentiomeric titration. Analysis of total phosphorus (P_{tot}) in unfiltered water followed Murphy and Riley (1962). Analyses of water samples from Central Yakutia are described by Kumke et al. (2007) and from the Lena Delta by Duff et al. (1998).

3.2.3. Chronology

The VORK5 sediment core was dated using ^{210}Pb and ^{137}Cs at the Bloomsbury Environmental Isotope Facility, UCL. Subsamples from the sediment cores were analysed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay using an ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector. ^{210}Pb was determined via its gamma emissions at 46.5 keV, and ^{226}Ra by the 295 keV and 352 keV gamma rays emitted by its daughter isotope ^{214}Pb following 3 weeks storage in sealed containers to allow radioactive equilibration. ^{137}Cs and ^{241}Am were measured by their emissions at 662 keV and 59.5 keV (Appleby et al., 1986). Radiometric dates were calculated using the CRS ^{210}Pb dating models (Appleby, 2001) and corrected by the AD 1963 depths determined from the ^{137}Cs and ^{241}Am stratigraphic records.

3.2.4. Modern climate and derivation of climate variables

Previous studies suggest that chironomid abundance and distribution are strongly influenced by mean air temperatures of the warmest summer month (e.g. Brooks, 2003, 2006b). Within the study area, July is the warmest month and mean July air temperature is included as an environmental variable. It was estimated for each lake by spatial interpolation of meteorological records from the three nearest weather stations, corrected for altitude. Sampling took place over a 9 year period in north-east European Russia and records from Syktyvkar suggest July air temperatures increased by 0.5 °C during the period 1977–2006 compared with 1968–97. Therefore mean July air temperatures were estimated from the instrumental data for the 30 years preceding sampling. Gorczynski (1920) derived a continentality index in which the annual difference in temperature is divided by the sine of latitude. Latitude is included as a parameter as solar radiation varies greatly with latitude. However near the equator, the sine of latitude approaches zero resulting in extremely high continentality indices, so later modifications of the index include the addition of constants (for example Grieser et al., 2006). The Grieser et al. (2006) modification of the Gorczynski's index (CI) was used in this study as it is easily computed and applicable to high latitudes:

$$CI = 1.7(A/\sin \phi) - 20.4$$

where A is the annual range of average monthly temperatures in °C and φ the latitude of the lake. Within the Russian study area the annual temperature range was based on mean July and January temperatures. CI values ranged from 0 to 29 in the Norwegian data-set and 31–91 in the 100-lake Russian data-set. Mean annual and summer (JJA) precipitation were estimated, for the 30-year period prior to sampling, from monthly observations in the Global Precipitation Climatology Centre (GPCC) database version 3, based on 0.5° grid intervals (Rudolf et al., 2003).

3.2.5. Numerical methods

The major cation and anion concentrations were strongly skewed and were therefore log transformed to normalise their distribution and to stabilise their variances (Birks, 1998). Detrended correspondence analysis (DCA), with detrending by segments, was used to assess the most appropriate numerical technique for further analyses of the chironomid data. Canonical correspondence analysis (CCA) was used to explore the relationship between the chironomid assemblages and the environmental variables. Several of the environmental variables were strongly correlated, and variables with the highest variance inflation factors (VIFs) were sequentially removed from the CCA until the VIFs were less than 20. Significant environmental variables were identified by forward selection and tested using a Monte Carlo permutation test (499 unrestricted permutations). Variables were considered significant if $p < 0.05$. CCAs were then run with each forward-selected variable individually. In this analysis, the ratio of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2) indicates the potential significance of the variable in explaining the cumulative variance in the taxon data. Inference models derived from explanatory variables with high ratios are therefore likely to have greater predictive power. Both DCA and CCA were performed using CANOCO 4.5 (ter Braak and Šmilauer, 2002) and in both analyses percentage species abundance data were square-root transformed and rare taxa down-weighted.

Two-way indicator species analysis (TWINSPAN) was undertaken using TWINSPAN for Windows version 2.3 (Hill and Šmilauer, 2005). TWINSPAN pseudospecies cut levels were set at 0, 2, 5, 10 and 20% to allow differences in taxon abundance to influence classification. The response of individual taxa to specific environmental variables was evaluated by fitting Huisman, Olff and Fresco (HOF) models (Oksanen and Minchin, 2002). These are a series of hierarchical models which are used to describe species responses to environmental variables. Temperature optima of taxa with more than 10 occurrences in both the Norwegian and Russian data-sets were estimated by Gaussian logit regression (GLR). Gaussian response curves were fitted to the data using the program GLR (Version 1.1, Juggins, 1994). The weighted averaging (WA) temperature optimum of each taxon was estimated using C2 (Juggins, 2005). General linear models (GLM) and general additive models (GAM), based on presence–absence data, were developed for taxa with more than 10 occurrences in both the Norwegian and Russian data-sets from the subset using R software (R Development Core Team, 2004). Models were fitted using the mgcv package for R, version 1.3–24 (Wood, 2007) and the statistical significance of additional parameters was tested using the Akiake Information Criterion (AIC) and Bayes Information Criterion (BIC).

The 100-lake Russian and 157-lake Norwegian data-sets were analysed to examine the relationship between the environmental

variables, including mean July air temperature and continentality, and chironomid distribution and abundance. Nineteen lakes with extremes of conductivity, pH or TP (total phosphorus) were removed to produce a second Russian 81-lake data-set with a more even distribution of lakes along the environmental gradients. A summary of the environmental variables in the 81-lake Russian data-set is given in Table 2 and the Norwegian data-set in Table 3. Chironomid-based temperature-inference models were developed from all three data-sets using weighted averaging (WA) and weighted averaging partial least squares (WA-PLS) methods (ter Braak and Looman, 1986; ter Braak and Juggins, 1993) using the program C2 version 1.4.3 (Juggins, 2005). The performance of the models and optimal number of components in the transfer function were assessed using leave-one-out, jack-knifed cross-validation.

To explore the relationship between chironomid distribution and continentality the 100-lake Russian data-set was combined with the Norwegian training set compiled by Brooks and Birks (2000, 2001) and unpublished data. Mean July air temperature is the main factor influencing the distribution of chironomids. Therefore to minimise the risk of wrongly attributing a temperature-driven response to continentality a subset of 149 lakes were selected from the Norwegian and Russian lakes. Lakes for inclusion were selected by stratified sampling; lakes were stratified by mean July temperature (at 0.5 °C intervals), then continentality at 1 CI intervals and finally by geographical location (longitude and latitude). If more that one lake from a similar location had the same mean July air temperature and same CI, a single representative lake was chosen by random selection. In the combined data-set the two extremes of the temperature gradient were restricted to a narrow range of continentality indices, the warmest lakes (18–18.9 °C) were located in central Yakutia with extremely high continentality and the coldest lakes (3.5–6.3 °C) in Svalbard have very low CIs of 10–15 so these two extremes were excluded from the continentality data-set by the stratification. The stratification process followed by selection of a single lake will minimise the risk of spatial autocorrelation and produce a data-set in which lakes with mean July air temperatures of 8–16 °C have a range of continentality indices (from 0 to 70). A summary of the environmental variables for this 149 Norwegian–Russian lake data-set is given in Table 4. A chironomid-based continentality inference model was produced and the performance evaluated as described for the temperature models.

Table 3
Summary of environmental data for the 157 Norwegian lakes.

	Norwegian lakes (157 lakes)				
	Minimum	Median	Mean	Maximum	Std dev
Latitude (N)	58.08	61.54	64.71	79.8	
Longitude (E)	5.005	8.862	11.27	31.038	
Altitude (m a.s.l)	5	260	484	1594	473
Distance to coast (km)	0	42	70	250	71
pH	4.66	6.37	6.4	8.4	0.7
Conductivity ($\mu S\,cm^{-1}$)	4	33	51.4	367	55.5
Water depth (m)	0.5	7	8.1	29	5.9
T_{july} (°C)	3.5	10.5	10.3	16	3.5
T_{jan} (°C)	−15.6	−7.6	−7.5	2.6	4.8
Continentality index	−1	12	14	29	7
Mean annual precipitation (mm)	390	796	995	2700	631
Cl^- ($\mu eq\,l^{-1}$)	2	67	147	2342	254
SO_4^{2-} ($\mu eq\,l^{-1}$)	7	46	72	1226	112
Ca^{2+} ($\mu eq\,l^{-1}$)	20	99	233	3004	355
Mg^{2+} ($\mu eq\,l^{-1}$)	7	44	95	930	140
Na^+ ($\mu eq\,l^{-1}$)	7	78	151	2127	224

4. Results

4.1. Species–environment relationships in the Russian lakes

Concentrations of sodium, magnesium and chloride ions, and consequently the conductivity of the lakes, are related to climatic parameters such as summer temperature, precipitation and continentality (Table 1, Appendix A). High concentrations of these ions and the associated high conductivity measured in lakes from Central Yakutia suggest their hydrology is strongly affected by the extreme continentality and negative hydrological balance of the region (Kumke et al., 2007). The extremes in electrical conductivity, chloride and sodium ions result primarily from extreme values in two lakes (Y1740 and Y1741). As expected, July air temperature is strongly negatively correlated to latitude (Pearson product-moment correlation coefficient, $r = -0.96$). Longitude is negatively correlated to January air temperatures, continentality index and annual and summer precipitation ($r > -0.77$). Annual precipitation shows strong positive correlation with summer precipitation ($r = 0.98$). Mg^{2+} and Na^+ ion concentrations and conductivity are

Table 2
Summary of environmental data for the subset of 81 Russian lakes.

	Russian lakes (81 lakes)				
	Minimum	Mean	Median	Maximum	Std dev
Latitude (N)	61.2140	67.2364	67.8667	71.9015	
Longitude (E)	50.5029	93.4761	92.2031	130.7293	
Altitude (m a.s.l)	2	154	102	805	195
Distance to coast (km)	16	408	259	5000	602
pH	5.1	7.5	7.4	9.5	0.8
Conductivity ($\mu S\,cm^{-1}$)	2.4	73.7	40.0	356.0	83.9
Water depth (m)	0.7	4.1	2.6	25.0	4.4
T_{july} (°C)	8.8	13.5	13.2	18.9	3.2
T_{jan} (°C)	−39.4	−27.8	−29.4	−15.5	8.8
Continentality Index	31	56	55	91	18
Mean annual precipitation (mm)	242	390	418	640	121
Cl^- ($\mu eq\,l^{-1}$)	2	43	27	288	49
SO_4^{2-} ($\mu eq\,l^{-1}$)	1	50	28	760	97
Ca^{2+} ($\mu eq\,l^{-1}$)	18	409	284	1587	379
Mg^{2+} ($\mu eq\,l^{-1}$)	15	261	123	1727	359
Na^+ ($\mu eq\,l^{-1}$)	10	115	52	813	156

Table 4
Summary of environmental data for the 149-lakes in the CI data-set.

	CI data-set lakes (149 lakes)				
	Minimum	Mean	Median	Maximum	Std dev
Latitude (N)	58.0767	64.7492	62.3833	71.9015	4.7694
Longitude (E)	5.0767	39.1043	11.4467	128.8992	42.1657
Altitude (m a.s.l)	2	345	206	1194	341
Distance to coast (km)	1	116	75	548	137
pH	4.66	6.64	6.68	9.10	0.75
Conductivity ($\mu S\,cm^{-1}$)	2.4	42.6	34.0	173.0	31.8
Water depth (m)	0.5	7.3	6.2	26.0	5.6
T_{july} (°C)	8.8	11.8	11.7	15.3	1.9
T_{jan} (°C)	−36.5	−13.2	−10.3	0.8	11.3
Continentality Index	0	26	20	70	19
Mean annual precipitation (mm)	269	921	570	2700	674
Cl^- ($\mu eq\,l^{-1}$)	2	96	41	677	127
SO_4^{2-} ($\mu eq\,l^{-1}$)	5	69	44	760	84
Ca^{2+} ($\mu eq\,l^{-1}$)	26	243	144	1585	258
Mg^{2+} ($\mu eq\,l^{-1}$)	11	93	62	609	97
Na^+ ($\mu eq\,l^{-1}$)	10	106	62	654	111

also positively correlated ($r > 0.78$). These relationships suggest there is considerable redundancy within the environmental variables.

In total, 132 chironomid taxa were identified from the surface sediment samples of the 100 Russian lakes. Of these 42 taxa occurred in 3 or fewer lakes. The majority of these rare taxa occur at less than 5% abundance in any lake, the exceptions are *Propsilocerus lacustris*-type with a maximum abundance of 7.4%, *Parachaetocladius* (6.2%), *Paralauterborniella* (6.7%) and *Propsilocerus jacuticus*-type (6.5%). Whilst none of the taxa occurred in all the lakes, the most common are *Psectrocladius sordidellus*-type which occurred in 87% of the lakes, *Procladius* (77%), *Tanytarsus lugens*-type (75%), *Cladotanytarsus mancus*-type (71%) and *Chironomus anthracinus*-type (66%). *Hydrobaenus conformis*-type, *Corynocera oliveri*-type, *Zalutschia* type B and *Abiskomyia* are predominately associated with mean July air temperatures of less than 12 °C (Fig. 2). *Chironomus plumosus*-type, *Paratanytarsus penicillatus*-type, *Glyptotendipes pallens*-type and *Cricotopus laricomalis*-type are more abundant in, and *Einfeldia* restricted to, lakes with July air temperatures greater than 16 °C.

Detrended correspondence analysis (DCA) of the species data produces an axis 1 gradient length of 3.78 standard deviation units, with an eigenvalue of 0.468, suggesting that unimodal-based numerical methods are most appropriate for further analysis (Birks, 1998). Canonical correspondence analysis (CCA) was undertaken on the 100-lake data-set with 18 environmental variables. Forward selection, using Monte Carlo permutation tests with 499 unrestricted permutations, indicates that six environmental variables (mean July air temperature, continentality, mean annual precipitation, tundra vegetation, water depth and Ca^{2+} concentrations) explain significant proportions ($p < 0.05$) of the explained variance (Fig. 3a, Table 5). The six selected variables were then used as single variables in a set of CCAs. The chironomid assemblages are most strongly correlated with mean July air temperature and continentality which give eigenvalue ratios of 1.169 ($\lambda_1/\lambda_2 = 0.374/0.320$) and 0.730 ($\lambda_1/\lambda_2 = 0.267/0.366$), respectively. These high

ratios indicate that these variables may be suitable for the development of inference models.

Fig. 3b presents correlation biplots of the CCA ordination based on 100 lakes, 132 taxa, and 6 significant environmental variables. The CCA results suggest *Zalutschia zalutschicola*-type and *Limnophyes* are closely associated with deep lakes and high mean annual precipitation (Fig. 3b). *Zalutschia* (Moller Pillot and Buskens, 1990) and some species of *Limnophyes* (Brodin, 1986) are associated with aquatic macrophytes. The majority of Russian lakes are on gently undulating tundra, so increasing precipitation may result in increased water depth and lake area, thereby increasing the size of the littoral zone and the area available for macrophyte growth. *Limnophyes* typically occurs in very shallow water (Kansanen, 1985; Hofmann, 1998), Massaferro and Brooks (2002) suggested that high abundances, in a sediment core from southern Chile, were associated with periods of low lake levels resulting from a decline in precipitation. The terrain in Chile is mountainous with steep-sided, tectonically controlled valleys. Therefore the impact of changing precipitation on water depth and the size of the littoral zone may depend on lake morphometry and the surrounding topography. From the CCA (Fig. 3b) it is difficult to distinguish if individual taxa are responding to mean July air temperatures and/or continentality as taxa such as *Einfeldia*, *C. plumosus*-type and *C. laricomalis*-type are most abundant in the Yakutian lakes with the warmest July air temperatures and most extreme continentality.

4.2. Comparisons of the Russian and Norwegian assemblages

The Norwegian training set comprises 157 lakes from Svalbard and mainland Norway. Fewer lakes were sampled in Russia (100 lakes) due to economic and logistic constraints. Potentially combining the data-sets could improve the representation of chironomid assemblages and individual taxa along the environmental gradients. But this would only be appropriate if the composition of the chironomid assemblages and responses of
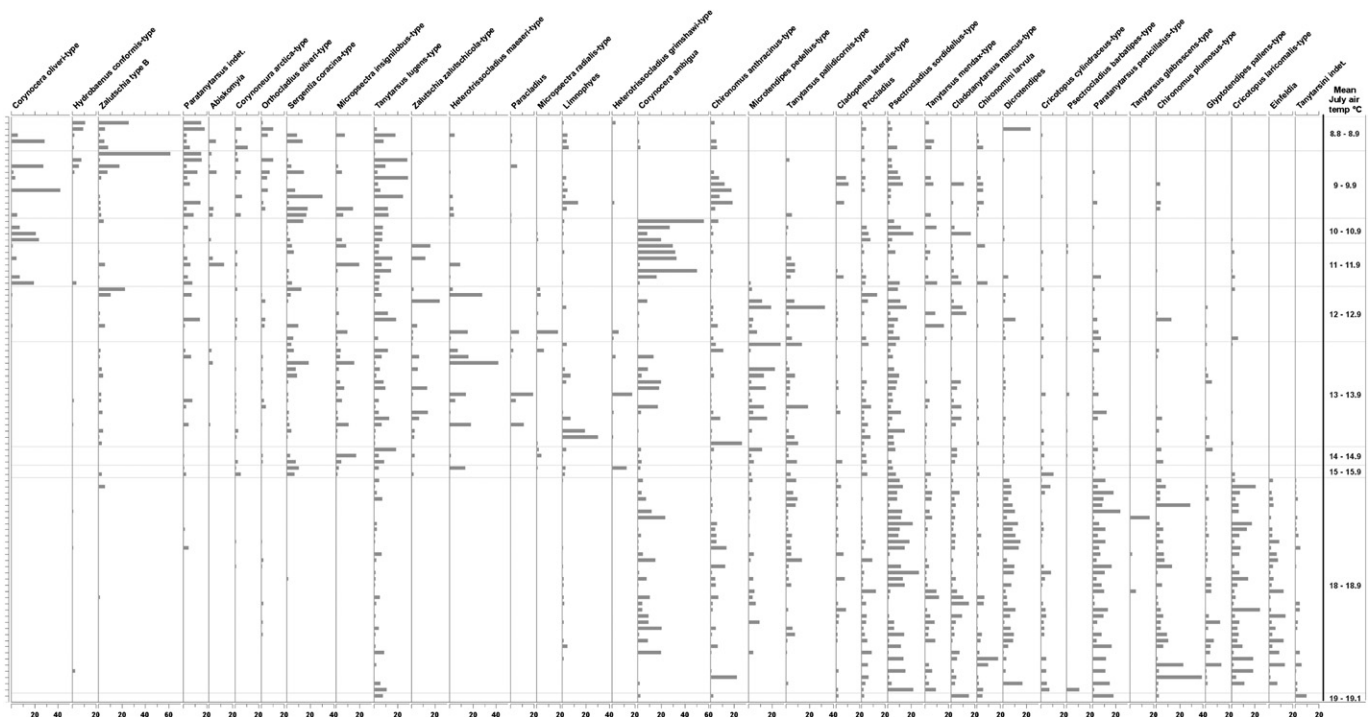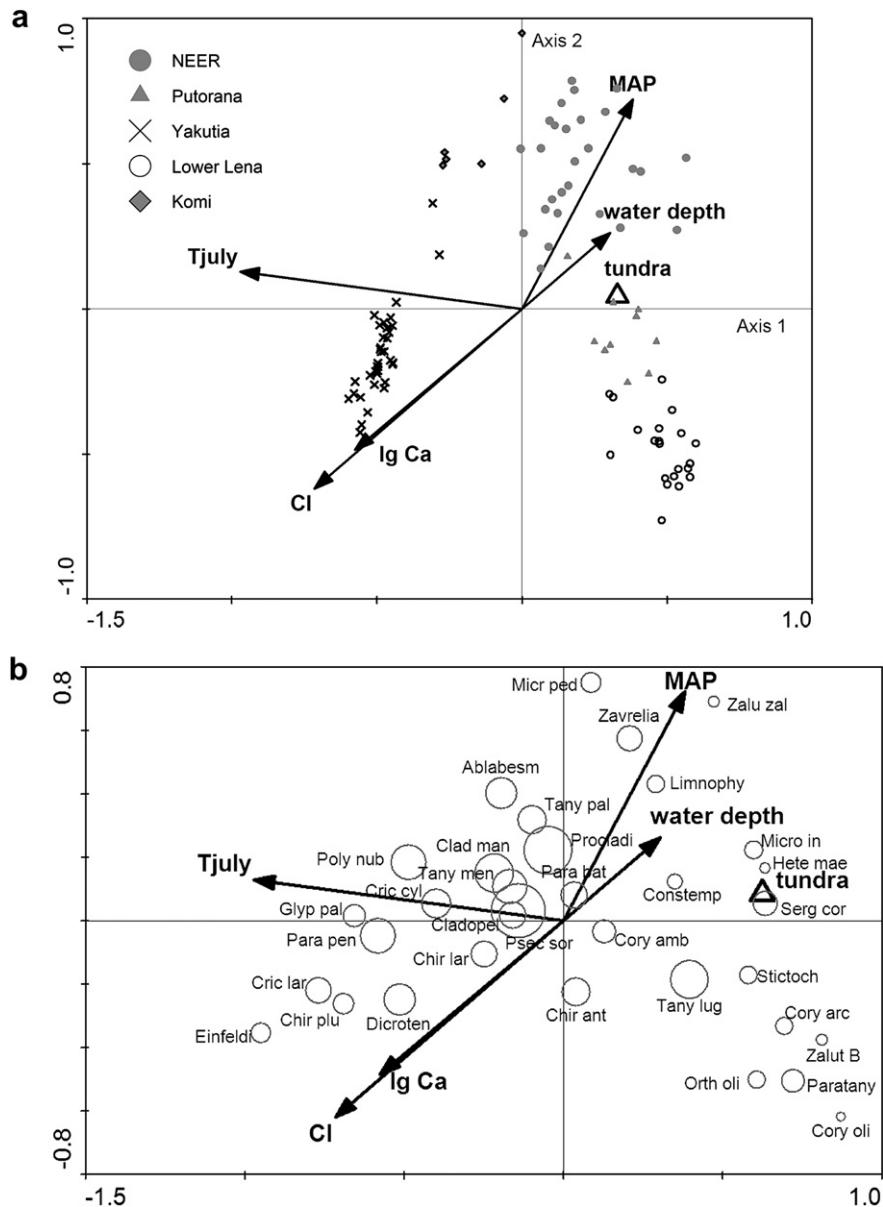

Fig. 2. Russian chironomid data-set ordered by mean July air temperature with the coldest lake at the top and the warmest at the bottom. Chironomids are shown as percentage abundance, for all taxa with abundances greater than 10% (100 lakes).

Fig. 3. CCA biplots of (a) 100 Russian lakes and significant environmental variables (black crosses: Yakutia, black diamonds; Komi Republic, grey filled circles; Pechora, grey triangles; Putoran, black unfilled circles Lena River) and (b) common taxa and significant environmental variables (circle size proportional to N2). (Abbreviations: T_{july}; mean July air temperature, CI; continentality index, MAP; mean annual precipitation, tundra; tundra vegetation and lg Ca; log of calcium ion concentrations).

Table 5
Significant environmental variables identified by forward selection in CCA of 100 Russian lakes and the variance they explain.

Variable	Variance explained	% total variance explained	Significance level
Mean July air temperature (T_{july})	0.37	43.0	$p < 0.002$
Continentality (CI)	0.16	18.6	$p < 0.002$
Mean annual precipitation (MAP)	0.09	10.5	$p < 0.002$
Tundra vegetation (tundra)	0.08	9.3	$p < 0.004$
Water depth	0.08	9.3	$p < 0.006$
Log Ca^{2+} conc (lg Ca)	0.08	9.3	$p < 0.002$
Total variance explained	0.86		
Total variance	3.99		

individual taxa are similar in the two geographic regions. The fauna from Birgervatnet, one of the Svalbard lakes, is composed of a single taxon *Hydrobaenus lugubris*-type so this lake was deleted from the Norwegian data-set reducing the gradient length of the first DCA axis from 6.6 to 4.4 SD units in the Norwegian set.

In compiling the Norwegian data-set, lakes were carefully selected to maximise the July temperature gradient and provide an even distribution of lakes over that gradient whilst minimising variation in the other parameters (Brooks and Birks, 2000). The standard deviations of variables such as pH, conductivity, and major cations are, therefore, lower in the Norwegian data-set compared to the Russian data (Table 3) as primarily naturally acid or circum-neutral, clear-water lakes were selected. However the maxima and standard deviation of altitude and annual precipitation are greater in the Norwegian data-set. These variables are spatially correlated as the main mountain range in Norway runs along the coast which results in high altitude lakes receiving greater orographic precipitation.

In total, 142 chironomid taxa or morphotypes were identified in surface sediments from the 156 Norwegian lakes. Some taxa identified in the Russian surface sediments, such as *Constempellina brevicosta* and *Einfeldia*, are not found in the sampled Norwegian lakes and other taxa including *Diamesa aberrata*-type are found in the Norwegian lakes only. Taxa recorded in both Norway and Russia, or the two data-sets individually, are listed in Appendix B. Several taxa found only in the Norwegian lakes are associated with springs, streams or running water; for example *Krenosmittia* (Schmid, 1993), *Rheotanytarsus* (Pinder and Reiss, 1983), *Rheocricotopus* spp. (Cranston et al., 1983) and *Parochlus* (Brundin, 1983). Their occurrence may reflect the greater importance of surface inflow into the Norwegian lakes due to the high precipitation and mountainous terrain compared to the Russian lakes. Many of the common morphotypes, such as *P. sordidellus*-type *T. lugens*-type, *Procladius* and *C. anthracinus*-type, appear to be widespread throughout Norway and Russia. The taxa may either have a cosmopolitan distribution due to wide environmental tolerances or the species composition, and therefore possibly the temperature optima of the morphotypes may vary between geographical regions, indicating the existence of distinct regional morphotypes.

Canonical correspondence analysis (CCA), with forward selection, suggest there is a relationship between chironomid distribution and abundance in the Norwegian lakes and July air temperature (not shown) with distance to the coast, chloride ion concentrations, and continentality also being important environmental variables. Chironomid distribution and abundance, in the combined Norwegian–Russian data-set, show strongest relationships with mean July air temperature and continentality (Fig. 4, Table 6) giving eigenvalue ratios in constrained CCA of 0.783 ($\lambda_1/\lambda_2 = 0.311/0.397$) for mean July air temperature and 0.479 ($\lambda_1/\lambda_2 = 0.231/0.482$) for continentality. July air temperature and continentality explain similar percentages of the variance in the chironomid data in both the Russian and combined data-sets, approximately 40–43% attributed to July air temperature and 19–24% to continentality.
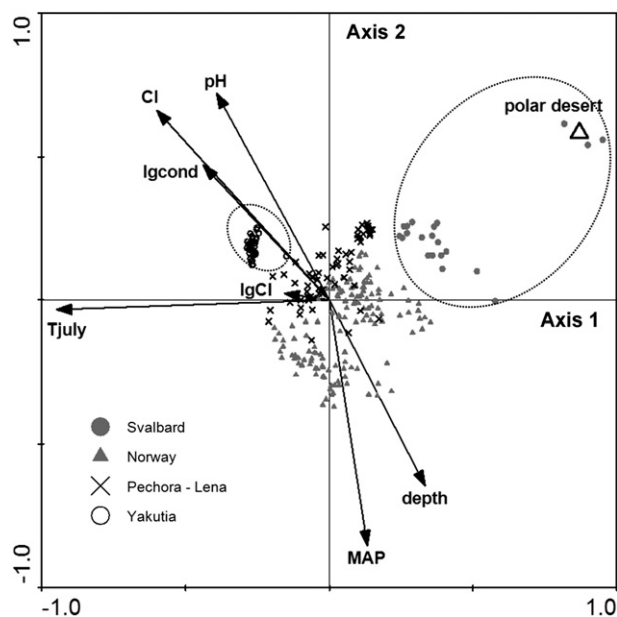
Table 6
Significant environmental variables identified by forward selection in CCA of the combined Norwegian and Russian lakes and the variance they explain.

<Variable	Variance explained	% total variance explained	Significance level
Mean July air temperature (T_{july})	0.31	39.7	$p < 0.002$
Continentality (CI)	0.18	23.1	$p < 0.002$
Log conductivity (lgcond)	0.08	10.3	$p < 0.002$
Water depth (depth)	0.06	7.7	$p < 0.002$
Polar desert vegetation (polar desert)	0.06	7.7	$p < 0.002$
Mean annual precipitation (MAP)	0.04	5.1	$p < 0.002$
Log Cl$^-$ conc (lgCl)	0.02	2.6	$p < 0.036$
pH	0.03	3.8	$p < 0.012$
Total variance explained	0.78		
Total variance	3.78		

4.3. Comparisons of species composition in Russian and Norwegian data-sets

Using squared chord distance as a measure of dissimilarity in an analogue analysis, Norwegian lakes were selected as the closest analogue for 14% of the Russian lakes. By comparison only 5% of Norwegian lakes selected a Russian lake as the closest analogue, probably reflecting the greater number and geographically close proximity of sampled Norwegian lakes compared to Russian lakes. TWINSPAN of the chironomid assemblages from Norway and Russia, excluding Birgervatnet, suggests the Svalbard (Groups 1 and 2) and Yakutian lakes (Group 3) have distinctive faunas (Fig. 5). The first level of the TWINSPAN division separates assemblages with greater than 2% *Orthocladius* type S and an absence of *Tanytarsus mendax*-type from the remaining lakes. Lakes with significant abundances of *Orthocladius* type S are on Svalbard and three lakes in northern Norway (B98-3, 99-23 and 99-25). The second division separates these three Norwegian lakes and lake N from Svalbard from the remaining Svalbard lakes, with the majority of Svalbard lakes are dominated by *Diamesa zernyi/cinerella*-type and *Pseudodiamesa*. The Svalbard lakes experience the coldest July air temperatures (3.5–6.5 °C) of the Norwegian data-set and these taxa are cold stenotherms (Brooks et al., 2007). In the fifth division the presence of *Einfeldia* and *C. laricomalis*-type at greater than 2% abundance and the absence of *Sergentia coracina*-type separates the Yakutian lakes and lake K-7 (36 lakes) from a larger group of 76 of Russian and Norwegian lakes. *S. coracina*-type is a cold stenotherm (Brundin, 1956; Brodin, 1986) and *Einfeldia* is usually indicative of eutrophic water (Sæther, 1979; Brooks et al., 2001). Eutrophic conditions are more common in warm lakes but *Einfeldia* is also found in relatively cool conditions in Switzerland (Heiri, 2001). With the exception of the assemblages from the Yakutian lakes and lake K-7, the remaining Russian assemblages are compositionally similar to the Norwegian assemblages at the fourth TWINSPAN level.

4.4. Species–July air temperature relationships

Taxon responses to July air temperature were examined in the Norwegian data-set (excluding Birgervatnet) and 100-lake Russian data-set by fitting response models to species abundance and presence/absence data for taxa with 10 or more occurrences using HOF and GLR models. Species mean July air temperature optima were also estimated by weighted averaging. The HOF models suggest 85% of the taxa in the Russian data-set with 10 or more occurrences have a statistically significant response to mean July air temperature, however only 47% have a unimodal response compared with 76% in the Norwegian data-set. A number of taxa were assigned zero values or values which clearly lay outside the environmental range of the study areas, for example −99.8 °C or

Fig. 4. CCA of the combined Norwegian and Russian lakes (157 from Norway and 100 from Russia) showing the significant environmental variables. Ovals highlight the compositionally distinct faunas from Svalbard (grey filled circles) and Yakutia (black unfilled circles). (Abbreviations: T_{july}; mean July air temperature, CI; continentality index, lgcond; log of conductivity, lgCl; log of chloride ion concentration, polar desert; polar desert vegetation, MAP; mean annual precipitation and depth; water depth).
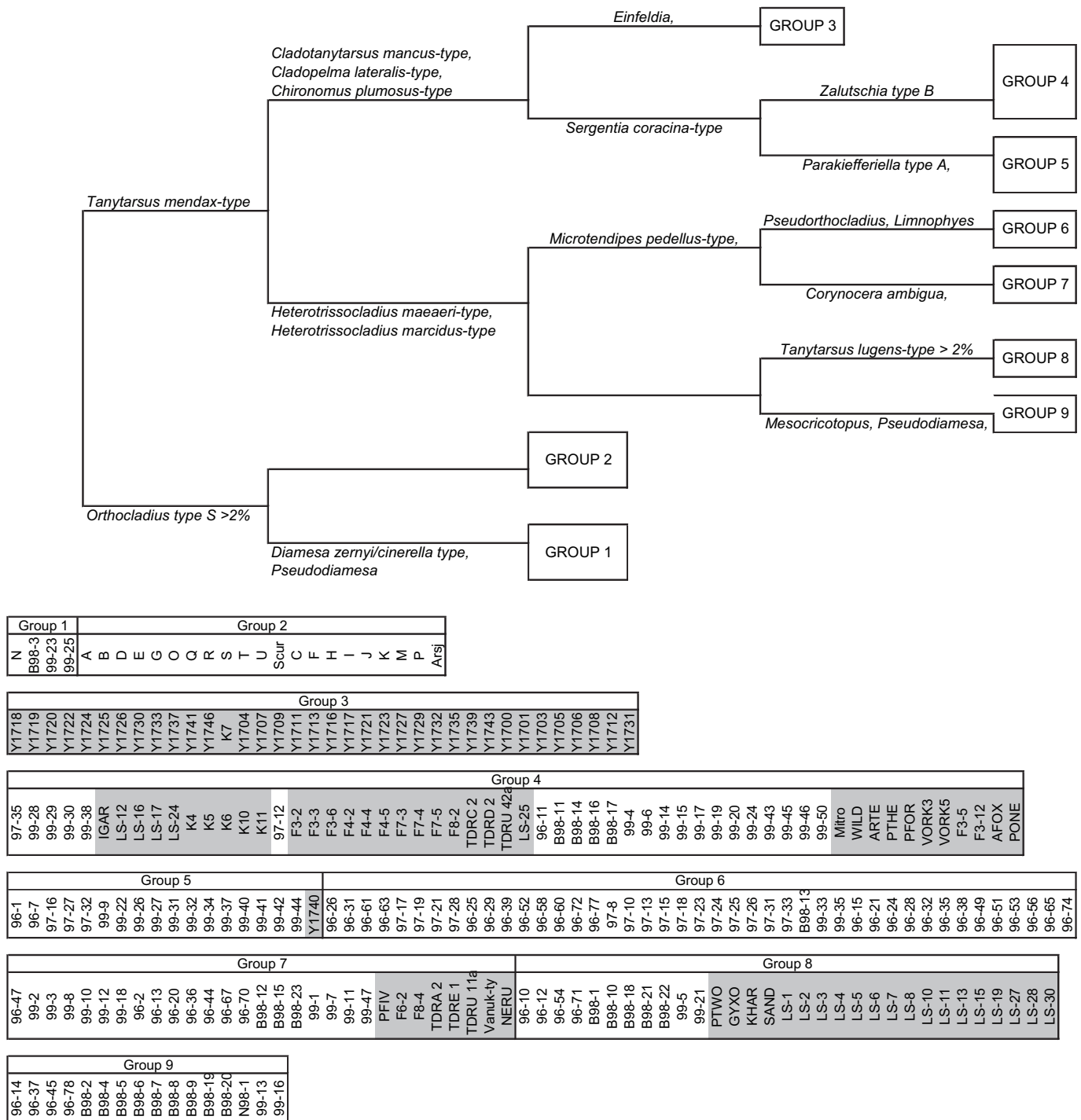
Fig. 5. TWINSPAN analysis of combined Norwegian and Russian lakes based on chironomid percentage abundance (Russian lakes highlighted in grey).

+47.5 °C in the Russian data-set (Table 7). GLR assumes all taxa have Gaussian responses to environmental variables and can give unrealistic results when unimodal responses are imposed on taxa that do not respond unimodally. When GLR-derived July air temperature optima for taxa shown to have a unimodal response (HOF model IV or V) in both data-sets and WA optima for all taxa are compared, the estimated optima are typically 1–3 °C higher in the Russian data-set than in the Norwegian data. The exceptions are S. coracina-type and Parakiefferiella triquetra-type which have higher GLR optima in the Norwegian data-set, although the WA optimum for S. coracina-type is 0.5 °C higher in the Russia data. The higher optima for the Russian taxa may be an artefact reflecting the gradient length and distribution of lakes along the July air temperature gradient in both data-sets. However, the higher optima for the Russian taxa remained after the coldest Svalbard lakes were removed from the analysis. Taxon response curves to July air temperature based on presence/absence data, modelled using GLMs and GAMs, also confirm the trend of higher optima for taxa in the Russian data-set. Examples of GLM response curves are shown in Fig. 6 for taxa in both data-sets.

Table 7
Number of occurrences (Count), maximum abundance (Max %), N2, and response to July air temperature (HOF model, GLR optima (GLR opt), and WA optima (WA opt)) for taxa with more than 10 occurrences and present in both Norwegian and Russian data-sets. (HOF model I shows no response to July air temperature; II a sigmoidal increasing or decreasing response, III a response which reaches a plateau; IV a unimodal response and V a skewed unimodal response).

	Norway (156 lakes)						Russia (100 lakes)					
	Count	Max %	N2	HOF	GLR opt °C	WA opt °C	Count	Max %	N2	HOF	GLR opt °C	WA opt °C
Tanypodinae												
Ablabesmyia	98	15.2	64.3	IV	13.1	12.4	46	8.2	32.5	V	15.8	15.7
Procladius	118	12.7	82.8	IV	12.6	11.4	77	13.6	50.3	IV	15.1	14.8
Chironomini												
Chironomus anthracinus-type	60	20.1	23.0	II	0	12.6	66	26.7	29.2	II	0	14.1
Chironomini 1st instar larvula	41	9.8	19.4	II	0	13.6	57	18.6	26.4	I	0	15.4
Chironomus plumosus-type	12	11.3	3.6	IV	13.7	13.6	49	39.4	21.2	II	0	17.3
Cladopelma	49	7.4	27.6	II	20.3	12.5	50	11.2	27.3	II	0	15.2
Dicrotendipes	72	20.7	28.5	IV	13.2	12.2	60	23.6	33.0	II	0	16.6
Microtendipes pedellus-type	74	46.2	20.5	IV	12.5	12.0	43	27.2	20.3	IV	14.6	14.3
Parachironomus varus-type	15	4.9	7.2	II	0	14.2	28	6.6	18.3	II	0	17.0
Phaenopsectra flavipes-type	16	4.7	9.6	IV	14.0	14.0	15	2.8	12.2	IV	14.6	14.0
Polypedilum nubeculosum-type	51	12.6	21.5	IV	15.4	13.3	52	8.3	36.5	IV	16.3	16.8
Sergentia coracina-type	119	55.0	53.8	IV	12.8	11.5	50	30.8	25.2	II	10.1	12.0
Stictochironomus	21	3.8	15.0	IV	11.5	11.3	29	8.3	17.7	II	11.4	12.3
Pseudochironomus	20	5.6	11.4	IV	15.9	14.5	18	9.5	12.7	II	18.2	18.3
Tanytarsini												
Cladotanytarsus mancus-type	42	23.4	13.5	IV	12.5	11.6	71	16.7	40.1	II	16.9	15.4
Corynocera ambigua	38	52.4	18.0	IV	9.9	10.1	60	56.5	23.9	IV	12.4	13.8
Corynocera oliveri-type	11	47.6	2.3	IV	8.0	8.7	20	41.8	8.5	IV	10.2	10.2
Micropsectra insignilobus-type	79	30.5	32.1	IV	9.5	9.7	39	20.1	18.2	IV	12.2	12.3
Micropsectra radialis-type	54	96.3	20.7	II	−2.4	5.2	14	18.2	4.8	IV	13.0	12.8
Paratanytarsus penicillatus-type	72	26.0	30.2	IV	11.7	11.3	64	24.1	36.7	II	29.2	17.1
Paratanytarsus undiff.	89	38.1	36.7	IV	8.6	9.3	41	18.6	23.2	II	0	11.1
Stempellinella − Zavrelia	28	4.1	18.8	IV	12.6	11.9	41	9.4	26.2	IV	14.4	14.2
Tanytarsus lugens-type	88	37.6	39.0	IV	8.9	9.6	75	28.8	39.6	V	−48.3	12.7
Tanytarsus mendax-type	94	18.8	55.6	IV	12.0	11.5	63	22.5	35.8	II	47.5	15.4
Tanytarsus pallidicornis-type	64	15.8	31.9	IV	13.2	12.1	58	33.3	29.5	IV	14.8	14.8
Orthocladiinae												
Corynoneura arctica-type	62	6.7	35.8	IV	13.5	11.9	31	11.3	17.4	II	−99.8	11.3
Cricotopus cylindraceus-type	51	19.0	18.3	IV	13.3	12.8	49	11.3	30.1	II	17.4	16.6
Cricotopus laricomalis-type	30	7.5	17.4	V	9.4	10.0	54	24.4	26.4	II	0	17.8
Cricotopus type P	29	2.5	22.2	IV	11.1	11.0	24	6.2	15.2	IV	12.7	12.6
Heterotrissocladius grimshawi-type	58	17.4	21.8	IV	11.5	11.2	13	17.9	5.8	IV	14.0	13.6
Heterotrissocladius maeaeri-type	48	69.3	15.2	IV	9.1	9.6	25	42.2	9.8	IV	12.8	12.7
Hydrobaenus conformis-type	19	46.1	4.0	II	0	5.4	17	11.2	8.4	II	0	10.4
Limnophyes − Paralimnophyes	85	18.8	42.1	IV	0	12.6	55	30.4	17.6	II	12.6	13.2
Orthocladius oliveri-type	34	22.9	8.6	I	0	10.2	29	11.0	17.1	II	0	11.5
Parakiefferiella bathophila-type	54	9.3	28.3	IV	12.3	11.9	40	7.4	27.3	I	0	14.5
Parakiefferiella triquetra-type	12	1.4	10.4	IV	12.3	11.8	16	7.4	10.4	II	10.1	11.2
Paraphaenocladius	22	8.0	8.1	IV	11.5	11.3	12	4.9	8.3	IV	17.4	15.6
Psectrocladius barbatipes-type	46	11.3	23.3	IV	12.7	12.3	14	13.0	4.1	IV	0	15.5
Psectrocladius septentrionalis-type	77	24.8	33.2	IV	11.6	11.4	21	5.7	11.0	IV	14.0	13.5
Psectrocladius sordidellus-type	133	30.8	91.9	IV	13.7	11.4	87	27.0	57.2	I	0	15.1
Pseudosmittia	24	7.3	13.1	II	22.1	12.7	13	3.8	9.9	IV	14.6	14.5
Zalutschia type B	42	24.6	13.7	IV	12.3	11.6	47	61.3	10.9	II	0	10.8
Zalutschia zalutschicola	23	41.8	11.4	V	11.4	11.2	24	24.3	10.5	IV	12.7	12.7

4.5. Species—continentality relationships

HOF models of the taxon—continentality relationship suggest 77% of the Russian taxa have a statistically significant response to the continentality index (CI). Fewer taxa (66%) have a significant response in the Norwegian lakes which may reflect the short CI gradient in Norway. Continentality is calculated from, and therefore is not independent of, T_{july}. Therefore to minimise the risk of attributing a response to T_{july} instead of continentality, the Norwegian and Russian data-sets were combined and a subset of 149 lakes selected. This excluded samples from the extremities of the T_{july} gradient as all the coldest lakes (in Svalbard) have low CIs and all the warmest lakes (in Yakutia) have high CIs and, for these lakes, it is difficult to separate out the effects of temperature and continentality on chironomid distribution and abundance. Additional samples were excluded to even out the distribution of samples along the continentality gradient. For each 0.5 °C interval along the July air temperature gradient, samples were selected so that the number of Norwegian lakes approximately equalled the number of Russian lakes for each interval, the total number of lakes in each 0.5 °C interval did not exceed 10 and the widest range of CI was retained in each temperature interval.

Taxon responses to CI were examined in the 149 lake data-set by fitting response models to species abundance and presence/absence data for taxa with 10 or more occurrences using HOF and GAM models. The fitted HOF models suggested 12 of the 82 taxa tested (14.6%) have no statistically significant relationship to continentality (Table 7). However, the GAM models for an additional 25 taxa show fluctuations in abundance, rather than a definite trend, along the CI gradient which mean that additional data are required to determine whether the inferred-HOF relationships are reliable. The results vary as the taxon responses are more complex than the five specified HOF models; GAMs are data-driven and therefore not limited to an *a priori* model as in HOF.

a *Heterotrissocladius maeaeri*-type

b *Paratanytarsus penicillatus*-type
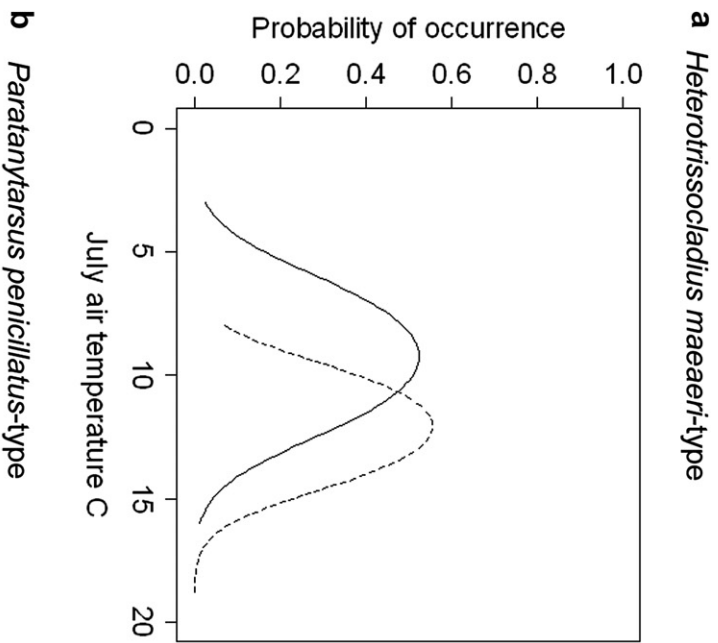
Fig. 6. Probability of occurrence of (a) *Heterotrissocladius maeaeri*-type and (b) *Paratanytarsus penicillatus*-type in the Norwegian (solid line) and Russian (dashed line) data-sets.

Nine taxa have a statistically significant sigmoidal increasing response to continentality (Table 8). These include *Abiskomyia*, *H. conformis*-type, *T. lugens*-type and *C. oliveri*-type which are cold stenothermic species (Brooks et al., 2007). Sixteen taxa have a statistically significant sigmoidal decreasing response to continentality, the majority of these taxa are terrestrial, semi-terrestrial or associated with the splash or very shallow littoral zone, for example *Paraphaenocladius* (Cranston et al., 1983) and *Thienemannimyia*-type (Fittkau and Roback, 1983). Fifteen taxa have statistically significant unimodal response to continentality and again many of these are associated with the shallow littoral or surf zones of lakes, for example *Psectrocladius barbatipes*-type (Lindegaard, 1992) and *Eukiefferiella claripennis*-type (Cranston

Table 8
HOF model responses to continentality in the combined Norwegian and Russian data-set (149 lakes, 82 taxa).

HOF model I null response	Show HOF response: but insufficient data for GAM model	HOF model II sigmoidal decreasing response	HOF model II sigmoidal increasing response	HOF models IV and V unimodal response
Cricotopus cylindraceus-type	*Cladopelma lateralis*-type	*Ablabesmyia*	*Abiskomyia*	*Cladotanytarsus mancus*-type
Cricotopus sylvestris-type	*Corynocera ambigua*	*Heterotanytarsus apicalis*-type	*Chironomus anthracinus*-type	*Corynoneura* type A
Cryptochironomus	*Corynoneura arctica*-type	*Orthocladius undiff.*	Chironomini 1st instar larvula	*Endochironomus albipennis*-type
Dicrotendipes	*Corynoneura edwardsi*-type	*Paracladopelma*	*Chironomus plumosus*-type	*Endochironomus impar*-type
Heterotrissocladius maeaeri-type	*Corynoneura lobata*-type	*Paraphaenocladius*	*Cricotopus intersectus*-type	*Eukiefferiella claripennis*-type
Heterotrissocladius grimshawi-type	*Cricotopus* type C	*Protanypus*	*Hydrobaenus conformis*-type	*Heterotrissocladius marcidus*-type
Limnophyes − Paralimnophyes	*Cricotopus* type P	*Psectrocladius septentrionalis*-type	*Orthocladius oliveri*-type	*Lauterborniella*
Orthocladius type S	*Glyptotendipes pallens*-type	*Psectrocladius sordidellus*-type	*Tanytarsus lugens*-type	*Micropsectra pallidula*-type
Pagastiella	*Macropelopia*	*Pseudorthocladius*	*Zalutschia* type B	*Parakiefferiella triquetra*-type
Paratanytarsus austriacus-type	*Mesocricotopus*	*Pseudosmittia*		*Parakiefferiella* type A
Parakiefferiella bathophila-type	*Microtendipes pedellus*-type	*Sergentia coracina*-type		*Phaenopsectra* type A
Phaenopsectra flavipes-type	*Micropsectra insignilobus*-type	*Smittia − Parasmittia*		*Psectrocladius barbatipes*-type
Zalutschia zalutschicola	*Micropsectra radialis*-type	*Synorthocladius*		*Pseudochironomus*
	Monodiamesa	*Tanytarsus chinyensis*-type		*Tanytarsus pallidicornis*-type
	Parakiefferiella nigra-type	*Thienemanniella clavicornis*-type		*Zavrelimyia*
	Paratanytarsus penicillatus-type	*Thienemannimyia*-group		
	Parachironomus varus-type			
	Paracladius			
	Paramerina		HOF model III plateau response	
	Paratanytarsus undiff.			
	Polypedilum nubeculosum-type		*Constempellina − Thienemanniola*	
	Stictochironomus rosenschoeldi-type		*Corynocera oliveri*-type	
	Tanytarsus 'no spur'		*Cricotopus laricomalis*-type	
	Zavrelia − Stempellinella		*Procladius*	
			Tanytarsus mendax-type	

et al., 1983; Lindegaard, 1992). Some thermophilic taxa such as *Heterotrissocladius marcidus*-type and *Micropsectra pallidula*-type (Brooks et al., 2007) have low CI optima of 12 and 13, respectively, whereas cold stenotherms such as *P. triquetra*-type have high CI optima, CI = 40 (Table 9). Many of the genera which show no statistically significant response to continentality have wide geographical distributions. *Limnophyes* (Cranston et al., 1983) and *Dicrotendipes* (Pinder and Reiss, 1983), for example, have world-wide distributions. Therefore each genus may be represented by different species along the continentality gradient.

4.6. Development of inference models

4.6.1. Chironomid-inferred July air temperature model

Chironomid assemblages show a strong relationship with mean July air temperature in both the Russian and Norwegian data-sets. The higher July temperature optima for the Russian taxa suggest that it is inappropriate to combine the two data-sets. A chironomid-based mean July air temperature transfer function was developed based on the 100 Russian lakes and 132 taxa. Performance statistics indicated the weighted average partial least squares (WA-PLS) 2-component model (Table 10a) performed best with a high coefficient of determination ($r^2_{jack} = 0.90$) and low RMSEP (1.09 °C). The lakes in the Russian data-set are unevenly distributed along the July air temperature gradient as 36 of 100 lakes were located in Central Yakutia with air temperatures of 18–19 °C. Many of these lakes have extremely high conductivity due to the low precipitation and/or have high nutrient levels (Table 1, Appendix A) and all are faunistically distinct from the majority of the remaining Russian lakes (Fig. 3). Therefore 19 lakes from Yakutia were excluded from the training set and a second chironomid-inferred July air temperature (C-IT) transfer function was constructed, based on 81 lakes. Only the 89 taxa with 3 or more occurrences were included in this inference model. To generate robust inference models the apparent and cross-validated predictive powers (RMSE/RMSEP ratio) must be similar. To achieve this the number of taxa should approximately equal the number of lakes (Racca et al., 2003). Performance statistics indicated the weighted average partial least squares (WA-PLS) 2-component model (Table 10b) performed better than the 100-lake model with a higher coefficient of determination ($r^2_{jack} = 0.92$) and lower RMSEP (0.89 °C). The model over-predicts temperatures below 13 °C and under-predicts above 13 °C and has a maximum bias of ±1.28 °C (Fig. 7a). These performance statistics compare favourably with other chironomid-based temperature-inference models (Brooks, 2006a).

Table 9
GLR and WA derived continentality indices optima for taxa showing a unimodal response to continentality. Abbreviations follow Table 7.

| Unimodal response	Count	Max %	N2	HOF	GLR opt.CI	WA opt CI
Cladotanytarsus mancus-type	65	4.8	48.7	IV	39	33
Corynoneura type A	24	2.9	20.1	IV	20	16
Endochironomus albipennis-type	17	1.7	15.4	V	42	38
Endochironomus impar-type	14	1.9	12.0	IV	36	34
Eukiefferiella claripennis-type	40	4.4	30.4	IV	0	16
Heterotrissocladius marcidus-type	63	5.0	50.2	IV	9	12
Lauterborniella	20	2.9	16.7	IV	18	16
Micropsectra pallidula-type	20	2.1	17.6	IV	15	13
Parakiefferiella triquetra-type	27	2.7	22.8	IV	54	40
Parakiefferiella type A	27	2.8	21.9	IV	21	17
Phaenopsectra type A	24	1.8	21.1	IV	18	15
Psectrocladius barbatipes-type	52	3.4	44.3	IV	21	21
Pseudochironomus	16	2.4	13.5	IV	16	15
Tanytarsus pallidicornis-type	82	5.8	65.0	IV	35	28
Zavrelimyia	26	2.6	22.2	IV	10	11

Table 10
Performance statistics for the chironomid-inferred mean July air temperature transfer functions for (a) the 100 Russian lake data-set, (b) the 81 Russian lake data-set and (c) the 157-lake Norwegian lake data-set. The model with the statistically best performance is shown in bold. Max = maximum, inv = inverse, cla = classical, TOL = tolerance.

Model	r^2_{jack}	RMSEP$_{jack}$	Mean bias$_{jack}$	Max bias$_{jack}$	Reduction in prediction error (%)
a					
Inverse					
WA (inv)	0.85	−0.01	2.17	1.36	–
WA − TOL (inv)	0.81	−0.25	2.47	1.53	–
Classical					
WA (cla)	0.85	−0.01	2.36	1.39	–
WA − TOL (cla)	0.81	−0.27	2.62	1.59	–
WA-PLS (1)	0.85	−0.04	2.15	1.36	–
WA-PLS (2)	**0.90**	**0.00**	**1.19**	**1.09**	**19.43**
WA-PLS (3)	0.90	−0.01	1.07	1.12	−1.91
WA-PLS (4)	0.88	−0.01	0.90	1.19	−6.71
WA-PLS (5)	0.86	−0.03	1.08	1.29	−8.00
b					
Inverse					
WA (inv)	0.86	1.19	−0.02	2.02	–
WA-TOL (inv)	0.80	1.47	−0.16	2.56	–
Classical					
WA (cla)	0.86	1.21	−0.02	2.06	–
WA-TOL (cla)	0.80	1.60	−0.19	2.68	–
WA-PLS (1)	0.86	1.19	−0.05	2.05	–
WA-PLS (2)	**0.92**	**0.89**	**−0.02**	**1.28**	**24.73**
WA-PLS (3)	0.93	0.86	−0.02	0.82	3.31
WA-PLS (4)	0.93	0.87	−0.02	0.74	−1.20
WA-PLS (5)	0.92	0.90	−0.03	0.78	−3.06
c					
Inverse					
WA (inv)	0.80	1.52	−0.01	2.29	–
WA-TOL (inv)	0.80	1.65	−0.01	2.62	–
Classical					
WA (cla)	0.83	1.39	−0.02	1.81	–
WA-TOL (cla)	0.84	1.44	−0.02	1.39	–
WA-PLS (1)	0.80	1.56	0.05	2.03	–
WA-PLS (2)	0.89	1.14	−0.01	1.16	26.88
WA-PLS (3)	**0.90**	**1.10**	**0.03**	**1.05**	**3.95**
WA-PLS (4)	0.89	1.15	0.02	1.01	−4.95
WA-PLS (5)	0.87	1.22	0.02	1.06	−6.00

4.6.2. Chironomid-inferred continentality model

The ordinations suggest that although there is a strong relationship between the distribution and abundance of chironomids and mean July air temperature, continentality is also an important factor. A chironomid-inferred continentality (C-IC) transfer function was constructed from a combined Norwegian–Russian data-set of 149 lakes. The 149 lakes, which include 120 taxa, were selected to ensure a range of continentality indices (CI) for each temperature interval (see Section 4.5). Within this data-set Pearson product–moment correlation coefficients suggest CI is weakly correlated with mean July air temperature ($r = −0.11$) and water depth ($r = −0.38$), but very strongly correlated to longitude ($r = 0.92$) and mean January air temperature ($r = −0.98$). Continentality increases with distance from the ocean (Atlantic and Arctic Oceans), but as the effect is dominated by the Atlantic Ocean this approximates to longitude in this data-set. CI is calculated from the annual temperature range (mean January–July temperatures). The extremely strong negative correlation to mean January air temperature results from the larger variation in January air temperatures than July temperatures within the data-set. However as the lakes in the training set are covered in ice and thermally insulated throughout the winter, coldest month temperatures are
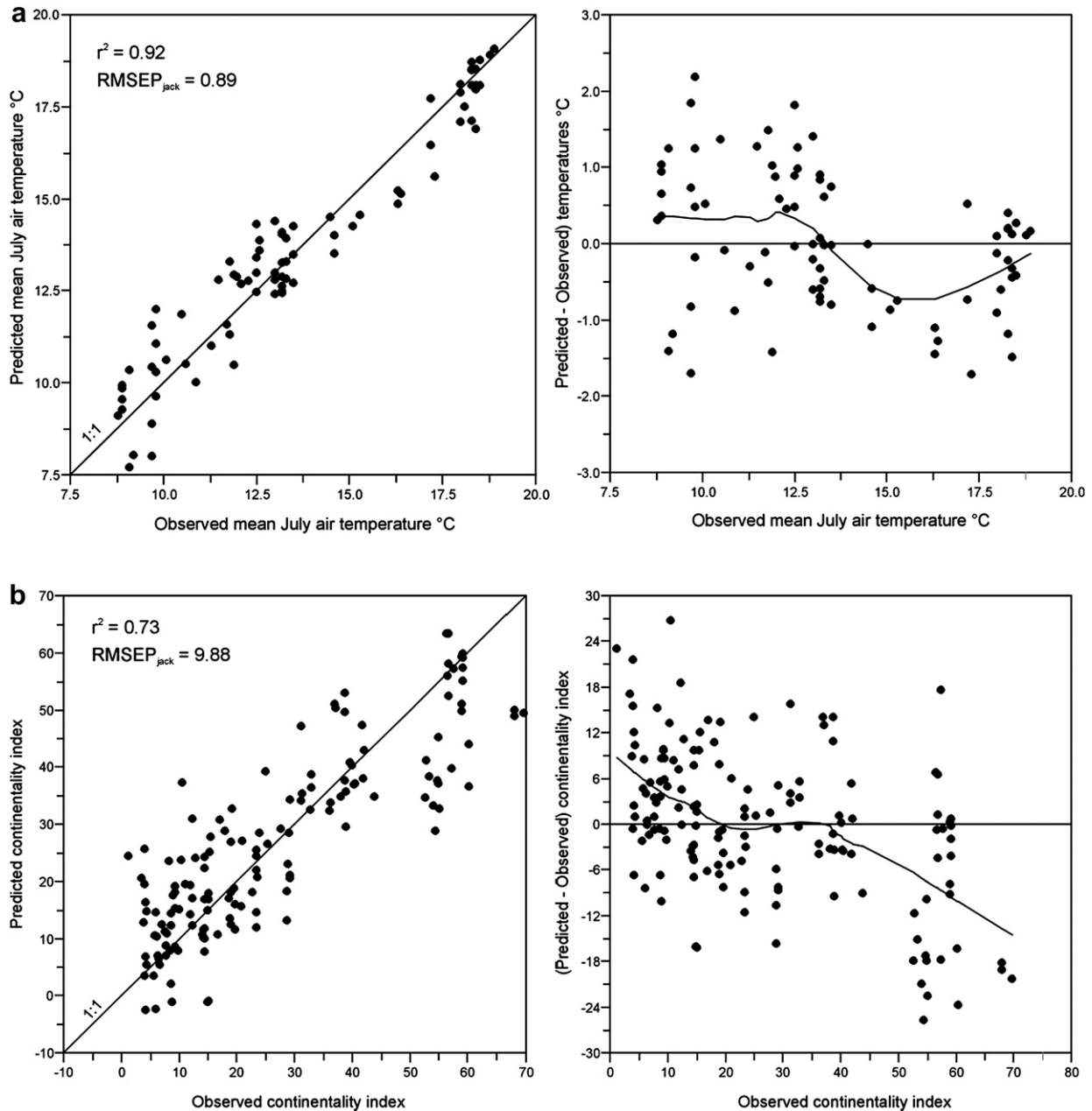
Fig. 7. Relationship between observed vs estimated and the residual (inferred − observed) for (a) the chironomid-inferred mean July air temperatures 2-component WA-PLS model and (b) chironomid-inferred continentality 2-component WA-PLS model. Trends in residuals are highlighted with a LOESS smoother (span = 0.45).

unlikely to have a direct impact on the chironomids. Variance partitioning by partial CCAs (Lepš and Šmilauer, 2003) showed that 31.6% of the total variation in the 149-lake species data can be explained by CI and mean July air temperature. Of this, 17.7% can be solely explained by the effects of continentality and 12.0% solely by July air temperature. The remaining 1.9% cannot be attributed solely to either environmental variable. Therefore the relationship with continentality in the 149-lake data-set appears to be independent of mean July air temperature.

The 2-component WA-PLS model represents the minimal adequate model (Birks, 1998) (Table 11) with a combination of high r^2_{jack} (0.73) and low RMSEP$_{jack}$ (9.88 CI units). Additional components did not reduce the prediction error by more than 5% and were not included in the model (Birks, 1998). The model predicts reasonably well over the CI range 10–40 but under-predicts above

an index of 50, which is typical of locations east and south of the Ural Mountains (Fig. 7b). Although the use of C-IT models for reconstructing July air temperatures is well established, the use of a chironomid−inference model to reconstruct continentality has not been attempted before.

4.7. C-IT and C-IC reconstructions from unnamed tundra lake VORK5

July air temperature and CI are estimated from chironomid assemblages prepared from a 15 cm short core collected from an unnamed tundra lake in NE European Russia, codenamed VORK5. The ^{210}Pb chronology suggested the core was deposited over the past 150 years, including the period from AD 1936 to present enabling comparison of inferred values with instrumental records.

Table 11
Performance statistics for the chironomid-inferred continentality transfer function. The model with the statistically best performance is shown in bold. Max = maximum, inv = inverse, cla = classical, TOL = tolerance.

Model	r^2_{jack}	RMSEP$_{jack}$	Mean bias$_{jack}$	Max bias$_{jack}$	Reduction in prediction error (%)
Inverse					
WA (inv)	0.65	11.16	0.06	25.39	–
WA-TOL (inv)	0.57	12.50	0.06	20.72	–
Classical					
WA (cla)	0.65	12.69	0.07	18.49	–
WA-TOL (cla)	0.58	15.00	0.05	14.65	–
WA-PLS (1)	0.65	11.16	−0.30	25.12	–
WA-PLS (2)	**0.73**	**9.88**	**0.08**	**19.26**	**11.53**
WA-PLS (3)	0.73	9.83	0.03	20.06	0.52
WA-PLS (4)	0.71	10.23	0.04	19.97	−4.07
WA-PLS (5)	0.69	10.69	0.07	18.79	−4.51
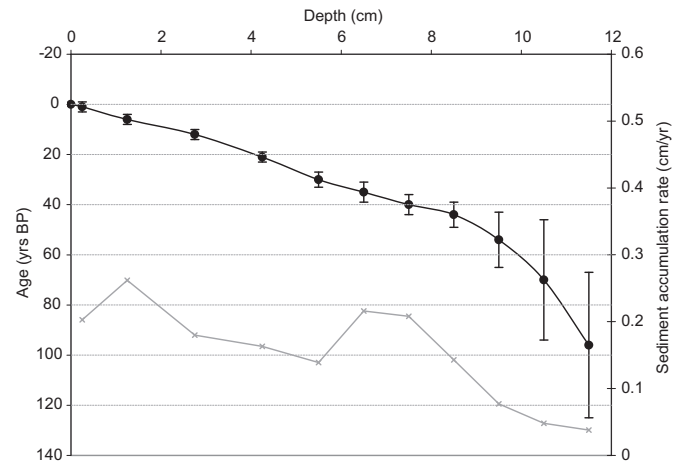
Fig. 8. Age−depth model and sediment accumulation rates for core VORK5 (sediment accumulation rates are shown in grey and ages in black with 2 SD error).

4.7.1. VORK5 chronology

Unsupported ^{210}Pb activities in VORK5 show a non-monotonic relationship with depth (Table 12) which indicates that changes have occurred in the initial ^{210}Pb concentrations supplied to the sediment over time. This precludes the use of the Constant Initial Concentration (CIC) model (Appleby, 2001) and, therefore, ^{210}Pb chronologies were calculated using the Constant Rate of Supply (CRS) dating model (Appleby and Oldfield, 1978). The raw CRS dating model places the AD 1963 layer at c.6 cm, above the AD 1963 layer suggested by the ^{137}Cs and ^{241}Am records. The final dates were calculated using the CRS model and corrected from the ^{137}Cs/^{241}Am records (Fig. 8).

4.7.2. Biostratigraphy

The diversity of the chironomid fauna in VORK5 is low and dominated by a small number of taxa (Fig. 9). Cold stenotherms such as *H. lugubris*-type (Cranston et al., 1983) and *T. lugens*-type (Brundin, 1956; Brodin, 1986) decline in abundance from the mid-twentieth century whilst thermophilic taxa such as *C. mancus*-type (Sæther, 1979; Brodin, 1986) increase in abundance. *Corynocera ambigua* increases from 3% in AD 1850 to a peak of 37% in AD 1962. Abundances of *C. ambigua* remain high but fluctuating until approximately AD 1990 before declining to late 19th century levels. Short-lived increases in *C. ambigua* in stratigraphic sequences are often associated with periods of environmental change within the lake.

4.7.3. Reconstructions and comparison with instrumental data

Despite the better performance statistics of the inference model based on the 81 Russian lake data-set the chironomid-inferred July air temperatures (C-IT) for VORK5 show little difference between the reconstructions based on the 81-lake data-set and those based on the 100-lake data (Fig. 10a). Individual reconstructions vary by less than 0.6 °C and remain relatively stable at approximately 12 °C throughout the period covered by the instrumental record (AD 1938 to AD 2006), although the decline in cold stenotherms since AD 1940 would suggest the climate had warmed. Minor cool fluctuations occur in the AD 1950s and late AD 1990s when temperatures decline by approximately 0.8 °C, whilst temperatures warm by 0.4 °C during the AD 1960s. However all these oscillations are within the prediction error of the C-IT models. Chironomid-based July air temperature reconstructions based on the Norwegian data-set reconstruct approximately 1.0−2.7 °C colder than the Russian models throughout the core. The variation between the reconstructions is greater than the prediction errors of the respective models.

Chironomid-inferred continentality reconstructions suggest the period from AD 1930s to AD 1970s was, in general, more continental than present (CI = 50, present-day CI = 39) with the exception of a period of low CI in the AD 1940s−50s. CI declined from 50 in AD 1971 to 32 in AD 1993, suggesting a more maritime climate. Over the last 25 years the continentality index has increased but shows greater inter-annual variation than earlier in the record.

Chironomid-inferred values are compared to instrumental records and the continentality index was calculated from the European Climate Assessment and Data-set records (Klein Tank et al., 2002) for Hoseda Hard (67.08°N, 59.38°E), approximately 90 km south of VORK5 (Fig. 10). The higher sampling resolution and sediment accumulation rates towards the top of the core mean the

Table 12
Summary table showing the ^{210}Pb, ^{241}Am and ^{137}Cs counting results, with respective errors, for the core VORK5.

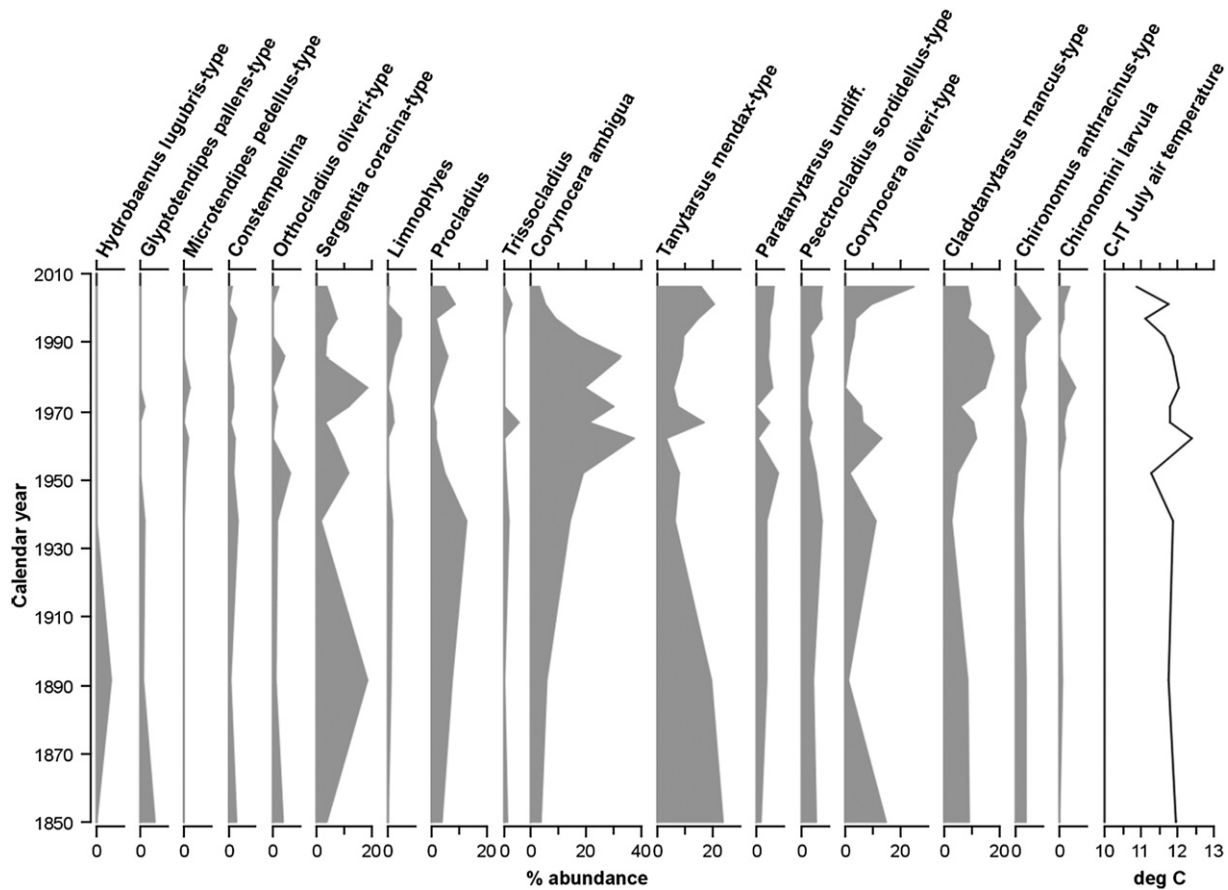| Sample depth (cm)	^{210}Pb activity (Bq kg^{-1})	Counting error (Bq kg^{-1})	^{210}Pb unsupported activity (Bq kg^{-1})	^{137}Cs activity (Bq kg^{-1})	Counting error (Bq kg^{-1})	^{241}Am activity (Bq kg^{-1})	Counting error (Bq kg^{-1})
0.25	223.54	32.85	175.1	18.83	4.3	0	0
1.25	155.93	17.47	118.98	17.29	2.48	0	0
2.75	167.67	19.84	137.76	15.16	2.71	0	0
4.25	134.57	21.38	105.28	26.53	3.31	0	0
5.5	115.76	13.79	85.71	38.61	2.41	0	0
6.5	84.47	14.08	43.58	45.52	2.64	0	0
7.5	70.03	13.67	37.17	65.5	2.68	0	0
8.5	60.72	12.23	19.93	82.67	2.83	2.14	1.17
9.5	47.51	10.9	20.66	58.37	2.05	0	0
10.5	54.11	12.78	23.22	24.23	2.02	0	0
11.5	47.82	10.87	13.23	6.56	1.52	0	0
12.5	43.07	11.17	10.62	0	0	0	0
13.5	23.17	10.43	−3.43	0	0	0	0

Fig. 9. Biostratigraphy of VORK5 showing taxa with >5% abundance.

subsamples from 0 to 0.5 cm and 1.0–1.5 cm depth typically represent 2–3 years accumulation of chironomid subfossils. The C-IT and C-IC estimates are in close agreement with the instrumental record for the mid-point, a single year, for these top two samples. Further down the core the lower sampling resolution and the greater uncertainty associated with the ^{210}Pb dating means the subsamples represent an amalgamation of several years. The sample from 9 to 10 cm depth, for example, accumulated over approximately 14 years from AD 1945 to AD 1959. Therefore the values represent a general trend for the time interval. In general the chironomid-inferred temperatures are 0.4–2.5 °C cooler and the CI values more continental than the instrumental records for Hoseda Hard which probably reflects the more northerly location of the lake. The chironomid-inferred July temperature reconstructions based on the Norwegian data-set are lower than those of the instrumental record. The Norwegian-based reconstruction also fails to reconstruct many of the decadal-scale fluctuations in the instrumental record. These results would suggest that the use of the Norwegian inference model would be inappropriate for this region of Russia.

On a decadal scale, the chironomid-inferred July air temperature (C-IT) reconstructions for VORK5 based on the Russian inference model show similar trends to the instrumental temperature over the period AD 1936–2006. Sample-specific prediction errors from the C-IT reconstructions are lower, ±1.0 °C than the high inter-annual variability in the instrumental record. Similarly the chironomid-inferred continentality (CI-IC) reconstructions from VORK5 show broad agreement to the instrument-derived record; both have a general trend to a more maritime climate over the last 25 years.

5. Discussion

The results suggest there is a strong relationship between chironomid distribution and abundance in north-west Russia and mean July air temperatures and continentality which dominate axes 1 and 2 respectively of the CCA plot (Fig. 3). These strong relationships also appear to persist over the wider geographical area of north-west Eurasia (i.e. Norway and north-west Russia) (Fig. 4). Of these, mean July air temperature is the most significant variable affecting chironomid distribution. The close relationship between chironomid assemblages and mean air temperature of the warmest month is well documented and has been used to develop chironomid-inferred temperature transfer functions in northern Eurasia (Lotter et al., 1997; Olander et al., 1999; Larocque et al., 2001; Luoto, 2008). The July air temperature gradient (8.8–19.0 °C) in the Russian data-set is comparable in length to the Swiss data-set (6.6–17.3 °C) (Lotter et al., 1997), but includes warmer temperatures than the Swedish (Larocque et al., 2001) or Norwegian data-sets (7.0–14.7 °C and 3.5–16.0 °C respectively). Water depth and mean annual precipitation were also statistically significant ($p \leq 0.05$) in the Russian (Fig. 3) and Norwegian–Russian ordinations (Fig. 4). Although the range of water depths were similar in the Russian and Norwegian data-sets, the lakes in the 100-lake Russian data were skewed towards shallower depth (mean = 3.8 m, median = 2.2 m). Chironomids in shallow lakes are probably more prone to be directly affected by winter ice and by winter temperatures than larvae living in deeper lakes. Furthermore, a negative water balance, which affects the continental interior such as central Yakutia in the study area, may also lead to shallow lakes. These relationships could provide a potential problem for the continentality inference model.
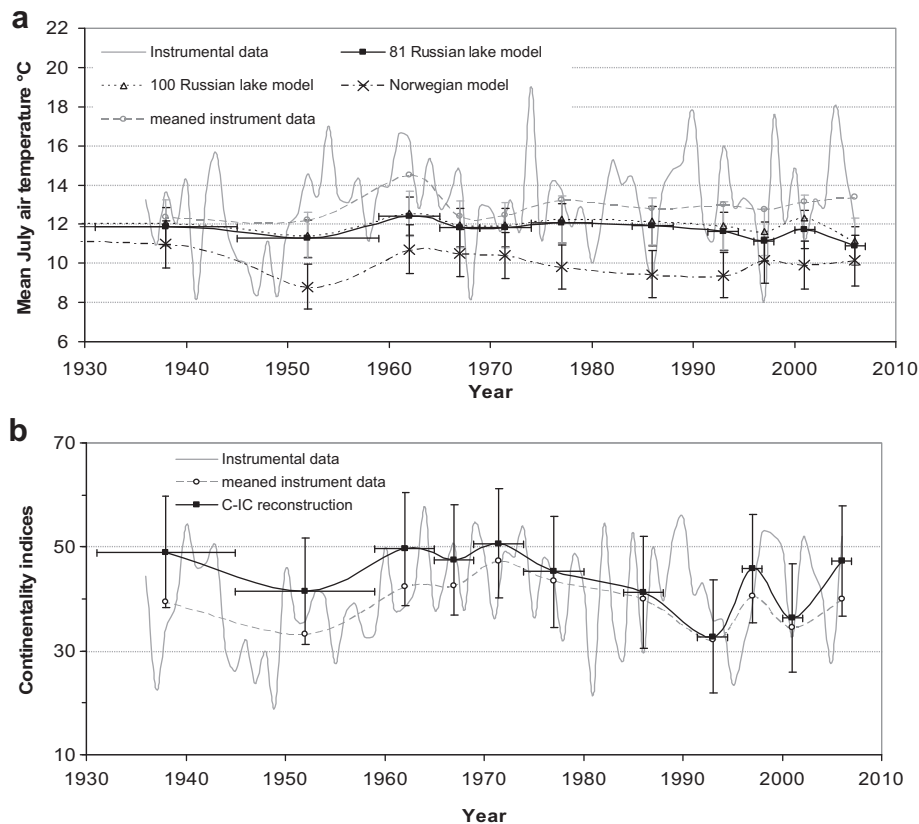
Fig. 10. Comparisons between chironomid-inferred reconstructions from VORK5 and instrumental records from Hoseda Hard showing (a) mean July air temperatures and (b) continentality indices. Annual instrumental values or CI calculated from the instrumental record are shown in grey. Sample-specific prediction errors for chironomid-inferred reconstructions are shown along the y-axis and the time interval represented by the sediment sample along the x-axis. Annual instrumental values are shown in grey, smoothed instrumental record (averaged instrumental data) is derived from the mean of the time interval represented by the sediment slice used to derive the chironomid-inferred reconstruction to give a comparable temporal resolution.

However, in both the 257-lake Norwegian–Russian data-set and 149-lake subset the correlation coefficients between water depth and CI were $r = -0.40$ and $r = -0.38$, respectively, which suggests only a moderate to weak correlation between the variables.

Previous studies have suggested that total phosphorus (TP) (Brooks et al., 2001), dissolved oxygen (Quinlan and Smol, 2001b), organic carbon (Langdon et al., 2008) and chlorophyll$_a$ (Brodersen and Lindegaard, 1999) are potentially important environmental variables in influencing chironomid distribution and abundance. The data-sets used in this study were compiled by different researchers. Therefore the above variables were either not recorded or not measured consistently so could not be used in the ordinations. The relationship with any of these variables may be stronger than the observed relationship with continentality. However no data are available for comparison as no previous chironomid studies have included continentality as an environmental variable.

The 100-lake and 81-lake Russian data-sets were used to produce C-IT transfer functions as mean July air temperature was the most significant variable in explaining chironomid distribution in NW Russia (Table 5). The use of chironomid-inferred temperature (C-IT) models is well established (Brooks, 2006b; Heiri, 2006) and the performance of the C-IT models developed in the current study are similar to previously published models in terms of RMSEP, r^2 and maximum bias (Brooks, 2006a). Chironomid-inferred mean July air temperature reconstructions for a short core from a tundra lake, VORK5, varied by less than 0.6 °C between the reconstructions based on the 81-lake data-set and those based on the 100-lake data (Fig. 10a). Nineteen lakes with high conductivity, salinity or eutrophic status were removed from the 100-lake data-

set to give values more similar to the Norwegian data-set. The deleted lakes were also from the warmest lakes (18.0–19.0 °C), therefore their deletion may have a more significant impact on reconstructions from warmer lakes than VORK5 where reconstructed temperatures varied between 10.9 and 12.5 °C. Chironomid-based July air temperature reconstructions based on the Norwegian data-set reconstruct approximately 1.0–2.7 °C colder than the Russian models and are lower than the instrumental record. The Norwegian-based reconstructions also fail to reconstruct many of the decadal-scale fluctuations in July temperature seen in the instrumental record, which are reflected in the Russian-based reconstructions.

Additionally, a combined Russian–Norwegian training set was used to produce a C-IC transfer function as continentality indices are statistically significant in explaining chironomid distribution and abundance in these countries (Table 6). The development of the chironomid-inferred continentality (C-IC) model represents a novel approach to palaeoenvironmental reconstructions. However the relationship with CI and the performance of the C-IC transfer function is considerably weaker than the relationship with July air temperature, r^2_{jack} is 0.92 for C-IT and 0.73 for C-IC. Gorczynski's continentality index (CI) is calculated from the difference between summer and winter temperatures but also provides an 'estimate of the influence of the ocean on the local climate' (Grieser et al., 2006). The climate regime experienced by a lake in Norway with a July air temperature of approximately 14 °C varies greatly from one in eastern Siberia with the same July temperature. For example Bergen (60.38°N, 5.33°E, CI = 5.6, mean July temperature 14.6 °C) had an average of 317 days per year with air temperatures above 0 °C,

between AD 1981–90, and Olenyok (68.5°N, 112.43°E, CI = 73.6, mean July temperature 14.0 °C) an average of 107 days per year above 0 °C (Royal Netherlands Meteorological Institute, 2009, http://climexp.knmi.nl/). Fig. 11 shows mean monthly air temperatures for Bergen and Olenyok. Although July air temperatures are similar, spring and autumn temperatures, the rates of spring warming and autumn cooling, and the duration of the warmest (summer) period vary considerably, in addition to the annual temperature range. Therefore, although continentality indices are calculated from the annual temperature range, continentality encapsulates more aspects of the climate regime than just the annual temperature range.

Chironomids in arctic environments generally overwinter in diapause or a quiescent state in frozen lakes in which water temperatures remain at or above 0 °C. Therefore it is unlikely they respond to winter temperature directly and may be responding to other climate variations. However, Larocque et al. (2001) showed that mean January air temperature also accounted for significant variation in chironomid assemblages in Sweden. Insects in the arctic are affected by the severity of the climate (cold temperatures, limited heat accumulation for growth), its seasonality (wide differences between summer and winter), short-term unpredictability (such as the potential for sudden changes in temperature even in summer) and variability (year-to-year changes in the factors governing development and survival) (Danks, 2004). Chironomids show a number of adaptations to arctic and subarctic environments. The number of generations per year is negatively correlated to latitude (Tokeshi, 1985) and extended life cycles of 2–7 years are common in many species at high latitudes (Welch, 1976; Butler, 1982) Chironomids, therefore, need to complete part of their life cycle during the summer and reach a resistant overwintering state before the onset of winter. The developmental rates of both eggs (Iwakuma, 1986) and larvae (Mackey, 1977; Edwards, 1986) are positively correlated to temperature, whereas daily growth rates appear to reach a maxima at a temperature optima (Storey, 1987; Hauer and Benke, 1991). This may ensure that larvae mature and pupate as fast as possible regardless of size. Variations in mean spring temperature, the rate of warming following ice-

melt and the duration of the summer period due to differences in continentality may all affect the ability of species to complete part of their life cycle within the summer period. In areas with the continuous daylight of the polar summer the emergence of adults is governed by thresholds in water temperature (Danks and Oliver, 1972a). Data from four taxa, *Corynoneura arctica*, *Stictochironomus* sp., *Micropsectra natvigi* and *Procladius culiciformis* on Bathhurst and Ellesmere Islands, Canada suggest thresholds of 4–5 °C for pupation and 7 °C for pupal ecdysis (Danks, 1971; Danks and Oliver, 1972b). These thresholds, particularly for pupal ecdysis, are relatively high and often close to the lake water maximum temperature in high arctic lakes and for completion of pupation the temperatures need to be sustained for periods of up to 21 days. If these thresholds are not met then the species will not develop further that year. Therefore any change in the time interval above the threshold may influence the composition of the chironomid assemblage. The duration of lake ice may also affect the oxygen tension of the water column and surface sediments. Chironomid taxa vary in their oxy-regulatory capabilities (Brodersen et al., 2004) and prolonged ice cover may favour taxa able to tolerate low oxygen tensions. Further work is required to determine the relative importance of these mechanisms.

Taxa showing a statistically significant sigmoidal increasing response to continentality include cold stenothermic species such as *Abiskomyia*, *H. conformis*-type, *T. lugens*-type and *C. oliveri*-type (Brooks et al., 2007). Their increased occurrence in more continental climates (CI above 40) suggests these species are ecologically or behaviourally adapted to completing part of their life cycle within the short continental summers and surviving the long ice-covered winters. The majority of taxa demonstrating a statistically significant sigmoidal decreasing response to continentality are terrestrial, semi-terrestrial or associated with the splash zone or very shallow littoral zone. Most species of *Smittia* and the larvae of many *Paraphaenocladius* species are terrestrial (Cranston et al., 1983) while *Pseudorthocladius* (Strenzlke, 1950; Saether and Sublette, 1983), *Synorthocladius* (Cranston et al., 1983), *Thienemanniella clavicornis*-type (Cranston et al., 1983) and *Thienemannimyia*-type (Fittkau and Roback, 1983) occur in littoral, splash zones or streams. Although terrestrial habitats and the splash zone derive thermal insulation from the snow layer this can melt and refreeze throughout the winter period or be removed by strong winds which could leave chironomids in these environments vulnerable to cellular damage from repeated freeze-thawing. Therefore the decline in these species in more continental areas may reflect their inability to survive in these environments during the long cold winters rather than their failure to complete part of their life cycle within the short summer. The decline of stream dwelling taxa, such as *Pseudorthocladius*, *Synorthocladius*, *Thienemanniella* and *Thienemannimyia*, with increased continentality may reflect a decline in the number of stream-fed lakes and an increase in ground-water fed, thermokarst lakes across the continentality gradient.

Whereas increasing or decreasing sigmoidal responses may reflect an adaptation to, or tolerance of, differences in the length of the summer or intensity of the winter; the concept of a continentality optimum is more difficult to explain in an ecologically meaningful way. Taxa with unimodal responses (Table 9) may have a competitive advantage under certain climate regimes but are outcompeted by better adapted species in more extreme maritime or continental climates. Alternatively the taxa may be restricted geographically for reasons unrelated to the present-day climate such as past dispersal patterns. Nevertheless of the 15 taxa showing unimodal responses, 12 occur in both the Norwegian and Russian data-sets. Some of these taxa, such as *P. triquetra*-type have a Holarctic distribution and have also been found in Patagonian
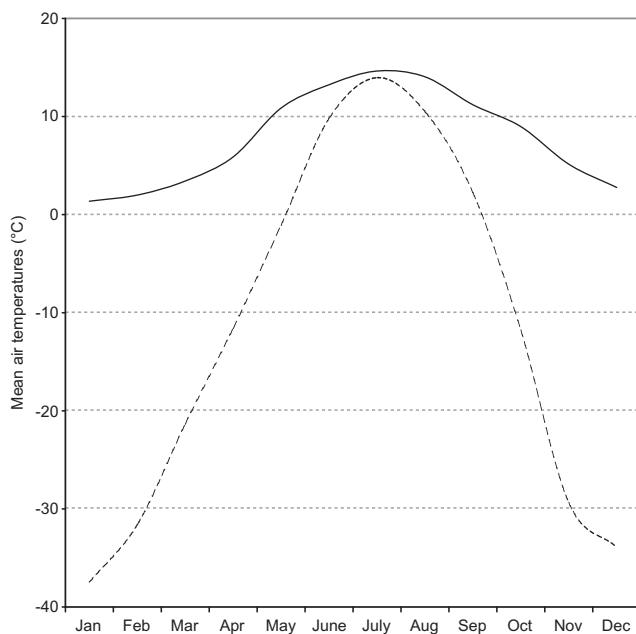
Fig. 11. Mean monthly air temperature for Bergen, 60.38°N, 5.33°E, (solid line) and Olenyok, 68.5°N, 112.43°E, (dashed line) between AD 1981–90 (Royal Netherlands Meteorological Institute, 2009, http://climexp.knmi.nl/).

lakes (Massaferro and Brooks, 2002). Their widespread distribution suggests they may be restricted by local environmental factors, which may or may not be related to climate such as pH. The remaining 3 taxa, *Corynoneura* type A, *M. pallidula*-type and *Zavrelimyia* were recorded in Norway only. This restricted distribution may reflect differences in biogeography, climate or the greater number of lakes in the Norwegian data-set. The eastern Palaearctic fauna includes a number of chironomid taxa which are not found in the western Palaearctic. Whilst this may be because climatic conditions are different in the eastern than western Palaearctic, a number of other insect groups have similar differences due to historical reasons such as glaciation, climate history and post-glacial dispersal (Konstantinov et al., 2009).

The ordinations suggest that the distribution and abundance of chironomids in both the Norway and Russian data-sets are influenced by many of the same environmental variables. The TWINSPAN results indicate the composition of the faunal assemblages from the two data-sets are similar and many taxa show similar responses to July air temperature. These characteristics are sometimes used to justify the merging of training sets or the application of inference models to areas outside the geographical region used to compile the data. However, the species–temperature optima are consistently higher, with 1–2 exceptions, in the Russian lakes than the Norwegian data-set regardless of the statistical modelling technique used. The July temperature reconstruction of the short core VORK5 based on the Norwegian inference model was consistently lower than that based on the Russian C-IT model and the instrumental record. This suggests continentality may play a role in the chironomid response either directly through climate parameters such as the duration of the ice-free period or spring temperatures or indirectly through the occurrence of ground-water fed thermokarst or stream-fed lakes. Further work is needed to confirm the relationship between chironomid distribution and continentality, and possible mechanisms for the response. However if confirmed this would imply that inference models should be considered specific to a geographical region with a similar continentality regime. Application to sites tens to hundreds of kilometres outside the geographic area covered by the training set may be acceptable but the use of western European inference models to cores collected in central Siberia is unlikely to yield reliable reconstructions. However, the use of transfer functions from geographically distinct areas may be justified when fossil taxa are poorly represented in local training sets. For example, Larocque-Tobler (2010) used North American and Swedish transfer functions to reconstruct July air temperatures at Egelsee, Switzerland as these data-sets had better representation of fossil taxa than the Swiss transfer function. The Swedish and North American-based reconstructions varied by up to 4 °C, suggesting that whilst the general pattern of temperature change could be inferred using a transfer function from another region, estimates of temperature and the amplitude of change may be less reliable (Larocque-Tobler, 2010).

6. Conclusions

Numerical analysis of environmental variables and subfossil head capsules remains in the surface sediments of 100 lakes showed that mean July air temperature is the most significant variable explaining contemporary chironomid distribution and abundance in northern Russia. This has been shown to be an important environmental variable in a number of previous studies, leading to the development of chironomid–temperature transfer functions (e.g. in Northern Europe by Olander et al., 1999; Brooks and Birks, 2001; Larocque et al., 2001). The performance of the WA-PLS temperature inference in the present study, with RMSEP of 0.89 °C and r^2 of 0.92, is comparable to these models. However, the Russian inference model improves the representation of a number

of taxa, such as *C. oliveri*-type, *Constempellina* and *Paracladius*, which frequently occur in subfossil assemblages from arctic Russian lakes, but are poorly represented in European training sets. These are cold-adapted taxa and their absence from the training sets could lead to overestimations of July temperatures, using European inference models, in fossil samples where these taxa form a major component (for example see Andreev et al., 2005).

Ordinations also suggest that continentality, expressed as the R continentality index, is also a statistically significant variable influencing the distribution and abundance of chironomid assemblages and also the temperature optima of chironomid species. Temperature optima are consistently higher in the Russian data than in the Norwegian data which implies that chironomid-based temperature reconstructions for subfossil assemblages in Russian sediment samples using the Norwegian inference model, or visa versa, are likely to be reliable. This was confirmed by reconstructions of the Russian core, VORK5, based on the Norwegian C-IT inference model which underestimated July air temperatures at this lake and did not reconstruct decadal-scale oscillations in temperatures. Therefore inference models should only be considered applicable to sediment cores collected within the broad geographic source area of the training set and to areas with similar continentality regimes. The relationships with continentality enabled the development of chironomid-inference models to reconstruct continentality over north-east Eurasia and July temperature in north European Russia to central Siberia.

July air temperature and continentality reconstructions from an unnamed lake in north-east European Russia gave similar value and trends to instrumental data over the past 70 years. The ability of the Russian models to estimate accurately past climate suggests the Russian chironomid–July air temperature-inference model represents an improvement over the Swedish and Norwegian inference models, for chironomid-inferred temperature reconstructions in northern Russia. The continentality inference model represents the first attempt to reconstruct past continentality using chironomids. This has the potential to make a valuable contribution towards reconstructing past climates in Arctic environments where recent summer (June, July and August) warming appears dampened compared to other months (Hirschi et al., 2007). However further work is necessary to confirm the observed relationship with continentality and establish the biological mechanisms for the response. Continentality reconstructions over the Holocene where seasonal insolation has varied and the variations are known may help to elucidate the relationship.

Appendix. Supplementary data

Supplementary data associated with this article can be found, in the on-line version, at doi:10.1016/j.quascirev.2011.01.022.

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