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An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia

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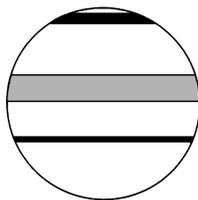
Abstract: Chironomid-temperature inference models based on an expanded data set of surface-sediment and limnological data from 53 Subarctic lakes in northern Fennoscandia have been developed using eight different numerical techniques, each based on slightly different underlying statistical models or ecological assumptions. The study sites are mostly small, shallow, bathymetrically simple, oligotrophic lakes, with a pH range from 5.0 to 7.8, a total organic carbon range from 2.5 to 12.6 mg l^{-1}, a mean July lakewater temperature ranging from 6.1 to 15.4°C, and a mean July air temperature ranging from 8.5 to 14.9°C. A series of redundancy analyses (RDA) identified sediment organic content, maximum lake depth, and lakewater temperature as being the most important explanatory variables. Variance partitioning by partial RDAs further suggested that each of these variables accounted for a significant fraction of variance independent from each other. Different calibration models were assessed on the basis of their statistical performance, with particular reference to prediction errors and the amount of bias along the temperature gradient. Of the eight calibration models, modern analogue techniques, weighted averaging partial least squares, simple weighted averaging with an 'inverse' deshrinking regression, and linear partial least squares consistently performed best. These methods can all be used to develop transfer functions for surface-water and air July temperatures with a root mean squared error of prediction (RMSEP) of about 1.5–1.6°C (water temperature) and 0.8–1.1°C (air temperature), as assessed by leave-one-out cross-validation. The resulting models do, however, have relatively high maximum biases (up to 3.9°C) in the lowest segments of the air and water temperature gradients, highlighting the need for enlarging and expanding the calibration data set to include lower temperatures.

Key words: Chironomidae, Subarctic, ordination techniques, calibration models, transfer function, summer temperature, palaeoclimate, Holocene, northern Fennoscandia.

Introduction

Global warming is among the most serious environmental problems in the future, as has recently been reported by the IPCC (Houghton *et al*., 1996; Watson *et al*., 1996; Bruce *et al.*, 1996). Climate change will have effects on terrestrial as well as aquatic ecosystems and may cause severe problems for the human environment. Reliable long-term information on natural climate variability is needed in order to test and validate results from General Circulation Models (GCMs), which are used to predict future climatic change as a result of human influences on global climate.

Meteorological measurements, or direct long-term monitoring of environmental data, do not offer time-series that are long enough for model validation. Palaeoclimates can be used as means of extending our knowledge on long-term natural climate variability that is required for model validation.

Most long-term quantitative information about past climates has been obtained so far from deep-sea cores and from Greenland and Antarctic ice cores, but quantitative information derived from continental environments is also needed. The lake-sediment record is potentially one of the most useful sources of quantitative palaeoclimatic proxy data (Battarbee, 1991; Smol *et al*., 1991).

Changes in both terrestrial and aquatic ecosystems are continuously recorded in lake sediments in the form of, for example, pollen, diatoms, cladoceran, or chironomid remains. Inferences of past temperatures may be made when the present-day thermal optima and tolerances of the taxa concerned are estimated (Birks, 1995). Such quantification involves modelling the values of a climatic variable (e.g., mean summer epilimnetic water temperature) as a numerical function of biological data using large modern-day calibration data sets (Charles and Smol, 1994; ter Braak, 1995).

The use of aquatic midge larvae in palaeolimnological research has increased recently. Improved knowledge on chironomid taxonomy and the development of appropriate statistical methods have made it possible to reconstruct quantitatively temperature changes, particularly from Lateglacial times (Walker *et al.*, 1991a, 1997; Levesque *et al.*, 1994; 1997). According to Walker *et al.* (1997), summer surface-water differences of up to 10°C occurred between the Younger Dryas and the Allerød periods in eastern Canada. Although temperature changes during the Holocene may have been much smaller, the reconstruction of Holocene climatic variations using midge larvae is, in theory, possible (e.g., Velle, 1998).

In a previous paper it was demonstrated that surface-water temperature is an important determinant of chironomid distributions and relative abundances in lakes within northwestern Finnish Lapland, an area of a high-latitude ecotone that is potentially sensitive to climatic change (Olander *et al.*, 1997). In this study the chironomid-based surface-water temperature model is developed further by means of an expanded calibration data set collected from the same area. The ultimate aim is to develop a reliable calibration model for the quantitative reconstruction of Holocene lakewater summer temperatures from fossil chironomid assemblages.

As many quantitative palaeoclimatic reconstructions, for example based on fossil pollen assemblages, beetles or plant macrofossils, are for mean July or mean summer *air* temperatures, we have also used our modern chironomid data set to develop a chironomid – air-temperature calibration model, following Lotter *et al.* (1997; 1999) and Brooks and Birks (1999). When applied to fossil chironomid assemblages, the resulting reconstructions can thus be for both summer lakewater and summer air temperatures. This permits direct comparison with independent palaeoclimatic reconstructions of summer air temperatures based on other proxy sources (e.g., tree-ring records) or different groups of organisms (e.g., pollen). Furthermore, in remote areas, such as northern Fennoscandia, basic data on variations in water temperature are sparse compared to air-temperature data that can usually be obtained at much higher temporal resolution. Accordingly, a marked improvement in the calibrations might be achieved by using air temperatures for calibration purposes rather than occasional water-temperature measurements only (Livingstone and Lotter, 1998). Ottosson and Abrahamsson (1998) discuss the problems in modelling epilimnetic and hypolimnetic temperatures in lakes and present a model driven by latitude, continentality and altitude to predict epilimnetic water temperatures in Swedish lakes.

Study area

In Olander *et al.* (1997), 30 lakes were selected from both sides of the northern tree-line in northwestern Finnish Lapland in order to examine the relationships between modern chironomid assemblages and selected physical and chemical variables. Particular attention was placed on surface-water temperature. For this study, 23 additional lakes were sampled to expand the data set and thus, it is hoped, to improve the reliability of the quantitative inference models (Figure 1). Most of the new sites are from the northernmost (Arctic) part of our initial transect. The inclusion of the 23
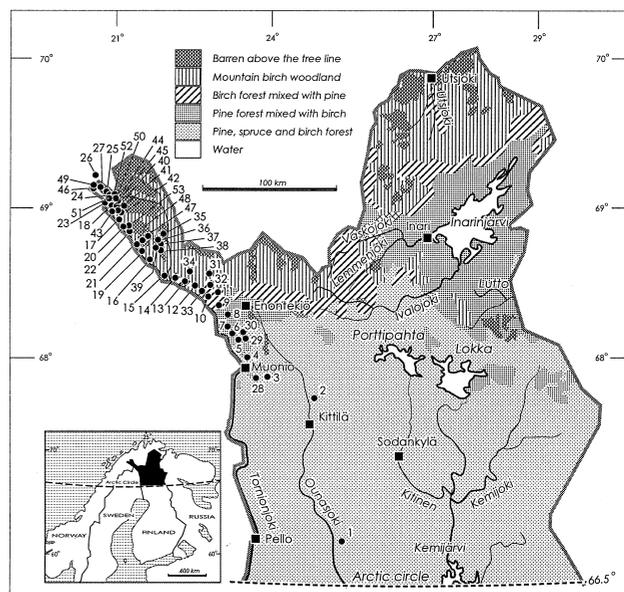
Figure 1 Distribution of the 53 lakes studied across the tree-line region in northernmost Fennoscandia.

new lakes does not, however, extend the initial temperature gradient to any significant amount. In the current 53-lake data set, July surface-water temperature ranges from 6.1 to 15.4°C, with a decreasing trend in temperatures from south to north. Most (79%) of the study sites were found to be thermally unstratified during the sampling period. The surface-water temperatures are, however, slightly skewed (Figure 2A). There are few lakes with surface-water temperatures below 9°C and there is a dip between the 11–12°C interval, whereas the 12–13°C interval is overrepresented. The uneven distribution of sites along this surface-water temperature gradient is associated with a relatively low density of lakes in the area, which makes it difficult to find lakes suitable for our purposes (i.e., lakes that are small and not too deep, and have minimal throughflow and undisturbed sedimentation conditions). Nevertheless, the steep water-temperature gradient observed is neither accidental nor dependent on a particular summer; it is clearly detectable in long-term water-temperature records from lakes in the area (Atlas of Finland, 1986; see also Weckström *et al.*, 1997). In general, there exists a close relationship between long-term air temperatures and long-term water temperatures in the area (Kuusisto, 1981).

Mean July air temperatures range from 8.5 to 14.9°C along the transect. The air temperatures are not significantly skewed (Figure 2B), in contrast to the surface-water temperatures. There is a significant relationship between the July air temperatures and the measured surface-water temperatures ($r = 0.65$, $p < 0.01$) in our data set (Figure 3).

Vegetation, climate and bedrock characteristics of the study area are described in detail by Olander *et al.* (1997). The study lakes are generally small (0.9–115.2 ha), headwater, clear, and oligotrophic. Their alkalinity ranges from 1.0 to 17.0 mg l⁻¹, total organic carbon (TOC) ranges from 2.5 to 12.6 mg l⁻¹, and the pH gradient varies between 5.0 and 7.8. The deepest lake is 25 m, whereas the shallowest lake is only 0.85 m deep. The catchment areas (excluding the lake area) vary from 5.45 to 2524 ha and the lake/catchment ratio is generally low (mean = 26.05). All the study sites are natural and there are no known direct impacts from human activity within their catchment areas. Further characteristics of the 53 lakes are given in Table 1.
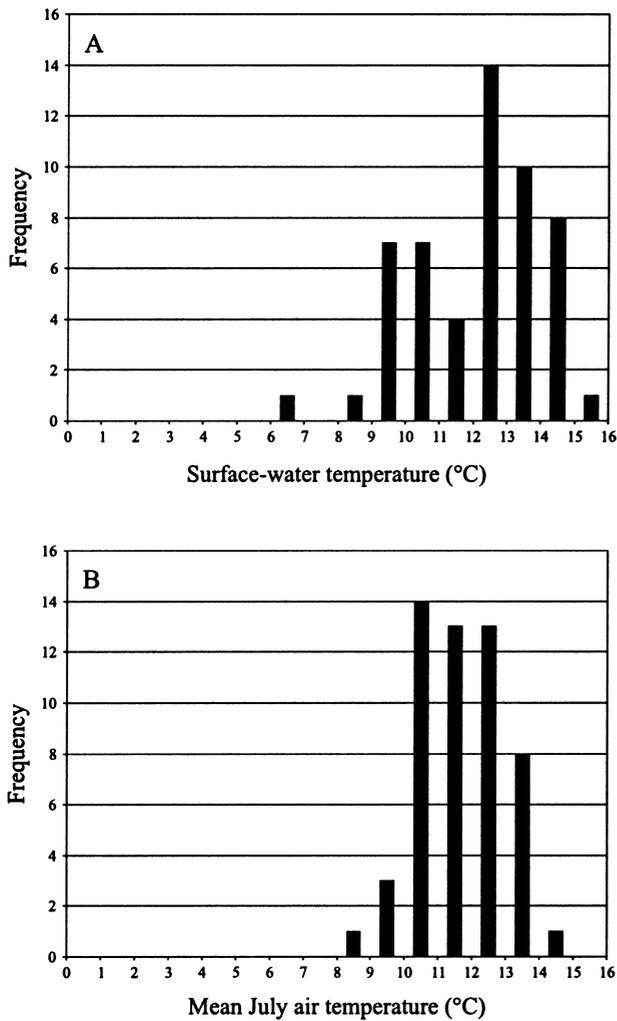
Figure 2 Frequency distributions of surface lakewater (A) and mean July air temperatures (B) for the 53 sampled lakes.
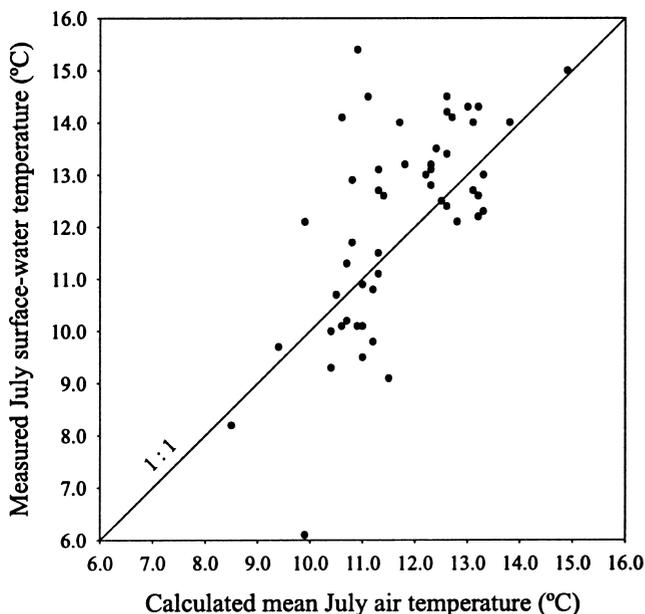
Figure 3 Scatter plot of measured July 1995 water temperatures (°C) and calculated mean July air temperatures (°C) based on the 1961–1990 period ($r = 0.65$, $p < 0.01$) for the 53 sampled lakes.

Methods

Sampling and laboratory methods

Sampling and laboratory procedures are described by Olander *et al.* (1997). Three new variables, distance beyond tree-line (DBT), sediment organic content measured by loss-on-ignition (LOI) and mean July air temperature, are included here. DBT acts as a surrogate for location factors in the data set. It was obtained by mapping the vegetation zones derived from 1:20 000 topographic maps of the study region. LOI was determined from three surface-sediment samples (combined to make one homogenized sample) taken from the deepest part of a lake according to the methods described in Bengtsson and Enell (1986) but with corrections to some of their formulae. For LOI analyses, quartz crucibles were used instead of porcelain crucibles in order to improve accuracy. Surface-water temperatures were measured twice in July 1994 and once in July 1995. Water-temperature measurements used in this study were all from July 1995. Mean July air temperatures were estimated for each lake using 1961–1990 Climate Normals data from 11 nearby climate stations (two in Norway, five in Finland, four in Sweden) and applying consistent regional lapse rates and a linear interpolation procedure to allow for the small but statistically significant trend in mean July air temperatures (reduced to sea level) within the study area. If a reference line is drawn from Skibotn in Troms, north Norway, southeastwards to Rovaniemi in northern Finland, and the positions of all 11 climate stations are drawn orthogonal to this line, there is a highly significant statistical relationship between mean July air temperature (reduced to sea-level values) at these climate stations and distance along this line (reduced mean July air temperature = $13.5 + 0.0544 *$ distance, $r = 0.97$, $p < 0.001$). The mean July air temperatures for each of the 53 lakes were estimated from the position of each lake along the line using this equation and allowing for the elevation of each lake by applying the regional lapse rate of 0.57°C per 100 m (Laaksonen, 1976).

Chironomid analysis

Subsamples of 0.5–28.5 g wet weight were deflocculated in warm 10% KOH for 30 minutes. Samples were then passed through a 105 μm sieve and transferred to a Bogorov counting tray. All head capsules were picked with fine forceps under a binocular microscope and mounted ventral side upwards on slides in Euparal. To obtain a minimum of 100 chironomid head capsules per sample, additional slides from the existing 30 lakes were also prepared. Chironomids were usually identified to generic level. However, the genera *Psectrocladius* and *Heterotrissocladius* and the tribe Tanytarsini were divided into smaller taxonomic units than in Olander *et al.* (1997) to improve taxonomic resolution. Their separation was mainly based on Hofmann (1971), Saether (1975) and Wiederholm (1983). Agreements in taxonomic harmonization emerged from workshops within the international MOLAR and NORD-CHILL projects and these were followed in this study. The genus *Psectrocladius* was divided into three separate groups (*Monopsectrocladius* gr., *P. sordidellus* gr. and *Allopsectrocladius* gr.) on the basis of the number and shape of median teeth in the mentum. The genus *Heterotrissocladius* was divided into four groups on the basis of the number and shape of middle median teeth in the mentum and the colour of the postmentum. In the cases when the head capsule was split into two halves, the distinction between *H. marcidus* and *H. maeari* was difficult or impossible. The tribe Tanytarsini was divided into separate taxonomic groups on the basis of the number of mandibular teeth and the presence/absence and shape of the projection on the antennal pedestal. *Micropsectra* species have a bifid premandible whereas *Tanytarsus* species have a trifid premandible. The premandible thus makes a good discriminator between *Micropsectra* and *Tanytarsus* species, but unfortunately the premandibles were only very rarely

Table 1 Locations and environmental characteristics of the 53 study lakes

Lake number	Latitude (°N)	Longitude (°E)	Altitude (m a.s.l)	Area (ha)	Perim. (km)	Catch. area (ha)	Catch/Area ratio	Mire area (%)	Forest zones *	DBT** (km)	Roughness (contours/km)	LOI*** (%)	Max.depth (m)	Secchi (m)	Water temp. (°C)	Air temp. (°C)	pH (units)	Cond. (µS/cm)	Alkalin.	K (mg/l)	Ca (mg/l)	Na (mg/l)	Mg (mg/l)	TOC (mg/l)	Fe (mg/l)
1	66.92	25.40	108.0	9.08	1.25	44.49	4.90	11.05	SPB	-148	4.55	37.4	10.15	6.15	15.0	14.9	6.2	15.1	4.0	0.37	0.60	0.40	0.40	6.2	0.12
2	67.82	24.87	197.5	2.90	0.66	17.87	6.16	0.00	SPB	-49	3.23	84.5	6.30	6.30	14.0	13.8	6.8	18.5	5.0	0.36	0.61	0.24	1.09	6.1	0.03
3	67.85	24.18	288.0	7.14	1.11	30.96	4.34	40.03	SPB	-51	5.17	64.1	4.00	4.00	13.0	13.3	6.2	16.4	3.0	0.24	1.01	0.69	0.28	9.9	0.53
4	67.98	23.68	262.0	10.67	1.18	59.07	5.54	28.81	SPB	-39	4.72	71.8	3.30	3.30	12.7	13.1	5.0	12.7	3.0	0.10	0.35	0.69	0.14	8.3	0.11
5	68.01	23.40	249.0	4.34	0.85	50.89	11.73	45.95	SPB	-24	4.21	50.1	3.35	2.70	12.6	13.2	6.9	36.4	14.5	0.31	2.79	1.29	0.94	11.0	1.20
6	68.12	23.37	252.0	1.52	0.50	5.91	3.89	4.45	PB	-21	0.00	88.0	4.30	4.30	14.0	13.1	5.0	9.5	1.0	0.11	0.26	0.19	0.06	5.1	0.48
7	68.20	23.18	283.0	0.90	0.37	5.45	6.06	0.00	PB	-11	0.00	61.2	4.40	4.40	14.3	13.0	6.5	16.0	4.5	0.22	0.88	0.80	0.36	7.2	0.16
8	68.20	23.22	294.0	33.99	3.04	327.29	9.63	43.32	BP	-2	2.72	37.3	6.95	3.00	12.1	12.8	6.9	24.8	9.0	0.71	1.31	1.05	0.64	12.0	0.74
9	68.33	22.95	290.0	2.62	0.77	33.20	12.67	64.20	MBW	7	0.00	63.8	1.75	1.75	14.1	12.7	6.8	25.0	9.0	0.43	1.84	1.00	0.58	12.6	0.41
10	68.40	22.88	317.0	2.58	0.80	11.04	4.28	1.50	BP	6	10.00	49.4	6.30	6.30	13.4	12.6	6.5	6.4	4.0	0.25	0.35	0.28	0.14	4.2	0.26
11	68.40	22.85	313.0	2.18	0.73	21.66	9.94	2.38	BP	5	9.02	58.6	4.10	4.10	14.5	12.6	6.8	11.7	6.5	0.30	0.56	0.24	0.24	8.0	0.27
12	68.42	22.58	332.0	1.97	0.61	8.80	4.47	58.82	BP	2	0.00	80.8	1.85	1.85	13.5	12.4	5.1	21.5	2.0	0.18	0.38	1.38	0.18	11.6	0.10
13	68.47	22.43	322.0	2.55	0.64	14.17	5.56	25.75	BP	1	7.14	60.4	4.00	4.00	12.5	12.5	6.9	18.5	5.5	0.43	0.98	0.61	0.40	8.5	0.39
14	68.50	22.30	330.9	40.64	3.23	348.23	8.57	52.24	BP	4	1.38	64.3	1.25	1.25	13.1	12.3	7.0	19.4	8.0	0.37	1.24	0.75	0.43	9.1	0.22
15	68.48	22.17	346.0	12.89	1.90	126.06	9.78	54.54	MBW	1	2.34	68.1	1.75	1.75	13.0	12.2	7.6	36.5	15.0	0.50	3.45	0.69	0.54	9.6	0.42
16	68.63	21.73	402.0	9.71	1.31	30.09	3.10	41.79	MBW	11	0.00	50.8	0.85	0.85	13.2	11.8	7.3	28.4	10.5	0.94	1.63	0.98	0.58	10.5	0.57
17	68.90	21.07	483.0	6.05	1.04	219.48	36.28	0.93	MBW	63	11.74	48.3	1.70	1.70	13.1	11.3	6.8	31.6	8.0	0.63	1.83	1.49	0.50	10.4	0.52
18	68.92	20.97	526.0	3.85	0.85	128.38	33.35	0.00	MBW	68	18.84	55.0	1.45	1.45	12.9	10.8	7.2	37.7	8.5	0.82	2.66	1.39	0.54	8.9	0.23
19	68.88	21.58	457.0	3.60	0.83	28.76	7.99	0.00	MBW	31	13.00	55.7	5.20	5.20	12.6	11.4	6.8	18.9	4.5	0.44	0.95	0.79	0.33	5.7	0.07
20	68.85	21.20	449.1	115.18	7.01	2524.73	21.92	3.13	MBW	54	4.74	28.7	5.15	5.15	13.1	11.3	7.2	32.6	9.5	0.81	2.21	1.18	0.56	8.5	0.13
21	68.70	21.48	480.6	18.01	2.00	108.14	6.00	7.10	MBW	36	8.21	28.1	25.00	9.50	11.5	11.3	7.4	44.7	12.5	0.64	3.90	1.01	0.64	4.9	0.05
22	68.80	21.28	476.0	9.58	1.38	353.96	36.95	1.47	MBW	77	6.99	59.5	1.05	1.05	12.7	11.3	7.4	31.1	8.0	0.66	2.21	1.06	0.46	5.3	0.10
23	68.98	20.95	547.0	4.92	0.90	447.59	90.97	0.84	MBW	74	9.52	27.3	7.95	7.95	11.3	10.7	7.2	33.9	8.5	0.49	2.35	1.31	0.38	4.5	0.07
24	69.05	20.87	679.4	69.86	4.17	530.45	7.59	0.00	Ba	81	21.56	20.5	24.00	9.20	6.1	9.9	7.2	45.2	9.0	0.26	2.81	1.10	0.59	3.1	0.04
25	69.07	20.88	930.9	1.69	0.53	7.94	4.70	0.00	Ba	84	4.69	41.4	3.35	3.35	8.2	8.5	6.2	7.2	2.0	0.09	0.38	0.33	0.08	3.5	0.05
26	69.18	20.72	355.0	7.21	1.15	356.79	49.49	0.00	MBW	98	22.67	59.6	3.40	3.40	14.0	11.7	6.9	34.2	6.5	0.70	2.29	1.69	0.43	9.8	0.08
27	69.08	20.80	588.2	15.68	1.84	192.49	12.28	0.00	Ba	87	18.42	17.5	13.75	9.50	9.3	10.4	7.1	24.0	5.5	0.23	1.69	0.86	0.22	4.1	0.02
28	67.88	23.87	254.0	18.80	2.47	713.30	37.94	17.25	SPB	-50	4.88	35.7	1.45	1.45	12.3	13.3	7.2	36.8	9.5	0.33	2.88	1.33	0.66	9.1	0.42
29	68.10	23.42	249.0	4.01	0.89	302.97	37.94	12.03	PB	-22	6.03	42.3	9.60	8.80	12.2	13.2	6.4	22.9	5.5	0.22	1.99	1.01	0.55	12.4	0.48
30	68.13	23.37	253.0	1.33	0.53	10.74	8.08	0.00	PB	-18	1.67	83.6	4.30	3.10	14.3	13.2	7.3	32.8	9.5	0.47	2.06	1.01	0.08	11.3	0.25
31	68.47	22.97	344.0	2.22	0.72	10.92	4.92	2.52	Ba	7	15.20	63.0	5.30	5.30	13.2	12.3	7.0	15.8	11.0	0.37	2.84	1.28	0.46	5.9	0.03
32	68.42	22.90	319.0	28.18	2.56	105.26	3.74	22.68	BP	4	6.30	42.3	6.00	6.30	12.4	12.3	7.6	33.5	12.5	0.65	3.43	1.28	0.94	8.3	0.20
33	68.40	22.85	314.0	2.78	0.82	24.08	8.66	0.00	BP	5	10.48	41.6	2.75	2.75	14.2	12.6	7.4	22.4	2.0	0.38	1.46	0.71	0.09	5.3	0.05
34	68.47	22.47	329.1	11.76	1.69	57.65	4.90	29.37	BP	3	7.69	47.9	4.05	4.05	12.8	12.3	7.7	32.0	12.0	0.49	2.46	0.69	0.79	7.5	0.13
35	68.88	22.05	526.0	8.35	1.62	113.22	8.14	0.00	MBW	24	12.89	38.2	3.70	3.70	10.9	11.0	7.4	28.0	9.0	0.35	2.08	0.94	0.40	4.8	0.06
36	68.67	22.05	498.0	10.27	2.08	302.97	29.50	0.33	MBW	23	10.66	35.7	5.10	5.10	11.7	10.8	7.5	33.5	9.5	0.40	2.38	1.01	0.48	6.5	0.05
37	68.67	22.03	508.0	1.39	0.54	52.39	37.69	0.00	MBW	22	8.18	38.2	2.85	2.85	9.8	11.2	7.3	32.8	9.5	0.47	2.06	1.01	0.38	4.8	0.02
38	68.65	22.05	551.0	45.28	2.92	213.24	4.71	4.39	Ba	19	8.07	63.0	9.05	7.10	10.1	11.0	7.0	15.8	9.5	0.25	0.93	0.58	0.46	5.4	0.05
39	68.65	22.02	503.0	26.78	2.23	367.93	13.74	1.58	Ba	21	8.51	38.6	6.45	6.45	9.5	11.2	7.8	48.3	10.0	0.49	2.40	1.28	1.29	3.5	0.04
40	68.93	21.03	613.0	15.39	1.83	464.64	30.19	0.00	Ba	66	15.14	41.8	5.50	5.50	10.0	10.4	7.4	31.0	6.5	0.38	1.46	0.71	0.24	4.1	0.07
41	68.92	21.05	506.0	3.47	0.95	16.00	4.61	0.00	MBW	65	6.12	54.5	8.15	8.15	10.7	10.5	7.2	20.5	5.5	0.37	0.91	0.94	0.28	4.0	0.06
42	68.92	21.00	555.0	8.35	1.62	113.22	8.14	0.00	MBW	65	8.00	54.1	3.70	3.70	10.2	10.7	7.2	27.9	7.5	0.49	1.88	0.94	0.33	4.8	0.05
43	68.92	21.00	538.0	6.66	1.42	45.44	6.82	10.57	MBW	65	15.84	49.8	5.10	5.10	11.7	10.8	7.4	29.8	8.0	0.50	2.05	1.01	0.40	5.4	0.09
44	68.93	20.98	584.4	11.95	1.61	184.31	15.42	0.00	MBW	68	9.29	27.7	14.30	8.10	10.1	10.8	7.5	48.6	13.0	0.75	3.71	1.26	0.50	4.4	0.10
45	68.92	20.98	528.0	15.23	2.70	2049.77	134.59	0.07	MBW	67	9.50	25.7	10.40	6.40	10.1	10.9	7.3	29.9	7.0	0.53	2.04	0.96	0.36	5.1	0.07
46	69.05	20.67	496.0	12.31	1.56	1161.78	94.38	1.58	MBW	87	8.28	25.3	3.00	3.00	9.5	11.0	7.8	48.3	17.0	0.18	3.49	1.03	1.29	3.5	0.05
47	68.70	21.57	446.1	31.43	3.01	603.93	19.22	3.96	MBW	35	10.43	32.8	7.30	6.20	9.1	11.5	7.4	31.0	9.5	0.64	1.65	0.91	0.48	6.6	0.05
48	68.70	21.50	487.9	28.04	2.26	329.51	11.75	6.63	MBW	37	5.68	35.1	12.60	6.70	9.8	11.2	7.5	31.3	9.0	0.47	2.28	0.85	0.44	6.5	0.05
49	69.08	20.67	776.3	16.10	1.91	1753.57	108.92	0.00	Ba	91	6.35	16.9	12.10	10.00	9.7	9.4	7.0	9.9	8.0	0.10	0.58	0.51	0.11	2.5	0.04
50	68.95	21.00	578.0	6.16	1.38	238.65	38.74	0.00	MBW	69	15.85	54.3	2.25	2.25	14.1	10.6	7.6	31.0	13.0	0.48	2.29	1.23	0.35	5.2	0.02
51	68.95	20.95	515.0	2.23	0.66	42.27	18.96	0.00	MBW	72	11.39	53.5	4.60	4.60	15.4	10.9	7.8	36.7	13.0	0.58	3.03	1.23	0.38	7.0	0.03
52	69.05	20.98	687.0	16.89	2.04	173.16	10.25	0.00	Ba	80	3.91	19.6	9.10	6.80	12.1	9.9	7.4	22.9	13.0	0.31	1.44	1.01	0.36	4.4	0.06
53	68.87	21.23	501.6	8.01	1.48	1166.31	145.61	1.87	MBW	56	5.64	35.9	5.05	5.05	14.5	11.1	7.6	30.4	13.0	0.75	1.95	1.38	0.55	7.4	0.06
Mean	68.59	22.07	434.9	14.16	1.59	331.30	26.05	18.28		26.45	8.02	47.78	6.30	4.70	12.1	11.7	7.0	26.6	8.1	0.42	1.78	0.92	0.44	6.9	0.19
Median	68.67	22.02	457.00	8.35	1.38	113.22	9.78	1.58		22.50	7.14	48.30	5.05	4.30	12.60	11.30	7.20	28.00	8.50	0.40	1.88	0.98	0.40	6.20	0.08
Minimum	66.92	20.67	108.0	0.90	0.37	5.45	3.10	0.07		-148.40	0.00	16.90	0.85	0.85	6.1	8.5	5.0	6.4	1.0	0.07	0.26	0.18	0.06	2.5	0.02
Maximum	69.18	25.40	930.9	115.18	7.01	2524.73	156.40	64.20		98.30	22.67	88.00	25.00	10.20	15.4	14.9	7.8	48.6	17.0	0.94	3.90	1.69	1.29	12.6	1.20

* SPB = spruce, pine and birch forest; PB = pine forest mixed with birch; BP = birch forest mixed with pine stands; MBW = mountain birch woodland; Ba = barren above the tree line

** DBT = Distance beyond treeline

*** LOI = Loss-on-ignition

preserved. Characters of the different Tanytarsini taxa used in this study are described by Brooks *et al.* (1997a).

Data analysis

Only chironomid taxa occurring in at least two lakes with a relative abundance of more than 2% in at least one lake were included in the numerical analyses (Table 2). Of the initial 63 taxa, 38 fulfilled these criteria. In all ordination, regression and calibration analyses, the chironomid percentage data were transformed to square-roots in an attempt to optimize the 'signal' to 'noise' ratio in the data (Prentice, 1980) and to stabilize the variances. All environmental variables, except pH and water and air temperatures, were log-transformed [ln (x + 1)] prior to numerical analyses to normalize their skewed distributions. The ordination analyses only used the measured chemical, limnological and catchment variables. The calculated mean July air temperature values were not used in the ordination analyses because they are estimated values and because of their high collinearity with some of the measured variables. The mean July air temperature values were solely used to derive chironomid–air-temperature calibration models that can be compared with the chironomid–surface-water-temperature inference model.

Detrended correspondence analysis (DCA) (Hill and Gauch, 1980), with detrending by segments, non-linear rescaling of axes, and downweighting of rare taxa, was undertaken on the chironomid data in order to explore the principal patterns of compositional variation, and to determine the gradient lengths of chironomid compositional turnover along the first few DCA axes. A series of exploratory DCAs were also run using the complete environmental data as predictor variables in an attempt to detect potential multicollinearity between environmental variables, and hence to identify variables that do not make a unique contribution to the overall regression model (ter Braak, 1988). When running these DCAs, all predictor variables were initially regressed onto the DCA axes (ter Braak, 1988). Variables with high (> 20) Variance Inflation Factors (VIFs) were eliminated one at a time beginning with the variable having the highest VIF, and the DCA was repeated until all VIFs were below 20 (ter Braak, 1988).

Redundancy analysis (RDA), a constrained gradient analysis technique (ter Braak, 1994), was used to explore the relationships between the chironomid assemblages and the measured environmental variables. The significance of the RDA axes was assessed using unrestricted Monte Carlo permutation tests (500 permutations; ter Braak, 1988; 1990; Birks, 1995). RDA was also used to identify a subset of environmental variables that explained statistically the greatest proportion of variance in the chironomid data.

Table 2 Basic information about the relative abundance (minimum, mean, maximum) number of occurrences, and Hill's N2 for each of the 38 taxa included in the 53-lake data set

Taxa	No. occurrences	N2	All values			Without zeroes	
			Minimum	Maximum	Mean	Minimum	Mean
Unidentified Orthocladiinae	48	29.5	0.0	18.4	3.6	0.6	3.6
Heterotrissocladius sp.	15	8.9	0.0	15.4	1.5	0.7	5.4
Heterotrissocladius maeari	13	8.4	0.0	9.7	0.7	0.5	3.0
Heterotrissocladius grimshawi	15	12.3	0.0	2.6	0.4	0.6	1.4
Heterotrissocladius subpilosus	12	3.1	0.0	37.5	1.3	0.6	5.8
Psectrocladius sp.	50	35.4	0.0	11.3	4.1	0.4	4.4
Psectrocladius sordidellus-group	53	29.5	0.9	36.8	6.4	0.9	6.4
Monopsectrocladius-group	42	21.5	0.0	30.5	7.0	0.5	8.9
Allopsectrocladius-group	27	13.6	0.0	9.1	1.0	0.4	1.9
Heterotanytarsus sp.	12	9.4	0.0	9.8	1.1	0.8	4.9
Orthocladius sp./*Cricotopus* sp.	47	26.7	0.0	20.7	4.3	0.5	4.8
Zalutschia zalutschicola	17	6.9	0.0	23.4	1.9	0.4	5.8
Zalutschia sp.	27	2.9	0.0	55.0	1.8	0.4	3.5
Corynoneura sp.	21	10.2	0.0	7.0	0.6	0.5	1.4
Abiskomyia sp.	3	3.0	0.0	4.5	0.2	3.5	4.2
Mesocricotopus sp.	5	3.6	0.0	2.8	0.1	0.8	1.6
Hydrobaenus sp.	4	1.6	0.0	18.7	0.5	0.4	6.1
Protanypus sp.	10	8.3	0.0	2.4	0.2	0.5	1.3
Unidentified Chironominae	29	21.8	0.0	3.3	0.7	0.4	1.2
Microtendipes sp.	42	24.3	0.0	22.5	5.3	0.7	6.8
Dicrotendipes sp.	41	27.7	0.0	8.7	2.2	0.7	2.8
Sergentia coracina	44	14.9	0.0	37.0	3.5	0.6	4.2
Unidentified Tanytarsini	53	40.0	2.5	49.6	15.4	2.5	15.4
Micropsectra gr. B/*Tanytarsina* gr. B	51	29.2	0.0	27.0	5.8	0.4	6.0
Tanytarsus lugens	36	12.9	0.0	18.1	1.9	0.4	2.7
Tanytarsus chinyensis	4	2.9	0.0	2.8	0.1	0.5	1.6
Paratanytarsus sp.	35	20.2	0.0	9.5	1.8	0.4	2.7
Cladotanytarsus mancus-group	25	17.9	0.0	3.6	0.6	0.4	1.3
Corynocera ambigua	34	11.2	0.0	55.0	4.6	0.6	7.2
Corynocera oliveri	9	5.7	0.0	8.5	0.7	0.9	4.1
Micropsectra sp.	24	12.8	0.0	20.8	3.2	0.9	7.1
Pagastiella sp.	23	15.3	0.0	5.3	0.8	0.5	1.8
Polypedilum sp.	22	11.6	0.0	6.4	0.5	0.5	1.2
Stempellinella sp.	19	11.8	0.0	4.4	0.5	0.4	1.4
Chironomus sp.	25	12.3	0.0	12.5	1.6	0.5	3.3
Cladopelma sp.	20	16.3	0.0	2.8	0.6	0.6	1.6
Stictochironomus sp.	4	3.5	0.0	3.2	0.2	1.1	2.0
Tanypodinae spp.	53	42.2	1.2	18.5	7.7	1.2	7.7

To do this, a series of constrained RDAs, in which the chironomid data were constrained to only one explanatory variable at a time, were run to assess the relative strength of each environmental variable. The statistical significance of each variable was assessed by means of a Monte Carlo permutation test (500 unrestricted permutations). The results of the permutation tests, canonical coefficients, approximate t tests, and the ratios of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2) were then used as criteria to identify the most appropriate environmental variables for quantitative reconstruction purposes (ter Braak, 1988; Birks *et al.*, 1990). Particular attention was paid to the latter criterion, as it serves as a good indicator of how effectively the variable is represented by axis 1 in the constrained analysis. As a general rule, quantitative inference models can be successfully developed for environmental variables that have high λ_1/λ_2 ratios (ter Braak, 1988).

Because many of the environmental variables in our data set are highly correlated with each other, we tested the strength and independence of various ecological gradients potentially suitable for the development of transfer functions by means of variance partitioning (Borcard *et al.*, 1992). By using a series of partial RDAs, the total variance in the chironomid data was partitioned into components representing different groups of explanatory variables (Borcard *et al.*, 1992). Particular attention was paid to assessing the power of lakewater temperature in explaining the variance in the chironomid data, as the primary aim is to develop a chironomid-based calibration function for palaeotemperature reconstructions. First, the variance in the chironomid data was partitioned among the chemical and physical components. In the second step, a subset of environmental variables was selected which explained best the variation in the chironomid data, as determined from a series of constrained RDAs and associated Monte Carlo permutation tests, and partitioned the variance between them. The overall results of variance partitioning helped to assess the proportion of independent variation in the chironomid data that can be explained by the various sets of environmental variables (Borcard *et al.*, 1992; Pienitz *et al.*, 1995; Jones and Juggins, 1995).

To determine whether to use linear- or unimodal-based numerical regression and calibration techniques (ter Braak and Prentice, 1988; Birks, 1995), the chironomid-water- and air-temperature data sets were initially analysed by detrended canonical correspondence analysis (DCCA) (ter Braak, 1986) to estimate the length of the chironomid compositional turnover (in standard deviation units; Hill and Gauch, 1980) along the water- or air-temperature gradients (ter Braak and Juggins, 1993). In these DCCAs, water or air temperature was the only explanatory variable and the DCCA options used were detrending-by-segments, non-linear rescaling, and downweighting of rare taxa.

The initial results of the DCA and DCCA were also used to identify potential outlying samples prior to regression and calibration. The following criteria were applied to identify unusual samples (e.g., Birks *et al.*, 1990; Korsman and Birks, 1996; Weckström *et al.*, 1997): (i) the sample score fell outside the 95% confidence limits of the sample score means on any of the first four DCA axes; and (ii) the lake had a large ($> 5\%$) residual distance to the constrained environmental axis in the DCCA using the environmental variable of interest as the sole explanatory variable, respectively. Additional checking of outliers in terms of an unusual combination of environmental variables was carried out using leverage diagnostics (ter Braak, 1990; 1994) in redundancy analysis (RDA), as well as principal components analysis (PCA) of the environmental data.

The statistical relationship of each individual taxon to water or air temperature was assessed using a hierarchical set of taxon response models (Huisman *et al.*, 1993; Oksanen 1997). This hierarchical set consists of a skewed unimodal response model, a symmetric (Gaussian) unimodal response model, a monotonically increasing or decreasing sigmoidal response model, and a null model of no relationship to temperature. The simplest statistically significant response model for each taxon was found by fitting the most complex model first and progressively removing parameters from the response model until the model could not be simplified further without a significant change ($p < 0.05$) in the deviance of the model. Deviance is a goodness-of-fit measure based on a likelihood ratio test that is analogous to the variance-ratio test (F-test) in normal least-squares regression (Crawley, 1993). Taxon response models were fitted by maximum likelihood estimation with a Poisson error structure and a logarithmic link function and were restricted to all taxa with occurrences in 10 or more (20% or more) of the samples in the data set. F-ratio tests were used to assess the significance of the response-model parameters rather than the simple chi-square test because the data are, as usual in biological data sets, over-dispersed as the deviance exceeds the degrees of freedom (Oksanen *et al.*, 1990; 1991; Crawley, 1993). Further details of maximum likelihood estimation, deviance, over-dispersion, etc. , are given in Crawley (1993). The numbers of taxa with statistically significant fits to the four types of response models are given in Table 3.

Table 3 Summary statistics for the modern chironomid-surface-water temperature calibration set. SD = standard deviation units of compositional turnover (Hill and Gauch, 1980; ter Braak and Juggins, 1993), λ = eigenvalue

	Surface-water	Air
Number of samples	53	
Number of taxa	38	
N2 for samples:		
minimum	8.16	
median	14.81	
maximum	19.83	
N2 for taxa:		
minimum	2.63	
median	19.63	
maximum	49.23	
DCCA axis 1:	Surface-water	Air
λ_1	0.122	0.110
Gradient length (SD)	1.627	1.748
% variance	12.0	10.9
DCA axis 2:		
λ_2	0.123	0.133
Gradient length (SD)	1.773	1.858
% variance	12.1	13.1
$\lambda_1\lambda_2$	0.992	0.827
Temperature (°C)	Surface-water	Air
minimum	6.1	8.5
mean	12.09	11.69
median	12.50	11.40
maximum	15.40	14.90
standard deviation	1.902	1.21
Taxon response models (maximum likelihood) for all taxa in $> 20\%$ of the samples:		
Skewed unimodal model	2	1
Symmetric unimodal model	3	11
Sigmoidal model	12	8
Null model	17	14

There are no strong theoretical reasons (Birks, 1995) for favouring the use of linear- or unimodal-based regression methods to develop chironomid temperature inference models. The chironomid data have a DCA gradient of 2.01 standard deviations (SD), the chironomid–water-temperature data have a DCCA gradient length of 1.63 SD (Table 3), the chironomid–air-temperature data have a DCCA gradient length of 1.75 SD (Table 3), 12 taxa show a statistically significant sigmoidal response and only five taxa show a statistically significant unimodal response to surface-water temperature (Table 3), whereas 11 taxa show a statistically significant unimodal response and eight taxa show a significant sigmoidal response to air temperature. These features of the data suggest that both linear- and unimodal-based techniques may be appropriate for these data (ter Braak and Prentice, 1988). Eight different calibration methods have thus been used, each based on slightly different underlying statistical models or ecological assumptions and we have selected the method(s) that performs best in a statistical sense by giving a low prediction error and a low maximum bias along the temperature gradients, as assessed in leave-one-out cross-validations (Birks, 1995), and represents a simple 'minimal adequate model' (*sensu* Crawley, 1993). The methods used are:

(1) simple weighted averaging (WA) with an 'inverse' deshrinking regression (Birks *et al.*, 1990; Birks, 1995);
(2) weighted averaging with taxon tolerance weighting (WA$_{tol}$) and an 'inverse' deshrinking regression (Birks *et al.*, 1990; Birks, 1995);
(3) simple weighted averaging (WA) with a 'classical' deshrinking regression (Birks *et al.*, 1990; Birks, 1995);
(4) weighted averaging with taxon-tolerance weighting (WA$_{tol}$) and a 'classical' deshrinking regression (Birks *et al.*, 1990; Birks, 1995);
(5) partial least squares (PLS) (Martens and Naes, 1989; ter Braak and Juggins, 1993; Birks, 1995; ter Braak, 1995);
(6) weighted-averaging partial least squares (WA-PLS) (ter Braak and Juggins, 1993; ter Braak, 1995; Birks, 1995);
(7) Gaussian logit model (GLM) (= maximum likelihood method) (ter Braak and van Dam, 1989; Birks *et al.*, 1990; Birks, 1995);
(8) modern analogue technique (MAT) (Bartlein and Whitlock, 1993; ter Braak, 1995; Birks, 1995) using Euclidean distance as a measure of dissimilarity between pairs of samples (with square-root transformed percentage values) and a weighted mean of the most similar modern samples, the weights being the inverse of the dissimilarity values so that samples that are most similar have the greatest weight.

The performance of each method was assessed on the basis of: (1) the root mean square error (RMSE) of the difference between the observed and the estimated temperature values; (2) the maximum bias along the temperature gradient (ter Braak and Juggins, 1993); and (3) the smallest number of 'useful' components in PLS and WA-PLS. To be considered 'useful', a component should give a reduction in prediction error of 5% or more of the RMSEP for the simplest one-component PLS or WA-PLS model (Birks, 1998). For calculating the bias statistics, the gradient is subdivided into 10 equal intervals, the mean bias (mean of the differences between (observed and inferred)) per interval is calculated, and the largest absolute value of mean bias for an interval is used as a measure of maximum bias. Estimating these statistics for the calibration set alone gives so-called 'apparent' statistics only (ter Braak and Juggins, 1993; Birks, 1995). As the same data are used to generate and to evaluate the inference model, the evaluation statistics will always be over-optimistic (Birks, 1995). A more realistic estimation of 'prediction error' or the likely error when the inference model is applied to additional independent data (e.g., fossil assemblages) is obtained by jack-knifing or leave-

one-out cross-validation (ter Braak and Juggins, 1993; Birks, 1995). All model assessments in terms of RMSEP, bias statistics, and the number of 'useful' components are based on leave-one-out cross-validation. For the modern analogue technique, prediction errors only are available as the algorithm specifically treats each sample as an independent sample and does not compare a sample with itself in finding close analogues within the calibration set. In MAT the RMSEP and maximum bias were estimated for 1,2, . . ., 10 closest matches and the number of matches that gave the lowest RMSEP and, if possible, the lowest maximum bias was selected as the final inference model.

All DCA, DCCA, RDA, PCA, and partial RDA were implemented by the program CANOCO 3.12 (ter Braak, 1988; 1990) and checked with version 3.12a using strict convergence criteria (Oksanen and Minchin, 1997). The WA, PLS and WA-PLS analyses were done by means of the program CALIBRATE version 0.81 (S. Juggins and C.J.F. ter Braak, unpublished program). GLM was implemented by the program GLR version 1.1 (S. Juggins, unpublished program) and WACALIB version 3.3 (Line *et al.*, 1994). MAT was implemented by the program MAT version 1.1 (S. Juggins, unpublished program). Taxon response modelling was done using the program HOF (Oksanen, 1997, and J. Oksanen, unpublished program). The program RMSEP (Birks, 1995) was used to calculate various of the inference-model statistics.

Results

The chironomid-water temperature data set is summarized in Table 3 in terms of the ranges and medians of the effective number of taxa per sample, and the effective number of occurrences per taxon, as estimated by Hill's (1973) N2 diversity measure (ter Braak, 1990; ter Braak and Verdonschot, 1995). The gradient length of DCCA axis 1 (constrained to water or air temperature) and the gradient length of the second unconstrained DCA axes are also presented, along with the eigenvalues and percentage variance of the chironomid data explained by each axis, as a guide to the presence of any large primary gradient and any large secondary gradients in the data. Water and air temperatures are summarized in terms of their range, median, mean and standard deviation. The thermal range of individual chironomid taxa is illustrated by their distribution and relative abundance along the water-temperature gradient (Figure 4).

Eigenvalues ($\lambda_1 = 0.26$, $\lambda_2 = 0.08$) of the first two DCA axes explain 33.1% of the cumulative variation in the chironomid data. This relatively low percentage of explained variance is not surprising, because the N2 values suggest a high degree of noise in the data, even after square-root transformation (Tables 2 and 3). DCA axis 1 is most influenced by sediment organic content, lakewater temperature, and maximum lake depth, the measured values of which showed statistically significant correlations with lake scores on the first DCA axis (Figure 5). Because DCA reveals environmental gradients of intermediate length, the choice between the ordination techniques based either on a unimodal response canonical correspondence analysis (CCA) or a linear response model (RDA) is somewhat subjective (ter Braak and Prentice, 1988). Therefore both sets of analyses were performed. The two methods produced results that are more or less similar. However, because the first two RDA axes explain a slightly larger proportion of the variance in the chironomid data, and because the ratio of the first eigenvalue (λ_1) to the second eigenvalue (λ_2) is slightly higher in RDA than in CCA (data not shown), only the results of the RDA are presented here.

After deleting collinear environmental variables (latitude, lake area and conductivity) on the basis of their high VIFs, RDA yields eigenvalues of 0.17 and 0.07 for the first two axes, respectively.

Figure 4 Distribution of common Chironomidae among the 53 sampled lakes from the coldest (top of diagram) to the warmest (bottom of diagram) in terms of measured surface-water temperatures (gr. = group).
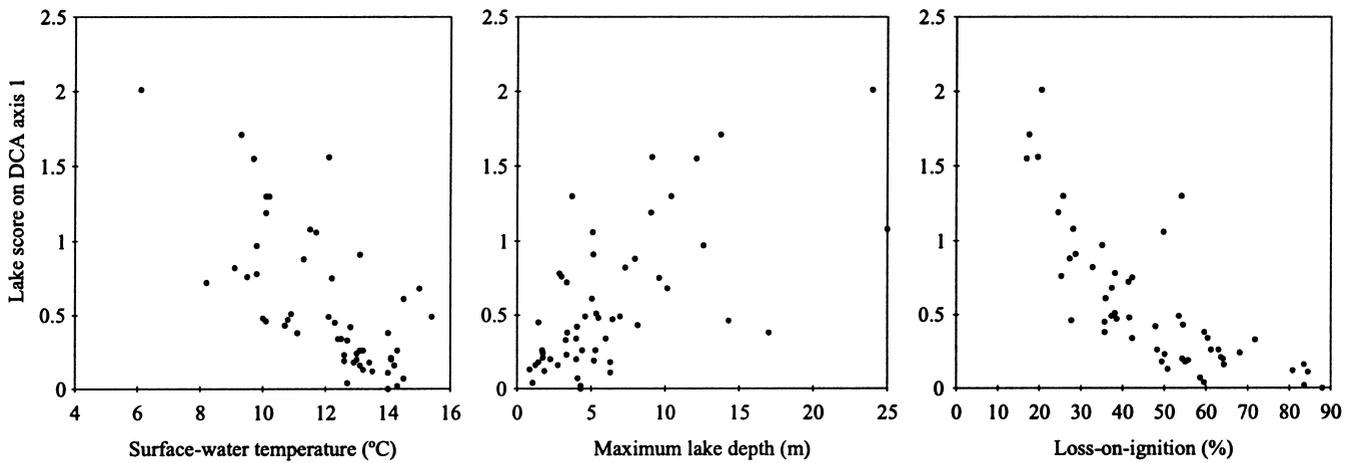
Figure 5 Results from detrended correspondence analysis (DCA) of surface-sediment chironomid assemblages in the 53 lakes as scatter plots of the first DCA axis samples scores against observed surface-water temperature (left), maximum lake depth (centre) and LOI (right).

Together these two axes capture 23.7% of the variance in the chironomid data. The species-environment correlations for RDA axes 1 (0.89) and 2 (0.88) are high, and together these first two axes account for 46.6% of the variation in the chironomid-environment relationship. Monte Carlo permutation tests indicate that both axes are statistically significant (p = 0.002). RDA axis 1 is strongly related to organic content (LOI), lakewater temperature (Temp), and maximum lake depth (Maxdepth), with interset correlations of –0.82, –0.68 and 0.65, respectively, whereas variables such as distance beyond treeline (DBT), sodium (Na), and longitude (Longitude) (interset correlations of –0.61, –0.59 and 0.55, respectively) contribute markedly to RDA axis 2 (Table 3). These interpretations are further confirmed by the canonical coefficients of the environmental variables and approximate *t* tests (Table 4).

In the RDA (Figure 6), axis 1 effectively separates 'an Arctic-Alpine lake type' (deep, cold, and oligohumic; e.g., lakes 24, 27, 38, 45, 49, 52), on the right-hand side of the biplot, from 'a Boreal lake type' (small, warm, meso/polyhumic; e.g., 2, 5, 6, 9, 12), positioned on the left-hand side of the biplot. Chironomid taxa that are most abundant in cold-water lakes are similarly positioned

on the right side of the RDA plot (e.g., *Heterotrissocladius* sp., *H. maeari* gr., *H. subpilosus*, *H. grimshawi*, *Heterotanytarsus* sp., *Protanypus* sp., *Mesocricotopus* sp., *Abiskomyia* sp., *Stempellinella* sp., *Micropsectra* sp., and *Corynocera oliveri*), whereas taxa characteristic of warmer and more humic waters are displayed on the left (e.g., *Dicrotendipes* sp., *Chironomus* sp., *Microtendipes* sp., *Cladotanytarsus* sp., *Tanytarsus* sp. *B*, *Psectrocladius sordidellus* gr., *Monopsectrocladius* gr., and *Allopsectrocladius* gr.).

The RDA in which the chironomid data were constrained to only one environmental variable at a time, show that LOI (a measure of sediment organic content), water temperature, and maximum water depth have the largest, statistically significant explanatory powers in explaining the variance in the chironomid data, as assessed by the amount of explained variance (15.0, 10.8 and 10.2%, respectively), as well as the highest λ_1/λ_2 ratios (1.23, 0.73 and 0.68, respectively) (Table 5). In this calibration data set, these three variables can therefore be considered to be potential candidates for quantitative environmental reconstruction. We now focus on testing the unique predictive power of water temperature in relation to other variables.

The results of the partial RDAs are summarized in Tables 6 and 7. The total explained variance in the (screened) data set is 50.8%. Physical variables (altitude, longitude, perimeter, catchment area, mire %, DBT, LOI, maximum depth and temperature) independent of lake chemistry account for the largest, statistically significant proportion (26.3%) of the variance, whereas lake chemistry independent of physical variables captures a non-significant proportion of 13.8% of the variation. There is also a large covariance or conditional effect (see Jones and Juggins, 1995) between the two sets of variables which represents an additional 10.7% (Table 6).

In a partial RDA where the effects of all other variables are partialled out, the three most significant environmental variables (LOI, temperature and maximum depth), as determined on the basis of the constrained RDAs (see above), independently account for 8.7% of the total variance in the data set (Table 6). When the effects of all other physical variables are partialled out, these three variables make an unique contribution of 10.7%. In such a test, the remaining physical variables make an unique contribution of 15.8%, while the covariance between these two sets of variables is 9.5% (Table 6).

Table 7 shows how the explained variance is partitioned between the three most significant components. The results indicate that lakewater temperature, maximum lake depth, and LOI can be considered to be statistically independent of each other, as each of these variables captures a significant amount of variation, regardless of the covariables used in each analysis. These tests

Table 4 Canonical coefficients, approximate *t* values and intra-set correlations of the environmental variables for RDA axes 1 and 2. Abbreviations are explained in Table 1

Variable	Canonical		*t* values		Intra-set correlations	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Longitude	–0.381	0.131	–0.140	0.045	–0.439	0.553
Altitude	–0.143	0.611	–0.039	0.156	0.509	–0.451
Lake perimeter	–0.084	0.109	–0.048	0.058	0.465	–0.025
Catchment area	0.127	0.436	0.069	0.219	0.487	–0.208
Mire – %	0.046	–0.062	0.030	–0.038	–0.315	0.129
DBT	–0.127	–0.849	–0.073	–0.453	0.123	–0.605
LOI	–0.646	0.620	–0.302	0.271	–0.821	0.169
Maximum depth	0.220	0.480	0.149	0.302	0.648	0.192
Water temperature	–0.227	–0.041	–0.126	–0.021	–0.682	0.087
pH	–0.034	–0.061	–0.013	–0.022	0.299	–0.485
Alkalinity	0.094	0.136	0.031	0.043	0.238	–0.488
K	–0.236	–0.277	–0.147	–0.161	–0.115	–0.459
Ca	0.030	–0.196	0.014	–0.087	0.182	–0.550
Na	–0.185	–0.448	–0.108	–0.244	0.054	–0.589
Mg	–0.050	0.004	–0.029	0.002	–0.027	–0.298
TOC	0.243	0.296	0.121	0.137	–0.568	0.006
Fe	–0.190	0.189	–0.139	0.130	–0.420	0.075
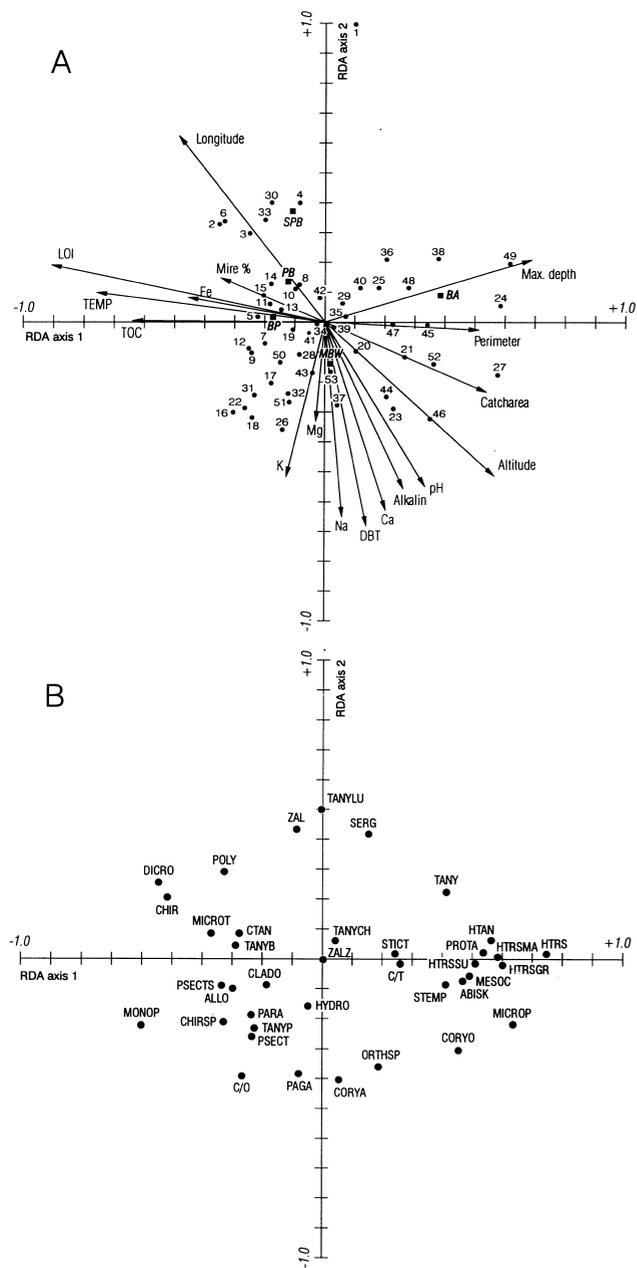
Figure 6 Redundancy analysis (RDA) correlation biplots showing the relationship between the 53 sites (A) and 38 chironomid taxa (B) and the measured environmental variables (screened data). Abbreviations for chironomid taxa: ABISK – *Abiskomyia*; ALLO – *Allopsectrocladius*; CHIR – Chironominae; CHIRSP – *Chironomus*; C/O – *Cricotopus/Orthocladius*; C/T – *Corynoneura/Thiemanniella*, CORYA – *Corynocera ambigua*; CORYO – *Corynocera oliveri;* CLADO – *Cladopelma*; CTAN – *Cladotanytarsus*; DICRO – *Dicrotendipes*; HTAN – *Heterotanytarsus*; HTRS - *Heterotrissocladius*; HTRSGR – *Heterotrissocladius grimshawi*; HTRSMA – *Heterotrissocladius maeari*; HTRSSU – *Heterotrissocladius subpilosus*; HYDRO – *Hydrobaenus*; MESOC – *Mesocricotopus*; MICROP – *Micropsectra*; MICROT – *Microtendipes*; MONOP – *Monopsectrocladius*; ORTHSP – unidentified Orthocladiinae; PAGA – *Pagastiella*; PARA – *Paracladopelma*; POLY – *Polypedilum*; PROTA – *Protanypus*; PSECT – *Psectrocladius*; PSECTS – *Psectrocladius sordidellus*; SERG – *Sergentia*; STEMP – *Stempellinella*; STICT – *Stictochironomus*; TANYP – Tanypodinae; TANY – Tanytarsini; TANYB – Tanytarsina group B; TANYLU – *Tanytarsus lugens*; TANYCH – *Tanytarsus chinyensis*; ZAL – *Zalutschia*; ZALZ – *Zalutschia zalutschicola*.

Table 5 The ratio of the first constrained eigenvalue to the second unconstrained eigenvalue, percentage variance explained by each environmental variable, and results of Monte Carlo permutation tests (500 unrestricted permutations) in a constrained RDA of the surface-sediment chironomid data (n = 53) where each variable is used as the sole constraining variable at a time

Variable	λ_1/λ_2	Variance explained (%)	P
Longitude	0.39	7.6	0.002
Altitude	0.44	8.4	0.002
Perimeter	0.38	6.9	0.002
Catchment area	0.39	7.0	0.002
Mire – %	0.26	5.5	0.002
DBT	0.20	4.4	0.024
LOI	1.23	15.0	0.002
Maximum lake depth	0.68	10.2	0.002
Water temperature	0.73	10.8	0.002
pH	0.23	4.9	0.006
Alkalinity	0.23	4.9	0.010
K	0.15	3.3	0.036
Ca	0.21	4.5	0.010
Na	0.18	4.1	0.018
Mg	0.12	2.6	0.148
TOC	0.51	9.2	0.002
Fe	0.31	6.3	0.002
Air temperature	0.50	9.2	0.002

Table 6 Results of partitioning the total variance in the surface-sediment chironomid data (53 lakes). P = significance level of Monte Carlo permutation test (99 unrestricted permutations); LOI = loss-on-ignition; MD = maximum lake depth; TEMP = water temperature

Source of variation	Percentage of covariation	P
a) Lake chemistry versus **physical variables**		
Explained by lake chemistry independent of physical variables	13.8	0.08
Explained by physical variables independent of lake chemistry	26.3	0.01
Explained by lake chemistry covarying with the physical variables	10.7	
Explained variance	50.8	0.01
Unexplained variance	49.2	0.01
b) LOI, MD and TEMP versus **other variables**		
Explained by LOI, MD and TEMP independent of other variables	8.7	0.01
Explained by other variables independent of LOI, MD, and TEMP	30.1	0.01
Explained by LOI, MD and TEMP covarying with other variables	10.4	
Explained variance	50.8	0.01
Unexplained variance	49.2	0.01
c) LOI, MD and TEMP versus **other physical variables**		
Explained by LOI, MD and TEMP independent of other physical variables	10.7	0.01
Explained by other physical variables independent of LOI, MD and TEMP	15.8	0.03
Explained by LOI, MD and TEMP covarying with the other physical variables	9.5	
Explained variance	36.0	0.01
Unexplained variance	64.0	0.01

Table 7 Summary of partial RDA of modern chironomid assemblages in 53 northern Fennoscandian lakes. P = significance level of Monte Carlo permutation test (300 unrestricted permutations); TEMP = water temperature; MD = maximum lake depth; LOI = loss-on-ignition

Variable	Covariables	Variance explained	P
TEMP	none	10.8	0.003
TEMP	MD, LOI	2.7	0.04
TEMP	LOI	2.8	0.03
TEMP	MD	5.6	0.01
LOI	none	15.0	0.003
LOI	TEMP, MD	4.6	0.01
LOI	TEMP	6.7	0.01
LOI	MD	7.5	0.01
MD	none	10.2	0.003
MD	TEMP, LOI	2.8	0.04
MD	TEMP	4.9	0.01
MD	LOI	2.9	0.02

also reveal that LOI is the strongest variable of these three variables, whereas much of the explanatory power of water temperature and maximum lake depth covaries with the remaining two variables. In a test where the effects of LOI and maximum depth are partialled out as covariables, water temperature makes a small (2.7%), but statistically significant independent contribution to the total variance.

In summary, these analyses indicate that the largest amount (26.3%) of the variation in the chironomid data is captured by physical environmental factors independent of lake chemistry, and that a large proportion of this variance (10.7%) is accounted for by only three physical variables, namely LOI, lakewater temperature, and maximum lake depth. The analyses further suggest that there is a large covariance between these three variables, yet the residual structure of each makes unique contributions to the variance. On the basis of all the ordination analyses, LOI, water temperature and maximum lake depth are identified as strong predictor variables in explaining the chironomid composition in our 53-lake calibration data set. Although reliable inference models can, at least in theory, be developed for each of these three variables, we present in this connection only the calibration function for reconstructing trends in lakewater temperature. The inference model for reconstructing lake depth using the same data set is presented elsewhere (Korhola *et al.*, 1999). We also present, for comparative purposes, the calibration function for mean July air temperature.

The results for the eight lakewater and air temperature inference methods are summarized in Tables 8 and 9. The full results in terms of taxon WA optima and tolerances, WA deshrinking equations, PLS and WA-PLS taxon beta-coefficients, GLM coefficients (b_0, b_1, b_2) and optima and tolerances, and MAT dissimilarity coefficients for the 16 analyses summarized in Tables 8 and 9 are available on request from H.O. or H.J.B.B. Comparison of the 'apparent' and 'jack-knifed' statistics for the eight inference methods for water temperature (Table 8) shows that the RMSEP

Table 8 Performance statistics for eight different inference models for summer surface-water temperature in terms of root mean square error (RMSE), coefficient of determination (r^2), mean and maximum bias, and root mean square error of prediction (RMSEP). For abbreviations and details of the inference models, see the text

Inference model	Apparent				Cross-validation jack-knifing			
	RMSE (°C)	r^2	Mean bias (°C)	Maximum bias (°C)	RMSEP (°C)	r^2	Mean bias (°C)	Maximum bias (°C)
WA (inverse)	1.335	0.517	0	3.564	1.560	0.342	–0.038	3.734
WAtol (inverse)	1.309	0.535	0	3.447	1.762	0.226	–0.033	3.732
WA (classical)	1.856	0.517	0	4.085	2.058	0.405	–0.031	3.818
WAtol (classical)	1.790	0.535	0	3.127	2.494	0.270	–0.029	3.760
PLS (1 component)	1.332	0.519	0	3.084	1.568	0.347	–0.001	3.564
WA-PLS (1 component)	1.335	0.517	0.0006	3.578	1.527	0.371	0.0005	3.879
GLM	1.490	0.398	0	3.624	2.162	0.321	0.0013	3.942
MAT (6 matches)	–	–	–	–	1.484	0.430	0.003	1.902

Table 9 Performance statistics for eight different inference models for mean July air temperature in terms of root mean square error (RMSE), coefficient of determination (r^2), mean and maximum bias, and root mean square error of prediction (RMSEP). For abbreviations and details of the inference models, see the text

Inference model	Apparent				Cross-validation jack-knifing			
	RMSE (°C)	r^2	Mean bias (°C)	Maximum bias (°C)	RMSEP (°C)	r^2	Mean bias (°C)	Maximum bias (°C)
WA (inverse)	0.846	0.512	0	2.701	0.951	0.388	–0.020	3.012
WAtol (inverse)	0.853	0.504	0	2.824	0.995	0.337	–0.019	3.099
WA (classical)	1.183	0.512	0	2.234	1.292	0.403	–0.042	2.787
WAtol (classical)	1.202	0.504	0	2.463	1.390	0.348	–0.053	2.943
PLS (3 components	0.420	0.880	0	0.682	0.749	0.626	–0.002	2.231
WA-PLS (2 components)	0.587	0.765	0	1.442	0.866	0.497	–0.004	2.925
GLM	0.959	0.360	0	1.879	1.383	0.342	–0.017	2.899
MAT (4 matches)	–	–	–	–	0.843	0.557	0.001	0.814

Figure 7 Relationship between observed and chironomid-inferred lakewater temperatures using a one-component partial least squares (PLS) model, with (predicted) and without (estimated) leave-one-out cross-validation.

are consistently higher (10.8–45.1%) than the 'apparent' RMSE, emphasizing the importance of using cross-validation as a means of deriving robust and realistic error estimates (Birks, 1995). With the exception of WA and WA$_{tol}$ with classical deshrinking, all the methods appear to perform moderately well as assessed by the 'apparent' errors (RMSE = 1.309–1.490°C, maximum bias = 3.084–3.624°C) but there are large differences between methods when the 'jack-knifed' errors are considered. Excluding WA and WA$_{tol}$ with classical deshrinking, GLM gives the highest RMSEP (2.162°C) in contrast to its apparent RMSE of 1.490°C. In terms of low RMSEP and low maximum bias, the MAT model gives the best performance, whereas in terms of low RMSEP

(1.527–1.568°C) only, there is little to choose between WA-PLS, WA (inverse deshrinking), and PLS. However, all these models give a maximum bias between 3.5 and 3.9°C. To give a visual impression of the performance of the models, the results of the water temperature transfer function based on linear PLS are shown in Figure 7.

Similar results are obtained for the mean July air temperature inference methods (Table 9) with a low RMSEP and the lowest maximum bias in the MAT model. In terms of low RMSEP (0.749–0.951°C) only, there is little to choose between the WA (inverse deshrinking), PLS, and WA-PLS models. All these models have a maximum bias between 2.2 and 3.0°C. The perform-
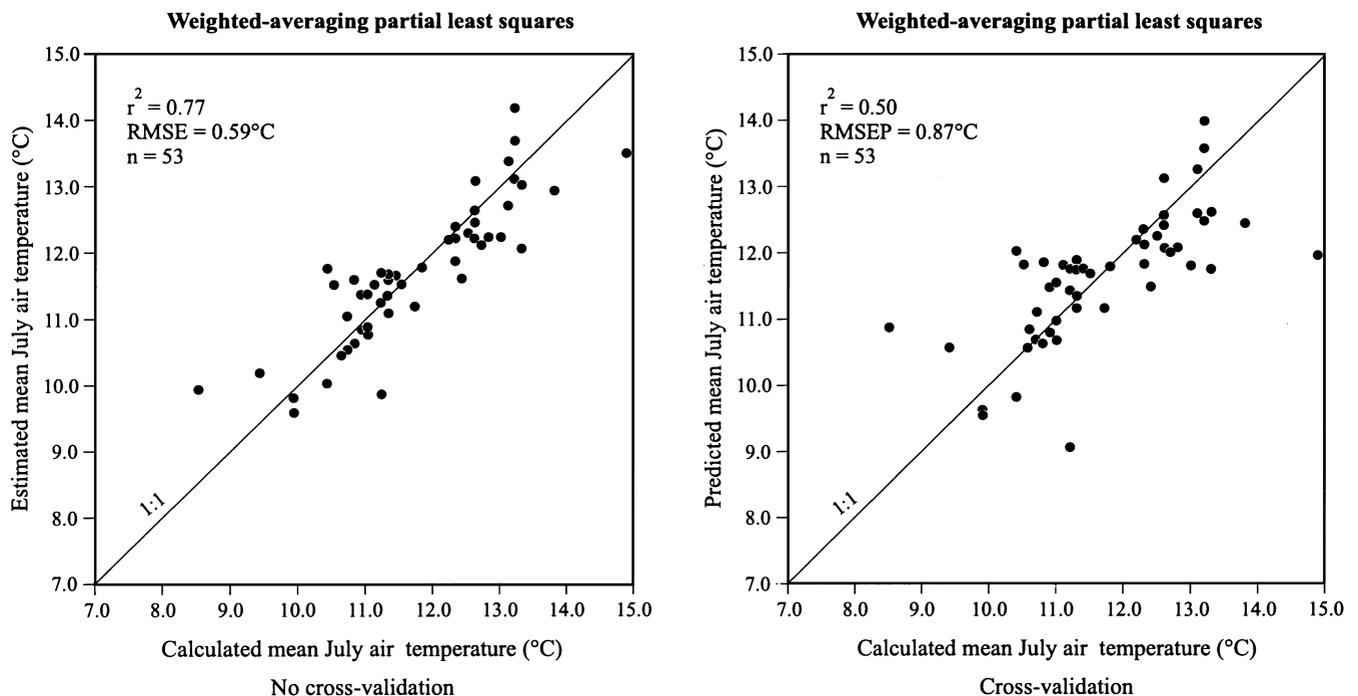
Figure 8 Relationship between calculated and chironomid-inferred mean July air temperatures using a two-component weighted-averaging partial least squares (WA-PLS) model with (predicted) and without (estimated) leave-one-out cross-validation.

ance of the two-component WA-PLS model for inferring mean July air temperatures is illustrated in Figure 8.

These results (Table 8) indicate that MAT, WA-PLS, WA (inverse deshrinking), and PLS can all be used to develop a transfer function for surface-water July temperature with a prediction error of about 1.5–1.6°C. This error is strikingly lower than the RMSEP (based on jack-knifing and a two-component WA-PLS model) of 2.26°C for a 39-sample calibration set from Canada that covers a summer surface-water temperature range of 6–27°C (Walker *et al*., 1997). However, this Canadian calibration set has a lower maximum bias of 2.4°C. A preliminary 44 sample chironomid calibration set from western Norway has a RMSEP of 2.22°C and a maximum bias of 5.29°C for summer surface-water temperature (range = 9.1–21.5°C) in a one-component WA-PLS model (Brooks and Birks, 1999).

Our results (Table 9) also show that MAT, WA-PLS, WA (inverse deshrinking), and PLS provide transfer functions for mean July air temperature with a prediction error of about 0.75–0.95°C and a maximum bias of 0.81°C (MAT) or 2.2–3.0°C (PLS, WA(inverse), WA-PLS). These results compare favourably with other chironomid–summer-air-temperature inference models. A 50-sample calibration set from the Swiss Alps has a RMSEP of 1.37°C and a maximum bias of 1.67°C for a two-component WA-PLS model in relation to mean July air temperature (range = 6.6–17.3°C) (Lotter *et al*., 1997). The 39-sample calibration set from Canada (Walker *et al*., 1997), when calibrated for mean July air temperature (range = 5–19°C) has a RMSEP of 1.54°C and a maximum bias of 1.71°C for a two-component WA-PLS model (Lotter *et al*., 1999). The 44-sample Norwegian data set covers a range of 5.7–14°C in mean July air temperature and has a RMSEP of 1.11°C and a maximum bias of 2.46°C in a one-component WA-PLS model (Brooks and Birks, 1999).

Discussion

The original chironomid–water-temperature (range = 6.1–15.0°C) calibration model based on 30 sites and WA with a classical deshrinking yielded a RMSEP of 1.13°C and maximum bias of 1.1°C (Olander *et al*., 1997). Thus, increasing the size of the training data set has led to a deterioration in model performance. Expansion of the data set has probably increased its biological and environmental heterogeneity, and consequently one would expect prediction errors to rise. It appears that there may be a critical size for a calibration data set after which the model improvement due to better estimates of taxon optima outweighs the inaccuracies introduced by heterogeneity in the data (Bennion *et al*., 1996; Walker *et al*., 1997). Obviously, this limit has not been reached in this study. However, as the data set increases in size, there may be a significant improvement in model performance, particularly when assessed by cross-validation techniques and by bias statistics (Birks, 1995; 1998).

The relationships between chironomids and temperature are generally well established (e.g., Walker and Mathewes, 1989; Walker *et al*., 1991b; Olander *et al*., 1997; Brooks *et al*., 1997a; 1997b; Lotter *et al*., 1997; Brooks and Birks, 1999), although opposing opinions have also been presented (Warwick, 1989; Warner and Hann, 1987; Hann *et al*., 1992). In general, chironomid taxa are known to differ in their temperature tolerances. Temperature may affect chironomid assemblages both directly (e.g. pupation, emergence, growth, flight, feeding and hatching) and indirectly (e.g., oxygen conditions, length of the ice-cover period, stratification, inflow rates, etc) (Smol *et al*., 1991). Many broad-scale biogeographical investigations have also documented a close connection between the present-day distribution patterns of Chironomidae and climate (Brundin, 1949; 1956; Walker and Mathewes, 1989; Rossaro, 1991).

All studies where both surface-water- and air-temperature inference models have been developed show that the statistical relationship between the composition of modern chironomid assemblages and mean July air temperature is as strong or stronger than for surface-water temperatures; for example, r^2*100 (based on leave-one-out cross-validation models) for three chironomid–temperature inference models based on WA-PLS shows that the variance in surface-water temperature modelled by the chironomid assemblages is 88% (N. America; Walker *et al*., 1997), 30.2% (Norway; Brooks and Birks, 1999), and 37.1% (northern Fennoscandia; this paper), whereas the modelled variance in summer air temperature is 85%, 69% and 49.7%, respectively. Ecological reasons for the good performance of chironomid assemblage composition in predicting mean July air temperatures are presented by Brooks and Birks (1999), whereas Birks (1998) discusses possible statistical reasons for the generally poorer performance in modelling surface-water temperature as a function of chironomid assemblages (see below).

Brooks and Birks (1999) argue that midge larvae are benthic organisms and therefore only those living in very shallow water will be exposed to surface-water temperatures. Most lakes in the current calibration set are shallow and clear and thus the temperature difference between the epilimnion and hypolimnion within the lakes is generally small or non-existent. On the other hand, air temperature is closely related to lakewater temperature, especially in the summer (Livingstone and Lotter, 1998) which in turn influences larval developmental rates. As the adult is the dispersal stage, the successful colonization of new localities is more likely to be dependent on air temperature than on water temperature (Brooks and Birks, 1999).

In contrast to a comparable study in western Norway (Brooks and Birks, 1999), there are relatively small differences in the percentage variance in mean July air temperature modelled by the northern Fennoscandian chironomid assemblages (mean r^2 for all eight inference models on Table 9 = 0.437 = 43.7%) compared to surface-water temperature (mean r^2 on Table 8 = 0.339 = 33.9%). In western Norway the comparable figures are 68.5% (air temperature) and 30.2% (surface-water temperature). Nilsson *et al*. (1996) and Birks (1998) discuss the possible sources of the unexplained variance $(1-r^2)$ in inference models and propose that the unexplained variance can be partitioned into (1) variance in the environmental variable consisting of repeatability and reproducibility errors ('pure error') and (2) variance in the model ('model error' or 'lack-of-fit'). The pure error sets the upper limit of the variance that it is possible to model and it is usually dominated by the repeatability error resulting from the natural variability in the environmental variable (Nilsson *et al*., 1996).

The unexplained variances in our northern Fennoscandian chironomid–temperature data are 56.3% (mean July air) and 66.1% (surface water), in contrast to 31% (mean July air) and 68.2% (surface water) in western Norway (Brooks and Birks, 1999). There are at least three possible explanations for these differences, particularly in the air-temperature models, between the two areas. (1) There may be difficulties in estimating reliable mean July air temperatures in a remote area such as northern Fennoscandia where there are few climatic stations compared to western Norway where there is a relatively dense network of climate stations. (2) In an extremely oceanic climate such as in western Norway, there may be large and unpredictable fluctuations in surface-water temperatures during the day and from day to day compared to areas with a less oceanic and more stable continental climate such as northwestern Finland. As a result the western Norwegian surface-water-temperatures may be inherently more variable than other surface-water-temperature data. (3) There is a significant correlation between the measured water temperature and the altitude-corrected air temperature in the northern Fennoscandian data set. This suggests that the entire water mass in these clear-water

lakes may be in close contact with the atmosphere (Blom *et al.*, 1998). As a result, there are no strong differences between the calibration models that use either air or water temperatures in our northern Fennoscandian data set.

In evaluating the performance of our chironomid-temperature calibration set, it is important to consider not only the random differences or error in its predictive abilities, as estimated by RMSEP, but also the systematic differences in the predictions (ter Braak and Juggins, 1995; Birks, 1995; ter Braak, 1995; Lotter *et al.*, 1997). The systematic differences are estimated by the mean bias and by the maximum bias in the predicted values. In all the models summarized in Tables 8 and 9, the highest maximum bias is always associated with the lowest temperature segments of the surface-water- or air-temperature gradients. The maximum bias for all the inference models (except for MAT) is about 3.5–3.8°C for surface-water temperature and 2.2–3°C for air temperature. These maximum bias values are high compared to the RMSEP and indicate that the predictive abilities of our chironomid data set are clearly worst at low temperatures. This is presumably due to the small number of lakes with low water or air temperatures (Figure 2) in the data set and hence to unreliable estimation of taxon parameters (WA optima, (WA)-PLS coefficients, etc) for taxa associated with the low end of the temperature gradient. As a result there is a strong tendency for predicted values to be seriously over-estimated for lakes with low water or air temperatures.

In contrast to Walker *et al.* (1991b), we found sediment organic content (as represented by LOI) to be a significant explanatory variable for chironomid distributions and relative abundances in our study lakes. This may, in part, be due to the multiple sampling approach applied here that may give a more reliable picture of the available substrates within a lake than the single surface-sediment sampling method used by Walker *et al.* (1991b). It may also be significant that the LOI gradient in this study is longer than the one in Walker *et al.* (1991b). Several studies on chironomid ecology have suggested correlations between chironomid taxa and substrate (e.g., McGarrigle, 1980; Pinder, 1986; Winnell and White, 1985). In the current data set, LOI and lakewater temperature are positively correlated in a way that the lakes with the most minerogenic sediments are usually also the coldest. Close coupling of these variables is obviously related to the decreased productivity of colder lakes and the low input of organic matter from their catchments. However, the results of the variance partitioning indicate that temperature and LOI both explain a statistically significant component of variation in the chironomid data that is statistically independent of each other. By examining sediments from lakes that commonly exhibit only minor fluctuations in LOI (e.g., relatively deep sites in the tundra) the risk of confusing sedimentological variations with temperature changes can thus be reduced. Fluctuations in LOI should therefore be viewed as a complementary source to the temperature inferences in palaeolimnological research of lakes in the study area. In lake Tšuolbmajavri (lake number 35 in the calibration set) sediment core the measured LOI values vary little (14–19%) during most parts of the Holocene (unpublished data). There are, however, distinct changes in the composition of the chironomid fauna; for example, in the proportions of *Heterotrissocladius maeari* (0–30%) and *Corynocera oliveri* (0–30%). Both are considered as northern cold-stenothermic taxa (Brundin, 1949; 1956; Pinder and Reiss, 1983). Warwick (1989) suggests *Heterotrissocladius* to be a sediphilic taxon. In lake Tšuolbmajavri *H. maeari* and *C. oliveri*, however, have responded to changes in some factor other than sediment organic content, quite possibly to changes in temperature.

In comparison to other existing regional chironomid–climate-calibration data sets (e.g., Walker *et al.*, 1997; Lotter *et al.*, 1997) we propose that our calibration set has certain important features. These are: (i) our lakes all are undisturbed and are in a natural condition; (ii) the calibration set has been sampled from a very restricted biogeographical area with a similar geological setting; (iii) the climate gradient in our study area has been shown to be stable; (iv) most of the study lakes are transparent and their water is thus in close contact with the atmosphere; and (v) the sediment organic content and thus the 'substrate' are more adequately measured in our study compared to previous investigations. All these features together with the addition of air-temperature data in our models are positive responses to the original criticisms raised by Hann *et al.* (1992) about the first chironomid–temperature-calibration study of Walker *et al.* (1991b).

In conclusion, we have developed transfer functions for inferring past lakewater and mean July air temperatures by means of chironomid assemblages preserved in lake sediments. However, the predictive abilities of our transfer functions are at present still relatively weak, particularly for an analysis of fine-scale Holocene climatic fluctuations. The current data set has large secondary gradients, with the second, unconstrained axes slightly larger than the first temperature-constrained axes, presumably reflecting variation in the chironomid assemblages that is unrelated to the measured water or air temperatures. Despite the expansion of the data set, many problems typical of small regional training sets, such as truncated species distributions, uneven distribution of sites along the environmental variable of interest (Jones and Juggins, 1995), and high maximum bias at the ends of the sampled gradient are still present. It is therefore necessary to expand further the geographical and temperature ranges of our data set, particularly at the low temperature end of the gradient, in an attempt to overcome these problems.

Acknowledgements

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