

A northwest North American training set: distribution of freshwater midges in relation to air temperature and lake depth

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Abstract Freshwater midges, consisting of Chironomidae, Chaoboridae and Ceratopogonidae, were assessed as a biological proxy for palaeoclimate in eastern Beringia. The northwest North American training set consists of midge assemblages and data for 17 environmental variables collected from 145 lakes in Alaska, British Columbia, Yukon, Northwest Territories, and the Canadian Arctic Islands. Canonical correspondence analyses (CCA) revealed that mean July air temperature, lake depth, arctic tundra vegetation, alpine tundra vegetation, pH, dissolved

organic carbon, lichen woodland vegetation and surface area contributed significantly to explaining midge distribution. Weighted averaging partial least squares (WA-PLS) was used to develop midge inference models for mean July air temperature ($r^2_{boot} = 0.818$, RMSEP = 1.46°C), and transformed depth ($\ln(x+1)$; $r^2_{boot} = 0.38$, and RMSEP = 0.58).

Key words Chironomidae · Transfer function · Beringia · Air temperature · Lake depth · Canonical correspondence analysis · Paleoclimate

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Introduction

Palaeoecologists seeking to quantify past environmental changes rely increasingly on transfer functions that make use of biological proxies (Battarbee et al. 2002; Lotter et al. 1997). Midges have been shown to be an excellent proxy organism for climate (Walker et al. 1991), and have been used to develop transfer functions for air and water temperature (Brooks and Birks 2001; Olander et al. 1999; Walker et al. 1997), and lake depth (Korhola et al. 2000). The application of temperature transfer functions has provided quantitative estimates of late-Quaternary climate conditions (Cwynar and Spear 2001; Heiri and Millet 2005; Larocque and Hall 2004.; Massferro

and Brooks 2002; Palmer et al. 2002; Rosenberg et al. 2004; Yelle et al 2005).

However, climate alone does not determine the distribution of midge taxa. For example, in North America *Corynocera ambigua* is common and abundant in Alaska, Yukon, Northwest Territories and adjacent regions, but is essentially absent farther north, east and south despite comparable temperatures and lake depths (Walker and MacDonald 1995; Walker et al 1997). Regional limnological trends and extremes in variables such as chemistry or salinity also influence midge distribution (Heinrichs et al 2001), and can override the impacts of climate (Walker 1995). In addition, chironomids are sensitive to other environmental variables, including metals (e.g., Brooks et al 2005), benthic oxygen levels (e.g., Quinlan and Smol 2001a), and other forms of pollution (e.g., Hynynen et al. 2004). In order to minimize these confounding environmental factors, the taxon assemblages and general climatic conditions of the site of interest should ideally be represented in the model to be used.

Alaska and much of Yukon form the eastern portion of Beringia, a region that remained largely unglaciated through the Last Glacial Maximum (LGM, 26,000–14,000 14C yr BP; Bradley 1999). The sediments of this region are therefore of great value for their potential to provide continuous palaeoclimatic records for the Arctic extending back through the LGM. Few quantitative palaeoclimatic data exist for this region; no midge temperature or lake depth reconstructions have yet been published.

The usefulness of midges as indicators of temperature and lake depth in northwestern Canada has recently been demonstrated (Gajewski et al 2005; Walker et al 2003; Wilson and Gajewski 2004), and the models presented here expand on those results. Lakes from Alaska and British Columbia are added to existing datasets from Yukon/ Northwest Territories (Walker et al. 2003) and Canadian Arctic Islands (Gajewski et al 2005), and temperature and depth transfer functions are developed and tested. The inclusion of sites from a broader geographical area makes these new models well suited for reconstructing temperature and lake depth throughout eastern Beringia.

Study area

Data were compiled from four independently collected datasets in Alaska, Yukon/ Northwest Territories (NWT), British Columbia (BC) and the Canadian Arctic Islands (Fig. 1). The 56 sites in Yukon and adjacent NWT were collected in July 1990; chemical, diatom and midge data for these sites have previously been published (Pienitz et al 1995, 1997; Walker et al. 2003). Samples and data from the Alaskan sites were collected in summer of 1996. Midge analysis of 34 Alaskan lakes is presented here; chemical, diatom and cladocera data for these and other lakes are found in Gregory-Eaves et al (1999, 2000) and Sweetman and Smol (2006). The 50 sites from the Canadian Arctic Islands were collected over a 10 year period from 1992 to 2002. Diatom, lake chemistry and chironomid data for these and other lakes are published elsewhere (Bouchard et al. 2004; Gajewski et al 2005). Fifty-seven lakes from BC were sampled in August 2001; midge, limnological and environmental data from 49 of these sites are presented here for the first time.

Collectively, these sites span a latitude range of 30°, and longitude range of 70°, and are distributed through seven ecozones in Canada alone (Natural Resources Canada 2003). Temperatures vary greatly in this region (Natural Resources Canada, 2003; Phillips 1990). In the Canadian Arctic Islands summer temperatures are cool, often having averages of less than 8°C, and winter temperatures often average less than -30°C. In interior BC summer temperatures average -15°C, and winter averages are about -8°C. In coastal Alaska and Yukon the arctic waters provide some moderating effect on climate, and temperatures are cold, although not extreme, year round. In comparison, the climate of interior Alaska and Yukon is continental and subject to some of the most extreme temperature ranges in North America with a greater than 40°C difference between the mean temperatures of the warmest and coldest months (Phillips 1990). Permafrost varies from continuous in the Arctic, to discontinuous in central Alaska and Yukon, and is absent in BC (Natural Resources Canada 2003).

Lakes selected for this study were ideally small, shallow and undisturbed. Lakes with little or no inflow were sought to ensure that all midge assemblages were

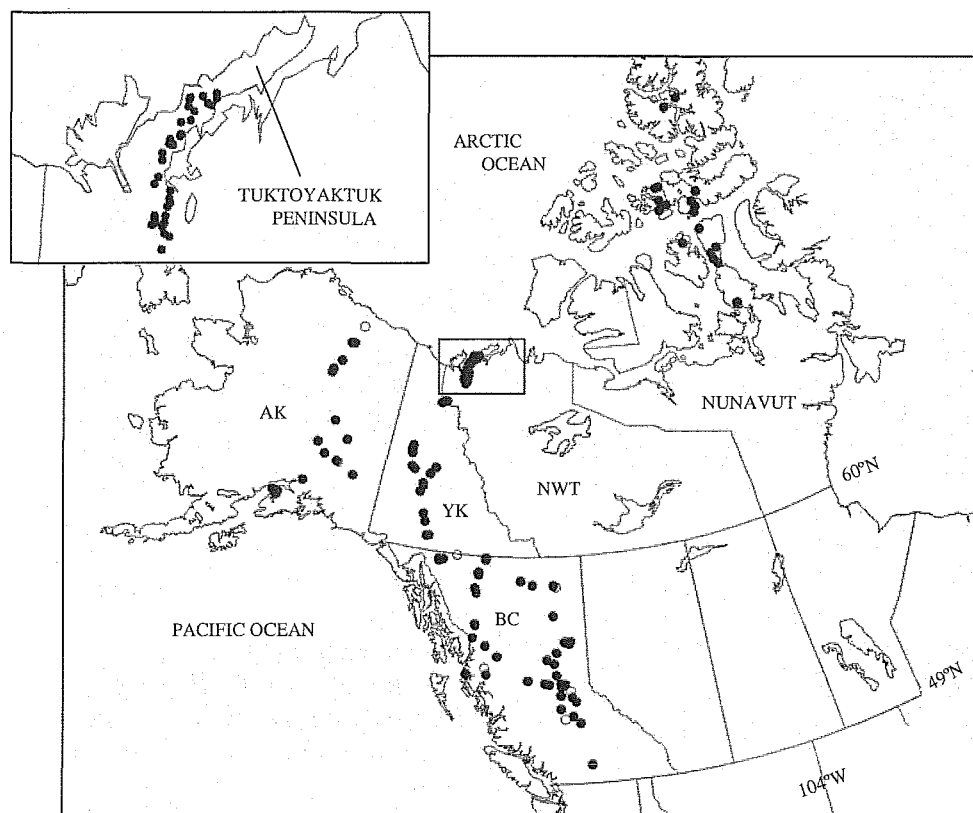


Fig. 1 Location of the 145 lakes of the northwest North American training set. Outliers are identified by open circles

influenced primarily by the local limnological and environmental data collected.

Methods and materials

Midge analysis

Sediment for midge analysis was obtained using a Kajak-Brinkhurst (Glew 1989) or mini-Glew (Glew 1991) gravity sediment corer, or an Ekman grab. Sediment samples were taken from approximately the deepest part of each lake, except for a few lakes whose depths exceeded the 30 m limits of sampling equipment. For each core, the top 1 or 2 cm of sediment were extruded on site, transferred to Whirlpak® bags, and kept cool until analysis at a later date. The volume of sediment available for analysis varied among datasets and depended on the type of corer and number of cores taken. In the laboratory, midges (chironomid head capsules, ceratopogonid head

capsules and *Chaoborus* mandibles) were processed and mounted following established protocol (Walker 2001; Walker et al, 1991).

Chironomids were identified primarily with reference to Wiederholm (1983), Walker (1988, 2000), and Oliver and Roussel (1983). A complete list of taxa and identification notes is available in Barley (2004; Appendix 1). Photos have been included to distinguish between *Zalutschia* type A and *Zalutschia* type B (Fig. 2). Chironomid head capsules were rarely identified to species, and more often to genus, or to groups of species or genera. Head capsules belonging to the subfamily Tanyptodinae are often fragmented; provided there were sufficient parts for them to be identified, they were always counted as whole. For consistent and precise counting of all other subfamilies, fragments of head capsules without the median teeth were not counted (except *Cladopelma* and *Cryptochironomus* which are easily identified by the lateral teeth), those with half the mentum were counted as a half, and those

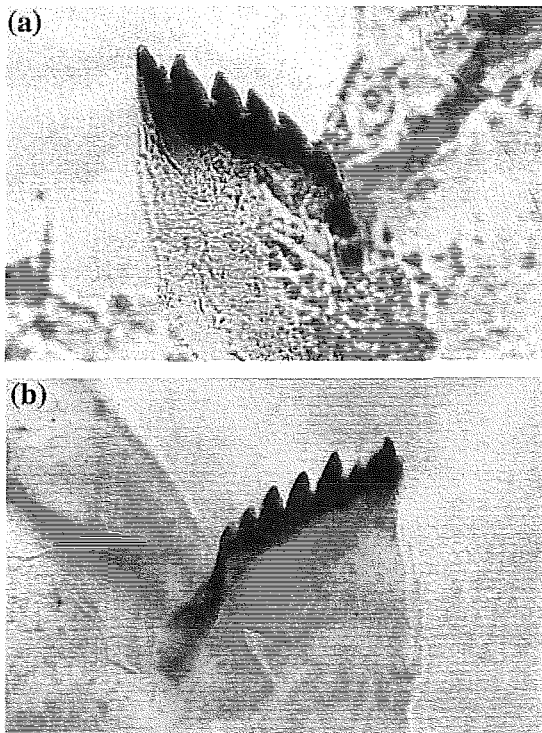


Fig. 2 Photos of the mentum of two types of *Zalutschia*. (a) *Zalutschia* type A: each median tooth has a small accessory tooth (unless worn), five pairs of lateral teeth, the last of which is sometimes shorter than the other laterals (though not on this specimen). (b) *Zalutschia* type B: each median tooth is asymmetrical with its peak on the median side of the tooth, the 1st pair of laterals is much reduced, and the 2nd to 6th pairs of laterals are of comparable size

with all median teeth were counted as whole. For *Chaoborus*, mandibles were counted individually (not as pairs). To ensure consistent identification among datasets, the authors (JK and EB) re-examined the midge slides from the Canadian Arctic Islands and Yukon/NWT datasets and updated the counts in accordance with the taxonomy described above.

A minimum count of 75 identifiable chironomids per sample was used. This value was chosen as a conservative estimate of the number of head capsules required to provide a statistically representative sample of the assemblage found at the deepest part of a given lake (Heini and Lotter 2001; Larocque 2001; Quinlan and Smol 2001b). A total of 145 lakes met this criterion, and constitute the sites of the northwest North American training set.

Environmental variables

Data for the Alaska, Yukon/NWT and Canadian Arctic Islands datasets were collected as part of independent studies and are presented elsewhere along with their accompanying methodologies (Gajewski et al. 2005; Gregory-Eaves et al. 2000; Pienitz et al. 1997). Physical, chemical and environmental data for the BC lakes are presented here (Table 1). Seventeen variables (with values above the limits of detection in >50% of lakes) were common to all four datasets.

Physical and environmental data were obtained from topographical maps (1:50,000) or collected in the field. Latitude (LAT) and longitude (LONG) were obtained at each site using a hand-held geographical positioning system, and recorded in decimal format. Elevation asl (ELEV), and surface area (SA) for each lake were determined using topographical maps. Maximum depth (DEPTH) was assessed by repeat sampling (except KW28 and KW46 where maximum depth exceeded equipment limits and sampling depth was substituted). pH readings were taken from a meter (Beckman FΦ255 pH/Temp/m V). Due to the failure of our conductivity meter during sampling, conductivity (COND) values were estimated using a linear regression model developed from 300 paired salinity and conductivity measurements ($y = 0.8754x + 0.6446$, where $y = \log(\text{cond})$, $x = \log(\text{salin})$, $r^2 = 0.987$). The salinities used in this model were calculated as the sum of major cations and anions (Ca, Na, Mg, K, Cl, SO₄, and DIC; Cumming et al. 1995).

Water samples for chemical analysis were collected near the center of each lake approximately 0.5 m below the water surface. Where necessary, samples were filtered and treated on site following the procedures outlined in the Analytical Methods Manual (Environment Canada 1994a, b). Water samples were stored under cool and dark conditions, and were analyzed by Environment Canada's Pacific Environmental Science Centre, Vancouver, BC. The variables with data for all four datasets are presented: calcium (Ca), chloride (Cl), potassium (K), sodium (Na), sulphate (SO₄), dissolved silica (SiO₂), dissolved organic carbon (DOC), and dissolved inorganic carbon (DIC).

Surrounding vegetation for all datasets was entered as binary variables after classification into one

Table 1 Environmental, limnological and chemical data for 49 BC lakes in the Northwest North American training set

Lake	LAT (metric)	LONG (metric)	ELEV (m)	SA (ha)	DEPTH (m)	pH	COND (μ S/cm)	JTEMP ($^{\circ}$ C)	Ca (mg/l)	Cl (mg/l)	K (mg/l)	Na (mg/l)	SO ₄ (mg/l)	SiO ₂ (mg/l)	DOC (mg/l)	DIC (mg/l)	Vegetation
KW02	49.90	120.17	1619	2	1.5	7.7	55	13.1	10.0	1.7	0.9	2.3	4.7	3.7	16.0	5.9	FOREST
KW03*	52.15	122.07	930	8	1.5	8.9	522	15.1	23.5	12.4	24.4	27.3	<0.5	17.8	31.3	99.2	FOREST
KW04	52.67	122.38	796	6	14.3	8.2	256	15.8	43.6	0.7	1.6	7.5	<0.5	20.4	8.8	48.6	FOREST
KW05	53.32	122.35	908	14	12.5	8.0	19	14.9	1.6	0.2	0.8	1.0	0.7	1.5	12.0	1.5	FOREST
KW06	53.88	123.25	762	6	7.3	8.2	123	14.9	18.8	3.6	1.4	3.2	1.0	15.0	2.6	20.2	FOREST
KW07	53.92	123.65	762	23	1.1	7.8	81	13.3	3.0	15.8	0.8	10.0	<0.5	<0.1	8.5	4.8	FOREST
KW08	54.05	125.05	939	31	8.5	8.4	77	14.2	12.8	0.2	1.2	3.9	2.5	0.2	13.0	10.1	FOREST
KW10	55.20	127.68	339	23	2.6	7.9	97	14.7	16.0	2.9	0.6	3.4	9.0	5.8	3.8	10.1	FOREST
KW11	54.32	128.55	183	6	8.7	8.1	38	15.7	0.8	7.5	<0.1	4.6	0.7	<0.1	1.7	0.8	FOREST
KW12	55.70	128.77	251	8	7.25	8.1	121	14.6	20.6	0.9	0.5	2.5	3.5	5.5	3.7	18.2	FOREST
KW13*	54.62	128.70	224	2	4.5	6.8	5	14.7	<0.1	0.2	0.2	0.2	<0.5	<0.1	3.4	0.9	FOREST
KW14*	54.23	130.12	73	2	8.5	5.4	17	12.4	0.6	1.4	<0.1	1.5	0.8	3.9	13.6	1.3	FOREST
KW15	54.28	130.27	60	2	0.75	6.6	43	12.4	3.2	3.3	0.2	3.1	2.9	0.8	16.0	1.3	FOREST
KW19	56.05	129.90	90	17	11	8.0	95	11.4	17.6	0.3	0.3	0.7	10.6	3.8	1.9	10.5	FOREST
KW20	56.67	129.75	550	6	4	7.0	14	11.9	1.4	<0.1	<0.1	0.9	0.6	3.3	9.6	1.4	FOREST
KW21	56.72	129.78	599	42	12.8	7.8	32	11.9	3.6	1.0	0.2	1.2	1.5	3.9	6.2	2.8	FOREST
KW23	58.22	129.83	1205	42	11.8	8.0	45	9.4	7.7	0.8	0.9	1.0	1.9	5.8	3.0	5.8	T-ALP
KW24	58.25	129.85	1209	25	12.5	8.0	26	10.0	4.8	0.1	0.3	1.1	1.1	7.8	1.6	4.5	T-ALP
KW25	58.43	130.00	799	39	19.2	8.8	148	11.3	23.5	0.6	1.1	4.8	5.3	6.3	4.7	23.0	FOREST
KW26	59.10	129.73	785	9	1.2	7.5	53	10.8	8.5	0.5	0.6	1.9	2.0	12.6	3.5	7.2	FOREST
KW27	59.18	129.80	955	5	6	7.9	56	10.1	8.7	0.7	0.8	1.5	5.2	8.9	0.9	6.0	FOREST
KW28	59.22	129.73	957	11	20.3	8.0	65	10.1	12.0	0.4	0.5	1.3	7.2	6.8	1.1	7.8	T-ALP
KW29	59.83	129.13	802	6	12.5	8.4	215	14.4	36.4	0.5	1.2	1.9	3.2	10.2	3.6	41.6	FOREST
KW30	59.87	129.15	842	16	2.5	8.3	170	14.1	36.1	3.1	0.3	1.9	<0.5	7.5	17.8	30.8	FOREST
KW31	59.92	129.10	835	6	5.1	8.4	192	14.1	29.5	1.2	0.4	1.9	0.6	5.1	16.0	35.4	FOREST
KW32*	59.95	132.00	790	6	2	7.7	75	12.0	14.4	0.2	0.9	1.1	2.1	9.4	4.2	13.1	FOREST
KW33	59.68	133.72	713	25	5.3	9.0	287	11.9	25.8	2.0	2.0	7.5	11.6	10.6	16.2	54.3	FOREST
KW34	59.70	133.30	1268	9	4.6	7.9	31	9.9	3.1	0.1	0.4	1.7	2.9	8.4	7.8	2.8	FOREST
KW35	59.60	133.68	758	41	13.8	8.8	448	12.1	15.3	3.3	5.3	7.2	37.3	9.1	19.7	86.0	FOREST
KW38	58.85	125.73	1066	2	2.3	8.2	104	11.3	26.3	0.3	<0.1	<0.1	9.7	2.2	0.5	27.0	FOREST
KW39	58.65	124.70	1289	2	2.2	9.0	125	9.7	21.4	13.8	0.3	7.8	<0.5	0.1	5.5	19.3	FOREST
KW40	58.62	122.70	482	19	1.6	7.1	50	16.2	6.1	0.9	0.6	1.8	5.5	0.3	19.8	2.9	FOREST
KW41*	58.62	122.50	472	28	9.1	8.0	133	16.5	27.5	0.2	0.3	1.9	7.6	3.9	21.6	19.3	FOREST
KW42	57.17	122.80	1205	8	3	6.6	13	13.8	2.6	<0.1	0.4	0.3	<0.5	2.0	20.0	1.1	FOREST
KW43	55.88	121.90	725	39	20	7.9	103	14.9	14.7	6.2	1.1	6.3	7.3	1.4	12.1	10.6	FOREST
KW44	55.80	121.52	706	38	5.5	7.9	189	14.9	38.7	0.4	1.7	2.4	3.5	4.4	14.9	33.9	FOREST
KW45	55.92	121.40	698	70	8.9	8.6	238	15.0	49.1	1.0	5.4	3.4	9.3	4.5	17.2	39.8	FOREST
KW46	55.38	122.62	868	95	30	8.5	109	13.0	24.7	1.2	0.2	1.1	5.6	1.0	1.7	18.1	FOREST
KW48	55.05	123.43	1029	17	4.7	7.9	45	13.0	8.6	<0.1	0.7	0.9	1.9	3.0	7.9	5.8	FOREST
KW49	54.87	122.83	879	14	10.2	7.8	20	14.4	2.7	<0.1	0.3	0.4	0.5	<0.1	5.0	2.6	FOREST

Table 1 continued

Lake	LAT (metric)	LONG (metric)	ELEV (m)	SA (ha)	DEPTH (m)	pH	COND (μ S/cm)	JTEMP (°C)	Ca (mg/l)	Cl (mg/l)	K (mg/l)	Na (mg/l)	SO ₄ (mg/l)	SiO ₂ (mg/l)	DOC (mg/l)	DIC (mg/l)	Vegetation
KW50	54.30	122.65	709	8	6	7.6	141	15.4	15.8	19.0	1.1	15.6	0.8	1.4	17.5	11.6	FOREST
KW51	53.90	122.30	739	6	1.8	8.3	71	15.0	11.4	1.5	0.6	2.2	0.8	2.8	14.5	9.7	FOREST
KW52	53.73	122.28	823	6	13.2	7.7	67	14.6	10.2	0.3	0.6	1.2	2.7	11.2	2.8	9.9	FOREST
KW53	53.85	121.98	743	8	11.6	8.0	37	14.1	6.7	<0.1	0.4	0.5	<0.5	0.4	7.0	5.8	FOREST
KW54*	53.50	121.53	985	6	13	7.3	9	13.2	0.6	<0.1	0.3	0.3	<0.5	<0.1	4.6	1.3	FOREST
KW55	53.22	121.45	1053	6	10.4	7.9	24	13.1	3.5	<0.1	0.2	0.5	0.6	1.4	7.6	3.1	FOREST
KW56	52.98	121.13	992	6	11.1	8.0	154	12.4	39.8	0.3	0.4	0.7	3.7	3.9	3.5	28.7	FOREST
KW57	52.30	121.43	845	11	6.5	7.8	188	14.2	37.0	0.8	0.9	6.5	1.3	13.6	15.2	36.2	FOREST
KW58	51.95	120.88	1011	17	7.5	7.9	80	14.7	14.0	0.2	0.8	1.2	0.6	8.1	11.8	13.2	FOREST

Readers are referred elsewhere for data from the Yukon/NWT (Pienitz et al., 1997), Alaska (Gregory-Eaves et al. 2000), and the Canadian Arctic Islands (Gajewski et al. 2005) datasets. Abbreviations: LAT = latitude, LONG = longitude, ELEV = elevation, SA = surface area, DEPTH = lake depth, COND = conductivity, JTEMP = mean July air temperature, DOC = dissolved organic carbon, DIC = dissolved inorganic carbon. *Outliers not included in models

of the following four categories: arctic tundra (T-ARC), alpine tundra (T-ALP), lichen woodland (L-WOOD), or boreal forest (FOREST).

Mean July air temperature (JTEMP) for each site was obtained from a climatic dataset compiled by New et al. (2002). The New et al. (2002) dataset uses climate normals from 1961 to 1990 to create a global climatic grid with a resolution of 10'. There are some shortfalls associated with this dataset worth noting. For example, the resolution of the climatic dataset remains coarse, and the climate normals used predate the collection of midge data and span a cold phase of the Arctic Oscillation (Overland and Wang 2005). However, the coarse resolution is more than made up for by the inclusion of sites from such a large geographic and climatic region. Specifically, the global nature of the New et al. (2002) dataset allowed us to include the 50 Canadian Arctic Island sites. This resulted in significant improvements to the correlation coefficient and errors of the model as compared with earlier model versions (Barley 2004), and indicates good correlation between the midge and climate data. It also increased the temperature range from 8.6-16.6°C (Barley 2004) to 3.9-16.5°C (present training set) and makes this new model better suited to reconstructing glacial conditions in Beringia.

Surface water temperatures were not included in these analyses. The potential problems associated with using single point measurements (Seppala 2001) are exacerbated here as measurements were subjected to diurnal, monthly and annual variation among the four different datasets.

Data analysis

Data screening

Analysis largely followed that described by Pienitz et al. (1995) and Gregory-Eaves et al. (1999). All taxon data are presented as percent abundances (calculated as percent of total identifiable midges) and were square-root transformed prior to further analysis. LAT, LONG and ELEV are fixed variables and so were entered as passive variables. Environmental variables with skewed distributions were transformed using $\ln(x+1)$, where x was the given environmental variable. Collinearity of environmental variables was assessed using a series of detrended

correspondence analyses (DCAs). Variables with an inflation factor ≥ 20 were eliminated one per DCA run (beginning with the variable with the largest inflation factor) until all remaining variables had values of < 20 . By this process, the variable FOREST was found to be redundant and was eliminated.

Sites with unusual midge assemblages and environmental characteristics were eliminated. A site was defined as an outlier if: (1) its sample score fell outside the 95% confidence interval of the sample score mean for both a DCA of the taxon data and a principal components analysis (PCA) of the environmental data; or (2) leverage diagnostics in canonical correspondence analysis (CCA) showed a sample to have an environmental variable with extreme influence ($> 8X$). Following these criteria, AK31, KW03, KW13, KW14, KW32, KW41, KW54 and E504 were eliminated. AK19 was also eliminated as it had high abundances of rheophilous taxa (*Eukiefferiella/Tvetenia* and *Rheotanytarsus*).

Rare taxa, defined here as taxa that were present in fewer than 5% of the lakes (i.e., present in fewer than 6 lakes), were eliminated.

Ordinations

All ordinations were performed using the program CANOCO, version 3.12 (ter Braak 1991). A DCA was used to explore principal patterns of faunistic variation in the dataset. The gradient length of species scores was relatively long (3.26 standard deviations), thus unimodal ordination techniques were used (ter Braak 1995). The relationships between individual environmental variables and midge distributions were assessed using CCA. Statistically significant ($P \leq 0.05$) environmental variables were determined using forward selection in CCA. Variables were sequentially selected such that each selected variable accounted for the greatest proportion of the remaining variance. Forward selected variables and CCA axes were also tested for significance by running Monte Carlo permutation tests (with 999 unrestricted permutations, $P \leq 0.05$).

Model development

Robust relationships between midges and both temperature (Brooks and Birks 2000, 2001; Lotter et al. 1997, 1999; Olander et al. 1997, 1999; Walker et al.

1991, 1997) and lake depth (Korhola et al., 2000) have previously been demonstrated. To explore the relationships between midges and these two variables for this dataset, CCAs constrained to temperature and depth respectively were run, and the first to second eigenvalues (λ_1/λ_2) compared.

The program C2 version 1.4 (Juggins 2003) was used to develop and assess midge transfer functions for temperature and depth. Several unimodal regression-calibration techniques were used: simple weighted averaging (WA) and weighted averaging with tolerance downweighting (WA_{tol}) both with classical and inverse deshinking, and weighted averaging partial least squares (WA-PLS). Each model was tested with 1000 bootstrap cycles, and evaluated by means of the bootstrapped co-efficient of determination (r^2_{boot}) and root mean squared error of prediction (RMSEP).

Results

Faunistic description

Over 28,000 midge subfossils from 80 taxa were examined. Ranking of taxa by temperature and depth (Figs. 3 and 4) revealed patterns in the distribution of many taxa. Sites with temperatures below 8°C were found exclusively in the Canadian Arctic Islands and were characterized by abundant cold stenotherms, especially *Pseudodiamesa*, *Hydrobaenus/Oliveridia*, *Procladius* and *Abiskomyia*, and a near absence of Chironomini. On the mainland *Abiskomyia*, *Mesocricotopus*, *Zalutschia* type B, *Procladius*, *Micropsectra* and *Parakiefferiella nigra* type were restricted to deep lakes in the colder regions, the first two taxa being further restricted to only the northernmost lakes. *Corynocera oliveri* type and *Derotanytus* (in low abundances, not graphed) showed a preference for cold and shallow lakes. *Sergentia*, commonly interpreted as a cold indicator (Palmer et al. 2002; Walker 1990), showed little relationship with temperature, but did show a pattern of higher abundances in deeper lakes. The warm indicators (*Labrundinia*, *Pseudochironomus* and *Glyptotendipes*) seemed to show little correlation with depth. Not surprisingly, common and taxonomically broad groups such as other Tanytarsina, *Procladius* and other Pentaneurini (not graphed) showed uniform distributions across temperature and depth. The broad distribution of

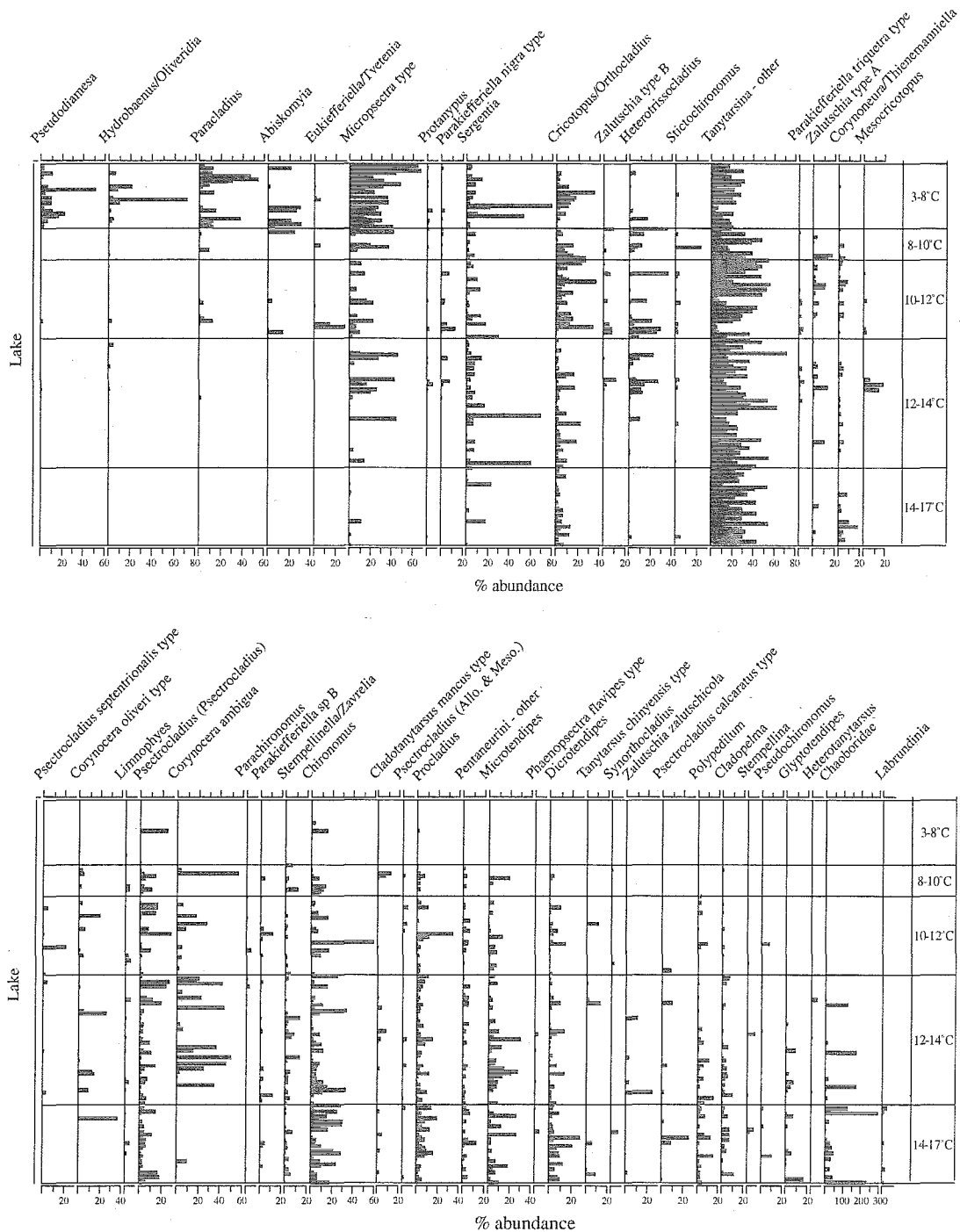


Fig. 3 Chironomid percentage diagram for the northwest North American training set, with taxa ranked by mean July air temperature (cold to warm) as determined by a constrained

canonical correspondence analysis (CCA). All taxon abundances are presented as a % of the total identifiable chironomids. Taxa that were rare or never exceeded 5% have been omitted

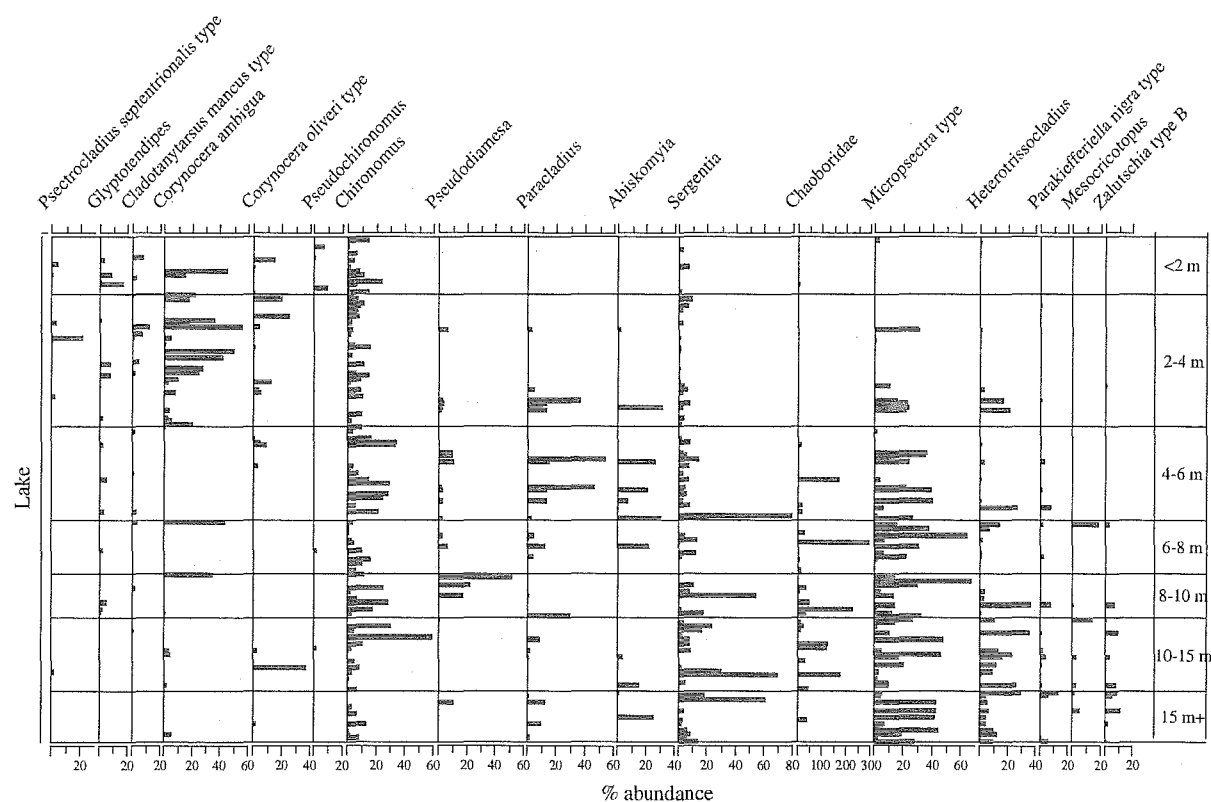


Fig. 4 Chironomid percentage diagram for the northwest North American training set, with select taxa ranked by mean depth (shallow to deep) as determined by a constrained canonical

correspondence analysis (CCA). All taxon abundances are presented as a % of the total identifiable chironomids

Chironomus suggests that it too might be composed of multiple species with different ecological niches. Both ceratopogonids and *Chaoborus* showed strong preferences for sites south of treeline (data not shown), with *Chaoborus* showing a further preference for the deeper lakes.

Corynocera ambigua and *Corynocera oliveri* type were mostly restricted to sites north of ~60° N on the mainland. In this region, they were common (found in 44% and 30% of lakes, respectively) especially in shallow lakes, and often attained high abundances within a lake (with maxima of 57% and 37% respectively). Within this region, *C. oliveri* type was found at the colder sites, whereas *C. ambigua* showed no correlation with temperature.

Ordinations

Ordination analyses included 62 non-rare taxa, 17 environmental variables and 136 sites (outliers ex-

cluded). In order to determine the extent to which individual environmental variables contributed to variation, forward selection in CCA was performed. In the initial run all variables were selected in the order dictated by forward selection. Eight environmental variables explained significant proportions ($P \leq 0.05$) of the explainable variance. In order, these were JTEMP, DEPTH, T-ARC, T-ALP, pH, DOC, L-WOOD and SA (Table 2).

With the selection of each variable in forward selection, the relative importance of the remaining variables is re-evaluated. A variable will decrease in relative importance if it is correlated with (i.e., explains some of the same variation as) the variables already selected. Thus, a variable that initially appears important might escape selection if it is correlated with variables already selected.

To test the robustness of the list of significant variables, a different order was forced by selecting the second ranked T-ARC ahead of JTEMP. Run 2

Table 2 Significant variables as identified by forward selection in CCA and the variance they explain

Run 1		Run 2	
Variable	Added with selection	Variable	Added with selection
JTEMP	0.35	T-ARC	0.24
DEPTH	0.10	JTEMP	0.18
T-ARC	0.07	DEPTH	0.11
T-ALP	0.05	T-ALP	0.05
pH	0.05	pH	0.05
DOC	0.04	DOC	0.04
L-WOOD	0.04	L-WOOD	0.04
SA	0.03	SA	0.03
Total variance explained	0.73	Total variance explained	0.74
Total variance	2.82	Total variance	2.82

Results are presented for: Run 1—CCA with all variables selected in the order presented; Run 2—CCA with T-ARC selected first, and all other variables selected in the order presented. Abbreviations: JTEMP = mean July air temperature (°C), DEPTH = maximum lake depth, T-ARC = arctic tundra vegetation, T-ALP = alpine tundra vegetation, DOC = dissolved organic carbon, L-WOOD = lichen-woodland vegetation, SA = lake surface area

produced the same list of significant variables with minor differences in the order: T-ARC, JTEMP, DEPTH, T-ALP, pH, DOC, L-WOOD and SA. The overall stability of this list supports the robustness of each of the selected variables.

Patterns in data structure of a CCA restricted to the 8 significant variables were compared with those of correspondence analysis (CA) to explore the impact of the environmental data on species and site ordination. Similar patterns were observed as assessed both visually, and by comparing CA and CCA values for the first 2 axes. Correlation between CA and CCA species scores of the first axis ($r^2 = 0.96$) and second axis ($r^2 = 0.74$), and site scores for the first axis ($r^2 = 0.99$) and second axis ($r^2 = 0.82$) were good. This confirms that the environmental variables included in CCA capture the general patterns of species distribution observed in CA. Therefore, only CCA is considered further.

The first four axes of the final CCA account for 22.4% of the species variance (Table 3). Monte Carlo tests (999 unrestricted permutations) confirmed the significance of all four axes ($P = 0.001$). Relationships between the significant environmental variables and the individual axes were examined through correlation coefficients, z -values and inter-set correlations (Table 4). All variables were significantly correlated with at least the first or second CCA axis ($P \leq 0.05$). JTEMP showed negative correlations with both the first and second axes, while DEPTH showed a

positive correlation with the first axis and negative correlation with the second axis.

A biplot of the final CCA sample scores (Fig. 5) shows strong clustering by vegetation type, with the forested sites falling in the top left quadrant and the arctic tundra sites in the bottom and top right quadrants. Within the Arctic tundra sites, those in the Canadian Arctic Islands fell at the cold end of the temperature gradient, while those on the mainland fell along the moderate portion of the temperature gradient. The majority of alpine tundra and lichen woodland sites fell along the boundary between the mainland arctic tundra and forest sites.

Table 3 Eigenvalues, taxon-environmental correlations, cumulative % variance and significance of the four CCA axes

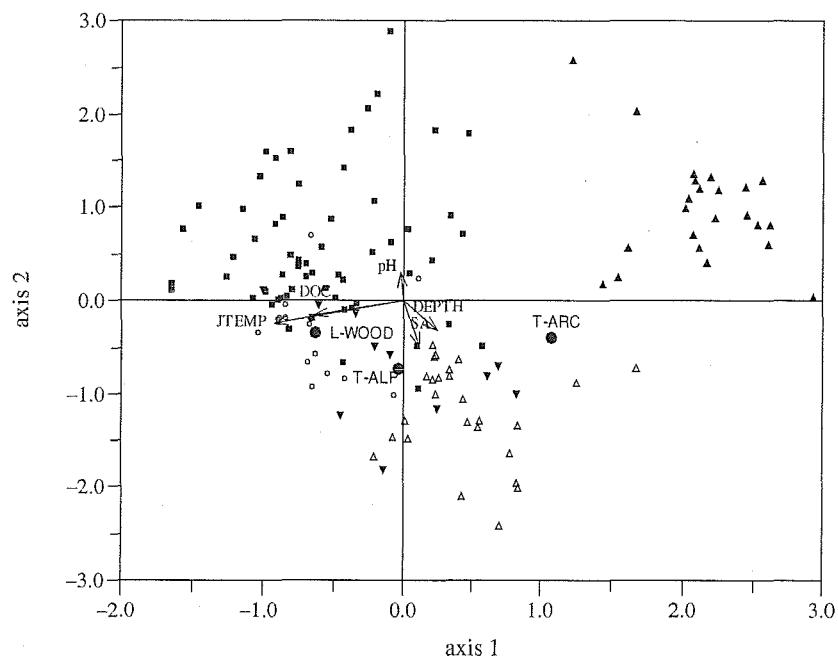
	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.396	0.116	0.079	0.043
Taxon-environment correlations	0.913	0.761	0.778	0.674
Cumulative % variance of taxon data	14.0	18.1	20.9	22.4
of taxon-environment relation	54.6	70.5	81.4	87.3
Significance (probability) of axis	0.001	0.001	0.001	0.001
Sum of all unconstrained eigenvalues				2.826
Sum of all canonical eigenvalues				0.726

Table 4 Canonical coefficients, their *t*-values and interset correlations for a CCA

	Canonical coefficients				<i>t</i> -values				Inter-set correlations			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
JTEMP	-0.73	-0.83	-0.30	0.25	-11.10*	-6.60*	-2.50*	1.60	-0.84	-0.19	-0.21	-0.05
DEPTH	0.32	-0.46	-0.69	-0.43	7.20*	-5.40*	-8.60*	-3.90*	0.22	-0.25	-0.62	-0.25
T-ARC	0.24	-1.05	0.23	0.06	3.60*	-8.10*	1.90	0.40	0.68	-0.21	0.23	0.01
T-ALP	-0.04	-0.56	0.30	0.24	-1.00	-6.60*	3.80*	2.20*	-0.01	-0.17	0.09	0.21
pH	-0.08	0.20	0.21	-0.75	-1.90	2.50*	2.80*	-7.40*	-0.01	0.23	0.07	-0.52
DOC	-0.12	-0.04	0.38	-0.40	-2.40*	-0.40	4.10*	-3.20*	-0.58	-0.12	0.21	-0.16
L-WOOD	0.06	-0.48	0.27	-0.27	1.40	-5.50*	3.20*	-2.40*	-0.22	-0.10	0.29	-0.04
SA	0.01	-0.20	0.26	-0.25	0.30	-2.20*	3.10*	-2.20*	0.10	-0.38	0.15	-0.27

* Significant at $P \leq 0.05$

Fig. 5 Canonical correspondence analysis (CCA) ordination showing the dispersion of sites by vegetation type relative to eight significant environmental variables. Symbols indicate: Δ arctic tundra (mainland), \blacktriangle arctic tundra (Canadian Arctic Islands), \blacktriangledown alpine tundra, \blacksquare forest, \circ lichen woodland



The distribution of CCA species scores reflects the environmental preferences of individual taxa (Fig. 6). In the top light quadrant are taxa typical of the coldest sites: *Pseudodiamesa*, *Abiskamyia*, *Eukiefferiella/Tvetenia*, *Hydrobaenus/Oliveridia*, *Metriocnemus*, *Paraladius* and *Micropsectra* type. Also typical of cold, and especially the deeper lakes were *Monodiamesa*, *Mesocricotopus*, *Parakiefferiella nigra* type, and *Zaluschia* sp. B in the bottom right quadrant. The two left quadrants include taxa typical of the warmer sites of shallow to moderate depth (e.g., *Psectrocladius* spp., *Cladotanytarsus mancus* type and *Labrundiniäi*). Taxa clustered in the central part of the CCA show no distinctive environmental or

vegetational preferences to the variables that are significantly correlated with these axes.

Model development

Mean July air temperature and depth were the first and second strongest variables as determined by forward selection. CCAs constrained first to temperature and then depth were run, and produced respective eigenvalue ratios of 1.282 ($\lambda_1/\lambda_2 = 0.350/0.273$), and 0.204 ($\lambda_1/\lambda_2 = 0.094/0.461$). WA and WA-PLS models were constructed using the screened training set (136 lakes; Table 5). For temperature, WA-PLS with the 2 component model (Fig. 7) was selected as it produced a

Fig. 6 Canonical correspondence analysis (eCA) ordination showing the dispersion of taxa relative to eight significant environmental variables. Taxon codes correspond with full taxon names listed in Table 6

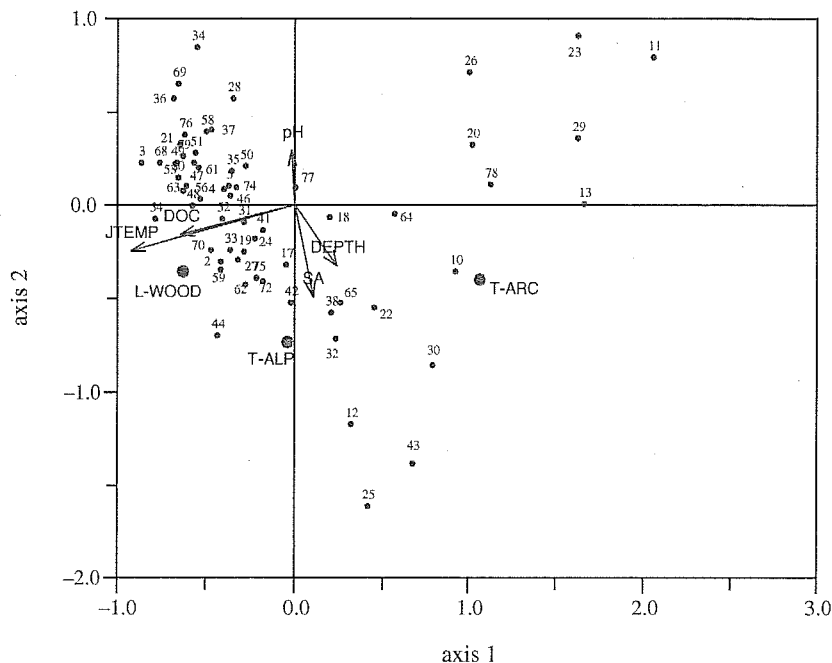


Table 5 A comparison of WA and WA-PLS models for reconstructing (a) mean July air temperature and (b) depth

Model	Apparent			Bootstrapped			
	r^2	RMSE	Max Bias	r^2	RMSEP	Max Bias	
(a) Mean July air temperature							
WA	Inverse	0.797	1.48	2.20	0.777	1.57	2.33
	Classical	0.797	1.66	2.45	0.779	1.71	2.47
WAtol	Inverse	0.821	1.39	2.46	0.797	1.55	2.83
	Classical	0.821	1.53	2.65	0.797	1.65	3.05
WA-PLS	1 component	0.797	1.48	2.28	0.777	1.58	2.40
	2 components	0.866	1.20	2.06	0.818	1.46	2.47
	3 components	0.903	1.03	1.57	0.830	1.46	2.37
	4 components	0.917	0.95	1.21	0.828	1.52	2.28
	5 components	0.923	0.91	1.17	0.820	1.61	2.34
(b) Depth							
WA	Inverse	0.362	0.55	1.48	0.247	0.62	1.56
	Classical	0.362	0.92	0.59	0.251	0.90	0.90
WAtol	Inverse	0.390	0.54	1.45	0.272	0.62	1.51
	Classical	0.390	0.87	0.67	0.277	0.88	0.95
WA-PLS	1 component	0.362	0.56	1.41	0.247	0.62	1.51
	2 components	0.567	0.46	1.08	0.382	0.58	1.32
	3 components	0.661	0.40	1.00	0.420	0.58	1.31
	4 components	0.706	0.38	0.92	0.419	0.60	1.28
	5 components	0.731	0.36	0.90	0.404	0.64	1.29

strong correlation coefficient ($r^2_{boot} = 0.818$), a low error (RMSEP = 1.46°C), and was more parsimonious than the higher component WA-PLS models. For depth, the WA-PLS model with 2 components

($r^2_{boot} = 0.382$, RMSEP = 0.58; Fig. 7) was again selected as the strongest and most parsimonious model.

Taxon specific optima and tolerances were generated using WA (Table 6). For temperature, *Pseud-*

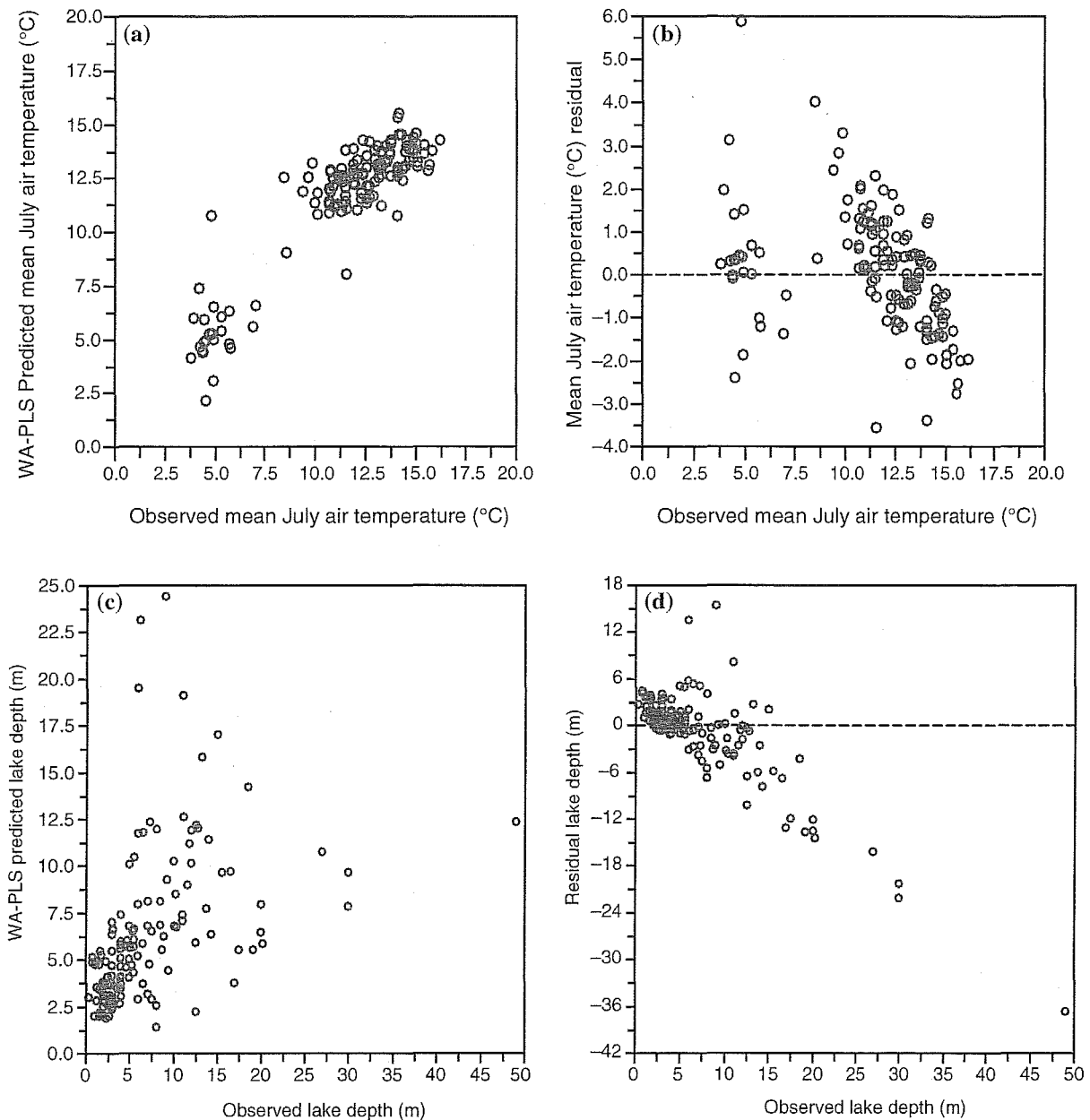


Fig. 7 For the WA-PLS (2 component; $r^2_{boot} = 0.818$, $RMSEP = 1.46^\circ C$) mean July air temperature model, (a) predicted versus observed values for mean July air temperature ($^\circ C$), and (b) residuals of predicted versus observed mean July air temperature are shown. Following the creation of the WA-PLS (2 component; $r^2_{boot} = 0.38$, and $RMSEP = 0.58$) lake depth

model with transformed depths ($\ln(x+1)$) lake depths and the residuals were untransformed, and these untransformed values are graphed as (c) predicted versus observed values for untransformed lake depth (m), and (d) residuals of predicted versus observed untransformed lake depth (m)

odiamesa has the coldest optimum at $5.4^\circ C$ and *Labrundinia* the warmest at $14.5^\circ C$. Estimates of the optima are limited by the range of actual temperatures corresponding to the sites (3.9 - $16.5^\circ C$). The

range of depths in the training set was 0.3 - 49 m (the distribution is skewed toward shallow lakes); *Metriocnemus* gave the lowest optimum (2 m) and *Zalutschia* type B the greatest (12 m). Beta values

Table 6 Values for all non-rare taxa for: taxon occurrence (i.e., percentage of 145 lakes in which the taxon was present), and for each of mean July air temperature (T) and depth (D): taxon minimum (Min), taxon maximum (Max), bootstrapped WA optimum (Opt), bootstrapped WA tolerance (Tol) and 2 component bootstrapped WA-PLS Beta coefficient (WAPLS Beta)

Taxon code	Taxon name	occurrence (%)	Temperature					Depth				
			T-Min (°C)	T-Max (°C)	T-Opt (°C)	T-Tol (°C)	WAPLS Beta	D-Min (m)	D-Max (m)	D-Opt (m)	D-Tol (m)	WA-PLS Beta ^a
1	<i>Derotanypus</i>	10	9.9	15.1	12.2	1.4	8.55843	1.2	10.1	3.5	0.6	-0.521247
2	<i>Labrundinia</i>	8	13.3	16.5	14.5	0.8	21.5318	1.1	14.3	6.3	1.0	3.70545
3	Tr: Pentaneurini	60	8.6	16.5	12.9	1.7	14.4651	0.8	49.0	5.7	1.2	2.90251
4	<i>Procladius</i>	77	4.9	16.5	12.9	1.8	14.4916	0.3	49.0	5.1	1.1	1.89073
5	<i>Protanypus</i>	23	4.0	15.7	9.7	3.4	10.3595	1.2	49.0	7.7	1.0	2.54175
6	<i>Pseudodiamesa</i>	16	3.9	12.7	5.4	1.8	-4.28936	2.1	17.0	5.6	0.6	0.144384
7	<i>Monodiamesa</i>	11	10.7	13.8	11.9	0.8	18.6806	1.5	15.5	7.2	0.8	2.00099
8	<i>Abiskomyia</i>	10	4.0	12.6	7.3	2.8	5.22535	2.1	20.0	6.8	0.8	0.911392
9	<i>Corynoneura/Thienemanniella</i>	50	4.0	15.8	12.2	2.4	12.3404	0.3	49.0	5.7	1.0	2.25716
10	<i>Cricotopus/Orthocladius</i>	86	4.5	16.5	11.1	3.2	8.27317	0.3	49.0	4.6	1.0	0.636493
11	<i>Doithrix/Pseudorthocladius</i>	12	8.6	15.6	12.6	2.1	17.3189	1.2	30.0	5.7	1.2	2.2834
12	<i>Eukiefferiella/Tvetenia</i>	10	4.0	15.8	8.5	3.6	3.38575	1.0	25.0	6.3	1.3	2.10552
13	<i>Heterotanytarsus</i>	5	12.4	14.9	13.9	0.7	17.9764	2.5	12.5	5.5	0.7	2.8603
14	<i>Heterotrissocladius</i>	43	4.0	15.7	11.2	2.5	14.9389	0.8	49.0	9.1	1.0	4.4659
15	<i>Hydrobaenus/Oliveridia</i>	17	3.9	13.0	6.5	3.1	0.218258	0.8	30.0	4.2	1.2	-0.787011
16	<i>Limnophyes</i>	37	4.9	15.6	12.5	2.3	12.5493	0.3	49.0	5.0	1.0	1.32133
17	<i>Mesocricotopus</i>	8	10.9	12.7	12.2	0.6	24.4048	5.5	18.5	10.2	0.5	4.3423
18	<i>Metriocnemus</i>	6	3.9	13.7	7.8	4.0	-12.3498	0.3	6.0	2.0	0.7	-5.10016
19	<i>Nanocladius</i>	21	10.1	15.4	12.9	1.6	15.2717	1.1	25.0	5.2	1.0	1.82859
20	Orthoclaadiinae sp. 2	8	8.5	15.6	12.4	2.5	8.31196	2.0	19.2	5.3	0.7	2.30534
21	<i>Paracladius</i>	28	3.9	13.3	6.9	3.1	-0.568018	1.5	49.0	6.2	0.8	0.893699
22	<i>Parakiefferiella nigra</i> type	17	4.0	13.3	10.3	2.7	12.3889	2.0	49.0	9.4	1.0	4.07897
23	<i>Parakiefferiella</i> sp. B	40	9.7	14.6	12.8	1.7	14.3364	0.8	49.0	5.9	1.1	2.84987
24	<i>Parakiefferiella triquetra</i> type	23	4.0	14.4	11.9	1.6	15.2153	1.2	49.0	6.9	1.0	2.76501
25	<i>Parametriocnemus/Paraphaeno.</i>	14	9.4	16.5	13.1	2.0	17.8585	2.0	49.0	7.0	1.0	4.10405
26	<i>Psectrocladius (Allo. & Meso.)</i>	15	9.7	16.5	12.9	1.9	10.286	1.1	49.0	4.2	1.3	0.890346
27	<i>Psectrocladius (Psectrocladius)</i>	79	4.9	16.2	12.6	2.2	11.5028	0.3	49.0	4.4	1.1	0.816704
28	<i>Psectrocladius calcaratus</i> type	12	11.2	16.0	13.3	1.4	14.1323	0.8	19.2	3.5	1.2	-0.594578
29	<i>Psectrocladius septentrionalis</i> type	15	8.5	15.1	12.3	1.4	7.20913	1.2	12.8	3.2	0.7	-1.13216
30	<i>Pseudosmittia/Smittia</i>	5	5.4	14.2	11.4	3.4	17.5977	1.5	15.5	6.2	0.8	1.48262
31	<i>Synorthocladius</i>	8	9.4	15.4	13.3	2.0	19.3277	6.0	49.0	11.6	0.6	7.7386
32	<i>Zalutschia</i> type A	45	5.4	15.8	11.9	1.7	10.3005	0.8	30.0	4.5	0.9	0.723882
33	<i>Zalutschia</i> type B	12	7.1	12.9	11.3	1.5	16.333	3.0	49.0	12.2	0.8	6.36254
34	<i>Zalutschia zalutschicola</i>	10	11.5	15.6	13.3	1.0	19.3334	2.0	18.5	4.0	0.6	-0.271165
35	<i>Chironomus</i>	72	4.5	16.5	12.8	2.1	13.2646	0.3	49.0	4.9	1.0	1.79733
36	<i>Cladopelma</i>	49	9.4	15.8	13.4	1.4	15.6021	0.8	49.0	4.4	0.9	1.3681
37	<i>Cryptochironomus</i>	30	9.6	16.2	13.2	1.4	14.6366	0.8	30.0	3.6	1.0	-0.057914

Table 6 continued

Taxon code	Taxon name	occurrence (%)	Temperature					Depth				
			T-Min (°C)	T-Max (°C)	T-Opt (°C)	T-Tol (°C)	WAPLS Beta	D-Min (m)	D-Max (m)	D-Opt (m)	D-Tol (m)	WA-PLS Beta ^a
38	<i>Cryptotendipes</i>	15	10.7	15.8	13.6	1.4	16.8331	1.1	49.0	4.1	1.4	0.741025
39	<i>Cyphomella/Harn./Paraclado.</i>	6	10.0	15.7	13.2	2.1	21.6488	3.1	30.0	8.7	0.9	5.18149
40	<i>Dicrotendipes</i>	62	9.7	16.5	13.3	1.6	15.1439	0.8	49.0	4.7	1.2	1.67409
41	<i>Einfeldia</i>	7	9.4	15.6	13.3	2.3	18.9558	4.0	30.0	11.3	1.1	8.7968
42	<i>Endochironomus</i>	21	10.7	16.5	13.6	1.5	17.5138	1.5	20.0	5.0	0.9	2.23864
43	<i>Glyptotendipes</i>	26	10.7	16.5	13.7	1.4	17.626	1.2	49.0	3.5	0.8	-0.215629
44	<i>Microtendipes</i>	59	9.9	16.5	13.1	1.4	15.7331	1.1	49.0	4.3	0.9	0.650976
45	<i>Pagastiella</i>	28	9.7	15.4	13.0	1.6	13.5439	0.8	49.0	5.3	1.4	2.59472
46	<i>Parachironomus</i>	21	10.7	15.4	12.7	1.7	11.8891	1.2	20.0	3.9	0.7	0.189731
47	<i>Paratendipes</i>	8	11.9	15.8	13.8	1.4	19.818	1.5	49.0	7.9	1.3	5.3797
48	<i>Phaenopsectra flavipes</i> type	17	9.4	15.4	13.2	1.5	17.9429	1.5	49.0	7.0	1.4	4.28231
49	<i>Polypedium</i>	54	9.6	16.5	13.4	1.4	16.2932	0.8	49.0	4.3	1.0	0.954915
50	<i>Sergentia</i>	63	4.0	16.5	10.3	3.5	7.39189	1.0	49.0	6.9	1.0	3.25181
51	<i>Stictochironomus</i>	22	4.9	15.7	11.6	2.3	13.1921	0.3	49.0	6.2	1.1	1.69157
52	<i>Pseudochironomus</i>	16	8.5	15.4	13.6	1.7	16.6973	0.8	30.0	4.0	1.2	0.385902
53	<i>Cladotanytarsus mancus</i> type	17	9.4	15.6	12.8	1.8	9.5801	0.8	30.0	3.5	0.8	-0.13548
54	<i>Corynocera ambigua</i>	28	9.4	15.4	12.6	1.2	11.9135	1.5	30.0	3.6	0.7	0.0346799
55	<i>Corynocera oliveri</i> type	17	7.0	14.4	12.3	1.6	11.4965	0.8	20.3	3.7	0.9	-0.422673
56	<i>Stempellina</i>	11	9.6	16.2	13.4	1.6	18.8694	1.6	30.0	10.0	1.0	6.84875
57	<i>Stempellinella/Zavrelia</i>	57	8.5	16.5	12.8	1.6	15.5702	1.2	49.0	5.6	1.0	2.23165
58	<i>Tanytarsus chinyensis</i> type	8	9.9	15.7	13.3	2.0	14.5632	0.8	13.2	4.2	1.2	0.847722
59	Tanytarsina—other	99	4.0	16.5	11.7	3.1	10.3357	0.3	49.0	5.2	1.0	1.6688
60	<i>Micropsectra</i> type	57	4.0	16.5	8.8	3.8	5.27437	0.3	49.0	7.9	0.9	3.28803
61	<i>Chaoborus</i>	45	9.9	16.5	13.9	1.4	18.9133	0.8	20.0	6.8	0.7	4.31676
62	Ceratopogonidae	30	10.0	15.4	13.5	1.5	17.0993	0.8	49.0	5.7	1.4	2.94702

^a The beta coefficients will infer transformed depths, which must be converted to real depths by $e^{\text{beta}-1}$

were generated by the WA-PLS (2 component) models as coefficients to be used in calculating temperature and depth estimates.

Discussion

Fauna

All taxa previously included in Canadian temperature models (Palmer et al. 2002; Walker et al. 1991, 1997) were also present in this training set. The higher number of taxa here is attributed both to the increased taxonomic resolution of some groups (e.g., *Psectrocladius*, *Zaluschia*, other Tanytarsina), and to the presence of a greater number of taxa in this study's larger geographical area. The most significant additions were three species of *Corynocera*, two of which were common and often abundant in this training set (the third was rare in the training set and excluded from the models), but which were entirely absent in the eastern training sets. Among the taxa included in the other Canadian model, only *Tribelos* was rare in this training set, and excluded from the model.

Corynocera ambigua has generated discussion for its unusual morphology, and interesting temporal and spatial distributions (Brodersen and Lindegaard 1999; Walker et al. 2003). It has often been characterized as a cold stenothermous taxon due largely to its abundance in late glacial sediments (see Brodersen and Lindegaard 1999). However, after examining the modern distribution of this taxon in Denmark, Brodersen and Lindegaard (1999) conclude that temperature is not a limiting factor in its distribution. Similarly, in a training set in northeastern Siberia, Porinchu and Cwynar (2000) find *C. ambigua* in their warmer sites south of treeline. In North America, Walker et al. (2003) suggest a Beringian refugium for this taxon during the last glacial interval, based on its present distribution and limited flight capabilities. The distribution of *C. ambigua* within this training set lends support to both these ideas. The modern distribution of *C. ambigua* generally correlates with Beringian boundaries: it is rare in the Canadian Arctic Islands (i.e., found in a single lake on Victoria Island) and is rare below -60° N (i.e., only 7 head capsules were found in northern BC). Within this region it shows no apparent correlation with temperature.

Some controversy surrounds the taxonomy and identification of *Corynocera oliveri*. *C. oliveri* has been described as having median teeth that are prominent or on a separate plane (Brooks 1999; Walker 2000). However, this description is shared by *Tanytarsus lugens*, and the separation of *C. oliveri* is dependent on the presence of a mandible with a large surface tooth. As a result, these two groups are sometimes lumped (e.g., Brooks and Birks 2000; Rosen et al. 2003). To further complicate matters, observations of subfossils from this training set and additional BC lakes (from Palmer et al. 2002; Walker and Mathewes 1988) revealed *C. oliveri* type mandibles (i.e., with a large surface tooth) on specimens with different mentum types that could both be described as having 'prominent median teeth' (personal observation). Our identification of *C. oliveri* type agrees with available descriptions, but is further restricted to a single mentum type characterized by a strong dorso-lateral curvature of the mentum, and is confirmed by the appearance of very subtle accessory teeth, or tooth-like shading where the first lateral and median teeth overlap (Fig. 8). In the Northwest North American training set, *C. oliveri* type shares a similar distribution pattern to *C. ambigua*: it is found only on the mainland and mostly north of -60° N, is moderately common, often abundant and is sometimes found in the same lakes as *C. ambigua*. Although it is absent from the warmest Yukon/NWT and Alaska regions, geography appears to be the strongest determinant of distribution. Again, its distribution supports the hypothesis of a Beringian refugium for this taxon.



Fig. 8 Photo of the mentum of *Corynocera oliveri* type (350 \times)

First reported by Walker and Mathewes (1988), *Corynocera* nr. *ambigua* (Fig. 9; which despite its name is quite distinctive from *C. ambigua*, see Bailey 2004) was identified at four sites in this training set and shows no geographical overlap with the other two *Corynocera* spp. The composite records indicate a strongly western/coastal BC distribution for this taxon. This again supports the suggestion that *C. m ambigua* survived the last glacial interval in a Queen Charlotte Island refugium (Walker and Mathewes 1988). *Corynocera* nr. *ambigua* was rare in the training set, and excluded from the model.

Training set and models

The temperature model developed from the midge training set benefits not only from the number and diversity of sites, but also from the large temperature gradient (3.9-16.5°C). This model gives high r^2 values ($r^2_{boot} = 0.818, r^2_{jack} = 0.818$) when compared with other Canadian models ($r^2_{jack} = 0.70$, Palmer et al. 2002; $r^2_{jack} = 0.73$, Rosenberg et al., 2004; $r^2_{jack} = 0.88$, Walker et al., 1997). In addition, it gives smaller error estimates (RMSEP_{boot} = 1.46°C, RMSEP_{jack} = 1.41°C) than those for the other models (RMSEP_{jack} = 1.98°C, Palmer et al. 2002; RMSEP_{jack} = 1.8°C, Rosenberg et al. 2004; RMSEP_{jack} = 2.26°C, Walker et al. 1997). These strong results were anticipated given the high ratio for the first to second axes $\lambda_1/\lambda_2 = 1.28$ in a CCA constrained to temperature. Regardless, caution is required in the interpretation of the palaeotemperatures derived from these models. For example, there is a bias in the temperature model to overestimate values at cold sites and underestimate values at warm sites. As well, errors generated by transfer functions



Fig. 9 Photo of the mentum of *Corynocera* nr *ambigua*. Mentum with a single median and five pairs of overlapping lateral teeth, mentum typically very worn, antennal pedestals with blunt projection (300 x)

are not absolute in that they represent only errors generated by the model, and do not incorporate potential errors in the data themselves (e.g., accuracy of the training set temperature data, or the representativeness of a given midge assemblage in a single sample for the whole lake).

The weak r^2_{boot} (0.38) for the depth model is not unexpected given the low ratio of first to second axes in a CCA constrained to depth ($\lambda_1/\lambda_2 = 0.20$). Earlier versions of the training set and models (Barley 2004) show by comparison that the strength of the depth model decreases when the temperature gradient is increased. In other words, depth is an important predictor of midge distribution, however for sites with extreme temperatures (i.e., the cold sites of the Canadian Arctic Islands), the effect of temperature largely overrides the influence of depth and other variables. Because Canadian Arctic Island sites were added with the specific aim of maximizing the temperature gradient, it is not surprising that this comes at the cost of a weaker depth model. The depth gradient captured is large (<1-49 m), but so too is the error (for example, after back transforming the data, an inferred depth of 5 m would have error bars from 2 to 10 m). As Walker et al. (2003) point out, fluctuations in water-levels are often too small to be satisfactorily reconstructed. However, atypical fluctuations of as much as 18 m have recently been identified in central Alaska (Abbott et al. 2000; Barber and Finney 2000; Bigelow and Edwards 2001). In regions where large depth fluctuations have occurred, the midge depth model provides a means to detect and describe these changes.

Forward selection in CCA indicates that eight environmental variables explained significant portions of the midge distribution. However, the difference (see Table 3) between the variance explained by the significant environmental variables and the total variance indicates that the distribution of midge taxa is also affected by additional factors not included in the statistical analyses. For example, water temperature (surface and profundal), lake substrate, organic content of the sediment, sources of food (e.g., within lake flora and fauna) and predators (e.g., presence of fish) might also contribute significantly to the dispersion of midge taxa. Where practical, inclusion of additional variables could provide additional information on the distributions of midge taxa.

In addition to providing data for the temperature and depth transfer functions, the northwest North American training set provides an excellent database for climate reconstruction by the Modern Analogue Technique. Here again, the diversity of sites and assemblages captured by the long transect and environmental gradients is an asset. Where close analogues exist, temperature and depth can be reconstructed, and insights can be gained into additional elements of the palaeoenvironment.

There is at present a paucity of quantitative palaeoclimatic data for eastern Beringia. Without these data, many palaeoclimatic questions remain unresolved such as how cold was the full glacial? What was the duration and magnitude of the Holocene Thermal Maximum (Kaufman et al. 2004)? What was the extent, in terms of both geography and magnitude, of the patterns of aridity from the full glacial through the Holocene (Guthrie 2001)? Did the Younger Dryas and other climatic events, so well documented for the North Atlantic, also influence eastern Beringia? Paradoxically, although there is some evidence for the occurrence of the Younger Dryas in eastern Beringia (Bigelow and Edwards 2001; Engstrom et al. 1990; Hu and Shemesh 2003; Hu et al. 2002), there is also evidence for a coeval early thermal maximum in parts of eastern Beringia (Cwynar, 1982; McCulloch and Hopkins 1966; Ritchie et al. 1983). It is hoped that the models presented here will prove useful in generating data that are independent of existing palaeoclimatic inferences (largely pollen based) and for testing hypotheses related to these and other questions.

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References

- Abbott MB, Finney BP, Edwards ME, Kelts KR (2000) Lake-level reconstructions and paleohydrology of Birch Lake, central Alaska, based on seismic reflection profiles and core transects. *Quat Res* 53:154-166
- Barber VA, Finney BP (2000) Late Quaternary paleoclimatic reconstructions for interior Alaska based on paleolake-level data and hydrologic models. *J Paleolimnol* 24:29-44
- Barley EM (2004) Paleoclimate analysis of southwestern Yukon Territory using subfossil chironomid remains from Antifreeze Pond. MSc thesis, Simon Fraser University, Burnaby, BC
- Battarbee RW, Grytnes J-A, Thompson R, Appleby PG, Catalan J, Korhola A, Birks HJB, Heegaard E, Lami A (2002) Comparing palaeolimnological and instrumental evidence of climate change for remote mountain lakes over the last 200 years. *J Paleolimnol* 28:161-179
- Bigelow NH, Edwards ME (2001) A 14,000 yr paleoenvironmental record from Windmill Lake, central Alaska: late glacial and Holocene vegetation in the Alaska range. *Quat Sci Rev* 20:203-215
- Bouchard G, Gajewski K, Hamilton PB (2004) Freshwater diatom biogeography in the Canadian Arctic Archipelago. *J Biogeogr* 31:1955-1973
- Bradley RS (1999) *Paleoclimatology: reconstructing climates of the Quaternary*. Academic Press, Toronto
- Brodersen KP, Lindegaard C (1999) Mass occurrence and sporadic distribution of *Corynocera ambigua* Zetterstedt (Diptera, Chironomidae) in Danish lakes. Neo- and palaeolimnological records. *J Paleolimnol* 22:41-52
- Brooks SJ (1999) Diagnosis of Janytarsini (June 1999)
- Brooks SJ, Birks HJB (2000) Chironomid-inferred late-glacial and early-Holocene mean July air temperatures for Kraknes Lake, western Norway. *J Paleolimnol* 23:77-89
- Brooks SJ, Birks HJB (2001) Chironomid-inferred air temperatures from lateglacial and Holocene sites in northwest Europe: progress and problems. *Quat Sci Rev* 20:1723-1741
- Brooks SJ, Udachin V, Williamson BJ (2005) Impact of copper smelting on lakes in the southern Ural Mountains, Russia, inferred from chironomids. *J Paleolimnol* 33:229-241
- Cunningham BF, Wilson SE, Hall RL, Smol JP (1995) Diatoms from lakes in British Columbia (Canada) and their relationship to lakewater salinity, nutrients and other limnological variables. *Bibliotheca Diatomologica*, J. Cramer, Stuttgart, p 207
- Cwynar LC (1982) A late-Quaternary vegetation history from Hanging Lake, northern Yukon. *Ecol Monogr* 52:1-24
- Cwynar LC, Spear RW (2001) Lateglacial climate change in the White Mountains of New Hampshire. *Quat Sci Rev* 20:1265-1274
- Engstrom DR, Hansen BCS, Wright Jr HE (1990) A possible Younger Dryas record in southeastern Alaska. *Science* 250:1383-1385
- Environment Canada (1994a) *Manual of Analytical Methods: Major Ions and Nutrients, Vol. 1*. National Laboratory for Environmental Testing, Canadian Centre for Inland Waters, Burlington, Ontario
- Environment Canada (1994b) *Manual of Analytical Methods: Trace Metals, Vol. 2*. National Laboratory for Environmental Testing, Canadian Centre for Inland Waters, Burlington, Ontario
- Gajewski K, Bouchard G, Wilson SE, Kurek J, Cwynar LC (2005) Distribution of Chironomidae (Insecta: Diptera) head capsules in recent sediments of Canadian Arctic lakes. *Hydrobiologia* 549:131-143

- Glew J (1989) A new trigger mechanism for sediment samplers. *J Paleolimnol* 2:241-243
- Glew J (1991) Miniature gravity corer for recovering short sediment cores. *J Paleolimnol* 5:285-287
- Gregory-Eaves I, Smol JP, Finney BP, Edwards ME (1999) Diatom-based transfer functions for inferring past climatic and environmental changes in Alaska, USA. *Arct Antarct Alp Res* 31:353-365
- Gregory-Eaves I, Smol JP, Finney BP, Lean DRS, Edwards ME (2000) Characteristics and variation in lakes along a north-south transect in Alaska. *Arch Hydrobiol* 147:193-223
- Guthrie RD (2001) Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quat Sci Rev* 20:549-574
- Heinrichs ML, Walker IR, Mathewes RW (2001) Chironomid-based paleosalinity records in southern British Columbia, Canada: a comparison of transfer functions. *J Paleolimnol* 26:147-159
- Heiri O, Lotter AF (2001) Effect of low count sums on quantitative environmental reconstructions: an example using subfossil chironomids. *J Paleolimnol* 26:343-350
- Heiri O, Millet L (2005) Reconstruction of Late Glacial summer temperatures from chironomid assemblages in Lac Lautrey (Jura, France). *J Quat Sci* 20:33-44
- Hu FS, Shemesh A (2003) A biogenic-silica 6^{18}O record of climatic change during the last glacial-interglacial transition in southwestern Alaska. *Quat. Res.* 59:379-385
- Hu FS, Lee BY, Kaufman DS, Yoneji S, Nelson DM, Henne PD (2002) Response of tundra ecosystem in southwestern Alaska to Younger-Dryas climatic oscillation. *Global Change Biol* 8:1156-1163
- Hynynen J, Palomäki A, Meriläinen JJ, Witick A, Mäntykoski K (2004) Pollution history and recovery of a boreal lake exposed to a heavy bleached pulping effluent load. *J Paleolimnol* 32:351-374
- Juggins S (2003) C2 version 1.4. University of Newcastle
- Kaufman DS et al (2004) Holocene thermal maximum in the western Arctic (0-180°W). *Quat Sci Rev* 23:529-560
- Korhola A, Olander H, Blom T (2000) Cladoceran and chironomid assemblages as quantitative indicators of water depth in subarctic Fennoscandian lakes. *J Paleolimnol* 24:43-54
- Larocque I (2001) How many chironomid head capsules are enough? A statistical approach to determine sample size for palaeoclimatic reconstructions. *Palaeogeogr Palaeoclimatol Palaeoecol* 172:133-142
- Larocque I, Hall RI (2004) Holocene temperature estimates and chironomid community composition in the Abisko Valley, northern Sweden. *Quat Sci Rev* 23:2453-2465
- Lotter AF, Birks HIB, Hofmann W, Marchetto A (1997) Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *J Paleolimnol* 18:395-420
- Lotter AF, Walker IR, Brooks SJ, Hofmann W (1999) An intercontinental comparison of chironomid palaeotemperature inference models: Europe vs North America. *Quat Sci Rev* 18:717-735
- Massaferro J, Brooks SJ (2002) Response of chironomids to Late Quaternary environmental change in Taitao Peninsula, southern Chile. *J Quat Sci* 17:101-111
- McCulloch D, Hopkins DM (1966) Evidence for an early recent warm interval in northwestern Alaska. *Geol Soc Am Bull* 77:1089-1107
- Natural Resources Canada (2003) Atlas of Canada. <http://www.atlas.gc.ca/site/index>
- New M, Lister D, Hulme M, Mankin I (2002) A high resolution data set of surface climate over global land areas. *Climate Res* 21:1-25
- Olander H, Korhola A, Blom T (1997) Surface sediment Chironomidae (Insecta: Diptera) distributions along an ecotonal transect in subarctic Fennoscandia: developing a tool for palaeotemperature reconstructions. *J Paleolimnol* 18:45-59
- Olander H, Birks HIB, Korhola A, Björn T (1999) An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia. *Holocene* 9:279-294
- Oliver DR, Roussel ME (1983) The Insects and Arachnids of Canada, Part 11: The Genera of Larval Midges of Canada, Diptera: Chironomidae. Research Branch, Agriculture Canada, Ottawa
- Overland IE, Wang M (2005) The Arctic climate paradox: the recent decrease of the Arctic Oscillation. *Geophys Res Lett* 32:1-5
- Palmer SL, Walker IR, Heinrichs ML, Hebda R, Scudder G (2002) Postglacial midge community change and Holocene palaeotemperature reconstructions near treeline, southern British Columbia (Canada). *J Paleolimnol* 28:469-490
- Phillips D (1990) The Climates of Canada. Canadian Government Publishing Centre, Environment Canada
- Pienitz R, Smol JP, Birks HIB (1995) Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *J Paleolimnol* 13:21-49
- Pienitz R, Smol JP, Lean DRS (1997) Physical and chemical limnology of 59 lakes located between the southern Yukon and the Tuktoyaktuk Peninsula, Northwest Territories (Canada). *Can J Fish Aquat Sci* 54:330-346
- Porinchu DF, Cwynar LC (2000) The distribution of freshwater Chironomidae (Insecta:Diptera) across treeline near the Lower Lena River, Northeast Siberia, Russia. *Arct Antarct Alp Res* 32:429-437
- Quinlan R, Smol JP (2001a) Chironomid-based inference models for estimating end-of-summer hypolimnetic oxygen from south-central Ontario lakes. *Freshwat Biol* 46:1529-1551
- Quinlan R, Smol JP (2001b) Setting minimum head capsule abundance and taxa deletion criteria in chironomid-based inference models. *J Paleolimnol* 26:327-342
- Ritchie JC, Cwynar LC, Spear RW (1983) Evidence from north-west Canada for an early Holocene Milankovitch thermal maximum. *Nature* 305:126-128
- Rosenberg SM, Walker IR, Mathewes RW, Hallett DJ (2004) Midge-inferred Holocene climate history of two subalpine lakes in southern British Columbia. *Holocene* 14:258-271

- Rosen P, Segerstrom U, Eriksson L, Renberg I (2003) Do diatom, chironomid, and pollen records consistently infer Holocene July air temperature? A comparison using sediment cores from four alpine lakes in northern Sweden. *Arct Antarct Alp Res* 35:279-290
- Seppälä M (2001) Unsatisfactory field data in a calibration model for inferring past temperatures from chironomid assemblages in northern Fennoscandia: a comment on Olander, Birks, Korhola and Blom. *Holocene* 11: 613-622
- Sweetman IN, Smol JP (2006) Patterns in the distribution of cladocerans (Crustacea:Branchiopoda) in lakes across a north-south transect in Alaska, USA. *Hydrobiologia* 553:277-291
- ter Braak CJF (1991) CANOCO version. Agricultural Mathematics Group, University of Wageningen, Wageningen, The Netherlands
- ter Braak CJF (1995) Ordination. In: Jongman RHG, ter Braak CJF, van Tongeren OPR (eds) *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge, pp 69-173
- Velle G, Brooks SJ, Birks HJB, Willassen E (2005) Chironomids as a tool for inferring Holocene climate: an assessment based on six sites in southern Scandinavia. *Quat Sci Rev* 24:1429-1462
- Walker IR (1988) Late-Quaternary Palaeoecology of Chironomidae (Diptera:Insecta) from Lake Sediments in British Columbia. Ph.D. thesis, Simon Fraser University, Burnaby
- Walker IR (1990) Modern assemblages of arctic and alpine Chironomidae as analogues for late-glacial communities. *Hydrobiologia* 214:223-227
- Walker IR (1995) Chironomids as indicators of past environmental change. In: Armitage PD, Cranston PS, Pinder LCV (eds) *The Chironomidae: Biology and Ecology of Non-biting Midges*. Chapman and Hall, London, UK, pp 405-422
- Walker IR (2000) The WWWFieldGuide to Subfossil Midges. <http://www.ouc.bc.ca/eesc/iwalker/wwwguide>
- Walker IR (2001) Midges: Chironomidae and related Diptera. In: Smol JP, Birks HJB, Last WM (eds) *Tracking Environmental Change using Lake Sediments: Zoological Indicators*. Kluwer Academic Publishers, Dordrecht, pp 43-66
- Walker IR, MacDonald GM (1995) Distributions of Chironomidae (Insecta:Diptera) and other freshwater midges with respect to treeline, Northwest Territories, Canada. *Arc Alp Res* 27:258-263
- Walker IR, Mathewes RW (1988) Late-Quaternary fossil Chironomidae (Diptera) from Hippa Lake, Queen Charlotte Islands, British Columbia, with special reference to *Corynocera* Zett. *Can Entomol* 120:739-751
- Walker IR, Smol JP, Engstrom DR, Birks HJB (1991) An assessment of Chironomidae as quantitative indicators of past climatic change. *Can J Fish Aquat Sci* 48:975-987
- Walker IR, Levesque AJ, Cwynar LC, Lotter AF (1997) An expanded surface-water palaeotemperature inference model for use with fossil midges from eastern Canada. *J Paleolimnol* 18:165-178
- Walker IR, Levesque AJ, Pienitz R, Smol JP (2003) Freshwater midges of the Yukon and adjacent Northwest Territories: a new tool for reconstructing Beringian paleoenvironments? *J N Am Benthol Soc* 22:323-337
- Wiederholm T (1983) Chironomidae of the Holarctic Region. Keys and Diagnoses. Part 1. Larvae. *Entomologica Scandinavica*, Suppl 19
- Wilson SE, Gajewski K (2004) Modern chironomid assemblages and their relationship to physical and chemical variables in southwest Yukon and northern British Columbia lakes. *Arct Antarct Alp Res* 36:446-455