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Article *in* Journal of Paleolimnology · July 2007

Impact Factor: 2.12 · DOI: 10.1007/s10933-007-9157-3

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J Paleolimnol (2008) 40:273–293
DOI 10.1007/s10933-007-9157-3

ORIGINAL PAPER

Environmental controls on modern chironomid faunas from NW Iceland and implications for reconstructing climate change

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Received: 11 May 2007 / Accepted: 30 September 2007 / Published online: 9 November 2007

Abstract Reconstructing climate change quantitatively over millennial timescales is crucial for understanding the processes that affect the climate system. One of the best methods for producing high resolution, low error, quantitative summer air temperature reconstructions is through chironomid analyses. We analysed over 50 lakes from NW and W Iceland covering a range of environmental gradients in order to test whether the distribution of the Icelandic chironomid fauna was driven by summer temperature, or whether other environmental factors were more dominant. A range of analyses showed the main environmental controls on chironomid communities to be substrate (identified through loss-on-ignition and carbon content) and mean July air temperature, although other factors such as lake depth and lake area were also important. The nature of the Icelandic landscape, with numerous volcanic centres (many of which are covered by ice caps) that produce large quantities of ash, means that relative lake carbon content and summer air temperature do not co-vary, as they often do in other chironomid datasets within the Arctic as well as more temperate environments. As the chironomid–environment relationships are thus different in Iceland compared to other chironomid training sets, we suggest that using an Icelandic model is most appropriate for reconstructing past environmental change from fossil Icelandic datasets. Analogue matching of Icelandic fossil chironomid datasets with the Icelandic training set and another European chironomid training set support this assertion. Analyses of a range of chironomid-inferred temperature transfer functions suggest the best to be a two component WA-PLS model with $r^2_{\mathrm{jack}} = 0.66$ and RMSEP = 1.095°C. Using this model, chironomid-inferred temperature reconstructions of early Holocene Icelandic sequences show the magnitude of temperature change compared to contemporary temperatures to be similar to other NW European chironomid sequences, suggesting that the predictive power of the model is good.

Keywords Chironomids · Iceland · Lakes · Climate change · Summer air temperature · Carbon

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Introduction

Chironomids (non-biting midges) are extremely sensitive to environmental change, and hence can be used as indicators of past climatic fluctuations on a variety of temporal and spatial scales. Modern day training sets (i.e. assemblage data from lake surface sediments from a transect of lakes) can be used to elucidate chironomid–environmental relationships over known environmental gradients of interest, and can subsequently produce quantitative chironomid-inferred reconstructions. Chironomid training sets sampled over large geographical gradients frequently show mean summer air temperatures to be the most significant variable in explaining faunal distribution (e.g. Brooks and Birks 2001; Larocque et al. 2001; Heiri et al. 2003a; Woodward and Shulmeister 2006; Barley et al. 2006). Predictive powers of these models are strong, and chironomid-inferred reconstructions of climate change throughout the Younger Dryas chronozone in NW Europe agree well with other proxy data (Brooks and Birks 2000; Bedford et al. 2004; Heiri and Millet 2005). Reconstructing changes during the Holocene, however, becomes more problematic as temperature changes were of a lower magnitude than during the Younger Dryas, and other parameters, notably changes in pH, nutrients and dissolved oxygen, can also affect chironomid communities (Velle et al. 2005), although some validation of chironomid-inferred temperature reconstructions for the last 100 years has been undertaken successfully against instrumental datasets (Larocque and Hall 2003; Holmes 2006). Some training sets which may have been originally designed to maximise temperature gradients have also shown other factors to be influential in explaining the distribution of Holarctic chironomid communities, including substrate (usually described using percentage loss-on-ignition (%LOI)) and lake depth (Korhola et al. 2000; Nyman et al. 2005; Barley et al. 2006; Larocque et al. 2006). Separating the effects of these individual factors on subfossil sequences is a major challenge for researchers, and impacts upon the choice of training sets/transfer functions that are used for evaluating fossil datasets.

One Northern Hemisphere location that is critical for reconstructing past climate change is Iceland, as it lies within the mid-North Atlantic, at the boundary of water masses with both 'polar' (the cold East Greenland current) and 'Atlantic' (the warmer Irminger current) characteristics. Recent marine records with high temporal resolution from the Icelandic Shelf and northern fjords close to the major thermal oceanographic boundary have demonstrated significant Holocene water mass and associated climatic fluctuations and also highlighted the deficiencies in the terrestrial record for the region (Jiang et al. 2002; Andrews and Giraudeau 2003; Andersen et al. 2004; Castañeda et al. 2004; Knudsen et al. 2004; Andresen et al. 2005; Smith et al. 2005). One way in which to address the shortcomings of the terrestrial record is to develop palaeoecological tools through which to reconstruct past climate quantitatively, and this study describes a chironomid-inferred temperature model for Iceland. The model has been used previously by Caseldine et al. (2006) who demonstrated for the first time close links between offshore sea surface temperature records (SSTs) and terrestrial summer temperatures for the early Holocene in Iceland, reflecting the influence of alternating warm/cold oceanic currents on the terrestrial climate. While the chironomid-inferred temperature model reconstructions of Caseldine et al. (2006) were convincing, it is important to consider model performance and other environmental factors which can affect chironomid distribution in Iceland, as well as assessing the validity of the Icelandic training set for reconstructing Icelandic Holocene climate change, which is the role of this paper.

Methods

Site selection and field methods

Approximately 2,750 km^2 of Iceland's surface area is covered by lakes, many of which are situated in the NW and W (Snæfellsnes peninsula) of Iceland. These regions were selected as a key area from which to create a chironomid training set (Fig. 1) due to the lack of geothermal activity within the region and the abundance of lakes at a range of altitudes. Holocene sequences have also been analysed from the region (Caseldine et al. 2003; Doner 2003), and a wealth of environmental data is available from the ocean core records from around NW Iceland (e.g. Eiríksson et al. 2000; Andrews et al. 2003; Castañeda et al. 2004; Ran et al. 2006; Bendle and Rosell-Melé 2007).

The geology of the NW is composed of tertiary basalts (mainly Miocene and Pliocene), with little variation except around parts of Snæfellsnes which include some younger rocks incorporating Holocene lavas (Einarsson 1994). Almost all the lakes are naturally oligotrophic, and both deep and shallow

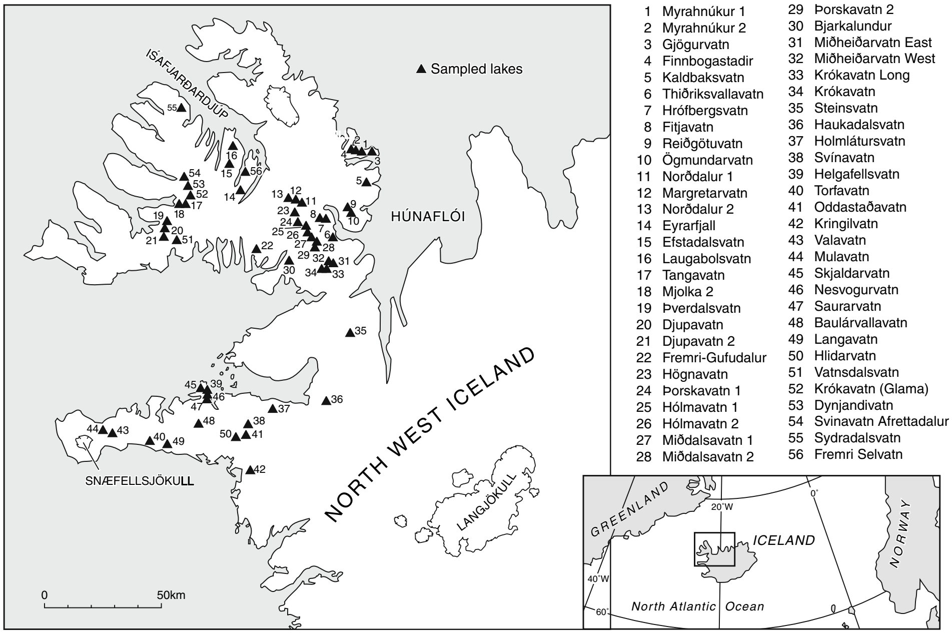

Fig. 1 Map of NW and W Iceland showing the sites sampled for the chironomid training set

lakes were incorporated into the training set. Fifty-six lakes were sampled over two summer field seasons in 2002 and 2003. Three lakes were rejected for further analysis as surface sediment could not be retrieved from one (Tangavatn, Glama), another was a saline lake (Kaldbaksvatn, near Djupavik), and the third lake (Fremri-Selvatn) had creamy coloured sediments, possibly influenced by local geothermal conditions, and contained no chironomid head capsules. A final total of 53 lakes were thus retained for the training set (Fig. 1, Table 1).

Surface sediment cores were extracted from the deepest part of the basin using a Renberg corer (Renberg 1991) and were sampled at 1 cm resolution. Water samples were collected at around 50 cm water depth and one sample was filtered on site, the filtrate being retained to be later analysed for chlorophyll-*a* (chl-*a*). The sediment samples, water samples and filtrate from each lake were stored at 4°C prior to laboratory analyses. Dissolved oxygen (DO) profiles were measured at each site and all lakes were found to be well-mixed, which is in accordance with other Icelandic lakes (H. Malmquist, personal communication). This is most likely to be due to the high levels of wind stress that Icelandic lakes suffer. As the lakes appear to be well mixed for most of the year (but may stratify periodically), it is unlikely that DO levels would affect chironomid communities in these lakes directly, and thus all DO data were left out of any subsequent statistical analyses. Conductivity, pH, water temperature and Secchi depth were also measured at each site. In total 25 environmental parameters were measured from each lake (Table 1).

Laboratory and desktop methods

Chironomid head capsules were extracted from the surface sediments (0–1 cm) following the methods within Brooks et al. (2007). Head capsules were identified using Wiederholm (1983), Oliver and Roussel (1983) and Schmid (1993), and the subfossil taxonomy was subsequently standardised to follow Brooks et al. (2007). A minimum of 50 head capsules were extracted from each sample (Heiri and Lotter 2001; Quinlan and Smol 2001). The surficial sediments were also analysed for percentage loss-on-ignition (% LOI) following standard methods (Dean 1974) and percentage total carbon (TC) and percentage total nitrogen (TN) using a Carlo Erba Elemental Analyser model NA2500. Particle size analysis was undertaken using laser diffraction with a Micromeritics Saturn Digisizer. Water samples were analysed for major anions and cations present, while the filtrate collected

Table 1 Key environmental data for the 53 lakes studied in NW and W Iceland

Lake name	Lake code	No.	Deg N	Deg W	Alt	Area	July T	Water T	MD	pH	Cond	Secchi	Chl-*a*	Mg^{2+}	Na^{+}
Myrahnúkur 1	Myrah1	1	66.00764	21.24362	73	0.053	7.79	6.5	1.3	6.39	189	0.95	8.1	2.4	12.5
Myrahnúkur 2	Myrah2	2	66.00643	21.24987	66	0.054	7.79	6.5	0.8	7.19	129	0.76	7.3	2.1	10.8
Gjögurvatn	Gjogur	3	66.00154	21.21614	43	0.383	7.70	5.8	1.1	7.25	243	0.90	16.2	3.6	19.6
Finnbogastadir	Finbog	4	66.00784	21.28617	23	0.026	7.35	5.9	0.5	7.40	188	0.46	1.8	2.9	14.7
Thiðriksvallavatn	Thidri	6	65.40966	21.44220	90	1.500	8.62	11.0	56.9	7.28	74	8.00	1.1	1.1	7.2
Hrofbergsvatn	Hrof	7	65.44481	21.46406	178	0.310	7.49	6.4	2.7	6.80	111	2.74	6.8	1.6	7.9
Fitjavatn	Fitja	8	65.44502	21.48052	175	0.125	7.77	5.6	0.4	6.69	112	0.37	5.1	1.6	7.5
Reiðgötuvatn	Reidgo	9	65.46055	21.37956	162	0.073	7.87	6.6	4.3	6.87	165	3.54	4.8	2.3	14.1
Ögmundarvatn	Ogmund	10	65.46025	21.36948	157	0.060	7.87	6.6	1.4	7.28	137	1.40	5.1	1.9	10.5
Norðdalur 1	Nord1	11	65.44936	22.06331	437	0.118	6.78	5.2	1.4	7.47	82	0.75	11.6	1.0	5.0
Margretarvatn	Marg	12	65.46396	22.10961	418	0.621	6.92	5.9	1.8	7.53	74	1.00	5.8	0.9	5.0
Norðdalur 2	Nord2	13	65.45347	22.08823	441	0.163	7.02	5.9	3.6	7.35	76	3.63	3.8	1.0	5.6
Eyrarfjall	Eyrar	14	65.47719	22.36712	317	0.036	7.89	6.1	0.9	7.37	87	0.61	6.3	1.0	6.6
Efstadalsvatn	Efst	15	65.56117	22.40638	123	0.578	9.32	7.7	3.8	7.50	88	3.00	5.8	0.6	7.0
Laugabolsvatn	Lauga	16	65.58784	22.39430	46	0.572	9.71	9.4	1.4	7.57	124	1.40	4.8	1.0	8.7
Mjolka2	Mjolk2	18	65.45973	23.07626	402	0.125	7.23	6.5	1.3	7.53	128	1.31	4.6	0.5	4.2
Þverdalsvatn	Pverd	19	65.37229	23.13390	381	0.045	7.69	6.4	0.6	6.25	78	0.61	5.1	0.8	4.9
Djupavatn	Djup1	20	65.39205	23.16032	498	0.056	6.93	6.6	2.3	6.07	68	2.32	5.6	0.9	4.4
Djupavatn 2	Djup2	21	65.39588	23.14341	426	0.050	7.22	7.9	0.6	6.95	68	0.61	4.0	0.6	5.3
Fremri-Gufudalur	FremGu	22	65.34615	22.23577	28	0.325	9.34	9.3	0.6	6.98	82	0.61	3.0	1.2	5.3
Högnavatn	Hogna	23	65.45022	22.09928	422	0.263	7.05	7.5	2.0	6.99	63	1.98	3.0	0.9	4.6
Þorskavatn 1	Porsk1	24	65.42695	22.08286	484	0.187	6.67	6.9	2.5	6.94	60	2.47	4.8	0.6	3.4
Hólmavatn 1	Holm1	25	65.42210	22.06408	453	0.092	6.73	6.9	7.6	6.80	59	4.80	4.0	0.8	4.2
Hólmavatn 2	Holm2	26	65.41574	22.04879	462	0.067	6.68	6.5	3.4	6.73	58	3.35	4.0	0.7	4.5
Miðdalsavatn 1	Midal1	27	65.47447	22.13165	369	0.107	7.23	9.0	0.7	7.08	87	0.70	3.8	1.1	6.0
Miðdalsavatn 2	Midal2	28	65.46615	22.12736	391	0.058	7.10	9.2	0.8	7.13	75	0.76	2.3	1.1	5.4
Þorskavatn 2	Porsk2	29	65.40395	22.01813	489	0.187	6.51	9.0	2.2	7.08	60	2.19	5.3	0.8	3.9
Bjarkalundur	Bjark	30	65.33226	22.06483	60	0.176	8.98	11.6	1.3	8.25	163	1.25	5.8	2.6	8.9
Miðheiðarvatn East	Midh E	31	65.33221	21.47068	396	0.168	6.84	6.7	21.3	6.88	92	3.75	5.8	1.1	6.4
Miðheiðarvatn West	Midh W	32	65.33214	21.47163	391	0.101	6.84	8.2	3.1	6.85	74	3.05	5.1	1.0	5.4
Krókavatn Long	Krok L	33	65.32325	21.48360	398	0.070	6.74	8.8	3.3	6.93	63	2.10	7.6	0.9	4.5
Krókavatn	Krokav	34	65.31693	21.49683	375	0.022	6.96	10.0	1.7	6.97	67	1.65	2.8	1.1	4.9
Steinsvatn	Stein	35	65.13210	21.15747	173	0.088	8.25	10.0	0.9	7.55	134	0.91	8.8	3.3	9.2
Haukadalsvatn	Hauka	36	65.03534	21.34884	52	2.600	9.86	9.6	40.0	7.70	103	4.30	4.3	1.5	5.0
Holmlátursvatn	Holmla	37	65.01013	22.03682	65	0.239	9.62	9.5	1.0	7.48	157	1.04	9.1	3.4	8.2
Svínavatn	Svinav	38	64.56354	22.13848	158	0.229	9.17	8.6	11.6	7.84	128	5.65	3.3	2.3	5.8
Helgafellsvatn	Helga	39	65.02465	22.44377	25	0.195	9.97	9.8	2.3	6.98	194	2.29	6.1	3.9	15.7
Torfavatn	Torfa	40	64.49195	23.10508	21	0.530	10.77	10.1	3.3	7.57	166	2.60	8.1	3.0	6.9
Oddastaðavatn	Oddas	41	64.54760	22.13618	72	2.700	9.82	9.0	17.8	7.14	194	7.00	4.6	2.8	6.2

Table 1 continued

Lake name	Lake code	No.	Deg N	Deg W	Alt	Area	July T	Water T	MD	pH	Cond	Secchi	Chl-*a*	Mg^{2+}	Na^{+}
Kringilvatn	Kring	42	64.45216	22.16065	46	0.167	10.10	10.4	0.7	7.10	143	0.67	12.1	4.0	8.6
Valavatn	Vala	43	64.52002	23.33651	301	0.061	9.15	11.3	1.3	7.14	54	1.30	2.2	0.8	4.9
Mulavatn	Mula	44	64.52259	23.35332	206	0.024	9.19	11.6	3.1	7.04	70	3.10	1.4	1.0	5.6
Skjaldarvatn	Skjald	45	65.02704	22.47775	12	0.099	10.06	11.5	1.3	8.39	203	1.30	3.9	5.3	18.1
Nesvogurvatn	Nesvog	46	65.03543	22.42839	21	0.071	9.93	11.6	1.2	7.17	143	1.00	5.0	3.1	17.7
Sauravatn	Saura	47	65.00885	22.43000	11	0.287	10.15	12.8	14.3	6.95	85	2.70	2.5	1.5	8.3
Baularvallavatn	Baular	48	64.54681	22.52806	198	1.600	9.62	10.9	32.4	7.03	46	8.20	1.8	1.0	4.5
Langavatn	Langa	49	64.48553	23.02193	25	0.812	10.80	11.6	1.2	7.72	122	1.20	6.1	2.1	13.1
Hlidarvatn	Hlidar	50	64.54059	22.09177	86	4.100	9.59	11.1	19.0	7.58	67	3.00	1.8	2.4	4.6
Vatnsdalsvatn	Vatns	51	65.35694	23.07261	20	2.100	10.01	11.9	33.8	6.70	31	9.20	1.1	0.2	3.7
Krókavatn Glama	Krok G	52	65.42504	23.06276	550	0.256	6.78	8.7	18.8	6.67	32	5.90	2.2	0.3	3.4
Dynjandivatn	Dynja	53	65.44066	23.09689	297	0.010	8.24	9.3	1.0	6.77	29	1.00	1.8	0.3	3.5
Svinavatn Afrettadalur	SvinAf	54	65.44881	23.09490	213	0.032	8.45	9.2	0.7	7.20	39	0.70	2.9	0.3	4.6
Sydradalsvatn	Sydra	55	66.07611	23.14772	8	1.000	9.68	8.0	1.5	7.08	73	1.50	1.8	1.1	8.9
Summary statistics		Min	64.45216	21.15747	8	0.010	6.51	5.2	0.4	6.07	29	0.37	1.1	0.2	3.4
		Max	66.07611	23.35332	550	4.100	10.80	12.8	56.9	8.39	243	9.20	16.2	5.3	19.6
		Mean	65.27530	22.19887	221	0.452	8.30	8.58	6.5	7.15	103	2.41	4.9	1.6	7.5
		SD	0.41976	0.66142	176	0.800	1.31	2.06	11.5	0.43	51	2.12	2.9	1.1	4.0

Lake Name	Lake code	No.	K^{+}	Ca^{2+}	SO^{4-}	Cl^{-}	TN	TC	C/N	LOI 500	LOI 850	Sand	Silt	Clay
Myrahnúkur 1	Myrah1	1	0.6	1.8	2.0	21.5	1.69	19.03	11.23	38.30	39.66	26.75	65.03	8.22
Myrahnúkur 2	Myrah2	2	0.5	1.1	1.2	19.4	0.18	2.14	11.67	6.15	6.33	46.20	47.80	6.00
Gjögurvatn	Gjogur	3	0.8	2.9	2.6	37.2	1.56	15.43	9.89	30.28	31.48	11.18	73.65	15.17
Finnbogastadir	Finbog	4	1.0	2.0	1.9	28.4	0.17	2.10	12.08	4.24	4.30	46.87	48.54	4.59
Thiðriksvallavatn	Thidri	6	0.2	1.8	0.1	12.3	0.23	3.48	15.34	11.02	12.22	21.20	69.73	9.07
Hrofbergsvatn	Hrof	7	0.5	1.6	1.2	17.4	0.70	6.79	9.74	16.47	17.85	12.51	79.98	7.51
Fitjavatn	Fitja	8	0.4	1.5	1.5	16.9	0.13	1.49	11.83	7.04	7.59	31.96	61.52	6.51
Reiðgötuvatn	Reidgo	9	0.6	2.7	3.2	30.5	1.46	13.46	9.24	30.93	32.85	13.57	76.35	10.08
Ögmundarvatn	Ogmund	10	0.5	2.1	2.8	24.0	0.63	9.15	14.47	18.35	19.01	27.00	69.30	3.70
Norðdalur 1	Nord1	11	0.3	0.9	2.4	10.9	0.46	4.67	10.25	11.44	12.13	12.10	81.00	6.90
Margretarvatn	Marg	12	0.3	0.8	1.7	9.6	0.55	5.52	10.08	14.18	14.94	5.71	84.28	10.01
Norðdalur 2	Nord2	13	0.2	0.6	2.2	11.2	0.59	5.59	9.49	18.23	19.53	10.37	77.17	12.46
Eyrarfjall	Eyrar	14	0.3	0.9	2.1	13.1	0.83	8.61	10.40	18.02	18.73	15.50	75.90	8.60
Efstadalsvatn	Efst	15	0.4	0.2	0.1	9.8	1.38	11.98	8.70	27.10	28.58	9.01	84.38	6.61
Laugabolsvatn	Lauga	16	0.4	0.8	0.1	11.6	1.46	13.10	8.95	33.35	37.20	21.79	74.60	3.61
Mjolka2	Mjolk2	18	0.2	0.6	1.9	8.0	0.71	5.54	7.84	13.36	14.84	9.58	81.14	9.28
Þverdalsvatn	Pverd	19	0.2	1.2	1.7	10.1	0.22	2.31	10.71	6.35	6.72	36.97	57.68	5.34
Djupavatn	Djup1	20	0.2	1.3	1.7	10.6	0.51	6.47	12.72	16.15	17.13	13.11	75.58	11.31
Djupavatn 2	Djup2	21	0.3	1.2	1.3	9.8	0.32	3.29	10.16	10.52	11.27	14.84	78.44	6.72
Fremri-Gufudalur	FremGu	22	0.3	2.1	2.4	10.8	0.02	0.28	14.87	2.19	2.67	64.37	33.26	2.37

Table 1 continued

Lake Name	Lake code	No.	K^+	Ca^{2+}	SO^{4-}	Cl^-	TN	TC	C/N	LOI 500	LOI 850	Sand	Silt	Clay
Högnavatn	Hogna	23	0.3	0.8	1.9	8.6	0.47	4.26	9.15	9.44	10.02	25.20	67.83	6.97
Þorskavatn 1	Porsk1	24	0.2	0.4	1.0	6.8	0.56	5.19	9.29	10.45	11.33	22.95	68.04	9.02
Hólmavatn 1	Holm1	25	0.2	0.6	1.7	8.6	0.63	6.09	9.68	14.89	16.04	8.32	80.04	11.63
Hólmavatn 2	Holm2	26	0.1	0.8	1.3	9.7	0.58	6.15	10.63	17.99	19.11	8.22	80.64	11.13
Miðdalsavatn 1	Midal1	27	0.2	1.5	2.3	10.4	0.19	2.15	11.20	8.65	9.09	23.19	69.88	6.93
Miðdalsavatn 2	Midal2	28	0.2	1.2	1.3	9.7	0.12	1.43	11.46	5.53	5.80	40.40	54.20	5.40
Þorskavatn 2	Porsk2	29	0.1	0.7	1.2	7.9	0.74	7.21	9.71	18.94	20.40	5.80	79.10	15.10
Bjarkalundur	Bjark	30	0.2	11.4	2.2	19.4	0.42	3.99	9.49	11.05	12.03	10.92	81.31	7.77
Miðheiðarvatn East	Midh E	31	0.3	1.1	1.2	12.5	0.45	3.91	8.66	13.65	14.55	12.34	77.33	10.33
Miðheiðarvatn West	Midh W	32	0.2	0.8	2.1	11.6	0.75	6.14	8.23	15.60	16.69	16.72	71.94	11.34
Krókavatn Long	Krok L	33	0.3	0.7	0.8	8.5	0.53	5.36	10.08	16.29	17.36	46.20	47.80	6.00
Krókavatn	Krokav	34	0.3	0.9	0.6	9.1	0.52	7.44	14.32	18.31	18.97	33.10	59.94	6.96
Steinsvatn	Stein	35	0.1	2.3	1.0	14.3	0.35	4.59	13.12	11.54	11.96	29.32	65.76	4.92
Haukadalsvatn	Hauka	36	0.2	2.3	0.1	7.2	0.15	1.81	12.19	5.97	6.66	17.52	73.37	9.11
Holmlátursvatn	Holmla	37	2.6	2.8	0.9	16.5	0.16	1.90	11.96	4.82	5.30	33.23	61.35	5.42
Svínavatn	Svinav	38	1.7	1.7	1.7	11.3	0.49	5.45	11.04	14.32	15.44	12.93	79.36	7.72
Helgafellsvatn	Helga	39	1.5	4.1	1.2	30.8	1.90	20.35	10.69	40.57	41.95	23.15	68.94	7.92
Torfavatn	Torfa	40	1.0	7.3	1.4	13.2	1.58	14.53	9.22	31.20	32.82	21.79	71.29	6.93
Oddastaðavatn	Oddas	41	0.2	2.5	0.1	8.2	0.45	4.53	10.13	13.26	14.45	13.80	78.00	8.20
Kringilvatn	Kring	42	0.8	3.7	1.2	13.3	0.51	7.24	14.12	22.97	23.79	18.56	77.23	4.21
Valavatn	Vala	43	0.4	0.5	0.1	8.7	0.47	4.72	10.10	22.93	24.65	13.01	76.41	10.58
Mulavatn	Mula	44	0.4	0.6	0.1	9.6	0.65	6.98	10.81	18.76	20.23	13.49	76.43	10.09
Skjaldarvatn	Skjald	45	0.6	8.8	0.0	24.5	0.71	9.93	13.95	29.21	30.29	22.69	70.86	6.45
Nesvogurvatn	Nesvog	46	0.9	2.5	0.1	29.1	1.07	16.50	15.41	45.98	47.50	19.69	75.08	5.23
Sauravatn	Saura	47	0.6	1.9	0.2	12.5	0.70	7.02	10.01	19.48	21.17	15.38	77.57	7.05
Baularvallavatn	Baular	48	0.3	0.6	0.1	7.5	0.47	4.89	10.46	15.13	16.41	10.48	81.88	7.64
Langavatn	Langa	49	0.4	3.4	0.1	23.3	1.53	18.39	12.05	41.28	42.60	12.00	76.28	11.71
Hlidarvatn	Hlidar	50	0.2	2.4	0.1	11.7	0.25	2.71	11.02	9.43	10.60	10.13	80.49	9.38
Vatnsdalsvatn	Vatns	51	0.2	0.1	0.1	5.7	0.64	4.83	7.59	11.97	13.45	9.39	82.24	8.37
Krókavatn Glama	Krok G	52	0.2	0.1	0.1	6.3	0.40	3.74	9.25	9.88	11.91	11.08	82.47	6.45
Dynjandivatn	Dynja	53	0.2	0.1	0.1	6.1	0.14	1.76	12.55	7.29	7.81	37.42	57.77	4.81
Svinavatn Afrettadalur	SvinAf	54	0.2	0.2	0.1	7.5	0.09	0.95	10.08	4.20	4.53	47.97	48.12	3.91
Sydradalsvatn	Sydra	55	0.3	0.8	0.1	13.0	0.10	1.08	10.42	4.40	4.89	31.49	64.88	3.64
Summary statistics		Min	0.1	0.1	0.0	5.7	0.02	0.28	7.59	2.19	2.67	5.71	33.26	2.37
		Max	2.6	11.4	3.2	37.2	1.90	20.35	15.41	45.98	47.50	64.37	84.38	15.17
		Mean	0.4	1.8	1.1	13.7	0.61	6.48	10.90	16.59	17.64	21.29	70.93	7.78
		SD	0.4	2.1	0.9	7.3	0.47	4.92	1.90	10.45	10.84	12.99	11.26	2.83

Alt, altitude (m); MD, maximum depth (m); Secchi depth was measured in metres, area was measured in km^2, anions and cations were measured in ppm, chl-*a* was measured in $\mu g\ l^{-1}$. TN, TC, LOI and the sand, silt, clay fractions were measured as percentages at each lake was analysed for chl-*a*. Mean monthly temperatures were taken from calculations based upon a spatial interpolation of analysis of Icelandic weather stations from the 1961–1990 period (Björnsson 2003). These data are at least 13 years older than the sampling period for the lake surface sediments. Whether this will affect the resulting models depends on the sedimentation rates for each lake and any shift in temperatures over this period. Analysis of temperature changes from the Stykkishólmur meteorological station shows that there has been a ~0.5°C increase in temperature for the 1995–2004 average compared with the 1961–1990 average (Holmes 2006). If we assume that average sedimentation rates of the upper 0–1 cm surface samples are in the order of 5–10 years cm^{-1} then the fact that we are using slightly older meteorological data may affect slightly the accuracy of the data produced by the model outputs but it will not affect the magnitude of the error of the model.

Statistical methods

The 25 environmental variables, with the exception of pH, were log transformed as none were normally distributed (see Birks 1998). Ordinations, including detrended correspondence analysis (DCA), principal components analysis (PCA) and canonical correspondence analysis (CCA), of the chironomid training set data were undertaken using CANOCO 4.5.2 (ter Braak and Smilauer 1998) in order to determine the main environmental controls on the chironomid assemblages. All analyses involved square root transforming the species data and downweighting of rare types. The program R (R, 2005) was used to analyse the data for analogues. Squared chord distance was calculated between the fossil samples and their closest analogue in both the Norwegian (Brooks and Birks 2001, unpublished data) and Icelandic chironomid training sets. TWINSPAN analyses were undertaken using Community Analysis Package (Seaby and Henderson 2006). TWINSPAN pseudospecies cut levels were set at 0, 2, 5, 10, and 20, which allowed the changes in minor taxon abundance to influence classification. The category for lowest abundances (0–2%) was downweighted by half. Transfer functions were developed and tested using C2 (Juggins 2003), which was also used for calculating Hill's N2 values.

Taxonomic notes

Previous research on Icelandic chironomids has been mainly restricted to ecological studies in the large lakes Thingvallavatn and Mývatn (e.g. Jónasson 1979, 1992; Lindegaard 1992; Einarsson et al. 2002) or in some of the river systems (e.g. Gíslason et al. 1994). A comprehensive study of adult populations has been undertaken by Hrafnsdóttir (2005) although the sampling strategies involved were not systematic between locations, precluding multivariate statistical analyses. The modern fauna is thought to consist of 35 genera with 80 species (Hrafnsdóttir 2005) although this is under constant revision. The study of subfossil chironomids from Icelandic sediments has relied mainly upon the work undertaken at Mývatn, a eutrophic lake fed mainly by spring waters which can reach temperatures of up to 30°C (Einarsson and Haflidason 1988). Little else has been published on Icelandic Holocene chironomid assemblages, with the exception of Caseldine et al. (2003, 2006).

In total 54 taxa were identified from the 53 lakes. A number of genera could be split into species morphotypes (sensu Brooks et al. 2007), although splitting some genera proved problematic. In particular, although some individuals of *Psectrocladius* could be identified as either *P. sordidellus*-type or *P. octomaculatus*-type (following Schmid 1993) based on the shape of the median teeth this was not always consistent, and often individuals, in particular early instars, resembled a hybrid state. Hence, all *Psectrocladius* were grouped into solely the genus. *Pseudodiamesa* species were split using Schmid (1993). *Orthocladius* type A was separated from other *Orthocladius*/*Cricotopus* morphotypes by having 6 lateral teeth, all subequal, and a reasonably wide median tooth. It is possible that this taxon might be similar to *Cricotopus* cf. *pilosellus* (T. Hrafnsdóttir, personal communication). Three *Micropsectra* species have been recorded from Icelandic lakes; *M. atrofasciata*, *M. recurvata* and *M. lindrothi* (Hrafnsdóttir 2005), although in the absence of reared larvae it was difficult to split the head capsules into these three species. Thus, the *Micropsectra* individuals were lumped into genus only in the final analyses presented below.

One species type that often causes problems taxonomically is *Tanytarsus lugens*-type. It can be possible to separate *Tanytarsus lugens*-type from *Corynocera oliveri*, due to the relatively large surface tooth on the mandible in *Corynocera*, and also the fact that the lateral teeth in *Corynocera oliveri* appear pressed together and partially super-imposed on each other; much more so than in *Tanytarsus lugens*-type (Brooks et al. 2007). In these Icelandic samples, however, there is a gradation between *Tanytarsus lugens*-type and *Corynocera oliveri*, and with many specimens also having a worn mentum it is difficult to ascertain which group they belong to. As no previous evidence has been found of *Corynocera* in Iceland, and withstanding the fact that absence of evidence is not evidence of absence, these taxa have been grouped under the *Tanytarsus lugens*-type category. A further complication exists, however, as a common *Tanytarsus* species from Iceland is *Tanytarsus gracilentus*, which has similar subfossil characteristics to *Tanytarsus lugens*-type, and hence in most subfossil studies would be grouped together with *Tanytarsus lugens*-type. *Tanytarsus gracilentus* head capsules do, however, have a defining characteristic of a large plate behind the mentum (Brooks et al. 2007). This has been found in a reasonable amount of samples from the lakes studied, and thus recorded as *Tanytarsus gracilentus* (Fig. 2). It is not clear though if this plate is always present in subfossil head capsules, and hence whether taphonomic processes (at any temporal scale) may influence the retention of this plate on the head capsule. Although *Tanytarsus gracilentus* is the most common *Tanytarsus* species in Iceland (Hrafnsdóttir 2005), Fig. 2 shows only a few occurrences of this taxon and much higher proportions of *Tanytarsus lugens*-type. It is thus possible that either all (or a great majority of) *Tanytarsus* are in fact *Tanytarsus gracilentus* but that the plate has been lost from many specimens, or that there are two (or more) different morphotypes, possibly with one that prefers warmer lakes (*Tanytarsus gracilentus*) and another that prefers cooler lakes (*Tanytarsus lugens*-type). This possible differentiation could account for the fact that some of the warmer lakes have a high abundance of *Tanytarsus lugens*-type, (as well as some *Tanytarsus gracilentus*), when it might be expected that they are all *Tanytarsus gracilentus*. The problem with not being able to always separate these taxa consistently unfortunately precludes the confirmation of this hypothesis.

Results

Chironomid distributions

The distribution of chironomid taxa within the study lakes has been ordered by mean July air temperature (Fig. 2). Although typically noisy for such a dataset, it is clear that some taxa have preferences for the generally cooler lakes such as *Micropsectra* spp., *Orthocladius* type I, *Orthocladius* (*Pogonocladius)* *consobrinus*, and *Tanytarsus lugens*-type, although there are some notable outliers regarding this taxon (see taxonomic notes above). Some cold stenotherms, e.g. *Oliveridia* and *Pseudodiamesa*, are almost exclusively present in one lake, Krókavatn Glama, which is one of the coldest lakes according to the model of Björnsson (2003), as well as being one of the most remote geographically from the studied lakes (Fig. 1). Other taxa appear more adapted to relatively warmer lakes, such as *Ablabesmyia*, *Arctopelopia*-type, *Procladius* and *Dicrotendipes*. Some taxa appear to be more eurythermic, although this might be a function of the relatively short contemporary mean summer thermal gradient present in Iceland, which ranges between ca. 4 and 12°C outside of the major ice caps (Björnsson 2003). Most lakes are dominated by *Heterotrissocladius grimshawi*-type and/or *Psectrocladius*, of which *Heterotrissocladius* is often assumed to be a cold stenotherm, whereas *Psectrocladius* is usually considered to be more thermophilous (Brooks et al. 2007). Diamesinae, which are typically considered cold stenotherms (Brooks et al. 2007) exhibit a normal distribution with respect to the relatively short temperature gradient present in this study (Fig. 3a), but show a clear association with TC, with greater abundances occurring in lakes with $<4\%$ TC (Fig. 3b).

Diversity and TWINSPAN analysis

The first level of TWINSPAN division separates the dataset into two groups of non-equal size, based on whether lakes are characterised by a fauna containing significant abundances of *Diamesa* and *Thienemanniella* (a smaller group of nine lakes), or lakes dominated by *Chironomus*, or *Micropsectra* and *Orthocladius* type I (a larger group of 44 lakes) (Fig. 4). The lakes with relatively high levels of

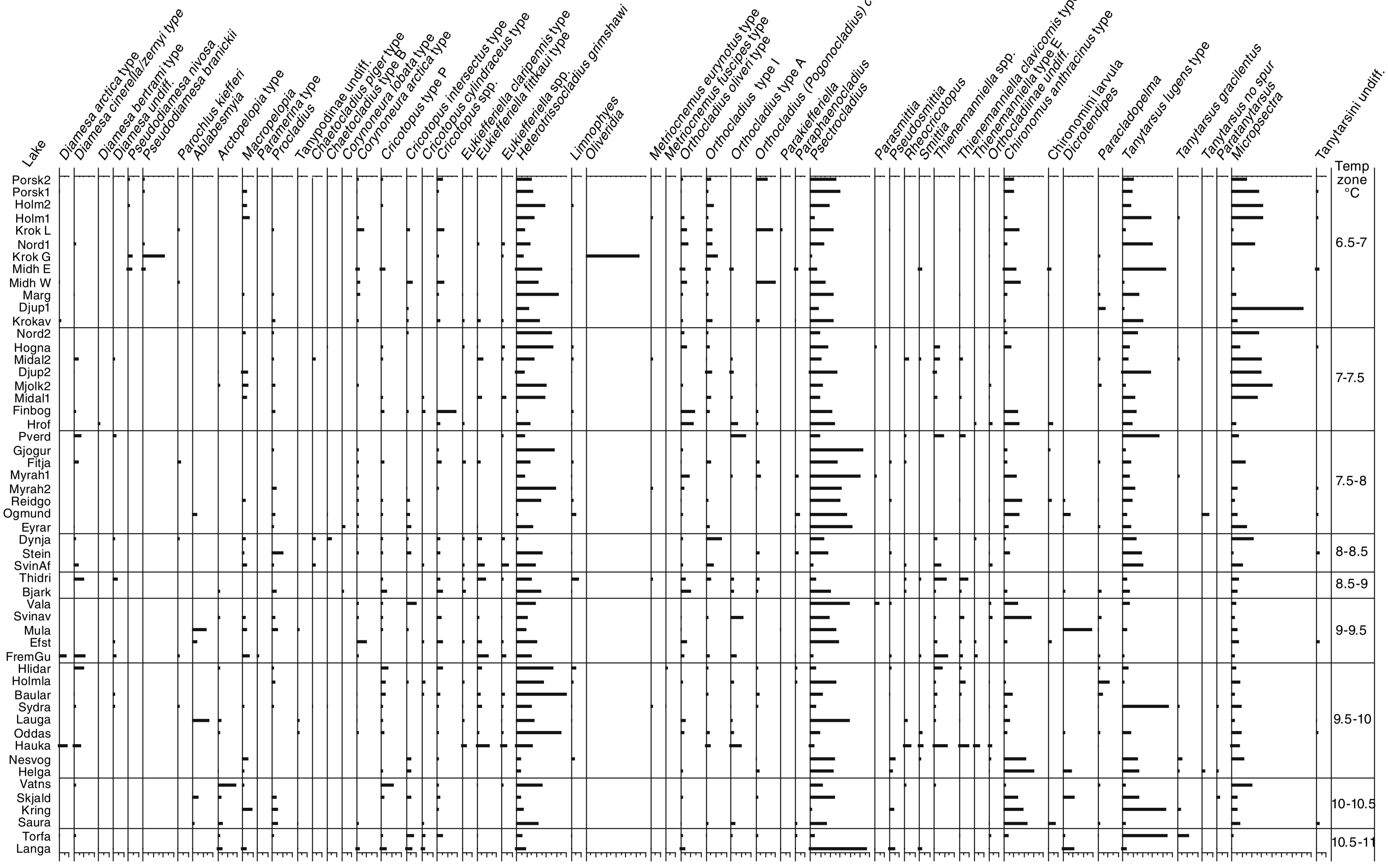

Fig. 2 Chironomid training set, classified by modern July air temperature at each site so the coldest lake is at the top with the warmest at the bottom. Chironomids are shown as percentage abundance

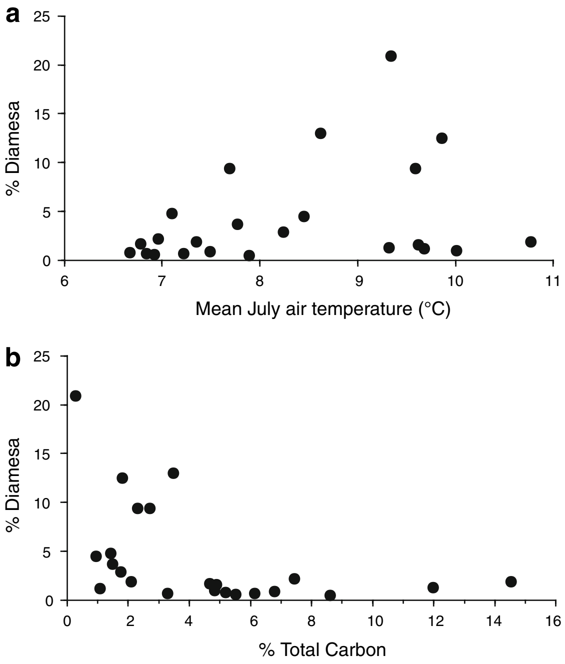

Fig. 3 Distribution of Diamesinae in the Icelandic training set plotted against (**a**) air temperature and (**b**) % TC

Thienemanniella and *Diamesa* have TC values <4%, as well as some of the most diverse chironomid faunas, based on Hill's N2 analyses whereas the other lakes are generally higher in % TC and conductivity (Fig. 5). The second level of division separates the larger group of 44 lakes into those dominated by *Chironomus*, which have higher % TC levels, and those more dominated by *Micropsectra* and *Orthocladius* type I that contain relatively lower levels of % TC. The second cut level on the smaller group of nine lakes separates out the one lake that contained *Oliveridia* (Krókavatn Glama), also identified as an outlier by DCA (see below). The third cut level splits lakes into groups that are characterised by the presence of thermophilous taxa such as *Dicrotendipes* (groups 1 and 2 in Fig. 4) and relatively cooler taxa such as *Heterotrissocladius* (groups 3 and 4 in Fig. 4). The group 1 and 2 lakes are all relatively warm, and situated in the southwest of the region, whereas groups 3 and 4 are relatively cooler (but not all) and situated more in the northeast of the region (Fig. 5). The third level cut on the lakes dominated by *Micropsectra* and *Orthocladius* type I splits those lakes that contain significant amounts of *Paracladopelma* (groups 7 and 8 in Fig. 4) and are comparatively warm from the relatively colder lakes dominated by *Micropsectra* (groups 5 and 6 in Fig. 4). The third cut level on the *Diamesa* and *Thienemanniella* dominated lakes separates sites that contain *Chaetocladius piger* type and are shallow lakes characterised by relatively significant riverine inputs from much deeper lakes (Fig. 5). A fourth cut level was retained on the TWINSPAN analysis as this discriminated between some groups based on key taxa, such as *Cricotopus intersectus* type and *Orthocladius* type A (groups 3 and 4 in Fig. 4). These two groups also had significantly different environmental characteristics, especially July temperature (Fig. 5). Overall, comparisons between the TWINSPAN lake groups (Fig. 4) and associated environmental parameters (Fig. 5) do further illustrate the range of environmental controls that influence chironomid distribution in Iceland.

Ordination analyses

Detrended correspondence analysis (DCA) of all the species and site/environmental data produced an axis 1 gradient of 2.42 (standard deviation units) with an eigenvalue of 0.258, suggesting that unimodal methods were appropriate for further analyses (cf. Birks 1998). The analysis produced a single clear outlier, lake 52 (Krókavatn Glama), which was dominated by *Pseudodiamesa* (20%) and *Oliveridia* (>50%), the latter being a taxon that does not occur in any other lakes within the training set. None of the lakes in the immediate vicinity of Krókavatn Glama were studied, although it is likely that other lakes nearby and at higher altitudes may also contain communities including *Oliveridia* as this is a cold stenotherm (Brooks et al. 2007). One other lake, Miðdalsavatn 2 (lake 28), was also identified as an outlier from the DCA and subsequent canonical correspondence analysis (CCA). This lake is situated towards the western side of the Þorskafjarðarheiði and is fed by the extensive network of rivers that drain the high ground, hence the relatively high number of rheophiles present in the sample. In periods of high flow the lake is more likely to resemble part of the river system, and for this reason was left out of subsequent data analyses, leaving 51 lakes in the final dataset. Principal component analysis (PCA) of the log transformed environmental data was also undertaken, in order to discern which of these variables

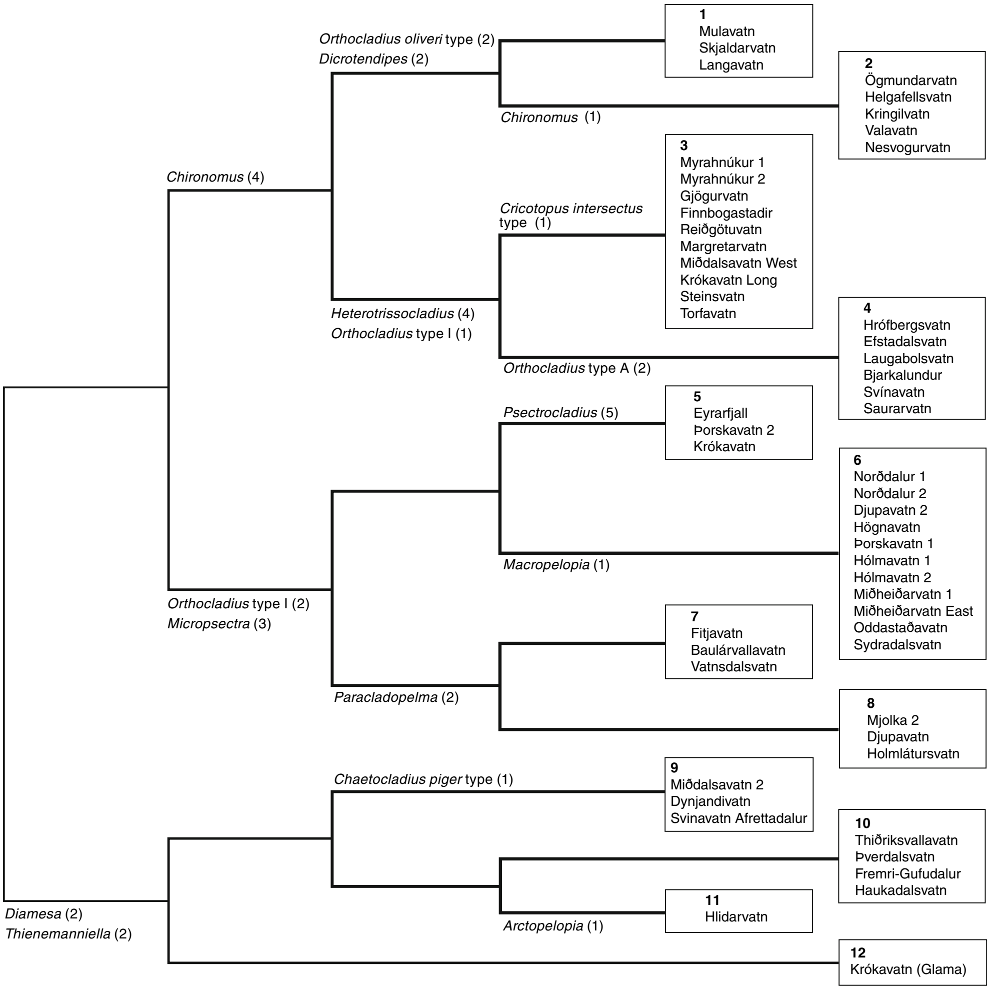

Fig. 4 TWINSPAN analysis of the lakes based on chironomid percentage abundance. The indicator species relative abundance levels are expressed on an ordinal scale

co-varied. There was clear co-variance between TC, TN, and % LOI at 550°C and 850°C (there is little carbonate in Icelandic lake sediments), and Secchi depth and maximum lake depth also showed a high degree of co-variance, as many of the lakes were shallow with the Secchi depth being equal to the maximum depth. Most of the elemental anions and cations showed a high degree of co-variance, along with conductivity.

CCA was undertaken on the dataset with 51 lakes (outliers excluded), 53 taxa and 25 environmental variables. Using forward selection and a Monte Carlo simulation with 999 unrestricted permutations, five environmental variables (TC, mean July air temperature, longitude, lake surface area and lake water Mg^{2+}) explained significant proportions ($p < 0.05$) of the explained variance (Fig. 6a, Table 2). Other CCA runs were undertaken selecting the significant variables in a different order to that in Table 2 , but the main 5 variables were always the same. Linear based methods were also undertaken (redundancy analysis: RDA) but the significant variables remained the same. Further ordinations were undertaken using a range of climate parameters, notably every mean monthly temperature and tri/tetratherms, but mean July air temperature was always the most significant climate parameter (Table 3).

The spatial pattern of lakes under CCA is clearly reflected in the distribution of some of the key taxa (Fig. 6b). The distribution of *Diamesa cinerella/*

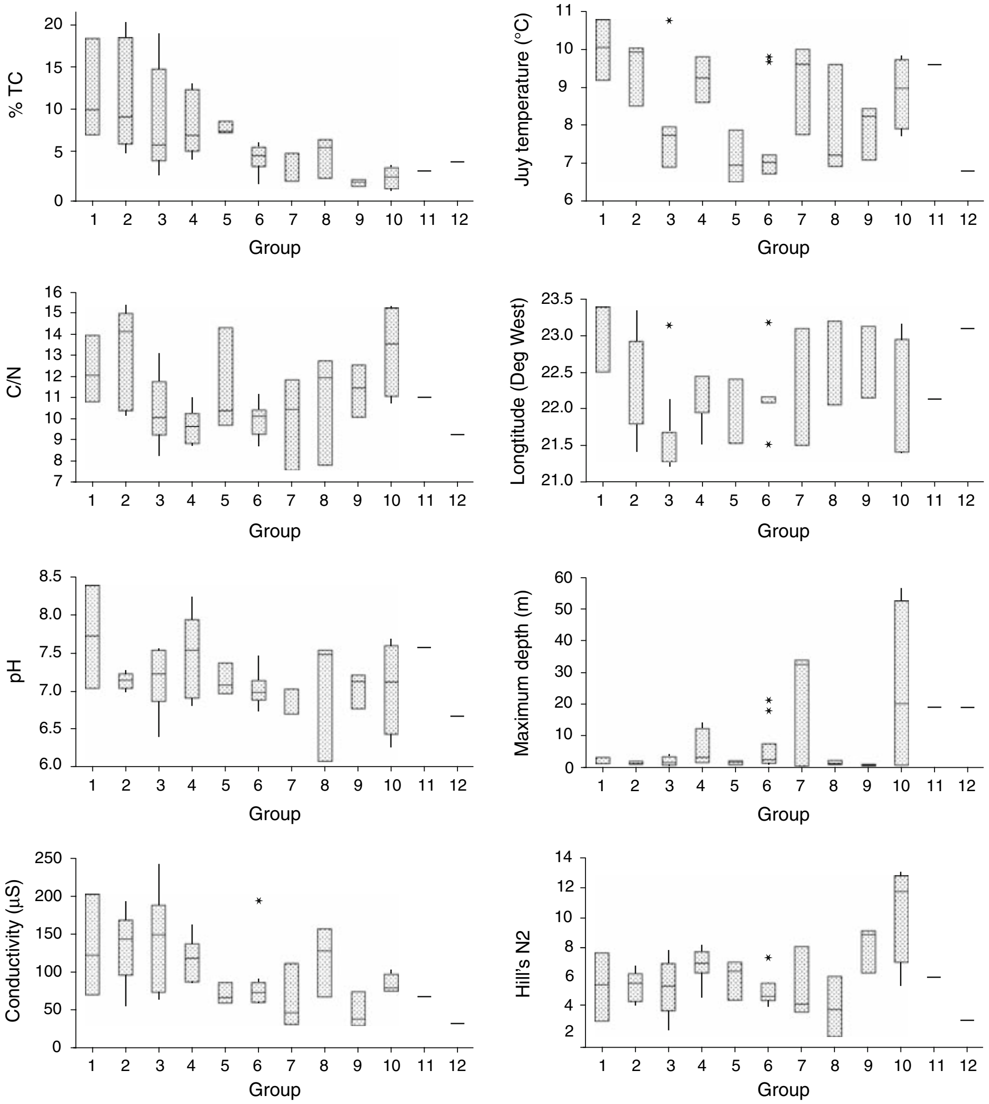

Fig. 5 Environmental parameters plotted against the main groups defined by TWINSPAN analysis

zernyi-type and *Thienemanniella* under CCA show a significant relationship with low TC levels ($p < 0.001$), whereas *Micropsectra* shows a significant relationship with low mean July air temperature ($p < 0.005$). *Tanytarsus lugens*-type is clearly separated from *Tanytarsus gracilentus* in Fig. 6b, although while the majority of colder sites have a reasonable abundance of this taxon (Fig. 2), there are other warmer sites in which *T. lugens*-type are also abundant, illustrating the problems of not being able to convincingly separate *T. lugens*-type and *T. gracilentus* in the subfossil taxonomy, as described above.

Transfer function

The two strongest variables as determined by forward selection, TC and mean July air temperature, were used as single variables in a constrained CCA producing eigenvalue ratios of 0.873 (λ_1/λ_2 = 0.137/0.157) and 0.331 (λ_1/λ_2 = 0.084/0.254) respectively. It was not considered necessary to construct a TC transfer function as this attribute can be measured directly from fossil sediments. A chironomid-inferred temperature (CI-T) transfer function was constructed from the data sets for the 51 lakes. The data were assessed using C2 (Juggins 2003) and a range of models considered. Performance statistics indicated that the weighted average partial least squares (WA-PLS) model using 2 components performed best (Fig. 7, Table 2) with a reasonably high $r^2_{\text{jack}} = 0.66$ and low RMSEP = 0.0396 (1.10°C). While these results seem acceptable, the climatic gradient over which these data have been assessed is somewhat short (6.5–10.8°C), which typically yields good quality models with relatively low error statistics (Walker and Cwynar 2006).

Modern analogues and model comparisons

Faunal (dis)similarity comparisons were undertaken between the Icelandic training set data and fossil samples from an early-mid Holocene sequence from Efstadalsvatn (EFST), NW Iceland. The chironomid dataset from Efstadalsvatn was previously published by Caseldine et al. (2003) and a CI-T reconstruction undertaken using the Norwegian training set developed by Brooks and Birks (2001). In order to test whether the Icelandic training set developed here provided better analogues than the Norwegian training set for palaeoclimatic reconstructions from subfossil Icelandic sequences, histograms showing the (dis)similarity between fossil samples from EFST and their closest analogue from each training set were produced (Fig. 8a, b). These results indicate that the downcore samples have much closer analogues in the

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

Variable	Variance explained	Significance level
Total carbon (TC)	0.137	$p < 0.001$
Mean July air temperature	0.085	$p < 0.001$
Longitude	0.065	$p < 0.001$
Lake area	0.060	$p < 0.001$
Mg^{2+}	0.047	$p < 0.005$
Total variance explained	0.394	
Total variance	1.492	

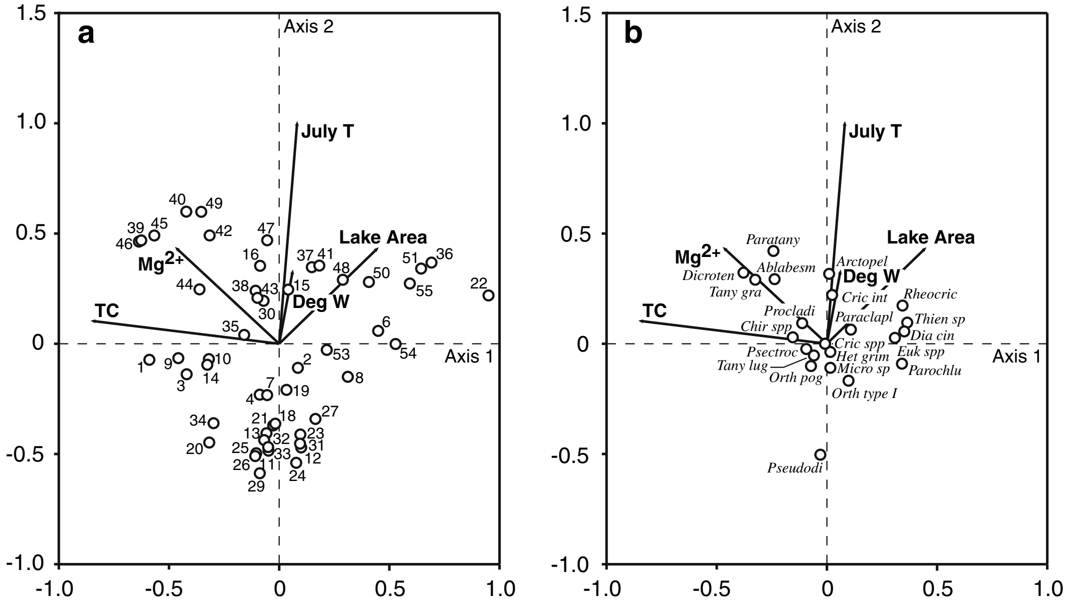

Fig. 6 CCA of the 51 lakes (outliers excluded), showing the significant environmental variables plotted with (**a**) sites (numbers refer to Fig. 1 and Table 1), and (**b**) selected chironomid taxa: Paratany = *Paratanytarsus*, Dicroten = *Dicrotendipes*, Ablabesm = *Ablabesmyia*, Arctopel = *Arctopelopia*, Tany gra = *Tanytarsus gracilentus*, Procladi = *Procladius*, Cric int = *Cricotopus intersectus* type, Rheocric = *Rheocricotopus*, Thien sp = *Thienemanniella* spp., Dia cin = *Diamesa cinerella/zernyi* type, Euk spp = *Eukiefferiella* spp., Paraclapl = *Paracladopelma*, Chir spp = *Chironomus* spp., Cric spp = *Cricotopus* spp., Psectroc = *Psectrocladius* spp., Tany lug = *Tanytarsus lugens* type, Het grim = *Heterotrissocladius grimshawi* type, Orth pog = *Orthocladius* (*Pogonocladius*) *consobrinus*, Micro sp = *Micropsectra* spp., Parochlu = *Parochlus kiefferi*, Orth type I = *Orthocladius* type I, Pseudodi = *Pseudodiamesa*

Table 3 Statistics showing the range of transfer function models utilised (best ones in italic), including WA Inverse, WA classical, PLS, WA-PLS, and WMAT

Model type	r^2_{jack}	Mean bias$_{\text{jack}}$	Max bias$_{\text{jack}}$	RMSEP
Inverse				
WA	0.55	− 0.000565	0.0592	0.0451
WA$_{tol}$	0.37	− 0.000161	0.1021	0.0536
Classical				
WA	*0.56*	*− 0.000643*	*0.0387*	*0.0473*
WA$_{\text{tol}}$	0.38	0.000396	0.0870	0.0740
PLS (1)	0.39	0.003370	0.0854	0.0522
PLS (2)	0.55	0.000782	0.0656	0.0450
PLS (3)	*0.57*	*0.001455*	*0.0516*	*0.0440*
WA-PLS (1)	0.55	-0.000772	0.0586	0.0451
WA-PLS (2)	*0.66*	*− 0.002935*	*0.0402*	*0.0396*
WA-PLS (3)	0.66	− 0.000652	0.0398	0.0394
MAT	0.53	0.027730	0.1005	0.0560
WMAT	*0.57*	*0.027787*	*0.0999*	*0.0549*

Icelandic training set than in the Norwegian training set. Based on a comparison of analogues, it therefore seems most appropriate to use the Icelandic training set for palaeoclimatic reconstructions from Icelandic subfossil sequences. A direct comparison between the reconstructions from the Icelandic and Norwegian transfer functions for EFST (Fig. 9) shows that very early Holocene reconstructions compare well between the models, with the exception of the coldest samples, but from ca. 10,200 cal. years BP onwards the model reconstructions differ consistently in terms of temperature reconstructions by ca. 1–1.5°C, but remain similar in terms of overall trends.

In order to further explore the relationship between training set analogues and the EFST subfossil sequence the data were combined and analysed using a 'time-track' CCA with the EFST samples plotted passively (Fig. 10). Modern analogues clearly exist in the training set for the mid-Holocene samples from EFST, although there are no contemporary analogues for the early Holocene samples. It is clear from Fig. 10 that the EFST chironomid samples are responding to July temperature rather than TC, with the colder early Holocene samples plotting at the base of the diagram where the coldest modern sites are located in the CCA, trending upwards through the mid to late-Holocene samples to warmer modern sites in the CCA. This analysis suggests that it is therefore appropriate to reconstruct summer temperatures from this sequence as shown in Fig 9.

Discussion

Factors affecting chironomid distribution

The two clear drivers of chironomid distribution in NW and W Iceland are TC and mean July air temperature, which dominate axes 1 and 2 of the CCA plot respectively (Fig. 6a). The Icelandic chironomid training set has been used to produce a CI-T transfer function, due to temperature being highly significant in explaining chironomid distribution in NW and W Iceland. However, while temperature is clearly important in the distribution of Icelandic chironomids, the main environmental driver from the training set was TC. Other chironomid training sets have also found levels of sediment organic matter to be influential in explaining chironomid distribution, for example sediment LOI was a key indicator for chironomid distribution in western Finnish Lapland (Nyman et al. 2005). In many other training sets sediment LOI and/or TC tend to co-vary with temperature (e.g. Larocque et al. 2001; Bigler et al. 2006), as warmer lakes tend to be more productive and enriched organically, whereas colder lakes are typically less productive with more clastic dominated sediments. These relationships are not so straightforward in Iceland, however, as temperature and TC follow different ordination axes in explaining chironomid distribution. The most likely explanation for the altered relationship is due to Iceland's active volcanic nature, the landscape being locally subjected to periodic tephra deposition during volcanic airfall events and subsequent remobilisation of tephra by variable wind patterns, even in the less volcanically active NW. Deposition from past eruptions plus the friable basalt from which the majority of the geology is comprised leads to most catchments being relatively rich in clastic material. Some lowland lakes situated within areas of extensive peat growth are relatively organically enriched, such as Torfavatn and Kringilvatn (the latter also by waterfowl), but other lowland shallow lakes are very clastic rich (e.g. Fremri-Gufudalur) due to large catchments and relatively little within lake productivity. The catchment and lake size are thus most likely to affect the

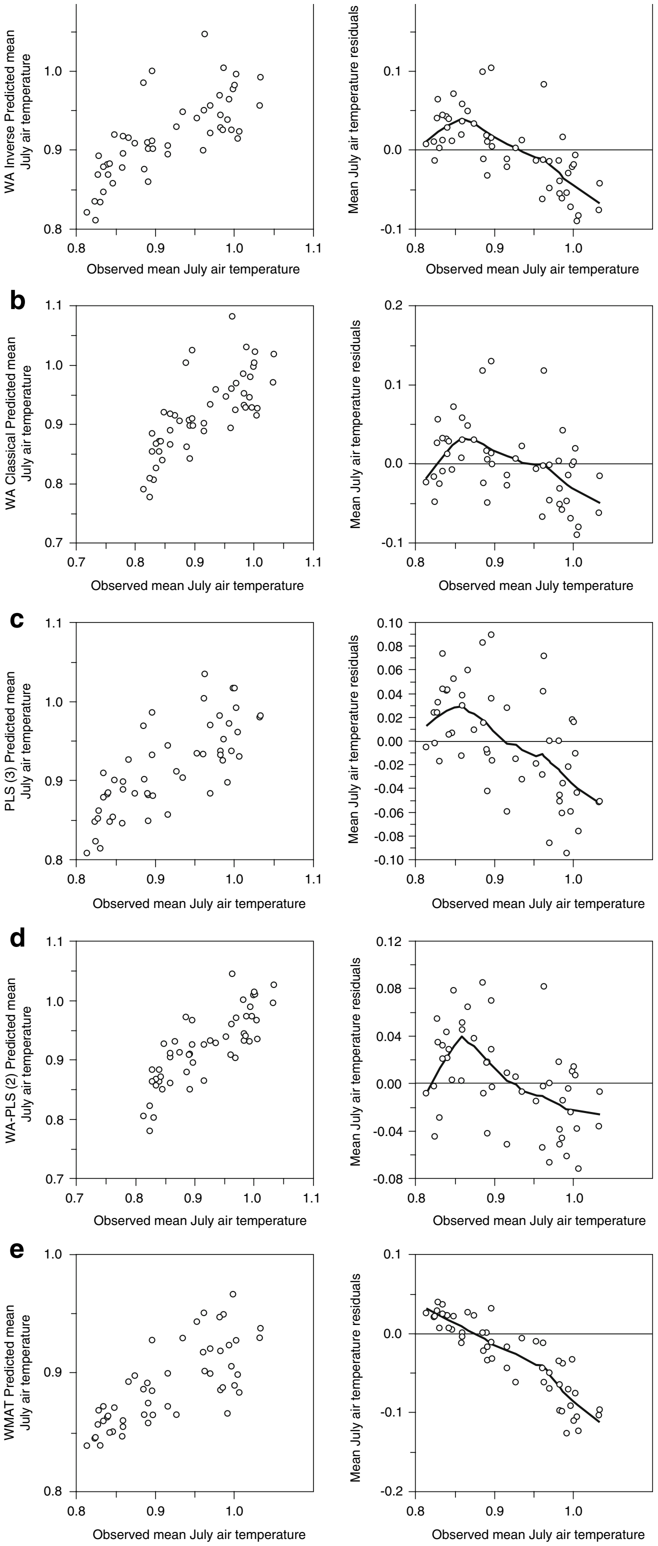

Fig. 7 Plots showing the observed vs predicted $\log_{10}$ mean July temperature and the residuals (inferred-observed) for a range of chironomid inferred mean July temperature models; **(a)** WA-inverse; **(b)** WA-Classical; **(c)** PLS (component 3); **(d)** WA-PLS (component 2); **(e)** Weighted MAT. Trends in residuals are highlighted with a LOESS smoother (span=0.45)

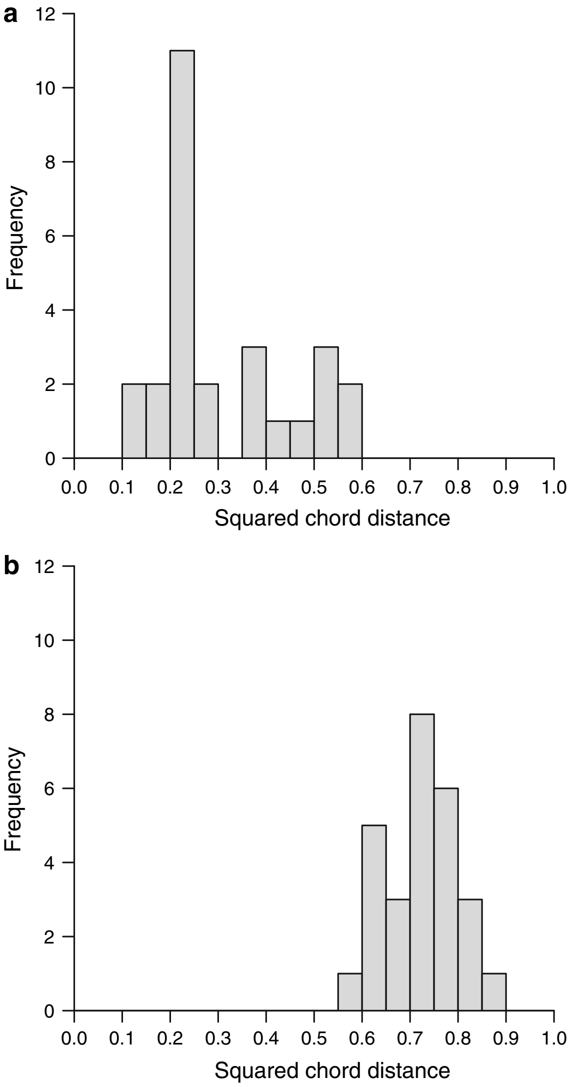

Fig. 8 Histograms showing the closest analogues (squared chord distance) between subfossil chironomids from Efstadalsvatn (Caseldine et al. 2003) and (**a**) the Icelandic training set developed in this paper, (**b**) the Norwegian training set developed by Brooks and Birks (2001, unpublished data)

TC content of the sediment and on the CCA plot (Fig. 6) lake area varies inversely with TC, with the larger lakes having on average the lowest carbon content per unit area. TC levels can influence the chironomid communities through a range of potential mechanisms, including relationships with substrate and larval feeding strategies. Low TC tends to relate to a relatively more clastic substrate and favours rheophiles, which are often found in the surf zone habitats of Icelandic lakes (Lindegaard 1992).

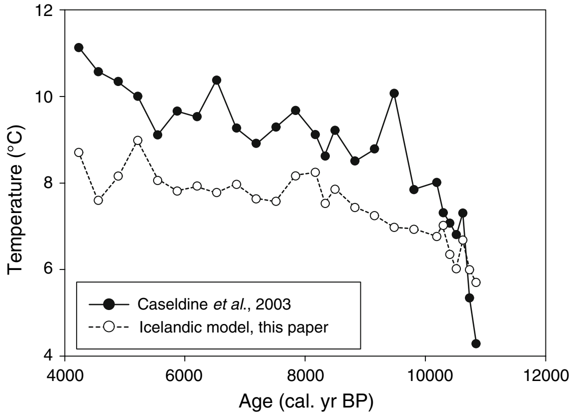

Fig. 9 Comparison between the CI-T reconstructions from the Icelandic and Norwegian transfer functions for the Efstadalsvatn sequence. The sample specific prediction errors (SSPE) are not plotted for each reconstruction to aid clarity, but the average SSPE for the Norwegian model reconstruction was 1.12°C, whereas it was 1.11°C for the Icelandic model reconstruction

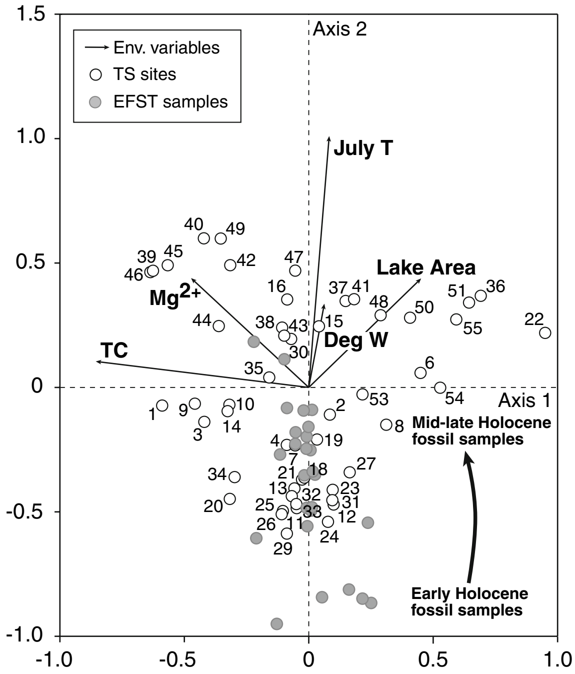

Fig. 10 CCA 'time track' plot showing the significant environmental variables and training set (TS) sites compared against early Holocene fossil samples from NW Iceland (EFST) which have been plotted passively. The fossil samples show early Holocene assemblages at the bottom part of the diagram, trending upwards towards mid-Holocene samples with analogues within the TS

Although lake depth was not significant statistically under CCA, the deeper lakes tend to have similar faunal communities which cluster together when plotted under DCA (not shown) and TWINSPAN analysis also suggested that the assemblages from the deeper lakes were distinctive. Lake depth is often a significant parameter in chironomid training sets (e.g. Korhola et al. 2000; Barley et al. 2006; Zhang et al. 2007). The low TC (clastic rich) lakes comprise both deep and shallow lakes and are predominantly composed of littoral taxa, especially *Thienemanniella* and Diamesinae. It is possible that the low carbon content of the lakes, coupled with the ultra-oligotrophic nature of the large lakes implies that food resources are scarce for benthic dwellers. Analyses of the larvae from large, deep lakes show very few individuals living in the profundal, whilst greater diversity and abundance occur at more shallow sites (Hrafnsdóttir, unpublished results). The head capsule samples we analysed from the profundal are therefore most likely to have washed in from the littoral, and hence these large, deep lakes tend to exhibit a fauna composed of more littoral taxa, and are ultimately governed by substrate (TC/LOI) and not depth with regard to their chironomid communities.

The thermal associations indicated by the Icelandic fauna are similar to relationships that have been found in other chironomid training set studies (e.g. Brooks and Birks 2001). Studies from the high Arctic, for example, indicate that temperature has a clear effect on the contemporary distribution of chironomids (Gajewski et al. 2005) and that aquatic communities are changing rapidly in response to recent warming (Smol et al. 2005; Quinlan et al. 2005). Temperature has also been shown to play a key role on chironomid distribution in sub-Arctic environments (Larocque et al. 2001), although some notable differences do exist within Iceland compared to other (sub)Arctic regions. The most obvious contradiction relates to the Diamesinae, which although present in some abundance, have a normal distribution around the temperature gradient in Iceland (Fig. 3a). A plot of the distribution of Diamesinae against TC (Fig. 3b), however, showed a clear relationship, with greater abundances occurring in lakes with <4% TC. Diamesinae commonly occur in proglacial rivers and lakes, although they are often found in the surf zone of Icelandic lakes (Lindegaard 1992), hence lakes with relatively clastic shorelines (as well as significant riverine inputs) are likely to have a fauna consisting at least partly of Diamesinae. This relationship may impact upon palaeoclimate reconstructions from fossil samples that consist of relatively large abundances of Diamesinae, although Diamesinae were rare in the sequences analysed previously using the Icelandic model described in this paper (Caseldine et al. 2006).

One other factor that might affect Icelandic chironomid distributions not yet discussed is the role of vegetation. Within lake vegetation (aquatic macrophytes) have been shown to significantly influence chironomid distribution within temperate shallow lakes (Brodersen et al. 2001; Langdon et al. 2008), although the presence/absence and quantification of macrophytes were not measured in this study. The majority of the lakes possessed some macrophytes, although density and plant community structure clearly varied amongst lakes. Some of the warmer lakes with low C/N ratios had relatively dense macrophyte communities (group 4 lakes from TWINSPAN analysis), but without detailed surveys it is difficult to ascertain the relative significance of this on overall chironomid community structure. Catchment vegetation has also previously been associated with chironomid distribution, particularly with reference to the tree-line (e.g. Porinchu and Cwynar 2000; Heiri et al. 2003b; Barley et al. 2006). The tree-line is not significant in Iceland at present as no real natural tree-line is recognised, but this may not have been the case earlier in the Holocene when more distinct tree lines probably emerged (Wastl et al. 2001). Any palaeoclimatic reconstruction using chironomids in Iceland should therefore also be associated with pollen reconstructions in order to assess the relevant influence of catchment vegetation on lacustrine dynamics (e.g. Caseldine et al. 2003, 2006).

Implications for temperature reconstructions

The individual environmental controls on chironomids in Iceland are similar to those identified from other regional training sets (i.e. TC and mean July air temperature), but the inter-relationships between these factors are markedly different. TC and mean July air temperature do not co-vary, and depth is not a significant factor statistically in explaining chironomid distribution from the surficial sediment head capsules. For these reasons, plus the relative significance of mean July air temperature in explaining chironomid distribution and subsequent model performance, it is advantageous to use an Icelandic model for interpreting past climate changes in Iceland. One other CI-T model has been used to reconstruct past climate in Iceland (Caseldine et al. 2003), and the trends for this reconstruction are similar to that of the Icelandic model (Fig. 9), although absolute values differ. This might be due to the relatively short air temperature gradient over which the Icelandic transfer function has been developed. Conversely, the Icelandic model reconstructions might be more accurate, as comparisons between early Holocene temperature reconstructions from Tröllaskagi with contemporary temperatures suggest that in northern Iceland early Holocene temperatures were at least ca. 2–2.5°C warmer than present (Caseldine et al. 2006), a magnitude of difference that compares well with other studies in northwest European low and sub-Arctic sites (Larocque and Hall 2004; Rosén et al. 2001; Seppä et al. 2002). The patterns of Icelandic reconstructions also agree consistently with offshore records (Caseldine et al. 2006) in addition to records from the Greenland ice cores (e.g. Cuffey et al. 1995; Cuffey and Clow 1997), suggesting that as well as showing similar trends for changes in temperature, these Icelandic chironomid records may also be reconstructing temperature accurately.

It is clear from the data presented in Figs. 8a and b that the Icelandic training set samples provide better analogues than the Norwegian training set samples for the fossil Icelandic sequences. These results withstanding, there are still a lack of modern analogues in the Icelandic training set for some of the early Holocene sequences (Fig. 10), further illustrating the differences between some early Holocene Icelandic assemblages and contemporary communities. The problem of finding suitable modern analogues for early Holocene samples is well known (e.g. Kurek et al. 2004; Velle et al. 2005) as this was a period of dynamic climate and landscape change with rapidly changing boundary conditions (e.g. regional/global ice volume and landscape development), unlike the majority of contemporary environments. Although the early Holocene faunas are species poor with few good community analogues, the reconstructed temperatures are calculated by using weighted average optima of individual taxa, and hence do not rely on the presence of modern community analogues.

As demonstrated above, the use of these reconstruction techniques in a range of studies imply that at many sites the early Holocene was warmer than present, although for an island like Iceland other factors need to be considered when evaluating early Holocene environmental change, in particular colonisation. Holarctic chironomid training sets have previously been developed in areas with large landmasses, where immediate postglacial colonisation would occur rapidly from taxa that may have been displaced southwards, or to the fringes of the ice covered areas. Iceland poses a greater problem for colonisation issues as it is a relatively small island, the nearest landmass being Greenland, itself covered in ice during the last glacial maximum (LGM). The question of faunal refugia in Iceland has been addressed elsewhere (Buckland and Dugmore 1991; Brochmann et al. 2003; Caseldine et al. 2004), but assuming the island was virtually devoid of insect life during the LGM it is likely, from comparison with other faunal and floral evidence (Rundgren and Ingólfsson 1999; Caseldine et al. 2004; Hallsdóttir and Caseldine 2005) that chironomids colonised rapidly from Europe, but through processes such as wind dispersal or survival on ice floes (Buckland and Dugmore 1991). Colonisation and subsequent survival of individual taxa may therefore be subject to stochastic mechanisms, and hence species distribution on Iceland may reflect communities that have expanded into niches which are only present, compared to more continental locations, due to the relatively impoverished fauna. While these rapid changes in population size and structure occurred in the early Holocene, the limited fossil evidence available suggests that by around 7,500 cal. years BP chironomid communities appear to have stabilised (Caseldine et al. 2003; 2006), although more sequences are required to fully test this hypothesis.

Conclusions

Contemporary chironomid faunal distribution in NW and W Iceland, based on subfossil head capsule remains from surficial lake sediments, are primarily influenced by lake substrate (% TC) and mean July air temperature. Unlike other chironomid training sets from low and sub-Arctic regions, these two variables do not co-vary, but dominate axes 1 and 2 respectively of CCA analysis. The altered relationship in Iceland is thought to arise due to the relatively frequent airfalls of volcanic ash that the landscape is subjected to, resulting in lakes with large catchments being far more likely to consist of relatively clastic materials, irrespective of altitude (and hence temperature), whereas only low altitude lakes with small catchments are likely to be higher in organic content. As the chironomid–environment relationships are different in Iceland compared to other chironomid training sets, we suggest that using an Icelandic model, such as the one developed in this study, is most appropriate for reconstructing past environmental change from fossil Icelandic datasets. While colonisation issues are clearly important for assessing the contemporary community structure of Icelandic chironomids, the taxa that presently exist in NW and W Iceland have a significant relationship with air temperature, and can be used successfully for Holocene temperature reconstructions.

Acknowledgements We are extremely grateful to Zoë Ruiz for help in the field, as well as Áslaug Geirsdóttir and Giff Miller for their support and technical assistance. This work has benefited from discussions with many other subfossil chironomid researchers, but in particular Thora Hrafnsdóttir, Jon Ólafsson and Yarrow Axford have contributed enormously to discussions regarding the Icelandic fauna. RANNIS are acknowledged for financial assistance, while Jim Grapes and Art Ames at Exeter University helped with the sedimentological and chemical analyses. Sue Rouillard and Bob Smith are thanked for producing the figures. NH was funded through a NERC studentship (NER/S/A/2002/10368A) and would also like to thank the QPALCLIM Marie Curie Training site which funded work she undertook in Bergen with John Birks and Steve Brooks, who are also thanked for providing the unpublished Norwegian chironomid data. Marjut Nyman and an anonymous referee are thanked for their valuable comments on an earlier draft of the manuscript.

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