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ORIGINAL PAPER

New Zealand chironomids as proxies for human-induced and natural environmental change: Transfer functions for temperature and lake production (chlorophyll *a*)

C. A. Woodward · J. Shulmeister

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Abstract The analysis of chironomid taxa and environmental datasets from 46 New Zealand lakes identified temperature (February mean air temperature) and lake production (chlorophyll *a* (Chl *a*)) as the main drivers of chironomid distribution. Temperature was the strongest driver of chironomid distribution and consequently produced the most robust inference models. We present two possible temperature transfer functions from this dataset. The most robust model (weighted averaging-partial least squares (WA-PLS), $n = 36$) was based on a dataset with the most productive (Chl $a > 10$ μg l^{-1}) lakes removed. This model produced a coefficient of determination (r^2_{jack}) of 0.77, and a root mean squared error of prediction ($RMSEP_{jack}$) of 1.31°C. The Chl *a* transfer function (partial least squares (PLS), $n = 37$) was far less reliable, with an r^2_{jack} of 0.49 and an $RMSEP_{jack}$ of 0.46 $Log_{10}\mu g\ l^{-1}$. Both of these transfer functions could be improved by a revision of the taxonomy for the New Zealand chironomid taxa, particularly the genus *Chironomus*. The *Chironomus* morphotype was common in high altitude, cool, oligotrophic lakes and lowland, warm, eutrophic lakes. This could reflect the widespread distribution of one eurythermic species, or the collective distribution of a number of different *Chironomus* species with more limited tolerances. The Chl *a* transfer function could also be improved by inputting mean Chl *a* values into the inference model rather than the spot measurements that were available for this study.

Keywords Chironomids · New Zealand · Transfer function · Temperature · Chlorophyll *a*

C. A. Woodward (✉) · J. Shulmeister
Department of Geological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand
e-mail: c.woodward@geol.canterbury.ac.nz

Introduction

The Dipteran family Chironomidae (non-biting midges) is the most widely distributed and frequently the most abundant group of insects in freshwater (Armitage et al. 1995). Taxon abundance, coupled with short life cycle duration, make this group an ideal target for use in paleolimnological studies (Walker 1995, 2001). As such, chironomids have been used extensively in the Northern Hemisphere in paleoenvironmental research to reconstruct climate change and to quantify the effects of human impact on lake ecosystems (e.g. Brooks and Birks 2000, 2001; Brooks et al. 2001; Quinlan and Smol 2002).

Paleoenvironmental analysis using chironomids is sparse in New Zealand, consisting of early qualitative work (Deevy 1955) and some later

more quantitative efforts (Boubee 1983; Schakau 1986, 1991, 1993) that attempted to determine the ecological tolerances of the New Zealand chironomid taxa. None of the earlier New Zealand investigations resulted in the production of quantitative inference models. Information derived from lake classification and ordination was applied to down-core chironomid fossil data, but the modern ecological results were applied qualitatively. Furthermore, the studies by both Boubee and Schakau were limited either by altitude and/or the length of the nutrient gradient covered by the 'training set'. Neither of the studies collected chironomid remains from lakes situated above the tree-line (~1000–1300 m a.s.l.).

Since those studies were completed, there has been major progress in the use of statistics in paleoecological research, and a major improvement in the resolution of the taxonomy of the New Zealand chironomid taxa, particularly the Orthocladiinae (see Boothroyd 1994, 1999, 2002). Despite these developments, there has been no attempt to develop chironomid-based inference models to enable the quantitative reconstruction of past environmental conditions. The most recent application of chironomids for paleoenvironmental reconstruction in New Zealand (Woodward and Shulmeister 2005) was still limited to making qualitative generalisations on past environmental conditions based mostly on the work of Boubee (1983) and Shakau (1986, 1991, 1993).

This paper presents preliminary transfers functions for temperature and lake production (chlorophyll *a* (Chl *a*)) based on chironomid data from a training set of 46 New Zealand lakes (Fig. 1). These are the first chironomid-based transfer functions to be developed in the Southern Hemisphere, although work is also underway to develop a temperature transfer function based on a larger training set with a deliberately reduced trophic gradient (M.J. Vandergoes et al. unpublished).

The impetus for this work comes from two sources:

Firstly, New Zealand paleoclimate history has become a focus for international studies, because New Zealand is seen as a good distal location to test paleoclimate hypotheses developed from Northern Hemisphere data (e.g. Broecker 1997). This is particularly true for the time interval from the last glacial maximum (ca. 21,000 years ago) to the start of the present interglacial (ca. 11000 years ago). Many studies of glacial systems (e.g. Denton and Hendy 1994; Shulmeister et al. 2005) and biotic indicators, notably pollen (e.g. McGlone et al. 2004; Vandergoes and Fitzsimons 2003) have been undertaken to investigate these changes but are limited by inadequate or contradicting estimates of temperature change.

Recently, there has been a focus on developing new quantitative paleoclimate tools for use in New Zealand. Transfer functions have been developed for phytoliths (Prebble et al. 2002) and testate amoebae (Wilmshurst et al. 2003) while bioclimatic modelling approaches have been applied to beetles (e.g. Marra et al. 2004). For some of these proxies (e.g. phytoliths) the inference of climate parameters from the data is not straightforward, while with others (e.g. testate amoeba) reconstructions appear to be affected by preservation biases. New, high resolution and widely applicable proxies are needed to test patterns of inferred climate change. Studies in the Northern Hemisphere have shown that even though chironomids are aquatic invertebrates, they can be used to reliably infer past air temperatures, and hence track climate change (e.g. Lotter et al. 1997; Brooks and Birks 2000). Hence, the development of a proxy for air temperature for a southern latitude land mass (New Zealand) will lead to the acquisition of critical data concerning climate change in this region during the Late Quaternary.

Secondly, there is growing concern in New Zealand about damage to waterways from changed agricultural practices (notably dairying in dry-land areas) and urbanisation. Even though a relatively small percentage of the lakes in New Zealand can be classified as eutrophic (22%) or hypertrophic (18%) (Taylor and Smith 1997), local councils have initiated 'long-term' water quality monitoring programmes (e.g. Burns and Rutherford 1998) and developed strategies and targets to facilitate the restoration of 'damaged' ecosystems (e.g. Hamilton 2003; Rutherford 2003). However, rigorous scientific

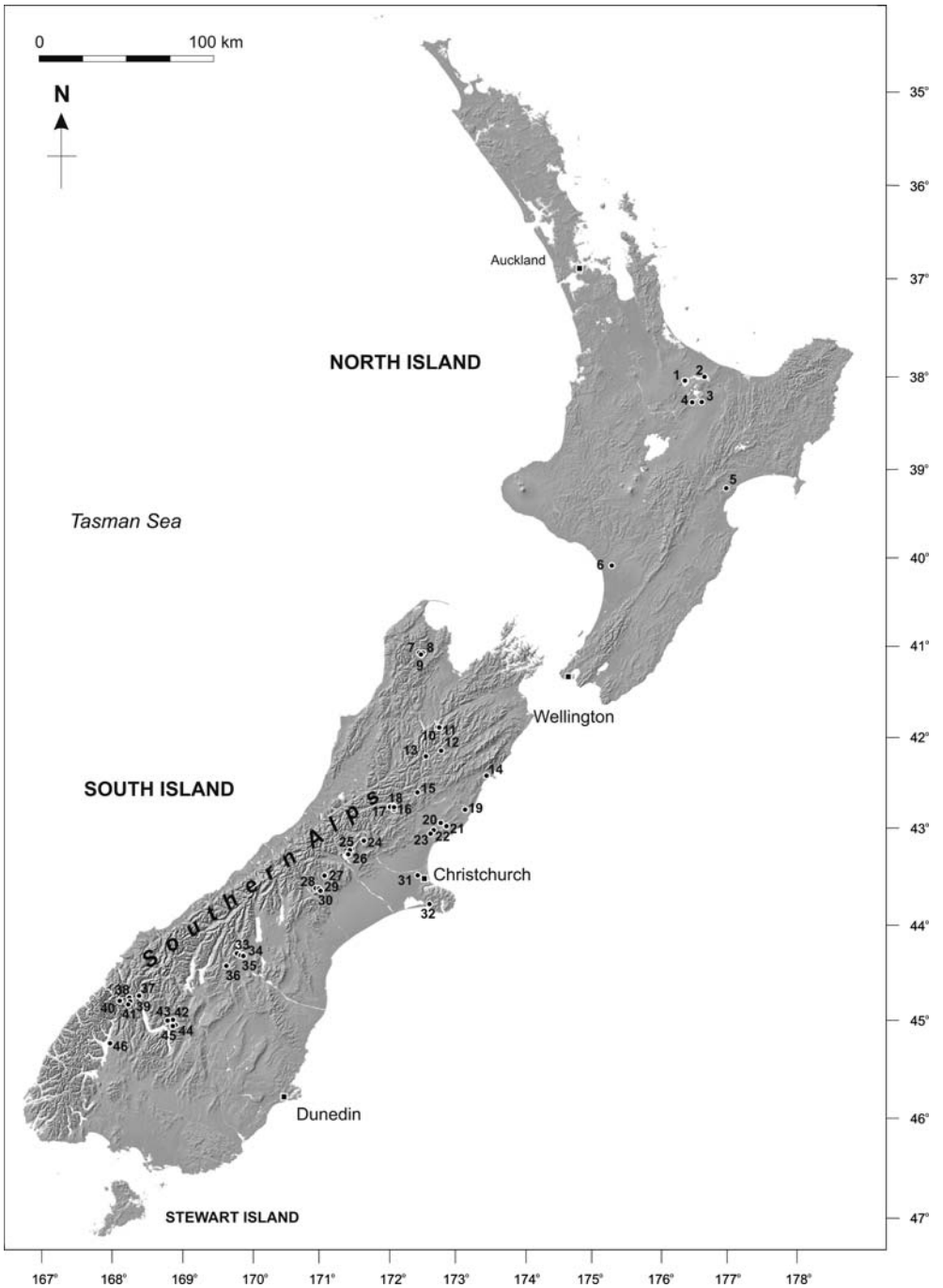

Fig. 1 Map showing the distribution of the 46 study lakes in New Zealand. Numbers refer to lakes listed in Table 1

monitoring of lakes and estuaries in New Zealand only extends back as far the early 1980s (Taylor and Smith 1997) and there are few continuous records of physical and chemical parameters. Therefore, it is difficult to establish base-line levels for lake productivity and set reasonable targets for lake restoration in the absence of long-term records.

Many studies in the Northern Hemisphere have successfully used transfer functions based on

biological proxies (e.g. chironomids and diatoms) to extend lake records beyond historical time. These long-term paleolimnological records (in tandem with other proxies, e.g. palynomorphs) provide valuable information on the natural functioning of lake/catchment systems and their response to anthropogenic disturbance (deforestation and intensive farming) (e.g. Bennion and Appleby 1999; Brooks et al. 2001; Kauppila et al. 2002; Quinlan and Smol 2002; Langdon et al. 2006). At this stage there is only one other robust published transfer function that is capable of quantifying past lake production (Chl *a*) in New Zealand (Reid 2005). Reid (2005) also produced diatom-based transfer functions for total phosphorus (TP) and dissolved reactive phosphorus (DRP), but these did not perform as well as the Chl *a* transfer function. The addition of a second, chironomid-based transfer function for lake productivity will allow comparison and cross validation between the chironomid and diatom-based transfer functions.

Description of sites studied

The training set comprised 46 lakes located in the North and South Island of New Zealand (38.04°S to 45.12°S latitude, 167.49°E to 176.16°E longitude) (Fig. 1, Table 1) The climate in this region is generally mild and oceanic. However, there are large temperature and precipitation gradients in the New Zealand region, particularly in the South Island. This is a product of the rugged topography of the Southern Alps and the influence of this mountainous terrain on the predominantly westerly airflow over the southern part of the country (Sturman and Wanner 2001). Orographic uplift of the airflow off the Tasman Sea results in an extreme contrast in average rainfall between the western and eastern sides of the mountains. Average annual precipitation near the divide on the western side of the Southern Alps can reach over 10,000 mm, while the eastern coastal plains and mountain basins receive an average annual rainfall of 600 mm (Griffiths and McSaveney 1983). Elevation of the sample sites ranges from 20 to 1880 m a.m.s.l. (above mean sea level), corresponding to estimated late summer (February) mean air temperatures of 8.2–18.1°C (Table 1).

The catchment vegetation of all the sample locations in the North Island and those located on the eastern coastal plains and foothills (below ~450 m a.m.s.l.) of the South Island has been subjected to intensive human modification. The original podocarp/broadleaf forest (e.g. *Podocarpus*, *Prumnopitys*, and *Dacrydium cupressinum*) cover in these areas has been largely cleared, firstly by Polynesian settlers, and more recently by Europeans to make way for pastoral farming (Ogden et al. 1998). Catchment vegetation of the lakes in these areas now comprises low scrub (e.g. *Discaria toumatou*, *Coprosma*, and *Leptospermum*), exotic trees (e.g. *Pinus radiata*), and introduced pasture grasses (e.g. *Pennisetum clandestinum*).

At higher altitudes up to the tree-line (~1000 to 1300 m a.m.s.l.) the natural vegetation comprises beech forest (four endemic species of *Nothofagus*) except for in the mid-central South Island 'Beech Gap' where podocarp/hardwood forests (e.g. *Podocarpus*) give way to other conifers (*Libocedrus*, *Phyllocladus*, and *Halocarpus*) at higher altitudes up to the tree-line. This natural forest cover now only exists in conservation reserves, and in remote, rugged un-farmed areas. Cleared forest has been replaced by indigenous grassland (montane tussock-land; e.g. *Poa*). Large tracts of this land are now used for low density sheep farming. Above the tree-line, forest and scrub gives way to sub-alpine tussock (e.g. *Chionochloa*) and other alpine flora (e.g. Asteraceae, Gentianaceae, and Ranunculaceae). Introduced grasses and composite weeds have also invaded this zone but less successfully than at lower elevations.

Methods

Forty-six lakes, selected to maximize the gradients of trophic status and temperature, were sampled in New Zealand during the summers (December to February) of 2002/2003, 2003/2004, and 2004/2005 (Fig. 1 and Table 1). Surface sediment samples, physical measurements and

Table 1 Lake number (nr) (corresponding to map, Fig. 1) and respective lake name

Lake Nr	Location	Lat (°S)	Long (°E)	Altitude (m)	Feb mean (°C)	Lake area (km^2)	Depth (m)	Secchi depth (m)	Cond ($\mu S\ cm^{-1}$)	NO_x-N (mg/l)	React P (mg/l)	TN (mg/l)	TP (mg/l)	Chl *a* ($\mu g/l$)	TC (mg/l)	DIC (mg/l)	DOC (mg/l)	Ca (mg/l)	Mg (mg/l)	Na (mg/l)	K (mg/l)	Cl (mg/l)	SO_4 (mg/l)	HC count	# Taxa
1	Lake Rotorua N	38.04	176.16	280	17.8	79.780	20.50	2.030	200.00	0.0005	0.0220	0.5905	0.0660	32.10	–	–	–	–	–	–	–	–	–	67	8
2	Lake Rotoehu	38.01	176.31	295	17.6	8.110	10.00	2.040	150.00	0.0180	0.0230	0.7100	0.0600	25.00	–	–	–	–	–	–	–	–	–	114.5	8
3	Lake Rerewhakaaitu	38.17	176.29	435	16.8	7.470	14.00	4.500	30.00	0.0040	0.0010	0.3400	0.0100	3.60	–	–	–	–	–	–	–	–	–	216.5	14
4	Lake Okaro	38.17	176.23	412	17	0.280	16.00	2.440	91.90	0.0110	0.0164	0.8765	0.0283	5.79	–	–	–	–	–	–	–	–	–	63	7
5	Lake Tutira	39.13	176.53	150	18.1	1.470	40.00	5.600	127.88	0.0430	0.0010	0.1047	0.0069	3.82	–	–	–	–	–	–	–	–	–	119.5	10
6	Lake Dudding	40.06	175.16	86	17.5	0.130	12.00	2.600	125.30	0.0280	0.0226	1.3185	0.0589	19.11	–	–	–	–	–	–	–	–	–	68	8
7	Iron Lake	41.06	172.36	1463	10.2	0.068	21.00	8.100	17.70	0.0220	0.0050	0.0700	0.0100	0.50	3.700	1.500	2.100	2.200	0.360	1.240	0.100	1.780	0.200	89	6
8	Lake Sylvester	41.06	172.37	1333	10.9	0.266	24.20	6.900	26.70	0.0190	0.0030	0.0500	0.0300	0.40	4.400	2.500	1.800	3.300	0.710	1.310	0.070	1.460	0.200	56.5	9
9	Little Sylvester Lake	41.06	172.37	1333	10.7	0.076	14.00	4.000	42.40	0.0210	0.0030	0.0900	0.0300	0.40	7.300	4.300	3.000	5.900	1.160	1.340	0.030	1.430	0.200	59.5	14
10	Rainbow Skifield W	41.52	172.51	1690	9.8	0.052	10.10	9.500	10.10	0.0190	0.0030	0.0800	0.0100	0.70	2.900	1.100	1.800	1.200	0.150	0.830	0.170	0.360	0.200	337	8
11	Rainbow Skifield E	41.53	172.52	1479	10.5	0.028	4.50	4.500	26.30	0.0180	0.0030	0.0600	0.0300	0.20	4.300	2.700	1.600	4.800	0.150	1.050	0.110	0.190	1.400	111.5	7
12	Lake Sedgemere	42.08	172.54	1008	12.9	0.080	1.30	1.300	30.90	0.0040	0.0375	0.3996	0.0427	0.50	10.597	4.103	6.494	3.447	1.015	2.814	0.600	0.986	0.378	235.5	16
13	Princess Bath	42.11	172.41	1757	9	0.070	15.50	10.500	13.40	0.0180	0.0030	0.1200	0.0100	2.30	2.600	1.400	1.100	2.200	0.090	0.630	0.020	0.020	0.500	81	3
14	Lake Rotorua S	42.24	173.34	20	17.3	0.550	2.08	0.380	185.00	0.0188	0.0269	6.0750	0.4529	15.30	56.987	2.850	54.137	5.887	3.178	20.891	1.965	23.702	0.200	104	13
15	Horseshoe Lake	42.35	172.31	468	15.4	0.040	10.30	3.700	83.70	0.0131	0.0087	0.4726	0.0100	0.40	16.076	8.132	7.944	10.693	2.181	6.693	1.065	3.098	3.160	331.5	13
16	Lake Taylor	42.46	172.13	588	14.1	1.850	35.00	6.650	53.00	0.0011	0.0030	0.1434	0.0069	2.27	–	–	–	–	–	–	–	–	–	134.5	11
17	Lake Mason	42.44	172.10	329	14.1	1.000	37.00	6.400	61.90	0.0009	0.0009	0.1054	0.0100	1.11	–	–	–	–	–	–	–	–	–	53.5	14
18	Lake Sheppard	42.45	172.15	587	14.6	1.150	17.00	1.450	56.40	0.0003	0.0046	0.2821	0.0223	8.10	–	–	–	–	–	–	–	–	–	51.5	12
19	St Annes Lagoon	42.46	173.16	33	17.1	0.200	1.00	0.245	340.50	0.0088	1.9701	2.7099	2.8038	7.30	65.472	19.094	46.377	20.329	9.734	43.640	4.362	48.618	11.678	95	6
20	Mill	42.55	172.55	146	16.6	0.060	2.70	0.500	256.00	0.0075	0.0214	1.5481	0.1737	9.80	34.085	10.171	23.914	16.332	5.631	24.340	1.937	29.748	20.932	76	8
21	Lake Greta	42.57	172.58	183	16.3	0.020	3.10	0.440	173.60	0.2440	0.0110	1.3000	0.1140	8.90	22.581	12.140	10.442	11.441	5.192	20.709	2.732	14.542	12.176	17	4
22	Glen	43.01	172.47	78	16.8	0.070	1.40	0.177	381.00	0.0058	0.0095	3.9306	0.2077	41.30	55.731	18.358	37.373	24.575	11.255	41.668	4.741	45.233	35.606	534	13
23	Hut	43.02	172.46	71	16.9	0.100	5.00	0.195	251.00	0.1161	0.4424	2.3297	0.7642	4.40	50.101	18.875	31.226	29.642	4.323	19.202	5.144	16.923	8.784	70	5
24	Lake Pearson	43.06	171.46	611	14.6	1.790	15.00	4.450	44.90	0.0018	0.0018	0.1954	0.0072	2.36	–	–	–	–	–	–	–	–	–	156	8
25	Mystery Tarn	43.12	171.34	854	13.3	0.020	8.00	3.800	6.90	0.0061	0.0058	0.3258	0.0306	0.40	7.202	0.557	6.645	0.386	0.139	1.228	0.218	1.637	0.326	425	16

Table 1 continued

Lake Nr	Location	Lat (°S)	Long (°E)	Altitude (m)	Feb mean (°C)	Lake area (km^2)	Depth (m)	Secchi depth (m)	Cond ($\mu S\ cm^{-1}$)	NO$_x$-N (mg/l)	React P (mg/l)	TN (mg/l)	TP (mg/l)	Chl *a* ($\mu g/l$)	TC (mg/l)	DIC (mg/l)	DOC (mg/l)	Ca (mg/l)	Mg (mg/l)	Na (mg/l)	K (mg/l)	Cl (mg/l)	SO_4 (mg/l)	HC count	# Taxa
26	Lake Evelyn	43.15	171.32	580	14.7	0.150	3.00	3.000	55.80	0.0060	0.0038	0.2259	0.0278	0.60	10.917	6.024	4.893	8.391	1.342	3.129	0.258	1.058	3.001	208	12
27	Lake Heron	43.29	171.10	691	13.7	6.300	36.00	5.600	51.10	0.0148	0.0002	0.1441	0.0046	0.95	–	–	–	–	–	-	–	–	–	64	7
28	Lake Camp	43.36	171.03	674	13.8	0.490	13.00	2.100	69.60	0.0041	0.0064	0.3290	0.0338	0.50	14.058	7.492	6.567	8.495	1.500	3.481	0.393	1.289	0.794	114	12
29	Lake Roundabout	43.37	171.05	653	13.9	0.130	0.74	0.740	57.90	0.0041	0.0220	0.7061	0.1129	1.20	14.028	4.590	9.438	7.315	2.111	4.267	0.213	2.900	1.128	63.5	8
30	Lake Emma	43.38	171.06	655.5	13.9	1.550	2.20	0.720	64.10	0.0048	0.0090	0.7253	0.0608	2.10	20.686	8.737	11.949	9.406	2.242	5.120	0.323	1.674	1.528	131.5	12
31	Groynes	43.27	172.36	25	16.8	0.018	1.25	1.250	62.40	0.0065	0.0043	0.3089	0.0445	2.50	10.818	5.500	5.318	8.322	1.057	3.321	0.585	2.128	4.857	120	6
32	Lake Forsyth	43.48	172.44	20	17	5.620	1.60	0.660	1180.00	0.0806	0.0090	2.5000	0.5500	181.00	–	–	–	–	–	–	–	–	–	30	1
33	Lake Middleton	44.16	169.50	526	15.5	0.230	4.50	2.300	21.80	0.0040	0.0069	0.4094	0.0100	0.60	10.270	3.049	7.220	3.663	0.742	2.240	0.223	1.082	0.581	173.5	8
34	Red Lagoon	44.18	169.52	589	15.2	0.160	1.25	1.200	37.60	0.0042	0.0056	0.5834	0.0372	0.15	11.521	1.987	9.535	3.285	0.740	3.094	0.171	1.209	0.381	150	21
35	Swan Lagoon	44.18	169.55	576	15.2	0.345	1.40	0.660	95.30	0.0054	0.0030	3.7637	0.0100	1.50	64.716	4.993	59.723	5.127	1.954	11.841	3.193	6.081	0.200	65	7
36	Avon	44.23	169.38	734	14.4	0.100	1.50	1.400	68.30	0.0040	0.0036	0.5083	0.0481	0.60	13.952	4.312	9.640	6.467	0.985	3.294	0.157	1.230	1.874	89	12
37	Lake Sylvan	44.42	168.19	383	14.3	0.720	19.15	3.800	45.00	0.0040	0.0043	0.1818	0.0322	0.50	7.771	1.752	6.019	5.334	0.569	1.516	0.348	1.623	2.254	88	18
38	Lake Harris	44.43	168.10	1231	9.6	0.250	40.00	8.000	16.13	0.0040	0.0297	0.1699	0.0100	0.15	3.571	2.275	1.296	2.562	0.109	0.551	0.077	0.951	0.524	112	19
39	Lake Mackenzie	44.45	168.10	885.5	11.4	0.200	34.20	11.500	15.52	0.0040	0.0280	0.0100	0.0310	0.15	1.033	0.282	0.750	0.612	0.059	0.222	0.135	0.778	0.316	156.5	14
40	Gertrude Saddle	44.44	168.01	1371.5	8.4	0.010	2.90	2.900	68.20	0.0040	0.0322	0.0989	0.0253	0.15	1.284	0.145	1.139	0.133	0.066	0.330	0.035	4.093	0.217	199	19
41	Lake Howden	44.49	168.08	684	12.4	0.100	9.40	2.500	102.00	0.0040	0.0292	0.1151	0.0100	0.20	14.309	10.087	4.222	22.230	0.333	1.327	0.148	1.336	2.832	255.5	19
42	Lake Hayes	44.58	168.48	329	15.8	2.030	31.00	4.750	141.46	0.0005	0.0028	0.2400	0.0100	1.99	–	–	–	–	–	–	–	–	–	50	12
43	Lake Johnson	45.00	168.43	406	15.4	0.200	28.30	1.940	216.00	0.0040	0.0067	0.7069	0.0100	0.40	34.450	14.547	19.902	26.443	2.784	5.113	2.300	4.336	7.120	27	7
44	''Sugarbowl Tarn''	45.03	168.49	1799.5	8.2	0.014	6.15	6.200	24.30	0.0040	0.0049	0.0936	0.0263	0.20	3.971	1.486	2.485	4.126	0.222	0.298	0.139	0.766	2.066	195	4
45	Lake Alta	45.04	168.48	1882	8.2	0.130	36.10	9.850	15.38	0.0040	0.0052	0.0920	0.0246	0.15	2.058	1.139	0.919	1.645	0.133	0.498	0.086	0.811	1.001	72.5	5
46	Lake Mistletoe	45.12	167.49	207	14.6	0.100	13.65	3.500	57.70	0.0040	0.0299	0.1494	0.0274	1.10	11.159	6.741	4.417	0.881	0.376	0.318	0.097	0.777	0.350	52.5	18

Global positioning was used to determine the latitude, longitude, and altitude. Abbreviations used for physical measurements and water chemistry parameters are listed in the body of the text

water chemistry for the lakes sampled in 2002/2003 were a product of a diatom training set developed by Reid (2005).

Prior knowledge of the trophic status of potential lakes was obtained from local government monitoring records (e.g. Christchurch Regional Council, unpublished dataset), data obtained from previous studies on New Zealand aquatic ecosystems (e.g. Stout 1985; Timms 1982, 1983) and the previous investigations of New Zealand chironomid ecology by Schakau (1993) and Boubee (1983).

Small (median 0.180 km^2), shallow (median 10.2 m depth) lakes were preferentially sampled to ensure a close relationship between bottom-water temperature and air temperature. Ideally, the sampling of deep (>30 m) lakes should be avoided to eliminate the effect of hypolimnetic anoxia on the chironomid species assemblages (Little and Smol 2001). All efforts were made to select such lakes, but due to the lack of bathymetric data for New Zealand's high altitude lakes, some of the high altitude lakes selected for sampling were found to be deep (Table 1). A preliminary ordination of the species and environmental data indicated that depth was not a significant ($P < 0.05$) driver of species variation in the training set, even when these deep lakes were included.

At each lake, maximum depth was located using bathymetric maps and a NorCross Hawkeye® DF2200PX portable depth finder. When bathymetric maps were not available, multiple transects were used to determine the deepest point of the lake. At the deepest point, two surface water samples (0–1 m) were collected in acid-washed 500 ml Nalgene bottles, which were rinsed with lake water. Surface water temperature, pH, and conductivity (Cond) were measured using a Hannah® HI 8424 pH meter and thermometer, and a Eutech® Cyberscan Con 20 conductivity meter. One of the surface water samples was immediately filtered using a syringe and Whatman® 25 mm Ø GF/F glass microfibre filters. Filters were wrapped in foil and kept for subsequent analysis for Chlorophyll *a* (Chl *a*) concentration determination, which was conducted in the Environment Canterbury laboratory in Christchurch, New Zealand. The 500 ml filtered and unfiltered samples were kept frozen until analysis at the Environment Chemistry Laboratory, Massey University, Palmerston North, New Zealand. Samples were analysed for ionic concentration (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Cl^{-}, SO_4^{2-}) and nutrients (reactive nitrogen (NO_x), reactive phosphorus (RP), total nitrogen (TN), total phosphorus (TP)), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and total carbon (TC). Water samples collected by Michael Reid in 2002/2003 (Reid 2005) were only analysed for nutrients (NO_x, RP, TN, TP) and Chl *a*. Even though other studies have shown that oxygen concentrations may have an influence on chironomid distribution (e.g. Little and Smol 2001), dissolved oxygen was not measured during this study. A summary of the physical measurements and chemistry of water samples from each lake is presented in Table 1.

Sediment cores were taken using a Glew Mini Corer (Glew 1991) at the deepest point in each lake. Where the main basin was large, or there was more than one sub-basin, several sites were sampled and the samples combined later to form a composite sample. The top 2 cm of each core were extruded while still in the boat, sampled at 1 cm intervals and placed in Whirl-paks®. Sediment samples were kept cool and out of direct sunlight until they could be processed.

Even though measurements for surface water temperature were taken in the field, the February mean (late austral summer) air temperature was used as the temperature variable in all numerical analyses. Chironomid assemblages are likely to be influenced by both air temperature (e.g., during pupation, flight, reproduction and dispersal (Hoffman 1986; Walker and Mathewes 1989)) and water temperature (e.g., larval development rates and mortality (Robb 1966)). Walker et al. (1991) and Olander et al. (1997) have demonstrated that there is a close relationship between air and water temperature for shallow polymictic lakes. Therefore, in the absence of long-term water temperature measurements, the use of mean monthly climate data is appropriate. February mean temperature measurements were extracted from a climate surface fitted to data from 346 weather stations covering a period of 30 years (Leathwick et al. 1998).

Sample preparation for chironomid analysis

Sediment samples were processed for chironomids following a modified version of the method outlined in Hofmann (1986). Samples were weighed, deflocculated in hot 10% KOH and washed on a 93-μm mesh with copious amounts of distilled water. Samples were then transferred to a Bogorov counting tray and examined for invertebrate remains under a dissection microscope, at 50× magnification. An average of 10 ml of wet sediment was required to achieve the target head-capsule quantity. A corresponding 2 ml sub-sample of un-processed sediment was dried at 50°C for 3 days for the purpose of chironomid head-capsule concentration calculations.

Chironomid head-capsules were mounted on glass slides in a drop of lactophenol PVA and covered with a glass coverslip. Head-capsules were mounted ventral side up to facilitate identification. Chironomids were identified using a transmission light microscope with the aid of publications by Forsyth (1971), Boubee (1983), Schakau (1993) and identification guides by Boothroyd (1994, 1999, 2002).

Statistical methods

Constrained and unconstrained ordinations were performed using CANOCO version 4.5 (ter Braak and Šmilauer 2002) to explore the relationships between modern chironomid assemblages and environmental variables, as well as to screen environmental and species data for outliers.

Secchi depth measurements were removed from the original environmental dataset as the secchi depth was potentially greater than the lake depth (i.e. the disc was visible on the bottom) in six lakes (Table 1). Latitude, longitude, altitude, and lake area values were also removed from the environmental dataset. These parameters indirectly affect chironomid distribution (i.e., they affect such factors as temperature and productivity) but are unlikely to have a direct effect on chironomid distribution.

In removing latitude and longitude it was assumed that the distribution of New Zealand chironomids is controlled by environmental tolerance and that biogeography plays only a minor role on the scale represented in this study. This hypothesis was confirmed by performing partial canonical correspondence analyses (CCA) in CANOCO 4.5 (ter Braak and Šmilauer 2002) constrained to latitude and longitude respectively (both parameters untransformed). Only longitude displayed a significant ($P \leq 0.05$) relationship to chironomid distribution. It was suspected that this was due to the prevalence of highly productive lakes on the lowlands to the east of the Southern Alps (Fig. 1). This was confirmed by partialling out the effect of Chl *a*, which reduced the significance (P) of longitude from 0.001 to 0.222 and the explanatory power (λ_1/λ_2) from 0.583 to 0.258.

The remaining 18 environmental variables were tested for normality using SPSS® statistical software (SPSS Inc. 2002). Log_{10} transformations were required to normalise all environmental data except for depth, February mean, and pH.

Two separate groups of analyses were performed based on the availability of environmental data. The first group of analyses (hereafter referred to as the non-ion data set) was performed using a dataset containing all 46 lakes. This group of analyses tested the explanatory power of the 9 environmental variables (depth, February mean, Cond, pH, NO_x, RP, TN, TP, and Chl *a*) available for all of the lakes (Table 1). The second group of analyses (hereafter referred to as the ion dataset) focused on a sub-set of 33 lakes for which data on all 18 environmental parameters (depth, February mean, conductivity, pH, NO_x, RP, TN, TP, Chl *a*, TC, DIC, DOC, Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Cl^{-}, and SO_4^{2-}) were available (Table 1).

Chironomid species data were used in the form of square root transformed percentage data (%) and log transformed (log (x+1)) concentration data (head-capsules/g dry sediment). All analyses were performed separately using datasets containing either: all taxa (concentration and % data), taxa with abundances ≥2% in at least 2 lakes (% data only), or taxa with $N2$ values ≥2 (concentration and % data).

All samples were removed from the dataset if the chironomid head-capsule count was less than 50. Quinlan and Smol (2001) argue that a minimum count of 40–50 head-capsules is sufficient for use in inference models where diversity is low.

Rarefaction analysis (see Fig. 2) of the species data (Birks and Line 1992) revealed that a sample size of at least 50 head-capsules captured an average of 80% of the actual taxonomic richness in the New Zealand chironomid assemblages. A regression of taxonomic richness vs. total head-capsule count (Fig. 2) revealed a low correlation (r^2 = 0.2253) between the sample size and taxonomic richness.

Unconstrained ordinations (principle components analysis (PCA), and detrended correspondence analysis (DCA)) were used to identify outliers in the training set and explore the patterns of compositional variation and biological species turnover (the gradient length). Partial, constrained ordinations (redundancy analysis (RDA), CCA) were used to determine which environmental variables were highly correlated to chironomid distribution. The statistical significance of each environmental variable was tested by Monte Carlo permutation test (999 unrestricted permutations under the full model). Variables with a significant ($P \leq 0.05$) were retained for further analyses. The unique explanatory power of each significant environmental variable was tested using a series of partial, constrained ordinations (RDA or CCA) with all other significant environmental parameters as co-variables. Only environmental parameters that retained their significance after these analyses were considered for transfer function development.

Quantitative transfer functions for the significant environmental variables selected in the CCAs and RDAs were developed in the computer program C2 (Juggins 2003). Gradient lengths for the first axis in a detrended canonical correspondence analysis (DCCA) constrained to a single environmental parameter were used to decide between linear (partial least squares (PLS)) or unimodal (weighted averaging (WA) and weighted averaging-partial least squares (WA-PLS)) models (Birks 1995, 1998).

Robust transfer functions were those that had a low root mean squared error of prediction (RMSEP), a high coefficient of determination (r^2_{jack}) and a low mean and maximum bias (Birks 1998).

Results and discussion

Data screening

Fifty chironomid taxa were identified and enumerated from the 46 lake training set (Appendix Table 4). Only 3 lakes failed to produce sufficient head-capsules (≥50; Lakes 21, 32, and 43: see Table 1). These lakes were excluded from further

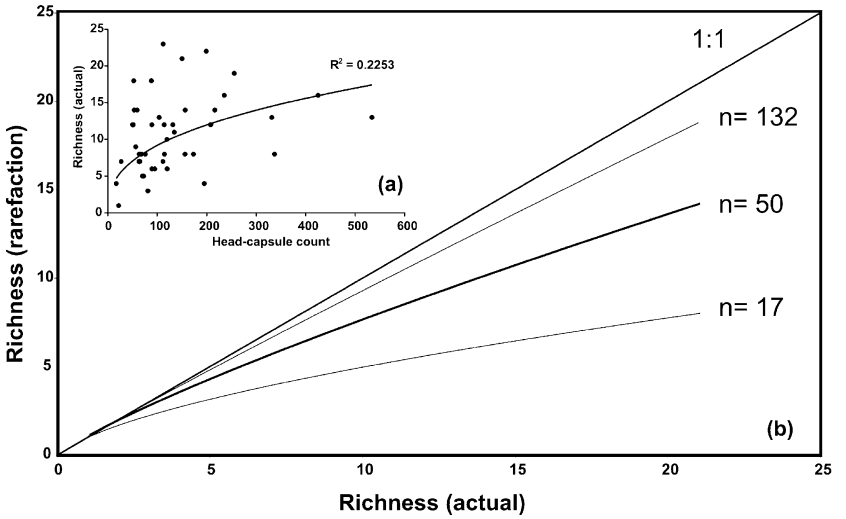

Fig. 2 Taxon richness in subfossil chironomid samples from New Zealand. (**a**) Relationship between total number of head-capsules and actual sample richness. (**b**) Comparison of richness before and after rarefaction analyses calculated for head-capsule numbers (n) = 17 (lowest count), 50 (accepted minimum count for inclusion of a lake) and 132 (mean number of head-capsules counted for each lake)

analyses. Analyses were performed using both percentage data (%) and concentration data (head-capsules/g dry sediment) for the larger (46 lake) dataset, and the smaller (33 lake) subset using all species datasets (all species, ≥2% and $N2 \geq 2$). Species percentage data outperformed species head-capsule concentration data in all cases. Concentration data also failed to produce any unique species/environment relationships.

The retention of all of the species in the analyses reduced the performance (significance (*P* value) and λ_1/λ_2) of environmental variables in partial constrained ordinations with and without co-variables; possibly due to the introduction of noise provided by rare taxa. Therefore, the following discussion will focus on the results from species percentage data (≥2% and $N2 \geq 2$) ordinations.

A PCA of the ion dataset indicated that there was a great deal of redundancy (i.e., colinearity). It was expected that the addition of the ionic data would not provide any extra relationships over those provided by the reduced dataset. A series of ordinations was used to test this theory. A CCA was performed using the ion set environmental parameters with species percentage data. Variables with high variance inflation factors (>20), (TC, Mg^{2+}, DOC, and Na^{+}), were removed one at a time starting with the largest value (TC) until all values were <20 (ter Braak and Šmilauer 1998). Out of the remaining 14 environmental variables only temperature (February mean) retained a significant relationship to chironomid species composition after partial, constrained ordinations with co-variables. Temperature (February mean) also emerged as the strongest predictor of chironomid species composition in the non-ion dataset. Therefore further statistical analyses focused on this dataset.

A PCA of the environmental data and a DCA of the chironomid data (≥2% and $N2 \geq 2$ deletion criteria) were performed for the non-ion dataset. Samples whose scores for axes 1 and 2 were outside one standard deviation (SD) of the mean for both axes in both the PCA and DCA (for environmental and species data, respectively) were considered outliers and were removed from further statistical analysis. Lakes 19 and 23 were identified as outliers in the PCA due to extreme values of area, TP, and RP, respectively. Both of these lakes are shallow, eutrophic, and located in catchments that are severely modified by human activities. Lake 1 was also removed from the dataset. Even though area was not considered as an environmental variable for reconstruction, the large size (79.78 km^2) and moderate depth (20.5 m) of this lake will quite likely result in a chironomid assemblage that is almost entirely dominated by profundal species in a sample taken from the lake centre.

No outliers were identified in a DCA using the smaller (≥2% deletion criterion) species dataset, but 3 lakes (40, 45, and 46) were identified as outliers in the DCA based on the larger ($N2 \geq 2$) species dataset. Lake 40 was an acidic (pH 5.3) high altitude (1371 m) lake with a high percentage (~22%) of head-capsules from *Parochlus*. Lake 45 was a deep (36.1 m) high altitude (1882 m) lake with high percentages of *Naonella forsythi* and *Tanytarsus vespertinus* (~11% and 30%, respectively). Both *Parochlus* and *Naonella forsythi* are common in cold, fast flowing streams and rivers (Brundin 1967; Taylor 2001). It is possible that where conditions in the lake are unfavourable (cold, deep, acidic) the contribution of river-borne head-capsules may be high. Lake 46 had a diverse (18 taxa) chironomid fauna. There were numerous species present in this lake that were rare (<2% relative abundance) elsewhere in the training set. This lake was highly stained (with high concentrations of dissolved tannic and humic substances) and situated in a forested catchment. Schakau (1993) found that species diversity (Shannon Weaver Index *H′*) was highest in lakes in heavily forested catchments.

The main environmental controls on New Zealand chironomid species

A series of ordinations were performed on the screened data to determine which environmental parameter(s) exerted the strongest influence on chironomid distribution in New Zealand. A DCA with detrending-by-segments was performed on both species datasets (≥2% and $N2 \geq 2$) to determine the most appropriate constrained ordination method. The results of the DCA for both datasets were similar. Axes 1 and 2 for each

analysis had eigenvalues of 0.270 and 0.135 (≥2% species dataset), and 0.294 and 0.147 ($N2 \geq 2$ species dataset). Axis 1 in the ≥2% species dataset accounted for 20% of the total variation in the chironomid dataset, compared to 18.2% for the $N2 \geq 2$ species dataset. Gradient lengths for Axis 1 were 2.901 SD for the ≥2% species dataset and 3.003 SD for the $N2 \geq 2$ species dataset. Gradient-length values <2 SD suggest the use of RDA while those >4 SD suggest the use of CCA (ter Braak 1995). Results for a CCA and a RDA were examined for both species datasets as the gradient lengths fall between the cut-off values suggested by ter Braak (1995). In both cases the CCA explained a higher percentage of the total species variation; therefore all further ordinations were performed using this method.

CCAs constrained to each of the 8 environmental variables for each species dataset identified February mean, Cond, TN, and Chl *a* as significant ($P \leq 0.05$) explanatory environmental variables for both species datasets (≥2% and $N2 \geq 2$), while CCAs on the ≥2% species dataset also extracted pH as a significant explanatory environmental variable for species distribution (Table 2, Fig. 3). In both cases (≥2% and $N2 \geq 2$) February mean explained the greatest significant amount of variation in the chironomid species data (13.6% and 10.6%, respectively), followed by Chl *a* (8.5% and 8.4%, respectively) and Cond (7.8% and 7.5%, respectively).

CCAs constrained to all significant environmental variables at once for both species datasets returned similar results (Table 3). A CCA of the ≥2% species data constrained to the 5 environmental parameters (February mean, Cond, TN, Chl *a*, and pH) explained slightly more of the variation in the chironomid species data (25.1% for 4 axes) than the $N2 \geq 2$ species dataset constrained to 4 environmental variables (21.1% for 4 axes). In both cases February mean was significantly correlated to CCA axes 1 and 2 (Table 3). The eigenvalue for axis 1 was high for both CCAs (0.169 and 0.160, respectively), and axis 1 explained >50% of the total variance of the species–environment relation in both cases.

Partial CCAs constrained to each variable, by itself, and with other significant environmental

Table 2 Results of a partial CCA for the significant ($P < 0.05$) environmental variables by themselves and with the effects of other variables partialled out

Environmental		≥2% deletion criterion				$N2 \geq 2$ deletion criterion			
Variable	Covariable(s)	λ_1	λ_1/λ_2	P	% variance	λ_1	λ_1/λ_2	P	% variance
Feb mean	None	0.173	0.935	0.001	13.6	0.106	0.488	0.001	10.6
	Cond	0.118	0.670	0.001	10.1	0.091	0.520	0.004	6.7
	TN	0.106	0.596	0.001	9	0.097	0.567	0.001	7
	Chl *a*	0.115	0.622	0.001	9.9	0.112	0.626	0.001	8.3
	TN, Cond, Chl *a*	0.103	0.640	0.001	9.2	0.081	0.482	0.002	6.4
	pH	0.157	0.853	0.001	12.9	–	–	–	–
	TN, Cond, Chl *a*, pH	0.096	0.568	0.001	9	–	–	–	–
Cond	None	0.099	0.442	0.001	7.8	0.075	0.333	0.004	7.5
	Feb mean	0.045	0.256	0.08	4.1	0.045	0.257	0.228	3.4
TN	None	0.094	0.152	0.002	7.4	0.065	0.289	0.01	6.5
	Feb mean	0.027	0.159	0.549	2.4	0.031	0.181	0.686	2.3
Chl *a*	None	0.109	0.537	0.001	8.5	0.126	0.609	0.001	8.4
	Feb mean	0.051	0.276	0.048	4.6	0.088	0.486	0.001	6.5
	Cond	0.062	0.312	0.02	5.3	0.06	0.324	0.032	4.4
	TN	0.048	0.249	0.09	4.3	0.076	0.388	0.005	5.4
	TN, Cond, Feb mean	0.047	0.297	0.058	5.2	0.059	0.351	0.049	4.8
	pH	0.092	0.465	0.001	7.6	–	–	–	–
pH	None	0.058	0.236	0.041	4.6	–	–	–	–
	Feb mean	0.043	0.234	0.114	3.9	–	–	–	–

The eigen value of the first CCA axis (λ_1), the ratio of the eigen value for axes 1 and 2 (λ_1/λ_2), the statistical significance (P), and the percentage of variance of the species data (% variance) are shown for both the smaller (≥2 in at least 2 lakes) and larger ($N2 \geq 2$) species datasets (left column and right column, respectively)

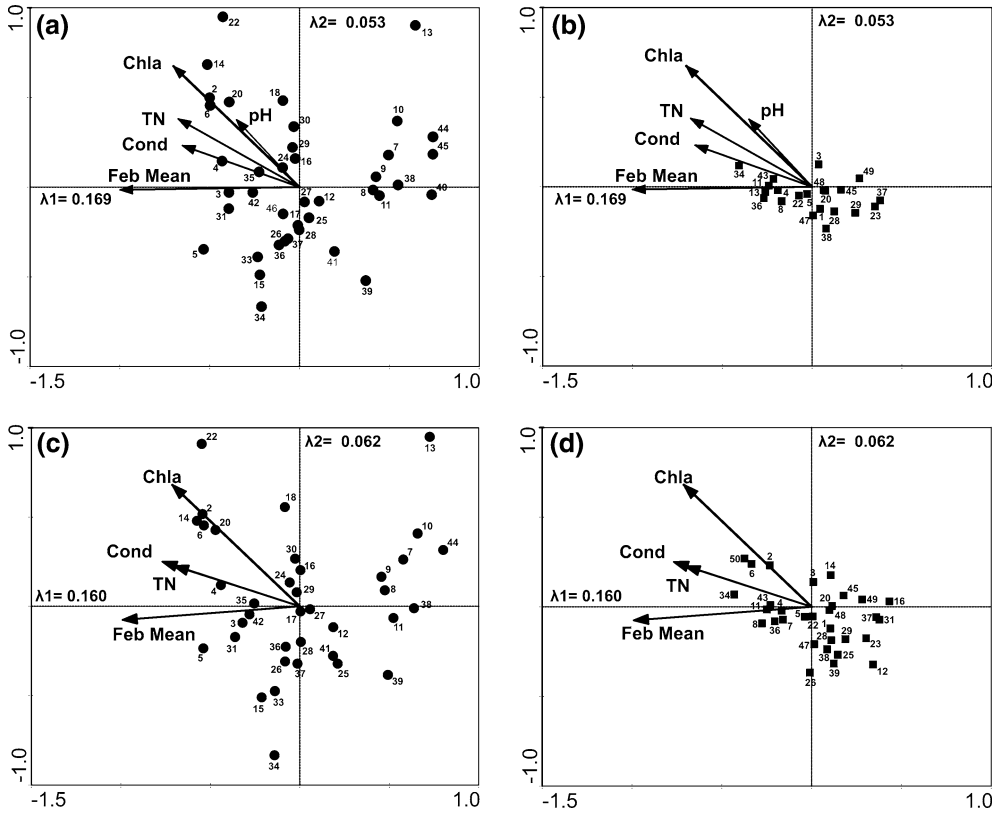

Fig. 3 CCA biplots for axis 1 vs. axis 2 (λ_1 vs. λ_2). Environmental variables (*arrows*) are shown. Chl *a*, TN, Cond, Feb mean and pH. Lake numbers (*points*) and species numbers (*squares*) correspond to Table 1 and Appendix A, respectively. (**a**) and (**b**) Partial CCA of sites and species respectively for the smaller (>2%) species dataset. (**c**) and (**d**) Partial CCA of sites and species respectively for the larger ($N2 \geq 2$) species dataset

parameters as co-variables were then performed to test the explanatory power of each individual variable (Table 2). Quantitative inference models (transfer functions) would only be attempted for environmental parameters that explained a significant proportion of the variation in the species data, both individually and when the effects of each of the other environmental variables were partialled out.

Analyses were run on both sets of species data (≥2% and $N2 \geq 2$) as Chl *a* seemed to perform slightly better with the larger species dataset. Chl *a* was significantly correlated to axis 2 in both CCAs constrained to all the environmental variables. However, the larger species dataset increased the canonical regression co-efficient and the significance as calculated by an approximate *t*-value (Table 3).

February mean was the only environmental variable to remain significant ($P \leq 0.05$) in a set of partial CCAs with other variables entered as co-variables for the ≥2% species dataset (Table 2). February mean remained significant ($P = 0.001$) and explained ≥9% of the variation in the chironomid species data after the removal of the effects of all of the other significant ($P \leq 0.05$) environmental variables separately and combined. Chl *a* was the only other environmental variable to remain significant ($P \leq 0.05$) after the effect of temperature was partialled out. However, the explanatory power of this variable was reduced after the effect of TN and the combined effect of February mean, Cond, and TN were partialled out (Table 2).

February mean remained the most significant environmental variable in a series of partial CCAs using the $N2 \geq 2$ species data, but did not perform quite as well as it did with the other species dataset (Table 2). The species–environment relationship remained significant ($P \leq 0.05$)

Table 3 Canonical co-efficients, *t*-values, and CCA summary from a partial CCA including all significant ($P < 0.05$) environmental variables for the smaller (≥2% in at least 2 lakes) and larger ($N2 \geq 2$) species datasets (left column and right column, respectively)

Axis:	Species deletion criteria							
	≥2%				*N*2 ≥2			
	AX1	AX2	AX3	AX4	AX1	AX2	AX3	AX4
Regression/canonical co-efficients								
Eigen value	0.169	0.053	0.044	0.035	0.160	0.062	0.027	0.019
Cum. % var. spp.	14.1	18.5	22.2	25.1	12.5	17.4	19.6	21.1
Variable								
Feb mean	−0.999	−1.079	−0.486	−0.195	−0.829	−1.081	0.607	0.564
Cond	0.026	0.015	1.210	0.735	−0.144	0.131	−1.454	0.052
TN	−0.076	0.298	0.129	−0.197	−0.088	0.094	0.184	−1.350
Chl *a*	0.043	1.226	−0.180	−0.603	−0.010	1.270	0.542	0.495
pH	0.007	0.096	−0.772	0.843	–	–	–	–
t-*values for regression co-efficients*								
FR explained	0.534	0.169	0.140	0.112	0.596	0.232	0.101	0.072
Variable								
Feb mean	−5.504	−3.999	−1.462	−0.577	−4.548	−4.641	1.940	1.014
Cond	0.160	0.061	4.077	2.432	−0.857	0.612	−5.044	0.101
TN	−0.450	1.193	0.419	−0.631	−0.564	0.468	0.684	−2.829
Chl *a*	0.248	4.783	−0.570	−1.877	−0.060	5.927	1.882	0.967
pH	0.051	0.484	−3.150	3.380	–	–	–	–

Eigenvalues are shown for the first 4 axes (AX1, AX2, AX3 and AX4) along with the cumulative % of variance in the species data explained by each axes (Cum. % var. spp.)

but the amount of variance this variable explained in the species data was reduced by the partialling out of the effect of Cond from 10.6% to 6.7%. Chl *a* performed slightly better in a series of partial CCAs using the $N2 \geq 2$ species dataset (Table 2). Chl *a* remained significant ($P \leq 0.05$) when the individual and combined effects of the other significant environmental variables were partialled out. The partialling out of the effect of Cond had the greatest detrimental effect on the explanatory power of Chl *a*. Partialling out the effects of conductivity reduced the amount of variance Chl *a* explained in the species data from 8.4% to 4.4% and reduced the statistical significance (P) from 0.001 to 0.032.

Chironomid species responses to the main environmental parameters

Temperature

New Zealand subfossil chironomid assemblages showed marked changes in species composition corresponding to gradients of altitude and temperature (Fig. 4). Six main zones of faunistic turnover (based on all 50 taxa) were returned in a zone analysis using the CONISS function in Zone 1.2 (Juggins 1992). The main zone of faunistic change approximated the tree-line (~1000–1300 m). Other workers (e.g. Porinchu and Cwynar 2000) have identified the tree-line as an important ecological boundary controlling chironomid distribution. *Cladopelma curtivalva*, *Cricotopus zealandicus*, *Cricotopus aucklandensis*, and *Polypedilum* were characteristic of warm (>13°C) temperatures. These genera (particularly *C. curtivalva* and *Polypedilum*) are also typical of warmer conditions in other parts of the world (Walker et al. 1991; Larocque et al. 2001). *Naonella kimihia* was also somewhat restricted to lower altitudes but remained as a component of the chironomid fauna at altitudes extending somewhat above the tree-line (~1300 m). The high altitude fauna (>1300 m) were dominated by 5 taxa; 4 species of Chironominae (*Chironomus*, *Corynocera*, *Tanytarsus funebris*, and *Tanytarsus vespertinus*) and head-capsules belonging to the tribe Macropelopiini. All of these species are also

present in high abundances in lowland lakes (Fig. 4). It appears that these species have a wide tolerance for temperature, but only occur in abundance below the tree-line in oligotrophic to mesotrophic lakes (with the exception of *Chironomus*) (Fig. 5). Brodersen et al. (2004) found that cold-water assemblages in low-arctic West Greenland were dominated by oxy-conformers; chironomids incapable of surviving low concentrations of dissolved oxygen. All the main high altitude species (except *Chironomus*), were rare or absent in eutrophic lowland lakes (Fig. 5); suggesting that this is also the case for the New Zealand fauna. The genus *Chironomus*, on the other hand, was also present in high concentrations in eutrophic lowland lakes.

Robb (1966) found that *Chironomus zealandicus* had a wide tolerance for extreme values for a large number of environmental gradients (e.g. temperature, pH, conductivity, and dissolved oxygen). So it could be that *Chironomus zealandicus* is the dominant *Chironomus* species represented in this training set and it becomes more common when conditions are outside the tolerance of other chironomid species. It could also be the case that the *Chironomus* morphotype represents more than one species in this training set. Preliminary work involving the integration of morphological, ecological and karyotypic studies (Assoc. Prof. Jon Martin and Don Forsyth unpublished data) suggests the existence of up to nine distinct *Chironomus* species on the New Zealand mainland. Future work should focus on relating easily identifiable features on the head-capsule to each of the nine karyotypes. Further attention to resolving the taxonomy of the Macropelopiini in New Zealand is also required. At present there is no consensus on the taxonomy of the larval stages (e.g. Schakau 1993; Stark 1981). The potential for the use of cephalic setation (see Rieradevall and Brooks 2001) was investigated briefly during the course of this study, but requires further work.

Species typical of rhithral (upland) streams (Orthocladiinae, Podonominae, and Diamesinae) were also common but not usually very abundant in high altitude lakes. Rhithral stream species are dominated by cold stenotherms (Burgherr and Ward 2001) so it is not surprising that these contribute to the chironomid fauna found in high altitude lakes.

Chlorophyll a

The distribution of the main (≥2% mean abundance) chironomid species with respect to the concentration of Chl *a* is shown in Fig. 5. The statistical significance of various models was tested in CANOCO 4.5 (ter Braak and Šmilauer 2002) for their ability to explain the distribution

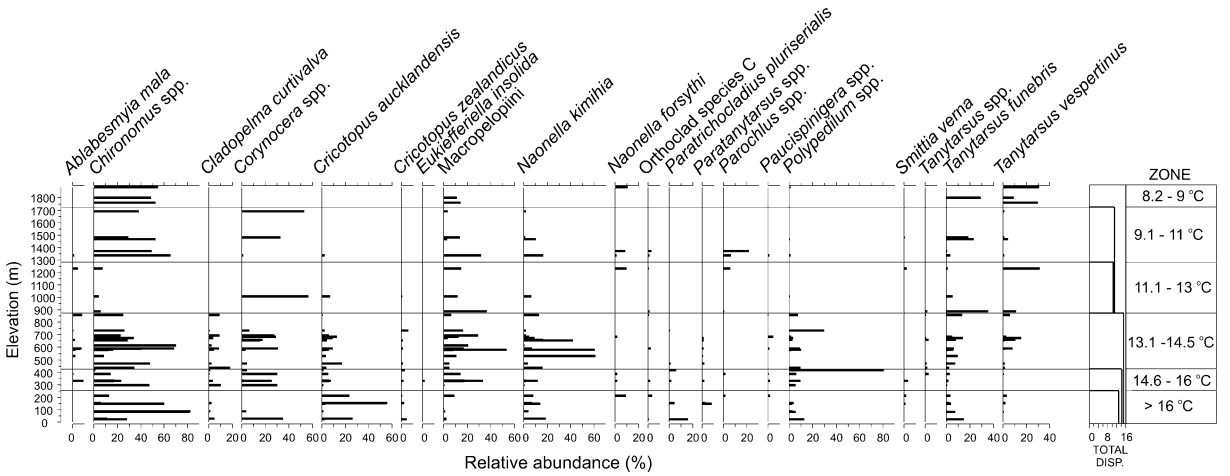

Fig. 4 Distribution and percentages of the main New Zealand chironomid species along an altitudinal gradient. All taxa present ≥2% in at least 2 lakes are shown. Lakes are ordered according to their elevations (m a.s.l.) and corresponding zones of mean February temperature are indicated

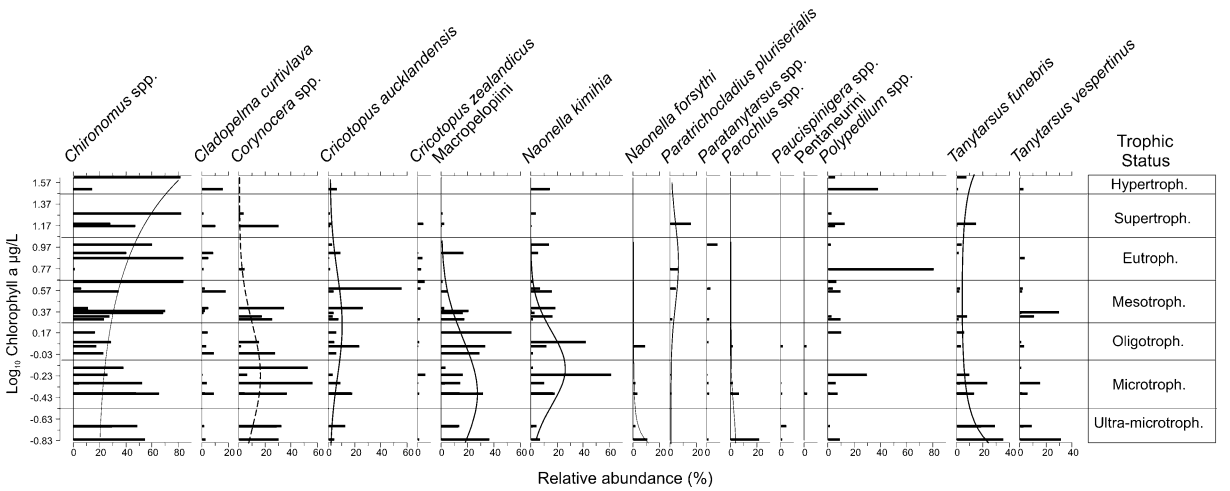

Fig. 5 Distribution and percentages of the main New Zealand chironomid species along a gradient of trophic status (Chl *a* concentration). Trophic classifications based on Burns et al. (2000). Solid curves are fitted significant ($P < 0.05$) models developed in CANOCO 4.5 (ter Braak and Šmilauer 2002). Dashed curve is less significant ($P = 0.09$)

of each of the main chironomid taxa with respect to Chl *a*. All of the curves plotted in Fig. 5 were significant ($P \leq 0.05$) except for the dashed curve which represents the distribution of *Corynocera* spp. ($P = 0.09$). In all cases a quadratic Poisson distribution explained the greatest significant amount of variation in the species data. The main trend to note is that most of the common (mean abundance ≥2%) New Zealand chironomid species have wide tolerances for Chl *a*. Species assemblages (particularly in the range of ultra-microtrophic to mesotrophic) are characterised by changes in relative abundance rather than the appearance and disappearance of different species. As mentioned in the previous section, *Chironomus* is common in lakes with a wide range of productivity, but tends to dominate the chironomid assemblages in hypertrophic lakes (Fig. 5). *Chironomus* is also characteristic of highly productive lakes in other parts of the world (e.g. Brodersen and Lindegaard 1999). Once again further investigation into the taxonomy of this genus may reveal that certain *Chironomus* species are characteristic of different levels of lake production. *Polypedilum* is also tolerant of a wide Chl *a* gradient and is common in eutrophic lakes. Temperature appears to be the main limiting factor on the distribution of *Polypedilum* however, as the best model fitted to the distribution of this species with respect to Chl *a* was not statistically significant ($P = 0.18$). This hypothesis was confirmed by testing the significance of the distribution of *Polypedilum* with respect to temperature in CANOCO version 4.5 (ter Braak and Šmilauer 2002) ($P = 0.01$, quadratic Poisson distribution).

Paratrichocladius pluriserialis was the only widely occurring species limited to the mesotrophic–hypertrophic end of the scale. *P. pluriserialis* is relatively rare (mean abundance 1.14%) and is most common in lake 22, a small (0.020 km^2), shallow (3.1 m) hypertrophic pond. Species typical of the ultramicrotrophic–mesotrophic end of the Chl *a* gradient also tended to be common in high altitude lakes (see discussion in the previous section). *N. kimihia* and *Cricotopus aucklandensis* are the only common species that are abundant in ultra-microtrophic to mesotrophic lakes that are not also common above the tree-line (~1000–1300 m). *C. aucklandensis* was a more tolerant species, with a wider distribution and an optimum at the transition from oligotrophic to mesotrophic trophic status (Fig. 5). *N. kimihia* was more limited in its distribution, occurring in low abundances in highly productive lakes. The *N. kimihia* species optimum was slightly lower than *C. aucklanden-*

sis, occurring at the transition from microtrophic to oligotrophic trophic status (Fig. 5).

Model development

The ratio of λ_1/λ_2 for February mean remained large (≥0.568) and significant (P=0.001) after a series of partial CCAs (Table 2), therefore confirming that this variable explains an independent and statistically significant amount of variation in the New Zealand chironomid species data. Chl *a* did not perform quite as well as February mean; the explanatory power (λ_1/λ_2) and significance (P) of this variable was reduced by the partialling out of other environmental parameters, particularly conductivity. Chl *a* remained significant ($P \leq 0.05$) after the partialling out of conductivity, but the ratio of λ_1/λ_2 was reduced to 0.351. Even though the value of λ_1/λ_2 value for Chl *a* is low, other studies with similarly low λ_1/λ_2 values (< 0.4) have produced robust quantitative inference models for the target variable (Rosén et al. 2000; Bloom et al. 2003).

A check for sites with extreme values (>8X) for each variable (February mean and Chl *a*) as identified by the leverage diagnostic, failed to identify any sites where these environmental variables had an unduly large effect on the ordination results. Gradient lengths for the first axis in a DCCA constrained first to temperature (with the ≥2% species data) and then to Chl *a* ($N2 \geq 2$ species data) were used to determine whether to use linear (e.g. PLS) or unimodal (e.g. WA) modelling methods (Birks 1995, 1998). The gradient lengths determined by DCCA with axis 1 constrained first to temperature (gradient length = 1.533 SD) and then to Chl *a* (gradient length = 1.602 SD) suggest the use of linear (PLS) models. However, ter Braak and Juggins (1993) argue that with short gradient lengths (< 2 SD) unimodal models may outperform linear models. Therefore both unimodal (WA, WA-PLS) and linear (PLS) models were tested for each environmental variable using the computer programme C2 (Juggins 2003).

Models were accepted if they had high r^2 values, a low RMSEP, RMSEP as a % of the gradient, and a low mean and maximum bias. A minimum adequate model was selected following the criterion recommended by Birks (1998). Extra components (1, 2, 3,...,*n*) were only included in the model if the new model improved on the RMSEP of the model with 1 component by at least 5%.

Model performance

Temperature

The best temperature model (r^2=0.80, r^2_{jack} = 0.62, $RMSEP_{jack}$ = 1.75°C, maximum $bias_{jack}$ = 2.15°C) was developed using unimodal methods (WA-PLS with 2 components, jack-knifing) including 40 lakes (lakes 1, 19, 21, 23, 32, 43 removed) and all species with abundances ≥2% in at least 2 lakes (Fig. 6a, b). There was a slight trend in the residuals, with the model having a tendency to over predict lower temperatures and under predict higher temperatures. This tendency is regarded as an inherent feature of WA-PLS based models (ter Braak and Juggins 1993; Lotter et al. 1997).

However, the presence of *Chironomus* in high altitude lakes and low altitude eutrophic lakes may also contribute to this effect. The beta coefficient for *Chironomus* is 12.3°C, therefore in warm (>16°C), lowland, eutrophic lakes (such as lakes 6 and 22 in Fig. 6) where the observed February mean was high, the abundance of *Chironomus* (>80%) will cause an under-prediction of the temperature. The reverse is the case for high altitude lakes where *Chironomus* is abundant (e.g. lakes 40, 44, and 45 in Fig. 6a, b). Observed February mean temperatures for these lakes are < 9°C, whereas the model over predicts the temperature in each case by up to 1.5°C (Fig. 6b).

A possible criticism of this chironomid training set (as far as temperature is concerned) is the presence of two long environmental gradients i.e., temperature *and* lake production (Chl *a*). Many studies (e.g. Brooks and Birks 2000) have selected sub-sets of an originally larger training set in order to focus on only one environmental parameter (temperature in the case of Brooks and Birks 2000). Larocque et al. (2001) also state that temperature inference models are likely to be more reliable if they are developed from training

sets where the amount of human impact is minimal.

Removing highly productive lakes from a training set intended for a temperature model is usually performed to avoid problems associated with disentangling the nutrient and climate signals from the biological training set. This problem has proven controversial in this field in the past (e.g. Walker and Mathewes 1987; Warner and Hann 1987). Even though this training set contained two long environmental gradients, the results of the partial CCAs (Table 2) show that temperature was by far the strongest environmental influence on the distribution of New Zealand chironomids. This remained then case, even when the effect of Chl *a* was partialled out. Investigating long temperature and nutrient gradients in this case revealed the problematic distribution of the *Chironomus* morphotype. Had we only examined a temperature gradient

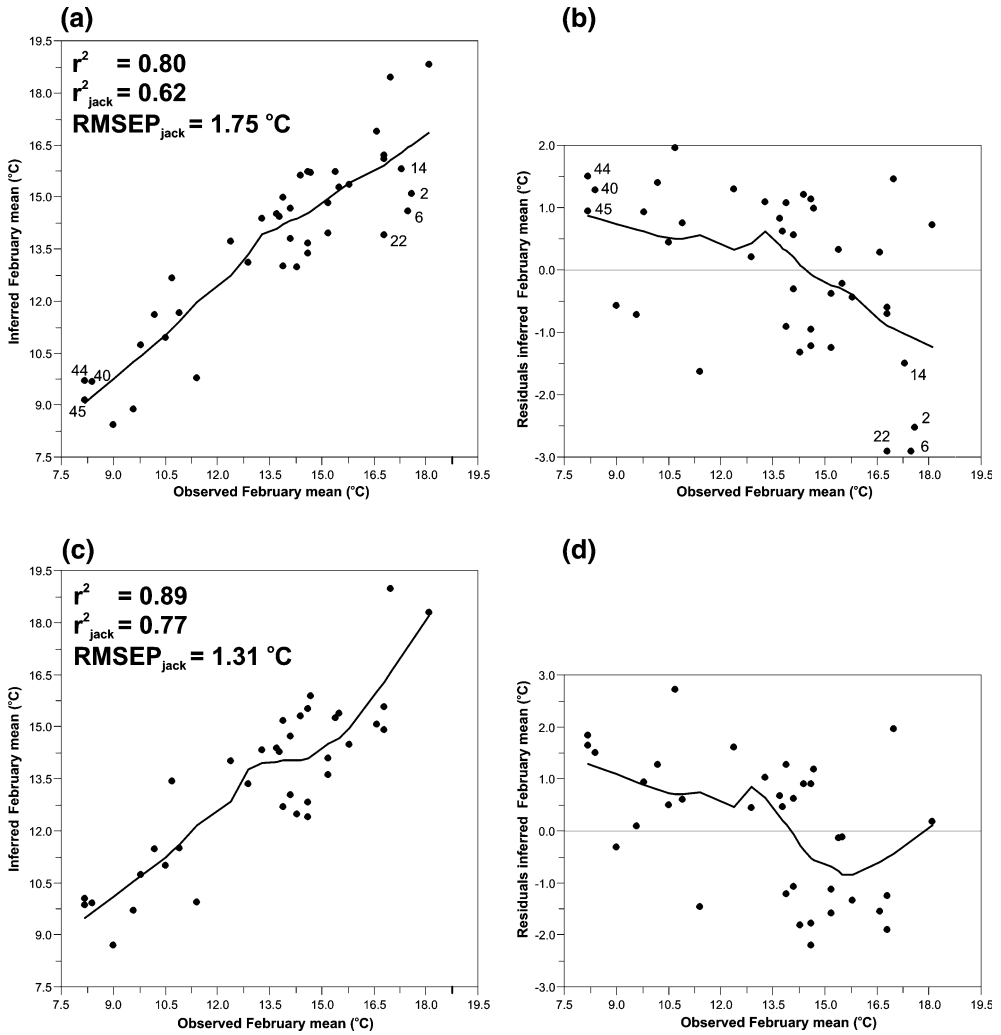

Fig. 6 (**a**) Plot of chironomid inferred February mean vs. observed February mean, and (**b**) observed vs. residual (chironomid-inferred minus observed February mean) using weighted averaging partial least squares (WA-PLS) regression. With the eutrophic lakes 2, 6, 14 and 22 included. (**c**) Plot of chironomid inferred February mean vs. observed February mean, and (**d**) observed vs. residual (chironomid-inferred minus observed February mean) using weighted averaging partial least squares (WA-PLS) regression lakes 2, 6, 14 and 22 removed. Loess smoother shown in all figures with a span of 0.45

and removed all of the highly productive lakes at the beginning, this trend would have gone un-noticed.

If we were to follow the strategy of Brooks and Birks (2000) (and others) and eliminate the highly productive (Chl *a* ≥10 μg/l) lakes from our dataset (lakes 2, 6, 14 and 22), the resulting model is far more robust (r^2 = 0.89, r^2_{jack} = 0.76, $RMSEP_{jack}$ = 1.3°C, maximum $bias_{jack}$ = 1.46°C) (Fig. 6c, d). The statistical significance (*P*) for February mean temperature in this reduced dataset was checked using a series of partial CCAs in CANOCO 4.5 (ter Braak and Šmilauer 2002) and confirmed that temperature remained significant ($P \leq 0.05$) after the partialling out of all other environmental variables. When the effect of temperature was partialled out in this reduced dataset, Chl *a* explained a relatively small (4.9%), and statistically insignificant ($P = 0.07$) amount of the total variance in the chironomid species data.

We can now say that this model would only be reliable in situations where the proportion of *Chironomus* is low, or if the proportion is high, where we could guarantee that conditions were not eutrophic or saline (Cond > 100 μS cm^{-1}). Obviously this temperature model would be unreliable when applied to brackish coastal lakes or Holocene records from lowland lakes with catchments that have experienced intensive human modification.

Highly eutrophic conditions are also possible in the absence of human impact (e.g., Brüchmann and Jörg 2004); therefore the presence of other fossils in lake sediments (e.g., *Isoetes* megaspores, charophyte oospores and the remains of other aquatic insects) could provide a guide to the past nutrient status of a particular lake. During the development of this training set it was observed that certain charophyte oospores, and *Isoetes* megaspores were absent from eutrophic, highly saline lakes. Other studies on New Zealand lakes (e.g., Stout 1985; Timms 1982, 1983) provide information on the presence or absence of particular aquatic insects in lakes of varying trophic status.

The future revision of the genus *Chironomus* may enable a differentiation between a high altitude cold stenothermic *Chironomus* species and a low altitude *Chironomus* species that is tolerant of low levels of dissolved oxygen. In the meantime this training set highlights the pitfalls of ignoring other environmental gradients, particularly nutrients in the development of a temperature inference model.

Chlorophyll a

The best model for Chl *a* (r^2 = 0.66, r^2_{jack} = 0.49, and $RMSEP_{jack}$ = 0.46 $\log_{10}$μg/l Chl *a*) was developed using linear methods (PLS with 2 components, leave-one-out cross validation) with 37 lakes (lakes 1, 19, 21, 23, 32, 40, 43, 45, and 46 removed) and all species with *N*2 values ≥2 included (Fig. 7a, b). There was a tendency for this model to under-predict the concentration of Chl *a* at the high end of the gradient (Fig. 7b).

Even though Chl *a* was shown to be a statistically significant independent driver of chironomid distribution in New Zealand (Table 2), the resulting transfer function is not particularly robust. Reid's (2005) New Zealand diatom-based Chl *a* transfer function has a lower $RMSEP_{jack}$ (0.18 Log_{10} μg/l Chl *a*) and a much higher r^2_{jack} (0.71). The only other published chironomid-based Chl *a* transfer function (Brodersen and Lindegaard 1999) also outperforms this transfer function in terms of r^2_{jack} (0.70), has a higher absolute $RMSEP_{jack}$ (0.63 Log_{10} μg/l Chl *a*), but covers a greater variation in Chl *a* concentration (0.55–2.51 Log_{10} μg/l Chl *a*).

There are several possible reasons for the poor performance of the Chl *a* transfer function. The first and most obvious possibility is that temperature is a much more powerful driver of chironomid distribution in New Zealand than Chl *a*. This possibility was certainly reflected in the results of the partial CCAs (Table 2). Chl *a* explained only 8.5% of the total chironomid species variation, while temperature (February mean) explained 13.6%. Even though Chl *a* was the only other environmental parameter to remain statistically significant in the partial CCAs (Table 2), the amount of variation that this parameter explained after partialling out the effect of temperature dropped to 4.6%.

The next 3 possibilities assume that New Zealand chironomids may in fact be useful proxies for Chl *a* and certain improvements to the training

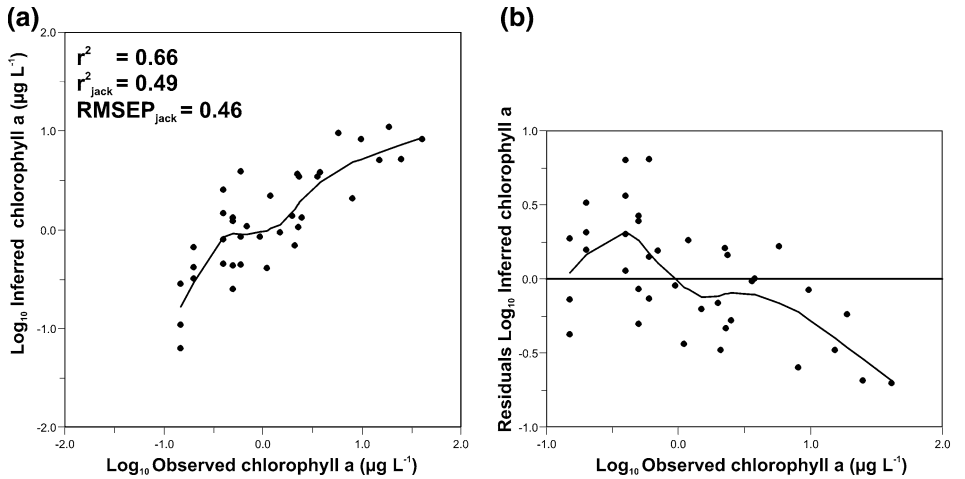

Fig. 7 (**a**) Plot of chironomid inferred Log_{10} inferred Chl *a* vs. Log_{10} observed Chl *a*, and (**b**) observed vs. residual Log_{10} Chl *a* (chironomid-inferred minus observed) using partial least squares (PLS) regression. Loess smoother shown in both figures with a span of 0.45

set may improve the performance of the chironomid-based Chl *a* transfer function. Firstly, improved taxonomy particularly of *Chironomus* (see the earlier discussion regarding this genus) may improve the performance of this model. Secondly, a more extensive set of Chl *a* data will certainly provide a more accurate impression of the long-term conditions in each lake. Brodersen and Lindegaard (1999) used summer mean Chl *a* values in the development of their robust Chl *a* transfer function (which has also been applied by Langdon et al. 2006). Future work should focus on obtaining more Chl *a* measurements to see if this improves the explanatory power of this variable. Long-term Chl *a* records were available for a small number of the lakes in this training set. We decided to use the spot measurements for the sake of consistency because these were available for the majority of the lakes. Finally, increasing the number of lakes at the high end of the Chl *a* gradient may also cause an improvement in the performance of this model.

Conclusions

The analysis of chironomid taxa, and environmental datasets from 46 New Zealand lakes identified temperature (February mean) and lake production (Chl *a*) as the most significant environmental influences on the distribution of chironomid taxa. Temperature explained the highest variation in the chironomid species data and consequently resulted in a more reliable transfer function. The most robust temperature inference model was based on a training set which excluded highly eutrophic lakes. The practice of eliminating other environmental gradients from a training set has been common practice in this field in the past. However, ignoring the effect of nutrients during the exploratory data analyses would have resulted in the failure to identify the problematic distribution of the ubiquitous *Chironomus* morphotype.

Problems attributed to the *Chironomus* morphotype may be resolved by an improved taxonomy of this genus in the future. Until this time the most robust temperature model (with highly productive lakes removed) should be applied with caution. The temperature model will certainly be unreliable if applied to eutrophic lakes or coastal brackish lakes.

Chl *a* was the only other environmental parameter to explain a statistically significant amount of variation in the chironomid taxa. The amount of variation explained by this variable was relatively low and therefore resulted in the production of a transfer function that was not particularly robust. The performance of this model could be improved by an increased taxonomic resolution of the New Zealand chironomid taxa (in particular *Chironomus* and the tribe

Macropelopiini) and by the input of mean Chl *a* concentrations into the model. The spot measurements available for most of the lakes in this study will not be truly representative of typical conditions in each lake.

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Appendix

Table 4 List of Chironomid taxa enumerated in this study

No.	Taxon name	*N*	Hill's *N*2	Maximum	Mean
1	*Ablabesmyia mala* Hutton	15	8.67	9.35	1.14
2	*Camptocladius* De Geer	3	2.40	1.90	0.08
3	*Chironomus* Meigen	46	30.74	100.00	36.71
4	*Cladopelma curtivalva* Kieffer	24	12.33	18.24	2.55
5	*Corynocera* Boothroyd	24	13.26	56.90	9.89
6	*Corynoneura* Winnertz	8	5.31	3.70	0.25
7	*Cricotopus* Boothroyd	12	4.79	6.28	0.34
8	*Cricotopus aucklandensis* Sublette and Wirth	34	12.37	56.07	5.88
9	*Cricotopus hollyfordensis* Boothroyd	1	1.00	0.96	0.02
10	*Cricotopus planus* Boothroyd	1	1.00	0.19	0.00
11	*Cricotopus zealandicus* Freeman	15	9.56	6.18	0.80
12	*Eukiefferiella brundini* Boothroyd and Cranston	4	2.75	3.81	0.16
13	*Eukiefferiella insolida* Boothroyd	1	1.00	2.00	0.04
14	*Eukiefferiella* Thienemann	4	3.28	1.94	0.11
15	*Harrisius pallidus* Freeman	2	1.77	1.90	0.06
16	*Hevelius carinatus* Sublette and Wirth	6	3.12	4.02	0.18
17	*Kaniwhaniwhanus chapmani* Boothroyd	2	1.79	2.27	0.07
18	*Kiefferulus opalensis* Forsyth	1	1.00	11.54	0.25
19	*Larsia* Wiedemann	1	1.00	1.87	0.04
20	Macropelopiini Fittkau	37	19.53	53.85	10.06
21	*Maoridiamesa* Pagast	3	1.34	7.14	0.18
22	*Naonella kimihia* Boothroyd	33	13.24	61.38	8.75
23	*Naonella forsythi* Boothroyd	11	6.57	11.03	1.15
24	*Naonella* ''305'' Unofficial morphotype	3	1.68	2.68	0.08
25	Orthoclad sp. A Boothroyd	5	3.84	1.90	0.13
26	Orthoclad sp. I Unofficial morphotype	5	3.27	2.94	0.13
27	Orthoclad sp. B Boothroyd	2	1.76	1.94	0.06
28	Orthoclad sp. C Boothroyd	11	7.81	3.81	0.40
29	Orthoclad sp. G Unofficial morphotype	6	4.29	1.70	0.12
30	Orthoclad sp. 1/6 Unofficial morphotype	2	1.95	0.89	0.03
31	Orthoclad sp. J Unofficial morphotype	3	2.76	0.85	0.04
32	Orthoclad sp. D Boothroyd	1	1.00	0.50	0.01
33	Orthoclad sp. E Unofficial morphotype	1	1.00	0.64	0.01
34	*Paratrichocladius pluriserialis* Freeman	7	3.61	20.59	1.14
35	*Parachironomus cylindricus* Freeman	2	1.62	1.14	0.03
36	*Paratanytarsus grimmii* Schneider	10	5.05	8.55	0.49
37	*Parochlus* Enderlein	12	4.07	22.11	1.09
38	*Paucispinigera* Stark	9	5.37	4.70	0.30
39	Pentaneurini	3	2.34	2.59	0.11
40	*Pirara matakiri* Boothroyd and Cranston	2	1.52	2.68	0.07

Table 4 continued

No.	Taxon name	*N*	Hill's *N*2	Maximum	Mean
41	*Podochlus* Brundin	1	1.00	0.50	0.01
42	*Podonomus* Philippi	2	1.91	2.01	0.07
43	*Polypedilum* Boothroyd	25	7.07	80.95	5.74
44	*Pseudochironomus* Malloch	2	1.81	0.46	0.02
45	*Smittia verna* Hutton	6	4.42	3.74	0.24
46	*Stictocladius* Edwards	1	1.00	1.87	0.04
47	*Tanytarsus* Boothroyd	14	8.58	3.41	0.38
48	*Tanytarsus funebris* Freeman	30	14.30	35.78	5.34
49	*Tanytarsus vespertinus* Hutton	24	9.91	32.14	4.22
50	*Xenochironomus canterburyensis* Freeman	3	2.99	0.96	0.06

Numbers correspond to CCA results (Fig. 3). The author of each taxonomic name is shown. The number of lakes were each taxon occurred (*N*), effective number of occurrences (Hill's *N*2), maximum and mean relative abundances (as a percent) are shown

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