

Midges (Chironomidae, Ceratopogonidae, Chaoboridae) as a temperature proxy: a training set from Tasmania, Australia

Andrew B. H. Rees · Les C. Cwynar ·
Peter S. Cranston

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Abstract Chironomid and ceratopogonid head capsules, along with *Chaoborus* mandibles, were used to model mean temperature of the warmest quarter (TWARM) in Tasmania. Our transfer function is based on midge assemblages and 21 environmental variables sampled from 47 lakes. Canonical correspondence analysis (CCA) revealed seven variables that account for a significant ($P \leq 0.05$) portion of the explainable variance. In order of explanatory power, these were pH, TWARM, annual radiation, magnesium, annual precipitation, SiO₂, and depth. TWARM was modeled using weighted averaging partial least squares (WA-PLS) and generated a model with $r_{\text{jack}}^2 = 0.72$ and RMSEP = 0.94. Advances in chironomid paleoecology are progressing very quickly in the Southern Hemisphere. Chironomid identification guides and autecological data are available for many regions, highlighting the potential for developing midge-based

quantitative models to address hemispheric and interhemispheric climate hypotheses.

Keywords Chironomids · Midges · Tasmania · Paleoclimate · Temperature · Transfer function · Australia

Introduction

The degree to which Northern Hemisphere paleoclimate affected its southern counterpart during the most recent deglaciation (20–10 ka BP) is a hotly debated issue (Turney et al. 2006; Alloway et al. 2007). Hypotheses are difficult to test with the few quantitative paleoclimate reconstructions currently available from south of the equator. Compounding the issue in terms of terrestrial records, only 2% of the Southern Hemisphere landmass is located within temperate regions corresponding to latitudes of extensive glaciation in the Northern Hemisphere (Clapperton 1990). At 41–44° S, the island-state of Tasmania, Australia (Fig. 1), is situated within this critical latitudinal range.

Tasmania is ideally located to detect synoptic-scale climate change within the Southern Hemisphere because it is positioned between two important controls of both atmospheric and oceanic circulation patterns: Australasia continental shelf regions to the north and Antarctica to the south (Kershaw and Nanson 1993). In addition, Tasmania may be distant

A. B. H. Rees (✉) · L. C. Cwynar
Department of Biology, University of New Brunswick,
Fredericton, Canada NB E3B 6E1
e-mail: a.rees@unb.ca

L. C. Cwynar
e-mail: cwynar@unb.ca

P. S. Cranston
Department of Entomology, University of
California – Davis, Davis, CA 95616, USA
e-mail: pcranston@ucdavis.edu

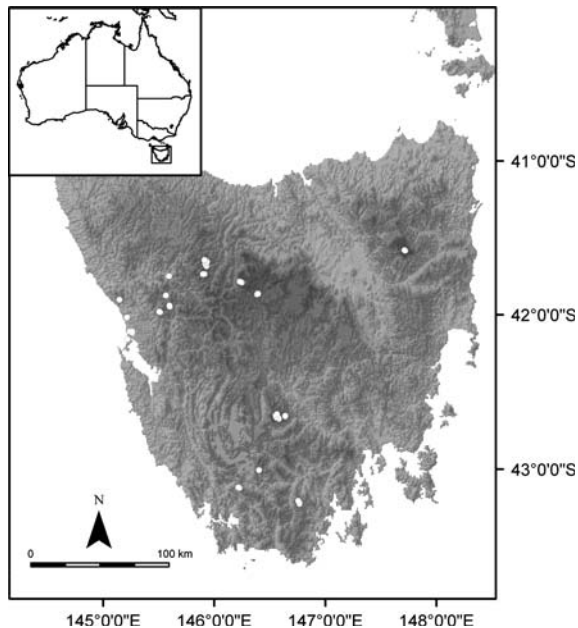


Fig. 1 Map of Tasmania with the 47 lakes comprising the training set. Map data provided by TASMAR, © State of Tasmania

enough from Northern Hemisphere ice sheet feedbacks and insolation-forcing mechanisms to register a genuinely Southern Hemisphere climate signal from the previous glaciation.

During the Last Glacial Maximum (LGM), ice-caps, along with valley and cirque glaciers, developed in western and central parts of Tasmania, covering ca. 1,000 km² (Colhoun and Shulmeister 2006; Colhoun 1985). With more ice coverage than mainland Australia, Tasmania's glaciers generated numerous lakes containing continuous sediment records dating to the Last Glacial Termination (LGT) and, where regions remained unglaciated, to the previous interglacial (120 ka BP). This presents a unique opportunity to address regional and hemispheric research questions. For example, what evidence is there from Tasmania for the Antarctic Cold Reversal (ACR) or Younger Dryas cooling event? Were there abrupt climate reversals during the Holocene? Does Tasmania register a hemispheric climate signal, i.e. how similar are Tasmanian records to those of Southern Hemisphere marine and ice cores? Does Tasmania's climate history show any similarity to other important Southern Hemisphere landmasses such as New Zealand or Patagonia? Obtaining answers to these questions is impeded by

the lack of inference models based on terrestrial proxies that can provide quantifiable estimates of past climate change.

Chironomids (Diptera: Chironomidae) are particularly useful environmental indicators, especially for reconstructing changes in temperature (Brooks and Birks 2001; Walker et al. 1997) and they are the most widely-distributed and often most abundant group of insects found in freshwaters (Armitage et al. 1995). The majority of species have short generation times and winged adults. Furthermore, as insects, chironomids respond to temperature during all stages of their lifecycle (Ward and Stanford 1982).

Although chironomid paleoecology has made tremendous progress over the past couple of decades in temperate regions of the Northern Hemisphere, progress in the Southern Hemisphere has lagged until recently. Chironomid-based, paleoecological studies in the tropics and Southern Hemisphere traditionally have remained relatively scarce because of an incomplete knowledge of the chironomid faunas, a lack of ecological data, and logistical problems that have prevented the development of calibration sets (Verschuren and Eggermont 2006). Because of these handicaps, many attempts to use chironomids for core-based paleoclimate/paleoenvironmental reconstructions in South America (Massaferro and Brooks 2002; Massaferro et al. 2005), Africa (Mees et al. 1991), and New Zealand (Deevey 1955) have been qualitative (see Verschuren and Eggermont 2006 for review). However, chironomid identification guides (e.g. Cranston 2000; Cranston and Dimitriadis 2004) and autecological data (e.g. Paterson and Walker 1974; Kokkin 1986) are available for many regions of the Southern Hemisphere, creating opportunities to develop robust, quantitative inference models.

While none of the earlier efforts in the Southern Hemisphere resulted in a quantitative temperature inference model, one of the first detailed studies to apply multivariate statistics to chironomid fossil data was conducted in New Zealand. Boubée (1983) used principal components analysis on modern chironomid remains to constrain down-core interpretations of fossil taxa. Similarly in New Zealand, Schakau (1986) applied classification techniques down-core in order to interpret shifts in fossil chironomid abundances qualitatively. Since these initial studies, there have been major improvements both in the statistics used in paleoecology and in the taxonomic

resolution of New Zealand chironomids, culminating in two transfer functions for temperature (Woodward and Shulmeister 2006; Dieffenbacher-Krall et al. 2007) and one for chlorophyll *a* (Woodward and Shulmeister 2006).

The first quantitative study of chironomid paleoecology in Australia was conducted by Dimitriadis and Cranston (2001) who calibrated subfossil assemblages using chironomid survey and physico-chemical data collected from eastern Australian lakes. With these data, they created a Holocene climate reconstruction from a tropical lake in north-eastern Queensland using mutual-climate-ranges (MCRs), a technique common to beetle paleoecology (Elias 1997). This method has encountered criticisms (see Birks 2003; Verschuren and Eggermont 2006 for a review), resulting in the need for a more robust approach to reconstructing the paleoclimates of Australia.

Here we present a temperature transfer function based on subfossil assemblages of Chironomidae (non-biting midges), Ceratopogonidae (biting midges), and Chaoboridae (phantom midges) from 47 Tasmanian lakes. This is the first such transfer function built for Australia and will add to the paleoclimatological tools available for testing climate hypotheses in the Southern Hemisphere.

Description of study area

Tasmania is located at the southern-most extent of the Australasian continental plate. During glacial stages, the island was connected to Australia by a land bridge; otherwise, Tasmania is separated from the mainland by the 250 km wide Bass Strait (Jackson 2005). Despite its association with a flat and dry continent, Tasmania possesses a predominately maritime climate and a mountainous landscape preserving many glacial features. The geology, climate, lake chemistry, and vegetation all change abruptly at what has been called “Tyler’s Line” by Shiel et al. (1989) and roughly coincides with the 146th meridian. The ensuing descriptions of climate, geology, and vegetation follow Jackson (2005) and Macphail (1978).

Climate

Westerlies known as the Roaring Forties provide western Tasmania with year-round precipitation.

Migration of a subtropical high pressure system over Australia governs the position of the Roaring Forties, forcing the westerlies south of Tasmania during summer months and across the island during winter (Harrison 1993), resulting in wet winters and relatively dry summers. In conjunction with Tasmania’s orography, the Roaring Forties produce a strong, west-east precipitation gradient. On the west coast, annual precipitation typically ranges from 1,029 to 1,270 mm. Rain-bearing winds move inland where they meet western mountain ranges, resulting in annual precipitation usually ranging between 2,540 and 3,560 mm on western mountains and a rain-shadow eastward. Consequently, the Midlands of east-central Tasmania typically receive less than 760 mm of precipitation annually. Above approx. 910 m, precipitation generally falls as snow during the winter months.

Tasmania’s climate is also moderated by the ocean, resulting in a maritime climate with only slight continentality on the Central Plateau. Mean austral summer and winter temperatures for Hobart (51 m a.s.l.), the capital city of Tasmania, are 18.9 and 11.7°C, respectively (Hobart meteorological station, Australian Bureau of Meteorology). However, like precipitation, temperature also is controlled by orography. For example, annual temperatures from a meteorological station in Liawenee (1,065 m a.s.l.), located on the Central Plateau, range from 16.1 (summer) to 5.3°C (winter). Irregular incursions of cold air from Antarctica can produce snow and frost at anytime of the year. On the other hand, warm, dry air from continental Australia occasionally causes extremely hot days in excess of 41°C.

Geology and vegetation

In western Tasmania, quartzose basement sediments have been intensely folded and reworked by erosion. This side of the island consists of jagged Precambrian siliceous rocks, namely quartzite, schist, and phyllite. In certain regions, older basement rock has been overlain by sedimentary limestones, sandstones, siltstones, and mudstones. However, extensive erosion has excised softer strata, leaving the hard quartzite rocks behind and filling valleys with the erosional by-products. In general, soils in the west are shallow, infertile, and acidic.

High annual precipitation in the west supports temperate, podocarp-broadleaf rainforests with

Nothofagus cunninghamii present from sea level to tree line. Low soil fertility produces breaks in the canopy, allowing the establishment of shade-intolerant mesophytic species such as *Eucryphia lucida*, *Anodopetalum biglandulosum*, and *Phyllocladus aspleniifolius*. Fire regimes encourage expansive communities of button grass moorland dominated by *Gymnoschoenus sphaerocephalus*.

In central and eastern Tasmania, extensive faulting has occurred with vertical down-drops of up to 1.5 km. Permian mudstones and Triassic siltstones, both modified by Jurassic doleritic intrusions, overlie the older basement rock. The younger strata weather rapidly, generating soils that are richer in clay and relatively more fertile than those in the west.

Reductions in moisture, along with enhanced soil fertility, drive the vegetational gradient from west to east. Temperate rainforests merge into a wet sclerophyll ecotone. In these landscapes, *N. cunninghamii*-dominated forests give way to eucalyptus forests containing an understory of *Pomaderris apetala* and the tree fern, *Dicksonia antarctica*. Wet sclerophyllous species are quick to colonize fire-cleared rainforest west of the ecotone.

Further east, in the rain-shadow of the western mountains, dry sclerophyllous eucalyptus forests contain an understory of small trees like *Casuarina*, *Acacia*, and *Banksia*, along with shrubs of the Epacridaceae, Proteaceae, and Asteraceae. This vegetation is eventually replaced by savanna woodland. Open eucalyptus forests dominate inland of the east coast.

Materials and methods

Midge collection and analysis

Sediment from 54 lakes was collected in replicates using a mini-Glew corer (Glew 1991) during the austral summer months of January and February, 2006 and 2007. Samples were obtained from the geographical centre of each lake. The upper 0–1 and 1–2 cm of each replicate was extruded on site, packaged in separate Whirlpaks[®], and kept cool until analysis. Lakes were selected along an altitudinal range to ensure a strong temperature gradient. While there was no strict cut-off in terms of lake depth, small and shallow lakes were preferentially sampled

to ensure a close relationship between bottom water temperature and air temperature (Livingstone et al. 1999). Sampling deep, stratified lakes should be avoided in order to prevent the effect of hypolimnetic anoxia on chironomid assemblages (Little and Smol 2001). However, due to the lack of bathymetric data for the majority of Tasmanian lakes, this was not always possible (Table 1).

In the laboratory, midge analysis was conducted according to the protocol established by Walker et al. (1991). Lake sediment was volumetrically sampled, deflocculated in hot 10% KOH, and washed with distilled water through a screen with 95 µm meshes. Aliquots of the residue were poured into a Bogorov tray and examined under a dissecting microscope at 50× magnification. Chironomid and ceratopogonid head capsules, along with *Chaoborus* mandibles, were hand-picked using fine forceps until the entire sample was processed. This procedure was repeated until a minimum of 100 head capsules was obtained per sample, which required, on average, 12 ml of wet sediment.

Quinlan and Smol (2001) suggest between 40 and 50 head capsules as sufficient for use in inference models where diversity is low. However, Heiri and Lotter (2001) caution against extrapolating this minimum count size to other geographical locations, arguing that minimum count size is model dependent. Therefore, rarefaction analysis was conducted using RAREPOLL (Birks and Line 1992) to estimate the taxon richness of samples processed with varying sampling effort. In total, three runs were performed, holding samples at constant counts of 50 (recommended count size), 77 (minimum count size of this study), and 144 (average count size of this study) chironomid head capsules, which captured an average of 84.3%, 92.8%, and 99.3% of actual taxonomic richness, respectively (Fig. 2).

Head capsules were positioned ventral-side up on a coverslip and mounted with Entallen[®]. Identification was conducted with a compound, light microscope at 400× magnification, following Wiederholm (1983), Oliver and Roussel (1983) and identification guides by Cranston (2000). Samples are archived with L. C. Cwynar's collection at the University of New Brunswick for eventual deposition in The Australian National Insect Collection, Canberra.

Table 1 Environmental variables of the 54 lakes sampled for the Tasmanian training set

Number	Lake	SOUTH metric	EAST metric	ELEV (m)	pH	TWARM (°C)	RAD (MJ/m ²)	Mg ²⁺ (mg/l)	PRECIP (mm)	SiO ₂ (mg/l)	DEPTH (m)	CON (µS/cm)	LOI (%)	TURB (mg/l)
1	Lake Mallanna	42.02	145.28	9.4	4.4	14.9	11.9	2.66	1,534	5.1	3.70	159	28.5	1.7
2	Lake Strahan	42.15	145.27	22.2	5.5	14.7	11.9	7.00	1,528	2.5	0.55	347	5.0	0.7
3	Lake Ashwood	42.10	145.29	39.7	5.8	14.6	11.8	3.17	1,573	0.2	0.13	158	34.5	0.9
4	Lake Bellingier	42.11	145.31	70.6	4.8	14.4	11.6	3.44	1,711	6.0	1.48	197	41.0	1.6
5	Lake Garcia	42.10	145.31	88.3	5.0	14.4	11.5	2.37	1,750	1.1	8.00	138	56.6	0.9
6	Cumberland Lake	41.90	145.21	411.4	4.9	12.7	10.6	1.07	2,638	2.8	1.35	62	37.5	1.7
7	Lake Selina	41.88	145.61	520.0	5.7	12.4	10.5	0.61	2,818	0.2	9.17	33	24.8	0.9
8	Basin Lake	41.98	145.55	576.7	4.7	12.0	10.2	0.65	3,170	0.5	1.90	45	50.6	0.6
9	Little Basin Lake ^a	41.98	145.56	599.0	4.6	11.9	10.2	0.71	3,219	0.3	2.90	47	38.4	0.9
10	Lake Herbert	41.75	145.64	618.7	4.8	11.9	10.9	0.63	2,378	0.5	5.35	39	31.0	0.7
11	Michael Tarn	41.95	145.64	751.5	5.2	11.1	10.4	0.49	2,935	0.4	5.10	30	34.7	1.0
12	Lake A ^a	41.95	145.64	764.7	5.9	11.0	10.5	0.54	2,899	0.2	2.80	32	21.8	1.2
13	Les Tam ^a	41.94	145.64	765.5	4.5	11.0	10.4	0.88	2,904	2.1	1.97	53	39.7	1.8
14	Lake 50 ^a	43.02	146.41	862.4	4.6	10.0	10.7	0.34	2,158	0.2	1.90	28	35.5	0.5
15	Lake Cygnus	43.13	146.23	873.4	4.9	9.7	10.3	0.51	2,457	0.1	8.30	34	5.0	0.4
16	Lake Fortuna	43.13	146.24	880.1	4.7	9.7	10.3	0.48	2,462	0.1	9.12	33	12.8	0.5
17	Lake Rodway	41.69	145.96	916.2	5.8	10.5	11.0	0.36	2,463	1.1	35.2	23	35.4	0.6
18	Lake Osborne	43.22	146.76	919.5	6.9	9.5	11.0	0.91	1,775	3.1	8.90	32	29.4	0.3
19	Lake Lilla	41.65	145.96	928.0	5.0	10.5	10.9	0.38	2,577	0.9	13.10	21	33.1	0.8
20	Flynns Tarn	41.69	145.96	936.0	6.2	10.4	10.9	0.54	2,482	1.2	0.58	20	18.6	0.7
21	Platypus Tarn	42.67	146.59	953.8	6.7	10.0	11.5	0.83	1,586	4.3	10.32	25	30.1	0.4
22	Ladies Tarn	43.24	146.77	971.0	6.5	9.2	11.0	0.88	1,808	3.1	8.80	25	40.1	0.3
23	Lake Esperance	43.23	146.77	976.0	6.4	9.1	11.0	0.60	1,811	2.0	19.2	27	33.6	0.3
24	Lake Nicholls	42.67	146.65	981.4	6.5	9.9	11.7	0.49	1,479	4.7	11.2	22	32.0	0.5
25	Twilight Tarn	42.65	146.57	999.1	6.1	9.7	11.4	0.57	1,663	1.6	0.74	19	41.6	0.7
26	Wombat Pool	41.65	145.95	1,001	4.6	10.1	11.0	0.32	2,499	0.4	2.15	27	38.6	1.0
27	Lake Hanson	41.66	145.97	1,002	4.8	10.1	11.0	0.27	2,466	0.8	10.4	20	39.5	1.0
28	Lake Rayner	42.66	146.65	1,020	6.8	9.6	11.6	0.57	1,523	5.9	0.94	27	23.7	0.4
29	Lake Dobson	42.68	146.59	1,027	7.0	9.5	11.4	1.60	1,651	7.3	4.47	39	21.7	0.4
30	Eagle Tarn	42.68	146.59	1,040	6.5	9.5	11.3	2.09	1,729	3.2	0.19	54	29.4	2.0

Table 1 continued

Number	Lake	SOUTH metric	EAST metric	ELEV (m)	pH	TWARM (°C)	RAD (MJ/m ²)	Mg ²⁺ (mg/l)	PRECIP (mm)	SiO ₂ (mg/l)	DEPTH (m)	CON (µS/cm)	LOI (%)	TURB (mg/l)
31	Andrew Tam ^a	41.74	145.94	1,066	5.2	9.7	10.9	0.33	2,472	0.1	0.95	22	10.1	2.8
32	Lake Holmes	41.74	145.95	1,076	5.0	9.6	11.0	0.38	2,441	0.1	0.95	23	16.1	1.8
33	Twisted Lakes	41.67	145.97	1,123	5.5	9.4	11.1	0.34	2,391	0.5	2.25	17	32.0	0.9
34	Lake Loane	41.79	146.26	1,126	6.5	9.6	11.8	0.44	1,700	1.4	1.80	18	29.2	0.8
35	Lake Newdegate	42.66	146.56	1,144	6.5	8.8	10.8	0.66	2,121	2.2	2.90	20	27.3	0.4
36	Central Plateau 2 ^a	41.87	146.41	1,184	6.3	9.4	12.9	0.42	1,080	0.2	3.30	20	29.4	0.5
37	Solomons Jewels 2	41.80	146.27	1,189	6.4	9.2	11.9	0.31	1,675	0.2	2.90	19	29.8	0.7
38	Central Plateau 1 ^a	41.87	146.41	1,193	6.6	9.3	13.0	0.63	1,043	0.3	0.46	24	44.2	1.6
39	Terry Tam	41.88	146.40	1,193	6.4	9.3	12.9	0.38	1,094	0.1	1.61	21	39.5	0.5
40	Solomons Jewels 1	41.80	146.27	1,199	6.1	9.2	11.9	0.32	1,678	0.5	2.35	16	36.0	0.9
41	Heather Tam ^a	41.80	146.28	1,201	6.1	9.2	11.9	0.37	1,678	0.2	0.37	20	25.3	2.6
42	Johnston Tam	42.67	146.57	1,210	6.7	8.4	10.6	0.70	2,441	2.7	9.03	21	21.7	0.9
43	MacKenzie Tam	42.67	146.57	1,210	6.5	8.5	10.6	0.63	2,407	2.8	10.15	18	28.9	0.1
44	Robert Tam	42.68	146.57	1,214	6.4	8.4	10.6	0.58	2,458	2.7	1.10	21	35.2	0.5
45	Lake Wilks	41.67	145.96	1,254	6.1	8.7	11.1	0.55	2,367	1.8	8.12	19	30.4	0.5
46	Lake Youl	41.59	147.69	1,302	6.7	9.0	12.4	0.45	1,456	0.5	0.71	16	14.9	0.4
47	Youls Tam	41.59	147.69	1,306	6.4	9.0	12.4	0.52	1,464	0.4	0.30	18	10.9	0.7
48	Lake Chisholm	41.13	145.06	149.3	4.9	14.5	12.4	4.00	1,497	3.5	10.07	117	44.3	0.9
49	Duckhole Lake	43.36	146.87	150.4	4.1	13.7	11.7	1.08	1,346	3.5	3.10	80	44.0	0.8
50	Lake Baker	41.59	147.72	1,357	6.5	8.7	12.4	0.52	1,498	1.8	0.40	19	-	3.1
51	Lake Baker 2 ^a	41.59	147.72	1,359	6.2	8.7	12.4	0.28	1,499	1.0	1.25	14	-	0.7
52	Menamatta Tams 1	41.54	147.63	1,446	6.2	8.2	12.3	0.52	1,549	0.2	0.16	23	-	2.3
53	Menamatta Tams 2	41.54	147.63	1,447	6.0	8.2	12.3	0.50	1,549	0.4	0.09	22	-	0.6
54	Menamatta Tams 3	41.54	147.63	1,451	5.9	8.1	12.3	0.46	1,551	0.2	0.10	26	28.7	10.1

Only the first 47 lakes were used in the final model. The lakes are ordered based on increasing elevation. Abbreviations of environmental variables are mentioned in the text

^a Lake names created by the authors

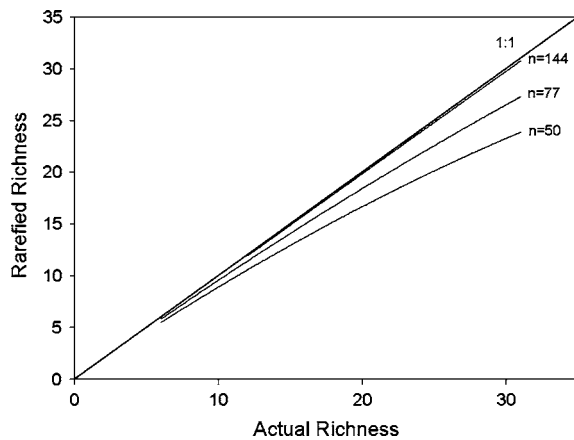


Fig. 2 Rarefaction plot comparing actual taxon richness to rarefied taxon richness. Samples were held at constant sizes of 50, 77, and 144 chironomid head capsules, which captured an average of 84.3%, 92.8%, and 99.3% of actual taxonomic richness, respectively

Environmental variables

Lake water for chemical analyses was sampled approx. 0.5 m below the water surface. A 250 ml plastic bottle was filled with lake water and kept cool until analysis. This particular sample was used to measure Na^+ , K^+ , Ca^{2+} , Mg^{2+} , Fe^{2+} , Mn^{2+} , Cu^{2+} , Zn^{2+} , Cl^- , SiO_2 , NH_3 , SO_4^{2-} , total organic carbon (TOC), turbidity (TURB), conductivity (CON), and pH. A 125 ml glass bottle was nearly filled with filtered (Sarstedt[®], 0.45 μm syringe filter) lake water; 1 ml of 30% H_2SO_4 was added for preservation, and the bottle was kept cool until analysis. This sample was used to measure Kjeldahl nitrogen (TKN) and total phosphorus (TP). Both general water chemistry protocols and TKN and TP protocols were conducted at the Research Productivity Council (RPC) located in Fredericton, New Brunswick, Canada.

Climate variables (Table 1) were acquired using the program BIOCLIM (Busby 1986, 1991; see also <http://cres.anu.edu.au/outputs/anuclim/doc/bioclim.html>). BIOCLIM uses a continent-wide, thin-plate smoothing spline derived from all available climate stations with adequate records (minimum of 30 years). For any given parameter, the software predicts point values for a specific latitude, longitude, and elevation within Australia. Of the 35 possible variables to choose from, we opted to use temperature of the warmest quarter (TWARM), annual precipitation (PRECIP), and annual radiation (RAD). Temperature estimates for Tasmania

were based on 76 meteorological stations, which were a minimum, maximum, and average distance of 1.9, 35.5, and 19.8 km away from sampling sites, respectively. The standard errors associated with temperature vary from 0.2 to 0.4°C (Houlder et al. 2000).

Water depth (DEPTH) was acquired by sounding with a Secchi disc at the geographical centre of each lake until a maximum depth was found. Loss-on-ignition (LOI), a coarse indication of the organic content of lake sediment, was measured on 1 ml of wet sediment ashed at 500°C for 4 h following Dean (1974).

Latitude (SOUTH), longitude (EAST), and elevation (ELEV) were measured using a Garmin[®] global positioning system. As these variables only affect midge distributions indirectly (i.e. through temperature, precipitation, soil fertility, etc.), they were removed from further analyses. Likewise, Secchi depth was also recorded; however, in the majority of cases, Secchi depth exceeded lake depth and was therefore excluded from modeling exercises.

Data screening and transformations

Prior to the ordinations, species count data were transformed into percentages. To remove noise, rare taxa, here defined as having a maximum abundance less than 2% and/or occurring in fewer than 2 lakes, were removed. Where applicable (i.e. detrended and canonical correspondence analyses), species were square-root-transformed and rare taxa were downweighted.

Prior to ordinations, environmental data were assessed for normality using the Kolmogorov-Smirnov normality test, and measurements of skewness and kurtosis (Zar 1999). Four transformations were considered in order to normalize the environmental data: square-root, inverse square-root, log 10, and inverse. LOI, pH, RAD, and TKN did not need to be transformed. K^+ and TOC were best normalized by inverse square-root transformations whereas DEPTH, Ca^{2+} , Fe^{2+} , Mn^{2+} , Zn^{2+} , SiO_2 , and TURB were best normalized by log 10 transformations. Na^+ , Mg^{2+} , Cl^- , TP, and CON were best normalized by inverse transformations. In the situation where no transformation normalized the data or significantly reduced skewness, the environmental parameter was left untransformed; this included TWARM, PRECIP, Cu^{2+} , and SO_4^{2-} .

Pearson's correlation tests and canonical correspondence analyses (CCAs) were run to assess the collinearity of the environmental variables. Variables with variance inflation factors (VIFs) greater than 20 were manually removed to reduce the redundancy of the training set. Variables with the highest VIFs were removed sequentially until all were less than 20 (ter Braak and Šmilauer 2002). Based on this criterion, only Na^+ was removed; the Pearson's correlation test revealed that Na^+ was highly correlated ($P \leq 0.01$) with pH, TWARM, K^+ , Mg^{2+} , Fe^{2+} , Cl^- , SO_4^{2-} , TKN, TOC, and CON.

Sites with fewer than 50 chironomid head capsules were removed from modeling exercises. Only four of the 54 lakes failed to meet this criterion (after processing all of the sediment, Menamatta Tarns 1 and 2 and Baker Lakes 1 and 2 all had fewer than 10 head capsules). A detrended correspondence analysis (DCA) of species data and a principal components analysis (PCA) of environmental data were run for the remaining 50 lakes. Sites with sample scores lying outside of one standard deviation from the means of axes 1 and 2 of both the DCA and PCA were considered for elimination. Although lakes Duckhole, Fortuna, Central Plateau 1, and Roberts Tarn were identified as outliers by the DCA, and lakes Strahan, Ashwood, and Chisholm were identified as outliers by the PCA, no lake was identified as an outlier by both.

A final consideration for site removal involved assessing the difference between observed versus predicted temperatures from weighted averaging partial least squares models (see Model development) constructed in C2 version 1.4 (Juggins 2003). The predicted temperatures for lakes Duckhole, Chisholm, and Little Basin were all considerably greater than the observed temperatures whereas the predicted temperature for Menamatta Tarn 3 was considerably lower. Lakes Duckhole and Chisholm are both sinkhole lakes with thick organic mats of coarse wood and leaves lining their basins with little other sediment and high concentrations of Mg^+ , Fe^{2+} , TOC, and TP. Menamatta Tarn 3 is an ephemeral lake that periodically dries out; the tarn is shallow and highly turbid. All three of these lakes were removed from the data set. Since there was no ecological reason to remove Little Basin Lake, it was retained for further analyses.

Ordinations

Ordinations were conducted using CANOCO version 4.5 (ter Braak and Šmilauer 2002). Relationships between midge distributions and environmental variables were assessed using CCA. Manual forward selection along with Monte Carlo permutation tests (999 unrestricted permutations) allowed identification of statistically significant ($P \leq 0.05$) environmental variables. Variables were selected such that each subsequent choice explained the highest proportion of the remaining variance. To test the robustness of the significant variables, a series of partial canonical correspondence analyses (pCCAs) were performed with and without the remaining significant variables included as covariables. The relationship between significant environmental variables and ordination axes was assessed with canonical coefficients, their associated *t*-values, and the inter-set correlations of the environmental variables with respective axes.

Taxon response models were constructed in CanoDraw, a component of CANOCO, using generalized linear models (GLM) set to a quadratic degree and Poisson distribution (ter Braak and Šmilauer 2002). The GLMs were used to detect significant relationships between taxa and the significant environmental parameters detected by the CCA (Table 2).

Model development

A midge transfer function was developed for temperature of the warmest quarter (TWARM) using the software package C2, version 1.4. A DCA was performed to assess the response of subfossil taxa across the gradients captured by our training set. The gradient length of DCA axis 1 was 2.206, indicating that either linear or unimodal methods could adequately model species response (Birks 1998). Hence, both partial least squares (PLS) and weighted averaging partial least squares (WA-PLS) techniques were employed. We used leave-one-out, cross-validation as this technique is more robust for data sets with fewer than 80 sites (Kim and Han 1997). Models were tested with 1,000 cycles and evaluated based on the performance of the jack-knifed coefficient of determination (r_{jack}^2), average bias of jack-knifed predictions ($\text{AveBias}_{\text{jack}}$), maximum bias of jack-knifed predictions ($\text{MaxBias}_{\text{jack}}$), and root mean square error of

Table 2 Taxa enumerated in this study. Occurrence is a percentage out of the 47 lakes comprising the final transfer function whereas the WA-PLS β coefficient is from the jack-knifed second component model

Number	Taxon name	Occurrence (%)	Hill's N2	Max (%)	Mean (%)	WA-PLS β coefficient	pH	TWARM	RAD	Mg	PRECIP	SiO ₂	DEPTH
1	Pentaneurini Genus E	51.1	14.4	9.5	1.7	12.7							
2	Larsia Fittkau	72.3	19.1	13.8	2.5	11.4	x	X	X				
3	Paramerina Fittkau	40.4	10.9	5.5	0.7	8.1							
4	Telmatopelopia Fittkau	21.3	7.2	8.1	0.9	6.3		x	X				x
5	Pentaneurini undifferentiated	76.6	17.7	14.7	2.0	9.6		X	X				
6	Macropelopini type 1 Unofficial morphotype	19.1	7.5	2.4	0.2	8.5						x	
7	Procladius Skuse	76.6	24.8	10.2	2.3	12.3		x	X	X			
8	Macropelopini undifferentiated	61.7	20.1	6.1	1.3	11.6	x						
9	Genus Australia	6.4	2.5	3.0	0.1	10.0	x	x					X
10	Botryocladus Cranston & Edward	68.1	14.6	12.6	1.8	6.5		X	X	x			
11	Cricotopus 'parbicintus'	48.9	9.8	13.3	1.4	7.7	X						
12	Echinocladius Cranston	61.7	13.6	27.9	3.0	7.3		x	X				
13	Gymmetriocnemus type 1 Unofficial morphotype	27.7	8.5	3.6	0.3	11.5							
14	Orthoclad type 1 Unofficial morphotype	14.9	5.5	2.3	0.2	12.3							X
15	Orthoclad type 2 Unofficial morphotype	10.6	4.1	2.6	0.2	5.1	x	x	X	x	X		x
16	Orthoclad type 3 Unofficial morphotype	48.9	15.8	3.6	0.6	11.2	x		X				x
17	Orthoclad type 4 Unofficial morphotype	17.0	6.4	3.7	0.4	4.7	X	X	x	X	x	X	x
18	Parakiefferiella type 1 Unofficial morphotype	63.8	11.4	55.5	7.1	7.5	x	X			x		
19	Parakiefferiella type 2 Unofficial morphotype	29.8	5.8	33.0	2.5	12.7	x	X	X	X			X
20	Parakiefferiella type 3 Unofficial morphotype	19.1	4.3	5.5	0.4	5.6	x		X				
21	Parakiefferiella type 4 Unofficial morphotype	6.4	2.3	16.4	0.6	8.4	x	X		X			x
22	Paralimmophyes type 1 Unofficial morphotype	83.0	18.9	44.6	7.1	9.4	X	X	X	X	X		x
23	Paralimmophyes type 2 Unofficial morphotype	25.5	4.3	12.9	0.7	6.0							x
24	Paralimmophyes type 3 Unofficial morphotype	34.0	12.1	2.3	0.4	11.3							

Table 2 continued

Number	Taxon name	Occurrence (%)	Hill's N2	Max (%)	Mean (%)	WA-PLS β coefficient	pH	TWARM	RAD	Mg	PRECIP	SiO ₂	DEPTH
25	'SO1'	6.4	2.8	4.2	0.2	3.2	X	X	X	x	X	X	X
26	<i>Stictocladus</i> Edwards	14.9	4.2	3.9	0.2	8.0		X				X	X
27	<i>Chironomus</i> Meigen	76.6	15.7	31.6	6.1	8.5				x			x
28	<i>Cladopelma</i> Kieffer	31.9	6.0	8.5	0.7	11.8	x					x	
29	<i>Cladotanytarsus</i> Kieffer	19.1	4.4	25.8	1.4	7.9	X	X			X		
30	<i>Cryptochironomus</i> Kieffer	27.7	10.1	2.3	0.3	12.2							
31	<i>Dicrotendipes</i> Kieffer	21.3	3.5	14.7	0.6	11.7	x			x	x		
32	<i>Kiefferulus martini</i> Freeman	6.4	2.4	6.2	0.2	31.4	X	X		X		X	
33	<i>Parachironomus</i> Lenz	46.8	16.6	3.2	0.7	15.8	X	X					
34	<i>Polypedilum vespertinus</i> Skuse	44.7	7.9	34.0	2.8	6.5	X			x			
35	<i>Polypedilum watsoni</i> Freeman	38.3	11.3	8.1	1.3	9.3	x		X		X		
36	<i>Polypedilum</i> type 1 Unofficial morphotype	27.7	10.7	2.6	0.3	10.9	X		X		X		
37	<i>Riethia</i> Kieffer	87.2	23.0	21.6	5.6	9.4			X				x
38	<i>Stempellina</i> Thienemann & Bause	53.2	12.0	57.8	8.4	17.0	X	X		x	x		x
39	<i>Tanytarsus</i> nr. <i>chinyensis</i>	31.9	7.0	15.1	1.0	21.0	X	X					
40	<i>Tanytarsus</i> type 1 Unofficial morphotype	61.7	14.0	37.2	6.8	11.9	X						
41	<i>Tanytarsus</i> type 2 Unofficial morphotype	46.8	12.3	20.3	3.1	13.2				X		X	x
42	<i>Tanytarsus</i> type 3 Unofficial morphotype	25.5	6.0	22.8	2.0	6.4			X		X		X
43	<i>Tanytarsus</i> type 4 Unofficial morphotype	12.8	1.7	37.8	1.1	1.7			X				
44	<i>Tanytarsus</i> type 5 Unofficial morphotype	8.5	3.2	2.0	0.1	16.7	x					X	
45	<i>Tanytarsini</i> undifferentiated	100.0	26.0	66.2	16.6	10.0	X	x				x	
46	<i>Parochilus</i> Enderlein	29.8	9.0	4.7	0.5	7.9			X		X	x	x
47	Ceratopogonidae type 1 Unofficial morphotype	34.0	10.7	3.9	0.5	6.3							x
48	Ceratopogonidae type 2 Unofficial morphotype	12.8	4.8	3.6	0.3	27.3	x	X			X		
49	<i>Chaoborus</i> Unofficial morphotype	29.8	7.9	7.0	0.7	21.6	X	X		X			X

Generalized linear modeling was used to determine significant relationships between taxa and environmental variables

x, significant at $P \leq 0.05$; X, significant at $P \leq 0.01$

prediction (RMSEP). The number of components included in the final model was selected based on reducing the RMSEP by at least 5% (Birks 1998).

Results

Midge analysis

After data screening, a total of 49 non-rare, midge taxa were identified from 47 Tasmanian lakes (Table 2). The minimum, maximum, and average count sizes were 77, 257, and 144 whole head capsules, respectively. Taxa restricted to cooler, high

elevation sites include *Telmatopelopia*, *Parakiefferiella* types 3 and 4, *Paralimnophyes* types 2 and 3, *Cladopelma*, *Cladotanytarsus*, *Polypedilum vespertinus*, *Polypedilum watsoni*, *Tanytarsus* types 3 and 4, and Ceratopogonid type 1 (Fig. 3). Taxa typifying warmer, low elevations include *Kiefferulus martini*, *Parachironomus*, *Stempellina*, *Tanytarsus* nr. *chinyensis*, *Tanytarsus* type 2, *Chaoborus*, and Ceratopogonid type 2 (Fig. 3). The majority of the remaining taxa reflect more cosmopolitan distributions. In several cases, these taxa are comprised of multiple species with broad ecological ranges, including *Procladius*, *Chironomus*, and the undifferentiated Pentaneurini, Macropelopini, and Tanytarsini.

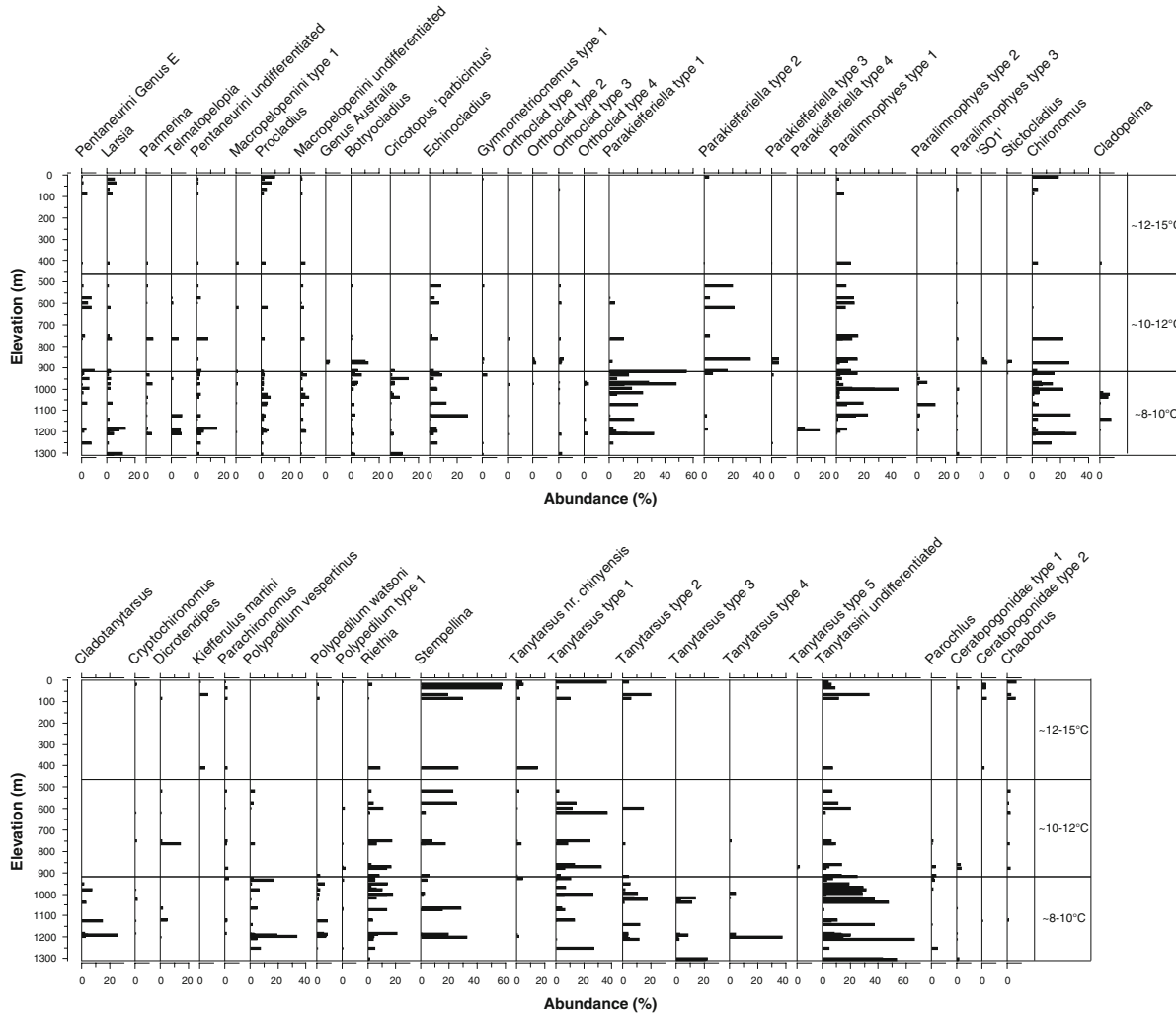


Fig. 3 Midge percent diagram of the 49 non-rare taxa included in the final model. Elevation is on the y-axis and the zones are based on approximate temperature ranges associated with the elevation gradient

Table 3 Partial CCAs of the seven significant environmental variables alone and with the effects of the remaining significant variables partialled out

Environmental variable	Covariable(s)	λ_1	λ_1/λ_2	<i>P</i>	% Variance
pH	None	0.203	1.010	0.001	11.6
	TWARM	0.152	0.879	0.001	9.6
	TWARM, RAD	0.099	0.589	0.001	6.8
	TWARM, RAD, Mg	0.057	0.365	0.010	4.3
	TWARM, RAD, Mg, PRECIP	0.060	0.395	0.009	4.7
	TWARM, RAD, Mg, PRECIP, SiO ₂	0.055	0.369	0.013	4.5
	TWARM, RAD, Mg, PRECIP, SiO ₂ , DEPTH	0.056	0.378	0.011	4.8
TWARM	None	0.161	0.668	0.001	9.2
	pH	0.110	0.636	0.001	7.1
	pH, RAD	0.099	0.589	0.001	6.8
	pH, RAD, Mg	0.095	0.609	0.001	6.9
	pH, RAD, Mg, PRECIP	0.085	0.559	0.001	6.5
	pH, RAD, Mg, PRECIP, SiO ₂	0.085	0.570	0.001	6.8
	pH, RAD, Mg, PRECIP, SiO ₂ , DEPTH	0.086	0.581	0.001	7.2
RAD	None	0.137	0.576	0.001	7.8
	pH	0.091	0.508	0.001	5.9
	pH, TWARM	0.080	0.476	0.001	5.6
	pH, TWARM, Mg	0.079	0.506	0.001	5.8
	pH, TWARM, Mg, PRECIP	0.084	0.553	0.001	6.5
	pH, TWARM, Mg, PRECIP, SiO ₂	0.085	0.570	0.001	6.8
	pH, TWARM, Mg, PRECIP, SiO ₂ , DEPTH	0.071	0.480	0.001	5.9
Mg	None	0.080	0.296	0.006	4.6
	pH	0.079	0.397	0.002	5.1
	pH, TWARM	0.078	0.500	0.002	5.4
	pH, TWARM, RAD	0.076	0.487	0.001	5.6
	pH, TWARM, RAD, PRECIP	0.063	0.414	0.004	4.9
	pH, TWARM, RAD, PRECIP, SiO ₂	0.055	0.369	0.007	4.5
	pH, TWARM, RAD, PRECIP, SiO ₂ , DEPTH	0.046	0.311	0.032	4.0
PRECIP	None	0.129	0.592	0.001	7.3
	pH	0.060	0.311	0.017	3.9
	pH, TWARM	0.052	0.301	0.029	3.6
	pH, TWARM, RAD	0.073	0.468	0.001	5.3
	pH, TWARM, RAD, Mg	0.060	0.395	0.004	4.7
	pH, TWARM, RAD, Mg, SiO ₂	0.062	0.416	0.002	5.1
	pH, TWARM, RAD, Mg, SiO ₂ , DEPTH	0.057	0.385	0.003	4.8
SiO ₂	None	0.100	0.417	0.001	5.7
	pH	0.071	0.353	0.003	4.6
	pH, TWARM	0.077	0.458	0.001	5.4
	pH, TWARM, RAD	0.069	0.416	0.001	5.1
	pH, TWARM, RAD, Mg	0.055	0.357	0.005	4.3
	pH, TWARM, RAD, Mg, PRECIP	0.057	0.383	0.004	4.7
	pH, TWARM, RAD, Mg, PRECIP, DEPTH	0.053	0.358	0.011	4.6

Table 3 continued

Environmental variable	Covariate(s)	λ_1	λ_1/λ_2	<i>P</i>	% Variance
DEPTH	None	0.089	0.335	0.001	5.1
	pH	0.085	0.455	0.001	5.5
	pH, TWARM	0.073	0.422	0.001	5.1
	pH, TWARM, RAD	0.056	0.335	0.010	4.1
	pH, TWARM, RAD, Mg	0.056	0.360	0.005	4.4
	pH, TWARM, RAD, Mg, PRECIP	0.050	0.446	0.016	4.1
	pH, TWARM, RAD, Mg, PRECIP, SiO ₂	0.046	0.311	0.025	4.0

Ordinations

CCAs were performed on the 49 non-rare, midge taxa, 21 remaining environmental parameters, and 47 lakes. Of the 21 environmental variables, seven accounted for a significant ($P \leq 0.05$) portion of the explainable variance. In order of explanatory power, these were pH (19.1%), TWARM (10.3%), RAD (7.5%), Mg²⁺ (7.1%), PRECIP (5.6%), SiO₂ (5.4%), and DEPTH (4.3%). All seven parameters retained their significance after testing with pCCAs (Table 3).

Combined, the first four axes of the reduced CCA (with only the seven significant explanatory variables) account for 30.3% of the variance in the species data (Table 4). All of the variables, except for DEPTH, are significantly correlated with the first ordination axis whereas only Mg²⁺ and SiO₂ are not correlated with the second. pH shows the strongest positive correlation with the first axis while both TWARM and DEPTH are strongly associated with the second (Table 4).

A biplot of the CCA sample scores shows a clear west-east dichotomy (Fig. 4a). In the majority of cases, lakes sampled west of Tyler's Line plot in the left quadrants while those east of the line plot in the right quadrants. Low elevation lakes (sites 1–5) plot in the upper, left quadrant, which is associated with warmer temperatures and coastal effects.

CCA species scores are indicative of taxa optima with respect to particular environmental variables (Fig. 4b). Warm-adapted taxa plot in the upper, left of the figure and are typical of low elevations (<600 m). Taxa plotting out in this quadrant of the figure and showing a significant relationship to temperature as indicated by the GLMs (Table 2) include *Kiefferulus martini*, *Parachironomus*,

Stempellina, *Tanytarsus* nr. *chinyensis*, Ceratopogonid type 2, and *Chaoborus*. Cold-adapted taxa occur on the opposite side of the figure in the lower, right quadrant. These taxa, as identified from the ordination plot and GLMs include *Botryocladus*, orthoclad type 4, *Parakiefferiella* type 1, *Paralimnophyes* type 2, and *Tanytarsus* type 4. Based on the ordination and GLMs, some taxa show preferences for deeper lakes, namely *Chironomus*, *Parochlus*, orthoclad type 2, and 'SO1'. Other taxa prefer acidic lakes, for instance *Cricotopus* 'parbicintus' and *Cladotanytarsus*, whereas *Parakiefferiella* type 2, *Paralimnophyes* type 1, *Polypedilum* type 1, and *Tanytarsus* types 1 and 5 all show a preference for more alkaline conditions.

Model development

Based on the final CCA ordination, TWARM explained the second largest amount of variance after pH. Both partial least squares (PLS) and weighted averaging partial least squares (WA-PLS) models were constructed for temperature. We selected the second component WA-PLS model (Fig. 5) as it was the most parsimonious, reducing the RMSEP by 8.4% and producing a strong r_{jack}^2 of 0.72, low AveBias_{jack} of -5.38×10^{-3} , low MaxBias_{jack} of 1.35, and low RMSEP of 0.94 (Table 5).

Beta (β) values generated by the model (Table 2) can be used as coefficients to construct temperature estimates. With the second component model, *Kiefferulus martini* has the highest coefficient (31.4) whereas *Tanytarsus* type 4 has the lowest (1.7). In general, β values are consistent with the CCA species scores and GLM results mentioned in the previous section.

Table 4 CCA summary including canonical coefficients, their associated *t*-values, and the interset correlations of the environmental variables with the ordination axes

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.242	0.147	0.081	0.061
Cum % var. spp.	13.8	22.2	26.9	30.3
Cum % var. spp.-env. relation	38.2	61.4	74.2	83.9
Regression/canonical coefficients				
<i>Variable</i>				
pH	0.308	0.490	-0.064	-0.512
TWARM	-0.676	0.873	-0.317	-0.568
RAD	0.677	1.164	1.194	-0.984
Mg	-0.392	0.125	0.323	-0.713
PRECIP	0.365	0.988	0.944	-1.479
SiO ₂	0.241	0.000	-0.313	-0.948
DEPTH	-0.114	-0.330	0.193	-0.235
<i>t</i> -values of regression coefficients				
<i>FR explained</i>				
	0.382	0.232	0.129	0.096
<i>Variable</i>				
pH	3.076*	3.105*	-0.331	-2.177*
TWARM	-6.295*	5.139*	-1.518	-2.248*
RAD	4.045*	4.404*	3.672*	-2.502*
Mg	-3.782*	0.760	1.604	-2.926*
PRECIP	2.231*	3.818*	2.967*	-3.841*
SiO ₂	3.236*	0.004	-2.168*	-5.424*
DEPTH	-1.788	-3.284*	1.563	-1.572
Inter-set correlation				
<i>Variable</i>				
pH	0.852	-0.015	-0.003	-0.047
TWARM	-0.575	0.523	-0.403	-0.026
RAD	0.527	0.487	0.229	0.166
Mg	-0.080	-0.228	0.733	-0.091
PRECIP	-0.595	-0.281	0.011	-0.254
SiO ₂	0.392	-0.072	-0.574	-0.407
DEPTH	-0.211	-0.522	0.046	-0.348

*Significant at $P \leq 0.05$ Cum % var. spp.,
Cumulative percent
variance of species data
Cum % var. spp.-env.
relation, Cumulative
percent variance of species-
environment relation

Discussion

Midge paleoecology in the Australasia region

The small number of transfer functions modeling midge temperature optima of Southern Hemisphere taxa makes it difficult to interpret results across studies. Before we can even compare subfossil chironomid remains from different regions of Australasia, paleoecologists need to develop a consensus on vouchered specimens. Survey and autecological data (e.g. Paterson and Walker 1974; Kokkin 1986) as well as identification guides (e.g. Cranston 2000; Cranston and Dimitriadis 2004) are available for

many regions of the Southern Hemisphere, however, there is a growing need for paleoecologists using fossil chironomids to make use of these resources and create robust, quantitative models in order to address local and regional climate hypotheses.

Although early inventories of chironomid taxa surveyed from Australian lake benthos reported low species richness (Fulton 1983a, b; Timms 1985), subsequent studies have shown richness in some Australian lakes to be comparable to lakes in the Northern Hemisphere (Wright and Cranston 2000; Cranston and Dimitriadis 2004). Wright and Burgin (2007) sampled 68 lakes dispersed between tropical northern Queensland, Fraser Island, south-eastern

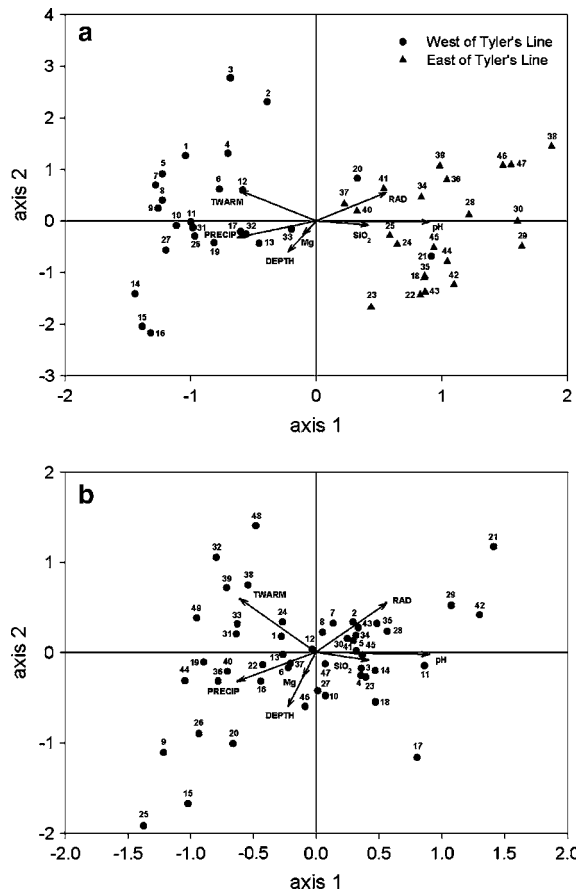


Fig. 4 Canonical correspondence analysis (CCA) of (a) sample scores for the 47 Tasmanian lakes where circles represent lakes west of Tyler's line and triangles represent lakes east of Tyler's line and (b) species scores. Both are plotted relative to the seven significant environmental variables. The numbers in the sample score plot correspond to Table 1 while the numbers in the species score plot correspond to Table 2

mainland Australia, and Tasmania and discovered more than double the number of taxa that had previously been reported in many early Australian studies. These authors used non-metric multidimensional scaling to evaluate the distribution of chironomid taxa and concluded that geographical location structured chironomid communities more strongly than geomorphic characteristics of lakes.

Within Tasmania, Wright and Burgin (2007) identified 57 species of chironomids based on pupal exuviae from 20 glacially-derived lakes and five dune lakes. At the generic level, the majority of the taxa are consistent with those identified in this study. We identified nine other genera not found in Wright and

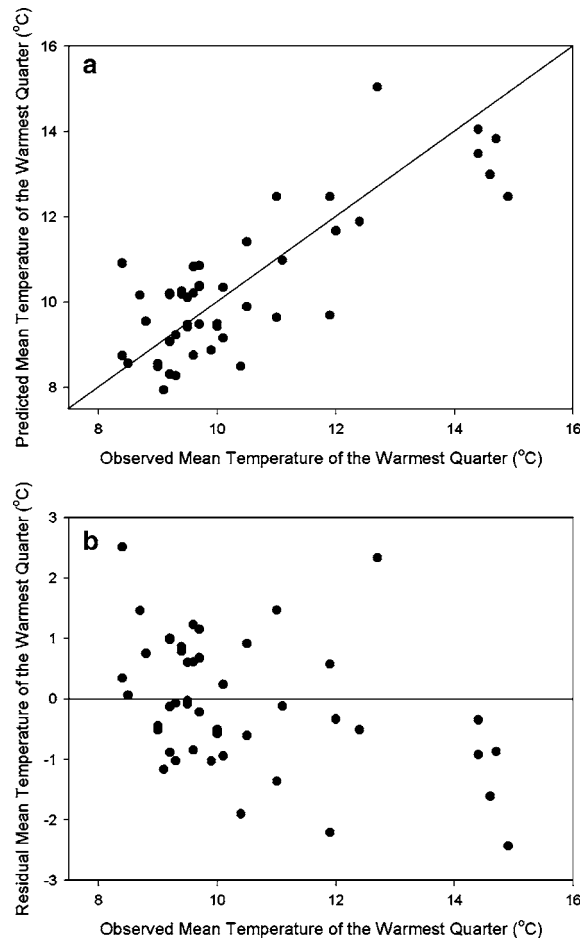


Fig. 5 Performance of second component WA-PLS model where (a) illustrates the predicted versus observed mean temperature of the warmest quarter and (b) illustrates residuals of the predicted versus observed mean temperature of the warmest quarter

Burgin's survey while they identified four not found in ours. Furthermore, working with pupal exuviae, Wright and Burgin obtained many more species-level identifications (compare Wright and Burgin 2007: Table 2 to our Table 2).

Geographic location appeared to be more important than geophysical lake characteristics with respect to structuring chironomid communities (Wright and Burgin 2007). Although this may be the case at their large, semi-continental scale, our data indicate that, at the state level, Tasmania's chironomid communities are structured most strongly by pH. Older, siliceous, rocks of western Tasmania are mantled by peat-forming rainforests and sedgeland, creating dystrophic lakes relative to those situated on the younger,

Table 5 Performance of PLS and WA-PLS models for reconstructing mean temperature of the warmest quarter. The bold indicates the model of choice

Model		Apparent				Jack-knifed				% Reduced
		r^2	Ave Bias	Max Bias	RMSE	r^2	Ave Bias	Max bias	RMSEP	
PLS	Component 1	0.62	1.51×10^{-15}	2.03	1.09	0.47	1.45×10^{-3}	2.66	1.29	
	Component 2	0.77	1.47×10^{-15}	0.86	0.84	0.56	-1.40×10^{-2}	1.63	1.18	8.7
	Component 3	0.84	1.32×10^{-15}	0.66	0.72	0.58	5.06×10^{-4}	1.52	1.15	2.6
	Component 4	0.87	1.40×10^{-15}	0.58	0.64	0.59	8.93×10^{-3}	1.46	1.15	-0.4
	Component 5	0.89	1.32×10^{-15}	0.50	0.59	0.56	8.98×10^{-3}	1.44	1.20	-4.0
WA-PLS	Component 1	0.78	1.70×10^{-2}	1.16	0.82	0.66	3.92×10^{-3}	1.92	1.02	
	Component 2	0.87	3.17×10^{-3}	1.29	0.64	0.72	-5.38×10^{-3}	1.35	0.94	8.4
	Component 3	0.90	-1.27×10^{-4}	0.62	0.57	0.69	9.42×10^{-3}	1.21	0.99	-4.3
	Component 4	0.92	8.34×10^{-3}	0.47	0.49	0.65	5.09×10^{-2}	1.24	1.07	-9.7
	Component 5	0.93	-4.09×10^{-4}	0.36	0.45	0.60	5.00×10^{-2}	1.36	1.16	-7.7

nutrient-rich rock types of the east. Further, the precipitation gradient, driven by the Roaring Forties in conjunction with Tasmania's orography, coincides with the geologic divide. Both factors combine to have a profound influence on Tasmania's flora and fauna, creating two distinct lake districts separated by the 146th meridian (Tyler 1992).

At Lake Barrine in northern tropical Queensland, Dimitriadis and Cranston (2001) identified 35 taxa based on pupal exuviae and larval head capsules. Because they used pupal exuviae (which allows for greater taxonomic resolution), MCR techniques, and surveyed a tropical lake, their results differed from ours. Of the taxa common to both studies at the generic level, Dimitriadis and Cranston (2001) found *Cladotanytarsus bilinearis*, *Tanytarsus richardsi*, *Dicrotendipes flexus*, and *Polypedilum convexum* to have warm MCRs whereas *Riethia* sp., *Procladius squamifer*, *Polypedilum kathleenae*, and *Stempellina australiensis* had relatively cold MCRs. A noticeable difference in our study is that *Cladotanytarsus* reconstructs with a relatively cool β coefficient (Table 2). In our calibration set, *Cladotanytarsus* (unidentified to species) is restricted to higher elevations. However, *Cladotanytarsus* is known to be a speciose taxon, inhabiting many ecological niches (Dimitriadis and Cranston 2007). The *Cladotanytarsus* morphotype identified here is more than likely a different species from *Cladotanytarsus bilinearis* identified at Lake Barrine. Dimitriadis and Cranston (2001) also indicate that *Riethia* sp. and *Stempellina*

australiensis are cold stenotherms requiring high oxygen concentrations. In our study, *Riethia* is assigned a relatively cool β coefficient (9.4) whereas *Stempellina* is here defined as a warm-adapted taxon. *Stempellina* requires coarse, grainy materials, like sand, to construct its casings. Since the dune lakes in this data set are effectively the warm analogues, *Stempellina* is assigned a warm β coefficient. However, as we can see from Fig. 3, *Stempellina* also occurs at higher elevations where it is likely responding to substrate rather than temperature.

Across the Tasman Sea in New Zealand, Woodward and Shulmeister (2006) identified *Cladopelma curtivalva*, *Cricotopus zealandicus*, *Cricotopus aucklandensis*, and *Polypedilum* as typical of warmer sites. At the generic level, all of these taxa differ from Tasmanian equivalents, which prefer intermediate to cool temperatures. Woodward and Shulmeister (2006) also identify *Chironomus*, *Tanytarsus funebris*, *Tanytarsus vespertinus*, and the Macropelopini tribe as taxa dominating high-altitude communities, although these taxa are also abundant at lower elevations. The same is true regarding the distribution of these taxa, at the generic level, in Tasmania (note that *T. funebris* and *T. vespertinus* are not present in Tasmania). Of the taxa common to our training set, at the generic level, Dieffenbacher-Krall et al. (2007) found *Chironomus*, *Cladopelma*, *Kiefferulus*, *Parachironomus*, *Polypedilum*, *Cricotopus aucklandensis* (which is restricted to New Zealand), and many types of *Tanytarsus* spp. to be significantly related to temperature; only

Kiefferulus martini, *Parachironomus*, and *Tanytarsus* type 4 are significantly related to temperature in Tasmania.

Woodward and Shulmeister (2006) found *Chironomus* to be abundant at both high-altitude, cool, oligotrophic lakes and low-altitude, warm, eutrophic lakes. Consequently, *Chironomus* reconstructs with an intermediate β coefficient of 12.3°C, under-predicting warm temperatures of lowland lakes and over-predicting cool temperatures of high-altitude lakes. This becomes a problem when *Chironomus* is present in high abundance as in the paleoclimate reconstruction of Lyndon Stream (Woodward and Shulmeister 2007). In Australia, adult morphology (Freeman 1961) and cytological variation (Martin 1979) reveal that *Chironomus* is a genus comprised of many species that cannot readily be distinguished morphologically as larvae. Although *Chironomus* is not significantly related to temperature in Tasmania, it is clearly most commonly found and most abundant at cooler, high-elevation lakes and has a β coefficient of 8.5°C (Table 2).

It is important to note that many New Zealand species are endemic as are some genera (e.g. *Hevelius*, *Kaniwhaniwhanus*, and *Naonella*) and so are not found in Tasmania. There is little endemism in the chironomid fauna of Tasmania at our level of taxonomic resolution. However, at the species level, Wright and Burgin (2007) found Tasmania to have the highest degree of endemism with respect to all four areas surveyed in Australia.

Modeling

The chironomid distributions of the 47 Tasmanian lakes surveyed in this study were strongly influenced by pH, TWARM, RAD, Mg^{2+} , PRECIP, SiO_2 , and DEPTH. Our results indicate that midges are an appropriate tool for modeling the temperature history of Tasmania. Although the r_{jack}^2 of our temperature transfer function is lower than that produced by some other models (e.g. Barley et al. 2006; Lotter et al. 1999; Walker et al. 1997), the AveBias_{jack}, Max-Bias_{jack}, and RSMEP (Table 5) compare well with other studies. Our lower r_{jack}^2 may be the result of a relatively short temperature gradient, which inherently produces lower r_{jack}^2 values (Larocque et al. 2001: Table 6).

Nevertheless, all models must be interpreted with caution. Errors created by the transfer function approach are partly an artifact of the statistical methods and do not necessarily incorporate errors associated with the data. Since inverse deshinking is implicit to weighted averaging, there is always a tendency to pull predicted values towards the mean of the training set, inevitably leading to overestimation of low and underestimation of high observed temperatures (ter Braak and Juggins 1993). In short, no matter the data entered, the model will still generate results. Therefore, it is important to interpret with scrutiny and test applications of transfer functions with historical data, analogue matching, multiproxy evidence, and knowledge of the autecology of taxa.

Future directions

Tasmania is a temperate region moderated by a maritime climate. Due to climate, geologic, and vegetation gradients, it may seem difficult to disentangle redundant variables. Furthermore, low to mid elevation sites (300–700 m) are not well represented in our model. The few potential sites within this elevation range are typically located on farms and pasturelands, sites to avoid due to anthropogenic influences. Despite these complications, we have produced a strong model. Observed temperatures from sample sites are significantly correlated with temperatures predicted from 1,000 jack-knifed cycles. However, the model could be improved by adding sites to both increase the gradient length as well as fill in the gap between 300 and 700 m (~12–14°C).

The next step is to apply this transfer function to a long-core record. Our goal is to compare the qualitative pollen-based climate inferences of Colhoun et al. (1999) from Lake Selina, Tasmania, to quantitative midge-inferred temperatures; the reconstruction extends back to the previous interglacial. The pollen record shows close correlation with the Vostok ice core from Antarctica, indicating that Tasmania may be recording climate change at a hemispheric scale. With our model, we will be able to determine quantitative temperature estimates for this long record and attempt to answer some of the questions posed in the introduction.

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References

- Alloway BV, Lowe DJ, Barrell DJA, Newnham RM, Almond PC, Augustinus PC, Bertler N, Carter L, Litchfield NJ, McGlone MS, Shulmeister J, Vandergoes MJ, Williams PW, NZ-INTIMATE Members (2007) Towards a climate event stratigraphy for New Zealand over the past 30 000 years (NZ-INTIMATE project). *J Quat Sci* 22:9–35. doi:10.1002/jqs.1079
- Armitage P, Cranston PS, Pinder LCV (eds) (1995) *The Chironomidae: the biology and ecology of non-biting midges*. Chapman and Hall, London, 572 pp
- Barley EM, Walker IR, Kurek J, Cwynar LC, Mathewes RW, Gajewski K et al (2006) A northwest North American training set: distribution of freshwater midges in relation to air temperature and lake depth. *J Paleolimnol* 36:295–314. doi:10.1007/s10933-006-0014-6
- Birks HJB (1998) Numerical tools in paleolimnology progress, potentialities, and problems. *J Paleolimnol* 20:307–332. doi:10.1023/A:1008038808690
- Birks HJB (2003) Quantitative palaeoenvironmental reconstructions from Holocene biological data. In: Mackay A, Battarbee R, Birks HJB, Oldfield F (eds) *Global change in the holocene*. Oxford University Press, New York, pp 107–123
- Birks HJB, Line JM (1992) The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *Holocene* 2:1–10
- Boubée JAP (1983) Past and present benthic fauna of Lake Maratoto, with special reference to the Chironomidae. Ph.D. thesis, University of Waikato, New Zealand, 151 pp
- Brooks SJ, Birks HJB (2001) Chironomid-inferred air temperatures from lateglacial and Holocene sites in northwest Europe: progress and problems. *Quat Sci Rev* 20:1723–1741. doi:10.1016/S0277-3791(01)00038-5
- Busby JR (1986) *Bioclimatic prediction system (BIOCLIM) user's manual version 2.0*. Australian Biological Resources Study Leaflet
- Busby JR (1991) *BIOCLIM: a bioclimatic analysis and prediction system*. In: Margules CR, Austin MP (eds) *Nature conservation: cost effective biological surveys and data analysis*. CSIRO, Melbourne, pp 64–68
- Clapperton CM (1990) Quaternary glaciations in the Southern Hemisphere: an overview. *Quat Sci Rev* 9:299–304. doi:10.1016/0277-3791(90)90024-5
- Colhoun EA (1985) Glaciations of the west coast range, Tasmania. *Quat Res* 24:39–59. doi:10.1016/0033-5894(85)90082-1
- Colhoun EA, Shulmeister J (2006) Late Pleistocene of the south west Pacific region. In: Elias S (ed) *Encyclopedia of quaternary science*. Elsevier, pp 1066–1075
- Colhoun EA, Pola JS, Barton CE, Heijnis H (1999) Late Pleistocene vegetation and climate history of Lake Selina, western Tasmania. *Quat Int* 57/58:5–23. doi:10.1016/S1040-6182(98)00046-9
- Cranston PS (2000) Electronic guide to the chironomidae of Australia. <http://www.science.uts.edu.au/sasb/chiropage/>
- Cranston PS, Dimitriadis S (2004) *The Chironomidae (Diptera) larvae of Atherton Tableland Lakes, north Queensland*. *Mem Queensl Mus* 49:573–588
- Dean WE Jr (1974) Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *J Sediment Petrol* 44:242–248
- Deevey ES (1955) Paleolimnology of the upper swamp deposit, Pyramid Valley. *Rec Canterb Mus* 6:291–344
- Dieffenbacher-Krall AC, Vandergoes MJ, Denton GH (2007) An inference model for mean summer air temperatures in the Southern Alps, New Zealand, using subfossil chironomids. *Quat Sci Rev* 26:2487–2504. doi:10.1016/j.quascirev.2007.06.016
- Dimitriadis S, Cranston PS (2001) An Australian Holocene climate reconstruction using Chironomidae from a tropical volcanic maar lake. *Palaeogeogr Palaeoclimatol Palaeoecol* 176:109–131. doi:10.1016/S0031-0182(01)00331-5
- Dimitriadis S, Cranston PS (2007) From the mountains to the sea: assemblage structure and dynamics in Chironomidae (Insect:Diptera) in the Clyde River estuarine gradient, New South Wales, south-eastern Australia. *Aust J Entomol* 46:188–197. doi:10.1111/j.1440-6055.2007.00592.x
- Elias SA (1997) The mutual climatic range method of palaeoclimate reconstruction based on insect fossils: new applications and interhemispheric comparisons. *Quat Sci Rev* 16:1217–1225. doi:10.1016/S0277-3791(97)00029-2
- Freeman P (1961) *The Chironomidae (Diptera) of Australia*. *Aust J Zool* 9:611–737. doi:10.1071/ZO9610611
- Fulton W (1983a) Macrobenthic fauna of Great Lake, Arthurs Lake and Lake Sorell, Tasmania. *Aust J Mar Freshw Res* 34:775–785. doi:10.1071/MF9830775
- Fulton W (1983b) Qualitative and quantitative variation in the macrobenthic fauna of the original lake and new lake areas of Great Lake and Arthurs Lake, Tasmania. *Aust J Mar Freshw Res* 34:786–803
- Glew J (1991) Miniature gravity corer for recovering short sediment cores. *J Paleolimnol* 5:285–287. doi:10.1007/BF00200351
- Harrison SP (1993) Late Quaternary lake-level changes and climates of Australia. *Quat Sci Rev* 12:211–231. doi:10.1016/0277-3791(93)90078-Z
- Heiri O, Lotter AF (2001) Effect of low count sums on quantitative environmental reconstructions: an example using subfossil chironomids. *J Paleolimnol* 26:343–350. doi:10.1023/A:1017568913302
- Houlder DJ, Hutchinson MF, Nix HA, McMahon JP (2000) *ANUCLIM user guide, version 5.1*. Centre for Resource

- and Environmental Studies, Australian National University, Canberra
- Jackson WD (2005) The Tasmanian environment. In: Reid JB, Hill RS, Brown MJ, Hovenden MJ (eds) *Vegetation of Tasmania*. Australian Biological Resources Study, Tasmania, pp 11–34
- Juggins S (2003) C2 software for ecological and paleoecological data analysis and visualisation. User guide version 1.4. University of Newcastle
- Kershaw AP, Nanson GC (1993) The last full glacial cycle in the Australian region. *Glob Planet Change* 7:1–9. doi:[10.1016/0921-8181\(93\)90036-N](https://doi.org/10.1016/0921-8181(93)90036-N)
- Kim N, Han JK (1997) Assessing the integrity of cross-validation: a case for small sample-based research. Hong Kong University of Science and Technology, Department of Marketing, Working Paper Series no. MKTG 97.096
- Kokkin M (1986) Identification of two Australian salt-lake chironomid species from subfossil larval head capsules. *Palaeogeogr Palaeoclimatol Palaeoecol* 54:317–328. doi:[10.1016/0031-0182\(86\)90131-8](https://doi.org/10.1016/0031-0182(86)90131-8)
- Larocque I, Hall RI, Grahn E (2001) Chironomids as indicators of climate change: a 100-lake training set from a sub-arctic region of northern Sweden (Lapland). *J Paleolimnol* 26:307–322. doi:[10.1023/A:1017524101783](https://doi.org/10.1023/A:1017524101783)
- Little JL, Smol JP (2001) A chironomid-based model for inferring late-summer hypolimnetic oxygen in southeastern Ontario lakes. *J Paleolimnol* 26:259–270. doi:[10.1023/A:1017562703986](https://doi.org/10.1023/A:1017562703986)
- Livingstone DM, Lotter AF, Walker IR (1999) The decrease in summer surface water temperature with altitude in Swiss alpine lakes: a comparison with air temperature lapse rates. *Arct Antarct Alp Res* 31:341–352. doi:[10.2307/1552583](https://doi.org/10.2307/1552583)
- Lotter AF, Walker IR, Brooks SJ, Hofmann W (1999) An intercontinental comparison of chironomid paleotemperature inference models: Europe vs. North America. *Quat Sci Rev* 18:717–735. doi:[10.1016/S0277-3791\(98\)00044-4](https://doi.org/10.1016/S0277-3791(98)00044-4)
- Macphail MK (1978) Vegetation and climates in southern Tasmania since the Last Glaciation. *Quat Res* 11:306–341. doi:[10.1016/0033-5894\(79\)90078-4](https://doi.org/10.1016/0033-5894(79)90078-4)
- Martin J (1979) Chromosomes as tools in taxonomy and phylogeny of Chironomidae (Diptera). *Entomol Scan Suppl* 10:67–74
- Massaferro J, Brooks SJ (2002) Response of chironomids to Late Quaternary environmental change in Taitao Peninsula, southern Chile. *J Quat Sci* 17:101–111. doi:[10.1002/jqs.671](https://doi.org/10.1002/jqs.671)
- Massaferro J, Brooks SJ, Haberle SG (2005) The dynamics of chironomid assemblages and vegetation during the Late Quaternary at Laguna Facil, Chonos Archipelago, southern Chile. *Quat Sci Rev* 24:2510–2522. doi:[10.1016/j.quascirev.2005.03.010](https://doi.org/10.1016/j.quascirev.2005.03.010)
- Mees F, Verschuren D, Nijs R, Dumont HJ (1991) Holocene evolution of the crater lake at Malha, Northwest Sudan. *J Paleolimnol* 5:227–253. doi:[10.1007/BF00200347](https://doi.org/10.1007/BF00200347)
- Oliver DR, Roussel ME (1983) The insects and arachnids of Canada, part 11: the genera of larval midges of Canada, Diptera: Chironomidae. Research Branch, Agriculture Canada, Ottawa
- Paterson CG, Walker KF (1974) Recent history of *Tanytarsus barbitarsus* Freeman (Diptera: Chironomidae) in the sediments of a shallow saline lake. *Aust J Mar Freshw Res* 25:315–325. doi:[10.1071/MF9740315](https://doi.org/10.1071/MF9740315)
- Quinlan R, Smol JP (2001) Setting minimum head capsule abundance and taxa deletion criteria in chironomid-based inference models. *J Paleolimnol* 26:327–342. doi:[10.1023/A:1017546821591](https://doi.org/10.1023/A:1017546821591)
- Schakau BL (1986) Preliminary study of the development of the subfossil chironomid fauna (Diptera) of Lake Taylor, South Island, New Zealand, during the younger Holocene. *Hydrobiologia* 143:287–291. doi:[10.1007/BF00026672](https://doi.org/10.1007/BF00026672)
- Shiel RJ, Koste W, Tan LW (1989) Tasmania revisited: rotifer communities and habitat heterogeneity. *Hydrobiologia* 186/187:239–245. doi:[10.1007/BF00048919](https://doi.org/10.1007/BF00048919)
- ter Braak CJF, Juggins S (1993) Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. *Hydrobiologia* 269/270:485–502. doi:[10.1007/BF00028046](https://doi.org/10.1007/BF00028046)
- ter Braak CJF, Šmilauer P (2002) CANOCO version 4.5. Biometris-Plant Research International, Wageningen
- Timms BV (1985) The structure of macrobenthic communities of Australian lakes. *Proc Ecol Soc Aust* 14:51–59
- Turney CSM, Haberle S, Fink D, Kershaw AP, Barbetti M, Barrows MTT et al (2006) Integration of ice-core, marine and terrestrial records for the Australian Last Glacial Maximum and Termination: a contribution from the OZ INTIMATE group. *J Quat Sci* 21:751–761. doi:[10.1002/jqs.1073](https://doi.org/10.1002/jqs.1073)
- Tyler PA (1992) A lakeland from the dreamtime: the second founder's lecture. *Br Phycol J* 27:353–368. doi:[10.1080/00071619200650301](https://doi.org/10.1080/00071619200650301)
- Verschuren D, Eggermont H (2006) Quaternary paleoecology of aquatic Diptera in tropical and Southern Hemisphere regions, with special reference to the Chironomidae. *Quat Sci Rev* 25:1926–1947. doi:[10.1016/j.quascirev.2006.01.008](https://doi.org/10.1016/j.quascirev.2006.01.008)
- Walker IR, Smol JP, Engstrom DR, Birks HJB (1991) An assessment of Chironomidae as quantitative indicators of past climatic change. *Can J Fish Aquat Sci* 48:975–987. doi:[10.1139/f91-104](https://doi.org/10.1139/f91-104)
- Walker IR, Levesque AJ, Cwynar LC, Lotter AF (1997) An expanded surface-water palaeotemperature inference model for use with fossil midges from eastern Canada. *J Paleolimnol* 18:165–178. doi:[10.1023/A:1007997602935](https://doi.org/10.1023/A:1007997602935)
- Ward JV, Stanford JA (1982) Thermal responses in the evolutionary ecology of aquatic insects. *Annu Rev Entomol* 27:97–117. doi:[10.1146/annurev.en.27.010182.000525](https://doi.org/10.1146/annurev.en.27.010182.000525)
- Wiederholm T (1983) Chironomidae of the holarctic region. Keys and diagnoses. Part 1. Larvae. *Entomol Scand Suppl* 19:457 pp
- Woodward CA, Shulmeister J (2006) New Zealand chironomids as proxies for human-induced and natural environmental change: transfer functions for temperature and lake production (chlorophyll *a*). *J Paleolimnol* 36:407–429. doi:[10.1007/s10933-006-9009-6](https://doi.org/10.1007/s10933-006-9009-6)
- Woodward CA, Shulmeister J (2007) Chironomid-based reconstructions of summer air temperature from lake deposits in Lyndon Stream, New Zealand spanning the MIS 3/2 transition. *Quat Sci Rev* 26:142–154. doi:[10.1016/j.quascirev.2006.06.004](https://doi.org/10.1016/j.quascirev.2006.06.004)

Wright IA, Burgin S (2007) Species richness and distribution of eastern Australian lake chironomids and chaoborids. *Freshw Biol* 52:2354–2368. doi:[10.1111/j.1365-2427.2007.01853.x](https://doi.org/10.1111/j.1365-2427.2007.01853.x)

Wright IA, Cranston PS (2000) Are Australian lakes different? Chironomid and chaoborid exuviae from Lake McKenzie,

a coastal temperate dune lake. *Int Ver Theor Angew Limnol Verh* 27:303–308

Zar JH (1999) *Biostatistical analysis*. Prentice Hall, Upper Saddle River, New Jersey, 931 pp