

## An expanded surface-water palaeotemperature inference model for use with fossil midges from eastern Canada

Ian R. Walker<sup>1,2,4</sup>, André J. Levesque<sup>1,2,3</sup>, Les C. Cwynar<sup>3</sup> & André F. Lotter<sup>4</sup>

<sup>1</sup>*Okanagan Institute for Freshwater Studies, and Department of Biology, North Kelowna Campus, Okanagan University College, 3333 College Way, Kelowna, British Columbia, Canada V1V 1V7*

<sup>2</sup>*Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6*

<sup>3</sup>*Department of Biology, University of New Brunswick, Bag Service No. 45111, Fredericton, New Brunswick, Canada E3B 6E1*

<sup>4</sup>*Geobotanisches Institut der Universität Bern, Altenbergrain 21, CH-3013 Bern, Switzerland*

Received 20 May 1996; accepted 26 October 1996

**Key words:** Ceratopogonidae, Chironomidae, *Chaoborus*, weighted averaging, weighted averaging partial least squares, temperature optima, error estimates, palaeoclimate, late-glacial, Younger Dryas

### Abstract

Using an expanded surface sample data set, representing lakes distributed across a transect from southernmost Canada to the Canadian High Arctic, a revised midge-palaeotemperature inference model was developed for eastern Canada. Modelling trials with weighted averaging (with classical and inverse deshrinking; with and without tolerance downweighting) and weighted averaging partial least squares (WA-PLS) regression, with and without square-root transformation of the species data, were used to identify the best model. Comparison of measured and predicted temperatures revealed that a 2 component WA-PLS model for square-root transformed percentage species data provided the model with the highest explained variance ( $r_{jack}^2=0.88$ ) and the lowest error estimate ( $RMSEP_{jack}=2.26\text{ }^{\circ}\text{C}$ ).

Comparison of temperature inferences based on the new and old models indicates that the original model may have seriously under-estimated the magnitude of late-glacial temperature oscillations in Atlantic Canada. The new inferences suggest that summer surface water temperatures in Splan Pond, New Brunswick were approximately 10 to 12 °C immediately following deglaciation and during the Younger Dryas. During the Allerød and early Holocene, surface water temperatures of 20 to 24 °C were attained. The new model thus provides the basis for more accurate palaeotemperature reconstructions throughout easternmost Canada.

### Introduction

Fossil midges are being used more frequently in recent palaeolimnological research. Much of this increased use can be attributed to the simultaneous development of quantitative means for inferring palaeotemperatures and palaeosalinities from these insects (Walker et al., 1991a; Walker et al., 1995; Wilson et al., 1993). Fossil midges have proven especially useful as means for recognizing past climatic oscillations, including the Killarney Oscillation and Younger Dryas cold events (Walker et al., 1991b; Levesque et al., 1993a, 1993b, 1994, 1996, in press; Wilson et al., 1993; Cwynar &

Levesque, 1995; Levesque, 1995). In these studies, chironomid faunal assemblages have provided clear, consistent evidence of late-glacial climatic events in Atlantic Canada. They could, however, also be used to reconstruct Holocene climatic fluctuations throughout the region.

The original palaeotemperature inference model was developed by Walker et al. (1991a), and was based on a limited surface sample data set derived from Labrador and adjacent Québec. However, surface samples from New Brunswick, Nova Scotia, and the Northwest Territories were later incorporated into the database and revised models, including those used

*Table 1.* Geographic co-ordinates, depths, and summer surface water temperatures for the study lakes used in developing the current midge-temperature inference model. Samples from lakes L23, L24, L29, L32, L48, L49, L52, L53, L68 and Immerk Lake contained fewer than 50 identifiable head capsules and were not used in the statistical analyses

Lake	Latitude	Longitude	Max. depth (m)	Area (ha)	Summer surface water temperature ( °C)
Immerk Lake	75 ° 41' N	84 ° 34' W	6.8	105	6.0**
Middle Beschel Lake	75 ° 39' N	84 ° 28' W	8.2	45	6.0**
Phalarope Lake	75 ° 39' N	84 ° 37' W	5.0	157	6.0**
Fish Lake	75 ° 39' N	84 ° 32' W	4.5	97	6.0**
Lake Instaar	62 ° 16' N	66 ° 16' W	10.0*	52	8.9
Lake Mercer	62 ° 16' N	66 ° 15' W	10.0*	38	9.0
Lake 46	57 ° 20' N	62 ° 48' W	23.0	73	9.0
Lake 68	57 ° 20' N	62 ° 55' W	9.0	59	12.0
Lake 45	57 ° 17' N	63 ° 08' W	24.0	54	10.2
Lake 48	57 ° 15' N	62 ° 46' W	15.0	103	11.1
Lake 43	57 ° 08' N	63 ° 05' W	50.0	173	7.6
Lake 49	56 ° 42' N	64 ° 09' W	14.0	86	9.8
Lake 50	56 ° 39' N	64 ° 32' W	9.0	57	9.8
Lake 52	56 ° 35' N	64 ° 30' W	11.0	84	10.0
Lake 53	56 ° 22' N	64 ° 15' W	9.0	86	11.0
Lake 54	56 ° 17' N	63 ° 57' W	3.0	114	10.0
Lake 56	56 ° 10' N	64 ° 25' W	6.0	57	11.1
Lake 36	55 ° 12' N	62 ° 44' W	3.0	59	12.0
Lake 35	55 ° 06' N	62 ° 44' W	17.0	68	11.0
Lake 64	55 ° 06' N	63 ° 07' W	13.0	57	11.1
Lake 61	54 ° 52' N	63 ° 15' W	7.0	76	12.0
Lake 58	54 ° 52' N	62 ° 44' W	4.0	97	11.9
Lake 42	54 ° 49' N	62 ° 23' W	5.0	189	11.8
Lake 41	54 ° 48' N	62 ° 21' W	14.0	100	12
Lake 32	54 ° 28' N	61 ° 12' W	27.0	78	13.8
Lake 29	54 ° 22' N	61 ° 09' W	14.0	78	12.8
Lake 34	54 ° 18' N	60 ° 53' W	26.0	162	13.2
Lake 28	54 ° 18' N	61 ° 08' W	3.0	165	13.5
Lake 23	53 ° 38' N	60 ° 41' W	24.0	59	11.5
Lake 22	53 ° 37' N	60 ° 45' W	14.0	70	12
Lake 24	53 ° 36' N	60 ° 37' W	11.0	65	12
Lake 10	52 ° 52' N	56 ° 52' W	2.0	130	18
Lake 14	52 ° 22' N	57 ° 43' W	1.0	84	17.1
Lake 20	52 ° 12' N	57 ° 33' W	1.0	130	18
Lake 16	52 ° 05' N	57 ° 50' W	8.0	135	15
Lake 17	52 ° 05' N	57 ° 52' W	6.0	54	15.2
Lake 2	51 ° 35' N	56 ° 45' W	5.0	4	14
Lake 3	51 ° 30' N	57 ° 14' W	23.0	105	12.4
Lake 1	51 ° 27' N	57 ° 12' W	14.0	59	14
Black Lake	46 ° 06' N	64 ° 22' W	6.0	18	24
Portey Pond	45 ° 51' N	64 ° 25' W	1.5	4	22
Leak Lake	45 ° 25' N	64 ° 21' W	14.2	16.5	24
Ritchie Lake	45 ° 25' N	65 ° 58' W	12.0	23	24
Long Lake	45 ° 19' N	66 ° 04' W	9.7	5	21.5
Joe Lake	46 ° 45' N	66 ° 40' W	1.75	4.0	25.2
Killarney Lake	46 ° 01' N	66 ° 38' W	9.8	10.5	27.0
Pine Ridge Pond	45 ° 34' N	67 ° 06' W	5.55	1.0	27.0
Splan Pond	45 ° 15' N	67 ° 20' W	10.6	4.0	25.6
Trout Lake	45 ° 05' N	68 ° 11' W	11.4	3	26.6
Minimum	45 ° 05' N	56 ° 45' W	1	1	6.0
Maximum	75 ° 41' N	84 ° 37' W	50	189	27.0
Mean	54 ° 52' N	64 ° 26' W	11.1	72.5	14.2

\* approximate.

\*\* beneath ice.

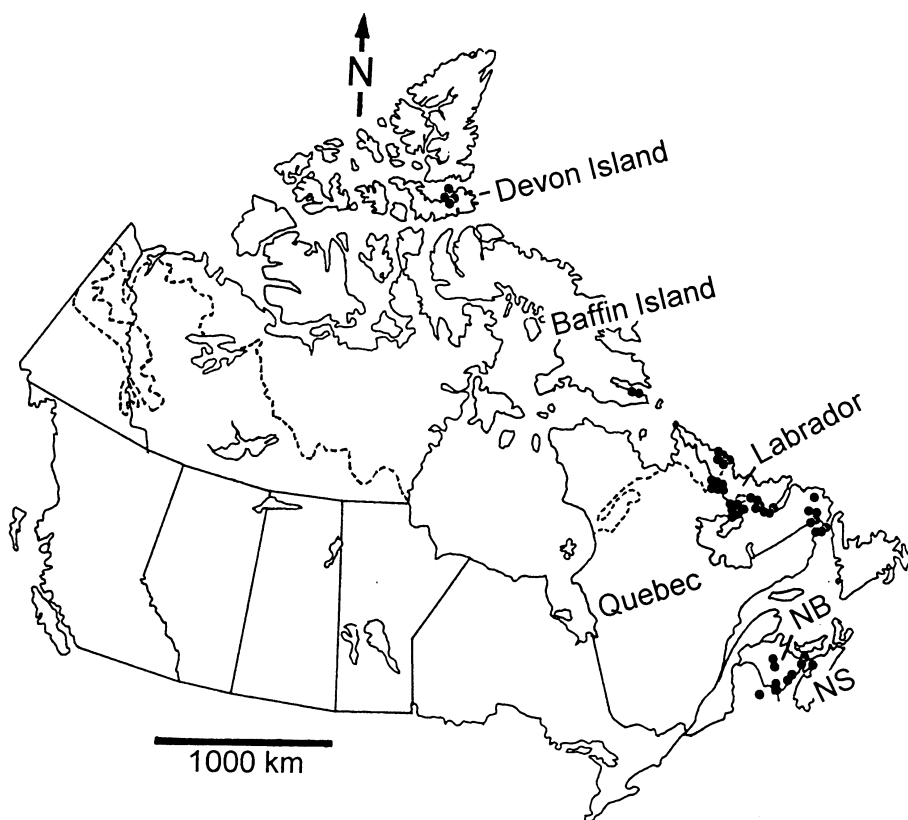


Figure 1. Map depicting the distribution of surface sample collection sites in eastern Canada. The approximate position of Arctic treeline is indicated by the dashed line. N indicates north. NB = New Brunswick, NS = Nova Scotia.

by Levesque et al. (1993a, 1993b, in press) and Wilson et al. (1993), were developed.

Recently, major advances have also been made in statistical methods relevant to Quaternary palaeoecological research (Birks, 1995). Thus, means now exist to obtain realistic error estimates via jackknifing and bootstrapping of the inference models (Birks et al., 1990; Line et al., 1994). Weighted averaging partial least squares regression (WA-PLS) provides another new modelling tool, which may further improve the predictive capabilities of chironomid palaeoecological research (ter Braak & Juggins, 1993; ter Braak et al., 1993). In this paper, we use these advances to develop an improved model for use in eastern Canada, and provide an assessment of errors associated with these temperature inferences.

## Methods

### *Chironomid analysis of surface sediments*

In its present form, the palaeotemperature inference model incorporates samples collected from a series of lakes, distributed from Devon Island, in the Canadian Arctic Archipelago, to Maine, and northern Nova Scotia in Atlantic Canada (Figure 1, Table 1). The samples were collected as a part of field work conducted independently by several palaeoecology research groups; thus, a variety of sampling gear was used.

Midge remains were isolated following a series of pretreatments, including deflocculation in warm 5% KOH, and sieving on a 93- to 95- $\mu\text{m}$  Nitex<sup>®</sup> mesh. Head capsules retained on the mesh were hand-sorted from a Bogorov counting tray at 50 $\times$  and mounted in Permount<sup>®</sup> or Entellan<sup>®</sup> on microscope slides. Identifications were made at 100 to 1000 $\times$ , with reference to available taxonomic literature, including especially Oliver & Roussel (1983), Walker (1988) and Wieder-

Table 2. Information pertaining to the percent abundance (minimum, maximum, and mean), number of occurrences, and Hill's N2 for each of the taxa included in the model

Taxa	All values...			Without zeroes...		Num Occ.	Hill's N2
	Min.	Max.	Mean	Min.	Mean		
<i>Paracladius</i>	0.0	29.5	1.61	1.83	15.7	4	2.5
<i>Pseudodiamesa</i>	0.0	7.1	0.52	0.92	4.0	5	3.9
<i>Eukiefferiella/Tvetenia</i>	0.0	8.6	0.45	0.48	4.4	4	2.5
<i>Oliveridia/Hydrobaenus</i>	0.0	4.5	0.23	0.50	2.2	4	2.7
<i>Parakiefferiella nigra</i>	0.0	5.5	0.49	0.92	3.2	6	4.8
<i>Abiskomyia</i>	0.0	14.0	1.05	2.61	8.2	5	3.6
<i>Mesocricotopus thienemanni</i>	0.0	4.6	0.42	0.30	1.7	10	5.7
<i>Sergentia</i>	0.0	31.9	3.33	0.26	6.8	19	9.1
<i>Stictochironomus</i>	0.0	7.1	0.80	0.14	2.4	13	6.7
<i>Heterotrissocladius</i>	0.0	66.1	15.34	1.84	18.1	33	17.2
<i>Protanypus</i>	0.0	4.3	0.76	0.15	1.4	21	13.6
<i>Cricotopus/Orthocladius</i>	0.0	7.3	1.45	0.44	2.3	25	16.6
<i>Corynoneura/Thienemanniella</i>	0.0	5.8	1.06	0.29	1.9	22	14.4
Subtribe Tanytarsina	9.2	60.8	38.86	9.24	38.9	39	35.6
Tribe Pentaneurini	0.0	17.4	3.42	0.24	4.9	27	15.3
<i>Microtendipes</i>	0.0	17.0	2.45	0.61	4.2	23	12.0
<i>Stempellina</i>	0.0	4.8	0.90	0.79	2.2	16	12.7
<i>Pagastiella</i>	0.0	5.2	0.71	0.32	2.0	14	9.0
<i>Psectrocladius</i>	0.0	38.7	6.26	0.60	8.1	30	14.2
<i>Procladius</i>	0.0	16.7	3.01	0.65	4.0	29	17.5
<i>Stempellinella/Zavrelia</i>	0.0	5.2	0.87	0.53	2.4	14	10.9
<i>Heterotanytarsus</i>	0.0	6.6	0.85	0.21	2.1	16	8.1
<i>Dicrotendipes</i>	0.0	14.0	2.97	0.79	4.8	24	15.2
Family Ceratopogonidae	0.0	3.0	0.25	1.02	1.9	5	4.2
<i>Cryptochironomus</i>	0.0	2.3	0.34	0.24	1.1	12	8.0
<i>Zalutschia</i>	0.0	18.5	2.13	0.29	4.9	17	7.1
<i>Cladopelma</i>	0.0	5.7	1.06	0.39	2.1	20	12.1
<i>Parakiefferiella</i> cf. <i>bathophila</i>	0.0	8.3	0.68	0.21	2.6	10	5.6
<i>Lauterborniella/Zavrelia</i>	0.0	2.9	0.36	0.73	1.6	9	7.6
<i>Polypedilum</i>	0.0	9.5	1.30	0.32	3.4	15	8.7
<i>Pseudochironomus</i>	0.0	4.7	0.43	0.29	1.9	9	6.2
<i>Tribelos</i>	0.0	14.1	0.78	0.15	3.0	10	3.2
<i>Chaoborus</i>	0.0	13.5	0.72	0.43	3.5	8	3.4
<i>Chironomus</i>	0.0	57.4	3.43	0.51	7.0	19	4.3

holm (1983). Identifications were normally made to the generic level. In instances where several genera could not be reliably distinguished, broader taxonomic categories have been used. For example, we were unable to reliably distinguish the genera *Cladotanytarsus*, *Micropsectra*, *Paratanytarsus*, and *Tanytarsus*; these genera are referred to collectively as subtribe Tanytarsina (Sæther, 1977). A collection of colour photographs has been prepared to document those taxa found, and to ensure taxonomic consistency in future work.

#### Statistical analysis

Several lakes and taxa were excluded prior to analysis. Samples were deleted if they contained fewer than 50 identifiable chironomid head capsules. All statistical analyses were based on either percentage data (expressed as a percentage of the total number of identifiable chironomid head capsules) or on square-root transformed percentage data. We included only those taxa that comprised greater than 2% of the fauna in at

Table 3. Table of optima and tolerances used in the WA models, and Beta values used in the 2 component WA-PLS models. Please note: Beta values are not to be interpreted as estimates of ecological optima

Taxa	WA				WA-PLS (2 components)	
	No transf.		Sqrt transf.		No transf.	Sqrt transf.
	Opt.	Tol.	Opt.	Tol.	Beta	Beta
<i>Paracladius</i>	6.3	1.2	6.8	1.6	−4.7	5.3
<i>Pseudodiamesa</i>	6.7	1.0	6.7	1.2	−6.5	2.0
<i>Eukiefferiella/ Tvetenia</i>	7.8	2.5	8.3	2.6	−1.2	5.3
<i>Oliveridia/ Hydrobaenus</i>	8.2	1.3	8.1	1.5	3.6	12.4
<i>Parakiefferiella nigra</i>	8.4	1.5	8.3	1.6	8.6	13.7
<i>Abiskomyia</i>	8.8	0.8	8.8	0.8	11.6	15.9
<i>Mesocricotopus thienemanni</i>	9.8	1.5	10.2	1.6	8.9	8.2
<i>Sergentia</i>	9.8	4.3	10.7	4.3	−7.3	−3.4
<i>Stictochironomus</i>	10.2	2.8	10.5	2.5	6.2	1.9
<i>Heterotrissocladius</i>	11.1	2.9	12.0	4.0	8.9	6.5
<i>Protanypus</i>	12.2	3.5	12.4	3.7	3.8	3.0
<i>Cricotopus/ Orthocladius</i>	12.5	5.7	13.5	6.1	5.9	7.0
<i>Corynoneura/ Thienemanniella</i>	14.3	6.6	14.3	6.3	16.4	12.5
Subtribe Tanytarsina	14.3	6.0	14.6	6.2	12.8	11.9
Tribe Pentaneurini	15.9	4.6	16.3	5.0	10.0	9.4
<i>Microtendipes</i>	16.5	4.7	16.9	5.3	15.9	14.1
<i>Stempellina</i>	16.8	5.3	16.8	5.3	23.1	16.5
<i>Pagastiella</i>	17.1	5.3	17.8	5.6	15.4	15.5
<i>Psectrocladius</i>	17.9	6.7	17.5	6.3	15.0	15.7
<i>Procladius</i>	18.1	5.6	17.6	5.8	22.2	16.8
<i>Stempellinella/Zavrelia</i>	18.3	5.8	17.6	5.7	25.4	17.2
<i>Heterotanytarsus</i>	18.8	4.5	18.4	5.0	27.6	20.8
<i>Dicrotendipes</i>	19.6	5.4	18.8	5.6	32.3	23.3
Family Ceratopogonidae	19.9	4.5	19.2	4.6	33.7	26.0
<i>Cryptochironomus</i>	20.4	5.5	20.6	5.5	30.9	29.7
<i>Zalutschia</i>	20.5	5.3	20.1	5.5	31.2	29.4
<i>Cladopelma</i>	21.1	5.8	20.3	5.9	40.4	30.7
<i>Parakiefferiella cf. bathophila</i>	22.3	3.5	22.0	4.5	47.7	40.7
<i>Lauterborniella/Zavreliella</i>	22.3	4.4	22.8	4.3	43.9	42.1
<i>Polypedilum</i>	23.3	4.0	22.3	4.8	51.8	40.5
<i>Pseudochironomus</i>	23.8	2.2	24.1	2.1	53.0	50.3
<i>Tribelos</i>	23.8	5.6	21.3	6.5	27.7	32.6
<i>Chaoborus</i>	24.4	3.4	24.1	4.0	45.6	48.1
<i>Chironomus</i>	24.7	5.3	21.6	6.5	31.0	35.9

least two of the 39 remaining lakes. Thus 20 rare taxa were excluded from our analyses.

Detrended canonical correspondence analysis (DCCA), implemented by the program CANOCO version 3.12 (ter Braak, 1987–1992) was used to assess the length of the temperature gradient in standard deviation units. The computer programs CALIBRATE version 0.61 (Juggins & ter Braak, unpubl.), WACALIB (Line et al. 1994), and WAPLS version 1.0 (Juggins & ter Braak, unpubl.) were used to develop calibra-

tion functions and for water palaeotemperature reconstruction. The calibration function was based on summer surface water temperatures measured during visits to the lakes at, or about, the time of sediment sampling. Temperature optima and tolerances were estimated as weighted averages and weighted standard deviations, respectively. Tolerance values were adjusted by dividing the weighted averaging tolerance by  $\sqrt{1 - (1/N2)}$ , where  $N2$  is Hill's (1973) diversity measure. Modelling trials using weighted averag-

## LATITUDINAL DISTRIBUTION OF MIDGES

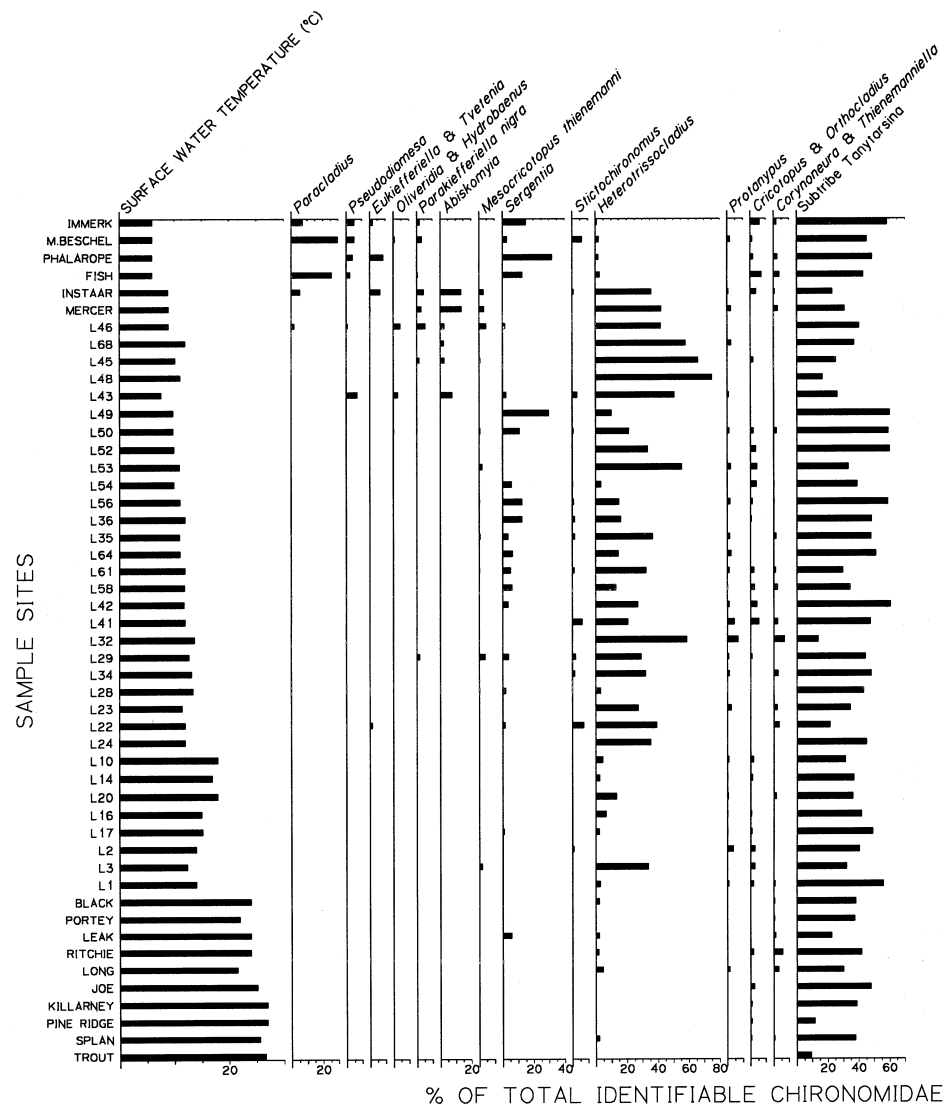


Figure 2. Distribution of those midges included in the model among lakes from Devon Island in the High Arctic (top of diagram) to southern Canada (bottom of diagram).

ing (with inverse and classical deshrinking, and with and without tolerance down-weighting) and weighted averaging partial least squares regression, with and without square-root transformation of the species data, were used to identify the best calibration function. The percentage data were transformed to square-roots (Prentice, 1980) as a means to optimize the 'signal' to 'noise' ratio in the data. The calibration equations derived from each trial were assessed via jack-knifed

and bootstrapped estimates of the root-mean-square-error of prediction (RMSEP), as well as the coefficient of determination ( $r^2$ ) between observed and predicted temperature values.



Descriptive statistics indicative of the relative abundance and frequency of occurrence of midge taxa used in the model are presented in Table 2. The temperature optima and tolerances for *Chaoborus*, Ceratopogonidae, and each of 32 different chironomid taxa are reported in Table 3. These values, together with the regression coefficients for the deshrinking equations (Table 4), provide the basis for inferring water

Estimated WA summer surface water temperature optima for the chironomid taxa range from 6.3 °C for *Paracladius* (a cold stenothermous taxon associated with arctic lakes, and the deep profundal habitats of large temperate lakes), to 24.7 °C for *Chironomus* (Table 3). Although much more abundant in temperate lakes, some *Chironomus* spp. are well known to occur even in high arctic ponds. The thermal range of

Table 4. Deshrinking regression coefficients used for calculating water palaeotemperatures with each of the WA models. For method of calculation, see Appendix 1

		Intercept (a)	Slope (b)
Untransformed data			
Classical deshrinking	WA	9.29	0.379
	WA(tol)	5.68	0.568
Inverse deshrinking	WA	-18.07	2.21
	WA(tol)	-6.83	1.54
Square-root transformed data			
Classical deshrinking	WA	9.89	0.368
	WA(tol)	6.07	0.571
Inverse deshrinking	WA	-19.22	2.22
	WA(tol)	-6.96	1.50

individual taxa is well illustrated by their distribution along the north–south transect (Figure 2).

A broad range of thermal tolerances was also observed, with taxa typical of high arctic lakes (e.g., *Paracadius*, *Pseudodiamesa*, and *Mesocricotopus*) occupying the narrowest thermal range (Table 3); thus, these taxa truly deserve the designation ‘cold-stenothermous’. In contrast, those taxa typical of lakes south of tree-line generally had much broader thermal tolerance. Nevertheless, some chironomids with high WA water temperature optima (e.g., *Pseudochironomus*) were also noted to have narrow thermal tolerances. Taxa with such narrowly defined temperature ranges are amongst the best temperature indicators; taxa with broad thermal tolerance and intermediate water temperature optima (e.g., subtribe Tanytarsina, *Corynoneura/Thienemanniella*, *Psectrocladius*) are least valuable for palaeotemperature inference.

The water temperature optima reflect similar trends to those revealed in stream studies by Rossaro (1992) and Lindegaard & Brodersen (1995); the Diamesinae and many Orthocladiinae are cold-stenothermous, whereas most Chironomini are restricted to relatively warm waters.

DCCA of the species data, with the first axis constrained to represent water temperature alone, revealed a gradient of 3.28 SD units. Modelling methods based on a unimodal response curve (as opposed to linear or monotonic responses) are recommended for such data (ter Braak, 1987; Birks, 1995). Thus, weighted-averaging (WA) and weighted averaging partial least squares (WA-PLS) regression provide appropriate means for modelling our data.

A variety of apparent, jack-knifed, and bootstrapped error statistics were obtained for the models (Table 5, 6). Error statistics based on cross-validation techniques (including both jackknifing and bootstrapping) provide more realistic means for assessing models than apparent error statistics (Birks, 1995). Consequently, we identified the best model on the basis of jack-knifed, rather than apparent, values of  $r^2$ , RMSEP, and bias. Bootstrapped statistics were available for the WA models (Table 5), but comparable information is not yet available for the WA-PLS models (Table 6).

WA-PLS using two components, and square-root transformed percentage species data, resulted in the highest  $r^2_{jack}$  (0.875), the lowest RMSEP<sub>jack</sub> (2.26 °C), and the lowest average and maximum bias<sub>jack</sub> (Tables 5, 6). This model therefore was considered superior to all other models. Figure 3 provides a comparison of the WA-PLS estimated and predicted water temperatures with our measured water temperatures, illustrating the fit of the model to our data.

To illustrate the differences between our new model and earlier models, we have used each model to recalculate late-glacial temperatures for Splan Pond in Atlantic Canada (Figure 4). The new WA-PLS model suggests much larger temperature oscillations during the late-glacial at Splan Pond than inferred by Walker et al. (1991b). For example, the original model had inferred a water temperature change of only 2 °C at the end of the Younger Dryas, from 12 °C to 14 °C (Figure 4a). Wilson et al. (1993) had later inferred a change of about 5 °C (Figure 4b). The model used by Levesque et al. (in press), and the new WA-PLS model (Figure 4c, 4d), infer a change of about 8 °C. The new WA-PLS model also suggests that the temperature change at the onset of the Younger Dryas may have been more gradual. Levesque (1995) has recently performed high resolution chironomid analyses on a second core from Splan Pond. His new data (Figure 4e, 4f) suggest that the temperature change was perhaps even larger (approximately 10 °C). Although the water temperature changes inferred by Walker et al. (1991b) might be regarded as being the result of minor climatic phenomena, the inferences obtained with our new model suggest very large and sudden shifts in late-glacial climate, between arctic and temperate thermal regimes.

It is interesting to note that Levesque’s (1995) core data produces inferred temperatures that are as much as 5 °C cooler than those inferred using Walker et al.’s (1991b) data. The differences in inferred temperatures between corresponding data points are not significant.



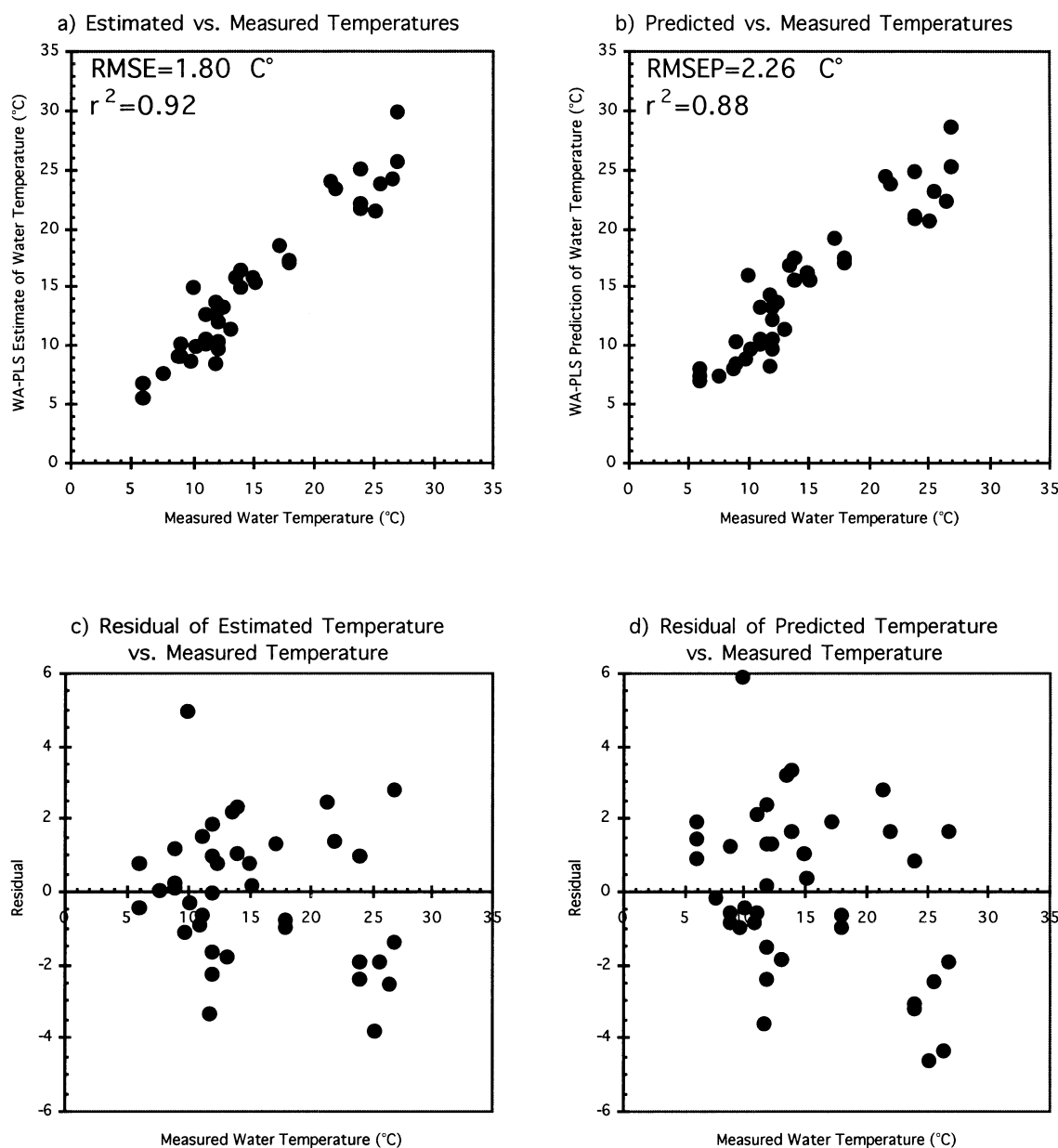


Figure 3. Comparison of estimated and predicted versus measured summer surface water temperatures for the 39 lake training set. The temperature inferences are based on the 2 component WA-PLS model for square-root transformed percentage data. (a) Estimated versus measured temperature, (b) Predicted (=jack-knifed) versus measured temperature, (c) Apparent residual (estimated minus measured) versus measured temperature, (d) Jack-knifed residual (predicted minus measured) versus measured temperature.

Nevertheless, the two cores were not taken at exactly the same location. If different proportions of deep-water (more cold tolerant) versus shallow-water (more warm-adapted) species were deposited at the coring sites, this might influence the inferred temperatures. However, Levesque's (1995) core was taken from the

shallower site; thus, we would expect this core to yield warmer, not colder, temperatures.

We have also applied bootstrapping to the WA model inferences, allowing us to estimate the standard error of prediction for each fossil sample (Birks et al., 1990; Line et al., 1994). A similar procedure in the program

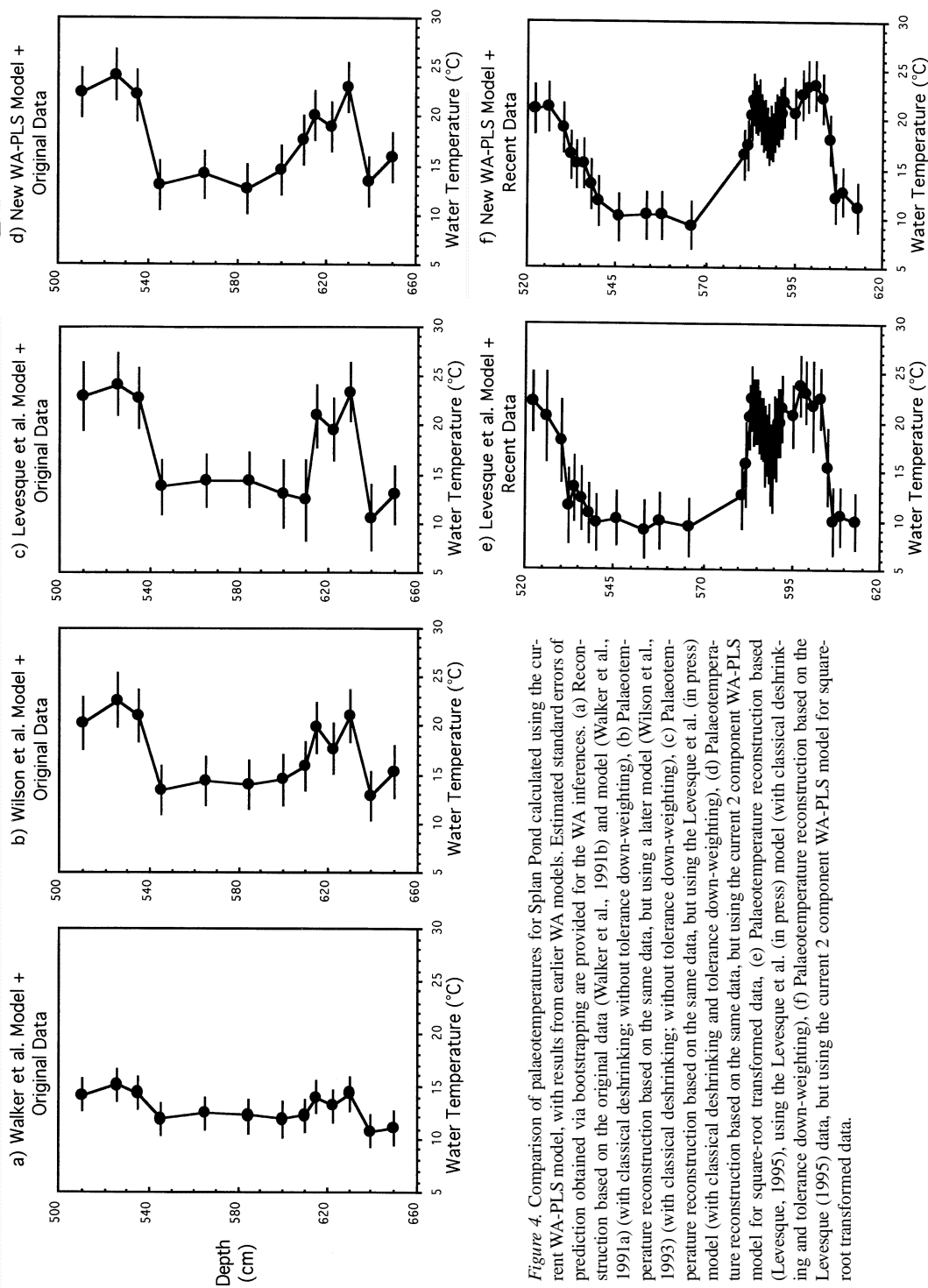


Figure 4. Comparison of palaeotemperatures for Splan Pond calculated using the current WA-PLS model, with results from earlier WA models. Estimated standard errors of prediction obtained via bootstrapping are provided for the WA inferences. (a) Reconstruction based on the original data (Walker et al., 1991b) and model (Walker et al., 1991a) (with classical deshrinking; without tolerance down-weighting). (b) Palaeotemperature reconstruction based on the same data, but using a later model (Wilson et al., 1993) (with classical deshrinking; without tolerance down-weighting). (c) Palaeotemperature reconstruction based on the same data, but using the Levesque et al. (in press) model (with classical deshrinking and tolerance down-weighting). (d) Palaeotemperature reconstruction based on the same data, but using the current 2 component WA-PLS model for square-root transformed data. (e) Palaeotemperature reconstruction based (Levesque, 1995), using the Levesque et al. (in press) model (with classical deshrinking and tolerance down-weighting). (f) Palaeotemperature reconstruction based on the Levesque (1995) data, but using the current 2 component WA-PLS model for square-root transformed data.

Table 5. Comparison of WA models obtained with inverse versus classical deshrinking, with and without tolerance down-weighting, and with and without square-root transformation of the species data

		$r_{app}^2$	$r_{jack}^2$	$r_{boot}^2$	RMSE <sub>app</sub>	RMSEP <sub>jack</sub>	RMSEP <sub>boot</sub>	Avg. bias	Max. bias	Avg. bias <sub>jack</sub>	Max. bias <sub>jack</sub>
Untransformed percentage species data:											
Classical deshrinking:	WA	0.84	0.81	0.80	2.82	2.99	3.11	0.0	2.4	−0.05	2.6
	WA <sub>tol</sub>	0.87	0.82	0.84	2.44	2.81	3.02	0.0	2.3	−0.11	2.7
Inverse deshrinking:	WA	0.84	0.80	0.80	2.58	2.84	3.09	0.0	2.7	−0.03	3.3
	WA <sub>tol</sub>	0.87	0.82	0.84	2.28	2.74	3.00	0.0	2.5	−0.09	3.6
Square root transformed percentage species data:											
Classical deshrinking:	WA	0.82	0.78	0.79	3.02	3.29	3.19	0.0	2.9	−0.04	3.1
	WA <sub>tol</sub>	0.86	0.80	0.83	2.61	3.08	3.15	0.0	2.8	0.02	2.7
Inverse deshrinking:	WA	0.82	0.77	0.78	2.73	3.04	3.10	0.0	3.7	−0.02	4.4
	WA <sub>tol</sub>	0.86	0.79	0.82	2.42	2.91	3.05	0.0	3.3	0.04	4.0

Table 6. Comparison of the different WA-PLS models, with and without square-root transformation of the species data

	$r_{app}^2$	$r_{jack}^2$	RMSE <sub>app</sub>	RMSEP <sub>jack</sub>	Avg. bias	Max. bias	Avg. bias <sub>jack</sub>	Max. bias <sub>jack</sub>
Untransformed percentage species data:								
Component 1	0.84	0.80	2.58	2.84	0.0	2.8	−0.04	3.3
Component 2	0.92	0.80	1.77	3.00	0.0	2.4	0.26	2.7
Component 3	0.94	0.77	1.58	3.32	0.0	2.2	0.29	3.5
Component 4	0.96	0.73	1.26	3.97	0.0	1.1	0.31	4.3
Square root transformed percentage species data:								
Component 1	0.82	0.77	2.74	3.05	0.0	3.4	−0.04	4.2
Component 2	0.92	0.88	1.80	2.26	0.0	1.9	0.02	2.4
Component 3	0.94	0.84	1.53	2.62	0.0	2.4	0.07	3.8
Component 4	0.95	0.80	1.36	2.99	0.0	1.7	0.07	4.0

WAPLS (Juggins & ter Braak, unpubl.) was used to derive sample specific standard errors for the new WA-PLS model. These errors are developed by (1) using jackknifing to obtain standard errors of the WA-PLS species coefficients, and (2) then using these errors to derive sample specific standard errors via Monte Carlo simulation (Juggins, pers. comm.). The estimated standard errors of prediction vary among the models, and for each fossil sample (Figure 4).

When bootstrapping was applied to the original model (Figure 4a), the estimated standard error of prediction varied from 1.48 to 1.56 °C for individual late-glacial samples. Larger estimated standard errors of prediction were calculated when bootstrapping was applied to the model used by Wilson et al. (1993) (Figure 4b), and the Levesque et al. (in press) model (Figure 4c, 4e). However, as noted by Walker et al. (1991a) and Wilson et al. (1993), the water temper-

ature inferences provided by the original model were artificially constrained, because of the comparatively narrow climatic gradient represented in the Labrador dataset. Consequently, the bootstrapped output does not provide an accurate portrayal of the actual errors associated with the original model.

The deficiencies of the original model are readily apparent if we use it to calibrate surface samples obtained from the Canadian Arctic Archipelago and southeastern Canada (Figure 5a). These surface samples were not available at the time the original model was being developed. It is clear that the water temperature inferences for these new samples, as inferred using the original model, are either too warm (samples collected north of Labrador), or too cold (samples collected south of Labrador). This deficiency was addressed by adding progressively more samples to the data set as they became available. The model used by

Wilson et al. (1993) seems to have largely addressed this problem (Figure 5b), although some slight further improvement may have occurred with subsequent development of the Levesque et al. (in press) model, and our new WA-PLS model (Figure 5c, 5d).

Thus, in evaluating the error estimates provided by bootstrapping, we cannot naïvely accept the conclusion that the original model was superior. It is clear that errors calculated for the original model were also constrained by the small thermal range of the lakes used in its development. Thus, we believe that the current model, developed from a larger surface sample dataset, provides more accurate water palaeotemperature inferences, and that the associated error estimates provide a more realistic assessment of the errors associated with midge-inferred water temperatures. Furthermore, as we continue to add new surface samples, we expect that the model inferences will become increasingly reliable.

Readers are also cautioned that the relationships between air and water temperatures are not always straight-forward. Air temperature, lake depth, inflowing meltwater streams, evaporation from lake surfaces, and loss of radiation by reflection off the water surface are among the many factors that influence water temperature (Walker & Mathewes, 1989). Because of the importance of incoming solar radiation to the heat budget of lakes, persistent cloud cover could have a pronounced impact on water temperatures. Mid-day summer surface water temperatures in the temperate lakes average approximately 25 °C, whereas mean July and August air temperatures at the same sites are commonly below 20 °C. The mean July air temperature for the Truelove Lowland, Devon Island, is about 6 °C. Although Truelove Lowland lakes may attain water temperatures of about 6 °C by late summer, these lakes also remain ice-covered in some years. Shallow arctic ponds may be several degrees warmer (Bliss, 1977).

Although midge-water temperature inferences have proven to be useful as proxy indicators of late-glacial climatic change, it must be emphasised that they are not a panacea. Sites and data for palaeotemperature reconstruction must be properly screened to ensure that the model is appropriately used, and that the basic assumptions of the model are met (Birks, 1995). The model was based almost entirely on oligotrophic, circumneutral, freshwater lakes which lacked summer stratification; thus, it is likely to give nonsensical results if applied to sites that are eutrophic, saline, brackish, or highly acidic, and should not be applied to large, deep, thermally-stratified lakes.

In conclusion, lakes are abundant throughout eastern Canada, and by the judicious selection of sites our inference model should be applicable throughout easternmost Canada, and over the entire postglacial period. Our model is likely also applicable to the late-glacial period of regions further south (e.g., New England) but is likely not applicable to more southerly Holocene records, since our data set contains few samples from such warm lakes. We will continue our efforts to expand the geographical and temperature ranges over which our model can be applied.

### Acknowledgments

This paper was completed while the senior author was on sabbatical leave at the University of Bern. We would like to thank the university for making the leave possible, and for making the Geobotanical Institute's facilities readily available for our research. We would also like to thank S. Juggins and C. J. F. ter Braak for providing pre-release copies of their CALIBRATE and WAPLS programs. Drs R. King, K. Williams, and A. Wolfe provided surface sediments and data from the Northwest Territories for our analyses. This work has been supported by the Natural Sciences and Engineering Research Council of Canada via research grants to I.R.W. and L.C.C., and a postdoctoral fellowship to A.J.L.

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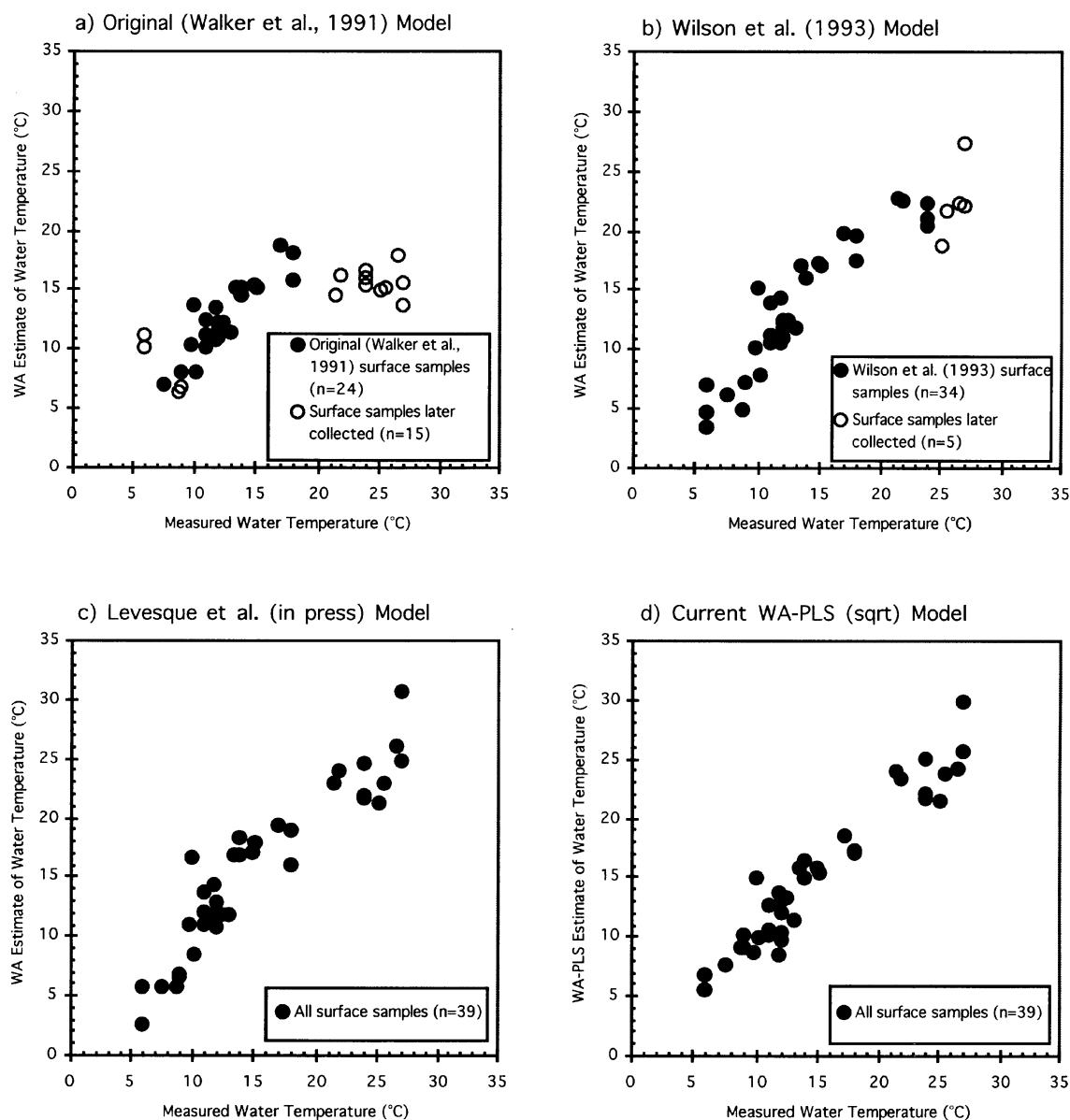


Figure 5. Comparison of older models with the new WA-PLS model, on the basis of estimated versus measured temperatures. (a) Walker et al. (1991a) model, (b) Wilson et al. (1993) model, (c) Levesque et al. (in press) model, (d) New 2 component WA-PLS model for square-root transformed data. Solid dots indicate those samples used in developing the model. Open circles indicate surface samples which were not available at the time each model was developed.

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## Appendix 1: Method for calculating chironomid-inferred temperatures.

Using WA inverse deshrinking models, inferred summer surface water temperatures (°C) for shallow lakes may be calculated as:

$$\hat{x}_i = a + b \left[ \left( \sum_{k=1}^m y_{ik} \hat{u}_k \right) / \sum_{k=1}^m y_{ik} \right]$$

(without tolerance down-weighting)

or

$$\hat{x}_i = a + b \left[ \left( \sum_{k=1}^m (y_{ik} \hat{u}_k / \hat{t}_k^2) \right) / \sum_{k=1}^m (y_{ik} / \hat{t}_k^2) \right]$$

(with tolerance down-weighting)

With WA classical deshrinking models, the inferred summer surface water temperatures (°C) are calculated as:

$$\hat{x}_i = \left[ \left[ \left( \sum_{k=1}^m y_{ik} \hat{u}_k \right) / \sum_{k=1}^m y_{ik} \right] - a \right] / b$$

(without tolerance down-weighting)

or

$$\hat{x}_i = \left[ \left[ \left( \sum_{k=1}^m (y_{ik} \hat{u}_k / \hat{t}_k^2) \right) / \sum_{k=1}^m (y_{ik} / \hat{t}_k^2) \right] - a \right] / b$$

(with tolerance down-weighting)

Using the WA-PLS models, inferred summer surface water temperatures (°C) may be calculated as:

$$\hat{x}_i = \left( \sum_{k=1}^m y_{ik} \hat{\beta}_k \right) / \sum_{k=1}^m y_{ik}$$

where,  $\hat{x}_i$  is the inferred temperature for sample  $i$ ,  $a$  and  $b$  are the intercept and slope of the deshrinking equation (see Table 4),  $y_{ik}$  is the abundance (depending on the model, either expressed as a percent of the total identifiable Chironomidae, or as the square-root of this value) of taxon  $k$  in sample  $i$ ,  $\hat{u}_k$  is the temperature optimum (°C) of species  $k$ ,  $\hat{\beta}_k$  is the Beta of species  $k$ , and  $\hat{t}_k$  is the tolerance (°C) of species  $k$  (Fritz et al. 1991; ter Braak 1987; Birks, pers. comm.). The required temperature optima, tolerances and Beta values are reported in Table 3.