Diatom-salinity relationships in 111 lakes from the Interior Plateau of British Columbia, Canada: the development of diatom-based models for paleosalinity reconstructions *

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Abstract

Diatoms were identified and enumerated from the surface sediments of 111 lakes, 45 from the Kamloops region and 66 from the Cariboo/Chilcotin region, located on the southern Interior Plateau of British Columbia, Canada. This paper is an extension of another study which investigated the relationship of diatoms to salinity and ionic composition in 65 lakes from the Cariboo/Chilcotin region. The 111 lakes spanned a large gradient in salinity, ranging from fresh through hypersaline (late-summer salinity values ranged from 0.04 to 369 g l^{-1}), and included both carbonate- and sulphate-dominated lakes with sodium and magnesium as the dominant cations. The Kamloops region had more sulphate-dominated, hypersaline lakes and fewer carbonate-rich lakes than the Cariboo/Chilcotin region. Most lakes had higher salinities in the late-summer compared to the spring.

Both salinity and brine-type were important variables that could explain the different diatom assemblages present in the lakes. The majority of diatom taxa had salinity optima in the freshwater to subsaline range (<3 g l^{-1}), and the taxa displayed a range of both narrow and broad tolerances along the salinity gradient. Weighted-averaging regression and calibration, and maximum likelihood techniques were used to develop salinity inference models from the diatom assemblages based on their relationship to the spring, late-summer and average lakewater salinity measurements. Simple weighted-averaging (WA) models generally produced the same or lower bootstrapped RMSEs of prediction than weighted-averaging with tolerance downweighting (WA(tol)) in the two regional and the combined datasets. Weighted averaging partial least squares (WA-PLS) showed little or no improvement in the predictive abilities of the datasets, as judged by the jackknifed RMSE of prediction. In all cases, the combined dataset of 102 lakes performed better than either of the smaller regional datasets, with relatively little difference between spring, average and late-summer salinity models. The maximum likelihood models gave lower apparent RMSEs of prediction in comparison to other methods; however, independent validation of this technique using methods such as bootstrapping were not undertaken because of the computer intensive nature of such analyses. These diatom-based salinity models are now available for reconstructing salinity and climatic trends from appropriately chosen closed-basin lakes in the Interior region of British Columbia.

Introduction

It is now widely accepted that high resolution paleoclimatic reconstructions are necessary to evaluate and test the various climate models that are being put forward in the scientific community. The sediment records of

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closed-basin lakes in arid and semi-arid regions are particularly good archives of paleohydrological and paleoclimatic signals, as the lake levels and ionic concentrations are governed largely by the balance between precipitation and evaporation (Last & Slezak, 1988). These changes in climate can be reconstructed using various biological, geochemical and sedimentological techniques. Among the fossils preserved in lake sediments, diatoms have proven to be sensitive indicators of a number of limnological variables (e.g. Dixit *et al.*, 1992; Hall & Smol, 1992), including salinity and ionic composition (e.g. Gasse *et al.*, 1983; Servant-Vildary & Roux, 1990; Blinn, 1993; Fritz *et al.*, 1993) and have been used in reconstructions of past salinity trends (e.g. Gasse *et al.*, 1987; Radle *et al.*, 1989; Fritz, 1990; Fritz *et al.*, 1991; Roux *et al.*, 1991).

The PISCES (Paleolimnological Investigations of Salinity, Climatic, and Environmental Shifts) project was initiated to develop and apply quantitative inference models (transfer functions) that could be used to estimate past lakewater salinities from sediment cores taken from lakes in western Canada (ICSLR, 1991). Recently, as part of the PISCES project, Cumming & Smol (1993) presented data showing the relationship of diatoms to salinity and brine-type along gradients of salinity and brine composition in 65 lakes from the Cariboo and Chilcotin Plateaux of British Columbia. Based on these diatom-salinity relationships, a quantitative inference model was developed to be used in regional paleoclimatic reconstructions. In this paper, the relationship of diatoms to salinity and ionic composition are re-evaluated with the addition of 45 lakes from the Kamloops region of British Columbia. The Kamloops region has a somewhat different geology and climate than that of the Cariboo/Chilcotin area, and therefore this combined 'training set' (*sensu* Birks *et al.* 1990b) should produce stronger and more realistic estimates of diatom salinity optima and tolerances, thereby providing a more powerful basis for paleosalinity and paleoclimatic reconstructions from appropriate closed-basin lakes in the southern Interior Region of British Columbia. This dataset has also been used to examine the distribution of chrysophyte cysts and scales and sponge spicule fragments along a gradient of salinity (Cumming *et al.*, 1993) as a means of enhancing paleolimnological interpretations.

Study region

The majority of saline lakes in British Columbia are located on the southern Interior Plateau, lying between the Coastal Ranges to the west and the Columbia-Rocky Mountain Ranges to the east. Located in the rainshadow of the Coast Mountains, the southern Interior experiences a semi-arid to sub-humid climate, with hot summers and cold winters. Annual precipitation averages between 240 to 400 mm y^{-1}, with an annual moisture deficit of approximately the same amount (Valentine & Schori, 1980; AES 1951–1980). A brief summary of the geology, vegetation and climate of the Kamloops and Cariboo/Chilcotin sampling regions is presented in Table 1.

Many of the saline lakes occupy shallow, closed depressions within glacial and glacial-fluvial deposits formed during the Wisconsinan glaciation (Renaut & Long, 1989). The lake types are diverse, and range from small, shallow, very saline, ephemeral ponds, to relatively deeper (>4 m) lakes that are meromictic. Lake catchments are typically small with the majority of inflow coming from groundwater discharge and precipitation (Renaut & Long, 1989). In addition to saline lakes, the southern Interior has an abundance of freshwater lakes that support a large recreational fishing industry. A more extensive description of the geology and lake basin characteristics can be found in Renaut & Long (1989), Renaut (1990) and Topping & Scudder (1977). The approximate locations of the 111 fresh and saline study lakes are shown in Fig. 1, and the coordinates are given in Appendix 1.

Materials and methods

Diatom analyses

Surface sediment samples (upper 1 cm) were collected in August and September of 1991 from near the center of 110 lakes using a Glew (1991) gravity corer (sediment was taken from lake K22 during the spring sampling and not in late-summer). A homogenized sediment subsample from each lake was placed in a polypropylene centrifuge tube and digested with a mixture of sulphuric acid and potassium dichromate following methods outlined by Smol (1983). A portion of the resulting slurry was then pipetted onto coverslips and allowed to evaporate. The dry coverslips
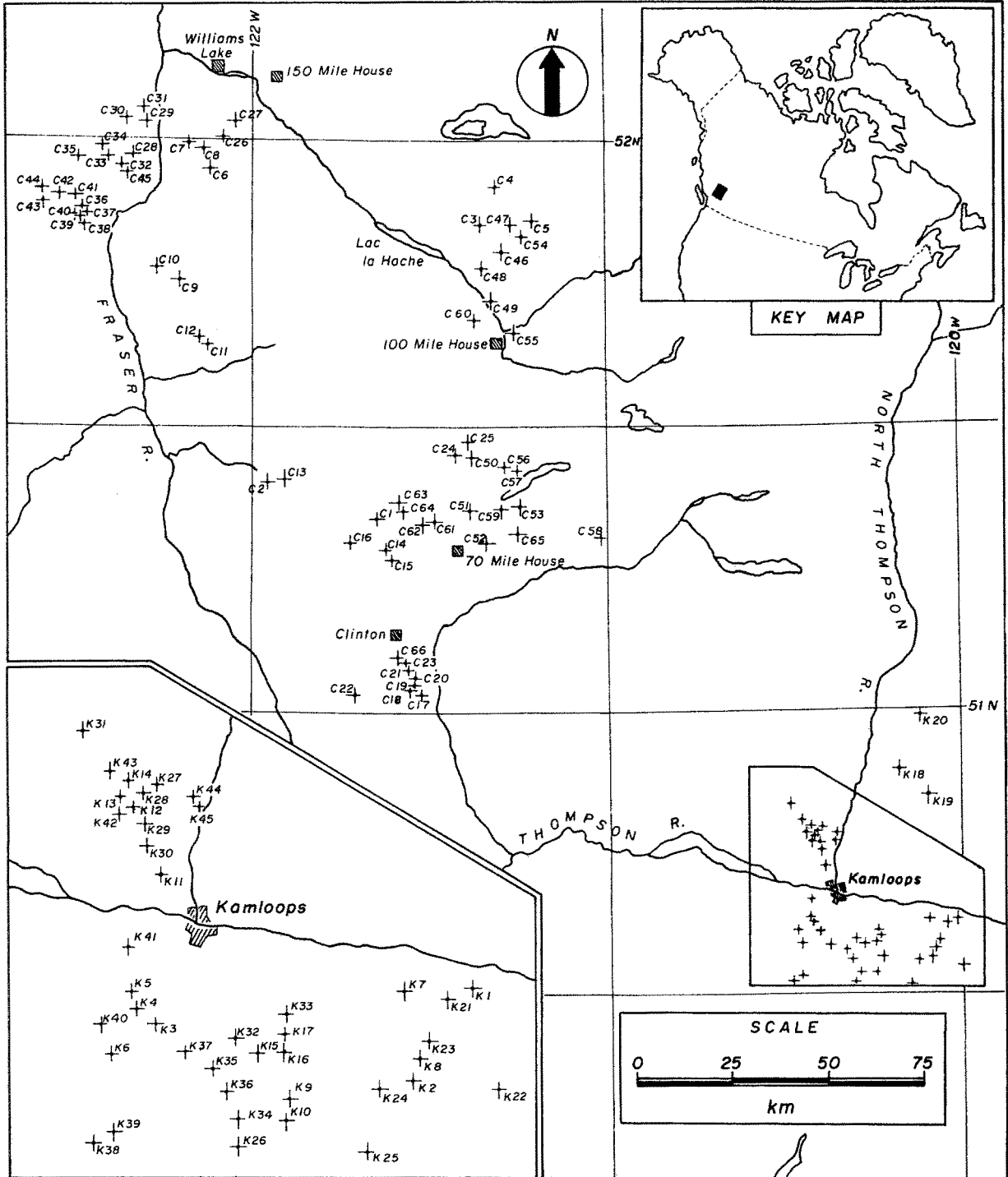
Fig. 1. Location of the 111 fresh and saline lakes sampled in the spring and late-summer of 1991. 'C' indicates Cariboo/Chilcotin lakes, and 'K' the Kamloops region lakes. Latitudes and Longitudes are in Appendix 1.

Table 1. A comparison of the geology, vegetation and general climate of the Kamloops and Cariboo/Chilcotin regions. Descriptions are taken from Farley (1979), Topping & Scudder (1977), and Renaut & Long (1989)

	Kamloops region	Cariboo/Chilcotin region
Geology	Paleozoic sedimentary and volcanic rock formations, intruded by granitic rock or early Tertiary lavas	Mainly flat-lying Miocene and Pliocene basalts with some Paleozoic sedimentary rocks
Vegetation	Open grassland with sagebrush (mainly *Artemisia*) and some ponderosa pine forest	Open grassland with mixed conifer forest consisting of Douglas-fir, aspen, and lodgepole pine
Annual Precipitation (mm yr^{-1})	~250	Cariboo: 300–400 Chilcotin: <300
Temperature (°C) (mean daily)	July: 20 to 22 January: −5 to −10	Cariboo July: 14 to 18 Cariboo Jan.: −9 to −12 Chilcot. July: 14 to 16 Chilcot. Jan.: −10 to −15

Table 2. The mean, median, minimum and maximum spring and late-summer salinities for the Kamloops, Cariboo/Chilcotin and combined datasets. All measurements are given in g L^{-1}

Dataset	Chemistry	N	Min	Max	Mean	Median
Combined	Spring	102	0.032	69.18	1.45	1.70
Combined	Late-summer	102	0.043	369.31	1.99	2.14
Cariboo/Chilcotin	Spring	60	0.032	54.95	1.15	1.62
Cariboo/Chilcotin	Late-summer	60	0.043	138.04	1.58	1.55
Kamloops	Spring	42	0.074	69.18	1.99	1.41
Kamloops	Late-summer	42	0.066	369.31	2.82	2.29

were mounted on glass slides using Hyrax® mounting medium (R.I. = 1.71).

Diatoms were identified and enumerated using either a Leitz Dialux 20 microscope (1250 × magnification with differential interference contrast optics, N.A. = 1.32) or a Nikon microscope (1000 × magnification with Nomarski optics, N.A. = 1.25). A minimum of 300 diatom valves (usually between 400 and 500) were identified from each sample, except in sediments where diatoms were especially uncommon (14 lakes) or absent (9 lakes). In the case of *Chaetoceros*, both valves and cysts were counted, and the cysts multiplied by 2 to represent valves. The higher of the two numbers was taken as representative of the population. Taxonomic consistency was established through the development of a comprehensive diatom iconograph (Cumming *et al.*, in press). Diatom nomencla-

ture followed Hustedt (1930–1966), Patrick & Reimer (1966, 1975), Håkansson & Stoermer (1984), Stoermer & Håkansson (1984), Krammer & Lange-Bertalot (1986–1991), the PIRLA Diatom Iconograph (Camburn *et al.*, 1984–1986), as well as other sources.

Water chemistry

Water chemistry surveys were undertaken in both the spring (April 30 to May 19) and late-summer (Aug. 21 to Sept. 13) of 1991 for 109 of the 111 study lakes. Lake C66 was sampled only in the late-summer of 1991, and K22 was sampled only in the spring. Temperature and conductivity profiles were taken on site with a YSI Model 33 S-C-T meter. Conductivity measurements were later corrected to the standard reference temperature of 25 °C. Oxygen profiles were taken with a YSI

Table 3. Eigenvalues of axes 1 through 4 of the correspondence analyses (CA) and canonical correspondence analyses (CCA), for the three datasets. NS indicates the axis was not significant based on a Monte Carlo permutation test (1000 permutations). The DCCA was performed with late-summer salinity data, and the gradient length is given in standard deviation units

Dataset		CA Axis 1	CA Axis 2	CA Axis 3	CA Axis 4	CCA Axis 1	CCA Axis 2	CCA Axis 3	CCA Axis 4	DCCA (Gradient Length)
Combined (101 Lakes)	Eigenvalue	0.86	0.81	0.73	0.71	0.76	0.60	0.44	0.34	5.19
Cariboo (59 Lakes)	Eigenvalue	0.84	0.81	0.71		0.76	0.55	0.48	NS	4.65
Kamloops (42 Lakes)	Eigenvalue	0.92	0.83			0.84	0.69	NS	NS	4.20

Table 4. Comparison of WA calibration models developed for estimating lakewater salinity based on the composition of diatom taxa in a sample. The Root Mean Squared Error after bootstrapping (RMSE$_{boot}$) was used as the main criterion for judging the predictive abilities of the various models. Notation follows Birks *et al.* (1990b). See text for details

Biological Dataset	Chemical Dataset	Model	Mean Salinity Inference	Number of taxa	Number of sites	r^2	Apparent RMSE	r^2_{boot}	RMSE$_{boot}$	s_1	s_2
Combined	Spring	WA	3.16	107	102	0.88	0.29	0.80	0.39	0.13	0.37
Combined	Spring	WA(tol)	3.16	107	102	0.91	0.25	0.83	0.40	0.20	0.34
Combined	Average	WA	3.25	107	102	0.89	0.30	0.82	0.42	0.13	0.39
Combined	Average	WA(tol)	3.25	107	102	0.92	0.26	0.84	0.41	0.21	0.36
Combined	Late-summer	WA	3.30	107	102	0.88	0.33	0.82	0.43	0.14	0.41
Combined	Late-summer	WA(tol)	3.30	107	102	0.92	0.28	0.83	0.45	0.23	0.39
Cariboo/Chilcotin	Spring	WA	3.06	75	60	0.87	0.28	0.78	0.40	0.15	0.37
Cariboo/Chilcotin	Spring	WA(tol)	3.06	75	60	0.89	0.26	0.78	0.42	0.21	0.36
Cariboo/Chilcotin	Average	WA	3.14	75	60	0.88	0.29	0.78	0.43	0.16	0.39
Cariboo/Chilcotin	Average	WA(tol)	3.14	75	60	0.89	0.28	0.79	0.45	0.23	0.38
Cariboo/Chilcotin	Late-summer	WA	3.20	75	60	0.87	0.31	0.77	0.45	0.17	0.42
Cariboo/Chilcotin	Late-summer	WA(tol)	3.20	75	60	0.89	0.29	0.79	0.48	0.27	0.40
Kamloops	Spring	WA	3.30	54	42	0.83	0.37	0.72	0.51	0.18	0.48
Kamloops	Spring	WA(tol)	3.30	54	42	0.87	0.33	0.78	0.51	0.29	0.42
Kamloops	Average	WA	3.40	54	42	0.85	0.38	0.75	0.53	0.18	0.50
Kamloops	Average	WA(tol)	3.40	54	42	0.88	0.35	0.81	0.52	0.30	0.43
Kamloops	Late-summer	WA	3.45	54	42	0.85	0.41	0.75	0.56	0.20	0.52
Kamloops	Late-summer	WA(tol)	3.45	54	42	0.87	0.37	0.81	0.56	0.32	0.46

model 54A dissolved oxygen (D.O.) meter equipped with a YSI model 5739 D.O. probe. Measurements of surface water pH were taken with a Fisher Scientific handheld electronic pH meter (resolution = 0.1 pH). Secchi disk measurements were taken using standard methods, but in most of the shallow lakes the Secchi disk could be clearly seen on the lake bottom. For this reason, Secchi depth was excluded as an explanatory variable of the diatom assemblages.

Surface water (~0.5 m depth) samples were collected from near the centre of each lake for laboratory analysis of nutrients, major ions, and metals. The samples were collected in polyethylene bottles that were rinsed with lakewater at the sampling site prior to the collection of the sample. These samples were stored on ice and shipped to Zenon Environmental Laboratories (Burnaby, B.C.) usually within 48 hrs (maximum 96 hrs) after the samples were taken. Chemi-

Table 5. Comparison of the various components for estimating lakewater salinity based on Weighted Averaging Partial Least Squares (WA-PLS) regression and calibration (Juggins & ter Braak, 1993). The Root Mean Squared Error after jackknifing ($RMSE_{jack}$) was used as the main criterion for selecting the number of stable components. The significant component for each dataset (one giving the lowest $RMSE_{jack}$) is shown in bold type. Note that WA-PLS with one component (WAPLS-1) = WA

Biological Dataset	Chemical Dataset	Component	r^2	Apparent RMSE	r^2_{jack}	$RMSE_{jack}$
Combined	Spring	**WAPLS-1**	0.88	0.29	0.80	**0.38**
Combined	Spring	WAPLS-2	0.92	0.24	0.79	0.39
Combined	Spring	WAPLS-3	0.94	0.21	0.78	0.41
Combined	Average	**WAPLS-1**	0.89	0.30	0.81	**0.39**
Combined	Average	WAPLS-2	0.92	0.25	0.81	0.40
Combined	Average	WAPLS-3	0.94	0.22	0.79	0.43
Combined	Late-summer	**WAPLS-1**	0.88	0.33	0.81	**0.42**
Combined	Late-summer	WAPLS-2	0.92	0.27	0.80	0.43
Combined	Late-summer	WAPLS-3	0.94	0.24	0.78	0.46
Cariboo/Chilcotin	Spring	WAPLS-1	0.87	0.28	0.79	0.36
Cariboo/Chilcotin	Spring	**WAPLS-2**	0.93	0.20	0.82	**0.33**
Cariboo/Chilcotin	Spring	WAPLS-3	0.95	0.17	0.81	0.34
Cariboo/Chilcotin	Average	WAPLS-1	0.88	0.29	0.79	0.38
Cariboo/Chilcotin	Average	**WAPLS-2**	0.93	0.21	0.82	**0.35**
Cariboo/Chilcotin	Average	WAPLS-3	0.95	0.18	0.81	0.36
Cariboo/Chilcotin	Late-summer	WAPLS-1	0.87	0.31	0.78	0.41
Cariboo/Chilcotin	Late-summer	**WAPLS-2**	0.93	0.23	0.81	**0.38**
Cariboo/Chilcotin	Late-summer	WAPLS-3	0.95	0.19	0.79	0.40
Kamloops	Spring	**WAPLS-1**	0.83	0.37	0.70	**0.49**
Kamloops	Spring	WAPLS-2	0.87	0.33	0.65	0.55
Kamloops	Spring	WAPLS-3	0.88	0.32	0.60	0.62
Kamloops	Average	**WAPLS-1**	0.85	0.38	0.73	**0.51**
Kamloops	Average	WAPLS-2	0.88	0.34	0.70	0.56
Kamloops	Average	WAPLS-3	0.88	0.35	0.63	0.65
Kamloops	Late-summer	**WAPLS-1**	0.85	0.41	0.73	**0.54**
Kamloops	Late-sunnmer	WAPLS-2	0.88	0.37	0.70	0.59
Kamloops	Late-summer	WAPLS-3	0.88	0.37	0.63	0.69

cal analyses followed standard procedures outlined by the American Public Health Association (1980) and in accordance with the quality control criteria described in Zenon's Laboratory Quality Assurance Manual (Jeffery, 1989).

Dissolved Al, Cd, Co, Cr, Cu, Fe, Mn, Mo, Ni, Pb, Bd, and Zn concentrations were below their respective detection limits in most of the lakes, and for this reason they were also eliminated as possible explanatory variables of the diatom distributions. Salinity was calculated as the sum of Ca, Mg, K, Na, SO_4, DIC and Cl concentrations.

Ordinations and inference techniques

All environmental variables were log transformed prior to analysis with the exception of pH, and surface and bottom temperature. Both B and Ba concentrations were very low in a number of lakes (between $0-1$ mg l^{-1}) and therefore a constant equal to half the lowest non-zero value was added prior to the transformations.

All ordinations were performed using the computer program CANOCO (version 3.21) (ter Braak 1988, 1990). The major gradients in the environmental and species data for the Kamloops (N = 42), Cariboo/Chilcotin (N = 59) and combined datasets

(N = 101) were determined by principal components analysis (PCA) and correspondence analysis (CA) respectively. Canonical correspondence analysis (CCA), a method of constrained ordination, was used to identify the environmental variables that could account for variations in the diatom data (ter Braak, 1986). In each CCA, the rare taxa were downweighted, and the species scores were scaled to be weighted averages of the site scores (ter Braak, 1990). A subset of environmental variables that could explain a majority of the variance in the dataset was selected by examination of the variance inflation factors (VIFs) in the CCA output. Variables with VIFs > 10 (i.e. multiple colinear variables) were eliminated one at a time beginning with the variable having the highest VIF. After each elimination, the CCA was re-run and the variance inflation factors re-examined, until no extreme VIFs remained. The t-values of the canonical coefficients were then examined to ensure that the remaining variables were significantly correlated with at least one significant ordination axis. Those variables not significantly correlated were eliminated. Monte Carlo permutation tests (1000 unrestricted permutations) were used to test the significance (P<0.05) of the first four ordination axes.

Because our goal was to develop models to reconstruct salinity, we used detrended canonical correspondence analysis (DCCA), with the first axis constrained to salinity, to determine the length of the salinity gradient in each of the three datasets.

The optima and tolerances of the diatom taxa to lakewater salinity were estimated using a weighted average and a weighted standard deviation, respectively (Birks et al., 1990a). The tolerances of the taxa were adjusted by dividing the weighted-average tolerances by $(1-1/N2)^{0.5}$, where N2 is Hill's (1973) diversity measure (e.g. Cumming et al., 1992). This resulted in proportionately broader tolerances for those taxa that had a lower effective number of occurrences.

Weighted-average regression and calibration salinity models (with inverse deshrinking) were developed from the three datasets using spring, late-summer and average salinity measurements. Average salinity was calculated as the arithmetic mean between spring and late-summer salinities. Models using simple weighted-averaging (WA) and weighted-averaging with tolerance downweighting (WA(tol)) were developed using the computer program WACALIB version 3.3 (Line et al., 1994). Weighted averaging partial least squares (WA-PLS) regression and calibration salinity models were developed using a beta-test version of the program CALIBRATE (Juggins & ter Braak, 1993). WA-PLS has improved the predictive ability of inference models in some datasets by utilizing the residual structure in the species data to improve the estimates of species parameters (ter Braak & Juggins, 1993; ter Braak et al., 1992). The bootstrapped RMSE of prediction for the WA and WA(tol) models, and the jackknifed RMSE of the individual components in the WA-PLS models were used as the criteria for assessing the predictive abilities of the salinity inference models. Bootstrapping is currently not available in CALIBRATE.

Ter Braak & van Dam (1989) used maximum likelihood calibration to reconstruct lakewater pH from diatom assemblages. The ML technique is theoretically desirable, but in practice its performance has been poorer than the simpler WA models (e.g. Birks et al., 1990b; Oksanen et al., 1988; Cumming et al., 1992). Maximum likelihood models were developed using the regression coefficients of Gaussian logit curves for those taxa that exceeded 1% relative abundance in three samples, using the maximum likelihood algorithm in WACALIB version 3.3 (Line et al., 1994). The Gaussian logit regression coefficients were calculated using GLR (S. Juggins unpublished program). Gaussian logit models were used to approximate the more complex multinomial logit model that can be difficult to fit and interpret (ter Braak, 1988).

Results and discussion

Water chemistry

The lakewater salinity of our combined dataset ranged from 0.03 to 69 g l^{-1} in spring and 0.04 to 369 g l^{-1} in late-summer (Table 2). Late-summer salinities were higher than those recorded in spring in almost all lakes, with the most pronounced changes occurring in lakes with spring salinities above 9 g l^{-1} (Fig. 2a). Lakes in the Kamloops region showed a larger discrepancy between spring and late-summer salinity (Fig. 2), which is not surprising considering the more arid climate (Table 1) and prominence of hypersaline (>50 g l^{-1}) lakes in the Kamloops area (Figs. 2 & 3).

The ionic compositions of the lakes in the spring and late-summer sampling periods were very similar, and therefore only late-summer ternary diagrams are presented (Fig. 3). In general, the freshwater lakes were dominated by carbonate/bicarbonate, although in a few cases they had relatively equal proportions
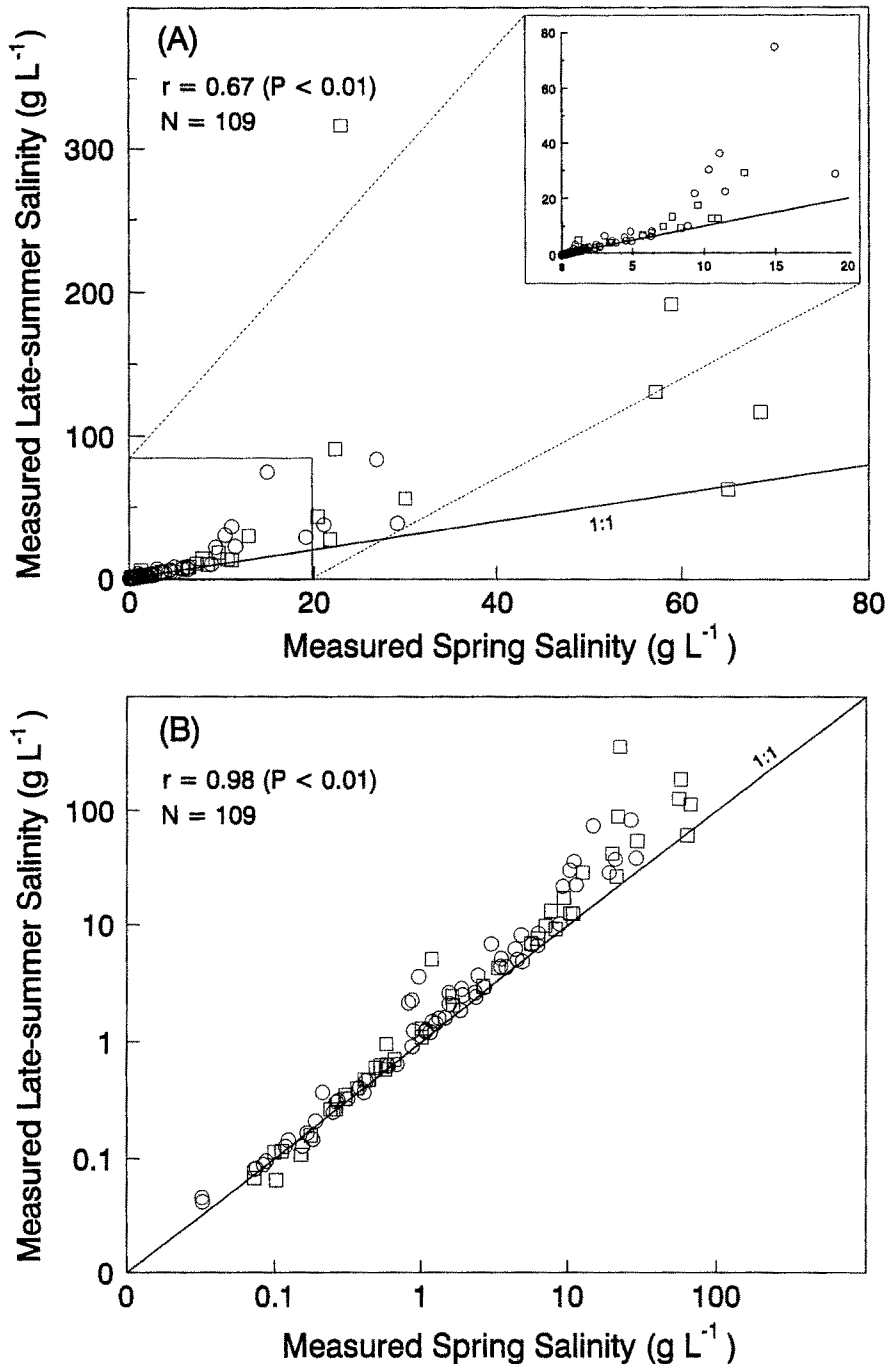
Fig. 2. The relationship between spring and late-summer salinities of the 109 lakes sampled in both the spring and late-summer, shown on a linear scale (A) and a log scale (B). □ = Kamloops lakes; ○ = Cariboo/Chilcotin lakes.

of carbonate/bicarbonate and sulphate (Fig. 3). The subsaline lakes were generally dominated by sulphate or carbonate/bicarbonate, or a combination of these anions. Hyposaline lakes were generally dominated by sulphate in the Kamloops region (Fig. 3b), where-

as both carbonate/bicarbonate and sulphate hyposaline lakes were sampled in the Cariboo/Chilcotin region (Fig. 3a). The hypersaline lakes were all sulphate-dominated. Chloride was rarely the dominant anion

(A) Cariboo/Chilcotin region lakes (Late-summer)
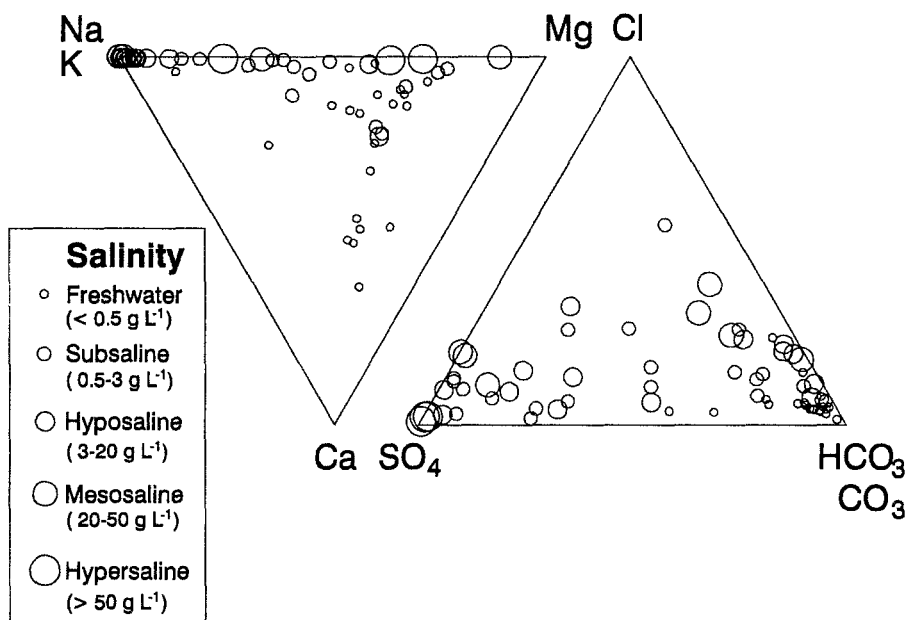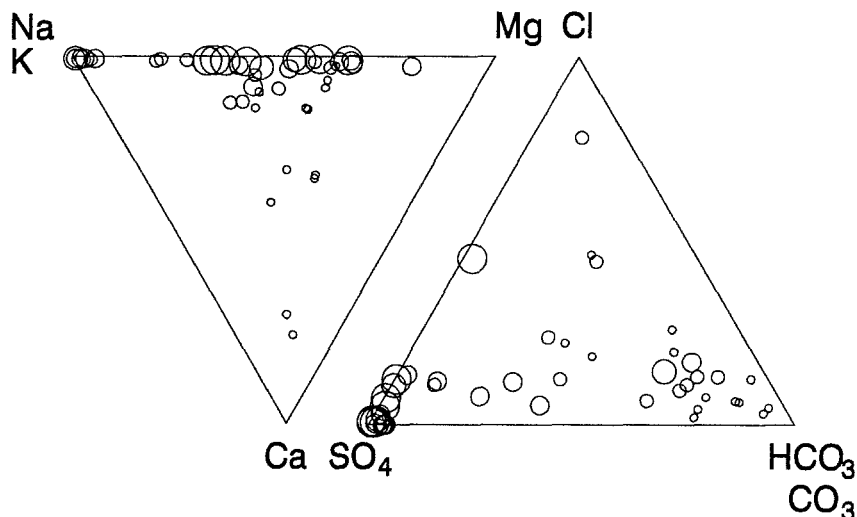

(B) Kamloops region lakes (Late-summer)

Fig. 3. Ternary diagrams showing mol% of cations and anions in the Cariboo/Chilcotin (A) and Kamloops lakes (B), during the late-summer sampling period. Saline lake classification follows Hammer *et al.*, 1983.

and only achieved high proportions in one fresh, three subsaline, and one hypersaline lake.

Calcium, sodium and magnesium cations were all common in the freshwater lakes, whereas only sodium and magnesium were dominant in the subsaline-hypersaline lakes. The majority of subsaline and saline Kamloops lakes had high proportions (>30 mol%)

of both sodium and magnesium, however six of the lakes had virtually all sodium and few other cations (Fig. 3b). In contrast, the Cariboo/Chilcotin subsaline-hypersaline lakes were mainly dominated by sodium, although ten lakes had magnesium as the dominant cation. Potassium was the dominant cation in one freshwater lake, and was the second most abundant cation

in five subsaline, 13 hyposaline, and five mesosaline lakes.

To summarize the regional water chemistry differences, the Kamloops area had primarily sodium- and magnesium-rich sulphate lakes (Na-Mg-SO$_4$ and Mg-Na-SO$_4$), whereas the Cariboo/Chilcotin subsaline and saline lakes displayed a greater diversity of ionic composition having various proportions of sodium and magnesium (but mainly sodium) dominating in sulphate- and carbonate/bicarbonate-rich systems (Cumming & Smol, 1993).

Gradient analyses

Diatoms were absent in the surface sediments of nine of the 111 lakes, and 14 additional lakes had low (<300 valves counted) diatom abundances. There was no obvious relationship between the absence of diatoms and lakewater salinity or ionic composition. The salinities of the lakes without diatoms ranged from 1 to 29 g l^{-1}. In some cases low light penetration (i.e. low Secchi disk transparency) or low Si concentrations (below detection limit) may have limited diatom production (Cumming & Smol, 1993); however there was no clear explanation for the other lakes, for which the apparent paucity may be related to high erosion rates rather than low diatom production, or a combination of these factors (Fritz *et al.*, 1993).

From the 102 lakes with diatoms present, approximately 325 taxa were identified, but only 107 had relative abundances ≥1% in a minimum of three lakes. The 107 taxa account for an average of 88.7% (SD = 14.5; median = 95.1%) of the relative abundance in the samples. The Cariboo/Chilcotin dataset of 60 lakes had approximately 289 diatom taxa, with 75 taxa present in ≥1% in at least three lakes. These 75 taxa represent an average 86.6% (SD = 18.6; median = 94.3%) of the relative abundance in the samples. Around 254 taxa were identified in the 42 Kamloops region lakes, with only 54 taxa having abundances ≥1% in three lakes. These taxa account for an average 72.7% (SD = 25.7; median = 79.7%) of the relative abundances. These surface-sediment species datasets (107 taxa × 102 lakes; 75 taxa × 60 lakes; 54 taxa × 42 lakes) were used to estimate the diatom optima and tolerances to lakewater salinity for the combined, Cariboo/Chilcotin, and Kamloops datasets, respectively.

For the ordinations, Lake C66, sampled only in the late-summer, was eliminated from the species matrix in order to make the spring and late-summer ordinations more comparable. Lake K22, which was sampled

only in the spring, was eliminated earlier as it was one of the nine lakes lacking diatoms in the surface sediment. The combined and Cariboo/Chilcotin datasets were therefore reduced to matrices of 107 taxa × 101 lakes, and 75 taxa × 59 lakes. In all cases, the spring and late-summer ordinations (CA and CCA) produced very similar results (e.g. eigenvalues, species and site scores), and therefore we present the eigenvalues of the late-summer ordinations only, and the late-summer CCA ordination plots.

The late-summer CCA ordination axes of the combined dataset are composed of linear combinations of the variables depth, surface temperature (Ttop), bottom temperature (Tbot), and concentrations of total Kjeldahl nitrogen (TKN), Si, B, Ba, Cl, dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), total phosphorus (TP), SO$_4$, and Mg. The selected variables for the spring ordination were virtually identical to late-summer, with the exception that Sr replaced Ba. All four ordination axes were significant (P<0.05) according to the Monte Carlo permutation tests. The late-summer species, site and environmental biplots for CCA axes 1 and 2, and axes 1 and 3 are presented in Fig. 4. The length and orientation of the environmental arrows reflect their relative importance and their approximate correlations to the ordination axes, respectively. The environmental variables not used in the construction of the CCA axes (passive variables), including the mol percentages (%) of the major cations and anions, are plotted in Fig. 5a, c, d & f.

CCA axis 1 is largely a gradient of salinity or overall ion concentration, with DIC, SO$_4$, Cl (inter-set correlations = 0.80, 0.72 and 0.81, respectively) as well as other variables, contributing to the first axis (Fig. 4b). Salinity and Na, entered as passive variables, are highly correlated to axis 1, and depth is negatively correlated with salinity (Fig. 5a & b). The second axis represents a gradient of ion composition with Mg, DIC, and SO$_4$ contributing (inter-set correlations = 0.69, 0.39, and 0.43, respectively). Both the salinity and brine-type gradients are important as indicated by their high and significant (P<0.05) eigenvalues (CCA axis 1 = 0.76; axis 2 = 0.60) (Table 3). A plot of CCA axis 1 versus 3 (Fig. 4e) indicates that total phosphorus (TP) and, to a lesser extent, depth are important variables contributing to the third axis (inter-set correlations = 0.45 and 0.35, respectively), with TP and depth inversely correlated.

The CA and CCA eigenvalues for axis 1 of the combined dataset were both high (Table 3). Correlations between CA axis 1 and CCA axis 1 species (r^2 = 0.85;

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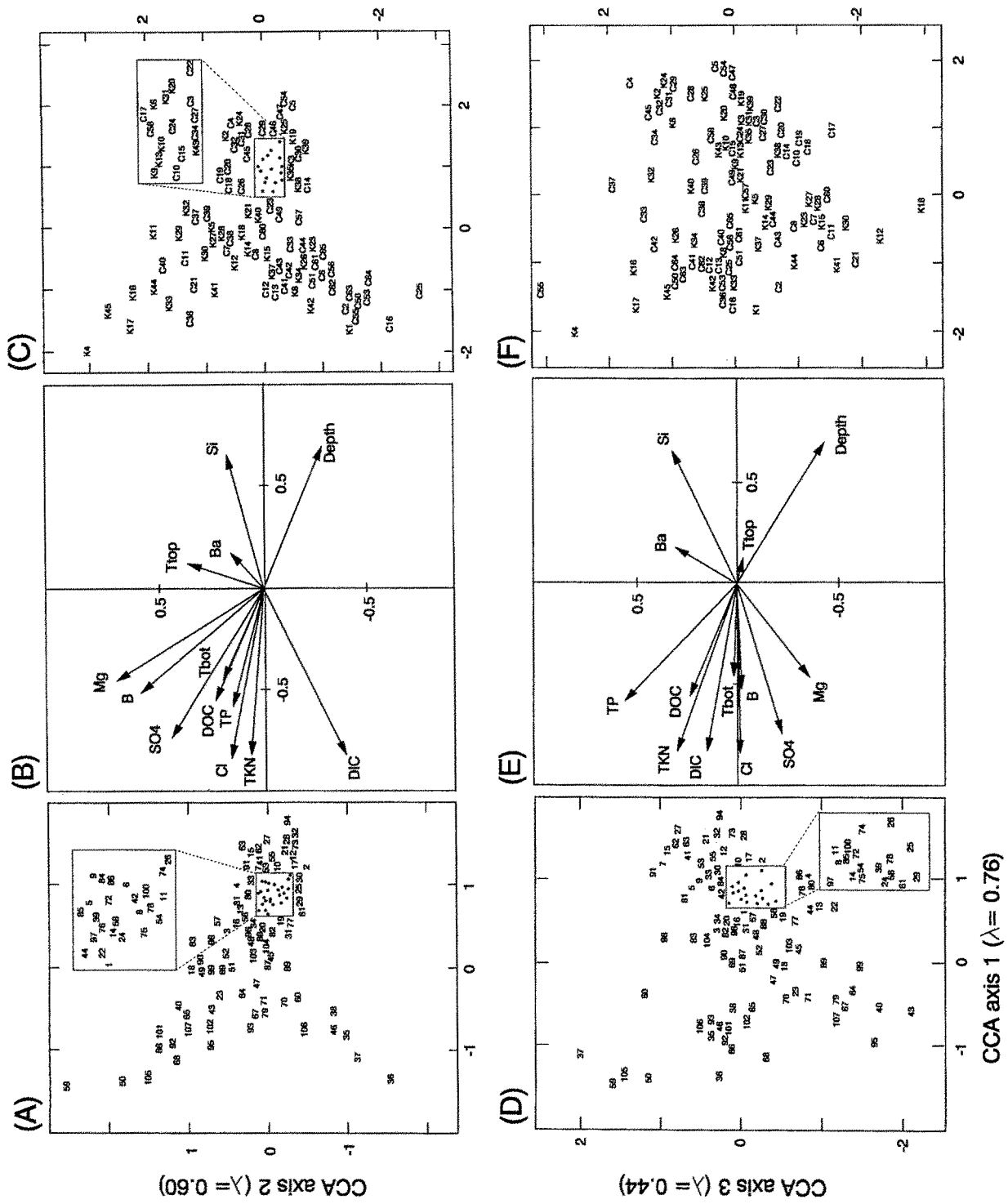
Fig. 4. Canonical correspondence analysis (CCA) ordination biplots showing species (A), environmental variables (B) and sites (C) of axis 1 versus axis 2 and species (D), environmental variables (E), and sites (F) of CCA axis 1 versus 3. The species scores presented are weighted averages of the site scores, and the site scores are positioned as linear combinations of the measured environmental variables. The species numbers correspond to those in Appendix 2, and the site numbers to those in Figure 1 and Appendix 1.

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Fig. 5. CCA ordination biplots showing only the environmental variables. Those variables used in the ordination are shown as solid arrows (B & E) and are identical to the plots in Fig. 4 (B & E). Passive variables are shown as dotted arrows. Once again the biplots of axis 1 versus 2 (A–C) and axis 1 versus 3 (D–F) are shown.

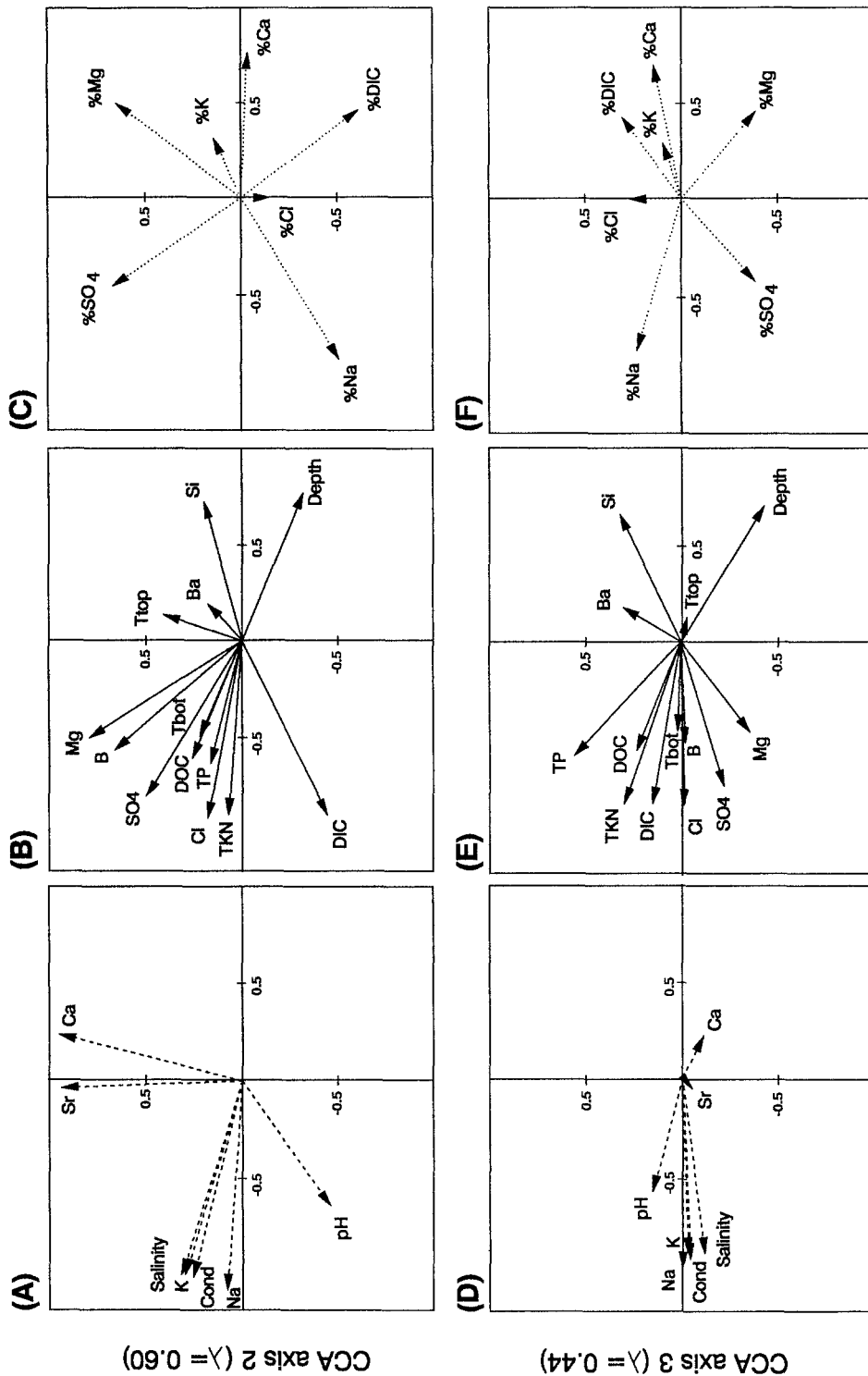P<0.01) and site ($r^2 = 0.92$; P<0.01) scores were also high and significant, suggesting that the environmental variables contributing to CCA axis 1 are sufficient to account for the major direction of variation in the diatom data. However, the correlations between CA axis 2 and CCA axis 2 species ($r^2 = 0.31$; P<0.05) and site ($r^2 = 0.43$; P<0.05) scores were not high, indicating that CCA axis 2 captured only part of the second major gradient in the species data. When CCA axis 3 and CA axis 2 species and site scores were compared, higher correlations ($r^2 = 0.45$ and 0.53 respectively) were observed than with CCA axis 2, suggesting that CCA axis 3 accounts for more of the variation in the second CA axis than CCA axis 2.

CCAs performed individually on the smaller Kamloops and Cariboo/Chilcotin datasets were similar to the combined CCA. DIC was once again highly correlated to axis 1 in the Cariboo/Chilcotin dataset (interset correlation = 0.87), with Mg and SO_4 strongly correlated to axis 2 (inter-set correlations = 0.68 and 0.59) (see Fig. 3 of Cumming & Smol, 1993). In the Kamloops CCA, salinity and related variables, such as Na, Mg and SO_4, were strongly correlated to axis 1, with TP and then Si contributing to axis 2 (figure not shown). Unlike the combined or the Cariboo/Chilcotin datasets, axis 2 did not represent a strong gradient of ionic composition. This is not surprising considering the lack of carbonate/bicarbonate-rich lakes in the Kamloops dataset and the fairly uniform ionic composition (i.e. Na-Mg-SO_4 or Mg-Na-SO_4) of the subsaline and saline lakes. Three of the ordination axes were significant in the Cariboo/Chilcotin dataset (see also Cumming & Smol, 1993), whereas only the first two axes were significant in the Kamloops dataset. The lengths of the DCCA gradients indicate that the datasets cover sufficiently large salinity gradients to develop reliable inference equations based on unimodal response curves of the individual taxa (Table 3).

Relationships of diatoms to salinity, ionic composition and other environmental variables

The position of each taxon (or site) on the CCA biplot approximates its weighted-average optimum relative to other taxa (or sites) along the environmental gradient. For example, diatoms that occur almost exclusively in freshwater lakes, such as *Nitzschia* cf. *bacillum* (#94 in Appendix 2), *Achnanthes conspicua* (32), *Fragilaria construens* var. *construens* (28), *F. pinnata* (27), *F. cyclopum* (21) and *Amphora inariensis* (73) are positioned at the far right of the plot (Fig. 4a) and

correspond to the high %Ca and %DIC lakes (Figs. 4c & 5c). Some of the planktonic taxa that are common in the fresh and deeper lakes include *Cyclotella bodanica* var. aff. *lemanica* (2), *Asterionella formosa* (12), *Tabellaria flocculosa* str. IIIp (30), and *Fragilaria crotonensis* (17) (Fig. 4a). *Stephanodiscus hantzschii* (5), *S. hantzschii* fo. 1 PISCES (6), *S. parvus* (11), *S. minutulus* (9), and *S.* cf. *oregonicus* (8) are other common planktonic taxa that have slightly higher salinity optima (Appendix 2), occurring in small numbers in subsaline and low hyposaline lakes, and therefore are positioned a little to the left of the other freshwater plankton. The majority of diatom taxa in the dataset are benthic and periphytic forms with optima in the freshwater to subsaline range, and thus are clustered to the right of the biplot origin. Some of the taxa with subsaline salinity optima that are positioned closest to the origin on the right or on the axis 2 boundary are *Craticula halophila* fo. 2 PISCES (45), *Nitzschia paleacea* (103), *Epithemia adnata* (87), *Rhopalodia gibba* (89) and *Navicula veneta* (51) (Fig. 4a).

The diatoms that occur in the most saline lakes are positioned in the upper left quadrant of the biplot, and correspond to the sulphate-rich lakes such as K4, K45, K17, K16, K44, K33, C40, and C36 in the upper left quadrant of Fig. 4c (Fig. 5c shows the location of the %SO_4 arrow). Those taxa with salinity optima in the hypersaline range (e.g. *Navicula* sp. 6 PISCES fo. 2 (59), *N. cincta* (50), *Nitzschia* cf. *communis* (105)) (Appendix 2) are positioned furthest from the biplot origin, and those taxa more common in the meso- and hyposaline lakes plot closer to the biplot origin. These include a number of mainly benthic and epiphytic forms such as *Amphora acutiuscula* (66), *Nitzschia frustulum* fo. 1 PISCES (101), *N. liebetruthii* fo. 1 PISCES (92), *Amphora* sp. 4 PISCES (68), *Mastogloia elliptica* (40), *Amphora coffeaeformis* (65), *Nitzschia perminuta* (95), *Navicula bulnheimii* (43), *Fragilaria pulchella* (23), and *Entomoneis paludosa* (64). *Chaetoceros muelleri* var. *muelleri* (107) (present as valves and cysts) was the only planktonic diatom with a salinity optimum in the saline range (Appendix 2). Diatom taxa present in high pH, carbonate-rich waters, such as lakes C16, C64, C53, C50, C55, and K1 (Fig. 4c), appear in the lower left quadrant at the far end of the DIC and %NA arrows, and to the left of the %DIC arrow (Figs 4a & b; Fig. 5c). These include mainly benthic diatoms with salinity optima in the hyposaline and subsaline ranges, such as *Anomoeoneis sphaerophora* fo. 1 & 2 PISCES (35, 36), *A. sphaerophora* (37), *A. sphaerophora* fo. *costata* (38), *Craticula halophila*

fo. 3 PISCES (46), *Surirella* sp. 1 PISCES (106), and *Navicula* sp. 1 PISCES (60). Taxa with low salinity optima (1.5–6.0 g l^{-1}) that occur in both carbonate- and sulphate-rich waters plot near the Axis 1 boundary, and include *Amphora subcapitata* (70), *A.* sp. 2 PISCES (71), *A.* sp. 1 PISCES (67), *Cymbella pusilla* (79), and *Craticula ambigua* (47).

Many of the very shallow, saline lakes and ponds sampled, such as lakes C55, K4, K16 and K17, have the highest TP and TKN concentrations (Fig. 4e & f), frequently reaching values between 8000 and 32 000 μg l^{-1}, and 10 000 to 70 000 μg l^{-1}, respectively. Extraordinarily high phosphorus and nitrogen values are not uncommon for many saline lakes in Canada (e.g. Campbell & Prepas, 1986) and in other parts of the world (Hammer, 1986). Furthermore, agricultural practices, particularly cattle ranching, have no doubt increased phosphorus and nitrogen loading to a number of the lakes in this region. Taxa that occur in these very saline, high phosphorus and nitrogen systems are positioned in the upper left quadrant of the ordination and include taxa such as *Anomoeoneis sphaerophora*, *Navicula* sp. 6 PISCES fo. 2, *Nitzschia* cf. *communis*, *Navicula cincta*, and *Navicula* sp. 1 PISCES (Fig. 4d). Interestingly, *Anomoeoneis sphaerophora* has been found in high nutrient saline lakes in other parts of the world, including the western United States, South Africa and Australia (reported in Gell & Gasse, 1994). The salinity optima and tolerances (upper and lower salinity limits) of the individual diatom taxa used in the ordinations are listed in Appendix 2. Photographs and taxonomic descriptions of the diatoms are available in Cumming *et al.* (in press).

Figure 6 shows the distribution of selected diatom taxa along the salinity gradient, arranged from low to high salinity optima. The scatters illustrate the range of tolerances (i.e. narrow versus broad distributions) exhibited by the diatoms. For example, in this dataset, *Navicula laevissima* and *Navicula* sp. 6 PISCES fo. 2 have very narrow tolerances as they only occur in freshwater and hypersaline lakes, respectively. Other taxa that show restricted distributions along the salinity gradient include *Anomoeoneis sphaerophora* fo. 1 PISCES (subsaline-hyposaline), *Amphora subcapitata* (subsaline-low hyposaline), and *Nitzschia perminuta* (meso-hypersaline). These contrast with other diatom distributions such as that of *Nitzschia frustulum* fo. 1 PISCES, which is present in lakes across the entire gradient from freshwater to hypersaline. *Cymbella pusilla* and *Amphora acutiuscula* also have fairly broad tolerances, achieving high relative abundances

in subsaline-hypersaline lakes, although *A. acutiuscula* is more prominent in the meso-hypersaline range (Fig. 6).

Lakewater salinity inference models

We developed diatom-based salinity inference models based on weighted-average estimates of diatom optima (WA models), and optima and tolerances (WA(tol) models), from 60 Cariboo/Chilcotin region lakes, 42 Kamloops region lakes and a combined dataset of the two regions (102 lakes) (Table 4). Models were developed from each dataset based on 1991 measurements of spring, late-summer and average lakewater salinity (spring and late-summer salinity values for each lake are given in Appendix 1). There was relatively little difference between spring, average, and late-summer salinity WA inference models within each of the three datasets, as judged by the RMSE of prediction after bootstrapping (RMSE$_{boot}$) (Table 4), due to the very high correlation between the measured spring and late-summer log salinity measurements (Fig. 2b, see also Cumming & Smol, 1993). However, the late-summer models had consistently higher bootstrapped RMSEs than those of the spring and average salinity models in each of the three datasets.

Simple WA models were equal to, or more reliable than, WA(tol) models based on the RMSE$_{boot}$ of prediction, with the exception of the combined and Kamloops average salinity models. However, the WA and WA(tol) RMSE$_{boot}$ values were very similar in each of the three datasets (Table 4). Overall, the combined dataset of 102 lakes produced lower RMSE$_{boot}$ values than either of the regional datasets, although there was little difference between the combined and Cariboo/Chilcotin prediction errors. In contrast, the bootstrapped RMSEs of the combined and Kamloops datasets differed by as much as 0.13 log salinity units (g l^{-1}). The relationship between the measured average salinity and the diatom-inferred salinity of the combined dataset is shown in Fig. 7.

A strong and significant relationship exists between the estimated diatom salinity optima derived from the Kamloops and Cariboo/Chilcotin datasets for the 36 taxa present in both datasets (Fig. 8a), whereas the relationship between the estimated tolerances is weak and not significant (Fig. 8b). These data suggest that the regional datasets are large enough to make comparable estimates of species optima, but not tolerances. Predictive diatom models developed using both species optima and tolerances have never shown superior predic-
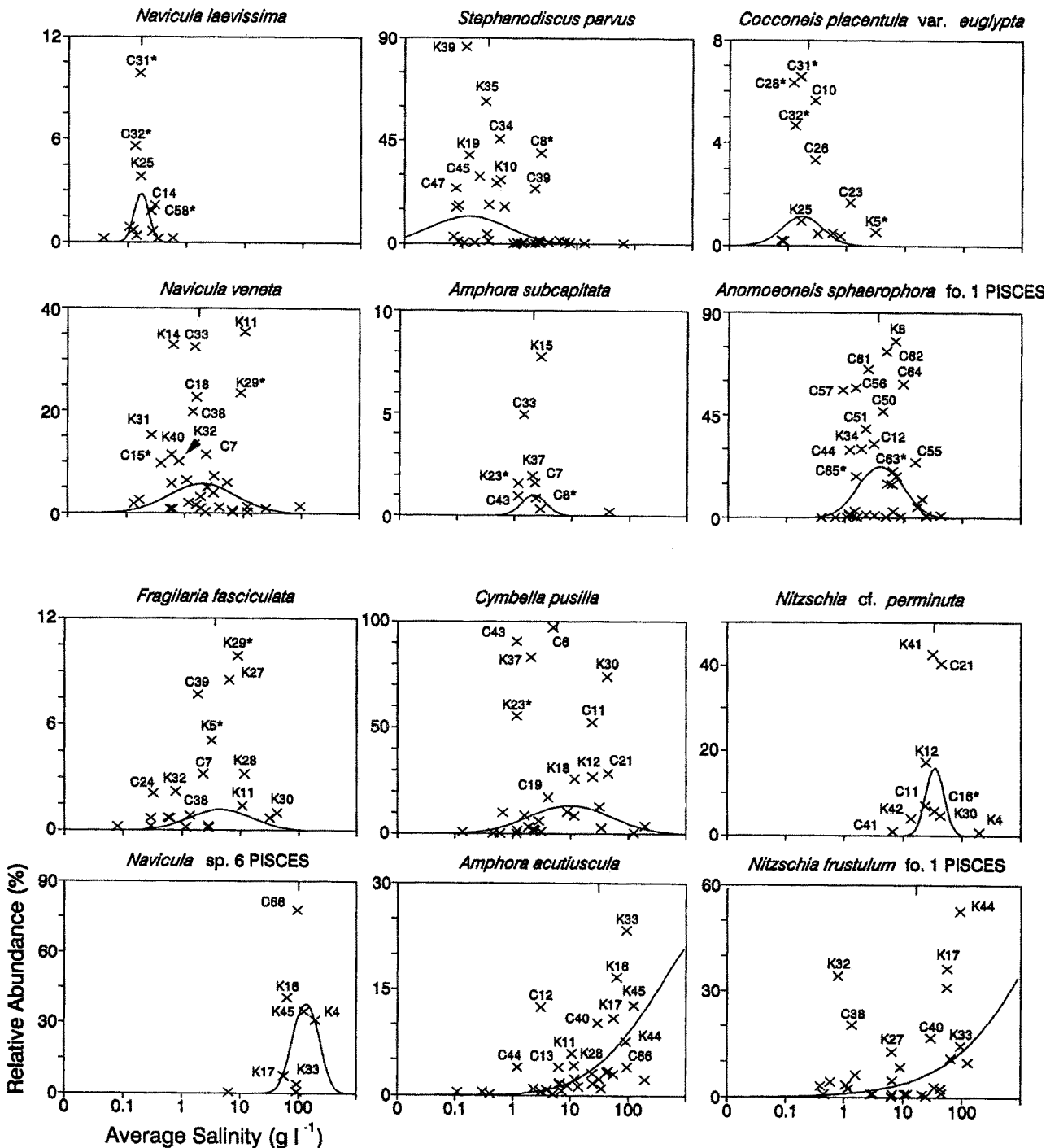
Fig. 6. Scatter diagrams of the relative abundance of 12 selected diatom taxa along the salinity gradient. Gaussian logit curves were fitted to these taxa using a quasi-likelihood model for proportions with binomial error structure as calculated by the computer program CALIBRATE (Juggins & ter Braak, 1993). The estimated WA optimum for each taxon is shown as a vertical line at the top of each plot. Many taxa (>80%) had Gaussian logit responses to the salinity gradient (e.g. all taxa shown here except *Amphora acutiuscula* and *Nitzschia frustulum* fo. 1 PISCES), whereas relatively few had sigmoid responses (e.g. *Amphora acutiuscula*).

(A) WA
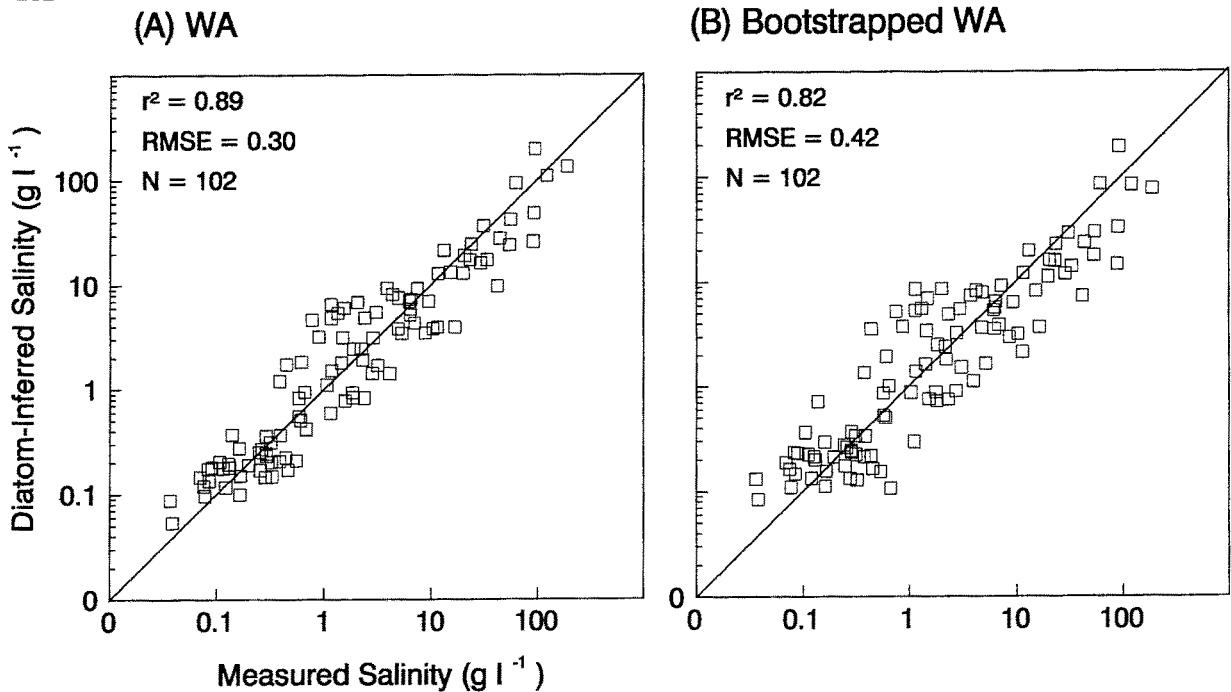
(B) Bootstrapped WA

Fig. 7. The relationship between measured average salinity and diatom-inferred salinity of the combined dataset (102 lakes) based on a simple weighted-averaging model with (B) and without (A) bootstrapping. The bootstrapped model provides a more realistic view of the predictive ability of the combined dataset.

tive abilities (after cross-validation or bootstrapping) to those that have been developed using species optima alone (e.g. Birks et al., 1990b; Hall & Smol, 1992). Species optima therefore appear to be reliably reproduced with the selection criteria we used (i.e. at least 1% relative abundance in three lakes), whereas species tolerances require more information. If we increase the number of required occurrences (e.g. at least 1% in five lakes), we see a coincident decline in the number of taxa operating the model. This initially results in an increase in the predictive ability of the WA(tol) inference model but, in our experience, this model never exceeds the predictive ability of the original WA model that is based solely on diatom species optima (unpublished data). As the number of required occurrences is increased further, the percent and number of taxa decline, and the predictive abilities of both the WA and WA(tol) models drastically decrease. One solution to this dilemma is to increase the size of the dataset from which ecological information is extracted. This will result in not only more accurate estimations of species parameters, but will also provide a better understanding of the relationship of many more taxa to multiple environmental variables, and provide a firmer basis for the development of more sophisticated paleoecologi-

cal inference techniques (e.g. multinomial regression, analogue matching, etc.).

Interestingly, many of the estimates of taxon salinity optima derived from the Kamloops dataset are higher than those of the Cariboo/Chilcotin dataset, as indicated by the position of points above the 1:1 line (Fig. 8a). The observed differences could result from the greater abundance of high salinity lakes sampled in the Kamloops area, and/or the lack of lower salinity carbonate-rich lakes in the Kamloops dataset that predominate in the Cariboo/Chilcotin region.

Recently it has been suggested that weighted averaging partial least squares (WA-PLS) models could be used to improve WA inference models (ter Braak & Juggins, 1993; ter Braak et al., 1993). However, WA-PLS did not yield superior results when compared to simple WA in the combined and Kamloops datasets, based on the jackknifed RMSE of prediction (Table 5). The three Cariboo/Chilcotin WA-PLS models did, however, show very slight improvements with the use of two WA-PLS components (WAPLS-2) (Table 5). The lower $RMSE_{jack}$ produced with WA-PLS in the Cariboo/Chilcotin dataset is not truely comparable to the WA $RMSE_{boot}$. Although the estimates of bootstrapped and jackknifed RMSEs are similar,
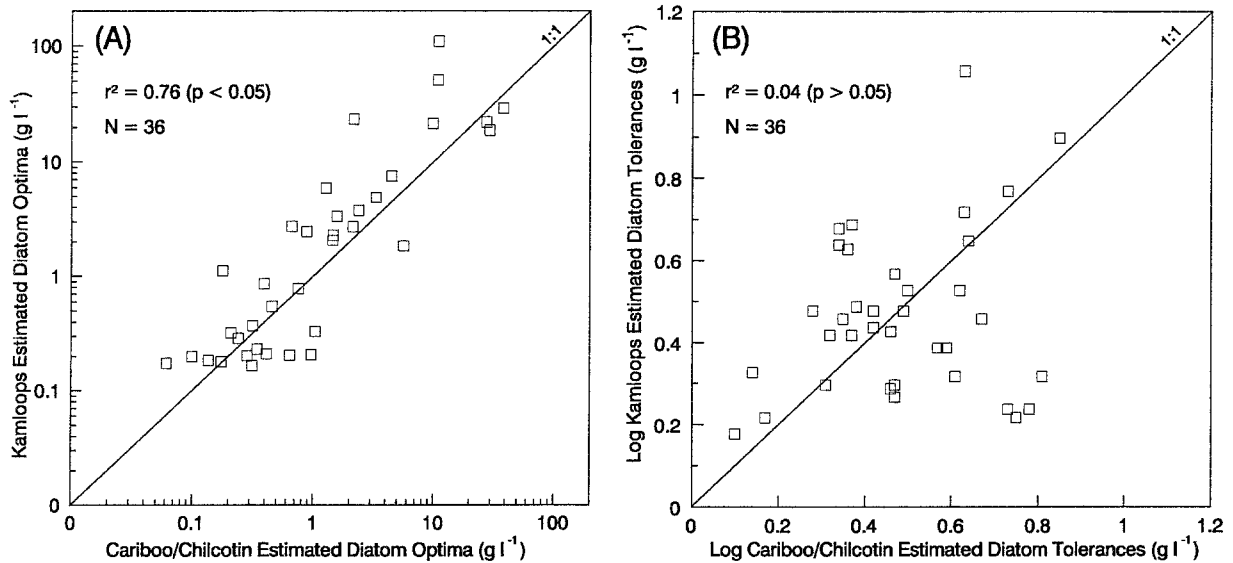
Fig. 8. Cariboo/Chilcotin versus Kamloops estimates of diatom salinity optima (A) and tolerances (B). The relationship is based on the 36 diatom taxa that were present in both of the datasets (i.e. Cariboo dataset = 75 taxa, Kamloops dataset = 54 taxa).

the jackknifed error estimates are slightly smaller than the more conservative error estimates produced from bootstrapping techniques (Tables 4 & 5).

Maximum likelihood salinity inference models generated from the combined dataset gave the same (spring salinity model) or lower apparent RMSEs of prediction than the simple WA models ($r^2 = 0.90$, RMSE = 0.27 in the average salinity model; $r^2 = 0.90$, RMSE = 0.29 in the late-summer salinity model). At present it is not possible to judge the significance of this result because bootstrapping ML models are computationally prohibitive. Data-rich ML models are ecologically preferable because more of the data are used, including the zero values. These results suggest that we may be approaching a large enough dataset to make accurate estimates of taxon parameters (e.g. optima and tolerances, maximum abundances) to lake-water salinity, however, larger datasets are still desirable in order to elucidate the ecological characteristics of diatom taxa. We recommend that simple WA models based on the optima of taxa be used in making quantitative paleosalinity reconstructions because it provides a robust and relatively simple way to reconstruct lakewater salinity from the species composition of diatoms.

Conclusions

The addition of lakes from the Kamloops region to the Cariboo/Chilcotin dataset only marginally improved the salinity inference models proposed by Cumming & Smol (1993), based on the bootstrapped RMSE of prediction. However, we believe the incorporation of these lakes into the model was still valuable in that more diatom species analogues, particularly for highly saline conditions, are now available to be used in long core paleosalinity reconstructions. On its own, the Cariboo/Chilcotin dataset had only a few sites which could supply such analogues. Furthermore, these additional, mainly sulphate-rich lakes have allowed us to more accurately estimate the optima and tolerances of the diatom taxa to lakewater salinity and to elucidate more clearly the relationship between ionic composition and diatom distributions.

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Appendix 1. Location of the 111 study lakes with spring and late-summer salinity measurements, as well as depth from which surface sediment cores were taken in the late-summer sampling period (the spring sampling depth is given for K22). The PISCES lake codes are used in Figures 1 and 4. ** indicates an absence of diatoms in the surface sediments (these lakes were excluded from the CCA), and * indicates lakes with low diatom abundances (<300 valves counted). Lake names in quotation indicate unofficial names.

PISCES Lake code	Lake name	Latitude	Longitude	Spring salinity (g l^{-1})	Late-summer Salinity (g l^{-1})	Sampling depth (m)
C1**	Goodenough	51°19.8'N	121°38.5'W	19.14	28.98	0.8
C2*	Long	51°23.9'N	121°57.4'W	10.36	30.45	2.5
C3	Greeny	51°51.2'N	121°21.0'W	0.17	0.17	7.0
C4	Fly	51°54.3'N	121°18.9'W	0.03	0.05	3.0
C5	Sneezie	51°51.5'N	121°12.7'W	0.08	0.09	21.0
C6	Boitano	51°56.7'N	122°07.5'W	3.04	6.90	2.6
C7	Sorenson	51°59.8'N	122°10.2'W	0.97	3.62	1.0
C8*	Westwick	51°59.3'N	122°09.0'W	1.91	2.86	1.8
C9**	Joes	51°45.2'N	122°12.5'W	1.27	1.46	3.5
C10	Alkali	51°46.6'N	122°16.7'W	0.27	0.32	4.0
C11	Sting	51°38.3'N	122°07.5'W	11.09	36.44	4.5
C12	'Putrid Pond'	51°38.9'N	122°08.5'W	2.46	3.71	1.5
C13	'White-2 (LE4) Pond'	51°23.9'N	121°55.0'W	5.71	6.85	0.7
C14	Beaverdam	51°16.3'N	121°37.0'W	0.21	0.37	3.3
C15*	No name	51°15.8'N	121°36.0'W	0.41	0.37	3.5
C16*	'Liberty'	51°17.2'N	121°43.0'W	29.13	38.91	0.7
C17	Six-mile	51°01.4'N	121°32.8'W	1.87	1.89	18.0
C18	'Lake south of Kersey'	51°01.8'N	121°33.0'W	0.87	2.30	3.5
C19	Kersey	51°02.1'N	121°32.8'W	3.83	4.37	8.5
C20	'North Alkali'	51°02.4'N	121°32.9'W	2.73	2.94	13.0
C21	Three-mile	51°03.4'N	121°33.6'W	14.93	74.75	2.5
C22	Leighwood	51°01.8'N	121°41.4'W	0.16	0.13	5.0
C23	No name	51°03.8'N	121°34.5'W	1.08	1.24	7.0
C24	Eighty-three	51°26.6'N	121°25.3'W	0.32	0.33	5.5
C25	'East of Eighty-three'	51°27.9'N	121°23.2'W	11.48	22.58	2.0
C26	Colpitt	52°00.3'N	122°04.8'W	0.27	0.32	1.5
C27	Brunson	52°02.0'N	122°02.8'W	0.27	0.31	7.0
C28*	McIntyre	51°58.3'N	122°20.9'W	0.12	0.13	4.0
C29	Leeches	52°02.3'N	122°19.0'W	0.03	0.04	2.5
C30	Till	52°02.8'N	122°21.5'W	0.38	0.41	13.0
C31*	No name	52°03.1'N	122°19.2'W	0.18	0.15	2.0
C32*	'Big' Doc English	51°57.5'N	122°22.8'W	0.13	0.14	3.0
C33	Rock	51°58.3'N	122°25.0'W	1.33	1.61	1.5
C34	East	51°59.3'N	122°25.9'W	0.43	0.47	3.5
C35**	Separating	51°58.3'N	122°30.0'W	1.57	2.63	0.5
C36	No name	51°52.3'N	122°29.2'W	26.86	83.84	0.2
C37	No name	51°52.2'N	122°29.0'W	0.90	1.26	0.1
C38	No name	51°51.7'N	122°29.3'W	1.20	1.52	0.9
C39	No name	51°52.0'N	122°30.0'W	1.57	2.13	1.0
C40	No name	51°51.9'N	122°30.8'W	21.10	37.96	0.7

Appendix 1. Continued.

PISCES Lake code	Lake name	Latitude	Longitude	Spring salinity (g l^{-1})	Late-summer salinity (g l^{-1})	Sampling depth (m)
C41	'Toosey'	51°54.2'N	122°31.0'W	4.86	8.28	2.0
C42*	No name	51°54.3'N	122°33.4'W	4.43	6.27	2.0
C43	No name	51°53.4'N	122°36.3'W	1.09	1.27	1.7
C44	No name	51°54.6'N	122°36.3'W	1.17	1.23	2.3
C45	'Lower' Doc English	51°56.9'N	122°22.0'W	0.19	0.21	3.8
C46	Chub	51°48.4'N	121°18.0'W	0.09	0.10	6.5
C47	Timothy	51°51.0'N	121°16.3'W	0.07	0.08	19.5
C48**	Soda	51°46.5'N	121°21.0'W	3.52	4.43	15.0
C49*	105-mile	51°43.0'N	121°19.3'W	0.60	0.63	4.0
C50	No name	51°26.5'N	121°22.6'W	3.55	5.16	0.2
C51	Loch Lomond	51°20.8'N	121°23.1'W	1.94	2.53	0.7
C52**	No name	51°18.8'N	121°21.3'W	4.55	5.08	0.6
C53	No name	51°21.2'N	121°14.4'W	6.35	8.58	1.0
C54	Dempsey	51°49.5'N	121°14.0'W	0.08	0.08	19.0
C55	Stephenson	51°39.4'N	121°15.4'W	9.34	21.94	0.2
C56	No name	51°23.3'N	121°18.5'W	0.82	2.19	0.8
C57	No name	51°23.4'N	121°18.0'W	0.88	0.93	3.1
C58*	No name	51°18.6'N	121°00.3'W	0.25	0.25	2.2
C59**	No name	51°22.1'N	121°18.5'W	2.36	2.65	0.5
C60	Savon	51°40.9'N	121°22.2'W	0.69	0.65	2.0
C61	No name	51°19.8'N	121°29.0'W	2.38	2.45	1.0
C62	No name	51°19.7'N	121°30.8'W	4.94	4.89	0.5
C63*	No name	51°20.2'N	121°33.6'W	6.29	6.71	0.7
C64	No name	51°20.1'N	121°33.4'W	8.87	10.30	0.5
C65*	Marsden	51°18.8'N	121°15.1'W	1.47	1.62	1.0
C66	'Clinton'	51°04.5'N	121°35.0'W	NA	136.60	0.1
K1*	Buse	50°37.5'N	120°01.7'W	12.83	29.24	3.0
K2	Campbell	50°33.5'N	120°05.5'W	0.07	0.07	2.0
K3	Jacko	50°36.7'N	120°25.0'W	0.31	0.33	23.0
K4	Inks	50°37.2'N	120°27.0'W	22.91	369.31	0.01
K5	'Lake north of Inks'	50°37.4'N	120°26.7'W	1.20	5.14	0.4
K6	Timber	50°34.8'N	120°28.0'W	0.50	0.61	4.3
K7**	'Barnhartvale'	50°37.8'N	120°06.5'W	7.16	10.03	0.8
K8	'Bestwick'	50°34.0'N	120°05.5'W	6.37	7.74	1.0
K9	Walker	50°33.2'N	120°14.0'W	0.67	0.72	4.3
K10	Shumway	50°31.5'N	120°15.0'W	0.45	0.49	8.5
K11	Batchelor	50°44.2'N	120°24.3'W	7.80	13.46	0.5
K12	'LB-1 Pond'	50°47.4'N	120°26.3'W	21.72	26.87	5.0
K13	Lac du Bois	50°48.0'N	120°27.4'W	0.37	0.41	7.2
K14	'McQueen Pond'	50°48.3'N	120°26.9'W	0.60	0.66	0.5
K15	Separation	50°34.8'N	120°17.5'W	2.70	3.01	3.3
K16	'East Beresford'	50°35.0'N	120°15.0'W	64.89	62.11	0.4
K17	'North Beresford'	50°35.5'N	120°15.5'W	22.25	90.46	0.02
K18	Lyons	50°53.4'N	120°11.2'W	11.00	12.76	10.5
K19	Little Heffley	50°50.6'N	120°06.6'W	0.15	0.11	8.0

Appendix 1. Continued.

PISCES Lake code	Lake name	Latitude	Longitude	Spring salinity (g l^{-1})	Late-summer salinity (g l^{-1})	Sampling depth (m)
K20	Knouff	50°59.4′N	120°07.3′W	0.10	0.12	2.0
K21	Upper Buse	50°37.2′N	120°03.0′W	0.58	0.59	2.5
K22**	Disdero	50°32.5′N	120°00.0′W	3.19	NA	3.1
K23	Curry	50°34.7′N	120°05.2′W	1.03	1.33	1.5
K24	Scuitto	50°32.9′N	120°08.2′W	0.10	0.07	6.0
K25	Hosli	50°30.5′N	120°08.8′W	0.18	0.16	15.0
K26*	Ussher	50°30.5′N	120°17.7′W	3.42	4.30	3.0
K27	No name	50°47.9′N	120°24.3′W	5.74	7.05	2.0
K28	No name	50°47.8′N	120°24.4′W	10.55	12.89	4.8
K29	Long	50°47.0′N	120°24.4′W	8.38	9.40	5.0
K30	'Southwest of Long'	50°46.1′N	120°25.5′W	29.93	55.42	1.5
K31	Pass	50°50.5′N	120°28.4′W	0.27	0.27	11.0
K32	'North of Knutsford'	50°35.3′N	120°18.8′W	0.59	0.97	0.5
K33	'Northeast of Beresford'	50°36.2′N	120°14.7′W	57.15	130.28	1.0
K34	Flat	50°31.6′N	120°18.1′W	1.68	2.10	0.7
K35	Edith	50°34.3′N	120°20.9′W	0.25	0.27	11.5
K36**	McLeod	50°33.0′N	120°19.2′W	1.03	1.12	3.2
K37	'Northwest of Edith'	50°34.9′N	120°23.4′W	1.66	2.48	0.8
K38	Stake	50°30.9′N	120°28.5′W	0.31	0.36	7.5
K39	McConnell	50°31.4′N	120°27.3′W	0.11	0.12	16.0
K40	'North of Timber'	50°36.2′N	120°28.2′W	0.54	0.64	1.8
K41	Bower	50°39.9′N	120°26.2′W	20.35	43.05	0.7
K42	'LB-2 Pond'	50°47.4′N	120°27.2′W	9.57	17.59	2.0
K43	'WSW of McQueen'	50°49.4′N	120°27.3′W	0.42	0.49	15.0
K44	'West of Deep'	50°47.7′N	120°22.0′W	68.38	116.32	1.0
K45	No name	50°47.4′N	120°21.3′W	58.82	191.15	0.02

Appendix 2. Estimates of taxon optima and tolerances (presented as upper and lower salinity limits, as in Fritz *et al.* (1993)), used in the salinity inference models for the combined B.C. dataset (i.e. those taxa that occurred in $\geq 1\%$ relative abundance in at least 3 of the 102 study lakes). The salinity limits for each taxon were calculated as $\pm$ two abundance-weighted standard deviation units from the log salinity optimum. Upper salinity limit values that exceeded the highest measured lakewater salinity in the dataset (369.31 g L^{-1}), were replaced with this same value. The salinity optimum and tolerance ranges are shown as back transformations from an average of the log spring and late-summer salinities. The taxon numbers correspond to those used in the ordination diagram (Fig. 4). N2 = effective number of occurrences (Hill, 1973). These taxa are further described in Cumming *et al.* (in press).

Taxon number	Taxon name and authority	Number of occurrences	N2	Maximum relative abundance (%)	Salinity optimum (g l^{-1})	Lower limit (g l^{-1})	Upper limit (g l^{-1})
1	*Aulacoseira subarctica* (O. Müll.) Haworth 1988	6	1.3	49.5	0.58	0.05	6.75
2	*Cyclotella bodanica* var. aff. *lemanica* (O. Müll. ex Schröt.) Bachm. 1903	20	4.4	39.4	0.26	0.05	1.38
3	*Cyclotella meneghiniana* Kütz. 1844	16	3.6	25.4	0.68	0.10	4.54
4	*Cyclotella michiganiana* Skvort. 1937	11	3.3	50.6	1.77	0.12	26.85
5	*Stephanodiscus hantzschii* Grun. in Cleve & Grun. 1880	23	6.8	16.1	0.33	0.03	3.77
6	*Stephanodiscus hantzschii* fo. 1 PISCES	25	8.9	35.9	0.26	0.04	1.82
7	*Stephanodiscus hantzschii* fo. *tenuis* (Hust.) Håkansson & Stoermer 1984	17	3.8	64.5	0.28	0.04	1.73
8	*Stephanodiscus* cf. *oregonicus* (Ehrenb.) Håkansson 1986	16	3.1	54.4	0.35	0.02	5.02
9	*Stephanodiscus minutulus* (Kütz.) Round 1981	15	5.6	5.6	0.23	0.01	6.27
10	*Stephanidiscus* cf. *minutulus*	5	2.9	13.1	0.20	0.06	0.66
11	*Stephanodiscus parvus* Stoermer & Håkansson 1984	35	11.4	86.3	0.29	0.03	2.59
12	*Asterionella formosa* Hass. 1850	19	4.5	26.3	0.18	0.03	0.99
13	*Diatoma tenue* var. *elongatum* Lyngb. 1819	4	2.7	4.6	2.21	0.60	8.11
14	*Fragilaria capucina* complex	17	4.9	11.5	0.30	0.11	0.82
15	*Fragilaria* sp. 1 PISCES	15	4.6	14.0	0.12	0.02	0.59
16	*Fragilaria capucina* var. *mesolepta* (Rabenh.) Rabenh. 1864	12	7.1	3.1	0.47	0.03	7.05
17	*Fragilaria crotonensis* Kitt. 1869	16	9.2	5.9	0.18	0.01	2.75
18	*Fragilaria fasciculata* (Agardh) Lange-Bertalot 1980	20	8.3	9.9	3.64	0.33	40.46
19	*Fragilaria nanana* Lange-Bertalot 1991	12	1.6	37.6	0.82	0.06	11.86
20	*Fragilaria ulna* var. *acus* (Kütz.) Lange-Bertalot 1980	28	6.5	17.3	0.50	0.09	2.73
21	*Fragilaria cyclopum* (Brutschy) Lange-Bertalot 1980	8	3.2	4.3	0.15	0.05	0.40
22	*Fragilaria famelica* (Kütz.) Lange-Bertalot 1980	9	4.6	3.4	1.08	0.01	187.93
23	*Fragilaria pulchella* (Ralfs ex Kütz.) Lange-Bertalot 1980	17	9.9	2.6	7.13	0.41	122.74
24	*Fragilaria* cf. *tenera* (W. Sm.) Lange-Bertalot 1980	17	5.7	18.9	0.71	0.06	8.61
25	*Fragilaria brevistriata* Grun. in Van Heurck 1885	29	4.5	82.1	0.25	0.04	1.40
26	*Fragilaria construens* var. *venter* (Ehrenb.) Grun. in Van Heurck 1881	13	1.5	36.7	0.17	0.02	1.50
27	*Fragilaria pinnata* Ehrenb. 1843	23	5.7	65.1	0.07	0.01	0.50
28	*Fragilaria construens* var. *contruens* (Ehrenb.) Grun. 1862	9	2.7	17.5	0.10	0.03	0.42
29	*Synedra delicatissima* var. *angustissima* Grun. in Van Heurck 1881	11	6.2	2.7	0.67	0.03	17.74
30	*Tabellaria flocculosa* str. IIIp sensu Koppen 1975	12	3.9	9.5	0.25	0.00	52.24
31	*Achnanthes minutissima* Kütz. 1833	50	22.7	13.8	0.62	0.03	12.97
32	*Achnanthes conspicua* A. Mayer 1919	7	3.4	2.9	0.13	0.03	0.53
33	*Cocconeis placentula* cf. var. *placentula* Ehrenb. 1838	13	6.5	6.6	0.22	0.05	0.95
34	*Cocconeis placentula* var. *euglypta* (Ehrenb.) Grun. 1884	21	7.7	11.1	0.54	0.06	5.16
35	*Anomoeoneis sphaerophora* (Ehrenb.) Pfitz. 1871 fo. 1 PISCES	35	14.6	77.6	3.57	0.66	19.28

Appendix 2. Continued.

Taxon number	Taxon name and authority	Number of occurrences	N2	Maximum relative abundance (%)	Salinity optimum (g l^{-1})	Lower limit (g l^{-1})	Upper limit (g l^{-1})
36	*Anomoeoneis sphaerophora* fo. 2 PISCES	16	9.0	95.8	12.62	2.74	58.21
37	*Anomoeoneis sphaerophora*	14	2.2	23.8	8.04	0.48	135.21
38	*Anomoeoneis sphaerophora* fo. *costata* (Kütz.) Schmid 1977	38	15.5	36.8	2.59	0.32	20.65
39	*Brachysira vitrea* (Grun.) Ross in Hartley 1986	13	8.2	7.1	0.39	0.04	3.37
40	*Mastogloia elliptica* (Agardh) Cleve ex A. Schmidt 1893	6	2.3	11.8	22.91	10.62	49.43
41	*Navicula laevissima* Kütz. 1844	12	4.6	9.9	0.17	0.08	0.35
42	*Navicula pupula* Kütz. 1844	20	12.5	4.6	0.28	0.01	7.24
43	*Navicula bulnheimii* Grun. in Van Heurck 1880	8	4.0	33.1	23.17	9.23	58.21
44	*Craticula halophila* (Grun. ex Van Heurck) D.G. Mann in Round *et al.* 1990 fo. 1 PISCES	14	6.5	8.1	1.12	0.08	16.26
45	*Craticula halophila* fo. 2 PISCES	43	14.0	20.9	1.12	0.10	11.99
46	*Craticula halophila* fo. 3 PISCES	3	2.8	52.7	1.92	1.34	2.75
47	*Craticula ambigua* (Ehrenb.) D.G. Mann in Round *et al.* 1990	30	6.8	41.0	1.87	0.18	19.05
48	*Craticula cuspidata* (Kütz.) D.G. Mann in Round *et al.* 1990	25	6.8	14.5	0.91	0.07	11.32
49	*Craticula cuspidata* fo. 2 PISCES	7	4.9	1.5	2.36	0.12	46.34
50	*Navicula cincta* (Ehrenb.) Ralfs in Pritch. 1861	19	5.1	19.8	47.75	1.04	369.31
51	*Navicula veneta* Kütz. 1844	33	13.5	35.5	1.75	0.15	20.80
52	*Navicula* aff. *veneta*	14	6.3	5.7	2.02	0.11	38.02
53	*Navicula cryptocephala* Kütz. 1844	19	4.9	19.4	0.16	0.01	1.92
54	*Navicula cryptotenella* Lange-Bertalot 1985 fo. 1 PISCES	20	7.8	12.7	0.24	0.04	1.68
55	*Navicula cryptotenella*	6	2.9	10.9	0.13	0.07	0.24
56	*Navicula libonensis* Schoeman 1970	16	7.1	5.7	1.10	0.13	9.12
57	*Navicula mutica* Kütz. 1844	11	3.0	11.1	1.01	0.00	369.31
58	*Navicula oblonga* (Kütz.) Kütz. 1844	26	8.1	18.0	0.49	0.05	4.56
59	*Navicula* sp. 6 PISCES fo. 2	8	3.9	77.8	100.69	40.83	248.31
60	*Navicula* sp. 1 PISCES	10	2.3	30.0	2.42	0.11	54.95
61	*Pinnularia microstauron* (Ehrenb.) Cleve 1891	10	3.1	7.0	0.29	0.03	3.04
62	*Stauroneis phoenicenteron* (Nitzsch) Ehrenb. 1843	7	4.6	2.9	0.10	0.02	0.52
63	*Stauroneis anceps* fo. *gracilis* Rabenh. 1864	8	1.3	37.3	0.12	0.03	0.56
64	*Entomoneis paludosa* (W. Sm.) Reimer in Patr. & Reimer 1975	8	3.7	4.9	4.74	0.57	39.45
65	*Amphora coffeaeformis* (Agardh) Kütz. 1844	11	4.4	6.3	9.91	1.32	74.13
66	*Amphora acutiuscula* Kütz. 1844	33	13.8	23.3	31.12	1.83	369.31
67	*Amphora* sp. 1 PISCES	9	3.9	19.4	4.80	0.62	37.24
68	*Amphora* sp. 4 PISCES	12	2.8	20.4	28.71	2.31	356.45
69	*Amphora veneta* Kütz. 1844	30	5.4	47.1	1.67	0.35	8.00
70	*Amphora subcapitata* (Kisselev) Hust. 1959	9	4.3	7.8	2.11	0.74	6.01
71	*Amphora* sp. 2 PISCES	12	3.8	44.6	2.42	0.99	5.87
72	*Amphora libyca* Ehrenb. 1840	32	9.4	25.3	0.33	0.05	2.29
73	*Amphora inariensis* Krammer 1980	13	7.6	4.5	0.12	0.03	0.54
74	*Cymbella microcephala* Grun. in Van Heurck 1880	19	8.0	3.2	0.24	0.03	1.87
75	*Cymbella minuta* Hilse ex Rabenh. 1862	18	9.3	3.9	0.36	0.02	7.50
76	*Cymbella cymbiformis* var. *nonpunctata* Font. 1917	11	7.3	2.3	1.13	0.13	9.64
77	*Cymbella* cf. *cistula* (Ehrenb. in Hemp. & Ehrenb.) Kirchn. 1878	14	9.0	2.9	0.77	0.16	3.76

Appendix 2. Continued.

Taxon number	Taxon name and authority	Number of occurrences	N2	Maximum relative abundance (%)	Salinity optimum (g l^{-1})	Lower limit (g l^{-1})	Upper limit (g l^{-1})
78	*Cymbella proxima* Reimer in Patr. & Reimer 1975	7	5.7	1.3	0.33	0.06	1.80
79	*Cymbella pusilla* Grun. ex A. Schmidt 1875	28	10.1	97.1	5.78	0.30	113.24
80	*Cymbella* sp. 1 PISCES	12	6.5	5.7	1.06	0.07	16.94
81	*Gomphonema parvulum* (Kütz.) Kütz. 1849	15	8.0	7.5	0.29	0.04	2.13
82	*Gomphonema* sp. 1 PISCES	19	4.7	20.5	0.50	0.12	2.03
83	*Gomphonema gracile* Ehrenb. 1838	7	4.8	2.8	1.00	0.03	33.81
84	*Gomphonema* cf. *angustum* Agardh 1831	10	3.8	12.6	0.21	0.08	0.56
85	*Gomphonema angustum*	14	7.4	4.5	0.28	0.06	1.32
86	*Denticula kuetzingii* Grun. 1862	13	4.0	31.7	0.51	0.02	12.50
87	*Epithemia adnata* (Kütz.) Bréb. 1838	13	8.2	2.5	0.64	0.21	1.92
88	*Epithemia turgida* (Ehrenb.) Kütz. 1844	11	6.2	3.6	0.43	0.07	2.62
89	*Rhopalodia gibba* (Ehrenb.) O. Müll. 1899	26	3.2	57.5	0.80	0.18	3.45
90	*Nitzschia hungarica* Grun. 1862	9	5.9	4.3	1.72	0.12	24.43
91	*Nitzschia acicularis* (Kütz.) W. Sm. 1853	6	2.0	10.0	0.24	0.09	0.67
92	*Nitzschia liebetruthii* Rabenh. 1864 fo. 1 PISCES	26	8.1	42.3	24.27	0.96	369.31
93	*Nitzschia liebetruthii* fo. 2 PISCES	33	9.0	74.0	5.09	0.27	96.61
94	*Nitzschia* cf. *bacillum* Hust. in A. Schmidt *et al.* 1922	4	3.5	2.1	0.09	0.06	0.14
95	*Nitzschia perminuta* Lange-Bertalot 1980	9	4.0	42.6	33.19	14.89	73.96
96	*Nitzschia palea* (Kütz.) W. Sm. 1856	20	9.1	15.4	0.69	0.11	4.33
97	*Nitzschia palea* var. *tenuirostris* sensu Lange Bertalot 1976 nec. Grun. in Van Heurck 1881	7	3.3	3.9	0.33	0.01	7.52
98	*Nitzschia amphibia* Grun. 1862	28	3.5	47.5	0.77	0.12	4.94
99	*Nitzschia obtusa* W. Sm. 1853	9	5.6	2.7	12.02	1.36	106.66
100	*Nitzschia* cf. *fonticola* Grun. in Van Heurck 1881	4	2.0	13.4	0.20	0.00	12.85
101	*Nitzschia frustulum* (Kütz.) Grun. in Cleve & Grun. 1880 fo. 1 PISCES	30	10.7	52.6	16.79	0.32	369.31
102	*Nitzschia frustulum* fo. 2 PISCES	20	5.7	25.4	8.18	0.09	369.31
103	*Nitzschia paleacea* (Grun. in Cleve & Grun.) Grun. in Van Heurck 1881	13	2.7	59.3	2.36	0.04	123.88
104	*Nitzschia radicula* Hust. 1942	21	1.9	44.0	0.58	0.10	3.33
105	*Nitzschia* cf. *communis* Rabenh. 1860	22	6.2	24.8	54.33	2.55	369.31
106	*Surirella* sp. 1 PISCES	8	2.3	31.1	4.36	1.00	19.01
107	*Chaetoceros muelleri* var. *muelleri* Lemm. 1898	7	2.8	15.8	19.72	3.17	122.74