DISPLAY ONLY

ISSN 1366-7300

ENVIRONMENTAL CHANGE RESEARCH CENTRE

University College London

RESEARCH REPORT

No. 3

Diatom / Water chemistry transfer functions for salinity, water-level and climate reconstruction

S. Juggins, R.W. Battarbee & S.C. Fritz

Final Report for the NERC Paleaoclimate Special Topic Award:

GST/02/494

1993

Environmental Change Research Centre
University College London
26 Bedford Way
London
WC1H 0AP

Table of Contents

List of Tables

List of Figures

Appendix 1

Appendix 2

1 Project Objectives

In arid and semi-arid regions the chemistry of closed-basin saline lakes responds directly to changes in the hydrological budget through the dilution or evaporative concentration of dissolved salts. Of the various biological indicators preserved in the sediments of these basins diatoms are one of the most useful, as a direct record of past water chemistry, especially palaeosalinity, and as an indirect measure of water level and climate change.

In the Northern Great Plains of North America (NGP), we have been developing quantitative approaches to salinity reconstruction using diatom-based transfer functions. Previous work has made progress in (i) clarifying diatom-taxonomic problems (Battarbee *et al.* 1983), (ii) constructing a modern diatom / salinity calibration dataset (Fritz & Battarbee 1988), and (iii) carrying out diatom analysis of cores from two sites, Devils Lake (Fritz 1990; Fritz *et al.* 1991), North Dakota, and Medicine Lake, South Dakota (Radle *et al.* 1989). This project aimed to extend this work by:

1. Exploring in detail the relationship between diatom assemblages and water chemistry for the calibration dataset, in relation to the adequacy of the existing dataset for the generation of a salinity transfer function, and its potential for generating transfer functions for secondary environmental gradients of cation and anion ratios.

2. Assessing the performance of a range of numerical approaches to the creation of a diatom / salinity transfer function and estimating the accuracy of prediction using a computer intensive method of cross-validation.

3. Applying the transfer function to existing late-glacial and Holocene cores from three sites, Medicine Lake, Devils Lake, and Pickerel Lake (Haworth 1972), which today span the gradient from hypersaline to freshwater, and which are known to have undergone major fluctuations in salinity or water level in the past.

4. Assessing the suitability of the transfer function for use in other saline lake regions, and its compatibility with other calibration datasets, e.g. for Africa.

2 Progress

All of the above objectives have been successfully achieved.

Statistical analysis of the existing diatom calibration dataset with respect to the main chemical gradients has been completed and results presented in Fritz *et al.* (in press). Comparison of the performance of different methodologies for quantitative salinity reconstruction is complete and reported in Juggins *et al.* (submitted a). The diatom taxonomy of Devils, Medicine and Pickerel Lakes has been harmonised with that of the calibration set. A diatom / salinity transfer function has been generated using weighted averaging and has been applied to the long core from Devils Lake (Fritz *et al.* 1991). A salinity reconstruction for Medicine Lake has been generated and compared with that from Devils Lake in Juggins *et al.* (submitted a).

Comparison of the NGP dataset with those from other regions has proceeded at three workshops (Appendix 1) and has led to the development of the CASPIA project and working group on salt-lake diatoms (Juggins *et al.* submitted b). In addition a large database of site, diatom, and environmental information has been created and will be made available to CASPIA participants (see 3.2 below).

3 Development of Methods & Techniques

3.1 New computer software

Four computer programs for use on IBM PCs have been developed to perform the various transfer function methods described in Section 4.2: 'WAPLS' - weighted averaging and weighted averaging partial least squares, 'MAT' - modern analogue technique, 'CA' - correspondence analysis regression and canonical correspondence analysis of environmental classes, and 'GLR' - Gaussian logit regression by maximum likelihood. These programs will shortly be made 'public domain' and placed at the anonymous ftp site *geology.wisc.edu.*

3.2 Database development

All data from the project are stored on the ECRC DISCO database running under ORACLE on a UNIX workstation. A PC version of this database is also being developed to facilitate the comparison and sharing of data from additional calibration datasets from other saline-lake regions (Section 4.4). The PC database currently contains information from c. 400 sites in North and South America and Africa.

4 Summary of Results

4.1 Relationships between diatom assemblages and water chemistry

A database of 66 calibration samples has been compiled from existing lake surface-sediment diatom samples and associated water chemistry analyses collected from Saskatchewan, North Dakota and South Dakota (Figure 1a). The dataset spans the range from freshwater to hypersaline (Figure 1b). Most lakes are dominated by sodium and magnesium sulphate, although carbonate and chloride lakes also exist (Figures 1b & 1c). Site locations and full chemistry for the calibration set are listed in Fritz *et al.* (in press), and reproduced in Appendix 2.2.

Canonical correspondence analysis (CCA) of the combined diatom / chemistry dataset reveals that diatom distribution is strongly and significantly related to salinity / conductivity and brine type ($p < 0.05$, assessed by 99 Monte Carlo permutations; Figure 2). Partial CCAs in which the effect of salinity, conductivity and lake depth were partialed out show a significant variation in diatom assemblages along the gradient from carbonate / bicarbonate to sulphate dominated waters (Fritz *et al.* in press).

The strong first-axis relationship between diatom composition and salinity is illustrated in Figure 3, which shows a plot of species optima (abundance-weighted means) and tolerances (abundance-weighted standard deviations) along the salinity gradient, from freshwater taxa such as *Aulacoseira ambigua* and *A. granulata* to hypersaline *Cyclotella* species and *Navicula bulnheimii*. Authorities, summary statistics and salinity optima and tolerances for all taxa greater than 1% in any one sample are listed in Appendix 2.2. The continuous distribution of the optima from 1 to c. 30 g l^{-1} shows that there are good indicators across the whole of this range and that prediction should be equally good across the range. Outside these limits the transfer function may be less accurate and it is clear that, as a result of the lack of very fresh sites in the dataset (< 0.5 g l^{-1}), the salinity optima of some taxa (e.g. *Aulacoseira* spp. and *Fragilaria* spp.) is overestimated in Figure 2. Additional samples have been collected from sites less than 0.5 g l^{-1} and will be used to extend the dataset and refine the estimates of the salinity optima and tolerances of freshwater taxa.

The significant relationship between diatom abundance and brine-type indicates the potential for developing transfer functions for reconstructing past changes in ionic ratios. However the small number of carbonate / bicarbonate (7) or chloride (1) dominated lakes in the dataset prevent this at present. Additional carbonate-dominated lakes have also been sampled to extend the dataset to allow the generation of transfer functions for ionic ratios.

4.2 Comparison of numerical methods

On the basis of the strong relationship between diatoms and salinity seven different numerical approaches were used to derive transfer functions between diatom relative abundances and $\log_{10}$ transformed salinity. These were correspondence analysis regression (CAR), canonical correspondence analysis of classes (CCAC), weighted averaging (WA) and tolerance downweighted weighted averaging (Tol-WA), weighted averaging partial least squares (WAPLS), maximum likelihood (ML), and modern analogues (MA). The performance of each method was assessed on the basis of (i) the root mean square of the error (RMSE), and (ii) the maximum bias along particular parts of the salinity gradient, each calculated for the whole calibration set to give 'apparent errors', and by jackknifing or 'leave-one-out' to give a more realistic estimate of the true prediction error.

Comparing apparent and prediction errors for each method shows the latter are 16-62% higher (Table 1), highlighting the importance of using a robust method of error estimation. Similarly, with the exception of CAR, all methods perform well as assessed by the apparent errors, but there are large differences between methods when the prediction errors are considered. Considering the prediction RMSE and bias, WA, Tol-WA, and CCAC give the best performance, although computational and model simplicity, and direct interpretation of regression coefficients (as species' optima) favour WA.

These results indicate that weighted averaging is the most reliable method for use with the NGP dataset, and that it can be used to derive a transfer function for inferring palaeosalinity with a prediction error of approximately 0.3 $\log_{10}$ units (Juggins *et al.* submitted a). The relationship between observed and diatom-inferred salinity using the

weighted average transfer function is shown in Figure 4.

4.3 Application of the transfer function to late-glacial and Holocene cores

After a process of taxonomic harmonisation to ensure taxonomic consistency between the calibration dataset and core data the weighted average diatom / salinity transfer functions has been applied to existing ^{14}C-dated late-glacial and Holocene diatom cores from Devils Lake, (North Dakota), Medicine Lake, (South Dakota), and Pickerel Lake, (South Dakota), (Figure 5).

Figures 6-8 show the late-glacial and Holocene diatom stratigraphy for Devils Lake, Medicine Lake, and Pickerel Lake respectively, with reconstructed salinity and jackknife-estimated errors. For each site taxa have been arranged according to their salinity optima, with freshwater species on the left. Also shown is the squared chord distance dissimilarity between each fossil sample and its closest modern analogue, with the dashed line indicating a cut-off for fossil samples that have no good analogues in the calibration set.

Despite the differences in present-day surface area and salinity of Devils Lake and Medicine Lake the two sites show broadly similar salinity histories (Figures 6, 7 and 9). Both started the early Holocene as freshwater lakes. At Medicine Lake salinity increased gradually after 9600 BP, and reached its maximum by c. 8000 BP. Devils Lake remained fresh until about 8200 BP when the salinity abruptly rose to 40 g l^{-1}. The high salinities recorded at both sites between 8000 BP and 7000 BP suggest that this is the time of maximum Holocene aridity. After 7000 BP salinities gradually fell at Devils Lake but were maintained at Medicine Lake until a period of low salinity recorded at both sites between 3000 BP and 2500 BP. The period between 2500 BP and the present is characterised at both sites by rapid and extreme fluctuations. Additionally, comparison of reconstructed salinities with the 100-year instrumental salinity record for Devils Lake suggests that the drought of the 1930s and 1940s was exceeded in aridity on at least four occasions in the last 2000 years.

The diatom record at Pickerel Lake is dominated throughout by freshwater assemblages which have no, or poor analogues in the modern dataset (Figure 8). Reconstructed salinities rise from 1.5 g l^{-1} in the early Holocene to 2.0 g l^{-1} at the present, and are certainly overestimates. Changes in the diatom record are interpreted as a response to a gradual increase in conductivity and nutrients as a result of soil development and erosion. There is no diatom evidence at this site for periods of climatically-induced high salinity or low lake-levels.

4.4 Assessing the suitability of the transfer function for use in other saline lake regions, and its compatibility with other calibration datasets

Comparison of the NGP diatom dataset with those from other saline-lake regions has proceeded at three workshops devoted to taxonomic, ecological, stratigraphic and statistical problems (See Workshop minutes in Appendix 1). At the first workshop in 1991 an initial comparison of the NGP dataset with a similar dataset developed for Africa by Francoise Gasse showed that although there were different dominant taxa in each dataset there was

considerable taxonomic overlap (Table 2), and that merging the two datasets would produce more powerful transfer functions by extending ecological gradients and providing more potential analogues for fossil samples. This was exemplified by a number of fossil assemblages in Africa characterised by small *Cyclotella* taxa that have no modern analogue in Africa but have potential analogues in the NGP.

As a result of these observations workshop participants set up the CASPIA project which aims to merge separate modern datasets from various saline-lake regions around the world, and, through a process of taxonomic harmonisation, generate a single dataset of modern diatom samples and water chemistry and habitat data for use in palaeoenvironmental reconstructions (Juggins *et al.* submitted b). The project currently has about 20 participants working on 10 regional datasets (Table 3, Figure 10) and has held two subsequent workshops focused on taxonomic problems and a programme of taxonomic quality control between laboratories (Appendix 1).

5 Conclusions

1. Statistical analysis of the modern diatom / water chemistry dataset using canonical correspondence analysis shows diatom distribution to be strongly and significantly related to total water salinity and brine type. The existing dataset is adequate for reconstructing salinities in the range 1 - 30 g l^{-1}, but there are too few carbonate/bicarbonate-dominated lakes for the relationship between diatoms and ionic ratios to be quantified. Additional samples have been collected to extend the dataset at both ends of the salinity gradient, and to give better coverage of carbonate/bicarbonate waters.

2. Comparison of the performance of seven numerical techniques shows weighted averaging to be the most robust method for deriving a diatom / salinity transfer function. The resulting transfer function may be used to reconstruct salinity with a prediction error estimated by jackknifing of approximately 0.3 $\log_{10}$ units.

3. The diatom stratigraphies from Devils Lake and Medicine Lake show that after a freshwater period during the late-glacial and early Holocene both sites were characterised by a series of oscillations between periods of high salinity and periods of freshwater or low to moderate salinity. Application of the transfer function to these cores significantly increases the information available from these cores by providing *quantitative* salinity reconstructions, allowing the absolute and relative magnitudes of these salinity fluctuations to be estimated. Preliminary results indicate that the period of maximum Holocene aridity occurred between between 8000 and 7000 BP, and that subsequent climatic fluctuations in the region were far more complex than the broad trends inferred from pollen and lake-level studies.

4. Comparison of the NGP dataset with other calibration sets at a series of workshops shows there is considerable taxonomic overlap between regions. As a result the CASPIA project has been set up to harmonise taxonomy between diatomists and laboratories and to merge individual datasets into a large, chemically diverse, central database. This will (i) allow the rapid distribution of taxonomic and ecological information in a consistent, machine-readable form, (ii) facilitate taxonomic

standardisation between laboratories, (iii) allow the development of more accurate transfer functions for salinity, and (iv) allow the development of transfer functions for other hydrochemical variables such as anion and cation ratios.

6 Future Research Arising from the Project

The project has identified the need to extend the calibration dataset to include more freshwater sites. This is required to enable more confident reconstructions of the Pickerel Lake core, and freshwater phases at Devils Lake and Medicine Lake. Partly as a result of the success of this project Fritz and Engstrom have obtained US-NSF funding which will allow the collection of additional freshwater samples, as part of a programme of palaeosalinity and palaeoclimate reconstructions in the NGP.

In addition, project has led to a number of successful research grant and studentship applications:

a) NERC Research Grant GR3/8854 to Battarbee, Juggins, Cox, and Sims at UCL and the British Museum, Natural History, 'Diatoms, salt lakes and climate change: inter-regional datasets and transfer functions for global application'. This two-year project will focus on the taxonomic harmonisation of the calibration datasets from the NGP and Africa, produce a diatom flora of this material for distribution to other laboratories, and derive new transfer functions for hydrochemical reconstructions. The project starts on March 1st. 1994.

b) British Council / Alliance Joint Research Programme (1993-94), 'Diatoms in saline lakes as a tool for reconstructing hydrologic and climate change in arid and semi-arid regions.' In collaboration with Francoise Gasse (Paris) this project is developing palaeoecological transfer functions using a modern diatom / chemistry dataset from Africa. These will be applied to fossil sequences to produce palaeosalinity maps of African lakes north of the Equator for the last 15000 years.

c) NERC studentship GT4/90/ALS/28 to David Ryves at UCL (1990-93), 'Diatom Dissolution in Saline Lakes: A case study from the Northern Great Plains of America'. This studentship has examined the effect of dissolution on the preservation of diatom assemblages, and its effect in biasing quantitative reconstructions.

d) NERC studentship GT4/91/ALS/23 to Jane Reed at UCL (1991-94), 'Palaeolimnology of Spanish salt lakes'. This studentship is investigating the potential of diatoms is Spanish salt lakes as indicators of climate change over the Holocene period.

And several pending research grant applications:

e) Joint Information Systems Committe, HEFC, 'Multimedia databases in micropalaeontology'. In collaboration with M. Barnsley (UCL, remote sensing) and A. Lord (UCL, geology) this project aims to develop software for the storage, retrieval and display of microfossil images, the integration of image and textural information, the computer-aided identification of taxa, and the rapid distribution of taxonomic information using CDROM or fast computer networks.

f) International Association for Promotion of Cooperation with FSU. 'Climate Change and Lake Sediments in South Eastern Russia and Southern Kazakhstan'. In collaboration with the Astrakhan Technical Institute of Fisheries and the Institute of Geography, Kazakh Academy of Sciences, this project aims to develop a diatom and ostracod core- and modern-sample approach to the study of past environmental change in these climatically sensitive regions.

7 Publications Arising from the Project

Fritz, S.C., Juggins, S., Battarbee, R.W. and Engstrom, D.R. 1991 A diatom-based transfer function for salinity, water level and climate reconstruction. *Nature* **352**, 706-708.

Fritz, S.C., Juggins, S. and Battarbee, R.W. Diatom assemblages and ionic characterization of freshwater and saline lakes of the Northern Great Plains, N.A.: a tool for reconstructing past salinity and climate fluctuations. *Canadian Journal of Fisheries and Aquatic Science.* (in press).

Juggins, S., Battarbee, R.W. & Fritz, S.C. Diatom / salinity transfer functions and climate change: an example from the northern Great Plains, North America. Proceedings of NERC/QRA 'Palaeoclimate '93' meeting, Durham. (submitted a).

Juggins, S., Battarbee, R.W., Fritz, S.C. and Gasse, F. The CASPIA project: diatoms, salt lakes, and environmental change. *Journal of Paleolimnology.* (submitted b).

8 Acknowledgements

We would like to thank Claire Keister and Liz Haworth for making available their original diatom data from Medicine Lake and Pickerel Lake.

9 Additional References

Battarbee, R.W., C.M. Keister & J.P. Bradbury 1983 The frustular morphology and taxonomic relationship of *Cyclotella quillensis* Bailey. *Proceedings of the Seventh International Diatom Symposium*, 173-184.

Fritz, S.C. 1990 Twentieth-century salinity and water-level fluctuations in Devils Lake, North Dakota: test of a diatom-based transfer function. *Limnology and Oceanography* 35: 1771-1781.

Fritz, S.C. & R.W. Battarbee 1988 Sedimentary diatom assemblages in freshwater and saline lakes of the Northern Great Plains, North America: preliminary results. *Proceedings of the Seventh International Diatom Symposium* 265-271.

Haworth, E.Y. 1972 Diatom succession in a core from Pickerel Lake, northeastern South

Dakota. Geological Society of America, Bulletin 83: 157-172.

Radle, N., C.M. Keister & R.W. Battarbee 1989 Diatom, pollen, and geochemical evidence for the palaeosalinity Medicine Lake, S. Dakota, during the Late Wisconsisn and early Holocene. *Journal of Paleolimnology* 2: 159-172.

Table 1 Performance of various transfer function methods using the Northern Great Plains dataset. Results are listed for the root means squared error ($\hat{x}$-x) and maximum bias in $\log_{10}$(salinity gl^{-1}) units, and are given as 'apparent' errors, estimated for the calibration set, and 'prediction' errors, estimated by jackknifing, a computer-intensive method of cross-validation.

Method		RMSE	Bias
Correspondence anal. regression	Apparent	0.30	0.24
	Prediction	0.35	0.28
Canonical CA of classes	Apparent	0.26	0.15
	Prediction	0.31	0.15
Weighted averaging (WA)	Apparent	0.22	0.10
	Prediction	0.32	0.10
Tolerance WA	Apparent	0.22	0.08
	Prediction	0.31	0.08
WA partial least squares	Apparent	0.22	0.10
	Prediction	0.32	0.10
Maximum likelihood	Apparent	0.21	0.25
	Prediction	0.34	0.49
Modern analog	Prediction	0.37	0.25

Table 2 Comparison of taxa between Northern Great Plains dataset and East African dataset of F. Gasse, in terms of number of occurrences, and maximum relative abundance (%) of each taxon. Within each dataset taxa are ranked in order of decreasing number of occurrences.

East Africa	N	Max
Nitzschia frustulum	88	85.3
Synedra ulna	87	17.0
Nitzschia amphibia	79	33.1
Nitzschia fonticola	79	88.0
Nitzschia palea	77	48.8
Gomphonema parvulum	67	57.7
Hantzschia amphioxys	64	6.0
Cyclotella meneghiniana	60	54.4
Stephanodiscus astraea	58	31.2
Aulacoseira granulata	56	90.2
A. granulata var. *angustissima*	56	80.3
Anomoeoneis sphaerophora	56	41.1
Aulacoseira ambigua	53	84.1
Nitzschia pusilla	53	48.8
Rhopalodia gibberula	53	57.5
Fragilaria brevistriata	52	20.0
F. construens var. *venter*	52	60.8
Navicula cincta	51	7.7
C. placentula var. *euglypta*	49	76.0
Cymbella turgida	48	10.3
Synedra acus	47	79.0
Aulacoseira agassizii	46	24.0
Synedra rumpens	43	50.0
Achnanthes minutissima	41	82.3
Gomphonema gracile	41	43.0
Amphora veneta	40	9.1
Cymbella muelleri	38	6.6
Epithemia adnata	38	17.0
Cymbella ventricosa	37	24.0
Amphora ovalis var. *libyca*	35	4.3
Gomphonema lanceolatum	34	19.2
Navicula seminulum	34	3.0
Navicula elkab	33	89.7
Amphora pediculus	32	26.1
Caloneis bacillum	31	8.0
Navicula halophila	30	24.3
Nitzschia bacata	30	9.7
Nitzschia lancettula	30	57.0
Thalassiosira rudolfi	30	65.2
Navicula cryptocephala	28	15.4
Rhopalodia gibba	28	7.0

Northern Great Plains	N	Max
Cyclotella meneghiniana	42	46.0
Chaetoceros cysts undiff.	38	60.1
Synedra pulchella	31	7.7
Anomoeoneis costata	30	22.0
Cyclotella quillensis	30	95.0
Synedra fasciculata	29	13.1
Nitzschia hungarica	28	11.8
Rhoicosphenia curvata	27	25.4
Amphora ovalis var. *affinis*	24	28.4
Campylodiscus clypeus	24	28.7
Nitzschia amphibia	24	12.3
Nitzschia [cf. *fonticola*]	24	68.0
Navicula cincta	23	64.7
Stephanodiscus parvus	23	68.6
Cymbella pusilla	22	48.7
Cocconeis placentula	22	41.9
C. placentula var. *lineata*	22	5.7
Stephanodiscus niagarae	22	13.0
Rhopalodia gibba	21	10.0
Surirella peisonis	21	36.8
Surirella ovata	20	5.8
Surirella striatula	20	4.2
Amphora coffeaeformis	18	11.6
Navicula halophila	18	5.9
Navicula oblonga	18	32.3
Navicula capitata var. *hungarica*	18	41.7
Cyclotella caspia	17	37.8
Nitzschia frustulum	17	17.9
Diatoma tenue var. *elongatum*	16	5.1
Mastogloia smithii var. *lacustris*	16	5.7
Navicula cuspidata	16	2.7
Stephanodiscus hantzschii	16	6.2
Stephanodiscus minutula	16	84.7
Amphora ovalis var. *pediculus*	15	4.2
Amphora veneta	15	5.9
Navicula capitata	15	20.0
Nitzschia frustulum var. *subsalina*	15	47.2
Nitzschia palea	15	5.8
C. placentula var. *euglypta*	13	8.3
Nitzschia tryblionella	13	3.0
Nitzschia apiculata	13	20.1

Table 3 The CASPIA Project, list of current participants and role.

Diatomists (modern datasets)

Rick Battarbee, University College London (Northern Great Plains, USA and Canada)
Sheri Fritz, Limnological Research Center (Northern Great Plains, USA and Canada)
Steve Juggins, University College London (S. Russia, statistics, database)
Francoise Gasse, Université de Paris-Sud (Africa, China, Australia, Madagascar)
Phil Barker, Loughborough University (Morocco, Turkey, taphonomy)
J. Platt Bradbury, USGS, Denver (Mexico, Argentina)
Brian Cumming, Queens University (British Columbia)
Peter Gell, University of Monash (Australia)
Leila Ben Khelifa, Université de Paris-Sud (Tunisia)
Sarah Metcalfe, University of Hull (Mexico)
Jane Reed, University College London (Spain)
Melanie Reidinger, Northern Kentucky University (Galapagos)
David Ryves, University College London (taphonomy)
Sue Wilson, Queens University (British Columbia)

Diatom taxonomy and iconograph production

Eileen Cox, British Museum Natural History
Pat Sims, British Museum Natural History
David Mann, Royal Botanic Garden, Edinburgh

Statistics and computing

John Birks, University of Bergen
Cajo ter Braak, Agricultural Mathematics Group, Wageningen

Figure 1 The Northern Great Plains modern diatom / chemistry dataset, showing (a) site locations, (b) anions and total salinity, and (c) cation composition, .

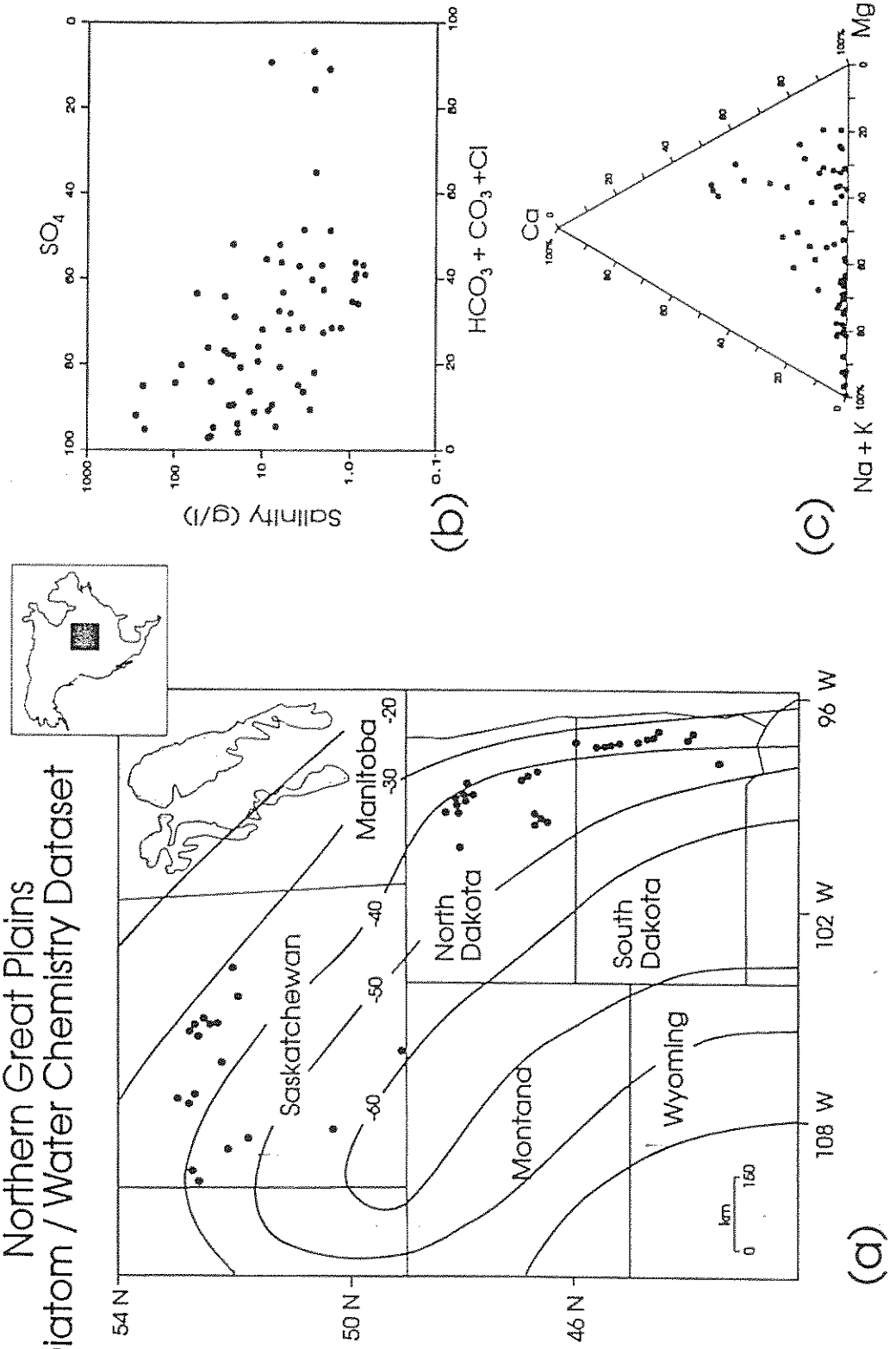


Figure 2 Canonical correspondence analysis ordination diagram (axes 1 & 2) of the NGP dataset.

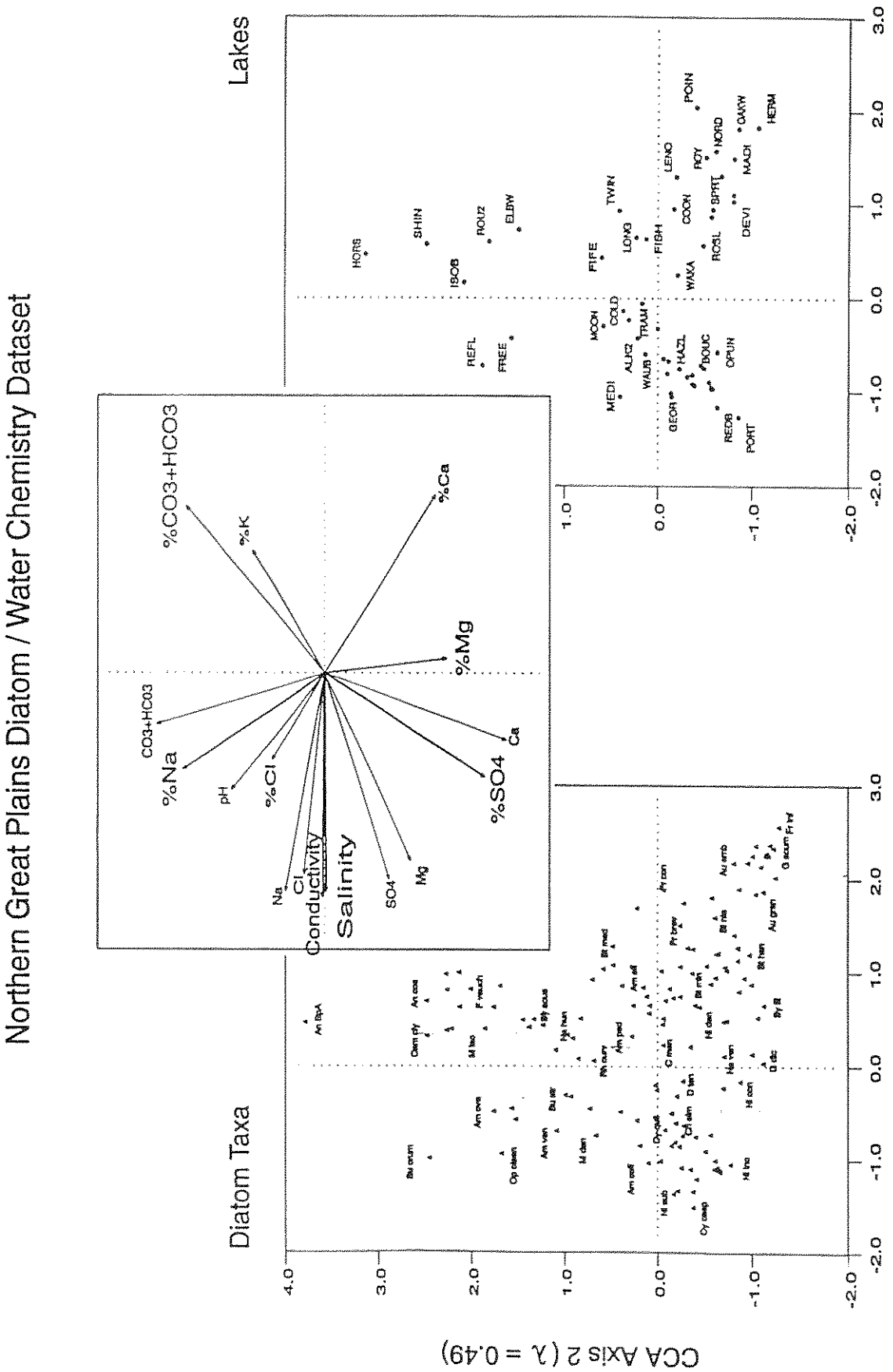


Figure 3 Salinity optima and tolerances of common taxa in the NGP dataset, calculated by weighted averaging.

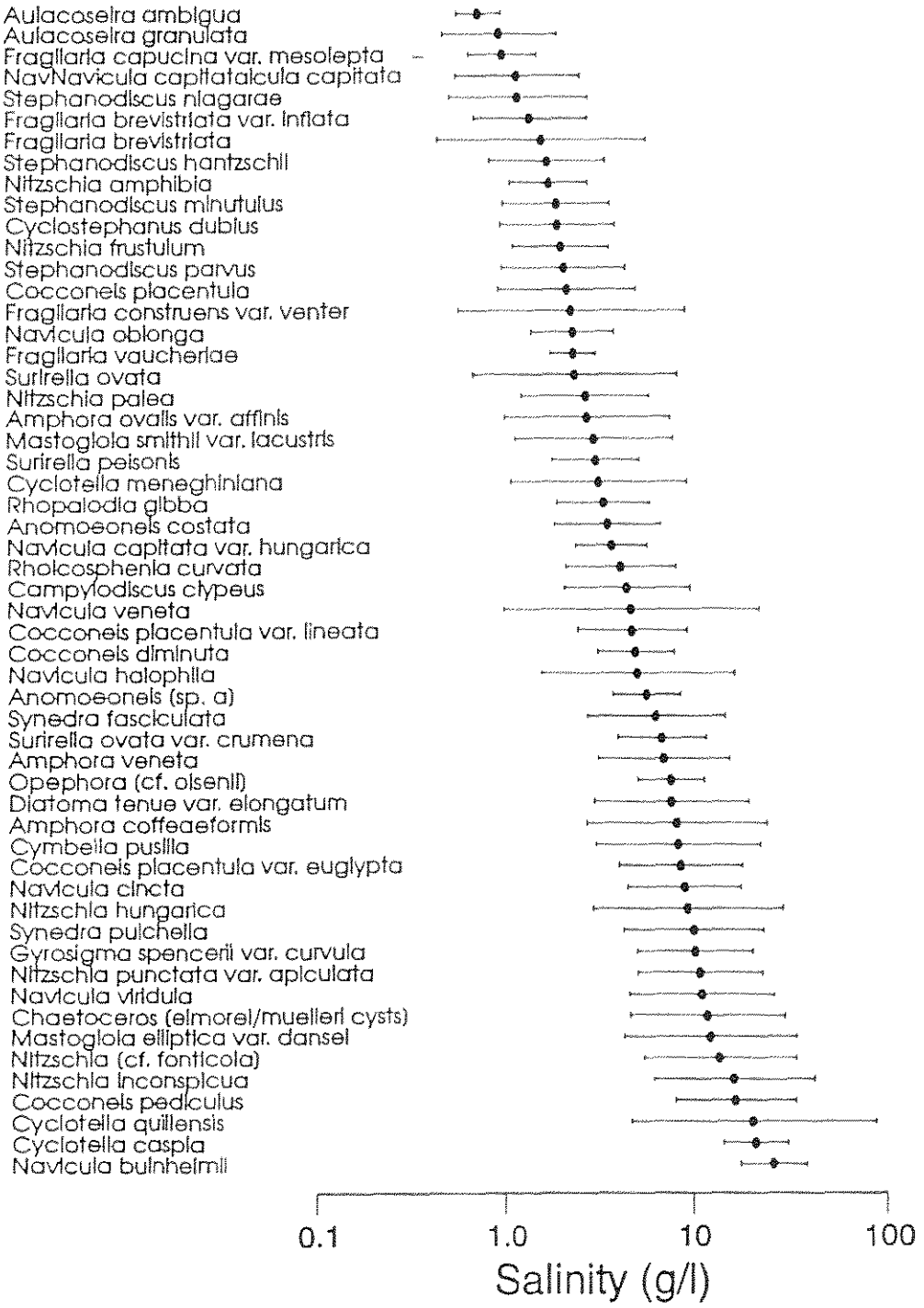
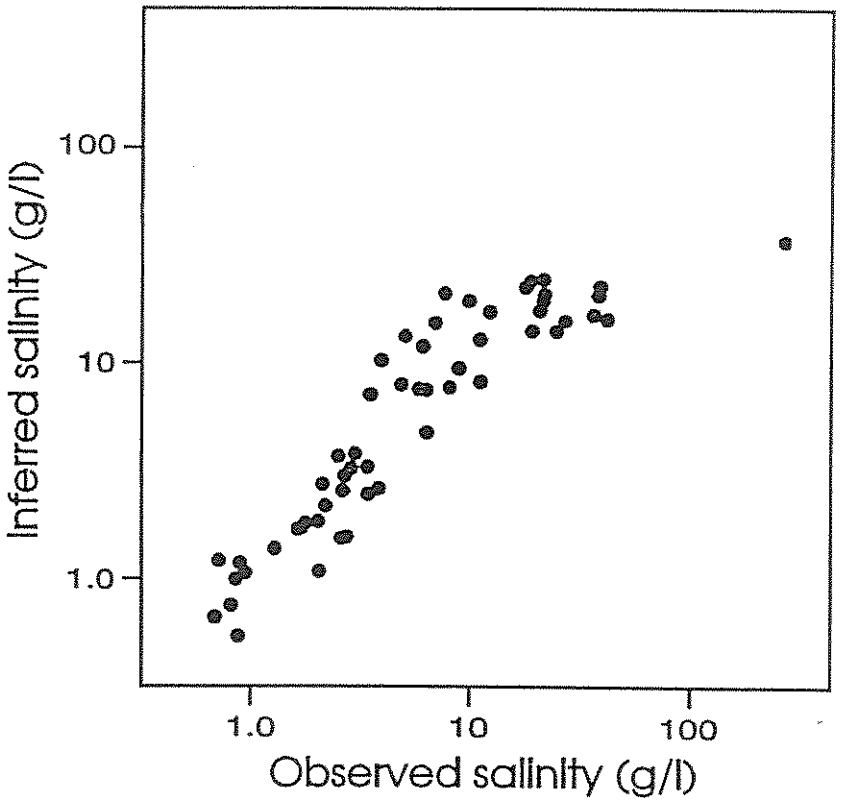


Figure 4 Relationship between observed and inferred salinity for lakes in the NGP calibration dataset, (r^2 = 0.84; RMSE = 0.22 $\log_{10}$ units; r^2_{jack} = 0.66; $RMSE_{jack}$ = 0.3 $\log_{10}$ units).



	Devils Lake	Medicine Lake	Pickerel Lake
Diatomist	S.C. Fritz	C.M. Keister	E.Y. Haworth
Surface Area (km^2)	55	1.8	3.9
Max depth (m)	8.5	9.0	13.4
Present salinity (g/l)	2.7	38.5	0.2

Figure 5 Devils Lake, Medicine Lake, and Pickerel Lake, site location, bathymetries, and summary statistics.

Figure 6 Devils Lake summary diatom diagram showing all taxa greater than 1% in any one sample, reconstructed salinity with jackknife errors, and chi-squared dissimilarity between fossil samples and modern dataset.

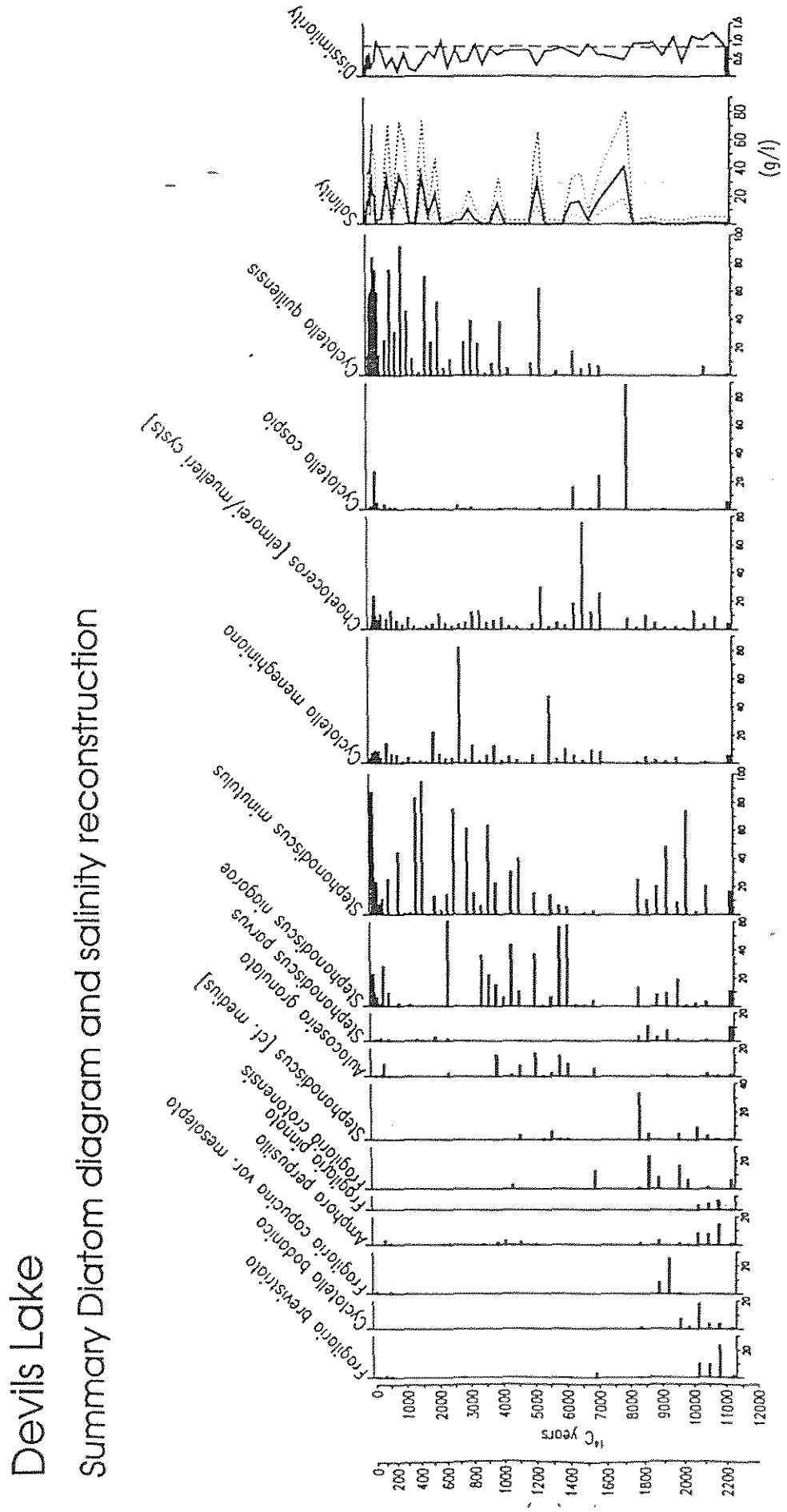


Figure 7 Medicine Lake summary diatom diagram showing all taxa greater than 1% in any one sample, reconstructed salinity with jackknife errors, and chi-squared dissimilarity between fossil samples and modern dataset.

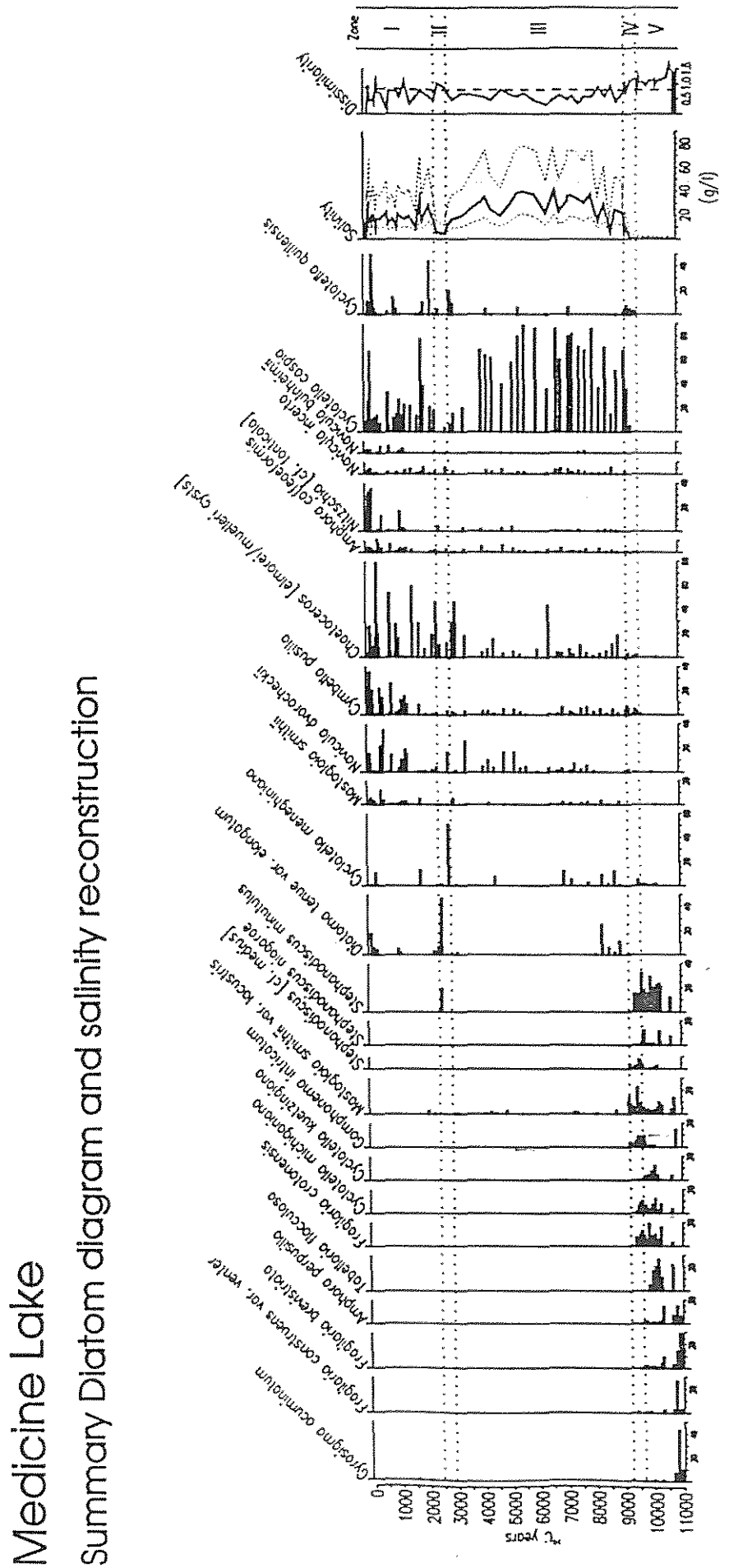


Figure 8 Pickerel Lake summary diatom diagram showing all taxa greater than 1% in any one sample, reconstructed salinity with jackknife errors, and chi-squared dissimilarity between fossil samples and modern dataset.

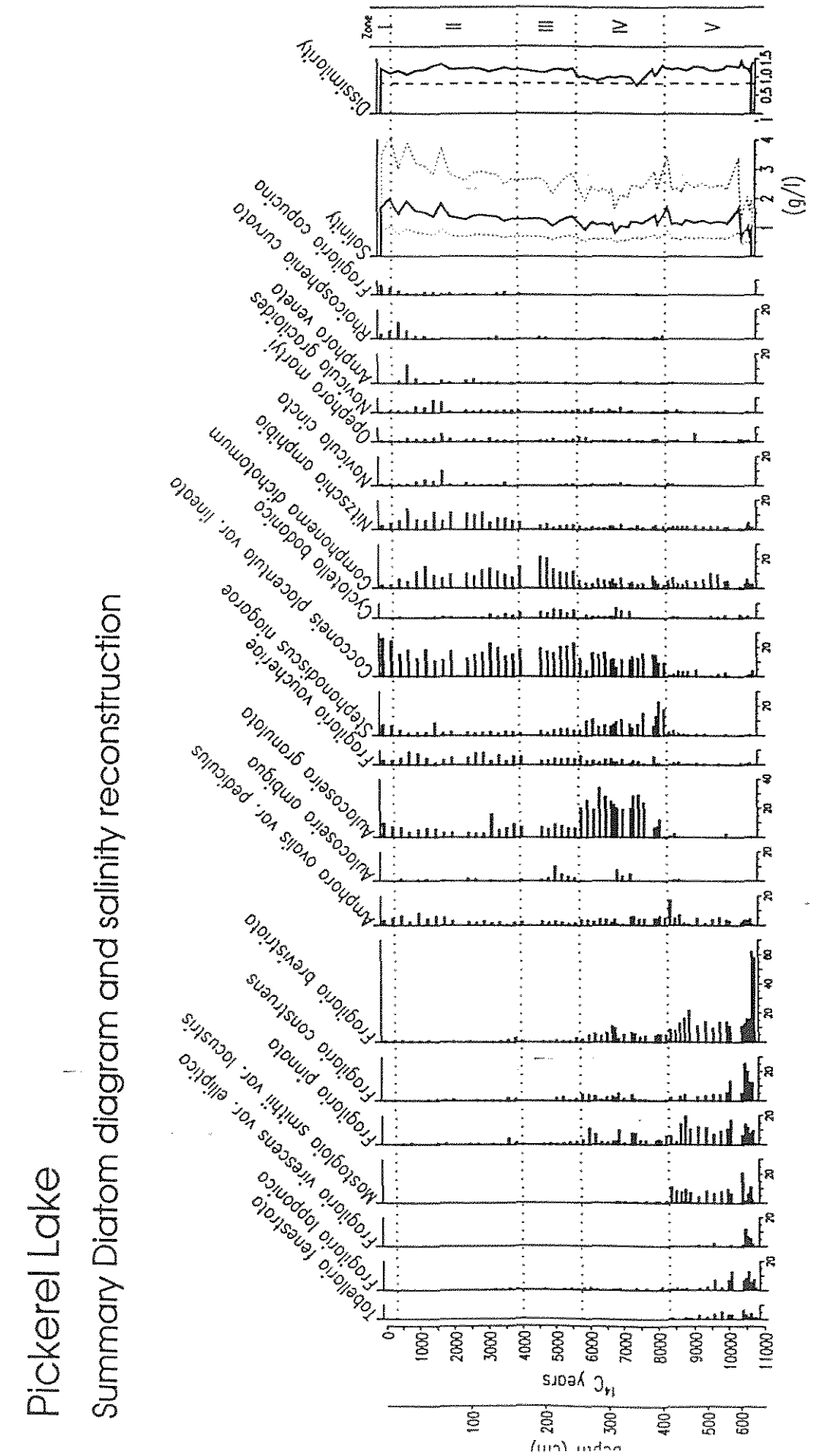


Figure 9 Devils Lake and Medicine Lake combined summary diagram showing main diatom taxa, reconstructed salinity with jackknife errors, and chi-squared dissimilarity between fossil samples and modern dataset.

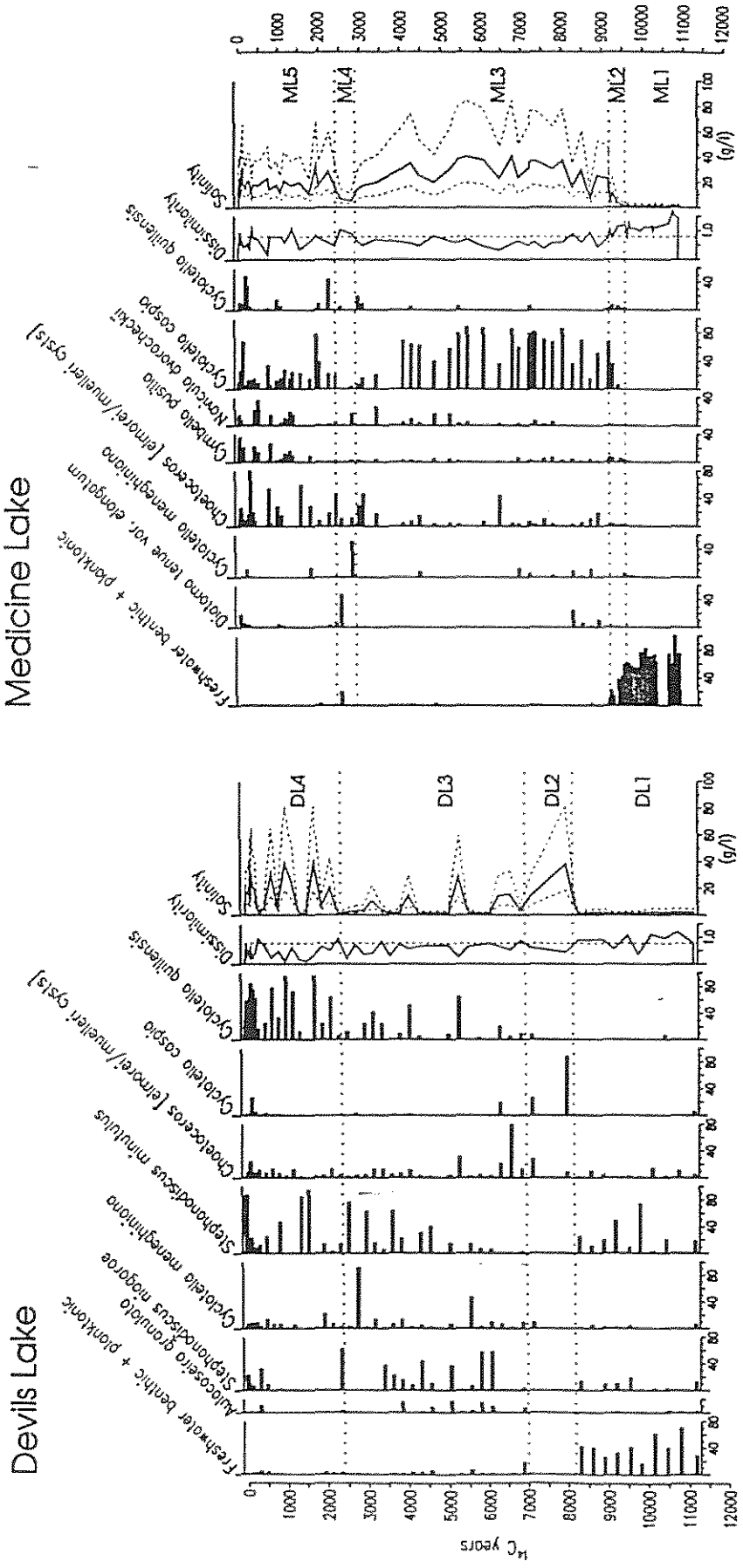
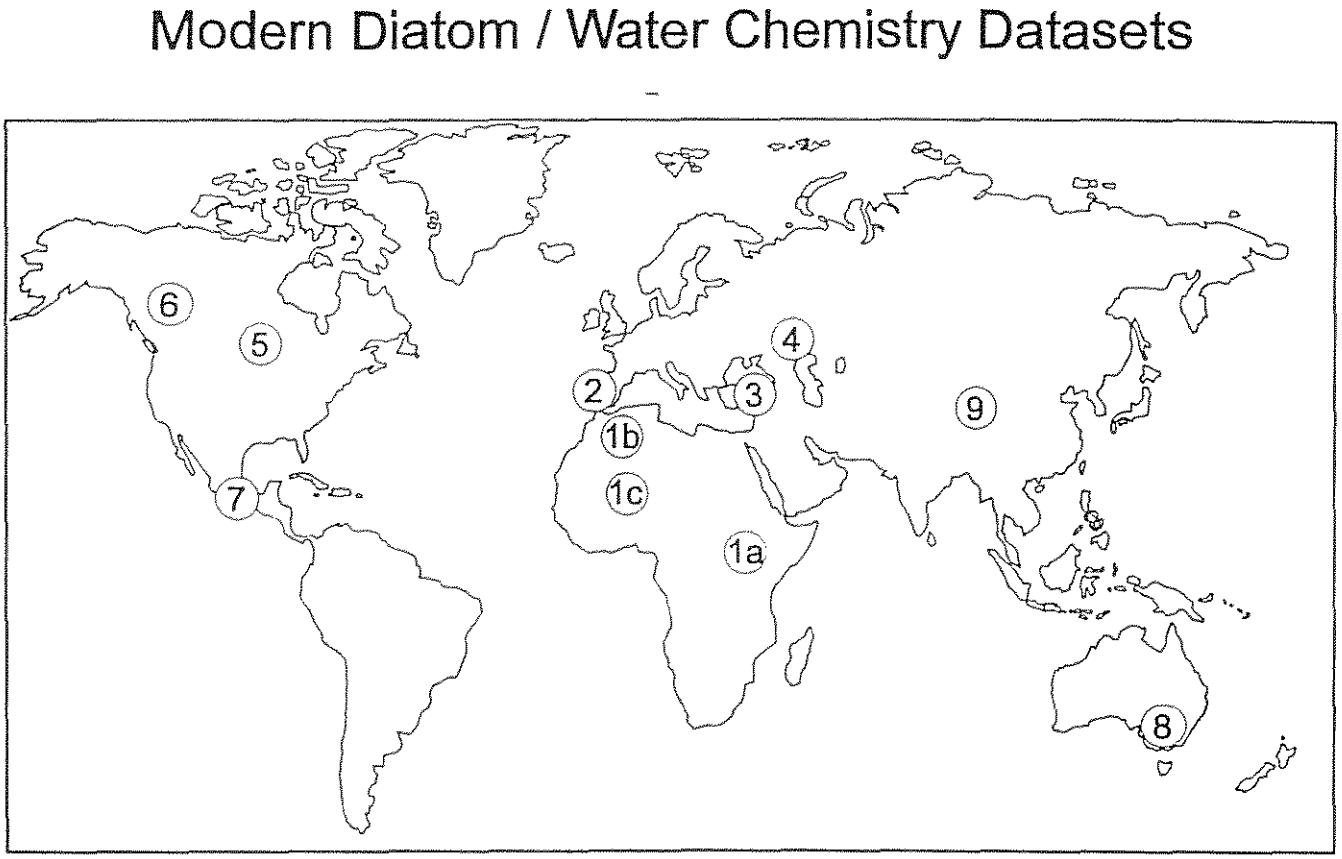


Figure 10 CASPIA Project, modern diatom / chemistry calibration datasets.



1	Africa	
1a	East Africa	Francois Gasse (n=170)
1b	North Africa	F. Gasse, Leila Ben Khelifa & Phil Barker (n=100)
1c	Sahara & Sahel	Francoise Gasse (n=60)
2	Spain	Jane Reed (n=60)
3	Turkey	Phil Barker (n=10)
4	Caspian Lowlands	Steve Juggins (n=10)
5	Northern Great Plains	Sheri Fritz & Rick Battarbee (n=95)
6	British Columbia	Sue Wilson & Brian Cumming (n=110)
7	Mexico	Sarah Metcalfe, Platt Bradbury (n=50)
8	S.E. Australia	Peter Gell & Francoise Gasse (n=90)
9	China	Francoise Gasse (n=30)

Appendix 1 Workshop Minutes

Minutes of the First CASPIA workshop, London 1991

Minutes of the Second CASPIA workshop, Paris 1992

Taxonomic notes from the Third CASPIA workshop, Melbourne 1993

Minutes of the First Saline Lake Workshop

(CASPIA)

held at UCL, April 8th-12th, 1991

Present :

Phil Barker, Rick Battarbee, Platt Bradbury, Roger Flower, Sheri Fritz, Françoise Gasse, Steve Juggins and David Ryves

Introduction

One of the main aims of CASPIA is to produce an ecological database allowing quantitative reconstruction of environmental variables through transfer functions. This entails collaboration at all stages, from standardisation of procedures for fieldwork, taxonomy and analysis to management of the database itself.

The range of lake salinity that CASPIA is concerned with ought to extend into the freshwater bracket (usually taken to be less than 3g/l TDS - Hammer 1986) and include as many saline lakes as possible, to cover the entire spectrum of salinity. At the moment there should not be any limits set as to exact salinity ranges, water types and so on.

The experiences of SWAP workshops can serve as a guide to those of CASPIA, particularly in the following areas :

1) Regular workshops
2) Taxonomic discussions and agreed guidelines
3) Quality control of participants in relation to (2)
4) Iconographs for in-house taxonomy
5) Museum involvement (especially taxonomic)
6) Database construction and statistical analyses

There are different, and greater, problems involved with saline lakes than freshwater systems but CASPIA can learn from the experiences of SWAP for international scientific collaboration.

1) Taxonomy

Lists of important species from the NGP (Sheri) and North Africa (Françoise) were produced from the separate databases, which for the NGP dataset included those of >1% abundance in two or more samples, and for North Africa (Algeria, Tunisia & Morocco), those of >5% abundance and 10 occurrences. The two lists were compared and taxa sorted according to 4 categories :

1 Appears only in one data set

2 Appears in both sets but common in one, rare in other - check?

3 Found in both datasets but:

a Probably no problem - check name/authority etc.
b Check for split with variety or similar taxon
c One of a difficult group, i.e. 3+ varieties in a species group

4 Unknown - needs work

Other taxa were added to this "master list" from East Africa (Françoise) and Mexico (Platt) and as a start to taxonomic standardisation, those taxa from category 3c were discussed during the week (see separate taxonomic guidelines). CASPIA agreed to the use of translation tables in the database which would allow individuals to work under their own systems but would standardise taxonomy for transfer function work within the database.

The NGP dataset consists of 66 lakes, of varying sizes (areas and depths) but most in the range 10^1-10^2 km^2. Salinity ranges from 0.8-100 ppt, but most lakes >50 ppt had no diatoms in the surface sediments. Most of the lakes are sulphate dominated, and pH 8-9. Water samples were taken of all the lakes at the time of surface sediment collection.

The African dataset includes 169 diatom samples and associated water samples taken from lakes, rivers, ponds and bogs, regionally divided into North and East African subsets. The African set covers a great range of lake sizes spread over a large geographical area, with salinity from 0.8-70 ppt, but this hides the enormous changes in water chemistry that can occur over very small spatial scales. Most East African lakes are of the carbonate/bicarbonate type, such that there is a relationship between pH, conductivity and salinity, while the North African subset includes sodium chloride as well as carbonate systems. Françoise has used the East African set for building pH transfer functions, and the North African for salinity.

Despite the differences in the lacustrine environments of Africa and North America, there are many taxonomic problems common to both. Although there is an apparent lack of common species in the surface sediment samples, the Holocene record from Africa includes many taxa found in the present day in the NGP dataset, so that the merging of the two datasets should solve many of the problems stemming from a lack of analogues in the individual sets. The relative lack of planktonic species in the African dataset may be related to water chemistry differences, but there is scope for increasing the African dataset by adding more lakes, especially from southern Africa.

Platt has data from 40 Central Mexican lakes, sampled in 1975, which include about 20 from Yucatan, dominated by calcium sulphate, with sodium chloride types towards the coast. There is

incomplete water chemistry data for the set, and many are only ephemeral lakes, showing great seasonal salinity variations. The diatom flora is very similar to that for East Africa, which may reflect similarities of water chemistry/geology, although the biogeography of diatoms must also be important. Sarah Metcalfe sampled 47 lakes in 1984-5 in Mexico, with considerable overlap with Platt's lakes.

There are other, smaller regional datasets which could be brought into CASPIA in due course, such as those from Australia and Tasmania (Pete Gell), Austria, Argentina and Chile/Tierra del Fuego. There might be problems of compatibility of such diverse sets, as even at the same salinity floras may be split into very different assemblages depending on ionic composition of the water as well as spatial (biogeographical) factors. This may make a truly global saline diatom database impossible, but need not preclude a hierarchical system based on regions of ecological space.

2) Dissolution and breakage

Discussion

CASPIA agreed that :

(1) There must be a standard procedure for collecting and preparing samples.

(2) Standardized indices of fracture and dissolution need to be developed.

(3) Steve and Rick can make a start on preservation indices using Rick's NGP countsheets from 1982 incorporating dissolution and breakage categories.

(4) Everyone can think about the boundaries and stages of preservation that individual species pass through, and where to split them in an objective system for counting on the LM.

3) Field sampling

Surface sediment samples

The main concern is to ensure that in the surface sediment sample represents as far as possible to the present day conditions found in the lake. Sites for coring must be chosen where reworking of older material is minimised, at least away from shallow areas where problems relating to water level fluctuations and perhaps wind-induced turbulence can be avoided.

It is not possible to give an absolute figure for the thickness of the surface sediment sample, as this depends on the rate of sediment accumulation and the rate of change of the water chemistry. From past experience, a thickness of up to 0.5 cms is about right for the top sample, but probably not much greater unless lake sedimentation and hydrology is known. Samples can be taken every 0.5 cms from the top of a short core to check that there are no significant differences between the top 0.5 cm level and that just below. The surface slurry can be separately sampled to distinguish the most recent (seasonal) crop.

Sediment traps

Sediment traps below the photic zone are useful for studying seasonal fluxes and the taphonomy of sedimentary assemblages, and are best emptied seasonally or at least annually. There may be problems of reworking and resuspension of sediment.

Live material

There are two approaches to live sampling as to whether to pool samples collected from all important habitats or not. If they are kept separately, the option is open to pool subsequently (but not vice versa). Live sampling ought to be as comprehensive as logistically possible, as different floristic assemblages of epiphytic diatoms (for example) can be found not only between plant species but between individuals within the same species. There is probably no need for artificial substrates.

Chemical analysis

Determination of the major anions and cations, including Si, P & N, will give the total salinity of the water (as TDS) as a by-product. In the field, the only measurements that need to be taken are pH, conductivity and Secchi disc depth. There is probably no need for carotenoid/pigment analysis. Water chemistry types and salinity ranges not well covered in the lake database at the moment should be explicitly targeted to fill in the ecological gaps. The basic difficulty remains of relating water chemistry to the diatom assemblage, given the variability of the chemistry and diatom flora and the representativity of the sediment sample to the contemporary diatom and water chemistry.

4) Transfer functions and databases

Discussion

The dataset should be extended to fill in the gaps in terms of analogues. Part of the problem concerns the geographic distribution of assemblages, as equally saline waters (in terms of TDS) support different floras which could result from changes in the physico-chemical environments or from changes in the genetic populations through isolation (or both).

Sheri agreed to investigate the most suitable database packages for CASPIA on the Apple Mackintosh system, with feedback from Steve and others. This system should include a central system for updating the database.

5) CASPIA and the wider community

At the moment, there are 4 labs involved in CASPIA - those of Françoise, Sheri, Platt and Rick - but others could be added later if they wished.

Taxonomic notes from the workshops will be circulated to as wide an audience as interested without prejudice. Those wanting to join the database at a later date must follow the taxonomic guidelines agreed by CASPIA and contribute a "significant amount" of new information/sites. A full protocol will be developed at the next workshop.

Slide exchange and quality control

Slides should be replicated and a copy made available for each lab and/or some museums. Slide exchange between all 4 labs for quality control of some problem taxa was agreed :

Sheri	*Navicula*	from Waldsea
	Amphora & Navicula	from Sayer
Françoise	*Na. cryptocephala var. veneta* (F.518)	
	Nitzschia subacicularis (JT.13)	
	Ni. bacillum (KE/H.7)	

The count for quality control slides will be 500 valves, to be completed by February 1992, and the results graphed etc to test the similarity.

In addition, one slide from each dataset from lakes of 2, 15 & 50 g/l TDS will be exchanged as well, together with hard copies of the datasets.

Future workshops and funding

The next workshop (CASPIA II) will hopefully be in Paris in 1992 at about the same date (13-17 April), in Françoise's lab or the museum. The third workshop will hopefully be in Minneapolis in 1993.

Funding is needed for workshops, production of iconographs and database Mackintosh hardware and packages (at about $5000 each for the last two). Possible sources of cash include the French Embassy, NATO, IBM, BP and perhaps NOAA.

6) Iconographs and museum involvement

Dave Mann (Edinburgh) and Pat Sims (British Museum) joined the workshop on the last day to discuss the possibility of museum involvement in the production of a saline diatom iconograph.

There is at present a major re-evaluation of marine diatoms found off the coast of Britain, and this may have spin-off effects in terms of general diatom taxonomy. BP have begun to develop an electronic taxonomic database for forams, and although the software is not sufficiently developed for high-resolution diatom work, it is improving, but funding is a problem. Central taxonomic institutions should not just be warehouses for storage of specimens, but research centres actively involved in and supplying information on the taxonomy, physiology and ecology of plants, particularly in the case of diatoms which are the second largest plant group.

Dave and Pat agreed to begin a pilot study, in about 2 months time, into the feasibility of museum involvement in producing an iconograph for saline athalassic diatoms, using both LM and SEM photography, and perhaps eventually the dissolution series for selected species (involving ion beam etching?). Taxonomy could be left "floating" as long as there was internally consistent identification of taxa and the associated environmental variables.

This preliminary investigation will involve the taxonomy of the *Nitzschia fonticola* group from

slides selected by CASPIA using SEM (Pat) and LM (Dave), including site information. In future, copies of type slides agreed by CASPIA can be sent to Pat and Dave for further investigation as well as curation.

The cost of an iconograph can be split into costs of photography (film, SEM fees, developing and other materials), printing and travel. Funding for an iconograph of all 200-300 saline taxa in hard copy form could be incorporated into a funded 3 year project, with the eventual aim of updating it to an electronic imaging system when the technology and the price allow. It was agreed to cost and write up a proposal in the next few months for this work, which could draw on a number of projects involving diatoms, for instance in saline lakes, eutrophic lakes, in the Antarctic, in Tertiary stratigraphy, and in SWAP, all of which need hard-copy and eventually electronic iconographs. Funding agencies, even the public, could be approached, and links with the EC in Brussels are worth cultivating.

7) Final remarks

It was agreed to publicise CASPIA by :

(a) Putting a short notice in *Diatom Research*

(b) Sending a letter to people outside the group who might be interested

(c) Producing and circulating the taxonomic "master list"

(d) Producing a poster at the next diatomists meeting (Haarlem, Netherlands, summer 1992), including a preliminary outline of Dave Mann's ideas on an iconograph. This will be designed at CASPIA II.

Taxonomic guidelines of the First Workshop on Saline Lakes

(CASPIA)

held at UCL, April 8th - 12th, 1991

Nitzschia fonticola group

axon	Length	Width	Striae per 10µm	Fibulae	Shape	Ref.
itzschia fonticola	10-65	2.5-5.0	23-33 (28-30[1])	central space (9-16)	lan.	p.103 #104
itzschia bacillum	12-20	2.0-3.5 (5.0)	27-32	evenly spaced (12-16)	lan.	p.108 #113
itzschia lacuum	10-20	2.0-3.0	35-40	evenly spaced (13-18)	lan.	p.107 #112
itzschia frustulum	5-60	2.0-4.5	19-30 (20-23[1])	central space (10-16)	linear-lin./lan.	p.94 #89
(var subsalina)[2]			23-32 (29)	central space (15)	linear-rounded ends[2]	[2]

Data and references from Krammer & Lange-Bertalot, 1988 (KLB 1988) except :

[1] Hustedt ("Die Susswasser-flora Mitteleuropas", 1930)

[2] *Nitzschia frustulum var subsalina* from Hustedt (1930), p.415; #796, is called *Nitzschia inconspicua* in KLB (1988), p.95; no.90. Examples of the **shape** are in KLB (1988), plate 69, p.354; #1-13.

Split of the *frustulum/fonticola* taxa is based on the striae density, as shape is more of a continuum. For those indeterminates that exhibit striae density of 23-28/10µm, the category "*frustulum/fonticola*" is proposed.

Similarly, the *bacillum/lacuum* split may prove difficult for any with striae density of 32-35/10µm, for which the category "*bacillum/lacuum*" is suggested.

Nitzschia inconspicua probably also includes *Nitzschia frustulum vars. perpusilla* and *perminuta*.

Slides will be ciculated for quality control of these divisions as follows :

Sheri	1 of *Ni. fonticola* from Big Quill 1 of *Ni. inconspicua* from Eckelson
Françoise	2 of *Ni. bacillum* (one freshwater, one saline)
Platt	1 of *Ni. frustulum* and/or *inconspicua* from Mexico

B) *Cyclotella caspia*

Cyclotella caspia is the same from the Northern Great Plains (NGP) and fossil African slides - Françoise to send over samples for LM & SEM. Rick to circulate SEM photos.

Reference : Hustedt ("Die Kieselalgen", 1930) Vol I, p.347, no.68; p.348, #177.

C) *Nitzschia punctata var apiculata/Nitzschia compressa*

Françoise has *Ni. punctata* forma minor, thought to be the same as *Ni. punctata var apiculata* - agree to rename as *Ni. compressa* forma minor.

References :

Hustedt ("Diatomeen-flora von Java, Bali und Sumatra", 1938), plate XL; #31 & #32 - given as *Ni. punctata* formae minores.
Gasse (1986), p.140; plate 31, #7 & #8 - given as *Ni. punctata* forma minor.
KLB (1988) transfers *Ni. punctata* to *Ni. compressa* which CASPIA agrees to follow, and plate 37, p.290; #6, #7 & #8 agree with forma minor.

D) *Nitzschia palea*

Françoise has distinguished a taxon *Ni. palea var debilis* but agrees to recombine with the nominate.

Reference : KLB (1988), p.85; no.80 - plate 59.

E) *Nitzschia* species 5 (and 4?) - Sheri's NGP data set

Both taxa are from Sayer Lake - Françoise thinks they are both forms of *Ni. subrostrata* (planktonic). Occur in African saline lakes at salinities of 15-30 ppt.

Reference : Gasse (1986), plate 36; #21.

CASPIA agrees to follow KLB (1988, p.118, no.130) who suggest

that *Ni. subacicularis* is synonymous with *Ni. subrostrata* and agree to use *Ni. subacicularis*.

Reference : KLB (1988) p.118; plate 67, #4-#10.

Nitzschia confinis still exists in the literature (for example Lange-Bertalot & Krammer 1987, p.12; plate 33, p.212 - #8-#10A) but Françoise has material which shows a continuum of forms. As it is difficult to separate it from *Ni. subacicularis*, CASPIA agrees not to recognize *Ni. confinis* but to subsume it under *Ni. subacicularis*.

F) ***Navicula cincta* group**

Na. cincta - references agreed :

KLB (1986), plate 28, p.496; #8-#15 (central area)
KLB (1985), plate 17, p.164; #6 (originally given as *Pinnularia cincta*).

Na. cincta forma minuta - reference : KLB (1986), plate 28, p.496; #16. Only difference is a finer appearance - more samples are needed to validate this.

Navicula cincta var heuflerii

CASPIA agree to rename *Na. cincta var heuflerii* as *Na. erifuga*. Called *Na.* affinis *cincta* in Sheri's NGP data.

References :

KLB (1985), p.69 : plate 17; #10-#12 (given as *Na. cincta var heuflerii)*
KLB (1986), p.116; no.43 (given as *Na. erifuga*).

Françoise has *Na. cincta var heuflerii* but this is probably *Na. heuflerii var leptocephala* (reference : Patrick & Reimer, 1966, Vol I, p.515; no.15).

G) ***Navicula halophila* & *Navicula elkab***

Na. elkab : 23-26 striae/10µm - ends rostrate-subrostrate.

Reference : Gasse (1986), p.93; plate 15 - #11-17; plate 16 - #10-#12.

Na. halophila : 15-24 striae/10µm.

Reference : KLB (1986), p.126, no.62.

Na. halophila var subcapitata : based on shape.

Reference : Gasse (1986), plate 16; #1.

Na. halophila var tenuirostris : based on shape.

Reference : Patrick & Reimer (1966), p.552; plate 44; #5.

Na. pseudohalophila

Reference : Schoeman & Archibald (1976-1980), No.2 (February 1977); #1-#39.

H) *Navicula cryptocephala* group

Na. cryptocephala : rounded central area and rostrate, drawn out ends.

References : Gasse (1986), plate 19; #10
KLB (1986), plate 31, p.502; #8-#13

Na. cryptocephala var veneta : CASPIA identify this taxon as *Na. veneta* from KLB (1986). Rectangular central area with regular, short striae in central area, and broad, subrostrate ends.

References : Gasse (1986), plate 19; #20-#22
KLB (1986), plate 32, p.504; #2-#4

Na. cryptonella : distinguish by its much smaller central area, formed by irregularly shortened striae. Regular shape - ends not drawn out.

Reference : KLB (1986), plate 33, p.506; #10 & #11.

I) *Navicula bulnheimii*

Occurs in both data sets - Sheri had it as *Navicula* species 5.

References : KLB (1986), p.552 : plate 56; #6 & #7
Simonsen (1987), Vol. II, plate 132; #17-#26 (as *Navicula longirostris*).

J) *Amphora* group

Am. perpusilla & *Am. ovalis var pediculus* : CASPIA maintains the distinction between these taxa, based on the key feature of the raphe.

References : Patrick & Reimer (1966), Vol. II - part 1, p.69-70; plate 13 -:
#8a-#11b - *Am. perpusilla*
#5a-#6b - *Am. ovalis var pediculus*

Am. inariensis Krammer : needs work.

Reference : KLB (1986), p.742; plate 150; #1-#6

Am. coffaeiformis var borealis : Françoise uses Cleve-Euler, 1953, Vol. III : #685c - smaller form with punctate striae in centre.

Am. macilenta : 9-13 striae/10µm - Cleve-Euler, 1953, Vol. III : #686A

Am. coffaeiformis : 13-20 striae/10µm.

Am. acutiuscula : Archibald & Schoeman (1984) give a good description, with clearly punctate striae (as opposed to *Am. coffaeiformis*).

K) Small *Stephanodiscus* species

It was agreed to defer consideration of the small *Stephanodiscus* spp. until the next workshop, but to take SEMs of them and consult the literature in preparation.

Minutes of the Second CASPIA workshop

Paris May 8th-13th, 1992

Participants: Francoise Gasse (Paris), Sheri Fritz (Minnesota), Steve Juggins (UCL), Philip Barker (Loughborough), Leila Ben Khelifa (Oxford & Paris), Brian Cumming (Queens), Sue Wilson (Queens), Peter Gell (Monash), Jane Reed (UCL), David Ryves ((UCL), Hui Fan (Paris), Tom Rhodes (Paris).

Introduction

The CASPIA project is concerned with the use of diatoms as indicators of salinity and ionic composition in inland waters. One of the main aims of the project is the production of an ecological database that will allow the quantitative reconstruction of environmental variables from fossil diatom assemblages through the use of transfer functions. Central to this work is the establishment of a common, harmonised approach to sample collection, diatom identification and nomenclature, and data storage and transfer, and these topics have been discussed at two workshops. The first was held at UCL in April 1991. These minutes describe the discussions of the second workshop, hosted by Francoise Gasse in Paris in May 1992.

The workshop concentrated on the examination of diatom material from Africa, North America, Australia and Spain, with special focus on the 'problem' groups identified at the 1991 workshop, namely members of the genera *Navicula*, *Nitzschia*, and *Amphora*. Sheri Fritz has already circulated notes of these discussions. If you did not receive a copy of these please contact Sheri or myself.

Between the taxonomy sessions members of the group gave informal presentations of their current work, and discussions followed on database development, iconographs, TQC, sources of funding, and publicity.

Modern Diatom / Chemistry Datasets

Several modern salt-lake diatom / chemistry datasets have been developed, or are being developed, in various parts of the world. Leading on from their taxonomic harmonisation, the amalgamation of these datasets will provide a powerful tool for both environmental reconstructions and for studies of diatom eeology and biogeography.

Opening the discussions Sheri Fritz described the background to the CASPIA project, with the initial desire to integrate the African (Gasse) and Northern Great Plains (NGP) (Fritz & Battarbee) modern datasets. One of the motivations for this work is that several fossil assemblages from African lakes have no analogue Africa today (e.g. planktonic assemblages dominated by *Cyclotella caspia*), but that analogues for these probably exist in the NGP dataset.

Northern Great Plains dataset

Sheri then described the NGP dataset of 66 lakes ranging from 0.5 to >100 gl^{-1}, and current work extending this by c. 30 additional lakes. These new samples were chosen to broaden the range into freshwaters, and to add more carbonate dominated lakes. The original samples consisted of surface sediments c. 3cm thick, which was probably too thick (although the lakes have rapid accumulation rates). The new samples consists of the top 0.5cm. The original dataset has been used to generate a salinity transfer function using weighted averaging which was applied to a Holocene core from Devil's lake. Additional analysis of this data shows significant response to diatoms to salinity and ion type. A discussion of the use of optima and tolerances followed, with the observation that taxa can show different ranges in different ion types, but that this has yet to be quantified. It was also pointed out that comparison of optima and tolerances between datasets is difficult unless the sampling range of each dataset is taken into account.

Sheri also described her current work looking at a transect of cores along an effective moisture gradient in the NGP region, and the work of a graduate student Kate Laird, on the seasonality and taphonomy of planktonic and periphyton diatoms in 6 lakes.

Canadian datasets

Brian Cumming and Sue Wilson described work on the PISCES I project (with J. Smol at Queens University) involving the generation of surface sediment datasets for two regions in CANADA, Cariboo/Chilcotin (Cumming) and Kamloops (Wilson). They also gave a brief report on a saline lake diatom taxonomy meeting held at Queen's University, March 21-23, 1992.

A total of 109 lakes were sampled, (65 in Cariboo/Chilcotin and 44 in Kamloops) covering a range 0 to >100 gl^{-1}. These were sampled in May and September 1991 for diatoms and chemistry, to give and idea of variability in chemistry and sediment diatom assemblage.

Brian indicated how the datasets will be used to generate transfer functions which will be used for environmental reconstruction in the PISCES II project.

Spanish dataset

Jane Reed described her work on salt lakes in southern Spain. Part of this work involves the development of a diatom / chemistry dataset for Spain, containing approximately 65 samples, spanning the range 0 to >100 gl^{-1}. Surface sediment samples (top 0.5 cm) were collected from each lake. Plankton samples and periphyton from the main habitats were also collected.

All the sites sampled for surface sediments were also examined for diatom preservation in short cores, with the aim to select suitable sites for long coring. A discussion followed on the problems of diatom preservation in relation to sediment type (and porosity) and lake permanence.

Australian dataset

Peter Gell described two datasets from western Australia. The first contains 32 lakes located in the Western Victoria volcanic plain, covering a range of 0.3 - 500 mS cm^{-1}. Samples consists of periphyton & phytoplankton. The second dataset contains sediment, plankton and periphyton samples from approximately 60 groundwater-fed lakes south of the Murray/Darling Basin.

Peter also described a sediment trap / monitoring study and proposed sediment-core work on three lakes, McGlashan's Lake, West Basin, and Lake Purrumbete.

African datasets

Francoise Gasse described three African datasets. The first, from East Africa, contains c. 160 sediment, plankton, and periphyton samples. The second, from the Sahel, contains about 60 samples, and the third, from North Africa, has about 50 samples. Francoise described the major chemical gradients in the datasets (conductivity, pH and ion type), and discussed the use of alkali / alkaline earth and $(CO_3+HCO_3)/ (Cl+SO_4)$ ratios in summarising the ionic composition. Previous work has derived transfer functions for pH and salinity from these datasets using the method of Gasse & Tekaia. Current work is developing new transfer functions for conductivity and exploring the quantitative relationships with ion type.

Francoise also described Baru Pond, Niger, a shallow stratified lake with surficial fresh and bottom saline waters. Sedimentary diatoms would contain a mixture of these two environments, so it was important to sample periphyton and associated chemistry. A discussion followed on sampling methods. Periphyton or plankton samples may be assumed to more comparable to a water sample collected at the same time (given problems of seasonality and stratification) but are not always representative of the taxa found in the surface sediments. Despite the problems of mixing several source communities, which may represent different salinities, it is the surface sediment samples that provide the direct analogues of the fossil material - if the past environment was highly seasonal then the fossil samples will also contain mixed assemblages. To interpret the fossil material correctly it is necessary to, at least in part, identify the source communities mixed in the sediments. To this end it was agreed that samples should be collected from both surface sediments and a wide range of periphyton and planktonic habitats, especially as most lakes would only be visited once. This reiterates the conclusions of the first workshop.

Leila Ben Kelifa then described a dataset of 74 surface sediment and periphyton samples from Tunisia spanning the range from freshwater to c. 75 gl^{-1}. A salinity transfer function has been derived from this dataset using the Gasse & Tekaia method and applied to a core from L'Oued Akarit to reconstruct Holocene salinity changes.

After the discussion on modern datasets Hui Fan described work on a sediment core from Pangong Lake, Tibet. The core contains a 16,000 yr diatom record, sampled at 10cm intervals. Coupled diatom and isotope ($\partial^{13}C$ and $\partial^{18}O$) evidence indicate 5 major stages of lake level changes.

Diatom preservation

Tom Rhodes described work on a core from Lac Manas, China, showing extremely poor diatom preservation. It is well known that diatom preservation is a major problem in salt lakes. If dissolution is complete then other indicators have to be found, but if only partial then it is important to understand the ways in which the assemblages may be biased if it is to be used for environmental reconstruction. The problem is threefold, (1) how to identify dissolution, (2) how to record it, and (3) how to incorporate this information in the transfer functions.

Phil Barker described experimental work looking at the effects of different salts of different molar strengths on the dissolution of sediment samples from Lake Geneva. $NaCO_3$ gave the fastest rate of dissolution, in agreement with the general observation that preservation is usually worst in carbonate lakes. Phil also described a simple dissolution index based on the ratio of central areas to whole valves of *Cyclotella meneghiniana*. If this (or a similar taxon) is present throughout a profile then the ratio could give an easily estimated but effective indication of the intensity of dissolution, and hence degree of assemblage modification, through time. Phil also showed how the surface area to volume ratio (averaged for an assemblage) decreased as the assemblage was dissolved and delicate forms with high A/V ratios were preferentially removed. Experiments also showed the effect dissolution would have on the inferred pH after the application of a transfer function, with inferred values differing by c. 0.5 pH units, but in a non-systematic and unpredictable way.

Dave Ryves then described work on diatom assemblages from the NGP, and attempts to quantify the dissolution state of an assemblage. Using the dominant taxa in the NGP dataset and an experimental approach making quantitative counts of valve loss with increasing dissolution, Dave described how each taxon could be ranked according to its susceptibility to dissolution. Dave also described plans to record a dissolution series for each taxon using LM and SEM, based on the distinct morphological changes each taxon undergoes as it dissolves. This will allow detailed dissolution information on each taxon to be collected during counting, and, coupled with a knowledge of the taxon's relative susceptibility to dissolution, will allow the interpretation of transfer function reconstructions to be modified according to intensity of dissolution. The ideas will be tested on a short core from Spiritwood Lake.

Taxonomic quality control (TQC)

Accurate and consistently applied taxonomy is central to the success of palaeolimnological investigations. Unfortunately diatoms are often taxonomically very difficult and conventions used for species distinctions between diatomists within and between countries can vary widely. The merging of calibration datasets and development of inter-regional transfer functions as envisaged by CASPIA is impossible without very careful attention to taxonomic consistency and the establishment of a worldwide baseline. Taxonomic workshops are central to the harmonisation of different datasets, and slide exchange and taxonomic quality control are essential to test the way in which taxonomic distinctions discussed and

decided at the workshops are used by individual diatomists in their own labs. Experience in both the SWAP and PIRLA projects has shown that by a programme of workshops, slide exchanges, and 'blind' counting, agreement amongst diatomists is possible and taxonomic convergence can be achieved. For example, cluster analysis of the final SWAP dataset which included 178 samples from 3 countries analysed by 5 diatomists showed no bias to country or laboratory.

It was therefore decided to implement a programme of slide exchanges focusing on the three main groups discussed at the workshop, that is *Navicula*, *Nitzschia*, and *Amphora* species. Each diatomist will select from their datasets three slides exemplifying taxa from these three genera, and send ten duplicates of each slide to UCL who will collate and redistribute to each laboratory. These are to be counted and the results discussed at the next workshop.

Databases and iconograph

To facilitate the combination of different datasets and their joint analysis it was decided at the first CASPIA workshop to develop a single 'user friendly' database that could be easily updated and distributed to CASPIA members.

Steve Juggins described the basic structure of the planned database. It is convenient to split the DB into two, a taxonomic database and an ecological database, though both would be integrated in practice. The ecological database would be an archive of diatom counts, water chemistry and site & sample information. A discussion followed on the range of site and sample information to include. The following would be a minimum requirement. For counts - analyst and a complete list of raw counts (ie. not just common taxa). For chemistry - date, analyst/lab, usual range of determinands, sample depth). For sites - location (Lat - Long), name, altitude, site type (permanent lake, river, playa etc.), site size. For samples - date, sample type (sediment, plankton, stone scrape, macrophyte etc.), sample depth.

Taxonomic workshops and quality control of the kind described above lead directly to the development of a salt-lake diatom flora and iconograph. The agreed floristic distinctions need to be recorded texturally and accompanied by light and scanning micrography. All taxa need to be checked against, and tied to type and other voucher material held in museum herbaria, and where no match can be found agreed temporary taxonomic status and nomenclature need to be established. The information on nomenclature, synonyms, hierarchy, morphological descriptions, cross references to related taxa, notes on the identification using CASPIA guidelines, together with scanned images of well and poorly preserved material, will form the taxonomic database.

For other diatomists working on core material to use the ecological information and transfer functions developed by CASPIA it is essential that they follow the same taxonomy. Dissemination of CASPIA results through the production of a project-based salt-lake diatom flora is therefore is a major goal of the project, but members recognised that this could not be accomplished without external funding (see below).

Publicity

1. It was agreed to publicise CASPIA at the 12th Int. Diatom Symp. at Renesse, The Netherlands, Aug. 30 - Sept. 5, 1992. A poster was designed at the workshop and constructed at UCL. Brian Cumming and Peter Gell presented the poster and described the project at the meeting. I have received 3 enquiries for information as a result.

2. Steve will present the project at the 6th Palaeolimnology Symposium in Australia, April 1993, and will submit a short description for the proceedings.

3. Steve will also send a short description to Bill Williams for possible inclusion in Salinet.

Funding

Steve reported that the UCL/Natural History Museum/Royal Botanic Gdn Edinburgh/ proposal to NERC to develop a salt-lake flora and associated taxonomic and ecological database and transfer functions has been rejected, but that we had been asked to resubmit emphasizing the taxonomic aspects of the work. The proposal has been rewritten and resubmitted. The outcome should be known by the time of the next workshop.

Next workshop

The next CASPIA workshop will be organised by Peter Gell and will be held 23-26th April 1993 at Monash University, Melbourne, Australia, immediately after the 6th Palaeolimnology Symposium. Please contact Peter if you have not received details.

Steve Juggins

Taxonomic Notes
CASPIA WORKSHOP #2
Paris, France - May 8-13 1992

Participants: Francoise Gasse (Paris), Sheri Fritz (Minnesota), Steve Juggins (UCL), Philip Barker (Loughborough), Leila BenKhelifa (Oxford), Brian Cumming (Queens), Peter Gell (Monash), Jane Reed (UCL), Tom Rhodes (Paris), David Ryves (UCL), Sue Wilson (Queens)

General comments: Most of the week was spent discussing difficult groups of *Nitzschia*, *Navicula*, and *Amphora*. For large groups of closely related species, we used various taxonomic references to construct tables of morphological features that characterize and distinguish the various taxa within a group. Below are more details and general comments on our discussions/confusions. Taxonomic references are given in the table, unless otherwise noted.

Nitzschia

Lanceolatae Subgroup - see table for more extensive description

1. N. latens group

Nitzschia communis Rabh. is coarser than other taxa in this group

Nitzschia bergii Cl. Eul. vs. N. latens Hust. + N. elliptica Hust.

K-LB discusses the similarity of *N. bergii*, *N. latens*, and *N. elliptica*. In our experience these taxa can be distinguished on the shape of the fibulae: *N. bergii* has elongate fibulae, the other 2 smaller rounded fibulae.

N. latens vs. N. elliptica

N. elliptica has broadly rounded ends, whereas *N. latens* has acutely rounded ends.

N. latens vs. N. ovalis Arnott

N. ovalis tends to have coarser fibulae and to be broader and shorter, but the two can overlap. K-LB has photos of type material. Pl. 79, Fig. 22 is our concept of a classic *N. latens*.

N. latens vs. N. perspicua Chol.

The differences between these 2 taxa are unclear. K.-LB suggests that they may be conspecific.

N. latens vs. N. pusilla Grun.

N. pusilla is more lanceolate in shape and has slightly protracted apices (see K-LB Pl. 79, Fig. 16-19). In Africa (F. Gasse) *N. pusilla* occurs in a diversity of environments, whereas *N. latens* is restricted to hyeralkaline systems.

N. pusilla vs. N. perspicua

N. pusilla is more lanceolate and has slightly protracted apices, but in practice the 2 are very difficult to tell apart.

N. aurariae Chol. vs. N. perspicua

N. aurariae has broadly rounded ends vs. acutely rounded ends in *N. perspicua*.

N. aurariae vs. N. elliptica

N. aurariae is finer

N. estoshensis Chol.

See Cholnoky 1966 for a good description of *N. estoshensis* & especially Plate 2, Fig. 83. In general Cholnoky is good for the *N. latens/N. elliptica/N. estoshensis* group.

Nitzschia unknown #1 (Gell). Peter Gell has a large taxon in the *N. latens* group, which we have been unable to find a name for. L: 50-90u B 9-11u.

2. Nitzschia fonticola/ N. frustulum/N. liebtruthii group

The various members of CASPIA continue to have difficulties in distinguishing amongst the related taxa in this group - see attached table and notes from 1991 CASPIA workshop for additional details. The presence of a central nodule, the major distinguishing feature according to K-LB, is often not easily determined in the light microscope, and many apparent populations seem to have some individuals with a well-developed nodule and other individuals where the nodule is not distinct. In general the shape of the ends seems to be an important distinguishing character.

N. hantzschiana Rabh. vs. N. acidoclinata L-B

The shape of the two species is similar, but *N. acidoclinata* is finer in both striae and fibulae density.

N. hantzschiana vs. N. frustulum (Kütz.) Grun.

The ends are drawn-out (attenuated) in *N. hantzschiana*, but are not in *N. frustulum*. The fibulae density in *N. hantzschiana* tends to be coarser, although there is some overlap in this character.

N. frustulum vs. N. perminuta (Grun.) Peragallo

N. frustulum has a central nodule, whereas *N. perminuta* does not. The ends of *N. frustulum* are bluntly rounded and in *N. perminuta* they are sub-capitate to capitate.

N. liebetruthii Rabh. vs. N. perminuta

N. liebetruthii has acute apices, whereas the apices in *N. perminuta* are capitate to sub-capitate. *N. liebetruthii* can be more lanceolate in shape.

N. liebetruthii vs. N. bacillum Hust.

N. bacillum has drawn-out capitate apices in contrast to the acute non-attenuated apices of *N. liebetruthii*.

N. liebetruthii vs. N. angustiforaminata Lang.-Bert.

We do not have a clear concept of how *N. angustiforaminata* differs from *N. liebetruthii* and do not use this epithet.

N. affinity N. lacuum L-B

A taxon similar to *N. lacuum*, but without the drawn-out & capitate ends of *N. lacuum*, is found in Australia (Gell), E. Africa (Barker), & China (Gasse, Rhodes). The shape varies somewhat from linear-lanceolate (Australia, E. Africa) to distinctly lanceolate (China, E. Africa). We tentatively agree to call this taxon *N. lacuum* var. 2.

N. affinity N. fonticola Grun.

Our concept of a typical *N. fonticola* has a distinct central nodule and attenuated sub-capitate ends. Specimens with a less clearly developed nodule and with acute ends occur in Africa (F. Gasse) and the Great Plains (Fritz). Gasse called these *N.* affn *fonticola* var. 1 in her monograph on E. African Diatoms (1986) and we agree to use that name for the time being.

N. affinity N. frustulum

Leila has specimens from Tunesia that are the shape of *N. subacicularis*, but are considerably coarser and, apart from shape, fit the general characteristics of *N. frustulum.*

3. Nitzschia palea group

Nitzschia palea v. debilis (Kütz.) Grun.& N. palea v. tenuirostris Grun.

The varieties of *N. palea* are not always easily differentiated from one another. *N. palea* var. *debilis* falls at the upper end of the range of *N. palea* v. *palea* in terms of striae and fibulae density, and the valves are more narrowly linear-lanceolate than the nominate. *N. palea* var. *tenuirostris* is narrower than the nominate or v. *debilis* and has more extremely protracted ends.

N. palea v. tenuirostris/ N. pumila Hust.

These taxa are seemingly differentiated based on a shape continuum from linear-lanceolate to lanceolate/rhombic and to more extremely protracted apices. In practice these taxa can be difficult to tell apart (compare, for example, Pl. 59, Fig. 23 with Pl. 81 Figs. 14-16 in K-LB).

N. gracilis Hantz. vs. N. palea v. tenuirostris & v. debilis

N. gracilis is generally larger, but the smaller forms can be confused with the varieties of *N. palea.*

4. Other Nitzschia species discussed

N. elegantula Grun.

Found in Spain (Reed) and Tunesia (Ben-Khelifa).

N. gracilis Hantz. vs. N. spiculum Hust.

N. gracilis is broader and has more protracted apices. The specimens identified as *N. gracilis* in Gasse (1986) are probably *N. spiculum.*

Amphora

A. coffeaeformis (Agardh) Kütz./A. acutiuscula Kütz.

Archibald & Schoeman (1984) have a good discussion of the confusions surrounding the circumscription of *A. coffeaeformis* and Archibald (1983) of *A. acutiuscula*. Archibald & Schoeman studied type material of *A. coffeaeformis*, and we thus follow their fairly broad concept of this taxon. It is clear from Archibald's discussion that the type of *A. acutuscula* is not clearly defined. We agree to follow Archibald and restrict the use of *A. acutiuscula* to specimens with distinctly punctate striae. In practice the "distinctness" of the punctation is not often clear in the LM, and there is confusion about whether to refer many individuals to *A. coffeaeformis* or *A. acutiuscula*. We agree to erect an intermediate category "*A. coffeaeformis/A. acutiuscula* for these specimens.

A. coffeaeformis v. aponina (Kütz.) Arch. & Sch.

A. coffeaeformis v. *aponina* is more lanceolate in shape than the nominate and falls at the lower end of the breath range of *A. coffeaeformis* . The ventral striae fall at the upper end of the range of *A. coffeaeformis*, and under TEM have a different structure than *A. coffeaeformis* v. *coffeaeformis*. See Archibald & Schoeman (1984).

A. castellata Giffen

A. castellata Giffen is characterized by a hyaline line across the center of the dorsal striae, formed by thickened longitudinal costae, and the structure of the rape, which has a thin siliceous flap covering the proximal ends. The striae are non-punctate. See Archibald (1983).

A. holsatica Hust.

Has coarsely punctate striae but is broader than *A. acutiuscula* and has coarser striae. Girdle bands are coarsely punctate.

A. affinity A. salina Wm Smith

Sue Wilson has populations of small *Amphora* sp. in British Columbia with rounded very distinctly punctate striae. These specimens resemble Figs. 42 & 43 in Archibald & Schoeman (1984) of *A. salina* from material of Wm Smith (BM23125), which according to Arch. & Sch. is not the same as the *A. salina* type material of Smith (=*A. coffeaeformis*) because of the punctate striae. The specimens are somewhat similar to *A. coffeaeformis* v. *borealis* of Cleve-Euler. They are probably most closely related to *A. acutiuscula.*

A. cognata Cholnoky

A small *Amphora* sp. somewhat similar to above, but raphe is very central and ends are sub-capitate. See Archibald (1983).

A. delicatissima Krasske

See K-LB for photos of type material. Found in Tunesia.

A. affinity A. micrometra Giffen

Specimens from Spain (Reed) resemble *A. micrometra* but have a distinct break in the dorsal striae.

Amphora unknown #1 (Gell)

Has finely punctate dorsal and ventral striae, which are finer than *A. acutiuscula* and other related species, with a hyaline line across the dorsal striae. The raphe is arched and nearly central. Common in NaCl systems.

1. Navicula cinta group

Navicula cincta f. minuta Grun./N. digoradiata f. minima Cl.Eul./N. microdigitoradiata LB

N. cincta f. *minuta* according to Van Heurck is a smaller version of *N. cincta* with finer striae. The taxonomic position of *N. cincta* f. *minuta* is uncertain according to Carter (1979 - Pl. 1, Fig. 31), and K-LB (1986 - vol. 1) suggest that this taxon does not belong to *N. cincta*, but is more closely related to *N. digoradiata* v. *minima* of Cleve Euler, although K-LB indicate that this combination has not generally been accepted. In a later volume of the Susswasserflora K-LB (1991 - vol. 4) apparently suggest that *N. cincta* f. *minuta* should be renamed as *N. microdigitoradiata*, but the photos depicting *N. microdigitoradiata* (Pl. 59, Fig. 23,24) are not the same taxon depicted in vol. 1 (Pl. 28 Fig. 16 & Pl. 34, Fig. 7) as *N. cincta* f. *minuta* from the Van Heurck slide. We agree to retain the name *N. cincta* f. *minuta* until its taxonomic position is clarified.

N. cincta v. heufleri Grun.

We agree to retain the name *N. cincta* v. *heufleri* for individuals with more widely spaced striae and without the characteristic central area of *N. cincta*. See Van Heurck Pl. 7 Fig 15.

2. Navicula elkab/N. halophila group (see also notes from 1991 CASPIA workshop & PISCES workshop)

Navicula elkab Müller

Has very drawn-out ends and striae composed of rounded punctae (FG). Gasse always finds it in shallow hyperalkaline environments.

N. affinity N. elkab

Specimens finer than *N. elkab* (26+ str/10u) and without distinctly punctate striae. In British Columbia material (Wilson) the striae are somewhat radiate at the center of the valve.

N. affinity N. halophila (Grun) Cleve

Gasse has populations that are more lanceolate in shape and without the characteristic pulled-out ends of *N. elkab*, but which are finer than *N. halophila*. These were originally counted it as *N. elkab*. Lakes with these populations plot in a different ecological space in an ordination, relative to those with classic *N. elkab*.

N. pseudohalophila Cholnoky

Has a shortened striae at center (e.g. K-LB. Pl. 44 Fig 2,3). K-LB synonymizes with *N. halophila*. Agree to retain name. Common in East Africa (Gasse & Barker).

Cyclotella

C. affinity C. quillensis Bailey

Similar to *C. quillensis* but with a half-ring of caentral strutted processes near the margin of the central area and with a marginal strutted process every 2 costae (vs. every 1 in *C. quillensis*). Populations with this morphology have been found in fossil material from Guatemala (Gasse), Algeria (Gasse), and Tanzania (Barker).

Cyclotella tripartita Hak./C. ocellata Pant./C. comensis Grun.

Gasse has a diversity of *Cyclotella* species in Chinese material that are related to each of the above 3 species, but are distinctly different.

Cymbella

Cymbella minuta Hilse ex Rabh. vs C. silesiaca Bleisch

The two can be distinguished based on size, the punctation of the striae (clearly visible in *C. silesiaca*), and the shape of the terminal fissures.

References

Archibald, R.E.M. 1983. The Diatoms of the Sundays and Great Fish Rivers in the Eastern Cape Province of South Africa. Bibliotheca Diatomologica Bd. 1. Cramer, Stuttgart.

Archibald, R.E.M. & F.R. Schoeman. 1984. *Amphora coffeaeformis* (Agardh) Kützing: a revision of the species under light and electron microscopy. S. Afr. Tydskr. Plantk. 3: 83-102.

Carter, J., 1979. On the identity of *Navicula cincta* Ehr. Bacillaria 2: 73-84.

Cholnoky, B. J., 1966. Diatomeenassoziationen aus Einigen Quellen in Sudwest-Africa und Bechuanaland. Beihefte, Nova Hedwigia 21: 163-244.

Gasse, F., 1986. East African Diatoms: taxonomy, ecological distribution. Bibliotheca Diatomologica Bd. 11. Cramer, Stuttgart.

Krammer, K. & H. Lange-Bertalot, 1986-1991. Susswasserflora von Mitteleuropa. Bacillariophyceae. Gustav Fischer Verlag, Stuttgart. Bd 2/1, 2/2, 2/4.

S.C. Fritz
26 May 1992

lumn 1	Column	Column 3	Column 4	Column 5	Column 6	Column 7	Column 8	Column 9	Column 10
SPECIES	NODE	LENGTH	WIDTH	STRIAE	FIBULAE	SIDES	ENDS	K & LB REF	
fossilis	+	30-85	3.5-5	18-21	7-9	lin lan	cap?, sharp rnd	T76;105	
incognita	+	20-70	2-3	28-30	10-15	lin lan	cap?, sharp rnd	T77;106	
fonticola	+	10-65	2.5-5	23-33	9-16	lan	cap?, sharp rnd	T75;103	
tropica	+	10-65	2.5-4	23-25	8-16	lan	cap? rnd	T76;104	
frustulum*	+	5-60	2-4.5	19-30	10-16	lin lan	cap?, sharp rnd	KLB T68;94	
hantzschiana	+	8-50	3-5	20-26	7-12.5	ell lan	cap? blunt rnd	KLB T73;101	
acidoclinata	+	8-45	2.5-3	27-34	10-16	lin	cap? blunt rnd	KLB T73;100	
archibaldii	?+	15-40	2-3	46-55	14-19	lan	cap?, sharp rnd	T81;115	
inconspicua	+	3-22	2.5-3.5	23-32	8-13	lin lan	blunt rnd	T69;95	
liebtruthii*		5-60	2-4.5	19-30	10-16	lin lan	sharp rnd	T69;96	
solita		18-50	4-6	24-28	11-16	lan,lin?	rost/cap, sharp rnd	T71;99	
perminuta		8-45	2.5-3	26-36	10-16	lin lin	cap, rnd?	T72;99	
bryophila		15-27	4-5	30-32	8-12	lin lan	short rost/cap	T74;103	
supralitoria		10-25	2.5-4	25-34	14-20	lin lin	cap?, rnd	T70;97	
modesta		16-24	3-3.5	19-21	8-10	lin	blunt-sharp rnd	T74;102	
justiforaminata		8-24	3-4	21-25	10-12	ell-lin	sharp rnd	T70;98	
desertorum		17-20	4-5	25	10-15	ell lin	rost, sharp rnd	T70;98	
bacillum		12-20	2-5	27-32	12-16	lan	cap, rnd?	T76; 106	
lacuum		10-20	2-3	35-40	13-18	lan	cap, sharp rnd	T78;107	
lacuum 2		"	"	"	"	"	not cap		
ATENS GROUP									
sp 1		58-80	11-15	+/-30	9-11	lin	brd rnd, wedge	Gell & Gasse XIth IDC	
etoshensis		20-60	4-5.5	'invis'	15-18	lin-lan	sharp rnd	Choi 1966 Pl 2 f81,83	round fibulae
bergii		14-60	4-5	35-40	14-18	lin-ell, lin	bl, rnd	KLB T80, f10,11,13; 110	dash-like fibulae
elliptica		11-17+?	4-5+?	invis	18-21	ell	brd rnd	Choi 1966 Pl 2 f76-79	irreg sp fibulae
latens		30	4	fine	17	lin lan	bl rnd	KLB T80, f22;113	
communis		6-40	4-6	28-38	10-14	ell, lin	br, rnd, bl	KLB T79, 110	
pusilla		8-33	2.5-5	40-55	14-20	lan	drn	KLB T79 f16,18, 111	
perspicua		17-25	3-4	+/- 50	15-17	narr ell	bl rnd	KLB T80; 112	
ovalis		13-22	4.5-6.6	+/-42	12-16	ell, lin-ell	bl, brd, rnd	KLB T79;110	
aurariae		6.5-18	2.5-3.5	46-53	13-18	lin-ell	brd, rnd	KLB T80; 113	bacilliform shape
PALEA GROUP									
palea		15-70	2.5-5	28-40	9-17	lin-lan	sharp rnd-cap?	KLB T59 1-18 ;85	
palea v.debilis		25-110	2-4	35-40	12-17	lin-lan	dr rnd cap	KLB T60 1-3;86	
v. tenuirostris		36-46	2-3	invis	11-18	lin-lan	drawn sub-cap	KLB T59 21-23 ;85	
subacicularis		20-80	(1.5)2-3	27-33	12-16	lan/lin-lan	drawn weak cap	KLB T67 4-10 ;118	
stantial overlap									
N. gracilis		30-110	2.5-4	invis	12-18	lin-lan	cap-sharp rnd	KLB T66 1-11 ;93	
(tenuirostris?)		30-37	2.5-3	invis	14-18	lan	drawn cap	KLB T61 14-15 ;115	
N. spiculum	+	70-100	1.5-2.5	invis	14-16	lan	drawn bl	Hust (1949) 13 1-4; 150	
gracilliformis	+	58-150	2-2.5	45-60	16-21	lin-lin/lan	drawn shp rnd	KLB T61 6-9 ;115	
N. paleacea	+	8-55	1.5-4	44-55	(12) 14-19	lin/lan-rhom	drawn shp rnd	KLB T61 1-7; 114	

nn 1	Column 2	Column	Column 4	Column 5	Column 6	Column 7	Column 8	Column 9	Column 10
	Length	Width	shape	str dens	str dir	central area	ends	punctae	ref.
radiosa	40-120	10-15	narr lan	10-12	rad->conv	±rhom, asym	±shp rnd	32	KLB 99, T29
angusta	30-72	5-8	lin	11-12	rad->conv	var, asym	bint rnd, drwn?	30	KLB 97, T28
argalithii	30-70	8-10	lin-lan	9-12	±rad->conv	±ext, asym	bint rnd	30	KLB 95, T27
punctatae	30-70	8-10	lin	9-12	±rad->±conv	rect	bint rnd	32	KLB 95, T27
anceolata	28-70	9-12	lan	10-13	rad->conv	rnd	bint rnd,±drwn	32	KLB 100, T29
locephala	20-40	5-7	ell-lan	14-17	rad->±conv	sm, ±circ	±rost	40	KLB 102, T31
erifuga	25-35	5-7	lan	12-14	rad->±conv	asym	bl, point, rnd	30-35	KLB 116, T36
phyllepta	12-45	4-8	lan	14-20	rad->//	rnd	drn	45	KLB 104, T32
liotenella	14-40	5-7	lan	14-16	rad->//,conv	sm, irreg	point, rnd	35-45	KLB 106, T33
trivialis	25-65	8-12.5	lan	11-13	rad->//,±conv	lge rnd	long drwn	28-32	KLB 110, T35
dridgiana	20-60	6-8	lin-lan	10-12.5	rad->conv	sm, lan-rhom	bint, shp rnd	24	KLB 97, T28
ibonensis	25-40	5.5-8	lan	12-13.5	±rad->conv	sm	bint rnd, ±drwn	26	KLB 99, T26
cari	25-80	6-11	lin-lan	9-12(16)	rad->//,±conv	var	bint->shp rnd	38	KLB 96, T27
cincta	13-45	5-8	lin-ell	8-12	rad->conv	sm, var	bint rnd	40	KLB 98, T28
f. minuta	15-21	4-5	lin-lan	14-16	rad->//	sm, var			KLB
r heufleri	20-25	4.5-5.5	lin-lan	10-13	rad->conv	wide,rnd	rnd		Van Huerck
recens	16-40	6.5-9	lin-ell	11-14	rad->±conv	±rnd	shp->bint rnd	35	KLB 95, I27
veneta	13-30	5-6	lin-rhom	13.5-15	±rad->conv	sm, ±sym	lightly drwn	35	KLB 104, T32
elkab	15-32	4-6	lan-ell	20-25	//(±rad)	abs	±rost	fine	Arch 270
elkab	1st CASPIA			23-26			rost->subrost		Gasse 1986, Pl 15-16
halophila	7-140	4.5-18	rhom/lin-lan	15-24	//->conv				KLB 126, T44
halophila	CASPIA WRKSHP			15-24					agree with KLB
bcapitata							subcapitate		Gasse 1986, Pl 16, #1
nukrostris	42-50	9-10	lan	20-22	/ /	sm->abs	capitate, drwn		P&R vol. 1, 1966
halophila	10-40	5-8	var, ell-lan-lin/lan	(18)19-24	rad->conv->arc	var	rnd, rost, cap	34-52	Schoe &Arch. 1976-80, No. 2
nmophila	17-30	5-6	lin-lan	10-14	±rad->//	±abs	±protr, sub-ac	dist	Arch 242-3
semenea	13-26	4-5.5	lan	18-20	rad->//	v. sm, asym	ac	fine	Arch 260
nelloides	14-21.5	2.5-4	lin-lan	16-21	rad->conv	±rnd	rnd, rost, ac	50	KLB 117, T36
ncertata	7-20	2.5-7	lin-lan	13-16	±rad->//	v. sm, rnd	obtuse	36-40	KLB 111, T35
erminuta	5.5-20	2-4	lin-lan	14-20	±rad->±conv	slm, wide rect	bint, rnd	33	KLB 112, T35
alsensis	9-12.5	2.5-3.5	lan	14-16->20-23	± / /	v. sm.	rnd	fine	Gasse, '86, pl18, f4-6,100
alinicola	7-17	2-3	lin-lan	17-20	±rad->//	abs	obt, rnd	fine	KLB 111, T35

Column 1	Column 2	Column 3	Column 4	Column 5	Column 6	Column 7	Column 8	Column 9
VICULA/STAURONEIS	Length	breadth	V shape	striae	str. form	central area	V end	
ula (W.Smith) Donkin	20-100	6-23	lan	14-18	rad-par	variab	rost	
af. crucicula	30-53	7-12	ell-lan	15-21	rad-par	variab	sub-rost	shape, ends dif from nominate
scodensis Krasske	15-36	6-7	lin	16-24	rad-par	asym large	rnd	
islouchii Poretz +Anis	20-38	5-9	ell-lan	22-24->28	lightly radial	mod wide +short striae	bint rnd-drawn?	
S. salina W.Smith	50-110	11-20	lan	18-25	rad-par	narr<wislouchii, asym	brd-shp rnd- not drawn	
S. tackei (Hust)K+LB	16-30	5-8	lin lan-lin ell	24-26->32	slightly rad-par ends	sm lin asym?	wk drawn sm rnd	
NAVICULA								
hyalosirella Hust	25-30	3	lan	20-24	par	small	sharp	
hartii Cholnocky	32-55	4-5.5	lin-lin lan	24-28->28	par cent-conv poles	asym, cent nod, rect fascia	acutely rnd	
bulheimii Grun	15.5-32	2-3.5	narr lan-lin lan	27-32	par	often abs, asym	drawn, sub rost-rost, cap?	

Column 10

KLB T54 1-7
BFC film 3/13
KLB T77 6-9
KLB T91 16-17
KLB T91 14-15
KLB T91 12-13

Hust (1961-6)p335
(1983) plate 16 286-287
(1983) plate 15 244-247

Column 1	Column 2	Column 3	Column 4	Column 5	Column	Column 7	Column 8	Column 9	Column 10	Column 11
	LENGTH	V WIDTH	D STRIAE	V STRIAE	PUNCT	RAPHE SHAPE	CENTRAL AREA	ENDS	AXIAL AREA	Other
formis (Ag +Pr)Kutz	14-55	3.5-7.3	16)17->16-26	21-36	indist	str. fil	sm vent	protr, brd rost-sub rost	narr lin	
castellata Giffen	15-67	2.7-6.1	19-21->24	28-32	indist	str. fil	sm, vent ?indist	protr,narr, rost-cap	nar dors,br ventr	long line
acutiuscula Kutz	18-49.5	3.4-6.4	15-20->20-24	22-28 (cent)	dist	str fil	sm vent	dist cap	narr dors, wider vent	
elicatissima Krasske	5-20	3-7	-30	indist	indist	str fil	none	rnd bent to vent	none	Not capit, dors convex
aff. salina W. Smith	11-17	2-3	20-22-finer	indist	dist	str fil	none	rostr - slightly cap	none	cent dors str dist
holsatica Hust	30-45	15-25	13-19	11-17	v.dist	str fil	ventr	sub rostr	narr	punct girdle band
micrometra Giffen	8-14	1.7-2.5	fin	indis	indist	str. fil	?invis	rnd	indis	
sp. 1	32-37	3.3-5	27-30		dist	arched	sm vent	drawn sub-cap	narr lin	long line, v stri dashed, equi

Column 12

Arch +Sch (1984)
ch 1983) plate 3 94-95
1 (1983) plate 3 89-92

KLB 351 T152 19-23
Sch (1984) figs 42-43
st (1930) fig 6:33 p345
1983) plate 4 123-125
P. Gell

ın 1	Column 2	Column	Column	Column	Column 6	Column 7	Column 8	Column 9	Column 10	Column 11	Column 12
I-CIRC	PUNCT DENS	LENGTH	WIDTH	STRIAE	COSTAE/100µ	STR/COST	SHAPE	VENTRAL SIDE	ENDS	COMMENTS	REF
sculus	10-15 single	12-80	10-16	15-20	30-50	2-4	sickle,semi-circ	±str-convex	brd rnd		KLB 163, T110,114
nctata	8-13 single	70-120	17-23	10-13	20-30	3-7	sickle,semi-circ	±str-convex	brd rnd		Krammer '88 164, Pl VI
berula	16-30 dble	25-100	5-12	15-19	30-100	2-8	sickle	concave	brd rnd		KLB 160, T110,112,113
minata	16-19	22-112	7.5-11	16-19	40-60	2-7	sickle	concave	sharp rnd, drn,bent?		KLB 162, T111A, 112, 113
lssonii	15-18(20)	15-40	5-8.5	17-22	35-60	2-5	≥semi-circ	str-convex	sharp rnd, drn, bent		KLB 164, T113, 113A
stricta	17-26	24-75	9-18	15-20	35-60	2-4	semi-circ	str	drn, ±bent	raphe constr	KLB 164, T110, 113A
culata	30-40 dble	18-52	5-10	16-18	30-60	2-7	semi-circ	str	rnd, drn-cap?±bent		KLB 165, T115
estris	>50 dble	20-74	5-8	15-17	30-50	2-7	semi-circ (rhom)	str	sharp rnd, bent	freshwater	KLB 165, T115

n 1	Column 2	Column 3	Column 4	Column	Column 6	Column 7	Column 8
ITELLA							
	Diam	costae	M fult	C fult	Rimop	CA diam:diam	
ensis	45-54	6-7	-	-	27-60	1:1.2ins 1:1.47out	Battarbee et al. (1984)
striata	18-48	6-10	1:3.3	1:3	1 (marg)	1:1.3ins, 1:1.6out	
iniana	3 9-15.6	6-15	1:1	1-3	1	1:1.76ins, 1:1.78out	
llensis			1:2				intermed menegh/quil

Taxonomic notes from the Third CASPIA workshop, Melbourne 1993

List of diatom slides circulated in April 1993 for CASPIA Taxonomic Quality Control programme. Taxonomic notes refer to workshop discussions of these slides.

CASPIA TQC Slide Exchange, April 1993

Slide No	Diatomist	Site Name	Sample Type
1/93	Dave Ryves	West Stump, North Dakota	epiphyton
2/93	Sheri Fritz	Sayer Lake, Saskatchewan	surface sediment
3/93	Sheri Fritz	Moon Lake, North Dakota	core (32cm)
4/93	Sheri Fritz	Madison Lake, South Dakota	surface sediment
5/93	Jane Reed	Podrido, Spain	algal mat
6/93	Sue Wilson	Site SK5, British Columbia	surface sediment
7/93	Sue Wilson	Site SK45, British Columbia	surface sediment
8/93	Brian Cumming	Site PC21, British Columbia	surface sediment
9/93	Brian Cumming	Site PC38, British Columbia	surface sediment
10/93	Peter Gell	McGlashan's Lake, Australia	artificial substrate
11/93	Peter Gell	Lake Purrumbete, Australia	artificial substrate
12/93	Peter Gell	Lake Milangil, Australia	wood scrape
13/93	Francoise Gasse	L. Chega, Algeria	surface mud
14/93	Francoise Gasse	Sonachi Crater Lake, Kenya	littoral mud
15/93	Francoise Gasse	Ouargla, Algeria	surface mud
16/93	Leila Ben Kelifa	Zafrane Ain Snam, Tunisia	surface sediment
17/93	Leila Ben Kelifa	Ain Dkouk, Tunisia	surface sediment
18/93	Leila Ben Kelifa	Ain Saber, Tunisia	surface sediment

* = not sent, insufficient duplicate slides

Steve Juggins, April 1993

CASPIA, April 1993, Melbourne

NITZSCHIA

Slide 1, Dave

N aff fonticola - ends not sufficiently sub-capitate for fonticola. Valve nodes variable, with and without. Suggest count them separately, but probably lump together when do diagram.

Slide 3, Kate (Minn)

N palea - striae c. 12/10 ie closer to palea than palea v debilis. Palea v debilis not valid as main distinction between it and palea is only the form of the ends.

Slide 5, Jane (Spain)

N frustulum - linear, coarser striae
N aff fonticola - lanc, finer.

(but appears to be a continuum, to me anyway)

Slide 10, Peter (Aus)

N liebetruthii - most valves have no node.
(not N bacillum - latter is more lanc and has definite capitate ends)

Slide 11, Peter, Purrumbete (Aus fresh)

N paleacea - w = c.2μ. Length to 78μ is longer than the main KLB defn but longer examples are known. Falls into two size categories to be counted separately, 50μ length dividing the two. (Isn't N spiculum from Simonsen's Hustedt since the ends of spiculum are more drawn)

Long and short N liebetruthii.

(nb Melanie, Galapagos, has valves where one frustule, with node, would be paleacea, and the other, without, would be graciloides)

Slide 12

N pusilla. Is a longer one, sim to no. 21 in KLB (= etoshensis/bergii).

N aff pusilla - fibulae 13/10. Is very fine but can see the striae; some close to supralitorea, others less so.

(nb - pusilla also overlaps perspicua in saline waters)

Slide 13, FG (6 ppm)

N desertorum
N solita (= steynii)
N microcephala

Slide 15, FG

N aff elegantula. Visibility of the punctate striae distinguish elegantula from microcephala. On Peter's microscope (quite low resolution), can just make out the striae. Check on better one - possibly is N elegantula.

N ?etoshenis.

Slide 16, Leila

N desertorum. Str 22-24/10. L = 24. W = 3.5. Fib 12/10

N solita - >50μ long. Fib 12/10. Str 24/10

N palea.

Slide 17, Leila

N aurariae. Distinct shape

N aff elegantula - cross bet elegantula and microcephala types; some +/- hyaline but punctate.

N elegantula
N microcephala

N liebetruthii.

Slide 18, Leila

N stompsii fragments. Distinct longit break in striae, similar to Anomoeoneis.

AMPHORA

We gave up before all the slides were looked at because too few are published to assign names to them. The distinctions between coffeaeformis and acutiuscula still stand from last meeting.

REFS -

Simonsen's Hustedt for A tenerrima, tenuissima, one of which has only been defined from a couple of diatoms in the type slide.
Peragallo
Cholnoky
Schoeman & Archibald papers incl descrn of v borealis and subacut
1987 Foged's Fiji - several distinct spp (Diatoms from Viti Levii, Fiji Islands. Bib Diat no 14. J Cramer, Berlin)

Slide 18, Leila

A coffeae

Slide 17, Leila

A acut

Slide 16, Leila

A libyca (KLB split to libyca and ovalis)

A holsatica - coarse G bands and ends point downwards.

Slide 15, FG

(See Leila's PhD)
A aff tenerescens - a poorly defined sp. See Simonsen Hustedt - isn't tenerrima)

sp 1 - +/- hyaline, L = 25, ends drawn down, sim shape to coffeae
sp 2 - +/- hyaline with hiatus in striae
sp 3 - very bent at centre valve

A coffeae

Slide 13, FG

A acut
A spp - poss several different hyaline ones
A tenerescens

Slide 12, PG

A acut v borealis - ie a small, dumpy version which is punctate (coffeae v borealis is the small, dumpy non-punctate form which is being kept in spite of KLB's lumping)

A acut - longer than v borealis
A micrometra - tiny, hyaline
A sp - larger hyaline

Slide 10, PG

A aff veneta - long and broad, without much narrowing towards ends

A acut v borealis or tenerrima: tenerrima usu more rounded ends and narrower than v borealis
A coffeae
A holsatica
A micrometra (but raphe usually more central)

Slide 7, Sue

A acut
A tenerrima/teneresCens type - small, fine with pinched-in ventral at centre.

NAVICULA

Slide 2, Sheri

N bulnheimii
N cincta
(nb N dvorcekii, Ehrlich, identified by Sue and Sheri, is the Brachysira aponina of KLB and FG's data)

Slide 5, Jane

N sp aff salinarum. Central area irreg, broad. Str = 17/10. W <7 - sim to Germain no 13 without the drawn ends. KLB has striae 13-17, Germain 14-16.
NOT:
cryptocephala - central area OK but striae here not long & sht at centre, too ellip ie ends not drawn enough.
phyllepta - shape OK but phyllepta lacks central area.
trivialis - too small and striae at ends are wrong.

Slide 6, Sue

N halophila
N veneta

Slide 7, Sue

N cincta f. minuta - very variable central area, long & sht striae at centre. Very radial striae, changing dirn towards ends. Too narrow and fine for cincta, and cincta's striae are less irregular.

nb N microdigitoradiata in the new KLB book isn't described and Sue's diatom is closer to the old cincta f. minuta. Overlap with digitoradiata, but stick to cincta.

N sp - no close fit. Isn't cruciculoides (see plates)

Slide 12, PG

N cincta f. minuta
N cincta - asymm central area

Slide 13, FG

N veneta
N incertata - coarser than salinicola, asymm valve and has a central area.

Slide 15, FG

N aff cancellata (KLB) - very variable. Asymm, coarse with gap in striae at centre. SJ - could be N aberrans

?N soodensis (Sundays River) - finer, parallel-sides, asymm with gap in striae at centre

Slide 17, FG

Stauroneis ?wesfluchii

Appendix 2 Publications Arising from the Project

1. Fritz, S.C., Juggins, S., Battarbee, R.W. and Engstrom, D.R. A diatom-based transfer function for salinity, water level and climate reconstruction. *Nature* **352**, 706-708.

2. Fritz, S.C., Juggins, S. and Battarbee, R.W. Diatom assemblages and ionic characterization of freshwater and saline lakes of the Northern Great Plains, N.A.: a tool for reconstructing past salinity and climate fluctuations. *Canadian Journal of Fisheries and Aquatic Science.* (in press).

3. Juggins, S., Battarbee, R.W. & Fritz, S.C. Diatom / salinity transfer functions and climate change: an example from the northern Great Plains, North America. Proceedings of NERC/QRA 'Palaeoclimate '93' meeting, Durham. (submitted a).

4. Juggins, S., Battarbee, R.W., Fritz, S.C. and Gasse, F. The CASPIA project: diatoms, salt lakes, and environmental change. *Journal of Paleolimnology*. (submitted b).

Sal-plim

Reconstruction of past changes in salinity and climate using a diatom-based transfer function

S. C. Fritz*, S. Juggins†, R. W. Battarbee† & D. R. Engstrom*

* Limnological Research Center, University of Minnesota, 310 Pillsbury Drive S.E., Minneapolis, Minnesota 55455, USA
† Environmental Change Research Centre, Department of Geography, University College London, 26 Bedford Way, London WC1H 0AP, UK

THE prospect of global warming has focused attention on the role of palaeoecology in testing the accuracy and sensitivity of climate-model predictions, in identifying past analogues for future climate change, and in placing model-predicted climate responses in the context of natural climate variability[1,2]. Proxy data for climate reconstruction can be derived from many sources, including the palaeolimnological record[3,4]. In closed-basin lakes in arid and semi-arid regions, shifts in effective moisture lead to the concentration or dilution of dissolved salts, and these changes in salinity are clearly reflected in the composition of lacustrine diatom assemblages[5–8]. Here we refine a previously published[9] diatom-based transfer function for the reconstruction of past changes in salinity of lakes in the northern Great Plains region of North America, and apply the refined transfer function to a late-glacial and Holocene sediment record from Devils Lake, North Dakota. Our results show that there were a number of alternations between fresh and saline conditions during the Holocene and hence demonstrate the utility of the technique in reconstructing past changes in regional climate.

Our transfer function for salinity reconstruction is based on the statistical relationship between regional modern diatom assemblages in surface sediments and lakewater chemistry. We collected surface-sediment samples for diatom analysis and associated data on water chemistry in 1982 and 1985 from 39 sites in North and South Dakota, USA and from 27 lakes in Saskatchewan, Canada. The lakes had salinity ranging from 0.7‰ to 270‰ and the sites had a strong gradient from east to west in their precipitation minus evaporation gradient (Fig. 1). Standard techniques were used for diatom analysis[10]. In most cases diatom counts were 400–600 valves, but in samples where diatoms were scarce or poorly preserved, fewer were counted. Cation concentrations were measured by d.c.-plasma atomic emission spectrometry, anions by ion chromatography and inorganic carbon by automated coulometric titration. Statistical analysis of the data on water chemistry and diatoms was carried out using principal-component analysis, detrended correspondence analysis and canonical correspondence analysis[11–13]. In all ordinations the first axis was strongly related to total salinity and many of its associated ionic components, and the second axis related to differences in brine type, in particular the difference between systems dominated by CO_3/HCO_3 and those dominated by SO_4. The combined data set was screened, and 11 samples where diatoms were absent or poorly preserved were omitted from further analysis.

On the basis of the strong first-axis relationship between diatom composition and salinity, we used weighted-averaging regression[14] of the log-transformed salinity data to estimate the salinity optima and tolerances of all taxa that occurred with at least 2% abundance in any one sample. We subsequently used weighted-average calibration with an inverse deshrinking regression[15] to estimate the diatom-inferred modern salinity for each site in the data set. A previously published transfer function[9], derived from canonical correspondence analysis[16], was based on classical regression, which produces larger root-mean-square errors and pulls inferred values away from the mean[15]. Optima

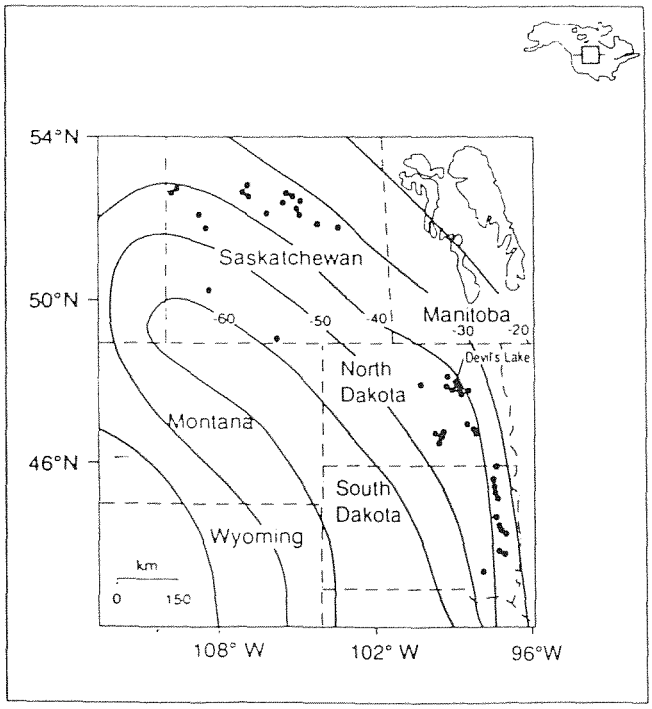


FIG. 1 Map of the northern Great Plains showing the location of surface-sample sites and Devils Lake. The contours are lines of equal precipitation minus evaporation, measured in cm yr^{-1} (ref. 18).

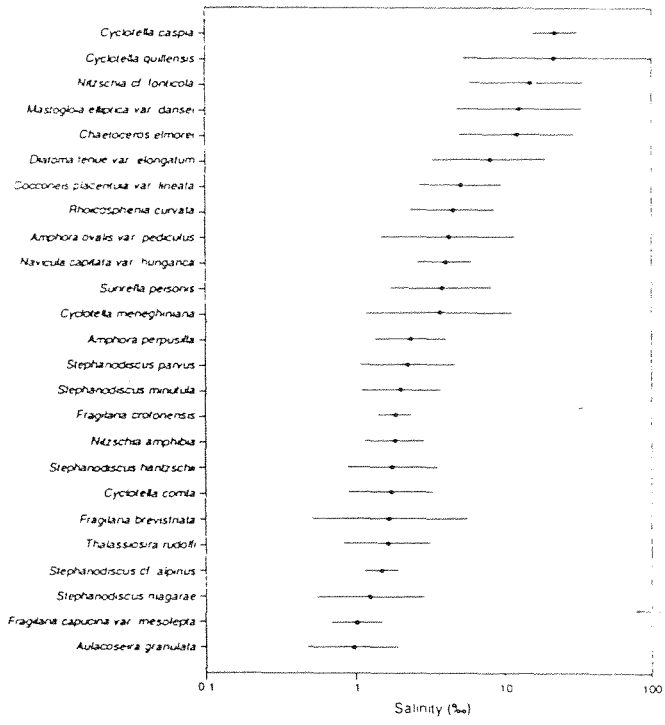


FIG. 2 Estimated optima (abundance-weighted means) and tolerances (abundance-weighted standard deviations) of taxa in the Devils Lake core with maximum abundance >5% and occurrences in five or more samples.

$$\hat{u}_k = \sum_{i=1}^{m} y_{ik} x_i \Big/ \sum_{i=1}^{n} y_{ik} \qquad \hat{t}_k = \left[\sum_{i=1}^{n} y_{ik} (x_i - \hat{u}_k)^2 \Big/ \sum_{i=1}^{n} y_{ik} \right]^{1/2}$$

where y_{ik} is the abundance of taxon k in sample i, x_i is the observed salinity of sample i, and $\hat{u}_k$, $\hat{t}_k$ are the optimum and tolerance of species k, respectively.

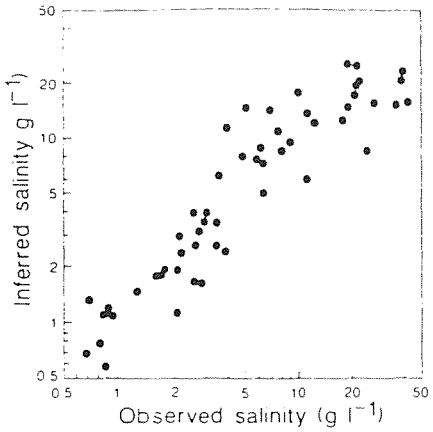


FIG. 3 Observed salinity against diatom-inferred salinity (derived from weighted-averaging regression) for the 55 surface-sample sites ($r = 0.91$).

$$\hat{x}_i = \sum_{k=1}^{m} y_{ik}\hat{u}_k \Big/ \sum_{k=1}^{m} y_{ik} \qquad \hat{x}_i = a + b\hat{x}_i$$

where y_{ik} is the abundance of taxon k in sample i, $\hat{u}_k$ is the optimum of species k, $\hat{x}_i$ is the inferred salinity, and a and b are the coefficients of the deshrinking regression of observed salinity x_i on $\hat{x}_i$ (ref. 72 in ref. 15).

and tolerances of selected diatom taxa and a comparison between inferred and measured salinity for each site are shown in Figs 2 and 3, respectively. The data indicate a very close agreement between inferred and measured salinity with no apparent outliers, despite the variable state of diatom preservation in the surface-sediment samples. These results suggest that diatom preservation is not significantly biased towards either the fresh or saline ends of the spectrum or that differential loss of entire valves is small.

To evaluate the use of the transfer function, we took cores from Devils Lake, North Dakota (48°05′ N 98°56′ W), where historical records show a strong hydrological response to climate change in the past century[17]. Lake levels fell and salinity rose from the late nineteenth century through the drought years of the 1930s and 1940s. Thereafter levels rose and salinity decreased to the present day (modern salinity is 2.8‰). This cycle of water-level change is recorded in the uppermost 30 cm of sediment by changes in the diatom composition. The recent freshwater phases are characterized by *Stephanodiscus minutulus* Kütz. Cleve and Moller and *S. niagarae* Ehr., whereas *Cyclotella quillensis* Bailey and resting spores of *Chaetoceros elmorei* Boyer dominate earlier saline periods. The highly saline low-water stands of the 1930s to 1940s also contain increased percentages of benthic diatoms and the meso-polysaline taxon *Cyclotella caspia* Grun. Application of both the preliminary[9] and the revised transfer functions to this time period showed that the salinity history could be accurately reproduced for periods of fresh water and low salinity (<10‰) and that high-salinity intervals could be clearly distinguished from those of low to moderate salinity. Discrepancies between the measured and diatom-inferred salinity during high-salinity episodes for Devils Lake probably result from problems with the sedimentary

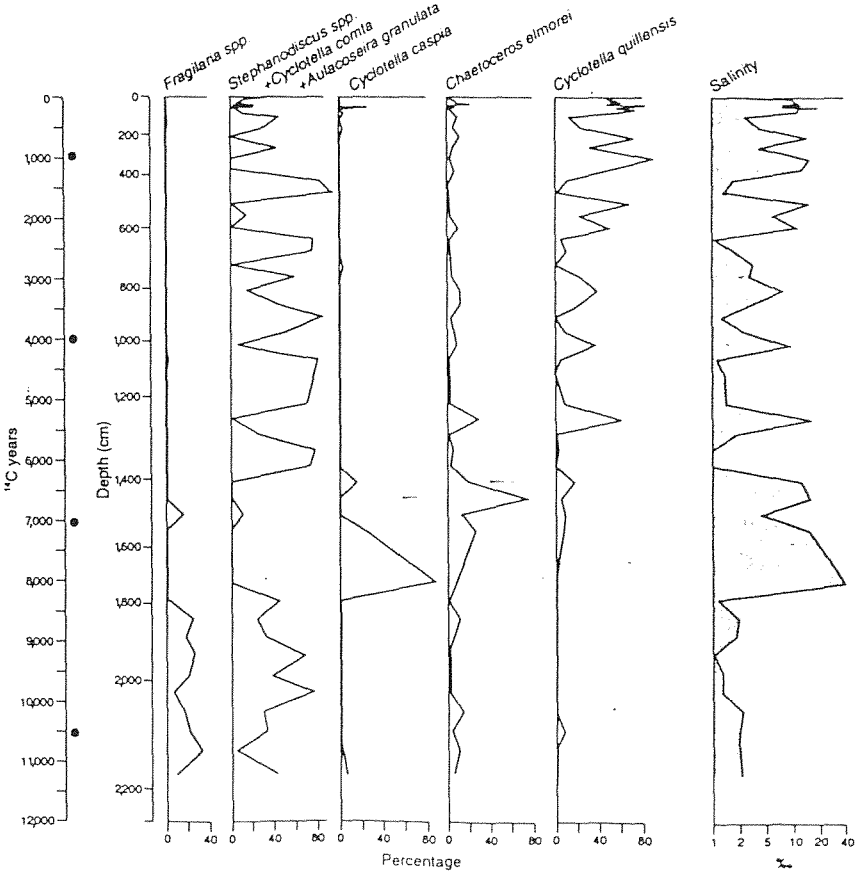


FIG. 4 Summary diatom diagram and diatom-inferred salinity for the late-glacial and Holocene record of Devils Lake, North Dakota. Core depth is measured from the sediment surface. Dates on the y-axis are derived from an age–depth relationship based on four AMS radiocarbon dates: Beta-21193/ETH-3022, 108–116 cm (woody fragment), 955 ± 120 BP; beta 21023/ETH-3009, 995–1003 cm (woody fragment), 3,950 ± 150 BP; beta-20471/ETH-2925, 1507–1515 cm (woody fragment), 6,855 ± 110 BP; beta-20472/ETH-2926, 2131–2139 cm (conifer twig), 10,580 ± 160 BP. The dating uncertainty limits represent 1 s.d. from counting statistics; dates are corrected by ^{13}C for total isotope effects; •, position of dates.

record, such as poor diatom preservation, sediment mixing and reworking, or dating inaccuracies, rather than from inadequacies in the inference method itself.

Diatom analysis of a 24-m-long, ^{14}C-dated by accelerator mass spectrometry (AMS) core from Devils Lake (Fig. 4) showed that the late-Wisconsin/early-Holocene was characterized by freshwater taxa, such as *S. minutulus*, *S. niagarae*, *Cyclotella comta* (Ehr.) Kütz. and *Fragilaria* sp. These freshwater species were abruptly replaced ~8,000 yr BP by *Cyclotella caspia* and other euryhaline species indicating a phase of low water level and high salinity that persisted until ~7,000 yr BP. A series of oscillations between fresh and saline episodes then followed, as shown by the alternation of freshwater *S. niagarae*, *S. minutulus* and *Aulacoseira granulata* (Ehr.) Ralfs. with the saline *C. quillensis* and *C. elmorei*.

Application of the transfer function to the Holocene stratigraphy suggests that salinities in the lake have fluctuated from ~1 to 40‰, with highest salinities in the early Holocene (Fig. 4). These oscillations in salinity, if repeated synchronously at other sites in the region, suggest that maximum aridity occurred ~8,000 yr BP, and that effective moisture fluctuated cyclicly throughout the remainder of the Holocene. At least seven oscillations are indicated by the Devils Lake data. The data further suggest that the lake was much more saline and conditions much drier in the past than the present day.

Because of high rates of sediment accumulation in many endorheic basins and a rapid chemical response to hydrological change, the diatom stratigraphy of saline-lake sediments can provide a sensitive, high-resolution record of climate change, without the lags characteristic of many other palaeoclimate proxies. We still need to extend our calibration data set at both ends of the salinity gradient to describe the weighted-averaged salinity optima of some taxa more accurately and to assess further the importance of variable diatom preservation in both the calibration data set and the core samples. Moreover, the relationship of salinity to water level and climate is complex and varies from lake to lake depending on hydrological and morphometric features of the lake and its watershed, as well as on geochemical characteristics of the lake water. For the northern Great Plains, where greenhouse warming could have a considerable impact on water availability and the agricultural economy, a series of accurately dated cores from additional sites are needed to substantiate the inferences that we have drawn here about effects on the climate. We can then use the pattern of events thus indicated to validate and refine moisture simulations from general circulation models, and to predict regional responses to climate change. □

Received 22 February; accepted 2 July 1991.

1. COHMAP Members *Science* **241,** 1043-1052 (1988).
2. Glantz, M. H. & Ausubel, J. J. in *Societal Responses to Regional Climatic Change* (ed. Glantz, M. H.) 113-142 (Westview, Boulder, Colorado, 1988).
3. Harrison, S. P. *Clim. Dyn.* **3,** 157-167 (1989).
4. Kutzbach, J. E. & Street-Perrott, F. A. *Nature* **317,** 130-134 (1985).
5. Fritz, S. C. & Battarbee, R. W. in *Proc. 9th Int. Diatom Symp.* 265-271 (Cramer, Stuttgart, 1988).
6. Bradbury, J. P., Forester, R. M. & Thompson, R. S. *J. Paleolimnol.* **1,** 249-267 (1989).
7. Radle, N. J., Keister, C. M. & Battarbee, R. W. *J. Paleolimnol.* **2,** 159-172 (1989).
8. Gasse, F., Talling, J. F. & Kilham, P. *Rev. Hydrobiol. Trop.* **16,** 3-34 (1983).
9. Fritz, S. C. *Limnol. Oceanogr.* **35,** 1771-1781 (1990).
10. Battarbee, R. W. in *Handbook of Holocene Palaeoecology and Palaeohydrology* (ed. Berglund, B.) 527-570 (Wiley, New York, 1986).
11. ter Braak, C. J. F. *Ecology* **67,** 1167-1179 (1986).
12. Jolliffe, I. T. *Principal Component Analysis*, 1-270 (Springer, New York, 1986).
13. Hill, M. O. & Gauch, H. G. *Vegetatio* **42,** 47-58 (1980).
14. ter Braak, C. J. F. & VanDam, H. *Hydrobiologia* **178,** 209-223 (1989).
15. Birks, H. J. B., Line, J. M., Juggins, S., Stevenson, A. C. & ter Braak, C. J. F. *Phil. Trans. R. Soc. Lond.* B**327,** 263-278 (1990).
16. ter Braak, C. J. F. *CANOCO—A FORTRAN program for Canonical Community Ordination* (TNO Institute of Applied Computer Science, Wageningen, 1987).
17. Swenson, H. A. & Colby, B. R. *US geol. Surv. Water-Supply Pap.* 1-79 (1955).
18. Winter, T. C. in *Northern Prairie Wetlands* (ed. Van Der Valk, A.) 16-54 (Iowa State University Press, Ames, 1989).

ACKNOWLEDGEMENTS. We thank E. Almgren, G. Battarbee, S. Björck, D. Haviland, H. Jacobson, S. Patrick, G. O. Seltzer, J. A. Wolin and H. E. Wright Jr for assistance with field work. This study was funded in the USA by the NSF (Ecology Program) and in the UK by the NERC (Palaeoclimate Special Topic).

Diatom assemblages and ionic characterization of lakes of the northern Great Plains, N.A.: a tool for reconstructing past salinity and climate fluctuations

S.C. Fritz

Limnological Research Center

University of Minnesota

310 Pillsbury Drive S.E.

Minneapolis, MN 55455 USA

S. Juggins and R.W. Battarbee

Environmental Change Research Center

Department of Geography

University College London

26 Bedford Way

London WC1H 0AP U.K.

Limnological Research Center Contribution # 444

Fritz, S.C., S. Juggins, and R.W. Battarbee. 1993. Diatom assemblages and ionic characterization of lakes of the northern Great Plains, N.A.: a tool for reconstructing past salinity and climate fluctuations. Can. J. Fish. Aquat. Sci. 50:0000-0000.

Abstract

The distribution of diatoms with respect to salinity and ionic gradients was studied in lakes of the northern Great Plains of North America. The lakes range from freshwater to hypersaline (0.65 to 270 g L^{-1}) and include a variety of brine types, although the majority are dominated by sulfate salts. Canonical correspondence analysis of diatoms in the surface sediments of 66 lakes and associated water-chemistry data indicates that diatom distributions are highly correlated with salinity. The ordination also suggests that brine type forms a significant environmental gradient and separates taxa characteristic of carbonate/bicarbonate lakes from those of sulfate-dominated systems. The salinity optima and tolerances of diatom species are calculated by weighted averaging regression, and these data provide a tool for the reconstruction of past salinity and the inference of climatic change in arid and semi-arid regions.

Introduction

Lakes in arid and semi-arid regions of the world respond rapidly to climate-driven hydrological change and, with their high sediment-accumulation rates, are significant repositories of high-resolution paleoecological and paleoclimatological information. Interpretation of stratigraphic records in these systems, however, requires detailed understanding of biological, geochemical, and sedimentological processes, as well as knowledge of the ecology and distribution of the biota that form the fossil record. Among the fossils contained in lake sediments diatoms are probably the most sensitive indicators of limnological change because of their widespread distribution, diversity, and rapid response to water-chemistry change. Although a vast literature exists on the ecological tolerances of freshwater diatom species, little is known about species in saline and subsaline systems, particularly for North America. A halobion system of classifying diatoms based on salinity preference was devised by Kolbe (1927) and later modified (Carpelan 1978; Hustedt 1953), however, this system is based primarily on waters of marine origin, where the dominant anion is chloride, and may not be broadly applicable to inland saline lakes where ionic composition is more diverse.

The Great Plains of North America contain a diversity of lakes that vary greatly in size and water chemistry and are important resources for local agriculture, mineral exploitation, and as wildlife habitat. We have studied diatom assemblages in a range of freshwater and saline lakes in the northern Great Plains of the United States and Canada and use these data to reconstruct regional changes in water chemistry, hydrology, and climate from the stratigraphic record (Fritz 1990; Fritz et al. 1991; Radle et al. 1989). Here we describe the data set that forms the basis for our stratigraphic interpretations and analyze the ionic characteristics of the lakes and the modern distribution of diatom assemblages with respect to salinity and ionic gradients.

Study Area

The northern Great Plains of North America are a region of flat to rolling topography in the continental interior (Fig. 1). The area has a cool continental climate. Daily mean temperatures range from ca. -18° C in January to 20° C in July in the north and from -10° C (Jan.) to 24° C (July) in the south, and mean annual precipitation decreases across the region from ca. 520 mm in the northeast to 350 mm in the southwest. The native vegetation reflects the negative effective-moisture gradient (P-E) (Fig. 1) and is predominantly grassland, with aspen parkland in northernmost portions and sagebrush steppe to the west. Presently the region forms one of the major agricultural belts of North America and is dominated by cultivated fields.

The lakes in this study are in glaciated portions of the northern Plains, where Cretaceous or Tertiary sedimentary bedrock is overlain by unconsolidated glacial deposits up to several hundred meters thick. The majority of lakes occupy morainal depressions or dammed valleys carved by glacial meltwater. They range from less than a few hectares to several-hundred square kilometers in size and from 0.1 to 28 m in depth. A few of the most saline systems are playas, but the majority of basins contain water throughout the year, except perhaps in years of extreme drought. Most of the shallower lakes do not stratify during the ice-free season as a result of frequent and intense winds. Several of the deepest lakes are known to be meromictic (Deadmoose, Waldsea, George, Medicine).

Lakes within the northern Great Plains show a great diversity in ionic concentration and composition and range from dilute freshwater to hypersaline. Salinity and ionic composition reflect both geology and precipitation minus evaporation gradients on a broad scale. However, within a small geographic area water chemistry can vary greatly, dependent on groundwater sources and topographic position within the drainage system (Almendinger 1990). The majority of sites described here were selected from earlier surveys in the north-Central U.S. (Gorham et al. 1983) and in Saskatchewan, Canada (Hammer 1978; Hammer and Haynes 1978).

Methods

Surface-sediment samples and associated water-chemistry data were collected in 1982 and 1985 from 39 lakes in North and South Dakota, USA and 27 in Saskatchewan, Canada (Fig. 1). The uppermost 3 cm of surficial sediment was collected for diatom analysis from a deepwater region of each lake, using a modified Hongve drop-corer (Wright 1990) or a rod-operated piston corer. ^{210}Pb dating of sediment cores from this region (Jacobson and Engstrom 1989; D.R. Engstrom, Limnological Research Center, University of Minnesota, Minneapolis, MN 55455, unpublished data) indicates that the uppermost 3 cm of sediment represents from 2 to 5 years of sediment accumulation.

At each lake a single water sample was taken in mid-summer with a Kemmerer sampler at 1 m depth, or just below the water's surface in basins of <1 m. Conductivity, pH, and water temperature were measured in the field. Measurements of pH were made on non-aerated samples with a Radiometer field pH meter, with a combination electrode and 2-buffer calibration. Cation concentrations were measured using matrix-matched external standards on a Spectrametrics SMI III d.c. plasma atomic-emission spectrometer, anions by ion chromatography on a Dionex 4000i machine with an As4A column, and inorganic carbon by automated coulometric titration on a Coulometrics CO_2 coulometer. All cation and anion measurements were made in the Aqueous Geochemistry Laboratory, Department of Geology, University of Minnesota. Salinity is calculated as the sum of all major cations and anions (Ca, Mg, K, Na, SO_4, Cl, HCO_3/CO_3).

Sediment samples for diatom analysis were processed in hot hydrogen peroxide or hot nitric acid with potassium dichromate to oxidize organic matter and subsequently rinsed several times with distilled water to remove the acid. Prepared samples were settled onto coverslips, and the coverslips mounted onto slides with Naphrax. Diatoms were counted in transects with an oil immersion objective (n.a. =1.32) on a Leitz Ortholux microscope at

a magnification of 1425X. A minimum of 400 valves was counted in most samples, but in sediments where diatom concentrations were low or diatom preservation was poor, fewer valves were counted. All recognizable valve fragments larger than one-half valve or represented as identifiable central areas were counted as a single valve. Diatom sums of less than 100 valves were excluded from further analysis. Slides, prepared sediment, and count data are archived in the Diatom Reference Collection of the Limnological Research Center, University of Minnesota and are available upon request.

The relationship between diatom distribution and environmental variables was explored using canonical correspondence analysis (CCA) (ter Braak 1986). Monte Carlo permutation tests were performed to test significance of ordination axes and of individual variables in a partial CCA (ter Braak 1990). Two lakes had incomplete chemistry, and a further 11 had no or very poorly preserved surface-sediment diatom assemblages and were excluded from the CCA. The resulting data set of 53 lakes contained a total of 149 taxa present at greater than 1% in at least one sample. In all analyses salinity and conductivity were log-transformed and lake maximum depth square-root transformed. Major cation and anions (Na, K, Mg, Ca, SO_4, Cl, HCO_3/CO_3) were included as both log-transformed concentrations and as proportions of total cations or anions, giving a total of 18 environmental variables (cation and anion concentrations and percents plus salinity, conductivity, pH, depth). All ordinations were performed using the CANOCO version 3.10 computer program (ter Braak 1988a; ter Braak 1990). Species optima and tolerances were calculated by weighted-averaging regression (ter Braak and VanDam 1989), using the program CALIBRATE version 1.5 (Juggins, unpublished program).

Results and Discussion

Water chemistry

The 66 lakes span a salinity gradient from 0.65 to 270 g L^{-1} and include a variety of brine types (Table 1). Most freshwater lakes (salinity <3 g L^{-1}) have sulfate as the dominant anion, although the majority also contain significant carbonate percentages (>20%), and in a few carbonate is the dominant anion (Fig. 2, Table 1). Sulfate is also the dominant anion in nearly all saline lakes, but occasionally carbonate and chloride may be abundant (>20%). Permanent water bodies dominated by chloride are rare in the northern Great Plains, and only one lake in the data set is so dominated (Reflex). Chloride is the sub-dominant anion in nine of the study lakes, and these include hyposaline (3-20 g L^{-1}) and mesosaline (20-50 g L^{-1}) systems.

Salts of magnesium and/or sodium are typical of both the fresh and saline systems, and in the lakes with salinity < 1 g L^{-1} calcium is also abundant (Table 1, Fig. 3). The freshwater gradient is truncated at 0.7 g L^{-1}, and this probably accounts for the absence of calcium-dominated lakes in the data set. Carbonate-dominated lakes have sodium as the dominant cation, whereas either magnesium or sodium may be dominant in sulfate-dominated lakes.

Diatom distribution and salinity

Results of canonical correspondence analysis with 18 environmental variables are shown in Figure 4 as a species-environment biplot (ter Braak 1987). The length and direction of environmental vectors reflects their relative importance and approximate correlation to the ordination axes. Axes 1 and 2 (eigenvalues of λ_1=0.59, λ_2=0.49) are both significant (p=0.01; Monte Carlo permutation test, 99 permutations) and together account for 11% of the cumulative variance in the diatom data. The low proportion of

variance accounted for by the first two axes is not unusual for data matrices with a large number of species and thus many zero values (Hall 1992).

Axis 1 is highly correlated with salinity (inter-set correlation 0.85) and its correlates, conductivity and major cation and anion concentration, and demonstrates the strong relationship between diatom distributions and total dissolved salts. The position of each taxon along this axis gives an indication of its weighted-average optimum with respect to the salinity gradient. For example, *Aulacoseira granulata, A. ambigua,* and *Fragilaria capucina* v. *mesolepta* are freshwater planktonic diatoms that, together with the attached species *Fragilaria brevistriata* v. *inflata, Gyrosigma acuminatum, Navicula capitata* and *N. vixvisibilis*, plot on the right of Figure 4. Other planktonic taxa characteristic of freshwater include *Stephanodiscus niagarae, Stephanodiscus* sp. affinity *S. medius*, and *Thalassiosira rudolfi* . Small *Stephanodiscus* taxa, including *S. hantzschii, S. minutulus*, and *S. parvus*, and *Cyclostephanos dubius* are most abundant in freshwater lakes, but occur at low abundance in weakly saline systems and therefore plot to the left of the other freshwater plankton. Other common epiphytic and benthic taxa with optima in the freshwater part of the gradient include *Nitzschia amphibia, N. frustulum, Amphora ovalis* v. *affinis, Fragilaria brevistriata, F. construens* v. *venter, F. vaucheriae, Cocconeis placentula,* and *Navicula oblonga. Cyclotella meneghiniana*, which is abundant in both freshwater and saline lakes, has its optimum near the biplot origin, which corresponds to a salinity of approximately 6 g L^{-1}, the weighted mean for the dataset.

Taxa that plot at the saline end of the gradient include *Navicula bulnheimii, Nitzschia inconspicua, Amphora coffeaeformis*, and the planktonic *Cyclotella caspia, Cyclotella quillensis*, and *Chaetoceros elmorei/muelleri* . Common benthic taxa with optima in the middle of the saline range include *Cymbella pusilla , Mastogloia elliptica* v. *dansei, Synedra pulchella, Nitzschia hungarica, N. fonticola, N. compressa* f. *minor, Navicula cincta*, and *N. viridula. Diatoma tenue* v. *elongatum, Opephora* sp. affinity *O. olsenii, Amphora veneta, Surirella ovata* v. *crumena, S. peisonis, Campylodiscus clypeus,*

Anomoeoneis costata, *Anomoeoneis* sp. a, *Synedra fasciculata*, *Nitzschia apiculata*, *Navicula veneta*, and *N. halophila* have optima in the lower end of the hyposaline range (<7 g L^{-1}).

Figure 5 shows the weighted-average salinity optima and tolerances (ter Braak and VanDam 1989) of the most abundant taxa in the surface-sample data set. The optima and tolerances of all taxa included in the CCA, as well the number of occurrences and each taxon's maximum abundance, are given in Table 2. Varied distributional patterns are apparent. A few taxa have very restricted tolerances, including *Aulacoseira ambigua*, *Fragilaria capucina* v. *mesolepta*, *Nitzschia amphibia*, and *Fragilaria vaucheriae* amongst the freshwater species and *Navicula bulnheimii*, *Cyclotella caspia*, *Opephora* cf. *olsenii*, and an unnamed *Anomoeoneis* species in saline parts of the range. The narrow ranges of several freshwater taxa may be in part an artifact of the data set, which presently does not extend to salinities below 0.7 g L^{-1}. *Navicula bulnheimii* was common only in deep meromictic saline lakes (Medicine, Redberry, Sayer, Basin, Waldsea, Deadmoose).

Some species have broad salinity tolerances and occur in both fresh and saline waters. These are primarily benthic diatoms, such as *Fragilaria brevistriata*, *F. construens* v. *venter*, *Surirella ovata*, and *Navicula veneta*. *Cyclotella meneghiniana* is the only planktonic taxon whose range extends from freshwater well into saline conditions, although several typically freshwater planktonic species (*Stephanodiscus parvus*, *S. minutulus*, *S. hantzschii*, *Cyclostephanos dubius*) can also be found in eutrophic hyposaline waters. Several of the taxa restricted to saline waters have broad ranges, most notably the planktonic *Cyclotella quillensis*, as well as benthic species including *Nitzschia inconspicua*, *N.* sp. affinity *N. fonticola*, *N. hungarica*, *Cymbella pusilla*, *Mastogloia elliptica* v. *dansei*, and *Amphora coffeaeformis*. *Chaetoceros* species are found in the sediments primarily as resting spores or cysts, which are not resolvable to the species level (Rushforth and Johansen 1986), and the apparent broad salinity tolerances of the *Chaetoceros elmorei/muelleri* group may be the result of combining taxa with more

restricted distributions. A few taxa that are restricted to saline lakes in the present data set clearly occur in freshwater elsewhere (*Cocconeis pediculus, C. placentula* v. *euglypta, C. diminuta, Gyrosigma spencerii* v. *curvula, Navicula viridula, N. cincta*). These were found primarily in small shallow saline lakes, and the restriction of their ranges is probably an artifact of the absence of analogous sites within the freshwater range.

The optima and tolerances presented here may be biased to some extent by the use of a single mid-summer sample to characterize water chemistry. The chemistry of closed-basin lakes varies seasonally and from year to year in response to changes in the balance between precipitation and evaporation. Salinity is commonly low in mid- to late-spring, following runoff from snow melt and spring rains, and increases gradually to maximum values in late summer and autumn, as a result of evaporative concentration of lakewater (Hammer 1978). Thus a mid-summer salinity measurement from a single year may not adequately characterize the range of water chemistries represented by an integrated surface-sediment sample, although it is probably a reasonable estimate of mean salinity. A more important consideration for the calculation of salinity optima is the seasonality of diatom blooms in saline lakes. For diatom taxa that bloom in the spring, an early spring salinity measurement may be more appropriate than a mean value and similarly autumn measurements may be more realistic for species that have autumnal population maxima. It is clear that we need more basic autecological studies to adequately address these sorts of issues.

Figure 6 shows the relative abundance of selected taxa along the salinity gradient, with taxa ordered top left to bottom right according to their salinity optimum. These plots reinforce some distributional patterns indicated in Fig. 5, including the narrow salinity distribution of *Aulacoseira ambigua, Nitzschia amphibia,* and *Fragilaria brevistriata* v. *inflata* at the freshwater end of the gradient and of *Cyclotella caspia* at the saline extreme. The broader ranges of taxa, such as *Stephanodiscus niagarae* and *Nitzschia frustulum* within freshwater systems and of *Cyclotella quillensis, Chaetoceros elmoreilmuelleri, Synedra pulchella, Amphora coffeaeformis*, and *Nitzschia inconspicua* across the saline

range, are also apparent. The plots also contrast the distributional patterns of the *Cyclotella meneghiniana*, with a broad range and high relative abundance across that range, with taxa such as *Surirella ovata* and *Surirella peisonis* that also have a broad distribution but rarely attain high relative abundance.

Diatom distribution and ionic composition

The second axis of the CCA ordination is correlated with HCO_3/CO_3, Ca, $\%SO_4$, %Mg, and %Na (inter-set correlation 0.64, -0.70, -0.62, -0.47, and 0.55 respectively) and relates to differences in brine type, separating the bicarbonate/carbonate lakes (Isabel, Shinbone, Elbow, Round #2, Horseshoe, Fife) which plot in the upper part of Figure 4, from sulfate-dominated waters. The ordination biplot also suggests some separation of Na versus Mg-dominated lakes along the second axis, although this gradient is created primarily by high relative abundance of Na in carbonate lakes of the upper part of the plot. Because there is a significant correlation between ionic composition and salinity in this data set (Fig. 2), the significance of brine type was further investigated using a partial CCA (ter Braak 1988b), in which the effects of salinity, conductivity, and depth were separated out, and the significance of ionic composition assessed using an unrestricted Monte Carlo permutation test. Forward selection of chemical variables relating to brine-type yielded 3 significant variables: $\%HCO_3/CO_3$, %Mg, and %Na ($p < 0.05$). A second partial CCA with anion-type additionally removed and cations as explanatory variables was not significant. These analyses indicate that both anion- and cation-type are important in explaining diatom distribution, but that their effects cannot be separated in this dataset.

Diatoms characteristic of the Na_2CO_3 lakes include *Campylodiscus clypeus, Anomoeoneis costata,* and an unknown *Anomoeoneis* species, as well as *Fragilaria vaucheriae, Gomphonema olivaceum, Cocconeis diminuta* and to a lesser degree *Navicula oblonga, Cymbella pusilla, Mastogloia smithii* v. *lacustris,* and *Surirella ovata* v. *crumena.* At the bottom left of the diagram are taxa characteristic of saline, sulfate-dominated lakes,

such as *Nitzschia compressa* f. *minor*, *N. constricta*, *N.* sp. affinity *N. fonticola*, *Gyrosigma spencerii* v. *curvula*, *Navicula cincta*, *Cocconeis pediculus*, and *Cyclotella caspia* .

Diatom preservation

Diatom preservation is variable in the lakes of the data set, and diatoms are absent or poorly preserved in sediments of 14 of the 66 lakes sampled (Table 1). Preservation is to some extent related to increased dissolution at high salinity, and diatoms are absent or poorly preserved in 7 of the 8 lakes with salinity > 40 g L^{-1}. Most of these lakes are also quite shallow ($z < 1.5$ m), and thus it is not possible to separate the relative contributions of salinity versus sediment mixing and desiccation to the poor state of diatom preservation. In some cases low concentrations of diatoms in the sediments may not be related to poor preservation but may result instead from low diatom production coupled with high erosion rates. Amongst the lakes of lower salinity with poor preservation, four have relatively high carbonate proportions (Manito, Shinbone, Alkaline, Horseshoe) and two of the others (Bitter, N. Blaine) are very shallow ($z<0.6$ m). However, neither depth nor carbonate concentration alone is sufficient to explain the poor preservation, because other shallow or carbonate systems in the data set do not suffer poor diatom preservation.

The relative abundance of diatom taxa in saline-lake sediments is biased in part by differential preservation. Heavily silicified diatom remains, such as *Chaetoceros* cysts, *Cyclotella quillensis*, *C. meneghiniana*, and various *Surirella* species, may be over-represented in sediments relative to their abundance in living communities, because they are less likely to be dissolved or broken in comparison with thin lightly silicified taxa. Similarly taxa with distinctive central areas, such as *Cyclotella caspia*, *Mastogloia smithii* v. *lacustris*, *Synedra pulchella*, *Navicula oblonga*, and *Rhoicosphenia curvata* may also be over-represented, because they are more easily distinguished than broken valves of other taxa.

Comparisons with other regional studies

The only well-developed literature on saline-lake diatoms is for the African continent, including studies of diatoms in relationship to water-chemistry variables in East Africa (Gasse 1986; Gasse et al. 1983; Hecky and Kilham 1973), the Sahara and Sahel (Gasse 1987; Gasse et al. 1987), North Africa (Khelifa 1989; F. Gasse, Laboratoire d'Hydrologie et de Géochimie Isotopique, Université de Paris Sud, F-91405 Orsay Cedex, France, unpublished data), and the extensive floras of from South Africa (e.g. Archibald 1983; Schoeman and Archibald 1976-1980). In other regions studies of diatoms with respect to ionic concentration and composition are limited (e.g. Ehrlich 1978; Ehrlich and Dor 1985), although in recent years a number of projects have been initiated in conjunction with studies of past environmental change (e.g. Bradbury 1989; Cumming and Smol 1993; Gell and Gasse 1992; Metcalfe 1988; Servant-Vildary and Roux 1990). The current North American literature on ecology of saline-lake diatoms includes primarily floristic studies of lakes in western regions of the United States and Canada (e.g. Bahls et al. 1984; Bailey 1922; Felix and Rushforth 1979; Hanna and Grant 1931; Kaczmarska and Rushforth 1983). In contrast to the sulfate-dominated lakes of the northern Great Plains, other published diatom studies from saline-lake regions are from areas dominated by carbonates or chlorides (E. Africa, Israel, central Mexico, south-eastern Australia, Bolivia, western U.S.), with the exception of those from North Africa.

Diatom distribution in the northern Great Plains with respect to salinity gradients is broadly similar to that seen in other areas. Taxa such as *Aulacoseira* spp., *Stephanodiscus* spp, *Nitzschia amphibia*, and *Fragilaria capucina* v. *mesolepta* are typical of freshwater, whereas *Nitzschia* sp. affinity *N. fonticola, Amphora coffeaeformis*, *Chaetoceros muelleri*, and *Cymbella pusilla* are characteristic of saline systems. Floristic comparisons of the sulfate-dominated lakes of the Great Plains with other regions, however, suggests significant differences related to brine type. Some of the common taxa in carbonate-

dominated lakes of Africa (Gasse 1987; Gasse et al. 1983), Australia (Gell and Gasse 1992), and Mexico (Metcalfe 1988), such as *Thalassiosira rudolfi*, *Anomoeoneis sphaerophora*, *Navicula elkab*, *Rhopalodia gibberula*, and *Nitzschia pusilla*, are rare or absent in the lakes studied here. Amongst the taxa apparently more common in the carbonate lakes of the Great Plains, *Anomoeoneis costata* is also common in carbonate lakes of Africa and Mexico, whereas in the African lakes *Campylodiscus clypeus* is also typical of chloride-dominated systems (Gasse 1987; Gasse et al. 1983). Many taxa that are characteristic of chloride lakes in Africa, such as *Amphora coffeaeformis*, *A. acutiuscula*, *Campylodiscus clypeus*, *Mastogloia elliptica*, *Nitzschia hungarica*, *N. tryblionella*, and *Cymbella pusilla* (Gasse 1987; Gasse et al. 1983) are also common in the sulfate lakes of the northern Great Plains, but a few taxa in African chloride systems, including *Amphora tenerrima*, *A. tenarescens*, *Nitzschia elegantula*, and *N. stompsii* (Gasse et al. 1987) have not been found.

A few of the differences in ecological distribution between the northern Great Plains and other regions undoubtedly result from taxonomic problems. For example, *Nitzschia frustulum* is common only in freshwater in the Plains, whereas in Africa it is characteristic of lakes of moderate to high salinity (Gasse et al. 1983). Similarly *Nitzschia* sp. affinity *N. fonticola* is characteristic of lakes with conductivity <3000 µS in East Africa (Gasse et al. 1983), appears to be indifferent to salinity in southwestern Australia (Gell and Gasse 1992), and in the northern Great Plains is common only in lakes of conductivity >3000 µS. Both of these groups are taxonomically difficult and morphologically variable, and the apparent discrepancies in distribution probably result from unrecognized taxonomic distinctions.

Cyclotella quillensis and *C. caspia* are common planktonic taxa in saline lakes of the northern Great Plains. *Cyclotella quillensis* was described from the Quill Lakes in Saskatchewan (Bailey 1922) and is closely related taxonomically to *C. meneghiniana* (Battarbee et al. 1982). Although it has not been reported in the literature from areas

outside the Americas, it has been found recently in deposits from Africa and China (F. Gasse, unpublished data). *Cyclotella caspia* has been reported from lakes, rivers, and estuaries in Europe (Kiss et al. 1988), North America (Fritz et al. 1991, S.R. Cooper, Department of Geography & Environmental Engineering, John Hopkins University, Baltimore, MD 21218, pers. comm.), and Australia (Gell and Gasse 1992). It is common in fossil deposits in Africa (Fontes et al. 1985; Gasse et al. 1987) and has been reported from riverine systems in South Africa (Archibald 1983), but to date it has not been found in lacustrine deposits elsewhere in Africa. This points to the broad utility of calibration data sets, in that modern lake systems in one region may provide analogs for fossil deposits that are not represented in the contemporary environments of another.

Summary and Conclusions

The distribution of diatoms is clearly related to salinity gradients, and thus sedimentary diatoms are excellent tools for the reconstruction of past changes in salinity and climate in arid and semi-arid environments. The available autecological information on saline-lake diatoms has permitted qualitative environmental interpretations from the sedimentary record (Begin et al. 1974; Bradbury et al. 1989; Fontes et al. 1985; Gasse et al. 1987), but the limited data on factors controlling diatom distributions in saline environments may preclude detailed stratigraphic interpretation. Regional studies of diatom distributions in relationship to water-chemistry and other environmental variables, such as the one presented here, enhance our ability to interpret stratigraphic records and also allow the development of models for the quantitative reconstruction of salinity and climate fluctuations (Fritz et al. 1991).

This paper presents an analysis of the distribution of diatoms with respect to gradients of ionic concentration and composition in lakes of the northern Great Plains of North America, a vast agricultural region where future water availability is of critical concern. The paper provides specific data on the salinity optima and tolerances of diatom taxa, which

can be applied to stratigraphic profiles from lakes within the region and in other areas under similar environmental controls. The data can also be compared with other regional data sets to address and pose questions related to diatom ecology and biogeography. The salinity optima and tolerances presented here are tentative and undoubtedly will be modified in the future as the data set expands to include a larger number and a broader range of lakes, particularly in the freshwater range.

The distribution of many diatom taxa within the northern Great Plains is clearly correlated with salinity gradients; however, the influence of ionic composition on distributional patterns is not clear because of the paucity of carbonate or chloride-dominated lakes within the current data set. Analysis of these patterns will necessitate the inclusion of sites from nearby areas in the Great Plains, such as the carbonate-dominated lakes of eastern Montana or those in the Nebraska Sandhills, and may be useful in the assessment of past changes in groundwater source or other hydrologic factors (Gasse 1987) from the stratigraphic record. Dissolution of diatoms in saline environments may also cause significant spatial and temporal variations in sedimentary diatom assemblages (Barker 1992), and analysis of the patterns and processes of valve dissolution is necessary for the clear interpretation of environmental change from sedimentary diatom assemblages.

These broad-scale distributional data, which clearly suggest a strong relationship of many diatom taxa to salinity gradients, do not allow us to disentangle the specific factors correlated with ionic concentration or composition that actually control diatom distributions or the extent to which these factors act directly on diatoms or through other components of the biological system. But the patterns suggested here are clearly useful for the reconstruction of past changes in lacustrine water chemistry and local moisture availability and can be used to pose hypotheses about patterns and processes of regional environmental change, as well as the biological interactions and physiological mechanisms that determine diatom distributions in saline and subsaline lakes.

Acknowledgments

We thank G. Battarbee, S. Björck, D. Engstrom, S. Patrick, and G. Seltzer for assistance with field work and D.R. Engstrom for analysis of the water-chemistry samples. This work was supported in the U.S. by NSF grants DEB80-04286, BSR84-15866, and ATM90-05875 and in the UK by the NERC (Paleoclimate Special Topic).

References

Almendinger, J. E. 1990. Groundwater control of closed-basin lake levels under steady-state conditions. J. Hydrol. 112: 293-318.

Archibald, R. E. M. 1983. The Diatoms from the Sundays and Great Fish Rivers in the Eastern Cape Province of South Africa. J. Cramer, Stuttgart, 362 pp.

Bahls, L. L., E. E. Weber, and J. O. Jarvie. 1984. Ecology and distribution of major diatom ecotypes in the southern Fort Union coal region of Montana. U.S. Geol. Survey Professional Paper 1289: 1-151.

Bailey, L. W. 1922. Diatoms from the Quill Lakes, Saskatchewan, and from Airdrie, Alberta. Contr. Can. Biol. 1921, No. 11: 157-165.

Barker, P. 1992. Differential diatom dissolution in Late Quaternary sediments from Lake Manyara Tanzania: an experimental approach. J. Paleolimnology 7: 235-251.

Battarbee, R. W., C. M. Keister, and J. P. Bradbury. 1982. The frustular morphology and taxonomic relationships of *Cyclotella quillensis* Bailey. *pp.* 173-184. *In* D. G. Mann (ed.), 7th International Diatom Symposium, Proceedings. J. Cramer, Stuttgart.

Begin, Z. B., A. Ehrlich and Y. Nathan. 1974. Lake Lisan, the Pleistocene precursor of the Dead Sea. Geol. Survey Israel, Bull. 63: 1-30.

Bradbury, J. P. 1989. Late Quaternary lacustrine paleoenvironments in the Cuenca de Mexico. Quat. Sci. Rev. 8: 75-100.

Bradbury, J. P., R. M. Forester, and R. S. Thompson. 1989. Late Quaternary paleolimnology of Walker Lake, Nevada. J. Paleolimnology 1: 249-267.

Carpelen, L. H. 1978. Revision of Kolbe's System der Halobien based on diatoms of California lagoons. Oikos 31: 112-122.

Cumming, B. F. and J. P. Smol. 1993. Diatoms and their relationship to salinity and other limnological characteristics from 65 Cariboo/Chilcotin region (British Columbia, Canada) lakes. Hydrobiol. (in press).

Ehrlich, A. 1978. The diatoms of the hyperhaline Solar Lake (NE Sinai). Israel J. Bot. 27: 1-13.

Ehrlich, A. and I. Dor. 1985. Photosynthetic microorganisms of the Gavish Sabkha. pp. 296-321. *In* G. M. Friedman and W. E. Krumbein (eds.), Hypersaline Ecosystems. Springer-Verlag, Berlin.

Felix, E. A. and S. R. Rushforth. 1979. The algal flora of the Great Salt Lake, Utah, USA. Nova Hedwigia 31: 163-195.

Fontes, J. C., F. Gasse, Y. Callot, J.-C. Plaziat, P. Carbonel, P. A. Dupeuble, and I. Kaczmarska. 1985. Freshwater to marine-like environments from Holocene lakes in northern Sahara. Nature 317: 608-610.

Fritz, S. C. 1990. Twentieth-century salinity and water-level fluctuations in Devils Lake, N. Dakota: a test of a diatom-based transfer function. Limnol. Oceanogr. 35: 1771-1781.

Fritz, S. C., S. Juggins, R. W. Battarbee, and D. R. Engstrom. 1991. Reconstruction of past changes in salinity and climate using a diatom-based transfer function. Nature 352: 706-708.

Gasse, F. 1986. East African Diatoms: taxonomy, ecological distribution. Cramer, Stuttgart, 201 pp.

Gasse, F. 1987. Diatoms for reconstructing palaeoenvironments and palaeohydrology in tropical semi-arid zones: examples of some lakes in Niger since 12000 BP. Hydrobiol. 154: 127-163.

Gasse, F., J. C. Fontes, J. C. Plaziat, P. Carbonel, I. Kaczmarska, P. De Deckker, I. Soulié-Marsche, Y. Callot, and P. A. Dupeuble. 1987. Biological remains, geochemistry and stable isotopes for the reconstruction of environmental and hydrological changes in the Holocene lakes from North Sahara. Palaeogeogr. Palaeoclimatol. Palaeoecol. 60: 1-46.

Gasse, F., J. F. Talling, and P. Kilham. 1983. Diatom assemblages in East Africa: classification, distribution, and ecology. Rev. Hydrobiol. trop. 16: 3-34.

Gell, P. A. and F. Gasse. 1992. Relationships between salinity and diatom flora from some Australian saline lakes. Proc. Cal. Acad. Sci (in press).

Gorham, E., W. E. Dean, and J. E. Sanger. 1983. The chemical composition of lakes in the north-central United States. Limnol. Oceanogr. 28: 287-301.

Hall, R. I. and J. P. Smol. 1992. A weighted averaging regression and calibration model for inferring total phosphorus concentration from diatoms in British Columbia (Canada) lakes. Freshwater Biol. 27: 417-434.

Hammer, U. T. 1978. The saline lakes of Saskatchewan. III. Chemical characterization. Int. Revue ges. Hydrobiol. 63: 311-335.

Hammer, U. T. and R. C. Haynes. 1978. The saline lakes of Saskatchewan. II. Locale, hydrography, and other physical aspects. Int. Revue ges. Hydrobiol. 63: 179-203.

Hanna, G. D. and W. M. Grant. 1931. Diatoms from Pyramid Lake, Nevada. Trans. Am.. Micr. Soc. 50: 282-297.

Hecky, R. E. and P. Kilham. 1973. Diatoms in alkaline saline lakes: ecology and geochemical implications. Limnol. Oceanogr. 18: 53-71.

Hustedt, F. 1953. Die Systematik der Diatomeen in ihren Beziehungen zur Geologie und Ökologie nebst einer Revision des Halobien-systems. Bot. Tidsskr. 47: 509-519.

Jacobson, H. A. and D. R. Engstrom. 1989. Resolving the chronology of recent lake sediments: an example from Devils Lake, North Dakota. J. Paleolimnology 2: 81-98.

Kaczmarska, I. and S. R. Rushforth. 1983. The Diatom Flora of Blue Lake, Tooele County, Utah. J. Cramer, Stuttgart, 123 pp.

Khelifa, L. B. 1989. Diatomees continentales et paleomillieux du Sud-Tunisien aux Quaternaire superieur. Ph.D. thesis, Université de Paris-Sud.

Kiss, K. T., M. Coste, R. LeCohu, and M. Nausch. 1988. *Cyclotella caspia* (Bacillariophyceae) in some rivers and lakes in Europe (morphological observations). Crypt. Algol. 9: 27-42.

Kolbe, R. W. 1927. Zur Ökologie, Morphologie und Systematik der Brackwasser-Diatomeen. Pflanzenforschung 7: 1-146.

Metcalfe, S. E. 1988. Modern diatom assemblages in Central Mexico: the role of water chemistry and other environmental factors as indicated by TWINSPAN and DECORANA. Freshwater Biol. 19: 217-233.

Radle, N. J., C. M. Keister, and R. W. Battarbee. 1989. Diatom, pollen, and geochemical evidence for the paleosalinity of Medicine Lake, S. Dakota, during the Late Wisconsin and early Holocene. J. Paleolimnology 2: 159-172.

Rushforth, S. R. and J. R. Johansen. 1986. The inland *Chaetoceros* (Bacillariophyceae) species of North America. J. Phycol. 22: 441-448.

Schoeman, F. R. and R. E. M. Archibald. 1976-1980. The Diatom Flora of South Africa. CSIR, Pretoria.

Servant-Vildary, S. and M. Roux. 1990. Multivariate analysis of diatoms and water chemistry in Bolivian saline lakes. Hydrobiol. 197: 267-290.

ter Braak, C. F. J. 1988a. CANOCO - A FORTRAN Program for Canonical Community Ordination by (Partial) (Detrended) (Canonical) Correspondence Analysis, Principal Components Analysis and Redundancy Analysis, Version 2.1. Agricultural Mathematics Group, Wageningen, the Netherlands.

ter Braak, C. F. J. 1988b. Partial canonical correspondence analysis. pp. 551-558. *In* H. H. Bock (ed.), Classification and Related Methods of Data Analysis. North-Holland Publishing Company, Amsterdam.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

ter Braak, C. J. F. 1987. Ordination. pp. 91-173. *In* R. H. G. Jongman, C. J. F. ter Braak and O. F. R. van Tongeren (eds.), Data Analysis in Community and Landscape Ecology. Pudoc, Wageningen.

ter Braak, C. J. F. 1990. Update notes: CANOCO, Version 3.10. Agricultural Mathematics Group, Wageningen, the Netherlands.

ter Braak, C. J. F. and H. VanDam. 1989. Inferring pH from diatoms: a comparison of old and new calibration methods. Hydrobiol. 178: 209-223.

Wright, H. E., Jr. 1990. An improved Hongve sampler for surface sediments. J. Paleolimnology 4: 91-92.

		N lat. W. long	mg L-1	mg L-1	mg L-1	mg L-1	mg L-1	mg L-1	mg L-1	mg L-1	mg L-1	mg L-1	Ion Dominance %	Salinity g L-1	Cond uS	pH	Depth m
ALBT	Albert, Hamlin Co., S.D.	44°32', 97°09'	33	20	59	62.5	0.383	0.068	280	10.4	241	6.1	$Mg(Ca)SO_4(CO_3)$	0.71	850	8.7	1.6
ALK2	Alkali, Sargent Co., N.D.	46°02', 97°23'	1610	56	207	27.1	0.135	0.025	2445	828.2	822	87.0	$NaSO_4(Cl)$	6.08	7350	9.1	2.6
ALKA	Alkaline, Kidder Co., N.D.*	46°40', 99°33'	1560	213	225	16.9	0.082	0.031	2922	273.5	1059	125.4	$Na(Mg)SO_4(CO_3)$	6.39	7250	9.2	2.4
ANTE	Antelope, Saskatchewan*	50°18', 108°25'	2460	196	1220	65.8	0.264	0.028	8580	342.7	843	138.1	$Na(Mg)SO_4$	13.85	14300	9.0	7.3
AROM	Aroma, Saskatchewan*	52°18', 108°33'	12900	1090	12000	153.6	0.499	0.057	61280	7052.0	1254	484.2	$Mg(Na)SO_4$	96.21	64700	9.0	1.5
BASI	Basin, Saskatchewan	52°38', 105°17'	2910	211	2480	135.9	0.402	0.024	14030	768.3	582	93.5	$Mg(Na)SO_4$	21.21	19600	8.9	11.3
BIT1	Bitter, Day Co., S.D.#	45°17', 97°19'	2450	515	3210	52.4	0.124	0.028	15620	702.7	880	98.2	$Mg(Na)SO_4$	23.53	21000	9.2	0.1
BITT	Bitter, Saskatchewan*	50°08', 109°50'	58700	1010	18000	551.0	19.500	0.247	178000	10630.0	862	263.8	$Na(Mg)SO_4$	268.04	100000	8.8	0.1
BOUC	Boucher, Saskatchewan	52°28', 105°41'	475	75	402	137.9	0.850	0.024	2426	159.4	245	16.4	$Mg(Na)SO_4$	3.94	4350	8.8	0.8
BQUI	Big Quill, Saskatchewan	51°55', 104°22'	6380	403	3870	201.9	0.728	0.032	23590	2890.0	481	97.5	$Mg(Na)SO_4$	37.91	33300	8.9	2.4
BYRN	Byron, Beadle Co., S.D.	44° 33', 98°10'												2.20	2777		1.3
COLD	Coldwater, McIntosh Co., N.D.	46°01', 99°04'	314	131	440	26.8	0.061	0.009	1789	95.7	708	19.5	$Mg(Na)SO_4(CO_3)$	3.52	3800	8.6	9.0
COON	Coon, Nelson Co., N.D.	47°58', 98°23'	225	22	114	90.8	0.619	0.061	807	48.5	320	3.5	$Na(Mg)SO_4(CO_3)$	1.63	1950	8.3	1.3
DEAD	Deadmoose, Saskatchewan	52°19', 105°10'	4880	235	1430	129.0	0.450	0.025	8712	5625.0	411	77.6	$Na(Mg)SO_4(Cl)$	21.50	25800	9.0	28.0
DEVI	Devils, Ramsey Co., N.D.	48°05', 98°56'	551	76	139	76.9	0.377	0.049	1151	246.4	500	20.3	$Na(Mg)SO_4(CO_3)$	2.76	3500	8.8	7.0
ECKL	Eckelson, Barnes Co., N.D.	46°56', 98°17'	9500	733	2620	151.0	0.528	0.026	22860	4728.0	682	130.1	$Na(Mg)SO_4(Cl)$	41.41	41300	9.0	0.5
ECOT	E. Coteau, Saskatchewan	49°03', 104°33'	631	106	869	163.3	0.533	0.032	4860	46.6	250	15.0	$Mg(Na)SO_4$	6.94	6350	8.7	5.4
EDEV	E. Devils, Ramsey Co., N.D.	47°57', 98°43'	2330	229	463	92.9	0.479	0.037	5040	1034.0	668	38.7	$Na(Mg)SO_4$	9.90	11800	8.8	6.5
ELBW	Elbow, Benson Co., N.D.	47°55', 98°43'	371	45	70	6.8	0.021	0.015	126	70.7	1000	83.4	$Na(Mg)CO_3$	1.77	1900	9.2	1.3
ESTU	E. Stump, Nelson Co., N.D.*	47°53', 98°22'	19300	990	4660	383.0	1.670	0.050	47970	8289.0	605	53.5	$Na(Mg)SO_4$	82.25	68200	8.6	1.0
FIFE	Fife, Saskatchewan	49°14', 105°53'	796	61	121	14.8	0.397	0.040	1077	28.5	1220	92.3	$Na(Mg)CO_3(SO_4)$	3.41	3800	8.9	2.5
FISH	Fishing, Saskatchewan	51°51', 103°33'	324	64	425	100.9	0.293	0.019	2154	56.8	318	6.5	$Mg(Na)SO_4$	3.45	3600	8.3	10.8
FREE	Free People, Benson Co., N.D.	47°56', 98°43'	2650	151	99	9.3	0.026	0.024	3383	868.8	1545	208.5	$NaSO_4(CO_3)$	8.92	11950	9.2	3.1
GEOR	George, Kidder Co., N.D.	46°45', 99°30'	5640	467	712	18.0	0.049	0.028	11460	1223.0	1407	308.0	$NaSO_4$	21.24	23300	9.2	24.3
HAZL	Hazelden, Day Co., S.D.	45°31', 97°28'	4340	750	4420	380.0	1.450	0.033	24940	747.3	345	43.0	$Mg(Na)SO_4$	35.97	30200	8.9	0.1
HERM	Herman, Lake Co., S.D.	44°00', 97°10'	39	16	58	89.9	0.520	0.081	372	7.3	218	7.2	$Mg(Ca)SO_4(CO_3)$	0.81	1000	8.8	1.7
HORS	Horseshoe, Eddy Co., N.D.	47°53', 98°48'	1900	151	31	17.3	0.165	0.032	2229	653.2	1213	140.5	$NaSO_4(CO_3)(Cl)$	6.33	7950	9.2	2.9
HUMB	Humboldt, Saskatchewan	52°09', 105°06'	167	61	316	108.9	0.327	0.030	1570	79.2	290	6.8	$MgSO_4$	2.60	2800	8.4	6.0
ISOB	Isabel, Kidder Co., N.D.	46°49', 99°44'	506	65	159	4.7	0.009	0.007	583	43.1	1046	122.1	$Na(Mg)CO_3(SO_4)$	2.53	2800	9.3	1.9
LENO	Lenore, Saskatchewan	52°30', 104°59'	43	16	111	40.7	0.120	0.012	376	14.2	285	3.6	$MgSO_4(CO_3)$	0.89	1050	8.3	7.5
LONG	Long, Benson Co., N.D.	48°01', 99°17'	312	67	150	76.2	0.389	0.064	816	97.7	595	12.4	$Na(Mg)SO_4(CO_3)$	2.13	2500	8.6	2.2
MADI	Madison, Lake Co., S.D.	43°57', 97°00'	56	14	66	99.5	0.524	0.064	443	44.9	217	2.0	$Mg(Ca)SO_4(CO_3)$	0.94	1150	8.3	2.9
MANI	Manito, Saskatchewan*	52°43', 109°43'	8080	214	371	12.5	0.194	0.024	12380	1930.0	1777	1862.9	$NaSO_4(CO_3)$	26.63	30600	9.7	15.0
MEDI	Medicine, Codington Co., S.D.	44°49', 97°21'	3100	511	5750	318.0	0.949	0.036	28120	532.9	214	33.1	$MgSO_4$	38.58	27900	8.9	9.2
MISS	Mission Bay, Benson Co., N.D.	48°01', 98°53'	5950	464	1230	107.0	0.412	0.027	13430	2359.0	765	69.0	$Na(Mg)SO_4$	24.37	27200	8.8	1.0
MOON	Moon, Barnes Co., N.D.	46°51', 98°10'	1320	242	274	11.9	0.014	0.008	2532	472.4	858	104.0	$Na(Mg)SO_4(CO_3)$	5.81	6850	9.2	11.5
MUSK	Muskiki, Saskatchewan*	52°20', 105°45'	43100	627	16400	503.0	5.670	0.094	145500	5133.0	372	118.7	$Na(Mg)SO_4$	211.76	101000	8.8	0.5
NBLA	N. Blaine, Saskatchewan*	52°50', 106°58'	643	128	847	96.6	0.520	0.028	6227	174.6	146	175.2	$Mg(Na)SO_4$	8.44	9350	9.9	0.5
NORD	Norden, Hamlin Co., S.D.	43°35', 97°12'	36	15	62	94.0	0.489	0.060	344	9.1	284	3.5	$Mg(Ca)SO_4(CO_3)$	0.85	1050	8.4	1.5
OAKW	Oakwood, Brookings Co., S.D.	44°26', 96°58'	20	16	61	65.1	0.400	0.074	278	7.8	226	2.3	$Mg(Ca)SO_4(CO_3)$	0.68	800	8.3	1.8
OPUN	Opuntia, Saskatchewan	51°48', 108°34'	1620	46	194	55.8	0.577	0.029	3493	230.4	624	22.6	$NaSO_4$	6.29	7400	8.5	1.5
PIYS	Piyas, Marshall Co., S.D.#	45°35', 97°20'												3.00	3164		1.6
POIN	Poinsett, Hamlin Co., S.D.	44°32', 97°05'	56	24	80	59.9	0.404	0.096	338	23.4	288	3.0	$Mg(Ca)SO_4(CO_3)$	0.87	1100	8.3	3.1
PORT	Porter, Saskatchewan	52°12', 106°17'	937	81	303	243.4	1.965	0.025	2688	740.6	35	15.6	$Na(Mg)SO_4(Cl)$	5.05	6150	9.6	0.3
RABB	Rabbit, Saskatchewan	52°36', 107°00'	947	89	934	61.0	0.154	0.033	4997	104.9	510	27.3	$Mg(Na)SO_4$	7.67	7450	8.6	4.8
REDB	Redberry, Saskatchewan	52°43', 107°09'	2100	168	2590	79.0	0.159	0.019	13140	212.8	546	85.2	$Mg(Na)SO_4$	18.92	16800	8.9	13.3
REFL	Reflex, Saskatchewan	52°40', 109°58'	2710	61	52	9.3	0.071	0.079	596	3356.0	1096	200.9	NaCl	8.08	12000	9.2	9.8
ROSL	Roslyn Pond, Day Co., S.D.	45°31', 97°26'	697	62	262	120.0	1.261	0.039	1588	517.8	559	35.1	$Na(Mg)SO_4(Cl)$	3.84	4850	9.0	2.0
ROU1	Round, Benson Co., N.D.	48°02', 99°16'	172	30	98	58.1	0.407	0.071	631	35.3	250	4.9	$Mg(Na)SO_4(CO_3)$	1.28	1950	8.6	2.2
ROU2	Round, McHenry Co., N.D.	48°02', 100°18'	657	47	83	6.0	0.009	0.012	256	61.8	1410	115.6	$NaCO_3$	2.64	3000	9.0	5.7
ROY	Roy, Marshall Co., S.D.	45°43', 97°27'	81	61	297	52.9	0.254	0.045	1083	25.5	445	16.2	$MgSO_4(CO_3)$	2.06	2400	8.8	3.8
SAYE	Sayer, Saskatchewan	52°34', 105°24'	1260	143	3020	144.5	0.300	0.027	13620	209.9	329	26.2	$MgSO_4$	18.75	14800	8.6	4.6
SBLA	S. Blaine, Saskatchewan*	52°46', 106°59'	10700	143	1550	405.3	4.050	0.031	27670	367.9	270	85.1	$Na(Mg)SO_4$	41.20	39200	9.1	0.8
SHIN	Shinbone, Benson Co., N.D.#	47°51', 98°42'	712	93	31	9.8	0.082	0.038	119	289.8	1355	94.4	$NaCO_3(Cl)$	2.70	3150	9.1	1.5
SPRG	Spring, Benson Co., N.D.	47°57', 98°49'	997	118	291	32.2	0.120	0.025	2333	406.9	640	25.7	$Na(Mg)SO_4$	4.84	5650	8.7	2.2
SPRT	Spiritwood, Stutsman Co., N.D.	47°05', 98°35'	339	50	165	27.3	0.084	0.024	888	137.3	399	21.9	$Na(Mg)SO_4(CO_3)$	2.03	2550	9.0	13.4
STI2	Stink, Stutsman Co., N.D.	46°52', 99°24'	6180	615	1570	53.4	0.275	0.025	14810	2830.0	454	171.0	$Na(Mg)SO_4$	26.68	28900	9.4	1.5
STIN	Stink, Benson Co., N.D.	48°13', 99°16'	4840	180	558	169.0	0.813	0.034	9913	1349.0	634	23.6	$NaSO_4$	17.67	20400	8.5	1.2
TRAM	Tramping, Saskatchewan	52°08', 108°47'	3200	131	232	37.1	0.702	0.032	6043	540.5	840	117.4	$NaSO_4$	11.14	13700	9.0	4.3
TWIN	Twin, Benson Co., N.D.	47°58', 99°06'	264	50	125	33.9	0.296	0.037	562	88.2	561	19.1	$Na(Mg)SO_4(CO_3)$	1.70	2000	8.8	1.9
WAKA	Wakaw, Saskatchewan	52°40', 105°35'	280	23	299	165.8	0.540	0.016	1902	58.9	144	2.8	$Mg(Na)SO_4$	2.88	3050	8.3	9.5
WALD	Waldsea, Saskatchewan	52°17', 105°12'	3020	228	2370	270.0	0.776	0.027	10860	3406.0	296	32.1	$Mg(Na)SO_4(Cl)$	20.48	21400	8.7	11.2
WAUB	Waubay, Day Co., S.D.	45°24', 97°26'	881	343	1750	79.0	0.235	0.021	8369	272.8	519	23.3	$MgSO_4$	12.24	11100	8.6	0.5
WHIT	Whiteshore, Saskatchewan*	52°08', 108°17'	47100	1130	17400	446.0	13.500	0.090	138200	17280.0	707	144.4	$Na(Mg)SO_4$	222.42	100000	8.6	0.8
WILL	Willowbunch, Saskatchewan*	49°27', 105°28'	18300	240	51	11.2	0.297	0.054	25470	4529.0	2461	4204.2	$NaSO_4(CO_3)$	55.27	59300	9.8	0.8
WSTU	W. Stump, Nelson Co., N.D.	47°55', 98°26'	2710	147	559	86.0	0.527	0.027	6069	1218.0	258	46.7	$Na(Mg)SO_4(Cl)$	11.09	14300	9.3	0.9

diatoms or very poor preservation. #Denotes additional samples with poor preservation. Ion dominance includes all ions that comprise at least 20% of the total cations or anions expressed in milliequivalents, listed in order of decreasing relative abundance.

Code	Site Name	Location N lat. W. long	Na mg L^{-1}	K mg L^{-1}	Mg mg L^{-1}	Ca mg L^{-1}	Sr mg L^{-1}	Ba mg L^{-1}	SO4 mg L^{-1}	Cl mg L^{-1}	HCO3 mg L^{-1}	CO3 mg L^{-1}
ALBT	Albert, Hamlin Co., S.D.	44°32', 97°09'	33	20	59	62.5	0.383	0.068	280	10.4	241	6.1
ALK2	Alkali, Sargent Co., N.D.	46°02', 97°23'	1610	56	207	27.1	0.135	0.025	2445	828.2	822	87.0
ALKA	Alkaline, Kidder Co., N.D.*	46°40', 99°33'	1560	213	225	16.9	0.082	0.031	2922	273.5	1059	125.4
ANTE	Antelope, Saskatchewan*	50°18', 108°25'	2460	196	1220	65.8	0.264	0.028	8580	342.7	843	138.1
AROM	Aroma, Saskatchewan*	52°18', 108°33'	12900	1090	12000	153.6	0.499	0.057	61280	7052.0	1254	484.2
BASI	Basin, Saskatchewan	52°38', 105°17'	2910	211	2480	135.9	0.402	0.024	14030	768.3	582	93.5
BIT1	Bitter, Day Co., S.D.#	45°17', 97°19'	2450	515	3210	52.4	0.124	0.028	15620	702.7	880	98.2
BITT	Bitter, Saskatchewan*	50°08', 109°50'	58700	1010	18000	551.0	19.500	0.247	178000	10630.0	862	263.8
BOUC	Boucher, Saskatchewan	52°28', 105°41'	475	75	402	137.9	0.850	0.024	2426	159.4	245	16.4
BQUI	Big Quill, Saskatchewan	51°55', 104°22'	6380	403	3870	201.9	0.728	0.032	23590	2890.0	481	97.5
BYRN	Byron, Beadle Co., S.D.	44° 33', 98°10'										
COLD	Coldwater, McIntosh Co., N.D.	46°01', 99°04'	314	131	440	26.8	0.061	0.009	1789	95.7	708	19.5
COON	Coon, Nelson Co., N.D.	47°58', 98°23'	225	22	114	90.8	0.619	0.061	807	48.5	320	3.5
DEAD	Deadmoose, Saskatchewan	52°19', 105°10'	4880	235	1430	129.0	0.450	0.025	8712	5625.0	411	77.6
DEVI	Devils, Ramsey Co., N.D.	48°05', 98°56'	551	76	139	76.9	0.377	0.049	1151	246.4	500	20.3
ECKL	Eckelson, Barnes Co., N.D.	46°56', 98°17'	9500	733	2620	151.0	0.528	0.026	22860	4728.0	682	130.1
ECOT	E. Coteau, Saskatchewan	49°03', 104°33'	631	106	869	163.3	0.533	0.032	4860	46.6	250	15.0
EDEV	E. Devils, Ramsey Co., N.D.	47°57', 98°43'	2330	229	463	92.9	0.479	0.037	5040	1034.0	668	38.7
ELBW	Elbow, Benson Co., N.D.	47°55', 98°43'	371	45	70	6.8	0.021	0.015	126	70.7	1000	83.4
ESTU	E. Stump, Nelson Co., N.D.*	47°53', 98°22'	19300	990	4660	383.0	1.670	0.050	47970	8289.0	605	53.5
FIFE	Fife, Saskatchewan	49°14', 105°53'	796	61	121	14.8	0.397	0.040	1077	28.5	1220	92.3
FISH	Fishing, Saskatchewan	51°51', 103°33'	324	64	425	100.9	0.293	0.019	2154	56.8	318	6.5
FREE	Free People, Benson Co., N.D.	47°56', 98°43'	2650	151	99	9.3	0.026	0.024	3383	868.8	1545	208.5
GEOR	George, Kidder Co., N.D.	46°45', 99°30'	5640	467	712	18.0	0.049	0.028	11460	1223.0	1407	308.0
HAZL	Hazelden, Day Co., S.D.	45°31', 97°28'	4340	750	4420	380.0	1.450	0.033	24940	747.3	345	43.0
HERM	Herman, Lake Co., S.D.	44°00', 97°10'	39	16	58	89.9	0.520	0.081	372	7.3	218	7.2
HORS	Horseshoe, Eddy Co., N.D.	47°53', 98°48'	1900	151	31	17.3	0.165	0.032	2229	653.2	1213	140.5
HUMB	Humboldt, Saskatchewan	52°09', 105°06'	167	61	316	108.9	0.327	0.030	1570	79.2	290	6.8
ISOB	Isabel, Kidder Co., N.D.	46°49', 99°44'	506	65	159	4.7	0.009	0.007	583	43.1	1046	122.1
LENO	Lenore, Saskatchewan	52°30', 104°59'	43	16	111	40.7	0.120	0.012	376	14.2	285	3.6
LONG	Long, Benson Co., N.D.	48°01', 99°17'	312	67	150	76.2	0.389	0.064	816	97.7	595	12.4
MADI	Madison, Lake Co., S.D.	43°57', 97°00'	56	14	66	99.5	0.524	0.064	443	44.9	217	2.0
MANI	Manito, Saskatchewan*	52°43', 109°43'	8080	214	371	12.5	0.194	0.024	12380	1930.0	1777	1862.9
MEDI	Medicine, Codington Co., S.D.	44°49', 97°21'	3100	511	5750	318.0	0.949	0.036	28120	532.9	214	33.1
MISS	Mission Bay, Benson Co., N.D.	48°01', 98°53'	5950	464	1230	107.0	0.412	0.027	13430	2359.0	765	69.0
MOON	Moon, Barnes Co., N.D.	46°51', 98°10'	1320	242	274	11.9	0.014	0.008	2532	472.4	858	104.0
MUSK	Muskiki, Saskatchewan*	52°20', 105°45'	43100	627	16400	503.0	5.670	0.094	145500	5133.0	372	118.7
NBLA	N. Blaine, Saskatchewan*	52°50', 106°58'	643	128	847	96.6	0.520	0.028	6227	174.6	146	175.2
NORD	Norden, Hamlin Co., S.D.	43°35', 97°12'	36	15	62	94.0	0.489	0.060	344	9.1	284	3.5
OAKW	Oakwood, Brookings Co., S.D.	44°26', 96°58'	20	16	61	65.1	0.400	0.074	278	7.8	226	2.3
OPUN	Opuntia, Saskatchewan	51°48', 108°34'	1620	46	194	55.8	0.577	0.029	3493	230.4	624	22.6

[illegible]	[illegible] S.D.	[illegible]	[illegible]	[illegible]	[illegible]	59.9	0.404	0.096	338	23.4	288	3.0
PORT	Porter, Saskatchewan	52°12', 106°17'	937	81	303	243.4	1.965	0.025	2688	740.6	35	15.6
RABB	Rabbit, Saskatchewan	52°36', 107°00'	947	89	934	61.0	0.154	0.033	4997	104.9	510	27.3
REDB	Redberry, Saskatchewan	52°43', 107°09'	2100	168	2590	79.0	0.159	0.019	13140	212.8	546	85.2
REFL	Reflex, Saskatchewan	52°40', 109°58'	2710	61	52	9.3	0.071	0.079	596	3356.0	1096	200.9
ROSL	Roslyn Pond, Day Co., S.D.	45°31', 97°26'	697	62	262	120.0	1.261	0.039	1588	517.8	559	35.1
ROU1	Round, Benson Co., N.D.	48°02', 99°16'	172	30	98	58.1	0.407	0.071	631	35.3	250	4.9
ROU2	Round, McHenry Co., N.D.	48°02',100°18'	657	47	83	6.0	0.009	0.012	256	61.8	1410	115.6
ROY	Roy, Marshall Co., S.D.	45°43', 97°27'	81	61	297	52.9	0.254	0.045	1083	25.5	445	16.2
SAYE	Sayer, Saskatchewan	52°34', 105°24'	1260	143	3020	144.5	0.300	0.027	13620	209.9	329	26.2
SBLA	S. Blaine, Saskatchewan*	52°46', 106°59'	10700	143	1550	405.3	4.050	0.031	27670	367.9	270	85.1
SHIN	Shinbone, Benson Co., N.D.#	47°51', 98°42'	712	93	31	9.8	0.082	0.038	119	289.8	1355	94.4
SPRG	Spring, Benson Co., N.D.	47°57', 98°49'	997	118	291	32.2	0.120	0.025	2333	406.9	640	25.7
SPRT	Spiritwood, Stutsman Co., N.D.	47°05', 98°35'	339	50	165	27.3	0.084	0.024	888	137.3	399	21.9
STI2	Stink, Stutsman Co., N.D.	46°52', 99°24'	6180	615	1570	53.4	0.275	0.025	14810	2830.0	454	171.0
STIN	Stink, Benson Co., N.D.	48°13', 99°16'	4840	180	558	169.0	0.813	0.034	9913	1349.0	634	23.6
TRAM	Tramping, Saskatchewan	52°08', 108°47'	3200	131	232	37.1	0.702	0.032	6043	540.5	840	117.4
TWIN	Twin, Benson Co., N.D.	47°58', 99°06'	264	50	125	33.9	0.296	0.037	562	88.2	561	19.1
WAKA	Wakaw, Saskatchewan	52°40', 105°35'	280	23	299	165.8	0.540	0.016	1902	58.9	144	2.8
WALD	Waldsea, Saskatchewan	52°17', 105°12'	3020	228	2370	270.0	0.776	0.027	10860	3406.0	296	32.1
WAUB	Waubay, Day Co., S.D.	45°24', 97°26'	881	343	1750	79.0	0.235	0.021	8369	272.8	519	23.3
WHIT	Whiteshore, Saskatchewan*	52°08', 108°17'	47100	1130	17400	446.0	13.500	0.090	138200	17280.0	707	144.4
WILL	Willowbunch, Saskatchewan*	49°27', 105°28'	18300	240	51	11.2	0.297	0.054	25470	4529.0	2461	4204.2
WSTU	W. Stump, Nelson Co., N.D.	47°55', 98°26'	2710	147	559	86.0	0.527	0.027	6069	1218.0	258	46.7

Ion Dominance %	Salinity g L^{-1}	Cond uS	pH	Depth m
$Mg(Ca)SO_4(CO_3)$	0.71	850	8.7	1.6
$NaSO_4(Cl)$	6.08	7350	9.1	2.6
$Na(Mg)SO_4(CO_3)$	6.39	7250	9.2	2.4
$Na(Mg)SO_4$	13.85	14300	9.0	7.3
$Mg(Na)SO_4$	96.21	64700	9.0	1.5
$Mg(Na)SO_4$	21.21	19600	8.9	11.3
$Mg(Na)SO_4$	23.53	21000	9.2	0.1
$Na(Mg)SO_4$	268.04	100000	8.8	0.1
$Mg(Na)SO_4$	3.94	4350	8.8	0.8
$Mg(Na)SO_4$	37.91	33300	8.9	2.4
	2.20	2777		1.3
$Mg(Na)SO_4(CO_3)$	3.52	3800	8.6	9.0
$Na(Mg)SO_4(CO_3)$	1.63	1950	8.3	1.3
$Na(Mg)SO_4(Cl)$	21.50	25800	9.0	28.0
$Na(Mg)SO_4(CO_3)$	2.76	3500	8.8	7.0
$Na(Mg)SO_4(Cl)$	41.41	41300	9.0	0.5
$Mg(Na)SO_4$	6.94	6350	8.7	5.4
$Na(Mg)SO_4$	9.90	11800	8.8	6.5
$Na(Mg)CO_3$	1.77	1900	9.2	1.3
$Na(Mg)SO_4$	82.25	68200	8.6	1.0
$Na(Mg)CO_3(SO_4)$	3.41	3800	8.9	2.5
$Mg(Na)SO_4$	3.45	3600	8.3	10.8
$NaSO_4(CO_3)$	8.92	11950	9.2	3.1
$NaSO_4$	21.24	23300	9.2	24.3
$Mg(Na)SO_4$	35.97	30200	8.9	0.1
$Mg(Ca)SO_4(CO_3)$	0.81	1000	8.8	1.7
$NaSO_4(CO_3)(Cl)$	6.33	7950	9.2	2.9
$MgSO_4$	2.60	2800	8.4	6.0
$Na(Mg)CO_3(SO_4)$	2.53	2800	9.3	1.9
$MgSO_4(CO_3)$	0.89	1050	8.3	7.5
$Na(Mg)SO_4(CO_3)$	2.13	2500	8.6	2.2
$Mg(Ca)SO_4(CO_3)$	0.94	1150	8.3	2.9
$NaSO_4(CO_3)$	26.63	30600	9.7	15.0
$MgSO_4$	38.58	27900	8.9	9.2
$Na(Mg)SO_4$	24.37	27200	8.8	1.0
$Na(Mg)SO_4(CO_3)$	5.81	6850	9.2	11.5
$Na(Mg)SO_4$	211.76	101000	8.8	0.5
$Mg(Na)SO_4$	8.44	9350	9.9	0.5
$Mg(Ca)SO_4(CO_3)$	0.85	1050	8.4	1.5
$Mg(Ca)SO_4(CO_3)$	0.68	800	8.3	1.8
$NaSO_4$	6.29	7400	8.5	1.5

	3.00	3164		1.6
$Mg(Ca)SO_4(CO_3)$	0.87	1100	8.3	3.1
$Na(Mg)SO_4(Cl)$	5.05	6150	9.6	0.3
$Mg(Na)SO_4$	7.67	7450	8.6	4.8
$Mg(Na)SO_4$	18.92	16800	8.9	13.3
NaCl	8.08	12000	9.2	9.8
$Na(Mg)SO_4(Cl)$	3.84	4850	9.0	2.0
$Mg(Na)SO_4(CO_3)$	1.28	1950	8.6	2.2
$NaCO_3$	2.64	3000	9.0	5.7
$MgSO_4(CO_3)$	2.06	2400	8.8	3.8
$MgSO_4$	18.75	14800	8.6	4.6
$Na(Mg)SO_4$	41.20	39200	9.1	0.8
$NaCO_3(Cl)$	2.70	3150	9.1	1.5
$Na(Mg)SO_4$	4.84	5650	8.7	2.2
$Na(Mg)SO_4(CO_3)$	2.03	2550	9.0	13.4
$Na(Mg)SO_4$	26.68	28900	9.4	1.5
$NaSO_4$	17.67	20400	8.5	1.2
$NaSO_4$	11.14	13700	9.0	4.3
$Na(Mg)SO_4(CO_3)$	1.70	2000	8.8	1.9
$Mg(Na)SO_4$	2.88	3050	8.3	9.5
$Mg(Na)SO_4(Cl)$	20.48	21400	8.7	11.2
$MgSO_4$	12.24	11100	8.6	0.5
$Na(Mg)SO_4$	222.42	100000	8.6	0.8
$NaSO_4(CO_3)$	55.27	59300	9.8	0.8
$Na(Mg)SO_4(Cl)$	11.09	14300	9.3	0.9

Diatoma tenue var. *elongatum*	Lyngb. 1819		16	5.08	7.96	3.13	20.27
Diploneis smithii	(Bréb. *ex* W. Sm.) Cleve 1894		1	1.39	18.92	18.62	19.22
Entomoneis paludosa	(W. Sm.) Reimer in Patr. & Reimer 1975		2	1.37	4.32	2.40	7.78
Epithemia adnata	(Kütz.) Rabenh. 1853		5	1.28	2.17	1.33	3.52
Epithemia argus	(Ehrenb.) Kütz. 1844		5	1.14	2.72	1.43	5.16
Epithemia turgida	(Ehrenb.) Kütz. 1844		5	2.00	2.92	1.83	4.65
Fragilaria brevistriata	Grun. in Van Heurck 1885	Fr bre	9	13.95	1.72	0.48	6.19
Fragilaria brevistriata var. *inflata*	(Pant.) Hust. 1930	Fr binf	8	35.02	1.49	0.74	2.99
Fragilaria capucina var. *mesolepta*	(Rabenh.) Rabenh. 1864	Fr mes	9	54.43	1.06	0.70	1.62
Fragilaria construens	(Ehrenb.) Grun. 1862	Fr con	6	3.25	1.00	0.72	1.38
Fragilaria construens var. *venter*	(Ehrenb.) Grun. in Van Heurck 1881		9	5.50	2.44	0.61	9.74
Fragilaria crotonensis	Kitton 1869	Fr cro	2	31.71	1.86	1.27	2.74
Fragilaria inflata	(Heiden) Hust. 1931	Fr inf	1	25.25	0.68	0.67	0.69
Fragilaria pinnata	Ehrenb. 1843		12	1.81	2.95	0.83	10.54
Fragilaria vaucheriae	(Kütz.) J.B. Petersen 1938	Fr vau	10	24.12	2.50	1.89	3.30
Fragilaria cf. *pinnata/sublitoralis*			1	4.02	17.67	17.39	17.95
Gomphoneis olivaceum	(Hornemann) P. Dawson *ex* Ross & Sims 1978	G oliv	5	18.81	2.95	2.41	3.61
Gomphonema angustatum	(Kütz.) Rabenh. 1864	G ang	8	2.19	3.29	1.83	5.93
Gomphonema dichotomum	Kütz. 1833	G dic	4	16.61	2.75	2.08	3.64
Gomphonema intricatum	Kütz. 1844		3	2.76	0.87	0.82	0.93
Gomphonema parvulum	(Kütz.) Kütz. 1849	G parv	9	2.47	2.49	1.38	4.47
Gomphonema subclavatum var. *commutatum*	(Grun.) A. Mayer 1928		1	1.14	5.81	5.72	5.90
Gyrosigma acuminatum	(Kutz.) Rabenh. 1853	Gy acu	2	5.81	0.92	0.86	0.97
Gyrosigma spencerii	(Quek.) Griffith & Henfrey 1856		1	1.58	12.24	12.05	12.44
Gyrosigma spencerii var. *curvula*	(Grun.) Reimer 1966	Gy curv	8	5.54	10.43	5.20	20.93
Mastogloia elliptica var. *dansei*	(Thwaites) Cleve 1896	M dan	12	10.61	12.45	4.41	35.12
Mastogloia smithii	Thwaites *ex* W. Sm. 1856		2	3.45	17.54	4.69	65.66
Mastogloia smithii var. *lacustris*	Grun. 1878	M lac	16	5.67	3.20	1.23	8.32
Navicula arvensis	Hust. 1937		2	2.76	0.92	0.58	1.46
Navicula bulnheimii	Grun. in Van Heurck 1880	Na bul	8	15.93	26.43	17.90	39.02
Navicula capitata	Ehrenb. 1838	Na cap	15	20.05	1.28	0.59	2.74
Navicula capitata var. *hungarica*	(Grun.) R. Ross 1947	Na hun	18	41.67	3.96	2.55	6.14
Navicula cari	Ehrenb. 1836		2	1.25	0.93	0.40	2.14
Navicula cincta	(Ehrenb.) Ralfs in Pritch. 1861		23	64.73	9.30	4.69	18.45
Navicula crucicula	(W. Sm.) Donk. 1871		3	1.79	22.03	10.15	47.84
Navicula cryptocephala	Kütz. 1844		9	5.00	2.71	0.86	8.57
Navicula cuspidata	(Kütz.) Kütz. 1844		16	2.65	2.20	1.19	4.07
Navicula gracilis	Ehrenb. 1830		7	1.09	2.77	1.47	5.20
Navicula halophila	(Grun. *ex* Van Heurck) Cleve 1894	Na hal	18	5.92	5.33	1.65	17.24
Navicula halophila forma *subcapitata*	Ostrup 1910		2	12.19	6.55	1.50	28.56
Navicula incerta	Grun. in Van Heurck 1880		5	2.30	21.10	18.03	24.68
Navicula oblonga	(Kütz.) Kütz. 1844	Na obl	18	32.34	2.48	1.50	4.10
Navicula pupula var. *rectangularis*	(Greg.) Grun. in Cleve & Grun. 1880		3	2.25	0.85	0.44	1.63
Navicula radiosa var. *tenella*	(Bréb. *ex* Kütz.) Grun. ex Van Heurck 1885		4	4.28	5.24	2.97	9.23
Navicula reinhardtii	Grun. in Van Heurck 1880		1	1.25	0.85	0.84	0.86
Navicula salinarum	Grun. in Cleve & Grun. 1880		2	2.27	2.16	0.58	8.01
Navicula veneta	Kütz. 1844	Na ven	9	11.99	4.94	1.05	23.23
Navicula viridula	(Kütz.) Ehrenb. 1836		10	9.36	11.33	4.73	27.15
Navicula vixvisibilis	Hust. 1937		5	9.34	1.09	0.56	2.14

Navicu[illegible]cryp[illegible]ata		Na cry	1	26.33	1.77	1.74	1.80
Navicula cf. *rhyncocephala* var. *amphiceros*		Na rhy	2	5.72	2.46	2.25	2.69
Navicula cf. *seminulum*		Na sem	1	5.32	9.90	9.74	10.06
Navicula cf. *spicula*			4	2.96	33.16	24.09	45.64
Neidium iridis	(Ehrenb.) Cleve 1894		2	2.67	1.76	1.74	1.79
Nitzschia amphibia	Grun. 1862	Ni amp	24	12.33	1.87	1.17	3.01
Nitzschia angustata	(W. Sm.) Grun. in Cleve & Grun. 1880		1	1.02	2.06	2.03	2.09
Nitzschia compressa forma *minor*	A. Cleve-Euler 1952	Ni comp	13	14.94	11.07	5.23	23.44
Nitzschia constricta	(Kütz.) Ralfs in Pritch. 1861	Ni con	4	20.11	4.25	3.09	5.84
Nitzschia denticula	Grun. in Cleve & Grun. 1880	Ni den	6	2.03	2.84	1.07	7.53
Nitzschia dissipata	(Kütz.) Grun. 1862		2	1.25	0.88	0.82	0.93
Nitzschia frustulum	(Kütz.) Grun. in Cleve & Grun. 1880	Ni fru	16	17.82	2.17	1.21	3.89
Nitzschia hungarica	Grun. 1862		27	11.81	9.55	3.03	30.11
Nitzschia inconspicua	Grun. 1862	Ni inc	15	47.17	16.45	6.28	43.09
Nitzschia linearis	W. Sm. 1853		6	1.05	2.72	1.96	3.77
Nitzschia obtusa	W. Sm. 1853		5	1.56	11.11	4.54	27.18
Nitzschia palea	(Kütz.) W. Sm. 1856		15	5.81	2.89	1.32	6.32
Nitzschia paleacea	(Grun. in Cleve & Grun.) Grun. in Van Heurck 1881		5	2.38	2.17	0.87	5.37
Nitzschia subacicularis	Hust. 1937	Ni sub	1	30.17	18.75	18.45	19.05
Nitzschia subtilis	Grun. in Cleve & Grun. 1880		1	1.26	0.71	0.70	0.72
Nitzschia tryblionella	Hantzsch in Rabenh. 1860		13	3.01	2.02	0.54	7.52
Nitzschia tryblionella var. *debilis*	A. Mayer 1913		2	7.84	3.43	3.30	3.55
Nitzschia cf. *fonticola*			24	67.99	13.91	5.61	34.48
Nitzschia cf. *palea*			3	1.63	3.29	1.52	7.14
Opephora cf. *olsenii*		Op ols	13	12.75	7.91	5.29	11.83
Plagiotropis arizonica	Czarnecki & Blinn 1978		5	4.56	6.69	4.15	10.80
Rhoicosphenia curvata	(Kütz.) Grun. 1860	Rc curv	27	25.38	4.38	2.25	8.55
Rhopalodia gibba	(Ehrenb.) O. Müll. 1895		21	9.91	3.57	2.02	6.29
Stephanodiscus alpinus	Hust. in Huber-Pestalozzi 1942		2	2.51	0.85	0.83	0.86
Stephanodiscus hantzschii	Grun. in Cleve & Grun. 1880	St han	16	6.15	1.83	0.90	3.70
Stephanodiscus minutulus	(Kütz.) Cleve & Moller 1882		16	86.53	2.06	1.07	3.97
Stephanodiscus niagarae	Ehrenb. 1846		21	13.00	1.29	0.55	3.04
Stephanodiscus parvus	Stoermer & Hakansson 1984		23	68.65	2.25	1.06	4.78
Stephanodiscus cf. *medius*		St med	4	11.75	1.55	1.12	2.14
Surirella linearis	W. Sm. 1853		2	1.00	1.44	0.22	9.25
Surirella ovata	Kütz. 1844	Su ova	20	5.75	2.54	0.73	8.82
Surirella ovata var. *crumena*	(Bréb. *ex* Kütz.) Hust. 1930	Su cru	9	32.84	7.13	4.17	12.18
Surirella peisonis	Pant. 1902	Su peis	20	36.84	3.27	1.92	5.58
Surirella striatula	Turpin 1828	Su str	20	4.30	7.03	3.64	13.56
Synedra acus	Kütz. 1844	Sy acus	12	1.33	1.78	1.15	2.74
Synedra acus var. *angustissima*	(Grun. in Van Heurck) Van Heurck 1885		4	2.21	3.58	2.30	5.57
Synedra berolinensis	Lemm. 1900		3	2.00	0.75	0.63	0.89
Synedra fasciculata	(Ag.) Kütz. 1844		29	13.07	6.70	2.89	15.51
Synedra nana	Meister 1912		1	3.07	2.06	2.03	2.09
Synedra parasitica	(W. Sm.) Hust. 1930		3	2.06	1.66	0.74	3.69
Synedra pulchella	Ralfs *ex* Kütz. 1844		29	7.69	10.32	4.44	23.99
Synedra ulna	(Nitzsch) Ehrenb. 1836	Sy uln	12	1.36	1.63	0.89	2.97
Synedra cf. *filiformis*		Sy fili	5	5.93	2.08	0.70	6.17
Synedra hartii	Cholnoky 1963		1	2.91	18.75	18.45	19.05

Thalassiosira lacus...	(Grun.) Hasle in Hasle & Fryxell 1977	1	1.71	3.84	3.78	3.90
Thalassiosira rudolfi	(Bach.)Hasle 1978	4	4.63	1.64	1.02	2.65

Figure Legends

Figure 1. Map showing the location of the northern Great Plains (shaded area) and isolines of equal precipitation minus evaporation (cm yr^{-1}). See Table 1 for additional site details.

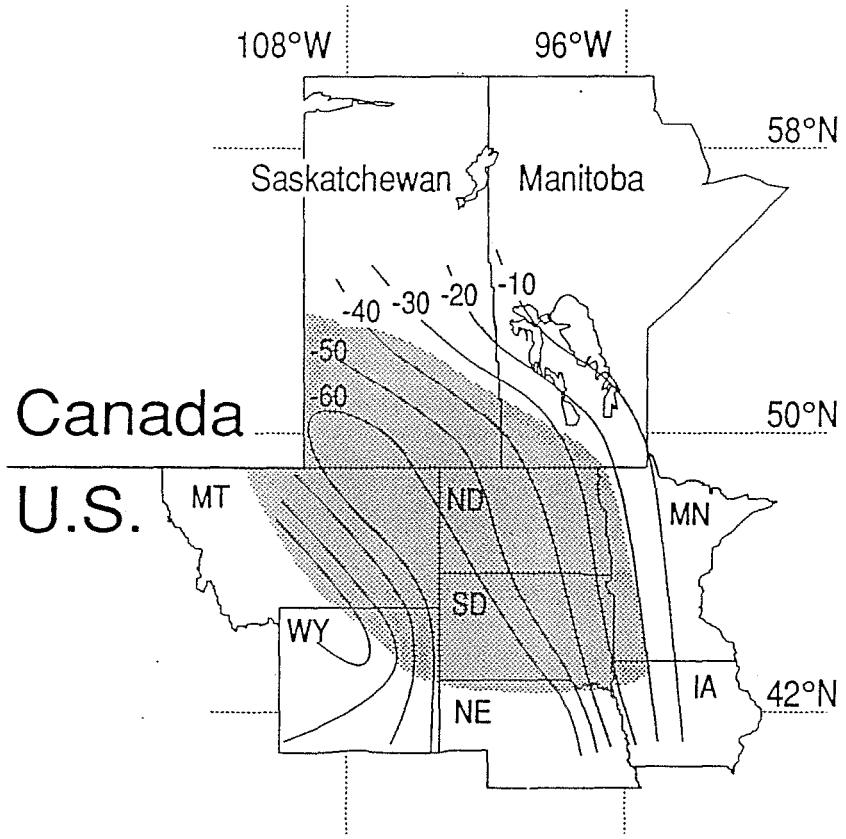
Figure 2. Plot of measured salinity and anion proportion for 64 lakes with full chemical data. Anions are expressed as a molar percent of total anions. Lake codes are given in Table 1.

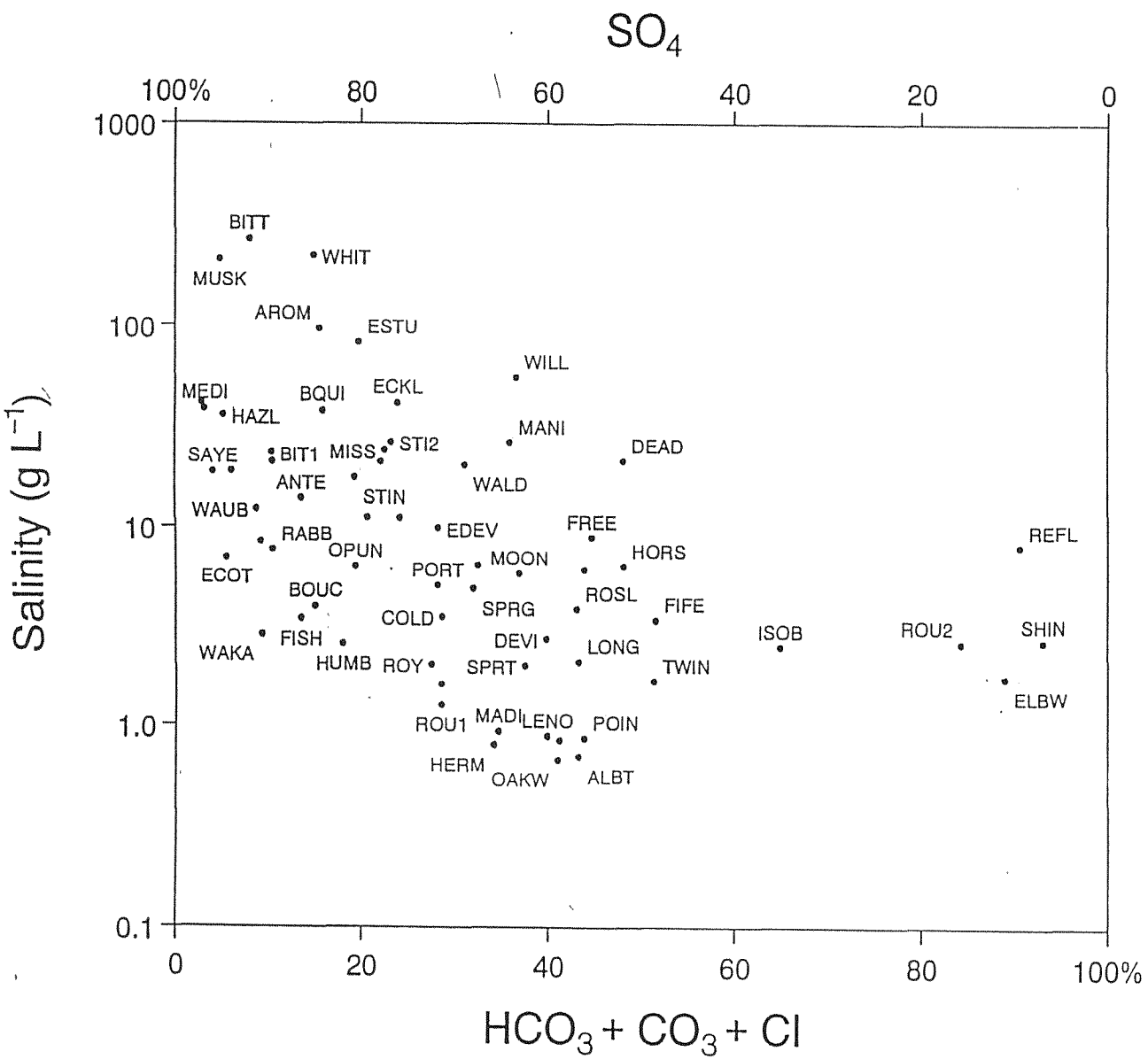
Figure 3. Cation proportions for 64 lakes with full chemical data. Cations are expressed as a molar percent of total cations. Lake codes are given in Table 1.

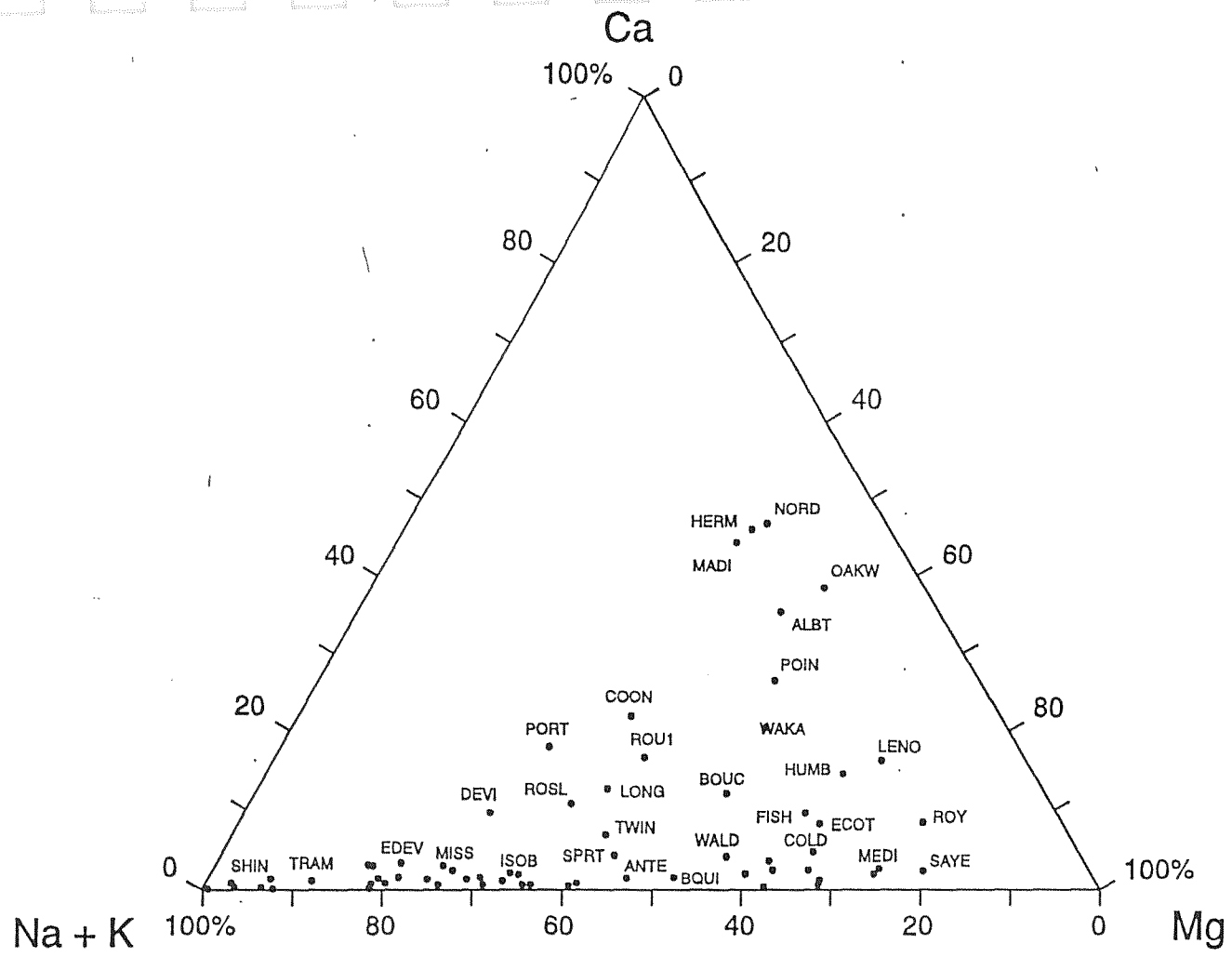
Figure 4. a) CCA ordination of diatom taxa identified from the northern Great Plains. Taxa with abundance of >5% and occurrence in >5 samples are plotted. See Table 2 for full species names, b) CCA plot of the 53 lakes with full chemical data and diatoms preserved in the surface sediments. See Table 1 for full lake names, c) Biplot of environmental variables. Arrows show the direction of maximum variation of the given variable across the diagram, and the arrow length indicates relative importance. Two environmental variables (K concentration and depth) are not plotted. Potassium lies directly on top of Cl concentration, and its vector is of similar length. The depth vector plots directly on top of Na concentration but is less than 0.1X its length.

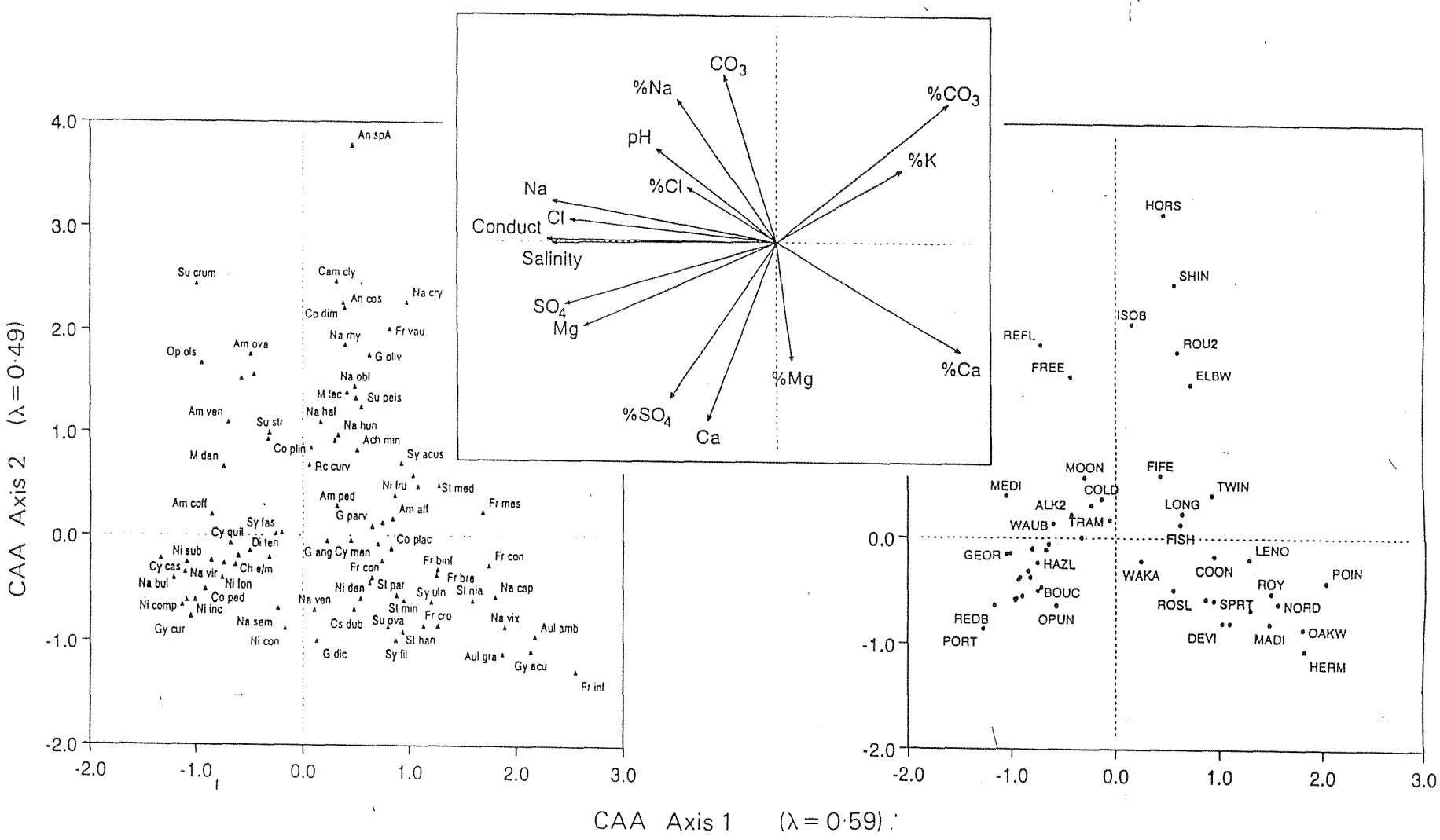
Figure 5. Estimated optima (abundance-weighted means) and tolerances (abundance-weighted standard deviations) of taxa in the surface sediments of the 55 lakes with salinity data. All taxa with abundance >5% and occurrence in >5 lakes are illustrated. See Table 2 for additional taxa.

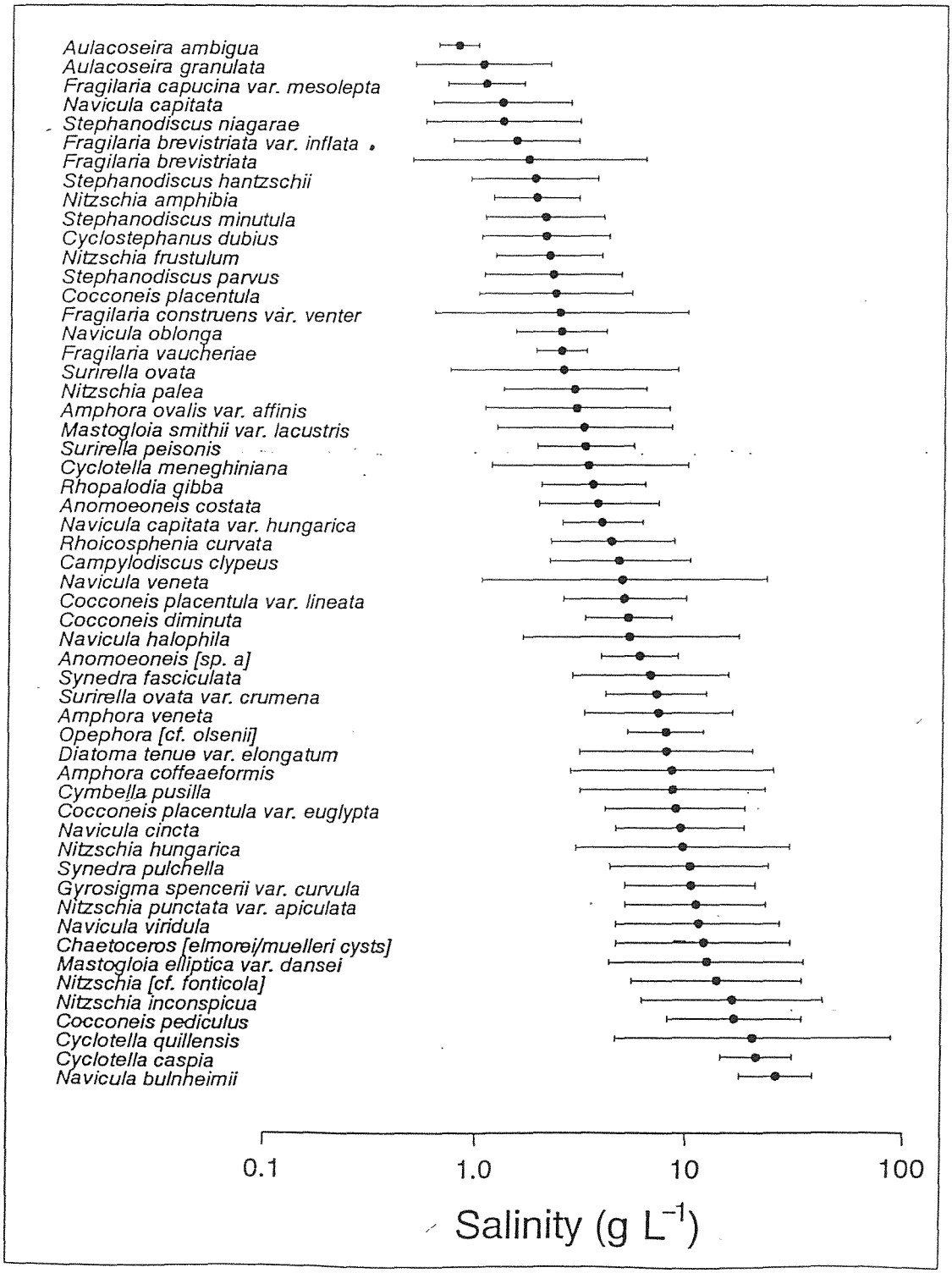
Figure 6. The relative abundance of selected taxa along the salinity gradient. Scaling of the vertical axis is proportional to the taxon's relative abundance and is not the same in each figure.

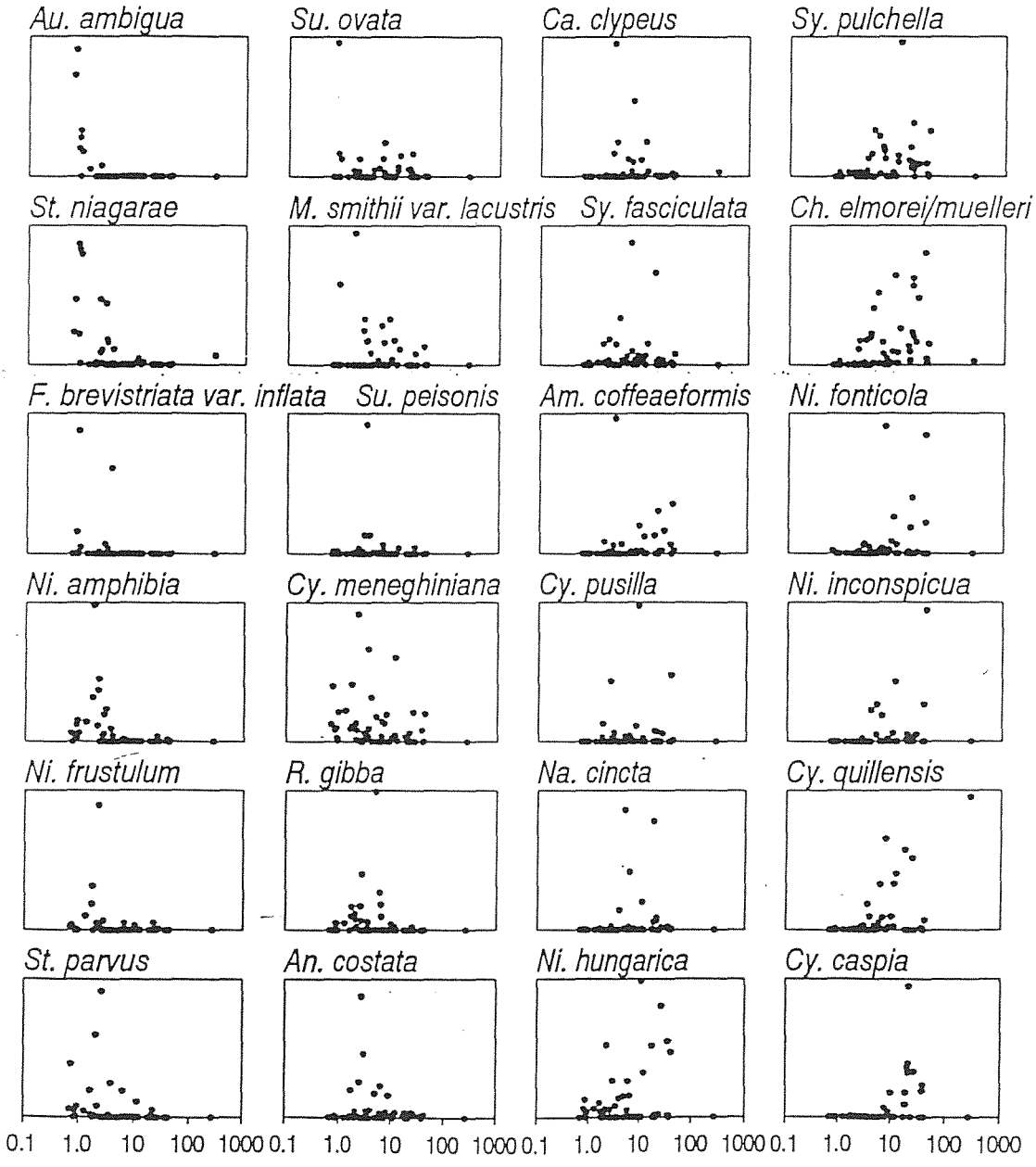

108°W
96°W
58°N
Saskatchewan
Manitoba
-40
-30
-20
-10
-50
-60
Canada
50°N
U.S.
MT
ND
MN
SD
WY
IA
42°N
NE


SO4
100%
80
60
40
20
0
1000
100
10
1.0
0.1
Salinity (g L-1)
BITT
WHIT
MUSK
AROM
ESTU
WILL
MEDI
BQUI
ECKL
HAZL
MANI
SAYE
BIT1
MISS
STI2
DEAD
ANTE
WALD
STIN
WAUB
RABB
EDEV
FREE
REFL
OPUN
HORS
ECOT
PORT
MOON
BOUC
ROSL
FIFE
COLD
SPRG
ISOB
ROU2
SHIN
FISH
DEVI
LONG
WAKA
HUMB
ROY
SPRT
TWIN
ELBW
ROU1
MADI
LENO
POIN
HERM
OAKW
ALBT
0
20
40
60
80
100%
HCO3 + CO3 + Cl


Ca
100%
0
80
20
60
40
40
60
20
80
0
100%
Na + K
100%
80
60
40
20
0
Mg
HERM
NORD
MADI
OAKW
ALBT
POIN
COON
PORT
ROU1
WAKA
LENO
HUMB
BOUC
DEVI
ROSL
LONG
FISH
ECOT
ROY
TWIN
WALD
COLD
MEDI
SAYE
SHIN
TRAM
EDEV
MISS
ISOB
SPRT
ANTE
BQUI


CO3
%Na
%CO3
pH
%K
%Cl
Na
Cl
Conduct
Salinity
SO4
Mg
%Ca
%Mg
%SO4
Ca
An spA
Su crum
Cam cly
An cos
Na cry
Co dim
Na rhy
Fr vau
Op ols
Am ova
G oliv
Na obl
M lac
Su peis
Am ven
Na hal
Su str
Na hun
Ach min
M dan
Co plin
Sy acus
Rc curv
Ni fru
St med
Am ped
Fr mes
G parv
Am aff
Am coff
Sy las
Cy quil
Di ten
Co plac
Ni sub
G ang
Cy man
Fr con
Fr bif
Fr con
Cy cas
Na vir
Ch e/m
Fr bre
Na bul
Ni lon
Ni den
St par
Sy uln
St nia
Na cap
Ni comp
Co ped
Ni inc
Na ven
St min
Fr cro
Na vix
Gy cur
Na sem
Cs dub
Su ova
Aul amb
Ni con
St han
G dic
Sy fil
Aul gra
Gy acu
Fr inf
HORS
SHIN
ISOB
REFL
ROU2
FREE
ELBW
MOON
FIFE
MEDI
COLD
TWIN
ALK2
LONG
WAUB
TRAM
FISH
GEOR
LENO
HAZL
WAKA
COON
POIN
BOUC
ROY
ROSL
SPRT
NORD
REDB
OPUN
DEVI
MADI
OAKW
PORT
HERM
4.0
3.0
2.0
1.0
0.0
-1.0
-2.0
-2.0
-1.0
0.0
1.0
2.0
3.0
CAA Axis 2 (λ = 0·49)
CAA Axis 1 (λ = 0·59)


Aulacoseira ambigua
Aulacoseira granulata
Fragilaria capucina var. mesolepta
Navicula capitata
Stephanodiscus niagarae
Fragilaria brevistriata var. inflata
Fragilaria brevistriata
Stephanodiscus hantzschii
Nitzschia amphibia
Stephanodiscus minutula
Cyclostephanus dubius
Nitzschia frustulum
Stephanodiscus parvus
Cocconeis placentula
Fragilaria construens var. venter
Navicula oblonga
Fragilaria vaucheriae
Surirella ovata
Nitzschia palea
Amphora ovalis var. affinis
Mastogloia smithii var. lacustris
Surirella peisonis
Cyclotella meneghiniana
Rhopalodia gibba
Anomoeoneis costata
Navicula capitata var. hungarica
Rhoicosphenia curvata
Campylodiscus clypeus
Navicula veneta
Cocconeis placentula var. lineata
Cocconeis diminuta
Navicula halophila
Anomoeoneis [sp. a]
Synedra fasciculata
Surirella ovata var. crumena
Amphora veneta
Opephora [cf. olsenii]
Diatoma tenue var. elongatum
Amphora coffeaeformis
Cymbella pusilla
Cocconeis placentula var. euglypta
Navicula cincta
Nitzschia hungarica
Synedra pulchella
Gyrosigma spencerii var. curvula
Nitzschia punctata var. apiculata
Navicula viridula
Chaetoceros [elmorei/muelleri cysts]
Mastogloia elliptica var. dansei
Nitzschia [cf. fonticola]
Nitzschia inconspicua
Cocconeis pediculus
Cyclotella quillensis
Cyclotella caspia
Navicula bulnheimii
0.1
1.0
10
100
Salinity (g L^{-1})


Au. ambigua
Su. ovata
Ca. clypeus
Sy. pulchella
St. niagarae
M. smithii var. lacustris
Sy. fasciculata
Ch. elmorei/muelleri
F. brevistriata var. inflata
Su. peisonis
Am. coffeaeformis
Ni. fonticola
Ni. amphibia
Cy. meneghiniana
Cy. pusilla
Ni. inconspicua
Ni. frustulum
R. gibba
Na. cincta
Cy. quillensis
St. parvus
An. costata
Ni. hungarica
Cy. caspia
0.1 1.0 10 100 1000
Salinity (g L^{-1})

Diatom / salinity transfer functions and climate change: an assessment of methods and application to two Holocene sequences from the northern Great Plains, North America

S. Juggins & R.W. Battarbee
Environmental Change Research Centre, University College London, UK

S.C. Fritz
Limnological Research Center, University of Minnesota, USA

ABSTRACT: The diatom record from the sediments of saline, closed-basin lakes provides a proxy record of salinity, water-level and climate change. The performance of seven different numerical approaches to salinity reconstruction was assessed using a calibration dataset of 55 lakes situated in the northern Great Plains, North America. Weighted averaging gave superior performance in terms of cross-validation prediction error and bias, and was used to reconstruct the late-glacial and Holocene salinity histories of two sites in the region. Both sites show major fluctuations in salinity throughout the Holocene and indicate a climatic history more complex than that inferred from pollen or lake-level studies.

1 INTRODUCTION

In arid and semi-arid regions the chemistry of closed basins responds directly to changes in the hydrological budget through dilution or evaporative concentration of dissolved salts. Of the various biological and geochemical indicators in these systems diatoms are one of the most useful, as a direct record of salinity, and an indirect measure of water level and climate change. Over the past decade the development of diatom-based transfer functions has replaced earlier classification schemes and revolutionised palaeolimnological interpretation by providing quantitative reconstructions of key hydrochemical variables.

Transfer functions are calibrated from a modern dataset of diatom samples collected from lake surface sediments, planktonic, or periphytic habitats, together with associated water chemistry. Several saline-lake calibration datasets have been generated for a number of regions (e.g. Gasse 1987), and although they have been used to give qualitative information on diatom / salinity relationships there are few examples of quantitative salinity reconstructions. In the northern Great Plains of North America we have been developing quantitative diatom-based salinity reconstructions (Fritz 1990; Fritz et al 1991). Here we compare the performance of seven different numerical approaches to salinity reconstruction and apply the results to two late-glacial and Holocene diatom records from this region.

2 THE NORTHERN GREAT PLAINS

The northern Great Plains (NGP) is a loosely defined physiographic region of flat to rolling topography in the North American continental interior (Figure 1). The native vegetation is predominantly prairie grassland and reflects the strong negative effective moisture gradient. Today the region forms one of the major agricultural belts of North America and is dominated by cultivated grassland.

Historical records show the strong hydrological response to climate change in the past century, with low lake levels and high salinity recorded at many sites through the drought years of the 1930s and 1940s (e.g.

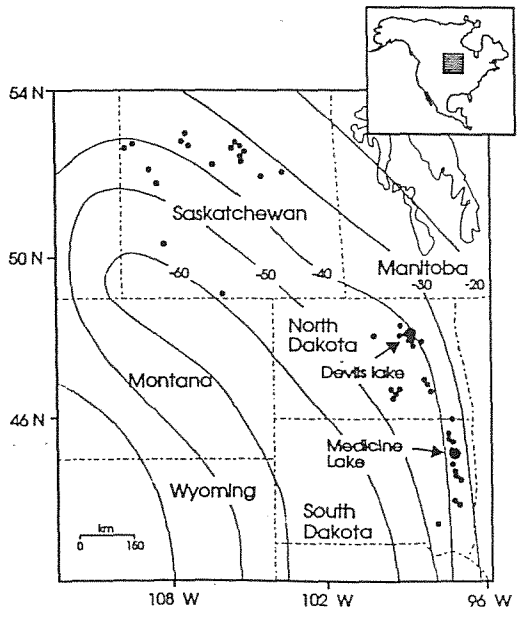


Figure 1. Northern Great Plains showing calibration and core sites. Contours are lines of equal P-E in cm yr^{-1}.

Swenson & Colby 1955). However, our knowledge of the long-term climate history of the region is poor, partly because there are only a few palaeoecological studies from the Great Plains (e.g. Watts & Bright 1966), and because climate reconstructions from existing pollen data are difficult in the prairies, where the pollen record is dominated by grasses and herbs of low taxonomic resolution and most sites are distant from ecotones.

3 DIATOM / SALINITY TRANSFER FUNCTION

The calibration set consists of surface sediment samples from 55 lakes situated in the glaciated areas of North and South Dakota and Saskatchewan (Figure 1). The lakes range in salinity from 0.8 to 260 g/l. Most are dominated by sodium and magnesium sulphate, although a few sodium carbonate and sodium chloride lakes are also included (Fritz et al. In press).

Ordination of the modern diatom and chemistry data by detrended correspondence analysis and canonical correspondence analysis shows that the major patterns of floristic composition are strongly and significantly related to salinity and its correlates (conductivity and major cation / anion concentrations) and to differences in brine type (Fritz et al. In press).

The strong first-axis relationship between diatom composition and salinity is illustrated in Figure 2, which shows a plot of species optima (abundance-weighted means) and tolerances (abundance-weighted standard deviations) along the salinity gradient, from freshwater taxa such as Aulacoseira ambigua and A. granulata to hypersaline Cyclotella species and Navicula bulnheimii. The continuous distribution of the optima shows that there are good indicators across the whole salinity gradient and that prediction should be equally good over this range.

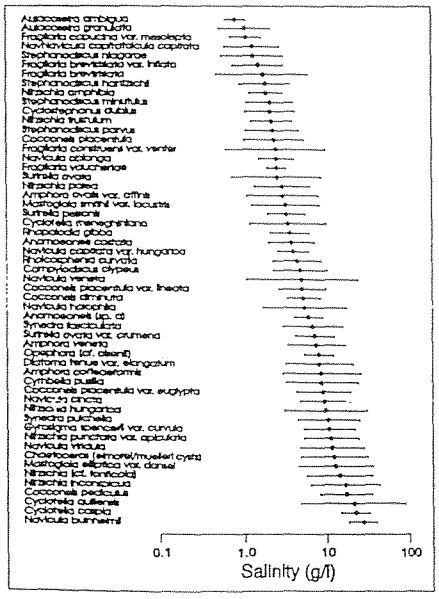


Figure 2. Salinity optima and tolerances of common taxa.

Table 1. Performance of various transfer function methods. Results are in $\log_{10}$(salinity gl^{-1}) units.

Method		RMSE	Bias
Correspondence anal. regression	Apparent	0.30	0.24
	Prediction	0.35	0.28
Canonical CA of classes	Apparent	0.26	0.15
	Prediction	0.31	0.15
Weighted averaging (WA)	Apparent	0.22	0.10
	Prediction	0.32	0.10
Tolerance WA	Apparent	0.22	0.08
	Prediction	0.31	0.08
WA partial least squares	Apparent	0.22	0.10
	Prediction	0.32	0.10
Maximum likelihood	Apparent	0.21	0.25
	Prediction	0.34	0.49
Modern analog	Prediction	0.37	0.25

On the basis of the strong relationship between diatoms and salinity seven different numerical approaches were used to derive transfer functions between diatom relative abundances and $\log_{10}$ transformed salinity; correspondence analysis regression (CAR), canonical correspondence analysis of classes (CCAC), weighted averaging (WA) and tolerance downweighted weighted averaging (Tol-WA), weighted averaging partial least squares (WAPLS), maximum likelihood (ML), and modern analogues (MA).

The performance of each method was assessed on the basis of (i) the root mean square of the error (RMSE), and (ii) the maximum bias along particular parts of the salinity gradient. Estimating these parameters for the calibration set alone gives so-called 'apparent errors'. Since the same data are used to both generate and evaluate the model these will always be over-optimistic. A better estimate of the 'prediction error', or the likely error when the transfer function is applied to new data, is obtained by jackknifing or 'leave-one-out', a computer intensive method of cross validation.

Comparing apparent and prediction errors for each method shows the latter are 16-62% higher (Table 1), highlighting the importance of using a robust method of error estimation. Similarly, with the exception of CAR, all methods perform well as assessed by the apparent errors, but there are large differences between methods when the prediction errors are considered. For example, ML gives the lowest apparent RMSE, but it is one of the worst methods in term of prediction error. Considering the prediction RMSE and bias, WA, Tol-WA, and CCAC give the best performance, although computational and model simplicity, and direct interpretation of regression coefficients (as species' optima) favour WA. WAPLS is unable to improve on WA in this dataset, although in a larger saline-lake dataset from Africa (n=254), both WAPLS and MA methods show promise (Gasse & Juggins unpubl).

These results indicate that weighted averaging is the

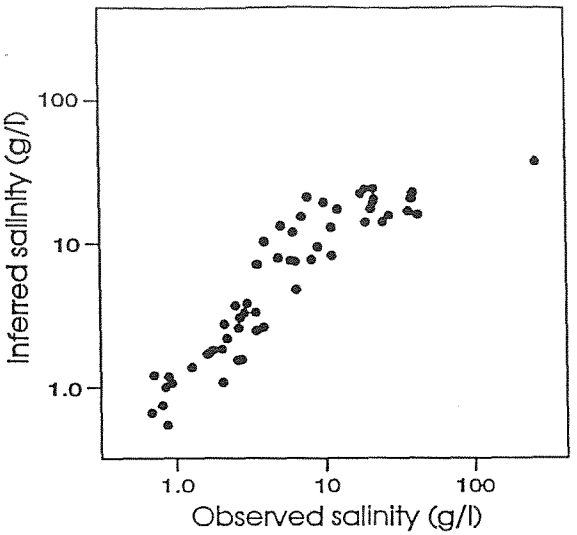


Figure 3. Relationship between diatom-inferred and observed salinity for the calibration set.

most reliable method for use with the NGP dataset, and that it can be used to derive a transfer function for inferring palaeosalinity with a prediction error of approximately 0.3 $\log_{10}$ units. This error has a similar relative magnitude to those associated with diatom / pH transfer functions.

The relationship between observed and diatom-inferred salinity using the weighted averaging transfer function is shown in Figure 3. The data indicate a close agreement between measured and inferred salinity, despite the variable state of diatom preservation in the surface sediment samples. The single outlying high-salinity sample is characterised by Cyclotella quillensis, a saline diatom with broad tolerance. This sample is therefore poorly modelled by the transfer function, but was not deleted since it gives additional information on the true range of this important taxon.

4 LATE-GLACIAL AND HOLOCENE SALINITY RECONSTRUCTIONS

The transfer function was applied to ^{14}C-dated late-glacial and Holocene cores from two sites, Devils Lake, North Dakota (Fritz et al. 1991), and Medicine Lake, South Dakota (Radle et al. 1989) (Figure 1). Figure 4 shows the late-glacial and Holocene diatom stratigraphy for the two sites, with reconstructed salinity and jackknife-estimated errors. For each site taxa have been arranged according to their salinity optima, with freshwater species on the left. Also shown is the squared-chord dissimilarity between each fossil sample and its closest modern analogue, with the dashed line indicating a cut-off for fossil samples that have no good analogues in the calibration set.

At Devils Lake the late-glacial and early Holocene were characterised by freshwater Fragilaria, Cyclotella and Stephanodiscus species (DL1). Salinity reconstructions for this period indicate values of around 1.5 g l^{-1}. These inferred values are certainly too high. Dissimilarities for this zone suggest that it has no good modern analogues due to the lack of very fresh sites in the calibration set. Additional information on the distribution of these taxa indicates that the salinity during this period was less than 0.5 g/l.

Around 8200 BP these freshwater taxa were abruptly replaced by Cyclotella caspia and other saline species, giving a reconstructed salinity of around 40 g l^{-1} (DL2). This saline phase lasted until about 7000 BP and was followed by a series of oscillations between fresher periods of 2-5 g l^{-1} indicated by Stephanodiscus and

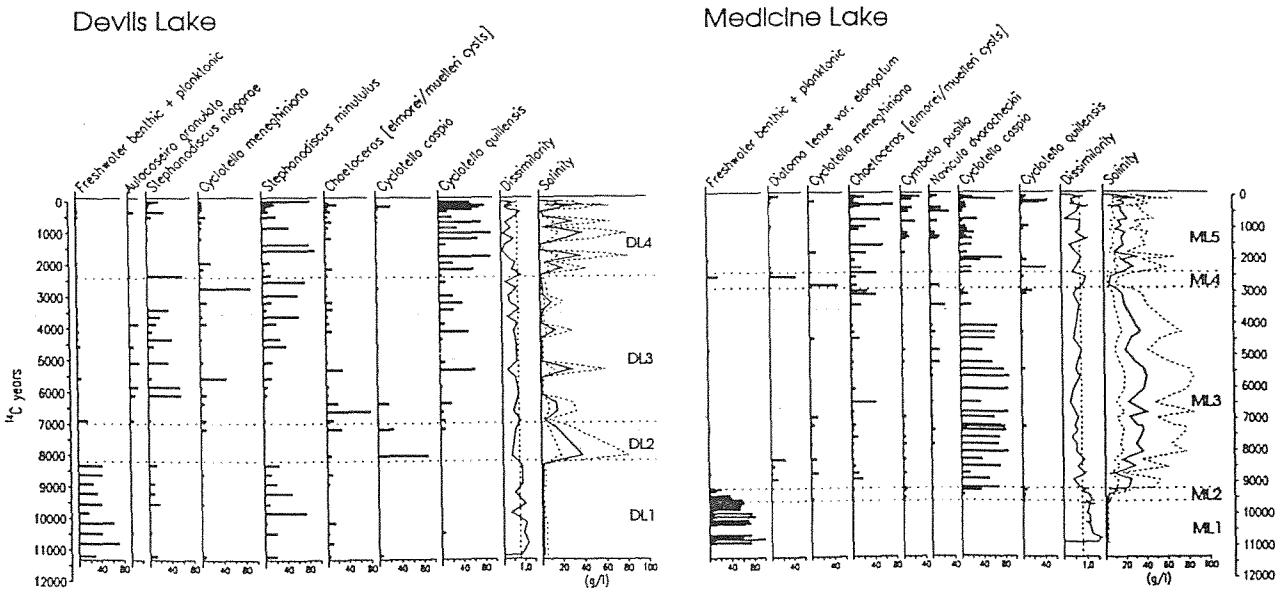


Figure 4. Devils Lake and Medicine Lake, summary diatom stratigraphy and salinity reconstructions.

Aulacoseira taxa, and Cyclotella meneghiniana, and shorter saline phases of between 12 and 30 g l^{-1} dominated by Cyclotella quillensis and Chaetoceros species (DL3). After 2400 BP the lake became more saline and was characterised by a period of more rapid oscillations between Cyclotella quillensis and Stephanodiscus minutulus, indicating excursions from less than 2 g l^{-1} to saline phases of 30 g l^{-1} (DL4).

The late-glacial and early Holocene periods at Medicine Lake were also characterised by freshwater benthic and planktonic taxa, and like the corresponding levels in Devils Lake this zone also lacks analogues in the calibration set (ML1). Between 9600 BP and 9200 BP there was an increase in saline taxa, in particular Chaetoceros species and Cyclotella quillensis (ML2). Freshwater taxa disappear completely around 9200 BP and there was a rapid transition to a flora dominated by the saline Cyclotella caspia which persisted until 2900 BP (ML3). Reconstructions for this period indicate an initial relatively stable salinity of 20 - 40 g l^{-1} declining to about 10 g l^{-1} after 4000 BP. This was followed by a fresher phase of 5 g l^{-1} which lasted from 2900 to 2400 BP (ML4). The period from 2400 BP to the present indicates a return to more saline conditions with salinity fluctuating between 10 and 30 g l^{-1} (ML5).

5 DISCUSSION

The relationship between salinity, water level and climate is complex and depends on the hydrological and morphological features of the lake and catchment. The two core sites reported here differ markedly in these respects. Devils Lake is today a large (55 km^2), relatively fresh (2.7 g l^{-1}) lake situated in a hydrologically complex catchment of c. 10,000 km^2. Medicine Lake is much smaller (lake area 1.8 km^2, catchment area 3.5 km^2) and more saline (> 30 g l^{-1}).

Despite these differences the two sites show broadly similar salinity histories. Both started the early Holocene as freshwater lakes. At Medicine Lake salinity increased gradually after 9600 BP, and reached its maximum by c. 8000 BP. Devils Lake remained fresh until about 8200 BP when the salinity abruptly rose to 40 g l^{-1}. The high salinities recorded at both sites between 8000 BP and 7000 BP suggest that this is the time of maximum Holocene aridity. After 7000 BP salinities gradually fell at Devils Lake but were maintained at Medicine Lake until a period of low salinity recorded at both sites between 3000 BP and 2500 BP. The period between 2500 BP and the present is characterised at both sites by rapid and extreme fluctuations. Additionally, comparison of reconstructed salinities with the 100-year instrumental salinity record for Devils Lake suggests that the drought of the 1930s and 1940s was exceeded in aridity on at least four occasions in the last 2000 years.

The diatom stratigraphies from the two lakes show that after a freshwater period during the late-glacial and early Holocene both sites were characterised by a series of oscillations between periods of high salinity and periods of freshwater or low to moderate salinity. Application of the transfer function enables the relative magnitude of these salinity fluctuations to be estimated, and shows that climatic fluctuations in this region were far more complex than the broad trends inferred from pollen and lake-level studies.

Current work is extending the calibration dataset at both ends of the salinity gradient to improve the accuracy of the transfer function, both by the collection of new samples from the NGP, and through the CASPIA project, which is focusing on the harmonisation and merging of different regional saline-lake datasets. The new transfer function will be applied to cores from additional sites to refine inferences about past climate and to help predict regional responses to future climate change.

ACKNOWLEDGEMENTS

We thank D. Engstrom for analysis of the calibration water-chemistry samples, and to C.M. Keister for providing the Medicine Lake diatom data. This work was supported by the NERC Palaeoclimate Special Topic Grant GST/02/494.

REFERENCES

Fritz, S.C. 1990. Twentieth-century salinity and water-level fluctuations in Devils Lake, North Dakota: test of a diatom-based transfer function. Limnol. Oceanogr. 35: 1771-1781.

Fritz, S.C., S. Juggins, R.W. Battarbee & D.R. Engstrom 1991. Reconstruction of past changes in salinity and climate using a diatom-based transfer function. Nature 352: 706-708.

Fritz, S.C., S. Juggins & R.W. Battarbee In press. Diatom assemblages and ionic characterization of lakes of the northern Great Plains, N.A.: a tool for reconstructing past salinity and climate fluctuations. Can. J. Fish. Aquat. Sci.

Gasse, F. 1987. Diatoms for reconstructing palaeoenvironments and paleohydrology in tropical semi-arid zones. Hydrobiol. 154: 127-163.

Radle, N., C.M. Keister, R.W. Battarbee 1989. Diatom, pollen, and geochemical evidence for the palaeosalinity of Medicine Lake, S. Dakota, during the Late Wisconsin and early Holocene. J. Paleolimn. 2: 159-172.

Swenson, H.A. & B.R. Colby 1955. Chemical quality of surface waters in Devils Lake Basin, North Dakota. U.S. Geol. Surv. Water-Supply Pap. 1-79.

Watts, W.A. & R.C. Bright 1966. Pollen, seed, and mollusk analysis of a sediment core from Pickerel Lake, northeastern South Dakota. Geol. Soc. Am. Bull. 79: 855-876.

The CASPIA Project: diatom, salt lakes, and environmental change

S. Juggins[1], R.W. Battarbee[1], S.C. Fritz[2] and F. Gasse[4]

[1]Environmental Change Research Centre, Department of Geography, University College London, 26 Bedford Way, London WC1H 0AP, UK

[2]Limnological Research Center, University of Minnesota, 310 Pillsbury Drive S.E., Minneapolis, MN 55455, USA

[4]Laboratoire d'Hydrologie et de Géochimie Isotopique, Université de Paris-Sud, Bâtiment 504, 91405 Orsay Cedex, France

Key words: diatoms, palaeolimnology, palaeoclimate, saline lakes, transfer functions

Submitted to Journal of Paleolimnology, Nov. 1993

Introduction

The sediments of closed-basin, saline lakes contain an unrivalled proxy record of hydrological and climatic change for arid and semi-arid regions of the world. Of the various palaeoclimatic indicators in these sediments the diatom record is one of the most useful, as a direct record of past water chemistry, especially palaeosalinity, and as an indirect measure of water-level and climate change (e.g. Bradbury et al., 1981; Gasse, 1987; Fritz et al., 1991). Consequently, there is a great demand for diatom-based salinity and water-level reconstructions for saline lakes world-wide.

Interpretation of the diatom record in these systems is dependant on a detailed knowledge of the ecology and distribution of constituent taxa, together with an understanding of the processes controlling the formation and preservation of the fossil assemblage. Although there is a large literature describing the range and tolerances of freshwater diatoms, the ecological requirements of taxa in saline systems are poorly understood. Schemes for classifying diatoms according to salinity have been developed for waters of marine (thalasic) origin (e.g. Kolbe, 1927; Hustedt, 1957; Simonsen, 1962) and modified for application to athalassic environments (Gasse et al., 1987). However, they have course resolution, allowing only semi-quantitative reconstructions, and many taxa remain unclassified.

Over the past decade the development of transfer functions has revolutionised palaeoecological interpretation by providing quantitative reconstructions of key hydrochemical parameters. Transfer functions are calibrated from a modern dataset of surface sediment, plankton or periphyton samples, and associated water chemistry. For certain regions, especially East and North Africa and the Northern Great Plains of North America, calibration datasets and salinity transfer functions have already been developed (Gasse et al., 1987; Fritz et al., 1991; Fritz et al., in press). Elsewhere diatomists are rapidly extending sampling networks to create new regional datasets which will be used to generate independent transfer functions.

In 1991 several people involved in the collection of these modern datasets set up a working group to compare saline-lake diatom floras from around the world. Since then the group has expanded and set up the CASPIA Project, with the aim to merge these different regional datasets into a single database of modern diatom and environmental data, and to use the database to generate regional and inter-regional transfer functions for core-based reconstructions. This paper describes the main objectives of the Project, shown in Figure 1.

Merging of Modern Datasets

The Project is currently focusing on nine modern datasets collected by 13 diatomists from various arid and semi-arid regions (Figure 2). These contain a total of ca. 800 diatom samples and cover a wide range of chemical environments and habitats. Where taxa are clearly identical between regions the increased

chemical diversity of the combined dataset will help refine estimates of species' optima and tolerances, and allow the development of more accurate transfer functions. Similarly, the increased biological diversity of the combined dataset will help in the search for modern analogues of fossil assemblages. Unfortunately these do not always exist within the same geographical region, and transfer functions are likely to be most accurate when they can be identified, even if they are geographically distant. For example, analogues for fossil planktonic taxa in Africa cannot be found in Africa today, but are potentially available in the Northern Great Plains dataset.

Accurate and consistently applied taxonomy is central to the success of all palaeolimnological investigations and the merging of modern datasets would be impossible without careful attention to taxonomic standardisation. It is especially important in the application of current weighted-averaging based transfer functions that are at their best with precisely quantified, species-rich assemblages (ter Braak & Looman, 1986; ter Braak & Juggins, in press). Unfortunately saline lake diatoms are often taxonomically very difficult, and nomenclature and the conventions used for species distinctions can vary between diatomists and laboratories. In CASPIA, taxonomic consistency is being achieved using methods of taxonomic quality control (TQC) developed during the SWAP (Munro et al., 1990) and PIRLA (Kingston et al., 1992) projects on lake acidification.

Taxonomic quality control involves (i) comparison of floras and identification of problem taxa or groups, (ii) comparison of problem taxa at workshops, agreement on protocols for identification, (iii) agreement on nomenclature, (iv) testing of protocols by controlled experiment, and (v) the progressive development of project-based floras linked, where possible, to type material. So far we have compared floras from North America, Africa, Australia, and Europe, and devoted three workshops to the examination of problem taxa within the genera Navicula, Nitzschia, and Amphora. A programme of slide exchange has been initiated to test workshop protocols relating to these taxa.

Diatom Iconograph and Ecological Database

Taxonomic quality control and workshop protocols are leading to the production of a project-based diatom iconograph, recording floristic distinctions using light and scanning micrographs of both project and type material. Since the iconograph will be a tool for both ecologists and micropalaeontologists it will contain images of specimens in various states of preservation, using criteria developed for recording dissolution and fragmentation series of individual taxa. The development of the iconograph is essential to maintain taxonomic consistency within the project, and to allow other diatomists working on core material to standardise taxonomy. Clearly core and calibration dataset taxonomy must be perfectly compatible before transfer functions can be applied.

One of the main aims of the project is to combine taxonomic and distributional information to construct a linked taxonomic and ecological database of saline lake

diatoms. This will contain, for each taxon, full taxonomic and nomenclatural history, synonyms, images and morphological descriptions, and ecological information. The latter will formalise the ad-hoc and varying ecological and distributional data that usually accompanies diatom floras by including detailed information derived from the modern datasets on the response of taxa to various environmental parameters.

The iconograph will consist of a library of hardcopy micrographs and scanned images, referenced to our existing database of diatom counts and environmental information. Using CD-ROM technology or fast computer networks this will allow the rapid distribution of the iconograph, taxonomic and ecological information, and transfer functions to the wider palaeolimnological community.

Transfer functions for palaeolimnological reconstruction

The ecological database will lead directly to the generation of transfer functions for palaeolimnological reconstruction. In studies of lake acidification and eutrophication the technique of weighted averaging regression and calibration (WA) has become a popular method for environmental reconstruction. Comparisons using the NGP dataset to reconstruct total salinity show WA to outperform a range of other methods in terms of prediction error (Juggins et al., submitted). However, with a larger dataset from Africa the method of weighted averaging partial least squares improves on WA (ter Braak & Juggins, in press; Juggins & Gasse, in prep.). Future work will examine in detail the performance of this new method and others based on analogue matching (Guiot, 1990) and response surfaces (Huntley, 1992), which are only practical with large modern datasets.

In addition to salinity it has been clearly shown that the composition of diatom communities is also controlled by brine type (e.g. Gasse *et al.*, 1983). Thus there is much scope for reconstructing changes in cation and anion dominance that may accompany changes in salinity, revealing past geochemical and hydrological pathways. However, the diatom response to changes in brine type is much weaker than the response to the salinity gradient, and our experience with soft-water calibration sets suggest that these secondary gradients can only be quantified using large (150+) datasets. For example, an initial dataset of 33 lakes was sufficient to generate a transfer function for pH reconstruction (Flower, 1986), but a dataset of 178 samples was needed before transfer functions for aluminium and dissolved organic carbon could be developed (Birks et al., 1990). This is known as the 'curse of dimensionality' - if n samples are needed to quantify diatom response along a single gradient, then n^2 samples are needed to quantify response along two independent gradients, if the same sampling density is to be maintained (Hastie & Tibshirani, 1990).

A basic assumption of the transfer function approach is that both the modern and fossil diatom assemblages are systematically related to the environmental variable to be reconstructed. By modifying the modern assemblages used to construct transfer functions and the fossil assemblages, taphonomic processes, in particular

the dissolution of diatom frustules, can lead to inaccurate transfer functions and biased reconstructions (Barker, 1992). An important part of the project is therefore examining the way both the morphology of individual diatom taxa, and the composition of diatom assemblages are modified by varying degrees of dissolution. This quantification of the preservation status of a particular sample can then be used to downweight or omit poorly preserved samples from the transfer function, or to modify error estimates of reconstructions which are based on degraded fossil assemblages.

Conclusions

CASPIA consists of 19 diatomists and statisticians involved in the collection of modern datasets, diatom taxonomy and iconograph production, diatom taphonomy, and database and transfer function development (Table 1). The project is currently proceeding by integrating results from members' individual research with taxonomic protocols developed at annual workshops. At the present time there is an excellent opportunity for diatomists to harmonise methodology and create a central database of taxonomic and ecological information that can be used to develop high-quality regional and inter-regional transfer functions that will provide Quaternary scientists with an ecologically and statistically sound basis for palaeoecological and palaeoclimate reconstructions. We welcome wider collaboration on any aspect of the project.

References

Barker P., 1992. Differential diatom dissolution in Late Quaternary sediments from Lake Manyara, Tanzania: and experimental approach. J. Paleolim. 7: 235-251.

Birks, H.J.B., S. Juggins & J.M. Line, 1990. Lake surface water reconstructions from diatom data. In The Surface Waters Acidification Programme. (ed. B.J. Mason). Cambridge University Press, 301-313.

Bradbury, J.P., B. Leyden, M. Salgado-Labouriau, W.M. Lewis, Jr., C. Schubert, M.W. Binford, D.G. Frey, D.R. Whitehead & F.H. Weibezahn, 1981. late Quaternary environmental history of Lake Valencia, Venezuela. Science 214:1299-1305.

Flower, R.J. 1986. The relationship between surface sediment diatom assemblages and pH in 33 Galloway lakes: some regression models for reconstructing pH and their application to sediment cores. Hydrobiologia 143: 93-103.

Fritz, S.C., S. Juggins, R.W. Battarbee & D.R. Engstrom, 1991. Reconstruction of past changes in salinity and climate using a diatom-based transfer function. Nature 352: 706-708.

Fritz, S.C., S. Juggins & R.W. Battarbee, in press. Diatom assemblages and ionic

characterization of freshwater and saline lakes of the Northern Great Plains, N.A.: a tool for reconstructing past salinity and climate fluctuations. Can. J. of Fish. aquat. Sci.

Gasse, F., J.F. Talling & P. Kilham, 1983. Diatom assemblages in East Africa: classification, distribution and ecology. Rev. Hydrobiol. trop. 16: 3-24.

Gasse, F., 1987. Diatoms for reconstructing palaeoenvironments and paleohydrology in tropical semi-arid zones. Example of some lakes from Niger since 12,000 BP. Hydrobiolia 154: 127-163.

Gasse, F., J.C. Fontes, J.C. Plaziat, P. Carbonel, I. Kaczmarska, P. De Dekker, I. Soulié-Marsche, Y. Callot & P.A. Dupeuble, 1987. Biological remains, geochemistry and stable isotopes for the reconstruction of environments and hydrological changes in the Holocene lakes from north Saraha. Palaeogr., Palaeoclimatol., Palaeoecol., 60: 1-46.

Guiot, J. 1990. Methodology of the last climatic cycle reconstruction in France from pollen data. Palaeogr., Palaeoclimatol., Palaeoecol., 80: 49-69.

Hastie, T.J. & R.J. Tibshirani, 1990. Generalised Additive Models. Chapman & Hall, London, 355pp.

Huntley, B., 1992. Pollen-climate response surfaces and the study of climate change. In Applications of Quaternary Research (ed. J.M. Gray). Quaternary Proceedings No. 2, Quaternary Research Association, Cambridge, 91-99.

Hustedt, F., 1957. Die Diatomeenflora des flussystems des Weser im Gebiet des Hansestadt Bremen. Abh. Naturw. Ver. Bremen 34: 18-140.

Juggins, S., R.W. Battarbee & S.C. Fritz, submitted. Diatom / salinity transfer functions and climate change: an example from the northern Great Plains, North America. Proceedings of NERC/QRA Palaeoclimate '93 meeting, Durham.

Kingston, J.C., B.F. Cumming, A.J. Uutala, J.P. Smol, K.E. Camburn, D.F. Charles, S.S. Dixit & R.G. Kreis, Jr., 1992. Biological quality control and quality assurance: a case study in paleolimnological biomonitoring. Proceedings International Symposium on Ecological Indicators. Elsevier, New York.

Kolbe, R.W., 1927. Zūr Okologie, Morphologie und Systematik des Brackwasser-Diatomeen. Die Kieselagen des Sperenberger Salzgebiet. Planzenforschung 7:1-146.

Munro, M.A.R., A.M. Kreiser, R.W. Battarbee, S. Juggins, A.C. Stevenson, D.S. Anderson, N.J. Anderson, F. Berge, H.J.B. Birks, R.B. Davis, R.J. Flower, S.C. Fritz, E.Y. Haworth, V.J. Jones, J.C. Kingston, & I. Renberg, 1990. Diatom quality control and data handling. Phil. Trans. R. Soc. Lond. B 327, 257-261.

Simonsen, R. 1962. Untersuchungen zur Systematik und Okologie der Bodendiatomeen der Westlichen Ostsee. Int. Rev. ges Hydrobiol., Syst. Beih. 1: 7-149.

ter Braak, C.J.F. & C.W.N. Looman, 1986. Weighted averaging, logistic regression and the Gaussian response model. Vegetatio 65: 3-11.

ter Braak, C.J.F. & S. Juggins, in press. Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. Hydrobiologia.

Tables

Table 1 List of current CASPIA participants and role.

Figure captions

Figure 1 CASPIA Project main objectives.

Figure 2 Map of modern diatom / water chemistry calibration datasets, and analysts.

Project coordination

Rick Battarbee, University College London (Northern Great Plains, North America)
Sheri Fritz, Limnological Research Center (Northern Great Plains, North America)
Francoise Gasse, Université de Paris-Sud (Africa, China, Tibet, Australia, Madagascar)
Steve Juggins, University College London (Southern Russia, statistics, database)

Diatomists - regional datasets

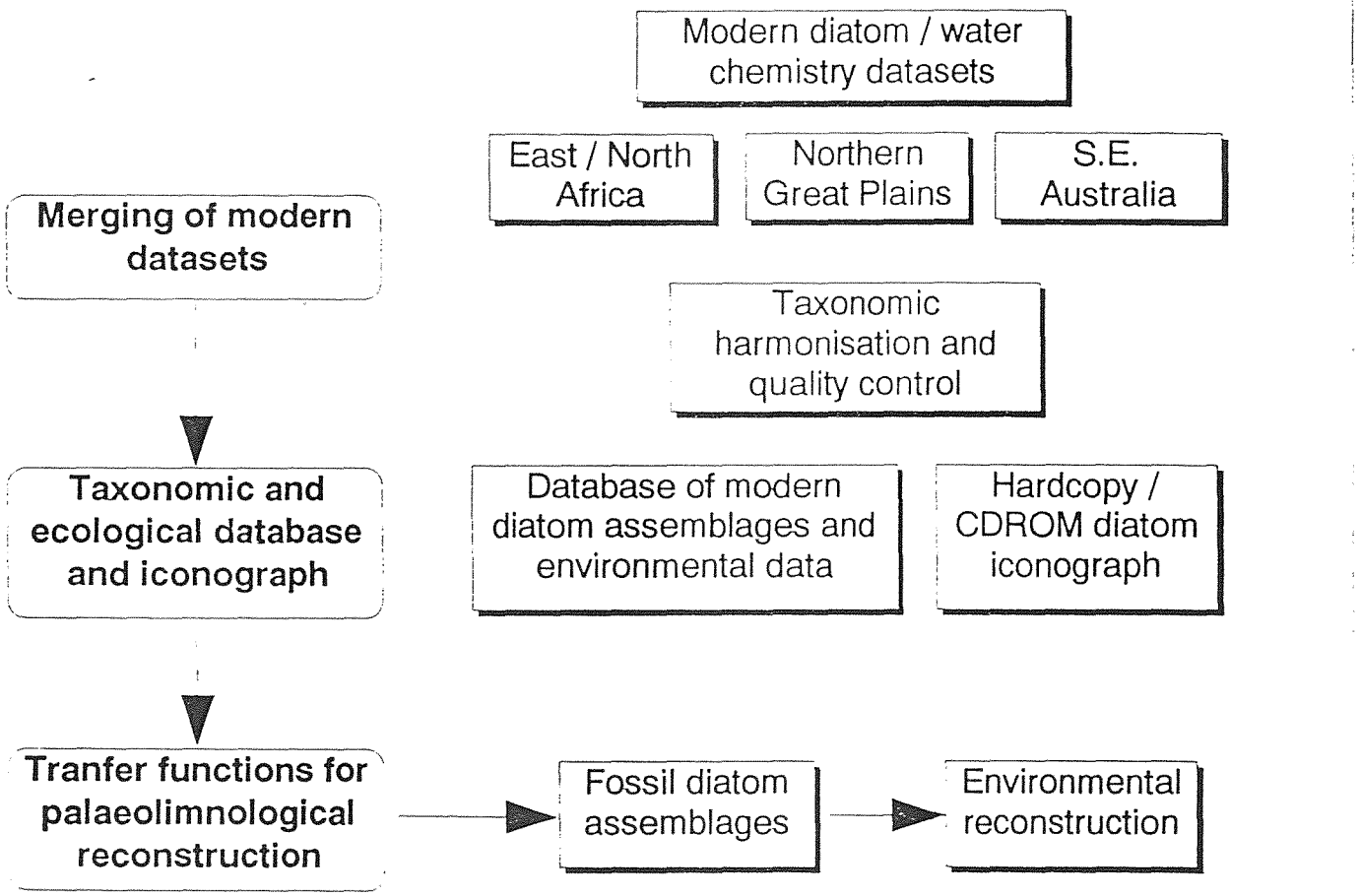
Phil Barker, Lancaster University (Morocco, Turkey, taphonomy)
J. Platt Bradbury, U.S. Geological Survey, Denver (Mexico, Argentina)
Brian Cumming, Queens University (British Columbia)
Peter Gell, University of Monash (Australia)
Leila Ben Khelifa, Université de Paris-Sud (Tunisia)
Sarah Metcalfe, University of Hull (Mexico)
Jane Reed, University College London (Spain)
Melanie Reidinger, Northern Kentucky University (Galapagos)
David Ryves, University College London (taphonomy)
Sue Wilson, Queens University (British Columbia)

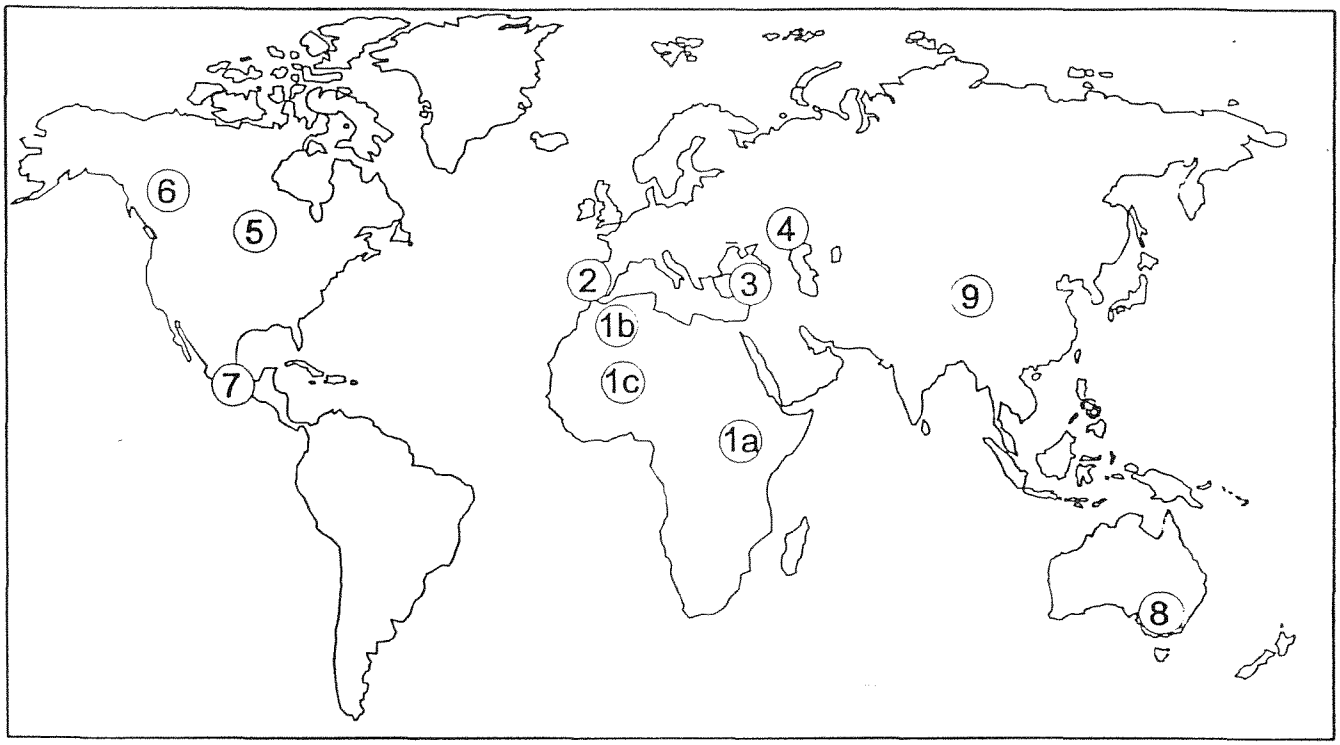
Diatom taxonomy and iconograph production

Eileen Cox, British Museum Natural History
Pat Sims, British Museum Natural History
David Mann, Royal Botanic Garden, Edinburgh

Statistics and computing

John Birks, University of Bergen
Cajo ter Braak, Agricultural Mathematics Group, Wageningen


Modern diatom / water chemistry datasets
East / North Africa
Northern Great Plains
S.E. Australia
Merging of modern datasets
Taxonomic harmonisation and quality control
Taxonomic and ecological database and iconograph
Database of modern diatom assemblages and environmental data
Hardcopy / CDROM diatom iconograph
Tranfer functions for palaeolimnological reconstruction
Fossil diatom assemblages
Environmental reconstruction



1	Africa	
1a	East Africa	Francois Gasse (n=170)
1b	North Africa	F. Gasse, Leila Ben Khelifa & Phil Barker (n=100)
1c	Sahara & Sahel	Francoise Gasse (n=60)
2	Spain	Jane Reed (n=60)
3	Turkey	Phil Barker (n=10)
4	Caspian Lowlands	Steve Juggins (n=10)
5	Northern Great Plains	Sheri Fritz & Rick Battarbee (n=95)
6	British Columbia	Sue Wilson & Brian Cumming (n=110)
7	Mexico	Sarah Metcalfe, Platt Bradbury (n=50)
8	S.E. Australia	Peter Gell & Francoise Gasse (n=90)
9	China	Francoise Gasse (n=30)