Freshwater Biology (2003) **48**, 1311–1328

Distribution of benthic diatoms in U.S. rivers in relation to conductivity and ionic composition

MARINA POTAPOVA AND DONALD F. CHARLES
Patrick Center for Environmental Research, The Academy of Natural Sciences, Philadelphia, PA, U.S.A.

SUMMARY

1. We quantified the relationships between diatom relative abundance and water conductivity and ionic composition, using a dataset of 3239 benthic diatom samples collected from 1109 river sites throughout the U.S.A. [U.S. Geological Survey National Water-Quality Assessment (NAWQA) Program dataset]. This dataset provided a unique opportunity to explore the autecology of freshwater diatoms over a broad range of environmental conditions.

2. Conductivity ranged from 10 to 14 500 μS cm^{-1}, but most of the rivers had moderate conductivity (interquartile range 180–618 μS cm^{-1}). Calcium and bicarbonate were the dominant ions. Ionic composition, however, varied greatly because of the influence of natural and anthropogenic factors.

3. Canonical correspondence analysis (CCA) and Monte Carlo permutation tests showed that conductivity and abundances of major ions (HCO_3^- + CO_3^{2-}, Cl^-, SO_4^{2-}, Ca^{2+}, Mg^{2+}, Na^+, K^+) all explained a statistically significant amount of the variation in assemblage composition of benthic diatoms. Concentrations of HCO_3^- + CO_3^{2-} and Ca^{2+} were the most significant sources of environmental variance.

4. The CCA showed that the gradient of ionic composition explaining most variation in diatom assemblage structure ranged from waters dominated by Ca^{2+} and HCO_3^- + CO_3^{2-} to waters with higher proportions of Na^+, K^+, and Cl^-. The CCA also revealed that the distributions of some diatoms correlated strongly with proportions of individual cations and anions, and with the ratio of monovalent to divalent cations.

5. We present species indicator values (optima) for conductivity, major ions and proportions of those ions. We also identify diatom taxa characteristic of specific major-ion chemistries. These species optima may be useful in future interpretations of diatom ecology and as indicator values in water-quality assessment.

Keywords: benthic diatoms, conductivity, ionic composition, rivers, U.S.A.

Introduction

Diatoms are the most common and diverse group of algae in many rivers and streams, and thus are important components of these ecosystems (Round, 1981). Although it is well known that salinity and concentrations of major ions have a strong influence on distributions of individual diatom taxa (Cholnoky, 1968), the relative importance of these factors has rarely been studied at large regional scales, and particularly not for the United States. Nor have ecological optima of taxa been quantified at these scales using large numbers of samples. This paper provides such information based on diatom data for samples collected by the USGS NAWQA Program. This information improves our understanding of how diatoms are distributed in U.S. rivers with respect to conductivity and major ions, and provides specific autecological data so that diatoms can be used more effectively in making assessments of ecological change.

Correspondence: M. Potapova, Patrick Center for Environmental Research, The Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103, U.S.A.
E-mail: potapova@acnatsci.org

Continental waters vary greatly in their mineral content and composition, mainly because of the variability in lithology, climate and vegetation. Anthropogenic factors are also important. Soil erosion, irrigation, or the direct input of industrial, municipal or agricultural wastes into rivers often increases total mineral content, or concentration of individual ions in river water (Meybeck & Helmer, 1989). For instance, the most noticeable environmental change in rivers of Massachusetts and New Jersey following development of their catchments was an increase in concentration of base cations (Dow & Zampella, 2000; Rhodes, Newton & Pufall, 2001), disrupting the natural communities of these rivers, which are adapted to low-alkalinity conditions. Agricultural land use often increases conductivity of river water and these changes are reflected in algal communities (Leland, 1995; Carpenter & Waite, 2000). Salt leaching from irrigated soils can further elevate the naturally high salinity of many rivers in arid and semi-arid zones. Mining operations can cause severe increases in the concentration of certain ions that not only dramatically alter natural communities, but also make water unsuitable for drinking, recreation and irrigation (Meybeck *et al.*, 1992).

Diatoms are often used to monitor these environmental changes because of their range of response to ionic content and composition. Their use in monitoring would be enhanced significantly if species responses to the concentration of major ions in fresh waters were better quantified.

Most knowledge of the relationship of diatoms to salinity comes from studies of the composition of diatom assemblages collected across strong salinity gradients in salt-polluted continental waters, estuaries, inland seas and saline lakes (Kolbe, 1927, 1932; Hustedt, 1957; Cholnoky, 1968; Stoermer & Smol, 1999). The most widely used salinity classifications (Kolbe, 1927; Hustedt, 1957; van der Werff & Huls, 1957–1974 as modified by van Dam, Mertens & Sinkeldam, 1994) assign diatoms to only a few salinity categories, based mostly on their occurrence in European inland and coastal waters. Consequently, these categories are most effective when used to determine whether observed assemblages are from fresh, brackish or saline waters. Strong responses of algal assemblages to the salinity or concentrations of certain ions are, however, not limited to major differences in salinity. A clear response to salinity is also often observed in sets of samples collected exclusively from fresh waters (e.g. Sabater, Sabater & Armengol, 1988; Sabater & Roca, 1992; Pipp 1997; Leland & Porter, 2000; de Almeida & Gil, 2001) and even for datasets limited to waters of very low concentration of dissolved salts (e.g. Potapova, 1996; Soininen, 2002).

Affinities of some freshwater diatoms towards certain ions can be found in widely used diatom floras (e.g. Patrick & Reimer, 1966, 1975). For instance, a number of taxa have been characterised as preferring calcium-rich or calcium-poor waters. It is difficult, however, to compile this information for water-quality monitoring purposes because it is scattered in floras and regional studies. Quantitative autecological characteristics derived from small-scale regional datasets are useful for regional monitoring programmes. However, as they are dependent on the restricted range and distribution of the environmental parameters in the dataset, they may not be appropriate for areas with different water chemistry characteristics. Reliable autecological data can be obtained only from a dataset with large numbers of observations representing the full range of environmental conditions. Here we characterise distributions of benthic diatoms along gradients of conductivity (as a measure of salinity) and ionic composition using data from samples collected as part of the National Water-Quality Assessment (NAWQA) programme from rivers throughout the U.S. Analysis of this dataset for samples collected in 1993–1998 showed that conductivity and ionic composition are among the most important determinants of diatom assemblage structure in U.S. rivers (Potapova & Charles, 2002). At the national scale the complex gradient of ionic strength and pH was the second most important after a so-called 'downstream' gradient, which combined gradients of river size, slope and nutrient concentration. Broad-scale differences in benthic diatom assemblages between rivers of the eastern coastal and western interior areas were largely because of a much higher mineral content in the arid western areas. In this study, we use an even larger NAWQA dataset, based on samples collected from 1993 to 1999, to study in more detail the relationship between these water chemistry properties and common diatom species. Our first objective was to investigate the influence of conductivity and ionic composition on diatom distributions in rivers of the U.S. The second objective was to calculate and present autecological data for use in environmental assessment.

Methods

Sample collection

Benthic algal samples were collected from 1993 to 1999 at 1109 sampling locations across the continental U.S., Alaska and Hawaii (Fig. 1). The USGS personnel collected benthic algal samples at each site once a year, during one to three consecutive years (Gurtz, 1993; Porter *et al.*, 1993). At the majority of the sites, two types of quantitative samples were collected: one from erosional habitats (rocks, usually from riffles and snags) and another from depositional (soft sediment, typically from pools and stream margins) habitats. Both types of samples were used in the present study. Algal samples were collected most often during low-flow conditions, usually in summer or early autumn.

Laboratory methods

Permanent diatom slides were prepared by oxidising organic material in samples with nitric acid and mounting cleaned diatoms in Naphrax. Diatom analysts at the Patrick Center of The Academy of Natural Sciences, Philadelphia (ANSP), the University of Louisville, Michigan State University, and independent contractors identified and counted diatoms. Analysts counted 600 diatom valves on each slide; fewer valves were counted on some slides when diatoms were scarce. Laboratory methods used at the ANSP are described in Charles, Knowles & Davis (2002). All slides were deposited in the ANSP Diatom Herbarium.

Taxonomy

The main diatom floras used for identification were those of Hustedt (1930a,b, 1959, 1961–1966), Patrick & Reimer (1966, 1975), Camburn, Kingston & Charles (1984–1986), Krammer & Lange-Bertalot (1986, 1988, 1991a,b), and Simonsen (1987). Other important works on diatom taxonomy were also consulted. A considerable effort was made to reach taxonomic consistency among analysts (Potapova & Charles, 2002). Some of the diatom taxa reported in this study have not yet been described in the literature; they are

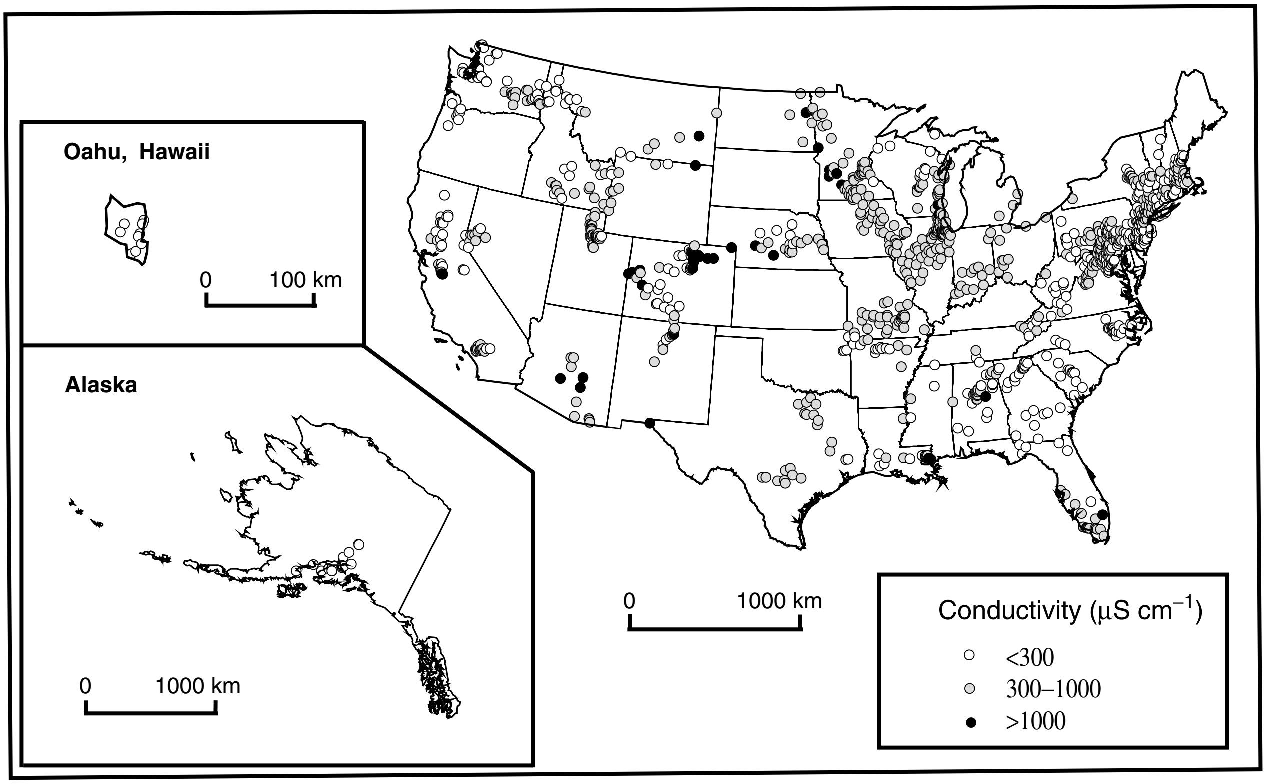

Fig. 1 Location of the 1109 NAWQA sampling sites and corresponding average conductivity values.

given temporary names that may include abbreviations of the name of the person making the determination and geographic location where the taxon was first collected. Images of these taxa are available at the ANSP Algae Image Database website (http://diatom.acnatsci.org).

Environmental data

Water chemistry samples were collected by the U.S. Geological Survey at least once a month. Conductivity, HCO_3^-, CO_3^{2-}, Cl^-, SO_4^{2-}, Ca^{2+}, Mg^{2+}, Na^+, K^+ were determined at the USGS National Water Quality Laboratory (Lakewood, CO, U.S.A.) (Fishman, 1993). For 70 sites where concentration of $HCO_3^- + CO_3^{2-}$ was not reported, we derived concentration of $HCO_3^- + CO_3^{2-}$ from alkalinity values. We used chemical measurements closest to the date of algal sampling in our analyses. Concentration of major ions is reported here in milliequivalents per litre (meq L^{-1}), and proportions of anions and cations are expressed as per cent equivalents of each ion of the sum of all anions or cations (% eq).

Data analysis

Conductivity was determined at all 1109 sampling sites, whereas major ions were analysed at 807 sites only. We constructed two datasets: a 'complete' dataset, consisting of 3239 samples collected from all 1109 sites, and a second 'limited' dataset, which included only the 2674 samples collected at sites where major ions were measured. We excluded all planktonic species from the diatom counts, calculating relative abundance of the benthic diatoms only. Distinction between benthic and planktonic diatoms in inland waters is somewhat arbitrary. Therefore, we excluded only those diatoms (mostly centric species) that are known to spend most of their life in the water column, not considering them being a part of the benthic communities. For analyses, we retained only those species that reached relative abundance of at least 1% in at least two samples per dataset. The resulting 'complete' dataset contained 717 diatom taxa and the 'limited' dataset had 683 taxa.

For numerical analyses, conductivity and concentrations of individual ions (expressed in μeq L^{-1}) were log-transformed to approximate a normal distribution.

To evaluate the strength of the relationship between composition of the diatom assemblages and conductivity, concentration, and proportion of each of the seven major ions, we used canonical correspondence analyses (CCA), with only one environmental variable at a time. A total of 15 CCAs corresponded to 15 tested variables (one for conductivity, seven for concentrations and seven for proportions of major ions). We evaluated the significance of the effect of each variable using Monte Carlo permutation tests with 199 unrestricted permutations, and used the ratio of the first to the second eigenvalue as a measure of the variable strength.

We ran another CCA to elucidate major coenclines and to estimate the relative importance of conductivity and proportions of the seven major ions in explaining variation among diatom assemblages. The eight parameters (conductivity and ion proportions) that were included in this CCA as constraining environmental variables were shown to explain a significant proportion of variation in species composition in previous CCAs and were not highly correlated ($r < 0.8$) with each other. Significance of the first four ordination axes was tested by permutation procedures in partial CCAs, as described by ter Braak & Šmilauer (1998). Significance of the second, third and fourth axes was checked in partial CCAs that used environment-derived sample scores for the first, second and third ordination axes, respectively, as covariables. The CCAs were performed with the CANOCO program (ter Braak & Šmilauer, 1998).

We calculated weighted average estimates of the species optima (u_k) as $u_k = \sum_{i=1}^{n} y_{ik}x_i / \sum_{i=1}^{n} y_{ik}$ where y_{ik} is the relative abundance of species k in sample *i*; x_i is the value of environmental parameter in sample *i*; *n* is the total number of samples in dataset. Tolerance or weighted standard deviation (t_k) was calculated as

$$t_k = \sqrt{\frac{\sum_{i=1}^{n} y_{ik}(x_i - u_k)^2}{\sum_{i=1}^{n} y_{ik}}}.$$

Results

Conductivity and ion concentrations

Conductivity varied from 10 μS cm^{-1}, corresponding to waters extremely poor in electrolytes, to

Table 1 Conductivity and concentration of major ions in NAWQA samples.

Parameter	Minimum	First quartile	Median	Third quartile	Maximum	Number of observations
Conductivity (μS cm^{-1})	10	180	363	618	14500	3040
HCO_3^-+CO_3^{2-} (meq L^{-1})	0.016	0.819	2.278	3.671	9.288	2674
Cl^- (meq L^{-1})	0.003	0.132	0.339	0.875	69.478	2674
SO_4^{2-} (meq L^{-1})	0.002	0.135	0.413	1.083	47.886	2674
Ca^{2+} (meq L^{-1})	0.026	0.749	1.846	2.958	27.455	2674
Mg^{2+} (meq L^{-1})	0.017	0.288	0.775	1.613	18.104	2674
Na^+ (meq L^{-1})	0.016	0.190	0.479	1.262	58.025	2674
K^+ (meq L^{-1})	0.003	0.035	0.059	0.092	1.291	2674

14 500 μS cm^{-1}, representing brackish water (Table 1). Median and interquartile range values for conductivity and concentration of individual ions indicated that most of the rivers had a moderate level of salt content (Meybeck & Helmer, 1989), and were of the calcium bicarbonate type. Highest conductivities were observed in rivers of south Florida and the Mississippi delta influenced by marine waters, rivers of the arid west, and some polluted rivers across the U.S. (black circles in Fig. 1).

Carbonate and bicarbonate were prevalent anions in samples from the majority of the 807 NAWQA sampling sites. Chloride and sulphate dominated only rarely (Fig. 2). Highest concentrations of chloride were found in the Mississippi delta and in some rivers of the arid west (Arizona Desert). The proportion of chloride was sometimes relatively high (up to 80% eq) in soft-water coastal rivers of North Carolina and Georgia. Highest concentrations of sulphate were recorded in some rivers of Colorado, Pennsylvania, Wyoming and Montana that receive coal-mining wastewater.

Alkaline earth metals, especially Ca^{2+}, were usually the dominant cations in studied rivers, while the percentage of Na^+ and K^+ was rarely high (Fig. 2). The ratio of Ca^{2+} and Mg^{2+} was especially high in rivers of medium conductivity (160–380 μS cm^{-1}) that drain carbonate bedrock (e.g. Ozark Plateaus and karst area in Georgia). The total concentration of Ca^{2+} and Mg^{2+} was, however, maximal in waters with the highest proportion of SO_4^{2-} among anions, mostly in rivers draining mining areas.

The highest concentrations of Na^+ and K^+ were observed in saline rivers of the Mississippi delta and western arid areas. A high proportion of Na^+ was also sometimes observed in the low-conductivity rivers of

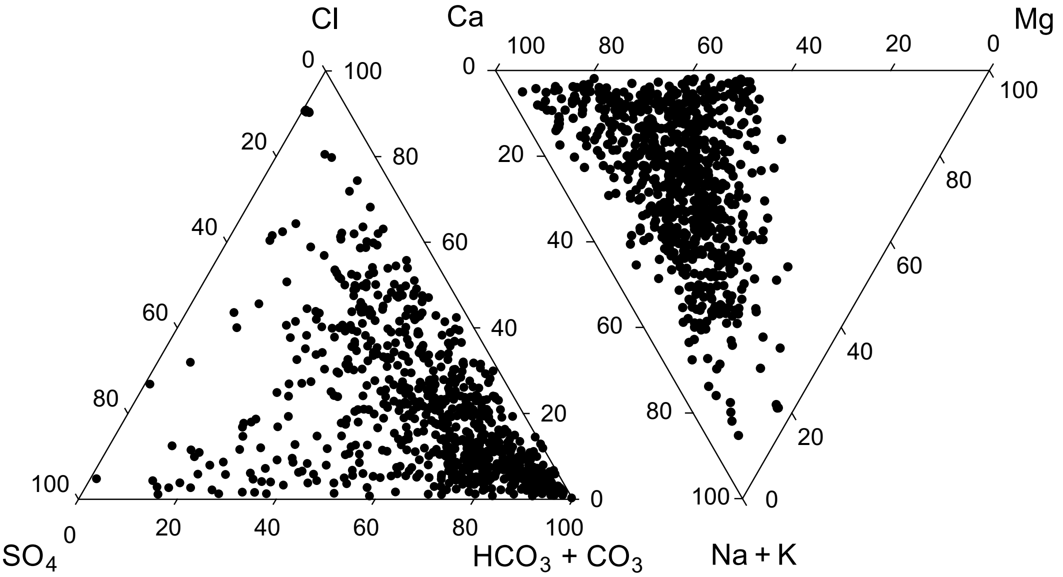

Fig. 2 Ternary diagrams showing ion composition in 807 NAWQA sampling sites.

Table 2 Correlation coefficients of conductivity and major ion concentrations in the 2674 sample NAWQA dataset. All correlations are significant at the $P < 0.01$ level

Parameter	$[HCO_3^- + CO_3^{2-}]$	$[Cl^-]$	$[SO_4^{2-}]$	$[Ca^{2+}]$	$[Mg^{2+}]$	$[Na^+]$	$[K^+]$
Cl^-	0.16	1					
SO_4^{2-}	0.31	0.32	1				
Ca^{2+}	0.71	0.28	0.75	1			
Mg^{2+}	0.67	0.52	0.74	0.74	1		
Na^+	0.27	0.91	0.56	0.38	0.65	1	
K^+	0.32	0.63	0.39	0.32	0.48	0.72	1
Conductivity	0.58	0.76	0.68	0.70	0.84	0.88	0.65

the eastern U.S. coast. K^+ was never a dominant cation – its ratio was highest in some dilute rivers of Washington, Alabama and Georgia.

There was no clear relationship between conductivity and dominant ions. Correlations between conductivity, $[Na^+]$, and $[Cl^-]$ are relatively high (indicating that highest values of conductivity were because of the increased concentration of these ions), but not much higher than between conductivity and other ions (Table 2). Relatively high correlation coefficients within sodium chloride and calcium carbonate/bicarbonate cation–anion pairs, combined with low correlation coefficients among them, indicate that the ratio of these salts forms a major gradient in ionic composition in the NAWQA dataset.

Community analysis

$[HCO_3^- + CO_3^{2-}]$ and $[Ca^{2+}]$, followed by conductivity and $[Mg^{2+}]$, explained the highest proportion of variation in diatom data (Table 3). Ion percentages explained less variation than ion concentrations, but nevertheless had a significant relationship with diatom assemblages when tested by permutation procedures ($P < 0.05$). Eigenvalues in all analyses were relatively low, but a moderate to high ratio of the first to the second eigenvalue indicated the important role of conductivity and concentrations of major ions in structuring diatom assemblages (Table 3).

Table 3 Results of CCA showing the strength of selected environmental variables. Only one environmental variable was used in each CCA

Variable	λ_1	λ_1/λ_2
Log_{10} conductivity ($\mu S\ cm^{-1}$)	0.189	0.47
$HCO_3^- + CO_3^{2-}$ (% eq)	0.089	0.23
Cl^- (% eq)	0.122	0.32
SO_4^{2-} (% eq)	0.049	0.12
Ca^{2+} (% eq)	0.086	0.22
Mg^{2+} (% eq)	0.054	0.13
Na^+ (% eq)	0.092	0.23
K^+ (% eq)	0.118	0.31
Log_{10} $[HCO_3^- + CO_3^{2-}]$ ($\mu eq\ L^{-1}$)	0.236	0.60
Log_{10} $[Cl^-]$ ($\mu eq\ L^{-1}$)	0.126	0.31
Log_{10} $[SO_4^{2-}]$ ($\mu eq\ L^{-1}$)	0.130	0.33
Log_{10} $[Ca^{2+}]$ ($\mu eq\ L^{-1}$)	0.201	0.51
Log_{10} $[Mg^{2+}]$ ($\mu eq\ L^{-1}$)	0.180	0.45
Log_{10} $[Na^+]$ ($\mu eq\ L^{-1}$)	0.144	0.36
Log_{10} $[K^+]$ ($\mu eq\ L^{-1}$)	0.135	0.33

λ_1, eigenvalue for axis 1; λ_2, eigenvalue for axis 2

Another CCA was conducted to explore the simultaneous effects of various ions on diatom assemblages. It employed only conductivity and ion ratios as environmental variables, because concentrations of specific ions were highly correlated with each other and conductivity (Table 1). This CCA showed that conductivity and the ratio of $Ca(HCO_3)_2 + CaCO_3$ to $NaCl + KCl$ were major factors explaining the structure of diatom assemblages (Fig. 3). The first four ordination axes were all significant ($P < 0.05$) and had eigenvalues of 0.23, 0.11, 0.07 and 0.05, respectively, thus indicating that the first two axes explained most of the variation in diatom data.

Fig. 3a shows that conductivity and the proportions of Ca^{2+}, $HCO_3^- + CO_3^{2-}$, Na^+, Cl^- and K^+ were highly correlated with the first two axes. Diatom taxa placed in the right upper quadrant of the first and second axes ordination plot (Fig. 3a), mostly species of *Eunotia*, are found in water low in alkaline (Ca^{2+}, Mg^{2+}) cations. Taxa in the lower right quadrant favour low conductivity waters but with a higher proportion of alkaline cations. Calciphilous species of *Cymbella* are found in the lower left quadrant of the ordination diagram. Diatoms with higher affinity for total salt content are placed in the left upper quadrant.

The third axis (Fig. 3b) can be interpreted as part of the variation in species composition along the gradient of monovalent–divalent cations (M : D) ratio. Another part of the variation along the M : D gradient was captured by the first, and especially, second axes, but that gradient also included the $(HCO_3^- + CO_3^{2-})$/

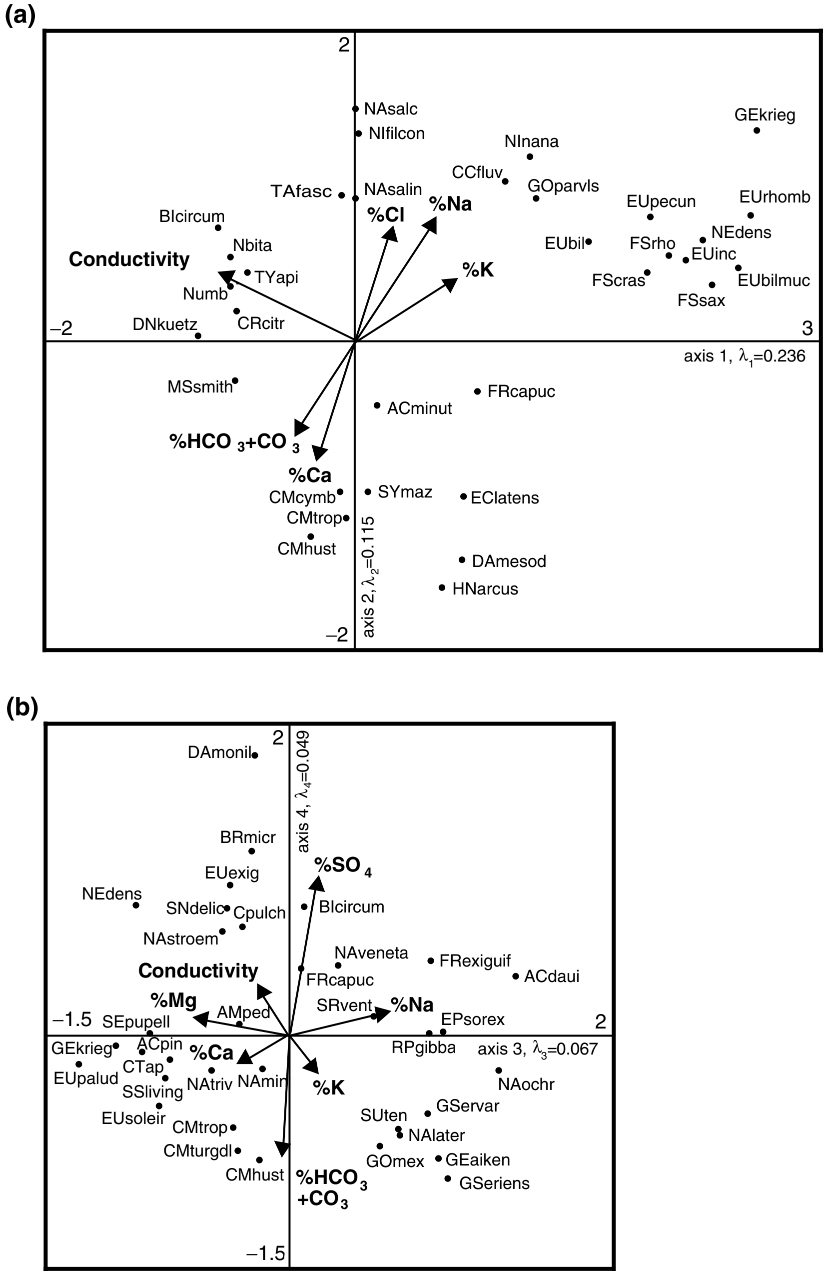

Fig. 3 Canonical correspondence analysis (CCA) diagrams showing environmental variables and diatom taxa centroids in the ordination space of the 1st and 2nd (A) and 3rd and 4th (B) CCA axes. Environmental variables that had low correlations with ordination axes are not shown. Taxa shown in the diagrams were found in at least 1% of all samples and either had high influence on the corresponding axes (8 species with highest fit) or extreme scores along corresponding axes (8 taxa with highest and 8 taxa with lowest scores). Taxa codes correspond to those in Table 4.

Cl^-ratio. The M : D gradient expressed along the third axis is a residual remaining after extraction of the stronger conductivity and $Ca(HCO_3)_2 + CaCO_3$ to NaCl + KCl gradients. In other words, species with high scores along the third axis can be found in waters with relatively high $\%Na^+$, even if the $\%Cl^-$ is low, and species with low scores favour waters with high $\%Mg^{2+}$ and $\%Ca^{2+}$, even if the $\%(HCO_3^- + CO_3^{2-})$ is low. The fourth axis can be interpreted as a gradient in $SO_4^{2-}/(HCO_3^- + CO_3^{2-})$ ratio (Fig. 3b). Species with high scores along this axis had high abundance in waters contaminated with mining discharge: they included halophilous (*Diatoma moniliformis, Biremis circumtexta, Ctenophora pulchella*) and acidophilous diatoms (*Brachysira microcephala, Eunotia exigua, Stenopterobia delicatissima*).

Species indicator values

Apparent optima of the most frequently occurring diatoms (found in at least 500 samples) are presented in Table 4. Optima are also shown for diatoms

Table 4 Position of 191 diatom taxa along gradients of conductivity, concentrations of major ions and ionic proportions. Taxa are in order of increasing conductivity optima. Conductivity optima (Opt.) and tolerance limits (low and high) are back transformed from weighted average and weighted standard deviation values of log-transformed conductivity (μS cm^{-1}). Optima for concentrations of major ions are calculated from weighted average values of log-transformed ion concentrations (μeq L^{-1}). Ionic proportion optima are weighted averages of per cent equivalents of total anions or cations. 'N occ.' is the number of samples in which the taxon occurred. Diatom taxa selected for the table were either common (found in at least 500 samples in the 2674 sample dataset) or had extreme optima among all taxa with occurrence reaching at least 1% of all samples in the 2674 sample dataset

		Conductivity (μS cm^{-1})			Anion optima (meq L^{-1})			Cation optima (meq L^{-1})				Anion optima (% eq)			Cation optima (% eq)				
Taxon name	Code	Opt.	Low	High	HCO_3 +CO_3	Cl	SO_4	Ca	Mg	Na	K	HCO_3 +CO_3	Cl	SO_4	Ca	Mg	Na	K	N occ.
Brachysira brebissonii Ross		40	21	76	0.16*	0.05*	0.05*	0.13*	0.08*	0.07*	0.01*	54	24	21	44	24	27	4.7	48
Eunotia tenella (Grun.) A. Cl.		48	23	100	0.17*	0.09*	0.04*	0.17*	0.08*	0.12*	0.02*	53	33	15	41	21	32	5.8	74
Frustulia saxonica Rab.	FSsax	50	26	97	0.17*	0.12	0.04*	0.12*	0.09*	0.15*	0.02*	50	38	13	32*	23	38**	6.7**	39
Eunotia bilunaris var. *mucophila* L.-B. & Nör.	EUbilmuc	66	35	125	0.13*	0.16	0.08	0.19*	0.13*	0.16	0.03	33*	41**	25	37*	24	32	6.8**	29
Eunotia rhomboidea Hust.	EUrhomb	66	34	127	0.11*	0.17	0.07*	0.18*	0.12*	0.16	0.04	32*	44**	24	36*	24	33	7.8**	75
Stauroneis livingstonii Reimer	SSliving	67	38	117	0.16*	0.15	0.03*	0.19*	0.14*	0.17	0.03	43	46**	12	36*	25	32	6.8**	30
Stenopterobia delicatissima (Lewis) Bréb.	SNdelic	68	33	143	0.10*	0.16	0.11	0.20*	0.13*	0.16	0.03	29*	39**	31**	37*	24	32	7.1**	34
Eunotia paludosa Grun.	EUpalud	69	46	102	0.14*	0.17	0.03*	0.22*	0.15	0.15	0.03	40*	48**	12	39*	26	28	6.9**	30
Encyonema latens (Krass.) Mann	EClatens	73	23	230	0.55	0.03*	0.16	0.50	0.20	0.13*	0.03*	70	6*	24	56	22	17	4.3	27
Navicula lateropunctata Wallace	NAlater	75	37	152	0.35	0.13	0.06*	0.25*	0.13*	0.19	0.04	62	26	13	40	21	32	7.0**	80
Geissleria cf. *kriegeri* (Krass.) L.-B. & Metzeltin	GEkrieg	76	45	130	0.12*	0.22	0.05*	0.22*	0.14*	0.19	0.05	31*	51**	18	35*	23	32	8.7**	53
Frustulia crassinervia (Bréb.) L.-B. & Kram.	FScras	79	42	147	0.23	0.16	0.06*	0.26*	0.13*	0.18	0.04	49	35	16	41	21	31	6.7**	157
Fragilariforma bicapitata (Mayer) Round & Will.		86	40	188	0.36	0.24	0.20	0.55	0.24	0.31	0.05	44	34	22	46	21	29	4.2	33
Eunotia naegelii Migula		89	39	200	0.18*	0.19	0.07*	0.29	0.15*	0.19	0.04	42	38	20	42	21	30	6.5**	102
Cymbella 'sp.1 JCK'	CM1JCK	89	43	186	0.62	0.10*	0.11	0.50	0.19	0.21	0.02*	70	14	16	52	21	24	3.0	95
Frustulia rhomboides (Ehr.) De Tony	FSrho	90	39	208	0.22	0.20	0.08	0.27*	0.15*	0.21	0.03	42	41**	17	39	21	33	6.0	165
Psammothidium helveticum (Hust.) Bukht. & Round		91	24	349	0.15*	0.18	0.10	0.23*	0.15	0.21	0.03	37*	43**	20	38*	21	36**	4.9	29
Eunotia flexuosa (Bréb.) Kütz.		94	30	295	0.26	0.19	0.05*	0.27*	0.13*	0.22	0.02*	49	38**	13	40	20	35**	4.7	46
Eunotia exigua (Bréb. ex Kütz.) Rab.	EUexig	94	39	229	0.15*	0.16	0.16	0.34	0.17	0.18	0.04	33*	33	34**	45	23	27	6	158
Eunotia incisa W. Sm. ex Greg.	EUinc	95	40	226	0.19*	0.21	0.09	0.27*	0.15*	0.22	0.03	37*	43**	20	38*	21	35**	5.5	143
Tabellaria flocculosa (Roth) Kütz.		95	36	248	0.25	0.09*	0.10	0.32	0.14*	0.15	0.02*	49	27	25	47	21	27	3.8	170
Neidium densestriatum (Østrup) Kram.	NEdens	97	58	164	0.12*	0.24	0.13	0.31	0.20	0.21	0.04	28*	42**	30**	40	25	28	6.5**	27
Hannaea arcus (Ehr.) Patrick	HNarcus	100	42	236	0.69	0.02*	0.12	0.59	0.18	0.11*	0.01*	77**	5*	18	63**	20	15	2.0	169
Neidium alpinum Hust.		101	49	209	0.19*	0.24	0.16	0.34	0.19	0.24	0.06	36*	37	28**	41	22	29	7.5**	57
Eunotia monodon Ehr.		102	51	203	0.31	0.22	0.07*	0.36	0.16	0.22	0.04	51	35	14	45	21	29	5.9	91
Diatoma mesodon (Ehr.) Kütz.	DAmesod	106	47	240	0.63	0.04*	0.13	0.57	0.19	0.14*	0.01*	71	8*	20	60**	21	17	2.1	167
Gomphonema olivaceiodes Hust.		107	54	214	0.77	0.03*	0.14	0.65	0.21	0.13*	0.01*	76**	7*	17	62**	20	15	2.1	122
Eunotia soleirolii (Kütz.) Rab.	EUsoleir	108	52	226	0.33	0.26	0.04*	0.39	0.21	0.23	0.04	50	38	12	44	24	26	6.6**	37
Stauroneis smithii var. *incisa* Pant.		109	53	226	0.28	0.18	0.14	0.39	0.19	0.20	0.05	47	28	25	46	22	25	6.6**	40
Cymbella aspera (Ehr.) Perag.		115	64	206	0.52	0.18	0.07*	0.39	0.22	0.31	0.04	63	25	12	39	23	33	5.1	35
Eunotia pectinalis var. *undulata* (Ralfs) Rab.		116	56	238	0.23	0.31	0.11	0.34	0.16	0.30	0.04	36*	44**	20	39*	19	37**	5.7	107
Geissleria aikenensis (Patr.) Torg. et Oliveira	GEaiken	119	68	208	0.68	0.14	0.07*	0.41	0.20	0.25	0.05	73	16	10*	44	22	28	5.7	50

Gomphonema rhombicum Fricke		119	53	265	0.92	0.09*	0.10	0.65	0.27	0.23	0.03*	77**	12	11*	53	23	22	2.7	124
Navicula longicephala Hust.		127	53	308	0.32	0.25	0.14	0.40	0.20	0.27	0.06	45	32	23	43	21	30	6.8**	90
Pinnularia appendiculata (Ag.) Cl.		129	41	398	0.33	0.31	0.22	0.48	0.27	0.36	0.07	39*	33	28	40	23	31	6.3	52
Achnanthes stewartii Patr.		134	40	451	0.48	0.26	0.15	0.42	0.26	0.33	0.04	53	29	18	39*	25	31	5.3	28
Achnanthidium 'sp. 10 NAWQA'		139	56	342	0.67	0.22	0.18	0.63	0.29	0.27	0.04	58	23	19	49	23	24	3.9	584
Achnanthes peragalli Brun & Heribaud		141	69	287	0.63	0.12	0.11	0.61	0.27	0.15*	0.03	68	18	14	54	25	17	3.1	34
Pinnularia intermedia (Lager.) Cl.		157	65	380	0.56	0.40	0.16	0.58	0.27	0.46	0.06	48	34	18	40	20	34**	5.4	61
Eunotia formica Ehr.		163	79	336	0.53	0.38	0.11	0.52	0.21	0.42	0.05	49	38	13	42	18*	36**	4.7	82
Fragilaria capucina Desmazières	FRcapuc	168	60	470	0.65	0.17	0.23	0.70	0.31	0.27	0.04	55	20	25	50	23	23	3.4	776
Stauroneis phoenicentron (Nitzsch) Ehr.		168	49	574	0.87	0.56	0.23	0.77	0.30	0.56	0.05	51	35	15	45	18*	34	3.4	35
Eucocconeis flexella (Kütz.) Cl.		185	88	389	0.81	0.11	0.22	0.89	0.30	0.21	0.02*	63	20	18	59**	20	19	1.7	37
Surirella tenera Greg.	SUten	189	66	541	1.08	0.19	0.17	0.80	0.36	0.48	0.08	68	19	13	46	21	29	4.9	26
Navicula viridula var. *linearis* Hust.		191	85	429	1.08	0.21	0.13	0.81	0.33	0.28	0.04	70	19	11*	51	22	24	3.8	147
Gomphoneis eriense (Grun.) Skv. & Meyer	GSeriens	192	99	372	1.19	0.11	0.14	0.76	0.35	0.38	0.07	78**	9.8	12	47	22	25	6.3	27
Synedra mazamaensis Sovereign	SYmaz	196	104	370	1.29	0.09*	0.31	1.02	0.36	0.24	0.03*	73	8*	19	59	20	18	1.9	45
Encyonema silesiacum (Bleisch) Mann		197	83	468	1.23	0.13	0.26	1.05	0.42	0.29	0.03	68	13	19	55	23	19	2.6	564
Nitzschia nana Grun.	NInana	201	60	676	0.44	0.50	0.22	0.61	0.34	0.55	0.08	40*	37	23	39*	21	34	6.3	61
Gomphonema apuncto Wallace		202	108	378	1.13	0.11	0.15	0.91	0.36	0.13*	0.03	73	13	14	59	24	14	2.8	79
Cymbella cymbiformis Ag.	CMcymb	204	112	369	1.58	0.06*	0.10	1.17	0.42	0.08*	0.02*	86**	6*	8*	66**	26	6*	1.7	55
Fragilaria vaucheriae (Kütz.) Petersen		209	79	555	1.07	0.18	0.28	0.97	0.44	0.35	0.04	62	17	21	51	24	22	3.0	1201
Encyonema minutum (Hilse) Mann	ECminu	209	81	545	1.04	0.22	0.27	0.97	0.42	0.34	0.04	61	19	20	52	23	22	3.1	1476
Gomphonema parvulum var. *parvulius* L.-B. & Reichardt	GOparvls	209	109	401	0.58	0.61	0.19	0.67	0.25	0.59	0.05	41	46**	13	39	15*	43**	3.4	26
Achnanthidium deflexum (Reim.) Kingston		211	97	456	1.42	0.12	0.17	1.11	0.48	0.16	0.03	75	9	16	57	27	13*	2.4	526
Navicula minuscula Grun.		212	85	526	1.29	0.09*	0.25	1.13	0.39	0.25	0.03	68	12	20	59	20	18	2.3	75
Fragilaria pinnata var. *lancettula* (Schum.) Hust.		216	89	528	1.52	0.13	0.22	1.02	0.53	0.35	0.05	76**	10	14	49	27	21	3	216
Geissleria decussis (Hust.) L.-B. & Metzeltin		220	83	583	1.29	0.28	0.23	1.06	0.46	0.38	0.05	66	18	16	51	23	22	3.7	654
Cymbella cf. *tropica* Kram.	CMtrop	221	143	343	1.69	0.11	0.14	1.36	0.39	0.12*	0.03	83**	8*	9*	68**	23	8*	2	63
Navicula cryptocephala Kütz.		222	88	562	1.12	0.29	0.23	0.98	0.45	0.36	0.05	63	21	16	50	24	23	3.8	1048
Brachysira microcephala (Grun.) Compère	BRmicr	225	61	832	0.57	0.17	0.34	0.91	0.44	0.26	0.03	48	17	35*	53	25	19	2.5	185
Surirella angusta Kütz.		225	86	593	1.14	0.27	0.26	1.00	0.48	0.36	0.06	62	19	18	49	25	22	4.3	546
Epithemia turgida (Ehr.) Kütz.		227	101	508	1.91	0.10*	0.16	1.33	0.59	0.18	0.04	81**	7*	11	57	28	13*	2.1	127
Achnanthidium minutissimum (Kütz.) Czarn.	ACminut	229	81	652	1.31	0.20	0.31	1.22	0.51	0.32	0.04	64	15	21	55	24	19	2.4	2019
Pinnularia acrosphaeria W. Sm.		234	100	551	1.08	0.42	0.13	1.04	0.31	0.50	0.06	61	26	13	53	17*	26	4.2	41
Navicula cf. *ochridana* Hust.	NAochr	237	91	614	1.52	0.24	0.36	1.07	0.41	0.70	0.08	66	15	19	45	19	32	3.7	49
Cymbella turgidula Grun.	CMturgdl	243	144	410	1.93	0.13	0.11	1.46	0.41	0.13*	0.04	86**	7*	7*	67**	24	8*	1.8	57
Reimeria sinuata (Greg.) Koc. & Stoermer		251	107	587	1.47	0.22	0.33	1.28	0.53	0.40	0.04	65	16	19	54	23	21	2.4	1385
Synedra ulna (Nitzsch) Ehr.		252	102	627	1.44	0.28	0.30	1.26	0.55	0.42	0.05	64	18	18	52	24	22	2.6	1311
Cymbella hustedti Krass.	CMhust	254	189	340	1.94	0.08*	0.11	1.69	0.35	0.09*	0.03*	88**	5*	7*	77**	17*	5*	1.3	48
Achnanthes rostrata Østrup		255	109	593	1.48	0.23	0.23	1.22	0.51	0.35	0.05	69	16	15	53	24	20	2.9	921
Gomphonema pumilum (Grun.) Reichardt		260	108	627	1.58	0.24	0.28	1.25	0.53	0.45	0.06	68	15	16	51	23	23	3.0	863
Cocconeis fluviatilis Wallace	CCfluv	261	98	692	0.59	0.63	0.30	0.63	0.39	0.71	0.08	39*	39**	22	35*	21	40**	4.5	83
Gomphonema sphaerophorum Ehr.		262	169	408	1.57	0.26	0.23	1.44	0.47	0.27	0.04	70	18	13	61**	21	16	2	64
Gomphonema angustatum Kütz.		264	106	659	1.31	0.20	0.28	1.21	0.54	0.30	0.04	65	16	19	54	25	18	2.9	637
Achnanthes exilis Kütz.		266	97	731	1.44	0.19	0.24	1.21	0.56	0.21	0.03	71	12	17	58	27	13*	2.2	47

Table 4 (*Continued*)

		Conductivity (μS cm^{-1})			Anion optima (meq L^{-1})			Cation optima (meq L^{-1})				Anion optima (% eq)			Cation optima (% eq)				
Taxon name	Code	Opt.	Low	High	HCO_3 CO_3	Cl	SO_4	Ca	Mg	Na	K	HCO_3 CO_3	Cl	SO_4	Ca	Mg	Na	K	N occ.
Epithemia sorex Kütz.	EPsorex	266	116	611	2.00	0.22	0.47	1.45	0.64	0.67	0.06	68	11	21	48	22	27	2.3	205
Cymbella delicatula Kütz.		269	135	533	1.75	0.10*	0.20	1.48	0.60	0.13*	0.03	78**	6*	16	63**	28	8*	1.6	204
Cocconeis placentula var. *lineata* (Ehr.) V.H.		270	111	655	1.64	0.31	0.33	1.35	0.61	0.49	0.05	65	18	16	51	24	23	2.3	1340
Staurosirella pinnata (Ehr.) Will. & Round		271	110	665	1.66	0.25	0.32	1.29	0.61	0.50	0.05	67	15	17	49	24	24	2.6	815
Epithemia adnata (Kütz.) Bréb.		279	104	746	2.11	0.17	0.21	1.59	0.75	0.29	0.04	76	13	11*	54	27	17	2	68
Gomphonema parvulum (Kütz.) Kütz.		284	101	794	1.33	0.39	0.34	1.21	0.55	0.53	0.06	59	22	19	48	23	25	3.4	1898
Achnanthes lanceolata (Bréb.) Grun.		286	114	719	1.52	0.30	0.32	1.27	0.60	0.47	0.05	65	17	17	50	24	22	2.9	1330
Nitzschia archibaldii L.-B.		288	114	728	1.51	0.38	0.37	1.31	0.57	0.57	0.07	61	20	19	49	23	25	3.3	726
Navicula submuralis Hust.		290	163	515	1.93	0.38	0.22	1.34	0.49	0.54	0.06	71	18	11*	50	21	27	2.4	28
Nitzschia sinuata var. *tabellaria* (Grun.) Grun.		294	155	557	1.87	0.21	0.32	1.69	0.52	0.24	0.05	72	11	17.4	64**	22	13*	2	164
Fragilaria exiguiformis L.-B.	FRexiguif	296	95	920	1.18	0.44	0.59	1.17	0.46	0.86	0.06	50	23	27	44.5	18	35**	2.6	61
Staurosira construens var. *venter* (Ehr.) Ham.	SRvent	300	109	822	1.60	0.31	0.44	1.36	0.62	0.66	0.07	61	17	22	47	22	27	2.9	617
Sellaphora seminulum (Grun.) Mann		305	131	714	1.42	0.43	0.31	1.22	0.57	0.55	0.06	60	23	17	48	23	26	3.2	706
Placoneis placentula (Ehr.) Hienzerling		308	157	607	1.55	0.52	0.42	1.58	0.47	0.69	0.07	57	23	20	53	17*	26	3.3	47
Melosira varians Agardh		309	138	690	1.66	0.36	0.36	1.40	0.70	0.49	0.06	64	18	18	50	26	22	2.7	1203
Gomphonema lingulatiforme L.-B. & Reich.		313	117	834	1.80	0.48	0.30	1.43	0.49	0.66	0.07	64	22	13.7	50	18*	28	3.3	130
Psammothidium lauenburgianum (Hust.) Round & Bukht.		317	159	631	2.88	0.25	0.30	1.94	1.33	0.34	0.04	81**	9	10*	52	36**	11*	1.3*	30
Navicula minima Grun.	NAmin	319	140	729	1.71	0.35	0.31	1.44	0.64	0.44	0.06	66	18	15	52	25	21	2.9	1672
Gomphonema mehleri Camburn		318	215	472	2.51	0.10	0.15	1.92	0.67	0.12*	0.04	85**	4*	11*	66**	29**	5*	1.4*	52
Gomphonema minutum (Ag.) Ag.		324	131	802	1.90	0.27	0.38	1.64	0.74	0.42	0.04	67	14	18	55	26	18	1.9	767
Cocconeis placentula var. *euglypta* Ehr.		326	146	726	2.00	0.30	0.34	1.57	0.71	0.47	0.06	70	14	16	52	25	20	2.4	1262
Nitzschia sinuata var. *delognei* (Grun.) L.-B.		335	231	485	2.48	0.19	0.30	1.76	0.75	0.33	0.04	80**	8*	12	57	26	16	1.6	25
Gomphonema mexicanum Grun.	GOmex	338	147	778	2.07	0.43	0.21	1.24	0.65	0.72	0.09	72	19	9*	44	23	29	3.5	35
Rhopalodia gibba (Ehr.) Müller	RPgibba	339	122	942	2.39	0.32	0.58	1.78	0.80	0.92	0.07	66	14	20	47	22	29	2.1	123
Navicula germanii Wallace		339	149	769	1.80	0.50	0.42	1.50	0.71	0.67	0.07	62	20	18	48	24	25	3.0	975
Sellaphora pupula (Kütz.) Mereschkowsky		342	143	820	1.74	0.42	0.42	1.52	0.65	0.64	0.07	61	20	19	49	22	25	3.1	1064
Ctenophora pulchella (Ralfs ex Kütz.) Will. & Round	Cpulch	342	163	716	0.86	0.67	0.53	1.18	0.57	0.70	0.06	41	32	27	45	22	30	2.7	66
Navicula stroemii Hust.	NAstroem	343	115	1021	1.98	0.20	0.65	1.79	0.98	0.30	0.03	65	8*	27	56	30**	12*	1.4*	26
Cymbella affinis Kütz.		347	170	708	2.28	0.21	0.41	1.95	0.76	0.37	0.05	70	10	20	58	25	16	1.8	870
Diatoma vulgaris Bory		355	188	670	2.10	0.35	0.48	1.75	0.80	0.56	0.05	66	15	19	52	25	21	2.1	693
Achnanthes exigua var. *elliptica* Hust.		359	207	622	1.67	0.78	0.54	1.77	0.59	0.82	0.11**	53	26	21.6	53	19	25	3.3	26
Diatoma moniliformis Kütz.	DAmonil	361	168	774	0.84	0.14	0.85	1.20	0.70	0.33	0.04	45	10	45**	52	30**	16	1.9	91
Nitzschia dissipata (Kütz.) Grun.		361	152	855	2.12	0.35	0.50	1.80	0.85	0.56	0.06	65	15	20	52	25	21	2.2	1324
Navicula menisculus Schumann		361	165	791	2.39	0.33	0.41	1.94	0.83	0.46	0.06	70	14	16	55	25	18	2.1	655
Navicula 'aff. *subminuscula* NAWQA EAM'		364	222	597	2.94	0.24	0.27	1.98	0.92	0.29	0.05	80**	9	11*	57	28	14*	1.6	33
Navicula capitata Ehr.	NAcapita	366	147	908	1.77	0.51	0.42	1.53	0.77	0.65	0.07	60	22	18	48	25	24	2.9	709
Nitzschia palea var. *tenuirostris* Grun.		368	159	853	1.93	0.47	0.41	1.64	0.97	0.55	0.06	64	20	16	49	29**	19	2.4	192

Caloneis bacillum (Grun.) Cl.		369	165	824	2.02	0.40	0.46	1.79	0.75	0.60	0.06	63	18	19	52	23	22	2.3	824
Navicula cryptotenella L.-B.		371	168	817	2.21	0.35	0.43	1.87	0.86	0.52	0.05	67	15	18	53	26	19	2.1	1620
Encyonopsis microcephala (Grun.) Kram.		380	169	857	2.20	0.23	0.40	2.20	0.76	0.35	0.04	67	10	23	62**	23	13*	1.5*	295
Rhoicosphenia curvata (Kütz.) Grun.		384	173	851	2.08	0.48	0.51	1.78	0.87	0.68	0.06	62	19	19	50	25	23	2.2	1548
Synedra delicatissima W. Smith		386	119	1253	1.95	0.33	0.10	1.96	0.50	0.56	0.03	68	12	20	60**	18	20	1.5*	33
Navicula symmetrica Patrick		388	172	877	2.18	0.50	0.51	1.74	0.86	0.79	0.07	63	18	19	48	25	24	2.7	608
Navicula capitatoradiata Germ.		390	195	782	2.33	0.36	0.49	1.96	0.90	0.52	0.06	67	14	19	54	26	19	2.1	1194
Navicula gregaria Donkin		392	169	910	1.95	0.58	0.53	1.70	0.86	0.76	0.07	59	21	20	48	25	24	2.4	1344
Nitzschia palea (Kütz.) W. Smith		398	170	933	2.08	0.53	0.55	1.82	0.87	0.77	0.08	60	20	20	49	24	24	2.7	1522
Diploneis parma Cl.		398	162	979	1.12	0.59	0.26	1.04	0.53	0.81	0.06	54	36	10*	40	19	38**	2.9	35
Nitzschia amphibia Grunow		400	201	794	2.26	0.51	0.45	1.87	0.81	0.69	0.07	65	19	16	51	24	23	2.5	1456
Navicula lanceolata (Ag.) Ehr.		406	196	843	1.94	0.59	0.63	1.83	0.92	0.81	0.06	56	21	23	49	25	24	2.0	679
Nitzschia inconspicua Grun.		407	167	995	2.07	0.55	0.65	1.77	0.88	0.92	0.08	58	20	22	47	24	27	2.5	1374
Nitzschia frustulum (Kütz.) Grun.		413	177	962	2.08	0.45	0.55	1.72	0.84	0.79	0.07	62	18	20	48	24	26	2.7	1153
Nitzschia heufleriana Grun.		416	215	805	2.56	0.35	0.71	2.11	1.08	0.72	0.05	65	12	23	50	26	22	1.5*	45
Amphora libyca Ehr.		416	188	918	2.38	0.47	0.53	2.05	0.92	0.67	0.07	64	17	19	52	25	21	2.3	582
Cocconeis pediculus Ehr.		422	223	798	2.59	0.41	0.62	2.26	1.03	0.61	0.06	65	15	20	54	25	19	1.8	969
Achnanthes pinnata Hust.	ACpin	424	200	895	3.18	0.79	0.59	2.52	1.39	0.68	0.06	67	20	13	51	29**	18	1.6	44
Diploneis pseudovalis Hust.		434	183	1026	2.70	0.70	0.48	2.39	0.63	0.99	0.06	65	20	16	56	17*	25	1.8	52
Denticula elegans Kütz.		436	226	838	2.48	0.30	0.87	2.59	0.86	0.55	0.07	62	10	28**	59	21	18	2.1	81
Nitzschia filiformis (W. Smith) V. H.		436	120	1581	1.20	0.80	0.57	1.26	0.69	1.19	0.09	47	30	23	41	20	36**	3.1	163
Navicula trivialis L.-B.	NAtriv	440	234	826	2.74	0.45	0.45	2.19	1.07	0.51	0.07	70	15	14	54	28	16	2.2	670
Surirella suecica Grun.		442	199	982	2.16	0.46	0.54	1.96	0.58	0.83	0.07	62	17	21	53	18*	27	2.9	32
Navicula reichardtiana L.-B.		442	225	867	2.68	0.39	0.59	2.31	1.08	0.56	0.06	66	14	19	54	26	17	1.7	764
Navicula lenzii Hust.		444	233	843	2.94	0.29	0.33	2.45	0.98	0.29	0.05	75	11	14	61**	26	11*	1.8	48
Achnanthes daui Foged	ACdaui	448	194	1033	2.56	0.37	1.09**	2.03	0.91	1.39	0.18**	58	11	32**	44	19	33	4.1	34
Navicula tripunctata (Müller) Bory		453	249	822	2.81	0.44	0.61	2.41	1.10	0.61	0.06	67	14	19	55	26	18	1.7	1039
Nitzschia acicularis (Kütz.) W. Smith		455	211	982	2.61	0.48	0.56	2.13	1.13	0.72	0.07	65	16	18	50	27	21	2.2	518
Nitzschia palea var. *debilis* (Kütz.) Grun.		460	214	989	2.56	0.52	0.61	2.06	1.12	0.79	0.08	64	17	19	48	27	22	2.6	595
Surirella minuta Bréb.		462	209	1023	2.49	0.50	0.61	2.13	1.11	0.65	0.07	63	17	20	51	27	20	2.4	661
Gomphonema olivaceum (Horn.) Bréb.		468	234	935	2.79	0.47	0.74	2.43	1.22	0.71	0.06	63	15	22	52	27	19	1.7	733
Fallacia pygmaea (Kütz.) Stickle & Mann		469	228	964	2.54	0.54	0.64	2.13	1.04	0.78	0.08	63	17	20	50	25	22	2.6	533
Amphora pediculus (Kütz.) Grun.	AMped	470	242	912	2.75	0.51	0.60	2.35	1.14	0.67	0.06	65	17	18	53	26	19	1.7	1626
Gomphonema affine Kütz.		481	275	839	2.96	0.50	0.48	2.32	1.29	0.51	0.05	73	15	13	53	30**	14	1.8	67
Navicula subminuscula Manguin		495	253	971	2.68	0.58	0.68	2.12	1.03	0.89	0.09	63	18	19	48	24	25	2.6	678
Craticula citrus (Krass.) Reichardt	CRcitr	499	356	700	3.62**	0.58	0.48	2.67	1.56**	0.79	0.09	74	13	13	51	30**	17	2.1	54
Surirella brebissonii Kram. & L.-B.		504	233	1090	2.02	0.71	0.86	2.06	1.72**	1.04	0.09	52	24	25	45	24	28	3	156
Nitzschia pusilla Grun.		505	165	1545	1.81	0.40	0.73	1.57	0.79	0.93	0.08	54	17	28**	45	23	30	2.9	88
Navicula ingenua Hust.		508	218	1183	1.71	1.00**	0.43	1.52	0.70	1.14	0.07	52	33	15	43	21	34	2.4	61
Amphora veneta Kütz.		515	246	1079	2.90	0.89	0.79	2.39	0.98	1.47**	0.11**	59	22	19	46	20	31	2.5	180
Navicula viridula (Kütz.) Kütz.		515	229	1159	2.74	0.65	0.86	3.08**	1.24	0.64	0.06	57	18	25	58	24	17	1.6	121
Mastogloia smithii Thwaites	MSsmith	519	249	1079	3.52**	0.48	0.53	2.88**	1.36	0.61	0.04	72	12	16	57	27	16	0.8*	38
Surirella brebissonii var. *kuetzingii* Kram. & L.-B.		520	254	1067	3.16	0.65	0.63	2.48	1.41	0.71	0.06	68	17	15	51	29**	18	1.4*	31
Nitzschia filiformis var. *conferta* (Reich.) L.-B.	NIfilcon	521	130	2089	1.29	1.29**	0.57	1.14	1.04	1.69**	0.11**	48	37	15	32*	23	42**	2.8	27

Table 4 (*Continued*)

		Conductivity (µS cm^{-1})			Anion optima (meq L^{-1})			Cation optima (meq L^{-1})				Anion optima (% eq)			Cation optima (% eq)				
Taxon name	Code	Opt.	Low	High	HCO_3 CO_3	Cl	SO_4	Ca	Mg	Na	K	HCO_3 CO_3	Cl	SO_4	Ca	Mg	Na	K	N occ.
Gyrosigma nodiferum (Grun.) Reimer		522	250	1091	3.03	0.75	0.80	2.52	0.80	1.32	0.07	63	19	18	51	17*	30	1.9	132
Simonsenia delognei (Grun.) L.-B.		524	304	902	3.27	0.70	0.53	2.45	1.55**	0.73	0.06	68	18	14	49	32**	18	1.5	181
Navicula caterva Hohn & Hellerman		525	292	942	3.52**	0.56	0.64	2.62	1.43**	0.72	0.06	69	15	16	52	28	19	1.4*	110
Navicula salinarum Grun.	NAsalin	527	243	1146	2.25	1.32**	0.68	1.90	1.16	1.24	0.08	51	32	17	42	26	29	2.6	51
Trybionella levidensis W. Smith		541	268	1091	2.89	0.92	1.03	2.44	0.95	1.47**	0.10**	56	22	22	46	20	32	2.4	125
Nitzschia elegantula Grun.		541	207	1416	2.79	0.39	1.07**	2.32	1.19	1.16	0.11**	57	14	29**	47	23	27	2.8	37
Navicula exilis Kütz.		547	308	973	3.28	0.81	0.63	2.54	1.58**	0.90	0.07	65	19	16	48	30**	20	1.8	261
Sellaphora pupula var. *elliptica* (Hust.) Bukht.	SEpupell	551	332	914	3.44**	0.63	0.64	2.85**	1.78**	0.64	0.07	68	16	16	52	32**	15	1.4*	28
Nitschia silicula Archibald		553	299	1026	3.74**	0.88	0.81	2.92**	1.58**	1.29	0.09	63	19	18	47	27	25	1.7	71
Nitzschia dubia W. Smith		553	225	1361	2.56	1.27**	0.57	1.81	1.28	1.37	0.07	56	29	15	40	26	32	1.6	30
Diploneis puella (Schumann) Cl.		569	290	1117	2.54	0.81	1.06**	2.53	0.9	1.3	0.1	54	21	26	49	20	29	2.6	158
Cymatopleura apiculata W. Smith	CTap	573	406	807	3.78**	0.77	0.67	2.99**	1.82**	0.68	0.07	70	16	14	52	32**	15	1.2*	54
Pleurosira laevis (Ehr.) Compère		573	292	1122	2.70	1.08**	0.80	2.28	1.50**	1.40	0.11**	53	27	21	41.2	27	30	2.4	44
Plagiotropis lepidoptera var. *proboscidea* (Cl.) Reimer		582	277	1225	3.01	1.47**	1.01	2.56	0.92	1.87**	0.11**	54	27	19	46	18*	34**	2.2	34
Navicula erifuga L.-B.		613	298	1262	2.92	0.66	0.96	2.55	1.38	1.15	0.10	58	17	24	47	26	25	2.2	625
Navicula recens L.-B.		614	345	1091	3.05	1.06**	1.21**	2.80	1.19	1.53**	0.09	55	22	24	47	22	29	1.9	319
Terpsinoe musica Ehr.		615	397	953	3.45**	1.47**	0.87	3.25**	0.71	1.88**	0.09	58	25	17	53	13*	32	1.9	35
Navicula sanctaecrucis Østrup		619	385	995	3.20	1.30**	1.16**	3.13**	0.93	1.83**	0.10**	55	24	22	50	17*	31	2.1	81
Denticula kuetzingii Grun.	DNkuetz	622	290	1334	3.66**	0.35	1.04**	2.80	1.52**	1.31	0.06	62	9*	29**	46	26	27	1.3*	34
Navicula veneta Kütz.	NAveneta	625	304	1285	2.95	0.48	1.08**	2.70	1.24	1.04	0.10	58	14	28**	50	24	24	2.5	442
Surirella brightwellii W. Smith		630	366	1081	3.22	1.11**	0.93	3.05**	1.22	1.69**	0.10	55	27	18	48	20	30	1.8	26
Amphora 'sp. 1 ANS WRC'		634	429	938	3.44**	1.65**	1.65**	3.69**	1.01	2.30**	0.11**	49	24	27	50	15*	33	1.9	37
Nitzschia liebetruthii Rab.		653	282	1510	2.13	0.73	1.01	2.28	0.81	1.21	0.11**	50	19	31**	50	19	29	2.7	66
Nitzschia supralitorea L.-B.		656	242	1778	2.70	0.69	0.84	2.20	1.20	1.54**	0.08	59	22	19	43	22	33	2	68
Tryblionella hungarica (Grun.) Mann		667	366	1213	3.38**	0.82	1.09**	3.07**	1.42**	1.29	0.10	58	18	24	49	24	25	1.9	265
Pleurosigma salinarum Grun.		673	454	998	3.62**	1.46**	1.21**	3.42**	1.22	1.97**	0.10**	56	24	20	49	18	31	1.7	38
Nitzschia solita Hust.		676	341	1340	3.05	0.57	0.93	2.63	1.37	1.09	0.10	60	15	25	48	26	24	2.3	212
Nitzschia bita Hohn & Hellerman	NBita	695	433	1117	3.86**	1.24**	1.27**	3.32**	1.05	2.22**	0.08	59	21	20	48	17*	33	1.4*	35
Tryblionella apiculata Greg.	TYapi	695	384	1259	3.55**	0.81	1.15**	3.05**	1.60**	1.30	0.08	59	17	23	48	26	25	1.6	325
Navicula salinicola Hustedt	NAsalc	697	150	3228	1.16	1.48**	0.80	1.47	1.14	2.31**	0.13**	38*	40**	22	34*	20	43**	2.8	29
Nitzschia reversa W. Smith		703	306	1614	2.62	0.91	1.34**	2.49	1.55**	1.77**	0.12**	49	21	30**	41	25	32	2.3	88
Tabularia fasciculata (Ag.) Snoeijs	TAfasc	719	181	2858	1.80	1.29**	0.60	1.69	1.17	1.47**	0.09	50	33	17	40	25	34	2.1	109
Nitzschia umbonata (Ehr.) L.-B.	Numb	759	476	1208	4.14**	0.96	1.14**	3.42**	1.98**	1.22	0.08	63	18	19	49	29**	21	1.2*	28
Biremis circumtexta (Meist. ex Hust.) L.-B. & Witkowski	BIcircum	902	461	1762	3.52**	0.62	2.07**	3.03**	2.20**	1.21	0.19**	53	12	35**	42	30**	24	3.4	36

* - extremely low, ** - extremely high optimum.

that had extreme (highest 15 and lowest 15) optima along any of the examined variables (conductivity, concentration and per cent equivalent of the seven major ions) and occurred in at least 25 samples. Conductivity optima for these diatoms ranged from 40 to 902 $\mu S\ cm^{-1}$. Most of the diatoms that exhibited highest affinity towards $Ca(HCO_3)_2$ water type had low (*Hannaea arcus, Diatoma mesodon, Gomphonema olivaceoides*) to moderate (*Gomphonema mehleri, Nitzschia sinuata* var. *delognei*) conductivity optima. Diatoms that had highest optima for the proportion of Na^+ and Cl^- either had very low (*Psammothidium helveticum, Eunotia flexuosa*) or relatively high conductivity optima (*Navicula salinicola*) thus reflecting two different types of rivers that had relatively high percentages of these ions: coastal soft-water rivers draining bedrock poor in alkaline cations and saline rivers of the arid zone. Many diatoms known as acidophilous taxa (*Eunotia bilunaris* var. *mucophila, E. rhomboidea, Stauroneis livingstonii, Stenopterobia delicatissima, Eunotia paludosa*) had relatively high optima for $\%Cl^-$ and $\%K^+$ and very low conductivity optima.

Discussion

Effect of conductivity

The relative position of species along the conductivity gradient in this study generally corresponds to the affinities reported by others. Many species with low conductivity optima were classified as halophobous by Kolbe (1927, 1932), Hustedt (1957) and other authors. Species commonly classified as halophilous or mesohalobous had relatively high, but probably underestimated, conductivity optima in our study. Species that are known to be abundant in brackish waters, such as *Diatoma moniliformis, Ctenophora pulchella* and *Tabularia fasciculata*, had apparent optima below 1000 $\mu S\ cm^{-1}$, which could be considered as a boundary between brackish and freshwaters. This underestimation of optima may be caused by the relatively low occurrence of brackish waters in our dataset and, hence, the truncated distribution of *T. fasciculata* and other species with relatively high position along the gradient of conductivity. The placement of optima of other brackish water species far from the high end of the conductivity gradient (i.e. *D. moniliformis, C. pulchella*) is more difficult to explain. Possibly, some populations in the NAWQA dataset could be freshwater ecotypes of those species. The apparent conductivity optima reported from some regional studies on U.S. rivers differ considerably from our results, but the rank of the diatom taxa on the conductivity scale is usually the same or nearly so. Optima reported by Bahls, Weber & Jarvie (1984) were generally much higher than those reported in the present study because conductivity was higher (median value 1752 $\mu S\ cm^{-1}$) in their Montana dataset. Conductivity optima reported by Leland, Brown & Mueller (2001) for California rivers were somewhat lower for the taxa with relatively low optima, and higher for diatoms with relatively high optima.

Effect of major ions

In most earlier studies of diatom species distribution in relation to salinity, the salinity gradient was primarily the result of a variation in concentration of a single salt, NaCl (Kolbe, 1927, 1932; Hustedt, 1957). As a result, it was difficult to distinguish the effects of specific ions from the overall effect of osmotic pressure. Hustedt (1957) noted that diatoms of continental waters respond mostly to osmotic pressure, and not the concentration of a particular salt. Experiments also showed that osmotic pressure in the medium is an important factor limiting growth of freshwater diatoms (Cleave, Porcella & Adams, 1981), or influencing their nutrient uptake (Tuchman, Theriot & Stoermer, 1984). As a result, conductivity or other measures of total ionic strength often explain much of the variation among diatom assemblages.

The importance of ionic composition to diatom distributions became obvious when datasets including various water types were studied. Investigations by Blinn (1993), Fritz, Juggins & Battarbee (1993), Gasse, Juggins & Ben Khelifa (1995), and Cumming *et al.* (1995) elucidated the importance of ionic composition in accounting for differences in diatom assemblages in saline lakes. Inclusion of different water types in river datasets revealed the importance of water chemistry for diatom community structure in lotic environments (e.g. Cholnoky, 1968; Sabater & Roca, 1992; Ziemann, 1997). Laboratory data provided additional evidence that concentration of specific ions influences growth of diatoms (e.g. Kopczyńska, 1979; Rao, Duraisamy &

Kannan, 1983; Saros & Fritz, 2000, 2002). Patrick & Reimer (1966), Ziemann (1971, 1997), Sabater & Roca (1992) , Round & Bukhtiyarova (1996), and Pipp (1997) pointed out the great difference between diatom communities in calcareous and calcium-poor rivers. In our study, the gradient of (Ca^{2+}) and ($HCO_3^- + CO_3^{2-}$) was the strongest among all variables related to major ions. We were able to distinguish species at the lower end of the conductivity gradient that had either high or low affinity towards calcium bicarbonate type of water. Not surprisingly, species with known low pH optima (*Eunotia* and *Frustulia* spp.) had lower optima for [Ca^{2+}] and [$HCO_3^- + CO_3^{2-}$] than alkaliphilous species of the genera *Gomphonema, Gomphoneis, Cymbella,* and diatoms *Hannaea arcus* and *Diatoma mesodon*. Sabater & Roca (1992) noted that calcareous springs in the Pyrenees were dominated by various species of *Cymbella,* along with *Denticula tenuis* and *Achnanthes minutissima*. In our dataset, the species with highest affinity towards calcium also belonged mainly to the genus *Cymbella* (Table 3, Fig. 3a). Calciphilous *Cymbella* and *Gomphonema* also have relatively high optima for [$HCO_3^- + CO_3^{2-}$], and it is difficult to distinguish the effect of that factor from the effect of [Ca^{2+}]. Some studies have shown that calcium affects diatom motility (Cohn & Disparti, 1994) and adhesion to surfaces (Cooksey & Cooksey, 1988), but exact physiological mechanisms responsible for the higher or lower affinity of diatoms to calcium (or the other alkaline cations) are still not known. Furthermore, concentration of divalent cations (Ca^{2+} and Mg^{2+}) is highly correlated with the amount of dissolved HCO_3^- and pH. It is not clear which of these factors has the greatest effect on the growth of diatoms.

Species with relatively high per cent equivalent optima for Mg^{2+} (*Bizemis circumtexta, Nitzschia umbonata, Cymatopleura apiculata, Sellaphora pupula* var. *elliptica, Navicula exilis, Simonsenia delognei*) were found mostly at the high end of the conductivity spectrum. Many diatoms with relatively high optima for per cent of base cations had low optima for %Na^+ or %K^+ and vice versa, once again confirming the observation that M : D ratio is an important factor affecting diatoms.

The position of diatom species along the [Cl^-] gradient in our study generally corresponds to the relative ranking of those species along this gradient given by Kolbe (1927, 1932), Hustedt (1957), and van Dam *et al.* (1994). Apparent chloride optima for diatoms in the dataset of 257 dilute lakes of the north-eastern U.S.A. (Dixit *et al.*, 1998) are, in general, lower than [Cl^-] optima in our study because of the lower [Cl^-] range of the former dataset. The highest optima for [Cl^-] and [Na^+] in the NAWQA dataset were observed in species with high conductivity optima (Table 4). When, however, the proportion of these ions was considered, the highest %Na^+ and %Cl^- optima were observed among species with either highest or lowest conductivity optima. Many of the species of *Eunotia, Stauroneis* and *Frustulia* had relatively high optima for the proportion of Na^+ and Cl^- in accordance with dominance of these ions in some dilute rivers of eastern coastal areas. Unlike species with high conductivity and high NaCl proportion optima, these diatoms also had relatively high %K^+ optima. Dionisio-Sese & Miyachi (1992) showed that chloride ions could be toxic to some freshwater algae because they inhibit carbonic anhydrase, an enzyme responsible for the hydration of carbon dioxide during photosynthesis. Our results confirm that the effect of Cl^- on diatom community composition is certainly different from the effect of total ionic strength.

The highest [SO_4^{2-}] optima were found in species with high conductivity optima (*Bizemis circumtexta, Nitzschia reversa*), but high per cent equivalent of SO_4^{2-} was favoured also by other diatoms such as *Diatoma moniliformis, Brachysira microcephala* and *Eunotia exigua*. In the coal-mining region of Montana, according to Bahls *et al.* (1984), diatoms with highest [SO_4^{2-}] optima were *Amphora coffeaformis, Diatoma tenue* (*D. moniliformis* accordingly to the drawing on p. 44), *Cymbella pusilla, Diploneis pumila* var. *smithii, Epithemia adnata, Navicula cincta* var. *rostrata, N. cryptocephala* var. *veneta, N. pavillardii, Nitzschia amphibia, N. closterium, N. obtusa, Rhopalodia gibba, Synedra famelica, S. fasciculata*. It is significant that, in the Montana dataset, increased conductivity was most often associated with Na_2SO_4 pollution, and that most of the mentioned species inevitably had high optima for all three parameters: Na^+, SO_4^{2-} and conductivity. There is little certainty which factor in particular was responsible for their competitive advantage in polluted rivers. We did not encounter many diatoms characteristic of sulphate-rich North American lakes (Fritz *et al.*, 1993; Cumming *et al.*, 1995), presumably because of the low representation of naturally highly mineralised sulphate-rich rivers in the NAWQA study. On the contrary, most of the rivers with high %SO_4^{2-} in our dataset had an increased conductivity and [SO_4^{2-}] because of mine drainage pollution. Sulphates in mine drainage often cause a significant decrease of water pH. In those cases, acidophilic diatom flora consisting mostly of *Eunotia*, *Frustulia* and *Pinnularia* develop despite relatively high total ionic content of the water (Hancock, 1973; Verb & Vis, 2000). High variation in diatom assemblages associated with elevated sulphate concentration is certainly because of a combined response of diatoms to the concentration of SO_4^{2-}, water pH and total mineral content.

Use of the autecological data

Optima presented in Table 4 are based on samples collected from a variety of habitats, from rivers ranging widely in size, slope and geographical location. All these factors undoubtedly introduce noise in the species response to ions. Nevertheless, the autecological characteristics calculated from the NAWQA dataset are more representative for most U.S. rivers than optima derived from datasets with limited number of observations. These autecological data are useful for the purposes of water quality assessment and further understanding of the ecology of diatoms.

Our results demonstrate that diatom assemblages are distributed continuously along gradients of conductivity and major ions. For practical application of the weighted average values to ecological assessments, the taxa could be assigned to categories according to their affinities. For example, conductivity range could be divided into low, medium and high-conductivity waters or into more finely defined categories. Sets of categories could be established to best meet the needs of individual studies. Differences in the proportion of individual diatoms in the categories could be used to assess differences among samples from different sites or between time periods. In the present paper, we preferred not to simplify autecological data by converting weighted average values to an arbitrarily chosen ordinal scale. The combination of optima presented in Table 4 could be considered as the optimal ionic composition of river water for each taxon. Monitoring the changes in the ionic composition could be carried out by simple observation of shifts in the dominant taxa or by inferring ion concentrations or conductivity using reported optima and some numerical procedure, for instance weighted averaging. Community analysis presented here shows that concentrations of the specific ions explain a higher proportion of variation in the diatom data than ionic proportions. This is mainly because the proportion of individual ions is usually important over a limited range of salinity or osmotic pressure. Therefore, ionic proportion optima are most meaningful when applied in conjunction with conductivity or other measure of the total salt content.

Future work on ecology and taxonomy of diatoms in North America will undoubtedly refine the data presented here. Creation of regional calibration datasets will make it possible to develop finely tuned models to quantitatively infer conductivity and ion concentrations, as is now often performed for lakes (e.g. Fritz *et al.*, 1993; Cumming *et al.*, 1995). The results obtained in this study also show the significant value of large-scale monitoring programmes, such as NAWQA, for obtaining autecological data for organisms important in biological monitoring.

Acknowledgments

This research was supported by the U.S. Geological Survey NAWQA Program through a cooperative agreement with The Academy of Natural Sciences. We thank C. Couch for her guidance. We are grateful to L. Bahls, T. Clason, W. Cody, K. Manoylov, L. Marr, E. Morales, C. Reimer, N.-A. Roberts, and D. Winter who analysed diatom samples, and to F. Acker, P. Cotter, and K. Sprouffske, who managed the Phycology Section database and assisted with technical aspects of data analysis.

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(Manuscript accepted 01 April 2003)