

Diatom metrics for monitoring eutrophication in rivers of the United States

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Abstract

Two major arguments in favor of using diatoms in water-quality assessments are that their distributions are cosmopolitan and their ecology is well studied. If these assumptions are true, diatom-based monitoring tools could be considered universal and used in any geographic area. Indeed, some diatom metrics based on species indicator values developed in Europe are often used in North America and many other parts of the world. There is considerable evidence, however, that diatom metrics are less useful when applied in a geographic area other than where species relations with environmental characteristics were originally studied to construct the metrics. We used U.S. Geological Survey National Water-Quality Assessment program data to create diatom metrics for monitoring eutrophication, and show here that these metrics provide better assessments in U.S. rivers than similar metrics developed for European inland waters. We also demonstrate that metrics developed by studying diatom–nutrient relationships on the continental-scale can be further refined if combined with regional-scale studies.

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1. Introduction

Diatoms are widely used to monitor river pollution because they are sensitive to water chemistry, especially ionic content, pH, dissolved organic matter, and nutrients. Wide geographic distribution and well-studied ecology of most diatom species are cited as

major advantages of using diatoms as indicator organisms (McCormick and Cairns, 1994). These assumptions imply that diatom-based water-quality assessment tools should have universal applicability across geographic areas and environments. There is evidence, however, that diatom metrics or indices developed in one geographic area are less successful when applied in other areas (Pipp, 2002). This is due not only to the floristic differences among regions, but also to the environmental differences (Kelly et al., 1998) that modify species responses to water-quality characteristics.

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The most commonly used sources of information on autecology of diatom species are diatom floras and compilations of numerous literature sources, such as those published by Lowe (1974), Beaver (1981), and van Dam et al. (1994). Since no formal quantitative procedure was used to assign species to ecological categories (e.g., oligo-, meso-, or eutraphentic) in those studies, they are essentially expert opinions. Such summaries of large amounts of information scattered in small-scale observational or experimental studies represented the most practical approach to quantify diatom autecology before large-scale consistent diatom datasets and appropriate numerical techniques became available. Recent developments of such techniques make it possible to use quantitative parameters of species distributions as measures of autecological characteristics. This type of approach is used increasingly often to characterize species responses to water-quality parameters (e.g., Rott et al., 1997; Kelly and Whitton, 1995; Pan et al., 1996; Winter and Duthie, 2000; Soininen and Niemelä, 2002; Potapova et al., 2004).

Various environmental agencies in the U.S. use diatoms as indicators of river health, usually relying on European studies as a major source of information about diatom ecology. van Dam et al. (1994), whose classification of diatoms into trophic categories is most commonly used in bioassessment studies (e.g., Fore, 2002; Fore and Grafe, 2002), pointed out, however, that their classification was “rather qualitative” and intended for use in The Netherlands. At the same time, large-scale monitoring programs carried out in the U.S. collect large amounts of information on water chemistry and diatoms in rivers of North America that might serve as a source of more objective information on diatom autecology. In particular, the U.S. Geological Survey National Water-Quality Assessment (NAWQA) program is gathering a nationwide set of diatom and nutrient data because nutrient enrichment is considered to be one of the main causes of river impairment in the U.S. The aim of our study was to determine whether quantitative data on diatom–nutrient relationships in U.S. rivers might be used to develop metrics better suited for use in the U.S. than metrics based on European studies. To this end, the NAWQA data were used to determine which diatom species were the best indicators of nutrients in U.S. rivers and a series of metrics were calculated based on

the relative abundance of these indicator species. Then abilities of these NAWQA metrics and similar European metrics to discriminate between low- and high-nutrient sites on U.S. rivers were compared.

2. Material and methods

2.1. Data sources

Two main sets of data were used in this study. One was necessary to identify diatom species indicative of river nutrient status and to develop metrics. Another independent set of data was needed to test these metrics. Like any other ecological models, metrics can be best validated by tests against independent data not used in building the model.

The data used to develop metrics were diatom counts and chemistry data downloaded from <http://water.usgs.gov/nawqa> on May 15, 2004. These data represented the NAWQA samples collected from 1993 to 2001 from 1240 river sites throughout the continental U.S. Algal samples were collected from hard substrate (rocks or submerged wood), most often during low-flow conditions, usually in summer or early autumn (Gurtz, 1993; Porter et al., 1993). Laboratory methods used for algal identification and enumeration are described in Charles et al. (2002). Samples were analyzed at the Patrick Center for Environmental Research of The Academy of Natural Sciences, Philadelphia (ANSP), the University of Louisville, Michigan State University, and by independent contractors. Water chemistry samples were analyzed at the USGS National Water Quality Laboratory, Lakewood, CO (Fishman, 1993). Total phosphorus (TP) and total nitrogen (TN) concentrations measured at 798 sampling sites within 14 days before algal sampling were used.

Algal and water chemistry data used to create an independent dataset to test the metrics were collected by the Environmental Protection Agency (EPA) Mid-Atlantic Highlands Streams Assessment (MAHA) program. The MAHA data were downloaded from the EPA website <http://www.epa.gov/emap/html/data1/surfwatr/data/ma9396.html> on June 26, 2004. Samples were collected from first- to third-order Mid-Appalachian streams from April 1993 to September 1996, according to protocols by Lazorchak et al. (1998). The

data for 397 sites located in the “Ozark, Quachita-Appalachian Forests” ecoregion were used.

2.2. National and regional datasets

To allow comparisons of the discriminative ability of diatom metrics based on datasets of different spatial extent, the national-scale NAWQA dataset was subdivided into smaller-scale (“regional”) datasets. The main goal in delineating the individual regional datasets was to limit environmental and floristic variation in the data. The EPA “nutrient” ecoregions were used as basic spatial units. “Nutrient” ecoregions are aggregations of Omernik’s level three ecoregions (Omernik, 1995) suggested by the EPA as a spatial framework to investigate impacts of nutrient enrichment on freshwater ecosystems throughout the U.S. (<http://www.epa.gov/waterscience/criteria/nutrient/ecoregions>). All 14 EPA “nutrient” ecoregions could not be used as spatial units, however, because the number of sites available in some ecoregions was limited. Therefore, some “nutrient” ecoregions were combined to obtain sufficiently large datasets. To do this, non-metric multidimensional scaling (NMS) was used to identify which “nutrient” ecoregions were relatively similar in diatom species composition. Those which had a low number of sites, were geographically adjacent, and were located relatively close to each other in the ordination diagrams were combined. Two ordinations were used to make decisions about combining “nutrient” ecoregions: one with the dataset that included all 1240 sampling sites (one randomly selected

sample per site), and another with a dataset that included only the 428 “less impacted” sites. These “less impacted” or reference sites were selected using the following criteria: percentage of agricultural land in the watershed <50%, percentage of urban land <5%, percentage of watershed occupied by mines and quarries <0.5%, $TP \leq 10 \mu\text{g L}^{-1}$, and $TN \leq 0.2 \text{ mg L}^{-1}$. The rationale for using reference or “less impacted” sites as a separate dataset was to delineate groups of sites and ecoregions that were relatively homogeneous in natural stream diatom assemblage composition. The national-scale diatom dataset was subdivided into five regional-scale datasets (Fig. 1), which corresponded to five groups of EPA “nutrient” ecoregions. Each group included at least 50 reference sites and at least 100 non-reference sites.

2.3. Indicator species lists

Several approaches were used to determine which diatom species were best indicators of nutrients. An indicator species analysis (Dufrene and Legendre, 1997) was carried out to identify which species were associated with the most nutrient-poor and the most nutrient-rich sites. This method searches for species, which not only have the highest specificity (mean relative abundance), but also the highest fidelity (frequency of occurrence) to a certain group of samples. All diatom samples that had corresponding $TP \leq 10 \mu\text{g L}^{-1}$ were designated as “low-TP” samples, those with $TP \geq 100 \mu\text{g L}^{-1}$ as “high-TP” sites, those with $TN \leq 0.2 \text{ mg L}^{-1}$ as “low-TN”

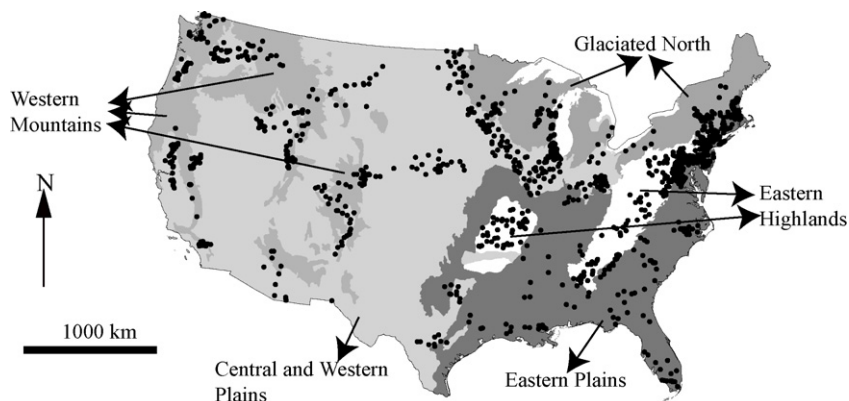


Fig. 1. Map showing 1240 sampling sites and aggregations of ecoregions into five groups based on diatom assemblage similarity, geographic proximity, and number of diatom samples available for analysis.

samples, and those with $TN \geq 3 \text{ mg L}^{-1}$ as “high-TN” samples. This classification is arbitrary and based on the chemical analyses detection limits ($10 \mu\text{g L}^{-1}$ for TP and 0.2 mg L^{-1} for TN) and the goal to have similar number of sites within low- and high-nutrient categories. For indicator species analysis, 1141 diatom samples from 798 sites where nutrients were measured within 14 days of algal sampling were used. The number of samples was higher than the number of sites because at 248 sites samples were collected two or three times, once a year. Indicator species analysis was carried out with PC-ORD/4, MjM Software, Gleneden Beach, OR.

Indicator species analysis selects as the best indicators taxa that are common in the dataset, and ignores relatively rare taxa. To identify less common species that might also be good indicators, TP and TN abundance weighted (WA) means (“optima”) and standard deviations (“tolerances”) were calculated

and examined. The following criteria were used to include species in the indicator list: species occurrence in at least five samples, WA optima either in the lowest (for low-nutrient indicators) or highest (for high-nutrient indicators) quartile of the species list, and tolerance-to-optimum ratio below 3.

2.4. Calculation and comparison of metrics

The following metrics were calculated using the indicator species list (Table 1): relative abundance (%) of diatoms assigned to categories “low-TP” (LP), “high-TP” (HP), “low-TN” (LN), and “high-TN” (HN), and an index related to ratio of high-nutrient to low-nutrient indicators. This index for total phosphorus indicators was calculated as:

$$RP = \frac{10HP}{HP + LP}.$$

Table 1
List of metrics based on relative abundance of diatom indicator species

Group of metrics based on	Metric	Abbreviation
List of NAWQA regional indicator species	% low-TP indicators	LPr
	% high-TP indicators	HPr
	Ratio of high/low-TP indicators	RPr
	% low-TN indicators	LNr
	% high-TN indicators	HNr
	Ratio of high/low-TN indicators	RNr
List of NAWQA national indicator species	% low-TP indicators	LPn
	% high-TP indicators	HPn
	Ratio of high/low-TP indicators	Rpn
	% low-TN indicators	LNn
	% high-TN indicators	HNn
	Ratio of high/low-TN indicators	RNn
Combined list of NAWQA regional and national indicator species	% low-TP indicators	LPr+n
	% high-TP indicators	HPr+n
	Ratio of high/low-TP indicators	RPr+n
	% low-TN indicators	LNr+n
	% high-TN indicators	HNr+n
	Ratio of high/low-TN indicators	RNr+n
List of indicator species by van Dam et al. (1994)	% oligotraphentic	
	% oligo-mesotraphentic	
	% mesotraphentic	
	% meso-eutraphentic	
	% eutraphentic	
	% hypertraphentic	
	% oligotraphentic + oligo-mesotraphentic (VDoligo)	VDoligo
% eutraphentic + hypertraphentic	VDeu	
Ratio of high/low nutrient indicators	VDr	

The index for total nitrogen indicators was calculated as:

$$RN = \frac{10HN}{HN + LN}$$

The factor of 10 was used to scale the ratio from 0 to 10, a range often used for water-quality indices. These metrics were calculated using various sets of indicator species: national-scale indicators, regional-scale indicators and combined lists of national-scale and regional-scale indicators (Table 1). In a few cases, national-scale and regional-scale indicator assignments were contradictory. For example, a species might have been assigned to the high-TP category on the national list and to the low-TP category on a regional list. In these cases, preference was given to the national-scale assignment when combining both lists.

To compare NAWQA metrics with similar metrics based on diatom indicator values published by van Dam et al. (1994), the relative abundance of diatoms that were assigned by these authors to various trophic categories (Table 1) was determined. The relative abundances of diatoms in categories “oligotraphentic” plus “oligo-mesotraphentic” (VDoligo) and “eutraphentic” plus “hypertraphentic” (VDeu), and an index related to their ratio:

$$VD_r = \frac{10VDeu}{VDeu + VDoligo}$$

were also calculated.

The ability of different metrics to discriminate low- and high-nutrient sites was compared by visually inspecting the box plots showing distribution of metric values in three categories of sites, designated as low-nutrient ($TP \leq 10 \mu\text{g L}^{-1}$ or $TN \leq 0.2 \text{ mg L}^{-1}$), high-nutrient ($TP \geq 100 \mu\text{g L}^{-1}$ or $TN \geq 3 \text{ mg L}^{-1}$), and intermediate ($TP 10.1\text{--}99.9 \mu\text{g L}^{-1}$ or $TN 0.21\text{--}2.99 \text{ mg L}^{-1}$). The overlap of or distance between the interquartile ranges (Klemm et al., 2003) was used to judge which metrics discriminated better between these categories of sites. Statistical tests of differences between median values of metric values between site categories were always highly significant (Mann–Whitney test, $P < 0.01$).

3. Results

3.1. Regionalization

NMS ordinations (Fig. 2) showed that five ecoregion groups varied in their relative homogeneity. For instance, ecoregions forming the group “Eastern Plains” appeared to be more diverse than other groups because their centroids were located further apart than ecoregion centroids in other groups. This heterogeneity may be partly a function of the different number of sites representing each

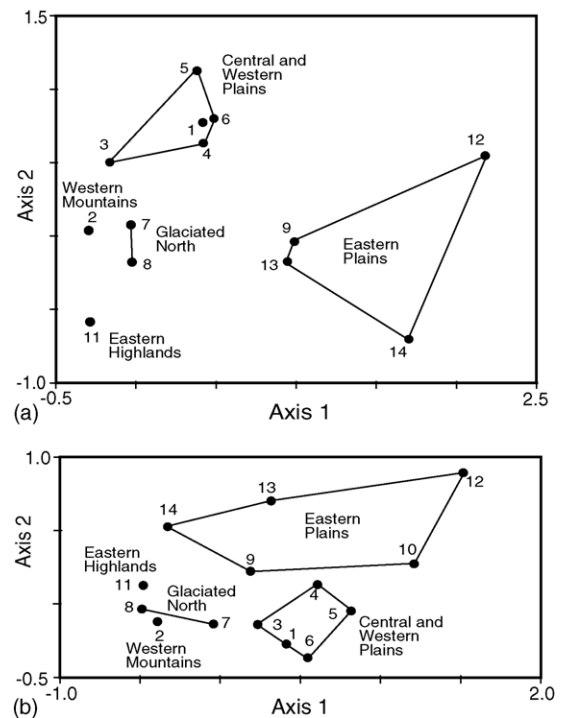


Fig. 2. NMS ordinations of 428 “reference” sites (a) and of all 1240 sites (b). Diagrams show positions of “nutrient” ecoregion centroids and their aggregation into five groups based on criteria described in the text. “Nutrient” ecoregions are: (1) Willamette and Central Valleys, (2) Western Forested Mountains, (3) Xeric West, (4) Great Plains Grass and Shrublands, (5) South Central Cultivated Great Plains, (6) Corn Belt and Northern Great Plains, (7) Mostly Glaciated Dairy Region, (8) Nutrient Poor Largely Glaciated Upper Midwest and Northeast, (9) Southeastern Temperate Forested Plains and Hills, (10) Texas–Louisiana Coastal and Mississippi Alluvial Plains, (11) Central and Eastern Forested Uplands, (12) Southern Coastal Plain, (13) Southern Florida Coastal Plain, and (14) Eastern Coastal Plain. No “reference” sites were available in “nutrient” ecoregion 10.

“nutrient” ecoregion. Some ecoregions in the “Eastern Plains” group were represented by a very small number of sites, and therefore could appear as very different from other ecoregions by pure chance. Conversely, centroids of “nutrient” ecoregions 2 (Western Forested Mountains), 7 (Mostly Glaciated Dairy Region), 8 (Nutrient Poor Largely Glaciated Upper Midwest and Northeast), and 11 (Central and Eastern Forested Uplands) clustered together, showing the relative similarity of diatom assemblages in these nutrient-poor regions. These ecoregions were, however, kept in three separate groups based on geographic position because there were relatively large numbers of observations in these areas.

3.2. Indicator taxa

There were 1246 diatom taxa in the national dataset of 1141 samples. Our analysis determined 371 of these as possible indicators of low or high nutrient concentration (Appendix A at <http://diatom.acnatsci.org/autecology>). Of the 83 taxa that were identified as indicators of high-TP in the national-scale NAWQA dataset, van Dam et al. (1994) listed 52 as high-nutrient indicators (meso-eutrathentic to hypertrathentic) and two (*Planothidium robustum* and *Nitzschia palea* var. *debilis*) as low-nutrient indicators (oligotrathentic). Of the 67 taxa that were identified as indicators of low-TP in the national-scale dataset, 25 were listed as oligo- to mesotrathentic, and two (*Cymbella affinis* and *C. cistula*) as eutrathentic. Of the 67 taxa that were identified as indicators of high-TN in the national-scale NAWQA dataset, 40 were listed as meso-eutrathentic to hypertrathentic, and three (*Nitzschia gracilis*, *N. palea* var. *debilis* and *Navicula pseudoventralis*) as oligo- to mesotrathentic. van Dam et al. (1994) listed only 17 of these 67 taxa as obligatory or facultative nitrogen-heterotrophs, and 30 as nitrogen-autotrophs. Of the 74 taxa that were identified as indicators of low-TN in the national-scale NAWQA dataset, only 23 were listed as oligo- to mesotrathentic, and 10 as meso-eutrathentic or eutrathentic.

Lists of indicator species derived from analysis of regional datasets were often considerably different from the national list, and only a few species were consistently identified as nutrient indicators in all datasets. These were very common diatoms: *Achnanthis minutissimum*, *Brachysira microcephala*,

Encyonopsis microcephala (low nutrient indicators), *Cyclotella meneghiniana*, *Navicula subminuscula*, *N. veneta*, and *Nitzschia amphibia* (high nutrient indicators).

3.3. Diatom metrics

In all five ecoregion groups, the NAWQA-based metrics separated low- and high-nutrient sites much better than metrics based on the van Dam et al. (1994) indicator species list, judging by the difference between 25th and 75th percentile values of metrics in low- and high-nutrient sites. Box plots in Figs. 3–6 show values of metrics in the “Western Mountains” and “Eastern Highlands” ecoregion groups. Relative abundances of oligotrathentic and oligo-mesotrathentic diatoms from van Dam’s list were very low in the NAWQA samples (Figs. 3–6). Therefore, ratios of eu- and hypertrathentic to oligo- and oligo-mesotrathentic diatoms discriminated poorly among low- and high-nutrient sites. In most cases, relative abundances of diatoms categorized as mesotrathentic or meso-eutrathentic by van Dam et al. (1994) did not show any relationship with nutrient concentrations. Discriminative abilities of regional, national, and “combined” (based on regional + national indicators) NAWQA metrics were similar.

Table 2 shows that NAWQA-based metrics always correlated more strongly with nutrient concentrations than corresponding metrics derived from van Dam et al.’s (1994) list.

Comparison of metrics calculated for the independent (MAHA) set of samples from Mid-Atlantic streams (Fig. 7) showed that NAWQA metrics based on the low-nutrient indicator taxa discriminated between low- and high-nutrient sites located on these streams better than analogous metrics derived from van Dam et al.’s list.

4. Discussion

4.1. Which metrics discriminate better between low- and high-nutrient sites and why?

Our results show that metrics created specifically for U.S. rivers are better suited for water-quality assessment of those rivers than metrics developed for

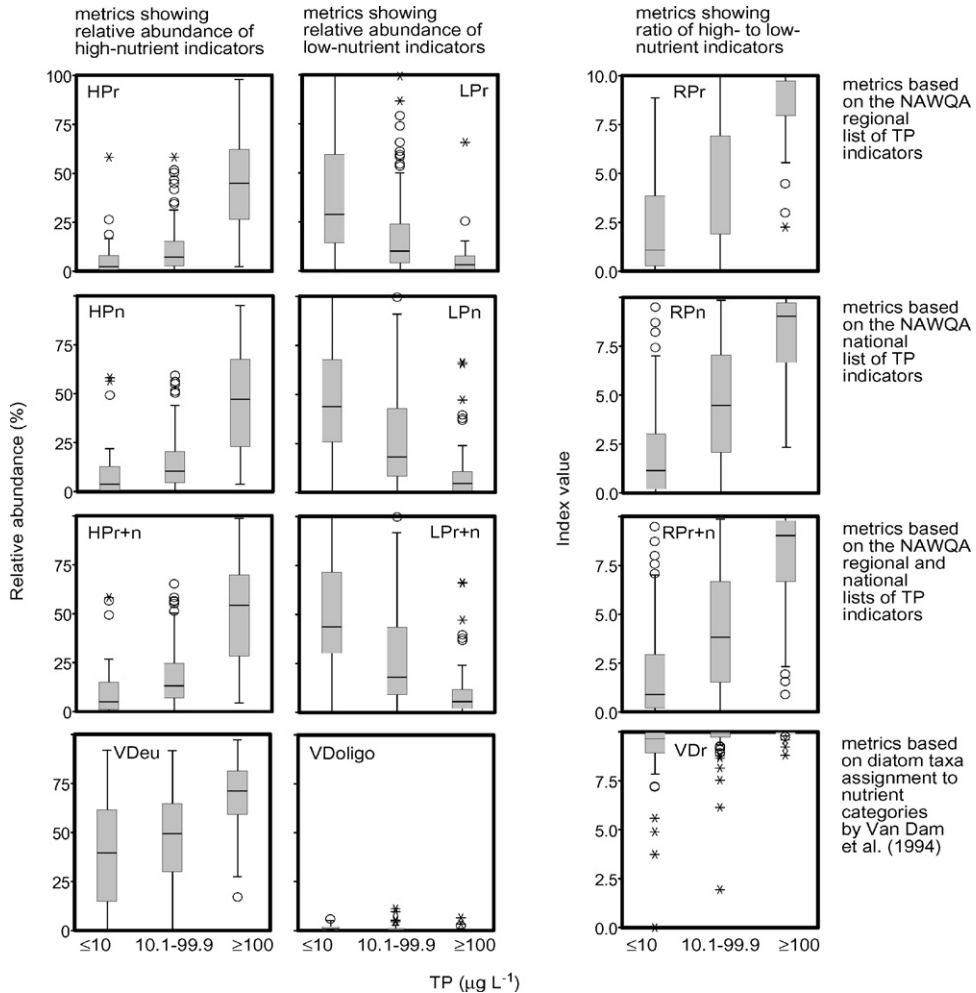


Fig. 3. Values of trophic diatom metrics for 209 sites in the “Western Mountains” ecoregion grouped into 3 TP categories. Metric abbreviations are given in Table 1. The gray bars in each box plot show the 25th and 75th percentiles of the data, the black bar inside the gray bar shows the median, the whiskers mark 1.5× interquartile range, circles show outliers between 1.5× and 3.0× interquartile range, and stars show extreme values outside 3.0× interquartile range.

other geographic areas. This conclusion is consistent with findings of several authors that diatom indices/metrics developed in certain parts of Europe are not effective when used in other areas of the same continent (Kelly et al., 1998; Pipp, 2002; Rott et al., 2003). Also, the national-scale U.S. metrics can be improved if they are tailored for particular regions. Although apparent discriminative powers of our NAWQA-based regional, national, and “combined” metrics were quite similar, it is important to keep in mind that the “combined” metrics were based on the

largest number of indicator taxa, and therefore should be more reliable when used on independent datasets.

A floristic difference between continents is the most obvious reason for better predictive abilities of NAWQA metrics in U.S. rivers. Box plots in Figs. 3–7 show that the relative abundance of diatoms considered as low-nutrient indicators in Europe is quite low in American rivers, and therefore, the metrics based on percentages of low-nutrient taxa from Van Dam et al.’s list do not discriminate well between nutrient-poor and nutrient-rich sites in the U.S. The

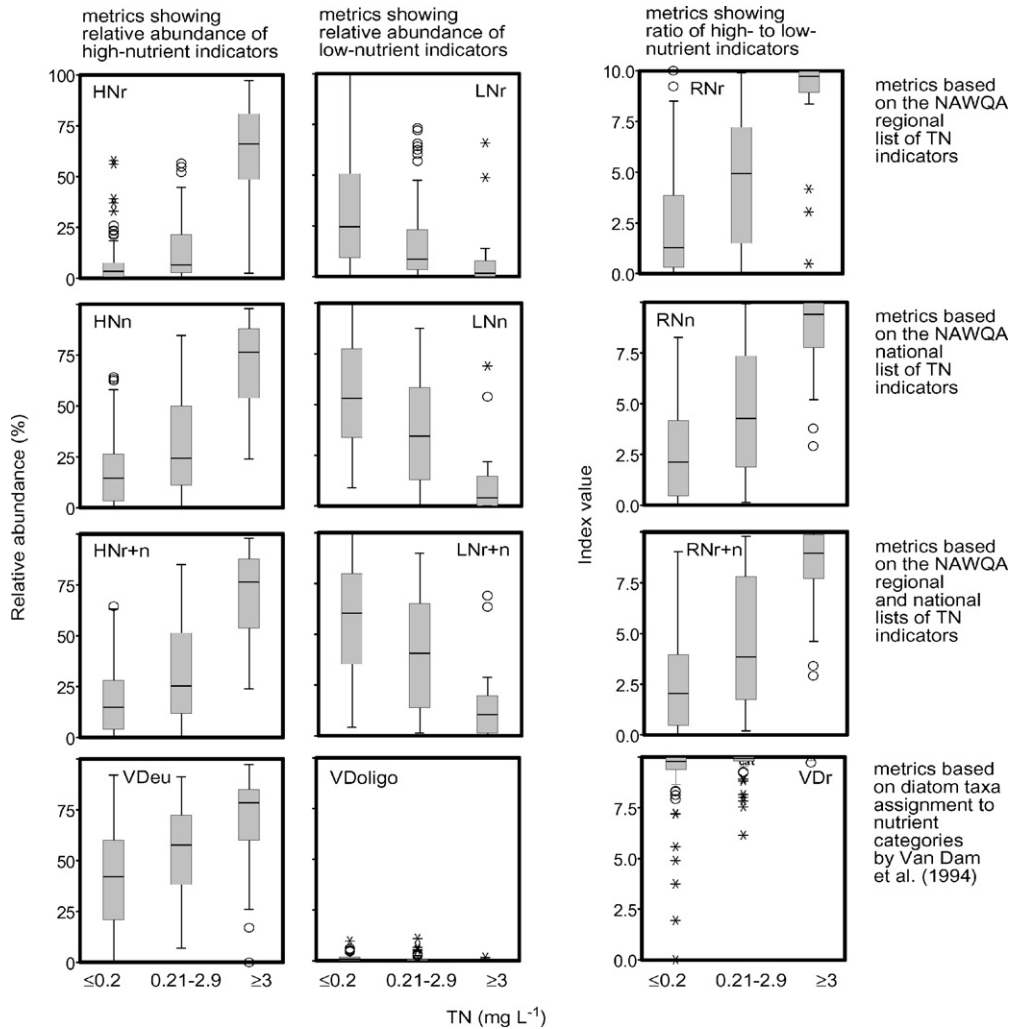


Fig. 4. Values of trophic diatom metrics for 209 sites in the “Western Mountains” ecoregion grouped into 3 TN categories. Metric abbreviations are given in Table 1. Box plot symbols as in Fig. 3. Fig. 4. Theoretical graphs and data plots of (a) u_w/U_h , (b) z_0/h , and (c) d_0/h vs. A for MODIS/IGBP land cover type grasslands.

relative abundance of European low-nutrient indicators also consistently correlates more weakly with nutrient concentrations in U.S. datasets. It is thus not advisable to use European indicators of low nutrients for monitoring U.S. rivers.

European high-nutrient indicator taxa are, on the contrary, quite abundant in U.S. rivers (Figs. 3–7). Discriminative power of metrics based in the high-nutrient indicators from van Dam et al.’s list is weaker, however, than that of the NAWQA metrics based on high-nutrient indicators, partly because European

high-nutrient indicators are often abundant even in low-nutrient U.S. rivers.

Besides floristic differences, the NAWQA indicator species list differs from that of van Dam et al.’s in ecological characterization of many, even common, diatoms. One striking difference is the placement of two extremely common taxa, *Achnanthes minutissimum* and *Synedra ulna* in the category of “low-nutrient” indicators in the NAWQA national and several regional lists, while van Dam et al. consider these taxa to be indifferent to nutrients (eurytraphen-

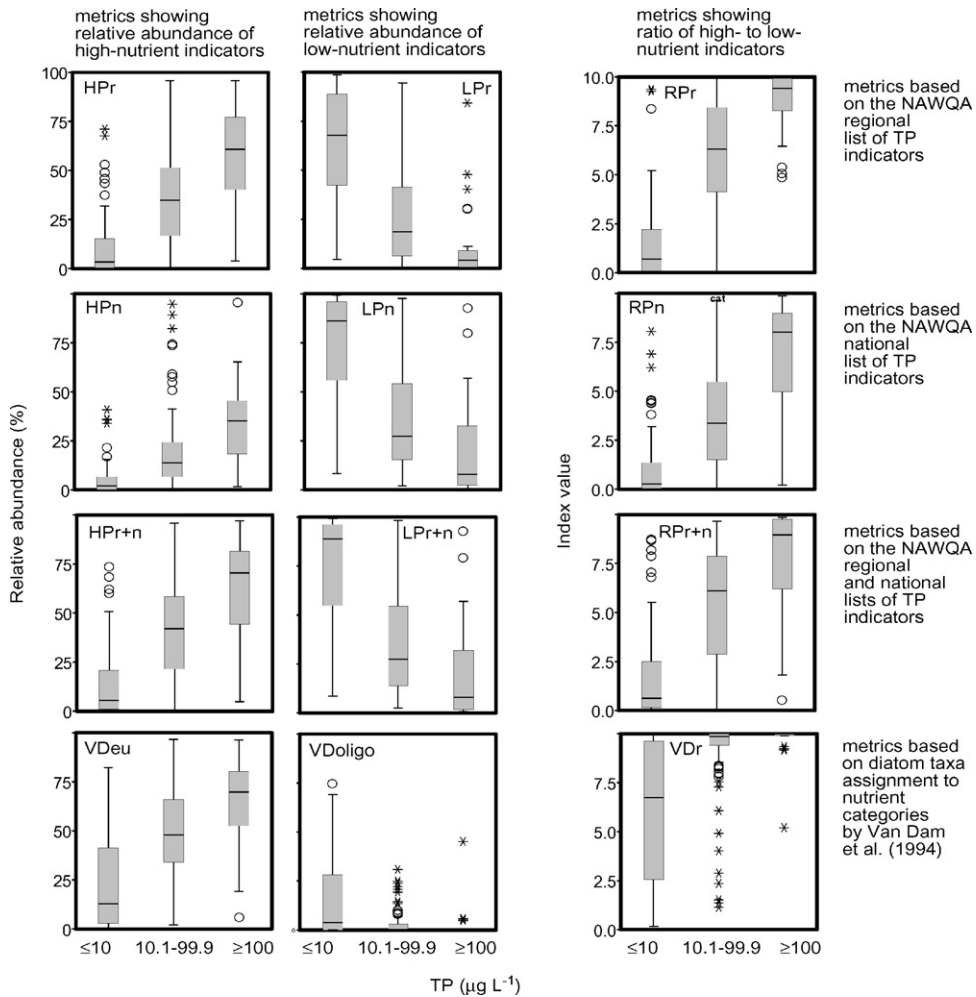


Fig. 5. Values of trophic diatom metrics for 138 sites in the “Eastern Highlands” grouped into 3 TP categories. Metric abbreviations are given in Table 1. Box plot symbols as in Fig. 3.

tic). Although these diatoms are reported from almost every survey of freshwater algae, the information about their distribution in relation to nutrients or about their responses to nutrient enrichment is often inconsistent. In experimental studies, absolute abundance of *A. minutissimum* has been found to respond positively to nutrients, in particular to nitrogen additions (e.g., Carrick et al., 1988; Fairchild et al., 1985), while in many observational studies relative abundance of this taxon was found to decrease with nutrient enrichment (Kelly and Whitton, 1995; Pan et al., 1996; Rott et al., 1997; Soininen and Niemelä,

2002). Stoermer’s (1980) characterization of *A. minutissimum* as “apparently tolerant of nutrient addition, but also quite abundant in more oligotrophic regions” effectively summarizes our current knowledge about the relation of this taxon to nutrients. The same can be said about *S. ulna*, which is also sometimes reported as having a relatively low nutrient optimum (Kelly and Whitton, 1995; Soininen and Niemelä, 2002), but occasionally as a high-nutrient indicator (Rott et al., 1997). Such widely distributed taxa as *A. minutissimum* or *S. ulna* might in fact be a mix of several species, which are difficult to separate

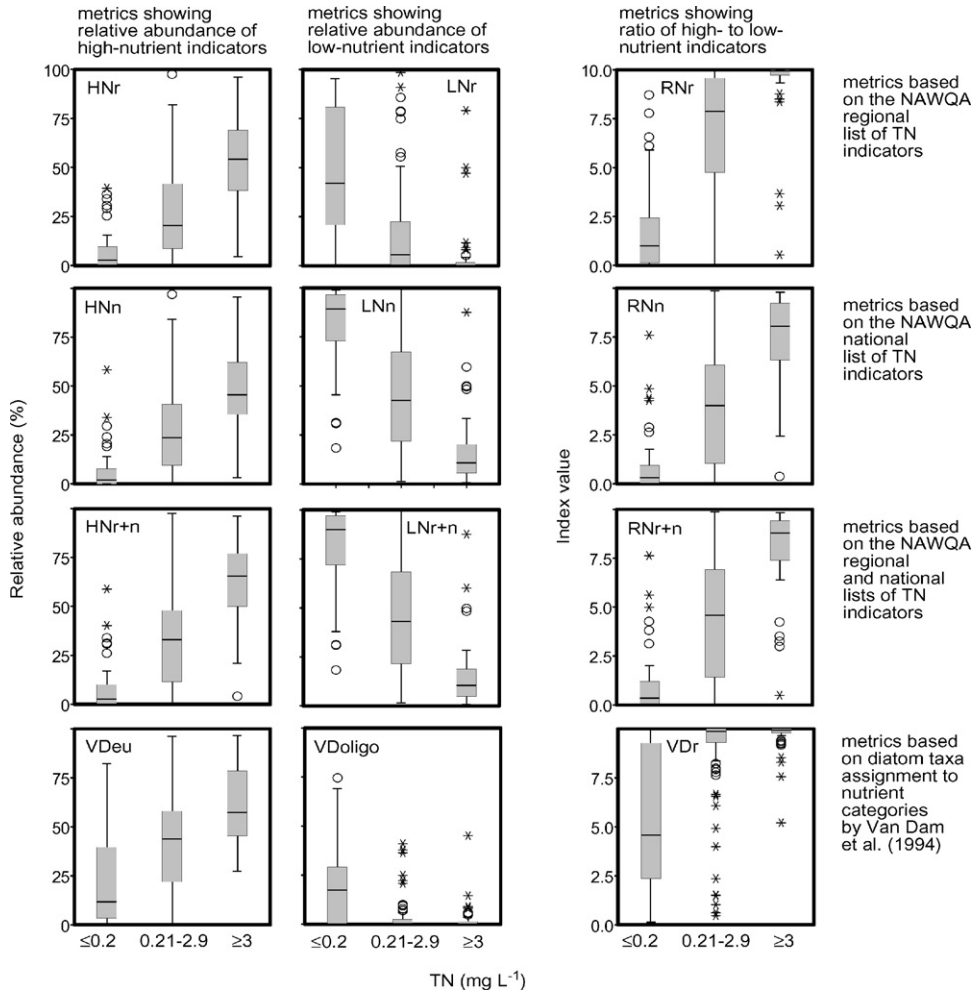


Fig. 6. Values of trophic diatom metrics for 138 sites in the “Eastern Highlands” grouped into 3 TN categories. Metric abbreviations are given in Table 1. Box plot symbols as in Fig. 3.

because there are relatively few distinguishing morphological characters. The presence of several indistinguishable species or ecotypes might explain conflicting information on the ecology of these taxa and the better performance of locally adjusted diatom metrics in comparison with “global” metrics.

4.2. What should be done to further improve diatom metrics?

Although the NAWQA dataset of diatom and nutrient data for 798 sites appears to be quite large, it is in fact too small to develop accurate metrics for all

regions of a country the size of the U.S. The number of sites in regional datasets used to study diatom distributions in relation to nutrients varied between 94 and 266. This is barely enough to characterize the distribution of the most common taxa, and clearly not sufficient to determine ecological properties of relatively rare diatoms across diverse and extensive geographic regions. In comparison, data from 1332 sites were used to develop diatom metrics and indices in France (Prygiel and Coste, 1996), from 671 sites in Austria (Rott et al., 2003), and from 553 sites in Japan (Watanabe et al., 1988). van Dam et al. (1994) combined data from hundreds of literature sources and

Table 2

Spearman correlation coefficients between diatom metrics (abbreviations in Table 1) and nutrient (TP or TN) concentrations in the five regional NAWQA datasets

Nutrient metric	Western Mountains	Central and Western Plains	Glaciated North	Eastern Plains	Eastern Highlands
TP					
LPn	−0.52	−0.52	−0.71	−0.53	−0.63
HPn	0.60	0.55	0.62	0.49	0.54
LPr	−0.52	−0.49	−0.75	−0.57	−0.62
HPr	0.63	0.53	0.68	0.57	0.62
LPn+r	−0.51	−0.53	−0.72	−0.58	−0.64
HPn+r	0.64	0.55	0.69	0.54	0.61
VDoligo	−0.30	−0.08	−0.12	−0.02	−0.35
VDeu	0.41	0.43	0.55	0.44	0.56
TN					
LNn	−0.52	−0.40	−0.71	−0.20	−0.67
HNn	0.55	0.56	0.73	0.27	0.66
LNr	−0.49	−0.43	−0.72	−0.40	−0.61
HNr	0.52	0.54	0.62	0.34	0.66
LNn+r	−0.50	−0.44	−0.72	−0.37	−0.68
HNn+r	0.54	0.57	0.75	0.34	0.70
VDoligo	−0.25	0.01	−0.14	−0.18	−0.37
VDeu	0.40	0.40	0.58	0.27	0.52

their own numerous observations made in The Netherlands, to assign diatom taxa to ecological categories. Correlations between metrics or indices and nutrient concentrations in test sites located in the same geographic areas for which metrics were developed were strong. For example, the correlation coefficient between the Austrian Trophic Index and TP in Austria was 0.85 (Rott et al., 2003). The correlation between the DAIpo index and TP in Japanese streams was approximately 0.70–0.80 (Watanabe et al., 1988). We think that better coverage (more sites per area) would further increase discriminative abilities of our metrics because autecology of more diatom species could be quantified.

Combining several datasets produced by different institutions or researches might provide a good way to increase the number of samples available for particular geographic regions and types of rivers. Such work, however, would be complicated by the taxonomic inconsistencies that exist between different datasets.

Lack of proper taxonomic treatment of many diatom taxa, even the most common ones, is another reason why diatom metrics do not reach higher potential. Lumping of several similarly looking taxa into one “morphospecies” diminishes discriminative ability of diatom metrics, while detailed taxonomic

and ecological studies allow recognition of taxa with good indicator properties (Round, 2004).

Metrics described in the present study were based on relative abundance of all diatoms found in a sample, benthic as well as planktonic. It could be argued that planktonic diatoms should be excluded from metric calculations because they are not part of a benthic assemblage and may reflect water quality upstream of the sampling site rather than local conditions. Nevertheless, inclusion of planktonic diatoms increases the number of indicator species and, therefore, robustness of the metrics. Future comparisons of metrics including and excluding planktonic diatoms will determine which metrics discriminate better between sites and are most useful for water-quality assessment.

One more way to increase the power of diatom metrics and indices is to improve the environmental data that are used to quantify diatom ecology. For instance, when studying diatom–nutrient relationships it is desirable to measure nutrient concentrations several times during the time of diatom assemblage development. Unfortunately, such data are rarely available from large-scale river monitoring programs.

The metrics presented in this paper are based on a rather crude assignment of taxa to only two categories:

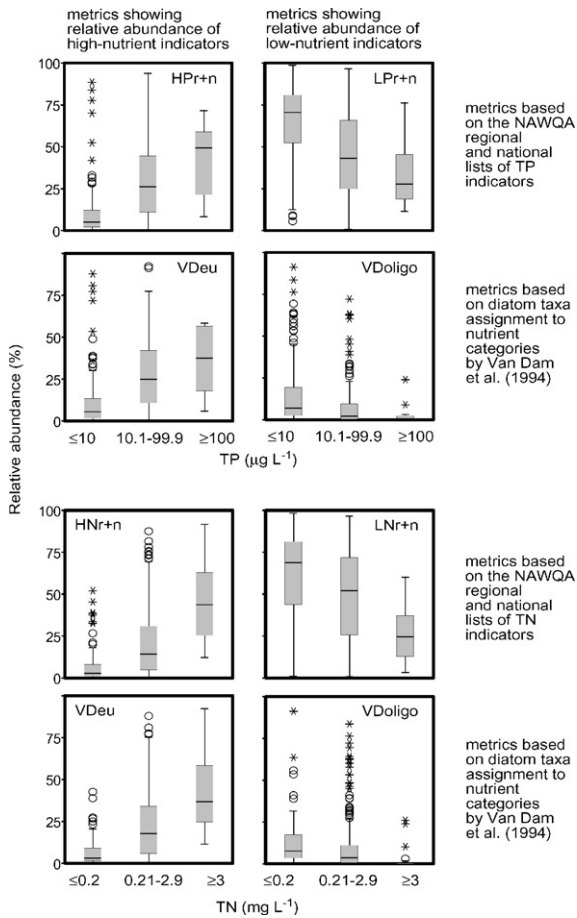


Fig. 7. Values of trophic diatom metrics for 397 Mid-Atlantic stream sites (MAHA dataset) grouped into 3 TP and 3 TN categories. Metric abbreviations are given in Table 1. Box plot symbols as in Fig. 3.

high- and low-nutrient indicators. This simplistic approach was chosen instead of a more advanced method, such as inference modeling, because of data limitations. One limitation was the rather high TP and TN detection limit ($10 \mu\text{g L}^{-1}$ and 0.2 mg L^{-1} ,

respectively) that made it impossible to accurately model species responses across full ranges of nutrient concentrations. Too many samples had corresponding nutrient values below these detection limits. Lower nutrient detection limits would allow better characterization of species ecology and therefore better performing metrics.

We conclude that to improve water-quality bioassessments, autecology-based diatom metrics should be developed (1) by quantifying species distributions along environmental gradients, (2) using datasets representative of the areas or river types where the metrics will be applied, (3) by assuring high-quality taxonomic identifications, and (4) by collecting environmental data that accurately represent conditions during algal growth.

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Appendix A

Diatoms indicating low (–) or high (+) nutrients in U.S. rivers. Species were included in this list as a result of two analyses. First, indicator species analysis (Dufrene and Legendre, 1997) determined species indicator values in groups of samples with corresponding $TP \leq 10 \mu\text{g L}^{-1}$ (low-TP), $TP \geq 100 \mu\text{g L}^{-1}$ (high-TP), $TN \leq 0.2 \text{ mg L}^{-1}$ (low-TN), and $TN \geq 3.0 \text{ mg L}^{-1}$ (high-TN). Diatoms with indicator values greater than 5 ($P < 0.05$) are listed here, and their indicator values are shown. The second analysis was based on calculation of species abundance-weighted means. Diatoms with TP and TN abundance-weighted means above the 75th percentile or below the 25th percentile of all values are listed here and marked by asterisks.

Taxon	All samples		Western Mountains		Central and Western Plains		Glaciated North		Eastern Plains		Eastern Highlands			
	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN		
<i>Achnanthes conspicua</i> Mayer		+*					+*	+52*		+*				
<i>A. exigua</i> Grun. + <i>A. exigua</i> var. <i>constricta</i> Grun. + <i>A. exigua</i> var. <i>heterovalva</i> Krass. + <i>A. exigua</i> var. <i>elliptica</i> Hust.	+*	+*	+*	+24*		+*				+29				
<i>A. lemmermannii</i> Hust.	+*				+5									
<i>A. oblongella</i> Østrup											+*			
<i>A. subhudsonis</i> var. <i>kraeuselii</i> (Choln.) Choln.											+27			
<i>Achnantheidium affine</i> (Grun.) Czarn.		–11				–27*				–9		–22*		
<i>A. altergracillima</i> (Lange-Bert.) Round et Bukht.	–*					–6				–*	–*			
<i>A. caledonicum</i> (Lange-Bert.) Lange-Bert.											+*			
<i>A. deflexum</i> (Reim.) Kingston	–24*	–21						–22	–27			–42	–41	
<i>A. exilis</i> (Kütz.) Round et Bukht.						–29*						–6	–7*	
<i>A. cf. latecephalum</i> Kobayasi												–7		
<i>A. minutissimum</i> (Kütz.) Czarn.	–69	–67	–66	–63	–71		–70	–70	–*	–21		–7	–*	
<i>A. rivulare</i> Potapova et Ponader	–32	–21					–52*	–56	–33*			–32		
<i>A. thienemannii</i> (Hust.) Lange-Bert.		–*												
<i>Adlafia bryophila</i> (Petersen) Lange-Bert.						–*	+*			+*				
<i>A. minuscula</i> (Grun.) Lange-Bert.			–6*	–*								–*	–*	
<i>Amphipleura pellucida</i> (Kütz.) Kütz.	–6*					–11*	–*			–17*	–*			
<i>Amphora acutiuscula</i> Kütz.	+*													
<i>A. coffeaeformis</i> (Agardh) Kütz.	+*	+*				+*								
<i>A. copulata</i> (Kütz.) Schoem. et Arch.												+27	+14	
<i>A. montana</i> Krass.	+13	+16											+15	
<i>A. ovalis</i> (Kütz.) Kütz.						+*								
<i>A. pediculus</i> (Kütz.) Grun.		+46										+36*	+49	+48
<i>A. veneta</i> Kütz.		+8	+14*	+26*								+7	+*	
<i>Asterionella formosa</i> Hassal												+8*		
<i>Aulacosira granulata</i> (Ehr.) Simonsen	+12	+10				+15								
<i>A. muzzaensis</i> (Meister) Kramm.						+5								
<i>Bacillaria paradoxa</i> Gmelin	+8*					+*		+*	+18					
<i>Brachysira brebissonii</i> Ross	–*	–*						–*	–*	–17*			–9*	
<i>B. microcephala</i> (Grun.) Compère	–12*			–*	–34*		–20*	–*	–*	–28	–14			
<i>Caloneis amphisbaena</i> (Bory) Cleve							+8							
<i>C. bacillum</i> (Grun.) Cleve													+39	
<i>C. macedonica</i> (Gregory) Kramm.										+*				

Appendix A. (Continued)

Taxon	All samples		Western Mountains		Central and Western Plains		Glaciated North		Eastern Plains		Eastern Highlands	
	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN
<i>Denticula elegans</i> Kütz.	-7	-7			-*		-14*	-30*			-14*	-19*
<i>D. kuetzingii</i> Grun.					-9							
<i>D. tenuis</i> Kütz.	-*	-*	-*	-*		-11						
<i>Diadesmis confervacea</i> Kütz.	+13		+*	+9	+*	+*	+14		+32			
<i>Diatoma mesodon</i> (Ehr.) Kütz.	-8*	-9	-20	-15		-11	-*					
<i>Didymosphenia geminata</i> (Lyngbye) Schmidt	-*	-*	-11*	-7*								
<i>Diploneis oblongella</i> (Naegeli ex Kütz.) Ross					-*	-32			-10	-21		
<i>D. parva</i> Cleve									-*	-*		
<i>Diploneis pseudovalis</i> Hust.					-10				-*			
<i>Diploneis puella</i> (Schumann) Cleve	+*											
<i>Encyonema auerswaldii</i> Rabh. + <i>E. caespitosum</i> Kütz.	-7						-*	-20	-23			
<i>E. brehmii</i> (Hust.) Mann		-*			-6*	-11*						
<i>E. lunatum</i> (Smith) V. H.	-*	-*	-*	-*	-18	-22	-12*		-*	-48*		
<i>E. minutum</i> (Hilse) Mann	-50	-44					-52	-62	-58			
<i>E. muelleri</i> (Hust.) Mann		-*			-17*	-*						
<i>E. perpusillum</i> (Cleve) Mann	-*											
<i>E. prostratum</i> (Berkeley) Kütz.									-11			
<i>E. silesiacum</i> (Bleisch) Mann		-24							-29			
<i>E. tenuissimum</i> (Hust.) Mann	-*	-*							-7*	-*		
<i>Encyonopsis cesatii</i> (Rabh.) Kramm.			-*	-*	-6	-11						
<i>E. evergladianum</i> Kramm.					-24*	-*						
<i>E. microcephala</i> (Grun.) Kramm.	-22*	-15	-15		-58*	-21	-28*	-34*	-17*	-20	-17	-24
<i>Epithemia adnata</i> (Kütz.) Bréb.	-6	-8	-15	-10						+8	-*	-9*
<i>E. reichelti</i> "var. 1 ANS OZRK"	-*	-*									-6*	-12*
<i>E. sorex</i> Kütz.		-24*			-*	-20*		-10*				-25*
<i>E. turgida</i> (Ehr.) Kütz.		-15*							+*	-11*	-23*	
<i>E. turgida</i> var. <i>westermanni</i> (Ehr.) Grun.	-*	-*	6*	-*	-*							
<i>Eucoconeis flexella</i> (Kütz.) Cleve	-*								-*			
<i>E. laevis</i> (Østrup) Lange-Bert.	-*	-*	-8*	-*					-*	-*		
<i>Eunotia arcus</i> Ehr.									-*	-*		
<i>E. bilunaris</i> var. <i>linearis</i> (Okuno) Lange-Bert. et Norpel									-*			-*
<i>E. exigua</i> (Breb. ex Kütz.) Rab.							-10*	-*				-*
<i>E. flexuosa</i> Breb. ex Kütz.	-*								-*	-22*		
<i>E. implicata</i> Norpel et al.	-*	-*			-9		-11*	-*			-11*	-10*
<i>E. incisa</i> Smith ex Greg.	-*	-*					-10*	-*			-*	-*
<i>E. microcephala</i> Krass. ex Hust.		-*									-*	-*
<i>E. monodon</i> Ehr.	-*	-*					-*	-*	-17	-27	-*	
<i>E. paludosa</i> Grun.		-*							-*			
<i>E. pectinalis</i> (Müller) Rabh. + <i>E. pectinalis</i> var. <i>undulata</i> (Ralfs) Rabh.	-*	-*					-7*	-*			-*	
<i>E. praerupta</i> Ehr.		-*										
<i>E. sudetica</i> Müller		-*								-*		
<i>E. tenella</i> (Grun.) Cleve		-*					-12*			-31	-*	-*
<i>Fallacia lenzii</i> (Hust.) Lange-Bert.					-*			+*				
<i>F. monoculata</i> (Hust.) Mann								+*				

Appendix A. (Continued)

Taxon	All samples		Western Mountains		Central and Western Plains		Glaciated North		Eastern Plains		Eastern Highlands		
	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN	
<i>F. pygmaea</i> (Kütz.) Stickle et Mann	+6										+7	+7*	
<i>F. subhamulata</i> (Grun.) Mann		+*				+*						+19*	
<i>F. tenera</i> (Hust.) Mann	+7								+*				
<i>Fistulifera pelliculosa</i> (Bréb. ex Kütz.) Lange-Bert.									—*	—*			
<i>F. saprophila</i> (Lange-Bert. et Bonik) Lange-Bert.								+11				+7*	
<i>Fragilaria capucina</i> var. <i>gracilis</i> (Østrup) Hust.	—*	—*	—6*					—22					
<i>F. capucina</i> var. <i>rumpens</i> (Kütz.) Lange-Bert.								—24					
<i>F. crotonensis</i> Kitton	—*					+*			—*		—18*		
<i>F. nanana</i> Lange-Bert.									—*			—*	
<i>F. synegrotasca</i> Lange-Bert.	—*								—*				
<i>F. tenera</i> (Smith) Lange-Bert.									—*		—9		
<i>F. vaucheriae</i> (Kütz.) Petersen		—40		—51									
<i>Fragilariforma bicapitata</i> (Mayer) Round et Williams			—*										
<i>F. constricta</i> (Ehr.) Williams et Round											—*		
<i>F. virescens</i> (Ralfs) Williams et Round								—*	—*				
<i>Frustulia amphipleuroides</i> (Grun.) Cleve-Euler					—*	—*				—11	+10	—*	
<i>F. crassinervia</i> (Bréb.) Lange-Bert. et Kramm.									—*		—40		
<i>F. rhomboides</i> (Ehr.) De Toni						—*	—*	—*			—45		
<i>F. saxonica</i> Rabh.									—*	—*			
<i>F. vulgaris</i> (Thwaites) De Toni												+22*	
<i>F. weinholdii</i> Hust.											—31		
<i>Geissleria acceptata</i> (Hust.) Lange-Bert. et Metzeltin						+*							
<i>G. aikenensis</i> (Patr.) Torgan et Olivera									—*	—*			
<i>G. decussis</i> (Hust.) Lange-Bert. et Metz.				+25									
<i>G. cf. kriegeri</i> (Krass.) Lange-Bert.											—23		
<i>G. schoenfeldii</i> (Hust.) Lange-Bert. et Metz.					—*	—*		+25		—*			
<i>Gomphoneis eriense</i> (Grun.) Skv. et Meyer		—*	—*	—*									
<i>G. eriense</i> var. <i>variabilis</i> Kociolek et Stoermer		—*											
<i>G. herculeana</i> (Ehr.) Cl.	—*							—17*	—*	+*			
<i>G. minuta</i> Kociolek et Stoermer	—*	—*	—*	—*	—*	—*							
<i>Gomphonema acuminatum</i> Ehr.									—18*				
<i>G. affine</i> Kütz.					—23							—12	
<i>G. angustatum</i> (Kütz.) Rab.						+19	+*	+50*	+20				
<i>G. angustatum</i> var. <i>intermedia</i> Grun.		—5										—23	
<i>G. apuncto</i> Wallace	—9*	—10*						—15*	—27*	—13*	—38*	—*	—15
<i>G. cf. pygmaeum</i> Kociolek et Stoermer			—*	—*									
<i>G. clavatum</i> Ehr.					—*	—11							
<i>G. gracile</i> Ehr. emend. V. H.			—6*		—29	—18							

Appendix A. (Continued)

Taxon	All samples		Western Mountains		Central and Western Plains		Glaciated North		Eastern Plains		Eastern Highlands	
	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN
<i>G. insigne</i> Greg.	+7						+*	+*				
<i>G. intricatum</i> Kütz.		-7	-7	-*	-5	-22					-*	-8
<i>G. intricatum</i> var. <i>vibrio</i> (Ehr.) Cl.					-17							
<i>G. kobayasii</i> Kociolek et Kingston								+25*				
<i>G. manubrium</i> Fricke	-*	-*								-13		
<i>G. mehleri</i> Camburn	-8*	-7									-26*	-25
<i>G. mexicanum</i> Grun.									-6	-23		
<i>G. minutum</i> (Ag.) Ag.		+29				+38						
<i>G. olivaceoides</i> Hust.	-7*	-12	-19	-18								
<i>G. olivaceoides</i> var. <i>hutchinsoniana</i> Patr.	-8*						-26*	-33*	-9	+15*		
<i>G. olivaceum</i> (Lyngb.) Kütz.							+54					
<i>G. parvulus</i> (Lange-Bert. et Reich.) Lange-Bert. et Reich.												+*
<i>G. parvulum</i> (Kütz.) Kütz.	+47	+45	+64	+61								+60
<i>G. pumilum</i> (Grun.) Reich. et Lange-Bert.		-20				-69			-36			
<i>G. rhombicum</i> Fricke		-12*			+*	+*			-*			-20*
<i>G. sarcophagus</i> Greg.	-*											
<i>G.</i> "sp. 23 NAWQA EAM"			-*									
<i>G. sphaerophorum</i> Ehr.	-8*	-6					-16*	-19*	-6*		-14	
<i>G. subclavatum</i> (Grun.) Grun.			-10									
<i>G. truncatum</i> Ehr.								-19	-9*	-23		+11*
<i>Gomphonitzschia agma</i> Hohn et Heller.					-*	-*						
<i>Gomphosphenia grovei</i> (Schmid) Lange-Bert.									-6*	-*		
<i>G. lingulatiformis</i> (Lange-Bert. et Reich.) Lange-Bert.												+*
<i>Gyrosigma acuminatum</i> (Kütz.) Rabh.	+8								+16		+*	+*
<i>G. attenuatum</i> (Kütz.) Rabh.										+*	+*	
<i>G. obtusatum</i> (Sull. et Wormley) Boyer	+10					+*		+14	+*			+11
<i>G. reimeri</i> Sterrenburg						-23	-*					
<i>G. scotoense</i> (Sull. et Wormley) Cl.		+5										+22*
<i>Hannaea arcus</i> (Ehr.) Patr.	-8*	-17*	-21	-26								
<i>H. arcus</i> var. <i>amphioxys</i> (Rabh.) Patr.		-*										
<i>Hantzschia amphioxys</i> (Ehr.) Grun.	+5											
<i>Hippodonta capitata</i> (Ehr.) Lange-Bert. et al.	+20	+15		+18			+36		+34	+28	+12	+22*
<i>H. hungarica</i> (Grun.) Lange-Bert. et al.				+9*		+*				-23*		
<i>Karayevia clevei</i> (Grun.) Bukht.						-11					+*	+*
<i>K. suchlandtii</i> (Hust.) Bukht.			-*	-*								
<i>Luticola cohnii</i> (Hilse) Mann				-*						-*		+*
<i>L. goeppertiana</i> (Bleisch) Mann		+9		+21				+23	+14			+28
<i>L. mutica</i> (Kütz.) Mann								+*				
<i>L. naviculoides</i> (Patr.) Johansen										-*		
<i>L. ventricosa</i> (Kütz.) Mann								+*				
<i>Mastogloia elliptica</i> (Ag.) Cl.					-12*	-*						

Appendix A. (Continued)

Taxon	All samples		Western Mountains		Central and Western Plains		Glaciated North		Eastern Plains		Eastern Highlands	
	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN
<i>M. smithii</i> Thw.	–*	–*			–22*	–*			–*			
<i>Mayamaea agrestis</i> (Hust.) Lange-Bert.					+	+						
<i>M. atomus</i> (Kütz.) Lange-Bert.	+21*	+29*	+41*	+60*		+35*						+
<i>M. atomus</i> var. <i>permitis</i> (Hust.) Lange-Bert.	+				+		+8	+				
<i>Melosira varians</i> Ag.								+				
<i>Meridion circulare</i> (Grev.) Ag.						+					+	+15*
<i>M. circulare</i> var. <i>constrictum</i> (Ralfs) V.H.				+		+						
<i>Navicula arvensis</i> fo. <i>major</i> Mang.	+											
<i>Navicula canalis</i> Patr.	+											
<i>N. capitatoradiata</i> Germain			+48								+54*	+50
<i>N. cari</i> Ehr.						+		+14				
<i>N. cf. pseudolanceolata</i> Lange-Bert.		–*										
<i>N. cincta</i> (Ehr.) Ralfs	+12				+11				+23			
<i>N. cryptocephala</i> Kütz.											+	+25
<i>N. cryptotenella</i> Lange-Bert.		+41									+	+56
<i>N. duerrenbergiana</i> Hust.					–*	–*						
<i>N. erifuga</i> Lange-Bert.	+29	+25*	+28	+27*				+37	+21*			+14
<i>N. exilis</i> Kütz.	+13	+15				+22				–*		
<i>N. festiva</i> Krass.		–*									–*	–7*
<i>N. genovefae</i> Fusey						+					+19*	
<i>N. germainii</i> Wallace	+25								+40*		+39	
<i>N. gregaria</i> Donkin	+33	+32	+36	+55			+67	+77*			+38	
<i>N. hambergii</i> Hust.		–*									–*	
<i>N. harderii</i> Hust.		+									+	
<i>N. hasta</i> Pant.								–10				
<i>N. hustedtii</i> Krass.												+12
<i>N. ingenua</i> Hust.	+5*	+			+	+			+			
<i>N. kotschyi</i> Grun.					–21		+13					
<i>N. lanceolata</i> (Ag.) Ehr.								+	+19	+27*	+	
<i>N. laterostrata</i> Hust.										–*		
<i>N. medioconvexa</i> Hust.	+	+5*	+9	+19	+	+6*						
<i>N. menisculus</i> Schum.		+11		–16						+		
<i>N. minima</i> Grun.	+43	+49	+37	+51		+45			+52		+28*	+55
<i>N. notha</i> Wallace						–11	–8	–19*		–*	–*	
<i>N. peregrina</i> (Ehr.) Kütz.							+14					+10*
<i>N. perminuta</i> Grun.						–*			–*	–*		
<i>N. pseudoventralis</i> Hust.		+				+						
<i>N. radiosa</i> Kütz.		–6		–*	–27*				–14			–12
<i>N. recens</i> Lange-Bert.	+19*	+14	+11				+11	+25*	+	+18*		
<i>N. reichardtiana</i> Lange-Bert.							+37					
<i>N. rhynchocephala</i> Kütz.											–*	
<i>N. rostellata</i> Kütz.	+16	+18	+	+36				+24*	+17*			+
<i>N. sanctaecrucis</i> Østrup	+											
<i>N. schroeteri</i> var. <i>escambia</i> Patr.			+7									+10
<i>N. seminuloides</i> Hust.						+						
<i>N. stroemii</i> Hust.	–5*				–29*	–*					–10	–8
<i>N. sublucidula</i> Hust.						+						
<i>N. subminuscula</i> Mang.	+48*	+46*	+52*	+68*	+52	+53	+23	+34	+29			+27*

Appendix A. (Continued)

Taxon	All samples		Western Mountains		Central and Western Plains		Glaciated North		Eastern Plains		Eastern Highlands	
	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN
<i>N. supralitorea</i> Lange-Bert.		+*		+9*		+*						
<i>N. thermaloides</i> Hust.			+7*	+14*								
<i>N. tropica</i> Hust.								+*				
<i>N. umbonata</i> Lange-Bert.	+*	+*		+*								
<i>N. vitrea</i> Norman						-18*						
<i>Nupela carolina</i> Potapova et Clason										+*		
<i>N. lapidosa</i> (Krass.) Lange-Bert.	-*											
<i>Pinnularia intermedia</i> (Lagerst.) Cl.										+*		
<i>P. mesogongyla</i> Ehr. sensu Patrick and Reimer, 1966						-23*	-21*					
<i>P. mesolepta</i> (Ehr.) W. Sm.										+*		
<i>P. microstauron</i> (Ehr.) Cl.						-11						
<i>Placoneis exigua</i> (Greg.) Mereschk.	+*						+11					
<i>P. placentula</i> (Ehr.) Hienzerling							-*					
<i>Plagiotropis lepidoptera</i> var. <i>proboscidea</i> (Cl.) Reim.	+*											
<i>Planothidium biporumum</i> (Hohn et Heller.) Lange-Bert.											+*	
<i>P. delicatulum</i> (Kütz.) Round et Bukht.										+*		
<i>P. frequentissimum</i> (Lange-Bert.) Lange-Bert.		+*	+*	23*		+*					+*	
<i>P. lanceolatum</i> (Bréb. ex Kütz.) Lange-Bert.		+32						+72	+33		+*	+39
<i>P. robustum</i> (Hust.) Lange-Bert.	+*			+10				+*				
<i>P. rostratum</i> (Østrup) Lange-Bert.				-22	+6							+56
<i>Pleurosigma delicatulum</i> W. Sm.	+*											
<i>P. elongatum</i> W. Sm.	+*											
<i>P. salinarum</i> Grun.	+*	+*			+*	+*				+*		
<i>Pleurosira laevis</i> (Ehr.) Compère	+7		+18									+*
<i>Psammothidium bioretii</i> (Germ.) Bukht. et Round										+*		
<i>P. laenburgianum</i> (Hust.) Bukht. et Round												-*
<i>P. marginulatum</i> (Grun) Bukht. et Round		-*		-*								
<i>P. subatomoides</i> (Hust.) Bukht. et Round												+9
<i>Pseudostaurosira brevistriata</i> (Grun.) Williams et Round		-11					-30			+*		
<i>P. brevistriata</i> var. <i>inflata</i> (Pant.) Edlund							-17	-14*				
<i>Reimeria sinuata</i> (Greg.) Kociolek et Stoermer	-37	-53	-7	-51*		-58	-47	-60	-8	+37		
<i>Rhoicosphenia abbreviata</i> (Ag.) Lange-Bert.	+38	+44								+46	+53*	+46
<i>Rhopalodia brebissonii</i> Kramm.					-*	-*						
<i>R. gibba</i> (Ehr.) O. Mull.	+*	-8		-11*	+*	-14				-*		
<i>R. gibberula</i> (Ehr.) O. Mull.	+*				+*					-*		
<i>Sellaphora bacillum</i> (Ehr.) Mann					-11*	-*						
<i>S. laevissima</i> (Kütz.) Mann						-35				-13*	-11*	

Appendix A. (Continued)

Taxon	All samples		Western Mountains		Central and Western Plains		Glaciated North		Eastern Plains		Eastern Highlands	
	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN
<i>S. mutata</i> (Krass.) Lange-Bert.									+	*		+8
<i>S. pupula</i> (Kütz.) Meresck.		+21		+46					+35	+39	+28	+37
<i>S. pupula</i> var. <i>elliptica</i> (Hust.) Bukht.										-12		
<i>S. rectangularis</i> (Greg.) Lange-Bert. et Metzeltin				-*								
<i>S. seminulum</i> (Grun.) Mann	+28*	+26*	+31	+70*	+25*	+29*			+43		+31	
<i>Simonsenia delognei</i> (Grun.) Lange-Bert.	+10											
<i>Stauroforma exiguiiformis</i> Flower et al.		-*		-*			-7*	-*	-*	-*		
<i>Stauroneis livingstonii</i> Reim.											-*	
<i>S. smithii</i> var. <i>incisa</i> Pant.											-34	
<i>Staurosirella lapponica</i> (Grun.) Williams et Round	-*						-*					
<i>S. leptostauron</i> (Ehr.) Williams et Round	-12	-14				-32*						+24*
<i>S. leptostauron</i> var. <i>dubia</i> (Grun.) Edlund			-6*	-5*								
<i>S. pinnata</i> (Ehr.) Williams et Round		-29				-49					+22	+31
<i>Stephanodiscus hantzschii</i> Grun.	+14	+13*	+10	+20	+20	+15	+	+		+10*		
<i>S. minutulus</i> (Kütz.) Cleve et Moller												
<i>S. niagarae</i> Ehr.												
<i>Surirella angusta</i> Kütz.									+34		+*	+21*
<i>S. brebissonii</i> Kramm. et Lange-Bert.	+	+			+	+						
<i>S. brebissonii</i> var. <i>kuetzingii</i> Kramm. et Lange-Bert.		+				+5*						
<i>S. minuta</i> Bréb.	+15	+17		+33		+21						+15
<i>S. ovalis</i> Bréb.									-*	-*		
<i>S. splendida</i> (Ehr.) Kütz.											-*	
<i>S. tenera</i> Greg.									-*			
<i>Synedra acus</i> Kütz.					-*	-*						
<i>S. delicatissima</i> W. Sm.					-*				-*			
<i>S. delicatissima</i> var. <i>angustissima</i> Grun.									-*			
<i>S. mazamaensis</i> Sover.	-*	-*		-6*								
<i>S. minuscula</i> Grun. sensu Patrick and Reimer, 1966	-*		-*	-*			-*	-*	11			
<i>S. parasitica</i> (W. Sm.) Hust.									+24	+	+	
<i>S. parasitica</i> var. <i>subconstricta</i> (Grun.) Hust.						-*					+	
<i>S. ulna</i> (Nitz.) Ehr. sensu lato	-45	-32				-62			-60	-16		-48
<i>Tabellaria fenestrata</i> (Lyngb.) Kütz.									-12*			
<i>T. flocculosa</i> (Roth) Kütz.	-9*		-*		-*				-27*	-*		-*
<i>Tabularia fasciculata</i> (Ag.) Williams and Round				+9								
<i>T. tabulata</i> (Ag.) Snoeijs				+								
<i>Thalassiosira pseudonana</i> Hasle et Heimdal									+			
<i>T. weissflogii</i> (Grun.) Fryxell et Hasle	+11			+14*						+17		

Appendix A. (Continued)

Taxon	All samples		Western Mountains		Central and Western Plains		Glaciated North		Eastern Plains		Eastern Highlands	
	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN	TP	TN
<i>Tryblionella apiculata</i> Greg.	+14	+14*	+*	+17							+*	
<i>T. calida</i> (Grun.) Mann	+10*	+6*	+11*	+14*								
<i>T. hungarica</i> (Grun.) Mann	+11*	+11*	+10*	+23*			+20*	+28*				
<i>T. levidensis</i> W. Sm.	+*				+*							
<i>T. victoriae</i> Grun.	+11				+12				+16			

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