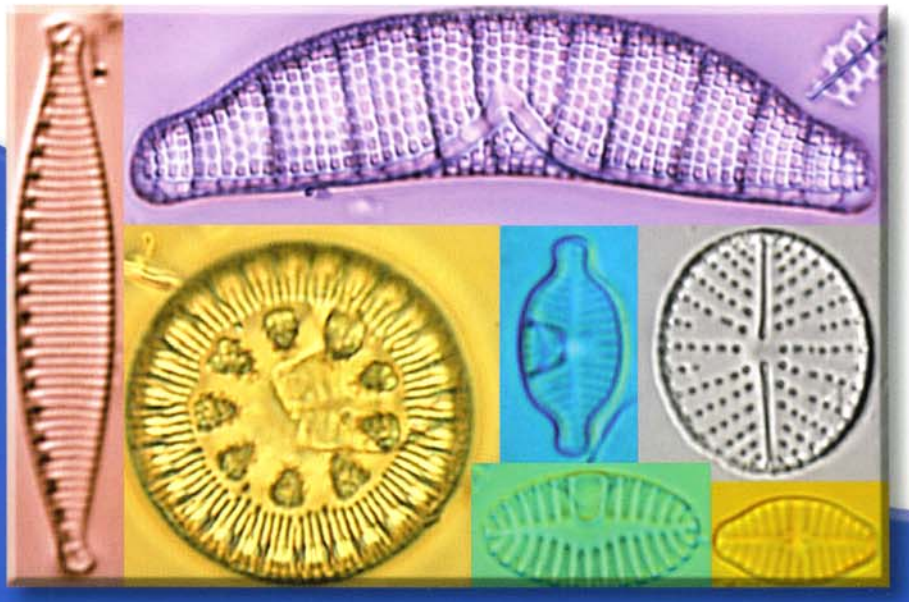
INTERNATIONAL ASSOCIATION
FOR GREAT LAKES RESEARCH

Journal of

GREAT LAKES RESEARCH

devoted to research on large lakes of the world
and their watersheds



Volume 32, Number 2, 2006

J. Great Lakes Res. 32:321–347
Internat. Assoc. Great Lakes Res., 2006

Diatom-based Weighted-averaging Transfer Functions for Great Lakes Coastal Water Quality: Relationships to Watershed Characteristics

Euan D. Reavie[1,*], Richard P. Axler[2], Gerald V. Sgro[3], Nicholas P. Danz[2], John C. Kingston[1,], Amy R. Kireta[1], Terry N. Brown[2], Thomas P. Hollenhorst[2], and Michael J. Ferguson[3]**

[1]*Center for Water and the Environment at the Natural Resources Research Institute*
University of Minnesota Duluth
1900 East Camp Street
Ely, Minnesota 55731

[2]*Center for Water and the Environment at the Natural Resources Research Institute*
University of Minnesota Duluth
5013 Miller Trunk Highway
Duluth, Minnesota 55811

[3]*Department of Biology*
John Carroll University
20700 North Park Boulevard
University Heights, Ohio 44118

ABSTRACT. *In an effort to develop indicators for Great Lakes near-shore conditions, diatom-based transfer functions to infer water quality variables were developed from 155 samples collected from coastal Great Lakes wetlands, embayments and high-energy shoreline sites. Over 2,000 diatom taxa were identified, and 352 taxa were sufficiently abundant to include in transfer function development. Multivariate data exploration revealed strong responses of the diatom assemblages to stressor variables, including total phosphorus (TP). Spatial variables such as lake, latitude and longitude also had notable relationships with assemblage characteristics. A diatom inference transfer function for TP provided a robust reconstructive relationship (r^2 = 0.67; RMSE = 0.28 log(µg/L); r^2jackknife = 0.55; RMSEP = 0.33 log (µg/L)) that improved following the removal of 13 samples that had poor observed-inferred TP relationships (r^2 = 0.75; RMSE = 0.22 log(µg/L); $r^2_{jackknife}$ = 0.65; RMSEP = 0.26 log (µg/L)). Diatom-based transfer functions for other water quality variables, such as total nitrogen, chloride, and chlorophyll* a *also performed well. Measured and diatom-inferred water quality data were regressed against watershed characteristics (including gradients of agriculture, atmospheric deposition, and industrial facilities) to determine the relative strength of measured and diatom-inferred data to identify watershed stressor influences. With the exception of pH, diatom-inferred water quality variables were better predicted by watershed characteristics than were measured water quality variables. Because diatom communities are subject to the prevailing water quality in the Great Lakes coastal environment, it appears they can better integrate water quality information than snapshot measurements. These results strongly support the use of diatoms in Great Lakes coastal monitoring programs.*

INDEX WORDS: *Great Lakes environmental indicators, diatoms, phosphorus, coastlines, watershed, stressors.*

*Corresponding author. E-mail: ereavie@nrri.umn.edu
** Deceased

INTRODUCTION

Bioindicators are receiving considerable attention in the Laurentian Great Lakes, particularly for assessing the condition of coastal waters (Keough and Griffin 1994, Maynard and Wilcox 1997, Lawson 2004). Developing effective indicators of ecological condition requires that indicators be calibrated to identify their responses to important environmental stressors (Niemi and McDonald 2004, Karr and Chu 1999, Seegert 2001). The main goals of calibration are to identify environmental optima and tolerances of indicator taxa, and to define systems with similar biota that respond similarly to anthropogenic stresses (e.g., Radar and Shiozawa 2001). Although bioindicator approaches in the Great Lakes have gained attention in the last decade (e.g., Environment Canada and U.S. EPA 2003, Wilcox *et al.* 2002, Albert and Minc 2004, Uzarski *et al.* 2004), most indicators proposed for Great Lakes coastal environments remain uncalibrated and untested throughout large parts of the basin or under the full range of environmental conditions. Bioindicators are particularly needed to monitor the impacts of human activities that increase the nutrient supply to water bodies, giving rise to cultural eutrophication, a human-driven process that has numerous adverse effects (Carpenter *et al.* 1998a, b). Phosphorus and nitrogen compounds from agricultural and urban activities are universally recognized to be the major causes of cultural eutrophication.

Modern datasets, also known as training sets, provide the basis for development of indicator transfer functions by relating contemporary assemblages with their corresponding environmental measurements (e.g., water quality stressors). Much utility has been realized for indicator groups in high (e.g., fish; Karr 1981) and low (e.g., algae; Stevenson *et al.* 1996) trophic levels. Algal assemblages, in particular, are proven robust indicators of stressors such as nutrients (e.g., Tibby 2004, Meriläinen *et al.* 2003, Ramstack *et al.* 2003), water clarity (Dixit and Smol 1994) and acidification (e.g., Siver *et al.* 2003), as well as a suite of other water quality problems in freshwater ecosystems (Smol 2002). Of the published water quality indicator transfer functions, diatom algae are popular because the taxa have definable optima along gradients of environmental conditions. In addition, the diatoms are taxonomically distinct, abundant in almost all aquatic environments, respond rapidly to changing conditions, and are well preserved in sediment deposits (Hall and Smol 1999). Hence, researchers can use changes in community composition (expressed as percent abundance of each taxon) to classify and quantify long-term environmental changes that result from anthropogenic activities.

A diatom transfer function is derived by relating diatom taxa assemblages in a training set of samples (e.g., from lakes, river reaches, coastal locales) to an environmental variable of interest (e.g., total phosphorus or nitrogen, pH, chloride, suspended solids) from a particular region (Charles 1990). The transfer function consists of taxa coefficients (e.g., environmental optima and tolerances) that can be used to infer quantitative information about the variable of interest, based on the abundance of each taxon in a sample assemblage. Transfer function evaluation and testing typically involves the comparison of diatom-inferred water quality to measured water quality to evaluate function robustness, which is usually characterized by a coefficient of determination (r^2) and an "error of prediction." While measured water quality variables are suitable for comparison to diatom-inferred water quality, contemporary measurements are often based on single ("snapshot") measurements from the epilimnetic environment at each site in the training set. This is not surprising because multiple time-integrated measurements can be costly and are often not logistically feasible in monitoring programs. Several studies have shown that, due to short-term fluctuations in freshwater parameters, snapshot measurements of water quality variables such as nutrients can misrepresent the prevailing water quality (e.g., Bradshaw *et al.* 2002, Detenbeck *et al.* 1996). Assemblages of algae, which are physiologically subject to water chemistry, have the potential to provide time-integrated inferences of limnological conditions.

Relationships between diatom-inferred (DI) water quality variables and watershed characteristics, such as urban and agricultural land use, have provided an important link between bioindicators and anthropogenic influences in the watershed (Dixit and Smol 1994). Such comparisons of diatom-inferred water quality to watershed stressors may reflect the strength of these transfer functions, particularly regarding their ability to infer more holistic stressor impacts beyond the water quality parameters that directly influence the indicator assemblages. Unfortunately, detailed data on watershed characteristics and human activities have yet to be integrated with most of these diatom-based transfer functions, and no such assessment has been performed for the Laurentian Great Lakes.

This study developed and tested several diatom-based transfer functions derived from a training set of coastal surface sediment and epilithic samples from the U.S. portion of the five Laurentian Great Lakes. The diatom indicators were derived from data collected as part of a larger study designed to develop and test indicators of ecological condition for Great Lakes coastal ecosystems (the Great Lakes Environmental Indicators (GLEI) project; Niemi *et al.* 2004, Danz *et al.* 2005). The larger study included measurements of other biotic assemblages, including birds, fish, amphibians, aquatic macroinvertebrates and wetland vegetation from coastal locations spread throughout the Great Lakes.

Diatom transfer functions were developed to infer nutrient concentrations, water clarity and possible loading from road salt pollution. Both diatom-inferred and measured water quality were regressed against watershed characteristics such as agricultural intensity and urban development to identify the ability of diatom assemblages to reflect watershed stressors. We compared this diatom-watershed relationship to the ability of measured water quality to reflect the same watershed stressors. The major goals of this study were to: (1) identify coastal water quality variables that are important in determining the composition of diatom assemblages in Great Lakes coastlines; (2) develop and evaluate the ability of diatom-based transfer functions to infer water quality variables such as phosphorus; and (3) compare measured and diatom-inferred water quality data to watershed characteristics to identify how well these measured and inferred data reflect landscape/watershed stressors.

METHODS

Coastal sample locations were selected as described in detail by Danz *et al.* (2005). Briefly, the entire U.S. coastline of the Great Lakes was divided into 762 segments, each consisting of a shoreline reach and associated watershed (i.e., a "segment-shed"). Each segment-shed was summarized using 207 geographic information system (GIS)-based environmental variables that included anthropogenic activities and soil data. Cluster analysis was carried out using these environmental data to create groups of segment-sheds with similar environmental profiles. Sample locations were randomly selected from each cluster, excluding inaccessible locations. This selection method provided a subset of sample locations that reflected the range of natural and anthropogenic environmental conditions present along the Great Lakes shorelines.

Five coastal ecosystem types, as described in detail by Danz *et al.* (2005), were sampled (Fig. 1), including embayments (EM), high-energy shorelines (HE), coastal wetlands (CW), riverine wetlands (RW), and protected wetlands (PW; i.e., physically protected from high-energy influences in the adjacent open-water system).

Field Work

Field sites were sampled from June to September 2002 and May to August 2003. A detailed suite of environmental measurements was collected at each sample location using a motorboat or canoe. Natural Resources Research Institute (NRRI) personnel used a Corning 313 pH/temperature meter, and a YSI (Yellow Springs Instruments) 85 T/DO/EC25 (specific conductance) meter calibrated according to standard methods (DO by air calibration, pH using 2 buffers, and EC25 using a 147 uS/cm KCl solution). John Carroll University (JCU) personnel used a YSI 30 (S-EC-T), YSI 63 (T-EC25-pH), YSI 95 (T/DO) meters and a Barnant 30 and YSI pH100 for surface pH. Clarity was estimated using 120 cm transparency tubes (Anderson and Davic 2004) and a Secchi disk (black and white 20 cm), where deep enough.

A 10-L Nalgene polypropylene compositing carboy with bottom spigot was rinsed and filled with lake water to provide enough water for field transparency tube measurements and water chemistry measurements. A 1-L polypropylene bottle attached to a polyvinyl chloride (PVC) pipe was used to dip water at sites less than 0.5 m deep, or at stations containing dense vegetation; the carboy was dipped manually where depths ranged from 0.5 m to approximately 2.5 m. A 2 m long, 4 cm diameter PVC pipe was used to collect a vertically integrated composite for depths > 2.5 m; both were filtered through a 500 μm nylon mesh funnel into the carboy to remove larger debris. Multiple samples were taken to collect 8–10 L of water. The carboy was vigorously shaken prior to dispensing water into various containers for water chemistry analyses. Transparency-tube clarity was measured from the composite in the field against a white background shaded by the body. Water from each site was used for fluorescence, turbidity and alkalinity measurements, performed on fresh samples at the end of each day. A 4-L cubitainer of water from each site was iced until processing for the other chemical

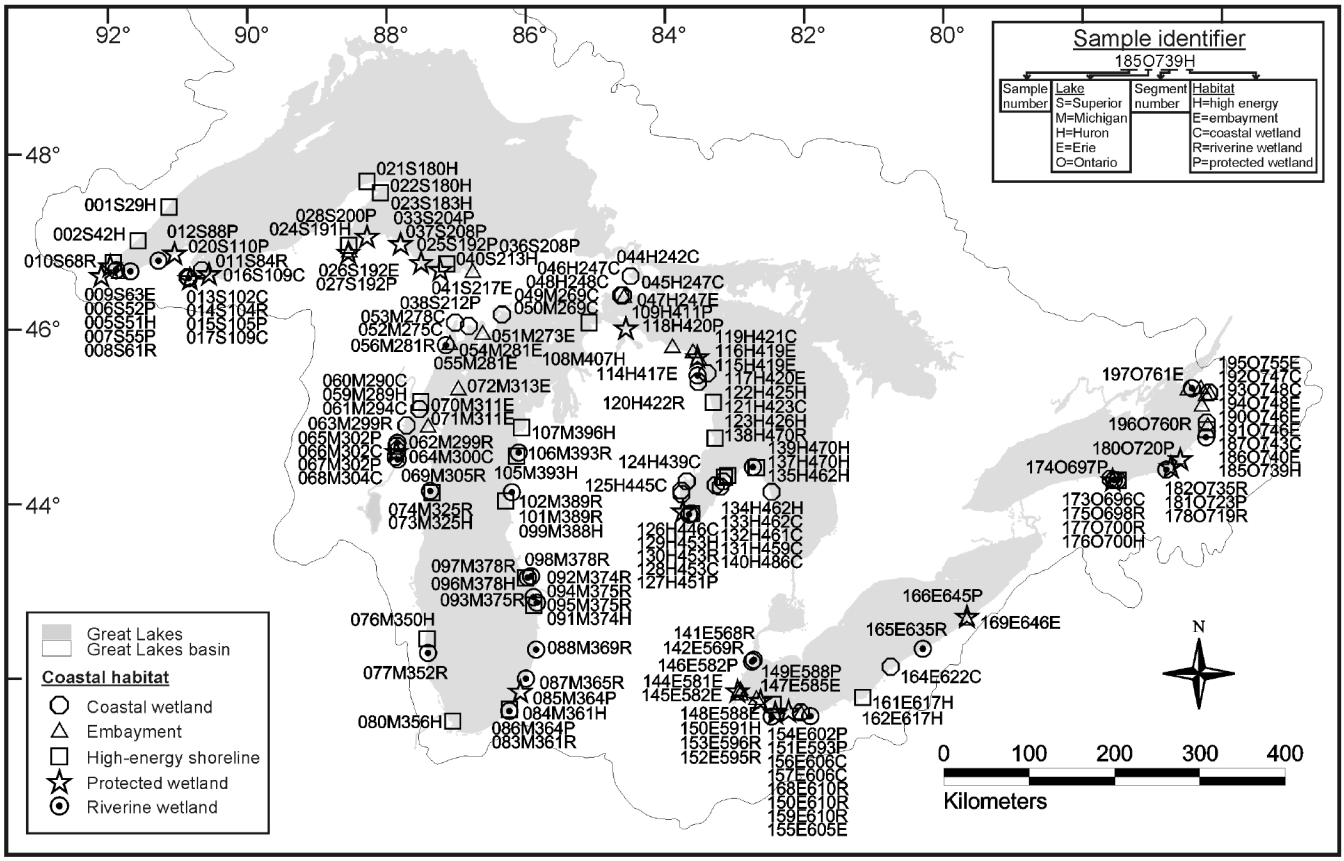


FIG. 1. Location map of the Great Lakes study area.

analyses (< 24 hours). Processing involved filtration and preservation: nitrate and ammonium subsamples were filtered through Millipore 0.45 µm membranes and the filtrates were frozen at –20°C until analysis; alkalinity was analyzed within 24 hours on 0.45 µm filtrate; DOC samples were preserved with Ultrex H_2SO_4 to pH 2; color and chloride samples were 0.45 µm-filtered and chilled; total suspended solids (TSS) and chlorophyll *a* filtrations used Whatman GF/C glass fiber filters for consistency with previous EPA Mid-Continent Ecology Lab Great Lakes stream and wetland studies; raw water was frozen for total phosphorus and total nitrogen analyses (TN/TP). TSS filters were immediately air-dried and chlorophyll *a* filters were wet-frozen. Turbidity and chlorophyll fluorescence were determined using a Turner Designs *Aquafluor* instrument on fresh samples (< 24 hours). Because only about 4 mL was used, each sample was replicated to minimize small sample artifacts. Fluorescence was calibrated to a reproducible arbitrary fluorescence unit using a manufacturer supplied solid standard (Solid Std HH Orange) made from synthetic ruby. Since non-chlorophyll fluorescence usually represented about half of the total signal obtained for unfiltered water, we determined both unfiltered and 0.45 µm-filtered fluorescence for each sample. We then calculated "particulate" fluorescence as a field estimate of chlorophyll *a*. These field measurements, along with transparency tube clarity and EC25 were performed at multiple stations within a designated site as surrogates for the more limited (due to cost) set of lab water chemistry analyses. In this manner, every diatom sample collected (see below) had an explicit set of surrogate measurements, and at least one per site also included the complete set of parameters. QA/QC procedures followed a Quality Assurance Project Plan submitted to EPA at the start of the project that followed EPA guidelines—Guidance for Quality Assurance Project Plans. At least 10% of all sites on a given day received replicate field sampling for complete water chemistry and diatoms. Analytical details for all parameters are included in Table 1.

Benthic and sedimented diatoms were sampled from natural substrates from 0.5 to 3 m depth. Sur-

TABLE 1. Water quality methods. QA/QC procedures followed a Quality Assurance Project Plan (QAPP) submitted to EPA that followed EPA guidelines - December 2002, Guidance for Quality Assurance Project Plans (QA/G-5; EPA/240/R-02/009; December 2002 at http://www.epa.gov/quality/qs-docs/g5-final.pdf).

Parameter	Methodology	Additional references
Chloride	Ion chromatography	
Specific conductance (EC25)	Field sensors (YSI 85, 63)	USGS 2004
pH	Lab or field pH meter—2 or 3 buffer calibration	USGS 2004
Alkalinity	Potentiometric titration (field)	Ameel *et al.* 1998
Dissolved oxygen (mg/L and % saturation)	Field sensors (YSI 85, 95)	Baker *et al.* 1997, USGS 2004
Turbidity	Nephelometry (Turner Designs *Aquafluor;*field)	APHA 2000, USGS 2004
TSS	Gravimetry using Whatman GF/C filtered seston	APHA 2000, Ameel *et al.* 1998
Transparency tube (1/T-tube)	120 cm visual clarity (field)	MPCA 2004a.
Secchi depth	20 cm black and white (field)	MPCA 2004b
Total phosphorus	Persulfate digestion + FIA (Lachat autoanalyzer)	Ameel *et al.* 1993, 1998; APHA 2000; USGS 2003
Total nitrogen	Persulfate digestion + FIA (Lachat autoanalyzer)	Ameel *et al.* 1993, 1998; APHA 2000; USGS 2003
(Nitrate+Nitrite)-N	FIA colorimetry (Cd reduction)	APHA 2000
Ammonium-N	FIA colorimetry (Salicylate)	APHA 2000
DIN (Nitrate+Nitrite+Ammonium-N)	Calculation	
Chlorophyll *a*	Lab fluorometer; 90% acetone extracts of GF/C filtered seston calibrated with pure chlorophyll *a*	Axler and Owens 1994
Chlorophyll-fluorescence	Field fluorometer (Turner Designs *Aquafluor;* field); filtrate corrected fluorescence; ruby calibration	Instrument manual
DOC	UV+persulfate oxidation; analysis for CO_2	APHA 2000, U.S. EPA 1987
Color	Lab spectrophotometry versus Pt-Co standards	Ameel *et al.* 1998, APHA 2000

face sediments were sampled using a 6.5 cm diameter push corer and core tube. Sediments were extruded in the boat or on shore and the top 1 cm of sediment was carefully removed using a spoon and/or spatula. In areas where coring was not feasible a "petite" Ponar sampler was used to collect unconsolidated bottom substrates, or rocks were carefully collected by hand. Approximately 1 cm of surface sediments from Ponar samples was removed using a spoon and/or spatula. The surfaces of rocks and pebbles were scrubbed clean with a small brush or plastic knife and collected in vials as epilithic samples. All samples were iced at 4°C until processing. Approximately 75% of sites were cored, 13% required Ponar grab samples, and 12% relied on epilithic samples collected by hand.

Diatom Sample Preparation and Analysis

In the lab, subsamples were taken from homogenized sediment samples and the diatom remains were cleaned using concentrated nitric or hydrochloric acid, or 30% hydrogen peroxide. Sam-

ples were digested in a water bath (85°C) for 1 hour. Samples were allowed to cool and settle at room temperature for 24 hours, and then were centrifuged at 1,800 RPM for 10 minutes. The tubes were aspirated, refilled with deionized water, and shaken to break up the pellet. This centrifugation process was repeated five times. Four microscope slides were prepared for each sample using the Battarbee (1986) method. For each sample, 400 diatom valves were counted along random transects at 1,000× magnification using oil immersion microscopy. Counts were made continuously along transects as wide as the field of view until sufficient valves were counted. Taxa were identified to the lowest taxonomic level possible using numerous diatom checklists and iconographs (e.g., Krammer and Lange-Bertalot 1986–1991, Stoermer *et al.* 1999, Patrick and Reimer 1966, Reavie and Smol 1998a, Cumming *et al.* 1995, and Camburn *et al.* 1984–1986). The sampling design included duplicate, and sometimes triplicate, diatom sampling and count replication for QA/QC. For analysis in this report replicate counts were combined (all sample replicates and/or count replicates), so some locations were characterized by more than 1,200 diatom valves. Because of the large set of samples, five analysts were needed to complete diatom assessments. In order to harmonize taxonomy among analysts, constant collaboration was maintained by phone and email, and annual taxonomic workshops were held during data collection. Workshops included invited diatom taxonomy experts to ensure the most modern, appropriate and consistent taxonomy.

Statistical Analyses

Three data matrices were developed for statistical analyses: diatom taxa relative abundances (155 records per taxon for exploratory analyses, 170 for TP transfer function development), site-level predictor variables (155 records per variable for exploratory analyses, 170 for TP transfer function development) and watershed-level predictor variables (109 records per variable). Taxon inclusion in the data matrix was based on either (1) occurrence in at least five samples with greater than 1% relative abundance in at least one of those samples, or (2) greater than 5% relative abundance in at least one sample. A total of 352 taxa met these criteria. The site-level predictors consisted of 17 water quality parameters measured at the same sites at which diatoms were collected, one spatial variable indicating lake membership for a site, and one habitat variable indicating ecosystem geomorphic type of a site (Table 2). Because the lake and geomorphic type variables were categorical (n = 5 categories for both), they were coded as dummy variables in the data matrices. For example, the Lake Superior variable (Sup) was coded as a series of zeroes and ones identifying whether a sample was from this lake. Additional site-level variables were collected, but were preemptively removed from exploratory multivariate analyses due to high numbers of unreliable measurements (Secchi depth; many sites were not deep enough), incomplete spatial coverage (silica, metals), or high redundancy with other variables based on preliminary correlation analyses (color, filtered aquafluor, turbidity, dissolved oxygen saturation, phaeophytin). Lognormal or square-root transformations were performed as appropriate on site-level predictors to improve distributional qualities required to meet statistical assumptions (Table 2).

A watershed was delineated for each sampled wetland (109 of the 155 sampled locales). A polygon was drawn encompassing sampling points for all GLEI indicator groups at a selected locale, and this wetland polygon was assumed to be the receiving area for the watershed. Topographic contributing areas were calculated for each of the wetland polygons from 30 meter digital elevation models (DEMs) using ArcInfo's WATERSHED command (ESRI 2000). Over 200 environmental variables in seven categories of environmental variation (Danz *et al.* 2005) were summarized for each watershed. Principal components analysis (PCA) within each category of environmental variation was used to reduce dimensionality and derive overall gradients. For example, 26 agricultural variables (including pesticide runoff and leaching, cropland area, nitrogen and phosphorous exports, percent of county treated for various pests, and livestock inventories) comprised an agricultural category. Principal component (PC) 1 of the agricultural PCA clearly characterized a gradient of agricultural activity for these watersheds (Fig. 2), so the PC 1 scores for each sample location were used in regressions against measured and diatom-inferred water quality data. In cases where PC axis 2 captured meaningful variation, axis 2 scores were also included as watershed variables. The watershed-level predictor matrix consisted of seven variables: the principal components from the agriculture (PC 1), atmospheric deposition (PCs 1 and 2), point source pollution (PC 1), soils (PCs 1 and 2), and urbanization (PC 1) categories.

TABLE 2. Environmental variables characterized for the Great Lakes coastal locations. The selected transformation was based on the closest approximation of a normal frequency distribution. Diatom-based model results for tested variables are presented as the jackknifed correlation coefficient ($r^2_{jackknife}$) and root mean square error of prediction (RMSEP). Model results are presented based on weighted averaging using species optima (WA) and with tolerance downweighting (WA_{tol}). All correlations were significant at P = 0.05 with Bonferroni correction. — = not applicable.

	Abbreviation	Min.	Max.	Average	Data transformation	$r^2_{jackknife}$ (WA)	RMSEP (WA)	$r^2_{jackknife}$ (WA_{tol})	RMSEP (WA_{tol})
Latitude (°N)	Lat	41.22	47.46	44.22	none	—	—	—	—
Longitude (°E)	Long	76.06	92.25	84.32	none	—	—	—	—
Field pH	pH	5.09	9.70	8.11	none	0.27	0.53	0.18	0.56
Field temperature (°C)	Temp	8.3	32.4	22.5	none	—	—	—	—
Field dissolved oxygen (mg/L)	DO	3.94	17.93	9.63	square root (x+1)	0.13	0.34	0.10	0.34
Field specific conductivity (µS/cm)	EC25	22.5	1,888.0	271.3	log(x+1)	0.42	0.20	0.40	0.21
Field transparency tube (cm)	TTurb	8.0	130.0	72.2	square root (x+1)	0.47	1.89	0.38	2.06
Lab turbidity	LTurb	0	80.3	4.7	log(x+1)	0.39	0.33	0.32	0.35
Lab total fluorescence (aquafluor)	Fluor	0.05	60.10	3.77	log(x+1)	0.32	0.30	0.27	0.31
Lab color (standard units)	Color	0	598	21.2	log(x+1)	0.39	0.41	0.31	0.44
Lab total suspended solids (mg/L)	TSS	0	260.8	6.8	log(x+1)	0.44	0.35	0.39	0.37
Lab chlorophyll *a* (µg/L)	Chla	0.17	114.14	4.12	log(x+1)	0.43	0.37	0.38	0.39
Lab total phosphorus (µg P/L)	TP	1	521	27	log(x+1)	0.55	0.33	0.49	0.35
Lab total nitrogen (µg N/L)	TN	110.5	8,060.0	706.3	log(x+1)	0.40	0.24	0.38	0.24
Lab alkalinity (meq/L)	Alk	2.0	15.8	9.9	square root (x+1)	0.22	2.06	0.23	2.05
Lab ammonium-N (µg N/L)	NH4	1	6,406	18	log(x+1)	0.16	0.40	0.13	0.41
Lab nitrate/nitrite-N (µg N/L)	NO3NO2	0	6,380	67	log(x+1)	0.18	0.78	0.13	0.80
Lab dissolved organic carbon (mg/L)	DOC	1.37	43.14	5.57	log(x+1)	0.37	0.22	0.29	0.23
Lab chloride (mg/L)	Cl	0.33	120.74	13.39	log(x+1)	0.43	0.33	0.37	0.35
Field sample depth (m)	Z	0.1	5.0	0.6	log(x+1)	—	—	—	—
Lake (nominal)	Sup, Mic, Hur, Erie, Ont	0	1	—	none	—	—	—	—
Geomorphic type (nominal)	CW, PW, RW, EB, HE	0	1	—	none	—	—	—	—

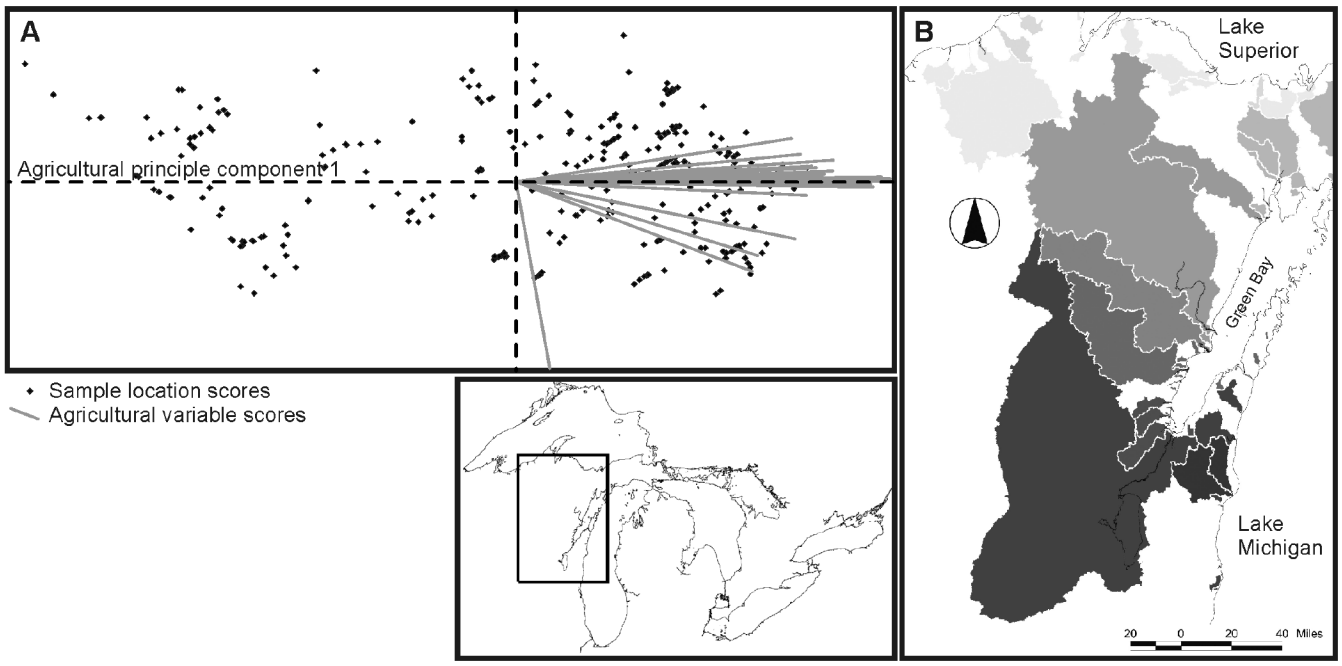


FIG. 2. Principal components analysis (PCA) of agricultural variables from watersheds associated with GLEI sample locations. Plate A illustrates the distribution of sample locations and the strong correlation of most agricultural variables with axis 1. Plate B illustrates the variation in agricultural intensity in a portion of the study area adjacent to lakes Superior and Michigan. Higher PCA scores (greater agricultural intensity) are mapped as darker shaded segment-sheds.

Diatom-environmental Relationships

Relationships among site-level variables and diatom taxa composition for all 155 samples in the training set were explored using canonical correspondence analysis (CCA), a multivariate ordination technique for direct gradient analysis (ter Braak and Prentice 1988) available in the CANOCO 4.5 software package (ter Braak and Šmilauer 2002). The distribution of site-level environmental variables and taxa among samples was initially explored with principal components analysis (PCA) and detrended correspondence analysis (DCA), respectively, to screen for outliers and determine gradient length. A CCA with forward selection was used to identify a subset of site-level variables that independently explained a significant portion of variance in the diatom taxa data (Monte Carlo test for significance; 999 permutations; $P < 0.05$).

Diatom-inference Transfer Functions

Transfer functions for 17 site-level water quality variables (Table 2) were developed using weighted averaging (WA) regression with inverse deshrinking and jackknife (leave-one-out) cross-validation for error estimation and lognormal taxa transformation (C2 software; Juggins 2003). DI estimates of water quality variables for each sample were calculated by taking the optimum of each taxon to that variable, weighting it by its abundance in that sample, and calculating the average of the combined weighted taxa optima. All transfer functions were similarly developed using tolerance downweighting of the taxa (Birks *et al.* 1994). The strength of the transfer functions were evaluated by calculating the squared correlation coefficient (r^2) and the root mean square error (RMSE) between measured values and transfer function estimates of those values for all samples. Jackknifing ($WA_{jackknife}$) was used in transfer function validation to provide a more realistic error estimate (RMSEP, the root mean square error of prediction) because the same data were used to both generate and test the WA transfer function.

Although 155 sample events had complete environmental and diatom data for exploratory analyses (CCA), an additional 15 sample events had TP mea-

surements (and corresponding diatom samples), so transfer function development for TP included a total of 170 records each for taxa and site-level variables. Further steps were taken in the evaluation of the total phosphorus (TP) transfer function. Samples with poor correspondence between observed and DI TP were identified from plots of $WA_{jackknife}$ residuals; samples with residuals greater than the standard deviation of measured TP ($SD_{log(TP)}$= 0.49) in the training set were removed for development of a "refined" transfer function, a technique often employed to improve diatom-nutrient coefficients (Reavie *et al.* 1995, Edlund and Kingston 2004). This choice to remove samples with apparent poorly-inferred TP is based on the idea that it will provide more accurate taxon coefficients (i.e., optima and tolerances) because it removes samples with apparently poor taxa-environmental relationships. This transfer function refinement is somewhat arbitrary, but is chosen to eliminate samples with atypical diatom-environmental relationships.

For each modeled water quality variable (Table 2), both measured and diatom-inferred values were regressed against the set of watershed-level predictors using multiple linear regression (using the software program NCSS) and evaluated using the coefficient of determination (r^2). The regressions tested the relationship between watershed properties and water quality in the adjacent coastal system, and were used to determine whether diatom-inferred or measured water quality is more closely related to watershed characteristics such as agricultural and urban development.

RESULTS

Diatoms

Rich diatom assemblages were the norm in the Great Lakes coastal samples. Approximately 2,100 taxa (including varieties, forms and subspecies) were identified, and 352 taxa were sufficiently common to be included in statistical analyses. Samples were dominated by periphytic taxa, with an average of only 11% planktonic composition in a sample. The most common taxa, based on effective number of occurrences across all samples (N2) were *Achnanthidium minutissimum* (12; code numbers and authorities are in Table 3), *Amphora pediculus* (24), *Staurosirella pinnata* (355), *Planothidium frequentissimum* (284) and *Navicula cryptotenella* (201). Based on the sum of all diatom counts, the most common taxa were *Achnanthidium minutissimum* (12; 9.2% of all valves counted), *Amphora pediculus* (24; 4.9%), *Pseudostaurosira brevistriata* (310; 2.6%), *Planothidium rostratum* (294; 2.3%) and *Staurosirella pinnata* (355; 2.2%). A number of taxa did not match specimens currently published in the literature, and so they have been assigned temporary numbers (Table 3). Genera such as *Martyana* especially require taxonomic reconciliation, as a wide variety of taxa that may be varieties or forms of *Martyana martyi* (180) were identified. Work is ongoing to characterize the taxonomy of these numbered taxa.

More details of the diatom taxonomy and count data will be available as a database on the Internet in 2007 (http://glei.nrri.umn.edu).

Diatom-environmental Relationships

DCA on the diatom taxa data matrix produced a gradient of 4.7 standard deviation units along the first axis, suggesting a long gradient in diatom taxa turnover and high diversity, and that unimodal methods (i.e., CCA and weighted averaging transfer function application) were appropriate (ter Braak and Šmilauer 2002). Neither PCA nor DCA identified any samples that were considered outliers in terms of both environmental and diatom data, respectively.

CCA revealed that 23% of the total variation in the diatom data was explained by the environmental variables included in the analysis. Forward selection identified 12 environmental variables that explained the maximum amount of variance in the diatom data (Fig. 3, Table 4). This subset of variables included, in order of selection (Monte Carlo, $P < 0.05$), Erie, TP, Lat(itude), HE, Ont(ario), RW, TN, NO3NO2, EC25, chlorophyll *a* (Chla), Sup(erior) and pH. Although many of these selected variables were correlated (e.g., TN, TP, and Chla), their selection indicates that they independently explained a unique proportion of variance in the diatom data. Also, relatively low variance inflation factors (Table 4) indicated that these selected variables independently explained a unique proportion of variance in the diatom data. Although the first four CCA axes merit environmental interpretation, for clarity we focused on the dissemination of sample and taxa score data distributed along the first two axes because they reflected the greatest proportion of explained variance.

Both CCA axes 1 and 2 defined gradients of nutrients and the overall lake effect on environmental conditions, with axis 2 capturing the pH gradient. As is typical for CCA biplots, a great deal more in-

TABLE 3. Common diatom species, their abundance statistics and total phosphorus coefficients. Although the diatom based model provides log-transformed total phosphorus values, the optima have been back-transformed for reference. Code numbers correspond to Figure 3. Taxa that could not be matched to published specimens are identified by temporary numbers or descriptions, including the identifying institution (UMD = University of Minnesota Duluth; JCU = John Carroll University; UMICH = University of Michigan). N = number of samples where taxon was encountered; N2 = effective number of occurrences.

Code	Taxon	Authority	Code number	N	N2	Max.	Opt. (µg/L)	Opt. (log(µg/L+1))	Tol. (log (µg/L))
ACECONSP	*Achnanthes conspicua*	A. Mayer	1	61	42.0	6.0	20.8	1.338	0.414
ACECURTI	*Achnanthes curtissima*	J.R. Carter	2	3	1.6	11.8	38.8	1.599	0.332
ACEDAUI	*Achnanthes daui*	Foged	3	7	4.0	8.8	67.6	1.836	0.471
ACEGRANA	*Achnanthes grana*	Hohn and Hellerman	4	23	14.9	10.1	32.2	1.521	0.401
ACEMINUS	*Achnanthes minuscula*	Hust.	5	15	9.3	4.3	34.5	1.551	0.535
ACEZIEGL	*Achnanthes ziegleri*	Lange-Bert.	6	32	20.9	2.7	15.2	1.210	0.383
ACHAFFIN	*Achnanthidium affine*	(Grunow) Czarn.	7	28	12.4	12.6	9.8	1.032	0.369
ACHBIACX	*Achnanthidium biasolettiana* complex	(Grunow) Bukht.	8	28	14.2	9.5	18.1	1.281	0.517
ACHEXIGU	*Achnanthidium exiguum*	(Grunow) Czarn.	9	57	35.9	4.0	28.9	1.476	0.395
ACHMACRO	*Achnanthidium macrocephalum*	(Hust.) Round and Bukht.	10	10	5.8	11.5	20.5	1.333	0.163
ACHMICRO	*Achnanthidium microcephalum*	Kütz.	11	22	13.6	13.0	8.6	0.984	0.354
ACHMINCX	*Achnanthidium minutissimum* complex	(Kütz.) Czarn.	12	145	111.7	70.5	18.7	1.296	0.441
ACHSAPRO	*Achnanthidium saprophila*	(H.Kobay. and Mayama) Round and Bukht.	13	10	6.8	3.5	17.9	1.276	0.287
ACLNORMA	*Actinocyclus normanii*	(W. Greg.) Hust.	14	15	11.1	1.5	80.7	1.912	0.232
ADLBRYOP	*Adlafia bryophila*	(Peterson) Lange-Bert.	15	9	4.0	5.9	12.1	1.119	0.250
ADLMINUS	*Adlafia minuscula*	(Grunow) Lange-Bert.	16	11	5.3	3.8	40.6	1.620	0.297
AMPAEQUA	*Amphora aequalis*	Krammer	17	10	7.6	2.1	24.8	1.412	0.453
AMPINARI	*Amphora inariensis*	Krammer	19	68	46.5	16.2	24.3	1.403	0.403
AMPLIBYC	*Amphora libyca*	Ehrenb.	20	49	31.4	9.8	35.6	1.563	0.406
AMPOVAAF	*Amphora ovalis* v. *affinis*	(Kütz.) VanHeurck ex DeToni	22	7	4.7	1.5	36.7	1.577	0.333
AMPOVALI	*Amphora ovalis*	(Kütz.) Kütz.	23	16	10.9	1.8	32.2	1.520	0.504
AMPPEDIC	*Amphora pediculus*	(Kütz.) Grunow	24	132	100.2	37.4	23.7	1.393	0.458
AMPPERPU	*Amphora perpusilla*	(Grunow) Grunow	25	34	24.5	13.7	19.1	1.304	0.486
AMPS1UMD	*Amphora* sp. 1 UMD		26	5	3.5	1.6	17.0	1.255	0.240
AMPSUBCO	*Amphora subcostulata*	Stoermer and J.J. Yang	27	21	11.7	13.4	24.8	1.412	0.440
AMPTHUME	*Amphora thumensis*	(Mayer) A. Cleve	28	20	14.6	2.2	17.4	1.264	0.322
AMPVENET	*Amphora veneta*	Kütz.	29	8	5.4	1.7	21.4	1.351	0.351
ANEMINOR	*Aneumastus minor*	(Hust.) Lange-Bert.	30	10	7.6	2.2	7.5	0.929	0.395
ASTFORMO	*Asterionella formosa*	Hass.	31	12	7.8	1.4	24.6	1.408	0.609
AULALPIG	*Aulacoseira alpigena*	(Grunow) Krammer	32	17	10.2	21.3	48.4	1.694	0.436
AULAMBIG	*Aulacoseira ambigua*	(Grunow) Simonsen	33	20	11.6	20.4	45.2	1.665	0.346
AULGRANU	*Aulacoseira granulata*	(Ehrenb.) Simonsen	34	33	20.0	5.3	70.6	1.855	0.449
AULISLAN	*Aulacoseira islandica*	(O. Müll.) Simonsen	35	14	11.2	1.1	103.6	2.020	0.376
AULITALI	*Aulacoseira italica*	(Ehrenb.) Simonsen	36	13	7.8	4.8	61.6	1.796	0.387
BACPARAD	*Bacillaria paradoxa*	Gmelin	38	5	3.2	2.3	120.0	2.083	0.354

BELBEROL	*Belonastrum berolinensis*	(Lemmermann) Round and Maidana	39	20	12.6	4.7	32.7	1.528	0.274
BRABREBI	*Brachysira brebissonii*	R. Ross	40	1	1.0	6.3	11.0	1.079	0.402
BRANEOEX	*Brachysira neoexilis*	Lange-Bert.	41	28	21.9	7.4	7.8	0.944	0.355
BRAVITRE	*Brachysira vitrea*	(Grunow) R. Ross	42	19	11.4	6.6	11.0	1.080	0.310
CALBACIU	*Caloneis bacillum*	(Grunow) Cleve	43	23	16.9	1.8	34.2	1.547	0.488
CAVCOCCO	*Cavinula cocconeiformis*	(W. Greg. ex Grev.) D.G. Mann and Stickle	44	11	7.5	2.1	16.3	1.238	0.274
CAVJAERN	*Cavinula jaernefeltii*	(Hust.) D.G. Mann and Stickle	45	7	4.0	6.0	8.4	0.973	0.181
CAVSCUTE	*Cavinula scutelloides*	(W. Sm.) Lange-Bert.	46	41	24.6	3.6	39.0	1.602	0.402
CAVUTERM	*Cavinula utermoehlii*	(auth. unknown)	47	21	16.3	1.1	23.9	1.397	0.405
COCNEODI	*Cocconeis neodiminuta*	Krammer	48	44	28.8	6.0	18.3	1.285	0.397
COCNEOTH	*Cocconeis neothumensis*	Krammer	49	90	57.7	17.2	23.6	1.391	0.429
COCPEDIC	*Cocconeis pediculus*	Ehrenb.	50	46	22.6	70.5	26.1	1.432	0.439
COCPLAEU	*Cocconeis placentula* v. *euglypta*	(Ehrenb.) Grunow	51	72	45.6	7.3	32.9	1.530	0.408
COCPLALI	*Cocconeis placentula* v. *lineata*	(Ehrenb.) VanHeurck	52	101	66.5	17.0	35.8	1.566	0.417
COCPLAPS	*Cocconeis placentula* v. *pseudolineata*	Geitler	53	7	4.5	9.3	32.8	1.528	0.715
COCPLACE	*Cocconeis placentula*	Ehrenb.	54	43	21.7	56.5	28.5	1.470	0.401
COCPSTHU	*Cocconeis pseudothumensis*	Reichardt	55	10	6.6	2.5	20.2	1.327	0.370
CRAACCOM	*Craticula accomoda*	(Hust.) D.G. Mann	56	6	2.7	3.6	44.4	1.657	0.232
CRACUSPI	*Craticula cuspidata*	(Kütz.) D.G. Mann	57	9	6.9	1.1	61.7	1.797	0.244
CRAS1NOR	*Craticula* sp. 1 UMICH		58	6	3.7	1.2	17.7	1.273	0.247
CTOPULCH	*Ctenophora pulchella*	(Ralfs ex Kütz.) D.M. Williams and Round	59	21	14.7	2.3	60.1	1.786	0.293
CSPDUBIU	*Cyclostephanos dubius*	(Fricke) Round	60	15	8.5	5.7	107.5	2.035	0.262
CSPINVIS	*Cyclostephanos invisitatus*	(Hohn and Hellermann) Theriot, Stoermer and Håk.	61	20	13.5	5.6	64.2	1.815	0.441
CSPTHOLI	*Cyclostephanos tholiformis*	Stoermer, Håk. and Theroit	62	25	13.9	7.2	97.9	1.995	0.309
CYCATO1J	*Cyclotella atomus* v. 1 JCU		64	6	4.6	8.0	103.8	2.020	0.453
CYCATOMU	*Cyclotella atomus*	Hust.	65	25	12.8	46.3	108.1	2.038	0.383
CYCCOMCX	*Cyclotella comensis* complex	Grunow	68	22	13.5	3.1	9.4	1.015	0.453
CYCCRYPT	*Cyclotella cryptica*	Reimann, Lewin and Guillard	69	5	4.4	1.5	129.9	2.117	0.267
CYCDISUN	*Cyclotella distinguenda* v. *unipunctata*	(Hust.) Håk.	72	14	7.2	3.0	20.8	1.339	0.334
CYCDISTI	*Cyclotella distinguenda*	Hust.	73	4	1.5	5.0	12.9	1.144	0.133
CYCDUBIA	*Cyclotella dubia*	Hilse	74	1	1.0	5.2	84.0	1.929	0.402
CYCOCELL	*Cyclotella ocellata*	Pant.	77	39	22.4	6.7	21.1	1.345	0.344
CYCOCECO	*Cyclotella* sp. 6 GLRD		78	7	5.1	1.8	64.1	1.814	0.639
CYCPSEUD	*Cyclotella pseudostelligera*	Hust.	79	37	25.3	5.0	56.8	1.762	0.338
CYCSTELL	*Cyclotella stelligera*	(Cleve and Grunow) VanHeurck	81	17	11.1	5.7	36.7	1.577	0.457
CYCSTOID	*Cyclotella stelligeroides*	Hust.	82	7	5.5	1.2	9.8	1.033	0.579
CYTSOLEA	*Cymatopleura solea*	(Bréb. and Godey) W. Sm.	84	19	15.6	1.1	48.7	1.697	0.186
CYMAFFIN	*Cymbella affinis*	Kütz.	85	16	12.2	1.3	10.6	1.063	0.424
CYMAMPHI	*Cymbella amphicephala*	Nägeli	86	7	4.3	2.0	14.2	1.182	0.429
CYMS111J	*Cymbella* sp. 111 JCU		87	1	1.0	6.6	9.0	1.000	0.402
DELDELIC	*Delicata delicatula*	(Kütz.) Krammer	88	13	8.2	12.0	5.3	0.803	0.474

(Continued)

TABLE 3. (Continued).

Code	Taxon	Authority	Code number	N	N2	Max.	Opt. (µg/L)	Opt. (log(µg/L+1))	Tol. (log (µg/L))
DENKEUTZ	*Denticula kuetzingii*	Grunow	89	19	12.7	10.9	7.6	0.934	0.379
DENTENCR	*Denticula tenuis crassula*	(Nägeli) W. West and G.S. West	90	8	4.4	8.2	4.0	0.695	0.205
DENTENUI	*Denticula tenuis*	Kütz.	91	22	10.7	29.1	8.9	0.994	0.542
DIATENEL	*Diatoma tenue elongatum*	Lyngb.	92	18	11.5	4.8	10.0	1.042	0.572
DIATENUE	*Diatoma tenue*	C. Agardh	93	23	13.3	4.5	27.2	1.450	0.409
DIAVULGA	*Diatoma vulgare*	Bory	94	13	9.5	1.3	47.5	1.685	0.508
DITASTER	*Distrionella asterionelloides*	D.M. Williams 1990	95	2	1.8	8.5	5.3	0.797	0.103
ENCCAESP	*Encyonema caespitosum*	Kütz.	96	27	14.6	6.7	16.8	1.250	0.379
ENCEVERG	*Encyonema evergladianum*	Krammer	97	7	5.5	4.5	5.6	0.821	0.185
ENCMINUT	*Encyonema minutum*	(Hilse ex Rabenh.) D.G. Mann	98	24	9.2	22.4	14.6	1.194	0.498
ENCREICH	*Encyonema reichardtii*	(Krammer) D.G. Mann	99	10	6.6	3.4	11.1	1.083	0.318
ENCSILES	*Encyonema silesiacum*	(Bleisch) D.G. Mann	100	66	44.2	9.4	18.6	1.293	0.460
ENCVENTR	*Encyonema ventricosum*	Kütz.	101	6	5.0	1.1	10.5	1.059	0.514
ENPCESAT	*Encyonopsis cesatii*	(Rabenhorst) Krammer	102	9	6.8	2.6	9.8	1.033	0.253
ENPKRAMM	*Encyonopsis krammeri*	Reich.	103	14	6.9	7.6	6.8	0.892	0.362
ENPMICRO	*Encyonopsis microcephala*	(Grunow) Krammer	104	67	42.6	30.3	14.8	1.197	0.397
ENPMINUT	*Encyonopsis minuta*	Krammer and Reichardt	105	20	11.6	6.0	15.3	1.212	0.480
ENPS1UMD	*Encyonopsis* sp. 1 UMD		106	5	4.1	2.4	10.8	1.071	0.205
ENPSUBMI	*Encyonopsis subminuta*	Krammer and Reichardt	107	18	12.0	5.3	8.2	0.965	0.352
ENPVANDA	*Encyonopsis vandamii*	Krammer and Lange-Bert.	108	5	3.9	3.0	3.4	0.639	0.315
EOLMINIM	*Eolimna minima*	(Grunow) Lange-Bert.	109	78	56.4	10.7	28.5	1.470	0.457
EPIARGUS	*Epithemia argus*	(Ehrenb.) Kütz.	110	11	7.4	1.5	63.3	1.809	0.433
EPISORE	*Epithemia sorex*	Kütz.	111	5	3.9	1.3	77.9	1.897	0.674
EPITURGI	*Epithemia turgida*	(Ehrenb.) Kütz.	112	7	5.4	2.0	43.0	1.644	0.625
EUCFLEAL	*Eucocconeis flexella* v. *alpestris*	(Brun) Hust.	113	15	11.0	2.2	8.6	0.982	0.287
EUCFLEXE	*Eucocconeis flexella*	(Kütz.) Cleve	114	21	15.5	3.5	8.7	0.988	0.363
EUCLAEVI	*Eucocconeis laevis*	(Østrup) Lange-Bert.	115	29	17.9	9.6	8.1	0.957	0.478
EUNBILUN	*Eunotia bilunaris*	(Ehrenb.) Mills	116	16	7.4	8.3	39.0	1.602	0.536
EUNFORMI	*Eunotia formica*	Ehrenb.	117	5	2.9	1.3	44.5	1.658	0.420
EUNIMPLI	*Eunotia implicata*	Norpel and Lange-Bert.	118	6	4.4	1.5	42.4	1.637	0.583
EUNINCIS	*Eunotia incisa*	W. Sm.	119	12	7.4	4.8	20.3	1.329	0.397
EUNPECMI	*Eunotia pectinalis minor*	(Kütz.) Rabenh.	120	7	4.6	3.4	18.7	1.294	0.258
EUNPRAER	*Eunotia praerupta*	Ehrenb.	121	6	3.8	1.5	44.3	1.656	0.702
EUNSOLEI	*Eunotia soleirolii*	(Kütz.) Rabenh.	122	5	2.0	16.6	12.4	1.126	0.495
FALPYGMA	*Fallacia pygmaea*	(Kütz.) D.G. Mann	123	11	8.6	1.3	97.5	1.993	0.311
FALSUBUL	*Fallacia sublucidula*	(Hust.) D.G. Mann	124	6	4.4	1.2	14.3	1.184	0.255
FALTENER	*Fallacia tenera*	(Hust.) D.G. Mann	125	10	7.2	1.5	87.5	1.947	0.280
FRACAPGR	*Fragilaria capucina* v. *gracilis*	(Østrup) Hust.	126	16	11.2	1.9	24.0	1.397	0.468
FRACAPME	*Fragilaria capucina* v. *mesolepta*	Rabenh.	127	36	16.0	35.9	58.5	1.774	0.371
FRACAPPE	*Fragilaria capucina* v. *perminuta*	(Grunow) Lange-Bert.	128	42	29.2	7.4	23.3	1.386	0.426

FRACAPVR	*Fragilaria capucina* v. *rumpens*	(Kütz.) Lange-Bert.	129	28	15.8	19.6	12.8	1.140	0.442
FRACAPUC	*Fragilaria capucina*	Desm.	130	74	42.9	30.6	31.2	1.508	0.449
FRACROTO	*Fragilaria crotonensis*	Kitton	131	20	12.8	2.8	15.6	1.219	0.483
FRADEL1E	*Fragilaria delicatissima* v. 1 UMD		132	1	1.0	23.2	4.0	0.699	0.402
FRADELIC	*Fragilaria delicatissima*	(W. Smith) Lange-Bert.	133	38	22.7	12.5	8.4	0.972	0.461
FRANANAN	*Fragilaria nanana*	Lange-Bert.	134	29	19.3	2.5	12.1	1.119	0.456
FRANITZS	*Fragilaria nitzschioides*	Grunow	135	2	1.2	23.2	112.6	2.055	0.312
FRAS7JCU	*Fragilaria* sp. 7 JCU		136	2	1.2	8.0	71.4	1.860	0.255
FRATENER	*Fragilaria tenera*	(W. Smith) Lange-Bert.	137	47	27.6	7.8	19.2	1.306	0.445
FRAVAUCH	*Fragilaria vaucheriae*	(Kütz.) J.B.Petersen	138	93	56.5	17.3	26.5	1.440	0.498
FRKSIMIL	*Frankophila similioides*	Lange-Bert.	139	17	8.2	25.1	43.3	1.646	0.516
FRUCRASS	*Frustulia crassinervia*	(Breb.) Lange-Bert. and Krammer	140	4	2.6	5.8	11.2	1.085	0.114
GEIACCEP	*Geissleria acceptata*	(Hust.) Lange-Bert. and Metz.	141	46	30.8	11.4	14.2	1.182	0.468
GEIARKEN	*Geissleria arkensii*	(auth. unknown)	142	1	1.0	5.3	83.0	1.924	0.402
GEICUMME	*Geissleria cummerowii*	(Kalbe) Lange-Bert.	143	8	4.8	9.6	20.2	1.326	0.458
GEIDECUS	*Geissleria decussis*	(Østrup) Lange-Bert. and Metz.	144	56	35.3	31.5	27.2	1.450	0.394
GEIPALUD	*Geissleria paludosa*	(Hust.) Lange-Bert. and Metz.	145	7	2.9	5.3	32.3	1.522	0.256
GEISCHOE	*Geissleria schoenfeldii*	(Hust.) Lange-Bert. and Metz.	146	13	4.9	15.8	32.3	1.523	0.333
GEISIMIL	*Geissleria similis*	(Krasske) Lange-Bert. and Metz.	147	5	3.6	1.5	41.1	1.624	0.442
GOMACUMI	*Gomphonema acuminatum*	Ehrenb.	148	8	6.5	1.0	34.0	1.545	0.606
GOMANGUS	*Gomphonema angustatum*	(Kütz.) Rabenh.	149	22	13.4	11.6	15.8	1.226	0.476
GOMANG1E	*Gomphonema angustatum* v. 1 UMD	(Kütz.) Rabenh. (no dot)	150	8	5.1	2.2	54.1	1.741	0.428
GOMANGUU	*Gomphonema angustum*	Agardh	151	48	23.2	52.3	14.5	1.190	0.473
GOMCBAVA	*Gomphonema* cf. *bavaricum*		152	1	1.0	5.1	8.0	0.954	0.402
GOMCPUMI	*Gomphonema* cf. *pumilum*		153	9	6.0	19.9	16.2	1.235	0.299
GOMCLAVA	*Gomphonema clavatum*	Ehrenberg	154	9	6.7	2.2	69.0	1.845	0.419
GOMGRACI	*Gomphonema gracile*	Ehrenb. emend. VanHeurck	155	20	16.0	1.2	49.0	1.699	0.374
GOMMINUT	*Gomphonema minutum*	(Agardh) Agardh	156	20	8.9	9.4	18.5	1.291	0.466
GOMOLIOL	*Gomphonema olivaceum* v. *olivaceoides*	(Hust.) Lange-Bert.	157	5	3.4	1.5	3.2	0.626	0.343
GOMOLIVA	*Gomphonema olivaceum*	(Lyngb.) Kütz.	158	34	20.8	8.0	33.1	1.533	0.592
GOMPARVU	*Gomphonema parvulum*	(Kütz.) Kütz.	159	54	37.0	8.1	47.1	1.682	0.372
GOMPUMEL	*Gomphonema pumilum* v. *elegans*	E. Reichardt and Lange-Bert.	160	8	5.8	1.7	28.8	1.474	0.288
GOMPUMIL	*Gomphonema pumilum*	(Grunow) Reich. and Lange-Bert.	161	21	10.0	36.9	16.0	1.229	0.595
GOMSAR1E	*Gomphonema sarcophagus* v. 1 UMD		162	1	1.0	5.4	8.5	0.978	0.402
GOMUTAE	*Gomphonema utae*	Lange-Bert. and Reich.	163	3	1.9	6.1	114.2	2.061	0.147
GYRATTEN	*Gyrosigma attenuatum*	(Kütz.) Rabenh.	164	5	3.1	5.9	111.2	2.050	0.208
GYRSPENC	*Gyrosigma spencerii*	(Quek.) J.W. Griff. and Henfr.	165	8	6.1	2.1	72.5	1.866	0.254
HIPCAPIT	*Hippodonta capitata*	(Grunow) Lange-Bert., Metz. and Witk.	166	53	35.0	6.6	62.3	1.801	0.352
HIPCOSTU	*Hippodonta costulata*	(Grunow) Lange-Bert., Metz. and Witk.	167	19	10.4	39.3	30.7	1.501	0.288
HIPHUNGA	*Hippodonta hungarica*	(Grunow) Lange-Bert., Metz. and Witk.	168	30	15.8	13.4	55.3	1.750	0.390

(Continued)

TABLE 3. (Continued).

Code	Taxon	Authority	Code number	N	N2	Max.	Opt. (µg/L)	Opt. (log(µg/L+1))	Tol. (log (µg/L))
KARCLERO	*Karayevia clevei* v. *rostratum*	(Hust.) Kingston	172	13	7.2	3.3	14.2	1.182	0.420
KARCLEVE	*Karayevia clevei*	(Grunow) Round and Bukht.	173	74	52.6	5.6	21.2	1.345	0.430
KARLATER	*Karayevia laterostrata*	(Hust.) Kingston	174	8	5.4	2.1	15.2	1.209	0.386
KOLPLOEN	*Kolbesia ploenensis*	(Hust.) Kingston	176	6	4.7	1.5	27.2	1.450	0.169
KOLSUCHL	*Kolbesia suchlandtii*	(Hust.) Kingston	177	10	6.1	3.3	16.6	1.246	0.394
LENHUNGA	*Lemnicola hungarica*	(Grunow) Round and Basson	178	6	4.0	1.5	99.6	2.003	0.415
MARMARTY	*Martyana martyi*	(Hérib.) Round	180	26	18.3	7.5	25.6	1.424	0.386
MARS2JCU	*Martyana* sp. 2 JCU		181	16	10.2	4.6	16.8	1.251	0.326
MARS2UMD	*Martyana* sp. 2 UMD		182	6	3.6	1.6	31.1	1.507	0.238
MARS3JCU	*Martyana* sp. 3 JCU		183	5	2.8	9.2	28.2	1.466	0.329
MARS3UMD	*Martyana* sp. 3 UMD		184	17	12.7	2.3	37.3	1.583	0.522
MARS4JCU	*Martyana* sp. 4 JCU		185	10	7.0	1.3	54.8	1.746	0.397
MARS4UMD	*Martyana* sp. 4 UMD		186	10	6.2	1.8	49.5	1.703	0.542
MARS5UMD	*Martyana* sp. 5 UMD		187	14	9.4	2.2	58.1	1.772	0.572
MARS8UMD	*Martyana* sp. 8 UMD		188	5	3.7	2.0	45.2	1.665	0.914
MAYAGRES	*Mayamaea agrestis*	(Hust.) Lange-Bert.	189	5	3.1	4.3	20.6	1.335	0.558
MAYATOMU	*Mayamaea atomus*	(Kütz.) Lange-Bert.	190	8	5.5	1.8	86.7	1.943	0.500
MELVARIA	*Melosira varians*	C. Agardh	191	15	9.7	8.4	84.0	1.929	0.500
NAVANGUS	*Navicula angusta*	Grunow	192	5	2.9	1.1	30.1	1.493	0.467
NAVANTON	*Navicula antonii*	Lange-Bert.	193	28	18.0	4.4	46.4	1.675	0.335
NAVBOURR	*Navicula bourrellyivera*	Lange-Bert., Witk. and Stach.	194	8	6.1	5.0	88.4	1.951	0.309
NAVCAPRA	*Navicula capitatoradiata*	Germain	195	32	17.5	16.4	61.3	1.795	0.350
NAVCARI	*Navicula cari*	Ehrenb.	196	16	12.7	1.0	23.5	1.389	0.458
NAVCATER	*Navicula caterva*	Hohn and Hellerman	197	12	10.2	1.0	61.5	1.796	0.423
NAVCNOVA	*Navicula* cf. *novaesiberica*		198	2	1.4	22.2	14.5	1.190	0.202
NAVCVIRI	*Navicula* cf. *viridula*		199	7	5.2	1.2	91.6	1.967	0.505
NAVCRYCP	*Navicula cryptocephala*	Kütz.	200	55	38.0	10.7	38.3	1.595	0.429
NAVCRYPT	*Navicula cryptotenella*	Lange-Bert.	201	107	70.8	18.0	22.7	1.376	0.422
NAVCRYOI	*Navicula cryptotenelloides*	Lange-Bert.	202	33	21.7	6.8	16.4	1.241	0.506
NAVERIFU	*Navicula erifuga*	Lange-Bert.	203	7	5.6	2.1	117.6	2.074	0.215
NAVGERMA	*Navicula germainii*	Wallace	204	14	8.1	3.7	125.7	2.103	0.327
NAVGREGA	*Navicula gregaria*	Donkin	205	75	49.2	22.9	67.0	1.833	0.392
NAVKOTSC	*Navicula kotschyi*	Grunow	206	7	5.8	1.2	17.4	1.266	0.278
NAVLANCE	*Navicula lanceolata*	(C. Agardh) Kütz.	207	26	12.5	12.7	56.7	1.761	0.242
NAVLIBON	*Navicula libonensis*	Schum.	208	15	9.5	2.2	62.7	1.804	0.408
NAVMENIL	*Navicula menisculus*	Schum.	209	31	20.4	5.6	52.2	1.726	0.413
NAVMENIS	*Navicula meniscus*	Schum.	210	5	2.5	7.0	66.5	1.829	0.285
NAVNOVAS	*Navicula novaesiberica*	Lange-Bert.	212	9	6.0	44.7	38.5	1.597	0.260
NAVPHYLL	*Navicula phyllepta*	Kütz.	213	19	10.7	5.0	81.5	1.916	0.352
NAVPSEUV	*Navicula pseudoventralis*	Hust.	214	8	4.6	5.9	16.4	1.241	0.416
NAVRADIO	*Navicula radiosa*	Kütz.	215	24	19.1	1.1	36.3	1.572	0.499

NAVREICH	*Navicula reichardtiana*	Lange-Bert.	216	35	20.1	12.5	38.5	1.597	0.357
NAVREINH	*Navicula reinhardtii*	Grunow	217	10	8.3	1.5	43.9	1.652	0.406
NAVRHYNC	*Navicula rhynchocephala*	Kütz.	218	17	10.9	2.8	62.9	1.806	0.487
NAVSALIN	*Navicula salinarum*	Grunow	219	14	11.0	8.8	102.6	2.015	0.238
NAVSCHAD	*Navicula schadei*	Krasske	220	8	4.6	6.1	18.6	1.292	0.344
NAVSLESV	*Navicula slesvicensis*	Grunow	221	5	3.1	8.9	81.7	1.917	0.433
NAVS132J	*Navicula* sp. 132 JCU (cf. *cincta*)		222	6	3.5	6.3	15.1	1.206	0.291
NAVS49JC	*Navicula* sp. 49 JCU		223	1	1.0	5.0	124.0	2.097	0.402
NAVSTROE	*Navicula stroemii*	Hust.	224	5	3.4	1.2	4.3	0.722	0.501
NAVSUBMI	*Navicula subminuscula*	Manguin	225	15	11.4	1.9	37.3	1.583	0.455
NAVSUBMU	*Navicula submuralis*	Hust.	226	13	9.1	6.3	18.7	1.294	0.378
NAVSUBRO	*Navicula subrotunda*	Hust.	227	9	5.7	2.1	22.5	1.371	0.497
NAVSUBTA	*Navicula subrotundata*	Hust.	228	15	10.6	1.4	26.0	1.432	0.422
NAVTANTU	*Navicula tantula*	Hust.	229	75	52.7	14.2	40.2	1.615	0.456
NAVTRIPU	*Navicula tripunctata*	(O.F. Müll.) Bory	230	37	19.9	19.5	32.0	1.519	0.474
NAVTRIVI	*Navicula trivialis*	Lange-Bert.	231	25	18.2	4.3	63.7	1.811	0.290
NAVUPSAL	*Navicula upsaliensis*	Grunow	232	23	18.2	1.0	55.6	1.753	0.340
NAVVANDA	*Navicula vandamii*	Schoemann and Archibald	233	16	11.7	3.8	71.2	1.858	0.404
NAVVENET	*Navicula veneta*	Kütz.	234	28	20.2	3.6	57.3	1.766	0.402
NAVVIRRO	*Navicula viridula* v. *rostellata*	(Kütz.) Cleve	235	6	4.1	1.2	111.7	2.052	0.323
NAVVIRID	*Navicula viridula*	(Kütz.) Ehrenb.	236	14	9.0	1.8	54.0	1.740	0.418
NAVWILDI	*Navicula wildii*	Lange-Bert.	238	5	4.1	1.1	9.4	1.017	0.170
NEIAMPLI	*Neidium ampliatum*	(Ehrenb.) Krammer	239	8	5.4	1.5	23.8	1.395	0.511
NITACI1U	*Nitzschia acicularioides* v. 1 UMD		240	6	4.2	1.5	107.7	2.036	0.444
NITACICU	*Nitzschia acicularis*	(Kütz.) W.Sm.	241	8	6.2	1.1	85.7	1.938	0.408
NITACIDO	*Nitzschia acidoclinata*	Lange-Bert.	242	11	6.1	3.6	52.6	1.729	0.485
NITAGNIT	*Nitzschia agnita*	Hust.	243	11	4.6	3.8	64.6	1.817	0.574
NITAMPHI	*Nitzschia amphibia*	Grunow	244	64	39.8	16.4	42.4	1.638	0.460
NITANGUS	*Nitzschia angustata*	(W. Sm.) Grunow	245	27	17.2	3.9	32.7	1.528	0.490
NITANGUL	*Nitzschia angustatula*	Lange-Bert.	246	14	9.4	2.4	54.8	1.746	0.362
NITAPICU	*Nitzschia apiculata*	(W. Greg.) Grunow	247	7	5.3	3.0	89.2	1.955	0.244
NITBACIL	*Nitzschia bacillum*	Hust.	248	28	22.5	1.7	18.2	1.282	0.396
NITCALID	*Nitzschia calida*	Grunow	249	7	5.5	2.5	93.0	1.973	0.225
NITDENTI	*Nitzschia denticula*	Grunow	250	8	5.1	2.3	67.1	1.833	0.562
NITDISME	*Nitzschia dissipata* v. *media*	(Hantzsch) Grunow	251	15	9.0	4.9	14.6	1.194	0.509
NITDISSI	*Nitzschia dissipata*	(Hantzsch) Grunow	252	53	32.6	6.4	41.5	1.628	0.425
NITFONTI	*Nitzschia fonticola*	Grunow	253	34	17.6	6.6	34.3	1.548	0.445
NITFRUST	*Nitzschia frustulum*	(Kütz.) Grunow	254	44	29.1	9.4	52.7	1.730	0.363
NITGRACI	*Nitzschia gracilis*	Hantzsch	255	17	12.2	2.3	40.5	1.618	0.593
NITHEUFL	*Nitzschia heufleriana*	Grunow	256	5	2.9	2.3	68.9	1.845	0.679
NITHUNGA	*Nitzschia hungarica*	Grunow	257	6	4.8	1.8	133.7	2.129	0.260
NITINCOG	*Nitzschia incognita*	Krasske	258	12	6.9	3.6	45.4	1.667	0.397
NITINCON	*Nitzschia inconspicua*	Grunow	259	33	19.6	14.5	48.0	1.690	0.423
NITINTER	*Nitzschia intermedia*	Hantzsch	260	7	5.8	1.0	69.5	1.848	0.434
NITLIEBE	*Nitzschia liebetruthii*	Rabenh.	261	13	9.3	1.7	58.9	1.777	0.501

(Continued)

TABLE 3. (Continued).

Code	Taxon	Authority	Code number	N	N2	Max.	Opt. (µg/L)	Opt. (log(µg/L+1))	Tol. (log (µg/L))
NITLINEA	*Nitzschia linearis*	(C. Agardh) W. Sm.	262	23	17.1	1.6	70.2	1.853	0.352
NITMICRO	*Nitzschia microcephala*	Grunow	263	11	7.8	1.8	52.6	1.729	0.396
NITMINUA	*Nitzschia minuta*	Bleisch	264	9	6.8	2.4	70.5	1.855	0.329
NITPALDE	*Nitzschia palea* v. *debilis*	(Kütz.) Grunow	265	7	4.4	1.3	44.1	1.654	0.390
NITPALTE	*Nitzschia palea* v. *tenuirostris*	Grunow	266	13	10.8	1.3	65.5	1.823	0.344
NITPALEA	*Nitzschia palea*	(Kütz.) W. Sm.	267	85	55.5	14.4	45.6	1.669	0.401
NITPALEC	*Nitzschia paleacea*	Grunow	268	26	13.8	8.3	51.8	1.723	0.525
NITPERMI	*Nitzschia perminuta*	(Grunow) M. Perag.	269	34	23.1	4.2	58.8	1.776	0.557
NITRADIC	*Nitzschia radicula*	Hust.	270	6	4.0	1.2	35.6	1.563	0.266
NITRECTA	*Nitzschia recta*	Hantzsch ex. Rabenh.	271	36	23.1	2.6	27.2	1.450	0.429
NITSILIQ	*Nitzschia siliqua*	Archibald	272	7	4.3	2.2	119.1	2.080	0.235
NITSOLIT	*Nitzschia solita*	Hust.	273	7	3.9	1.7	69.1	1.846	0.226
NITSUBAC	*Nitzschia subacicularis*	Hust.	274	8	6.6	1.1	53.6	1.737	0.291
NITSUPRA	*Nitzschia supralitorea*	Lange-Bert.	275	38	22.8	8.4	63.6	1.810	0.420
PLQCLEME	*Placoneis clementis*	(Grunow) E.J. Cox	276	16	13.2	1.2	46.4	1.676	0.440
PLQEXIGU	*Placoneis exigua*	(W. Greg.) Mersechk.	277	9	6.0	1.9	62.0	1.800	0.331
PLAGASTM	*Placoneis gastrum*	(Ehrenb.) Mersechk.	278	8	6.2	1.6	36.3	1.572	0.309
PLQPSEUD	*Placoneis pseudanglica*	(Lange-Bert.) E.J. Cox	279	20	12.8	2.3	40.4	1.617	0.347
PLABIPOR	*Planothidium biporomum*	Hohn and Hellerman	280	12	7.0	7.1	50.2	1.709	0.568
PLADELIC	*Planothidium delicatulum*	(Kütz.) Round and Bukht.	281	45	24.8	23.8	63.1	1.807	0.462
PLADUBIU	*Planothidium dubium*	(Grunow) Round and Bukht.	282	46	29.6	11.0	30.8	1.502	0.422
PLAENGEL	*Planothidium engelbrechtii*	(Cholin.) Round and Bukht.	283	37	22.2	14.8	55.5	1.752	0.467
PLAFREQU	*Planothidium frequentissimum*	(Lange-Bert.) Round and Bukht.	284	106	77.2	10.4	38.8	1.600	0.469
PLAHAUCK	*Planothidium hauckianum*	(Grunow) Round and Bukht.	285	12	6.4	3.2	47.5	1.686	0.475
PLAJOURS	*Planothidium joursacense*	(Héribaud) Lange-Bert.	286	24	20.3	1.7	18.1	1.280	0.472
PLALANCE	*Planothidium lanceolatum*	(Bréb.) Round and Bukht.	288	50	29.0	12.8	45.3	1.666	0.382
PLAOESTR	*Planothidium oestrupii*	(A. Cleve) Round and L.Bukht.	289	12	5.8	11.1	10.0	1.042	0.373
PLAPERPA	*Planothidium peragalli* v. *parvulum*	(R.M. Patrick) Andresen, Stoermer and Kreis	290	4	1.7	9.5	27.1	1.449	0.174
PLAPERAG	*Planothidium peragalli*	(Brun and Hérib.) Round and Bukht.	291	15	9.0	6.6	28.8	1.475	0.419
PLALANCA	*Planothidium robustum* v. *abbreviata*	(auth. unknown)	292	9	5.7	1.8	26.9	1.446	0.456
PLAROSV1	*Planothidium rostratum* v. 1 UMD		293	6	5.3	3.9	23.4	1.388	0.586
PLAROSTR	*Planothidium rostratum*	(Østrup) Round and Bukht.	294	92	63.6	34.0	28.2	1.465	0.422
PSABIORE	*Psammothidium bioretii*	(Germain) Bukht. and Round	295	41	24.7	5.8	24.3	1.403	0.330
PSADAONE	*Psammothidium daonense*	(Lange-Bert.) Lange-Bert.	296	9	6.6	1.2	15.8	1.225	0.300
PSAHELVE	*Psammothidium helveticum*	(Hust.) Bukht. and Round	297	11	7.9	1.5	25.6	1.425	0.450
PSALACVU	*Psammothidium lacus-vulcani*	(Lange-Bert.) Bukht.	298	13	9.4	1.4	12.4	1.127	0.472
PSALAUEN	*Psammothidium lauenburgianum*	(Hust.) Bukht. and Round	299	19	15.6	1.5	15.4	1.214	0.496
PSALEVAN	*Psammothidium levanderi*	(Hust.) Bukht. and Round	300	11	6.0	7.2	8.4	0.972	0.248

PSAPSSWA	*Psammothidium pseudoswazi*	(J.R.Carter) Bukht. and Round	301	2	1.3	6.9	14.0	1.175	0.621
PSAROSEN	*Psammothidium rosenstockii*	(Lange-Bert.) Bukht.	302	39	22.8	33.1	12.8	1.139	0.314
PSASACCU	*Psammothidium sacculum*	(J.R.Carter) Bukht.	303	11	6.7	6.5	24.7	1.410	0.340
PSASUBAT	*Psammothidium subatomoides*	(Hust.) Bukht. and Round	304	20	13.4	3.2	19.5	1.311	0.267
PSAVENTR	*Psammothidium ventralis*	(Krasske) Bukht. and Round	305	9	4.7	3.2	13.4	1.157	0.247
PRABRE1J	*Pseudostaurosira brevistriata* v. 1 JCU		306	5	4.2	1.0	33.7	1.540	0.192
PRABREBI	*Pseudostaurosira brevistriata* v. *binodis*	(Pantocsek) N.A. Andresen, Stoermer and Kreis	307	10	7.8	2.4	36.3	1.571	0.530
PRABREIN	*Pseudostaurosira brevistriata* v. *inflata*	(Pant.) M.B. Edlund	308	68	42.4	23.4	30.3	1.495	0.418
PRABR1NO	*Pseudostaurosira brevistriata* v. "lopsided"		309	9	4.4	7.3	24.2	1.401	0.699
PRABREVI	*Pseudostaurosira brevistriata*	(Grunow) D.M. Williams and Round	310	90	62.3	53.3	33.6	1.538	0.474
PRAMICRO	*Pseudostaurosira microstriata*	(Marciniak) Flower	311	8	3.4	7.4	36.8	1.577	0.449
PRAPOLON	*Pseudostaurosira polonica*	*sensu* Morales and Edlund	312	5	3.8	6.8	128.4	2.112	0.681
PRAS1JCU	*Pseudostaurosira* sp. 1 JCU		313	5	3.6	1.1	65.3	1.822	0.207
PRAS2JCU	*Pseudostaurosira* sp. 2 JCU		314	8	5.3	11.5	18.9	1.298	0.367
PRAZEILL	*Pseudostaurosira zeilleri*	(Hérib.) D.M. Williams and Round	315	10	4.1	4.3	38.5	1.596	0.425
PUNS1JCU	*Punctastriata* sp. 1 JCU		316	22	16.8	1.5	23.0	1.380	0.355
REISINUA	*Reimeria sinuata*	(W. Greg.) Kociolek and Stoermer	317	50	27.6	21.3	15.3	1.213	0.422
RHOABBRE	*Rhoicosphenia abbreviata*	(C. Agardh) Lange-Bert.	318	53	35.2	11.9	35.2	1.559	0.424
RHPGIBBA	*Rhopalodia gibba*	(Ehrenb.) O.Müll.	319	8	5.6	2.5	99.8	2.003	0.331
ROSLINCU	*Rossithidium linearis* f. *curta*	(auth. unknown)	320	20	13.5	4.1	19.4	1.309	0.316
ROSLINEA	*Rossithidium linearis*	(W. Sm.) Round and Bukht.	321	75	46.4	12.2	21.5	1.351	0.403
ROSPETER	*Rossithidium petersennii*	(Hust.) Round and Bukht.	322	17	10.0	4.9	19.7	1.317	0.467
ROSPUSIL	*Rossithidium pusillum*	(Grunow) Round and Bukht.	323	7	4.6	3.2	15.9	1.227	0.352
SELBACIL	*Sellaphora bacillum*	(Ehrenb.) D.G. Mann	324	9	6.7	1.1	35.3	1.560	0.344
SELLAEVI	*Sellaphora laevissima*	(Kütz.) D.G. Mann	326	13	8.9	1.2	65.2	1.821	0.449
SELMUTAT	*Sellaphora mutata*	(Krasske) Lange-Bert.	327	10	6.9	3.5	24.6	1.408	0.298
SELPUPUL	*Sellaphora pupula*	(Kütz.) Mereschk.	329	66	40.4	12.6	46.3	1.674	0.448
SELSEMOI	*Sellaphora seminuloides*	(Grunow) D.G. Mann	330	80	54.5	31.1	23.1	1.382	0.443
SELSEMIN	*Sellaphora seminulum*	(Grunow) D.G. Mann	332	46	30.8	5.9	27.2	1.451	0.506
SELS1JCU	*Sellaphora* sp. 1 JCU		333	7	5.7	1.5	27.0	1.446	0.198
SELVITAB	*Sellaphora vitabunda*	(Hust.) D.G. Mann	334	22	17.6	2.2	16.8	1.251	0.432
SKEPOTAM	*Skeletonema potamos*	(Weber) Hasle	335	5	4.8	2.0	63.4	1.809	0.276
SRACON2J	*Staurosira construens* v. 2 JCU		336	5	2.1	3.7	23.0	1.380	0.191
SRACON7J	*Staurosira construens* v. 7 JCU		337	1	1.0	18.5	17.0	1.255	0.402
SRACONBI	*Staurosira construens* v. *binodis*	(Ehrenb.) P.B. Hamilton	338	42	25.4	16.1	55.7	1.753	0.444
SRACOB1U	*Staurosira construens binodis* f. 1 UMD		339	8	5.8	2.0	74.8	1.880	0.427
SRACONON	*Staurosira construens* "deformed"		340	6	4.2	2.0	29.2	1.479	0.719
SRACONPU	*Staurosira construens pumila*	(Grunow) Kingston	341	30	17.1	12.8	65.6	1.824	0.552
SRACONSU	*Staurosira construens subsalina*	(Hust.) Andresen, Stoermer and Kreis	342	13	7.9	5.2	87.8	1.948	0.582

(Continued)

TABLE 3. (Continued).

Code	Taxon	Authority	Code number	N	N2	Max.	Opt. (µg/L)	Opt. (log(µg/L+1))	Tol. (log (µg/L))
SRACONVE	*Staurosira construens venter*	(Ehrenb.) Hamilton	343	72	47.4	24.9	33.6	1.539	0.505
SRACOV4J	*Staurosira construens venter* f. 4 JCU		344	3	1.2	5.7	19.4	1.310	0.155
SRACONST	*Staurosira construens*	(Ehrenb.) D.M. Williams and Round	345	86	51.0	68.9	34.9	1.555	0.443
SRAELLIP	*Staurosira elliptica*	(Schum.) D. M. Williams and Round	346	38	25.4	7.1	52.4	1.727	0.482
SRAPSCON	*Staurosira pseudoconstruens*	(Marciniak) D.M. Williams and Round	347	34	20.5	27.1	40.9	1.623	0.581
SRAS108J	*Staurosira* sp. 108 JCU		348	1	1.0	5.0	112.0	2.053	0.402
SLLLAPPO	*Staurosirella lapponica*	(Grunow) D.M. Williams and Round	349	6	4.1	1.2	28.3	1.467	0.360
SLLLEPTO	*Staurosirella leptostauron*	(Ehrenb.) D.M. Williams and Round	350	18	10.0	4.8	13.9	1.172	0.298
SLLMINUT	*Staurosirella minuta*	Morales and M.B. Edlund	351	42	27.8	9.3	33.8	1.542	0.452
SLLPINAC	*Staurosirella pinnata* v. *acuminata*	A. Mayer	352	29	19.9	6.9	43.8	1.651	0.464
SLLPININ	*Staurosirella pinnata* v. *intercedens*	(Grun.) P.B. Hamilton	353	26	16.7	5.3	27.9	1.460	0.570
SLLPINLA	*Staurosirella pinnata* v. *lancettula*	(Schum.) E.Y. Haw. and M.G. Kelly	354	71	49.5	5.7	38.1	1.592	0.494
SLLPINCS	*Staurosirella pinnata* complex	(Ehrenb.) D.M. Williams and Round	355	124	82.5	55.7	28.3	1.467	0.466
SLLS1JCU	*Staurosirella* sp. 1 JCU		356	5	4.7	1.1	22.2	1.366	0.293
SCYMENPL	*Stephanocyclus meneghiniana* v. *plana*	(auth. unknown)	358	17	9.1	8.5	120.6	2.085	0.269
SCYMENEG	*Stephanocyclus meneghiniana*	(auth. unknown)	359	54	28.2	24.0	89.6	1.957	0.312
SUSAGASS	*Stephanodiscus agassizensis*	Håk. and Kling	360	14	10.8	2.7	77.2	1.893	0.309
SUSALPIN	*Stephanodiscus alpinus*	Hust.	361	8	5.7	2.5	56.6	1.761	0.281
SUSHANTE	*Stephanodiscus hantzschii* f. *tenuis*	(Hust.) Håk. and Stoermer	362	21	11.7	3.9	111.6	2.052	0.329
SUSHANTZ	*Stephanodiscus hantzschii*	Grunow	363	43	26.3	9.5	65.8	1.825	0.435
SUSMINUS	*Stephanodiscus minutulus*	(Kütz.) Cleve and J.D. Möll.	365	12	7.4	2.3	63.1	1.807	0.526
SUSNIAGA	*Stephanodiscus niagarae*	Ehrenb.	366	3	1.8	6.7	102.7	2.016	0.376
SUSPARVU	*Stephanodiscus parvus*	Stoermer and Håk.	368	30	20.9	5.2	62.8	1.805	0.352
SURBREBK	*Surirella brebissonii* v. *kuetzingii*	Krammer and Lange-Bert.	371	7	4.6	7.5	84.6	1.933	0.195
SURMINUT	*Surirella minuta*	Bréb.	372	29	16.1	10.1	86.3	1.941	0.348
SYNAMPAU	*Synedra amphicephala* v. *austraica*	(Grunow) Hust.	373	5	3.2	2.6	17.6	1.268	0.306
SYNRADIA	*Synedra radians*	Kütz.	374	9	4.7	5.2	14.9	1.203	0.669
SYNULNA	*Synedra ulna*	(Nitzsch) Ehrenb.	375	31	21.5	1.6	35.4	1.561	0.604
SYLPARAS	*Synedrella parasitica*	(W. Smith) Round and Maidana	376	18	10.5	2.5	37.3	1.583	0.317
TABFLOCX	*Tabellaria flocculosa* complex	(Roth) Kütz.	377	24	12.3	6.3	19.4	1.310	0.434
TABQUADR	*Tabellaria quadriseptata*	Knuds.	378	5	3.0	3.9	10.9	1.076	0.397
TALFASCI	*Tabularia fasciculata*	(C.Agardh) D.M. Williams and Round	379	13	8.6	1.8	71.0	1.858	0.395
THMPSEUD	*Thalassiosira pseudonana*	Hasle and Heim.	380	9	6.3	1.8	84.5	1.932	0.430

TABLE 4. T-test values for the canonical coefficients and variance inflation factors (VIF) of the forward-selected environmental variables for each of the first four CCA axes. Significant (P < 0.01) t-values are in boldface.

NAME	Axis 1	Axis 2	Axis 3	Axis 4	VIF
Eigenvalue	0.416	0.209	0.193	0.133	
EC25	**2.65**	–1.23	–2.24	2.15	2.73
Lat	–2.45	1.78	**2.79**	**–3.28**	4.84
Chla	1.49	0.87	–0.32	**–3.18**	3.58
NO3NO2	**3.28**	**–5.66**	**–3.27**	0.15	1.85
TN	–0.87	**4.11**	**4.80**	**3.17**	3.34
TP	**3.37**	–0.02	**–6.22**	**–2.74**	5.06
pH	–0.45	**–3.04**	–2.04	2.43	1.50
Sup	**3.85**	1.17	–1.21	**4.06**	2.99
Erie	**9.43**	–0.66	**6.96**	**–4.34**	2.58
Ont	**5.75**	**–3.69**	2.33	**6.61**	1.34
HE	0.02	**–4.89**	0.28	**–4.05**	1.54
RW	1.36	1.50	3.64	**4.29**	1.69

formation is presented in Figure 3 than can be assimilated in our interpretation, and much of the detail in the diagram may be useful to readers with specific interests in taxa-environmental relationships in the Great Lakes. Some notable relationships are as follows. The positive portion of the first axis reflects high-nutrient samples (e.g., 151E593P, 152E595R and 160E610R) and taxa (e.g., *Nitzschia siliqua* (272), *Stephanocyclus meneghiniana* v. *plana* (358), and *Lemnicola hungarica* (178)) typical of Lake Erie. The two left-hand quadrants contain samples (e.g., 001S29H, 017S109C, and 109H411P) and taxa (e.g., *Denticula tenuis* (91), *Geissleria acceptata* (141), and *Staurosirella leptostauron* (350)) that are typical of lower nutrient conditions in Lakes Superior and Huron. Although pH was not a dominant variable in explaining the variation in the diatom data, a gradient of low to high pH runs from the upper left to the lower right quadrant, with acid tolerant (e.g., *Frustulia crassinervia* (140) and *Eunotia bilunaris* (116)) and alkaline tolerant (e.g., *Navicula novaesiberica* (212) and *Amphora aequalis* (17)) taxa lying on opposite ends of this gradient.

CCA ordination suggested statistically significant relationships between diatom distributions and the twelve forward-selected environmental variables. Therefore, these variables can potentially be inferred from diatom assemblages collected from Great Lakes coastal environments. From a management perspective there is little use in designing transfer functions to infer "lake" or coastal habitat type since these are geomorphic features. However, a forthcoming study identifies the lake and habitat specificity of the diatom assemblages, and characterizes diatom-environmental relationships on these smaller spatial and geomorphic scales (Kireta *et al.*, pers. comm., Center for Water and the Environment, Natural Resources Research Institute). Particularly useful transfer functions for future monitoring or downcore applications would be DI TP and DI EC25, to infer nutrient and ionic water quality, respectively.

Forward selection does not necessarily preclude a non-selected variable from subsequent diatom-inference transfer function development, but it should always be noted that such a function is actually inferring a suite of intercorrelated variables. For example, measured TSS is correlated with TP (r = 0.79), and so after the removal of TP during forward selection, no significant amount of the remaining variation in the diatom data was explained by TSS. However, in an independent comparison of TSS to diatom assemblages in a CCA (data not presented), TSS captured a significant amount of variation. In fact, in a series of such independent tests, all variables explained some significant proportion of variation in the diatom data. So, diatoms can be used to infer TSS, keeping in mind that the inferred TSS should be assumed to be correlated with nutrient concentrations and other variables.

Diatom-inference Transfer Functions

Because of the known strength of diatoms in monitoring and paleoecological applications, diatom-based transfer function development and assessment has become a fairly routine practice (Hall and Smol 1999). A series of transfer functions was developed to test the ability of the diatoms to infer water quality variables (Table 2). TP, field transparency tube clarity (TTurb), TSS, Chla, Cl and EC25 with $r^2_{jackknife}$ values of 0.55, 0.47, 0.44, 0.43, 0.43, and 0.42, respectively, provided the best apparent transfer functions to infer water quality. DO, NH4, and NO3NO2 provided the poorest transfer functions, with $r^2_{jackknife}$ values of 0.13, 0.16, and 0.18, respectively. Because of low diatom-environmental correlations for certain environmental variables during CCA, it was expected that some of these transfer functions (e.g., DO) would not be able to estimate values with sufficient accuracy to be useful in actual monitoring programs. However, we developed these transfer functions and their performance metrics to compare

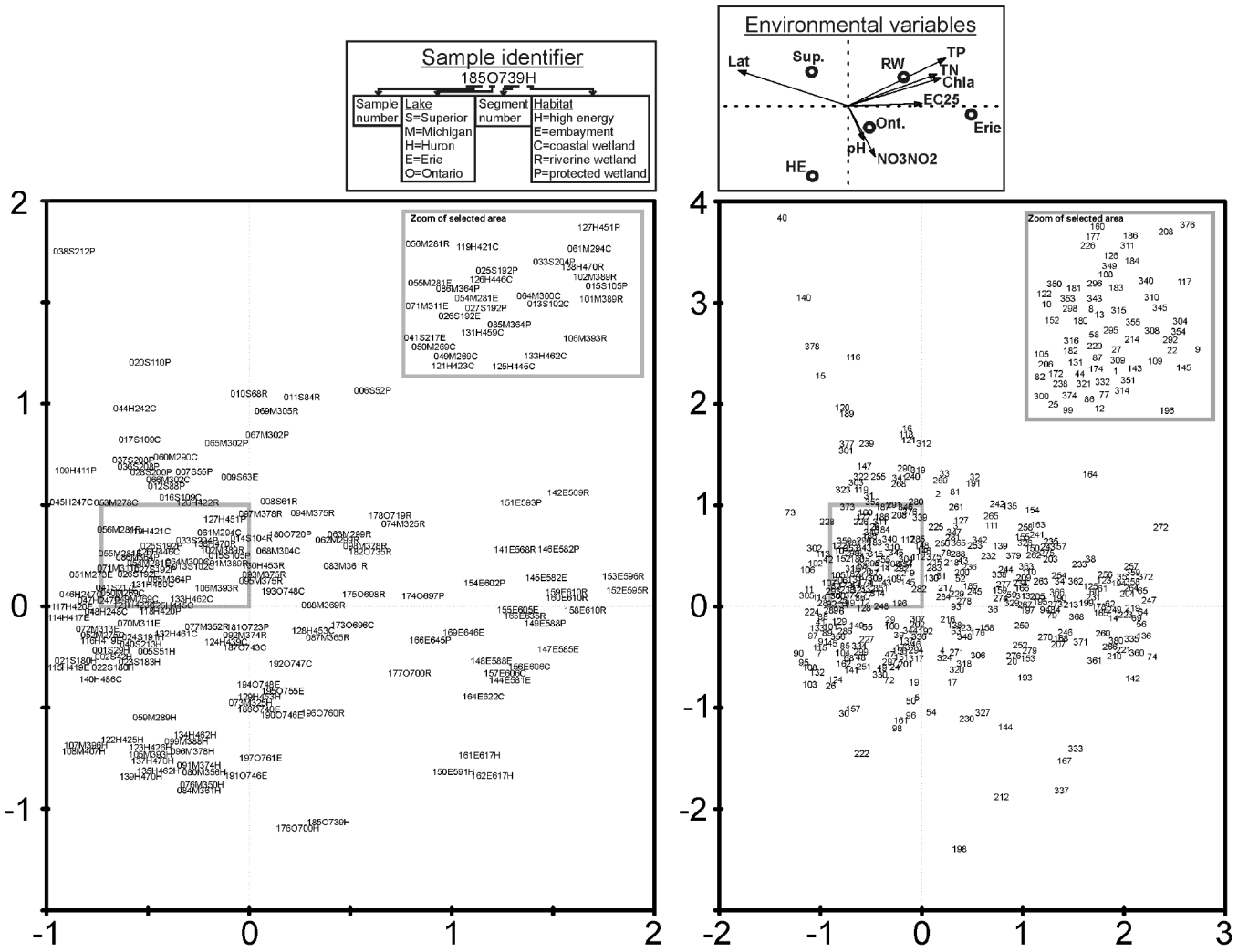


FIG. 3. Ordination plots of samples (left), taxa (right) and forward-selected environmental variables (upper right) from the 155 coastal sample training set. Samples are marked by their sample code and taxa are marked by numbers that correspond to those in Table 3. Centroids of nominal variables are illustrated by open circles.

inferred water quality data to adjacent watershed characteristics (discussed below). We have minimized some of the detail that is often presented in such assessments and present results for total phosphorus as an example. Additional details on all transfer functions, such as taxa coefficients and performance metrics, are available from the authors on request.

Based on a comparison of observed and DI TP, the transfer function has high reconstructive ability (Fig. 4). Even with critical investigation ($WA_{jackknife}$) the observed-inferred relationship only decreased to a still highly significant r^2 (WA = 0.67, $WA_{jackknife}$ = 0.55) and RMSE increased from 0.28 to 0.33 log (µg TP/L). This degradation in the observed-inferred relationship following jackknifing is typical of such transfer functions, as the standard transfer function without jackknifing provides some circularity in the diatom-inferred values; each sample's diatom-inferred TP value is derived from a transfer function that includes the measured data and diatom assemblage from that sample. The jackknife approach provides a more realistic test by sequentially creating transfer functions that do not include each sample as it is tested. In this way, $WA_{jackknife}$ results provide an estimate of error that would be assumed when the transfer function is ap-

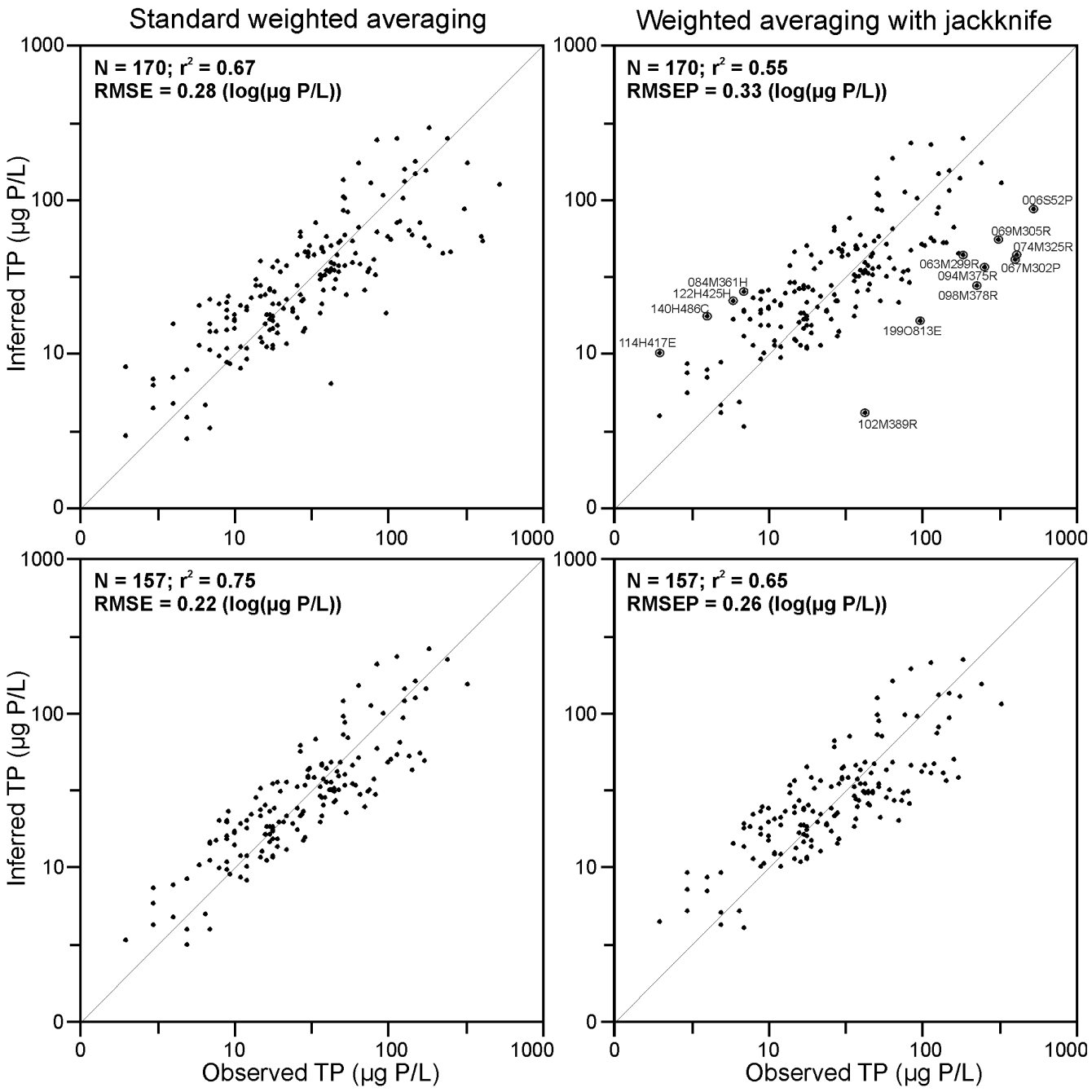


FIG. 4. Diatom-based predictive transfer functions for total phosphorus (TP) for 155 Great Lakes coastal samples. All transfer function evaluations shown were obtained using weighted averaging with lognormal taxa transformation. Observed-inferred relationships on the left are based on standard WA, and relationships on the right applied jackknife (leave-one-out) methods. Observed-inferred relationships on the bottom are based on a redeveloped transfer function with 13 samples (labeled in the upper right diagram) removed.

plied to diatom samples that were not used in model construction. Presenting results with and without jackknifing allows the assessment of the effect of single samples on the power of the transfer function. A greater discrepancy in r^2 is typically observed between WA and $WA_{jackknife}$ transfer functions when the set of samples does not effectively capture enough information to adequately define the diatom-environmental relationships in a region. For example, Reavie and Smol (1998b) observed a drop from $r^2 = 0.48$ to $r^2_{jackknife} = 0.23$ when testing a transfer function using epilithic diatoms in the St. Lawrence River to infer suspended solids. The corresponding decrease in the GLEI data for WA versus $WA_{jackknife}$ in the Great Lakes was much smaller, thus indicating that our training set effectively captured the variety of diatom assemblages and corresponding TP concentrations present in the Great Lakes coastal systems.

Taxa tolerance data did not improve apparent transfer function performance (Table 2). With the exception of alkalinity, WA transfer functions with tolerance downweighting consistently provided a poorer observed-inferred relationship (lower r^2 and higher RMSEP) than WA transfer functions based on optima alone.

In published diatom training sets developed to infer phosphorus (e.g., Reavie *et al.* 1995, Edlund and Kingston 2004), and pH (e.g., Davis *et al.* 1994), suggestions have been made to optimize transfer functions by eliminating samples that provide poor observed-inferred relationships during testing, and redeveloping the transfer functions without those samples. While it is generally assumed that inaccurate inferences are the result of incongruous diatom assemblages, consideration has rarely (Bradshaw *et al.* 2002) been given to the accuracy of the measured data used in these transfer functions. Removing 13 samples with a poor observed-inferred relationship (Fig. 4) resulted in an improvement in transfer function performance; $r^2_{jackknife}$ increased from 0.55 to 0.65 and RMSEP decreased from 0.33 to 0.26 log(µg TP/L), following transfer function refinement.

Regressions with Watershed Variables

In general, the agricultural, industrial and soil properties of the watershed explained the most variation in measured and DI water quality data (Fig. 5). Urban and atmospheric properties generally explained little additional variation in water quality, although urban development is correlated to both

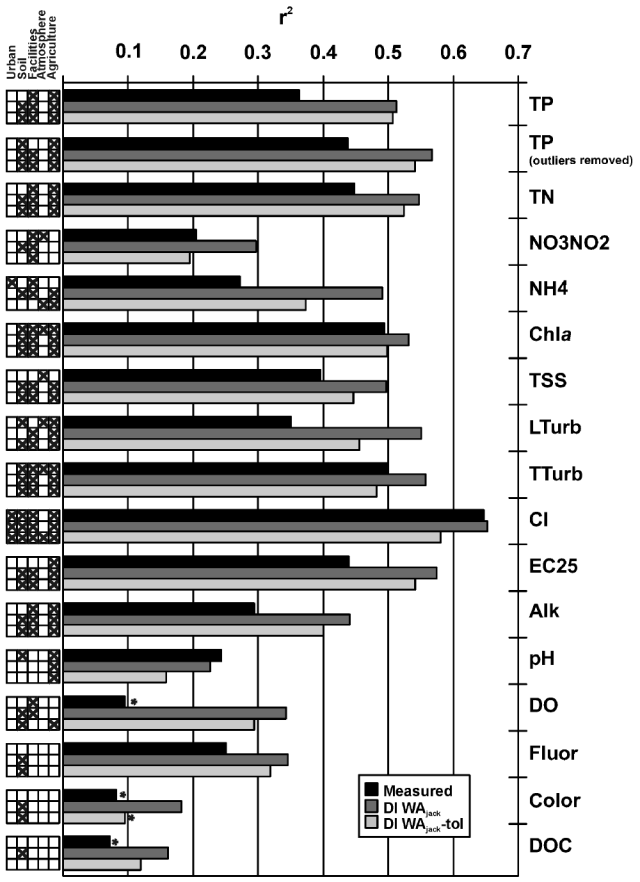


FIG. 5. Multiple regressions of observed and diatom-inferred water quality variables against watershed characteristics. Horizontal bars represent coefficients of multiple determination of regression models. Diatom-inferred results were compared using weighted averaging with jackknife cross-validation (DI WA_{jack}) and weighted averaging with jackknife cross-validation and taxa tolerance downweighting (DI WA_{jack}-tol). Squared correlation coefficients (r^2) were based on multiple linear regressions of each set of water quality values to watershed principal component scores (e.g., Fig. 2) for urban development (Urban), soil characteristics (Soil), industrial facilities (Facilities), atmospheric deposition (Atmosphere) and agricultural development (Agriculture). Watershed characteristics with significant ($P < 0.05$) correlations to water quality in a multiple linear regression are marked by an X. Correlations marked with an asterisk were not significant ($P < 0.05$ with Bonferroni correction).

measured and DI Cl, a possible relationship to road salt applications in urban areas.

There are strong relationships between watershed predictors and diatom-inferred water quality (Fig. 5, black bars). In most cases, watershed characteristics predicted DI water quality data better than measured water quality, although these relationships varied based on the modeling procedure (i.e., with or without tolerance downweighting). The fact that tolerance downweighting generally resulted in poorer relationships in both DI-measured and DI-watershed comparisons indicates that using the tolerance coefficients provides little advantage over taxa optima alone in these modeling procedures.

Based on transfer function testing presented above, we identified the most appropriate approach for Great Lakes coastal environments to be the jackknifed weighted averaging calculation using taxa optima ($WA_{jackknife}$; Fig. 4). With the exception of pH, DI water quality data from these transfer functions provide sets of water quality data that are more highly correlated to watershed characteristics than measured water quality from a single point in time. Although slightly higher, the correlation of DI Cl to watershed characteristics is little better than that for measured Cl. These results suggest that for water quality variables such as nutrients, DI data better reflect the prevailing condition (e.g., integrated over several days or weeks) than the measured data. Apparently no additional information about contemporary pH in these coastal environments can be gained from the diatom transfer function, likely because a single pH measurement is sufficient to characterize the prevailing condition in these well-buffered systems.

DI TP shows a marked improvement over measured TP to identify watershed characteristics such as agricultural and industrial development that have an influence on limnological nutrient load. Following the removal of 13 samples with poor observed-inferred relationships, correlations to watershed characteristics improved for both measured and DI TP. This finding indicates that the poor observed-inferred relationship may have been due to TP measurements that poorly represented the prevailing condition at those sites. Alternatively, incongruous diatom assemblages may reflect characteristics besides TP. The removal of these 13 samples resulted in an improvement of the diatom taxa coefficients (TP optima). It was anticipated that the removal of these samples might reduce the number of unreliable TP measurements and so improve the measured TP-watershed relationship relative to the DI-watershed relationship. However, even with transfer function refinement, DI TP was better correlated to watershed characteristics than measured TP. Of all the measured parameters, DI NH4 and DI DO provided markedly higher correlations to watershed characteristics than measured data, suggesting that these measurements were especially ineffective at capturing the prevailing condition for these variables.

DISCUSSION

This study provides convincing evidence that diatom assemblages can integrate important water quality information in coastal ecosystems better than snapshot measurement procedures. The diatom community at a site is subject to its prevailing water quality condition, and so diatom-inferred water quality data should also reflect this condition. Diatoms are likely to integrate water quality conditions over longer temporal periods (e.g., past days to weeks) compared to water chemistry measurements (e.g., past hours). While there are small errors associated with sampling and lab analyses for water quality, we attribute the primary error to the vulnerability of these measurements to short-term fluctuations that are inherent in coastal environments (e.g., Morrice *et al.* 2004). Furthermore, unlike individual chemical variables, the diatoms can capture the influence of multiple stressors on the biological community at a locale.

We expect that validation of these transfer functions will continue as they are applied in the future, but our results indicate robust nutrient (e.g., TP) and ionic (e.g., EC25) inferences. EC25 and Cl are related to seasonal road salt applications. We expected that salt inputs from the previous winter's road applications would have been flushed from the watershed and coastal aquatic system by the time samples were collected, although it is possible there is chronically elevated Cl in groundwater at urban locales that receive large amounts of salt treatments.

Ammonium-N would be expected to be the most dynamic of the measured nutrients, and so the most poorly represented by snapshot sampling because of its central role in plant and microbial nitrogen metabolism and rapid recycling rates (Mitsch and Gosselink 2000). The fact that measured DO did not correlate significantly with any watershed characteristics while DI DO did suggests that single DO measurements may not adequately capture prevailing DO concentrations. Low DO periods may exist

due to persistent low-flow periods and/or storm events that bring in organic soils, detritus and waste. Note that DOC, the only direct measure of organic matter in the water, responded similarly. These results corroborate the short-term, stochastic fluctuations that may be affecting these water quality variables, and the power that the algal assemblages have to integrate their prevailing condition in the water column.

We used watershed characteristics as a measure of site quality. Ideally we would have also compared actual prevailing water quality (if such a thing is possible to quantify) to snapshot-measured and DI data. We do not know the degree to which the prevailing water quality conditions at the sampled locales are directly related to the watershed characteristics. While in theory an infinite number of samples would be required to determine the prevailing condition, multiple water quality samples collected at a GLEI locale could be used to determine the number of samples required to closely approximate this condition. Such a thorough assessment would be costly, but would provide for a true cost-benefit comparison of physicochemical methods to diatom-based assessments. However, based on known project costs the assessment of the diatom community for environmental interpretation is a cost-effective alternative to snapshot assessment of a suite of water quality parameters. The use of diatoms is further supported by their ease of collection, preparation, and observation, and unlike chemical samples, diatom samples can be stored indefinitely for reference purposes.

Our results confirm that the diatoms provide a powerful tool to track the impacts of anthropogenic stressors in Great Lakes coastal monitoring programs. There is also considerable value in these indicators for retrospective assessments. Because long-term measured water quality data can be sparse or unreliable, and pre-European settlement data are unavailable, diatom-based paleoecological studies in the Great Lakes have been valuable in describing background conditions and anthropogenic impacts (Stoermer *et al.* 1993). To date, these studies have focused on sediment cores collected from deep, open water areas, and so provide integrated assessments of long-term water quality from a large coastal region or lake. The diatom-environmental relationships in this report can also provide a tool for nearshore paleoecological studies and the assessment of more localized impacts, such as the paleolimnology of wetlands that have been impacted by cultural eutrophication.

Because the diatom-based transfer function is derived using coastal measurements, one might wonder how the transfer function can provide more accurate data than those used in creating the transfer function. The answer is difficult to substantiate, but we hypothesize that by deriving taxa coefficients (i.e., optima) from a large dataset of assemblages and environmental samples the optima of the taxa are accurate, and not heavily influenced by those samples where the measured water quality does not satisfactorily match the prevailing water quality. In a sense, the modeling approach smoothes out some of the error associated with snapshot measurements. In other words, the diatom taxa optima which comprise these transfer functions are not heavily influenced by a subset of "poor" measured data in the calibration set. Assuming an equal number of higher- and lower-than-prevailing water quality measurements in our calibration set, the taxa optima should remain relatively consistent. Combined with the large number of taxa in the transfer function, precise environmental inferences can be provided through weighted-averaging. This hypothesis could also explain the decline in performance of the WA_{tol} transfer functions; it appears that the taxa tolerances are enlarged by these nonrepresentative measurements, and so provide inferences that are not as well correlated to stressors.

We make the following recommendations for the development of future taxa-based transfer functions that will be used to reconstruct the impacts of anthropogenic stressors. First, comparison of measured and diatom-inferred data to watershed data (if available) provides a valuable tool to validate transfer function performance, as the typical observed/inferred water quality relationship is based on the assumption that poorly-inferred water quality in a sample is caused by an incongruous taxa assemblage. Such a comparison does not identify whether a major weakness with a transfer function lies with the environmental or assemblage data. Representation of the prevailing condition by snapshot water quality measurements is an important consideration, but even with the use of these one-time measurements a robust diatom transfer function can be developed. Second, some improvement in the accuracy of taxa coefficients (optima and tolerances) can be achieved by eliminating samples with poor observed/inferred water quality relationships. Third, it appears that the power of diatom-based transfer functions derived from training sets may be better than that assumed from traditional observed-inferred water chemistry comparisons; we

recommend vigilance when comparing DI data to measured chemical data during testing.

In the context of the suite of biological indicators sampled in the GLEI program, the diatoms provide a reliable tool to infer water quality in Great Lakes coastal ecosystems. In combination with other bioindicator groups such as invertebrates and fish, we expect to describe many aspects of the limnological condition at a coastal locale. Furthermore, because the diatoms clearly respond to anthropogenic stressor influences from the watershed, integrating the diatom indicators with upland indicators (e.g., vegetation, birds) should provide a strong holistic view of overall disturbance, and a powerful management tool for Great Lakes decision makers.

ACKNOWLEDGMENTS

We dedicate this paper to the memory of John C. Kingston. We are grateful to V. Brady for coordinating and assisting with the sampling design. Diatom identification and enumeration results were supported by N. Andresen, and diatom taxonomic support was provided by E. Stoermer and J. Johansen. This work was made possible through the efforts of many other GLEI and EPA researchers who assisted in the field, laboratory, and with project logistics; J. Henneck was a lead individual in these efforts; J. Ameel analyzed much of the water chemistry; and J. Reed helped in the field and laboratory. We thank the EPA-MED laboratory and L. Anderson for analyzing DOC, and for constructive discussions with J. Thompson, J. Morrice, J. Kelly, and R. Kreis. This work also benefited from critical project review by E. Stoermer, R. Kreis, and S. Dixit. This research was supported by a grant to G. Niemi from the U.S. Environmental Protection Agency's Science to Achieve Results (STAR) Estuarine and Great Lakes (EaGLe) program through funding to the Great Lakes Environmental Indicators (GLEI) project, U.S. EPA Agreement EPA/R-8286750. This document has not been subjected to the Agency's required peer and policy review and therefore does not necessarily reflect the view of the Agency, and no official endorsement should be inferred. This is contribution number 397 of the Center for Water and the Environment, Natural Resources Research Institute, University of Minnesota Duluth.

REFERENCES

Albert, D.A., and Minc, L.D. 2004. Plants as regional indicators of Great Lakes coastal wetland health. *Aquat. Ecosys. Health Manage.* 7:233–247.

Ameel, J.J., Axler, R.P., and Owen C.J. 1993. The use of persulfate digestion for determination of total nitrogen and phosphorus in low nutrient waters. *Am. Environ.* Lab 5:1–11.

———, Ruzycki, E., Owen, C.J. and Axler,R. 1998. Analytical chemistry and quality assurance procedures for natural water, wastewater, and sediment samples (revised 2003). Natural Resources Research Institute, University of Minnesota Duluth, MN. Technical Report NRRI/TR-98/28.

Anderson, P., and Davic, R.D. 2004. Use of transparency tubes for rapid assessment of TSS and turbidity in streams. *Lake Reservoir Manage.* 20:110–120.

APHA (American Public Health Association). 2000. *Standard methods for the examination of water and wastewater,* 21st ed. American Public Health Association, Washington, D.C.

Axler, R.P., and Owens, C.J. 1994. Fluorometric measurement of chlorophyll and phaeophytin: Whom should you believe? *Lake Reservoir Manage.* 8:143–151.

Baker, J.R, Peck, D.V., and Sutton, D.W. 1997. *Environmental Monitoring and Assessment Program Surface waters: field operations manual for lakes.* U.S. Environmental Protection Agency, Washington, DC. EPA/620/R-97/001.

Battarbee, R.W. 1986. Diatom analysis. In *Handbook of Holocene palaeoecology and palaeohydrology,* B.E. Berglund, ed., pp. 527–570. New York, NY: J. Wiley.

Birks, H.J.B., Line, J.M., Juggins, S., and ter Braak, C.J.F. 1994. WACALIB version 3.3—a computer program to reconstruct environmental variables from fossil assemblages by weighted averaging and to derive sample-specific errors of prediction. *J. Paleolim.* 10:147–152.

Bradshaw, E.G., Anderson, N.J., Jensen, J.P., and Jeppesen, E. 2002. Phosphorus dynamics in Danish lakes and the implications for diatom ecology and palaeoecology. *Freshwater Biol.* 47:1963–1975.

Camburn, K.E., Kingston, J.C., and Charles D.F. 1984–1986. *PIRLA diatom iconograph.* PIRLA Report Series 3. Indiana University, Bloomington, IN.

Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., and Smith, V.H. 1998a. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Appl.* 8:559–568.

———, Cole, J.J., Kitchell, J. F., and Pace, M.L. 1998b. Impact of dissolved organic carbon, phosphorus and grazing on phytoplankton biomass and production in experimental lakes. *Limnol. Oceanogr.* 43:73–80.

Charles, D.F. 1990. A checklist for describing and documenting diatom and chrysophyte calibration data sets

and equations for inferring water chemistry. *J. Paleolim.* 3:175–178.

Cumming, B.F., Wilson, S.E., Hall, R.I., and Smol, J. P. 1995. Diatoms from British Columbia (Canada) lakes and their relationship to salinity, nutrients, and other limnological variables. *Bibliotheca Diatomologica*. Berlin: J. Cramer.

Danz, N.P., Regal, R.R., Niemi, G.J., Brady, V.J., Hollenhorst, T.P., Johnson, L.B., Host, G.E., Hanowski, J.M., Johnston, C.A., Brown, T.N., Kingston, J.C., and Kelly, J.R. 2005. Environmentally stratified sampling design for the development of Great Lakes environmental indicators. *Envir. Monit. Assess.* 102:41–65.

Davis, R.B., Anderson, D.S., Norton, S.A., Ford, J., Sweets, P.R., and Kahl, J.S. 1994. Sedimented diatoms in northern New England lakes and their use as pH and alkalinity indicators. *Can. J. Fish. Aquat. Sci.* 51:1855–1876.

Detenbeck, N.E., Taylor, D.L., Lima, A., and Hagley, C. 1996. Temporal and spatial variability in water quality of wetlands in the Minneapolis/St. Paul, MN metropolitan area: Implications for monitoring strategies and designs. *Environ. Monit. Assess.* 40:11–40.

Dixit, S.S., and Smol, J.P. 1994. Diatoms as indicators in the Environmental Monitoring and Assessment Program—Surface Waters. *Environ. Monit. Assess.* 31:275–306.

Edlund, M.D., and Kingston, J.C. 2004. *Expanding sediment diatom reconstruction model to eutrophic southern Minnesota lakes.* Minnesota Pollution Control Agency Report, Contract No. A45276.

Environment Canada and U.S. EPA (Environmental Protection Agency) 2003. *State of the Great Lakes 2003.* U.S. Environmental Protection Agency, Washington, D.C. EPA 905-R-03-004.

ESRI (Environmental Systems Research Institute, Inc.) 2000. *ArcGIS spatial analyst*, Environmental Systems Research Institute, ESRI Press, Redlands, CA, USA.

Hall, R.I., and Smol, J.P. 1999. Diatoms as indicators of lake eutrophication. In *The diatoms: applications for the environmental and earth sciences*, E.F. Stoermer and J.P. Smol, eds., pp. 128–168. Cambridge, UK: Cambridge University Press.

Juggins, S. 2003. C2 User Guide. Software for ecological and paleoecological data analysis and visualisation. University of Newcastle, Newcastle upon Tyne, UK.

Karr, J.R. 1981. Assessment of biotic integrity using fish communities. *Fisheries* 6:21–27.

_____, and Chu, E. W. 1999. *Restoring life in running waters: better biological monitoring*. Washington, DC: Island Press.

Keough, J. R., and Griffin, J. 1994. *Technical workshop on EMAP indicators for Great Lakes coastal wetlands. Summary Report.* U.S. Environmental Protection Agency and National Biological Service, Duluth, MN.

Krammer, K., and Lange-Bertalot, H. 1986–1991. Bacillariophyceae. In *Susswasserflora von Mitteleuropa 2/1–4*, eds. H. Ettl, J. Gerloff, H. Hyenig and D. Mollenhauer. Stuttgart: Fischer.

Lawson, R. 2004. Coordinating coastal wetlands monitoring in the North American Great Lakes. *Aquat. Ecosys. Health Manage*. 7:215–221.

Maynard, L., and Wilcox, D.A. 1997. *Coastal Wetlands of the Great Lakes.* State of the Lakes Ecosystem Conference 1996. Environment Canada and U.S. Environmental Protection Agency, Washington, DC. EPA 905-R-97-015b.

Meriläinen, J.J., Hynynen, J., Palomäki, A., Mäntykoski, K., and Witick, A. 2003. Environmental history of an urban lake: a palaeolimnological study of Lake Jyväsjärvi, Finland. *J. Paleolim.* 30:387–406.

MPCA (Minnesota Pollution Control Agency) 2004a. *Citizen Stream Monitoring Program Annual Report for 2003*. Environmental Outcomes Division , St. Paul, MN. Sep 2004; www.pca.state.mn.us/publications/reports/wq-csm2-03.pdf.

_____. 2004b. *Citizen Lake Monitoring Program. Report on the transparency of Minnesota lakes, March 2004.* Annual Report for 2003. Minnesota Pollution Control Agency, Environmental Outcomes Division, St. Paul, MN. Sep 2004; www.pca.state.mn.us/publications/reports/wq-csm2-03.pdf; www.pca.state.mn.us/water/clmp.html.

Mitsch, W.J., and Gosselink, J.G. 2000. *Wetlands*, Third ed. New York, NY: Van Nostrand Reinhold.

Morrice, J.A., Kelly, J.R., Trebitz, A.S., Cotter, A.M., and Knuth, M.L. 2004. Temporal dynamics of nutrients (N and P) and hydrology in a Lake Superior coastal wetland. *J. Great Lakes Res.* 30 (Supplement 1):82–96.

Niemi, G.J., and McDonald, M. 2004. Application of ecological indicators. *Annu. Rev. Ecol. Syst.* 35:89–111.

_____, Wardrop, D., Brooks, R., Anderson, S., Brady, V., Paerl, H., Rakocinski, C., Brouwer, M., Levinson, B., and McDonald, M. 2004. Rationale for a new generation of ecological indicators for coastal waters. *Environ. Health Perspect*. 112:979–986.

Patrick, R., and Reimer, C.W. 1966. *The diatoms of the United States exclusive of Alaska and Hawaii, Volume 2, Part 1.* Monographs of Natural Sciences of Philadelphia 13. Lititz, PN: Sutter House.

Radar, R.B., and Shiozawa, D.K. 2001. General principles of establishing a bioassessment program. In *Bioassessment and management of North American freshwater wetlands*, R.B. Radar, D.P. Batzer, and S.A. Wissinger, eds., pp. 13–43. New York, NY: John Wiley and Sons, Inc.

Ramstack, J.M., Fritz, S.C., Engstrom, D.R., and Heiskary, S.A. 2003. The application of a diatom-

based transfer function to evaluate regional water-quality trends in Minnesota since 1970. *J. Paleolim.* 29:79–94.

Reavie, E.D., and Smol, J.P. 1998a. Freshwater diatoms from the St. Lawrence River. *Bibliotheca Diatomologica.* Berlin: J. Cramer.

_____, and Smol, J.P. 1998b. Epilithic diatoms from the St. Lawrence River and their relationships to water quality. *Can. J. Bot.* 76:251–257.

_____, Hall, R.I., and Smol, J.P. 1995. An expanded weighted-averaging regression and calibration model for inferring past total phosphorus concentration from diatom assemblages in eutrophic British Columbia (Canada) lakes. *J. Paleolim.* 14:49–67.

Seegert, G. 2001. The development, use, and misuse of biocriteria with and emphasis on index of biotic integrity. *Environ. Sci. Pollut.* 3:51–58.

Siver, P.A., Ricard, R., Goodwin, R., and Giblin, A. E. 2003. Estimating historical in-lake alkalinity generation from sulfate reduction and its relationship to lake chemistry as inferred from algal microfossils. *J. Paleolim.* 29:179–197.

Smol, J. P. 2002. *Pollution of lakes and rivers: a paleoenvironmental perspective*. London, UK: Arnold Publishers.

Stevenson, R.J., Bothwell, M.L., and Lowe, R.L. 1996. *Algal ecology: freshwater benthic ecosystems*. San Diego, CA: Academic Press.

Stoermer, E.F., Wolin, J.A., and Schelske, C.L. 1993. Paleolimnological comparison of the Laurentian Great Lakes based on diatoms. *Limnol. Oceanogr.* 38:1311–1316.

_____, Kreis, R.G., Jr., and Andresen, N.A. 1999. Checklist of diatoms from the Laurentian Great Lakes. *J. Great Lakes Res*. 25:515–566.

ter Braak, C.J.F., and Prentice, I.C. 1988. A theory of gradient analysis. *Adv. Ecol. Res*. 18:271–317.

_____, and Šmilauer, P. 2002. *CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5)*. Microcomputer Power, Ithaca, NY.

Tibby, J. 2004. Development of a diatom-based model for inferring total phosphorus in southeastern Australian water storages. *J. Paleolim*. 31:23–36.

U.S. EPA (Environmental Protection Agency) 1987. Handbook of methods for acid deposition studies. Laboratory analyses for surface water chemistry. U.S. Environmental Protection Agency, ORD, Washington, DC. 600/4-87-026.

USGS (United States Geological Survey) 2003. Evaluation of alkaline persulfate digestion as an alternative to Kjeldahl digestion for determination of total and dissolved nitrogen and phosphorus in water by Charles J. Patton and Jennifer R. Kryskalla. U.S. Geological Survey Water-Resources Investigations Report 03-4174.

_____, 2004. National field manual for the collection of water-quality data: U.S. Geological Survey techniques of water-resources investigations, book 9, chapters A1–A9. http://pubs.water.usgs.gov/twri9A.

Uzarski, D.G., Burton, T.M., and Genet, J.A. 2004. Validation and performance of an invertebrate index of biotic integrity for Lakes Huron and Michigan fringing wetlands during a period of lake level decline. *Aquat. Ecosys. Health Manage*. 7:269 288.

Wilcox, D.A., Meeker, J.E., Hudson, P.L., Armitage, B.J., Black, M.G., and Uzarski, D.G. 2002. Hydrologic variability and the application of Index of Biotic Integrity metrics to wetlands: a Great Lakes evaluation. *Wetlands* 22:588–615.

Submitted: 22 August 2005
Accepted: 22 February 2006
Editorial handling: Rex L. Lowe