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Coastal Geomorphic and Lake Variability in the Laurentian Great Lakes: Implications for a Diatom-based Monitoring Tool

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

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

[2]*Center for Water and the Environment*
Natural Resources Research Institute
University of Minnesota Duluth
5013 Miller Trunk Highway
Duluth, Minnesota 55811-1442

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

ABSTRACT. *In an evaluation of diatoms as indicators of human disturbance in coastal ecosystems of the Laurentian Great Lakes, we characterized assemblage specificity to lake and habitat type to identify non-anthropogenic factors influencing indicator models. Surface sediment assemblages and environmental variables were collected along the U.S. coastline at 191 sample sites, which were classified by lake and geomorphic type: high-energy (HE), embayment (EB), coastal wetland (CW), riverine wetland (RW), protected wetland (PW), and open water (OP). Diatom inferred (DI) total phosphorus (TP) transfer functions (models) were developed for each lake and geomorphic type. Robust models included: the overall model (RMSEP; $r^2_{jack} = 0.65$; RMSEP = 0.005), Lake Superior ($r^2_{jack} = 0.73$; RMSEP = 0.003), Lake Ontario ($r^2_{jack} = 0.73$; RMSEP = 0.007), PW ($r^2_{jack} = 0.64$; RMSEP = 0.003), and EB ($r^2_{jack} = 0.64$; RMSEP = 0.007). Weaker models, indicating poorer diatom-TP relationships, included: RW ($r^2_{jack} = 0.03$; RMSEP = 0.005), OP ($r^2_{jack} = 0.15$; RMSEP = 0.059), and Lake Michigan ($r^2_{jack} = 0.38$; RMSEP = 0.006). DI TP data were regressed against landscape characteristics to quantify the relationships to adjacent watershed stressors. RW data were further scrutinized as a case study to investigate the suitability of diatom-based approaches in systems with poor diatom-TP relationships. Despite poor performance of the RW model, DI phosphorus data for riverine wetlands, derived from the overall model, were strongly related to watershed characteristics ($r^2 = 0.61$), indicating the overall model's ability to integrate stressors from the surrounding watershed in areas where measured phosphorus did not adequately characterize prevailing conditions. This study confirms that physical properties (e.g., lake or habitat type) can influence indicator models; however, weaknesses may be overcome by robust calibration techniques.*

INDEX WORDS: *Great Lakes Environmental Indicators, diatoms, transfer functions, phosphorus, habitat, nearshore.*

[*]Corresponding author. E-mail: akireta@nrri.umn.edu
[**]Deceased

INTRODUCTION

Readily accessible monitoring data are essential to assess conditions, prioritize research, and evaluate effectiveness of current policies (Messer *et al.* 1991). Water chemistry is frequently used as a water quality indicator, but snapshot measurements may not reflect the prevailing conditions in an area (Detenbeck *et al.* 1996, Bradshaw *et al.* 2002). Biological indicators are often chosen as indicators of condition and change in freshwater systems because they integrate environmental conditions over time (Yoder and Rankin 1998). For example, diatoms (Dixit *et al.* 1992), fish communities (Brazner 1997, Rahel 2000), wetland vegetation (Herdendorf 1992), birds (Robinson *et al.* 1995), and amphibians (Kutka and Bachman 1990) have been used to assess impacts from stressors. The U.S. Environmental Protection Agency (U.S. EPA) Science to Achieve Results program established the Estuarine and Great Lakes (EaGLe) research program with a major goal of developing new approaches to assess environmental condition (Niemi and McDonald 2004, Niemi *et al.* 2004). One of the EaGLe projects, the Great Lakes Environmental Indicators (GLEI: https://glei.nrri.umn.edu) project, was specifically designed to develop indicators for the Laurentian Great Lakes. This paper focuses on the diatom algae; other groups worked with fish, birds, amphibians, benthic macroinvertebrates, and sediment contaminants.

Diatom algae are powerful tools for inferring environmental variables. Diatoms are especially well suited for environmental inferences for several reasons: as primary producers they integrate and correlate well with ambient water quality conditions, they possess a rapid turnover rate and therefore a short response time to environmental change (Vinebrooke 1996), they have numerous species with a range of tolerances to various environmental measures (Patrick and Reimer 1966a, b; Werner 1977; Round *et al*. 1990), and they manufacture siliceous cell walls that leave floristic fossils (Hall and Smol 1999). Diatoms have been used to reveal past lake conditions (Hall and Smol 1992, Fritz *et al.* 1993, Bennion 1994, Reavie and Smol 1997) as an instrument for investigating climate change (Gregory-Eaves *et al.* 1999) and as monitors of present day conditions (Reavie and Smol 1998a, Ramstack *et al.* 2003).

Phosphorus is a proxy of cultural eutrophication (Vollenweider 1968, Dillon and Rigler 1975) and has been used to characterize trophic gradients (Hustedt 1939). Diatoms are a natural choice for assessing environmental condition in freshwater systems that are potentially impacted by cultural eutrophication, due to the clear responses they have to phosphorus conditions (Dixit and Smol 1994). Many diatom inferred (DI) phosphorus models (also known as transfer functions) have been developed and illustrate this strong relationship to phosphorus concentration (e.g., Hall and Smol 1992, Bennion 1994, Reavie and Smol 1998a, Ramstack *et al.* 2003). Indeed, phosphorus has already been identified as an important chemical influencing the diatoms from the nearshore Laurentian Great Lakes (Reavie *et al.* 2006). The basin-wide diatom-based transfer function developed from various coastal habitats across the Great Lakes (Reavie *et al.* 2006) would be useful to researchers and lake managers working anywhere in the nearshore system. However, the lakes are physically and chemically variable and there are distinct habitats with unique properties within each lake. For example, Lake Huron is classified as an oligotrophic lake, although some areas in the lake have historically ranged from eutrophic to ultra-oligotrophic (Vollenweider *et al.* 1974). Additionally, there are differences in benthic diatom assemblages within and between lakes (Stoermer 1975, 1998). Furthermore, geographic gradients are known to confound diatom-based transfer functions and overwhelm the biological-water quality relationship used to develop indicator models (Potapova and Charles 2002).

It has been recommended that more studies concentrate on the dominant features of the coastal zone of the Great Lakes to investigate the relationship of geomorphology and hydrology on organisms and processes (Keough *et al.* 1999). A better understanding of these and other non-anthropogenic factors helps to better distinguish natural variability from stressor-influenced variability (Smith 1998). The present study design enabled us to obtain a large sample size specifically targeting six pre-defined geomorphic types across all five Great Lakes to develop indicators. This study uses data from an existing Great Lakes coastal inference model (Reavie *et al.* 2006). Here our goal was to investigate the effects of these geomorphological and geographical properties on diatom-based phosphorus models, and to find whether specific geomorphic types or lakes were less amenable to developing phosphorus transfer functions (i.e., inference models).

Comparing diatom-inferred water quality to measured water quality is an established method used to determine model robustness. Additionally, by comparing DI measures to adjacent landscape characteristics, we can quantify the ability of diatom assemblages to detect upland stressor influences. The previous study, which used a basin-wide model, demonstrated how DI water quality had a stronger relationship with landscape stressors than snapshot measures of water quality (Reavie *et al.* 2006). Landscape stressor data provide a means to assess inference models and relate indicator organisms to perturbations on the surrounding landscape. Hence, we also sought to investigate the relationship between landscape stressors and DI phosphorus from individual habitat and lake models, and in doing so further evaluate diatom transfer function performance. Furthermore, the present study expanded the Reavie *et al.* (2006) dataset to determine the effect of including offshore samples in the diatom transfer function.

The major goals of this study were to: 1) determine the specificity of diatom assemblages and environmental variables to each of the five Great Lakes and each of the six coastal region geomorphic types, 2) determine whether we can consistently develop robust transfer functions within these 11 subgroups, and if not, 3) identify which natural factors weaken diatom indicator models and recommend approaches to resolve these weaknesses.

METHODS

Study Area

A detailed explanation of the GLEI study design is given by Danz *et al.* (2005). Briefly, sites were randomly selected across natural and anthropogenic gradients in all five Great Lakes in two ecoprovinces; the southerly, warmer Eastern Broadleaf Forest and the more northerly Laurentian Mixed Forest (Keys *et al.* 1995). The U.S. coast of the Great Lakes was divided into 762 “segment-sheds” defined as the area draining to a shoreline segment beginning and ending halfway between second order streams. The sampling area covered the U.S. side of Lakes Superior (SU), Michigan (MI), Huron (HU), Erie (ER), and Ontario (ON) from Silver Bay, Minnesota to Bedford Corners, New York. Site characterization was performed at a segment-shed level using landscape characteristics, including potential stressor variables, from various geographical information system (GIS) sources. A subset of sites was selected which maximized the coverage of natural (e.g., habitat and soil types) and anthropogenic (e.g., urban and agricultural development) gradients across the basin (Danz *et al.* 2005).

Diatom and water quality samples were collected at 191 sites (Fig. 1) in six types of coastal ecosystems characterized by hydrogeomorphic features: high-energy (HE), embayment (EB), coastal wetland (CW), riverine wetland (RW), protected wetland (PW), and open water (OP). Figure 2 represents a conceptual model of our geomorphic types, revised and expanded from Keough *et al.* (1999). Five of these geomorphic types involved sampling less than 1 km from shore, typically at a depth of 0.5 m, and were classified as nearshore (HE, EB, CW, RW, and PW), and a sixth geomorphic type, OP, was sampled farther from shore and was considered an offshore habitat. All six geomorphic types were categorized in the present study as “coastal” since they were within 5 km of shore. Grouping of the “nearshore” sites was used to simplify referral to the five shallow habitats. The inclusion of the offshore (OP) samples is unique to other GLEI analyses published thus far and was undertaken to investigate the inclusion of these deeper samples with the nearshore model (Reavie *et al.* 2006). HE sites were defined as exposed shoreline that did not support vegetation and were subjected to wind and wave energy. EB sites were at least one square kilometer, had a reduced exposure to wind and wave energy, contained no more than one smaller bay, and had a bay opening that was smaller than the distance from the open lake to the innermost bay section. CW sites were found in open coastlines and relatively open bays. These were exposed wetlands vulnerable to the most wind and wave energy of the three wetland types. RW sites were influenced by a second order or higher river, had a surface water connection to the lake, and were somewhat protected from wind and wave action. PW sites were least disturbed by wind and wave energy. They were behind a sand-spit or other land barrier, were characterized by high sedimentation and may have had a surface water connection. Detailed characteristics of the three wetland types are given by Keough *et al.* (1999). Our best judgment was used to accurately categorize nearshore sampling sites, as there were a few instances where a sample location had characteristics of more than one geomorphic type. OP sites were deeper, open-water habitats sampled 3 to 5 km from shore where the water column was approximately 30 m deep. OP sites were also collected along the landscape stressor gradient, with a goal of selecting four to five locations within each lake.

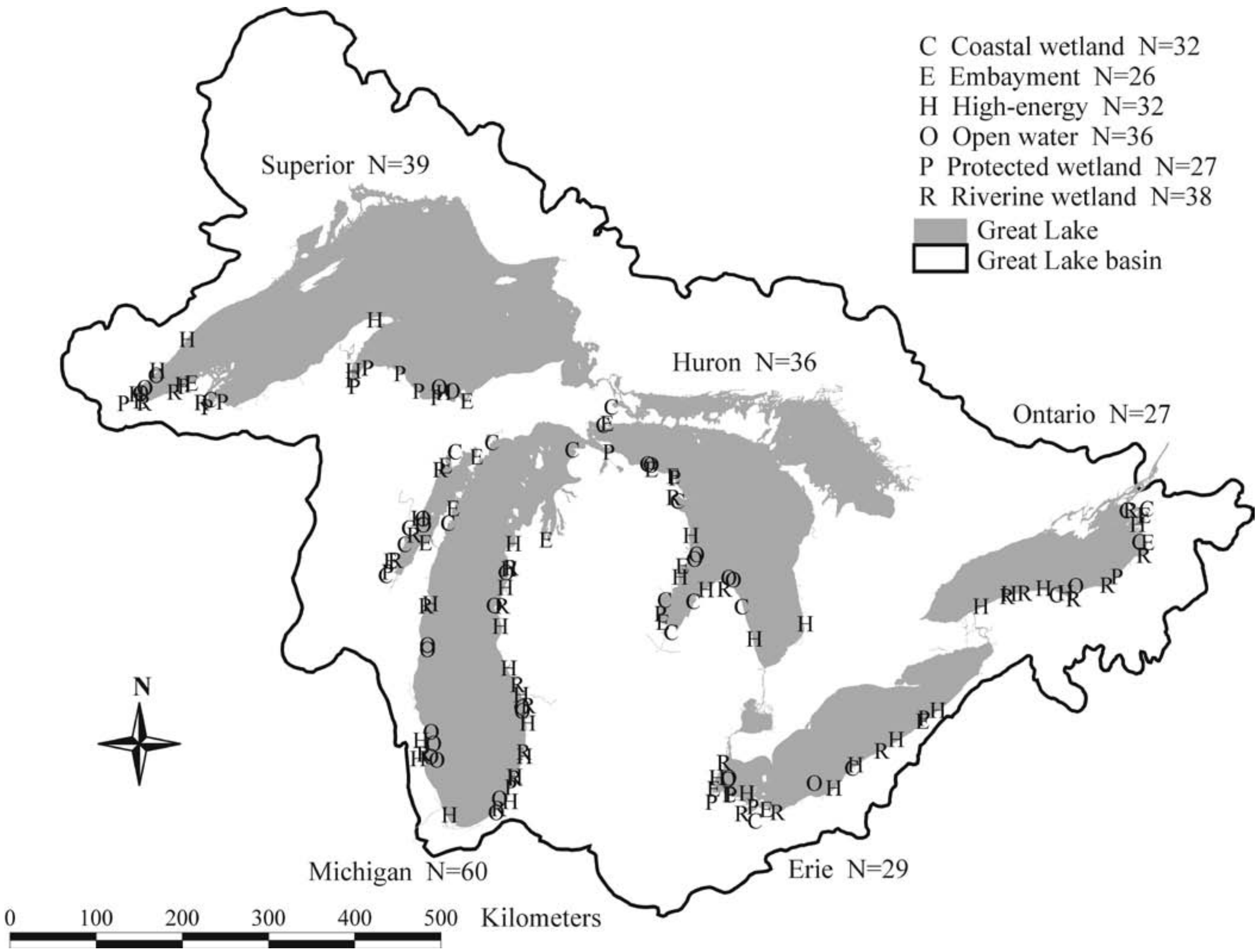

FIG. 1. Map of the Laurentian Great Lakes and basin with sampling sites. Sites of same geomorphic type within 10 km of each other were pared down for visualization.

Field Sampling

Field data were collected from nearshore sites from 9 Jun. through 18 Sept. in 2002, and from 22 May through 10 Aug. in 2003. OP samples and chemistry were collected by the U.S. EPA Mid-Continent Ecology Division (MED) from 7 Aug. through 11 Sept. in 2002, and 11 Jun. through 9 Sept. in 2003 using the research vessel *Lake Explorer* (http://www.epa.gov/facilities_network/lakeexplorer.html).

A motorboat or canoe was used to sample each nearshore site based on ease of access. Field measurements or samples were collected for: dissolved oxygen (DO), pH, specific conductance, total suspended solids (TSS), chlorophyll *a* (chl *a*), fluorescence, turbidity, chloride, dissolved organic carbon (DOC), total phosphorus (TP), total nitrogen (TN), nitrate/nitrite [$(NO_2$+$NO_3)$-N], and ammonia (NH_4-N). Water sample processing for nearshore samples occurred within 24 hours at temporary labs set up near field locations. A Turner Designs Aquafluor™ was used to determine fluorescence and turbidity at the time of sample processing. Raw water samples were analyzed for both turbidity and fluorescence, and filtered samples for background fluorescence, each reading performed twice. A replicate sample, blank, turbidity calibration standard, and solid fluorescence standard were also analyzed every ten samples. TN, TP, $(NO_2$+$NO_3)$-N, NH_4-N, color, and chloride were later analyzed using standard methods (Ameel *et al*. 1998, APHA 2000) at University of Minnesota Duluth's Natural Resources Research

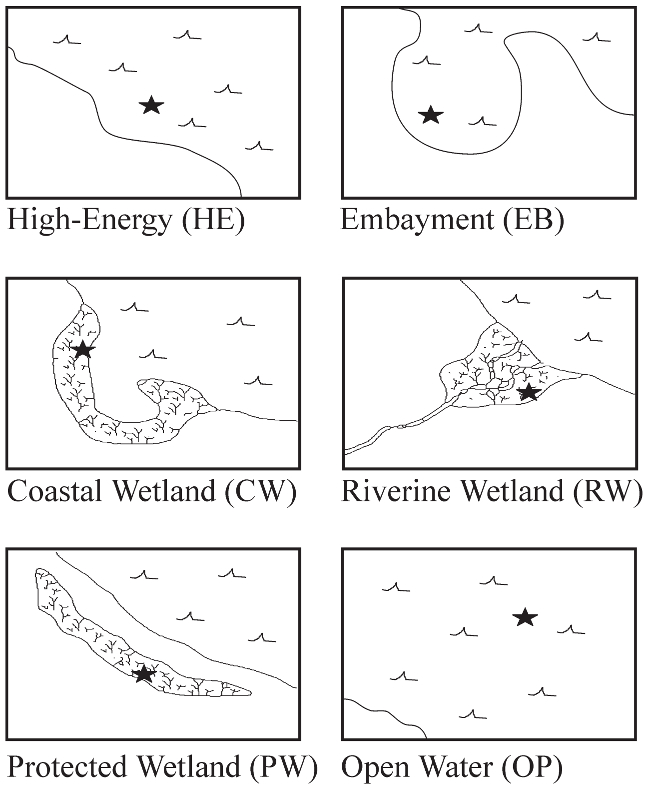

FIG. 2. Conceptual models of geomorphic types used in this study, modified from Keough* et al. *(1999). High-energy (HE) = exposed shoreline, embayment (EB) = sites incorporated in a bay, coastal wetland (CW) = exposed shoreline wetland, riverine wetland (RW) = influenced by a second order or higher river, protected wetland (PW) = at least partially enclosed by sand spit or other land barrier, and open water (OP) = ~30 m deep, open water sites. Stars mark approximate sampling sites within habitats.

Institute (NRRI). DOC was analyzed by UV-persulfate/IR absorption (APHA 2000) at the EPA-MED water quality laboratory (Duluth, MN).

Samples were processed (filtered, preserved, iced, or frozen) at temporary labs in the field within 24 hours. TSS was later determined gravimetrically at the collector's institution (NRRI's Ely Field Station or John Carroll University). Chlorophyll-*a* (ppb) and phaeophytin-*a* (ppb) were analyzed at NRRI.

Alkalinity was analyzed within 24 hours of sample collection by acid titration to endpoint pH 4.5, unless the initial pH was greater than 8.3, in which case 8.3 was the first of two endpoints. Reavie *et al.* (2006) provide complete additional details on chemistry methods and references used in this investigation.

For nearshore samples, diatoms were collected from sediment with a 6.5 cm diameter push core (approximately 75% of samples). The entire top 1 cm of sediment was carefully removed with a putty knife, spoon, and/or large pipette. A Ponar sampler was used to obtain sediment and the top 1 cm was collected whenever a core was not possible. Rock or wood was collected and scraped with a knife or scrubbed clean with a small brush into a container to collect attached algae when other collection methods were not possible. Diatom samples were refrigerated until processing. Field replicates of diatom and water samples were taken for 10% of samples.

Water was collected from 8 L Niskin bottles on a rosette sampler near the water's surface for OP water quality measures. Measures included all those performed for nearshore samples except for phaeophytin-*a*, alkalinity, color, and turbidity. Benthic diatom samples were preferably collected with a 6.5 cm diameter gravity corer, but the top of a Ponar sample was obtained when a core was not possible, which occurred in many instances due to hard substrates. U.S. EPA-MED performed all water quality analyses on open-water samples following standard methods that were virtually identical to those used for the nearshore samples analyzed by NRRI-UMD.

Diatom Preparation

Diatom sub-samples were taken from sediment samples that were homogenized by hand mixing. Diatom frustules were cleaned using one of the following digestion methods: strong acid (concentrated nitric or hydrochloric acid) and boiling, or by using 30% hydrogen peroxide (H_2O_2) in either a warm water bath (~78°C) or with potassium dichromate ($K_2Cr_2O_7$) as a catalyst. Larger sub-samples were processed using approximately 10 g wet sediment and 100 mL 30% H_2O_2 with ~0.2 g catalyst in 1 L beakers. Smaller sub-samples (~0.2 g wet sediment) were prepared in 20 mL borosilicate glass scintillation vials with ~15 mL 30% H_2O_2, using a water bath to heat samples. Another digestion method used approximately 20–30 ml of strong acid in beakers with 1 g of sediment that had been dried on low heat for 24 hours. Samples were rinsed at least five times for all methods, using a centrifuge, or by settling overnight, followed by aspiration of the supernatant. Remaining, undigested sample material was freeze-dried for preservation and is stored at NRRI's field station in Ely, Minnesota.

Slides were prepared by pouring a sub-sample of diatom slurry and deionized water over four circular 18 mm coverslips in a Battarbee settling tray (Battarbee 1986). Dried coverslips were mounted on slides using a mountant with a high refractive index, either Pleurax (refractive index ~1.7+) or Naphrax (refractive index ~1.65+). One slide was used per count, slide transects were recorded, and every diatom valve that was more than 50% in the field of view and with more than 50% of the valve intact was enumerated, with a goal of 400 valves per sample. A small percentage of samples had very sparse diatom assemblages, so considering logistic constraints we enumerated to the highest feasible number. In most instances, over 350 valves were counted per sample with the exception of OP samples, which had notably sparser diatom density, in which case over 300 valves were usually counted.

The following references were employed to assist in taxonomic identification: Krammer and Lange-Bertalot (1986-1991), Stoermer *et al.* (1999), Patrick and Reimer (1966a, b), Reavie and Smol (1998b), Cumming *et al*. (1995), and Camburn *et al.* (1984-1986). Taxonomic meetings were held to ensure harmony of identifications among different taxonomists (Reavie *et al.* 2006). In addition to the field replicates, slide count (a minimum of 10% of samples), temporal, and spatial replicates were assessed. Field and slide count replicates were later combined for analyses in this paper. Temporal replicates were treated as unique samples and represented 8% of total samples (10% of nearshore samples). Spatial replicates had unique chemistry for most measures and were independently analyzed at 5% of sample locations.

Data Analyses

Unique sampling events with associated diatom and chemical data were used in analyses. Raw counts of taxa were transformed into percent (relative) abundance. Taxa were defined as non-rare and included in all further analyses if they occurred in at least five samples and represented at least 1% relative abundance in one or more samples, or if they represented at least 5% relative abundance in at least one sample. Site diatom assemblages and environmental profiles underwent outlier analysis as described in Reavie *et al.* (2006); no outliers were identified. Some taxa were combined into "complexes" of similar taxa, which may have been categorized differently by separate taxonomists (i.e., *Achnanthidium biasolettiana* (Grunow) Bukhtiyarova, *Achnanthidium minutissimum* (Kütz.) Czarnecki, *Cyclotella comensis* Grunow, *Staurosirella pinnata* (Ehrenb.) D.M. Williams and Round, and *Tabellaria flocculosa* (Roth) Kützing). Preliminary analysis using detrended correspondence analysis on our species data produced a gradient length of 4.7 standard deviation units, suggesting unimodal analysis methods were most appropriate for these data (ter Braak and Šmilauer 2002).

We carried out correspondence analysis (CA) using Canoco 4.5 (ter Braak and Šmilauer 2002) to visualize variation in the diatom assemblages and to develop scores for testing differences among the sample subgroups. We used scaling focused on inter-species distances, applying downweighting of rare species. Species ordinations were initially performed on the entire set of samples (N = 191). Preliminary analyses showed strong species differences between the OP and the collective nearshore sites, so exploratory analyses were also performed on nearshore sites alone to better reveal variability within these data.

We carried out principal components analysis (PCA) to reduce the dimensionality of our water quality measures to visualize and test environmental patterns among geomorphic types and lakes. Water chemistry variables were transformed (e.g., log(x + 1) or square root (x+1)) when necessary to obtain or approximate normal distribution and to reduce the influence of outliers (see Reavie *et al.* 2006 for transformation details). Variables included in the analysis were: DO, pH, conductivity, TSS, chlorophyll *a*, fluorescence, chloride, DOC, TP, TN, (NO_2+NO_3)-N, and NH_4-N. Scaling was focused on inter-variable correlation, variable scores were divided by the variable's standard deviation (sd) after extraction of the axes, and centering and standardization were carried out on the correlation matrix. Like the species data, PCA was performed on the complete sample set (N = 191) and subsequently on the nearshore samples (N = 155), because the OP samples exhibited distinct environmental characteristics.

We tested for statistical differences in species assemblages and water chemistry among sites using 2-way multivariate analysis of variance (MANOVA; SAS Institute 2003). There were two tests, one using the first two CA axes (species assemblages) as dependent variables and one using the first two PCA axes (water chemistry) as dependent variables. Lake identity and geomorphic type were the two main effects (independent variables) in both tests. We carried out multiple comparisons between all pairs of lakes and all pairs of geomorphic types using CONTRAST statements ($P < 0.05$ with Bonferroni correction; SAS Institute, 2003). CA scores were first log transformed (log (x+1)) because preliminary analysis on raw scores yielded high residuals resulting from skewness.

Models

C2 software (Juggins 2003) was used to develop models using the total (omnibus) training set (i.e., set of sample locations) and lake- and geomorphic type-specific training sets. C2 uses the training set to calculate optima and tolerances for each taxon to a selected environmental variable. In the model inference step, weighted averages of the species optima are used to calculate the inferred value for an assemblage, with optional downweighting by the species tolerance coefficients (Birks *et al.* 1994). To test a model's ability to infer the selected variable, C2 compares observed to diatom-inferred values for each training set sample. The strength of a model is denoted by the squared correlation coefficient (r^2) and the root mean square error (RMSE) of the observed-inferred comparison for the calculated variable. A leave-one-out cross-validation technique called jackknifing is used to avoid circularity by independently estimating environmental data (Juggins 2003). The power of the jackknifed model is denoted by r^2_{jack} and model error is calculated as root mean square error of prediction (RMSEP). Comparisons of RMSEP could not be directly made among the various models we developed because the range of measured total phosphorus differed among geomorphic type and lake training sets. To standardize each RMSEP value, it was divided by the standard deviation of measured total phosphorus from the corresponding model training set. In general, models with higher r^2_{jack} values and lower standardized RMSEP values were considered more robust. Maximum and average bias data were also evaluated, lower bias reflecting less prediction error. Maximum bias data were divided by the range of model input data to provide a percent maximum bias. Average bias values were consistently less than 10^{-16}% of the range of measured data in each model, so these data are not presented.

Total phosphorus was the environmental variable used for model evaluation since phosphorus is associated with cultural eutrophication and was most the influential chemical variable explaining variation in the diatom assemblage data (Reavie *et al.* 2006). Total phosphorus models were developed for: (A) all samples (the omnibus training set), (B) each lake, and (C) each geomorphic type. The omnibus model included all lakes and geomorphic types comprising 191 samples and 380 taxa. A nearshore model (excluding OP samples) was also developed based on preliminary evidence that these samples had very different water quality and species characteristics from the nearshore environments (155 training set samples, 372 taxa). A model was also created excluding RW samples based on apparent poor transfer function performance of this geomorphic type, and riverine wetland DI TP was independently reconstructed using C2 software (Juggins 2003). Weighted averaging with classical deshrinking (C2 software; Juggins 2003) was the chosen method for all models, based on preliminary evaluations of model performance.

Multiple Linear Regression with Landscape Stressors

Landscape data were created from landscape and soil characteristics summarized in a previous study (Danz *et al.* 2007). Landscape stressor data were characterized adjacent to each wetland site sampled (N=109) and were used to evaluate the relationship between watershed characteristics and both measured and DI TP for the three wetland types. Associated landscape data for OP, HE, and EB sites were unavailable at the time of analyses; this subset of wetland watershed characteristics is consistent with Reavie *et al.* (2006). Analyses were expanded in the current study to evaluate the effect of inclusion of offshore (OP) sites in the inference model. A polygon "complex" for sampling events was drawn around each GLEI wetland sampling area, and a watershed contributing area to each complex was determined by using GIS-based elevation models (Hollenhorst *et al.* 2007 this issue). Effort was taken to ensure best boundary placement for complex characterization and included sampling events from other GLEI subcomponents when appropriate.

ArcView (GIS; ESRI 1996) was used to summarize over 200 environmental variables from seven categories: agriculture, atmospheric deposition, land use and land cover, human population density and development, point and non-point source pollution, shoreline modification, and soils. The first six categories represent anthropogenic disturbances, while the soils category represents a landscape characteristic important to physical and chemical water quality measures. PCA was performed on the datasets for each of these seven environmental categories to reduce the dimensionality and to establish principal component (PC) scores for each complex (Danz *et al.* 2005). We used eight PCs that were interpreted as gradients across the basin: *agricultur*e (PC axis 1) indicates overall agriculture pressure, *atmosphere1* (PC axis 1) refers to atmospheric deposition, *atmosphere2* (PC axis 2) indicates values reflecting basicity (calcium, ammonium, and magnesium cation deposition), *facilities1* (PC axis 1) illustrates overall point source facility density, *facilities2* (PC axis 2) indicates density of facilities that either physically disturb the environment or discharge polycyclic aromatic hydrocarbons (PAHs), *urban* (PC axis 1) represents urbanization, population, road, and land cover densities, *soils1* (PC axis 1) reflects a suite of landscape variables related to soil permeability, and *soils2* (PC axis 2) reflects water holding capacity, cation exchange capacity, and organic matter.

These eight PCs were regressed against corresponding observed and DI total phosphorus using multiple linear regressions (using the software program NCSS 97). DI total phosphorus was developed using the transfer function including all habitats, due to the robust performance in comparison to weaker individual wetland transfer functions (RW, CW) and applicability across the basin. Regressions were similarly performed on the transfer function excluding OP sites to investigate the relationship of estimated total phosphorus from nearshore sites to landscape characteristics. In a subsequent analysis, various observed and inferred RW data manipulations were performed to evaluate apparent poor model performance of the riverine wetland geomorphic type. The reliability of measured riverine wetland TP data and the effect of their inclusion in the total model were investigated. Landscape data were regressed against observed TP and: (A) all wetland DI TP developed from the nearshore model, (B) CW and PW DI TP developed from the nearshore model, (C) RW DI TP developed from the nearshore model, (D) independently reconstructed RW DI TP, and (E) independently reconstructed RW DI TP added to CW and PW DI TP developed from the modified nearshore model that excluded RW observed data.

RESULTS

Diatoms

A diatom taxa list for all nearshore samples can be found in Reavie et al. (2006). Samples contained a rich diversity of diatoms. Over 2,000 taxa were enumerated, 380 of which met our criteria to be included as non-rare taxa. Additional taxa encountered in this study due to the inclusion of OP samples are listed in Table 1. Environmental characteristics, including optimum, tolerance, and frequency of occurrence, are provided for each taxon based on the total phosphorus model derived from all samples.

Species Assemblage and Water Quality Analyses

Ordination diagrams illustrate the variations in diatom assemblages and water quality characteristics among geomorphic types (Fig. 3) and lakes (Fig. 4), and Table 2 lists the summary data for the multivariate analyses. MANOVA testing revealed overall diatom assemblage and water quality differences among lakes (Wilks' Lamda, $F = 22.39$; $P = < 0.0001$) and geomorphic types ($F = 34.92$; $P = < 0.0001$). No significant interaction effect between lake and geomorphic type was detected. Species assemblages in OP samples were significantly different from the other geomorphic types, clearly visible in Fig. 3, top; the separation of OP from nearshore samples defines the primary (axis 1) gradient in the CA, which is primarily related to planktonic taxa in the diatom assemblages. The group of RW species assemblages was also significantly different from those in all other geomorphic types (Fig. 3, top; Fig. 5). No significant differences in species assemblages were observed among HE, EB, CW, and PW.

Water quality variations were influenced by a nutrient gradient (axis 1) and a pH gradient (axis 2), as was the case in Reavie *et al.* (2006; no data presented here). OP water quality was also distinct from all other geomorphic types, possessing a more narrow range of environmental variation, which is evident from the limited extent of the OP PCA polygon in the lower left quadrant (Fig. 3, bottom). HE water quality was additionally distinguished from the three wetland categories (CW, PW, RW), while EB was distinguished from PW and RW water quality.

In terms of species assemblages, ER and ON were distinct from the other three lakes and from each other (Fig. 4, top; Fig. 5). In terms of water

TABLE 1. Common diatom species in addition to those presented in Reavie* et al. *(2006). Taxa not matching published specimens were given temporary names and codes including the identifying institution (UMICH = University of Michigan, JCU = John Carroll University). N = number of samples where a taxa was encountered; N2 = effective number of occurrences; Max. = maximum relative abundance in any sample; Opt. = total phosphorus optimum; Tol. = log-transformed total phosphorus tolerance. The first optima values have been back-transformed since the model provided log-transformed total phosphorus values (second Opt. column).

Code	Taxon	Authority	N	N2	Max.	Opt. (µg/L)	Opt. (log(µg/L+1))	Tol. (log(µg/L))
AMPCOFFE	*Amphora coffeaeformis*	(C.Agardh) Kütz.	5	3.6	1.2	20.3	1.3	0.8
AMPNEGLE	*Amphora neglecta*	Stoermer and J.J. Yang	6	4.5	1.6	11.3	1.1	0.2
AULSUBAR	*Aulacoseira subarctica*	(O.Müll.) E.Y. Haw.	14	8.8	9.9	6.9	0.9	0.3
CYCBODAN	*Cyclotella bodanica*	Eulenst.	12	8.4	6.1	5.3	0.8	0.3
CYCCATOM	*Cyclotella cf. atomus*		3	1.5	5.2	12.8	1.1	0.2
CYCCOMUN	*Cyclotella aff. comta v. unipunctata*	Hust.	14	10.2	4.3	3.5	0.7	0.3
CYCCYCLO	*Cyclotella cyclopunctata*	Håk. and J.R. Carter	9	6.0	4.9	3.3	0.6	0.3
CYCDELIC	*Cyclotella delicatula*	Hust.	10	5.9	17.3	6.0	0.8	0.3
CYCKUETZ	*Cyclotella kuetzingiana*	Thwaites	10	8.8	2.8	6.1	0.9	0.4
CYCMICHI	*Cyclotella michiganiana*	Skvortsov	21	15.0	4.9	4.4	0.7	0.3
CYCNOR13	*Cyclotella* sp. 13 UMICH		15	11.7	16.3	5.2	0.8	0.3
CYCTRIPA	*Cyclotella tripartita*	Håk.	7	5.7	2.1	4.5	0.7	0.3
HIPNEGLE	*Hippodonta neglecta*	Lange-Bert., Metz. and Witk.	9	7.1	1.6	3.0	0.6	0.2
HIPSUBCO	*Hippodonta subcostulata*	(Hust.) Lange-Bert., Metzelin and Witkowski	9	6.1	2.9	5.9	0.8	0.3
KARCLEBO	*Karayevia clevei v. bottnica*	(Cleve) Bukhtiyarova	13	9.1	6.0	3.7	0.7	0.4
KOLAMOEN	*Kolbesia amoena*	(Hust.) Kingston	10	6.3	14.1	3.0	0.6	0.2
LUTMUTIC	*Luticola mutica*	(Kütz.) D.G. Mann	5	4.0	2.0	9.2	1.0	0.8
NAVMOSKA	*Navicula moskalii*	Metzeltin, Witkowski and Lange-Bert.	5	4.1	1.7	32.3	1.5	0.7
NAVVITIO	*Navicula vitiosa*	Schimanski	5	3.3	2.5	11.8	1.1	0.2
PLALANVM	*Planothidium lanceolatum v. minutissima*	(unofficial)	8	6.3	3.9	6.1	0.9	0.5
SELCPUPU	*Sellaphora cf. pupula*		5	2.7	3.7	36.7	1.6	0.5
SELNYAMI	*Sellaphora nyassensis fo. minor*	(O. Muller) Andresen, Stoermer and Kreis	6	3.9	1.9	4.2	0.7	0.1
SELSEMHU	*Sellaphora seminulum v. hustedtii*	(R.M. Patrick) D.G. Mann	4	2.5	3.8	30.5	1.5	0.5
SLLS2JCU	*Staurosirella* sp. 2 JCU		4	1.6	11.7	8.8	1.0	0.6
SUSMEDIU	*Stephanodiscus medius*	Håk.	13	9.4	4.6	8.1	1.0	0.6
SUSOREGO	*Stephanodiscus oregonicus*	(Ehrenb.) Håk.	7	3.7	6.1	3.9	0.7	0.1
SUSS13NO	*Stephanodiscus* sp. 13 UMICH		11	8.7	9.5	5.1	0.8	0.3
SUSTRANS	*Stephanodiscus transylvanicus*	Pant.	5	4.1	1.7	4.7	0.8	0.0

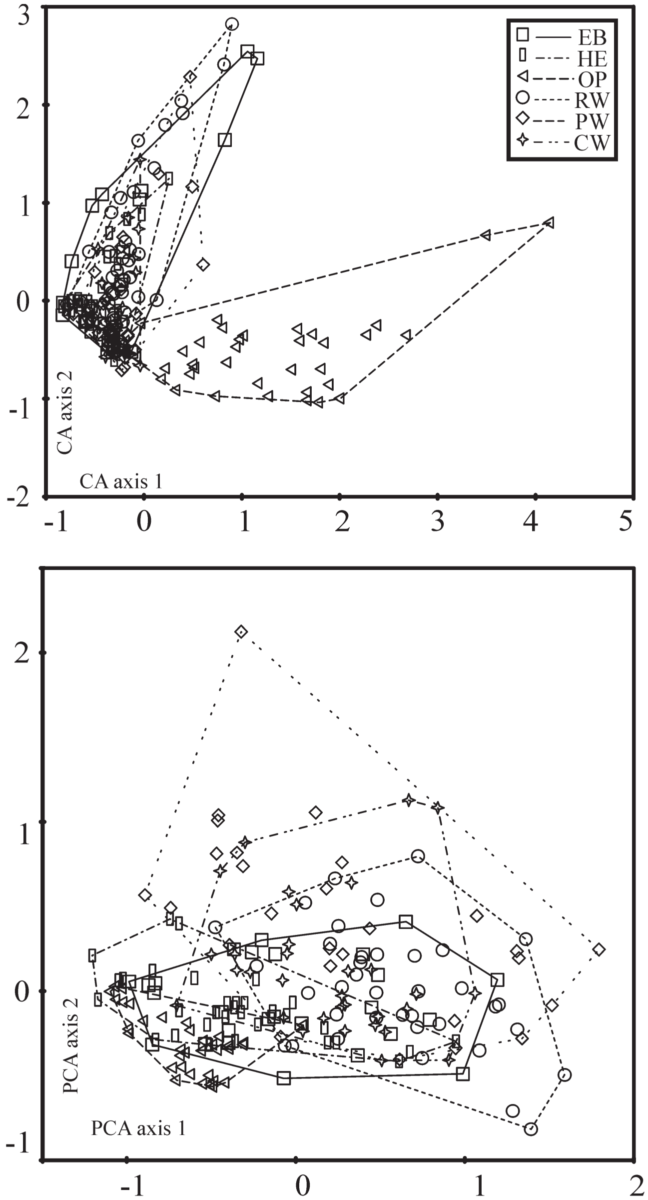

FIG. 3. Correspondence analysis (CA) and principal components analysis (PCA) for diatom assemblages (top) and water quality (bottom), respectively. Score distributions for habitat types are illustrated using unique symbols and are enveloped in polygons.

quality ER was distinct from SU, HU, and ON, but overlapped with MI. SU had significantly different water quality from all other Great Lakes. Analyses of nearshore samples yielded the same significant assemblage and water quality differences among geomorphic types and lakes as analyses that included the deeper OP sites (results not shown).

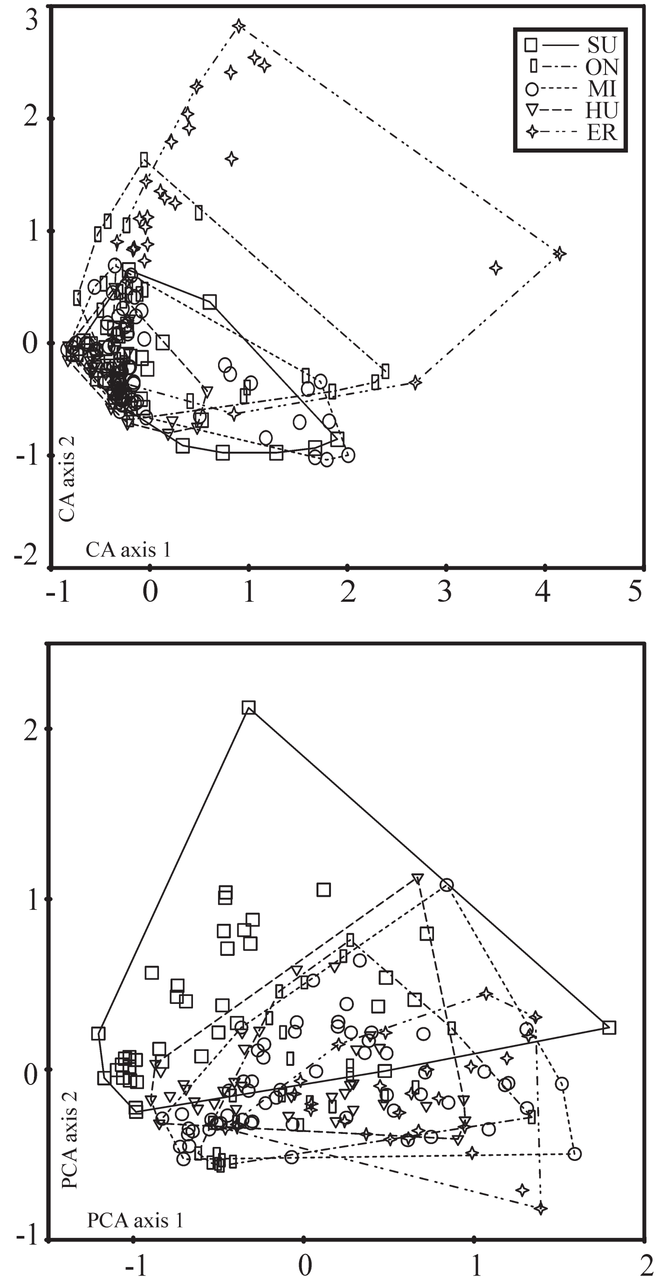

FIG. 4. Correspondence analysis (CA) and principal components analysis (PCA) for diatom assemblages (top) and water quality (bottom), respectively. Score distributions for each lake are illustrated using unique symbols and polygons.

Total Phosphorus Inference Models by Geomorphic Type and Lake

The range of measured total phosphorus varied among models created in this study (Fig. 6a). Based on comparisons of r^2_{jack} (Fig. 6b) and RMSEP/sd

TABLE 2. Eigenvalues and proportions of captured variance for correspondence analysis and principal components analysis.

		Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
CA All	Eigenvalue	0.540	0.483	0.461	0.396	11.867
	Cumulative percentage variance	4.5	8.6	12.5	15.8	
CA Nearshore	Eigenvalue	0.530	0.490	0.388	0.335	10.262
	Cumulative percentage variance	5.2	9.9	13.7	17	
PCA All	Eigenvalue	0.455	0.159	0.122	0.083	standardized to 1.00
	Cumulative percentage variance	45.5	61.4	73.5	81.9	
PCA Nearshore	Eigenvalue	0.436	0.155	0.136	0.09	standardized to 1.00
	Cumulative percentage variance	43.6	59.1	72.8	81.8	

TP (standardized prediction error; Fig. 6c), model performance was most robust when all geomorphic types were included. Percent maximum bias values were relatively similar among models (ranging from 10 to 23%), providing limited information on characterizing model robustness: although ON, ER, and SU models appeared to have the lowest predictive bias in the residuals (Fig. 6d). EB and PW models were also relatively robust, followed by the nearshore and HE models. Some geomorphic types appeared to be unreliable as stand-alone models: CW and RW had particularly low r^2_{jack} values, as did the OP model, which also had a markedly high standardized prediction error.

Lakes Superior and Ontario provided the best transfer functions in the lake-specific evaluations. Lake Erie was also a fairly strong stand-alone model while Lakes Huron and Michigan had markedly poorer performance. Standardized prediction errors for lake inference models were similar to the error in the model including all lakes, except for the model derived for Lake Huron, which exhibited higher error.

Multiple Linear Regression with Landscape Stressors

As in Reavie *et al*. (2006) wetland DI total phosphorus was more strongly associated with landscape stressors than was measured total phosphorus (Fig. 7). DI TP had a significant relationship with agriculture, facility density (facilities1), and soil properties (soils1 and soils2). The relationship between landscape stressors and DI TP increased slightly when open-water samples were excluded from the model. Measured TP had weak relationships with all of the watershed categories except for agriculture and facilities that discharge PAHs or physically disturb the environment (facilities2).

Riverine Wetland Investigations

Based on the poor performance of the RW model, more detailed investigations were performed on measured and DI TP data from the riverine wetlands to better understand the apparent poor diatom-TP relationship (Fig. 8). When compared to the full nearshore model (graph A, Fig. 8), the r^2 for DI TP versus landscape characteristics slightly decreased when RW samples were excluded from the multiple regression (graph B). However, the measured TP in the RW samples was not as well linked to watershed characteristics, as the watershed relationship to measured TP simultaneously increased with the removal of RW values. This weak relationship of measured RW TP to landscape stressors was best illustrated in graph C. We also found more evidence for a more robust watershed stressor relationship with DI TP for RW sites alone (graph C) than the full nearshore model (graph A), suggesting that despite a much poorer relationship between measured TP and watershed characteristics, the DI TP data in the RWs still well reflected watershed conditions. When the nearshore model was developed without RW samples, and RW samples were reconstructed independently, the DI TP/watershed relationship for RW sites alone remained similarly high (graph D). However, when the independently reconstructed values were added to estimates from the other sites, which were determined without RW inclusion, the relationship to landscape stressors slightly decreased (graph E) when compared to the

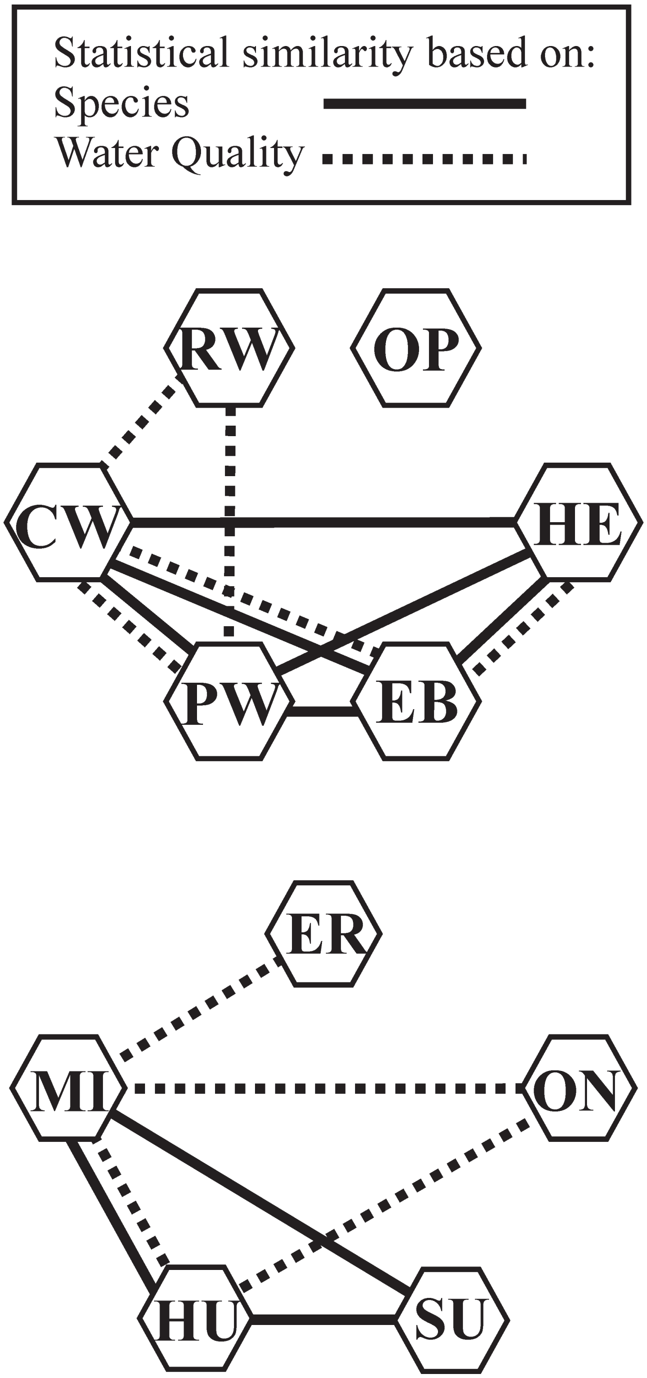

FIG. 5. Geomorphic types and lakes with statistically similar results from multiple pairwise comparisons in the MANOVA. Non-significant differences between diatom assemblages (from correspondence analyses) are indicated by solid lines and water quality (from principal components analyses) by dotted lines for each habitat and lake category ($P < 0.05$ with Bonferroni correction).

original nearshore estimates (graph A). Thus, excluding measured RW data from model development slightly decreased the relationship of watershed characteristics to DI TP from other sites, suggesting that the diatom and TP data from riverine wetlands are important contributions to the model in terms of being able to track watershed characteristics.

DISCUSSION

The specificity of diatom assemblages and water quality was evaluated for the five Great Lakes and various coastal habitat types that comprise the Laurentian Great Lakes system. Diatom assemblages and water quality varied among the geomorphic types and lakes but did not necessarily vary in concord; significant differences in water quality between two habitats did not necessarily imply that diatom assemblages would also be different. For example, water quality was distinct in the three wetland categories compared to high-energy sites, but diatom assemblages overlapped between all nearshore categories except for riverine wetlands. Moreover, this distinction of riverine wetland diatom assemblages was evident in coastal and protected wetlands where water quality characteristics overlapped with riverine wetland data. In addition, diatom assemblages showed clear lake affinity in Lakes Erie and Ontario, although both had overlapping water quality with Lake Michigan, the latter also possessing similar water quality to Lake Huron. Furthermore, Lake Superior had distinct water quality from all other lakes, but overlapping species assemblages with Lakes Michigan and Huron. This indicates variables other than measured water quality collected for this study were important in determining diatom community composition.

Offshore samples had clear water quality differences from nearshore samples and so, not surprisingly, diatom assemblages in these samples were similarly unique (i.e., mainly planktonic). Open water diatoms and water quality values were so distinctive in our coastal dataset that we believed their inclusion in multivariate analyses might have obscured our evaluation of variation among other geomorphic types, which was not the case according to analyses. However, the distinction between nearshore and deeper open-water diatom assemblages was enough to suggest that the offshore samples offered little to a model that would be used to infer nearshore conditions. Previous studies have used fundamental differences in diatom assem-

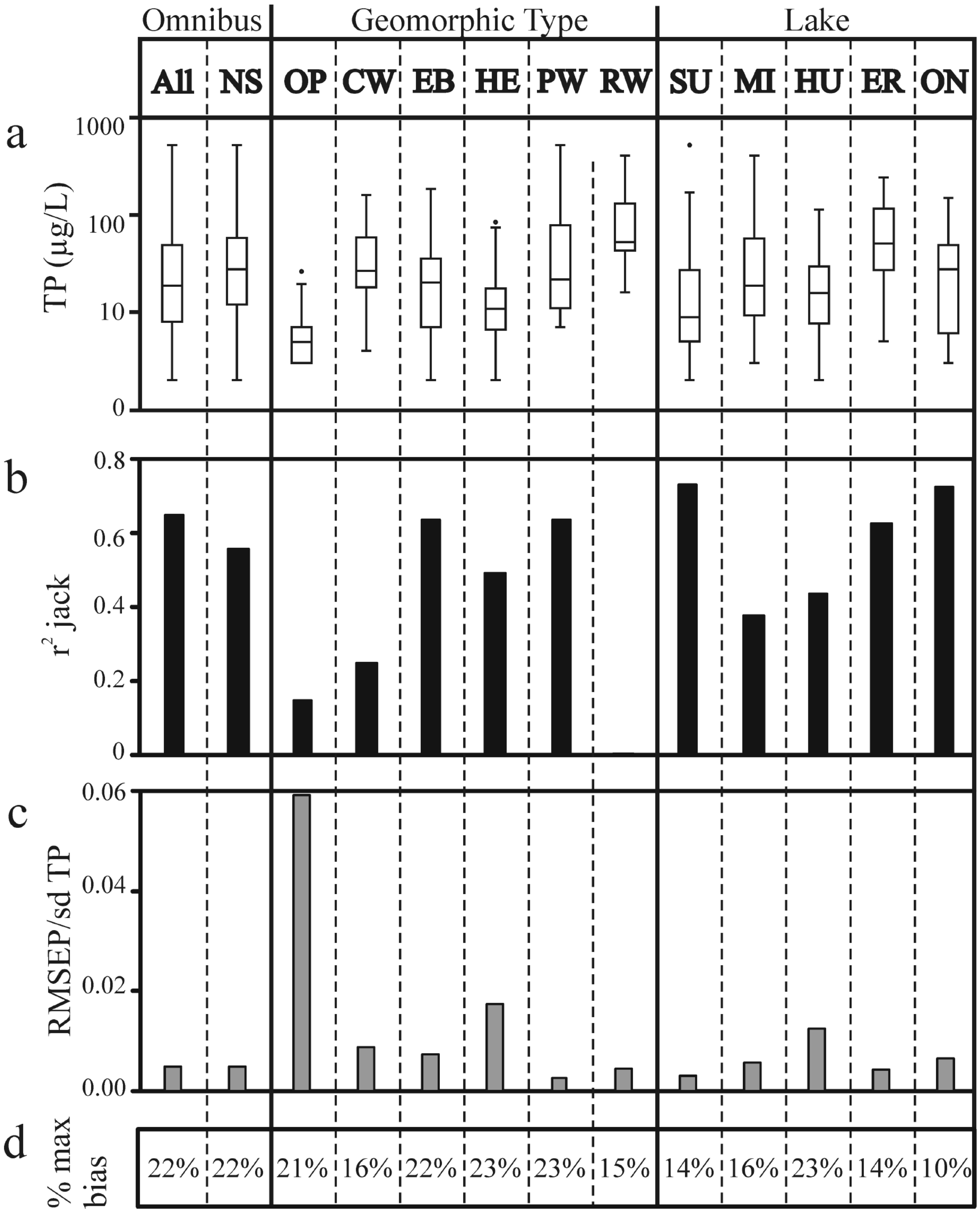

FIG. 6. Range of total phosphorus boxplots (a), diatom-inferred total phosphorus (DI TP) jackknife model r^2 (b), DI TP model standardized RMSEP (c), percent maximum bias (% max bias) for the DI TP residuals (d). For measured TP boxplots, boxes represent the interquartile range (IQR, the middle 50% of phosphorus measurements). Upper and lower adjacent values (largest observation within the 75^{th} percentile plus 1.5 times IQR, and smallest observation within the 25^{th} percentile minus 1.5 times IQR, respectively) are displayed as T-shaped lines. Small circles indicate mild outliers (within 3 IQRs from the 25th and 75th percentiles).

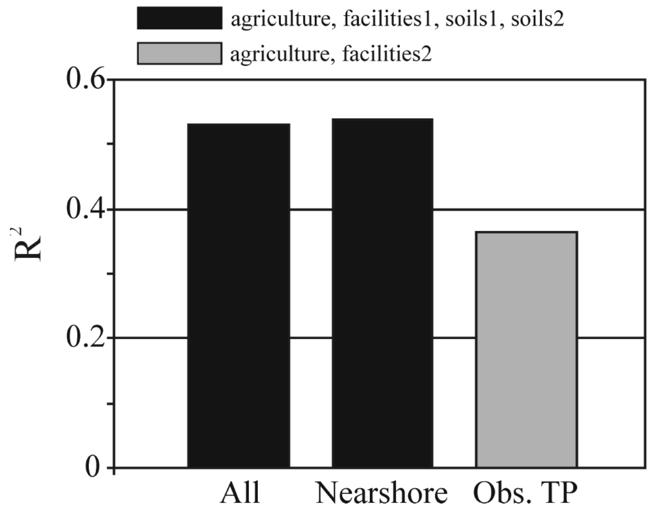

FIG. 7. Multiple regression r^2 values between wetland landscape characteristics (PC scores) and diatom-inferred (black) and measured (gray) TP. Wetland diatom inferred phosphorus from the "All" and "Nearshore" models showed significance ($p < 0.05$) with agriculture, facilities1, soils1, and soils2 PCs, while observed total phosphorus showed significance with agriculture and facilities2.

blages as a justification for developing separate diatom transfer functions for these communities (Werner and Smol 2005). Periphyton and phytoplankton, which respectively dominate the nearshore and offshore assemblages, experience very different physicochemical conditions; therefore, it has been suggested that in some cases it is necessary to focus on one of these functional groups when developing inference models (Philibert and Prairie 2002). However, this suggestion was not supported by the omnibus model testing, which showed the strongest model included all samples.

We surmise the superior performance of the omnibus model is in part a result of consistently low measured TP in the offshore samples, which account for most of the low end of the measured TP gradient encountered in this study. Because of the unique assemblage properties of the offshore samples, it is not surprising that we were able to adequately estimate TP in these samples during the model-testing phase (phytoplankton-dominated assemblages generally resulted in low TP reconstructions), and consequently obtain good model performance metrics. However, because these offshore assemblages were so different from nearshore assemblages, the inclusion of offshore assemblages in a model to reconstruct wetland condition, for example, does not seem appropriate. Total phosphorus varied little in the OP sites, at least during our sampling periods, relative to the nearshore sites. The poor performance of the individual OP model indicates that a broader range of water quality calibration data would be required to develop useful offshore diatom models

We originally anticipated poorer transfer function performance in the wetlands relative to the HE and EB sites based on Werner and Smol's (2005) work in wetland systems, in which macrophytes were believed to be related to decreased model performance. Two of our wetland models (CW and RW), in fact, performed poorly, but protected wetlands (also dominated by macrophytes) produced the strongest geomorphic type-specific model. We hypothesize that the robust performance of the PW model resulted because these sites were likely the least physically disturbed of our geomorphic types, in contrast to the others that were either hydrologically "flashier" (e.g., RW) or more exposed to physical and chemical perturbations from the adjacent lake associated with seiches, storms, ice push, and currents (CW, RW; Keough *et al.* 1999). In addition, water velocity and seiche and incoming tributary magnitude are important to wetland habitat patterns (Trebitz *et al.* 2005) and may well be important to diatom community composition. Trebitz *et al.* (2002) found that physical characteristics, such as mouth size and tributary flow, of the same type of wetland on the same lake could account for significant hydrologic variability. Differences in these physical stressors may account for variability among or within habitat categories and may be reflected in poorer diatom transfer functions. Protected wetland locales were less likely to manifest short-term chemical and physical fluctuations, thus enhancing our ability to track diatom-water quality relationships through the spot sampling used for model calibration.

On the other hand, riverine wetlands, in general, are typically subject to fluctuating runoff conditions to a greater degree than other habitat types (Bedford 1992, Keough *et al.* 1999, Detenbeck *et al.* 2005), which likely influenced the discrete point-in-time water quality measurements performed at our RW sites. We attribute poor performance of the RW model to the naturally higher variability of TP at these sites, resulting in relatively poorer characterization of the prevailing or average water quality condition by spot sampling, and consequently a

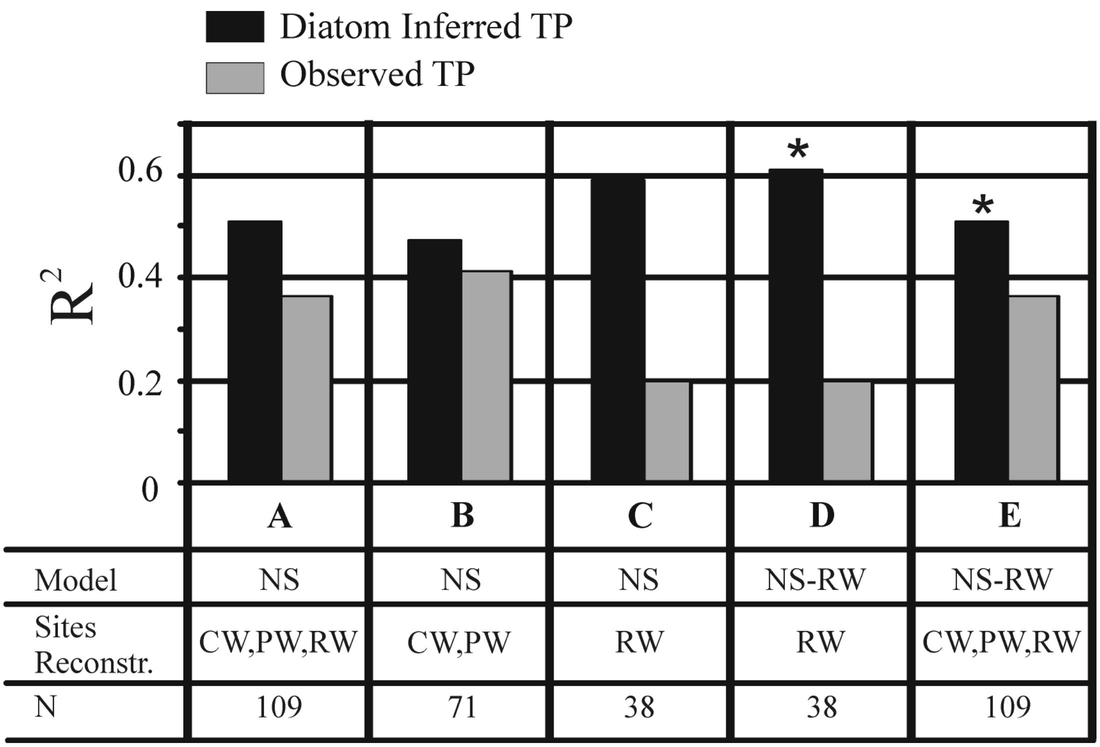

FIG. 8. Multiple regressions of diatom inferred phosphorus and measured phosphorus with landscape PCs. Diatom inferred phosphorus estimates are jackknife r^2 values derived from nearshore (NS) models, which exclude open water (OP) sites. Models were evaluated with (NS) and without (NS-RW) riverine wetland samples included in the training set. Sites Reconstructed indicates the source of DI TP estimates included in the multiple regression and N is the number of samples included in the multiple regression. CW = coastal wetlands, PW = protected wetlands, RW = riverine wetlands. Bars marked with an asterisk included independently reconstructed riverine wetland values derived from the NS-RW model.

poor diatom-environmental relationship. Measured phosphorus, in these instances, would be expected to have a weaker link to landscape stressors, which was the case for this habitat. In contrast, landscape stressors were strongly correlated with DI phosphorus estimates for riverine wetlands, indicating that diatom inferred estimates of phosphorus were more representative of surrounding landscape characteristics than measured total phosphorus. Nevertheless, our testing of various model permutations revealed that including the measured RW values in the model strengthened the relationship to landscape stressors. So, despite apparently poor diatom-environmental relationships in riverine wetlands (and in RW-specific models) it appears that one can still reliably reconstruct TP as a proxy for landscape stress in these wetlands using the nearshore model. Overall, these results suggest that poor diatom-environmental relationships may be expected in models developed for habitats that are frequently physically disturbed, and that including samples from more stable habitats may strengthen models.

Lake-specific models for Superior, Ontario, and Erie produced robust transfer functions, suggesting that lake-specific models may be appropriate when working in those lakes. Superior and Ontario models were each more robust than the all-lake model, and Superior and Erie produced the lowest prediction errors. Potapova and Charles (2002) recommend limiting geographical scope and environmental characteristics to all but the indicator metric (in our case, phosphorus) when developing calibration sets. Although lake-specific models for Michigan and Huron were less robust, none of the lakes appear to be a "weak link" in the omnibus Great Lakes model. However, managers and researchers might favor the omnibus nearshore model for investigations on Lakes Michigan and Huron. Model development investigations such as this, and the related model using integrated water quality (Reavie 2007 this issue), not only provide information on robust environmental indicators, but enable further understanding of complicated ecosystems, such as the Laurentian Great Lakes.

In conclusion, we were able to develop strong diatom total phosphorus transfer functions for several individual lakes and nearshore habitats. In some cases the physical influences of geographic and geomorphic variability may have weakened diatom indicator models, but these variations in transfer function robustness provided insight into the lake and geomorphic systems from which they were derived. With this manuscript we do not wish to recommend specific transfer functions for management and research use; the appropriate transfer function to use may vary according to future study designs and goals. Further investigations of water quality and biological dynamics, including regression against watershed characteristics, in habitats and lakes with weaker transfer functions will improve the accuracy of these indicators. Environmental assessments of large systems such as the Laurentian Great Lakes provide insight into the challenges for the discreet habitat types within them, and for others working in large lakes and coastal regions worldwide.

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