BioOne RESEARCH EVOLVED

Benthic diatom assemblages as indicators of water quality in the Everglades and three tropical karstic wetlands

Author(s): Josette M. La Hée and Evelyn E. Gaiser
Source: Freshwater Science, 31(1):205-221. 2012.
Published By: The Society for Freshwater Science
DOI: http://dx.doi.org/10.1899/11-022.1
URL: http://www.bioone.org/doi/full/10.1899/11-022.1

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Freshwater Science, 2012, 31(1):205–221
© 2012 by The Society for Freshwater Science
DOI: 10.1899/11-022.1
Published online: 24 January 2012

Benthic diatom assemblages as indicators of water quality in the Everglades and three tropical karstic wetlands

Josette M. La Hée[1] AND Evelyn E. Gaiser[2]

Department of Biological Sciences, Florida International University, Miami, Florida 33199 USA

Abstract. Limestone-based (karstic) freshwater wetlands of the Everglades, Belize, Mexico, and Jamaica are distinctive in having a high biomass of $CaCO_3$-rich periphyton mats. Diatoms are common components of these mats and show predictable responses to environmental variation, making them good candidates for assessing nutrient enrichment in these naturally ultraoligotrophic wetlands. However, aside from in the Everglades of southern Florida, very little research has been done to document the diatoms and their environmental preferences in karstic Caribbean wetlands, which are increasingly threatened by eutrophication. We identified diatoms in periphyton mats collected during wet and dry periods from the Everglades and similar freshwater karstic wetlands in Belize, Mexico, and Jamaica. We compared diatom assemblage composition and diversity among locations and periods, and the effect of the limiting nutrient, P, on species composition among locations. We used periphyton-mat total P (TP) as a metric of availability. A total of 176 diatom species in 45 genera were recorded from the 4 locations. Twenty-three of these species, including 9 that are considered indicative of Everglades diatom flora, were found in all 4 locations. In Everglades and Caribbean sites, we identified assemblages and indicator species associated with low and high periphyton-mat TP and calculated TP optima and tolerances for each indicator species. TP optima and tolerances of indicator species differed between the Everglades and the Caribbean, but weighted averaging models predicted periphyton-mat TP concentrations from diatom assemblages at Everglades ($R^2 = 0.56$) and Caribbean ($R^2 = 0.85$) locations. These results show that diatoms can be effective indicators of water quality in karstic wetlands of the Caribbean, but application of regionally generated transfer functions to distant sites provides less reliable estimates than locally developed functions.

Key words: Caribbean, Belize, Mexico, Jamaica, periphyton, phosphorus, weighted averaging models.

Much of the Caribbean and Central American region is underlain by ancient limestone bedrock (Eocene karst), which can contain isolated riverine or tidal freshwater depression wetlands where elevated from the ocean. These wetlands are characterized by low concentrations of water-column nutrients and a distinctive biological community, particularly abundant thick, calcareous benthic periphyton mats (Rejmánková and Komárková 2000, Novelo and Tavera 2003, Gaiser et al. 2006, La Hée 2010). These wetlands are naturally depleted in nutrients, so any organic and inorganic nutrients that enter the system (primarily via surface-water runoff from agricultural and industrial activities) can significantly alter the physical and chemical environment. Such changes in the environment tend to bring about long-lasting ecosystem effects (Hagerthey et al. 2009) that begin with the microbial community and subsequently cascade up through the food chain (Gaiser et al. 2005).

Most investigations of nutrient-induced state changes in karstic wetlands have been done in the Florida Everglades, a 5000-km^2 subtropical wetland that has been exposed to decades of enrichment resulting mainly from agricultural development and runoff in the upstream drainage (Noe et al. 2001, 2003). Experiments and observations along enrichment gradients developed downstream of canal inflows have demonstrated that periphyton productivity is limited by P (McCormick and O'Dell 1996, McCormick et al. 1996) and that excess P added to natural ecosystems is removed within hours or days by microbial communities existing in periphyton, detritus, and sediments (Noe et al. 2001). Together with adsorption to associated $CaCO_3$ (Scinto and Reddy 2003), these communities maintain water-column concentrations <5 to 6 μg TP/L (Thomas et al. 2006), except in locations with a long history of

[1] E-mail addresses: jlahee@ymail.com
[2] gaisere@fiu.edu

enrichment (McCormick et al. 1996). P is removed efficiently by microbes, but it drives marked physiological, physical, and compositional changes (McCormick and O'Dell 1996, McCormick et al. 2001, Gaiser et al. 2005, Iwaniec et al. 2006, Munyon 2010), such that even very low supplies of total P (TP) (<5 μg/L above ambient) can initiate a change in ecosystem state (Gaiser et al. 2005). Persistent increases in P loading lead to changes in soil respiration, macrophyte growth and composition, and consumer function (Reddy et al. 1993, DeBusk et al. 2001, Smith et al. 2009).

Native Everglades wetlands are noted for the presence of abundant benthic periphyton, referred to as *mats* because of their tendency to grow as attached masses on benthic, submerged, and floating substrates (Van Meter-Kasanof 1973, Browder et al. 1994; Fig. 1A, B). These mats can maintain high standing crop and productivity in this system (Browder et al. 1994, Goldsborough and Robinson 1996, Ewe et al. 2006, Gaiser et al. 2011) and serve as a food source and protective refuge for micro- and macroinvertebrate consumers and fish (Williams and Trexler 2006, Liston et al. 2008). Periphyton mats also contribute to production of detritus after death and decomposition of mat material (Neto et al. 2006), influence gas flux (McCormick et al. 1996, 1997, McCormick and Laing 2003, Munyon 2010), and can modify soil quality through the deposition of $CaCO_3$ throughout the system. Filamentous cyanobacteria (primarily *Schizothrix* spp. and *Scytonema* spp.) dominate the periphyton-mat assemblage and form an interwoven structure in which diatoms, green algae, and heterotrophic bacteria grow amid polysaccharide mucilage strands and interstitial deposits of $CaCO_3$ (Van Meter-Kasanof 1973, Swift and Nicholas 1987, Stal 2000, Donar et al. 2004).

Periphyton mats remove P rapidly from the water column and exhibit marked responses to increases in P availability. The most obvious response is an anomalous decrease in overall mass and an increase in % organic content (Pan et al. 2000, McCormick et al. 2001, Gaiser et al. 2006, La Hée 2010). The response to increased P availability is echoed in the algal assemblage as a loss of $CaCO_3$-precipitating cyanobacteria and a switch from an assemblage dominated primarily by endemic taxa to one dominated by weedy benthic taxa (Swift and Nicholas 1987, Grimshaw et al. 1993, Raschke 1993, McCormick and O'Dell 1996, McCormick et al. 1996, Pan et al. 2000). Because the diatom assemblage is particularly responsive to P availability, diatom-based inference models have been developed to infer water TP (Slate and Stevenson 2007), soil TP (Cooper et al. 1999), and periphyton-mat TP concentrations (Gaiser et al. 2006), which provide a more integrated understanding of P-load history than that afforded by highly variable water-column TP measurements (McCormick and Stevenson 1998, Gaiser et al. 2004). Therefore, within the Everglades wetland system, periphytic diatom assemblages are a highly effective tool for monitoring water-quality changes.

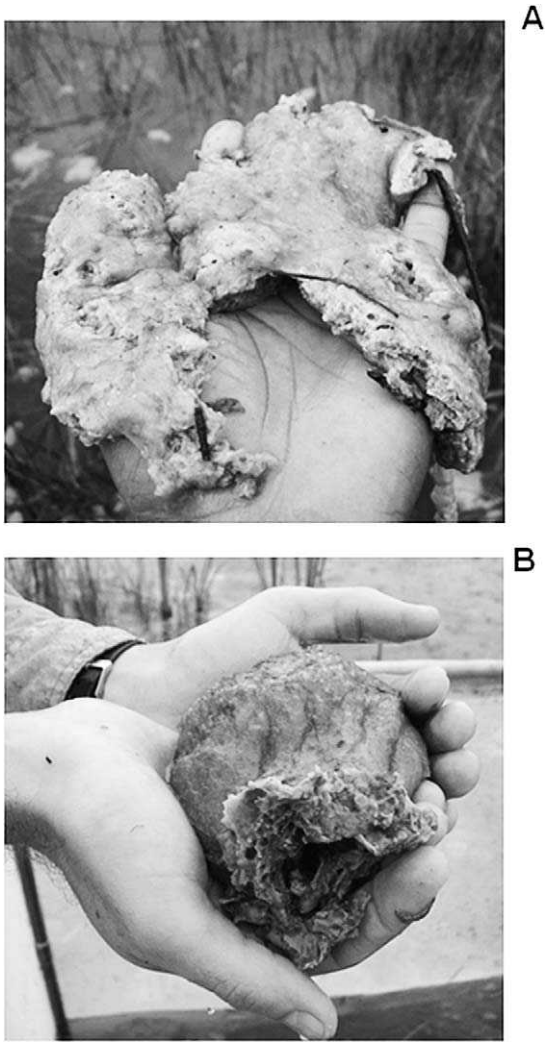

Fig. 1. Benthic (A) and epiphytic (B) periphyton mats from marsh habitats in Mexico and Belize, respectively.

Karstic wetlands with marsh habitats and periphyton mats comparable to those in the Everglades recently have been found in the Caribbean region (Rejmánková 2001, Novelo et al. 2007). In these wetlands, periphyton-mat biomass is extremely high and shows a negative relationship in response to P enrichment, a pattern that parallels the response in the Everglades (La Hée 2010). These wetlands have a less extensive history of enrichment than the

Everglades. However, areas that have been subjected to agricultural and industrial activities exhibit significant changes in water quality and concomitant ecosystem degradation (Rejmánková and Komárková 2005). Use of diatoms as biological indicators would be valuable in the management of these wetlands. However, a pervasive lack of environmental and species data across much of the region precludes development of site-specific diatom inference models.

Under these circumstances, diatom-based TP inference models developed for the Everglades might be useful for predicting environmental changes in these Caribbean wetlands. Cross-system application of calibration models has been attempted in other systems (Charles et al. 2006, Weilhoefer and Pan 2006) and in palaeoecological work, in which the response of modern diatom flora to present environmental conditions is used to infer past environmental conditions (Battarbee 1986, Smol et al. 1986, Dixit et al. 1992, Fritz et al. 1999). However, use of cross-system models is contingent on environmental similarity and an overlapping species assemblage that exhibits a parallel response to water-quality change among the systems. Whether the diatom assemblages and their responses to P in these wetlands are the same as in the Everglades is not known.

The main objectives of our study were to: 1) examine periphytic diatom assemblages from karstic wetland habitats in Belize, Mexico, and Jamaica, and compare them to assemblages in similar Everglades wetlands, 2) examine and compare the relationship between periphyton-mat TP concentrations and diatom assemblages at the Everglades and Caribbean locations, 3) determine the feasibility of using models relating diatom assemblage to water quality in the Everglades in similar systems in the wider Caribbean region.

Site Description

We sampled wetlands of similar geology, climate, hydrology, and vegetation in 3 regions in the northern Caribbean Basin (Fig. 2A): the Sian Ka'an Biosphere Reserve in Quintana Roo, Mexico (lat 19°52.342N, long 87°57.579W; Fig. 2B); the New River Lagoon in Orange Walk, Belize (lat 17°47.111N, long 88°39.212W; Fig. 2C); and the Broad River in the Black River Morass, St. Elizabeth, Jamaica (18°03.182N, long 77°48.874W; Fig. 2D). We compared data from these 3 locations to a larger data set from 110 sites across the Everglades National Park, in southern Florida, USA (Fig. 2E).

The Sian Ka'an Biosphere Reserve lies within a 6500-km^2 area along the southeastern coast of the

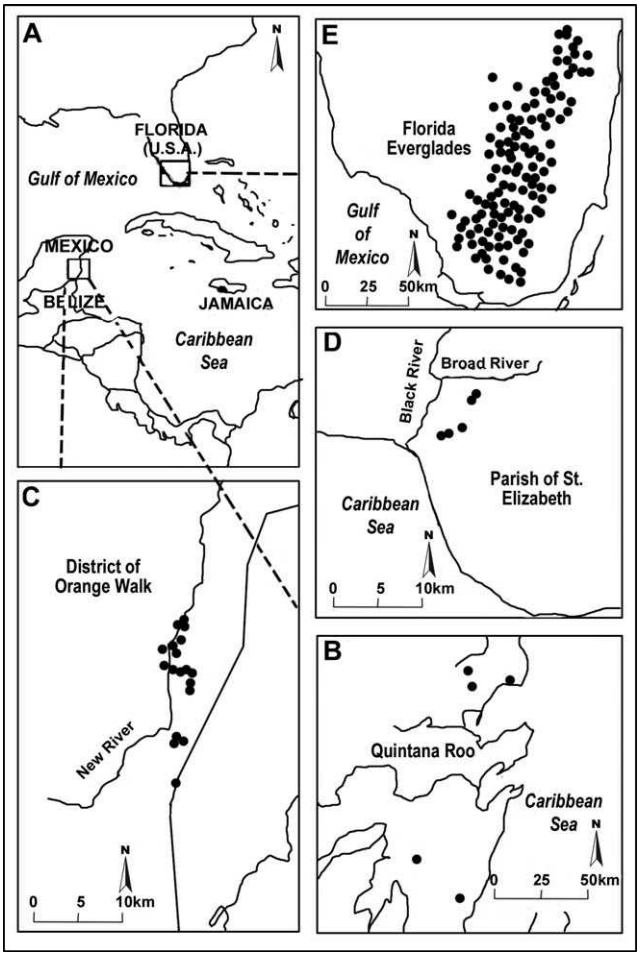

FIG. 2. Northern Caribbean region (A) showing the sampling sites in Mexico (N = 10) (B), Belize (N = 21) (C), Jamaica (N = 10) (D), and the Everglades (N = 110) (E).

Yucatan Peninsula in Quintana Roo, Mexico (Cairns et al. 2005). The Yucatan peninsula is an uplifted marine platform that extends from the greater Yucatan platform, separating the Gulf of Mexico from the Caribbean Sea. The geological formation consists of a 2- to 3-km thick sequence of limestone with intermittent layers of dolomite, anhydrite, and gypsum (Weidie 1985). In this region, karstic wetlands exist as low-P, inland, freshwater, marl-based habitats and coastal, mesohaline habitats. Macrophytic vegetation is generally dominated by *Cladium jamaicense* (sawgrass), *Eleocharis* spp. (spikerush), and *Typha domingensis* (southern cattail), which tend to dominate at low, intermediate, and high water depths, respectively (Rejmánková et al. 1996). In the coastal brackish water marshes, increased salinity levels encourage the growth of dwarfed populations of *Rhizophora mangle* (red mangrove). Calcitic periphyton mats are abundant in both freshwater and brackish water, marl-based

habitats (Rejmánková et al. 1996). We confined inland sampling sites at this location to freshwater *Eleocharis* spp. marshes, whereas closer to the coast, we sampled brackish water sites dominated by a mixture of *Eleocharis* spp. and dwarf *R. mangle*.

The New River Lagoon is an ~23-km-long and 750-m-wide stretch of the New River, the longest river contained entirely within Belize (Meerman 2006). The area is in the district of Orange Walk in northern Belize, just to the southeast of the basal portion of the Yucatan Peninsula and has geological features similar to this adjacent land mass (Weidie 1985). The New River Lagoon is bordered by freshwater marshes in which *C. jamaicense, Eleocharis cellulosa*, and *Eleocharis interstincta* are dominant. Intermittent deeper pools that support dense assemblages of *Nymphea ampla* (dotleaf waterlily) also are present. We confined sampling sites in this area to *Eleocharis* spp. marshes adjacent to the lagoon.

The Black River Morass is the largest freshwater wetland and river system in the Greater and Lesser Antillean archipelago in the Caribbean Sea (Davis et al. 1998, Massa and Haynes-Sutton 1998). The watershed, referred to as the Black River Basin, occupies an area of ~1488 km^2 in the southwestern region of Jamaica. The area is divided into a northern and southern section: the Upper and Lower Morass. The Upper Morass is ~97 km^2 (Cronberg 1983) and is composed of a mass of swampy lowlands with limestone bedrock covered by peat deposits. The Lower Morass, which is ~57 km^2 (Enell 1984), is an area of down-faulted, poorly karstified limestone, overlain by a relatively thin clay and peat sequence. Inland marsh areas are dominated by *C. jamaicense* and *Eleocharis* spp., with large stands of *T. domingensis* present in some areas (Azan and Webber 2007). In coastal habitats, *R. mangle* dominates as large trees bordering the main waterways as they meander through the wetland system. We sampled in *C. jamaicense* and *Eleocharis* marshes along the Broad River, a major tributary of the Black River.

The Everglades is one of the largest contiguous wetland systems in North America and encompasses an area of ~5000 km^2 (McCormick et al. 1998, Childers et al. 2001). These wetlands are <5000 y old and formed as a result of extended hydroperiod regimes that encouraged deposition of peat and marl in the midst of a limestone depression (Gleason and Stone 1994). The vegetation structure of Everglades marsh habitats is similar to that of the Caribbean locations, with *C. jamaicense* and *Eleocharis* spp. common in inland marshes and *Nymphaea odorata* (American white waterlily), *Nymphaea aquatica* (water shield), and *Nuphar advena* (spatterdock) characterizing deeper sloughs (Gunderson 1994, Richardson 2009). We used data drawn from a larger data set derived from multiple seasonal sampling events throughout the Everglades as part of the Comprehensive Everglades Restoration Plan (CERP 2005, Gaiser 2009).

Methods

We visited each of the 3 Caribbean study locations twice, once during a wet period and once during a dry period. Because of abnormal seasonal rainfall patterns during the study period, wet and dry *periods* did not necessarily coincide with the typical regional wet and dry *seasons*. Therefore, we applied wet and dry designations based on rainfall levels at each location during the sampling period relative to typical wet and dry seasonal rainfall levels. At each location, we defined dry periods as those in which no significant rain events were recorded for 1 mo prior to sampling and wet periods as those in which significant rain events occurred during the month preceding sampling. The Everglades samples were collected during October to December 2005 (wet period) and September to December 2006 (dry period) as part of the periphyton component of the CERP seasonal sampling regime. The Mexico sites were visited in December 2006 (wet period) and March 2008 (dry period), the Belize sites in May 2007 (dry period) and November 2007 (wet period), and the Jamaica sites in December 2007 (wet period) and May 2008 (dry period). We made an effort to sample as many sites as possible in each location. However, during dry periods the number of sites sampled varied according to our ability to find areas with water depths >5 cm. During wet periods, sampling efforts were contingent on our ability to gain access to sites and were limited to sites with water depths <~1 m because deeper-water habitats are less likely to support accrual of calcitic periphyton mats (Iwaniec et al. 2006).

Within each location, we sampled 3 main types of marshes: 1) sloughs dominated by *Eleocharis* spp. or *Nymphaea* spp., 2) ridges dominated by *C. jamaicense*, and 3) wet prairies dominated by *Eleocharis* spp. and dwarf *R. mangle*. At each sampling site, we recorded global positioning system (GPS) coordinates. We used a 1-m^3 throw trap to delineate 1-m^2 areas, which were treated as sampling plots (Kushlan 1981). We collected periphyton-mat samples from 4 plots at each site. We photographed plots to record the surface view, and measured water depth, pH, and conductivity with a YSI 63 meter (Yellow Springs Instruments, Yellow Springs, Ohio).

We collected all periphyton material in each plot with successive sweeps of a bar-seine net and coarsely sorted

the material to remove animals and attached marl or rocks. We removed live submerged and emergent aquatic vegetation entrained in the mat (especially *Utricularia purpurea*, *Chara* sp., and stems of *E. cellulosa* and *C. jamaicensis*) and collected the remaining periphyton mass in a perforated 2000-mL graduated cylinder, which allowed water to drain from the total sample. The total mass of periphyton collected in each plot could be measured as a volume because consolidated periphyton forms a jelly-like mass that pours easily into a measuring container. We measured the total biovolume of periphyton in the sample plot with the graduated cylinder, and from this total biovolume, we collected a 120-mL subsample to be used for TP and diatom analyses. We collected the subsample in a 120-mL sample cup, placed it in a sterile sample bag, and stored it in a cooler with ice for transport to the laboratory. When no observable calcitic periphyton mats were present, we collected nonquantitative epipelon samples from the benthos with successive sweeps of a bar-seine net along the surface of the sediment and scraped epiphytic films from any macrophytes present.

In the laboratory, we transferred each 120-mL subsample to a clean 500-mL beaker and added 20 mL of distilled water to facilitate homogenization with a hand-held homogenizer. We removed a 50-mL subsample from the total homogenized volume, poured it into a labeled 120-mL sample cup, and dried it at 80°C to constant mass. We ground the dried contents in a mortar and pestle and analyzed for TP following the methods of Solórzano and Sharp (1980). We removed a 10-mL subsample and processed it for quantitative diatom analysis with the sulfuric acid oxidation method of Hasle and Fryxell (1970). We then pipetted a measured amount of cleaned/processed material onto a glass coverslip and permanently fixed it to a glass slide with Naphrax® mounting medium. We identified diatom species using standard available taxonomic reference sources (see La Hée 2010). We counted a minimum of 500 diatom valves along random transects on each slide at a magnification of 1000× with a Nikon Eclipse E600 compound light microscope (Nikon, Melville, New York). For each sample, we recorded the number of cells of each species as species abundance and calculated % abundance for each species as the number of cells of species x/total number of cells counted for all species in the sample and multiplied by 100.

Data analysis

We calculated maximum, minimum, and mean values for water depth, pH, and conductivity separately for wet and dry periods at each location. No conductivity and pH values were available for the Everglades sites for the period during which samples were collected. Therefore, we derived values from data recorded from the same sites during the CERP 2008 wet and dry-season sampling episodes. These values serve primarily to characterize the physicochemical features of these sites.

Prior to statistical analysis, we $\log_{10}(x)$-transformed periphyton-mat TP (μg TP/g periphyton-mat dry mass) data and $\sqrt[4]{(x)}$-transformed diatom species % abundance data to satisfy assumptions of normality (Clarke and Gorley 2006). Rare species are often excluded from assemblage analyses because their presence can create noise in the data and reduce the clarity of underlying patterns (McCune and Grace 2002). We removed from the analysis any species that occurred in <1% of all samples in a location *and* had % abundance <5% where it did occur.

Sampling effort was not the same at all locations. However, the bias of unequal sampling effort can be circumvented by fitting asymptotic rarefaction curves to species accumulation rates to calculate total richness provided that samples are collected in a similar manner, from similar habitats, and overlap with respect to species composition (Tipper 1979). Rarefaction allows calculation of the expected number of species in a subsample (n) that has been randomly selected from a larger sample (N) (Krebs 1999). We generated rarefaction curves for each location and for the combined Caribbean sites with EstimateS (version 8.2.0; Colwell 2009). We assigned a logarithmic function with forward forecasting to each curve to allow determination of the rate of accumulation (slope) and expected species richness (asymptote) given the same sampling effort at all locations (i.e., sampling effort equal to that in the Everglades). We compared the generated curves among locations to determine the effectiveness of sampling in capturing the full complement of species present in the community and differences in species accumulation rates and richness (Hughes et al. 2001). Where few species are present or species are distributed evenly across sampling sites, curves tend to be convex (i.e., steep initial incline that begins to level off quickly). Where species richness is high or species are not evenly distributed across the sampled landscape, the likelihood of finding new species with each new sampling event is increased, and the shape of the curve tends to be more linear (Hughes et al. 2001).

We calculated mean per-sample species richness and Shannon–Weiner diversity based on samples collected at each location and used analysis of variance (ANOVA) to test for differences within and among locations. When the ANOVA was significant,

we used Tukey's test to locate specific differences. We examined relationships between richness, diversity, and periphyton-mat TP at each location with regression analysis. We used SPSS (version 18.0; SPSS, Chicago, Illinois) to run these analyses.

We used 6 data sets when analyzing diatom assemblages: Everglades (E), Belize (B), Mexico (M), Jamaica (J), a composite of Belize, Mexico, and Jamaica (Caribbean [C]), and all samples (T). We visualized patterns of similarity among sites and locations with nonmetric multidimensional scaling (NMDS) ordination (PC-ORD, version 5; McCune and Grace 2002) and tested the magnitude and significance of differences tested with Analysis of Similarity (ANOSIM) (PRIMER, version 6; Clarke and Gorley 2006). Each NMDS was based on a Bray–Curtis distance dissimilarity matrix, with 50 runs done in search of an optimal solution in a minimum number of dimensions above which no appreciable loss of stress was detected. The stress value for the NMDS analysis is an indication of the goodness of fit between the original Bray–Curtis distance dissimilarity matrix and the NMDS-generated distances among points. We used ANOSIM to determine the significance of patterns observed in the NMDS plots by evaluating the differences within and among sample categories. A global R value is reported as a measure of among-sample dissimilarity, where the level of dissimilarity increases from 0 to 1. Significant dissimilarity is indicated by the probability of a sample pair originating from the same community <0.05.

NMDS and ANOSIM analyses were done on the T data set to examine differences among all sites and locations based on diatom assemblages. We used ANOSIM pairwise comparison tests to evaluate significant differences in diatom assemblages between paired groups of samples (e.g., M wet-season samples vs J dry-season samples) and reported the resultant pairwise R statistics and significance levels. We used Pearson correlation (PC-ORD, version 5) to evaluate the direction and strength of the relationship between periphyton-mat TP and Bray–Curtis diatom-assemblage dissimilarity for each NMDS analysis. We applied the vector representing this relationship to the NMDS plot and report Pearson's r- and p-values.

To determine whether the diatom assemblage at each site was influenced by sampling period, we categorized samples as wet-period and dry-period samples. We examined differences in diatom assemblages between wet and dry periods with separate NMDS and ANOSIM analyses of E and C data sets categorized by period.

To evaluate the relationship between diatom assemblage and TP at each location, we categorized samples from each location as having periphyton mats with either high or low TP. We derived these designations by averaging the periphyton-mat TP concentrations among sites within a given location. We expressed the TP concentrations for any given assemblage at a site within the location as the deviation from the local mean as $P = (OTP - ATP)/(STP)$ where P = the designated TP category, OTP = observed periphyton-mat TP concentration at the *site*, ATP = mean periphyton-mat TP for the *location*, and STP = standard deviation of periphyton-mat TP for the *location*. Low TP sites had $P < 0$ (site concentration < location mean), and high TP sites were those where $P \geq 0$ (site concentration ≥ location mean).

We examined differences in diatom assemblages between high- and low-TP sites with separate NMDS and ANOSIM analyses of E, B, M, J, and C data sets categorized by periphyton-mat TP. For each location, we used Pearson's correlation to test for significant correlations between periphyton-mat TP and diatom assemblage Bray–Curtis dissimilarity. We reported Pearson's r- and p-values for all locations, but we show NMDS plots only for E and C data sets. We applied the vector representing the direction and strength of the relationship between periphyton-mat TP and diatom-assemblage dissimilarity to each NMDS plot.

We used the program C2 (Juggins 2003) to determine TP optima and tolerance levels of diatom species and subsequently created weighted-averaging models based on the % abundances of the various diatom species at different periphyton-mat TP concentrations. This analysis was done initially for each location data set (E, B, M, J). However, the fewer the number of sites included in the analyses, the shorter the length of the TP gradient over which averages can be calculated for each species and the greater the variation around the mean. Thus, relatively small data sets tend to produce less reliable models with elevated prediction errors. Therefore, we combined the B, M, and J data sets, which contained 21, 10, and 10 sites, respectively, to form a single C data set with 41 sites. For the E and C data sets, we regressed observed periphyton-mat TP against diatom-inferred periphyton-mat TP and calculated the predictive power (R^2) and the root mean square error of prediction (RMSEP expressed as μg TP/g periphyton-mat dry mass) by bootstrapping. Bootstrapping allows comparison of the bootstrapped sample variability with the original sample variability to improve estimates of predictive errors and RMSEP (Birks 1995).

Only species that occurred at all locations *and* at more than one site within each location were included

TABLE 1. Number of sites sampled (*N*) and mean (SD) values for water characteristics and periphyton attributes at each location during wet and dry periods. TP = total P, DM = periphyton-mat dry mass, – indicates missing data.

Location_season	*N*	pH	Conductivity (µS/cm)	Water depth (cm)	Periphyton biovolume (mL/m^2)	Periphyton TP (µg P/g DM)
Belize_wet	12	7.3 (0.5)	441.8 (208.6)	73.2 (8.5)	857.1 (1486.4)	239.7 (106.7)
Belize_dry	9	8.3 (0.2)	690.3 (104.0)	31.6 (11.8)	101.6 (264.6)	543.1 (187.9)
Jamaica_wet	5	8.4 (0.5)	447.6 (137.3)	11.6 (12.7)	2251.3 (1712.6)	200.3 (16.5)
Jamaica_dry	5	7.9 (0.2)	522.6 (62.4)	9.6 (3.6)	–	405.2 (158.3)
Mexico_wet	6	–	1259.0 (952.5)	37.9 (10.3)	6772.6 (2957.6)	212.5 (93.7)
Mexico_dry	4	9.2 (0.4)	15,047.7 (16,670.5)	30.3 (23.4)	4144.6 (2720)	193.7 (210.9)
Everglades_wet	55	7.2 (0.3)	496.1 (525.3)	54.5 (20.5)	3352.5 (3003.0)	146.0 (111.1)
Everglades_dry	55	7.4 (0.3)	445.9 (261.7)	39.4 (21.1)	3756.8 (2980.6)	157.1 (104.1)

in calculations of TP optima. If a species occurred at only one site within a location, then it could not be included in the weighted averaging calculations, because there were not enough occurrences to average (i.e., a species has to occur more than once to calculate an average). We identified the 23 species fitting these criteria and regressed the TP optima calculated for the C data set against the optima values of the same species calculated for the E data set to examine whether species optima were consistent between locations. We ran indicator species analysis (PC-ORD) to identify species that indicated high or low periphyton-mat TP concentrations. Indicator species analysis uses weighted averaging to determine environmental preferences for each species and requires a sizeable number of data points to yield an effective estimate that is representative of the true mean, so we did these analyses with the E and C data sets. We selected indicator species with a strong relationship to TP (identified by regression analysis) and a weighted-average estimated tolerance less than the mean tolerance for all species.

Results

Environmental conditions at the sampling sites overlapped. Ranges of pH (6.3–9.4), conductivity (214–38,000 µS/cm), water depth (5–113 cm), and TP (20–789 µg TP/g dry mass) reflected the level of variation in shallow marl-based marshes across all locations (Table 1). Conductivity was notably higher in the coastal brackish water sites in Mexico than in other locations during wet and dry periods. Periphyton-mat biovolume was lowest in Belize during the dry period (101.6 mL/m^2) and highest in Mexico during the wet season (6772.6 mL/m^2).

A total of 176 diatom species representing 45 genera was recorded from the 4 locations (Appendix; available online from: http://dx.doi.org/10.1899/11-022.1.s1). Ninety-four of these species were included in diatom assemblage analyses after removal of rare species. Twenty-five of the 94 species were present at all 4 locations, and of these, 23 were present at >1 site within each location. The most common among the 23 species (mean abundances >1% at all locations) were *Brachysira neoexilis*, *Encyonema evergladianum*, *Encyonema* spp., *Fragilaria synegrotesca*, *Mastogloia smithii* var. *lacustris*, *Mastogloia smithii*, *Navicula cryptotenella*, *Nitzschia palea*, and *Nitzschia serpentiraphe*.

Five rarefaction curves were generated, one each for the Everglades, Belize, Mexico, and Jamaica data sets and 1 for the Caribbean data set (Fig. 3). A large proportion of the species present at Everglades sites was captured in a relatively small proportion of the samples collected, a result suggesting that the assemblage was sampled adequately. The curves generated for Belize, Mexico, Jamaica, and the Caribbean all had approximately the same shape, a result that implies that these assemblages were sampled with equal effort relative to their overall richness. However, the curves tended to be linear without reaching an asymptote, a result that suggests that these locations had greater rates of species accumulation, greater richness, and required a greater sampling effort to capture the complement of species present than at Everglades locations. The disparity between the Caribbean and the Everglades also was reflected in the slopes of the curves, which were much steeper for Caribbean than for Everglades sites (Fig. 3).

Mean per-sample species richness was significantly lower ($p < 0.001$) at Everglades sites (14.88) than at Belize, Mexico, and Jamaica sites (18.48, 18.70, and 21.90, respectively; Table 2). Estimated species richness derived from forward forecasting of the logarithmic function of each curve to a maximum of 140 sampled sites also showed that Everglades sites had lower species richness (~80) than Belize, Mexico, Jamaica, and Caribbean sites (~170, 140, 140, and 225, respectively; Fig. 3). Mean per-sample species diversity was significantly lower at Everglades and Belize

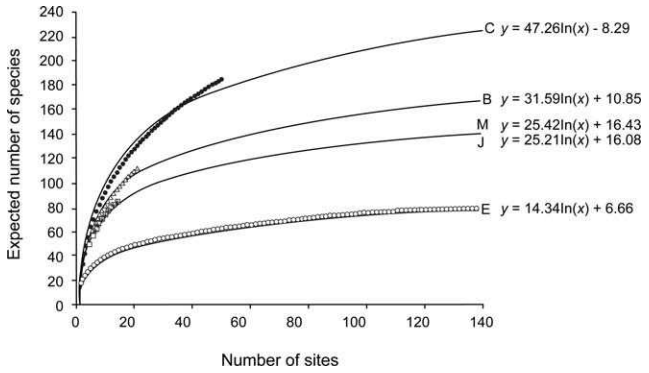

FIG. 3. Rarefaction curves for Everglades (E), Belize (B), Mexico (M), Jamaica (J), and a composite of the Caribbean (C) samples. A logarithmic function with forward forecasting was assigned to each curve to allow the determination of the predicted asymptote and curve of the slope.

sites (1.59 and 1.67, respectively) than at Mexico and Jamaica sites (2.00 and 2.01, respectively) ($p < 0.001$; Table 2). Per-sample species diversity (H) was not significantly related to periphyton-mat TP at any location. However, per-sample species richness was positively linearly related to periphyton-mat TP at the Belize sites ($R^2 = 0.36$, $p < 0.01$).

Diatom assemblages from the 4 locations showed some compositional overlap (NMDS stress = 0.17; Fig. 4). However, some separation of locations was observed. Assemblages differed significantly between E and C locations (global $R = 0.42$, $p < 0.001$). Pairwise ANOSIM comparisons detected significant differences between all pairs of assemblages (all pairwise $R > 0.36$, $p < 0.02$), except for Jamaica assemblages during the wet period and Mexico assemblages during the dry period (pairwise $R < 0.27$, $p > 0.09$). This exception probably was an artifact of the small sample size at these 2 locations (probable type I error). Belize assemblages during the dry period differed most strongly from all other assemblages (all pairwise $R > 0.63$; $p < 0.003$). Assemblage dissimilarity was correlated with periphyton-mat TP ($r = 0.64$, $p < 0.05$), and Belize assemblages during dry and wet periods clustered at the high end of the TP range (Fig. 4). At all locations, composition of wet- and dry-period assemblages overlapped, and no distinct separation between the paired groups was detected except for Belize assemblages (ANOSIM, pairwise $R = 0.02$, $p = 0.01$).

TABLE 2. Mean per-sample species richness (S) and diversity (H) for all locations. N = number of locations, * = significantly low values ($p < 0.001$).

Site	N	Total no. of species	S	H
Belize	21	113	18.48 (6.51)	1.67 (0.49)*
Mexico	10	84	18.70 (4.45)	2.00 (0.33)
Jamaica	10	87	21.90 (4.41)	2.01 (0.22)
Everglades	134	87	14.88 (3.40)*	1.59 (0.30)*

Assemblage composition differed between high- and low-TP periphyton mats in Belize (NMDS stress = 0.14, global $R = 0.43$, $p < 0.001$), Mexico (NMDS stress = 0.05, global $R = 0.52$, $p < 0.017$), Jamaica (NMDS stress = 0.11, global $R = 0.32$, $p < 0.033$), the Everglades (NMDS stress = 0.19, global $R = 0.23$, $p < 0.001$; Fig. 5A), and the Caribbean sites (NMDS stress = 0.12, global $R = 0.20$, $p < 0.001$; Fig. 5B). Assemblage dissimilarity was significantly correlated with periphyton-mat TP in all locations (Belize: $r = 0.66$, Mexico: $r = 0.68$, Everglades: $r = 0.66$, Caribbean: $r = 0.75$, $p < 0.05$) except Jamaica ($r = 0.41$, $p = 0.24$).

Weighted-averaging models were developed based on % abundances of species in mats with different periphyton-mat TP concentrations. Observed periphyton-mat TP was compared to periphyton-mat TP inferred from diatom optima and tolerances for Caribbean and Everglades assemblages separately (Fig. 6). Diatoms predicted the observed periphyton-mat TP with greater accuracy for Caribbean sites ($R^2 = 0.85$, RMSE = 66.1 μg TP/g) than for Everglades sites ($R^2 = 0.56$, RMSE = 113.4 μg TP/g). A positive relationship existed between the optima of the 23 shared species in Everglades and Caribbean sites ($R^2 = 0.55$, $p < 0.001$; Fig. 7A), but TP optima generally were lower at Everglades sites than at Caribbean sites ($p < 0.0001$; Table 3). A positive relationship also existed between the ranked TP optima of the same 23 species at Everglades and Caribbean sites ($R^2 = 0.50$, $p < 0.001$; Fig. 7B). These 2 results suggest that although the same species had, on average, higher TP optima at Caribbean than at Everglades sites, species maintained their ranking along the spectrum of TP preference regardless of location.

Indicator species analysis identified 17 Everglades species and 12 Caribbean species that indicated either high or low periphyton-mat TP concentrations (Table 3). One indicator species (*Eunotia flexuosa*) was shared by both locations and indicated high TP concentrations at both.

Discussion

We identified a core diatom assemblage of relatively common species that occurred across all Caribbean locations and is composed of taxa common in Everglades marshes. This assemblage, which includes

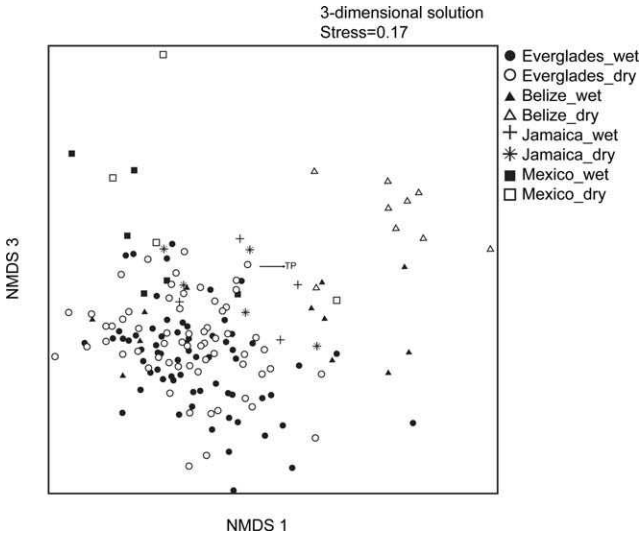

FIG. 4. Nonmetric multidimensional scaling (NMDS) plot showing dissimilarity between diatom assemblages from sites from all locations (stress = 0.17). The vector represents the direction and strength of the relationship between periphyton-mat total P (TP) concentrations and diatom assemblage dissimilarity.

Brachysira neoexilis, *Encyonema evergladianum*, *Encyonema* spp., *Fragilaria synegrotesca*, *Mastogloia smithii* var. *lacustris*, *Mastogloia smithii*, *Navicula cryptotenella*, *Nitzschia palea*, and *Nitzschia serpentiraphe*, is distinctive of subtropical/tropical freshwater karstic wetlands. Some of these species were thought to be endemic to the Everglades (Slate and Stevenson 2000, 2007, Gaiser et al. 2006). Others had been recorded in freshwater habitats in Cuba (Foged 1984) and Jamaica (Podzorski 1985), and periphyton mats in the El Eden Ecological Reserve in Quintana Roo, Mexico (Novelo et al. 2007, Ibarra et al. 2009). However, ours is the first study in which this distinctive core assemblage was described in periphyton mats in Belize and Jamaica. Despite the ubiquity of this core assemblage across locations, compositional differences did exist among the 4 locations and among sites within each location. This variation is often interpreted as a result of habitat heterogeneity and microhabitat variability (Weilhoefer and Pan 2006), but also can be caused, in part, by environmental variables other than TP that were not evaluated in our study (e.g., salinity).

The greatest disparity among locations was between assemblages collected from Belize in the dry period and all other assemblages. The dry-season Belize samples were collected during an intense drought from *Eleocharis* spp. marshes adjacent to a river lagoon, and some of these marshes probably are influenced by periodic, inland excursions of lagoon water. Periphyton samples from some of these sites

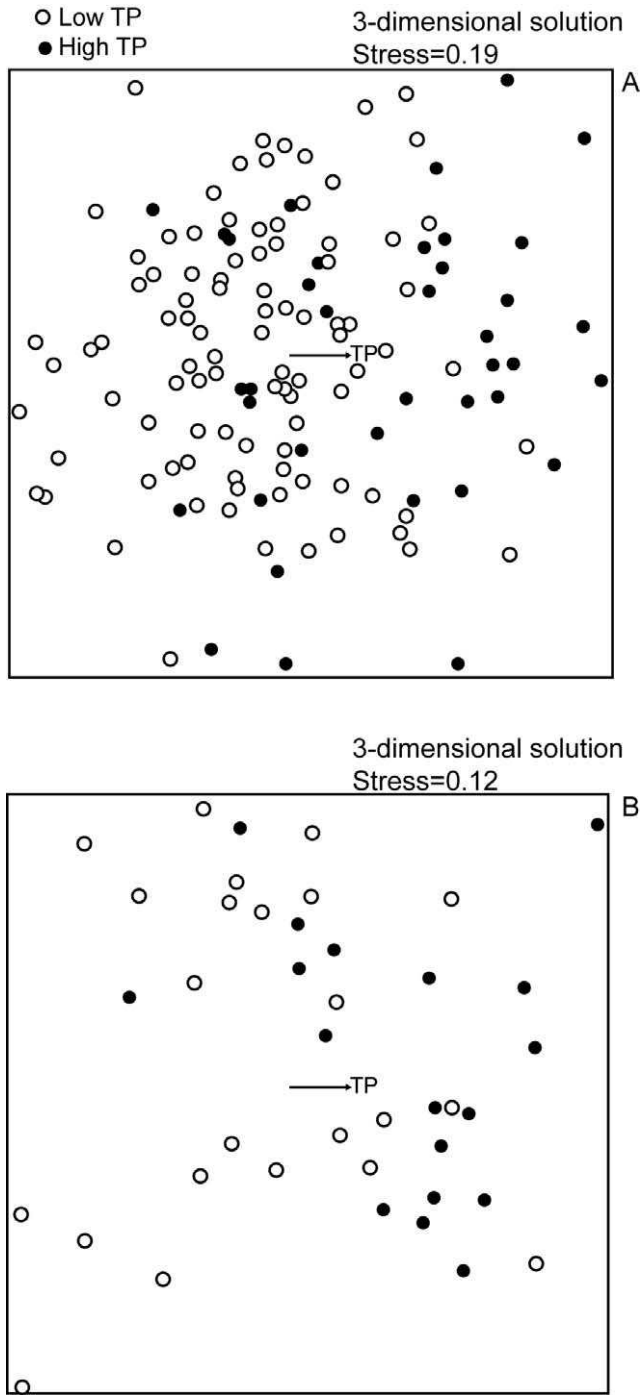

FIG. 5. Nonmetric multidimensional scaling (NMDS) plot showing dissimilarity between diatom assemblages associated with periphyton mats of high and low total P (TP) from the Everglades (stress = 0.19) (A) and a composite of the Caribbean locations (stress = 0.12) (B). The vector represents the direction and strength of the relationship between periphyton-mat TP concentration and diatom assemblage dissimilarity.

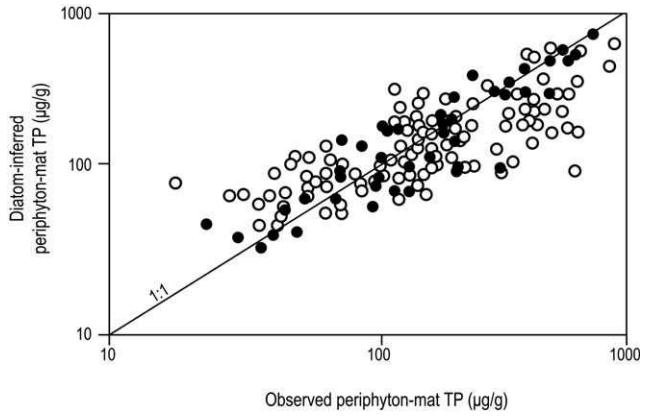

FIG. 6. Scatter plot showing the relationship between diatom-inferred periphyton-mat total P (TP) concentrations and observed periphyton-mat TP concentrations for Caribbean (R^2 = 0.85, RMSE = 66.1 µg TP/g) and Everglades sites (R^2 = 0.56, RMSE = 113.4 µg TP/g).

were noncalcitic, unconsolidated, and had elevated P concentrations, characteristics reminiscent of the form of periphyton present in the Everglades in deep water with elevated P concentrations (McCormick and O'Dell 1996). Similar mat types were rare at other sites in our study, so these samples were recognized as different in the community analyses.

Differences in sampling effort among locations could have influenced derived diversity and richness estimates because of possible underestimation of diversity at undersampled sites (Hughes et al. 2001). However, the shapes and slopes of the rarefaction curves showed that periphyton mats from Caribbean locations supported a greater number of diatom species than those from the Everglades even though fewer sites were sampled at the Caribbean locations. This result, which was reinforced by mean per-site richness and diversity, suggests that the diversity of the diatom flora is lower in the Everglades than in the Caribbean karstic wetlands. However, the underlying reason for this difference is unclear.

Species diversity within a given locale is determined by a combination of factors. These factors include, but are not limited to, the distance between the locale and species source locations, the availability and efficiency of transport mechanisms, the frequency of immigration and emigration events, competitive interactions, habitat heterogeneity, evolutionary processes of speciation, stochastic disturbances, and the length of time over which these factors are allowed to exert their various influences (Kristiansen 1996, Rosenzweig 1997, Hubbell 2001, Charalambidou and Santamaria 2002, Figuerola and Green 2002). The geographically isolated position of the Everglades and

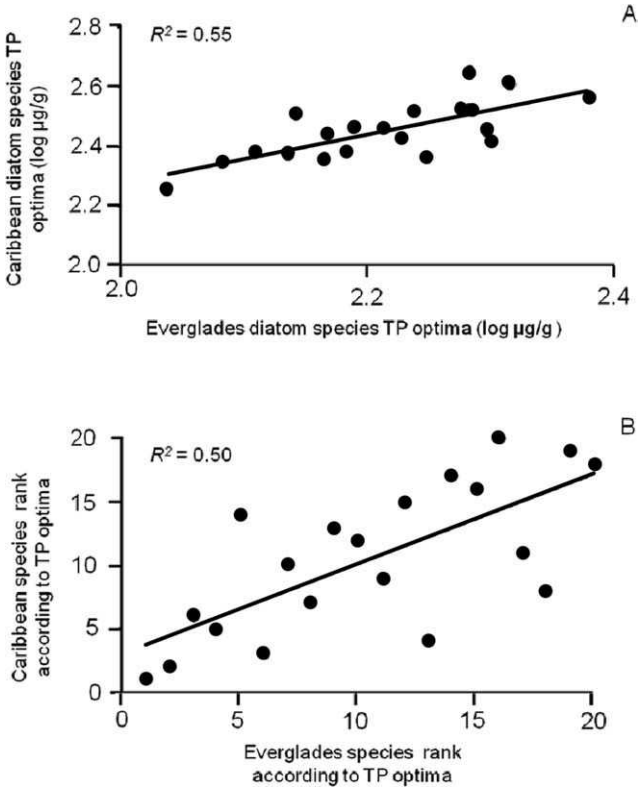

FIG. 7. Scatter plot showing the relationships between Everglades and Caribbean diatom species total P (TP) optima (R^2 = 0.55) (A) and between Everglades and Caribbean ranked diatom species TP optima (R^2 = 0.50) (B).

its relatively young geological age (~5000 y old) support the assumption that diatom assemblages may have developed following species introductions from older regional wetlands (Slate and Stevenson 2007). This hypothesis could explain why the locations all share a core diatom assemblage, which under this scenario, would have developed first in the older wetlands and subsequently been introduced to the Everglades following a series of dispersal events. This hypothesis also could help to explain the lower diversity in the Everglades relative to in the Caribbean sites. First, increases in the number of species present in the Everglades system would depend on continuous introductions from the older systems (and subsequent periods of establishment), and it is reasonable to assume that the younger system (sink) would have lower numbers of species than the older systems (source pools) until an equilibrium level was attained (Ricklefs 1979). Second, species numbers also can increase as a result of local speciation events. Again, older systems would have a longer period over which such events could occur compared to younger systems (Ricklefs 1979). Both of these explanations rest on the idea that the younger Everglades would

TABLE 3. Mean % abundance (based on cell counts) of all indicator species (I) at all locations (E = Everglades, B = Belize, M = Mexico, J = Jamaica). Total P (TP) optima and with lower and upper tolerance values are given for the 23 indicator taxa present at all locations. Species are identified as indicating high or low total P (TP) for Everglades (** = high TP, * = low TP) and Caribbean (^{tt} = high TP, ^{t} = low TP). – indicates taxon absence from a location.

Taxon	% abundance				TP optimum (μg/g) (lower/upper tolerance)		I	
	E	B	M	J	E	C	C	E
Achnanthidium neomicrocephalum H. Lange-Bertalot & F. Staab	1.4	27.0	0.7	1.2	191 (99/369)	442 (281/696)	tt	
Brachysira neoexilis Lange-Bertalot	7.8	25.3	5.9	7.6	147 (67/321)	273 (142/525)		
Cyclotella meneghiniana Kützing	0.4	0.4	1.2	0.4	163 (71/373)	289 (165/507)		
Diploneis oblongella (Naegelii ex. Kutzing) Ross	0.6	0.2	0.9	1.9	128 (62/265)	225 (118/428)		
Diploneis parma Cleve	0.7	0.2	0.3	1.5	137 (57/326)	235 (118/467)		
Encyonema evergladianum Krammer	23.2	16.3	20.3	29.6	146 (68/313)	229 (118/445)	t	
Encyonema sp. 5	3.4	1.7	5.8	3.3	177 (83/378)	230 (122/432)		**
Encyonema sp. 6	0.6	0.2	0.6	0.1	177 (83/378)	230 (122/432)		
Encyonopsis microcephala (Grunow) Krammer	2.7	0.2	1.1	10.8	189 (84/423)	334 (215/520)		**
Eunotia flexuosa (Brébisson) Kützing	0.6	0.5	0.2	0.5	239 (120/478)	368 (245/554)	tt	**
Fragilaria nanana Lange-Bertalot	0.7	2.8	3.5	2.2	199 (100/395)	263 (141/489)		
Fragilaria synegrotesca Lange-Bertalot	11.2	14.0	6.0	6.6	168 (80/355)	266 (145/488)		**
Fragilaria ulna var. *ulna* (Nitzsch) Lange-Bertalot	1.0	2.3	0.2	0.6	266 (137/516)	281 (151/521)		
Gomphonema cf. *vibrioides* Reichardt & Lange-Bertalot	0.9	1.7	4.0	0.2	206 (107/399)	406 (254/649)	tt	
Gomphonema intricatum var. *vibrio* (Ehrenberg) Cleve	0.9	1.2	0.5	0.7	172 (79/375)	329 (186/582)		**
Mastogloia cf. *smithii* Thwaites ex. W. Smith	37.6	6.3	21.8	6.7	152 (70/332)	240 (125/461)		*
Mastogloia smithii var. *lacustris* Grunow	2.5	1.8	1.6	0.4	128 (59/275)	239 (133/429)		
Navicula cf. *radiosa* Kutzing	0.9	1.2	1.6	1.0	198 (97/402)	282 (139/572)		**
Navicula cryptotenella Lange-Bertalot	1.6	1.2	1.7	1.1	190 (86/420)	332 (197/561)		**
Navicula subtilissima Cleve	1.1	1.4	0.3	1.2	154 (70/339)	291 (148/573)		
Nitzschia palea (Kutzing) W. Smith	4.3	2.3	6.6	7.1	120 (59/247)	222 (124/398)		*
Nitzschia serpentiraphe Lange-Bertalot	4.0	1.2	3.1	3.5	109 (52/226)	180 (108/301)		*
Sellaphora laevissima Krammer	0.6	0.2	0.5	0.4	138 (63/304)	321 (179/577)		
Encyonema silesiacum (Bleisch) Mann	4.5	0.4	0.3	–				**
Eunotia camelus Ehrenberg	6.7	5.1	0.9	–			tt	
Achnanthidium sp. 2	0.8	0.5	–	0.3			tt	
Amphora sulcata (Brébisson) Cleve	8.9	–	3.0	2.4			t	
Eunotia cf. *karenae* Metzeltin & Lange-Bertalot	–	1.8	0.4	–			tt	
Nitzschia tubicola Grunow	–	–	14.1	2.8			t	
Achnanthidium exiguum (Grunow) Czarnecki	–	2.8	–	0.4			tt	
Synedra acus var. *angustissima* Ehrenberg	–	0.6	–	0.1			tt	
Rhopalodia gibba (Ehrenberg) O. Muller	0.4	–	–	3.9				**
Brachysira pseudoexilis Lange-Bertalot & Moser	1.5	–	–	–				*
Eunotia incisa W. Smith ex. Gregory	0.4	–	–	–				**
Eunotia naegelii Migula	0.4	–	–	–				**
Eunotia sp. 1	0.8	–	–	–				**
Nitzschia amphibia (Grunow) Lange-Bertalot	0.8	–	–	–				**
Nitzschia scalaris (Ehrenberg) W. Smith	–	0.2	–	–			tt	

Freshwater Science jnbs-31-01-25.3d 11/1/12 09:40:34 215 Cust # 11-022R

have had less time to develop a more diverse flora than the older Caribbean sites.

The latitudinal diversity gradient, which is evidenced by the reduction in species richness with distance from the tropics, has been best documented in plant and animal communities from terrestrial and marine systems (Willig et al. 2003). The pattern of change in diversity has not been examined sufficiently as a forcing factor in freshwater microbial communities (Hillebrand 2004, Leighton 2005), but could potentially influence diatom diversity patterns, such that subtropical systems like the Everglades would have lower diversity than the more tropical Caribbean locations. The diversity of diatom species in the Everglades also might be restricted by features of the subtropical climate that are not experienced in the more tropical Caribbean locations. Foremost among these climatic features is temperature, which exhibits greater annual extremes in the Everglades than in Caribbean wetlands. Species contributing to diatom diversity in the Everglades may be limited to those that can tolerate such fluctuations in temperatures, whereas the more moderate tropical climate would support a wider range of species.

We examined the influence of season on diatom assemblages to rule out the possibility that seasonal effects would mask or enhance the influence of TP on diatom assemblages. Seasonal variability in light and temperature is muted in the subtropics/tropics relative to temperate ecosystems, so the greatest seasonal change in tropical wetlands is mediated through hydrologic responses to seasonal differences in precipitation (McCormick et al. 1998, Gottlieb et al. 2006, Thomas et al. 2006). Seasonal changes in periphyton mats do occur in the Everglades. In particular, assemblages shift from dominance by filamentous cyanobacteria during the wet season to dominance by diatoms during the dry season (McCormick et al. 1998). Water depth affects the spatial distribution of diatoms (Gaiser 2009), but differences in diatom assemblages between wet and dry periods have not been reported, and we found no such differences in our study. Spatial variation in water depth and periphyton-mat TP usually are correlated (Gaiser et al. 2010), but we found no differences in periphyton-mat TP between wet and dry periods, except for at the Belize sites where the lagoon influenced dry-period samples.

Experimental and observational studies in the Everglades (McCormick et al. 1996, Cooper et al. 1999, Gaiser et al. 2005) demonstrated the relationship between diatom assemblages and TP availability and led to the development of diatom-based predictive models that are now used in system-wide habitat assessment (Gaiser 2009). These models provide a more accurate and meaningful assessment of habitat state than previous models, but their use has highlighted an important consideration, i.e., the validity of cross-system applications of these models. In a study examining periphyton responses to eutrophication within the Everglades, Gaiser et al. (2006) found that ambient periphyton-mat TP concentrations from unaffected wetland areas varied from 97 to 430 μg TP/g dry mass. The variation in periphyton mat-TP concentrations among sites produced associated variations in diatom assemblage response to TP. Thus, a unique calibration model was needed for each individual wetland basin, and no single model could be used reliably to infer quantitative TP concentrations across all sites. This result indicated that diatom species were responding to local *relative* changes in periphyton-mat TP at each site instead of to *absolute* periphyton-mat TP concentrations across all sites. We expressed periphyton-mat TP concentration at each site as its deviation from the local mean periphyton-mat TP concentration instead of as an absolute value. This method revealed a clear pattern, in which distinct high- (above average) and low-TP (below average) diatom assemblages could be identified at all locations, despite differences in absolute average periphyton-mat TP concentrations among locations. This pattern also was evident in the species optima and tolerances, which differed among locations, but when ranked, revealed a consistent pattern in which species preferences for low or high TP concentrations were similar among locations. The underlying mechanisms that allow species optima to vary among areas are not well understood. However, it is reasonable to think that a diatom assemblage at any given location could include populations of species that adapt to local conditions over time. Population studies would be required to examine this hypothesis, but under this hypothesis, the same species or group of species adapted to different local conditions could exhibit different optima and tolerances in different regions. Alternatively, ecosystem shifts might occur in response to local changes in the environment, such that excess P is processed or stored in a way that effectively prevents diatom species from being exposed to higher P levels. Further examination of this issue is warranted, especially considering the fact that regional differences in the response of indicator species to environmental conditions could potentially invalidate the broad-scale use of indicator species in cross-system comparisons.

Subsequent analyses also identified species that were indicative of relatively high or low TP concentrations, but only 1 indicator species (*E. flexuosa*, which

indicated high periphyton-mat TP concentrations) was shared by Everglades and Caribbean locations. Several of the Everglades indicator species identified in our study also were identified by Gaiser et al. (2006), including *E. flexuosa*, *N. cryptotenella*, *E. incisa*, *R. gibba*, and *N. amphibia* (as indicators of elevated periphyton-mat TP concentrations) and *M. smithii* (as an indicator of low periphyton-mat TP concentrations). *Mastogloia smithii* has been identified as an indicator of low TP concentrations in the Everglades in several studies (McCormick et al. 1996, Cooper et al. 1999, Pan et al. 2000, Slate and Stevenson 2007) and has been proposed as a potential keystone taxon in these mats (Gaiser et al. 2010). Of the 12 species identified as indicators for the Caribbean locations, 1 species, *Eunotia* cf. *karenae*, had not been described previously as occurring in this region. Therefore, although we found this species indicative of high periphyton-mat TP concentrations, no other information could be found regarding its tolerance for P enrichment in other karstic wetland habitats. All of the remaining indicators of high periphyton-mat TP concentrations throughout the Caribbean locations are species that also occur in the Everglades. However, none have been reported previously as indicator species. Three species were identified as indicators of low periphyton-mat TP concentration. One of these was *E. evergladianum*, which was previously reported as an indicator of low P in the Everglades (Gaiser et al. 2006).

At both Everglades and Caribbean locations, diatom-inferred and observed periphyton-mat TP were strongly related. This result confirms that diatom assemblages can be used to infer periphyton-mat TP in these wetlands. However, the smaller sample size from the Caribbean locations reduced the confidence with which our model can be applied elsewhere. Both models were strong, but the model produced for Caribbean locations was more robust and had a higher R^2 and lower RMSEP than the model for the Everglades location. Sampling was conducted along similar TP gradients at both Everglades and Caribbean locations, so an argument cannot be made that a longer TP gradient in the Caribbean increased model strength. However, the difference in model strength may be a consequence, in part, of the greater number of sites sampled in the Everglades than in the Caribbean locations. Including more sites could have introduced greater variability in habitat and environmental factors that can influence diatom assemblages and, thus, reduce the strength of the P signal (Slate 1998). Also, species richness was lower in the Everglades location than in the Caribbean locations. Thus, fewer species were contributing information to the Everglades model, which would reduce the predictive ability of the model.

Our results are consistent with findings from examinations of relationships between diatom assemblages and water quality across spatial expanses and support the growing concern regarding the cross-system application of diatom-based water-quality assessment tools (Potapova and Charles 2007). Diatom species assemblages and the specific responses of individual species to environmental factors can vary considerably even within habitat or geographic boundaries (Kelly et al. 1998, Pipp 2002, Charles et al. 2006, Gaiser et al. 2006). This variability can reduce the predictive power of models developed outside the target system. In addition, discrepancies in diatom taxonomic identification often arise when work is done by multiple investigators, and this problem can reduce comparability of data across systems.

Diatom-based monitoring techniques are a powerful tool for water-quality assessment, and careful application of this technique for the purposes of wetland monitoring and management of karstic wetlands in the Caribbean region should be encouraged. Development of site-specific models relating diatom assemblages to water quality would provide the most reliable and accurate information for use in biomonitoring programs in these systems. However, in the absence of data to develop such models, cross-system application of inference models developed for the well studied Everglades system may suffice, but only as a way to determine relative, as opposed to absolute, water-quality state.

The use of diatoms in aquatic biomonitoring programs is well established for lakes (e.g., Dixit and Smol 1994), rivers (e.g., Charles 1996, Stevenson and Pan 1999), and to a lesser extent, wetlands (e.g., Pan and Stevenson 1996). Development of standardized diatom indices (e.g., Lowe 1974, van Dam et al. 1994) and diatom-based inference models (e.g., Gaiser et al. 2006) has allowed a more quantitative approach to water-quality assessment and encourages cross-system comparisons. However, challenges arise when intrinsic ecosystem variability reduces the predictive power of these indices and models, even when applied within and across similar systems (Charles et al. 2006, Gaiser et al. 2006, Weilhoefer and Pan 2006). Our study provides an example of the value of diatoms as bioindicators for inferring water quality in karstic wetlands, but our results emphasize the need for caution when applying diatom-inference models across systems. This strategy may occasionally be the only recourse available, but in the absence of a robust monitoring program, even moderate sampling within a given

system can provide valuable supplementary information regarding water quality.

Acknowledgements

We thank the Sian Ka'an Biosphere Reserve in Quintana Roo, Mexico, and Lamanai Outpost in Orange Walk, Belize, for facilitating site access and supporting researchers during field excursions. We also thank Joel Trexler, William Loftus, Clifton Ruehl, Raul Urgelles, and collaborators from Universidad Nacional Autónoma de México for their assistance with the field collections in Mexico and Belize, and the periphyton laboratory at Florida International University (FIU) for data collection in the Everglades. This research was funded by an international supplement award to the Florida Coastal Everglades Long-Term Ecological Research program through the National Science Foundation under Grant No. DBI-0620409 and DEB-9910514 and a grant to JML from the Latin American Caribbean Center at FIU. The Southeast Environmental Research Center (SERC) at FIU also provided travel and analytical funding for this research. This is publication number 537 from SERC and 214 from the Tropical Biology Program of the Department of Biological Sciences at FIU.

Literature Cited

Azan, S., and D. Webber. 2007. The characterization and classification of the Black River Upper Morass, Jamaica, using the three-parameter test of vegetation, soils and hydrology. Aquatic Conservation: Marine and Freshwater Ecosystems 17:5–23.

Battarbee, R. W. 1986. Diatom analysis. Pages 527–570 *in* B. E. Berglund (editor). Handbook of Holocene palaeoecology and palaeohydrology. John Wiley and Sons, Chichester, UK.

Birks, H. J. B. 1995. Quantitative palaeoenvironmental reconstructions. Pages 161–254 *in* D. Maddy and J. S. Brew (editors). Statistical modeling of Quaternary science data. Volume 5. Quaternary Research Association, Cambridge, UK.

Browder, J. A., P. J. Gleason, and D. R. Swift. 1994. Periphyton in the Everglades: spatial variation, environmental correlates, and ecological implications. Pages 379–418 *in* S. M. Davis and J. C. Ogden (editors). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.

Cairns, C. E., R. Villanueva-Gutiérrez, S. Koptur, and D. B. Bray. 2005. Bee populations, forest disturbance, and Africanization in Mexico. Biotropica 37:686–692.

CERP (Comprehensive Everglades Restoration Plan). 2005. 2005 report to Congress. Department of the Army, Washington, DC. (Available from: http://www.evergladesplan.org/pm/pm_docs/rtc_2005/030606_rtc.pdf)

Charalambidou, I., and L. Santamaria. 2002. Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. Acta Oecologica – International Journal of Ecology 23(3):165–176.

Charles, D. F. 1996. Use of algae for monitoring rivers in the United States: some examples. Pages 109–118 *in* B. A. Whitton and E. Rott (editors). Use of algae for monitoring rivers II. Institut für Botanik, Universität Innsbruck, Innsbruck, Austria.

Charles, D. F., F. W. Acker, D. D. Hart, C. W. Reimer, and P. B. Cotter. 2006. Large-scale regional variation in diatom-water chemistry relationships: rivers of eastern USA. Hydrobiologia 561:27–57.

Childers, D. L., R. D. Jones, J. C. Trexler, C. Buzzelli, J. Boyer, A. L. Edwards, E. E. Gaiser, K. Jayachandran, D. Lee, J. F. Meeder, J. Pechmann, J. H. Richards, and L. J. Scinto. 2001. Quantifying the effects of low level phosphorus enrichment on unimpacted Everglades wetlands with in situ flumes and phosphorus dosing. Pages 127–152 *in* J. Porter and K. Porter (editors). The Everglades, Florida Bay, and coral reefs of the Florida Keys. CRC Press, Boca Raton, Florida.

Clarke, K. R., and R. N. Gorley. 2006. PRIMER v6. User manual/tutorial. PRIMER-E, Plymouth UK.

Colwell, R. K. 2009. EstimateS: statistical estimation of species richness and shared species from samples. Version 8.2. User's guide and application. (Available from: http://purl.oclc.org/estimates)

Cooper, S. R., J. Huvane, P. Vaithiyanathan, and C. J. Richardson. 1999. Calibration of diatoms along a nutrient gradient in Florida Everglades Water Conservation Area-2A, USA. Journal of Paleolimnology 22: 413–437.

Cronberg, G. 1983. Plankton of the Negril and Black River Morasses, Jamaica: Report to the Petroleum Corporation of Jamaica, Kingston, Jamaica. Institute of Limnology, University of Lund, Lund, Sweden. (Available from: Environmental Protection Agency, Headquarters and Chemical Libraries, 1301 Constitution Ave NW, Washington, DC 20004 USA.)

Davis, M., G. C. Lalor, and R. Rattrap. 1998. Nutrient status of the Black River System, St. Elizabeth, Jamaica. Jamaican Journal of Science and Technology 9:45–62.

DeBusk, W. F., S. Newman, and K. R. Reddy. 2001. Spatiotemporal patterns of soil phosphorus enrichment in Everglades WCA-2A. Journal of Environmental Quality 30:1438–1446.

Dixit, S. S., and J. P. Smol. 1994. Diatoms as indicators in the Environmental Monitoring and Assessment Program-Surface Waters (EMAP-SW). Environmental Monitoring and Assessment 31:275–306.

Dixit, S. S., J. P. Smol, J. C. Kingston, and D. F. Charles. 1992. Diatoms: powerful indicators of environmental change. Environmental Science and Technology 26:23–33.

Donar, C. M., K. W. Condon, M. Gantar, and E. E. Gaiser. 2004. A new technique for examining the physical structure of Everglades floating periphyton mat. Nova Hedwigia 78:107–119.

ENELL, M. 1984. Water chemistry of the Negril and Black River Morasses, Jamaica. Petroleum Corporation of Jamaica, Kingston, Jamaica. (Available from: University of the West Indies, Mona Campus, Main Library, Mona, Kingston 7, Jamaica.)

EWE, S. M. L., E. E. GAISER, D. L. CHILDERS, V. H. RIVERA-MONROY, D. IWANIEC, J. FOURQUREAN, AND R. R. TWILLEY. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) in the Florida Coastal Everglades LTER (2001–2004). Hydrobiologia 569: 459–474.

FIGUEROLA, J., AND A. J. GREEN. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshwater Biology 47: 483–494.

FOGED, N. 1984. Freshwater and littoral diatoms from Cuba. Bibliotheca Diatomologica, Cramer, Berlin, Germany.

FRITZ, S. C., B. C. CUMMING, F. GASSE, AND K. F. LAIRD. 1999. Diatoms as an indicator of hydrologic and climate change in saline lakes. Pages 41–73 *in* E. F. Stoermer and J. P. Smol (editors). The diatoms: applications for the environmental and earth sciences. Cambridge University Press, Cambridge, UK.

GAISER, E. E. 2009. Periphyton as an indicator of restoration in the Florida Everglades. Ecological Indicators 9: S37–S45.

GAISER, E. E., J. M. LA HÉE, F. A. C. TOBIAS, AND A. H. WACHNICKA. 2010. *Mastogloia smithii* var. *lacustris* Grun.: a structural engineer of calcareous mats in karstic subtropical wetlands. Proceedings of the Academy of Natural Sciences of Philadelphia 160:99–112.

GAISER, E. E., P. MCCORMICK, AND S. E. HAGERTHEY. 2011. Landscape patterns of periphyton in the Florida Everglades. Critical Reviews in Environmental Science and Technology 41(S1):92–120.

GAISER, E. E., J. H. RICHARDS, J. C. TREXLER, R. D. JONES, AND D. L. CHILDERS. 2006. Periphyton responses to eutrophication in the Florida Everglades: cross-system patterns of structural and compositional change. Limnology and Oceanography 51:617–630.

GAISER, E. E., L. J. SCINTO, J. H. RICHARDS, K. JAYACHANDRAN, D. L. CHILDERS, J. C. TREXLER, AND R. D. JONES. 2004. Phosphorus in periphyton mats provides the best metric for detecting low-level P enrichment in an oligotrophic wetland. Water Research 38:507–516.

GAISER, E. E., J. C. TREXLER, J. H. RICHARDS, D. L. CHILDERS, D. LEE, A. L. EDWARDS, L. J. SCINTO, K. JAYACHANDRAN, G. B. NOE, AND R. D. JONES. 2005. Cascading ecological effects of low-level phosphorus enrichment in the Florida Everglades. Journal of Environmental Quality 34: 717–723.

GLEASON, P. J., AND P. STONE. 1994. Age, origin and landscape evolution of the Everglades peatland. Pages 149–197 *in* S. Davis and J. C. Ogden (editors). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.

GOLDSBOROUGH, L. G., AND G. G. C. ROBINSON. 1996. Pattern in wetlands. Pages 77–117 *in* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). Algal ecology in freshwater benthic ecosystems. Academic Press, San Diego, California.

GOTTLIEB, A. D., J. H. RICHARDS, AND E. E. GAISER. 2006. Comparative study of periphyton community structure in long and short hydroperiod Everglades marshes. Hydrobiologia 569:195–207.

GRIMSHAW, H. J., M. ROSEN, D. R. SWIFT, K. RODBERG, AND J. M. NOEL. 1993. Marsh phosphorus concentrations, phosphorus content and species composition of Everglades periphyton communities. Archiv für Hydrobiologie 128: 257–276.

GUNDERSON, L. H. 1994. Vegetation of the Everglades: determinants of community composition. Pages 323–340 *in* S. M. Davis and J. C. Ogden (editors). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.

HAGERTHEY, S. E., S. E. JONATHAN, J. COLE, AND D. KILBANEA. 2009. Aquatic metabolism in the Everglades: dominance of water column heterotrophy. Limnology and Oceanography 55:653–666.

HASLE, G., AND G. FRYXELL. 1970. Diatoms: cleaning and mounting for light and electron microscopy. Transactions of the American Microscopical Society 89:470–474.

HILLEBRAND, H. 2004. On the generality of the latitudinal diversity gradient. American Naturalist 163:192–211.

HUBBELL, S. P. 2001. A unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey.

HUGHES, J. B., J. J. HELLMAN, T. H. RICKETTS, AND B. J. M. BOHANNAN. 2001. Counting the uncountable: statistical approaches to estimating microbial diversity. Applied and Environmental Microbiology 67:4399–4406.

IBARRA, C., R. TAVERA, AND E. NOVELO. 2009. Diversity and structure of periphyton and metaphyton diatom communities in a tropical wetland in Mexico. Revista Mexicana de Biodiversidad 80:763–769.

IWANIEC, D. M., D. L. CHILDERS, D. RONDEAU, C. J. MADDEN, AND C. J. SAUNDERS. 2006. Effects of hydrologic and water quality drivers on periphyton dynamics in the southern Everglades. Hydrobiologia 569:223–235.

JUGGINS, S. 2003. C2 user guide. Software for ecological and palaeoecological data analysis and visualisation. University of Newcastle, Newcastle upon Tyne, UK.

KELLY, M. G., A. CAZAUBON, E. CORING, A. DELL'UOMO, L. ECTOR, B. GOLDSMITH, H. GUASCH, J. HÜRLIMANN, A. JARLMAN, B. KAWECKA, J. KWADRANS, R. LAUGASTE, E. A. LINDSTRØM, M. LEITAO, P. MARVAN, J. PADISÁK, E. PIPP, J. PRYGIEL, E. ROTT, S. SABATER, H. VAN DAM, AND J. VIZINET. 1998. Recommendations for the routine sampling of diatoms for water quality assessments in Europe. Journal of Applied Phycology 10:215–224.

KREBS, C. J. 1999. Ecological methodology. 2nd edition. Addison–Wesley Educational Publishers, Menlo Park, California.

KRISTIANSEN, J. 1996. Dispersal of freshwater algae—a review. Hydrobiologia 336:151–157.

KUSHLAN, J. A. 1981. Sampling characteristics of enclosure fish traps. Transactions of the American Fisheries Society 110:557–662.

LA HÉE, J. M. 2010. The influence of phosphorus on periphyton mats from the everglades and three tropical karstic wetlands. PhD Dissertation, Florida International University, Miami, Florida.

LEIGHTON, L. R. 2005. The latitudinal diversity gradient through deep time: testing the 'Age of the Tropics' hypothesis using carboniferous productidine brachiopods. Evolutionary Ecology 19:563–581.

LISTON, S. E., S. NEWMAN, AND J. C. TREXLER. 2008. Macroinvertebrate community response to eutrophication in an oligotrophic wetland: an in situ mesocosm experiment. Wetlands 28:686–694.

LOWE, R. L. 1974. Environmental requirements and pollution tolerance of freshwater diatoms. National Environmental Research Center, Office of Research and Development, US Environmental Protection Agency, Cincinnati, Ohio.

MASSA, A. K., AND A. HAYNES-SUTTON. 1998. Environmental policy framework, Parish of St. Elizabeth, Jamaica. Technical Support Services, Inc. Prepared for the Natural Resources Conservation Authority Protected Areas Management Branch and the United States Agency for International Development, Kingston, Jamaica. (Available from: http://pdf.usaid.gov/pdf_docs/PNACF307.pdf)

MCCORMICK, P., M. CHIMNEY, AND D. SWIFT. 1997. Diel oxygen profiles and water column community metabolism in the Florida Everglades, USA. Archiv für Hydrobiologie 140:117–129.

MCCORMICK, P. V., AND J. A. LAING. 2003. Effects of increased phosphorus loading on dissolved oxygen in a subtropical wetland, the Florida Everglades. Wetlands Ecology and Management 11:199–216.

MCCORMICK, P. V., AND M. B. O'DELL. 1996. Quantifying periphyton responses to phosphorus in the Florida Everglades: a synoptic-experimental approach. Journal of the North American Benthological Society 15: 450–468.

MCCORMICK, P. V., M. B. O'DELL, R. B. E. SHUFORD, J. G. BACKUS, AND W. C. KENNEDY. 2001. Periphyton responses to experimental phosphorus enrichment in a subtropical wetland. Aquatic Botany 71:119–139.

MCCORMICK, P. V., P. S. RAWLIK, K. LURDING, E. P. SMITH, AND F. H. SKLAR. 1996. Periphyton-water quality relationships along a nutrient gradient in the northern Everglades. Journal of the North American Benthological Society 15:433–449.

MCCORMICK, P. V., R. B. E. SHUFORD, J. B. BACKUS, AND W. C. KENNEDY. 1998. Spatial and seasonal patterns of periphyton biomass and productivity in the northern Everglades, FL, USA. Hydrobiologia 362:185–208.

MCCORMICK, P. V., AND R. J. STEVENSON. 1998. Periphyton as a tool for ecological assessment and management in the Florida Everglades. Journal of Phycology 34:726–733.

MCCUNE, B., AND J. B. GRACE. 2002. Analysis of ecological communities. MjM Press, Gleneden Beach, Oregon.

MEERMAN, J. C. 2006. Ecological characterization of the New River Lagoon, Orange Walk District, Belize. Report prepared for the Freshwater Programme for Belize, Belize City, Belize. (Available from: http://biological-diversity.info/Downloads/AWS_REA.pdf)

MUNYON, J. 2010. The effects of hydrology and phosphorus on Everglades productivity. MS Thesis, Florida International University, Miami, Florida.

NETO, R. R., R. N. MEAD, J. W. LOUDA, AND R. JAFFÉ. 2006. Organic biogeochemistry of detrital flocculent material (floc) in a subtropical, coastal wetland. Biogeochemistry 77:283–304.

NOE, G. B., D. L. CHILDERS, AND R. D. JONES. 2001. Phosphorus biogeochemistry and the impact of phosphorus enrichment: why is the Everglades so unique? Ecosystems 4: 603–624.

NOE, G. B., L. J. SCINTO, J. TAYLOR, D. L. CHILDERS, AND R. D. JONES. 2003. Phosphorus cycling and partitioning in an oligotrophic Everglades wetland ecosystem: a radioisotope tracing study. Freshwater Biology 48:1993–2008.

NOVELO, E., AND R. TAVERA. 2003. The role of periphyton in the regulation and supply of nutrients in a wetland at El Edén, Quintana Roo. Pages 217–239 *in* A. Gómez-Pompa, M. F. Allen, S. L. Fedick, and J. J. Jiménez-Osornio (editors). The Lowland Maya Area. Three millennia and the human-wildland interface. Food Products Press, New York.

NOVELO, E., R. TAVERA, AND C. IBARRA. 2007. Bacillariophyceae from karstic wetlands in Mexico. Bibliotheca Diatomologica 54:1–136.

PAN, Y., AND R. J. STEVENSON. 1996. Gradient analysis of diatom assemblage in western Kentucky wetlands. Journal of Phycology 32:222–232.

PAN, Y., R. J. STEVENSON, P. VAITHIYANATHAN, J. SLATE, AND C. J. RICHARDSON. 2000. Changes in algal assemblages along observed and experimental phosphorus gradients in a subtropical wetland, USA. Freshwater Biology 44: 339–353.

PIPP, E. 2002. A regional diatom-based trophic state indication system for running water sites in Upper Austria and its over-regional applicability. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 27:3376–3380.

PODZORSKI, A. C. 1985. An illustrated and annotated checklist of diatoms from the Black River Waterways, St. Elizabeth, Jamaica. Bibliotheca Diatomologica 7:1–177.

POTAPOVA, M., AND D. F. CHARLES. 2007. Diatom metrics for monitoring eutrophication in rivers of the United States. Ecological Indicators 7:48–70.

RASCHKE, R. L. 1993. Diatom (Bacillariophyta) community response to phosphorus in the Everglades National Park, USA. Phycologia 32:48–58.

REDDY, K. R., R. D. DELAUNE, W. F. DEBUSK, AND M. A. KOCH. 1993. Long-term nutrient accumulation rates in the Everglades. Soil Science Society of America Journal 57: 1147–1155.

REJMÁNKOVÁ, E. 2001. Effect of experimental phosphorus enrichment on oligotrophic tropical marshes in Belize, Central America. Plant Soil 236:33–53.

REJMÁNKOVÁ, E., AND J. KOMÁRKOVÁ. 2000. Function of cyanobacterial mats in phosphorus-limited tropical wetlands. Hydrobiologia 431:135–153.

REJMÁNKOVÁ, E., AND J. KOMÁRKOVÁ. 2005. Response of cyanobacterial mats to nutrient and salinity changes. Aquatic Botany 83:87–107.

REJMÁNKOVÁ, E., K. O. POPE, R. POST, AND E. MALTBY. 1996. Herbaceous wetlands of the Yucatan peninsula: communities at extreme ends of environmental gradients. Internationale Revue der gesamten Hydrobiologie 81: 223–252.

RICHARDSON, C. J. 2009. The Everglades: North America's subtropical wetland. Wetlands Ecology and Management 18:517–542.

RICKLEFS, R. E. 1979. Ecology. 2nd edition. Chiron Press, New York.

ROSENZWEIG, M. L. 1997. Species diversity in space and time. Revised edition. Cambridge University Press, Cambridge, UK.

SCINTO, L. J., AND K. R. REDDY. 2003. Biotic and abiotic uptake of phosphorus by periphyton in a subtropical freshwater wetland. Aquatic Botany 77:203–222.

SLATE, J. E. 1998. Inference of present and historical environmental conditions in the Everglades with diatoms and other siliceous microfossils. PhD Dissertation, University of Louisville, Louisville, Kentucky.

SLATE, J. E., AND R. J. STEVENSON. 2000. Recent and abrupt environmental change in the Florida Everglades indicated from siliceous microfossils. Wetlands 20:346–356.

SLATE, J. E., AND R. J. STEVENSON. 2007. The diatom flora of phosphorus-enriched and unenriched sites in an Everglades marsh. Diatom Research 22:355–386.

SMITH, S. M., J. A. LEEDS, P. V. MCCORMICK, P. B. GARRETT, AND M. DARWISH. 2009. Sawgrass (*Cladium jamaicense*) responses as early indicators of low-level phosphorus enrichment in the Florida Everglades. Wetlands Ecology and Management 17:291–302.

SMOL, J. P., R. W. BATTARBEE, R. B. DAVIS, AND J. MERILÄINEN. 1986. Diatoms and lake acidity. Reconstructing pH from siliceous algal remains in lake sediments. W. Junk, Dordrecht, The Netherlands.

SOLÓRZANO, J. H., AND L. SHARP. 1980. Determination of total dissolved phosphorous and particulate phosphorous in natural waters. Limnology and Oceanography 25:754–758.

STAL, L. J. 2000. Cyanobacterial mats and stromatolites. Pages 61–120 *in* B. A. Whitton and M. Potts (editors). The ecology of Cyanobacteria: their diversity in time and space. Kluwer Academic Publishers, Dordrecht, The Netherlands.

STEVENSON, R. J., AND Y. PAN. 1999. Assessing ecological conditions in rivers and streams with diatoms. Pages 11–40 *in* E. F. Stoermer and J. P. Smol (editors). The diatoms: applications to the environmental and earth sciences. Cambridge University Press, Cambridge, UK.

SWIFT, D. R., AND R. B. NICHOLAS. 1987. Periphyton and water quality relationships in the Everglades Water Conservation Areas, 1978–1982. Technical Publication 872. South Florida Water Management District, West Palm Beach, Florida. (Available from: South Florida Water Management District Library, 3301 Gun Club Road, West Palm Beach, Florida 33416-4680 USA.)

THOMAS, S., E. E. GAISER, M. GANTAR, L. SCINTO, AND R. D. JONES. 2006. Quantifying the response of calcareous periphyton crusts to rehydration: a microcosm study (Florida Everglades). Aquatic Botany 84:317–323.

TIPPER, J. C. 1979. Rarefaction and rarefiction—the use and abuse of a method in paleoecology. Paleobiology 5: 423–434.

VAN DAM, H., A. MERTENS, AND J. SINKELDAM. 1994. A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. Netherlands Journal of Aquatic Ecology 28:117–133.

VAN METER-KASANOF, N. 1973. Ecology of the microalgae of the Florida Everglades. Part I. Environment and some aspects of freshwater periphyton, 1959 to 1963. Nova Hedwigia 24:619–664.

WEIDIE, A. E. 1985. Geology of the Yucatan platform. Pages 1–19 *in* W. C. Ward, A. E. Weidie, and W. Back (editors). Geology and hydrology of the Yucatan and Quaternary geology of northeastern Yucatan peninsula. New Orleans Geological Society, New Orleans, Louisiana.

WEILHOEFER, C. L., AND Y. PAN. 2006. Diatom-based bioassessment in wetlands: how many samples do we need to adequately characterize the diatom assemblage in a wetland? Wetlands 26:793–802.

WILLIAMS, A. J., AND J. C. TREXLER. 2006. A preliminary analysis of the correlation of food-web characteristics with hydrology and nutrient gradients in the southern Everglades. Hydrobiologia 569:493–504.

WILLIG, M. R., D. M. KAUFMAN, AND R. D. STEVENS. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics 34:273–309.

Received: 11 March 2011
Accepted: 4 November 2011