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ARTICLE

Diatom-based Models for Inferring Hydrology and Periphyton Abundance in a Subtropical Karstic Wetland: Implications for Ecosystem-Scale Bioassessment

Sylvia S. Lee · Evelyn E. Gaiser · Joel C. Trexler

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Abstract We developed diatom-based prediction models of hydrology and periphyton abundance to inform assessment tools for a hydrologically managed wetland. Because hydrology is an important driver of ecosystem change, hydrologic alterations by restoration efforts could modify biological responses, such as periphyton characteristics. In karstic wetlands, diatoms are particularly important components of mat-forming calcareous periphyton assemblages that both respond and contribute to the structural organization and function of the periphyton matrix. We examined the distribution of diatoms across the Florida Everglades landscape and found hydroperiod and periphyton biovolume were strongly correlated with assemblage composition. We present species optima and tolerances for hydroperiod and periphyton biovolume, for use in interpreting the directionality of change in these important variables. Predictions of these variables were mapped to visualize landscape-scale spatial patterns in a dominant driver of change in this ecosystem (hydroperiod) and an ecosystem-level response metric of hydrologic change (periphyton biovolume). Specific diatom assemblages inhabiting periphyton mats of differing abundance can be used to infer past conditions and inform management decisions based on how assemblages are changing. This study captures diatom responses to wide gradients of hydrology and periphyton characteristics to inform ecosystem-scale bioassessment efforts in a large wetland.

Keywords Restoration · Bioassessment · Diatoms · Hydroperiod · Biovolume · Periphyton · Everglades

Introduction

In wetlands, hydrology is an important driver of ecosystem change because it maintains both the abiotic and biotic components that contribute to the defining features and function of wetland habitats (Mitsch and Gosselink 2007). Many wetlands undergo ecosystem-scale changes as anthropogenic agents, including accelerating rates of land-use and climate change (Batzer and Sharitz 2006), as well as restoration efforts, alter their hydrology. To predict the ecosystem effects of hydrologic changes and to direct adaptive assessment efforts, it is important to understand the complex relationships between hydrology and biotic assemblages. Because biotic assemblages can actively change wetland hydrology and physicochemistry through feedbacks (Mitsch and Gosselink 2007), hydrologic alterations by restoration efforts could modify these relationships if assemblage changes occur.

Bioassessment tools permit interpretation of the direction of environmental change and are useful for developing management targets to inform and assess restoration efforts (EPA 2011a). Because diatom assemblages are sensitive to environmental changes, including hydrologic changes, they can be used to develop robust inference models for early detection of shifts due to habitat degradation or restoration projects (Davis et al. 1996; Stevenson 1998). Sensitivity to hydrologic changes have been shown by the immediate recovery of diatom production in desiccated periphyton (benthic algae; Browder et al. 1994) upon rehydration (Thomas et al. 2006), and the influence of hydroperiod on

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S. S. Lee (✉) · E. E. Gaiser · J. C. Trexler
Department of Biological Sciences, Florida International University, Miami, FL 33199, USA
e-mail: sylvia.lee1@fiu.edu

the relative abundance of desiccation-resistant species inhabiting the periphyton matrix (Gottlieb et al. 2005). Periphyton is an important indicator of wetland degradation and restoration progress because it undergoes rapid and measurable structural, functional, and compositional responses to environmental changes (especially hydrology and water quality; Browder et al. 1994) at a large range of spatial scales (McCormick and Stevenson 1998; Gaiser 2009).

Diatom-based assessments conducted over long time periods should be used to inform wetland adaptive assessment tools about the rates, causes, and functional consequences of change to improve future management strategies (Gaiser and Rühland 2010). Because diatoms persist in the fossil record, they provide quantitative measures of past conditions that give ecologically-based context for current and future management plans (Smol and Stoermer 2010). Along with long-term monitoring, reconstructing the hydrologic history of wetlands is important, as past settings can provide hydrologic targets for restoration (Marshall et al. 2009), particularly in the face of changes in rainfall and inundation due to climate change (Mulholland et al. 1997). In addition to assessment over time, the inherent spatial attribute of diatom-based models provide an opportunity to examine responses at multiple spatial scales. The degree of consistency of species responses to ecosystem properties and the distribution of environmental gradients among hydrologically connected wetland subbasins determine whether models should be basin-specific (e.g., Gaiser et al. 2006) or regional.

Wetland assessment programs have lagged behind other aquatic systems, such as lakes and streams (EPA 2011b). Robust diatom-based inference models will provide a means for examining both the drivers and biological feedbacks of regulatory variables at a range of spatial scales. Most diatom-based assessments of wetlands have addressed water quality parameters such as nutrients (Pan and Stevenson 1996; Cooper et al. 1999; Gaiser et al. 2006; Lane and Brown 2007; Velinsky et al. 2011; La Hée and Gaiser 2012), salinity (Taffs 2001; Hicks and Nichol 2007; Wachnicka et al. 2010, 2011), dissolved oxygen (Zhang et al. 2011), and pH (Owen et al. 2004; Taffs et al. 2008). Some studies have employed diatoms to assess wetland vegetation (Huvane and Cooper 2001; Gaiser et al. 2005a), and several have employed diatom-based assessment of wetland hydrologic characteristics such as hydroperiod (Gaiser et al. 1998; Mackay et al. 2011). To date, inference models that reflect biological feedbacks, such as periphyton characteristics, to hydrologic conditions have not been developed. Reconstructions of ecosystem properties using regional inference models were successful for several wetlands (Gaiser et al. 1998; Taffs 2001; Owen et al. 2004), while other studies used or advocated basin-specific models (Cooper et al. 1999; Gaiser et al. 2006; La Hée and Gaiser 2012).

In the Florida Everglades, restoration goals, targets, and assessment tools are at the forefront of scientifically-sound adaptive management of the multi-billion dollar, landscape-scale Comprehensive Ecosystem Restoration Plan (C & SF Project 1999). Restoration efforts propose to redirect unused freshwater to areas that historically had greater periods of inundation, as well as to areas that would benefit cities and farmers. Without robust inference models, however, changes to hydrology could result in unintended consequences for wetland structure and function (e.g., Surratt et al. 2012). While development of diatom response models to water quality parameters such as periphyton total phosphorus (TP) concentrations (McCormick et al. 1996; Pan et al. 2000; Gaiser et al. 2006; La Hée and Gaiser 2012) have allowed paleoecological reconstructions of historical environments (e.g., Cooper et al. 1999; Slate and Stevenson 2000), hydrologic reconstructions have been impeded by the lack of robust diatom-based inference models (but see Sanchez et al. 2012). Also, diatom responses to periphyton characteristics reflective of biological feedbacks and responses to hydrologic changes have not been defined. If specific diatom assemblages inhabit periphyton of differing characteristics (e.g., biovolume), diatoms could be used to infer past wetland conditions even though the characteristics of the periphyton itself are not conserved in monitoring or paleoecological records. The numerous biogeochemical processes attributed to periphyton make the maintenance of native periphyton structure an important aspect of Everglades restoration (Hagerthey et al. 2011). Examination of periphyton along hydroperiod gradients in a marl-based wetland area found little effect of hydroperiod on periphyton biomass (Wachnicka, unpublished data), but patterns across the long hydrologic gradients present in the larger Everglades landscape, including the hydrologically different (but connected) Water Conservation Areas (WCAs) and Everglades National Park (ENP) (Light and Dineen 1994), are expected. Extensive studies have been conducted on the periphyton and paleoecological indicators of the historically P-enriched and hydrologically-managed WCA-2A (e.g., McCormick et al. 1996, 1998; Cooper et al. 2008). However, a quantitative evaluation of diatom sensitivity to periphyton characteristics occurring across the broader hydrologic gradients represented in the Greater Everglades could elucidate landscape-scale responses to hydrologic change.

In this study, we examined the diatom assemblages of periphyton samples that were gathered in 2006 as part of a landscape-scale monitoring program across the Everglades. Our first objective was to quantify diatom assemblage patterns and associations with habitat characteristics. We used the term ‘habitat characteristics’ to include both the abiotic physicochemical factors of the environment and the biological features of the periphyton mat that influence, and are influenced by, the diatoms embedded in the mat matrix. We hypothesized that hydroperiod, periphyton biovolume, and periphyton TP concentration would be associated with the differences in diatom assemblages across the Everglades. Our second objective was to test whether the responses of diatom assemblages across the Everglades were consistent throughout the landscape. We hypothesized that a spatially extensive dataset would enable detection of basin-specific responses, if they exist, but also provide an opportunity to develop landscape-scale models. Our final objective was to evaluate the predictive capacity of diatom-based inference models. In addition, we mapped inferences relative to actual patterns to illustrate the utility of visualizing landscape-scale patterns for application in restoration planning and management.

Methods

Site Description

Located in Florida, USA, the Everglades is an expansive wetland (>6,000 km^2) encompassing a mosaic of environmental conditions resulting from natural gradients and differences in biogeochemistry, as well as anthropogenic compartmentalization and eutrophication (Davis and Ogden 1994). Owing to the limestone bedrock underlying much of the southern Everglades, periphyton assemblages can contain an abundance of calcium carbonate precipitates that allows the formation of thick, calcareous mats. However, areas of higher nutrient levels contain organic, filamentous films that are easily disrupted (McCormick and O’Dell 1996; McCormick et al. 2001; Gaiser et al. 2005b, 2011). This study focuses on calcareous communities occurring throughout the spatially complex WCAs and ENP, exclusive of soft-water regions (the Arthur R. Marshall Loxahatchee National Wildlife Refuge, also known as WCA-1) with a very different algal assemblage and suite of environmental stressors (Harvey and McCormick 2009; Gaiser et al. 2011; Hagerthey et al. 2011). The Everglades has a subtropical climate with a distinct wet and dry season, the duration of which are controlled by climate variability and water management and can have significant influences on variability in species abundances and ecosystem properties.

Sample Collection and Processing

Periphyton samples were collected during the 2006 wet season (September through December) as part of the Monitoring and Assessment Program of the Comprehensive Everglades Restoration Plan (RECOVER 2004). A total of 86 sites were included in this study (refer to Fig. 5; see Online Resource for exact locations). Generalized random-tessellation stratification (Stevens and Olsen 2004) was used to choose a spatially balanced set of sampling locations. The landscape was divided into 800 m × 800 m grids and a representative sample of these was drawn as primary sampling units (PSU); three sampling sites were randomly selected from the samplable habitat in each PSU (Philippi 2005). Samplable habitat included all locations where vegetation was not too dense for our sampling device to enclose 1 m^3 of the water column and less than 1 m deep; primarily wet prairies and sloughs met these conditions (Gunderson 1994).

At each sampling location, water depth was measured, and water samples were taken for measurement of pH and conductivity (μS cm^{-1}). Other hydrologic variables, including hydroperiod (days flooded) and days since dry (number of days since flooding of the marsh surface after the latest drying event when water levels were <5 cm), were estimated by calibration to nearby continuous water level gauges using digital elevation models provided by the Everglades Depth Estimation Network (EDEN) (http://sofia.usgs.gov/eden/stationlist.php). The sampling device used to delineate the sampling area was a 1 m^3 enclosure with mesh sides and open on the top and bottom (Jordan et al. 1997). Visual assessment for aerial cover (percent of the surface of the enclosed area covered by periphyton) was conducted before all periphyton within the enclosure was collected and measured for biovolume using a perforated graduated cylinder. Extraneous plant matter, animals, and other debris were on average less than 0.5 % of the volume of the sample and did not affect biovolume measurements. If no benthic, epiphytic, or metaphytic periphyton was present, flocculent detritus from the benthos was collected (Troxler and Richards 2009; Pisani et al. 2011).

Periphyton samples were taken back to the laboratory and frozen before further processing. Animals, plant matter, and other debris were removed, and subsamples were taken for the measurement of dry weight (g m^{-2}) by drying at 80 °C to constant weight, ash-free dry mass (g m^{-2}) by combustion at 500 °C for 1.5 h, chlorophyll *a* mass (μg m^{-2}) and chlorophyll *a* concentration (μg g^{-1} dry weight) by fluorometry (Welschmeyer 1994), total periphyton P (μg g^{-1} dry weight) by colorimetry after dry combustion (Solorzano and Sharp 1980; EPA 1983), and diatom species composition analysis. Organic content was calculated as the ratio of ash-free dry mass to total dry mass expressed as a percent. Periphyton P concentrations were used as a metric of P availability because periphyton P has a strong correlation with P load (Gaiser et al. 2004, 2005b, 2006). See Online Resource for full dataset of all habitat characteristics mentioned above. Diatom samples were cleaned of calcite and organic matter using strong acids and chemical oxidizers (Hasle and Fryxell 1970), and then permanently affixed to glass slides using Naphrax®. A minimum of 500 valves were counted and identified per slide (Weber 1973) using a compound light microscope at 1,000× magnification. Identifications were made to the lowest taxonomic level possible (variety or forma) using a database of South Florida diatom taxa (http://fce.lternet.edu/data/database/diatom) and other references (e.g., Slate and Stevenson 2007).

Data Analysis

Species abundances were relativized by the maximum abundance achieved by each species over all samples to reduce the differential impact of common and uncommon species on inferences. All species were included in the analyses after checking for outliers more than two standard deviations from the mean Sørenson distance measure (McCune and Grace 2002). Three categories of habitat characteristics were analyzed: hydrology, periphyton abundance, and periphyton quality (Table 1). Hydrology included days since dry (DSD), hydroperiod (HYPER), and water depth (DEPTH). Periphyton abundance included periphyton biovolume (PBIOV), aerial cover (AERCO), chlorophyll *a* mass (CHLMA), dry weight (DRYWT), and ash-free dry mass (AFDM). Periphyton quality included periphyton organic content (ORGCO), periphyton total phosphorus (TP), chlorophyll *a* concentration (CHLCO), water column pH (pH), and water column conductivity (CONDU). We used the term 'periphyton quality' to include measurements of periphyton and water column attributes because of the intimate relationship between water quality (nutrient and ion concentrations) and the composition and function of periphyton mats, including both the influence of the water column on mats and the influence of mats on the surrounding water column (Gottlieb et al. 2005; Thomas et al. 2006; Hagerthey et al. 2011). Each habitat characteristic was transformed to bring skewness (a metric to assess normality) closest to zero, including square root, arcsine square root, tenth root, and log transformations (McCune and Grace 2002) (Table 1). Samples more than two standard deviations from the mean Euclidean distance measure were considered outliers and removed from the dataset; subsequent analysis of species confirmed the absence of outlier species. Samples were categorized a priori into three wetland subsets based on landscape pattern and management practices: Shark River Slough (SRS), Water Conservation Areas 2A and 2B (WCA-2), and Water Conservation Areas 3A and 3B (WCA-3).

To examine diatom assemblage patterns associated with gradients of habitat characteristics, we used non-metric multidimensional scaling (NMS) ordination (Kruskal and Wish 1978; Minchin 1987) with the Bray-Curtis dissimilarity measure (Bray and Curtis 1957). Because our data are observational, we did not attempt to identify causal relationships between assemblages and habitat characteristics. The statistical program DECODA (Database for Ecological Community Data; Minchin 1990) was used to run ordinations and to fit vectors of maximum correlation of habitat characteristics with assemblage difference. To detect whether assemblages had consistent responses to habitat characteristics throughout the landscape or if there were distinct regional differences, analysis of similarity (ANOSIM) was conducted using Primer-E statistical software (version 6.0) to determine differences in diatom assemblages among and within the three wetland subsets (Clarke and Gorley 2006). Following the results of the ANOSIM, separate ordinations of wetland subsets were

Table 1 Summary statistics of habitat characteristics (before transformations) and transformations used to bring skewness of values closest to zero

Category	Habitat characteristics (units)	Code	Mean	Standard deviation	Minimum	Maximum	Transformation
Hydrology	Days since dry (days)	DSD	556	802	0	2523	Log(x+1)
	Hydroperiod (days)	HYPER	239	61	39	333	none
	Water depth (cm)	DEPTH	41.8	21.4	6.0	90.0	Square root
Periphyton abundance	Periphyton biovolume (mL m^{-2})	PBIOV	3000	3200	0	14000	Square root
	Aerial cover (% of 1 m^2 quadrat)	AERCO	50	40	0	100	Arcsine square root
	Chlorophyll *a* mass (µg m^{-2})	CHLMA	1.35×10^{-4}	1.34×10^{-4}	0	5.80×10^{-4}	Square root
	Periphyton dry weight (g m^{-2})	DRYWT	50.3	79.7	0	437	Log(x+1)
	Periphyton ash-free dry mass (g m^{-2})	AFDM	17.4	23.2	0	121	Log(x+1)
Periphyton quality	Organic content of periphyton (%)	ORGCO	51	18	23	84	Square root
	Total periphyton phosphorus (µg m^{-2})	TP	190	140	20	660	(Log(x+10))−1
	Chlorophyll *a* concentration (µg g^{-1})	CHLCO	927	1340	65.5	8260	Log(x+1)
	Water column pH	pH	7.9	0.34	7.2	9.1	Tenth root
	Conductivity of water (µS cm^{-1})	CONDU	284	216	2.13	1170	Square root

TP was transformed by taking the log of x+10 (the decimal constant) and then subtracting 1 (the order of magnitude constant) from the resulting value (refer to McCune and Grace 2002). See Online Resource for full dataset of all habitat characteristics. Sample size=86 sites

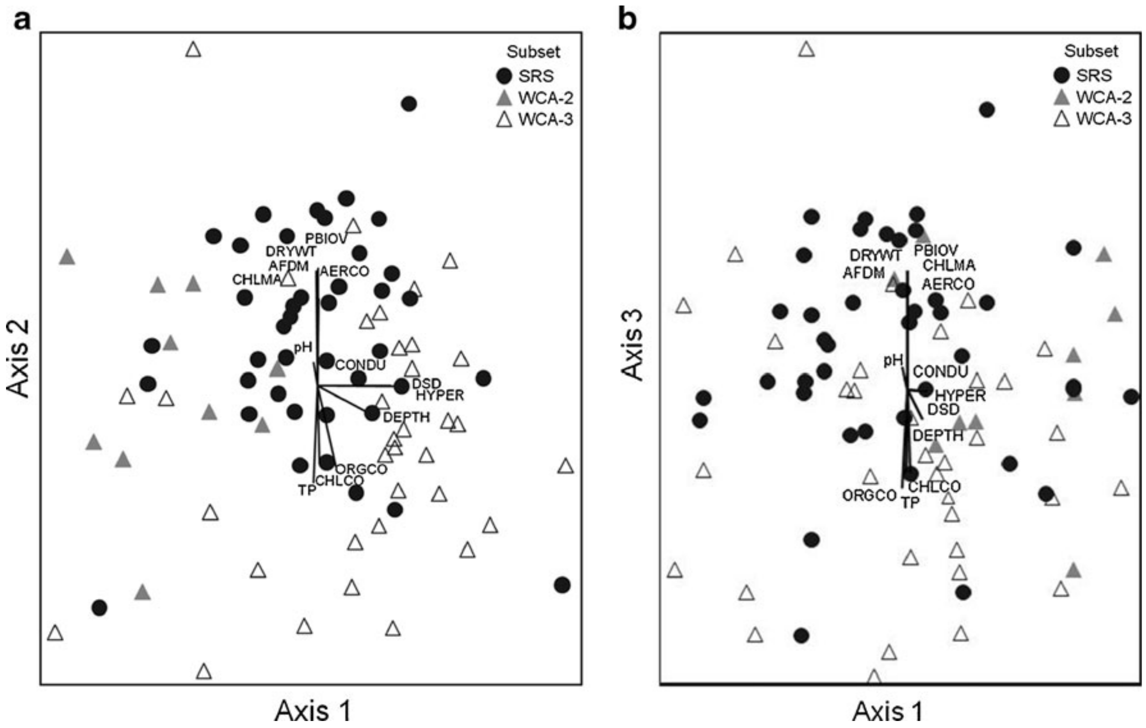

Fig. 1 Non-metric multidimensional scaling ordination plot (multivariate representation of dissimilarities between samples based on rank order differences in assemblage composition). Three-dimensional ordination shown in two-dimensional plots for easier visualization: Axis 2 vs. 1 (**a**) and Axis 3 vs. 1 (**b**). Plots rotated 260° (maximizing association between hydroperiod and Axis 1) to show relative distribution of environmental vectors. Wetland subsets: Shark River Slough (SRS), Water Conservation Areas 2A and 2B (WCA-2), and Water Conservation Areas 3A and 3B (WCA-3)

conducted to determine any subset-specific assemblage patterns. To test the null hypothesis that species responses to habitat characteristics are not associated among subsets, we used Kendall's coefficient of concordance with correction for tied ranks, W_c (Zar 1996).

We used the Bio-Env (Biota-Environment) procedure in Primer to determine the habitat characteristics most correlated with differences in diatom assemblages (Clarke and Ainsworth 1993). Bio-Env determines the correlation (Spearman) between the ranked dissimilarities of all possible pairs of samples based on the assemblage matrix and the ranked dissimilarities based on subsets of the environmental (habitat characteristics) matrix (Clarke and Warwick 2001). Rank correlation $\rho=1$ indicates complete agreement, whereas $\rho=-1$ indicates complete opposition (Clarke and Warwick 2001; Clarke and Gorley 2006). Because Bio-Env attempts to match all possible combinations of habitat characteristics to explain differences in the assemblage data, correlations could be found by chance. We tested the null hypothesis that the biota and the environment are not linked by using the BEST (Biota Environment STepwise) permutations test (999 permutations) in Primer to determine statistical significance (Clarke et al. 2008).

For the selected habitat characteristics, weighted averaging calibration models were constructed using C2 software to obtain species optima and tolerance values (Juggins 2005). The weighted averaging models were tested by simulating prediction errors using the bootstrapping resampling method repeated 1000 times (Efron 1982; Birks et al. 1990). The resulting Root Mean Square Error of Prediction (RMSEP) and bootstrapped (boot) r^2 were used as more conservative estimates of model fit compared to the apparent Root Mean Square Error (RMSE) and r^2 (Efron 1983; Birks et al. 1990; ter Braak and Juggins 1993; Birks 1995). For variables that were previously transformed, we present the upper and lower limits of tolerance values because of transformation-generated scale changes. For the same reason, we present RMSE and RMSEP values in transformed units. Finally, observed, diatom-inferred, and the difference between the observed and diatom-inferred values were mapped using ArcGIS version 10 (ESRI 2011). Interpolation techniques were not applied due to the inaccuracies that could result from the use of a limited number of sampling points across a large area.

Results

Assemblage Patterns and Habitat Characteristics

We observed 59 species of diatoms representing 21 genera. The most abundant species among all samples were

Table 2 Pearson's correlation matrix of habitat characteristics (prior to transformations). Sample size=86

Category	Hydrology			Periphyton abundance					Periphyton quality				
	DSD	HYPER	DEPTH	PBIOV	AERCO	CHLMA	DRYWT	AFDM	ORGCO	TP	CHLCO	pH	CONDU
DSD													
HYPER	0.73^{a}												
DEPTH	0.58^{a}	0.47^{a}											
PBIOV	−0.32^{a}	−0.26	−0.50^{a}										
AERCO	−0.23	−0.16	−0.41^{a}	0.82^{a}									
CHLMA	−0.30^{a}	−0.23	−0.47^{a}	0.92^{a}	0.79^{a}								
DRYWT	−0.32^{a}	−0.30^{a}	−0.54^{a}	0.94^{a}	0.82^{a}	0.91^{a}							
AFDM	−0.31^{a}	−0.28^{a}	−0.52^{a}	0.95^{a}	0.80^{a}	0.92^{a}	0.99^{a}						
ORGCO	0.24	0.27^{a}	0.46^{a}	−0.60^{a}	−0.65^{a}	−0.57^{a}	−0.76^{a}	−0.65^{a}					
TP	0.11	0.01	0.40^{a}	−0.62^{a}	−0.62^{a}	−0.54^{a}	−0.66^{a}	−0.60^{a}	0.72^{a}				
CHLCO	0.38^{a}	0.42^{a}	0.56^{a}	−0.65^{a}	−0.57^{a}	−0.47^{a}	−0.73^{a}	−0.68^{a}	0.71^{a}	0.59^{a}			
pH	−0.21	−0.31^{a}	−0.38^{a}	0.42^{a}	0.37^{a}	0.41^{a}	0.49^{a}	0.48^{a}	−0.40^{a}	−0.25^{a}	−0.43^{a}		
CONDU	0.06	0.04	0.07	0.02	0.05	−0.02	0.00	−0.01	−0.01	−0.06	−0.07	−0.31^{a}	

[a] Significant correlation at the 0.05 level

Mastogloia cf. *lacustris* (also reported as *Mastogloia smithii* and *M. smithii* var. *lacustris*; Gaiser et al. 2010), *Encyonema evergladianum*, *Fragilaria synegrotesca*, and *Brachysira neoexilis*, making up 36 %, 24 %, 12 %, and 9 % of all diatom valves counted, respectively. *Mastogloia* cf. *lacustris* was the most abundant species in WCA-3, SRS, and WCA-2 (38 %, 35 %, and 34 % of all valves counted, respectively). There were 15 species common to all wetland subsets that contributed 95 % of the total relative abundance, indicating high overlap of species among regions.

Differences among sites in the relative abundance of species generally grouped samples by wetland subset in the NMS ordination, though overlap was also common (Fig. 1a). A three-dimensional solution resulted in the greatest decrease in minimum stress level (stress=0.183) and was rotated by degree increments until the relative distribution of the vectors of habitat characteristics could be clearly depicted (Fig. 1a and b). The total rotation was 260°, which also maximized the association between hydroperiod and Axis 1. The percentages of variance represented by Axis 1, 2, and 3 for the rotated ordination were 23 %, 29 %, and 20 %, respectively. Periphyton biovolume, dry weight, AFDM, and TP had the largest magnitude of association with the ordination axes, as indicated by the length of the vectors (refer to Table 4 for exact correlation values). The relative placement and angles of the vectors showed patterns in diatom assemblages were correlated with hydrology (hydroperiod, days since dry, and water depth), periphyton quantity (periphyton biovolume, AFDM, dry weight, aerial cover, and chlorophyll *a* mass), and periphyton quality (TP, organic content, chlorophyll *a* concentration, and pH).

The habitats included in this study ranged from short (min=39 days) to very long (max=333 days) hydroperiod sites; periphyton biovolumes were as low as 0 $\mathrm{mL\,m^{-2}}$ (4 WCA-3 sites and 1 SRS site) to as high as 14,000 $\mathrm{mL\,m^{-2}}$ (Table 1). Most habitat characteristics were positively skewed; hydroperiod, however, was negatively skewed, indicating a greater number of long hydroperiod sites relative to short hydroperiod sites in our samples (Table 1). Habitat characteristics within the same category (hydrology, periphyton abundance, and periphyton quality) were correlated ($p<0.05$), except for conductivity; conductivity was only correlated with pH (Table 2). Organic content and other metrics of periphyton quality were correlated with metrics of periphyton abundance. SRS sites exhibited a negative relationship between hydroperiod and periphyton biovolume, while longer hydroperiod sites in WCA-2 and WCA-3 tended to have mats of higher periphyton biovolume but less organic content (Table 3).

Landscape-Scale Patterns

Relative abundances of diatom species varied consistently among the three wetland subsets according to ANOSIM

Table 3 Pairwise correlations between three habitat characteristics describing hydrology (HYPER), periphyton abundance (PBIOV), and periphyton quality (ORGCO) of wetland subsets: SRS (Shark River Slough) WCA-2 (Water Conservation Areas 2A and 2B), and WCA-3 (Water Conservation Areas 3A and 3B)

	SRS			WCA-2			WCA-3	
	HYPER	PBIOV		HYPER	PBIOV		HYPER	PBIOV
PBIOV	−0.32[a]		PBIOV	0.20		PBIOV	0.24	
ORGCO	0.42[a]	−0.51[a]	ORGCO	−0.21	−0.42	ORGCO	−0.28	−0.53[a]

Sample size=86 sites

[a] Significant correlation at the 0.05 level

(Global $R=0.26$; $p<0.01$). Pairwise tests showed that SRS and WCA-2 were the most different ($R=0.52$), while SRS and WCA-3 were most similar ($R=0.17$), but differences between all pairs were statistically significant ($p<0.01$). Ordinations performed for the subsets (stress=0.17, 0.03, and 0.16; SRS, WCA-2, and WCA-3, respectively) showed that SRS assemblages had similar associations with habitat characteristics as the combined dataset (Fig. 2a), except for responses to pH (Table 4). The WCA-3 assemblage also showed similar associations as those of the combined dataset (Fig. 2b), except associations with days since dry, hydroperiod, chlorophyll *a* mass, conductivity and pH were not statistically significant. The WCA-2 assemblage was only associated with TP but, more importantly, had similar placement of vectors relative to each other as in the combined dataset (Fig. 2c). Kendall's test of concordance between subset-specific species responses to habitat characteristics rejected the null hypothesis that species responses were not associated ($W_c=0.76$, $\chi^2=27.4$, $p<0.01$). Therefore, concordant associations of assemblage patterns among subsets allowed development of landscape-scale metrics using the entire dataset.

Weighted Averaging Models and Maps

Hydroperiod, days since dry, water depth, periphyton biovolume, TP, and chlorophyll *a* concentration were selected by the Bio-Env procedure as the subset of habitat characteristics that formed the most correlated ($\rho=0.27$) ranked set of dissimilarities with that of the assemblage matrix. The procedure was repeated with forced exclusions because of high correlations between hydroperiod and days since dry, hydroperiod and water depth, and between TP and chlorophyll *a* concentration (refer to Table 2). In the second run, hydroperiod, periphyton biovolume, and TP were selected as the subset to reach the highest rank correlation ($\rho=0.25$), with no improvement with the addition of any number of the remaining variables. Because the observed rank correlation could not be obtained after 999 permutations using randomized environmental matrices, we rejected the null hypothesis that there is no link between the assemblages and the environment ($p<0.001$). The variance in assemblage composition explained by hydroperiod, periphyton biovolume, and TP was 12.4 %, 13.6 %, and 17.9 %, respectively ($p<0.005$ for all).

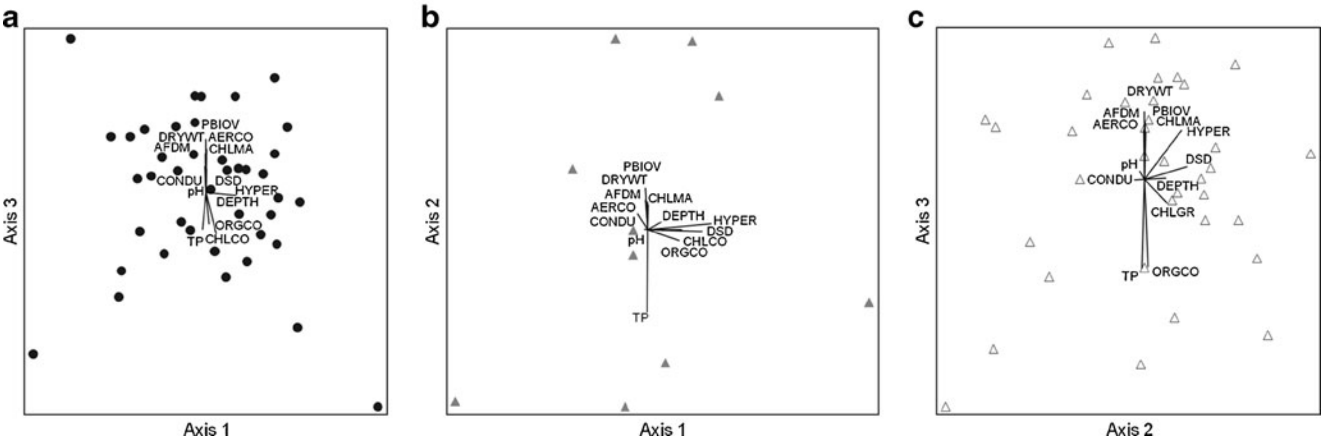

Fig. 2 Non-metric multidimensional scaling. Three-dimensional ordination of wetland subsets: SRS (**a**), WCA-2 (**b**), and WCA-3 (**c**). Plots rotated to show relative distribution of environmental vectors

Table 4 Maximum correlation to vectors of habitat characteristics from three-dimensional NMS of the entire dataset and each subset separately

Habitat characteristics	All subsets (n=86)	SRS (n=41)	WCA-2 (n=10)	WCA-3 (n=35)
DSD	0.36[a]	0.37	0.52	0.37
HYPER	0.35[a]	0.57[a]	0.71	0.45
DEPTH	0.44[a]	0.59[a]	0.61	0.49[a]
PBIOV	0.61[a]	0.63[a]	0.42	0.52[a]
AERCO	0.56[a]	0.60[a]	0.50	0.52[a]
CHLMA	0.53[a]	0.48[a]	0.33	0.46
ORGCO	0.52[a]	0.67[a]	0.81	0.71[a]
DRYWT	0.61[a]	0.70[a]	0.42	0.55[a]
AFDM	0.59[a]	0.65[a]	0.34	0.47[a]
TP	0.59[a]	0.68[a]	0.80[a]	0.65[a]
CHLCO	0.53[a]	0.77[a]	0.76	0.57[a]
CONDU	0.27	0.36	0.48	0.27
pH	0.32[a]	0.33	0.27	0.31

[a] Significant correlation at the 0.05 level

Because hydroperiod, periphyton biovolume, and TP best matched assemblage patterns, these three metrics best informed inference models for assessment applications. Our TP weighted averaging models were comparable to previous models generated from Everglades diatom assemblages (Gaiser et al. 2006; La Hée and Gaiser 2012). Thus, we do not reiterate the results in this study. We evaluated the performance of weighted averaging models constructed for hydroperiod and periphyton biovolume by comparing diatom-inferred values with observed values (Fig. 3). Diatom-inferred hydroperiod was correlated with observed values with r^2=0.63 (RMSE=35 days) and boot r^2=0.19 (RMSEP=55 days); diatom-inferred periphyton biovolume was correlated with observed values with r^2=0.56 (RMSE=19 square root mLm^{-2}) and boot r^2=0.41 (RMSEP=23 square root mLm^{-2}) (Table 5).

Hydroperiod optima of diatom species ranged from 99 to 303 days and tolerances ranged from 8 to 81 days above and below optima; periphyton biovolume optima ranged from 0 to 6,000 mLm^{-2} and tolerances ranged from as low as 0 mLm^{-2} (where flocculent matter from the benthos, rather than periphyton, was sampled) and as much as 11,000 mLm^{-2} (Table 6). *Pinnularia microstauron* was associated with shorter hydroperiod sites, while *Encyonema* sp. 02 was associated with longer hydroperiod sites; *Eunotia naegelii* was associated with low periphyton biovolume, while *Nitzschia serpentiraphe* was associated with high periphyton biovolume, though it had a wide tolerance range of 850 to 8,700 mLm^{-2} (Fig. 4).

Maps of observed values, diatom-inferred values, and differences (observed minus inferred values) for hydroperiod (Fig. 5a, b and c) and periphyton biovolume (Fig. 5d, e and f) allowed visualization of the spatial distribution of these important habitat characteristics and the accuracy of diatom-based inferences. The highest predicted values of hydroperiod were in WCA-3, while the northern part of SRS had the lowest predicted values. In SRS, very long hydroperiod conditions (>280 days) were underestimated and shorter hydroperiod conditions (<190 days) were overestimated. Inferred periphyton biovolume estimates were very similar to observed values, with the highest predicted values in SRS, and lower values (<5,000 mLm^{-2}) in WCA-2 and WCA-3. Differences between observed and diatom-inferred values were generally no more than one standard deviation of the observed variability in hydroperiod and periphyton biovolume (Fig. 5c and f, respectively).

Discussion

Hydroperiod, periphyton biovolume, and periphyton TP content were the habitat characteristics most strongly associated with diatom assemblage structure in the Everglades. The underlying geology and geomorphology influence the natural hydropatterns of the Everglades (McVoy et al. 2011), while an extensive system of canals, levees and water control structures control the present flow of water (Sklar et al. 2002). Alterations to the hydrology of the Everglades influence periphyton biovolume and nutrient content, especially when canal inputs increase delivery of minerals or P and encourage the development or disintegration of periphyton communities (Iwaniec et al. 2006; Hagerthey et al. 2011; McCormick et al. 2011). Periphyton biovolume has been used as a metric of productivity (e.g., Ewe et al. 2006; Iwaniec et al. 2006), but has not been analyzed as a habitat characteristic for diatom assemblages. Because mats of high and low abundance appear to support distinct diatom assemblages, assemblage composition is useful for inferring the abundance of periphyton in given wetland locations in the past (before drainage and management) to inform restoration target-setting. A known relationship between assemblage

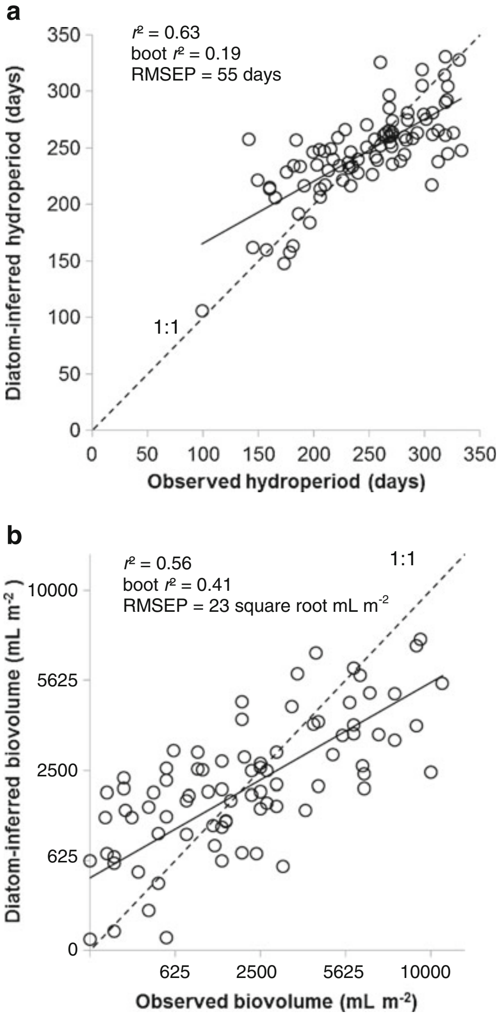

Fig. 3 Diatom-inferred vs. observed hydroperiod (**a**) and periphyton biovolume (**b**). Diatom-inferred values calculated using weighted averaging models with bootstrapping cross validation method. Weighted averaging method with the lowest RMSEP (Root Mean Square Error of Prediction) chosen. Strength of model prediction indicated by r^2 of trendline (apparent and bootstrapped r^2 values (boot r^2) shown). Dashed line indicates 1:1 line of 100 % correlation. Axes scaled to back-transformed values for periphyton biovolume

composition and periphyton biovolume would also aid restoration assessment because obtaining measurements of periphyton biovolume in the field is simple compared to the additional processing required to obtain measurements of chlorophyll *a* or nutrients in the laboratory. Because certain diatom species (e.g., *Eunotia camelus*, *Gomphonema gracile*, and *Stenopterobia curvula*) are associated with flocculent detrital material but absent or infrequent at sites with periphyton (zero minimum biovolume optimum and tolerance), their relative abundances can indicate the absence of periphyton. Thus, diatoms are comprehensive indicators of periphyton abundance that can provide inferences about a range of wetland environments that may or may not support periphyton.

While the relationship between phosphorus concentrations and diatom assemblage structure is well-documented (McCormick et al. 1996, 1998; Pan et al. 2000; Gaiser et al. 2006; Cooper et al. 2008; La Hée and Gaiser 2012), this study shows the important effects of hydroperiod and periphyton biovolume on diatom composition. We have yet to uncover the exact mechanisms driving diatom assemblage composition, but feedbacks among hydroperiod, periphyton biovolume, and composition could shape wetland structure and function. Since short hydroperiod areas tend to have high periphyton abundance (Gottlieb et al. 2006), the periphyton mats in these areas could favor desiccation-resistant species capable of surviving annual drying. In turn, desiccation-resistant diatoms and other algal species produce biomass, including anti-desiccative mucilage (Hoagland et al. 1993), that contribute to high biovolume periphyton mats, while also playing a role in controlling nutrient and mineral concentrations in the surrounding water column (Gottlieb et al. 2005; Thomas et al. 2006; Hagerthey et al. 2011). Further investigations are needed to understand how changes in hydrology affect these feedbacks.

The responses of individual diatom species, especially species with narrow tolerance ranges, had a key role in determining predictive relationships of diatom assemblages with hydroperiod and periphyton biovolume. For example, *Fragilaria synegrotesca* preferred long hydroperiod habitats; this agreed with previous findings by Gottlieb et al.

Table 5 Performance of weighted-averaging models by linear regression of diatom-inferred values against observed values of entire dataset and each subset separately

	Hydroperiod				Periphyton biovolume			
	r^2	RMSE (days)	Boot r^2	RMSEP (days)	r^2	RMSE (square root mLm^{-2})	boot r^2	RMSEP (square root mLm^{-2})
All subsets (n=86)	0.63	35	0.19	55	0.56	19	0.41	23
SRS (n=41)	0.67	29	0.26	48	0.57	18	0.37	23
WCA-2 (n=10)	0.71	28	0.10	54	0.59	12	0.02	23
WCA-3 (n=35)	0.76	29	0.23	54	0.67	14	0.31	22

Slope of regression line (r^2) and Root Mean Square Error (RMSE) compared to slope of regression line of bootstrap cross-validated values (boot r^2) and Root Mean Square Error of Prediction (RMSEP). See text for more details on model evaluation

Table 6 Frequency, maximum abundance, and weighted-average optima and tolerance ranges of diatom species for hydroperiod (HYPER) and periphyton biovolume (PBIOV)

Taxon name	Freq. (%)	Max. abund. (%)	HYPER		PBIOV		
			opt. (days)	tol. (days)	opt. (mL m^{-2})	tol. lower lim. (mL m^{-2})	tol. upper lim. (mL m^{-2})
Caponea caribbea Podzorski	0.005	0.397	99	50	3500	1300	6900
Nitzschia cf. *obtusa* W. Smith	0.005	0.395	145	50	1600	300	4000
Nitzschia amphibia var. *frauenfeldii* Grunow	0.009	0.781	157	50	6000	2900	10200
Pinnularia cf. *gibba* Ehrenberg	0.002	0.188	173	50	3700	1400	7100
Stauroneis phoenicenteron (Nitzsch) Ehrenberg	0.005	0.302	178	50	400	0	1900
Eunotia camelus Ehrenberg	0.151	13.200	181	50	0	0	600
Gomphonema gracile Ehrenberg	0.014	1.200	181	50	0	0	600
Frustulia rhomboides var. *crassinervia* (Brébisson) Ross	0.023	1.208	192	44	700	100	1900
Pinnularia microstauron (Ehrenberg) Cleve	0.071	2.000	192	57	1500	0	5400
Frustulia sp. 01	0.005	0.378	196	50	0	0	600
Stenopterobia curvula (W. Smith) Krammer	0.005	0.378	196	50	0	0	600
Rhopalodia gibba (Ehrenberg) Muller	0.048	1.439	203	43	1400	200	3600
Diploneis parma Cleve	0.503	7.273	205	53	1500	100	4400
Gomphonema affine Kützing	0.050	1.186	208	62	1600	200	4700
Diploneis oblongella (Naegeli ex Kuetzing) Ross	0.190	2.183	209	60	2200	600	4900
Navicula subtilissima Cleve	0.343	7.031	216	64	2800	700	6300
Nitzschia palea var. *debilis* (Kützing) Grunow	3.300	16.80	219	51	3100	800	6700
Brachysira brebissonii Ross	0.114	3.021	227	77	1000	0	3300
Enyconopsis microcephala (Grunow) Krammer	1.560	34.170	230	46	1600	100	5000
Nitzschia serpentiraphe Lange-Bertalot	2.461	33.100	230	52	4400	1400	9300
Cyclotella meneghiniana Kützing	0.263	1.188	233	50	1800	200	5000
Nitzschia amphibia (Grunow) Lange-Bertalot	0.192	1.727	234	57	700	0	2100
Brachysira neoexilis morph. 1 Lange-Bertalot	0.149	4.626	234	43	4400	900	10700
Navicula cryptotenella Lange-Bertalot	0.835	7.364	237	46	1000	100	3200
Eunotia naegelii Migula	0.069	3.008	237	45	100	0	1100
Eunotia monodon Ehrenberg	0.007	0.377	239	81	1100	500	2000
Nitzschia palea (Kutzing) Smith	0.828	23.730	239	38	2000	500	4500
Amphora sulcata (Brébisson) Cleve	1.630	43.380	241	46	2000	500	4500
Eunotia flexuosa (Brébisson) Kützing	0.194	8.271	242	37	100	0	900
Brachysira neoexilis morph. 2 Lange-Bertalot	9.106	50.850	242	61	2200	400	5700
Brachysira pseudoexilis Lange-Bertalot & Moser	0.341	2.923	243	56	4100	1400	8300
Mastogloia cf. *lacustris* Grunow	36.37	75.900	243	55	2100	300	5600
Brachysirea vitrea (Grunow) Ross	0.023	1.547	244	47	5200	2300	9400
Gomphonema intricatum var. *vibrio* (Ehrenberg) Cleve	0.595	7.200	245	48	900	0	3400
Sellaphora laevissima (Kützing) Krammer	0.133	0.985	245	54	1500	100	4600
Mastogloia lanceolata Thwaites	0.091	2.603	248	42	2600	900	5100
Navicula radiosa Kützing	0.464	4.494	251	47	1400	200	4000
Encyonema evergladianum Krammer	23.30	60.790	252	53	2200	400	5600
Achnanthes minutissima f. *gracillima* (Meister) Cleve-Euler	0.078	1.912	253	53	1100	100	3100
Fragilaria synegrotesca Lange-Bertalot	12.58	72.540	258	48	900	0	2900
Enyconema silesiacum var. *elegans* Krammer	0.229	6.667	260	40	900	0	3100
Gomphonema coronatum Ehrenberg	0.005	0.355	260	50	100	600	5000
Amphora holsatica Hustedt	0.005	0.562	260	50	2300	0	900
Encyonema sp. 01	2.387	31.670	261	51	1400	100	3900
Eunotia incisa Gregory	0.018	0.388	262	10	300	0	1600
Nitzschia nana Grunow	0.174	5.618	263	61	1400	200	3700

Table 6 (continued)

Taxon name	Freq. (%)	Max. abund. (%)	HYPER		PBIOV		
			opt. (days)	tol. (days)	opt. (mL m^{-2})	tol. lower lim. (mL m^{-2})	tol. upper lim. (mL m^{-2})
Sellaphora pupula (Kützing) Mereschkowsky	0.027	1.509	265	8	100	0	1200
Aulacoseira italica (Ehrenberg) Simonsen	0.002	0.192	265	50	4400	1800	8100
Gomphonema vibriodes Reichardt & Lange-Bertalot	0.297	4.610	266	55	1000	0	3200
Encyonema silesiacum (Bleisch) Mann	0.220	14.750	268	50	100	0	100
Brachysira serians (Brébisson) Round & Mann	0.002	0.217	268	50	100	0	1100
Fragilaria nanana Lange-Bertalot	0.153	2.000	272	52	100	100	3100
Achnanthes caledonica Lange-Bertalot	0.300	11.260	280	62	1300	300	3100
Fragilaria ulna var. *ulna* (Nitzsch) Lange-Bertalot	0.027	0.901	287	56	1200	200	3300
Navicula radiosafallax Lange-Bertalot	0.014	0.538	291	41	200	0	500
Stauroneis javanica (Grunow) Cleve	0.002	0.186	298	50	2500	1000	6100
Achnanthes cf. *minutissima* v. *gracillima* (Meister) Lange-Bertalot	0.005	0.407	298	50	3000	700	5400
Encyonema sp. 02	0.018	0.377	303	28	1200	200	3000
Fragilaria delicatissima (W. Smith) Lange-Bertalot	0.009	0.538	303	50	300	0	700

Species sorted from low to high hydroperiod optima. PBIOV tolerance lower and upper limits reported due to transformation-generated changes in scale. Sample size=86 sites

(2005) and Gaiser et al. (2011). The diatom species with the longest hydroperiod optimum was *Fragilaria delicatissima*, a planktonic species (Patrick and Reimer 1966). *Pinnularia microstauron* was associated with shorter hydroperiod habitats; the type specimen of this species was found in soil on the roots of plants from Rio de Janeiro, Brazil, indicating its ability to survive in drier conditions (Patrick and Reimer 1966). The holotype of *Caponea caribbea*, which had the shortest hydroperiod optimum in our analyses, was collected by Podzorski (1985) from algal mats on the surface of a Jamaican peat swamp that had experienced a fire some months prior. Podzorski's (1985) findings suggest that *C. caribbea* is adapted to surviving periodic desiccation and fire, which are frequent in short-hydroperiod wetlands; this species may even indicate time since fire. Species associated with habitats with very little periphyton, such as *Eunotia camelus* and *Stenopterobia curvula*, are acidophilic diatoms not usually found in calcium-rich habitats like calcareous periphyton mats (Patrick and Reimer 1966; Krammer and Lange-Bertalot 1988; Furey 2010). *Gomphonema gracile* and *G. coronatum* have been reported to prefer high P habitats with pH<7 (Tobias and Gaiser 2006; Slate and Stevenson 2007).

Some of the more common diatom species in the flora of Everglades calcareous periphyton had broad tolerance ranges that were not useful for inferring habitat characteristics. *Nitzschia serpentiraphe*, a very common species in slough periphyton mats with a moderate (Slate and Stevenson 2007) to low TP optimum (Gaiser et al. 2006), reached its highest abundance in the thick, calcareous mats from SRS. Calcareous periphyton mats disintegrate due to a shift in community structure from a calcite-precipitating filamentous flora (species of *Utricularia* and cyanobacteria that provide substrates for diatom growth) to dominance by green algae and eutrophic diatoms following P enrichment (McCormick and O'Dell 1996; McCormick et al. 2001; Gaiser et al. 2005b, 2006, 2011). This phenomenon supports the association of *N. serpentiraphe* with high periphyton biovolume and correspondingly low to moderate TP habitats. However, *N. serpentiraphe* also had a wide tolerance range, which is expected because species in this genus are known to tolerate eutrophic conditions (Van Dam et al. 1994). The species with the highest periphyton biovolume optima (including *N. amphibia* var. *frauenfeldii*, *N. serpentiraphe*, *Brachysira vitrea*, and *B. neoexilis*) had an average tolerance range of greater than 8000 mL m^{-2}. The wide tolerance ranges of these species restrict optima from reaching higher values, even though periphyton abundance can exceed 10,000 mL m^{-2}. Inferences about periphyton abundance and enrichment based on diatoms with wide tolerance ranges should be made with caution because other factors may allow some species to thrive in both enriched and unenriched habitats.

We found that although the wetland subsets in our study differed in species' relative abundances, similar assemblage responses to habitat characteristics allowed development of a landscape-scale model encompassing gradients broader than those present in individual subsets. None of the NMS ordinations captured a response to conductivity, likely because of the shorter conductivity gradient encompassed by

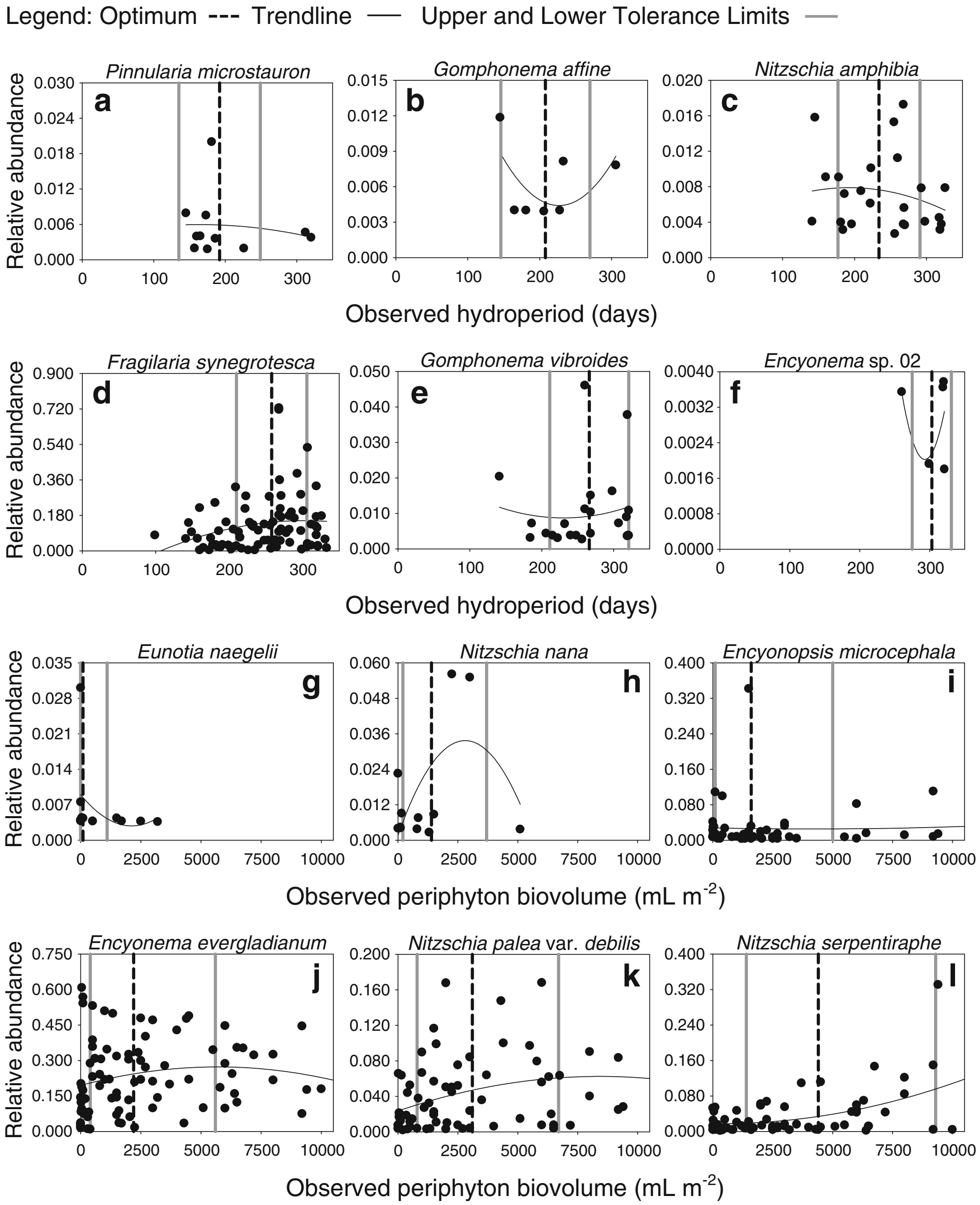

Fig. 4 Relative abundances of diatom species indicating preferences (optima and tolerance ranges) for a range of hydroperiod (**a–f**) and periphyton biovolume (**g–l**). Second order polynomial trendlines. Note different y-axis scales for each taxon

our focus on alkaline freshwater habitats (where calcareous periphyton thrives) relative to gradients of other habitat characteristics. The lack of response by WCA-3 assemblages to metrics of inundation (days since dry and hydroperiod) may reflect how the impoundment of water for flood control in the WCAs limits the natural variability of inundation (Light and Dineen 1994; Romanowicz and Richardson 2008). In contrast, historic P enrichment in WCA-2 affected nutrient removal (Craft and Richardson 1993), peat accretion (Reddy et al. 1993), and vegetation (Urban et al. 1993). In our study, species assemblages in WCA-2 were not associated with any of the variables measured except TP. The lack of response to the other habitat characteristics could be attributed to the low sample size of the subset (n=10). Despite these differences, hydroperiod and periphyton biovolume weighted averaging models made separately for each subset had lower boot r^2 values (especially models for WCA-2) or only slightly improved boot r^2 values (the hydroperiod models for SRS and WCA-3) (Refer to Table 5), probably because of the decrease in sample size (Birks et al. 1990; Reavie and Juggins 2011). The lack of improvement in correlation values of subset-specific models validated combining wetland subsets for landscape-scale assessment.

The weighted averaging models for hydroperiod and periphyton biovolume showed the utility of diatom assemblages for wetland assessment. Our Everglades model was not as strong as the hydroperiod model by Gaiser et al. (1998) for diatoms from surface sediments of intermittent ponds on the Atlantic Coastal Plain (r^2=0.81), because the Everglades

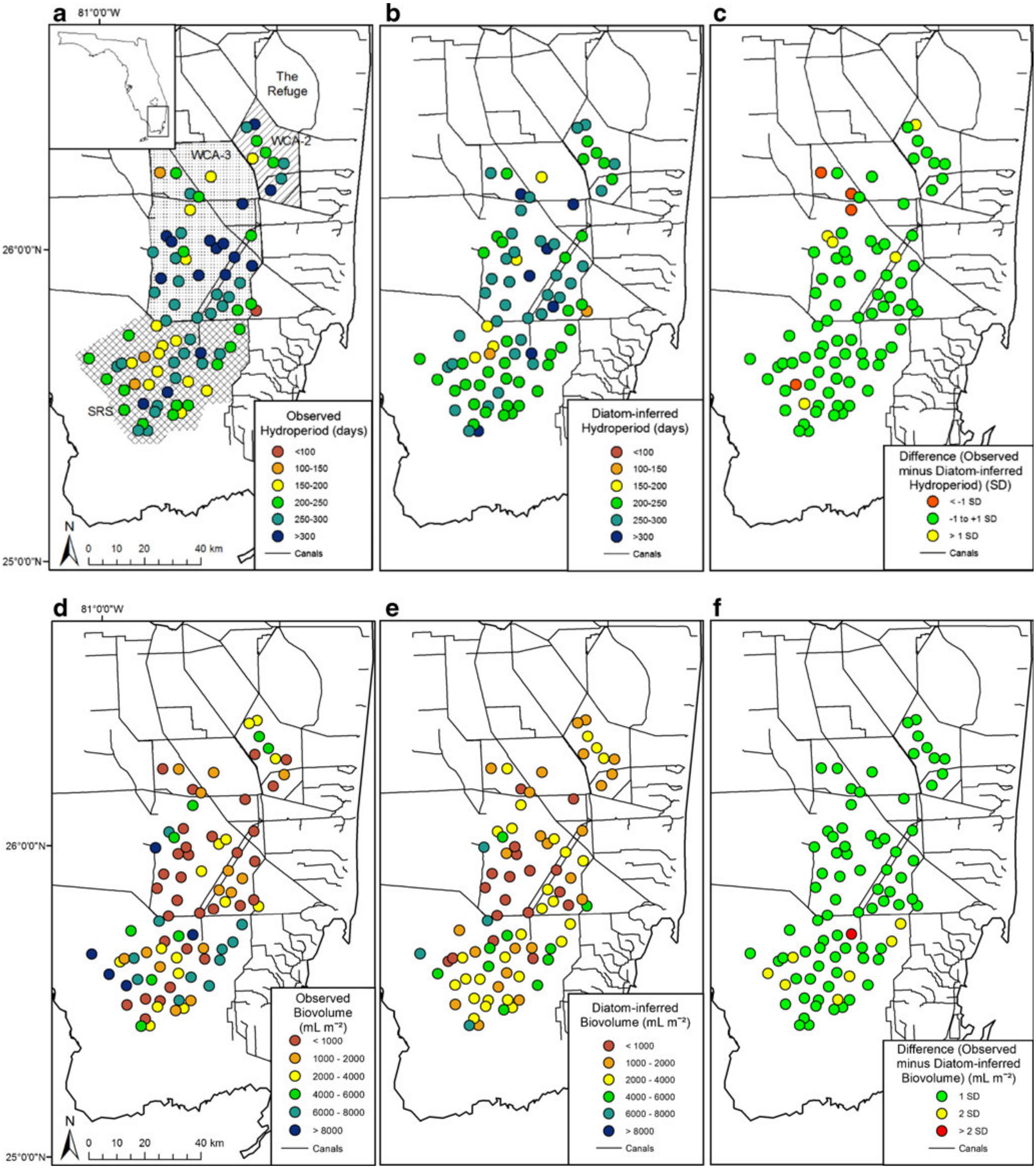

Fig. 5 Observed, diatom-inferred, and difference (observed minus diatom-inferred values) maps of hydroperiod (**a**, **b**, **c**) and periphyton biovolume (**d**, **e**, **f**), respectively. Black values in difference maps (**c** and **f**) indicate values within one standard deviation of observed values. Standard deviations of hydroperiod and periphyton biovolume are 61 days and 3200 mL m^{-2}, respectively. Patterning delineates wetland subset boundaries. Color version available online

model underestimates long hydroperiod conditions and overestimates short hydroperiod conditions. The limitations of the Everglades model could be a result of higher spatial and temporal variability within a wetland compared to ponds that are similar in geology, vegetation, and water source but range broadly in hydroperiod, permitting a more extreme gradient for developing inferences. Because we also recognized that unimodal-based calibration methods are prone to the 'edge effect' (ter Braak and Juggins 1993; Birks 1998), which biases inferred values towards the mean of the observed values, we evaluated but did not employ weighted averaging models using partial least squares regression (ter Braak and Juggins 1993) to conserve parsimony and because improvements were not statistically significant.

Visualizing the weighted averaging models showed that for both hydroperiod and periphyton biovolume, most of the differences between observed and diatom-inferred values were within the variability (one standard deviation) of the observed values. Because wetlands are spatially complex, we emphasize the utility of maps to summarize biotic responses to the environment by visualization of biological patterns across a landscape in a way that integrates spatial and environmental heterogeneity. Maps can complement tools already developed for restoration assessment (Gaiser 2009), to visualize compliance or deviation of current conditions from reference or restoration targets.

We emphasize the utility of analyzing diatom assemblage composition as a way to develop predictive models about the environment that coarser metrics may not always capture, especially in dynamic systems such as wetlands. Unlike one-time direct measurement of physical or chemical conditions such as periphyton biomass or water quality, assemblage composition is less prone to sampling variability because it integrates environmental conditions over larger spatial and temporal scales (Stevenson 1998). The relationship between diatom assemblages and hydrology is especially important in the Everglades because hydrologic manipulation is the basis of current restoration plans. As advances in diatom taxonomy continue to develop, it is imperative to make identifications to the species level in order to reconcile any current taxonomic discrepancies with future datasets (Julius and Theriot 2010). This effort would facilitate the combination of datasets for analyses at larger spatial and temporal scales. While assessment based on the presence or absence of a few indicator species can be less time consuming and costly, this method is prone to non-detection resulting from variable species detectability or inadequate sampling (MacKenzie 2005). Gottlieb (2003) found that long and short hydroperiod assemblages differed in species relative abundances, rather than in the presence or absence of species. Likewise, we found that wetland subsets had differing species relative abundances, not species identities, which permitted us to develop inference models at the landscape scale. The laborious process involved in species identification and enumeration is worthwhile, considering the wealth of information it provides about how the species within assemblages respond, as a whole, to the environment and should be incorporated in assessments of other wetland systems.

Sound ecologically-based assessment of change in wetlands requires an understanding of how assemblages respond to ecosystem parameters to make interpretations about past conditions, develop targets for the future, and aid assessment. This study found diatom assemblage composition has predictable relationships with two very important habitat characteristics of wetland ecosystem function: hydroperiod and periphyton biovolume. Wetland management programs should use this information to infer landscape-scale biological responses to hydrologic change and to inform restoration targets, especially in the Everglades where hydroperiod regimes no longer follow natural spatial and temporal patterns (Romanowicz and Richardson 2008). This study quantitatively described the hydroperiod and periphyton biovolume optima and tolerance ranges of Everglades diatom taxa. This autecological information should be used to futher investigate the poorly described flora of tropical karstic wetlands (La Hée and Gaiser 2012). Finally, this study found landscape-scale models are possible in the Everglades because diatom assemblage patterns were consistent across wetland subsets. Spatially-explicit visualizations of these models are useful for assessing the performance of diatom-based inferences over a large area. Landscape-scale diatom-based models from the Everglades should be used as an example for other large wetlands around the world with high hydrologic connectivity, such as boreal wetlands (Spence et al. 2011), the Pantanal (Alho et al. 1988), and the Okavango Delta (McCarthy et al. 2000). Although most tropical wetlands have received inadequate attention to date, advancements made by monitoring, restoration, and assessment efforts for the subtropical Everglades can guide newly developing wetland protection programs.

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References

Alho CJR, Lacher TE Jr, Gonçalves HC (1988) Environmental degradation in the pantanal ecosystem. BioScience 38(3):164–171

Batzer DP, Sharitz RS (2006) Ecology of freshwater and estuarine wetlands. University of California Press, Los Angeles

Birks HJB (1995) Quantitative paleoenvironmental reconstruction. In: Maddy D, Brew JS (eds) Statistical modelling of quaternary science data. Quaternary Research Association, Great Britain, pp 161–254

Birks HJB (1998) Numerical tools in palaeolimnology—progress, potentialities, and problems. Journal of Paleolimnology 20:307–332

Birks HJB, Line JM, Juggins S, Stevenson AC, ter Braak CFJ (1990) Diatoms and pH reconstruction. Philosophical Transactions of the Royal Society of London B 327:263–278

Bray JR, Curtis JT (1957) An ordination for the upland forest of Southern Wisconsin. Ecological Monographs 27:325–349

Browder JA, Gleason PJ, Swift DR (1994) Periphyton in the Everglades: spatial variation, environmental correlates, and ecological implications. In: Davis SM, Ogden JC (eds) The Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, pp 379–418

C & SF Project (1999) Central and Southern Florida Comprehensive Review Study Final Integrated Feasibility Report and Programmatic Environmental Impact Statement. In: Get a Copy of the Plan. Everglades Restoration. http://www.evergladesplan.org/pub/restudy_eis.aspx. Accessed May 2012

Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92:205–219

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. Primer-E, Plymouth

Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology 366:56–69

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

Cooper SR, Goman M, Richardson CJ (2008) Historical changes in water quality and vegetation in WCA-2A determined by paleoecological analyses. In: Richardson CJ (ed) Everglades experiments: lessons for ecosystem restoration. Ecological Studies 201: 321–350

Craft CB, Richardson CJ (1993) Peat accretion and N, P, and organic C accumulation in nutrient-enriched and unenriched Everglades peatlands. Ecological Applications 3:446–458

Davis SM, Ogden JC (1994) Everglades: the ecosystem and its restoration. St. Lucie Press, Boca Raton

Davis WS, Snyder BD, Stribling JB, Stoughton C (1996) Summary of state biological assessment programs for streams and wadeable rivers. EPA 230-R-96-007. U. S. Environmental Protection Agency; Office of Policy, Planning, and Evaluation; Washington D. C., USA

EDEN (Everglades Depth Estimation Network). http://sofia.usgs.gov/eden/stationlist.php. Accessed October 2012

Efron B (1982) The jackknife, the bootstrap, and other resampling plans. SIAM, Philadelphia

Efron B (1983) Estimating the error rate of a prediction rule: improvement on cross-validation. Journal of the American Statistical Association 78:318–331

EPA (1983) Methods for chemical analysis of water and wastes. Chapter 365.1 Revision March 83. Cincinnati, OH: United States Environmental Protection Agency

EPA (2011a) A primer on using biological assessments to support water quality management. United States Environmental Protection Agency. Accessed October 2012. Retrieved from http://water.epa.gov/scitech/swguidance/standards/criteria/aqlife/biocriteria/upload/primer_update.pdf

EPA (2011b) National aquatic resource surveys. United States Environmental Protection Agency. Accessed October 2012. Retrieved from water.epa.gov/type/watersheds/monitoring/aquaticsurvey_index.cfm

ESRI (2011) ArcGIS Desktop: release 10. Environmental Systems Research Institute, Redlands

Ewe SML, Gaiser EE, Childers DL, Iwaniec D, Rivera-Monroy VH, Twilley RR (2006) Spatial and temporal patterns of aboveground net primary productivity (ANPP) along two freshwater-estuarine transects in the Florida Coastal Everglades. Hydrobiologia 569:459–474

Furey P (2010) Eunotia. In: Diatoms of the United States. http://westerndiatoms.colorado.edu/taxa/genus/eunotia. Accessed 19 August 2011

Gaiser EE (2009) Periphyton as an indicator of restoration in the Florida Everglades. Ecological Indicators 9:S37–S45

Gaiser EE, Rühland K (2010) Diatoms as indicators of environmental change in wetlands and peatlands. In: Smol JP, Stoermer EF (eds) The diatoms: applications for the environmental and earth sciences. Cambridge University Press, New York, pp 473–496

Gaiser EE, Philippi TE, Taylor BE (1998) Distribution of diatoms among intermittent ponds on the Atlantic Coastal Plain: development of a model to predict drought periodicity from surface-sediment assemblages. Journal of Paleolimnology 20:71–90

Gaiser EE, Scinto LJ, Richards JH, Jayachandran K, Childers DL, Trexler JC, Jones RD (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 EE, Wachnicka AH, Ruiz P, Tobias FAC, Ross M (2005a) Diatom indicators of ecosystem change in coastal wetlands: evidence from diatom records. In: Bortone S (ed) Estuarine indicators. CRC Press, Boca Raton

Gaiser EE, Trexler JC, Richards JH, Childers DL, Lee D, Edwards AL, Scinto LJ, Jayachandran K, Noe GB, Jones RD (2005b) Cascading ecological effects of low-level phosphorus enrichment in the Florida everglades. Journal of Environmental Quality 34:717–723

Gaiser EE, Childers DL, Jones RD, Richards JH, Scinto LJ, Trexler JC (2006) Periphyton responses to eutrophication in the Florida Everglades: cross-system patterns of structural and compositional change. Limnology and Oceanography 51:617–630

Gaiser EE, La Hée JM, Tobias FAC, Wachnicka AH (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 (1):99–112

Gaiser EE, McCormick PV, Hagerthey SE, Gottlieb AD (2011) Landscape patterns of periphyton in the Florida Everglades. Critical Reviews in Environmental Science and Technology 41:1–29

Gottlieb AD (2003) Short and long-hydroperiod Everglades periphyton mats: community characterization and experimental hydroperiod manipulation. Dissertation. Florida International University, Miami, Florida, USA

Gottlieb AD, Richards JH, Gaiser EE (2005) The effects of desiccation resistance and rewetting on the community structure of Everglades periphyton. Aquatic Botany 82:99–112

Gottlieb AD, Richards JH, Gaiser EE (2006) Comparative study of periphyton community structure in long and short-hydroperiod Everglades marshes. Hydrobiologia 569:195–207

Gunderson LH (1994) Vegetation of the Everglades: determinants of community composition. In: Davis SM, Ogden JC (eds) The

Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, pp 323–340

Hagerthey SE, Bellinger B, Wheeler K, Gantar M, Gaiser EE (2011) Everglades periphyton: a biogeochemical perspective. Critical Reviews in Environmental Science and Technology 41:309–343

Harvey JW, McCormick PV (2009) Groundwater's significance to changing hydrology, water chemistry, and biological communities of a floodplain ecosystem, Everglades, South Florida, USA. Hydrogeology Journal 17:185–201

Hasle GR, Fryxell GA (1970) Diatoms: cleaning and mounting for light and electron microscopy. Transactions of the American Microscopical Society 89:469–474

Hicks H, Nichol SL (2007) A marine to freshwater sediment succession from Kowhai Beach wetland, Northland: implications for Holocene sea level. Journal of the Royal Society of New Zealand 37(3):91–107

Hoagland KD, Rosowski JR, Gretz MR, Roemer SC (1993) Diatom extracellular polymeric substances: function, fine structure, chemistry, and physiology. Journal of Phycology 29(5):537–566

Huvane JK, Cooper SR (2001) Diatoms as indicators of environmental change in sediment cores from northeastern Florida Bay. In: Wardlaw BR (ed) Paleoecological studies of South Florida. Bulletins of American Paleontology 361:145–158

Iwaniec DM, Childers DL, Rondeau D, Madden CJ, Saunders C (2006) Effects of hydrologic and water quality drivers on periphyton dynamics in the southern Everglades. Hydrobiologia 569:223–235

Jordan F, Coyne S, Trexler JC (1997) Sampling fishes in vegetated habitats: effects of habitat structure on sampling characteristics of the 1 m^2 throw trap. Transactions of the American Fisheries Society 126:1012–1020

Juggins S (2005) The C2 software for ecological and palaeoecological data analysis and visualisation. University of Newcastle, Newcastle-upon-Tyne

Julius ML, Theriot EC (2010) The diatoms: a primer. In: Smol JP, Stoermer EF (eds) The diatoms: applications for the environmental and earth sciences. Cambridge University Press, New York, pp 8–22

Krammer K, Lange-Bertalot H (1988) Bacillariophyceae. 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. Gustav Fisher Verlag, Jena

Kruskal JB, Wish M (1978) Multidimensional scaling. Sage Publications, Beverly Hills

La Hée JM, Gaiser EE (2012) Benthic diatom assemblages as indicators of water quality in the Everglades and three tropical karstic wetlands. Freshwater Science 31(1):205–221

Lane CR, Brown MT (2007) Diatoms as indicators of isolated herbaceous wetland condition in Florida, USA. Ecological Indicators 7:521–540

Light SS, Dineen JW (1994) Water control in the Everglades: a historical perspective. In: Davis SM, Ogden JC (eds) The Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, pp 47–84

Mackay AW, Davidson T, Wolski P, Woodward S, Mazebedi R, Masamba WRL, Todd M (2011) Diatom sensitivity to hydrological and nutrient variability in a subtropical, flood-pulse wetland. Ecohydrology. doi:10.1002/eco.242

MacKenzie DI (2005) What are the issues with presence-absence data for wildlife managers? Journal of Wildlife Management 69 (3):849–860

Marshall FE, Wingard GL, Pitts P (2009) A simulation of historic hydrology and salinity in Everglades National Park: coupling paleoecologic assemblage data with regression models. Estuaries and Coasts 32:37–53

McCarthy TS, Cooper GRJ, Tyson PD, Ellery WN (2000) Seasonal flooding in the Okavango Delta, Botswana: recent history and future prospects. South African Journal of Science 96(1):25–33

McCormick PV, O'Dell MB (1996) Quantifying periphyton responses to phosphorus in the Florida Everglades: a synoptic-experimental approach. Journal of the North American Benthological Society 15(4):450–468

McCormick PV, Stevenson RJ (1998) Periphyton as a tool for ecological assessment and management in the Florida Everglades. Journal of Phycology 34:726–733

McCormick PV, Rawlick RS, Lurding K, Smith EP, Sklar FH (1996) Periphyton-water quality relationships along a nutrient gradient in the northern Florida Everglades. Journal of the North American Benthological Society 15(4):433–449

McCormick PV, Shuford RBE III, Backus JG, Kennedy WC (1998) Spatial and seasonal patterns of periphyton biomass and productivity in the northern Everglades, Florida, U.S.A. Hydrobiologia 362(1):185–210

McCormick PV, O'Dell MB, Shuford RBE, Backus JG, Kennedy WC (2001) Periphyton responses to experimental phosphorus enrichment in a subtropical wetland. Aquatic Botany 71:119–139

McCormick PV, Harvey JW, Crawford ES (2011) Influence of changing water sources and mineral chemistry on the Everglades ecosystem. Critical Reviews in Environmental Science and Technology 41:28–63

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach

McVoy CW, Said WP, Obeysekera J, VanArman JA, Dreschel TW (2011) Landscapes and hydrology of the predrainage Everglades. University Press of Florida, Gainesville

Minchin PR (1987) An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69:89–107

Minchin PR (1990) Database for Ecological COmmunity DAta (DECODA) Software. Australian National University, Canberra

Mitsch WJ, Gosselink JG (2007) Wetlands. Wiley, Hoboken

Mulholland PJ, Best GR, Coutant CC, Hornberger GM, Meyer JL, Robinson PJ, Stenberg JR, Turner RE, VeraHerrera F, Wetzel RG (1997) Effects of climate change on freshwater ecosystems of the southeastern United States and the Gulf Coast of Mexico. Hydrological Processes 11:949–970

Owen RB, Renaut RW, Hover VC, Ashley GM, Muasya AM (2004) Swamps, springs and diatoms: wetlands of the semi-arid Bogoria-Baringo Rift, Kenya. Hydrobiologia 518:59–78

Pan Y, Stevenson RJ (1996) Gradient analysis of diatom assemblages in western Kentucky wetlands. Journal of Phycology 32:222–232

Pan Y, Stevenson RJ, Vaithiyanathan P, Slate J, Richardson CJ (2000) Changes in algal assemblages along observed and experimental phosphorus gradients in a subtropical wetland, USA. Freshwater Biology 44:339–353

Patrick R, Reimer CW (1966) The diatoms of the United States. The Academy of Natural Sciences of Philadelphia, Philadelphia

Philippi T (2005) Final report. CERP MAP Implementation: Transect and Sentinel Site Sampling Design. South Florida Water Management District Agreement CP040131

Pisani O, Yamashita Y, Jaffé R (2011) Photo-dissolution of flocculent, detrital material in aquatic environments: contributions to the dissolved organic matter pool. Water Research 45:3836–3844

Podzorski AC (1985) An illustrated and annotated check-list of diatoms from the Black River waterways, St. Elizabeth, Jamaica. Lubrecht & Cramer Ltd., Germany

Reavie ED, Juggins S (2011) Exploration of sample size and diatom-based indicator performance in three North American phosphorus training sets. Aquatic Ecology 45:529–538

RECOVER (2004) CERP Monitoring and Assessment Plan: Part 1. Monitoring and Supporting Research—January 2004. Comprehensive Everglades Restoration Plan, Restoration Coordination and Verification (RECOVER). U.S. Army Corps of Engineers Jacksonville District, Jacksonville, Florida, and South Florida Water Management District, West Palm Beach, Florida, USA

Reddy KR, DeLaune R, DeBusk WF, Koch M (1993) Long-term nutrient accumulation rates in the Everglades. Soil Sciences Society American Journal 57:1147–1155

Romanowicz EA, Richardson CJ (2008) Geologic settings and hydrology gradients in the everglades. In: Richardson CJ (ed) Everglades experiments: lessons for ecosystem restoration. Ecological Studies 201:167–189

Sanchez C, Gaiser EE, Saunders CJ, Wachnicka AH, Oehm N, Craft C (2012) Challenges in using siliceous subfossils as a tool for inferring past water level and hydroperiod in Everglades marshes. Journal of Paleolimnology. doi:10.1007/s10933-012-9624-3

Sklar FH, McVoy C, VanZee R, Gawlik DE, Tarboton K, Rudnick D, Miao SL, Armentano T (2002) The effects of altered hydrology on the ecology of the Everglades. In: Porter JW, Porter KG (eds) The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: an ecosystem sourcebook. CRC Press, Boca Raton, pp 39–82

Slate JE, Stevenson RJ (2000) Recent and abrupt environmental change in the Florida Everglades indicated from siliceous microfossils. Wetlands 20:346–356

Slate JE, Stevenson RJ (2007) The diatom flora of phosphorus-enriched and unenriched sites in an Everglades marsh. Diatom Research 22:355–386

Smol JP, Stoermer EF (2010) The diatoms: applications for the environmental and earth sciences, 2nd edn. Cambridge University Press, New York

Solorzano L, Sharp JH (1980) Determination of total dissolved P and particulate P in natural waters. Limnology and Oceanography 25:754–758

Spence C, Guan XJ, Phillips R (2011) The hydrological functions of a boreal wetland. Wetlands 31:75–85

Stevens DL, Olsen AR (2004) Spatial balanced sampling of natural resources. Journal of the American Statistical Association 99(465):262–278

Stevenson RJ (1998) Diatom indicators of stream and wetland stressors in a risk management framework. Environmental Monitoring and Assessment 51:107–118

Surratt D, Shinde D, Aumen N (2012) Recent cattail expansion and possible relationships to water management: changes in upper Taylor Slough (Everglades National Park, Florida, USA). Environmental Management 49(3):720–733

Taffs KH (2001) Diatoms as indicators of wetland salinity in the Upper South East of South Australia. The Holocene 11(3):281–290

Taffs KH, Farago LJ, Heijnis H, Jacobsen G (2008) A diatom-based Holocene record of human impact from a coastal environment: Tuckean Swamp, eastern Australia. Journal of Paleolimnology 39:71–82

ter Braak CJF, Juggins S (1993) Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. Hydrobiologia 269(270):485–502

Thomas S, Gaiser EE, Gantar M, Scinto LJ (2006) Quantifying the responses of calcareous periphyton crusts to rehydration: a microcosm study (Florida Everglades). Aquatic Botany 84:317–323

Tobias FAC, Gaiser EE (2006) Taxonomy and distribution of diatoms in the genus *Gomphonema* from the Florida Everglades, USA. Diatom Research 21:379–405

Troxler TG, Richards JH (2009) [delta]13C, [delta]15 N, carbon, nitrogen and phosphorus as indicators of plant ecophysiology and organic matter pathways in Everglades deep slough, Florida, USA. Aquatic Botany 91:157–165

Urban NH, Davis SM, Aumen NG (1993) Fluctuations in sawgrass and cattail densities in Everglades Water Conservation Area 2A under varying nutrient, hydrologic, and fire regimes. Aquatic Botany 46:203–223

Van Dam H, Mertens A, Sinkeldam J (1994) A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. Aquatic Ecology 28:117–133

Velinsky D, Sommerfield C, Enache M, Charles D (2011) Final report: nutrient and ecological histories in Barnegat Bay, New Jersey. Patrick Center for Environmental Research Report No. 10-05. New Jersey Department of Environmental Protection, New Jersey, USA

Wachnicka AH, Gaiser EE, Collins L, Frankovich T, Boyer J (2010) Distribution of diatoms and development of diatom-based models for inferring salinity and nutrient concentrations in Florida Bay and adjacent coastal wetlands of south Florida (USA). Estuaries and Coasts 33:1080–1098

Wachnicka AH, Gaiser EE, Boyer J (2011) Ecology and distribution of diatoms in Biscayne Bay, Florida (USA): implications for bioassessment and paleoenvironmental studies. Ecological Indicators 11:622–632

Weber C (1973) Biological field and laboratory methods for measuring the quality of surface waters and effluents: plankton. National Environmental Research Center U.S. Environmental Protection Agency, Cincinnati, pp 1–17

Welschmeyer NA (1994) Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. Limnology and Oceanography 39(8):1985–1992

Zar JH (1996) Biostatistical analysis, 3rd edn. Prentice Hall, New Jersey

Zhang N, Fan Y, Liu Y (2011) Relationship between diatom communities and environmental conditions at Honghe wetland, China. African Journal of Biotechnology 10(76):17506–17518