Spatial and temporal distributions of epiphytic diatoms growing on *Thalassia testudinum* Banks *ex* König: relationships to water quality

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Abstract

The spatial and temporal distributions of the epiphytic diatom flora on *Thalassia testudinum* was described within the Florida Bay estuary and at one Atlantic site east of the Florida Keys over a 1-year period. Species of the genus *Mastogloia* dominated the epiphytic diatom flora (82 out of 332 total species). Nonmetric Multidimensional Scaling (NMDS) and Analysis of Similarity (ANOSIM) revealed four distinct spatial assemblages and two temporal assemblages. Eastern and western Florida Bay assemblages were identified within the estuary. The eastern diatom assemblage was characterized by high relative abundances of *Brachysira aponina* and *Nitzschia liebetruthii*, while the western assemblage was characterized by the abundance of *Reimerothrix floridensis*, particularly during summer. Two diverse and distinct marine assemblages, one located in the Gulf of Mexico along the western edge of Florida Bay and the other behind the Florida reef tract in the Atlantic Ocean, were also identified. Analysis of the spatial distribution of diatoms and water quality characteristics within Florida Bay suggest that these assemblages may be structured by salinity and nutrient availability, particularly P. The Gulf of Mexico and the western Florida Bay assemblages were associated with higher water column salinities and TP concentrations and lower DIN concentrations and TN:TP ratios relative to the eastern Florida Bay assemblage. The temporal variation in diatom assemblages was associated with water temperature, though temporal indicator species were few relative to the number of spatial indicators.

Introduction

Benthic diatoms, both edaphic and epiphytic, are ubiquitous in shallow water environments and may be the most taxonomically diverse group of organisms in estuarine ecosystems (Sullivan & Currin, 2000). These highly productive diatom assemblages support upper trophic levels and affect the cycling and availability of silicate, nitrogen and phosphorus (Admiraal, 1984). Benthic diatom species assemblages affect ecosystem processes by binding surface sediments and consequently reducing the occurrence of turbidity events (Paterson, 1989; Smith & Underwood, 1998; Lucas et al., 2003). Fossil diatom distributions have also proven useful in inferring paleoenvironmental conditions (Dixit et al., 1992), and the strength of these inferences is dependent upon defining the environmental relationships of contemporary diatom assemblages.

Despite the importance of benthic diatoms and the growing need for species–environment relationships in biomonitoring and paleoecological applications, their taxonomic composition and ecology are poorly known, especially for tropical and subtropical ecosystems (Round et al., 1990;

Gaiser et al., 2005). This paucity is largely due to the very high diversity of diatoms in benthic marine ecosystems and the deficiency of taxonomic work in tropical regions (Round et al., 1990). Early descriptions of the marine diatom floras were concentrated in temperate Northwest Atlantic estuaries (Peragallo & Peragallo, 1897–1908; Van Heurck, 1899; Hendey, 1964; Admiraal & Peletier, 1980), especially on the unvegetated intertidal mudflats common to these regions. From these beginnings, investigations have expanded geographically and into vegetated marine ecosystems (Main & Mcintire, 1974; Montgomery, 1978; Jacobs & Noten, 1980; John, 1988; Snoeijs, 1994).

Spatial and temporal differences in diatom distributions in estuaries have been attributed to variability in physico-chemical and resource availability gradients (Amspoker & McIntire, 1978; Snoeijs, 1994; Underwood et al., 1998). The high degree of spatial and temporal variability of environmental conditions in estuaries (Day et al., 1989) causes diatom composition to be similarly variable. Within estuaries, salinity and the variability thereof, has shown to be a major structuring variable on diatom assemblages (Snoeijs, 1999). McIntire (1978) found that 41% of the variability in species data could be associated with salinity. Amspoker & McIntire (1978) and Snoeijs (1994) noted marked transitions in diatom species composition from freshwater species to brackish and marine species at approximately 5 ppt salinity. Snoeijs (1994) found differences in epiphytic diatom community composition between three macroalgal hosts in the Baltic Sea, but she concluded that the epiphytic diatom community composition was more affected by physical factors (i.e., season and salinity) than by host preference.

Changes in nutrient availability often coincide with salinity gradients (Day et al., 1989; Boyer et al., 1999) and may also explain diatom community structure (Archibold, 1972; Podzorski, 1984; Underwood et al., 1998). Within Colne estuary in temperate England, ammonium concentrations were important in determining diatom species compositions (Underwood et al., 1998), while in tropical Jamaica, phosphate and organic nitrogen were the important nutrients (Podzorski, 1984).

Vegetated ecosystems are ideal habitats for benthic diatoms and other epiphytes (Main & Mcintire, 1974; Penhale, 1977). Seagrass leaves and algal thalli may represent an order of magnitude greater surface area relative to sediments (Main & Mcintire, 1974; Zieman et al., 1989) for the colonization and growth of diatoms. Modern marine epiphytic diatom distributions in south Florida have been described from Biscayne Bay, Florida (Reyes-Vasquez, 1970), northeast Florida Bay (DeFelice & Lynts, 1978) and the Florida reef tract (Montgomery, 1978), but the details of the relationships between these diatom assemblages
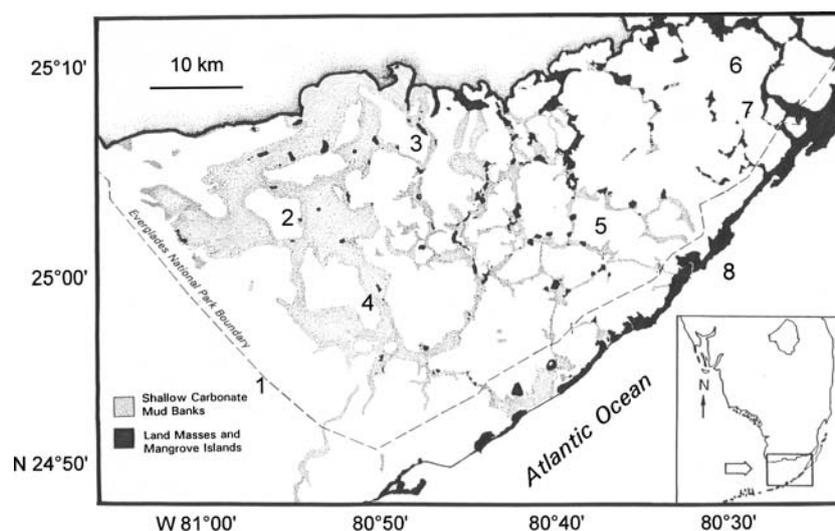

Figure 1. Florida Bay, USA, showing sampling locations for epiphytic diatoms (sites 1–8) and water quality variables (sites 1–6).

and water quality characteristics remain incomplete. The purpose of the present investigation was to characterize the temporal and spatial variation of the epiphytic diatom flora on *Thalassia testudinum* at seven sites in the Florida Bay estuary and at one Atlantic Ocean site east of the upper Florida Keys (Fig. 1). We hypothesized that different diatom assemblages exist across the study area and that distributional differences may be explained by water quality characteristics.

Materials and methods

To describe the regional and temporal variation of epiphytic diatom assemblages on the seagrass *T. testudinum*, the relative abundances of diatom taxa were determined at the eight study sites. The sites are representative of the various environments within Florida Bay and the Florida Keys. Sites 1–6 were chosen because of the availability of monthly water quality data and their location relative to the pronounced nutrient and productivity gradient within Florida Bay. Eastern Florida Bay is characterized by low primary productivity and phosphorus limitation. Primary productivity is higher and less nutrient-limited in western Florida Bay (Zieman et al., 1989; Fourqurean et al., 1993a; Armitage et al., 2005). Site 7 is adjacent to an island used as a seabird rookery and was chosen because the point source nutrient input has produced elevated levels of seagrass biomass and epiphytes relative to other areas in the eastern Florida Bay (Frankovich & Fourqurean, 1997). Site 8 was included to determine the similarity of diatoms within Florida Bay to composition outside of the bay. Each site was sampled at approximately bi-monthly intervals in March, June, August, October, and December 2000, and February 2001.

Using a razor blade, epiphyte material was scraped from the leaves of approximately 20 *T. testudinum* short-shoots collected from each site. The epiphyte material was combined yielding one homogeneous sample. Organic material was removed from the epiphytic diatoms by oxidation in 30% nitric acid followed by addition of potassium dichromate. The cleaned diatoms were settled from the solution for a minimum of 6 h and decanted; this process was repeated until the solution

reached a neutral pH. Cleaned diatoms were air-dried on cleaned no. 1 coverslips which were then mounted onto glass slides using Naphrax®. At least 500 diatom valves from one slide per sampling event were counted along arbitrary linear transects of suitable diatom density. Identifications and enumerations were made using differential interference contrast (DIC) and an oil immersion lens on a Nikon E600 microscope ($\times$1200 magnification, NA = 1.40). Diatom identifications were based on descriptions, drawings and photomicrographs in published keys (see Electronic Supplemental Materials). Shannon species diversity (natural logarithmic base, e) was determined for each sample and temporal and spatial differences were tested for using Friedman's repeated-measures ANOVA by ranks and Tukey type multiple comparisons (Zar, 1996).

Monthly water quality data that corresponded closest to the time of diatom sampling from sites 1 to 6 in Florida Bay were used to relate diatom assemblages to water quality characteristics. Previous analyses (Fourqurean et al., 1993b; Boyer et al., 1997; Frankovich & Fourqurean, 1997) led us to select six independent variables for analyses of diatom assemblages: DIN (dissolved inorganic nitrogen), TON (total organic nitrogen), TP (total phosphorus), TN:TP [calculated as: (DIN + TON)/TP], turbidity, bottom temperature, and bottom salinity. These water quality variables were ln-transformed and adjusted to the standard deviate (z-scored) to normalize water quality variables that were measured in different units to the same scale (McCune & Grace, 2002).

A species by sampling event similarity matrix (species by sampling events) and a water quality data matrix (water quality variables by sampling events) were constructed. Species present in fewer than 5% of samples and having a mean abundance (when present) of less than 2 valves per sample were removed prior to analyses. Analyses of similarity (ANOSIM, PRIMER_E/ANOSIM® software) using the Bray-Curtis similarity and the Euclidean distance metrics for the species and water quality data, respectively, were performed to identify *a priori* differences among sites and sampling periods. Nonmetric multidimensional scaling ordination (NMDS, PC-ORD vers. 4 software) (Kruskal, 1964; McCune & Mefford, 1999) was used to illustrate differences identified by

ANOSIM. The dimensionality (number of axes) of all NMDS solutions was assessed using a Monte Carlo test with 20 randomized runs. Significant dimensions were determined when simulated stress values were less than observed stress value at $p < 0.05$ (McCune & Grace, 2002). Diatom species significantly influencing site groupings were identified using Indicator Species Analysis (ISA) (Dufrêne & Legendre, 1997). ISA identifies indicator species based on the concentration of species abundances in a particular group and on the fidelity of occurrence in that group. ISA calculates an indicator value from the product of the proportional abundance of a particular species in a particular group relative to the abundance of that species in all groups and the proportional frequency of the species in each group (Dufrêne & Legendre, 1997; McCune & Grace, 2002). The indicator values range from 0 (no indication) to 100 (perfect indication). Taxa having an indicator value (based on relative abundance and frequency among sites) above 40% of perfect indication ($p < 0.05$) were considered reliable indicators.

Spatial and temporal differences in the individual water quality parameters were tested using Friedman's repeated-measures ANOVA and Tukey type multiple comparisons (Zar, 1996). The water quality variables that exhibited significant spatial and temporal differences as indicated by Friedman repeated-measures ANOVA were overlaid on NMDS ordination plots and correlated with NMDS axes.

A species by sampling event similarity matrix (92 species by 36 sampling events) from the six water quality sites was compared to the corresponding water quality data matrix (seven water quality variables by 36 sampling events) using the Mantel test to evaluate the correlation between these two matrixes (Mantel, 1967). In this way, we were able to determine correlations in variability in the environmental and species matrixes while avoiding having to assume independence of the influence of the multiple environmental variables on species distributions (Faith & Norris, 1989). The water quality variables that exhibited significant spatial and temporal differences according to the ANOVA analysis were plotted as vectors onto NMDS joint plots to indicate the direction and strength of the relationships of the variables with the site and period ordination scores. Taxa optima and tolerances in relation to the water quality variables were calculated using weighted-averaging (Ter Braak & Looman, 1995). The taxa optima and tolerances of select spatial and temporal indicator species were compared to their spatial and temporal distributions. NMDS, ISA, and the Mantel test were performed using PC-ORD vers. 4 software (McCune & Mefford, 1999), and taxa optima and tolerances were calculated using C2 software (Juggins, 2003).

Results

Our requirements for minimum abundance of species to include in samples led to exclusion of many taxa from our analyses. A total of 25,202 diatom valves were counted from 48 samples. From these samples, 255 taxa from 65 genera were identified under light microscopy (LM). We scanned additional material (beyond the 500 count needed for quantitative purposes) and identified 77 additional rare taxa. After removing rare and infrequent taxa from the distance matrixes, the number of taxa analyzed was reduced to 92 (see Electronic Supplemental Materials[1]). Although these species constituted only 28% of the total species identified from the collections, they represented > 95% of the total cell count. The seven most abundant species from pooled samples were *Cocconeis placentula* Ehrenberg, *Brachysira aponina* Kützing, *Nitzschia liebetruthii* Rabenhorst, *Hyalosynedra laevigata* (Grunow) Williams and Round, *Amphora* sp. 1, *Mastogloia crucicula* (Grunow) Cleve, and *M. pusilla* (Grunow) Cleve. These seven species collectively accounted for 51.7% of all valves counted and occurred in at least 85% of all samples (see Electronic Supplemental Materials[1]). Shannon species diversity ranged from 1.34 at site 7 in February 2001 to 3.55 at site 8 outside of Florida Bay in June 2000. Significant temporal and spatial differences in Shannon species diversity were not observed (Friedman test, $p > 0.05$).

ANOSIM identified four distinct epiphytic diatom assemblages across the study region (Table 1). The diatom assemblages at the two most

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[1] Electronic Supplementary Material is available for this article at http://www.dx.doi.org/10.1007/s10750-006-0136-x.

Table 1. Comparison of sampling sites and periods based on Analysis of Similarities (ANOSIM-Primer) using Bray-Curtis dissimilarities of species composition

Site designation	8	1	4	2	3	5	6	7
Community group	A	B		C			D	

Sampling period designation	JUN00	AUG00	OCT00	DEC00	FEB01	MAR00
		S				
				T		
					W	

Continuous horizontal lines denote non-significant differences in species composition. Community groups are identified by similar species composition. Significance level = 0.05. Site numbers correspond to sampling locations in Figure 1. Period groups are designated as follows: S – June and August 2000, T – October and December 2000, W – February 2001 and March 2000.

marine sites (group A = site 8 on the Atlantic ocean side of the Florida Keys and group B = site 1 along the western edge of Florida Bay) were significantly different from each other and from two distinct diatom assemblages in the interior of Florida Bay. The two interior diatom assemblages consisted of group C = sites 2, 3, and 4 in western Florida Bay and group D = sites 5, 6, and 7 in the eastern bay (Table 1). ANOSIM also revealed temporal differences in the diatom assemblages

sampled at seasonal extremes, but each assemblage showed a gradual temporal progression from one sampling period to the next. The diatom assemblages in June and August 2000 were significantly different from those in March 2000 and February 2001. These two period groups may be represented as a summer (S) diatom assemblages and winter (W) diatom assemblages (Table 1).

Three major gradients identified by NMDS captured most of the variation in the diatom
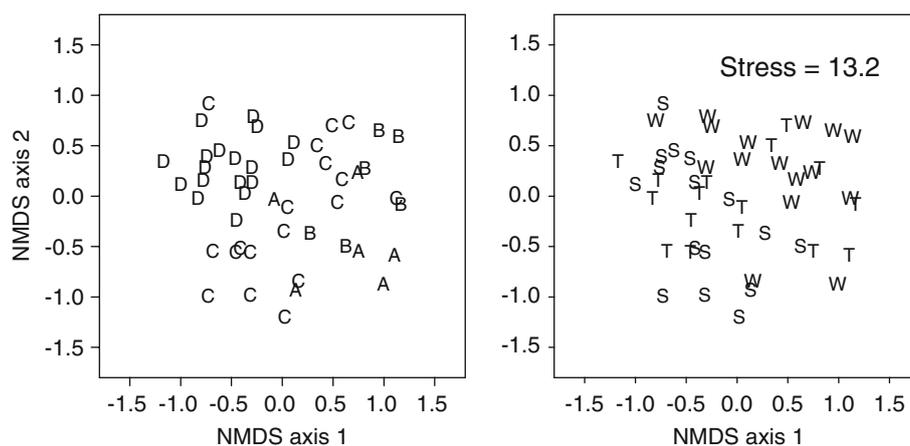

Figure 2. Ordination site scores in two of the dimensions generated by non-metric multidimensional scaling (NMDS) using the Bray-Curtis similarity metric of diatom species relative abundances. Sites are coded by community groups and sampling period groups. All community groups are significantly-different in ANOSIM and are designated as: A – Site 8; B – Site 1; C – Sites 2, 3, and 4; D – Sites 5, 6, and 7. Sampling period group designations are: S = summer – June and August 2000; W = winter – March 2000 and February 2001; T = transition periods – October and December 2000. S and W period groups are significantly different from each other in ANOSIM.

Table 2. Indicator species by site and sampling period

Taxon name	Indicator	*p*-value
Site analysis		
Group A site 8		
Mastogloia cribrosa	74.0	0.002
Cymatosira lorenziana	70.7	0.001
Seminavis delicatula	66.6	0.002
Mastogloia ovalis	61.4	0.001
Dimerogramma dubium	53.0	0.003
Mastogloia corsicana	50.7	0.022
Neofragilaria nicobarica	45.0	0.010
Mastogloia crucicula	45.0	0.041
Mastogloia lacrimata	43.0	0.010
Group B site 1		
Cocconeis woodii	75.8	0.002
Mastogloia pusilla	71.6	0.001
Rhopalodia pacifica	70.2	0.001
Amphora sp. 1	60.9	0.007
Cymatosira belgica	53.8	0.004
Mastogloia manokwariensis	50.0	0.003
Cocconeis barleyi	48.7	0.005
Group C sites 2, 3, and 4		
Reimerothrix floridensis	71.5	0.003
Amphora lineolata	53.5	0.002
Cocconeis britannica	44.1	0.009
Licmophora grandis	42.0	0.026
Group D sites 5, 6, and 7		
Brachysira aponina	68.7	0.001
Nitzschia liebetruthii	59.5	0.001
Sampling period analysis		
Summer group – June, August 2000		
Reimerothrix floridensis	65.0	0.002
Hyalosynedra laevigata	51.9	0.035
Mastogloia biocellata	50.8	0.002
Mastogloia erythraea	47.7	0.025
Winter group – March 2000, February 2001		
Amphora sp. 1	58.1	0.001
Cocconeis placentula	49.7	0.045
Navicula cf. *salinicola*	41.1	0.017

Indicator species identified by Indicator Species Analysis (Dufrêne & Legendre, 1997) using PC-ORD, version 4.17 with 1000 permutations in the Monte Carlo test. The indicator values range from 0 (no indication) to 100 (perfect indication). Site groupings based on results of ANOSIM (Primer).

Table 3. Results of Friedman's repeated-measures ANOVA (Zar, 1996) examining differences in water quality parameters by site group and sampling period

	Site group differences		Period differences	
	χ^2	Significance	χ^2	Significance
Temperature	6.22		31.30	S
Salinity	18.62	S	12.31	
Turbidity	6.59		12.37	
TON	8.66		11.25	
DIN	23.26	S	1.58	
TP	15.34	S	12.13	
TN:TP	17.01	S	16.43	S

Site groups identified by ANOSIM. "S" denotes statistical significance of χ^2 at experimentwise Type I error rate = 0.05 and comparisonwise Type I error rate = 0.007.

assemblages; the three dimensions contained 40.0, 28.0, and 13.8%, respectively, of the information in the analytical dataset (cumulative = 81.7%). The four distinct spatial assemblages and the winter and summer temporal assemblages identified by ANOSIM are well separated in the NMDS plots (Fig. 2). The ordination plotted by site shows the two most marine site groups (i.e., group A = site 8 and group B = site 1) were most different from the eastern interior site group (i.e., group D = sites 5, 6, and 7) (Fig. 2). The diatom assemblages of the western interior sites (i.e., group C = sites 2, 3, and 4) exhibit some overlap with the most marine sites and the eastern bay sites. In the NMDS plots coded by time of year, February and March diatom assemblages were most different from June and August assemblages. Diatom assemblages sampled from the intervening months overlap with the summer and winter assemblages.

ISA identified many species significantly influencing the spatial and temporal site groupings (Table 2, see Electronic Supplemental Materials for photomicrographs). Site 8 was characterized by many different *Mastogloia* species and some epipsammic (sand-grain associated) diatoms (i.e., *Cymatosira lorenziana* Grunow, *Dimerogramma dubium* Grunow, and *Neofragilaria nicobarica* Desikachary, Prasad, and Prema). *Mastogloia pusilla*, *Rhopalodia pacifica* Krammer, and *Cocconeis woodii* Reyes were strong indicators of site 1.

Reimerothrix floridensis Prasad was particularly abundant in the western interior of Florida Bay (i.e., sites 2, 3, and 4) during summer months. The eastern interior of Florida Bay was characterized by high relative abundances of *Brachysira aponina* and *Nitzschia liebetruthii*.

The water quality parameters also exhibited significant spatial and temporal variation (Table 3). Water temperature exhibited significant temporal variation only (Table 3), with bay wide mean temperatures ranging from 23.0 °C in December 2000 to 29.2 °C in June 2000. Mean salinity at site 6 in eastern Florida Bay was 27.8 ppt and was significantly lower ($p < 0.001$) than the mean salinity (37.2) at western sites 1–3. Turbidity was more variable than temperature and salinity and ranged from 1.1 NTU at site 2 in December 2000 to 16.8 NTU at site 3 in October 2000. Site 3 exhibited the highest turbidity during four of the six sampling periods, but these differences were not statistically significant. TON concentrations varied greatly, spanning an order of magnitude and ranging from 5.5 μM at site 1 in March 2000 to 67.1 at site 3 in February 2001. TON did not exhibit significant spatial and temporal differences due to large intra-site and intra-period variability (coefficients of variation = 40, 42%, respectively). DIN concentration exhibited significant spatial variation only (Table 3). Mean DIN concentration ranged from 0.5 μM at site 1 to 4.7 μM at site 5. Mean DIN concentrations at sites 3, 5, and 6 were significantly higher than site 1 located on the western edge of the bay ($p < 0.001$). TP concentration exhibited significant spatial variation and ranged from 0.05 μM at site 1 in February 2001 to 1.75 μM at site 3 in December 2000. Mean TP concentration at site 3 was significantly higher than at sites 5 and 6 in northeast Florida Bay ($p = 0.003$). Site 6 in eastern Florida Bay exhibited the highest mean TN:TP ratio of water column nutrients and was significantly different from the ratios at sites 1 and 4 in the western bay ($p = 0.001$). Mean TN:TP ratio was highest in March 2000 ($p = 0.002$). The ratios at two sites in the eastern bay (sites 5 and 6) spiked during this time period because of very low concentrations of TP.

ANOSIM of the water quality parameters revealed that three sites in outer Florida Bay (sites 1, 2, and 4) were characterized by similar water quality characteristics that were significantly different from that at site 3 and sites 5 and 6 in the bay interior (Table 4). ANOSIM revealed fewer temporal differences in water quality characteristics (Table 4). Similar to the ANOSIM of the species data, water quality characteristics exhibited much overlap between all sampling periods except December 2000 which was significantly different from all others, likely due to the spike in TP concentrations during this time period.

NMDS revealed three major gradients that captured most of the variation in the water quality characteristics in Florida Bay. These dimensions contained 39.2, 35.4, and 21.0%, respectively, of the information in the water quality dataset (cumulative = 95.5%). The two distinct water quality groups identified by ANOSIM [i.e., outer (O) and interior (I)], are well separated in the

Table 4. Comparison of sampling sites and periods based on Analysis of Similarities (ANOSIM-Primer) using Euclidean distance measures of "z transformed" water quality parameters

Site designation	2	4	1	3	5	6
Water quality group	Outer Florida Bay (O)			Interior Florida Bay (I)		
Sampling period designation	AUG00	JUN00	MAR00	OCT00	FEB01	DEC00

Continuous horizontal lines denote non-significant differences in water quality parameters. Water quality groups are identified by similar species composition. Significance level = 0.05. Site numbers correspond to sampling locations in Figure 1.
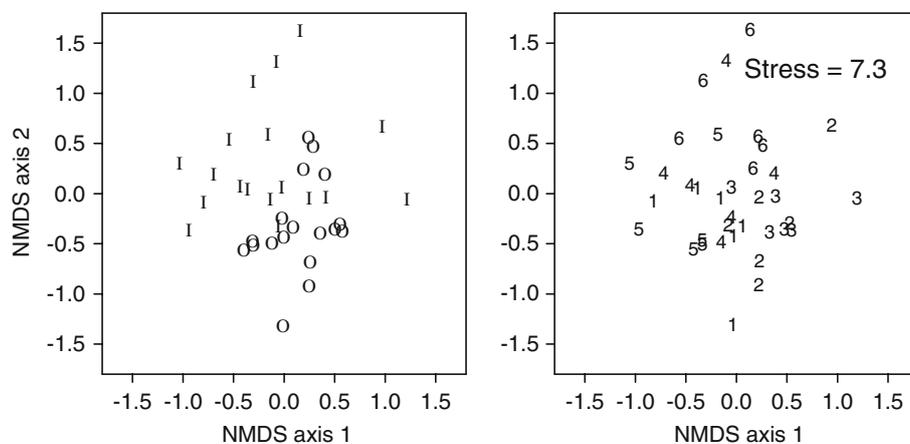
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Figure 3. Ordination site scores in three dimensions generated by non-metric multidimensional scaling (NMDS) using the Euclidean distance metric of z-transformed water quality parameters for sites 1–6. Sites are coded by water quality groups and sampling periods. Both water quality groups are significantly different in ANOSIM and are designated as: I = interior Florida Bay – Sites 3, 5, and 6; O = outer Florida Bay – Sites 1; 2, and 4. Sampling period groups were similar and designated as: 1 – March 2000; 2 – June 2000; 3 – August 2000; 4 – October 2000; 5 – December 2000; 6 – February 2001.

NMDS plots (Fig. 3). Outer Florida Bay sites 1, 2, and 4 are more similar to each other than to the more interior sites 3, 5 and 6. The NMDS plots coded by sampling period illustrates the similarity of water quality between sampling periods as revealed by ANOSIM.

The distribution of epiphytic diatoms was related to water quality. The Mantel test revealed that dissimilarity in diatom species composition was positively, but weakly related to dissimilarity in the water quality parameters (Mantel statistic $r = 0.224$, $p < 0.001$). Overlaying the water quality parameters that exhibited significant spatial and temporal variation as vectors onto the NMDS joint plots, revealed that higher DIN concentrations and TN:TP ratios were associated with the interior Florida Bay sites while higher salinities and TP concentrations were associated with the outer Florida Bay sites (Fig. 4). Higher water temperatures were associated with the summer samplings (i.e., June and August) (Fig. 4).

Taxa optima and tolerances of indicator species in relation to the water quality variables (see Electronic Supplemental Materials) indicated that the indicator species group of eastern Florida Bay (*Brachysira aponina* and *Nitzschia liebetruthii*) had the lowest mean salinity optima (33.2 ppt) and the largest salinity tolerance (5.2 ppt) compared to the mean salinity optima and tolerances of the other three spatial indicator species groups.

The eastern Florida Bay indicator species group also exhibited the highest mean DIN (3.11 μM) and TN:TP (102) optima relative to the other spatial indicator groups.

Discussion

The epiphytic diatom flora in Florida Bay and at the adjacent Atlantic Ocean site conforms to the epiphytic diatom flora of the Florida Keys (Montgomery, 1978), upper Florida Bay (DeFelice & Lynts, 1978), Biscayne Bay (Reyes-Vasquez, 1970), and the Bahamas (Hein et al., in review). The epiphytic diatom assemblage on the seagrass *T. testudinum* in Florida Bay was also similar to that on the prop roots of the mangrove *Rhizophora mangle* Linnaeus in the Indian River, Florida (Navarro & Torres, 1987). A common characteristic of the epiphytic flora in these subtropical areas is the predominance in the number and relative abundance of *Mastogloia* species (Reyes-Vasquez, 1970; DeFelice & Lynts, 1978; Montgomery, 1978). *Mastogloia* accounted for 24.6% of the species and 19.7% of the total cell counts in the present study. Similarly, 16% of the benthic diatoms identified by DeFelice & Lynts (1978) were *Mastogloia* species. DeFelice & Lynts (1978) and Montgomery (1978), reported relative abundances of *Mastogloia* ranging from 34.5 to 70.7%.
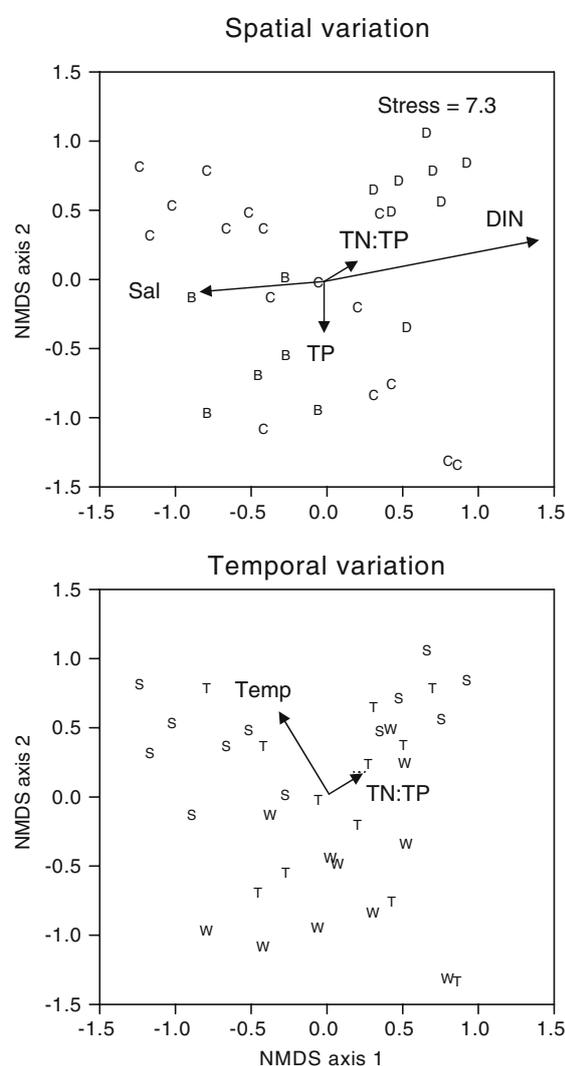
Figure 4. Vectors corresponding to the direction of maximum correlation of the water quality variables with NMDS site scores coded by community groups and sampling period groups. The water quality vectors depicted correspond only to those water quality variables that exhibited significant spatial and temporal variation as indicated by Friedman's repeated-measures ANOVA. Community group designations are: B – Site 1; C – Sites 2, 3, and 4; D – Sites 5 and 6. Sampling period group designations are: S = summer – June and August 2000; W – winter – March 2000 and February 2001; T = transition periods – October and December 2000.

The lower mean species diversity of the Florida Bay epiphytic diatom assemblages (2.14, DeFelice & Lynts, 1978; 2.77, present study) relative to the oceanic back-reef sites (3.42, Montgomery, 1978) is likely due to the more variable physical environment and nutrient limitation in Florida Bay. DeFelice & Lynts (1978) and Huvane (2002) noted a general trend of increased diatom diversity away from terrestrial environments towards more marine sites. Similarly, the highest mean diversity observed in this study (3.23) was at marine site 8 outside of Florida Bay, though the differences between this site and the Florida Bay sites were statistically insignificant. DeFelice & Lynts (1978) hypothesized that the diatom assemblages in Florida Bay are controlled by variability in physical factors such as temperature and salinity that result in low diatom diversity. The shallow waters of Florida Bay (0–2 m) cool and heat quicker than deeper adjacent marine waters producing more variable water temperatures (Boyer et al., 1999). Salinity is also more variable within Florida Bay with variability increasing towards the restricted eastern bay (Frankovich & Fourqurean, 1997: p. 43, Fig. 9). Low freshwater runoff and limited exchange with Atlantic and Gulf of Mexico (GOM) waters restrict circulation and increase water residence time resulting in variable salinities ranging from hyposaline during wet years to hypersaline during droughts (Boyer et al., 1999; Nuttle et al., 2000).

The alignment of indicator species of the four distinct spatial assemblages along the estuarine gradient suggests that salinity is a structuring variable. The observed epiphytic diatom assemblages in this study transition from the predominance of marine *Mastogloia* species at the two marine sites (sites 1 and 8, Fig. 1) to a *Reimerothrix floridensis* species assemblage (sites 2, 3, and 4) to the assemblage dominated by brackish-occurring *Brachysira aponina* and *Nitzschia liebetruthii* in the eastern bay (sites 5, 6, and 7). The predominance of marine *Mastogloia* species at the two marine sites is similar to the characteristics of the Florida Keys back-reef sites analyzed by Montgomery (1978). This spatial distribution of species is also consistent with descriptions of the salinity preferences of these diatoms (Witkowski et al., 2000; Prasad et al., 2001). Differences in diatom species composition were expected at the eastern Florida Bay site 7, which was characterized by elevated seagrass and epiphyte biomass in response to nutrient addition by the resident bird colony (Powell et al., 1991). Surprisingly, the diatom assemblage at site 7 was similar to other

eastern Florida Bay sites, suggesting reduced importance of nutrient availability.

Within estuaries, diatom community composition has been shown to be driven by salinity characteristics (McIntire, 1978; John, 1988; Snoeijs, 1994, 1999; O'Connell et al., 1997). Salinity is believed to be the predominant environmental factor that determines the community structure of diatoms along estuarine gradients (Snoeijs, 1999). Huvane & Cooper (2001) and Huvane (2002) examined diatom valves in Florida Bay sediment cores and surface sediments, respectively, and concluded that diatoms were good indicators of historic salinity conditions. In contrast, Reyes-Vasquez (1970) concluded that salinity does not appear to have a direct effect on the distribution and succession of the diatoms living on *T. testudinum* in Biscayne Bay, FL, though the observed salinity range was small (30.05–38.95 psu). During the time period of this study, salinities were consistent with the classic estuary model with lower salinities towards the head of the estuary and higher marine salinities at the mouth. During extended drought periods, which periodically occur in Florida Bay over larger time scales, the gradient is reversed with hypersaline conditions toward the restricted interior of the bay. Snoeijs (1999) suggested that diatoms may be selected more according to their ability to flourish in variable salinity environments than to their observed salinity optimum. This may also be the case in Florida Bay. The indicator species of the eastern Florida Bay sites exhibited the lowest mean salinity optima and the largest mean salinity tolerance relative to the indicator species at the more marine sites. To determine if salinity variability is the major structuring variable, observations of diatom community structure must be made over longer time periods (e.g., multiple years) in order to capture the climatic variation occurring over the larger time scales.

Differences in nutrient availability are often reflected in the structure and species composition of algal communities (Sundbäck & Snoeijs, 1991; Underwood et al., 1998; Snoeijs, 1999). Sundbäck & Snoeijs (1991) found that nutrient addition produced some changes in the species dominance of the diatoms, but changes were more evident at the macroscopic level (i.e., an increase in filamentous green algae) than in the microflora. The distinct epiphytic diatom assemblages in Florida Bay, aligned along a nutrient gradient (Fig. 4), suggest that nutrient availability may also structure these communities. In this study, DIN concentrations explained the most variation in the distribution of the epiphytic diatoms. The nutrient and productivity gradient in Florida Bay, increasing from east to west, is created by phosphorus limitation of primary production and the limited exchange of relatively phosphorus-rich marine water from the GOM (Fourqurean et al., 1993a, b; Fourqurean & Zieman, 2002; Armitage et al., 2005). Western Florida Bay sites exhibited higher TP concentrations and lower DIN concentrations and TN:TP ratios relative to eastern Florida Bay sites (Table 3). In P-limited Florida Bay, any available phosphorus is quickly removed from the water column by biological uptake and adsorption to carbonate particles (Boyer et al., 1999; Koch et al., 2001). As phosphorus is removed during the exchange of GOM waters with Florida Bay waters, phosphorus availability decreases toward the restricted interior of Florida Bay, DIN concentrations become elevated due to the accumulation of excess nitrogen relative to phosphorus, and the TN:TP ratio increases (Fourqurean et al., 1993a, b). Excess DIN may be a better indicator of the P-limited conditions, because water column P concentrations are often below detection limits (Boyer et al., 1999). The high DIN and TN:TP optima of the abundant eastern Florida Bay indicator species (*Brachysira aponina* and *Nitzschia liebetruthii*) suggest that these species are able to thrive under *P*-limited conditions.

In addition to spatial variation, the epiphytic diatoms also exhibited temporal variation though this variation was subtler. Differences in community structure were gradual between summer and winter diatom assemblages and the temporal indicator species were few relative to the number of spatial indicators. The temporal variation was significantly associated with water temperature. Changes in diatom species composition have been observed in the heated water effluent from nuclear power plants (Hein & Koppen, 1979; Snoeijs, 1999). Hein & Koppen (1979) observed a decrease in species richness and diversity in the Forked River, Barnegat Bay, N.J. nuclear power plant effluent. Snoeijs (1999) observed increases in the abundance of large colonial diatoms (e.g.,

Melosira spp.) and large epiphytic diatoms (e.g., *Tabularia tabulata* (C. A. Agardh) Snoeijs and *Licmphora* cf. *gracilis* (Ehrenberg) Grunow) in the heated waters of the Forsmark Biotest basin, Bothnian Sea, Sweden. The size of the temporal indicator species of the present study exhibited a temporal trend that was similar to that observed in the Forsmark Biotest basin. In the present study, two large synedroid taxa (*Reimerothrix floridensis* and *Hyalosynedra laevigata*) and two smaller *Mastogloia* species (*M. biocellata* (Grunow) Novarino & Muftah and *M. erythraea* Grunow) were more prevalent during summertime. Three relatively small species (*Amphora* sp. 1, *Cocconeis placentula*, and *Navicula* cf. *salinicola* Hustedt) were more prevalent during the winter.

As hypothesized, distinct spatial and temporal distributions of epiphytic diatoms were observed in Florida Bay and at one Atlantic back-reef site. The diatom assemblages were aligned along a salinity and nutrient limitation gradient formed by restricted circulation in the bay interior (Boyer et al., 1999). Multivariate analyses revealed that the diatom assemblages may be structured spatially by salinity and nutrient availability, particularly phosphorus. As hypothesized, diatom assemblages also varied temporally with the variation associated with temperature. These inferences were based on correlational evidence and therefore must be verified by future experimentation.

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