NUTRIENT EFFECTS ON SEAGRASS EPIPHYTE COMMUNITY STRUCTURE IN FLORIDA BAY[1]

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A field experiment was employed in Florida Bay investigating the response of seagrass epiphyte communities to nitrogen (N) and phosphorus (P) additions. While most of the variability in epiphyte community structure was related to uncontrolled temporal and spatial environmental heterogeneity, P additions increased the relative abundance of the red algae–cyanobacterial complex and green algae, with a concomitant decrease in diatoms. When N was added along with P, the observed changes to the diatoms and the red algae–cyanobacterial complex were in the same direction as P-only treatments, but the responses were decreased in magnitude. Within the diatom community, species relative abundances, species richness, and diversity responded weakly to nutrient addition. P additions produced changes in diatom community structure that were limited to summer and were stronger in eastern Florida Bay than in the western bay. These changes were consistent with well-established temporal and spatial patterns of P limitation. Despite the significant change in community structure resulting from P addition, diatom communities from the same site and time, regardless of nutrient treatment, remained more similar to one another than to the diatom communities subject to identical nutrient treatments from different sites and times. Overall, epiphyte communities exhibited responses to P addition that were most evident at the division level.

Key index words: diatoms; epiphytes; fertilization; Florida Bay; nitrogen; nutrients; phosphorus; photopigments; seagrass

Abbreviations: ANOSIM, analysis of similarity; ANOVA, analysis of variance; C, control; DIC, differential interference contrast; H, Shannon diversity index; N, nitrogen; NA, numerical aperture; NMS, nonmetric multidimensional scaling; NP, nitrogen + phosphorus; P, phosphorus; RA, relative abundance; S, site; T, time

Increased loadings of N and P in coastal ecosystems require further understanding and greater predictive capabilities of the community-level responses to these nutrient additions. Increased nutrient loadings can have dramatic effects on estuarine ecosystems. In extreme cases, dominance may shift from benthic primary production to phytoplankton production (Orth and Moore 1983, Cambridge et al. 1986, Duarte 1995). In less extreme cases, nutrient effects may be most evident as changes between taxonomic groups (e.g., diatoms vs. cyanophytes) within a particular primary producer community (Pinckney et al. 1995, Wear et al. 1999). In other instances, changes may occur in the relative abundances of individual species within a taxonomic group (Sundbäck and Snoeijs 1991, Marks and Power 2001).

Benthic diatom communities are very diverse and have turnover rates on the order of days or weeks (Round et al. 1990). As suggested by the alignment of these communities along nutrient availability gradients (Underwood et al. 1998), the species composition of these fast-growing organisms may be reflective of changing nutrient conditions (Stoermer et al. 1978, Manoylov and Stevenson 2006). Benthic diatoms are abundant in seagrass epiphyte assemblages (Harlin 1980), yet little is known about how

epiphyte communities, in general, and the diatom assemblages, in particular, respond to changing nutrient availability. Changes within epiphyte communities may translate into larger changes in the ecosystem because of the importance of epiphytes in supporting higher trophic levels (Kitting et al. 1984, Mutchler et al. 2004). Nutrient addition may shift algal species composition toward species that may be more or less palatable or toxic to herbivores (Sommer 2001).

Within estuaries, the relationships between diatom distributions and nutrients are complex because diatom communities are often aligned along covarying gradients of salinity and nutrient availability (Archibold 1972, Podzorski 1984, Underwood et al. 1998, Frankovich et al. 2006). Underwood and Provot (2000) determined that the distribution of some of the common taxa of epipelic diatoms from the Colne estuary, United Kingdom, could be explained by individual species' preferences for inorganic nitrogen as determined in unialgal cultures. Because most studies reporting nutrient responses of benthic diatoms and microalgae have been conducted in freshwater lotic habitats (see Borchardt 1996 for review), and because natural field experiments on mixed-species assemblages (Ault et al. 2000) in marine environments are scant (Cox 1993), there is a need for further field experimentation on benthic marine microalgae.

The goal of the present investigation was to determine how in situ changes in N and P supply alter seagrass epiphyte communities by examining the changes in photopigments that are specific to larger taxonomic groups and the changes in the relative abundances of diatom species. The present experiment utilizes an existing experimental design that, after 1.5 years of N and P additions, both singly and in combination, had successfully established nutrient-enriched plots containing elevated levels of N and P in the sediments, seagrass leaf tissue, and epiphytes (Armitage et al. 2005, 2006). Armitage et al. (2005, 2006) reported increases in epiphyte P content and increased absolute abundances of epiphyte photopigments in response to sediment nutrient additions, and they confirmed P limitation of seagrass biomass and epiphyte communities in eastern Florida Bay. The present study differs from these previous investigations by further investigating changes in epiphyte community structure resulting from nutrient additions by reporting changes evident in the relative abundances of diatom species and epiphyte photopigments. In the present investigation, we hypothesized that the relative abundances of epiphytic photopigments and of the epiphytic diatom species in Florida Bay would change in response to P additions especially in eastern Florida Bay, and that these communities would not exhibit any response to N additions.

MATERIALS AND METHODS

Experimental design. To determine the response of epiphytic photopigments and diatom communities to nutrient additions, epiphytes were sampled from 0.25 m^2 study plots from an existing experiment that, after 1.5 years, had successfully established nutrient-enriched conditions containing elevated levels of N and P in the sediments, seagrass leaf tissue, and epiphytes (Armitage et al. 2005, 2006). This experimental design was employed to examine nutrient effects on seagrass, macroalgae, and epiphyte biomass (results in Armitage et al. 2005, 2006). Two study sites were located at 25°10.59 N, 80°29.39 W (site 1) and 24°58.62 N, 80°50.35 W (site 2) and correspond to sites C2 and B1, respectively, in Armitage et al. (2005). Site 1 and site 2 were chosen to represent areas of severe and moderate P limitation, respectively (Armitage et al. 2005). At each site, a total of 24 study plots were separated at 1 m intervals. N additions, P additions, both N and P additions (NP), and no nutrient additions (C) were randomly assigned to six plots per site. Bimonthly additions of N, P, and NP to the sediment surface began in October 2002 and continued throughout the experiment. N was added at a loading rate of 1.43 g N · m^{-2} · d^{-1} in the form of slow-release nitrogen capsules (Polyon fertilizer, 94% N as urea, Agrium Advanced Technologies, Sylacauga, AL, USA). P was added at a loading rate of 0.18 g P · m^{-2} · d^{-1} as defluorinated rock phosphate granules [Multifos, Ca$_3$(PO$_4$)$_2$, The Mosaic Company, New Wales, FL, USA]. These loading rates (N:P molar ratio = 17.6:1) approximate potential sewage loading rates (MCSM 2001) in the Florida Keys. Application of fertilizer to the sediment surface has been shown to be accessible to seagrasses, macroalgae, microphytobenthos, and seagrass epiphytes (Ferdie and Fourqurean 2004, Mutchler et al. 2004, Armitage et al. 2005). At the times of sampling, N and P additions to the sediment surface had significantly increased epiphyte N and P content relative to controls at both study sites (Armitage et al. 2005), indicating that nutrients were reaching the epiphyte community. At the times of sampling, P additions had also increased *Thalassia testudinum* cover by 50%–75%, relative to unfertilized controls at site 1, but epiphyte biomass (as estimated by chl *a* concentration) had not changed in response to nutrient additions at either site (Armitage et al. 2005). Plots were sampled during summer (August 3–4, 2004) and winter (February 7–9, 2005) to capture any differential nutrient response of the epiphyte communities due to season.

Epiphyte accessory photopigment analyses. To determine nutrient addition effects on epiphytes at higher taxonomic levels (i.e., division), the relative molar abundances of the photopigments fucoxanthin, zeaxanthin, and chl *b* were determined using HPLC according to the methods described in Armitage et al. (2006). Fucoxanthin is specific to Heterokontophyta and Dinophyta, while chl *b* is specific to green algae (Chlorophyta, Prochlorophyta, Euglenophyta, and Chlorarachniophyta; Van den Hoek et al. 1995). Zeaxanthin is an abundant pigment in Rhodophyta and Cyanophyta (Van den Hoek et al. 1995). Pigments were extracted from lyophilized epiphytes scraped from an entire *T. testudinum* short-shoot from all 24 plots at each site and time (*n* = 6 for each treatment). Four-way analysis of variance (ANOVA) was utilized to determine effects of site (S), time (T), phosphorus (P), and nitrogen (N) additions on relative abundance of the three taxa-specific photopigments measured. When significant effects were identified by ANOVA, Tukey's multiple comparison tests were employed to detect significant differences between levels (Zar 1996).

Diatom analyses. To determine the response of diatom communities to nutrient enrichment, epiphytic diatoms were identified and enumerated from the leaves of the most

abundant seagrass, *T. testudinum*. Due to greater lab time requirements for diatom identification and enumeration, only a subset of the sites, times, and plots in Armitage et al. (2005) were selected for analyses of epiphyte relative species composition. Three study plots of each fertilizer treatment at each site and time (48 total) were randomly selected for the diatom determinations.

Epiphyte material was scraped from the leaves of 10 *Thalassia* short-shoots within each study plot using a razor blade and pooled into one homogenous sample per study plot. Organic material was removed from the epiphytic diatoms by oxidation in a boiling solution of 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 that were then mounted onto glass slides using Naphrax® (The Biology Shop, Hazelbrook, Australia). At least 500 diatom valves from one slide per study plot (>24,000 total) 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 Eclipse E600 microscope (×1,200 magnification, NA = 1.40) (Nikon Instruments Inc., Melville, NY, USA). Diatom identifications were based on descriptions, drawings and photomicrographs in published keys (Peragallo and Peragallo 1897–1908, Hustedt 1930–1966, 1955, Voigt 1942, 1952, 1956, 1963, Reyes-Vasquez 1970, Montgomery 1978, Stephens and Gibson 1980, Navarro 1982, Yohn and Gibson 1982, Foged 1984, Round et al. 1990, Honeywill 1998, Witkowski et al. 2000, Prasad et al. 2000, 2001, Danielidis and Mann 2002, Prasad 2003).

Species richness, Shannon diversity, and individual species relative abundances were calculated for each study plot. Four-way ANOVAs ($S \times T \times N \times P$) were performed on species richness and Shannon diversity using the Bonferroni adjustment (Zar 1996) for two tests. A comparison-wise Type I error rate of 0.025 was used, ensuring an experiment-wise error rate of < 0.05.

A species relative abundance by study plot matrix (all sites and times) was constructed to investigate patterns in diatom community structure that are represented when all sampling sites and times are considered. Nonmetric multidimensional scaling ordination (NMS, Primer v6) (Kruskal 1964, Clarke and Warwick 2001), using calculated Bray-Curtis similarity coefficients, was used to illustrate differences in community structure. To decrease the importance of the rarest species in the ordination, whose occurrence in a particular study plot may be due largely to chance (McCune and Grace 2002) and as required by ordination analyses (Clarke and Warwick 2001), the rarest species were removed from the matrix. Species present in <5% of samples or with a maximum abundance of <1% in all samples were removed prior to analysis. After removal of the rare and infrequent taxa, the number of taxa analyzed for NMS ordination of all samples was reduced to 71. Although these taxa constituted only 39% of the total species identified, they represented 97.4% of the total valve count. Species relative abundances were square-root transformed to enhance community patterns produced by species of intermediate abundance (Clarke and Warwick 2001). The dimensionality (number of axes) of all NMS solutions was assessed using a Monte Carlo test with 50 randomized runs. Significant dimensions were determined when simulated stress values were less than observed stress values at $P < 0.05$ (Clarke and Warwick 2001).

Distinct spatial and temporal epiphytic diatom communities were previously observed in Florida Bay (Frankovich et al. 2006). Because nutrient addition effects may be obscured by larger spatial and temporal variations in diatom community structure (Clarke and Warwick 2001), and because large

clusters representing the separate site and time combinations were observed in the NMS plot for all samples, nutrient addition effects were analyzed separately for each of the four separate site and time combinations (i.e., site 1, August 2004; site 1, February 2005; site 2, August 2004; site 2, February 2005). Using the same data-screening methods described for the full-sample ordination analysis, NMS ordinations were repeated within each large cluster (i.e., each distinct site and time combination) to reveal a more accurate display of the finer structure (Clarke and Warwick 2001) produced by nutrient addition effects.

Because the epiphytic diatom community in Florida Bay is species rich (>300 spp.) and diverse (Frankovich et al. 2006), and each species is subject to "high statistical noise," the diatom community data need to be analyzed "en masse to elicit the important biological signal" (Clarke and Warwick 2001, pp. 1–3). In reference to community data, Clarke and Warwick (2001, pp. 1–3) state, "standard parametric modeling is totally invalid." For these reasons, ANOVA on individual diatom species was not employed, even though the present study sampled the diatom communities from an existing factorial experimental design (Armitage et al. 2005). One-way analyses of similarity (ANOSIM, Primer v6) with all species retained (Clarke and Warwick 2001) were employed to test for differences in diatom community structure resulting from four nutrient treatments (control, N, P, N + P) on each of four spatiotemporal communities. If overall differences between the four nutrient treatments were detected ($P \leq 0.05$, Clarke's Global R statistic), R values were examined for each pair-wise comparison.

RESULTS

Accessory photopigment analyses. Macro- and microscopic examination of the seagrass epiphytes at the time of sampling revealed that diatoms and coralline red algae [*Melobesia membranacea* (Esper) J. V. Lamour. and *Hydrolithon farinosum* (J. V. Lamour.) Penrose et Y. M. Chamb.] were the most commonly observed epiphyte components. Larger encrustations of coralline algae were observed in February 2005 than in August 2004. Filamentous red algae (*Polysiphonia binneyi* Harv. and *Ceramium brevizonatum* var. *caraibicum* H. E. Petersen et Børgesen), cyanobacteria (*Lyngbya* sp.), and green algae (*Ulvella lens* P. Crouan et H. Crouan) were also observed in some of the fertilized plots, particularly in February 2005. Brown algae were not observed. Consequently, we interpreted fucoxanthin to represent diatoms, zeaxanthin to represent a red algal/cyanobacterial complex, and chl *b* to represent green algae.

Fucoxanthin responded to spatial, temporal, and nutrient factors and their interactions (Fig. 1). A significant $S \times T \times P$ interaction ($P \leq 0.05$, Table 1) resulted from the lack of a fucoxanthin response to P in August 2004 at site 2, but P additions reduced the relative abundance of fucoxanthin for all other time and site combinations (Fig. 1). The directions of the changes in fucoxanthin relative abundances resulting from S and T effects were mixed. A significant $P \times N$ interaction ($P \leq 0.05$, Table 1) indicated that the effects of P additions on fucoxanthin relative abundances were consistently negative, but the additions of N

diminished the negative effects of P addition ($P \leq 0.05$, Tukey's multiple comparison test) (Figs. 1 and 2). A significant T × P interaction ($P \leq 0.05$, Table 1) indicated that the effects of P additions on

fucoxanthin relative abundance were consistently negative during both time periods, but the reduction was greater during February 2005 (Fig. 1). With the exception of the lack of P effect in August 2004

FIG. 1. (a–f) Responses of relative molar abundances of epiphytic pigments to site (S, $n = 48$), time (T, $n = 48$), nitrogen (N, $n = 48$), and phosphorus (P, $n = 48$) additions. φ indicates that pigment was not detected. Significant sources of variation at experiment-wise Type I error rate of $P < 0.05$ and comparison-wise Type I error rate of $P < 0.017$ are listed.
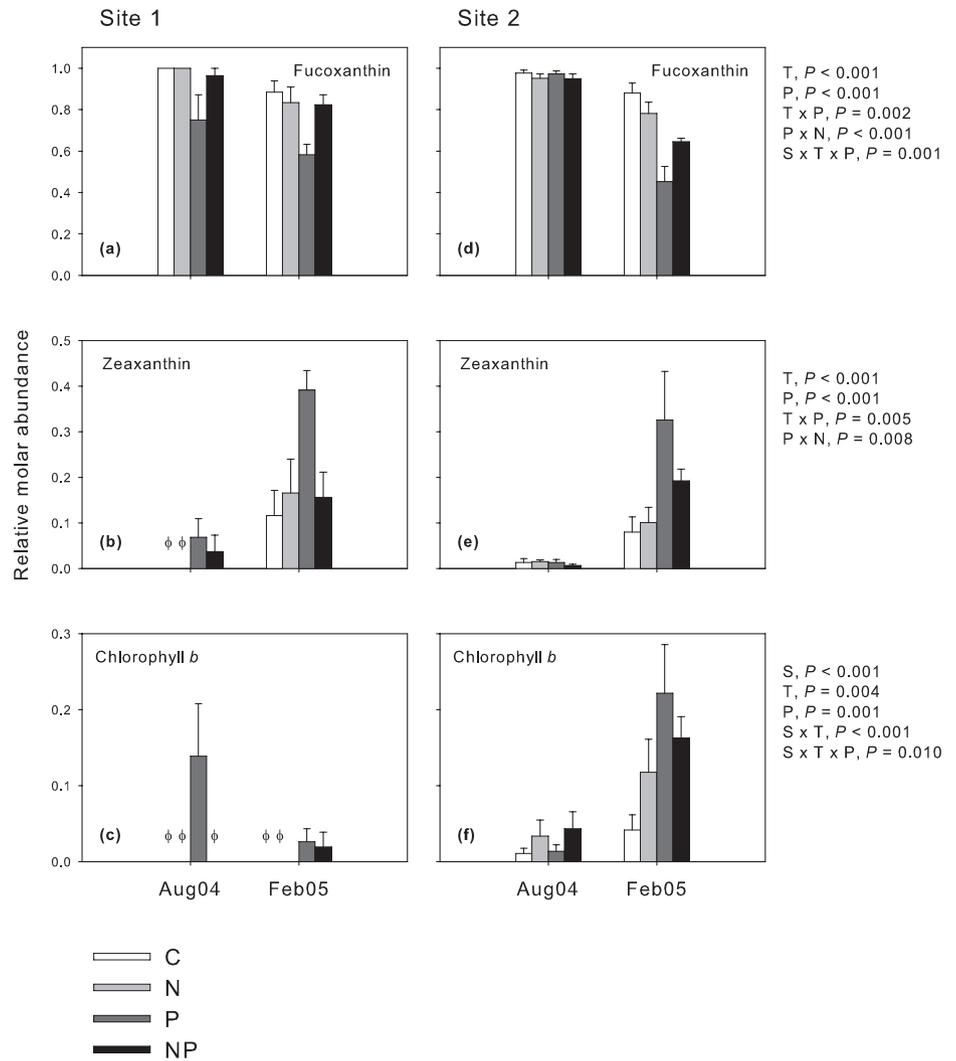
TABLE 1. Results of univariate four-way analysis of variance [site (S) × time (T) × nitrogen (N) × phosphorus (P)] of effects of S, T, N, and P on the relative abundances of fucoxanthin, zeaxanthin, and chl b ($n = 24$, all factors).

Source	Epiphyte pigment relative abundance		
	Fucoxanthin	Zeaxanthin	Chl b
S	–	–	9.5
T	31.8	32.6	5.4
P	13.5	8.5	8.0
S × T	–	–	12.7
T × P	4.2	4.4	–
P × N	6.1	4.0	–
S × T × P	2.6	–	4.2

Entries in table indicate the relative amount of variation (r^2, percent) accounted for by each effect, by those sources significant at an experiment-wise error rate of $P \leq 0.05$ and comparison-wise error rate of $P \leq 0.017$. Only significant main factors and interactions are listed.

FIG. 2. Comparison of nutrient treatments based on Tukey's multiple comparison tests using relative molar abundances of epiphytic pigments. Continuous horizontal lines denote nonsignificant differences in pigment relative abundance.

at site 2, the negative P effects in the higher-order interactions (Table 1) support the significant main effect of P addition on fucoxanthin relative abundances.

Zeaxanthin also responded to spatial, temporal, and nutrient factors and their interactions (Fig. 1). A significant P × N interaction ($P \leq 0.05$, Table 1) indicated that the effects of P additions on zeaxanthin relative abundances were consistently positive, but the additions of N diminished the positive effect of P additions ($P \leq 0.05$, Tukey's multiple comparison test) (Figs. 1 and 2). A significant T × P interaction ($P \leq 0.05$, Table 1, Fig. 1) indicated that both T and P had consistent effects on zeaxanthin relative abundances that supported the significant main effects of both P and T ($P \leq 0.05$, Table 1). P additions increased xeaxanthin relative abundances at both sampling times, while xeaxanthin relative abundances were greater in February 2005 than in August 2004 (Fig. 1).

Chl b responded to spatial, temporal, and P treatment factors and their interactions (Table 1, Fig. 1). Nitrogen additions did not affect chl b relative abundances. A significant S × T × P interaction ($P \leq 0.05$, Table 1) indicated that the effects of P additions on chl b relative abundances were consistently positive across all site and time combinations. Site and time effects modulated the positive effects of P but were not consistent in direction. A significant S × T interaction ($P \leq 0.05$, Table 1) indicated that the effect of site was entirely dependent on sampling time, and vice versa. The consistently positive P effects in the higher-order interactions (Table 1) support the significant main effect of P addition on chl b relative abundances. At site 1, chl b was absent from all the C and N plots at both times and was only present in P and NP plots (Fig. 1).

Diatom analyses. A total of 181 species representing 46 genera were observed in the diatom floras. Different diatom floras were observed at each site during each sampling time (Table 2). Four or fewer species constituted the majority (>50%) of the cell counts in control plots at each site during each sampling time (Table 2, Fig. S1 in the supplementary material). In August 2004 at site 1, the most P-limited site (Armitage et al. 2005), *Nitzschia liebetruthii, Mastogloia punctifera, Brachysira aponina,* and *Cocconeis placentula* var. *euglypta* were the most abundant diatoms (see Table 2 for taxonomic authors). In February 2005 at site 1, diatom abundance was dominated by *C. placentula* var. *euglypta* and *B. aponina.* At site 2, the most abundant species were different between the summer and winter sampling times. During August 2004, the large erect diatoms *Hyalosynedra laevigata* and *Riemerothrix floridensis* were most abundant, while in February 2005, the most abundant species were the much smaller species *C. placentula* var. *euglypta, Navicula* cf. *salinicola,* and *Mastogloia crucicula* (Table 2).

As indicated by distinct site and time clusters of sampling points, the NMS ordination of relative species abundances from all samples revealed spatial and temporal patterns in epiphytic diatom community structure (Fig. 3), which agree with the description of distinct epiphytic diatom floras in Florida Bay that are dependent on location within the bay and season (Frankovich et al. 2006). The stress value of 0.07 indicated that the spatial patterns depicted in the NMS two-dimensional configuration are representative of the overall structure of the diatom assemblages. The presence of distinct site and time clusters in the NMS ordination also indicates that any nutrient addition effects on diatom community structure were site and time specific. Differences in diatom community structure resulting from nutrient addition effects were much smaller than differences resulting from spatial and temporal effects. Figure 3 best illustrates the larger, overall structure of the samples formed by spatiotemporal variation. Smaller ''local'' variations possibly produced by nutrient effects are more accurately

TABLE 2. Species constituting majority (>50%) of cell counts from control plots ($n = 3$) for each site and time.

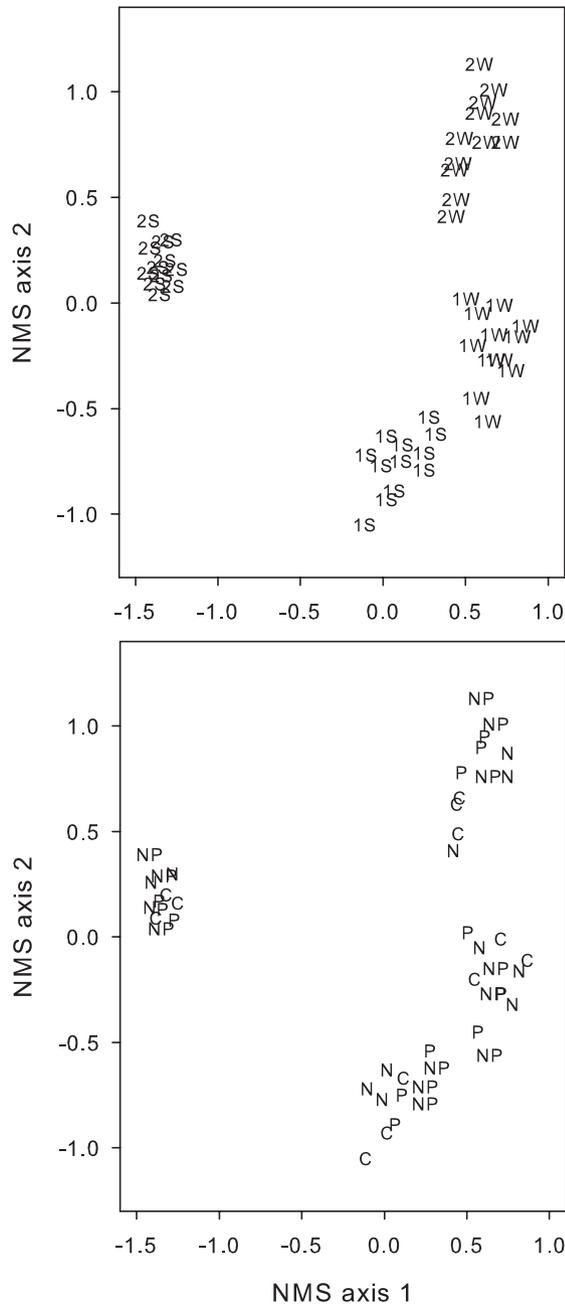| Site and time	Species	Relative abundance (%)
Site 1 August 2004 Total spp. = 74	*Nitzschia liebetruthii* Rabenh. *Mastogloia punctifera* Brun *Brachysira aponina* Kütz. *Cocconeis placentula* var. *euglypta* (Ehrenb.) Cleve Total	17.3 13.7 12.9 7.1 51.0
Site 1 February 2005 Total spp. = 58	*Cocconeis placentula* var. *euglypta* (Ehrenb.) Cleve *Brachysira aponina* Kütz. Total	43.4 9.7 53.1
Site 2 August 2004 Total spp. = 53	*Hyalosynedra laevigata* (Grunow) D. M. Williams et Round *Reimerothrix floridensis* A. K. S. Prasad Total	44.3 20.9 65.2
Site 2 February 2005 Total spp. = 55	*Cocconeis placentula* var. *euglypta* (Ehrenb.) Cleve *Navicula* cf. *salinicola* Hustedt *Mastogloia crucicula* Grunow Total	33.9 15.1 6.6 55.6

FIG. 3. Ordination scores in two dimensions generated by nonmetric multidimensional scaling (NMS) using the Bray-Curtis similarity metric of diatom species relative abundances. (a) Scores are coded by site numbers (1 and 2; $n = 24$) and sampling time (S = summer, August 2004; W = winter February 2005; $n = 24$). (b) Scores are coded to indicate control (C), nitrogen (N), phosphorus (P), and nitrogen + phosphorus (NP) plots.

TABLE 3. Results of univariate four-way analysis of variance [S (site) × T (time) × N (nitrogen) × P (phosphorus)] of effects of site ($n = 24$), time ($n = 24$), nitrogen ($n = 24$), and phosphorus ($n = 24$) additions on species richness and Shannon diversity.

	Measure	
Effect	Species richness	Shannon diversity
S	20.0	34.8
T	31.3	6.2
S × T	–	25.1
S × T × N	5.2	–

Entries in table indicate the relative amount of variation (r^2, percent) accounted for by each effect, by those sources significant at an experiment-wise error rate of $P \le 0.05$ and comparison-wise error rate of $P \le 0.025$. Only significant main factors and interactions are listed.

displayed by NMS ordination repeated within each distinct cluster (Clarke and Warwick 2001).

Diatom species richness responded to spatial, temporal, and N treatment factors and their interactions (Table 3, Fig. 4). A significant S × T × N interaction ($P \le 0.05$, Table 3) indicated that time effects on species richness were consistent across all site and N treatment combinations, and that N and site affected the magnitude of the temporal differences, but the effects were mixed in direction (Fig. 4). The consistent T effects in the S × T × N interaction (Table 3) support the significant main effect of time ($P \le 0.05$, Table 3) on species richness. Diatom species richness was greater in August 2004 compared to February 2005.

Shannon diversity responded only to spatial and temporal factors (Table 3). A significant S × T interaction ($P \le 0.05$, Table 3) indicated that site 1 exhibited higher Shannon diversities compared to site 2 at both sampling times (Fig. 4). The direction of the time effects was site dependent (Fig. 4). The consistent site effects in the S × T interaction supported the main effect of site ($P \le 0.05$, Table 3).

One-way analyses of similarity (ANOSIM, Primer v6), performed for each site and time combination, identified changes in diatom community structure resulting from the nutrient treatments (C, N, P, N + P) (Table 4). At site 1 in August 2004, diatom assemblages of the P addition treatments (P and NP) were both significantly different from controls, while the N treatment was not (ANOSIM, $P \le 0.05$). At site 2 in August 2004, only the P treatment was significantly different from control (ANOSIM, $P \le 0.05$). Nutrient addition effects on diatom community structure were not evident at either site in February 2005 (ANOSIM, $P > 0.05$). The P effects at site 1 in August 2004 on diatom community structure and identified by ANOSIM are illustrated as a separation of the P and NP treatments from the C treatments in the low-stress NMS ordinations (defined as stress ≤ 0.10, Clarke 1993) (Fig. 5). At site 2 in August 2004, the low-stress NMS ordination illustrates the difference in community structure between P treatments and controls (Fig. 5).

DISCUSSION

Spatial and temporal factors were most important in structuring the seagrass epiphyte communities
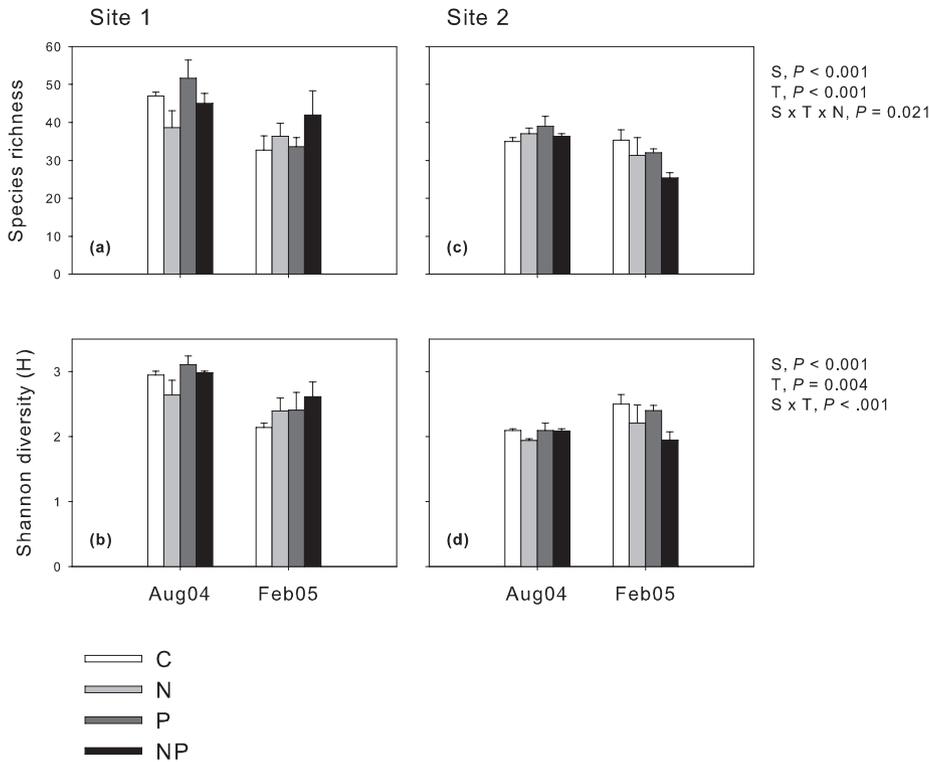
Fig. 4. (a–d) Responses of diatom species richness and Shannon diversity to site (S, $n = 24$), time (T, $n = 24$), nitrogen (N, $n = 24$), and phosphorus (P, $n = 24$) additions. Significant sources of variation at experiment-wise Type I error rate of $P < 0.05$ and comparison-wise Type I error rate of $P < 0.025$ are listed.

TABLE 4. Results of one-way analysis of similarity (ANOSIM) using Bray-Curtis dissimilarities of species composition identifying differences between nutrient treatments (C, N, P, NP).

Overall differences between nutrient treatment groups		Global R	P
Site 1 August 2004*		0.336	0.04
Site 1 February 2005		−0.127	0.79
Site 2 August 2004*		0.306	0.02
Site 2 February 2005		0.151	0.16
Pair-wise tests	Groups	R	P
Site 1 August 2004	C, NP**	0.593	0.10
	C, P**	0.444	0.10
	C, N	0.037	0.60
	NP, N**	0.778	0.10
	NP, P	−0.111	0.70
	N, P	0.333	0.20
Site 2 August 2004	C, NP	0.370	0.20
	C, P**	0.48	0.10
	C, N	−0.111	0.60
	NP, N	0.296	0.20
	NP, P**	0.593	0.10
	N, P	0.333	0.20

Significant effects at *$P \leq 0.05$ and **$P \leq 0.10$.

P indicates statistical significance of Clarke's Global R statistic. C, control; N, nitrogen; P, phosphorus; NP, nitrogen + phosphorus.

studied in Florida Bay. Nutrient effects were generally smaller, mostly site and time specific, and mainly due to P additions. The pattern of greater relative abundances of diatoms (fucoxanthin) and decreased relative abundances of red and cyanobacteria (zeaxanthin) and green algae (chl *b*) during summer (August 2004) compared to winter (February 2005) is consistent with macro- and microscopic epiphyte observations of the present study and also with descriptions of the seasonality of macroalgae (Armitage et al. 2005) and seagrass epiphytes (Frankovich and Zieman 1994) in Florida Bay. The factors responsible for the observed seasonality of the epiphyte communities are not known. The observed epiphytic diatom community structure and the changes within due to temporal and spatial variation are similar to previous descriptions of the Florida Bay flora (DeFelice and Lynts 1978, Prasad et al. 2001, Huvane 2002, Lewis et al. 2004, Frankovich et al. 2006). DeFelice and Lynts (1978) first described the epiphyte assemblages in eastern Florida Bay. Their one-time sampling (May 1974) revealed an epiphyte community dominated by *C. placentula*, which was also abundant at site 1 of the present study. The diatom assemblage at site 1 of the present study was also characterized by *N. liebetruthii* and *B. aponina* and conforms to the eastern Florida Bay assemblage (Lewis et al. 2004, Frankovich et al. 2006). Site 2 was characterized by the dominance of *H. laevigata* and *R. floridensis* and conforms to the western Florida Bay assemblage (Prasad et al. 2001, Frankovich et al. 2006). The temporal variation observed in the present study is also consistent with the pattern described previously (Frankovich et al. 2006). *H. laevigata* and *R. floridensis*, which were dominant at site 2 during the summer sampling, were identified as summer indicator species, while the increased relative abundances of *C. placentula* var. *euglypta* at both sites and *N.* cf.
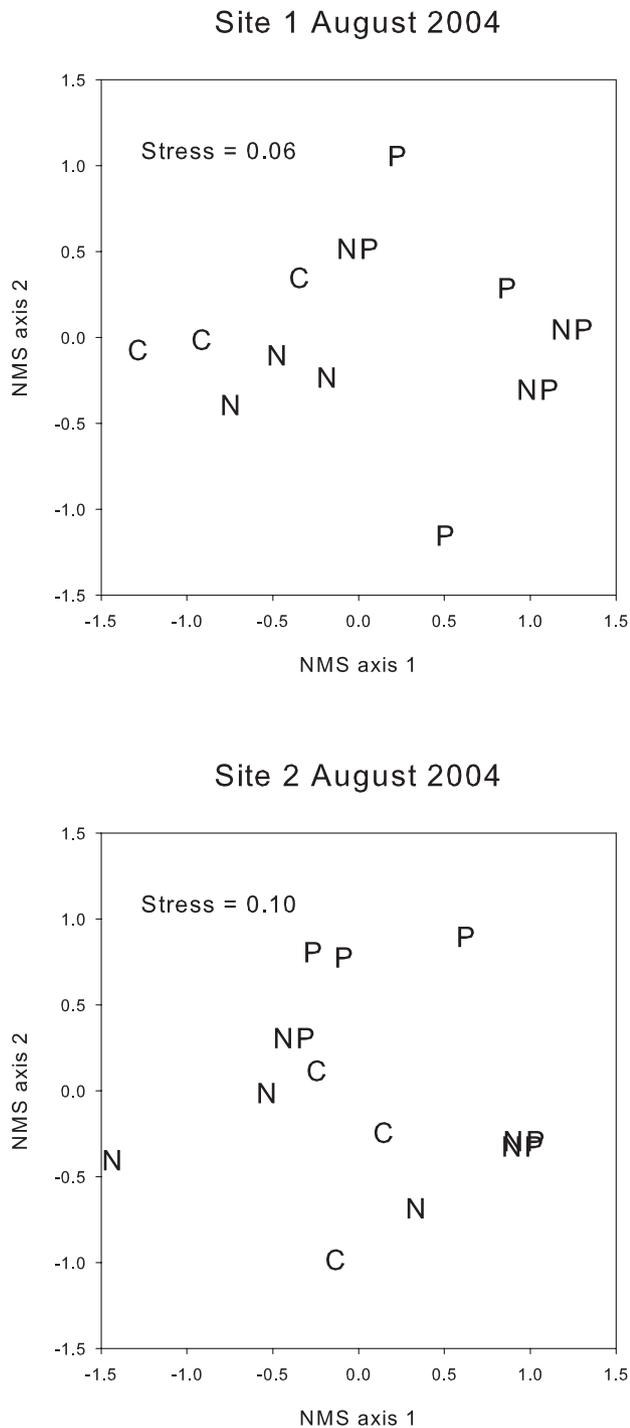
Site 1 August 2004

Site 2 August 2004

FIG. 5. Ordination scores in two dimensions generated by nonmetric multidimensional scaling (NMS) using the Bray-Curtis similarity metric of diatom species relative abundances. Scores are coded to indicate control (C), nitrogen (N), phosphorus (P), and nitrogen + phosphorus (NP) plots ($n = 3$, all treatments). Nutrient addition effects on diatom community structure were only evident in August 2004 (analysis of similarity [ANOSIM], $P > 0.05$).

salinicola at site 2 during winter are consistent with the identification of these taxa as winter indicator species (Frankovich et al. 2006). Three previously

described spatial assemblages in Florida Bay were aligned along an estuarine salinity and nutrient availability gradient (Frankovich et al. 2006), suggesting that salinity, salinity variability, or nutrients might be responsible for structuring these communities. Salinities were polyhaline and differed little during the present study. Bottom salinities at sites 1 and 2 measured during the August sampling were 39.5 ppt and 39.0 ppt, respectively. During February 2005, these were 38.4 ppt and 33.4 ppt, respectively. Despite the greater spatial difference in observed salinities during February 2005, diatom assemblages from both sites were more similar to one another during that period than during August 2004 when the observed salinities at both sites were approximately equal. The small differences in observed salinities (all salinities polyhaline) do not appear to be influencing diatom community structure. Snoeijs (1999) suggested that diatoms might be selected more according to their ability to flourish in variable salinity environments than to their observed salinity optimum. In her review of brackish-water diatoms, Snoeijs (1999, p. 306) concluded that salinity is the ''overruling environmental factor'' structuring estuarine communities; however, realized abundances in different brackish waters may be limited by other environmental constraints (e.g., nutrients). Salinities in Florida Bay vary from hyposaline to hypersaline depending on the amount of rainfall (Nuttle et al. 2000) with variability increasing from the Gulf of Mexico to northeast Florida Bay (Frankovich and Fourqurean 1997). Monthly measurements of bottom salinity from 1991 to 2006 (http://serc.fiu.edu/wqmnetwork/SFWMD-CD/Pages/DataDL.htm) indicate a lower mean salinity and greater variability at site 1 (mean = 29.2 ppt, coefficient of variation = 24.5%) than at site 2 (mean = 35.1 ppt, coefficient of variation = 10.0%), but the importance of salinity and salinity variability can only be determined with controlled salinity experiments.

The epiphyte responses to nutrient additions, particularly P, were most evident as changes in algal composition at the division level. As reported in Armitage et al. (2005), changes in epiphyte chl *a* concentrations resulting from nutrient additions were not evident. This finding suggests that changes in chl *a* concentrations, which are often used as proxies for epiphyte biomass, are not as sensitive as epiphyte response variables as changes in the relative abundances of accessory photopigments. This is likely due to the diverse nature of algal epiphyte communities and their associated photopigments (Harlin 1980). In response to P addition, the relative abundance of zeaxanthin (red and blue-green algae) and chl *b* (green algae) increased. Fucoxanthin (mainly diatoms), though still the most abundant accessory photopigment, decreased in relative abundance in response to P addition. Similarly, Wear et al. (1999) reported that diatoms were the most abundant seagrass epiphytes under both

control and nutrient-enriched conditions, but red and brown algae increased greatly in their enriched plots. The changes in photopigment abundances of this study are consistent with nutrient-induced shifts from diatom production to production by cyanobacteria (Pinckney et al. 1995, Armitage and Fong 2004), red algae (Wear et al. 1999), and green algae (Valiela et al. 1997, Lotze et al. 2000) observed in previous studies, though diatoms may still be most abundant under enriched conditions (Sundbäck and Snoeijs 1991, Coleman and Burkholder 1994). The response of photopigment relative abundances to P addition and the limited response to N additions confirm P limitation of seagrass epiphytes in Florida Bay (Frankovich and Fourqurean 1997, Armitage et al. 2006). With the exception of site 2 in August 2004, the observed division-level shifts in algal relative abundances were greatest in those plots of the present study that had received only P additions ($P < 0.05$, Tukey's multiple comparison test) (Figs. 1 and 2). Those plots receiving both N and P additions also shifted relative algal abundance from diatoms to a red algal and cyanobacterial complex, though those changes were not as great as those observed in plots receiving only P ($P < 0.05$, Tukey's multiple comparison test) (Figs. 1 and 2).

Similar to the epiphyte photopigments, epiphytic diatom communities were structured mainly by spatial and temporal factors unrelated to nutrient additions. Diatom species richness and Shannon diversity responded mostly to site and time factors with only one significant nutrient three-way interaction ($S \times T \times N$) for species richness that explained only 5% of the variation in species richness (Table 3). The diatom floras were site and time specific and remained that way despite nutrient enrichment. Nutrient enrichment, particularly P addition, changed diatom community structures during August 2004, but the diatom floras subject to nutrient enrichment remained more similar to those not receiving nutrient additions within the same site and sampling time than to all other diatom assemblages (enriched and nonenriched) from other sites and times. The changes in epiphytic diatom community structure resulting from P addition were only observed in August 2004 (Table 4).

Changes in community structure resulting from nutrient enrichment are expected to be greatest when and where competition for the limiting nutrient is greatest (Tilman 1977). Significant changes in diatom community structure relative to controls were observed in both P and NP treatments at site 1 in eastern Florida Bay, while at site 2 in western Florida Bay, significant changes relative to controls were limited to only the P treatments. The observed spatial pattern in the P responses of the epiphytic diatoms is consistent with the spatial variation of P limitation in Florida Bay (Fourqurean and Zieman 2002). P availability decreases from western Florida Bay to eastern Florida Bay (Fourqurean and Zieman 2002). Western Florida Bay receives P inputs from the Gulf of Mexico (Fourqurean et al. 1992), while extensive shallow carbonate mudbanks in western and central parts of the bay and the nearly continuous barrier of the upper Florida Keys restrict circulation in eastern Florida Bay waters. The calcium carbonate sediments and bedrock underlying a shallow water column in Florida Bay bind P and reduce its availability to primary producers (Fourqurean et al. 1992). These conditions set up large gradients in primary productivity and nutrient availability in Florida Bay with greater levels in the western bay decreasing to lower levels in the very P-limited eastern bay (Fourqurean et al. 1992, Fourqurean and Zieman 2002). If the community structure within the diatom communities responds to the relative availability of N and P, high levels of P limitation would be evidenced by a response to both P and NP treatments. Lower levels of P limitation, especially levels approaching nutrient-replete conditions, may only permit a response to P-only treatments. The P added when P limitation is low may be more than enough to satisfy the P demand, establishing N-limiting conditions. When N is added in addition to P (i.e., NP treatments) under low ambient levels of P limitation, the relative availability of N and P approaches control conditions.

The limitation of the epiphytic diatom responses to P addition at the August 2004 sampling time may be consistent with greater P limitation during the summer seasons when primary productivity and the demand for nutrients are greater (Fourqurean et al. 2001), but contrasts with greater photopigment (fucoxanthin and zeaxanthin) responses to P additions during February 2005. Therefore, competition for nutrients cannot explain the seasonality of the P effects.

The results of the field nutrient manipulations suggest that P additions increased the relative abundance of the red algae–cyanobacterial complex and green algae and decreased that of diatoms, but within the diatom communities, responses to P additions, though evident, were not as strong. Nutrient availability may be less important in structuring estuarine diatom communities than other spatial and temporal factors. Strong nutrient responses have been evident in freshwater habitats (Stoermer et al. 1978, Pan and Lowe 1994, Manoylov and Stevenson 2006), but in marine habitats, the overwhelming influence of salinity variability may mute the response to nutrient availability (Snoeijs 1999). The conclusions of this study are in agreement with statements made by Snoeijs (1999). In her review of brackish water diatoms, she states, ''Different algal species have different nutrient requirements, but often species belonging to the same taxonomic group have similar requirements. Eutrophication effects on the composition of microalgal communities are therefore often clearly reflected on the Class

or Division levels. The most typical compositional change following eutrophication is usually a decrease in the relative importance of diatoms ...'' (Snoeijs 1999, p. 312). The observed changes in epiphyte communities resulting from nutrient addition are consistent with patterns of P limitation in Florida Bay, but the nutrient-induced changes in epiphyte community structure were small relative to spatial and temporal variation of the epiphyte communities, suggesting that testing of other factors (e.g., salinity variability, grazing) will be needed to further understand epiphyte distribution.

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Supplementary Material

The following supplementary material is available for this article:

Figure S1. Species constituting majority of cell counts from control plots at each site during each sampling time (species listed in Table 2). Scale bars = 10 μm. (a) *Reimerothrix floridensis*; (b) *Mastogloia punctifera*; (c) *M. punctifera*, focus on partectae; (d) *Hyalosynedra laevigata*; (e) *Mastogloia crucicula*; (f) *M. crucicula*, focus on partectae; (g) *Navicula* cf. *salinicola*; (h) *Brachysira aponina*; (i) *Cocconeis placentula* var. *euglypta*; (j) *Nitzschia liebetruthii*.

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