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Nutrient impacts on epifaunal density and species composition in a subtropical seagrass bed

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Abstract

The capacity of epifauna to control algal proliferation following nutrient input depends on responses of both grazers and upper trophic level consumers to enrichment. We examined the responses of *Thalassia testudinum* (turtle grass) epifaunal assemblages to nutrient enrichment at two sites in Florida Bay with varying levels of phosphorus limitation. We compared epifaunal density, biomass, and species diversity in 2 m^2 plots that had either ambient nutrient concentrations or had been enriched with nitrogen and phosphorus for 6 months. At the severely P-limited site, total epifaunal density and biomass were two times higher in enriched than in unenriched plots. Caridean shrimp, grazing isopods, and gammarid amphipods accounted for much of the increase in density; brachyuran crabs, primary predatory fish, and detritivorous sea cucumbers accounted for most of the increase in biomass. At the less P-limited site, total epifaunal density and biomass were not affected by nutrient addition, although there were more caridean shrimp and higher brachyuran crab and pink shrimp biomass in enriched plots. At both sites, some variation in epifaunal density and biomass was explained by features of the macrophyte canopy, such as *T. testudinum* and *Halodule wrightii* percent cover, suggesting that enrichment may change the refuge value of the macrophyte canopy for epifauna. Additional variation in epifaunal density and biomass was explained by epiphyte pigment concentrations, suggesting that enrichment may change the microalgal food resources that support grazing epifauna. Increased epifaunal density in enriched plots suggests that grazers may be able to control epiphytic algal proliferation following moderate nutrient input to Florida Bay.

Introduction

Alterations of communities through bottom-up processes such as nutrient enrichment can produce complex direct and indirect impacts on entire communities, including primary producers and associated fauna (Hunter & Price, 1992; Dyer & Stireman, 2003; Valiela et al., 2004). Increased input of limiting nutrients can shift primary producer composition, causing blooms of opportunistic, weedy species (Duarte, 1995; Smith et al., 1999; Hauxwell et al., 2001; Cardoso et al., 2004), which can directly alter food supply and trophic support for consumers. Potential outcomes include increases in food availability (Nixon & Buckley, 2002) or quality (Hemmi & Jormalainen, 2002) or, conversely, shifts towards less palatable, lower nutritive value, or toxic species (Leibold, 1999; Armitage & Fong, 2004).

Nutrient enrichment is also associated with changes in the physical structure of the habitat in both terrestrial and marine systems (Ostertag & Verville, 2002; McManus & Polsenberg, 2004). Alterations of primary producer species composition can indirectly impact associated faunal communities by changing primary producer structural complexity (Tolan et al., 1997). Replacement of slower-growing species with fast-growing, opportunistic species can increase habitat complexity (Fourqurean et al., 1995; Cardoso et al., 2004). In other cases, nutrient-induced decreases in structural complexity can occur, as when phytoplankton blooms increase light attenuation and subsequently reduce submerged aquatic vegetation growth (Short et al., 1995).

Watershed development renders coastal communities vulnerable to nutrient (e.g., nitrogen (N) and phosphorus (P)) input from anthropogenic sources (Howarth, 1988; Nixon, 1995; Smith et al., 1999). Seagrass beds in particular have declined due in part to nutrient-induced increases in phytoplankton (Duarte, 1995; Short et al., 1995), macroalgae (Hauxwell et al., 2001), or epiphytes (Hughes et al., 2004) that increase light attenuation. Epifaunal grazers may mitigate the negative effects of nutrient enrichment on seagrasses by reducing epiphyte loads (Williams & Ruckelshaus, 1993; Hays, 2005), but upward cascading effects of enrichment on seagrass fauna are variable. Faunal density and biomass can increase with nutrient input (Bustamante et al., 1995; Wootton et al., 1996), but in other cases, minimal (Widbom & Elmgren, 1988; Posey et al., 2002) or negative (Deegan et al., 2002) impacts on upper trophic levels have been detected. The capacity of epifaunal assemblages to control algal proliferation following nutrient input depends on responses of both grazers and upper trophic level consumers to enrichment.

Florida Bay is a shallow, semi-enclosed system that may experience increased freshwater and nutrient input following Everglades restoration. The bay is largely phosphorus (P) limited, with stronger limitation within the seagrass community in the eastern, more enclosed region of the bay (Fourqurean & Zieman, 2002; Armitage et al., 2005). This natural spatial gradient of P limitation provides an ideal habitat to experimentally examine the effects of nutrient input on epifaunal assemblages with varying levels of background limitation. Previous work in this system has demonstrated that nutrient addition causes a relative increase in epiphytic red algae, cyanobacteria, and green algae (Armitage et al., 2006), which may represent a shift in trophic support for an epiphyte-based food web. In addition, nutrient enrichment causes long-term changes in the structural features of the seagrass community, increasing *Halodule wrightii* Ascherson (shoalgrass) relative to *Thalassia testudinum* Banks *ex* König (turtle grass) (Fourqurean et al., 1995). *Halodule wrightii* leaves are also much thinner than *T. testudinum* leaves, suggesting that enrichment may alter the seagrass canopy structure. In this study, we hypothesized that epifauna density would increase in response to nutrient-induced changes in epiphyte composition and seagrass canopy structure, particularly in the severely P-limited area. We also predicted that epifaunal responses to nutrient addition would be strongest in grazers due to changes in epiphytic microalgal food resources.

Methods

To determine the effects of nutrient enrichment on faunal community structure, we established two study sites in Florida Bay with differing levels of nutrient limitation (see Armitage et al., (2006) for map of study area). The eastern site, Duck Key (25° 10.59′ N, 80° 29.39′ W), is in an area of severe phosphorus limitation and is characterized by sparse, short *Thalassia testudinum* and some calcareous green macroalgae (esp. *Penicillus capitatus* Lamarck and *P. lamourouxii* Decaisne) (Armitage et al., 2005). The western site at Nine Mile Bank (24° 56.21′ N, 80° 51.65′ W) experiences less nutrient limitation and is characterized by dense, tall *T. testudinum* and patchy calcareous green macroalgae (esp. *Halimeda incrassata* (J. Ellis) J.V. Lamouroux and *Halimeda monile* (J. Ellis & Solander) J.V. Lamouroux).

In April 2004, 12 2 m^2 quadrats were established in a grid at each site, with two meters between plots. The grids were located 25 m east of a plot array from separate ongoing study in the region (Armitage et al., 2005). Study plots were demarcated with steel stakes at each corner. Two treatments (control [C] and nutrient addition [nitrogen (N) + phosphorus (P)]) were randomly assigned to the study plots ($n = 6$ per site). The plots were fertilized bimonthly for 6 months with N in the form of slow release nitrogen fertilizer

(Polyon™, Pursell Technologies Inc., 38-0-0) and P as granular phosphate rock (Multifos™, IMC Global, $Ca_3(PO_4)_2$, 18% P) at loading rates of 1.43 g N m^{-2} day^{-1} and 0.18 g P m^{-2} day^{-1} based on maximum potential loading rates and previous studies in the region (Ferdie & Fourqurean, 2004; Armitage et al., 2005). The fertilizer was sprinkled evenly on the plot and gently worked onto the sediment by hand.

In October 2004, we characterized the primary producer assemblages in each plot. We estimated the percent cover of each seagrass (*T. testudinum*, *Syringodium filiforme* Kützing [manatee grass], and *Halodule wrightii*) and macroalgal species in each plot using a modified Braun-Blanquet abundance scale: 0 = absent; 0.1 = one individual, <5% cover; 0.5 = few individuals, <5% cover; 1 = many individuals, <5% cover; 2 = 5–25% cover; 3 = 25–50% cover; 4 = 50–75% cover; 5 = 75–100% cover (Fourqurean et al., 2002).

The seagrass epiphyte community was described using high performance liquid chromatography (HPLC). One seagrass shoot was collected from each plot and epiphytes were removed by gently scraping with a razor blade. Epiphytes were freeze dried and weighed to determine total epiphyte load, including adhered sediments. Pigments were extracted with 90% acetone for at least 12 hours at −20 °C. Extracts were injected into a Hewlett Packard 1090 HPLC, and solvents and flow rates followed Pinckney et al. (1999). Pigments were identified based on retention times and comparisons with pure standards obtained from DHI Water & Environment (Denmark). The concentrations of characteristic pigments were determined: fucoxanthin (diatoms), zeaxanthin (cyanobacteria and red algae), and chlorophyll *b* (green algae).

To assess faunal responses to nutrient treatments in October 2004, a 1 m^2 throw trap with solid sides and a 2 mm mesh removable top was placed over each plot by a single snorkeler to minimize faunal disturbance. Sweep nets (2 mm mesh) were then pulled through the trap three times to collect all epifauna. This method primarily captures slow moving, benthic organisms. Two snorkelers performed all sweeps to standardize collection effort. Samples were frozen (−20 °C) until further analysis. In the laboratory, fauna were separated from plant and sediment debris, identified to the lowest practical identification level (most often to species), enumerated, and dried to determine dry weights. Gastropods and bivalves were dissected prior to drying in order to obtain body and shell weights separately. All other organisms were dried and weighed intact. We calculated the Shannon-Wiener species diversity index (H′), which is sensitive to changes in rare species, where $H' = -\sum(p_i)(\ln p_i)$ and p_i was the proportion of the faunal community belonging to the *i*th species (Krebs, 1994). Species evenness E (the equitability of abundance among species) was calculated for each treatment, where $E = H'/H'_{max}$. The maximum species diversity is given by $H'_{max} = \ln(S)$, where S was species richness (the total number of species observed) (Krebs, 1994).

The effects of nutrient enrichment were determined separately for all habitat (macrophyte and epiphyte) characteristics and all epifaunal characteristics with MANOVA and Bonferroni-Dunn post-hoc tests within each site. We used backward stepwise regressions to evaluate relationships between each of the epifaunal parameters (total density, total biomass, diversity, species richness, and species evenness) and the characteristics of the epiphyte and macrophyte communities within each site. Prior to regression analyses, we calculated the tolerance values of each pair of variables to confirm that collinear conditions did not exist. Regression models used a Type III sums of squares. We plotted predicted values from the results of these stepwise regressions against observed values for each dependent variable to assess how well the regression models explained the observed patterns. We used analyses of similarity (ANOSIM) to test for enrichment effects on epifaunal community structure, as measured by the relative number of individuals in each species and the distribution of biomass among species at each site (Clarke, 1993). ANOSIM yields an R statistic, where a value > 0.75 indicates that communities are highly dissimilar and a value < 0.25 indicates that communities are indistinguishable from each other.

Results

Epiphyte resources and macrophyte structural characteristics differed more between enriched and

Table 1. Mean values ± standard error of epiphyte resources and macrophyte structural characteristics to nutrient (N and P) enrichment at (a) Duck Key and (b) Nine Mile Bank

	Unenriched	Enriched
(a) *Duck Key*		
Epiphyte chlorophyll *b* (ng cm^{-2} leaf)	ND	53.4 ± 15.9
Epiphyte fucoxanthin (ng cm^{-2} leaf)	106.8 ± 29.4	72.8 ± 6.9
Epiphyte zeaxanthin (ng cm^{-2} leaf)	ND	7.4 ± 2.8
Total epiphyte load (mg cm^{-2} leaf)	6.6 ± 3.3	10.8 ± 4.2
Thalassia testudinum % cover	3.7 ± 0.2	4 ± 0.4
Halodule wrightii % cover	0.1 ± 0.1	1.4 ± 0.6
Calcareous green algae % cover	0.4 ± 0.2	0.8 ± 0.2
(b) *Nine Mile Bank*		
Epiphyte chlorophyll *b* (ng cm^{-2} leaf)	58.7 ± 13.1	53.4 ± 7.7
Epiphyte fucoxanthin (ng cm^{-2} leaf)	108.0 ± 29.2	60.5 ± 10.0
Epiphyte zeaxanthin (ng cm^{-2} leaf)	1.0 ± 0.6	2.1 ± 0.8
Total epiphyte load (mg cm^{-2} leaf)	5.5 ± 2.7	4.4 ± 2.1
Thalassia testudinum % cover	4.3 ± 0.3	4 ± 0.5
Halodule wrightii % cover	0	0
Calcareous green algae % cover	1.8 ± 0.5	1.9 ± 0.9

Percent cover is represented by Braun-Blanquet scores. ND = none detected.

unenriched plots at Duck (MANOVA, Hotelling T-Square = 68.96, $F = 5.747$, $p = 0.0372$) than at Nine Mile Bank (MANOVA, Hotelling T-Square = 26.10, $F = 3.132$, $p = 0.0985$). At Duck Key, there was higher epiphytic chlorophyll *b* (Bonferroni-Dun post-hoc test, $p = 0.0074$), zeaxanthin ($p = 0.0230$), and *H. wrightii* cover ($p = 0.0530$) in enriched plots (Table 1, panel a). At Nine Mile Bank, macrophyte and epiphyte characteristics were similar between nutrient treatments (Table 1, panel b).

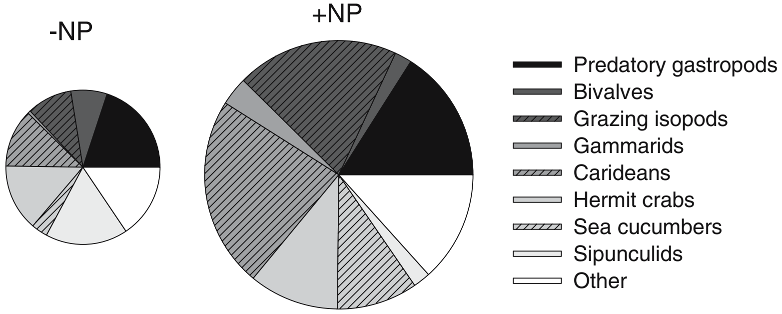
Epifaunal characteristics differed more between enriched and unenriched plots at Duck (MANOVA, Hotelling T-Square = 47.96, $F = 5.755$, $p = 0.0274$) than at Nine Mile Bank (MANOVA, Hotelling T-Square = 12.90, $F = 1.547$, $p = 0.3033$). At Duck Key, there was higher density (Bonferroni-Dun post-hoc test, $p = 0.0028$) and biomass ($p = 0.0092$) in enriched plots (Table 2, panel a; Figs. 1, 2). At Nine Mile Bank, epifaunal characteristics were similar between nutrient treatments (Table 2, panel b; Figs. 1, 2).

Backward stepwise regression produced a model that could explain 83% of the variation in total epifaunal density at Duck Key (Fig. 3a). Faunal density was positively related to total epiphyte load and *Haoldule wrightii* cover and negatively related to epiphytic fucoxanthin concentration (Table 3, panel a). Backward stepwise regression produced a model that could explain 54% of the variation in species evenness (Fig. 3b). Species evenness was negatively related to epiphytic chlorophyll *b*; no significant increase in the model fit was obtained by adding other independent variables. Variation in species richness, species diversity, and total

Table 2. Mean values ± standard error of epifaunal responses to nutrient (N and P) enrichment at (a) Duck Key and (b) Nine Mile Bank

	Unenriched	Enriched
(a) *Duck Key*		
Total # organisms $plot^{-1}$	107.2 ± 15.2	185.5 ± 12.8
Species diversity	3.6 ± 0.1	3.5 ± 0.2
Species richness	21.2 ± 2.0	26.2 ± 1.2
Species evenness	0.83 ± 0.01	0.74 ± 0.04
Total biomass (g m^{-2})	1.3 ± 0.2	2.8 ± 0.4
(b) *Nine Mile Bank*		
Total # organisms $plot^{-1}$	89.0 ± 12.4	212.7 ± 53.5
Species diversity	3.2 ± 0.2	2.9 ± 0.2
Species richness	23.5 ± 2.7	28.0 ± 1.0
Species evenness	0.72 ± 0.02	0.61 ± 0.05
Total biomass (g m^{-2})	9.1 ± 2.0	10.0 ± 2.9

(a) Duck Key



(b) Nine Mile Bank

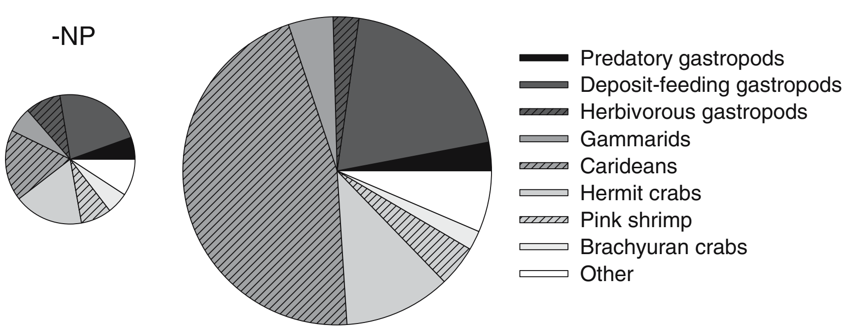
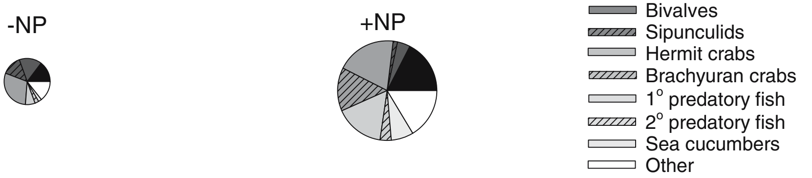


Figure 1. Proportion of total density in common epifaunal groups at (a) Duck Key and (b) Nine Mile Bank. Charts are scaled to represent the average total density per plot.

(a) Duck Key



(b) Nine Mile Bank

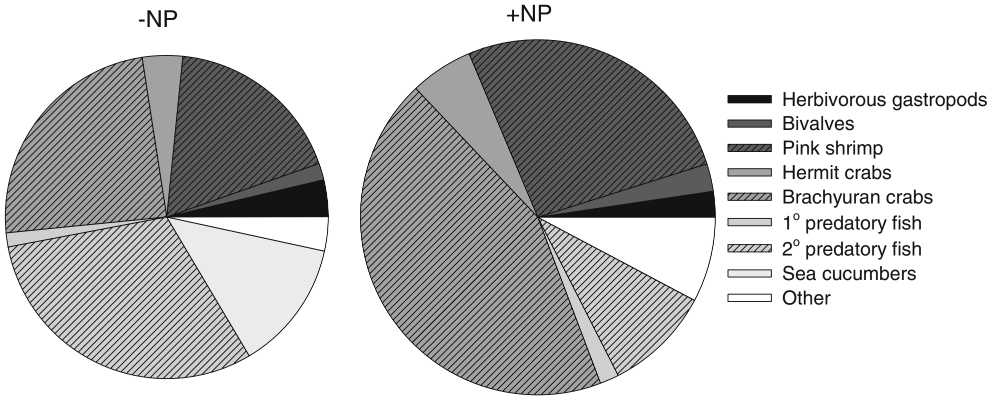


Figure 2. Proportion of total biomass in common epifaunal groups at (a) Duck Key and (b) Nine Mile Bank. Charts are scaled to represent the average total biomass per plot.

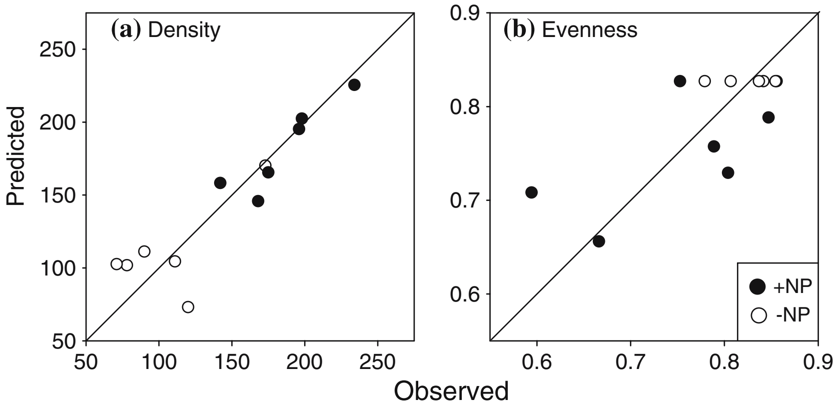


Figure 3. Predicted versus observed values for stepwise multiple linear regression models of (a) epifaunal density (# m^{-2}) as a function of total epiphyte load, epiphytic fucoxanthin concentration, and *Halodule wrightii* percent cover and (b) species evenness as a function of epiphytic chlorophyll *b* concentration at Duck Key.

epifaunal biomass were not explained using stepwise regression and the measured habitat variables.

At Nine Mile Bank, the measured habitat variables produced models generally explained small portions of the variability in epifaunal characteristics (Fig. 4). Backward stepwise regression produced a model that explained 34% of the variability in epifaunal density (Table 3, panel b). Epifaunal density was negatively related to *Thalassia testudinum* cover; no significant increase in the model fit

Table 3. Results from backward stepwise regressions of epifaunal characteristics on macrophyte and epiphyte features at (a) Duck Key and (b) Nine Mile Bank

	p	r^2	Variables entered	Coefficient
(a) *Duck Key*				
Total faunal density (# m^{-2})	0.0020	0.828	*Halodule wrightii* cover	25.643
			Epiphyte load	4.674
			Epiphytic fucoxanthin	−471.548
			Intercept	129.399
Species diversity	NS			
Species richness	NS			
Species evenness	0.0066	0.538	Epiphyte chlorophyll *b*	−1.547
			Intercept	0.827
Total biomass (g m^{-2})	NS			
(b) *Nine Mile Bank*				
Total faunal density (# m^{-2})	0.0471	0.339	*Thalassia testudinum* cover	−62.886
			Intercept	412.857
Species diversity	0.0070	0.668	*Thalassia testudinum* cover	0.291
			Epiphytic fucoxanthin	3.730
			Intercept	1.572
Species richness	NS			
Species evenness	0.0326	0.381	*Thalassia testudinum* cover	0.061
			Intercept	0.413
Total biomass (g m^{-2})	0.0496	0.333	Epiphytic zeaxanthin	2011.905
			Intercept	6.480

NS = regression not significant.

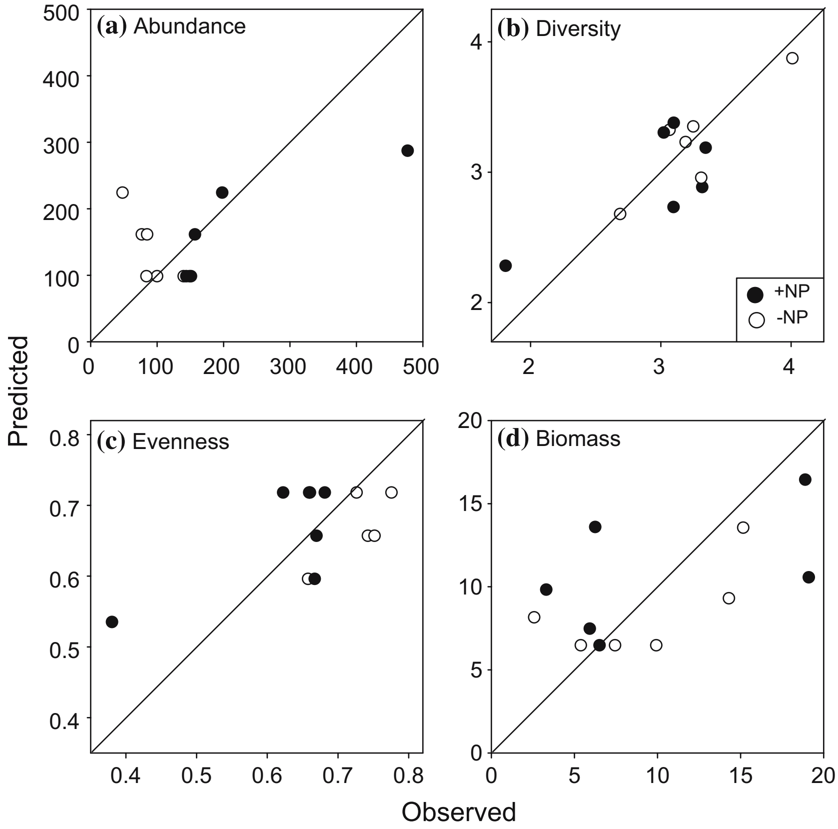


Figure 4. Predicted versus observed values of (a) epifaunal density (# m^{-2}) as a function of *Thalassia testudinum* percent cover, (b) species diversity as a function of *T. testudinum* cover and epiphytic fucoxanthin, (c) species evenness as a function of *T. testudinum* cover, and (d) total biomass (g m^{-2}) as a function of epiphytic zeaxanthin concentration at Nine Mile Bank.

was obtained by adding other independent variables. Backward stepwise regression produced a model that explained 67% of the variability in species diversity. Species diversity was positively related to *T. testudinum* cover and epiphytic fucoxanthin concentration. Backward stepwise regression produced a model that explained 38% of the variability in species evenness. Species evenness was positively related to *T. testudinum* cover; no significant increase in the model fit was obtained by adding other independent variables. Backward stepwise regression produced a model that explained 33% of the variability in epifaunal biomass. Epifaunal biomass was positively related to epiphytic zeaxanthin concentration; no significant increase in the model fit was obtained by adding other independent variables.

At Duck Key, communities were similar between enriched and unenriched treatments in terms of the relative number of individuals in each species and the distribution of biomass among species (ANOSIM, density R = 0.25, biomass R = 0.11). Qualitative comparisons of the densities of each species between enrichment treatments suggest that caridean shrimp (e.g., *Thor manningi* Chace), grazing isopod (e.g., *Erichsonella attenuata* Harger), gammarid amphipod, and sea cucumber (e.g., *Leptosynapta* sp.) densities were higher in enriched plots and sipunculid and bivalve (especially Family Veneridae) densities were higher in unenriched plots (Fig. 1, see electronic supplemental materials[1]). Qualitative comparisons of the biomass of each species between enrichment treatments suggest that brachyuran crabs (e.g., *Pitho*

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[1] Electronic supplementary material is available for this article at < http://dx.doi.org/ 10.1007/s10750-006-0147-4 > and accessible for authorised users.

quadridentata Miers, *Neopanope packardii* Kingsley), first-order predatory fish (fish that primarily consume grazers, e.g., *Hippocampus zosterae* Jordan & Gilbert) and sea cucumbers had higher biomass in enriched plots and sipunculids and bivalves had higher biomass in unenriched plots (Fig. 2).

At Nine Mile Bank, community structure was similar between enriched and unenriched treatments in terms of the relative number of individuals in each species and the distribution of biomass among species (ANOSIM, density $R = 0.05$, biomass $R = -0.07$). Qualitative comparisons of the densities of each species between enrichment treatments suggest that caridean shrimp (especially *T. manningi* and *Hippolyte zostericola* Smith) densities were substantially higher in some of the enriched plots (Fig. 1, see electronic supplemental materials). Qualitative comparisons of the biomass of each species between enrichment treatments suggest that brachyuran crabs (e.g., *P. quadridentata*, *N. packardii*) and pink shrimp (*Farfantepenaeus duorarum* Burkenroad) had higher biomass in enriched plots and second-order predatory fish (fish that primarily consume other predators, e.g., *Opsanus beta* Goode & Bean) and sea cucumbers (*Holothuria* sp.) had higher biomass in unenriched plots (Fig. 2).

Discussion

Increased nutrient input to coastal habitats often causes the replacement of slower-growing macrophyte species that dominate in oligotrophic habitats with opportunistic, fast-growing species (Duarte, 1995; Fourqurean et al., 1995; Smith et al., 1999; Hauxwell et al., 2001; Cardoso et al., 2004), but impacts of nutrient enrichment on fauna are less predictable. We observed large differences in total epifaunal density and biomass between enriched and unenriched treatments, particularly at the more phosphorus limited site. Faunal density and biomass are sometimes enhanced in enriched conditions, particularly when associated with a moderate increase in primary productivity that augments food availability for grazers (Bustamante et al., 1995; Wootton et al., 1996). Cases where there are minimal or negative effects of enrichment on fauna can be attributed to interannual variability or degradation of the primary producer infrastructure that overwhelms any enhancement of food availability (Deegan et al., 2002; Posey et al., 2002). At the severely P-limited site, changes in the primary producers may reflect an early eutrophication shift, where macrophyte structure and epiphyte biomass increased enough to benefit fauna without reaching a more detrimental end state (Isaksson & Pihl, 1992).

Epifaunal communities were similar between enrichment treatments in terms of the relative number of individuals in each species and the distribution of biomass among species at both sites. However, changes in a few individual species explained most of the nutrient-induced increases in density and biomass that we observed. Grazing crustaceans, such as caridean shrimp, largely accounted for the higher density in enriched plots. Upper trophic level consumers, particularly brachyuran crabs and primary predatory fish, had greater biomass in enriched treatments. Nutrients are often linked to shifts in community composition and biomass allocation in epifaunal and meiofaunal communities in estuarine and marine habitats (Widbom & Elmgren, 1988; Isaksson & Pihl, 1992; Keats et al., 2004). Within a community, grazers often show the strongest responses to increase in primary production (Wootton et al., 1996; Bologna & Heck, 1999). Impacts of nutrient enrichment on upper trophic levels are observed less frequently. The nutrient-related differences in fish density and biomass that we detected were likely influenced by the patchy distribution of these larger epifaunal organisms, where collection of few large individuals could greatly influence total biomass.

Epifaunal density and biomass were related to features of the macrophyte canopy and to epiphyte characteristics. At the phosphorus-limited Duck Key, *Halodule wrightii* cover was higher in enriched plots. *H. wrightii* has thinner, shorter, and more numerous leaves than *Thalassia testudinum*, and the two species may provide different habitat values for associated epifauna (Tolan et al., 1997). By influencing seagrass species composition, nutrient enrichment may have altered the refuge value of the seagrass canopy for epifauna, particularly at Duck Key. Nutrient enrichment can cause changes in macrophyte structure in a variety of habitats, including phase shifts from coral reefs to macroalgal assemblages (McManus & Polsenberg, 2004) and replacement of native tree species with invasive underbrush species (Ostertag & Verville, 2002). Nutrient-induced increases in primary producer structural complexity can be associated with an increase in epifaunal density and biomass (Parker et al., 2001). Increased light attenuation in canopies with higher macrophyte leaf surface area has been shown to attract caridean shrimp (Zupo & Nelson, 1999) and may partially explain the higher caridean densities we observed in enriched treatments, though we did not directly measure leaf surface area. Alternatively, increased habitat complexity can have negative impacts on associated fauna, particularly when species replacement occurs, such as the overgrowth of *Zostera marina* with filamentous algae (Isaksson & Pihl, 1992; Deegan et al., 2002).

Nutrient enrichment may have directly modified the epifaunal food web by altering epiphyte community composition. Epiphytes often play an important trophic role in seagrass communities (Bologna & Heck, 1999; Moncreiff & Sullivan, 2001). The increased density of caridean shrimp, herbivorous isopods, and gammarid amphipods, particularly at Duck Key, suggests that grazing epifauna may have been attracted to the altered epiphytic community composition or to the increased microalgal food quality in the enriched plots (Hemmi & Jormalainen, 2002; Goecker et al., 2005).

Increased grazer density may explain why little algal overgrowth of *T. testudinum* occurred in enriched conditions in this and other studies in the region (Armitage et al., 2005), despite frequent documentation of algal replacement of seagrasses following increased nutrient input in other habitats (Duarte, 1995; Valiela et al., 1997; Hauxwell et al., 2001; Cardoso et al., 2004). Effective grazer control of algal proliferation in moderately enriched conditions has been demonstrated in a variety of marine habitats, including rocky intertidal (Wootton et al., 1996) and temperate (Williams & Ruckelshaus, 1993) and subtropical (Hays, 2005) seagrass beds. However, the ability of grazers to regulate epiphytic algae over longer time periods may be limited by seasonal variations in herbivore populations (Frankovich & Zieman, 2005). Predation pressure may also restrict grazing epifaunal abundance over a longer time scale. Further research evaluating the persistence of faunal assemblages over time as well as the trophic relationships within epifaunal communities under enriched conditions will facilitate predictions of community-level impacts of nutrient enrichment on the Florida Bay ecosystem.

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