Responses of seagrass communities to fertilization along a gradient of relative availability of nitrogen and phosphorus in a carbonate environment

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Abstract

Patterns of relative nutrient availability in south Florida suggest spatial differences regarding the importance of nitrogen (N) and phosphorus (P) to benthic primary producers. We did a 14-month in situ fertilization experiment to test predictions of N and P limitation in the subtropical nearshore marine waters of the upper Florida Keys. Six sites were divided into two groups (nearshore, offshore) representing the endpoints of an N:P stoichiometric gradient. Twenty-four plots were established at each site with six replicates of each treatment (+N, +P, +N+P, control), for a total of 144 experimental plots. The responses of benthic communities to N and P enrichment varied appreciably between nearshore and offshore habitats. Offshore seagrass beds were strongly limited by nitrogen, and nearshore beds were affected by nitrogen and phosphorus. Nutrient addition at offshore sites increased the length and aboveground standing crop of the two seagrasses, *Thalassia testudinum* and *Syringodium filiforme,* and growth rates of *T. testudinum.* Nutrient addition at nearshore sites increased the relative abundance of macroalgae, epiphytes, and sediment microalgae. N limitation of seagrass in this carbonate system was clearly demonstrated. However, added phosphorus was retained in the system more effectively than N, suggesting that phosphorus might have important long-term effects on these benthic communities. The observed species-specific responses to nutrient enrichment underscores the need to monitor all primary producers when addressing questions of nutrient limitation and eutrophication in seagrass communities.

The initial response of a coastal ecosystem to eutrophication will be influenced by the status of nutrient limitation at the time of enrichment. In coastal marine systems, nitrogen (N) limitation is common in temperate ecosystems with siliciclastic sediments, whereas phosphorus (P) limitation is often assumed to be restricted to tropical ecosystems with carbonate sediments (reviewed by Short 1987; Howarth 1988). This generalization is largely attributed to biogeochemical sorption processes: strong P affinity to carbonate sediments results in a loss of phosphorus available for plant uptake. However, not all tropical carbonate benthic ecosystems are P-limited (e.g., Erftemeijer 1994; Udy et al. 1999), so there must be other determinants of the limiting nutrient in coastal marine ecosystems.

Confirming the quality (N vs. P or some other element)

of nutrient limitation in an ecosystem can be achieved by nutrient addition assays, but these assays require relatively involved experimental designs, and their interpretation is not always clear-cut. In order to generate hypotheses about the nature of nutrient limitation, it is possible to examine the elemental content of organic matter from ecosystems. The elemental content of plant tissue and the ratios of elements (i.e., C:N:P) might reflect relative availability and nutrient limitation status. Stoichiometry has been used to infer nutrient limitation of phytoplankton (e.g., Redfield 1958), wetland macrophytes (e.g., Bedford et al. 1999), sediment microalgae (e.g., Hillebrand and Sommer 1999), macroalgae (e.g., Lyngby et al. 1999), and seagrass (e.g., Atkinson and Smith 1983).

The benthic ecosystem of the Florida Keys are an interesting locale to study nutrient limitation of coastal systems. The dominant primary producers in this environment are seagrasses and macroalgae, and the water column is transparent and unproductive. Spatial patterns in elemental stoichiometric ratios suggest varying importance of nitrogen and phosphorus. Elemental analysis of seagrass (Fourqurean and Zieman 2002), water quality (Jones and Boyer 2001), and sediment (Szmant and Forrester 1996) display a pattern of relatively high N:P nearshore and relatively low N:P offshore toward the Florida Keys Barrier Reef (~10 km from the shoreline). On the basis of these stoichiometric patterns, it has been hypothesized that the benthic communities in the nearshore waters of the Florida Keys are P-limited and offshore waters are N-limited, despite the fact that the entire region is underlain with carbonate sediments (Fourqurean and Zieman 2002). This implies that benthic community responses to localized nutrient enrichment might differ significantly on the spatial scale of a few kilometers. However,

nutrient limitation hypotheses derived from stoichiometric evidence should be confirmed with nutrient addition assays.

The classic response of benthic communities to coastal marine eutrophication is a shift in vegetation structure from slow-growing seagrass and macroalgae to fast-growing microalgae and phytoplankton (e.g., Valiela et al. 1992). This sequence is a consequence of interspecific competition and changing resource availability. The relative availability of resources (e.g., nutrient and light) at a given time will favor those species with greater competitive ability for the most limiting resource (Tilman 1982). In low-nutrient environments, seagrasses and slow-growing macroalgae are competitive dominants because they have relatively low nutrient requirements, can access nutrients in the sediment porewater, and possess efficient internal nutrient recycling (*see* review by Duarte 1995). An increase in environmental nutrient availability is concomitant with a decrease in light availability to the benthos. Seagrasses have higher light requirements compared with algae because they support metabolism for greater belowground biomass. As nutrient availability continues to increase, epiphytes and fast-growing macroalgae dominate because they take up nutrients more effectively and quickly than seagrass and have relatively lower light requirements to sustain growth (e.g., Harlin and Thorne-Miller 1981; Twilley et al. 1985).

Seagrass communities are ideal candidates for nutrient limitation studies because they tend to proliferate in shallow oligotrophic waters. The seagrass plants themselves are good indicators of changes in nutrient regimes because they are rooted plants with relatively long lives, they are sensitive to changes in water quality, and tissue nutrient content reflects the relative availability of nutrients in a system (Atkinson and Smith 1983; Duarte 1990). Knowledge of species-specific life history traits and shifts in species dominance might also provide insight on changes in nutrient regimes. The three most common seagrass species in the Caribbean region are *Thalassia testudinum, Syringodium filiforme,* and *Halodule wrightii.* From a life history perspective, *T. testudinum* is often dominant in areas of high light and low nutrients. *S. filiforme* and *H. wrightii* possess faster colonization rates and are relatively more efficient at nutrient uptake compared with *T. testudinum* (Williams 1990). We could then predict that the relatively slow-growing *T. testudinum* would be replaced by faster-growing species if nutrient loads were increased. Changes in the distribution and abundance of seagrass, relative to other seagrass species or primary producers, could therefore be used to infer changes in the nutrient status of a system.

In this study, we sought to test the hypothesis that seagrass-dominated benthic communities close to shore with high N : P ratios are P-limited, whereas those further offshore with low N : P are N-limited. We expected that these ecosystems would respond to nutrient enrichment with increasing biomass and productivity. We further expected that additions of nitrogen, phosphorus, or both would alter the N : P of the primary producers and that we would see a shift from dominance by slow-growing *T. testudinum* to more rapidly growing primary producers as a consequence of nutrient addition.

Materials and methods

Study site—The Florida Keys (ca. 25°N, 80°S) are a 250-km-long archipelago of low-lying islands stretching from Key Largo to the Dry Tortugas (Fig. 1). The Keys are flanked by the Straits of Florida and Atlantic Ocean to the south and east and the Gulf of Mexico and Florida Bay to the north and west. South Florida contains the largest continuous seagrass beds in the continental United States and some of the most expansive documented seagrass communities in the world (Fourqurean et al. 2002). *T. testudinum* is a common component of the oceanside benthos in the Florida Keys. *S. filiforme* distribution is patchy in the nearshore oceanside areas but increases in density in an offshore direction. *T. testudinum* was selected as a primary response species because it is the dominant seagrass species in the region and has been identified as nutrient limited in adjacent Florida Bay (Powell et al. 1989).

Experimental design and statistical analyses—A factorial nutrient loading experiment was conducted at six sites, divided into two groups that represent the endpoints of the stoichiometric gradient: nearshore (<1 km from the shoreline) and offshore (<1 km inside the reef tract). The number of replicates for each treatment was determined by a preliminary power analysis. At each site, 24 plots were established in a grid (50 × 50 m) with six replicates of each treatment (nitrogen addition, +N; phosphorus addition, +P; nitrogen and phosphorus addition; +N+P; and control, C). Treatment plots (0.5 m²) were evenly spaced within the grid with 10 m of separation between treatments.

This experimental design was of the form of a split plot. Sites (*n* = 6) were the (random) whole plots; onshore versus offshore were fixed whole-plot "treatments." Quadrats within plots were the subplots (random); nutrient treatments were fixed subplot treatments. We treated N and P additions as separate factors, with two levels of nitrogen (control, +N) and two levels of phosphorus (control, +P).

Response variables that were only measured at the termination of the experiment were tested with mixed-model analyses of variance (PROC MIXED, SAS v9.0), with denominator degrees of freedom calculated via the containment method. Nearshore–offshore was tested against sites (1 and 4 degrees of freedom); nutrient treatments and all interactions between nutrient treatments and nearshore–offshore were tested against quadrats (1 and 132 degrees of freedom). For response variables sampled repeatedly throughout the experiment, sampling dates as categorical repeated measures with quadrats within sites as subjects were added to the above split plot design. Sampling date was treated as categorical rather than ordered, and error covariances were treated as unstructured rather than autoregressive because of the underlying seasonality in many of the measured response variables. In order to evaluate differences in environmental conditions between onshore and offshore sites, *t*-tests assuming equal variances were performed on physicochemical and sediment parameters. Unless otherwise stated, we deemed a comparison statistically significant at $p \leq 0.05$.
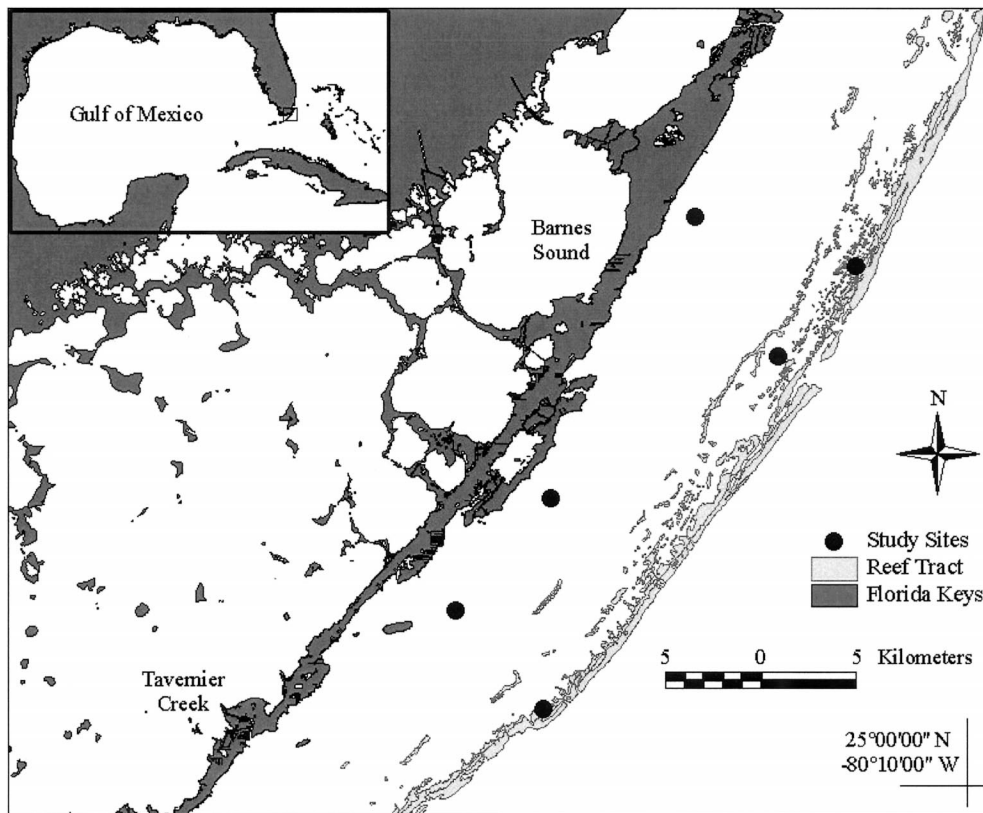
Fig. 1.   Map of study sites in the upper Florida Keys.

Nutrient loading rates—Loading rates used in nutrient enrichment experiments ideally must satisfy the following two requirements: they must be ecologically relevant, and they must be sufficient to ameliorate nutrient limitation. Loading rates used in previously published experiments in seagrass ecosystems vary widely, and these rates rarely have been justified. The use of excessive loading rates in experiments is problematic when the goal is to apply experimental results to ecological and coastal management applications. To ensure the ecological relevance of this experiment, nutrient loading rates were based on regulatory estimates of potential maximum wastewater and stormwater discharge (MCSM 2001), which are the dominant sources of anthropogenic nutrient inputs to the nearshore marine waters of the Florida Keys and have been identified as severe threats to regional water quality (EPA 1999). Adjustments were made for geochemical (e.g., sorption) and biological (e.g., denitrification) processes. A final loading rate of 0.77 g N m^{-2} d^{-1} and 0.12 g P m^{-2} d^{-1} represented a N:P (mole:mole) ratio of 14. The rate used in this experiment exceeded the N and P demand of *T. testudinum* during peak growth as assessed by multiplying peak growth rates by nutrient content (Fourqurean et al. 1992).

Fertilizer was added monthly to the sediment. Nitrogen was added in the form of urea-coated slow-release N fertilizer (Polyon, Pursell Technologies; 38-0-0, 94% nitrogen as urea and phosphorus as deflourinated granular phosphate rock [Multifos, IMC Phosphates] Ca$_3$(PO$_4$)$_2$, 18% P). Urea is rapidly converted via microbial activity to ammonium

(Fenchel and Blackburn 1979), which is the dominant form of inorganic nitrogen in the coastal waters of the Florida Keys (Boyer and Jones 2002). Fertilizer was applied evenly to each 0.5-m^2 plot and was gently mixed by hand into the surface 5 cm of sediment. The sediment surface of control plots was also mixed in a similar manner. Fertilizer application near the sediment–water column interface allowed for nutrients to diffuse through the sediment porewater and from the sediment into the water column, thus exposing both above- and belowground macrophyte biomass to nutrient manipulations.

Sampling—The experiment was initiated in May 2001 and was terminated in July 2002. Sediment fertilization and collection of abiotic data (light availability, salinity, surface water temperature, turbidity) occurred monthly at each site. Light attenuation by the water column was assessed with a 4π photosynthetically active radiation (PAR) sensor (LI-COR, Lincoln, Nebraska). Biotic response variables were measured during four major sampling events that occurred over the course of 14 months (May 2001, September 2001, March 2002, July 2002), in which the first represented a prefertilization sampling event. Biomass and nutrient sampling was conducted on those primary producers considered most sensitive to changes of nutrient availability in coastal marine systems: seagrass, macroalgae, epiphytes, and sediment microalgae. The following response variables were measured at all sampling events: *T. testudinum* leaf productivity, morphology, standing crop, and leaf elemental con-

tent. At the end of the experiment, we measured sediment porosity, bulk density, and organic content, as well as *T. testudinum* rhizome and *S. filiforme* leaf elemental content; *S. filiforme* leaf length and standing crop; *T. testudinum* total epiphyte load and epiphyte chlorophyll *a* (Chl *a*) content; sediment microalgae abundance; sediment total N and P content; and nonepiphytic macroalgae abundance.

At each sampling event, a quadrat (10×10 cm) was placed inside each treatment plot. *T. testudinum* growth rates were measured on plants within this quadrat by the modified hole-punch methodology (Fourqurean et al. 2001). Morphological measurements of all *T. testudinum* leaves (length and width) were recorded, and seagrass standing crop (g m^{-2}), areal productivity (g m^{-2} d^{-1}), and leaf emergence rates of marked short shoots (SS) (leaves SS^{-1} d^{-1}) were calculated. The number of *S. filiforme* short shoots, leaves, and leaf length found within the productivity quadrats were recorded. Epiphytic material, including inorganic carbonates, adhering to *T. testudinum* leaves was removed by gentle scraping with a razor blade. Epiphytes were placed into preweighed 20-ml glass scintillation vials and stored at $-20°$C. Seagrass leaf material within each productivity quadrat was pooled by species, dried at 70°C, and ground to a fine powder. Carbon and nitrogen contents were determined with a CHN analyzer (Fisons NA1500). Phosphorus content was determined by a dry-oxidation, acid hydrolysis extraction followed by colorimetric analysis of phosphate concentration (Fourqurean et al. 1992). Elemental content and ratios were calculated on a dry weight and mole : mole basis, respectively.

Epiphytes were freeze-dried to obtain dry weight, and total epiphyte load (g dry weight of epiphytes g^{-1} dry weight of seagrass leaves) was determined. Twenty milliliters of 90% acetone was added to each vial. Vials were shaken and stored at $-20°$C for a minimum of 72 h. Chl *a* content of the acetone extracts was measured fluorometrically (Strickland and Parsons 1972) on a Gilford Fluoro IV spectrofluorometer (excitation = 435 nm, emission = 667 nm). Epiphyte autotrophic content (μg Chl *a* mg^{-1} epiphyte) was used to estimate the relative contribution of algal epiphytism (Frankovich and Fourqurean 1997).

Abundance of macrophytes (seagrasses and macroalgae) was assessed by the Braun–Blanquet procedure (Fourqurean et al. 2001). This technique results in a score of relative cover, in which cover is defined as the fraction of the bottom that is obscured by specific benthic taxa when viewed by a diver from directly above. Score values were as follows: 0, absent; 1, <5% cover; 2, 5–25% cover; 3, 25–50% cover; 4, 50–75% cover; 5, 75–100% cover.

Two sediment cores (1.15 cm diameter, 2.61 cm depth) were taken from each treatment plot. One core was used to estimate sediment microalgal abundance via determination of Chl *a* content of the sediment (mg Chl *a* m^{-2}). Sediment samples were transferred into 20-ml glass scintillation vials and placed on ice in the dark. In the lab, 10 ml of 100% acetone was added to the wet sample to extract Chl *a*, and further analysis followed the method used for epiphyte Chl *a* content. The second core was used to analyze sediment porosity, bulk density, organic content, and elemental content (C, N, P). Sediment was transferred into preweighed 20-ml glass scintillation vials, and wet weight was calculated.

The sample was dried at 70°C for 48 h to obtain a dry weight. Dry samples were ground with a ceramic mortar and pestle. Sediment total nutrients were analyzed by the same methods as seagrass nutrients. Sediments were ashed at 500°C for 5 h, and percent organic content was calculated as loss on ignition.

T. testudinum rhizomes for nutrient analysis (C : N : P) were randomly collected from each quadrat, rinsed to remove carbonate sediments, dried at 70°C, ground to a fine powder, and analyzed in the method described above. Nonepiphytic macroalgal abundance was calculated for each treatment plot with a modification of the Braun–Blanquet quadrat method (Fourqurean et al. 2001).

Retention efficiency calculations—Changes in community structure often occur on timescales greater than this experiment. In order to gain insight into the fate of added nutrients and the relative long-term importance of N and P additions, we estimated the retention efficiency of nitrogen and phosphorus in both nearshore and offshore seagrass systems. Absolute quantities of nitrogen and phosphorus were calculated for compartments within a 0.25-m^3 ($25 \times 100 \times 100$ cm) seagrass habitat containing 200 liters of water column and 50 liters of sediment. The following compartments were included: water column, *T. testudinum* leaves, *T. testudinum* rhizomes, *S. filiforme* leaves, nonepiphytic macroalgae, *T. testudinum* epiphytes, and sediment. Water quality data were obtained from the Southeast Environmental Research Center Water Quality Monitoring Network at Florida International University. Absolute quantities (g) of nitrogen and phosphorus in each component were calculated by multiplying nutrient content (percent dry weight) and total mass (g m^{-2}). Estimates for macroalgal biomass (113 g dry weight m^{-2}; Davis and Fourqurean 2001) and epiphyte nutrient content ($N = 1.48\%$ of ash free dry weight (AFDW), P = 0.22% of AFDW; Lin et al. 1996) were obtained from the literature. *T. testudinum* belowground biomass was estimated as 85% of total *T. testudinum* mass. The remaining data were derived directly from this experiment. Mass balances were calculated for control and +N+P treatments at both nearshore and offshore sites. Net system retention ([total system nutrient (g), +N+P] − [total system nutrient (g), control]) and retention efficiency ([net system retention (g)/mass applied (g)] $\times$ 100%) were calculated.

Results

Nearshore and offshore waters exhibited similar mean water temperature and salinity (Table 1). There was an inverse relationship between depth and light attenuation: the deeper offshore sites had higher water clarity, as evidenced by lower light attenuation and lower turbidity, compared with nearshore sites. Despite the difference in water clarity, the amount of light reaching the benthos (% I_0) was not very different between nearshore and offshore locations: between 14.2% and 27.8% of the incoming solar radiation reached the seagrass canopy. Sediments at nearshore sites had higher porosity, lower bulk density, and higher organic content compared with offshore sites, which consisted of coarser sand and a low contribution of organic material. Nearshore

Table 1. Summary of site descriptions and environmental parameters. Temperature and salinity are annual means ($n = 10$–18). The diffuse attenuation coefficient (k_d) and the amount of light reaching the benthos (% I_0) are means of quarterly measurements from 1995 to 2002 ($n = 18$–27). Turbidity was measured in Nephelometric Turbidity Units (NTU). Sediment characteristics and abundance values are site means ($n = 24$) from the beginning of the experiment. Differences in means between onshore and offshore sites were evaluated by t-tests. Parameters with different means ($p \leq 0.05$) are bold.

	Nearshore			Offshore			t-test
	I-1	I-2	I-3	O-1	O-2	O-3	p value
Water							
Depth (m)	5	5	4	8	8	6	**0.023**
Salinity	35.9	36.0	36.1	36.2	36.2	36.1	0.067
Temperature (°C)	24.6	26.2	26.5	26.7	26.6	26.9	0.180
Turbidity (NTU)	0.64	0.39	0.59	0.30	0.26	0.25	**0.026**
Light attenuation, k_d (m^{-1})	0.32	0.39	0.33	0.23	0.16	0.29	0.051
I_0 (%)	20.2	14.2	26.7	15.9	27.8	17.6	0.990
Sediment							
Porosity (g cm^{-3})	0.71	0.69	0.77	0.54	0.52	0.60	**0.007**
Bulk density (g cm^{-3})	0.77	0.79	0.93	1.20	1.21	1.23	**0.002**
Organic content (%)	4.52	3.78	3.47	2.25	2.07	1.91	**0.005**
Macrophyte abundance							
Thalassia	3.1	4.0	3.9	3.9	3.7	3.6	0.834
Syringodium	0.0	0.1	0.3	0.6	1.1	2.5	0.092
Nonepiphytic macroalgae	1.5	1.0	1.0	0.1	0.8	1.4	0.386

seagrass beds were dominated by *T. testudinum* interspersed with abundant mounds of fine mud deposited by infauna. Offshore seagrass beds were more homogeneous, and *S. filiforme* was more abundant in offshore compared with nearshore sites. *T. testudinum* rhizomes were primarily located in the top 10 cm of sediment at nearshore sites, whereas offshore rhizomes were found at greater depth (~5–20 cm). Nonepiphytic macroalgal composition consisted primarily of calcareous green algae species (*Penicillus* spp., *Halimeda* spp., *Udotea* spp., *Rhipocephalus* spp.). Also present in sparse amounts were green algae (e.g., *Avrainvillea* spp., *Codium* spp., *Dasycladus* spp., *Batophora* spp., *Caulerpa* spp.), red algae (e.g., *Laurencia* spp., *Gracilaria* spp.), and brown algae (e.g., *Dictyota* spp.).

Seagrass morphology, standing crop, and growth responses—Sediment fertilization increased sediment nutrient content and increased plant nutrient content, providing evidence that fertilization increased availability of both nitrogen and phosphorus. Plant nutrient enrichment resulted in significant changes in *T. testudinum* leaf nutrient content (Fig. 2) and elemental ratios (Fig. 3). Nitrogen addition led to rapid uptake of nitrogen by seagrass at both nearshore and offshore sites, as evidenced by increases in leaf N content and decreases in C:N. The response to P addition was delayed compared with N addition. Whereas the effects of N addition were evident at both nearshore and offshore sites in September 2001 (4 months of fertilization), elevated leaf P content was not observed at nearshore sites until March 2002 (10 months) and at offshore sites until July 2002 (14 months). The nutrient contents of *S. filiforme* leaves and *T. testudinum* rhizomes were significantly affected by nutrient addition (Fig. 4). Nitrogen addition decreased *S. filiforme* leaf and *T. testudinum* rhizome C:N. Phosphorus addition decreased *S. filiforme* leaf C:P. Significant changes in rhizome P content

and C:P values with P addition were observed at nearshore, but not offshore, sites.

Nutrient addition significantly affected *T. testudinum* length, standing crop, and growth rates (Fig. 5). Leaf length, standing crop, and areal productivity increased with N addition at offshore sites, but not at nearshore sites. There were no significant effects of P addition on *T. testudinum* productivity. Nitrogen addition significantly increased *S. filiforme* length and standing crop at offshore, but not nearshore, sites (Fig. 6). There were no significant effects of nutrient additions on *T. testudinum* leaf emergence rates.

Algal responses to nutrient enrichment occurred primarily at nearshore sites (Fig. 7). Nonepiphytic macroalgal abundance increased with N addition at nearshore sites only (significant Location × N interaction). Both N and P additions affected epiphyte loads, but in a complex manner (significant main effects of N and P additions on epiphyte load). Nearshore, P addition increased epiphyte loads, whereas offshore, N additions decreased loads on the seagrass blades. Additions of both nitrogen and phosphorus significantly increased the epiphyte Chl *a* content at inshore sites, but at offshore sites, only N addition increased the autotrophic index. Sediment microalgae abundance increased only with +N+P enrichment at nearshore sites.

Retention efficiency of nitrogen and phosphorus—The relative allocation of nitrogen and phosphorus to various seagrass system compartments was similar between nearshore and offshore sites. However, the net retention of added nutrients varied considerably on the basis of nutrient and location (Table 2). The majority of nitrogen and phosphorus was located in the sediment, and the water column contribution was negligible (<0.1%). Nutrient enrichment nearly doubled both nearshore and offshore total nitrogen in the system, and greatly elevated total nearshore phosphorus and
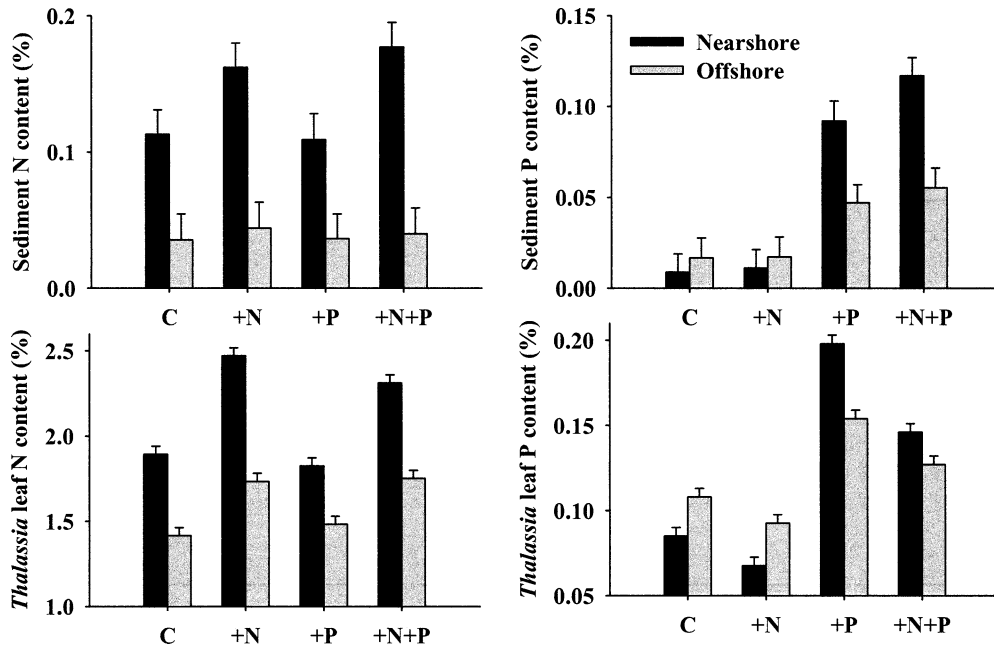
Fig. 2. Phosphorus and nitrogen content of sediments and leaves of *Thalassia testudinum* at nearshore and offshore sites following 14 months of fertilization, expressed as percentage of dry weight. Values are treatment means (*n* = 18), and error bars are ±1 SE.

offshore phosphorus. Net system retention for both nitrogen and phosphorus were higher at nearshore sites compared with offshore sites. Retention efficiency was large for phosphorus (nearshore = 82%, offshore = 49%) and relatively small for nitrogen (nearshore = 9%, offshore = 4%).

Discussion

This experiment demonstrated that nearshore benthic communities in south Florida are indeed nutrient limited, but the nature of that limitation differs for nearshore and off-
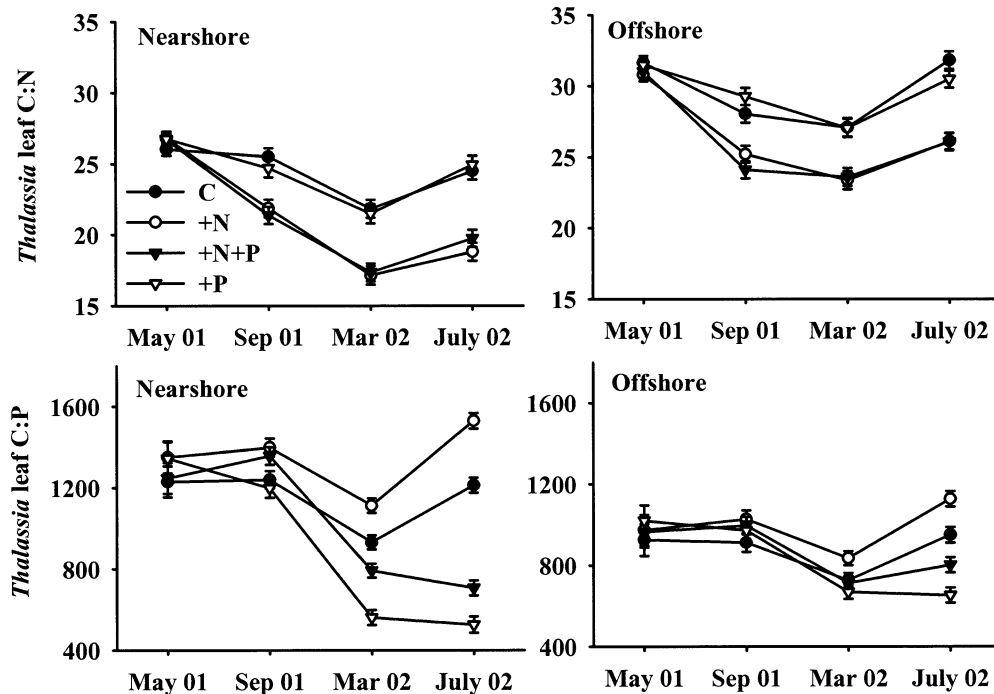

Fig. 3. *Thalassia testudinum* leaf nutrient ratios during the course of the experiments. Values are treatment means (*n* = 18), and error bars are ±1 SE.
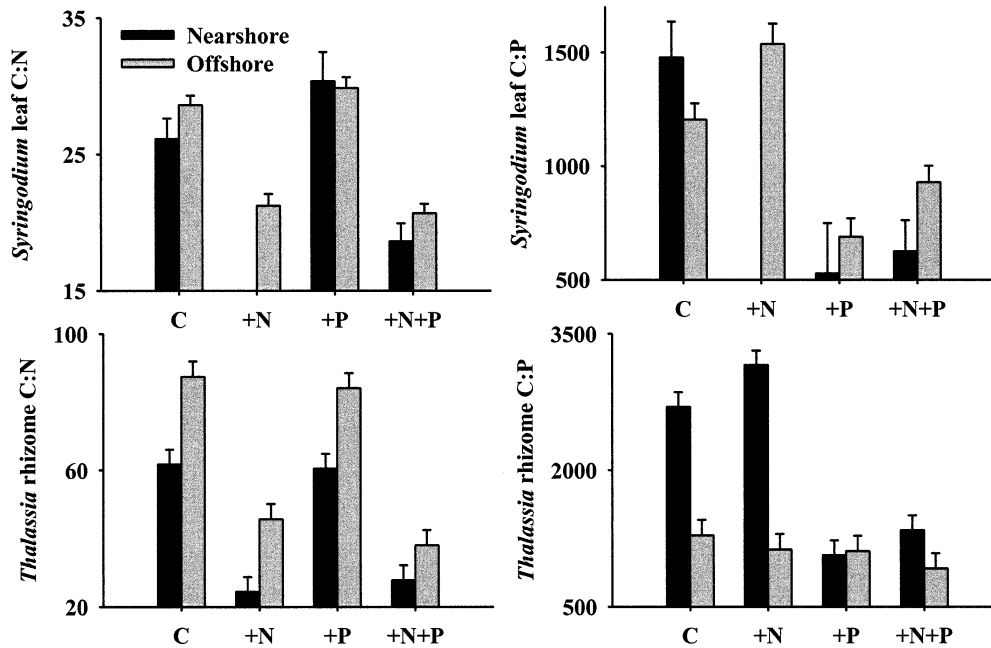
Fig. 4.   *Thalassia testudinum* rhizome and *Syringodium filiforme* leaf nutrient content responses at nearshore and offshore sites following 14 months of fertilization, expressed as percentage of dry weight. Values are treatment means ($n = 18$), and error bars are ± 1 SE. *Syringodium filiforme* was not present in any +N treatments at nearshore sites.

shore sites and for seagrass and algae (Table 3). The original hypothesis that seagrass communities are P-limited nearshore and N-limited offshore was partially supported by the responses of primary producers to nutrient enrichment. There was an increase in *T. testudinum* leaf length, standing crop, and growth rates (Fig. 5) in response to N, but not P, addition at offshore sites. Offshore *S. filiforme* leaf length and standing crop also increased with N addition. This implies that seagrass in offshore habitats in the upper Florida Keys are N-limited. Nutrient addition at nearshore sites had no significant effect on *T. testudinum* or *S. filiforme* length or standing crop. *T. testudinum* areal productivity at nearshore sites increased with +N and +N+P treatments, suggesting that nearshore *T. testudinum* might be nutrient limited, but this limitation is not as severe as offshore seagrass. Contrary to our a priori predictions based on stoichiometric evidence, there was no clear increase in biomass or primary productivity of seagrasses at nearshore sites in response to P addition.

Significant increases in the relative abundance of nonseagrass primary producers were found almost exclusively at nearshore sites (Fig. 7) and encountered with all nutrient treatments (+N, +P, +N+P). Macroalgal abundance, total epiphyte load, epiphyte autotrophic content, and sediment microalgae abundance increased with nutrient addition at nearshore sites. A decrease in total epiphyte loads at offshore sites with +N and +N+P addition might have been caused by higher leaf production and leaf mass associated with offshore N addition. The only significant effect of nutrients on an offshore algal response variable was an increase in epiphyte Chl *a* content with N addition (+N, +N+P), although the increase was not as great in magnitude as the nearshore

response. This suggests that the autotrophic component of the offshore epiphyte complex might be N-limited, as was observed for the offshore seagrass.

The strong epiphyte responses at nearshore sites might be a function of benthic microalgal mats. Qualitative observations by divers of microalgal blooms were identified exclusively in nutrient treatments (+N, +P, +N+P) at nearshore, but not offshore, sites. The absence of benthic algae increases at offshore sites might be a result of higher water energy and strong water mixing at offshore sites, which might have physically inhibited the development of benthic microalgal mats, or of observation times that do not coincide with mat formation, or of microalgal mats that are not nutrient limited at offshore sites. The dynamics of benthic microalgae in response to nutrient enrichment deserve more attention in future research.

The competitive outcome following changes in nutrient availability plays a critical role in determining the community response to eutrophication. Although the time frame of this experiment was not long enough to observe community structure shifts, changes in the relative abundance of primary producers allowed us to predict the future trajectory of community composition. Increases in *S. filiforme,* macroalgae, and epiphyte abundance observed in this study might lead to direct competition with *T. testudinum* for resources. Mean leaf length for *S. filiforme* in offshore +N+P treatments (198 $\pm$ 48 mm) were higher than *T. testudinum* (176 $\pm$ 39 mm), suggesting that shading effects on *T. testudinum* by *S. filiforme* can occur with fertilization. These shading effects might be exacerbated by a higher *T. testudinum* minimum light requirement than *S. filiforme* (Wiginton and McMillan 1979). Macroalgal species, especially rhizophytic calcareous

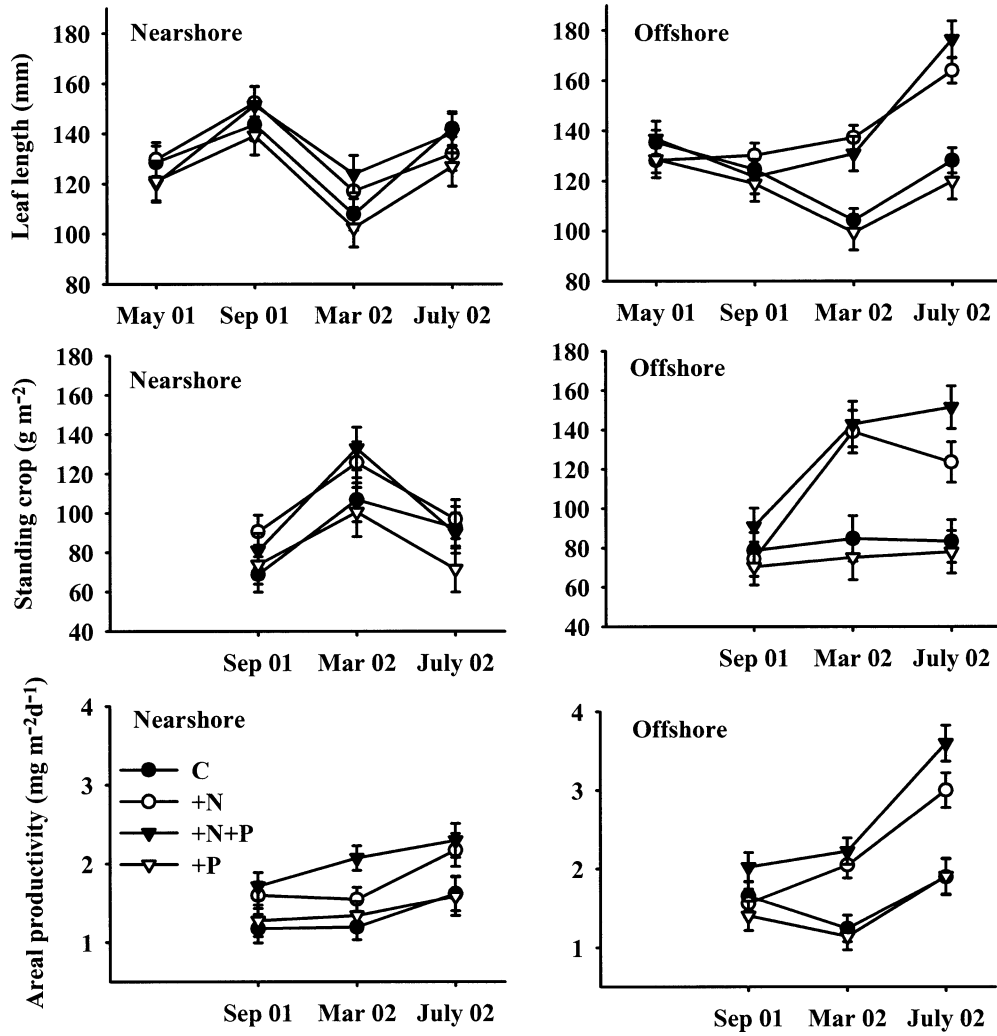Fig. 5. Morphology and growth measurements of *Thalassia testudinum* over the course of the experiments at nearshore and offshore sites. Values are treatment means ($n = 18$), and error bars are ± 1 SE.
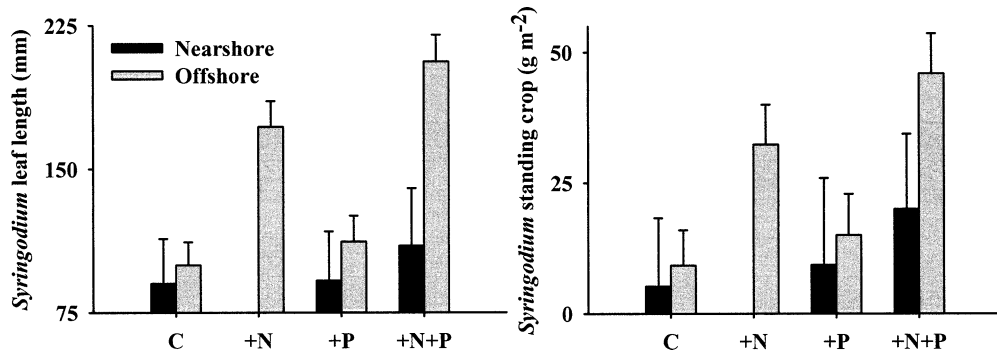

Fig. 6. *Syringodium filiforme* mean leaf length and standing crop at nearshore and offshore sites following 14 months of fertilization. Values are treatment means ($n = 18$), and error bars are ± 1 SE.
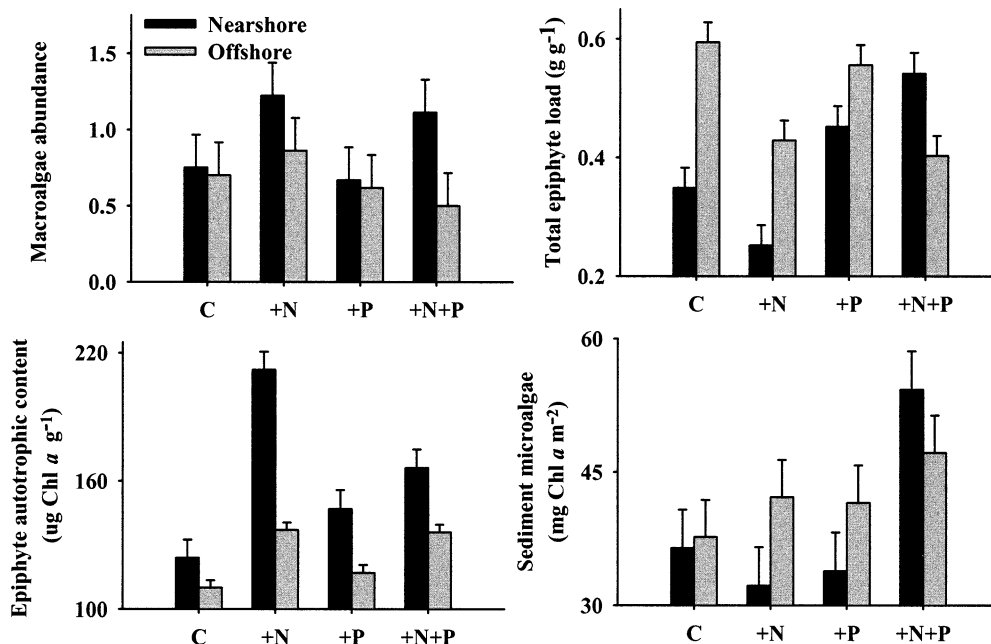
Fig. 7. Epiphyte load and autotrophic content and nonepiphytic macroalgal and sediment microalgal responses at nearshore and offshore sites following 14 months of fertilization. Values are treatment means ($n = 18$), and error bars are ± 1 SE.

greens, are conspicuous in south Florida seagrass communities and might compete with seagrasses for light, space, and nutrients (Davis and Fourqurean 2001). Seagrasses are especially prone to the negative shading effects of epiphytes and benthic algal blooms (e.g., Twilley et al. 1985). Nutrient enrichment in this experiment resulted in an increase in seagrass biomass at offshore sites and an increase in algal biomass at nearshore sites. This demonstrates that both regions are nutrient limited but that taxon-specific responses to nutrient enrichment are different. Continuous nutrient enrichment could lead to a shift from *T. testudinum* to *S. filiforme* dominance at offshore sites and to algae dominance at nearshore sites.

The time course of seagrass community responses to changes in nutrient availability has been shown to occur on the scale of years and decades. In Florida Bay, a monoculture *T. testudinum* bed was replaced by *H. wrightii* following 8 yr of fertilization (Fourqurean et al. 1995). Changes have also been shown to occur following the cessation of nutrient addition. In the Mediterranean, a *Posidonia oceanica* meadow displayed persistent seagrass declines 3 yr following the closure of a fish farm (Delgado et al. 1999). These long-term community changes suggest that nutrients were retained and recycled in the system. Benthic communities in this experiment differed dramatically in their retention of nitrogen and phosphorus (Table 2). Although total system nitrogen dou-

Table 2. Absolute quantities (g) and retention efficiency (%) of nitrogen and phosphorus for compartments within 0.25 m³ of seagrass habitat containing 200 liters of water column and 50 liters of sediment. Measurements are listed for control (C) and nutrient (+N+P) treatments at nearshore and offshore sites.

Component [g (0.25 m⁻³)⁻¹]	Nitrogen				Phosphorus			
	Nearshore		Offshore		Nearshore		Offshore	
	C	+N+P	C	+N+P	C	+N+P	C	+N+P
Sediment	43.5	67.1	21.4	24.5	3.4	44.3	10.2	33.7
Thalassia aboveground	1.7	2.2	1.2	2.6	0.1	0.1	0.1	0.2
Thalassia belowground	3.4	7.8	2.4	10.6	0.2	0.4	0.4	1.0
Syringodium leaves	0.1	0.4	0.1	0.9	0.003	0.03	0.01	0.05
Macroalgae	0.3	0.3	0.3	0.3	0.04	0.04	0.04	0.04
Epiphytes	0.4	0.6	0.6	0.7	0.07	0.1	0.1	0.1
Water column	0.04	0.04	0.04	0.04	0.001	0.001	0.001	0.001
Total system (g)	49.4	78.5	26.1	39.7	3.8	45.1	10.8	35.2
Net retention (g)		29.1		13.6		41.2		24.4
Mass applied (g)		323		323		50		50
Retention efficiency (%)		9.0		4.2		82.5		48.7

Table 3. A summary of statistically significant (ANOVA main effects, $p \leq 0.05$) responses after 14 months of fertilization. A plus (+) indicates that the variable was greater than the controls, a minus (−) indicates a decrease compared with controls. ND indicates there was no comparison possible, because *Syringodium filiforme* was absent from all +N treatments at the inshore locations.

Response variable	Nearshore +N	Nearshore +P	Nearshore +N+P	Offshore +N	Offshore +P	Offshore +N+P
Thalassia testudinum						
Areal productivity	+		+	+		+
Specific productivity	+	+	+			
Productivity per short shoot			+	+		+
Standing crop				+		+
Leaf length				+		+
Syringodium filiforme						
Standing crop	ND			+		+
Short shoot density	ND					+
Leaf length	ND			+		+
Macroalgae						
Abundance	+		+			
Epiphytes						
Load			+	−		−
Chl *a* load	+	+	+			
Autotrophic index	+	+	+	+		+
Sediment microalgae						
Abundance			+			
Nutrient content of seagrasses						
Thalassia						
Leaf N content	+		+	+		+
Leaf P content	−	+	+	−	+	+
Leaf C:N	−		−	−	−	−
Leaf C:P	+	−	−	+	−	−
Leaf N:P	+	−	−	+	−	
Rhizome N content	+		+	+		+
Rhizome P content		+	+			+
Rhizome C:N	−		−	−		−
Rhizome C:P	+	−	−			
Rhizome N:P	+	−		+		
Syringodium						
Leaf N content	ND		+	+		+
Leaf P content	ND	+	+		+	+
Leaf C:N	ND		−	−		−
Leaf C:P	ND	−	−	+	−	−
Leaf N:P	ND	−	−	+	−	

bled with N addition, <10% of the added nitrogen was retained. In contrast, these sites were extremely efficient at P retention: 82% and 49% of added phosphorus was retained at nearshore and offshore sites, respectively. These differences suggests that long-term P enrichment, unlike N enrichment, has the potential to be an important driver of long-term community changes because most of the phosphorus was retained within the system, whereas much of the nitrogen was lost from the system. Nutrients can be lost from a system via several pathways, including mineralization processes, sedimentation, diffusion from the sediment, physical removal, and herbivory. The sediment served as a large sink for phosphorus in this study. The high loss rates of nitrogen was likely a function of microbial transformations (e.g., denitrification). Because of the high affinity of carbonate sed-

iments for phosphate, it is also likely that inorganic nitrogen is more mobile and therefore more easily lost from the system.

Seagrass leaf nutrient content increased at all sites with the addition of nutrients, but the magnitude of these responses varied by time and location. Increases in *T. testudinum* leaf N content were apparent quickly (4 months of fertilization), whereas significant increases in P content were not observed at nearshore sites until 10 months and at offshore sites until 14 months (Fig. 3). The overall delayed response of *T. testudinum* leaf P content with P addition might have been caused by sorption of added phosphorus on carbonate sediments (Short et al. 1990). However, this geochemical process does not explain the difference between nearshore and offshore *T. testudinum* P content responses to +P ad-

dition. Sediment grain size has been shown to possess an inverse relationship to sorption potential: smaller grain sizes provide more surface area for P adsorption, resulting in less phosphorus available for plant uptake (Erftemeijer 1994). On the basis of this phenomenon, we could predict that nearshore sites, with smaller grain size, would display delayed P uptake by seagrass compared with offshore sites. The opposite pattern was observed. Dissolution and precipitation of carbonates are also influenced by organic matter (Morse et al. 1985) and sediment pH (Jensen et al. 1998), where $CaCO_3$ dissolution is related to higher organic content. Nearshore sediments have relatively higher organic content (Table 1), so this factor might affect P availability. It is also possible that the greater depth of the root zone at offshore sites might account for the delay in seagrass P uptake. An alternate explanation is that P uptake by *T. testudinum* did not occur at offshore sites because phosphorus was not limiting. The increase of rhizome P content with +P at nearshore, but not offshore, sites is further evidence that phosphorus did not limit seagrass growth or metabolic processes at offshore sites (Fig. 4).

The addition of nitrogen not only increased *T. testudinum* N content, but it also affected the metabolism and uptake of phosphorus. A significant decrease in leaf P content with N addition was observed at both nearshore and offshore sites (Figs. 2, 3). A probable explanation is that the addition of nitrogen increased N assimilation and led to higher P demand, a phenomena observed with nutrient enrichment in an Australian seagrass bed (Udy and Dennison 1997). This net decrease was not seen with +N+P, presumably because the increased P demand was met by fertilization. The addition of phosphorus alone did not have a significant negative effect on N content, emphasizing the difference in metabolic characteristics of specific nutrients.

Growth and biomass responses in this experiment did not consistently follow the nutrient content responses. Although N addition increased leaf N content at all sites, increases in leaf length and standing crop were found only at offshore sites. The addition of phosphorus alone to nearshore and offshore sites increased leaf P concentrations but did not affect length, standing crop, or growth rates. Increases in *T. testudinum* leaf nutrient content in the absence of a positive standing crop or growth response implies that nutrient availability in the study area was either insufficient to satisfy all plant metabolic demands for nitrogen, phosphorus, or both, or that *T. testudinum* is capable of storing excess nutrients when demand is less than supply, also known as luxury consumption. Luxury consumption of nutrients by algae is common (e.g., Campbell 2001) and has also been identified in seagrass (e.g., Murray et al. 1992; Van Lent et al. 1995). Nutrient storage differs between *T. testudinum* photosynthetic (leaves) and structural (rhizomes) tissues; the photosynthetic short shoots contain the largest amount of nitrogen and phosphorus, whereas rhizomes serve as important carbohydrate storage organs. The only instance in this study in which the addition of a solitary nutrient (N or P) had no effect on plant nutrient content for that particular nutrient was for rhizome C : P and P content (Fig. 4) at offshore sites. The absence of a rhizome P increase might be a function of accessibility, in which the added phosphorus did not migrate

downward to the relatively deep rhizome–root complex because of sorption activity, relatively lower mobility, or both compared with nitrogen. It is also possible that the added phosphorus was not integrated into offshore rhizome tissue because the element is in excess at offshore sites and not required, which is likely because offshore P availability is relatively high and offshore growth is strongly N-limited.

Ecological applications of this study—Phosphorus limitation of coastal primary production is frequently associated with tropical marine carbonate systems in which the strong sorption affinity of phosphorus to calcium carbonate mineral surfaces reduces the amount of phosphorus available for plant uptake (Morse et al. 1985). Biological availability of phosphorus is further regulated by geochemical processes, such as sediment grain size (Erftemeijer 1994), sorption-site saturation (McGlathery et al. 1994), and carbonate dissolution dynamics (e.g., Jensen et al. 1998; Burdige and Zimmerman 2002). There is building evidence that seagrass communities found in carbonate-rich systems can be limited by nitrogen rather than phosphorus. A review of in situ seagrass fertilization experiments that included separate N and P enrichment found only one out of seven studies which clearly identified P limitation of seagrass growth in a carbonate system (Table 4). In this frequently cited investigation, Short et al. (1990) found significant effects of P addition on *S. filiforme* growth only when porewater P concentrations were increased to 2,000 times ambient levels, a concentration that might be excessive in real-life scenarios. Other fertilization experiments that used only +N+P combined addition have inferred P limitation with changes in leaf nutrient content, biomass measurements, or both (Agawin et al. 1996; Powell et al. 1989), but at this time, adequate experimental data is lacking to justify a broad assumption of P limitation in carbonate systems. In temperate systems, three out of six fertilization studies identified seagrass growth with P addition (Harlin and Thorne-Miller 1981; Perez et al. 1991; Murray et al. 1992), suggesting that P limitation is more common on a global scale and that parameters such as locale (tropical vs. temperate) and sediment composition (carbonate contribution) are not effective predictors of seagrass nutrient limitation. This experiment clearly demonstrated N limitation of *T. testudinum* and *S. filiforme* in the offshore waters of the upper Florida Keys, despite predictions of P limitation in carbonate systems.

This study partially supports our original hypotheses of nutrient limitation on the basis of patterns of nutrient availability: nearshore algae were affected by nitrogen and phosphorus, and offshore seagrasses were affected by nitrogen. Predictions of nearshore P limitation were not strongly supported by our experimental results. It is possible that nearshore habitats are P-limited, but the signal was not observed because of factors such as the relatively short experimental time period, high nutrient conservation, and recycling of *T. testudinum* as an adaptation to low nutrient environments. These problems are associated with P-loading, sediment sorption, or the indirect effects of microalgal mats, which can cause direct shading of seagrass photosynthetic tissue or affect sediment processes such as oxygen demand. Predicting the response of a system to eutrophication is confounded

Table 4. Responses of seagrass to in situ nutrient enrichment experiments involving separate nitrogen (N) and phosphorus (P) addition. Entries are grouped by climate (temperate vs. tropical/subtropical) and by sediment regime (carbonate vs. siliciclastic).

Location	Species	Response Tissue	Response Growth	Source
Tropical/subtropical carbonate				
Indonesia (coral islands)	*Thalassia hemprichii*	+N	None	Erftemeijer et al. (1994)
Bahamas	*Syringodium filiforme*	+N+P	+P	Short et al. (1990)
NE Australia	*Halodule uninervis*	+N	+N	Udy et al. (1999)
NE Australia	*Syringodium isoetifolium*	+N	+N	Udy et al. (1999)
Florida Keys	*Thalassia testudinum*	+N+P	+N	This investigation, offshore
Florida Keys	*T. testudinum*	+N+P	+N+P	This investigation, nearshore
Tropical/subtropical siliciclastic				
Indonesia (coastal site)	*T. hemprichii*	None	None	Erftemeijer et al. (1994)
E Australia	*H. univervis*	+N	+N	Udy and Dennison (1997)
E Australia	*Zostera capricorni*	+N+P	+N+P	Udy and Dennison (1997)
E Australia	*Cymodocea serrulata*	+N	None	Udy and Dennison (1997)
Temperate carbonate				
NE Spain	*Cymodocea nodosa*	+P	+P	Perez et al. (1991)
Temperate siliciclastic				
SE Australia	*Heterozostera tasmanica*	+N+P	+N	Bulthuis et al. (1992)
Italy	*C. nodosa*	None	None	Ceccherelli and Cinelli (1999)
Rhode Island	*Zostera marina*	+N	+N+P	Harlin and Thorne-Miller (1981)
Chesapeake Bay	*Z. marina*	+P	+P	Murray et al. (1992)

by the fact that primary producers in coastal systems have species-specific nutrient requirements and can exhibit dissimilar forms of limitation. The limiting nutrient has been shown to vary among trophic levels such as plants and bacteria in coastal ecosystems (Sundareshwar et al. 2003), but this study clearly demonstrates that members within a trophic level might also respond differently to N and P enrichment. The response of seagrass communities in the upper Florida Keys to N and P enrichment varies appreciably between the nearshore and offshore environment, and the responses of all primary producers should be considered before categorizing a natural system with a specific nutrient limitation.

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