Journal of Experimental Marine Biology and Ecology 339 (2006) 65–74

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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The short-term influence of herbivory near patch reefs varies between seagrass species

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Received 1 December 2005; received in revised form 25 February 2006; accepted 15 July 2006

Abstract

The coexistence of multiple species within a trophic level can be regulated by consumer preferences and nutrient supply, but the influence of these factors on the co-occurrence of seagrass species is not well understood. We examined the biomass and density responses of two seagrass species in the Florida Keys Reef Tract to grazing pressure near patch reefs, and evaluated how nutrient enrichment impacted herbivory dynamics. We transplanted *Halodule wrightii* (shoalgrass) sprigs into caged and uncaged plots in a *Thalassia testudinum* (turtlegrass) bed near a patch reef. Nutrients (N and P) were added to half of the experimental plots. We recorded changes in seagrass shoot density, and after three months, we measured above- and belowground biomass and tissue nutrient content of both species. Herbivory immediately and strongly impacted *H. wrightii*. Within six days of transplantation, herbivory reduced the density of uncaged *H. wrightii* by over 80%, resulting in a decrease in above- and belowground biomass of nearly an order of magnitude. *T. testudinum* shoot density and belowground biomass were not affected by herbivory, but aboveground biomass and leaf surface area were higher within cages, suggesting that although herbivory influenced both seagrass species, *T. testudinum* was more resistant to herbivory pressure than *H. wrightii*. Nutrient addition did not alter herbivory rates or the biomass of either species over the short-term duration of this study. In both species, nutrient addition had little effect on the tissue nutrient content of seagrass leaves, and N:P was near the 30:1 threshold that suggested a balance between N and P. The different impacts of grazing on these two seagrass species suggest that herbivory may be an important regulator of the distribution of multiple seagrass species near herbivore refuges like patch reefs in the Caribbean.

Keywords: Epiphytes; Grazers; Parrotfish; Seagrass; *Sparisoma aurofrenatum*; Trophic dynamics

1. Introduction

The coexistence of multiple species within a trophic level can be influenced by numerous factors, including competitive abilities, consumer preferences, resource availability, and environmental conditions (Tilman, 1977; Emery et al., 2001; Gross et al., 2001; Del-Val and Crawley, 2005). In nearshore marine communities, patterns of species coexistence are temporally and spatially dynamic, with fluctuations in species composition often occurring following ecosystem-level changes, including natural disturbances like storms (Fourqurean and Rutten, 2004) and anthropogenic impacts such as overharvesting of top consumers (Jackson et al., 2001) and coastal nutrient enrichment (Cardoso et al., 2004).

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doi:10.1016/j.jembe.2006.07.013

Understanding how both natural and anthropogenic forces influence species composition aids in the prediction of responses to ecosystem changes and the development of management strategies.

Seagrass beds are widespread in temperate and tropical nearshore habitats, and seagrass species composition is linked to ecosystem functions including trophic support (Jernakoff and Nielsen, 1998) and production export dynamics (Zieman et al., 1979). However, factors influencing the coexistence of multiple seagrass species are not well understood. Nutrient addition can shift seagrass species composition in oligotrophic habitats (Fourqurean et al., 1995), and there is some evidence that grazing parrotfish prefer faster-growing, pioneering seagrass species over slow-growing, climax species (Mariani and Alcoverro, 1999). Similar processes have also been documented in terrestrial (Coley, 1983) and marine algal (Hay, 1981a) communities. In addition, grazers may select plant tissue that has been nutrient enriched (McGlathery, 1995; Boyer et al., 2004). Nutrient enrichment can also stimulate epiphyte growth (Tomasko and Lapointe, 1991), which in turn can shade seagrass leaves and reduce seagrass growth if not controlled by grazers (Howard and Short, 1986). Simultaneous manipulations of both grazers and nutrient supply are necessary to determine how these factors influence the coexistence of multiple seagrass species.

In south Florida, two of the common seagrass species are *Thalassia testudinum* Banks ex KD König (turtlegrass) and *Halodule wrightii* Ascherson (shoalgrass). Over long time scales, *H. wrightii* can replace *T. testudinum* in high nutrient conditions (Fourqurean et al., 1995), but monitoring in the Florida Keys National Marine Sanctuary (FKNMS) over the last ten years has revealed that *H. wrightii* is patchily distributed and does not persist for long periods of time, even in areas of relatively high nutrient availability near the Florida Keys coral reef tract (Fig. 1a, Fourqurean and Escorcia, 2005). The rapid disappearance of transplanted *H. wrightii* in this environment (W.J. Kenworthy, personal communication) suggests that selective grazing on *H. wrightii* may contribute to scarcity of shoalgrass in the FKNMS. *H. wrightii* can proliferate in enriched conditions (Fourqurean et al., 1995), possibly due to rapid nutrient uptake rates. Preferential grazing on enriched tissue may further increase herbivory rates (McGlathery, 1995; Boyer et al., 2004). However, the impact of herbivory on *H. wrightii* biomass and the potential influence of nutrient enrichment on seagrass grazing rates in the FKNMS have not been experimentally established. The objectives of our study were to evaluate the role of grazing on *H. wrightii* and *T. testudinum* density near patch reefs and investigate the impacts of nutrients on herbivory dynamics. We hypothesized that selective grazing by reef-associated herbivores, particularly parrotfish (Family Scaridae) and urchins (Class Echinoidea), would limit *H. wrightii* biomass in the vicinity of patch reefs. We also expected that *H. wrightii* would take up added nutrients faster than *T. testudinum* and that herbivory would be higher on enriched tissue.

2. Methods

2.1. Study system

Carysfort Reef, near Key Largo, Florida, is characteristic of the seagrass bed-patch reef matrix on the ocean side of the Florida Keys. The seagrass bed in the region is dominated by *Thalassia testudinum* and *Syringodium filiforme* Kützing (Fig. 1b). Long-term monitoring at this

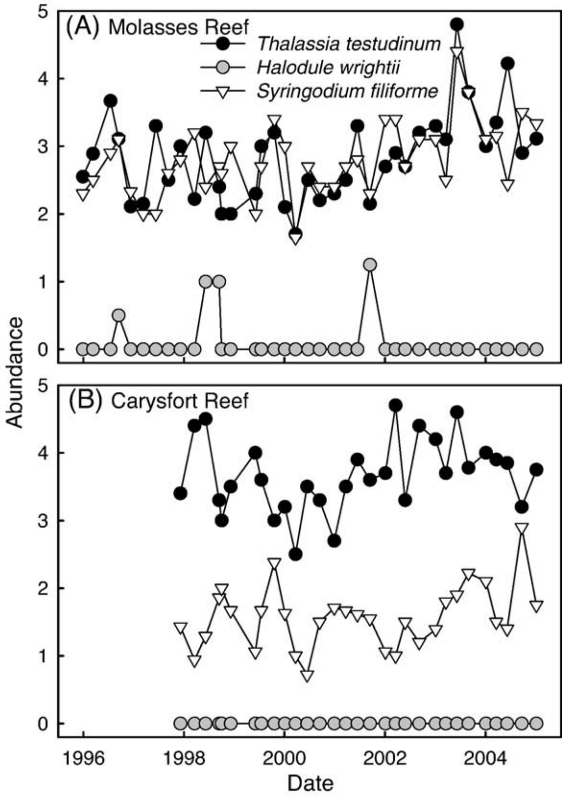

Fig. 1. Abundance of *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme* at two sites in the Florida Keys National Marine Sanctuary: (A) Molasses Reef (25° 00.807 N, 80° 22.677 W); (B) Carysfort Reef (25° 13.314N, 80° 12.881W, about 100 m from the experimental study site). Abundance represents the Braun–Blanquet score of percent cover (on a scale of 0–5) in study plots where that species occurred, adapted from Fourqurean and Escorcia (2005). No measurements were taken at Carysfort Reef prior to 1998.

Table 1
Results from two-way Model I ANOVA of caging and nutrient enrichment treatments on *Halodule wrightii* and *Thalassia testudinum* shoot density

		df	MS	*F*	P
Halodule wrightii	Cage	2	561.47	21.82	<0.001
	Nutrient	1	5.81	0.23	0.640
	Cage * Nutrient	2	15.17	0.59	0.564
	Error	21	25.74		
Thalassia testudinum	Cage	2	3483.61	4.20	0.029
	Nutrient	1	1242.15	1.50	0.235
	Cage * Nutrient	2	811.01	0.98	0.392
	Error	21	829.09		

site revealed that *Halodule wrightii* was generally absent from this site but occurred nearby (Fig. 1a, Fourqurean and Escorcia, 2005). Our study site at Carysfort (25° 12.965 N, 80° 13.682 W) was a patch reef (approx 450 m^2) encircled by a grazed halo extending out about three meters into the surrounding seagrass bed at a water depth of 5 m. Inside the halo, cropped *T. testudinum* dominated the plant biomass. Outside the halo, *S. filiforme* (manatee grass) and small clumps of macroalgae (e.g., *Dictyota* spp.) also occurred.

Herbivore assemblages and grazing behavior at the study site were qualitatively characterized in July 2004 along a 50 m transect bisecting the reef. A single SCUBA diver swam along the transect three times at a rate of ~15 m min^{-1}, each time counting the number and species of fish and invertebrate grazers within visual range. The dominant fish grazing on seagrass was *Sparisoma aurofrenatum* Valenciennes (redband parrotfish; approx. 1 fish 50 m^{-2}). *Meoma ventricosa* Lamarck (heart urchins) were also observed grazing on seagrass surrounding the reef (approx. 1 urchin 15 m^{-2}). These densities were comparable to those of urchins and other species of parrotfish at other sites in the FKNMS (Keller, 2003).

Background water column nutrient concentrations at the study site were relatively low, similar to other sites along the Florida Keys Reef Tract, with a total organic nitrogen concentration of approximately 8 μM and a total phosphorus concentration of approximately 0.2 μM (Keller, 2003). Despite low water column nutrient content, long-term monitoring revealed that *Thalassia testudinum* at this site had a tissue N:P ratio of approximately 30:1, suggesting a balance in N and P supply (Atkinson and Smith, 1983; Fourqurean et al., 2005).

2.2. Experimental design

In July 2004 we established 30 plots in two parallel rows within a 3 × 30 m band around the perimeter of the patch reef. Each plot was separated by at least 1 m from other plots and from the reef. We randomly assigned one of three caging treatments to each plot: full cage, partial cage, or open. Cages were constructed from 1.25 cm steel mesh hardware cloth and held in place with steel rods. Full cages had four 0.5 × 0.5 m side panels and a top, restricting access of all macroherbivores. Partial cages consisted of three sides and a top to control for hydrological and shading caging artifacts but allow full herbivore access. Open plots (0.25 m^2) were demarcated with steel rods. We randomly assigned nutrient enrichment treatments to half of the experimental plots from each caging treatment ($n=5$ per treatment). Nitrogen was added to the sediment in the form of slow release nitrogen fertilizer (Polyon™, Pursell Technologies Inc., 38-0-0) and phosphorus as granular phosphate rock (Multifos™, IMC Global, $Ca_3(PO_4)_2$, 18% P). Loading rates of 1.43 g N m^{-2} day^{-1} and 0.18 g P m^{-2} day^{-1} (molar N:P ratio 17.6:1) were selected based on potential sewage loading rates (MCSM, 2001) and previous studies in the region (Ferdie and Fourqurean, 2004; Armitage et al., 2005). Benthic fertilizer applications ensured accessibility of nutrients to both above-ground and benthic primary producers (Ferdie

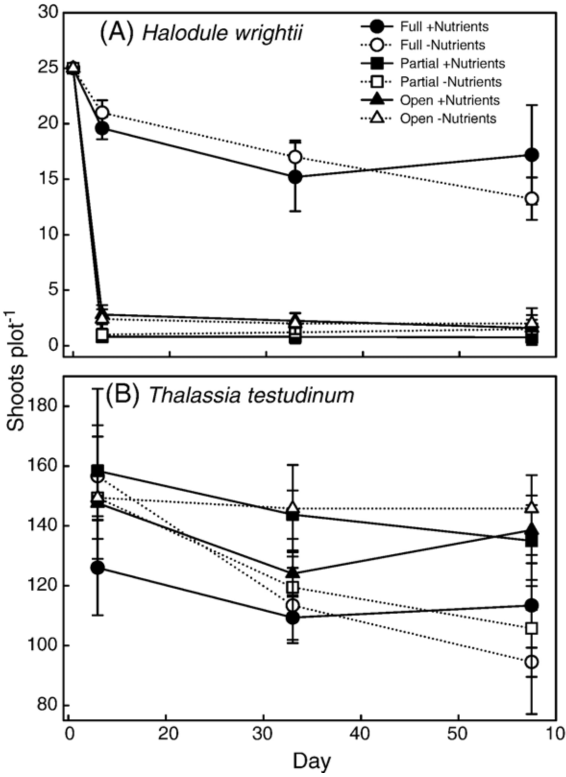

Fig. 2. Changes in (A) *Halodule wrightii* and (B) *Thalassia testudinum* shoot density in experimental plots over the study period in response to caging and nutrient enrichment treatments. Error bars represent ± 1 SE.

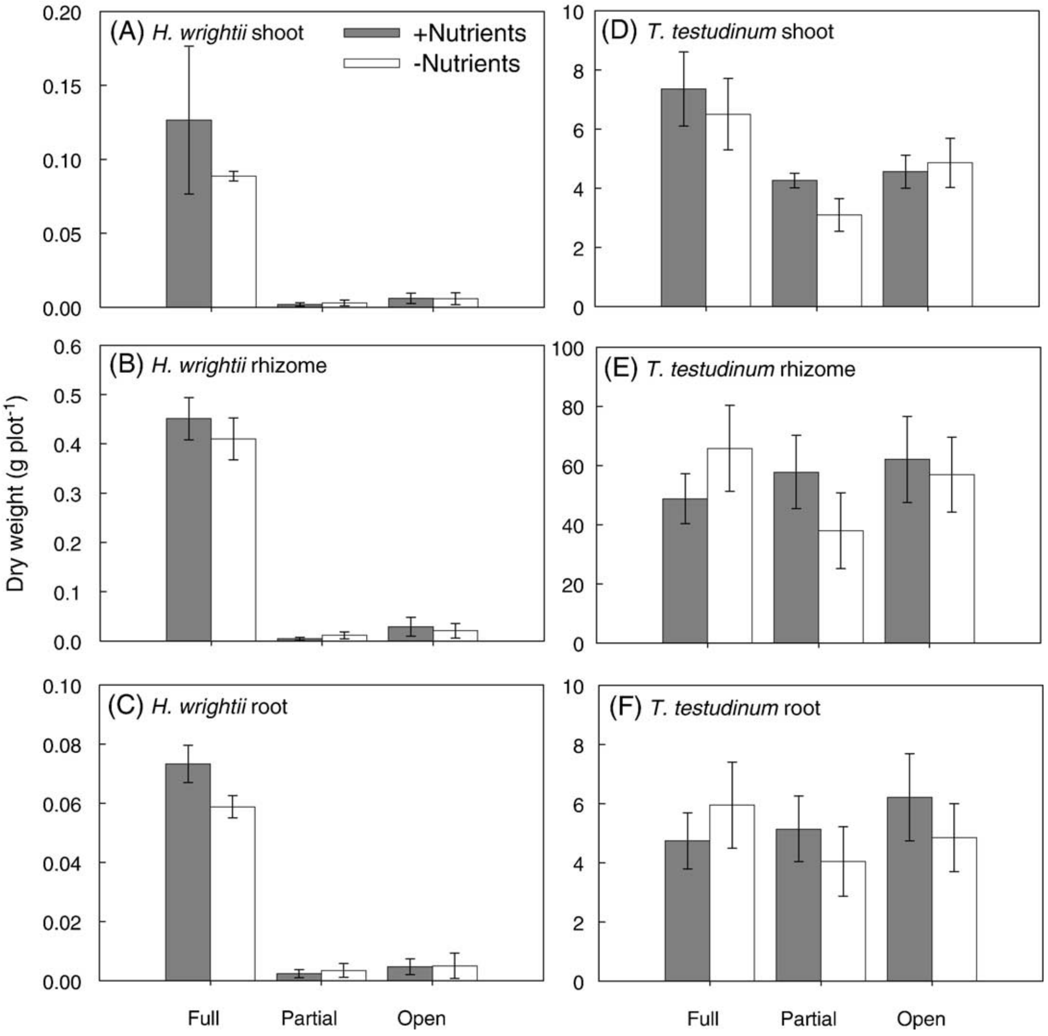

Fig. 3. Response of seagrass biomass to caging and nutrient enrichment treatments: (A–C) *Halodule wrightii* shoot, rhizome, and root biomass; (D–F) *Thalassia testudinum* shoot, rhizome, and root biomass. Error bars represent ±1 SE.

and Fourqurean, 2004; Mutchler et al., 2004; Armitage et al., 2005), and since the preponderance of nutrients in the water column in this region are bound to particulates (Fourqurean et al., 1993), sediment addition most closely mimics natural nutrient loading. Although *T. testudinum* rhizomes can be longer than 1 m, nutrient enrichment effects using our benthic addition protocol have been highly localized (Armitage et al., 2005), indicating that spacing plots at least 1 m apart was sufficient to separate nutrient treatments.

In order to explore the causes of temporal and spatial patchiness of *Halodule wrightii* in the FKNMS, sprigs of *H. wrightii* were collected by hand from a robust population at a nearby site (24° 47.820 N, 80° 43.609 W) with similar sandy sediments and ocean exposure as at Carysfort Reef but not close to any patch reefs. All sprigs consisted of five shoots connected by a horizontal rhizome and an apical meristem. Sprigs were aerated in buckets of seawater during transport to the study site and transplanted into the study plots within four hours of collection. Five sprigs were secured to the bottom of each plot using metal garden staples and the rhizomes were gently buried under 1–2 cm of sediment. We recorded the density of *H. wrightii* and *Thalassia testudinum* shoots in the study plots 6, 46, and 95 days after transplantation.

At the end of experiment (October 2004, 98 days after transplantation), we collected all *H. wrightii* above- and belowground biomass from each plot by flushing away the top layer of sediment by hand and carefully removing the rhizomes and attached shoots and roots. *T. testudinum* above- and belowground biomass was then

Table 2
Results from two-way ANOVA of caging and nutrient enrichment treatments on *Halodule wrightii*, *Thalassia testudinum*, and epiphyte characteristics

		df	MS	*F*	P
H. wrightii shoot biomass	Cage	2	0.97	96.58	<0.001
	Nutrient	1	<0.01	0.07	0.792
	Cage * Nutrient	2	<0.01	0.23	0.795
	Error	21	0.01		
H. wrightii rhizome biomass	Cage	2	0.14	66.25	<0.001
	Nutrient	1	<0.01	0.32	0.578
	Cage * Nutrient	2	<0.01	0.30	0.744
	Error	21	<0.01		
H. wrightii root biomass	Cage	2	0.01	154.71	<0.001
	Nutrient	1	<0.01	1.69	0.208
	Cage * Nutrient	2	<0.01	2.32	0.123
	Error	21	<0.01		
T. testudinum shoot biomass	Cage	2	0.19	6.79	0.005
	Nutrient	1	0.02	0.63	0.436
	Cage * Nutrient	2	0.01	0.39	0.681
	Error	21	0.03		
T. testudinum rhizome biomass	Cage	2	2.65	0.45	0.642
	Nutrient	1	0.38	0.07	0.802
	Cage * Nutrient	2	5.92	1.01	0.382
	Error	21	5.87		
T. testudinum root biomass	Cage	2	2.03	0.35	0.707
	Nutrient	1	0.23	0.04	0.842
	Cage * Nutrient	2	5.91	1.03	0.375
	Error	21	5.75		
T. testudinum leaf surface area	Cage	2	95.99	9.12	0.001
	Nutrient	1	39.43	3.75	0.067
	Cage * Nutrient	2	9.55	0.91	0.419
	Error	21	10.53		
Epiphyte dry weight	Cage	2	0.21	2.07	0.151
	Nutrient	1	0.02	0.21	0.649
	Cage * Nutrient	2	0.01	0.07	0.936
	Error	21	0.10		
Epiphyte chlorophyll *a*	Cage	2	<0.01	0.86	0.437
	Nutrient	1	0.10	2.42	0.135
	Cage * Nutrient	2	<0.01	0.24	0.792
	Error	21	<0.01		

subsampled using a 15 cm diameter, 15 cm deep core placed in the center of each plot. All epiphytes, including encrusting coralline algae and adhered sediments, were removed from *T. testudinum* leaves by gently scraping each leaf with a razor blade and dried to determine epiphyte dry weight. Epiphytes were generally sparse on *H. wrightii* leaves, so any epiphytes were removed and discarded. We separated aboveground (photosynthetic) tissue from the roots and rhizomes of each seagrass species. To estimate areal loss of *T. testudinum* due to herbivory, images of the cleaned *T. testudinum* leaves were created using a digitizing pad and the remaining leaf surface area was calculated using ImageJ 1.33u software (National Institutes of Health, USA). We calculated areal loss as the percent difference in leaf area between open or partial cages vs. full cages. *H. wrightii* leaves are too thin to utilize this imaging method. Each of the three tissue types (shoot, rhizome, root) for each species was dried separately at 60 °C and weighed to estimate biomass. To estimate the net effect of grazing on aboveground biomass, we calculated the loss rate using the exponential decay equation $\ln(B_t/B_o) = -Ht$, where H was the herbivory rate and B_t/B_o was the proportion of biomass remaining in partial cages or open plots relative to full cages at time t. We defined t as the number of days over which most biomass loss occurred (6 days for *H. wrightii* and 98 days for *T. testudinum*). We assumed that new tissue production rates were the same in all caging treatments, and that in the absence of herbivory, loss rates from senescence were equivalent to production rates, resulting in a steady state. In the partial cages and open plots, the loss rate that we calculated represented tissue loss from herbivory.

We determined the nitrogen content of each seagrass tissue type for each species separately using a CHN analyzer (Fisons NA1500). Phosphorus content was determined by a dry-oxidation, acid hydrolysis extraction followed by a colorimetric analysis of phosphate concentration of the extract (Fourqurean et al., 1992). Tissue nutrient content analyses were performed only for tissue from full cages because insufficient *H. wrightii* tissue for processing was available from partial and open caging treatments.

We collected one additional intact *T. testudinum* shoot and removed the epiphytes with a razor blade. There was not sufficient *H. wrightii* tissue to provide enough epiphyte material for analysis. Epiphytes were freeze dried and pigments extracted with 90% acetone. The epiphyte chlorophyll *a* concentration was determined

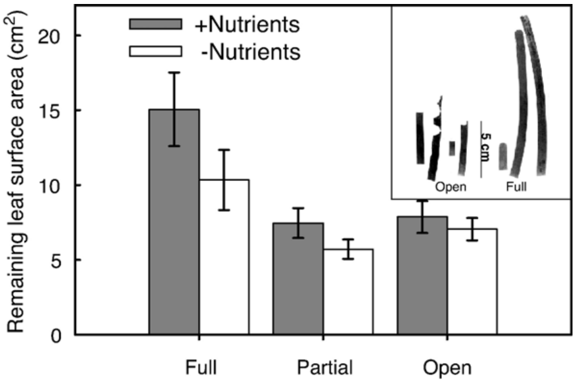

Fig. 4. Remaining one-sided *Thalassia testudinum* leaf surface area following 98 days of caging and nutrient enrichment treatments. Inset depicts patterns of bite marks on tissue from open plots and from full caging treatments. Error bars represent ± 1 SE.

Table 3
Epiphyte dry weight and chlorophyll *a* concentration (mean±SE) in response to caging and nutrient enrichment treatments

	Epiphyte dry weight (mg cm^{-2})	Epiphyte chlorophyll *a* (μg cm^{-2})
Full +nutrients	0.519±0.054	0.233±0.027
Full −nutrients	0.631±0.079	0.194±0.014
Partial +nutrients	0.415±0.080	0.194±0.024
Partial −nutrients	0.413±0.127	0.181±0.009
Open +nutrients	0.692±0.251	0.205±0.035
Open −nutrients	0.755±0.157	0.157±0.027

following the high performance liquid chromatography method of Pinckney et al. (1999).

All data were tested for homoscedasticity using the $F_{\max}$ test and log transformed if necessary to conform to the assumptions of ANOVA. Three cages were damaged during the course of the study and discarded from the statistical analyses (one each of partial +nutrients, partial −nutrients, and full −nutrients). *H. wrightii* and T. *testudinum* final shoot density, shoot, root, and rhizome dry weight, *T. testudinum* leaf area, epiphyte dry weight, and epiphyte chlorophyll *a* concentration were analyzed with two-way Model I ANOVA, where the factors were caging treatment and nutrient addition. For each group of primary producers, we adjusted *P*-values for multiple comparisons with the Bonferroni procedure, where the corrected $P=\alpha/c$, $\alpha=0.05$, and c was the number of comparisons within each group (*T. testudinum*: 5 comparisons, adjusted $P=0.010$; *H. wrightii*: 4 comparisons, adjusted $P=0.013$; epiphytes: 2 comparisons, adjusted $P=0.025$). The nitrogen and phosphorus contents of each seagrass tissue type were determined only for full cage treatments due to the lack of sufficient tissue for analysis from partial and open treatments, so nutrient contents were analyzed with unpaired *t*-tests with nutrient addition as the grouping variable.

3. Results

Halodule wrightii shoot density in the open and partial treatments was dramatically and rapidly reduced by herbivory, resulting in a highly significant cage effect (Table 1). In full cages, *H. wrightii* density decreased over the study period from 25 shoots plot^{-1} to about 15 shoots plot^{-1}. In open and partial cage treatments, *H. wrightii* density was reduced by 91% to approximately two shoots plot^{-1} by the sixth day of the study and did not recover over the study period (Fig. 2a). Nutrient addition did not affect *H. wrightii* shoot density in any of the caging treatments and there were no interactions between factors. After adjusting *P*-values for multiple comparisons, *Thalassia testudinum* shoot density was not significantly affected by cage treatment (Table 1), though there was lower density in full cages than in open plots (Fig. 2b). *T. testudinum* density in partial cages was similar to open plots, suggesting that there was no caging artifact. *T. testudinum* shoot density was not affected by nutrient addition and there were no interactions between factors.

Halodule wrightii shoot, rhizome, and root biomass were all significantly lower in open and partial cage treatments than in full cages (Fig. 3a–c, Table 2). Shoot, rhizome, and root biomass were 98%, 98%, and 96% lower, respectively, in partial cages and 95%, 94%, and 93% lower in open plots relative to full cages. Nutrients did not affect the biomass of any tissue type and there were no interactions between factors. The estimated

Table 4
Tissue nitrogen (N) and phosphorus (P) content as a percent of dry weight (mean±SE) in *Halodule wrightii* and *Thalassia testudinum* shoot, rhizome, and root tissues from full cages, and results from unpaired *t*-tests of nutrient enrichment treatment on plant tissue nitrogen and phosphorus content

N content	*H. wrightii* shoot	*H. wrightii* rhizome	*H. wrightii* root	*T. testudinum* shoot	*T. testudinum* rhizome	*T. testudinum* root
Enriched	1.99±0.11	0.86±0.32	0.84±0.05	1.88±0.10	0.78±0.03	0.89±0.03
Unenriched	1.74±0.03	0.52±0.03	0.73±0.02	1.68±0.05	0.64±0.03	0.87±0.02
t-value	2.08	1.05	1.99	1.76	3.02	0.75
P	0.095	0.351	0.106	0.134	0.020	0.484
P content						
Enriched	0.112±0.009	0.041±0.004	0.053±0.003	0.114±0.003	0.148±0.024	0.046±0.005
Unenriched	0.131±0.005	0.039±0.004	0.045±0.001	0.133±0.007	0.121±0.017	0.043±0.007
t-value	−1.47	0.45	2.25	−2.42	0.89	0.37
P	0.209	0.670	0.075	0.074	0.405	0.728
N:P ratio						
Enriched	39.4±1.2	44.4±13.6	36.4±2.0	36.5±2.1	12.8±1.9	45.0±4.8
Unenriched	29.5±0.9	29.9±1.4	36.3±1.1	28.3±2.3	12.7±2.6	49.1±8.8
t-value	6.07	1.06	0.04	2.65	0.03	−0.41
P	<0.001	0.347	0.969	0.034	0.981	0.700

daily net loss of *H. wrightii* due to grazing was 65.2% day^{-1} in partial cages and 50.0% day^{-1} in open plots. *Thalassia testudinum* shoot biomass was significantly lower in open and partial cages than in full cages (47% loss in partial cages and 32% loss in open plots relative to full cages) but was unaffected by nutrient addition (Fig. 3d, Table 2). *T. testudinum* rhizome and root biomass were not affected by nutrients or caging treatment with no interactions between factors (Fig. 3e–f). The estimated daily net loss of *T. testudinum* due to grazing was 0.6% day^{-1} in partial cages and 0.4% day^{-1} in open plots.

The average per-plot one-sided *T. testudinum* leaf surface area was significantly lower in the open and partial treatments than in full cages (Fig. 4, Table 2). Leaf area was reduced by 48% in partial cages and 41% in open plots relative to full cages. Bite mark patterns were characteristic of parrotfish herbivory (Fig. 4, McClanahan et al., 1994). There was no significant nutrient effect on leaf surface area and there were no interactions between factors (Table 2).

Both estimates of epiphyte biomass, epiphyte dry weight and chlorophyll *a* concentration, were not affected by caging or nutrient treatments with no interactions between factors (Tables 2 and 3).

Nitrogen and phosphorus content of *H. wrightii* and *T. testudinum* tissues were largely unaffected by nutrient addition (Table 4). N content of *T. testudinum* rhizomes was significantly higher in enriched treatments, and the N:P ratios of both *H. wrightii* and *T. testudinum* shoots were significantly higher in enriched treatments, but the nutrient contents of all other tissue types were not affected by nutrient addition.

For all response variables, results were similar between open plots and partial cages, suggesting that caging artifacts on the measured variables were minimal.

4. Discussion

We observed a strong and immediate effect of herbivory on seagrass species composition. Herbivory is known to be an important influence on seagrass density (Thayer et al., 1984; Valentine and Heck, 1999; Maciá and Robinson, 2005), and can have particularly pronounced impacts around patch reefs, where halos of heavily or completely grazed seagrass occur (Randall, 1965). More of this grazing is attributed to parrotfish (Scaridae) than urchins (Tribble, 1981; Hay et al., 1983), and the patterns of bite marks on leaves in our study (Fig. 4) indicated that parrotfish (particularly *Sparisoma aurofrenatum*) were largely responsible for the grazing we observed. Previous work has revealed that 3–10% of transplanted *Thalassia testudinum* tissue is often consumed within 24 h (Hay et al., 1983; Kirsch et al., 2002; Goecker et al., 2005). In our study, grazing rates on *T. testudinum* appeared to be somewhat lower, as comparisons between open and full cage treatments estimated that consumption rates were less than 0.6% day^{-1}, which is roughly 25% of the daily gross leaf production of ca. 2% day^{-1} typical of south Florida seagrass beds (Fourqurean et al., 2001). Our lower grazing rates are likely a function of different grazer densities in our field manipulations compared to earlier studies. The grazing rate on *Halodule wrightii* was substantially higher than for *T. testudinum*, as high as 65% day^{-1}. This intense grazing on *H. wrightii* corresponds with previous studies documenting stronger grazing pressure on faster growing species in seagrass (Mariani and Alcoverro, 1999), marine algal assemblages (Hay, 1981a), and tropical forests (Coley, 1983). We assumed that new tissue production rates were the same in all caging treatments. We detected few caging artifacts, but if cage shading altered production rates, the daily net loss rates we calculated may not be absolute values. Regardless, our estimates illustrated that net daily loss of *H. wrightii* due to grazing was much higher than for *T. testudinum*.

Reef-associated grazers such as parrotfish and damselfish can have strong impacts on algal assemblages and on the co-occurrence of algal and coral species (Hay, 1997; Ferreira et al., 1998; Overholtzer and Motta, 1999; Ceccarelli et al., 2005). Although grazers can have large impacts on seagrass biomass (e.g., Thayer et al., 1984; Valentine and Heck, 1999), the influence of herbivores on the co-occurrence of multiple seagrass species is not as well understood. We demonstrated that the impacts of grazing can vary among seagrass species near herbivore refuges like patch reefs over a short time scale, suggesting that herbivory may be an important regulator of the distribution of multiple seagrass species in the FKNMS. *H. wrightii* is relatively sparse throughout the FKNMS (Fourqurean et al., 2002), so reef-associated herbivory, though important at our study site, is not the only source of grazing that may limit its distribution. Other grazers that are not as closely linked to reef structures, including urchins and other parrotfish (e.g., bucktooth parrotfish *Sparisoma radians*) may regulate *H. wrightii* distribution in areas that are further away from patch reefs (Kirsch et al., 2002; Maciá and Robinson, 2005). Selective grazing on particular seagrass species has been documented in the US Virgin Islands (Lobel and Ogden, 1981) and Kenya (Mariani and Alcoverro, 1999), though the implications of selective consumption for seagrass species distribution was not examined in those studies. Tribble (1981) demonstrated that grazing intensity influenced the relative abundance of *Thalassia testudinum* and *Syringodium filiforme* near patch reefs in the western Caribbean, and McClanahan et al. (1994) observed that seagrass species distribution correlated with grazer species composition in Kenya. The mechanisms driving selective grazing may include selection for a mixed diet in which varied components provide a range of protein and nutrient contents (Lobel and Ogden, 1981; Raubenheimer et al., 2005). In addition, *T. testudinum* and *H. wrightii* may have different lignin content, which can alter nutritive value and influence herbivory patterns (Thayer et al., 1984).

Transplant stress may have made *H. wrightii* more susceptible to herbivory than *T. testudinum*, which was not transplanted into the study site. The overall decrease in *H. wrightii* shoot density within full cages over the course of the study period suggests that some degree of transplant stress occurred, but a similar decrease was detected for *T. testudinum* as well, indicating that the change in shoot densities was probably attributable to a more general temporal trend at this site. Herbivorous reef fish often rapidly graze transplanted plant tissue (Hay, 1981b), which may have augmented the parrotfish preference for *H. wrightii* in our study. In addition, if all of the transplants had been initially caged to facilitate establishment before exposing them to herbivory, the *H. wrightii* rhizome system would have become more firmly attached in the sediment. Subsequent herbivory might not have removed the rhizome system as well as the shoots and allowed cropped but well-rooted *H. wrightii* to persist. Although these factors suggest that the absolute rate of herbivory on *H. wrightii* that we observed may have been somewhat inflated, it is also likely that *H. wrightii* is more susceptible to grazing because its thin leaves are clipped entirely by herbivores, whereas wider *T. testudinum* leaves can remain partially intact and attached to the shoot even under heavy grazing pressure (Fig. 4, Zieman et al., 1979).

Nutrient enrichment had few effects on seagrass species composition or on herbivory patterns. This contrasts with studies in other marine systems, which have documented elevated grazing pressure on enriched plant tissue (McGlathery, 1995; Boyer et al., 2004; Goecker et al., 2005). Seagrass with more than 1.8% N tissue content is not predicted to respond to N enrichment (Duarte, 1990). Accordingly, shoot N content in our study for both *T. testudinum* and *H. wrightii* was near or above the 1.8% threshold for N limitation, and we did not observe any responses to N addition. Furthermore, the shoot N:P ratios of both species were near the 30:1 value that indicates a balance between N and P supply (Atkinson and Smith, 1983), suggesting that neither N nor P were limiting seagrass growth at our study site on the short time scale of this study. The effects of nutrient enrichment on seagrass community structure often manifest over longer time scales (Fourqurean et al., 1995; Armitage et al., 2005). The slight but significant increases in shoot N:P ratios that we observed in nutrient addition plots suggest that longer-term enrichment, particularly of N, might impact the patterns of herbivory on *T. testudinum* and *H. wrightii* in this oceanic, well-flushed environment, though herbivory appears to be a strong short-term influence on the coexistence of these species at this site. We know of no other studies that simultaneously evaluated the roles of grazers and nutrients on the co-occurrence of seagrass species, and further investigation is necessary to understand these longer-term dynamics.

In addition to excluding seagrass grazers, our full caging treatment also prevented large epiphyte grazers (e.g., Acanthuridae such as tangs and surgeonfish) and micrograzer predators (e.g., Chaetodontidae such as butterflyfish) from foraging in the study plots. Though we did not directly measure herbivore response to caging treatments, small grazers such as amphipods can control epiphyte biomass (Duffy and Harvilicz, 2001), subsequently increasing seagrass productivity (Howard and Short, 1986). We detected no difference in epiphyte biomass among caging treatments and there was no response of epiphytes to nutrient addition, despite nutrient-induced increases in biomass and shifts in species composition that have been observed in other studies (McGlathery, 1995; Ferdie and Fourqurean, 2004; Armitage et al., 2006). The consistently low epiphyte biomass across treatments suggests that an increase in micrograzers inside full cages following a release from predation pressure compensated for the exclusion of macrograzers. Further examination of interactions between guilds of grazers is necessary to understand the indirect effects of the removal of large omnivorous and carnivorous fish from reef–seagrass habitats.

The strong short-term influence of herbivory on the co-occurrence of *T. testudinum* and *H. wrightii* may vary along a spatial gradient, decreasing in importance further away from patch reefs. A similar pattern of decreasing herbivore influence on *S. filiforme* abundance was observed in the San Blas Islands (Tribble, 1981). The influence of parrotfish grazing can also change relative to the distance from refuges in blowouts (bare patches) within seagrass beds (Maciá and Robinson, 2005). These spatial gradients in herbivory pressure can be altered by ecosystem management practices. Overfishing, for example, can directly remove the herbivores that controlled *H.*

wrightii density in our study (McClanahan et al., 1994). In addition, the foraging behavior of herbivorous parrotfish can be altered by removal of top predators through heavy fishing pressure, effectively increasing the distance parrotfish will forage off patch reefs, which is largely governed by predation risk (Randall, 1965; Sweatman and Robertson, 1994). Alternatively, increased human presence on reefs may increase parrotfish sheltering behavior, decreasing the distance of herbivore influence on seagrass species distribution. The seagrass beds we studied may be particularly sensitive to changes induced by alterations of the food web, since short-term grazing activity strongly influenced the coexistence of *H. wrightii* and *T. testudinum*. The FKNMS includes areas that are fully protected, partially protected, and open to commercial and recreational fishing (Pattengill-Semmens, 2002). Regulation of fishing pressure in these protected areas is known to benefit several commercially and recreationally targeted fish species, including multiple grouper species (Ault et al., 2005), which in turn may influence the off-reef foraging behavior of grazing fish such as parrotfish. The impacts of this management strategy on seagrass communities is not well understood, but our study suggests that because the influence of grazers on seagrass species composition can be very strong, management zones in the FKNMS may have cascading effects on lower trophic levels as well. Further studies of the links between the management of fishing pressure and the composition of primary producer communities will aid in the effective planning and implementation of management strategies in this region.

Acknowledgments

This project was funded as part of the Water Quality Protection Program of the Florida Keys National Marine Sanctuary, and jointly funded by the U.S. Environmental Protection Agency (cooperative agreement x97468102-0) and the National Oceanic and Atmospheric Administration's Coastal Oceans Program (contract NA04NOS4780024). Fred McManus of the EPA is the coordinator of the Water Quality Protection Program; without his continued support our work would not have been possible. Our permit to work in the Florida Keys National Marine Sanctuary was expedited by Joanne Delaney and Brian Keller of NOAA. Thanks to the many people who helped in the field and the laboratory, especially Ginny Cornett and Kevin Cunniff. Pursell Technologies Inc. and IMC Global generously donated the nitrogen and phosphorus fertilizers, respectively, for this study. This is contribution #332 of the Southeast Environmental Research Center at FIU. **[SS]**

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