

Role of sea urchin *Lytechinus variegatus* grazing in regulating subtropical turtlegrass *Thalassia testudinum* meadows in the Florida Keys (USA)

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ABSTRACT: In previous work, in St. Joseph Bay, Florida (30° N, 85.5° W), in the northeastern Gulf of Mexico, we found that sea urchin *Lytechinus variegatus* grazing usually controlled seasonal changes in turtlegrass *Thalassia testudinum* abundance. In this study, we tested the generality of those conclusions by conducting new grazing studies in 2 turtlegrass habitats in the subtropical Florida Keys (USA). In the first experiment, we varied the duration of sea urchin grazing bouts in order to understand the impacts of temporally varying herbivory on seasonal changes in turtlegrass biomass in shallow water (<2 m) near Big Pine Key (~25° N, 85° W). In the second experiment, we examined the effects of chronic low levels of grazing on seagrass growth and biomass in a deeper-water seagrass habitat (6 to 7 m) in Hawk Channel (~25° N, 80° W). These new studies suggest that the impacts of sea urchin grazing are highly variable in the Florida Keys. Depending on the season, urchin grazing (at densities of 20 ind. m⁻²) had both negative and positive effects on seagrass biomass in Big Pine Key. If grazing occurred during spring, turtlegrass biomass was significantly reduced by short bouts of sea urchin herbivory. The impacts of this spring grazing extended into early summer. If grazing occurred in summer, sea urchins reduced turtlegrass biomass for only short periods of time, after which urchin grazing stimulated turtlegrass production. These findings are similar to those of previous grazing experiments conducted in St. Joseph Bay. In contrast, we found little evidence that ambient (0 to 8 ind. m⁻²) densities of sea urchins could control either seagrass production or biomass in the deeper waters of Hawk Channel. The differences we found in grazer impacts on turtlegrass growth and abundance, in a well-lit shallow water habitat and deeper-water habitat with less light, suggest that there is a critical need not only to repeat experiments in environments with differing physical conditions but also to develop a more complete understanding of the mechanisms by which seagrasses can compensate for losses of tissues to marine herbivores under varying environmental conditions.

KEY WORDS: Seagrass · Herbivory · Sea urchins · Food webs

INTRODUCTION

Herbivores often determine the productivity and abundance of plants in aquatic environments (e.g., Porter 1973, 1977, Lynch & Shapiro 1981, Lewis 1985, Vanni 1987a, Mallin & Paerl 1994). For example, in freshwater lakes, zooplankton grazing can reduce the

abundance of small or naked phytoplankton species, favoring the survival of larger phytoplankton species with gelatinous sheaths or other structures that reduce their vulnerability to grazing (e.g., Porter 1973, 1977, McCauley & Briand 1979, Demot & Kerfoot 1982, Vanni 1987b). In marine environments, grazing by coral reef fishes and invertebrates can cause dramatic shifts in macroalgal community structure from dominance by highly competitive, fast-growing, edible algae to competitively inferior, slower growing, but

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chemically defended algae (reviewed by Hay & Steinberg 1992). Similarly, gastropod grazing can alter macroalgal community structure in temperate rocky intertidal zones by consuming competitively dominant, fast-growing, more palatable species, which are then replaced by competitively inferior, slower growing, less palatable species (reviewed by Lubchenco & Gaines 1981, Gaines & Lubchenco 1982). In perhaps the most dramatic example of herbivore impacts on marine plants, sea urchin grazing can convert macroalgal kelp forests to grazer-resistant coralline-dominated algal pavements in temperate and boreal settings (reviewed by Lawrence 1975). These observations suggest that herbivores can, at times, play an important role in determining both the composition of ecological communities and the manner in which energy flows from plants to higher order consumers.

In contrast to these better-studied habitats, grazing rates in seagrass meadows are believed to be very low. In part, this is because seagrasses are thought to contain little nutritional value, owing to the high C/N ratios of their leaves (e.g., Bjorndal 1980, Duarte 1990) and the apparent inability of most invertebrate grazers to digest cellulose (Lawrence 1975). Current levels of seagrass herbivory are also thought to be low because of the low densities of larger vertebrate herbivores (e.g., green turtles, dugongs, manatees, fishes, and waterfowl) (Randall 1965, Heinsohn & Birch 1972, Lipkin 1975, Charman 1979, Bjorndal 1980, Kiorbøe 1980, Jacobs et al. 1981, Thayer et al. 1984). In some areas, the proportion of seagrass production directly entering food webs via grazing is quite low (less than 15% of annual net aboveground primary production (NAPP) (Nienhuis & Van Ierland 1978, Nienhuis & Groenendijk 1986, Cebrián et al. 1996, Cebrián & Duarte 1998). Most seagrass production is believed to enter coastal food webs through the detrital pathway (e.g., Fenchel 1970, 1977, Kikuchi & Pérès 1977, Kikuchi 1980, Nienhuis & Van Ierland 1978, Thayer et al. 1984, Nienhuis & Groenendijk 1986, Zieman & Zieman 1989).

There is evidence, however, that the underlying assumptions of this grazing paradigm need reevaluation (Klumpp et al. 1993, Cebrián & Duarte 1998, Valentine & Heck 1999). For example, investigators have shown that the nitrogen concentration of the leaves of many seagrasses, often considered to be an indicator of plant nutritional quality, is similar to that of algal tissue (Lowe & Lawrence 1976, Lobel & Ogden 1981; reviewed in Thayer et al. 1984). There is substantial evidence that detrital seagrass, the predominant pathway for the flow of energy from seagrasses to higher order consumers, is an even poorer source of nutrition (i.e., has lower leaf nitrogen content) for consumers than are living leaves (Harrison & Mann 1975,

Zieman 1975, Fenchel 1977, Thayer et al. 1977, Rice 1982, Klumpp & van der Walk 1984). The use of C/N ratios to assess the nutritional value of seagrasses to herbivores can be traced to Russell-Hunter (1970), who concluded that food with a C/N ratio < 17 was required to satisfy human protein requirements. Surprisingly, the relevance of this frequently used ratio as an indicator of the low nutritional quality of seagrass leaves has never been verified with marine herbivores (cf. Thayer et al. 1977, Hatcher 1994). It has been suggested, however, that the C/N ratio in seagrass leaves may actually be poor descriptors of their nutritional quality (Harrison & Mann 1975, Klumpp et al. 1989, Hatcher 1994). Therefore, based on available data, it seems premature to conclude that the nutritional content of seagrass leaves, by itself, limits the rate at which seagrasses are grazed (cf. Cebrián & Duarte 1998).

In St. Joseph Bay, Florida, we found that the sea urchin *Lytechinus variegatus*, at densities of 10 to 40 ind. m⁻², could have important impacts on turtlegrass *Thalassia testudinum* abundance during the fall, winter, and spring (Valentine & Heck 1991). However, once grazing pressure was relaxed, seagrass biomass rapidly reached levels that exceeded those measured in nearby ungrazed seagrass habitats (Valentine & Heck 1991). During summer, we found little evidence of grazing impacts on seagrass abundance, even at very high urchin densities. We also found that persistent grazing in plots where rhizomes were severed at the borders of the plots, thus preventing the allochthonous input of belowground reserves, could create persistent barren unvegetated substrates in short periods of time, especially during the winter and spring (Heck & Valentine 1995). From this, we concluded that belowground reserves allow turtlegrass to persist where herbivory is intense and can, depending on the season, allow seagrasses to recover rapidly to levels that equal or exceed nearby ungrazed plots (Valentine & Heck 1991, Valentine et al. 1997). During summer months we found that grazing triggered an increase in areal NAPP (Valentine et al. 1997). These results suggested to us that seagrasses have as yet undescribed abilities to compensate for losses of leaf tissue to herbivores, the existence of which could lead to a significant underestimate of the amount of seagrass material consumed by herbivores (Valentine & Heck 1999).

Through this study, we evaluate the generality of our previous work in the northeastern Gulf of Mexico by describing the findings of 2 additional experiments done in the Florida Keys. These experiments were designed to (1) assess the impact of varying intensities of sea urchin grazing on turtlegrass abundance and (2) the ability of turtlegrass to compensate for losses to grazers in both shallow (<2 m) and deeper-water (6 to 7 m) sites.

METHODS AND APPROACH

Description of study sites. The 2 study sites were located in the Florida Keys—one in the northern Keys (Hawk Channel) the other in the middle Keys (Big Pine Key) (Fig. 1). The depths at the Big Pine Key and Hawk Channel study sites were approximately 1.5 and 7 m, respectively. As such, these sites are representative of the range of depths at which turtlegrass is commonly found in much of south Florida (Zieman & Zieman 1989). Water temperatures vary seasonally, ranging from 14°C in winter to 35°C in summer in this region (Roessler & Tabb 1974).

The seagrass habitats of south Florida are dominated by monospecific stands of turtlegrass *Thalassia testudinum*, but shoalgrass *Halodule wrightii* and manatee grass *Syringodium filiforme* are also present (Roessler & Tabb 1974, Roessler et al. 1975, Thorhaug & Roessler 1977, Kenworthy & Schwarzschild 1998). As in north Florida, turtlegrass production is seasonal in south Florida but the growing season is longer, extending over some 7 to 8 mo (Zieman 1975, Thorhaug & Roessler 1977). South Florida standing crops of turtlegrass peak at 1800 g dry wt m⁻², while leaf densities have been reported as high as 5800 m⁻² (Zieman 1975).

The grazing experiments. **Big Pine Key:** Two experiments were designed to (1) assess the impacts of varying intensities of episodic sea urchin grazing on turtlegrass abundance in a seasonally productive shallow water seagrass meadow and (2) determine the rate at which turtlegrass biomass recovers following the relaxation of grazing pressure. Experiments were conducted in 2 seasons, spring (February through May) and summer (June through August), to assess the range of seagrass responses to herbivory to changing seagrass productivity. The cages used in the spring grazing experiment were sustained through July in order to assess the potential for sea urchins to create barren unvegetated substrates, as we found in St. Joseph Bay. Grazing experiments were conducted using 12 replicate 5 m² cages which were randomly assigned to a 2 × 6 array haphazardly located in an undisturbed turtlegrass meadow along the northern edge of Big Pine Key. Cages were constructed

with 30 mm plastic mesh that was attached to rebar stakes. Experimental treatments consisted of an ungrazed control and 3 grazing treatments of varying duration. In the first grazing treatment, sea urchin density was held constant at 20 sea urchins m⁻² for 1 mo, after which time the sea urchins were removed. In the second grazing treatment, this same sea urchin density was sustained for 2 mo, and then sea urchins were removed. In the third treatment, sea urchin density was held constant for 3 mo and then sea urchins were removed. The duration of the grazing treatments and sea urchin densities used in these experiments were based on the temporal range of reported patterns of sea

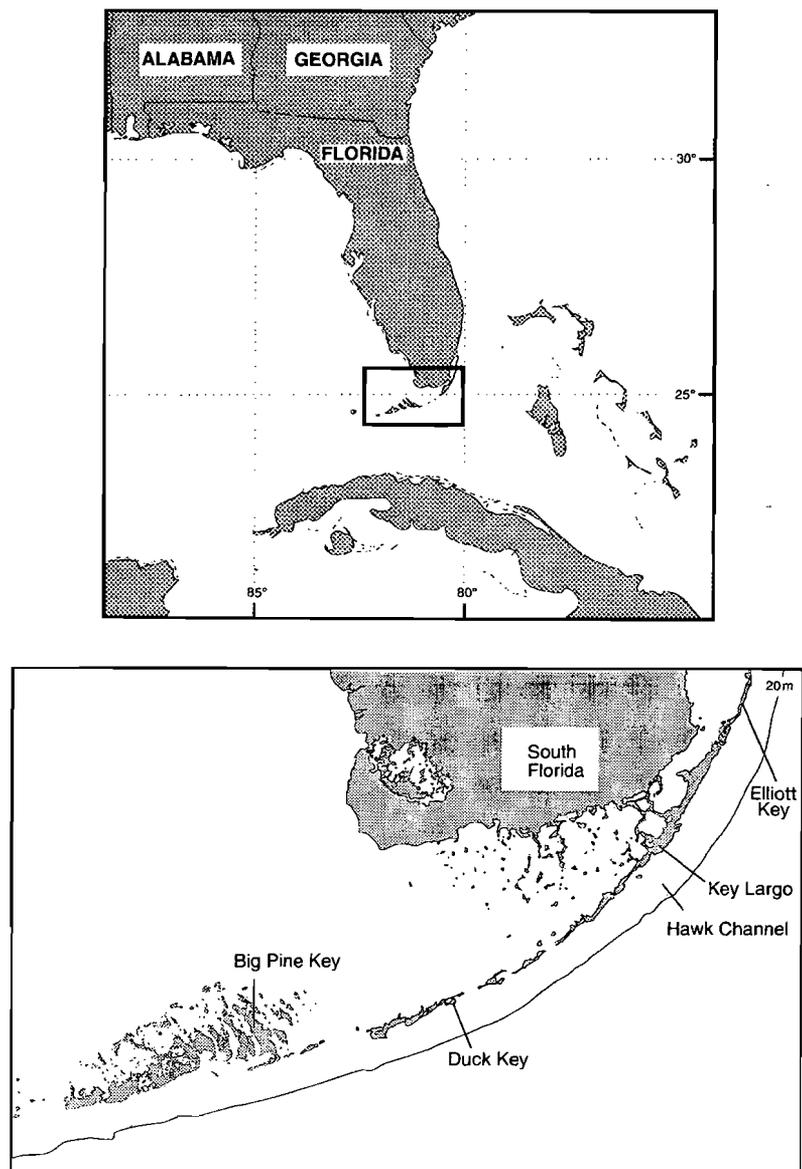


Fig. 1. Locations of the study sites in the Florida Keys (USA)

urchin grazing (Camp et al. 1973, Greenway 1976, Bach 1979, Engstrom 1982, Valentine & Heck 1991, Rose et al. 2000). The density of 20 ind. m^{-2} used in this experiment was chosen because it was the median density used in our previous experiments in St. Joseph Bay (Valentine & Heck 1991). Following the relaxation of grazing pressure, we maintained the integrity of the cages in an effort to determine the rate of seagrass recovery following the cessation of grazing. Each treatment was replicated 3 times.

The impact of sea urchin grazing was monitored by collecting 3 haphazardly located, 0.01 m^2 clippings of aboveground biomass from each cage, and 3 core samples (5 cm diameter \times 15 cm deep) of belowground turtlegrass biomass from each cage at 3 to 4 wk intervals. Core samples were collected from the same location as the aboveground biomass clippings. Sampling locations were marked with labeled wire stakes to ensure that no area was sampled more than once. The total amount of area sampled from each replicate cage was calculated to be 0.6% mo^{-1} . Samples were frozen and returned to the laboratory for analysis.

In the laboratory, aboveground biomass (g dry wt), was measured by drying clipped leaves in an oven at 60°C following the removal of leaf epiphytes by scraping with a razor blade. Leaves were dried to a constant weight. Core samples were washed over a 500 μm sieve to separate plant biomass from all sediments. Plant material was placed in pans and separated from infaunal organisms, dried to a constant weight, at 60°C, and weighed (± 0.01 g).

Hawk Channel: Twenty-one 1 m^2 cages constructed with 30 mm mesh plastic aquaculture netting and iron rebar were placed in a continuous turtlegrass habitat during the onset of the seagrass growing season. Sea urchins placed in these enclosures ranged in size from 45 to 55 cm horizontal diameter. Grazing intensity was manipulated in 3 treatments of 0, 4, and 8 ind. m^{-2} . These densities were based on the range of average densities found in Hawk Channel in an initial survey of the study area ($n = 49$). Each treatment was randomly assigned to 7 of 21 cages.

Sea urchins were enclosed in cages from May through July, after which time they were removed for 1 wk. During this interruption of grazing, several estimates of turtlegrass abundance, growth and biomass were made. The grazing impact on areal NAPP was measured (using a modified hole punch technique; Kirkman & Reid 1979) by marking all turtlegrass shoots within 3 haphazardly placed 0.01 m^2 quadrats in each cage. Leaves in each shoot were marked by punching holes through all leaves at the top of each shoot sheath. After 6 d, all of the marked shoots were clipped where the shoot attaches to the rhizome. Harvested shoots were frozen and returned to the laboratory for analy-

ses. Sea urchins were restocked following the harvesting of the marked shoots. From these samples, we recorded shoot density, aboveground seagrass biomass, and leaf epibiont biomass.

We also documented changes in belowground biomass. Belowground plant material was collected from three 15.24 cm diameter cores pushed 15 cm into the sediment. These core depths are within the turtlegrass rhizosphere (Williams 1990). Extruded cores were placed in a 500 μm sieve to separate the belowground plant material from the sediment. Belowground plant material was frozen and returned to the laboratory for analysis.

In the laboratory, areal NAPP (g ash free dry wt [AFDW] $m^{-2} d^{-1}$), aboveground seagrass biomass (g AFDW m^{-2}), shoot-specific growth (g AFDW shoot $^{-1} d^{-1}$), shoot density (no. m^{-2}), and epibiont biomass (g AFDW m^{-2}) were determined from each sample. Areal NAPP was defined as the mass of all blade tissue between the initial puncture scar and the top of the shoot sheath, plus any new unmarked blades formed during the 6 d period. Aboveground seagrass biomass was calculated as the sum of all blade tissue collected in each quadrat. All growth and biomass samples were dried to a constant weight at 60°C. After dried samples were weighed (± 0.1 mg), they were ashed in a muffle furnace at 500°C for 5 h. Ashed samples were placed in desiccators to cool and then reweighed (± 0.1 mg). Epibiont mass was measured by scraping attached animals and plants from each side of each leaf with a razor blade then drying and weighing epibionts as described above (± 0.01 mg). We measured epibiont biomass because these organisms can shade seagrass blades and potentially alter NAPP.

Surveys of sea urchin density in the northern and middle Florida Keys: To assess the distribution and density of *Lytechinus variegatus* at our study sites in the northern and middle Florida Keys, we conducted 3 separate surveys. In one, we recorded the densities of this sea urchin at stations located at 4.8 km intervals along the center of Hawk Channel from 2.5 n miles ESE of Elliott Key southwest to just offshore of Duck Key. At each station, we recorded sea urchin densities from three 1 m^2 quadrats haphazardly dropped within a turtlegrass meadow. The total length of this survey covered some 80 km. In the second survey, we documented changes in sea urchin densities at our study site in Hawk Channel over a 17 mo period by haphazardly dropping a 1 m^2 quadrat ($n = 10$) and counting all sea urchins within the quadrat during each visit. In the third survey, at Big Pine Key, we recorded sea urchin densities from 21 haphazardly located 1 m^2 quadrats at 3 locations around the island.

Statistical analyses. The Big Pine Key experiment: To determine the impacts of sea urchin grazing on sea-

sonal changes in seagrass abundance, growth and biomass we used a repeated measures analysis of variance (RMANOVA). Before conducting RMANOVA, Levene's test of equality was used to inspect data for homogeneity of variance on each sample date. In some cases, the data violated this assumption. These violations did not lead to increased incidence of Type I error (rejecting a true null hypothesis), as in none of these cases did we find evidence of significant grazing effects on seagrass abundance, growth, or biomass.

RMANOVA analyzes repetitively sampled replicates using both univariate and multivariate approaches. Output is in the form of between-subject effects and within-subject effects. Each examines data from a different perspective.

Between-subject effects represent a test of the overall significance of the experiment and treatment effects averaged over time. Computationally, the univariate and multivariate analyses of between-subject effects are the same. When significant between-subject differences were detected, *a posteriori* comparisons were made using the least significant difference test.

Within-subject effects comparisons represent a test of how treatments affect changes in a variable over time. For within-subject effects, the univariate approach is more powerful than the multivariate approach but has more restrictive assumptions (i.e., the circularity of the variance covariance matrix) (von Ende 1993). To test if the data met this assumption, we used Mauchly's test of sphericity. When sphericity is violated the *F* statistic can be inflated, thus increasing the probability of making a Type I error. When the sphericity assumption was violated, we made a Huynh-Feldt adjustment by multiplying the numerator and denominator degrees of freedom by epsilon (ϵ) (von Ende 1993), and *F* values and probabilities were recalculated (von Ende 1993). Once the probabilities were recalculated, results were inspected for significant within-subject treatment effects. When data were adjusted in this way, we also used the output of the RMANOVA multivariate testing of within-subject effects to interpret the data. While the MANOVA approach does not require that the matrix be circular, it does assume that the variance-covariance matrices across cells are the same. To test this assumption we used a Box M test. In some cases, we were unable to conduct the Box M test and multivariate output was not used. In those cases, our interpretation of within-subject effect data is based on the results of the univariate test. In addition, we calculated the statistical power of each comparison, at the 5% level of significance, as an indication of the strength of the *F* test for each main effect. In this case power is the probability that our *F* test will detect the difference between groups equal to those implied by the sample differences.

The Hawk Channel experiment: Initially, we intended to conduct this experiment from May until the end of September. Sampling was to take place in May, July and September. However, the passage of a tropical low that generated gale force winds for over 11 d in September breached 7 of our cages and allowed sea urchins to escape. The week before the storm, divers had checked the cages and found them intact. Consequently, we limit our analyses of the experiment to 2 sets of data. The first collected in May, prior to the inclusion of sea urchins in our grazing treatments. The second, collected in July, was the last month that we sampled.

One-way ANOVA was used to separately analyze samples collected in each month. Shoot density was transformed using a square root transformation to ensure that the variances were independent of the means. Other measured parameters satisfied the assumptions of ANOVA and were not transformed. Results were considered highly significant at the 5% level of significance and marginally significant at the 10% level of significance. All statistical analyses were conducted using the SPSSTM statistical package for personal computers.

RESULTS

Grazing in Big Pine Key

Sea urchin grazing, regardless of duration, significantly affected turtlegrass biomass (both above- and belowground) in each of our experiments (Tables 1 to 4, both between-subject effects and within-subject effects: time \times treatment interactions). The manner in which sea urchin grazing affected biomass varied between seasons, indicating a need to account for seasonal variation in seagrass growth when studying seagrass herbivory (Tables 1 to 4, within-subject effects: time \times treatment interactions).

Grazing had a highly significant effect on turtlegrass aboveground biomass in the spring experiment (Fig. 2a, Table 1, between-subject effects). The marginally significant interaction between time and grazing (Table 1, within-subject effects: time \times treatment interaction [univariate only]) indicates that treatment also had a weak effect on the rate at which aboveground biomass changed during this experiment (Fig. 2a).

A posteriori contrasts of the grazing treatments (between-subject effects) showed that the impacts of grazing on aboveground turtlegrass biomass were not uniform. For example, in the first month of the experiment, when sea urchins were present in all of the grazing treatments, aboveground biomass decreased faster in the

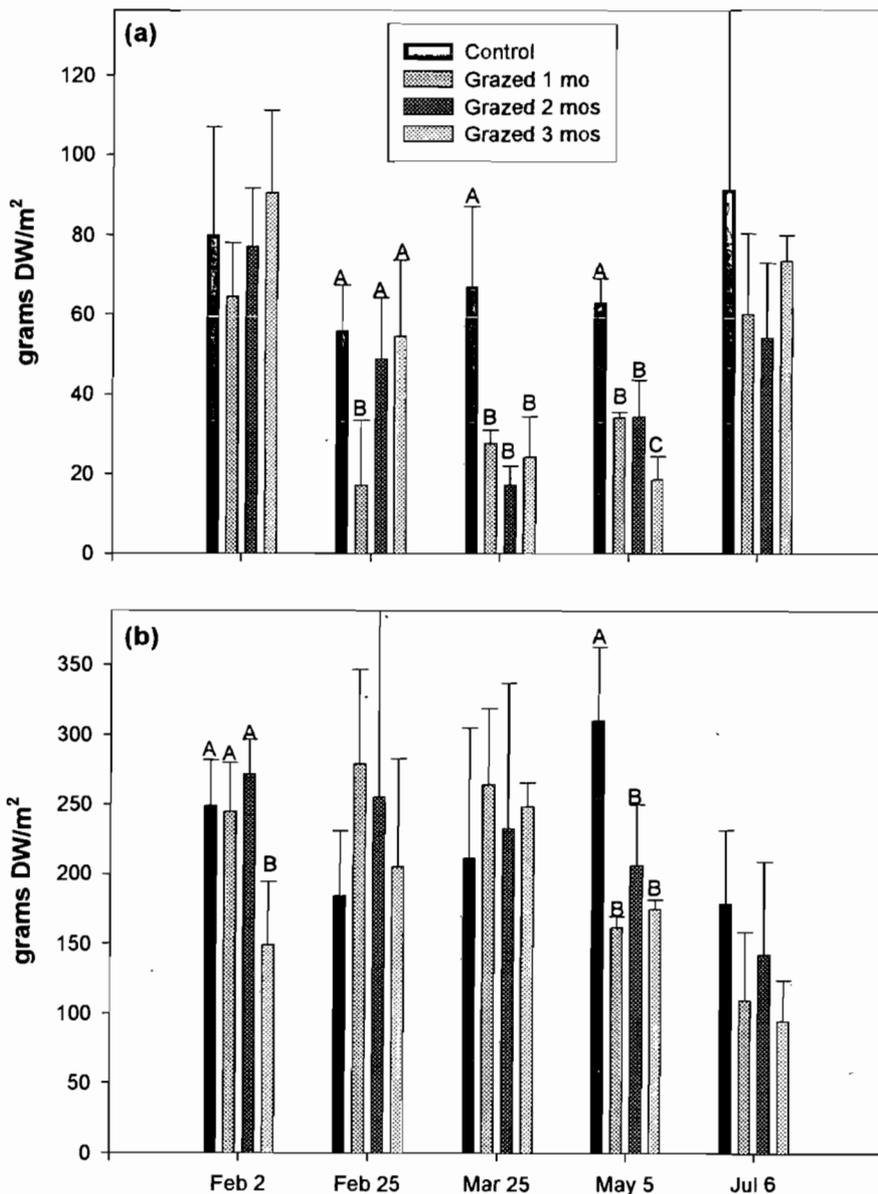


Fig. 2. (a) Aboveground and (b) belowground biomass in cages grazed by sea urchins for either 1, 2 or 3 mo during spring in Big Pine Key (mean + 1 SE, n = 3). Letters indicate treatments that were significantly different

grazing treatments than in the ungrazed control treatment (Fig. 2a). Despite this, only 1 grazing treatment had significantly lower aboveground biomass (i.e., the treatment grazed for only 1 mo) than the control (ungrazed) treatment. In the second month of the experiment, *a posteriori* comparisons found that all grazing treatments, even the treatment where grazing pressure was released a month earlier, had significantly less biomass than the control treatment. These significant differences persisted until the end of the experiment, when significant differences among the treatments no longer existed. A marginally significant interaction between the grazing treat-

ments and time shows that grazing also had a small effect on changes in belowground biomass during spring (Table 2, within-subject effects). The manner of this interaction is unclear, as there were no consistent increases or decreases in belowground biomass among treatments. Pairwise contrasts on successive sampling dates show that the interaction became significant in May, when all of the grazing treatments had significantly less belowground biomass than the ungrazed control treatment (Fig. 2b).

Sea urchin grazing also had a significant impact on aboveground turtlegrass biomass in summer, although

Table 1. Repeated measures ANOVA of spring grazing effects by *Lytechinus variegatus* on aboveground biomass in Big Pine Key, Florida. **Bold** indicates statistically significant differences among treatments. Differences were considered to be highly significant when $p < 0.05$ and marginally significant when $p < 0.10$. Note: data do show homogeneity of treatment variances (Sphericity test, $p = 0.065$; $df = 2$). Box M test could not be computed because there were fewer than 2 nonsingular cell covariance matrices

(A) Between subjects										
Source	df	MS		F	p	Power				
Treatment	3	0.266		5.14	0.029	0.733				
Error	8	0.0519								
(B) Within subjects										
Source	df	Univariate analysis				Multivariate analysis				
		MS	H-F F	H-F p	Power	Num. df	Den. df	Wilk's λ	p	Power
Time	4	0.881	18.903	0.000	1.0	4	5	0.083	0.000	0.997
Treatment \times Time	12	0.0504	2.01	0.058	0.815	12	14	0.023	0.014	0.819
Error	32	0.0251								

Table 2. Repeated measures ANOVA of spring grazing effects by *Lytechinus variegatus* on belowground biomass in Big Pine Key, Florida. **Bold** indicates statistically significant differences among treatments. Differences were considered to be highly significant when $p < 0.05$ and marginally significant when $p < 0.10$. Note: data do show homogeneity of treatment variances (Sphericity test, $p = 0.053$; $df = 2$). Box M test could not be computed because there were fewer than 2 nonsingular cell covariance matrices

(A) Between subjects										
Source	df	MS		F	p	Power				
Treatment	3	0.839		1.618	0.26	0.28				
Error	8	0.518								
(B) Within subjects										
Source	df	Univariate analysis				Multivariate analysis				
		MS	H-F F	H-F p	Power	Num. df	Den. df	Wilk's λ	p	Power
Time	4	2.343	7.03	0.00	0.987	4	5	0.096	0.009	0.940
Treatment \times Time	12	0.634	1.91	0.072	0.789	12	14	0.026	0.019	0.786
Error	32	0.33								

the pattern was different. While we found no significant overall impacts of sea urchin grazing on turtlegrass biomass (Table 3, between-subject effects), grazing did have a highly significant impact on how aboveground turtlegrass biomass changed in summer (Table 3, within-subject effects: time \times treatment interaction [univariate only]). In the first month of the experiment, aboveground biomass increased somewhat in the control treatment, while it decreased dramatically in each grazing treatment (Fig. 3a). Even though sea urchin densities were identical in all grazing treatments during the first month of the experiment, pairwise contrasts showed that only 2 of the 3 grazing treatments had significantly lower biomass than the ungrazed control treatment. In the second month of the experiment, no significant differences were detected among treatments as turtlegrass bio-

mass had increased in all of the grazing treatments. Biomass changed little in the ungrazed treatment during this same period of time. In Month 3, pairwise contrasts showed that the treatment grazed for 1 mo had significantly higher turtlegrass biomass than the other treatments (Fig. 3a). When grazing pressure was relaxed in summer, aboveground biomass increased rapidly in each of the grazing treatments (Fig. 3a). In the treatment grazed for 1 mo (i.e., the treatment where sea urchins were removed in July), biomass was double that observed in the ungrazed control at the end of the experiment. In the treatment where sea urchins remained for 2 mo (i.e., the treatment where sea urchins were removed in August), aboveground biomass decreased during the first month as well (by some 40%) then rapidly increased to levels that were statistically indistinguishable from those of the control

Table 3. Repeated measures ANOVA of summer grazing effects by *Lytechinus variegatus* on aboveground biomass in Big Pine Key, Florida. **Bold** indicates statistically significant differences among treatments. Differences were considered to be highly significant when $p < 0.05$ and marginally significant when $p < 0.10$. Note: data do show homogeneity of treatment variances (Sphericity test, $p = 0.762$; $df = 2$). Box M test could not be computed because there were fewer than 2 nonsingular cell covariance matrices

(A) Between subjects										
Source	df	MS	<i>F</i>	<i>p</i>	Power					
Treatment	3	0.09315	0.818	0.52	0.158					
Error	8	0.0519								
(B) Within subjects										
Source	df	Univariate analysis			Power	Multivariate analysis				
		MS	H-F <i>F</i>	H-F <i>p</i>		Num. df	Den. df	Wilk's λ	<i>p</i>	Power
Time	3	0.355	10.6	0.000	0.966	3	6	0.208	0.018	0.828
Treatment \times Time	9	0.111	0.33	0.009	0.926	9	15	0.134	0.098	0.491
Error	24	0.0334								

Table 4. Repeated measures ANOVA of summer grazing effects by *Lytechinus variegatus* on belowground biomass in Big Pine Key, Florida. **Bold** indicates statistically significant differences among treatments. Differences were considered to be highly significant when $p < 0.05$ and marginally significant when $p < 0.10$. Note: data do not show homogeneity of treatment variances (Sphericity test, $p = 0.010$; $df = 2$). Huynh-Feldt corrected degrees of freedom, *F* values and probabilities (*P* H-F) are given for the univariate within subjects analysis (H-F $\epsilon = 0.7$). Box M test could not be computed because there were fewer than 2 nonsingular cell covariance matrices

(A) Between subjects										
Source	df	MS	<i>F</i>	<i>p</i>	Power					
Treatment	3	1.805	23.43	0.000	1.0					
Error	8	0.0787								
(B) Within subjects										
Source	df	Univariate analysis			Power	Multivariate analysis				
		MS	H-F <i>F</i>	H-F <i>p</i>		Num. df	Den. df	Wilk's λ	<i>p</i>	Power
Time	2.1	2.97	6.9	0.006	0.876	3	6	0.10	0.000	0.995
Treatment \times Time	6.3	0.61	1.417	0.265	0.413	9	15	0.05	0.01	0.786
Error	16.8	0.43								

treatment. In the treatment where grazers remained for 3 mo, the lowest aboveground biomass was observed in July (some 37% of initial values), after which there was a substantial recovery (some 66% of original biomass).

This pattern of initial losses was followed by rapid accumulation of 'new' biomass, to the point that we could not detect statistically significant differences among treatments. This suggests that grazing stimulated large increases in aboveground NAPP in the summer experiment. Grazing had a highly significant impact on belowground biomass in summer (Table 4, between-subject effects). Belowground biomass in the control treatment changed little during the experi-

ment, whereas belowground biomass oscillated widely in the grazing treatments. Pairwise contrasts of treatment effects found a single significant difference to exist after 1 mo of grazing (i.e., between the cages grazed for 2 mo and all other treatments) (Fig. 3b). In the second month, cages grazed for 1 and 3 mo were significantly different from either those grazed for 2 mo or controls. In the third month of the experiment, significant differences among treatments grazed for 1 and 2 mo were found. The higher levels of biomass in 2 of the 3 grazing treatments than in the ungrazed control at the end of the experiment again point towards increased levels of primary production as a result of grazing (Fig. 3b).

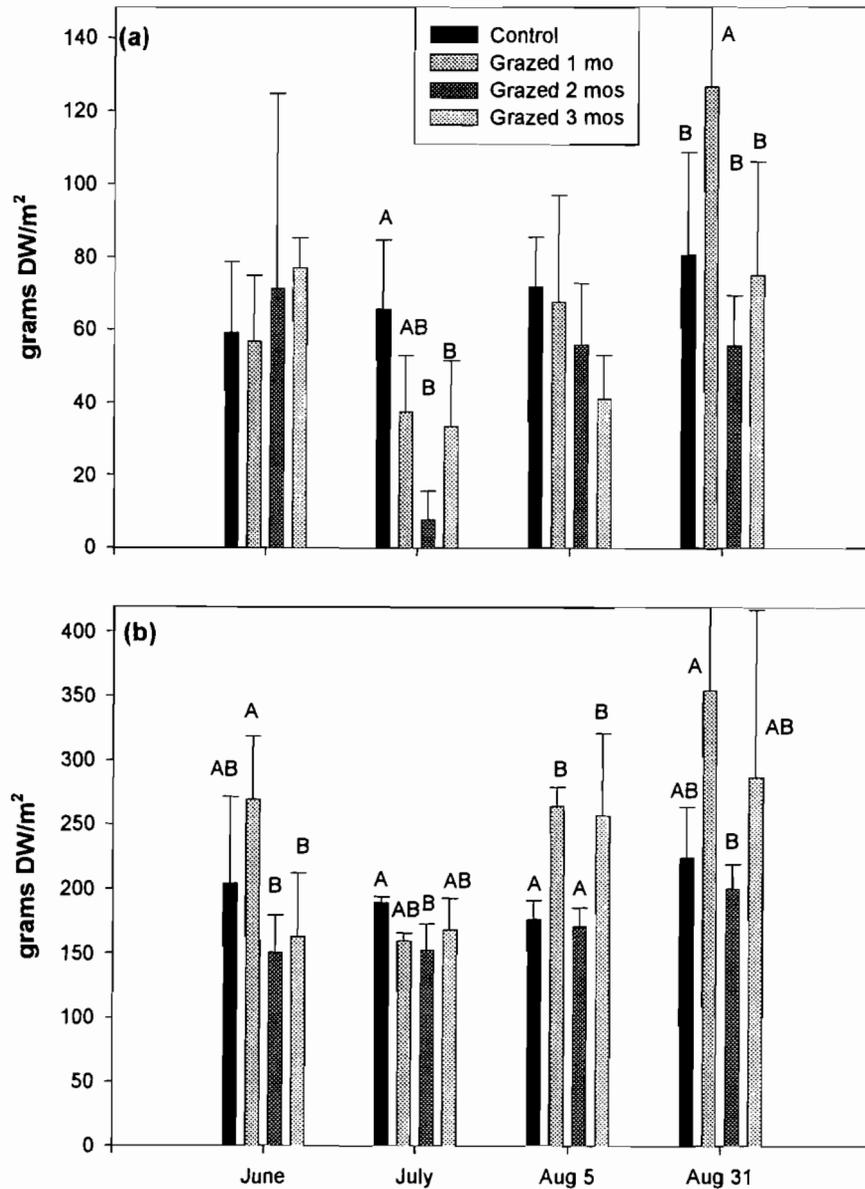


Fig. 3. (a) Aboveground and (b) belowground biomass in cages grazed by sea urchins for either 1, 2 or 3 mo during summer in Big Pine Key (mean + 1 SE, n = 3). Letters indicate treatments that were significantly different

Grazing in Hawk Channel

Initial comparisons of the selected parameters found no statistically significant differences among treatments ($p > 0.1$). This indicates that our study area was relatively homogeneous with regard to the selected response measures of turtlegrass growth and abundance (Figs. 4 to 7). Further analysis showed that grazing marginally affected only 1 of these parameters (leaf length) in Hawk Channel (Table 5). Pairwise comparisons found that leaves were significantly

longer in the cages with sea urchins at densities of 4 ind. m⁻² than in either of the other 2 treatments. These results suggest that grazing plays only a small role in controlling the distribution and abundance of turtlegrass in Hawk Channel. However, unlike our experiments in Big Pine Key, the statistical power of this experiment in Hawk Channel to detect significant differences among treatments was low for each response variable (Table 5). As a result, the probability of making a Type II error (i.e., not rejecting a false null hypothesis) is very high.

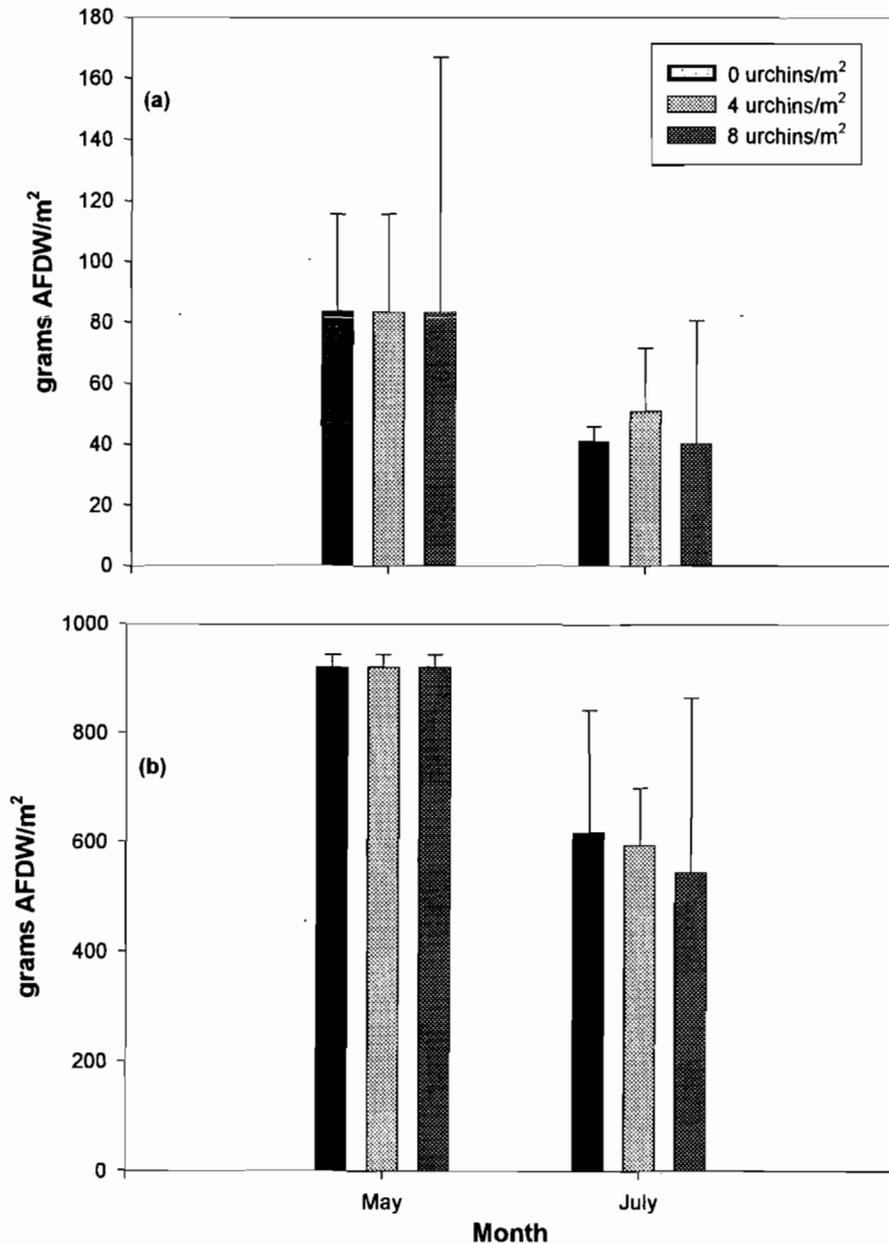


Fig. 4. (a) Aboveground and (b) belowground biomass in cages grazed by sea urchins in Hawk Channel (mean + 1 SE, $n = 7$)

Surveys of sea urchin densities in northern and middle Florida Keys

Sea urchin densities were similar at all study sites. Initial densities of *Lytechinus variegatus* ranged from 0 to 7 ind. m^{-2} ($n = 49$) in the Hawk Channel vicinity and from 0 to 6 ind. m^{-2} ($n = 20$) in the Big Pine Key area. Of the 3 sites selected to record densities, sea urchins were not found north or west of Big Pine Key but occurred along the southern shoreline of Big Pine Key

at an average density of 3.9 ind. m^{-2} . Sea urchins were found commonly throughout Hawk Channel. Of the 22 locations sampled, *L. variegatus* was present at 19. Average densities at the selected sites along the 80 km segment of Hawk Channel surveyed ranged from 0 to 3.33 ind. m^{-2} . Longer-term monitoring of sea urchin density showed a steady decline between April 1995 and September 1996 at our study site in Hawk Channel (Fig. 8). Over the 1.5 yr period, average sea urchin densities dropped from 1.7 to 0.7 ind. m^{-2} .

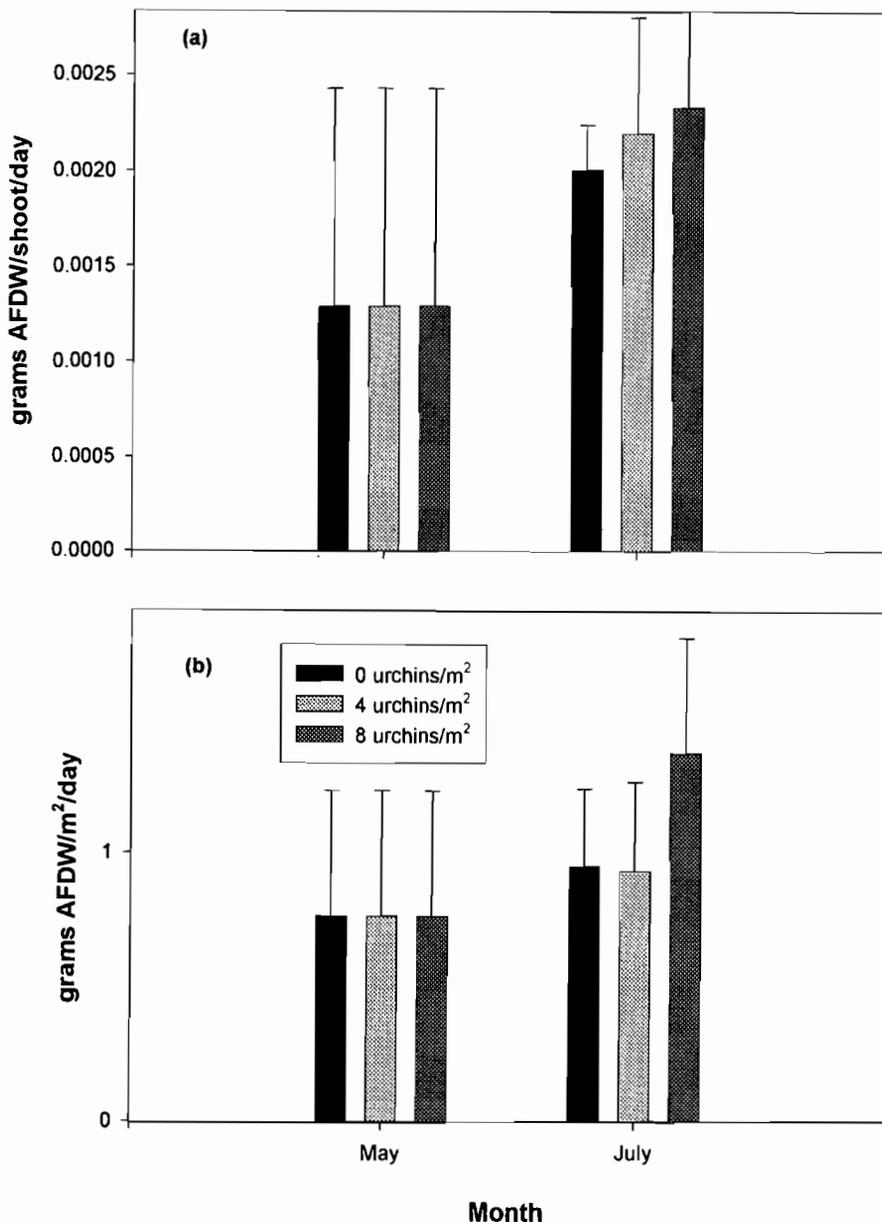


Fig. 5. (a) Short-shoot-specific production and (b) net aboveground primary production in cages grazed by sea urchins in Hawk Channel (mean + 1 SE, n = 7)

DISCUSSION

We found that sea urchin grazing can control seasonal changes in turtlegrass abundance in some areas of the Florida Keys. At Big Pine Key, grazing had a significant, negative impact on turtlegrass biomass throughout the spring. Grazing duration had little effect on seagrass abundance, as short grazing bouts were as effective as longer periods of grazing in reducing aboveground biomass. The lack of biomass accu-

mulation, once grazing pressure was relaxed, indicates that seagrass growth was minimal during spring. Once the growing season began, turtlegrass regrew and reached levels exceeding those in ungrazed cages by mid-summer. This is similar to what we found in the northern Gulf of Mexico (Valentine & Heck 1991). We also found that sea urchin grazing controlled how belowground biomass changed in spring at Big Pine Key but the manner in which grazing affected these changes remains unclear.

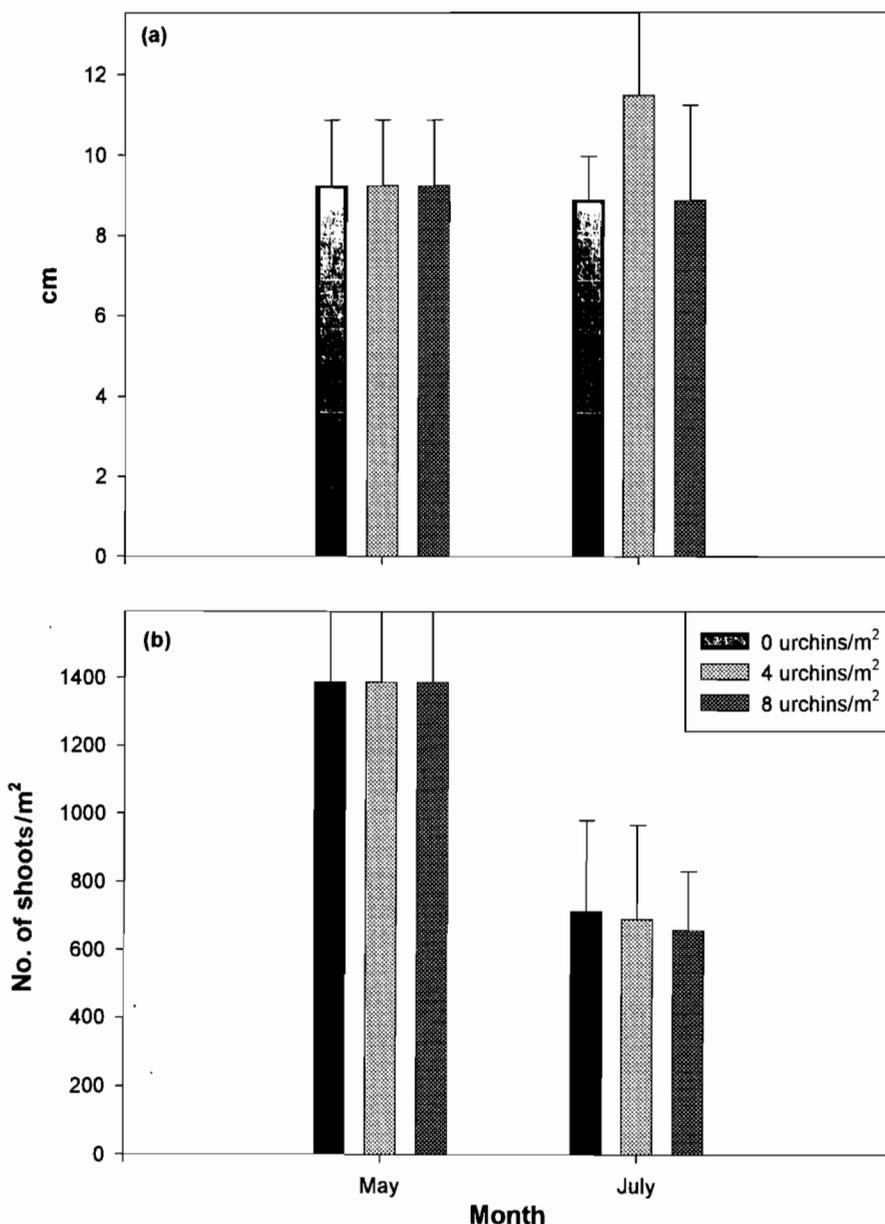


Fig. 6. (a) Leaf length and (b) short shoot density in cages grazed by sea urchins in Hawk Channel (mean + 1 SE, n = 7)

In summer, however, when seagrass growth is at its zenith (Zieman & Zieman 1989), the impacts of grazing on turtlegrass biomass were far less uniform. The rapid regrowth of aboveground seagrass biomass, which in some cases reached higher levels than observed in the ungrazed control treatment, indicates that grazing must have stimulated seagrass production during the summer months. While we did not directly measure NAPP at Big Pine Key, it is possible to estimate the total amount of production that occurred in our treatments using a simple mass balance equation (NAPP = the change in biomass [i.e., $\text{biomass}_{t+1} - \text{biomass}_{t0}$] + bio-

mass consumed by sea urchins + leaf loss due to senescence, over an interval of time). We cannot use this formula to estimate aboveground production, as we have no direct estimates of consumption by grazers or leaf loss. We can, however, use this formula to estimate net belowground primary production if we assume that the sea urchins do not consume belowground tissue and no tissue was differentially lost among treatments. Since sea urchins cannot reach belowground biomass and there are no transport processes that can carry the belowground material away from our cages, we believe these are reasonable assumptions. Using this

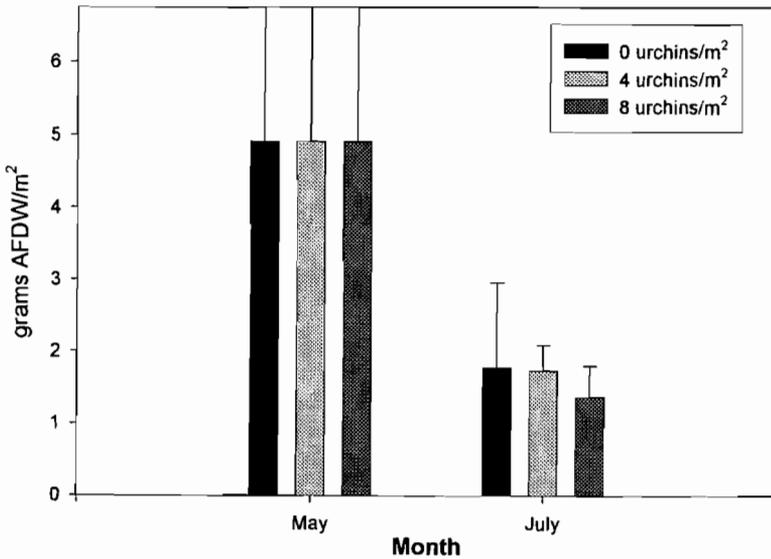


Fig. 7. Epibiont biomass in cages grazed by sea urchins in Hawk Channel (mean + 1 SE, n = 7)

formula, we estimate that net belowground primary production (from June through August) in our experiment was 0.198, 0.8483, 1.2963, and 0.4759 g dry wt m^{-2} in treatments with no sea urchins and those with sea urchins enclosed for 1, 2 and 3 mo, respectively. We estimate that belowground primary production in the grazing treatment was more than double that of the ungrazed control treatment during summer. Since rhizome growth occurs at rhizome apices, and new shoots are produced almost always at rhizome apices (Tomlinson & Vargo 1966, Tomlinson 1974), it is likely that

sea urchin grazing also led to increased aboveground production in our summer experiment. Based on these observations, and our earlier work showing that sea urchin grazing can stimulate aboveground seagrass production (Valentine et al. 1997), we conclude that determining the importance of seagrass herbivory to nearshore food webs based solely on relative reductions in seagrass biomass in grazed versus ungrazed cages is inappropriate, as it substantially underestimates the amount of plant consumption by marine herbivores.

We anticipated that sea urchins would have highly significant negative impacts on turtlegrass biomass at the Hawk Channel study site, even though the densities used in this experiment were lower than those in the Big Pine Key experiments. We anticipated this, in part, because the increased depth of our study site in Hawk Channel would have much lower light levels than the shallow water at the Big Pine Key study site. However, we found no evidence that the lower densities significantly influenced turtlegrass growth or abundance in Hawk Channel. The reasons for this are unclear, but one obvious possibility is that the lower densities of sea urchins used in this experiment were below the threshold necessary to significantly affect either seagrass growth or the accumulation of biomass. However, experiments conducted in the shallow waters of St. Joseph Bay showed that only slightly higher sea urchin densities (i.e., 10 ind. m^{-2}),

Table 5. Summary of ANOVAs describing the grazing impacts on turtlegrass within our cages in Hawk Channel, Florida, during July. Degrees of freedom for all tests are 2 and 12. **Bold** indicates statistically significant differences among treatments. Differences were considered to be highly significant when $p < 0.05$ and marginally significant when $p < 0.10$

Plant characteristic	Source	SS	F	p	Power
Aboveground biomass	Model	349.02	0.53	0.6	0.12
	Error	3983.3			
Belowground biomass	Model	13809.66	0.13	0.88	0.07
	Error	649700.4			
Shoot density	Model	7614.5	0.06	0.94	0.06
	Error	712959.8			
Shoot-specific NAPP	Model	0.0000001	0.6	0.56	0.13
	Error	0.0000002			
Areal NAPP	Model	0.632	0.12	0.88	0.40
	Error	1.52			
Leaf length	Model	22.54	3.1	0.08	0.49
	Error	43.72			
Epibiont biomass	Model	0.49	0.44	0.65	0.11
	Error	6.73			

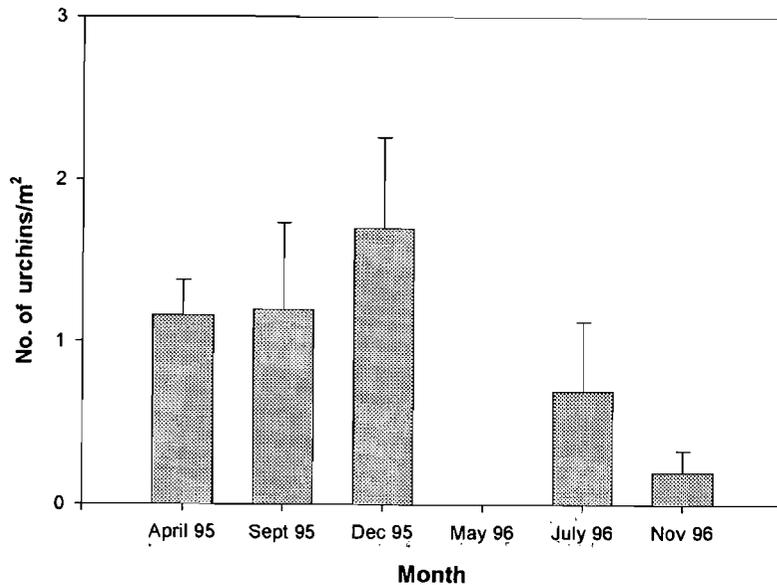


Fig. 8. Sea urchin density in Hawk Channel (mean + 1 SE, n = 10)

had a major impact on seagrass growth (Valentine et al. 1997). It is also possible that modest increases in production observed in July, albeit not statistically significantly higher, were sufficient to allow turtlegrass to persist in our experiments. Alternatively, the statistical power of the Hawk Channel experiment was extraordinarily low and we may have simply made a Type II error. This low power was surprising, as treatment replication and the densities used were similar to our previous studies (Valentine & Heck 1991, Heck & Valentine 1995, Valentine et al. 1997, this study at Big Pine Key).

Overall, sea urchin densities at our study sites were much lower than in St. Joseph Bay (Valentine & Heck 1991). These new experiments suggest that *Lytechinus variegatus* is unlikely to have the same major effects on turtlegrass abundance in the Florida Keys that we reported from the northern Gulf of Mexico (but see Moore et al. 1963, Bach 1979, Maciá & Lirman 1999). However, sea urchins may produce substantial effects on other species of seagrass in south Florida. In 1997, local fishermen reported that high numbers of sea urchins were found in lobster traps in Florida Bay (Rose et al. 2000). Divers discovered that aggregations (with localized densities exceeding 300 ind. m⁻²) of *L. variegatus* were grazing heavily on manatee grass *Syringodium filiforme* throughout the area (Rose et al. 2000). The result was the conversion of a lush seagrass meadow into a heterogeneous landscape, composed of barren unvegetated sand flats, and a combination of heavily grazed and ungrazed patches of *S. filiforme*. Aerial photography and ground-truthing suggest that

this grazing covered at least 10 km² and extended across a 2 km southward-migrating front (Rose et al. 2000).

In this study, the differences in grazer impacts on turtlegrass growth and abundance, in a well-lit shallow water habitat and deeper-water habitat with less light, suggest that there is a critical need not only to repeat experiments in environments with differing physical conditions, but also to develop a more complete understanding of the mechanisms by which seagrasses can compensate for losses of tissues to marine herbivores under varying environmental conditions. Only then will we be able to accurately estimate the amount of energy entering nearshore food webs via the grazing pathway. To date, there have been no field experiments that have simultaneously considered the multiple controlling factors that determine just how much energy actually flows from seagrasses to herbivores.

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