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Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow

Abstract The sea urchin, *Lytechinus variegatus*, has been estimated to consume between 50 and 90% of annual net aboveground production in selected turtlegrass (*Thalassia testudinum*) meadows in the eastern Gulf of Mexico. Nevertheless, turtlegrass persists where sea urchin grazing is intense. We hypothesized that turtlegrass productivity is stimulated by grazing, as has been reported from terrestrial grassland systems, and that this best explains the persistence of heavily grazed turtlegrass in St. Joseph Bay, Fla. This hypothesis was tested by manipulating sea urchin densities (0, 10, and 20 individuals/m^2) in 1-m^2 enclosures. These densities encompass the range of average densities at the study site and those reported in the literature. Changes in turtlegrass abundance (e.g., short shoot density and biomass), production by short shoots, and leaf width were monitored in these enclosures during the summer. Repeated-measures ANOVA showed that production by short shoots, leaf density/shoot, and leaf width decreased over time in all treatments. Leaf density/shoot and leaf width were not significantly impacted by grazing, nor did grazing significantly reduce seagrass biomass, but it did lead to significantly higher densities of short shoots than found in control cages. Our results indicate that turtlegrass compensates for the effects of sea urchin herbivory by increasing the recruitment of short shoots during the growing season. We estimate that this increased shoot density led to a 40% increase in net aboveground primary production (g dry weight/m^2) in grazing treatments, which helps to explain the lack of significant reductions of sea grass biomass during the growing season.

Key words Herbivory · Sea urchins · Turtlegrass

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Introduction

The importance of herbivory in controlling plant productivity and abundance in terrestrial ecosystems is well established (e.g., Dixon 1971; Harper 1977; Morrow and LaMarche 1978; Rausher and Feeny 1980; Cumming 1982; Crawley 1985; Whitham and Mopper 1985). In evaluating plant responses to herbivory, ecologists are polarized, hypothesizing that plants either (1) benefit from increased nutrient recycling, light availability, flowering, and/or seed production brought on by grazing (e.g., Owen and Wiegert 1976; McNaughton 1979a, b, 1986; Floate 1981; Cargill and Jeffries 1984; Paige and Whitham 1987), or (2) are damaged by herbivores and any apparent benefits are limited to short periods of time (Belsky 1986, 1987; Belsky et al. 1993). The controversy centers on interpretations of the selective processes underpinning plant responses to herbivore-induced damage (Belsky et al. 1993).

In the sea, although there have been many examinations of the effects of grazing on macroalgae (reviewed by Lubchencho and Gaines 1981; Gaines and Lubchencho 1982), sea grass-herbivore interactions are poorly understood. In general, herbivory on sea grasses is believed to be relatively unimportant (cf. Thayer et al. 1984) due, in part, to the loss of important vertebrate herbivores [e.g., green turtles, dugongs, manatees, fishes, and waterfowl (Randall 1965; Heinsohn and Birch 1972; Lipkin 1975; Charman 1977, 1979; Bjorndal 1980; Kiorboe 1980; Jacobs et al. 1981)]. In addition, sea grasses are perceived to be a poor-quality food source (Bjorndal 1980). Consequently, investigations of the factors controlling seagrass productivity and abundance emphasize the primacy of sediment porewater nutrient

supply (e.g., Patriquin 1972; Short 1987; Powell et al. 1989; Fourqurean et al., 1992; Short et al. 1993), light availability, and/or other physical factors (e.g., Patriquin 1975; Backman and Barilotti 1976; Dennison and Alberte 1982; Thom and Albright 1990).

In previous papers, we demonstrated that sea urchins [*Lytechinus variegatus* (Lamarck)] can reduce sea grass biomass in the eastern Gulf of Mexico (Valentine and Heck 1991; Heck and Valentine 1995). Furthermore, using reported *L. variegatus* densities, their ingestion rates and estimates of net sea grass aboveground production, we determined that this sea urchin alone can consume between 50 and 90% of the annual aboveground turtlegrass production in some regions of the Gulf of Mexico and Caribbean Sea (cf. Moore et al. 1963; Greenway 1976, 1995; Heck and Valentine 1995). Observations elsewhere show that other sea urchins can also control local sea grass abundance (Ogden et al. 1973; Bach 1979; Bak and Nojima 1980; Kirkman and Young 1981; Hulings and Kirkman 1982; Vicente and Rivera 1982; Verlaque and Nedelec 1983; Jafari and Mahasneh 1984; Larkum and West 1990; Klumpp et al 1993; F. Short, personal communication). In addition, waterfowl, green turtles [*Chelonia mydas* (Linnaeus)] and sirenians [i.e., manatees and dugongs], which can still be locally abundant, are intense sea grass grazers (Lipkin 1975; Charman 1977; Anderson and Birtles 1978; Bjorndal 1980; Jacobs et al. 1981; Nietschmann and Nietschmann 1981; Ogden et al. 1983; Williams 1988; Nietschmann 1990; Provancha and Hall 1991; Baldwin and Lovvorn 1994), and can have even greater impacts on sea grass biomass and productivity than sea urchins (Zieman et al. 1984). Together these data suggest that herbivory on sea grasses, although reduced in a historical context, may still be important in determining sea grass productivity and abundance in many areas.

Despite grazing impacts, sea grasses can persist in areas where herbivory is intense (e.g., Bach 1979; Hulings and Kirkman 1982; Vicente and Rivera 1982; Jafari and Mahasneh 1984) and can, depending on the season, recover to rapidly exceed aboveground standing crops in ungrazed areas (Valentine and Heck 1991). This suggests that grazing may stimulate net aboveground sea grass production (NAPP), as has been suggested for both terrestrial grasses and marine algal turfs (e.g., McNaughton 1979a, b; Carpenter 1986; Williams and Carpenter 1988). To address this possibility, we experimentally examined the impact of chronic sea urchin grazing on turtlegrass productivity in the eastern Gulf of Mexico. Specifically, we asked whether herbivory could lead to increases in turtlegrass productivity and abundance.

Materials and methods

Study site

The study site, St. Joseph Bay, Fla, is located in the northeastern Gulf of Mexico. St. Joseph Bay is a protected, shallow coastal embayment with little freshwater input: salinities usually range from 30 0/00 to 36 0/00 (Stewart and Gorsline 1962; Folger 1972; personal observation). Temperatures vary seasonally from 8° to 30°C (personal observation) and the mean tidal range is 0.5 m (Rudloe 1985).

Enclosed within the bay is an extensive sea grass habitat estimated to occupy some 26 km^2 (McNulty et al. 1972). This sea grass habitat is dominated by large monospecific stands of *Thalassia testudinum* (Banks ex König) interspersed with smaller patches of *Halodule wrightii* Aschers, unvegetated sand flats, and small amounts of *Syringodium filiforme* Kutzing (Iverson and Bittaker 1986). Sea grass production is highly seasonal with leaf biomass and density peaking near 150 g ash free dry mass (AFDM)/m^2 and approximately 3,000 leaves/m^2 during the summer months (Iverson and Bittaker 1986). Only the shallowest portions of the sea grass habitat are exposed during low tides, and wave energy is minimal.

Turtlegrass (*T. testudinum*) is the dominant sea grass species in the tropical and subtropical western Atlantic Ocean. It is a clonal sea grass with horizontal rhizomes growing beneath the sediment surface. Regularly spaced, erect, vertical branches (called short shoots) arise from the horizontal rhizome and extend into the water column. New leaves grow from a centrally located basal meristem and are held together by old leaf sheaths. Short shoots can have as many as five leaves present during the growing season (Tomlinson and Vargo 1966; Zieman and Zieman 1989).

St. Joseph Bay occurs near the northernmost extent of an offshore, high-salinity, sea grass habitat that covers more than 3,000 km^2 of substratum on the broad continental shelf of the eastern Gulf of Mexico (Iverson and Bittaker 1986). Turtlegrass forms a physically complex habitat on otherwise featureless substrate. Annual epibenthic macroinvertebrate production in this habitat can exceed 400 g AFDM/m^2 per year, some eight times higher than observed on nearby unvegetated substrates (Valentine and Heck 1993).

The dominant turtlegrass grazer along the west coast of Florida is the sea urchin *L. variegatus* (Lamarck). *L. variegatus* is a generalist herbivore that ingests whatever plant material it encounters (Lawrence 1975; Ogden 1976). This sea urchin is commonly found in subtropical and tropical sea grass beds in the western Atlantic Ocean, with average densities of up to 20 individuals/m^2 reported from several locations in the tropical and subtropical western Atlantic Ocean (see Table 1 in Valentine and Heck 1991).

Grazing experiment

During May to August 1992, 21 1-m^2 circular cages, constructed with 30-mm mesh plastic aquaculture netting and iron rebar, were placed along a turtlegrass habitat edge, approximately 1 m from a sand/sea grass boundary. This location was selected to standardize the location of experimental treatments within a sea grass habitat. Grazing intensity was manipulated in three treatments consisting of 0, 10, and 20 sea urchins/m^2. These densities encompassed commonly reported average sea urchin densities in the Gulf of Mexico and Caribbean Sea (e.g., Moore et al. 1963; Greenway 1976, 1995; Keller 1983; Valentine and Heck 1991). Each treatment was randomly assigned to 7 of 21 cages. Based on earlier experiments (Valentine and Heck 1991), we estimated that seven replicates would provide us with a 90% chance of detecting a 0.5 g dry mass (DM)/m^2 difference in aboveground biomass between treatments at the 5% level of significance. A 0.5-g DM difference was selected based on the range of observed effects of the manipulated sea urchin densities on aboveground seagrass biomass (Valentine and Heck 1991).

Sea urchins were enclosed in cages for 3 weeks/month and removed from cages for 1 week/month. During the week-long period without urchins, we made several estimates of turtlegrass production and abundance using established techniques. Grazing impacts on production by turtlegrass short shoots (hereafter called production) were measured monthly. This was done using a syringe to puncture all the leaves in a shoot at the base of the leaf sheath

(Dennison and Alberte 1982). Five haphazardly selected turtlegrass short shoots were so marked within each cage. After 6 days, all leaves of the marked shoots were clipped at the sediment-water interface, frozen, and returned to the laboratory for the analyses described below. Because turtlegrass leaves grow from a basal meristem, the production by marked shoots can be determined by measuring the amount of new growth distal to the hole in punctured leaves, plus any new, unpunctured leaves that appear within a marked bundle.

The removal of sea urchins from the cages ensured that their grazing activities would not lead to loss of marked leaves during the week when production estimates were being made. After production samples had been harvested, sea urchins were restocked in grazing treatments. This procedure was repeated each month.

Changes in turtlegrass abundance were also monitored monthly by counting the short shoots present in five haphazardly located 0.01-m² quadrats in each cage. To minimize potential destruction of sea grass associated with aboveground biomass sampling (see below), sampling within the cages was limited to the beginning and end of the experiment. Aboveground biomass was determined from three 0.01-m² clippings of sea grass leaves taken from each cage in May and August.

In the laboratory, mean leaf density, leaf width (mm), and aboveground production (g DM/shoot per day), and epibiont biomass on sea grass leaves were determined for each cage from the harvested shoots. The production by marked short shoots was defined as the mass of all leaf tissue, dried to a constant mass at 90°C, between the location of the initial marking scar and base of the leaf sheath, plus the mass of any new unmarked leaves formed during the 6-day period. Unmarked leaves were seldom encountered. Mean leaf density/marked shoot was determined by counting leaves on the five marked shoots. Leaf width (± 1 mm) on the leaves of each marked shoot was measured at the widest point on the leaf. For comparisons with other studies, all data have been standardized to 1 m².

Epibiont fouling of sea grass leaves can limit sea grass growth by inhibiting leaf from collection of light for photosynthesis (Neckles et al. 1993; Williams and Ruckleshaus 1993). The extent of leaf fouling was characterized by epibiont biomass. Epibiont biomass was determined by scraping fouling organisms and algae from each leaf with a razor blade, then drying and weighing epibionts as described above for seagrass biomass. The term epibiont is used instead of epiphyte since many plants and animals, including barnacles, bryozoans, hydroids, polychaetes, and ascidians, along with coralline and filamentous algae and diatoms, typically colonize turtlegrass leaves along the northern coast of Florida (Chernoff 1985; personal observation). For comparisons with other studies, all data have been standardized to 1 m².

Statistical analyses

We used analysis of variance (ANOVA) to ensure that the study site was homogeneous with respect to the selected parameters at the beginning of the experiment. Treatment effects on all of the sea grass parameters, measured monthly, were compared using a repeated measures ANOVA (Winer 1971). Prior to the analysis, several transformations were performed to either normalize the data or ensure that count variances were independent of their means. The effects of these transformations were verified using Mauchly's criteria for repeated-measures ANOVA (cf. von Ende 1993). Probability plots for normality and Bartlett's test for homogeneity of variance were used to determine the effects of these transformations on ANOVAs conducted for single dates. Leaf growth, leaf width, and aboveground biomass were each normalized using a natural log transformation. Shoot densities were transformed using a square root transformation. If significant differences were detected, a posteriori comparisons were conducted using the Sheffé multiple-comparison test. All other measured parameters satisfied the assumptions of these ANOVAs and were not transformed. All differences were considered significant at $P < 0.05$.

Results

Initially, ANOVA showed that none of the measured parameters, except epibiont biomass, differed significantly among treatments, indicating that the study site was relatively homogeneous at the beginning of our experiment (Table 1). Over time, all of the measured plant parameters changed significantly (Tables 2, 3). Production by individual short shoots decreased in all treatments during the course of the experiment but was not affected by the presence of sea urchins (Table 3; Fig. 1a). Leaf width and density also decreased significantly with time. Leaf density per shoot decreased by approximately one leaf in all treatments (Table 2). Neither of these parameters was affected by sea urchin grazing, as significant interactions between grazing and time were not noted. While aboveground biomass more than doubled in all treatments (Table 2), there were no significant differences among treatments at the end of this experiment (Table 3).

Sea urchin grazing significantly interacted with time to control the rate at which short shoot density increased (Table 3). Short shoot density in the control treatment changed little from May through July, after which there was an approximately 16% increase in August (Fig. 1b). Sheffé comparisons of shoot densities among treatments at the end of the experiment found significant differences between the control and grazing treatments (both 10 and 20 individuals/m²), but not between grazing treatments, suggesting that grazing by as few as 10 urchins/m² could trigger the increased production of new short shoots by turtlegrass enclosed within these cages. On average, the two grazing treatments contained 40% more short shoots than the control treatment at the end of the experiment (Fig. 1b, Table 2).

Initially, significant differences in epibiont biomass (g DM/shoot) were noted among treatments (Table 1). Sheffé comparisons of the treatments found significantly more epibiont biomass on leaves in cages that were selected to exclude sea urchins than on leaves within the

Table 1 Summary of ANOVAs describing the initial conditions in May within our cages prior to the enclosure of sea urchins. Degrees of freedom for all tests are 2 and 18. Differences were considered to be significant when $P < 0.05$

Plant characteristic	Source	SS	F	P
Aboveground biomass	Model	0.348	2.02	0.16
	Error	1.549		
Production	Model	0.00026	0.54	0.59
	Error	0.04340		
Epibiont biomass	Model	0.016	9.79	0.0001
	Error	0.014		
Leaf density/shoot	Model	0.1067	0.95	0.40
	Error	1.0057		
Leaf width	Model	3.349	2.16	0.14
	Error	13.9331		
Short shoot density	Model	0.203	2.38	0.12
	Error	0.767		

Table 2 Measured plant characteristics in the three sea urchin grazing treatments in May and August 1992 (mean ± 1 SE) $n = 7$ (*DM* dry mass)

Characteristic	Urchin density/m²					
	0		10		20	
	May	August	May	August	May	August
Aboveground biomass (g DM/m²)	92 (±32)	189 (±42)	69 (±29)	145 (±39)	64 (±29)	154 (±31)
Production (g DM/shoot per day)	0.008 (±0.001)	0.004 (±0.001)	0.007 (±0.001)	0.004 (±0.001)	0.009 (±0.003)	0.005 (±0.001)
Epibiont biomass (g DM/shoot)	0.09 (±0.03)	0.293 (±0.33)	0.04 (±0.03)	0.217 (±0.22)	0.03 (±0.02)	0.10 (±0.11)
Leaf density/shoot	3.63 (±0.37)	2.76 (±0.14)	3.77 (±0.29)	2.69 (±0.43)	3.63 (±0.27)	2.89 (±0.40)
Leaf width (mm)	7.90 (±0.73)	6.84 (±0.78)	7.13 (±0.99)	7.99 (±0.78)	7.77 (±1.40)	7.32 (±0.98)
Short shoot density (mean/m²)	637 (±86)	836 (±202)	670 (±104)	1171 (±174)	714 (±166)	1170 (±108)
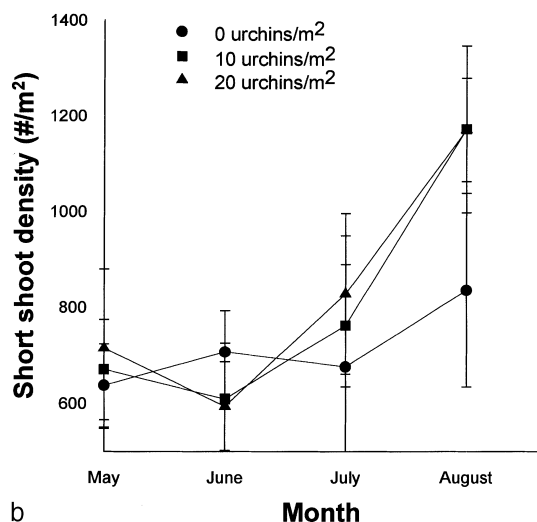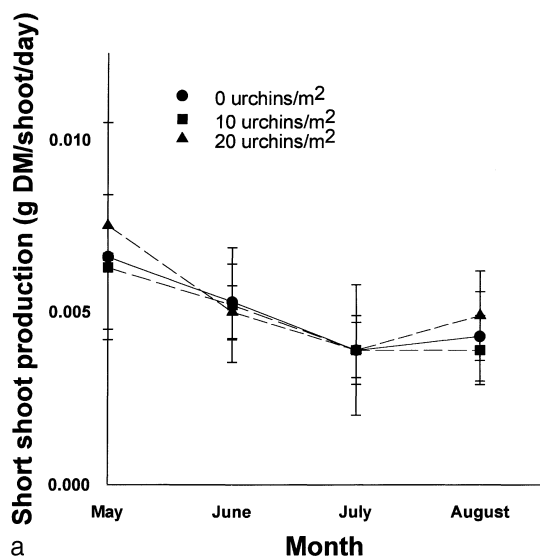
Fig. 1 Net aboveground turtlegrass short shoot production (**a**) and short shoot density (**b**) in our experiment in St. Joseph Bay, Fla., during summer 1992 (mean ±1 SE, $n = 7$) (*DM* dry mass)

Table 3 Repeated-measures analysis of monthly turtlegrass growth parameters. Degrees of freedom = 3,2,6. Differences were considered to be significant when $P < 0.05$ (TM = time, UD = urchin density)

Parameter	Factor	MS	F	P
Aboveground biomass	TM	51.9	1.83	0.15
	UD	4.07	0.14	0.87
	TM*UD	47.9	1.69	0.14
Production	TM	1.65	5.14	0.003
	UD	0.409	1.27	0.29
	TM*UD	0.190	0.59	0.74
Epibiont biomass	TM	34.7	5824.67	0.0001
	UD	0.012	2.0	0.14
	TM*UD	0.0004	0.67	0.68
Leaf density	TM	0.162	14.39	0.0001
	UD	0.036	3.2	0.047
	TM*UD	0.008	0.7	0.65
Leaf width	TM	0.068	5.12	0.003
	UD	0.077	5.78	0.005
	TM*UD	0.0006	0.05	1.00
Short shoot density	TM	1.78	7.92	0.0001
	UD	0.376	0.17	0.52
	TM*UD	0.671	2.99	0.006

cages selected for the two grazing treatments. There were no significant differences between the two grazing treatments. While epibiont biomass increased significantly over time, sea urchin grazing was not found to significantly affect how it did so (Table 3).

Discussion

Turtlegrass responses to sea urchin grazing in the northeastern Gulf of Mexico are complex, and depend on seasonal patterns of primary productivity and grazing intensity (Valentine and Heck 1991; Heck and Valentine 1995). We previously demonstrated that sea urchins at the manipulated densities (i.e., 10 and 20 urchins/m²) could reduce turtlegrass habitats to barren, unvegetated substrates from fall through early spring

(Valentine and Heck 1991; Heck and Valentine 1995). In this study we showed that sea urchin grazing can also lead to increased short shoot densities during the summer, which helps to explain the persistence of turtlegrass habitats in the northeastern Gulf of Mexico despite intense grazing.

Earlier studies have shown that the repeated removal of turtlegrass leaves by sea urchins can lead to decreased aboveground production, leaf width, and leaf density/shoot (e.g., Greenway 1976; Zieman et al. 1984). In our study we also observed temporal decreases in each of these parameters. While ANOVA failed to relate these changes directly to the presence of sea urchins (interaction between time and treatment was not significant), we suggest that the decreases in leaf characteristics may be due to the presence of more younger shoots in the grazed plots at the end of the experiment. Contradicting the suggestion that these differences were due to greater numbers of young shoots in the grazing treatments is the fact that epibiont biomass increased significantly in all treatments (i.e., 0, 10, and 20 individuals/m^2) during this experiment.

L. variegatus readily consumes turtlegrass (Valentine and Heck 1991; Heck and Valentine 1995), yet aboveground biomass, while reduced, did not differ significantly from the control treatment at the conclusion of the experiment. One reason for the failure to detect a significant difference was the low statistical power of the comparison. We estimate, for example, that the power of our test to detect a 50% difference in the aboveground biomass mean for all untransformed data collected in August was 0.201 (at $\alpha = 0.05$). Power diminished to 0.05 for the natural-log-transformed data (at $\alpha = 0.05$). To have an 80% chance of detecting a 50% difference in untransformed means, the minimum replicate number needed would have been 32 while for transformed means we would have needed $n = 581$ (at $\alpha = 0.05$). Therefore, the probability of making a type II error (failing to reject a false null hypothesis of no significant treatments effects) is very high.

We can crudely estimate turtlegrass aboveground production in our treatments by multiplying short shoot density by our estimates of shoot-specific production. Since the production of individual short shoots was not significantly different among treatments, the approximately 40% greater shoot density in the 10 and 20 individuals/m^2 treatments means that net aboveground primary production is some 40% higher in grazing treatments than in the control cages (average of ca. 4.68 g DM/m^2 per day vs. ca. 3.34 g DM/m^2 per day, respectively, during this experiment). Additionally, because the production of new shoots is closely linked to the rate of rhizome growth (Gallegos et al. 1993) and occurs only at rhizome apices (Tomlinson and Vargo 1966), sea urchin grazing at the manipulated densities must have also led to increased rhizome growth rates and belowground production.

Herbivores have been shown to stimulate increased production of grasses in terrestrial systems (McNaugh-ton 1979a, b, 1985; Cargill and Jeffries 1984; Frank and McNaughton 1993), phytoplankton in freshwater lakes (Martin 1967; Porter 1976; Lehman and Scavia 1982; Scavia et al. 1984; but see Bartell 1981; Taylor 1984), marine algal turfs (Carpenter 1986), coralline algae (Littler et al. 1995) and marine benthic diatoms (Bianchi 1988). To date, however, this possibility has not been investigated in sea grass systems. Thayer et al. (1982) hypothesized that grazing green turtles "short-circuit" detrital cycling by making nitrogen-rich fecal material available to detritivores. This same nitrogen-rich fecal material could also stimulate turtlegrass growth in tropical sea grass systems. This hypothesis has not been supported by field observations, which have associated grazing on turtlegrass, either by sea urchins or green turtles, with reduced leaf growth and sediment nutrient depletion (Zieman et al. 1984; Williams 1988).

The increased production in our treatments is similar to that reported from terrestrial grasslands (e.g., McNaughton 1985, 1986). Based on descriptions of herbivore impacts on terrestrial perennial grasses and on examples from the sea grass literature, we suggest that sea grasses have as-yet-unrecognized physiologically based mechanisms for compensating for herbivory. Belsky et al. (1993) suggested that plants can tolerate herbivory and regrow if they possess (1) storage organs that contain carbohydrate, amino acid and protein reserves, (2) dormant meristems or buds that can replace destroyed organs, (3) the ability to reallocate energy and reserves from undamaged to damaged tissues, (4) the ability to increase photosynthetic rates in residual tissues, and (5) the ability to use photosynthate from newly growing tissue. Of these five traits required for regrowth and potentially increased growth following grazing, sea grasses possess at least three. During peak production, sea grass rhizomes serve as storage sites for carbohydrates and proteins that are used for leaf regeneration (e.g., Dawes and Lawrence 1979; Iizumi and Hattori 1982; Short and McRoy 1984; Tomasko and Dawes 1989a). In addition, there is evidence that stored carbohydrates are translocated along rhizomes to areas of increased metabolic activity such as new leaf growth (Libes and Bourdouresque 1987; Tomasko and Dawes 1989a). Tomasko and Dawes (1989b) further showed that the loss of the outside leaves on a sea grass shoot will lead to increased rates of primary production in the remaining undamaged leaves.

Our results, plus lessons learned from the terrestrial literature, suggest that interactions between sea urchins and turtlegrass in the eastern Gulf of Mexico are more complicated than previously suggested. To date, our studies show that the same sea urchin densities (i.e., 10, and 20 urchins/m^2) that stimulate increased production of short shoots during the summer may lead to destructive overgrazing of the habitats during fall and winter (Valentine and Heck 1991). If grazing is persistent during the spring, when new leaf growth is initiated, urchins can create unvegetated patches in what was previously continuously vegetated habitat, presumably

because stored plant reserves are insufficient to support regrowth (Heck and Valentine 1995). Because of this, we hypothesize that these apparent contradictions in sea grass responses to grazers will be better understood only when the role of stored materials in rhizomes, nutrient recycling, along with shifts in growth rate following grazing, are considered. Perhaps most importantly, because turtlegrass can respond to herbivory by increasing the density of new shoots, we suggest that simply measuring sea grass biomass as a response variable may have led to a large underestimate by earlier investigators of the effects of herbivory on sea grass (cf. Sand-Jensen et al. 1994).

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