Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay

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ABSTRACT: Unusually dense aggregations of the sea urchin *Lytechinus variegatus* overgrazed at least 0.81 km^2 of seagrass habitat in Outer Florida Bay (USA) between August 1997 and May 1998. Initially, sea-urchin densities were as high as 364 sea urchins m^{-2}, but they steadily declined to within a range of 20 to 50 sea urchins m^{-2} by December 1998. Prior to this event, sea-urchin densities were <1 sea urchin m^{-2} in this area of Outer Florida Bay. Seagrasses in Outer Florida Bay consist primarily of manatee grass *Syringodium filiforme*, of which 82% or 390 g dry weight m^{-2} of total seagrass biomass and >95% of the short-shoot apical meristems were removed by sea-urchin grazing in our study area. Such extensive loss may severely limit recovery of this seagrass community by vegetative reproduction. Effects of the removal of seagrass biomass have already resulted in the depletion of epifaunal-infaunal mollusk assemblages and resuspension of fine-grained (<64 μm) surface sediments—which have caused significant changes in community structure and in the physical properties of the sediments. These changes, coupled with the loss of essential fishery habitat, reductions in primary and secondary production, and degradation of water quality, may lead to additional, longer-term, indirect effects that may extend beyond the boundaries of the grazed areas and into adjacent coastal ecosystems.

KEY WORDS: Seagrass · Sea urchin · Herbivory · *Syringodium filiforme* · *Lytechinus variegatus* · Florida Bay · Disturbance

INTRODUCTION

Investigations of fish and sea-urchin grazing on the structure of seagrass communities have been limited mostly to defoliated halos surrounding tropical coral reefs (e.g. Randall 1965, Ogden et al. 1973, Tribble 1981, Hay 1984, McAfee & Morgan 1996), and the

maintenance of bare areas in subtropical seagrass beds (Valentine & Heck 1991, Heck & Valentine 1995). Large-scale, destructive grazing, or overgrazing, by sea urchins does not appear to occur with either the frequency or magnitude in seagrass communities as in kelp forests (e.g. Breen & Mann 1976, Bernstein et al. 1981), though the role of sea urchins on overfished coral reefs can become increasingly important in limiting the distribution and abundance of algae and sea-

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grasses adjacent to the reef when densities increase due to the absence of predatory fishes (Hay 1984). Few small-scale, seagrass overgrazing events have been reported (e.g. Bak & Nojima 1980, Kirkman & Young 1981, Cambridge et al. 1986). Experimental manipulations have suggested that sea-urchin densities >20 sea urchins m^{-2} have the potential to completely denude seagrass beds of *Thalassia testudinum* Banks ex König in some areas of the Caribbean Sea and the northern Gulf of Mexico (Greenway 1976, Valentine & Heck 1991). In one of the more extraordinary reports of overgrazing, ca 20% of a large meadow of *T. testudinum* in the northeast Gulf of Mexico was denuded by the sea urchin *Lytechinus variegatus* (Lamarck) with densities as high as 636 sea urchins m^{-2} (Camp et al. 1973).

We report a similar incidence of seagrass overgrazing by sea urchins in Outer Florida Bay (24° 54' N, 81° 05' W). In August 1997, a commercial spiny lobster fisherman directed us to an unusually large patch of sea urchins ca 19 km north of Marathon in Outer Florida Bay (Fig. 1). Aggregations (with localized densities exceeding 300 sea urchins m^{-2}) of the sea urchin *Lytechinus variegatus* were found along a 2 to 3 km, east-west portion of the northern extent of a large, highly productive *Syringodium filiforme* Kützing seagrass meadow (see Kenworthy & Schwarzschild 1998). To the north of the sea-urchin aggregation, seagrasses were overgrazed, leaving a mostly barren bottom with small, isolated patches of vegetation. As the aggregations migrated southward into the ungrazed seagrass beds, they created nearly defoliated channels of barren mud (ca 20 to 50 m long and 3 to 10 m wide). The leading edge of these channels (i.e. at the interface between grazed and ungrazed *S. filiforme*) generally contained the highest densities of sea urchins.

This overgrazing event in Outer Florida Bay is located within the boundaries of the Florida Keys National Marine Sanctuary (FKNMS), where seagrass monitoring has been conducted since 1995 (Fourqurean et al. in press). Between 1996 and 1997, we surveyed benthic communities at 509 random sites within the FKNMS (Fourqurean et al. in press) using modified Braun-Blanquet scoring techniques (Braun-Blanquet 1932). We also estimated sea-urchin densities (in 1997 only) at 276 sites. Because the monitoring was conducted prior to August 1997, we have the opportunity to compare the seagrass and sea-urchin populations in the overgrazed areas to background levels. The data from these surveys reveal that the benthos in Outer Florida Bay is dominated by *Syringodium filiforme*, having a mean Braun-Blanquet density between 4 and 5 (i.e. equivalent to ca 75 to 100% cover) (Fig. 2). Sea urchins were present at only 25% of the sites sampled in 1997, with a mean (± SD) density of 0.2 ± 0.6 sea urchins m^{-2} (median = 0) and a maximum site density of 5.2 sea urchins m^{-2}. The large disparity between background and overgrazing densities of sea urchins, the location of the overgrazing aggregations at the edge of one of the most dense, luxuriant seagrass beds in south Florida, and the recent history of widespread seagrass die-offs, phytoplankton blooms, sponge mortality, and reduced spiny lobster populations in Florida Bay (Robblee et al. 1991, Butler et al. 1994, Phlips & Badylak 1996, Fourqurean & Rob-

Fig. 1. Aggregations of the sea urchin *Lytechinus variegatus* in a seagrass bed consisting primarily of *Syringodium filiforme* in Outer Florida Bay. The wooden box in the background is a commercial lobster trap, and the fish swimming above the sea-urchin aggregation are mangrove snapper
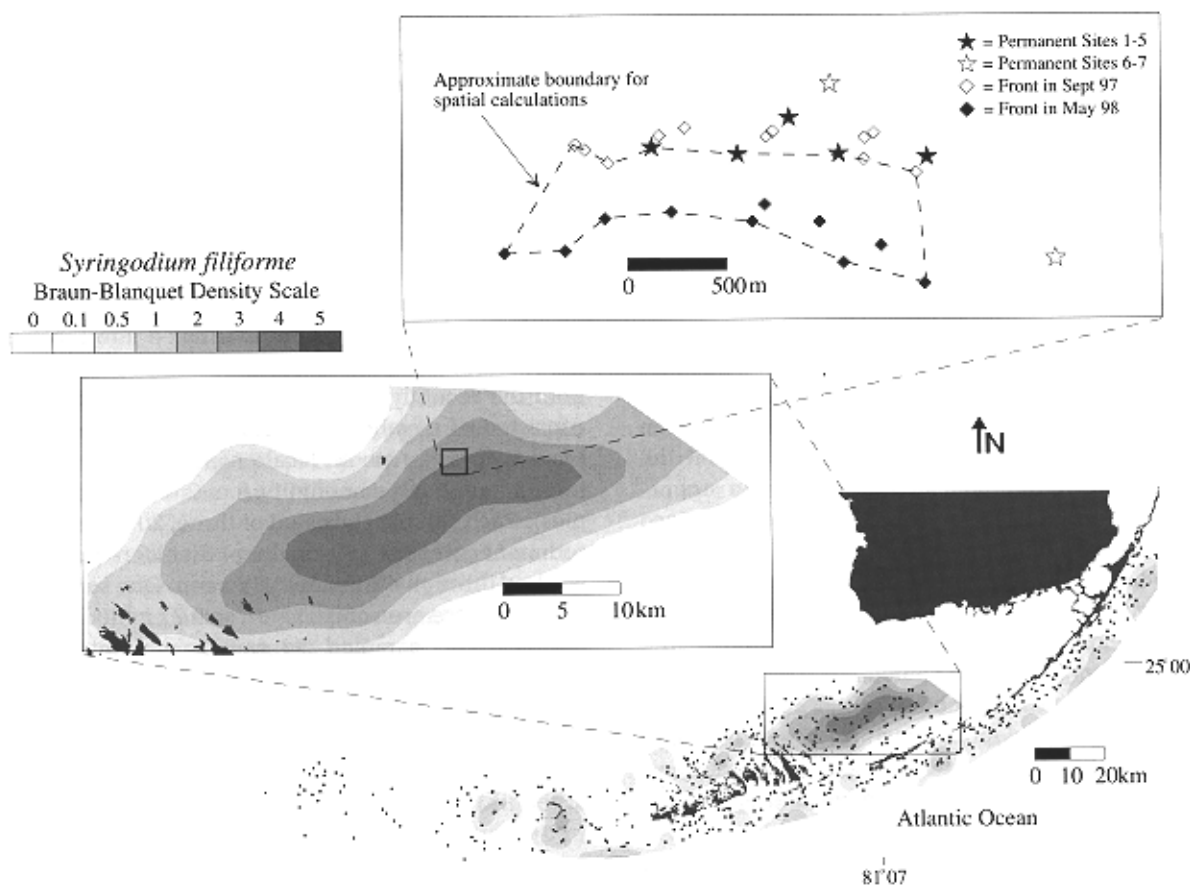
Fig. 2. Contour map of Braun-Blanquet density measurements of the seagrass *Syringodium filiforme* in the Florida Keys National Marine Sanctuary (FKNMS) sampled in 1996 and 1997. Enlarged area shows the location of the sea-urchin aggregation in relation to the large seagrass bed of *S. filiforme* in Outer Florida Bay. Box shows the outline of the fronts observed in September 1997 and May 1998, location of permanent sites, and approximate boundary of the spatial extent of the disturbance between September 1997 and May 1998

blee in press) prompted us to study the effects of this seagrass overgrazing event.

Because seagrass overgrazing by sea urchins has been poorly documented, and even less well understood, this event in Outer Florida Bay provided us with a unique opportunity to study how grazers (at high densities and over a large spatial scale) have the potential to greatly affect seagrass communities. In September 1997, we initiated a study of the seagrass overgrazing in Outer Florida Bay with the following objectives: (1) to characterize the initial sea-urchin population structure in order to obtain a mean age of the sea urchins in the aggregation and determine the number of recruitment events that added to the aggregations; (2) to determine the extent of damage to the seagrass communities and the potential for recovery via vegetative propagation; and (3) to describe the indirect effects of sea-urchin overgrazing on epifaunal-infaunal mollusk communities and the

physical composition of the substrate. Because mollusks constitute ca 75% of the diet of the spiny lobster *Panulirus argus* Latreille (Espinosa et al. 1991, Cox et al. 1997), they may be an important indicator of the potential of this event to impact other trophic levels within this system.

MATERIALS AND METHODS

Migration of the sea-urchin front. We labeled the general east-west portion of the grazed-ungrazed interface encompassing the high-density aggregations of sea urchins as the 'sea-urchin front'. Most of Outer Florida Bay is shallow, with depths ranging between 2 and 4 m. Thus, we were able to map the visible east-west extent of the sea-urchin front in September 1997 and in May 1998 by following the outline of the grazed-ungrazed interface from a boat.

Periodically, a diver verified the presence of the grazed-ungrazed interface. Mapping ceased when we could not discern the interface because of water clarity. Positions along the sea-urchin front were recorded by a differential global positioning system (DGPS) and maps were constructed using GIS-software. Migration rates of the sea-urchin front were estimated based on 10 north-south differences in the positions of the sea-urchin front from September 1997 and May 1998.

We conducted a second, independent measurement of the movement of the sea-urchin aggregation by following the southward migration of the grazed-ungrazed interface of a nearly defoliated channel. In January 1998, a submerged buoy was placed at the grazed-ungrazed interface of the sea-urchin aggregation. The location of the grazed-ungrazed interface was periodically checked by divers from January to July 1998, and linear measurements were made between successively marked locations to determine the extent of the migration.

Initial observations. In September 1997, we conducted several studies to obtain initial information on the sea-urchin population structure, the extent and potential of the damage to the seagrass beds, and changes to the sediment environment and epifaunal-infaunal mollusk communities.

Sea-urchin densities were measured at the grazed-ungrazed interface of 5 nearly defoliated channels (hereafter referred to just as channels). A 6 m transect, parallel to and placed in the middle of each channel, was set across the grazed-ungrazed interface, with 3 m of the transect in the channel and 3 m in the seagrass bed. Three haphazardly placed 0.25 m^2 quadrats were sampled at 5 locations along each transect: at 3 and 1 m within the channel, at 0 m (i.e. the grazed-ungrazed interface), and at 1 and 3 m within the ungrazed seagrass bed. These locations along the transect are referred to as −3, −1, I, +1, and +3, respectively. We also measured the horizontal test diameter (nearest mm) of 111 sea urchins sampled from all 5 channels to obtain size-frequency information.

Three, 0.25 m^2 seagrass sod samples were collected from 3 channels and from 3 adjacent ungrazed patches to examine the effects of grazing on biomass and key population attributes of *Syringodium filiforme*. The sod samples were obtained by severing the rhizomes around the outside perimeter of a quadrat and excavating roots, rhizomes, and short shoots from the sediment. The number of apical meristems (both rhizome and aerial) and short shoots were recorded (see Kenworthy & Schwarzschild 1998 for a more detailed description of vegetative morphology). Short shoots in the grazed samples were classified as being intact or

damaged (hereafter referred to as SS or stems, respectively). Seagrass biomass was separated into leaves, leaf-sheath material, SS (or stems), and roots + rhizomes; rinsed in 5% phosphoric acid to remove adhering carbonates; and dried to a constant weight at 60°C (nearest 0.001 g).

To investigate the effects of loss of seagrass biomass on the molluscan epifaunal-infaunal communities, we compared molluscan assemblages at 2 locations in 3 different communities: ungrazed, 'recently' grazed (i.e. 5 to 10 m behind the grazed-ungrazed interface), and 'previously' grazed (i.e. 100 m behind the interface). Both the recently and previously grazed communities consisted of mostly barren soft mud with some damaged seagrass. At both locations, 5 samples were collected from each community (i.e. $2 \times 5 \times 3 = 30$ samples). Each sample consisted of three, 20 cm (diameter) sediment cores (8 to 10 cm deep) that were pooled and washed through a 1 mm mesh screen. One sample covered a surface area of 0.054 m^2, so 0.27 m^2 (0.054 $m^2 \times 5$ samples) was sampled for each community at each location.

Grain-size analysis was conducted on sediments also collected from ungrazed, recently grazed, and previously grazed communities. Three short cores (0.35 cm in length) were collected from each community, and wet-sieving techniques were used to determine the grain-size distribution.

Continuous monitoring. Sea-urchin densities along the front were determined in January and April 1998. Due to water turbidity and the increasing dispersal of sea urchins, identifying distinct channels became difficult. Thus, rather than measuring sea-urchin densities at the grazed-ungrazed interface of the channels as before, we chose to sample every 10 m along a haphazardly selected 100 m east-west portion of the front (n = 10). At each site, a 6 m transect was placed across a grazed-ungrazed interface as before—but this time, the grazed-ungrazed interface was not necessarily placed in distinct, identifiable channels. So, even though the same sampling protocol was followed (i.e. 3, haphazardly placed 0.25 m^2 quadrats were sampled at 5 positions [−3, −1, I, +1, +3] along each transect), all samples were pooled at each site (n = 15) because of the uncertainty with the placement and orientation of the transects relative to the position of the channels.

In addition to the samples from the 100 m portion of the front described above, 7 permanent sites (Sites 1 to 7) were haphazardly placed and established in September and November 1997 directly north of the sea-urchin front (Fig. 2) so that we could observe both sea-urchin and seagrass densities within the grazed areas and monitor seagrass recovery. At Sites 1 to 5, a permanent 50 m northward transect was established,

along which divers sampled 10 random 0.25 m² quadrats in order to measure percent cover of *Syringodium filiforme*. These measurements were recorded using Braun-Blanquet abundance scores (Braun-Blanquet 1932), using the following modified scale: no SS within a quadrat had a score of 0; 1 SS with <5% cover received a score of 0.1; 2 to 3 SS with <5% cover received a score of 0.5; multiple SS with <5% cover, a 1; SS with 5 to 25% percent cover were given a score of 2; 25 to 50% cover, a 3; 50 to 75% cover, a 4; and 75 to 100% cover, a 5. These scores were averaged for all 10 quadrats to provide a measure of Braun-Blanquet density of *S. filiforme* at each site. Densities of sea urchins were also measured from counts made within the sampled quadrats. These 5 permanent sites were sampled in September and November 1997 and June 1998.

Permanent Sites 6 and 7 were also haphazardly placed, and were established in November 1997 so that we could examine the response and recovery of seagrasses in grazed channels and ungrazed patches. At both sites, nine, 1 m² plots were permanently marked: 3 were placed 3 to 5 m into the ungrazed seagrass bed (referred to as 'ungrazed'), 3 along the vegetated edge of the ungrazed patches (referred to as 'edge'), and 3 in nearly defoliated channels (referred to as 'grazed'). The location of each plot was fixed by DGPS with 2 of the corners marked by anchoring devices. Seagrass abundance was measured by positioning four, 0.25 m² quadrats on each 1 m² plot. The 0.25 m² quadrats were subdivided into one-hundred 0.0025 m² squares and all the squares occupied by seagrass were counted. Percent occupancy in each 1 m² plot was calculated by dividing the number of occupied squares by the total (400). The 3 plots for each stratum (ungrazed, edge, and grazed) were averaged at each site. We calculated sea-urchin densities by counting sea urchins within each 1 m² quadrat. These sites were sampled in January and May 1998.

Statistics. All values presented are means ±1 SD. Statistical tests included *t*-tests and ANOVA (both 1- and 2-way designs) with significance levels at p ≤ 0.05. When needed, data were log transformed to reduce deviations from normality and homogeneity of variances; however, the Mann-Whitney Rank Sum Test was used when significant deviations were still present after transformations. Post hoc tests for 1-way ANOVA included the Student-Newman-Keuls Method or Dunn's Method, and Tukey's test for 2-way ANOVA designs.

RESULTS

Migration of the sea-urchin front

Based on the distance between 10 positions mapped in September 1997 and May 1998 (Fig. 2) we estimated that the leading edge of the sea-urchin front advanced, on average, 390 m. The total area grazed within the area defined by the eastern- and westernmost positions of the front in September 1997 and the corresponding positions in May 1998 was 0.81 km²—for an estimated grazing rate of 3375 m² d⁻¹ or 1.52 m d⁻¹. Data collected from our second, independent measurement of grazing rates along a single channel monitored from January to July 1998 provided an estimated grazing rate of ca 0.91 m d⁻¹.

Initial observations

In September 1997, densities of sea urchins at the grazed-ungrazed interface in 5 channels were as high as 364 sea urchins m⁻², with a mean of 167 ± 85 sea urchins m⁻² (Fig. 3). As we moved ±1 m from the grazed-ungrazed interface ('I' in Fig. 3) into either the grazed channel or ungrazed seagrass bed, sea-urchin densities did not significantly differ from those at the interface (p > 0.05, $F = 8.62$, df = 23, 1-way ANOVA, Student-Newman-Keuls Method post hoc); but as we moved ±3 m from the interface, densities were significantly lower than at the interface (p < 0.001). Sea urchins collected and measured in September 1997 ranged from 45 to 71 mm, with a mean size of 54.9 ± 5.0 mm (Fig. 4).
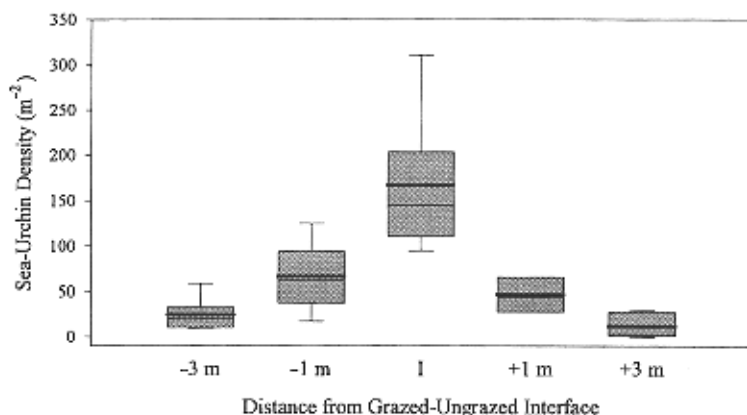

Fig. 3. Mean (thick solid line) and median (thin solid line) sea-urchin densities at the grazed-ungrazed interface at 5 channels in September 1997. Error bars represent the range of the 10th and 90th percentiles, and the length of the box indicates the 25th and 75th percentiles. A 6 m transect was employed from the grazed barren mud (−3 and −1 m) across the grazed-ungrazed interface (I), and into the ungrazed grass bed (+1 and +3 m)
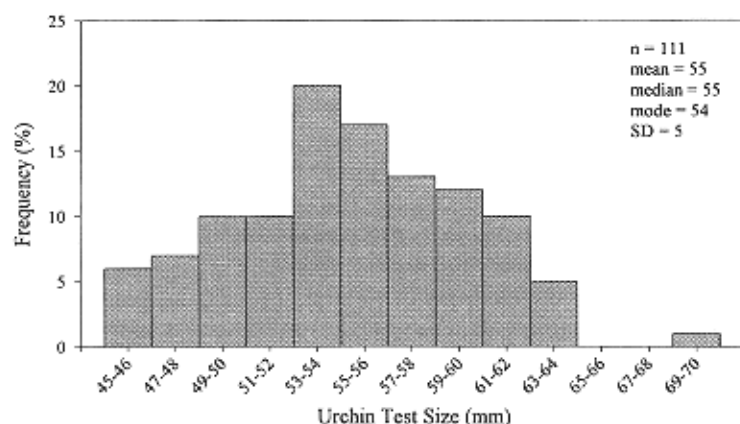
Fig. 4. Frequency histogram of sea-urchin test sizes (mm) for 111 sea urchins collected at the grazed-ungrazed interface in September 1997

The density of intact SS of *Syringodium filiforme* at ungrazed sites was ca 2.8× greater than the combined densities of intact SS and stems (i.e. damaged SS) in channels (Fig. 5). A similar ratio was observed for rhizome apical meristems. No aerial apicals (i.e. rhizome apical meristems occurring above the sediment interface) were present in samples collected from channels. There was a 5-fold difference in mean total biomass of *S. filiforme* collected from sites in the ungrazed patches to seagrass collected in the channels (Fig. 6). A majority (84%) of the biomass collected from channels was composed of below-ground roots and rhizomes, whereas below-ground biomass accounted for only 28% of the total biomass in ungrazed patches (Fig. 6). Leaves and leaf-sheath material accounted for <0.5 and 29% of the total biomass of samples collected from the channels and ungrazed sites, respectively.

A total of 749 living mollusks representing 58 species in 3 classes (35 gastropods, 22 bivalves, and 1 polyplacophoran) were identified from sediment cores collected in 3 communities (i.e. ungrazed, recently grazed, and previously grazed) at 2 locations. There were no significant differences in mollusk communities between the 2 locations (p = 0.145, location main effect, $F = 2.269$, df = 1, 2-way ANOVA), but the ungrazed community at both locations had a significantly higher number of individual mollusks (p < 0.001, community main effect, $F = 17.96$, df = 2, 2-way ANOVA) and number of species (p < 0.001, $F = 41.95$, df = 2, 2-way ANOVA) relative to both the recently and previously grazed communities (Table 1). Fifteen 'common' species (9 gastropods, 6 bivalves) contributed 85% of the specimens. The gastropod *Schwartziella catesbyana* (d'Orbigny, 1842) contributed 45% of all specimens (Table 1); *S. catesbyana* is

a prominent member of seagrass communities in southern Florida (Moore 1969). Sixty-seven percent of all *S. catesbyana* occurred in the ungrazed communities, but 32% persisted in the recently grazed areas—presumably on sparse, scattered vegetation that remained there. Only 1% survived in previously grazed areas. Ratios of overall abundance (n_T) among the other common species of gastropods (8 spp.: $n_T = 129$; ratio = 74:11:15) and bivalves (6 spp.: $n_T = 166$; ratio = 64:11:25) showed a slightly different pattern: the abundance sharply declined from the ungrazed to the recently grazed communities, followed by small increases in the previously grazed communities—caused principally by recruitment of infaunal bivalves.

Ungrazed, recently grazed, and previously grazed communities have sediments dominated by mud (<62 μm), but as the time since the grazing increased, percentage of mud decreased, as evidenced from the regression of percent mud from 82% in the ungrazed to 78% in the recently grazed to 55% in the previously grazed communities (Fig. 7). The proportion of coarse material exhibits the opposite trend being greatest in the previously grazed communities.

Continuous monitoring

Sea-urchin densities at the grazed-ungrazed interface at 10 sites along a 100 m portion of the front were 22.45 ± 22.42 sea urchins m^{-2} in January 1998 and
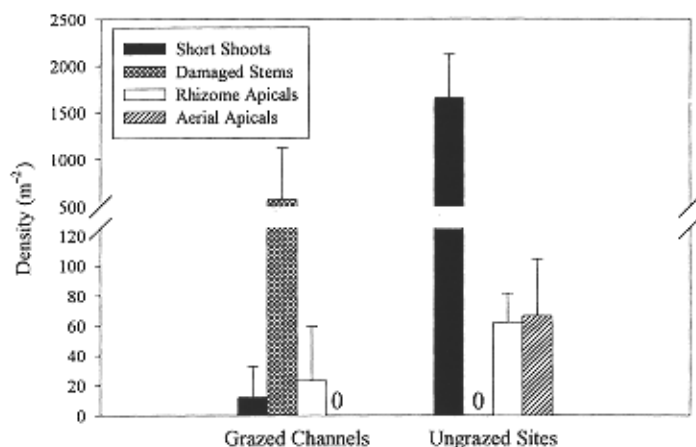

Fig. 5. Mean (± SD) densities of intact short shoots (SS), damaged stems, and rhizome and aerial apical meristems from grazed channels and ungrazed communities of *Syringodium filiforme* sampled in September 1997. Note: no aerial meristems were found in grazed channels, and damaged stems were not present at undisturbed sites

Table 1. Abundances of the 15 most common mollusks in ungrazed, recently grazed, and previously grazed communities in Outer Florida Bay. Samples were collected in September 1997. Values represent pooled numbers of individuals from 5 samples at 2 locations within each of the 3 types of communities

Species		Habitat		Total
	Ungrazed	Recently grazed	Previously grazed	
Gastropoda				
Schwartziella catesbyana	225	108	5	338
Caecum pulchellum	28	1	4	33
Meioceras nitida	19	1·	1	21
Jaspidella sp.	10	1	8	19
Turbonilla sp.	16	0	1	17
Rissoina cancellata	9	3	0	12
Nassarius albus	5	3	2	10
Nassarius sp.	6	2	1	9
Gibberula lavalleeana	2	3	3	8
Total	320	122	25	467
Bivalvia				
Nucula proxima	49	3	10	62
Anodontia alba	20	2	15	37
Lucinisca nassula	20	10	4	34
Codakia orbiculata	10	1	1	12
Lucina amianta	6	1	5	12
Chione cancellata	1	2	6	9
Total	106	19	41	166

18.48 ± 15.24 sea urchins m^{-2} in April 1998. Sea-urchin densities did not significantly differ between January and April 1998 (p = 0.995, Mann-Whitney Rank Sum Test).

At permanent Sites 1 to 5 (installed north of the front in September 1997), seagrass and sea-urchin populations were monitored from September 1997 to June 1998. Braun-Blanquet density of *Syringodium filiforme* along the 5 permanent transects behind the urchin front was 2.04 ± 1.07 in September 1997, 1.76 ± 0.64 in November 1997, and 0.46 ± 0.76 in June 1998 (Fig. 8A). Markers for 2 sites (Sites 2 and 3) were lost over the winter and were not sampled in June 1998. Though a 77% difference in the means was observed from September 1997 to June 1998, these differences were not significant (p = 0.08, F = 3.35, df = 12, 1-way ANOVA). The lack of statistical significance between sampling dates may be attributed to the high degree of variability between sites (% CV ranged between 34 and 178%), low statistical power (0.36), and missing data from Sites 2 and 3. When we re-examined the data to only include Sites 1, 4, and 5 for all sampling dates, percent loss of the Braun-Blanquet density of *S. filiforme* at Sites 1, 4, and 5, was 100, 97, and 55%, respectively. These losses at Sites 1, 4, and 5 between September 1997 and June 1998 are significant (p = 0.039, F = 5.89, df = 8, 1-way ANOVA, Dunn's Method post hoc).

Sea-urchin densities at permanent Sites 1 to 5 also exhibited a decreasing trend—from 4.56 ± 3.56 sea urchins m^{-2} in September 1997 to 2.72 ± 1.48 sea urchins m^{-2} in November 1997 to 0.80 ± 0.70 sea urchins m^{-2} in June 1998 (Fig. 8B). The highest densities were recorded in September 1997, when quadrat densities were as high as 9.6 sea urchins m^{-2}; but no significant differences in sea-urchin densities were detected among the 3 months (p = 0.157, F = 2.24, df = 12, 1-way ANOVA, Student-Newman-Keuls Method post hoc). The lack of statistical significance did not change if we only analyzed the data from Sites 1, 4, and 5.

At permanent Sites 6 and 7 (installed in November 1997), seagrass recovery was monitored in January and May 1998 in permanent quadrats originally placed in ungrazed seagrass beds, along the edges between grazed and ungrazed areas, and in grazed, nearly defoliated areas (Fig. 8C). Abundance (or percent occupancy) of *Syringodium filiforme* in permanent quadrats significantly differed between dates (p < 0.001, date main effect, F = 65.203, df = 1, 2-way ANOVA, Tukey test post hoc), mainly due to the higher abundances in ungrazed plots sampled in January. Ungrazed plots, for both sampling dates, were significantly higher (p < 0.001, community main effect, F = 96.647, df = 2, 2-way ANOVA, Tukey test post hoc) than permanent plots initially located on
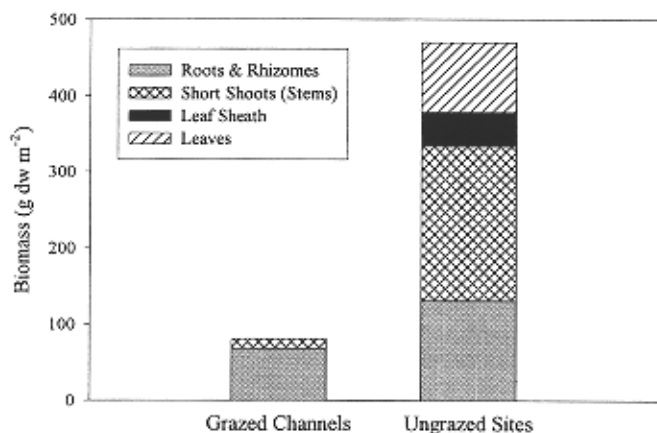

Fig. 6. Mean total biomass (g dwt m^{-2}) of *Syringodium filiforme* from grazed channels and ungrazed sites in September 1997. Plant organs are separated into 4 categories: roots and rhizomes, short shoots (referred to as stems in grazed areas), leaf sheath material, and leaves
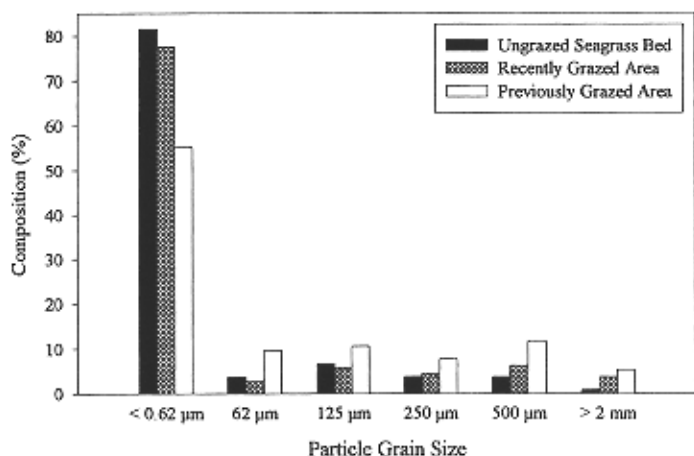
Fig. 7. Sediment grain size distribution for cores collected from ungrazed, recently grazed, and previously grazed seagrass communities. Samples were collected in September 1997

DISCUSSION

Between September 1997 and May 1998, a dense aggregation of *Lytechinus variegatus* along a 2 to 3 km front in Outer Florida Bay severely impacted ≥0.81 km^2 of a luxuriant and productive meadow of *Syringodium filiforme*. Approximately 3375 m^2 of seagrass was grazed daily, transforming a relatively homogeneous system dominated by *S. filiforme* into a nearly unvegetated landscape with small, isolated patches of *S. filiforme*; sparsely distributed surviving individuals of the seagrasses *Thalassia testudinum* and *Halodule wrightii* Ascherson; and small patches of the green algae *Halimeda* spp. and *Caulerpa* spp. (pers. obs.). The loss of *S. filiforme* is evidenced by the significant difference ($p < 0.001$, $F = 17.7$. df = 32, 1-way ANOVA, Student-Newman-Keuls Method post hoc) between the Braun-Blanquet densities at the 5 permanent sites compared to a mean of 3.97 ± 1.03 from 20 nearby (i.e. located within a 15 km radius of the front) sites sampled from May to August 1997 as a part of our benthic surveys in the FKNMS.

In addition to the removal of the canopy of *Syringodium filiforme*, a large biomass of decaying vertical stems, rhizomes, and roots remained in the sediment immediately behind the front. Because
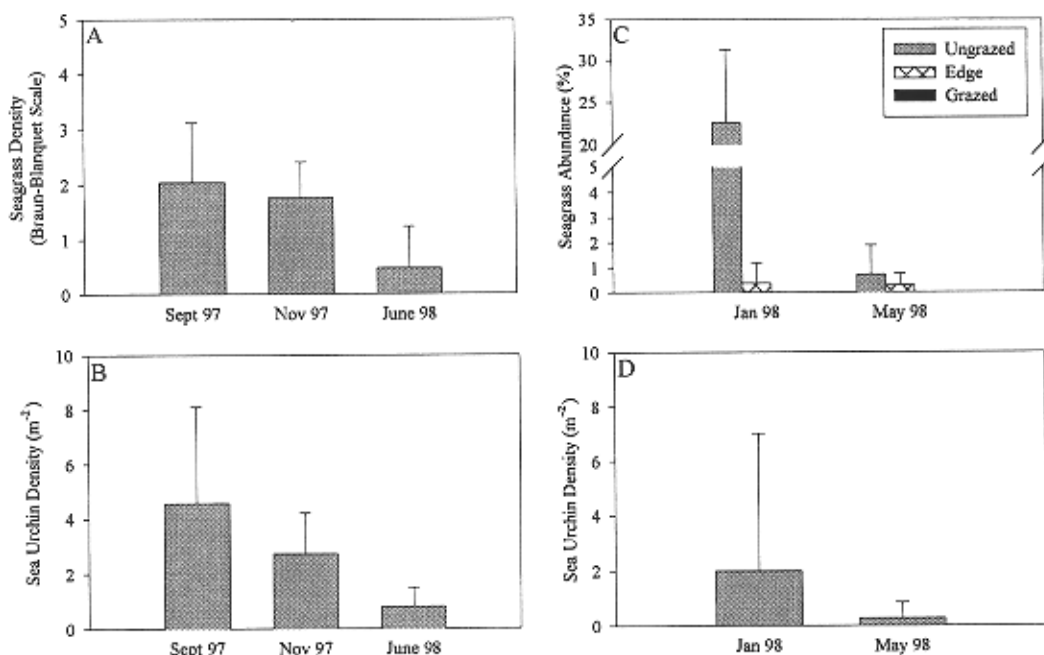
the edge and within grazed areas. All of the *S. filiforme* present (in all quadrats) in January 1998 was eaten by May 1998—except for the emergence of seedlings (with densities as high as 12 m^{-2}) observed in 6 of the 18 quadrats located at both sites. Sea-urchin densities (Fig. 8D), enumerated from all 9 quadrats at each site, did not significantly differ between sites or sampling dates ($p > 0.05$).

Fig. 8. Seagrass and sea-urchin populations at permanent sites north of the grazed-ungrazed interface. Mean ± SD (A) Braun-Blanquet density of *Syringodium filiforme* and (B) sea-urchin density along 50 m transects at permanent Sites 1 to 5 sampled in September 1997, November 1997, and June 1998. Mean ± SD (C) percent abundance of *S. filiforme* and (D) sea-urchin densities from permanent quadrats at Sites 6 and 7 sampled in January and May 1998

nearly all of the photosynthetic material of *S. filiforme* was destroyed by the overgrazing of sea urchins, rhizome meristems buried in the sediments lost the support of living SS and consequently had a high mortality. However, the mean density of rhizome apical meristems sampled from 3 channels in September 1997 was greater than we anticipated, but appears to be disproportionately influenced by 1 site (with site averages of 0, 1.3, and 68 rhizome apicals m^{-2}). Reasons for this disparity may be due to a lesser degree of grazing or that the 1 site (with 68 rhizome apicals m^{-2}) was sampled at an earlier stage of grazing.

Because seagrass growth is meristem dependent and branching of existing SS to form new rhizome apicals is rare (Tomlinson 1974), the catastrophic loss of apical growing tips suggests that recovery by vegetative reproduction will be inhibited and that the general loss of seagrass may continue. This conclusion is supported by the measured decrease in seagrass abundance at permanent Sites 6 and 7 between January and May 1998. In May 1998, sea-urchin densities at these 2 sites were considerably less than densities recorded along the front, several hundred meters to the south. Also in May 1998, the only sign of potential recovery was the presence of *Syringodium filiforme* seedlings, which were patchily distributed with densities ≤12 m^{-2} at permanent Sites 6 and 7. The contribution of seedlings of *S. filiforme* to the recovery dynamics has never been documented for a disturbance of this magnitude, so it is unknown whether this system will recover via seedling recruitment. Furthermore, in a sampling of Sites 6 and 7 in December 1998, after Hurricane Georges passed over the area, we did not find any surviving seedlings presumably because of the disturbance to the benthos caused by the storm. The pattern of continued degradation of heavily grazed areas at Sites 6 and 7, along with the persistence of a low density of sea urchins throughout the area behind the front, raises some concern as to whether recovery will proceed. Peterken & Conacher (1997) reported that the seagrass *Zostera capricorni* Ascherson recovered to pre-grazing SS densities within a year after intense grazing by a herd of dugongs, despite continuous grazing throughout the year. Densities of germinating seeds and flowering shoots were as high as 86 and 1219 m^{-2}, respectively, indicating that for at least that population of *Z. capricorni* sexual reproduction was an important process in responding to a large-scale disturbance event.

The role of grazers in structuring seagrass communities has been well-documented. The most publicized accounts of grazing involve the formation of halos surrounding coral reefs by resident herbivorous fish and sea urchins (e.g. Randall 1965, Ogden et al. 1973, Tribble 1981, Hay 1984, McAfee & Morgan 1996) and the

formation of grazing scars by sea turtles (Bjorndal 1980, Ogden et al. 1983). Vicente & Rivera (1982) suggest that sea-urchin densities of ca 3 sea urchins m^{-2} may limit the lower depth penetration of *Thalassia testudinum* in Jobos Bay, Puerto Rico; and clumps of 17 to 19 sea urchins m^{-2} result in intense grazing and the formation of bare patches. Formation and maintenance of bare areas by sea urchins in seagrass beds have also been reported for subtropical communities of *T. testudinum* in the northern Gulf of Mexico where densities were >20 sea urchins m^{-2} (Valentine & Heck 1991, Heck & Valentine 1995), and in communities of *Posidonia* spp. in Cockburn Sound, Western Australia, where densities were as high as 250 sea urchins m^{-2} (Cambridge et al. 1986).

The extent and severity of the recent seagrass overgrazing event in Outer Florida Bay make it difficult to compare our results to previous reports of the role and effects of sea-urchin grazing. Until now, seagrass overgrazing by sea urchins has generally been represented by the lone report of Camp et al. (1973), where high densities (as high as 636 sea urchins m^{-2}) of the sea urchin *Lytechinus variegatus* denuded ca 20% of a meadow of *Thalassia testudinum* (but also see Bak & Nojima 1980). Though Camp et al. (1973) report a maximum of sea-urchin densities almost 2× higher than we observed in Outer Florida Bay, sea-urchin densities behind the fronts and in the grazed areas are similar (<5.6 m^{-2}). Active feeding channels in the seagrass beds of *T. testudinum* grazed through the seagrass beds at an average rate of 0.23 m d^{-1}, and denuded 1 to 2 m^2 of seagrass daily. These rates are greatly lower than those observed in Outer Florida Bay. Linear grazing rates in Florida Bay were estimated at 0.91 to 1.52 m d^{-1}. The range of estimates of grazing rates only highlights the spatial heterogeneity of this disturbance. Areal grazing rates are an estimated 3375 m^2 d^{-1}, which result in 1586 kg dry weight of seagrass biomass lost on a daily basis (Table 2). This could result in a loss of ca 578 981 kg dry weight (dwt) of seagrass biomass after 1 yr, which equates to a loss of ca 1 231 875 m^2 of seagrass cover.

The origins of this extraordinary 'feeding front' remain unclear. One hypothesis, based on the relatively small range of sea-urchin test sizes sampled in September 1997, is that the high densities and aggregations of sea urchins were the result of a highly successful recruitment. Using the estimates presented by Moore et al. (1963), this sea-urchin population appears to be between 1 and 2 yr old, with a greater percentage of individuals greater than 1 yr old (i.e. >50 mm) and no individuals <45 mm (Fig. 4). Alternatively, a release from predation pressure could partially explain the formation of the dense aggregations of sea urchins now present in Outer Florida Bay.

Table 2. Summary of estimates and predictions of sea-urchin grazing rates and loss of *Syringodium filiforme* in Outer Florida Bay between September 1, 1997, and May 15, 1998. Annual calculations are based on data presented in this paper

Parameter	Estimate
Linear east-west extent of sea-urchin front	3100 m
Southward migration of sea-urchin front	390 m
Linear grazing rate	1.52 m d^{-1}
Areal extent of grazing event	0.81 km^2
Areal grazing rates	3375 m^2 d^{-1}
Biomass of *Syringodium filiforme*	0.47 kg dwt m^{-2}
Daily loss of seagrass biomass	1586 kg dwt d^{-1}
Total loss of seagrass biomass	406 080 kg dwt
Predicted loss of seagrass biomass after 1 yr	578 981 dwt kg
Predicted loss of seagrass cover after 1 yr	1 231 875 m^2

Based on studies of sea-urchin grazing in kelp forest habitats and coral reefs, the consequences of the removal of large apex predators (e.g. spiny lobsters and stone crabs) in nearshore food webs could change food web composition and lead to significant changes in ecological community composition and ecosystem function (Parsons 1992, 1996, Botsford et al. 1997, Vitousek et al. 1997). Regardless of the origins of this feeding front, these seagrass communities in Outer Florida Bay have been at least temporarily altered. Sea-urchin densities in Outer Florida Bay, prior to August 1997, were <1 sea urchin m^{-2}. If sea urchins persist in these areas at densities >1 sea urchin m^{-2}, this event is likely to have longer-term impacts on the structure of these seagrass communities in Outer Florida Bay.

Catastrophic losses in this seagrass community and uncertainty for recovery may have far-reaching implications for both the Florida Bay and Florida Keys ecosystems. The area overgrazed in this event is located at the northernmost extent of a large (ca 600 km^2), extremely productive meadow of *Syringodium filiforme* (Kenworthy & Schwarzschild 1998). We have estimated that this meadow stabilizes 1.8 × 10^8 m^3 of fine-grained, unconsolidated sediment. Because it is located at the convergence point of water masses flowing south along the eastern Gulf of Mexico shelf and water ebbing from Florida Bay, the stabilizing properties of the meadow must have a significant influence on the quality of the water flowing into the Gulf of Mexico, Hawk Channel, and the Florida Keys reef tract (Smith 1994). Loss of seagrass biomass in the grazed areas resulted in smaller amounts of fine-grained particles in the surface sediments. Post-grazing sediments were proportionally coarser in composi-

tion. These results help explain the high levels of turbidity within the region being actively grazed and suggest that nutrients and other substances bound within the upper sediment surfaces will most likely be exported from the region. Resuspension of these fine-grained sediments is partly responsible for attenuating light needed by the surviving plants and the recruits attempting to recolonize the sediments (Gallegos & Kenworthy 1996). Since September 1997, water transparency in the overgrazed area has been relatively poor compared to areas south of the front, overlying the ungrazed seagrass bed. Secchi disk depths taken from November 1997 through July 1998 were less than the water depth at the permanent sites, indicating that light reaching the bottom was insufficient to sustain long-term seagrass growth and meadow development (Kenworthy & Fonseca 1996).

The loss of seagrass biomass can also have a substantial impact on animal communities. The density of mollusks in previously grazed areas decreased 84% relative to that of undisturbed seagrass beds, and similar losses were probably experienced by crustaceans and other groups that favor the seagrass habitat (e.g. Sheridan 1992). From September 1997 through May 1998, mollusks lost from the grazed areas exceeded 9.68 × 10^8 individuals. Impacts on the populations of smaller seagrass biota will, in turn, affect the animals that depend upon them for food. The extensive meadows of *Syringodium filiforme* in Outer Florida Bay serve as habitat for several of Florida's most important fishery species. For instance, juvenile *Panulirus argus* (spiny lobster) and *Farfantepenaeus duorarum* (pink shrimp) predominantly eat mollusks and crustaceans (Eldred et al. 1961, Espinosa et al. 1991, Cox et al. 1997). Our results indicate that the loss of *S. filiforme*, and the associated losses of epifaunal-infaunal mollusks, may deleteriously affect the abundance of these 2 comercially important species.

The spatiotemporal extent of this sea-urchin overgrazing event in Outer Florida Bay is uncertain. The suspended sediments and high turbidity associated with the front have made it difficult to determine the exact boundaries of the overgrazed area with either aerial photography or SCUBA. However, observations as far as 4 km north of the front (and in a few isolated areas west of the front) indicate that severe grazing occurred over a broad area prior to August 1997.

In December 1998, 2 mo after the passage of Hurricane Georges, sea-urchin densities of 20 to 50 sea urchins m^{-2} were found at a grazed area of the seagrass bed ca 100 m south of where the sea urchins had last been observed, in September 1998. Thus, questions remain concerning the sea-urchin population structure, its reproductive potential, the ability of the seagrass to recover, and the effects of a reduced

light regime on nearby, ungrazed seagrass communities. The effects of the continued loss of seagrass on sediment properties and animal communities have the potential to cascade through the Florida Bay ecosystem and extend to the nearby Florida Keys reef tract.

The immediate impacts of this grazing event—which include loss of seagrass biomass and primary production, loss of infauna, and increased water column turbidity caused by destabilized sediments—are evident over 10 to 15 km^2 in the FKNMS. We know of no reason, however, to predict that the seagrass beds affected by this event will not eventually recover. It is entirely possible that there are some long-term, beneficial consequences of this grazing event as the nearly complete removal of the dense, monospecific seagrass canopy may increase habitat complexity as other seagrass and algae species recolonize these barren areas. On the other hand, frequent and long-lived events of this magnitude have the potential to seriously alter the environment of the FKNMS, as well as seagrass communities in other systems.

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