

DESTRUCTION OF FLORIDA BAY SEAGRASSES BY A GRAZING FRONT OF SEA URCHINS

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Florida Bay is a shallow lagoon (mean depth <1 m) located at the southern tip of Florida, USA. As one of the largest estuarine ecosystems in the world (2200 km²), the Bay has great regional importance as permanent habitat and nursery grounds for a large number of economically important fish and shellfish species such as seatrout, snook, tarpon, snappers, pink shrimp, blue crabs and spiny lobsters (Tilmant, 1989; Zieman et al., 1989; McIvor et al., 1994).

Approximately 80% of the Florida Bay bottom is covered by seagrass beds composed of three main species, *Thalassia testudinum* Banks ex König, *Halodule wrightii* Ascherson, and *Syringodium filiforme* Kütz (Zieman et al., 1989). Seagrasses are critical components of the ecosystem, providing both the structural and trophic foundations for a highly productive food web. Seagrasses also play a major role in controlling the water quality of the bay by capturing and storing nutrients, binding and stabilizing bottom sediments, and trapping suspended sediments (Ginsburg and Lowenstam, 1958). In this study, we document the significant effects of a large (several kilometers long) aggregation of the sea urchin *Lytechinus variegatus* (Lamarck) that was first detected in August 1997 grazing on dense beds of the seagrass *S. filiforme* in the western portion of Florida Bay.

L. variegatus is a common grazer of seagrass beds in the western Atlantic. Although in some areas it occurs at population densities from 20–40 ind m⁻², populations usually have fewer than 10 ind m⁻² (Moore et al., 1963; Engstrom, 1982; Keller, 1983; Oliver, 1987; Montague et al., 1988; Valentine and Heck, 1991; McGlathery, 1995). In 1973, Camp et al. reported that an aggregation of *L. variegatus* had severely overgrazed a *T. testudinum* bed in the northeastern Gulf of Mexico (Camp et al., 1973). The aggregation formed a grazing front with maximum densities of over 600 ind m⁻², by far the highest density ever reported for this species. Until now, this was the only report of such localized high population densities for *L. variegatus*.

METHODS

We initiated our study in September, 1997 following several reports of local fishermen who had observed an unusually high number of sea urchins in the western portion of Florida Bay. A well-defined urchin front was located in September and November of 1997. On these dates, we measured urchin density with a series of 1 m-wide belt transects perpendicular to the front. In January, March, and July of 1998, the urchins were not distributed as a distinct front; randomly placed 1 m² quadrats were used to assess urchin density. Test diameter of haphazardly collected urchins was measured with calipers. Above-ground seagrass and rhizophytic algae samples were collected with haphazardly located 30 × 30 cm quadrats within which all biomass was clipped with scissors. Below-ground biomass was collected with 15 cm diameter corers to a depth of 15–25 cm. Seagrass and algae samples were dried to constant weight at 70°C.

In November, 1997, two permanent plots (2 × 1 m) were established within the field site 10 m south of the urchin front in the ungrazed seagrass bed. At the time these plots were established, the bottom had 100% cover of *S. filiforme* and exhibited no signs of grazing. No urchins were found within the plots. These plots were surveyed again in January, 1998 after passage of the urchin front.

Sediment depth was measured in November, 1997 by driving a pole marked in 1 cm increments into the sediment. Measurements were taken in the ungrazed area ahead of the front and in the completely grazed area behind the front. Also in November 1997, sediment samples for grain size and organic content analyses were taken in three areas: ahead of the front (ungrazed), behind the front in bare sand (completely grazed), and behind the front in areas with some seagrass cover remaining (partially grazed). Samples were collected with 2.5 cm diameter corers to a depth of 13.5 cm. A subsample from each core was dried at 70°C and then ashed at 500°C for 24 h. Organic content was calculated as percent weight loss after ignition. A second subsample from each core was used to determine grain size composition. Samples were mixed with 10 ml of dispersant (10% chemical water softener in water) and allowed to sit for at least 48 h. The sediment/dispersant mixture was washed through two sieves (0.5 mm and 0.64 μ), and the portion retained on each sieve was dried at 70°C and weighed. Three grain size categories were used: gravel (>0.5 mm), sand (0.5 mm–64 μ), and silt/clay (<64 μ).

RESULTS

In the summer of 1997, a grazing front of *L. variegatus* was observed moving southward within a bed of *S. filiforme* in Florida Bay (Figs. 1,2). Water depth at the site was 3 m. In September 1997, the grazing urchins were distributed as a distinct front 2–3 m wide with a mean density of 96 ± 11.5 (SE) ind m^{-2} (maximum density = 160 ind m^{-2}). The density of urchins dropped sharply a few meters in front of and behind this front, but urchins were still present in lower numbers for many tens of meters behind the front. This type of grazing front formation was again observed in November 1997, with a mean density of 124 ± 18.4 ind m^{-2} (maximum = 222 ind m^{-2}). By January 1998, however, the urchins were no longer organized as a dense narrow band, but were grazing in a more diffuse aggregation with a mean density of 18.5 ± 3.8 ind m^{-2} and a maximum density of 86 ind m^{-2} . A similar diffuse formation was observed in July 1998 when mean urchin density was $16.0 (\pm 3.7)$ ind m^{-2} and maximum density was 36 ind m^{-2} .

The low visibility encountered in the area during each survey (usually less than 1.5 m of horizontal visibility) prevented us from determining the length of the grazing front. Given the area affected by the urchins (Fig. 2), however, the front was estimated to be approximately 4 km long. Similar difficulties prevented us from determining the movement rates of the front with accuracy. Nevertheless, a movement rate was estimated by using the coordinates recorded during our September and November 1997 surveys, when the urchins were found in a distinct front formation. During this period, the estimated movement rate of the front was 6.7 m d^{-1} in a southerly direction. Although the same general direction was maintained, the calculated movement rate decreased to 2.7 m d^{-1} between November 1997 and January 1998. This was also the time when the front dissipated into a more diffuse formation.

Mean test diameter of urchins in September 1997 was 55.9 ± 0.3 mm (Fig. 3A). By January 1998, mean test diameter had increased to 60.3 ± 0.4 mm (Fig. 3B). In July 1998, mean test diameter again increased to 62.3 ± 0.4 mm (Fig. 3C).

After passage of the urchin front, percent bottom cover of the two permanent plots, which was initially 100% *S. filiforme*, was reduced to <5%. *S. filiforme* biomass throughout the site was significantly affected by the urchin front. Eleven weeks after passage of the urchins, above-ground biomass decreased significantly from a pre-grazing value of 232 ± 30 g dry wt m^{-2} to less than 3.3 ± 2.9 g m^{-2} (Wilcoxon test; $Z = 3.92$; $P < 0.001$). Below-ground biomass also decreased significantly from 243.2 ± 37.5 g m^{-2} prior to grazing to

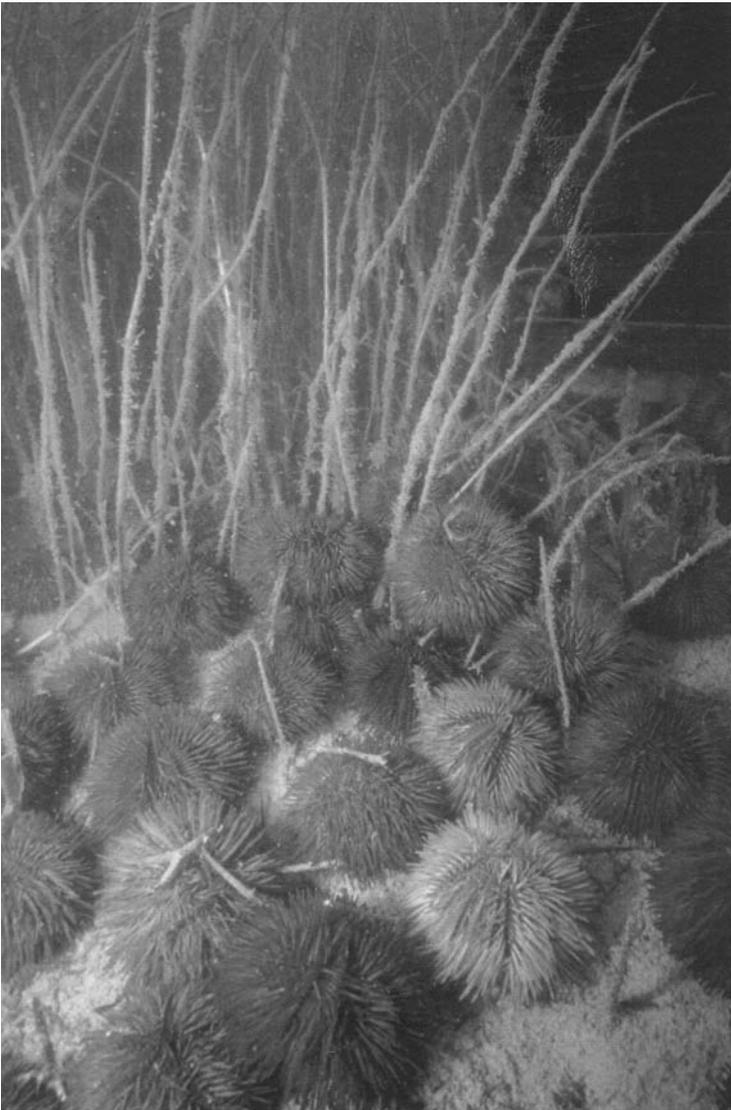


Figure 1. Photograph of the sea urchin *Lytechinus variegatus* feeding on a seagrass meadow of *Syringodium filiforme* in Florida Bay. Note the bare sediment in the foreground, a result of urchin overgrazing.

$63.2 \pm 17.7 \text{ g m}^{-2}$ (Student's t-test on ln-transformed data; $t = 5.19$, $df = 16$, $P < 0.001$). Both above- and below-ground biomass continued to decline until 37 wks after passage of the front (July 1998), at which time no seagrass biomass was detected.

In November 1997, the urchin front passed through a small patch of calcareous rhizophytic macroalgae (*Halimeda*, *Penicillus*, *Caulerpa*, and *Udotea* spp.). Although the seagrass canopy surrounding the algal patch had been completely grazed, algae remained present with a dry weight within the patch of $61.4 \pm 11.5 \text{ g m}^{-2}$.

Mean sediment depth in the undisturbed seagrass bed ($25.8 \pm 1.2 \text{ cm}$) was significantly greater than in the grazed areas ($12.3 \pm 1.3 \text{ cm}$) behind the front (Wilcoxon test $Z = 5.11$,

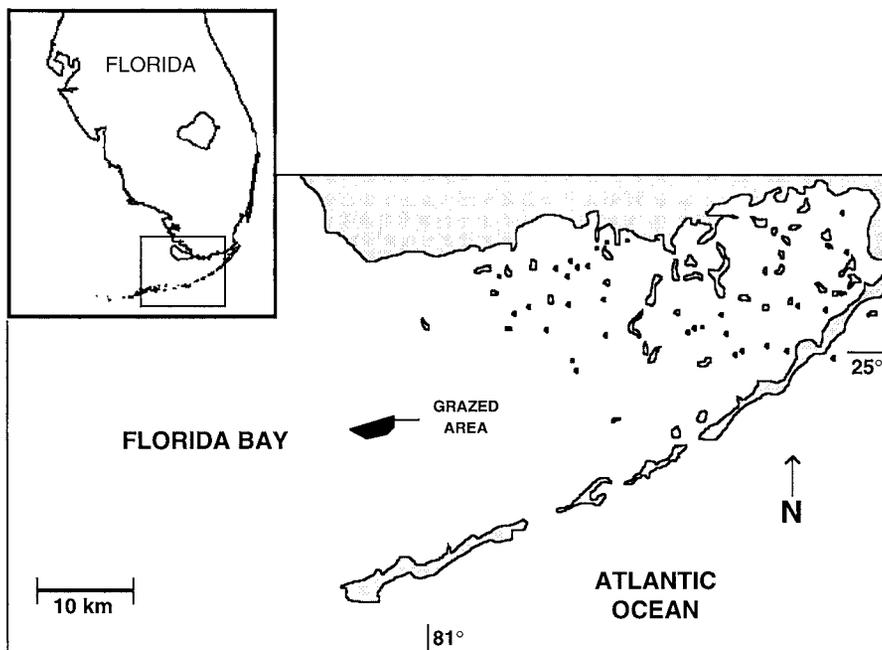


Figure 2. Map of Florida Bay showing the area (9.3 km²) affected by the grazing activities of the sea urchin front as estimated from aerial surveys conducted in August 1997 by Bill Sharp, Department of Environmental Protection, Florida.

$P < 0.001$). Grain size analysis indicated that the frequency distribution of the different sediment size fractions (gravel, sand, silt/clay) differed among ungrazed, partially grazed, and completely grazed areas ($\chi^2 = 36.76$, $df = 4$, $P < 0.001$). A significantly smaller percentage of the sediment was composed of silt/clay in the completely grazed area ($6.0 \pm 0.1\%$) than in the ungrazed area ($36.0 \pm 0.04\%$) ($F = 36.95$, $df = 14$, $P < 0.001$). There was also a concurrent increase in the gravel fraction from ungrazed ($9.0 \pm 0.02\%$) to grazed ($33.0 \pm 0.05\%$) areas ($F = 9.28$, $df = 14$, $P < 0.01$). Percent organic matter in the sediment increased significantly from the ungrazed ($3.0 \pm 0.1\%$) to the partially grazed ($4.6 \pm 0.4\%$) to the completely grazed area ($6.7 \pm 0.3\%$) ($F = 43.08$, $df = 14$, $P < 0.001$).

DISCUSSION

Given the uniformity in size, the urchins in the Florida Bay aggregation appear to be of a single year class, as were those in the previously reported *L. variegatus* front in the Gulf of Mexico (Camp et al., 1973). Based on data collected by Moore et al. (1963) on *L. variegatus* in Biscayne Bay, Florida, the urchins in the Florida Bay front would have been approximately 2 yrs old at the time the front was first discovered in the summer of 1997. Camp et al. (1973) estimated the age of the Gulf of Mexico urchins to be 1 yr old at the time of their discovery. Just 2 mo later, however, the urchins suffered a mass mortality, possibly as a result of decreased salinity (Lawrence, 1975). Our study in Florida Bay indicates that *L. variegatus* can remain in grazing front formation for much longer than 1 yr (up to approximately 2.5 yrs). Had salinity changes not decimated the Gulf of Mexico

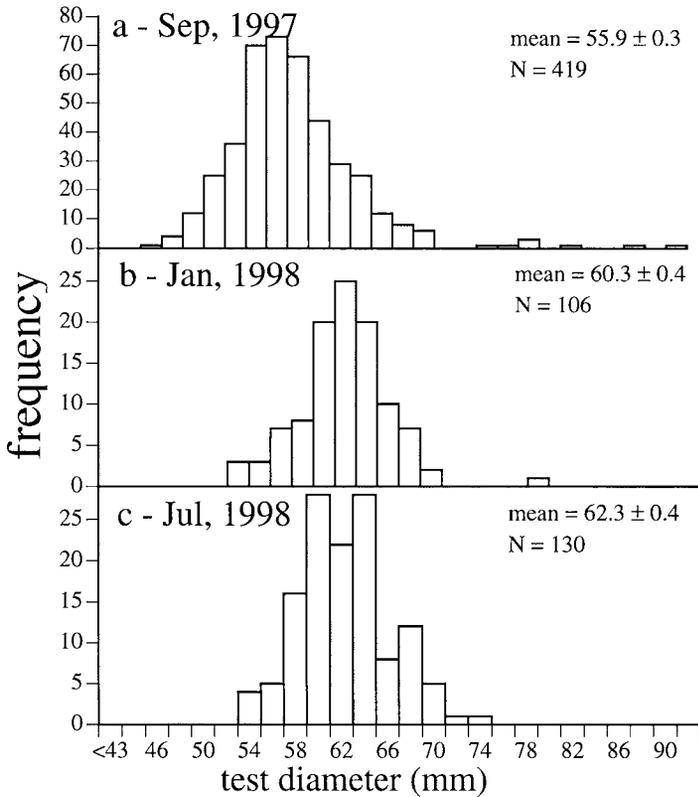


Figure 3. Size frequency distribution of *Lytechinus variegatus* within the grazing front on a) September 1997, b) January 1998 and c) July 1998.

population, its impact could have been even greater than that reported.

The growth rates estimated from the crowded conditions in the front (1 mm mo⁻¹ between September 1997 and January 1998) are high, given that this species has a constant growth rate up to a test diameter of 50 mm, after which growth rate declines rapidly (Moore et al., 1963). Because the sudden mass mortality prevented the estimation of growth rate for the Gulf of Mexico urchins, our study represents the first estimate of *L. variegatus* growth rate at an extremely high population density.

The most obvious effect of the urchin grazing activities in Florida Bay has been removal of the seagrass canopy, which in large areas has been completely grazed away. Because seagrass roots and rhizomes are normally buried within the sediment and out of reach of the urchins, immediate effects of the grazing front were less pronounced (though still significant) for below-ground than for above-ground biomass of *S. filiforme*. *S. filiforme* rhizomes, however, are found at relatively shallow depths in the sediment (Zieman, 1982) and, following the grazing event and the subsequent decrease in sediment depth, many of the remaining *S. filiforme* rhizomes were exposed at the surface of the sediment. Thus, with time, even belowground biomass was eliminated. In November, 1997, the front passed through a small patch of rhizophytic algae. While the seagrass surrounding the algae was completely grazed, the algae were not. Although the algae species avoided are chemically and morphologically defended (reviewed by Paul, 1992) previous studies have shown

that they are consumed by urchins (Lowe and Lawrence, 1976; Vadas et al., 1982). This feeding pattern suggests that, despite the overcrowded conditions, the urchins within the front are able to acquire enough food from the seagrass alone.

While the work of Camp et al. (1973) focused primarily on the biological effects of the urchin grazing front, our study has shown that, in addition to changes to the biota of the seagrass bed, the urchin front appears to have caused profound changes to the physical characteristics of the sediment as well. The changes in sediment grain size composition and depth are most likely a result of the elimination of the baffling effect normally provided by the seagrass canopy. Slowing of the current by the seagrass blades allows the settling and retention of fine particles; when the sediment is exposed, currents can easily resuspend and carry away finer particles (Ginsburg and Lowenstam, 1958).

The chemical composition of the sediment also appeared to have been affected. The amount of organic matter in the sediment increased significantly within days of passage of the grazing front, resulting in unvegetated areas with relatively high organic content. This situation is the reverse of that normally found in the sediment of seagrass beds, which usually have a higher organic content than nearby unvegetated areas (Marshall and Lukas, 1970; Kenworthy et al., 1982). Although experimentally untested, the increase in sediment organic matter may be caused by the deposition of urchin fecal matter.

The formation of grazing fronts is well documented among temperate sea urchins in the genus *Strongylocentrotus*. Grazing front behavior has been observed in these urchins in the kelp beds of California, Nova Scotia, and Norway, where urchin grazing forms large barren areas that persist over time (Lang and Mann, 1976; Bernstein et al., 1983; Dean et al., 1984; Vadas et al., 1986; Watanabe and Harrold, 1991; Hagen, 1995). Grazing fronts have also been observed in various other benthic marine invertebrates. The queen conch, *Strombus gigas*, in the Central Bahamas forms fronts averaging 78 m and 2.8 m in length and width, respectively, and with densities as high as 295 ind m⁻² (Stoner, 1989; Stoner and Lally, 1994). Detritus, epiphytes and drift algae, the primary food of queen conch, are almost completely removed from the seagrass bed after passage of the conch fronts. The Caribbean starfish *Oreaster reticulatus*, which feeds on organic matter in the sediment, has been observed in a grazing front 3–5 m wide with a mean density of 131 m⁻² (Scheibling, 1985). Passage of the *Oreaster* front resulted in substantial reductions in the organic content of the sediment. Another starfish, *Asterias ruber*, forms grazing fronts 10–35 m wide and hundreds of meters long with densities up to 400 m⁻² (Dare, 1982). These fronts move over mussel beds, consuming all of the mussels present.

Grazing fronts such as those mentioned above have one important feature in common—they have the potential, often realized, to completely eliminate the food source of the species involved. Grazing fronts of the urchin *L. variegatus* are particularly damaging, however, as they also eliminate the structural foundation of the local benthic community. Aside from providing a substratum for direct attachment for many epiphytic plants and animals, the seagrass canopy plays an important role in providing a refuge from predation for many invertebrates. The wholesale removal of the seagrass or kelp canopy will have serious effects on those species which depend directly or indirectly on them for food and shelter, and in seagrass beds these species are very numerous (Santos and Simon, 1974; Heck and Wetstone, 1977; Stoner, 1980; Virnstein et al., 1983; Edgar et al., 1994; Conolly and Butler, 1996).

Because there was no follow-up to the initial report by Camp et al. (1973) on the previous *L. variegatus* overgrazing event in the Gulf of Mexico, direct comparisons of recovery

rates after intense grazing cannot be made with certainty between their study and ours. Camp et al. (1973) did find some sparse regrowth in the form of short *Thalassia* shoots several meters behind the urchin front, but they felt complete recovery would be very slow as the rhizomes remaining after passage of the front appeared to be decaying. Our study provides direct evidence to support this concern about recovery of the seagrass bed. In the 9 mo that we have been monitoring our site, no signs of recovery of *S. filiforme* have been observed. In fact, *S. filiforme* biomass, both above- and below-ground, has been completely eliminated from the area. The loss of root and rhizome biomass does not bode well for the recovery of the seagrass bed in Florida Bay. Without the possibility of vegetative regrowth, recovery will depend entirely on sexual recruitment and growth of seedlings, a process that can be much slower than asexual regrowth.

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