Trampling in a seagrass assemblage: direct effects, response of associated fauna, and the role of substrate characteristics

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ABSTRACT: Human wading in shallow coastal waters is a common activity that inherently involves trampling of the substrate. An experiment was conducted in *Thalassia testudinum* seagrass beds in Puerto Rico to determine how seagrass and associated mobile fauna respond to this anthropogenic disturbance. Three trampling intensities were applied to replicate seagrass beds throughout a 4 mo period. Seagrass biomass was inversely related to trampling intensity and duration. There was moderate recovery in the trampled areas 7 mo after the last trampling event. Intense levels of trampling resulted in decreased shrimp abundances, especially for *Thor manningi*. Fish abundances and composition of shrimp and fish assemblages did not change significantly after 4 mo of trampling. *T. testudinum* beds with softer substrates lost more seagrass biomass as a result of trampling than seagrass beds with firm substrates, suggesting that substrate firmness can modify disturbance effects. Educators and resource managers should limit trampling by large groups, or confine it to small areas with firm substrates, and researchers should be mindful of artifacts arising from trampling in and around sampling areas.

KEY WORDS: Trampling · Disturbance · Seagrass · Recovery · Recreation · *Thalassia testudinum* · Decapods · Fishes

INTRODUCTION

Despite the current surge in outdoor recreation, we know surprisingly little about the most basic consequences of this increased usage. For instance, we are often enjoined to 'take nothing but photos, leave nothing but footprints', but are those footprints really innocuous? In terrestrial assemblages, damage to flora is directly related to the amount of foot traffic (Bayfield 1979, Cole 1995a,b). On rocky shores, trampled areas generally have lower densities and diversities of algae and sessile organisms than less trampled areas (e.g. Addessi 1994, Keough & Quinn 1998). Trampling experiments on coral reef flats resulted in direct breakage and/or mortality of coral colonies, and reduced live coral cover (Woodland & Hooper 1977, Hawkins & Roberts 1993).

Unlike terrestrial grasslands, seagrasses have no history of trampling pressure by large herbivores, and therefore may not have the same resistance to trampling as terrestrial flora. Seagrasses grow in saturated substrates, which may make them more prone to trampling damage than terrestrial flora growing in soils that are drier and more compact. Seagrasses also lack certain supportive tissues that are present in many terrestrial grasses (Cronquist 1981).

Although it is known that human trampling reduces cover of plants and sessile fauna, there is little knowledge of effects on mobile fauna associated with trampled vegetation in any system (but see Liddle 1975, Keough & Quinn 1998, Brown & Taylor 1999). The high diversity and abundance of animals living within seagrass beds is largely due to habitat selection and the refugium from predation provided by the complexity of the seagrass

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habitat (Stoner & Lewis 1985, Sogard et al. 1987). Structural complexity and heterogeneity are believed to be the most important factors influencing changes in faunal composition (e.g. Heck & Orth 1980, Lewis 1984). However, Bell & Westoby (1986a,b) found that density of some species of seagrass-associated decapods increased with decreasing seagrass leaf height and density, whereas density of others decreased. Similarly, some studies have found no clear relationship between fish abundances and seagrass cover, leaf height, and density (Bell & Westoby 1986a,b, Connolly 1994).

An important emphasis of previous work has been the relative resistance of different plant species and growth forms to trampling. In terrestrial habitats, herbaceous plant species that are low-growing, have tough leaves, and form mats or tufts are generally more resistant to trampling than other growth forms (Cole 1995b). Terrestrial grasses are more resistant to trampling than some forest plant species, such as leafy, stemmed forbs (Cole 1985). However, very little is known about how habitat characteristics, such as substrate quality, modify trampling disturbance, although substrate has been suggested as a potentially important factor (Harrison 1980/1981, Hylgaard 1980/1981, Wynberg & Branch 1997).

This study reports the results of a trampling experiment in seagrass beds at La Parguera, Puerto Rico. We tested the null hypotheses that human trampling does not damage *Thalassia testudinum* shoots or rhizomes and does not alter the abundance or composition of associated fauna. Further, sediment composition and substrate penetrability were examined as potential modifiers of trampling disturbance. Disturbance regimes have many components/descriptors, including spatial distribution, frequency, area affected, intensity, landscape topography, context, and history (e.g. Connell 1978, Pickett & White 1985). The experiment was designed with these diverse parameters in mind, and manipulations were based on observed usage patterns.

MATERIALS AND METHODS

Study area and sampling design. The study area was located near La Parguera (Fig. 1), in southwestern Puerto Rico (17° 58′ N, 67° 03′ W). The shallow seagrass beds in the area are composed mainly of *Thalassia testudinum*, but are sometimes interspersed with, or bordered by, *Syringodium filiforme* and *Halodule wrightii*. Calcareous green algae (species of *Halimeda*, *Penicillus*, and *Udotea*) and unattached red and brown algae (particularly species of *Acanthophora* and *Dictyota*) are common in the study area. Zoanthids often grow among *T. testudinum* blades, sometimes forming dense mats. Most study sites were located in the lee of coral-

reef crests or shallow rubble cays, but several of the sites closer to the coast were near mangrove islands with limited coral-reef development (see Eckrich 1998 for more detailed site description).

The experimental design consisted of 3 experimental trampling 'lanes' at each of 10 sites (Fig. 2). Trampling lanes were used so that the results could be compared with other marine and terrestrial experimental trampling studies (see also Sun & Walsh 1998, Keough & Quinn 1998, Schiel & Taylor 1999). The lanes were wider than some experimental lanes used in terrestrial studies (Cole & Bayfield 1993) to avoid an edge effect that could have influenced the abundances of mobile fauna. The 10 replicate sites were chosen in seagrass beds of <1 m depth where no known trampling had occurred. At each site, the 3 lanes (5 × 2.5 m: control, low-intensity trampling, and high-intensity trampling) were marked with PVC stakes. The lanes were 1.5 m apart to minimize inter-lane trampling effects.

Sites were selected by identifying widely dispersed, shallow seagrass beds and haphazardly throwing markers into the beds. At 2 of the study sites, strong currents were perpendicular to the trampling lanes. Lane arrangement on these 2 sites was not haphazard; rather, the upcurrent lane was the control, and the lanes to be trampled were staggered so as to minimize sediment transport from one lane to another. Five sites were trampled from March through July 1996, and another 5 sites were trampled from September 1996 through January 1997. Measurements were taken from each lane before trampling, 2 and 4 mo after trampling began, and 7 mo after the last trampling
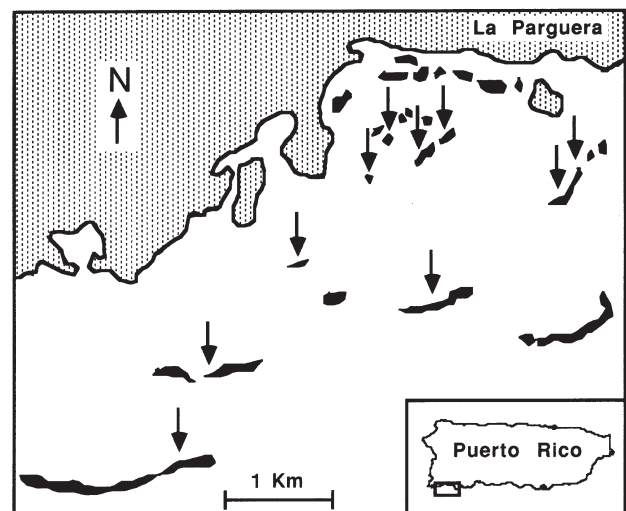

Fig. 1. South coast of Puerto Rico near town of La Parguera. Stippling: 'mainland' Puerto Rico; black shapes: coral reefs and/or mangrove islands with which extensive seagrass meadows are associated. Arrows indicate 10 study sites
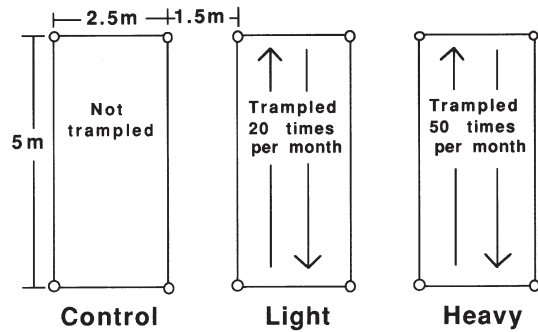
Fig. 2. Treatment lanes: control with no trampling, lightly-trampled lane (trampled 20 times mo^{-1} for 4 mo), and heavily-trampled lane (trampled 50 times mo^{-1} for 4 mo). Arrows indicate directions of trampling

event (the latter was to assess recovery). We sampled at 2 time periods because the volume of fieldwork prohibited us from sampling all 10 sites simultaneously and because we wished to maximize the general applicability of our results. In other words, our sampling of multiple sites at multiple times was aimed at providing spatial and temporal replication rather than revealing site or seasonal differences per se.

In the low- and high-intensity trampling lanes, a 57 kg person wearing rubber-soled shoes walked to the end of the lane and back 20 and 50 times, respectively. The trampling was applied evenly across each lane (i.e. the person began trampling back and forth on the left side of the lane and slowly worked back to the right side and so on from one side to the other). Treatments were applied once a month for 4 mo. Trampling intensities and frequencies were based on multi-year departmental records for visitor group usage of shallow seagrass beds (Eckrich 1998). Records included number of groups per year, group size, and duration of grassbed use. Our low- and high-intensity levels of disturbance bracketed the observed level of usage.

Seagrass. During each sampling series, a 1 m^2 quadrat was placed near each end of each lane at each study site (avoiding the edges). Within each of these quadrats, the number of short shoots lying within 2 randomly placed 0.063 m^2 (25 × 25 cm) quadrats was counted to determine short-shoot density. Also, all short shoots within 2 randomly placed 0.016 m^2 (12.5 × 12.5 cm) quadrats were collected within each of the 1 m^2 quadrats. Five short shoots were randomly selected from each of these samples. Number of blades per short shoot, blade lengths and blade widths were measured to calculate leaf-area index (LAI). Calcium carbonate was removed from the photosynthetic material of the samples with a dilute hydrochloric acid solution and gentle scraping (similar to the protocol of Dauby & Poulicek 1995). Samples were then dried at 90°C for 24 h and weighed to determine standing crop (photosynthetic biomass).

Seven months after the last trampling treatment, short-shoot density, LAI, and canopy height data were collected from each of the 10 sites. Field sampling and laboratory processing were identical to the protocol described above, except that short shoots were counted in 2 (instead of 4) randomly placed 0.063 m^2 quadrats and collected from 2 (instead of 4) randomly placed 0.016 m^2 quadrats within each trampling lane.

Cover estimates were also obtained. Four quadrats (1 m^2) were randomly placed in each lane, and the percent cover of *Thalassia testudinum*, algae (all species combined), zoanthids, and sand were visually estimated. These data were collected before trampling and 2 and 4 mo after trampling began.

Two rhizome cores were taken from the outside perimeter of each trampling lane before trampling began. The cores were taken from the perimeter because coring within the lanes would have directly affected the experimental area. The holes left from the corer were subsequently plugged with cores from nearby seagrass so that predators such as octopuses and stomatopods would not move into some of the holes and bias the experiment. One month after the last trampling treatment, 2 cores were taken from the middle of each lane to assess trampling disturbance, and the holes were subsequently filled. The cores were collected using a 15 cm diameter corer that penetrated to an average depth of 25 cm. There was no rhizome development below this depth at the 10 sites studied. Samples were rinsed and sorted in the laboratory, and the non-senescent rhizomes (rootlets not included) were oven-dried at 90°C and weighed.

Fauna. Faunal sampling occurred before seagrass sampling at each interval; samples were taken during daylight hours. A 0.56 m^2 (75 × 75 cm) throw-trap (Kushlan 1981, Holmquist et al. 1989a,b, Rozas & Minello 1997) with a depth of 50.5 cm was thrown into the center of each lane and held in place with 2.27 kg weights on the outside of each trap corner. A 0.75 m wide bar-seine (a rectangular net with rigid edges and 2 handles) with 2 mm square mesh was passed through the seagrass canopy within the trap 10 times, and the contents of the seine were emptied into a container between scoops. Live animals were transported to the laboratory and sorted immediately. Species abundances of shrimps and fishes were recorded.

Sediment composition. Two sediment samples were haphazardly collected from each site and separated into 3 categories: mud (<0.062 mm), sand (0.062 to 2 mm), and gravel (>2 mm). Sediment cores to a depth of 15 cm were collected using a 5.1 cm diameter PVC corer. In the laboratory, organic particles were dissolved from the samples with a 30% hydrogen peroxide solution, and the clay portions of each were subsequently separated by wet-sieving with distilled water.

The clay samples were then dried at 40°C and weighed (Folk 1974). The remaining sediments of each sample were also dried at 40°C, dry-sieved to separate sand and gravel components, and then weighed (Folk 1974).

Substrate penetrability. Substrate penetrability was measured using 2 methods, one to measure penetration as a function of impact, the other to measure penetration as a result of steady pressure. Eight haphazard measurements were taken at each of the study sites using each of the 2 methods. Measurements were taken on the perimeters of the sampling lanes.

The 'impact' method used a speargun (Hawaiian sling). The elastic band of the sling was retracted with a force of 9.5 kg and, when released, shot the pole spear directly into the substrate. The tip of this impact penetrometer was fitted with a pan-head machine screw (5×0.8 cm) and held 1 m above the substrate. Before releasing the elastic band, the penetrometer was fitted into a 2.54 cm diameter PVC pipe that was perpendicular to the substrate to assure a 90° angle of impact. After the penetrometer had been released, the distance that the screw penetrated the substrate was measured.

The 'pressure' method used a steady pressure exerted by a rod and measured with a scale. The scale was attached on one end of a 2.4 m long pipe fitted with a wood cylinder (2.54 cm diameter) at the other end. By pulling down on the scale, a constant force of 9 kg cm^{-2} was applied towards the substrate until the pressure penetrometer stopped sinking. The distance the base penetrated the substrate was then measured.

Data analysis. Before-after, before-intermediate, and intermediate-after differences between treatments were contrasted for short-shoot density, standing crop, LAI, canopy height, percentage cover, and faunal abundances. Because of high temporal variance, contrasts were made using changes in given measures, during individual time periods. We also report mean values, in addition to tests on changes, because these values are more intuitive and provide additional perspective. No intermediate data were collected for rhizome biomass, and therefore only before-after differences between treatments were contrasted for this variable. Normality was tested for changes in variables using residuals and scatterplots. Equality of variances was tested using F-max and Cochran's

tests (Kirk 1982). In order to meet assumptions of normality and homogeneity of variance, various transformations were required. Changes in short-shoot density, leaf-area index, canopy height, and standing crop were log-transformed, and change in percentage cover of seagrass was arcsine-transformed. Changes in shrimp and fish abundances were given transformations of $y^{1/2} + (y+1)^{1/2}$ and $\log(y+1)$, respectively. Seagrass variables were examined by paired Student's t-tests (1-tailed, following significant randomized-block ANOVAs) when assumptions of normality were met, and non-parametric Wilcoxon signed-ranks were performed on contrasts for the remaining variables. Simple chi-square tests were performed on shrimp and fish species abundances. The sequential Bonferroni correction (Holm 1979, Rice 1989) was used to compensate for multiple comparison errors. We also present limited ANOVA results of seasonal differences in trampling impact. However, we believe that our 2 sets of concurrent samples do not allow a robust test of seasonal differences (see the excellent discussion in Morrisey et al. 1992). Linear regressions (one-tailed) were used to investigate the influence of substrate characteristics. All statistical analyses were done using SYSTAT (Wilkinson 1990).
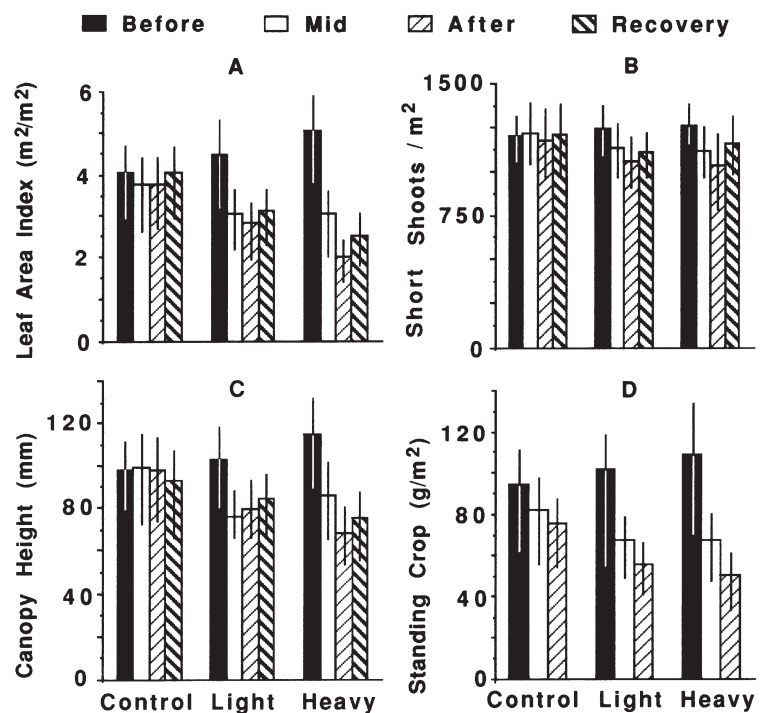

Fig. 3. Leaf area index, short-shoot density, canopy height, and standing crop before (Before), after 2 mo (Mid), after 4 mo (After) trampling, and 7 mo after last trampling treatment (Recovery) for controls, lightly-trampled lanes (20 passes mo^{-1}), and heavily-trampled lanes (50 passes mo^{-1}). Data are means ±95% confidence intervals

RESULTS

Seagrass

In general, *Thalassia testudinum* biomass decreased with increasing trampling intensity and trampling time. After 4 mo of trampling (before-after), LAI, short-shoot density, canopy height, and standing crop all decreased in the heavily-trampled lanes (Fig. 3, Table 1), whereas only canopy height and LAI decreased significantly (after Bonferroni correction) in the lightly-trampled lanes. Declines for these latter variables were greater in the heavily-trampled lanes. Decreases in LAI, short-shoot density, canopy height, and standing crop were greater in spring than in fall (p < 0.001 for all; F = 33.5, 19.2, 33.7, and 33.7, respectively).

Trampling resulted in decreased seagrass and increased sand cover (Fig. 4, Table 1). After 4 mo of trampling (before-after), percentage cover of seagrass decreased in both types of trampled lanes and declined more in the heavily-trampled lanes than in the lightly-trampled lanes (Fig. 4, Table 1). Percentage cover of sand increased in the heavily-trampled lanes and, to a lesser extent, in the lightly-trampled lanes (Fig. 4, Table 1); 2 of the 10 heavily-trampled lanes developed large sand patches. Algal cover was unaffected (Fig. 4, Table 1).
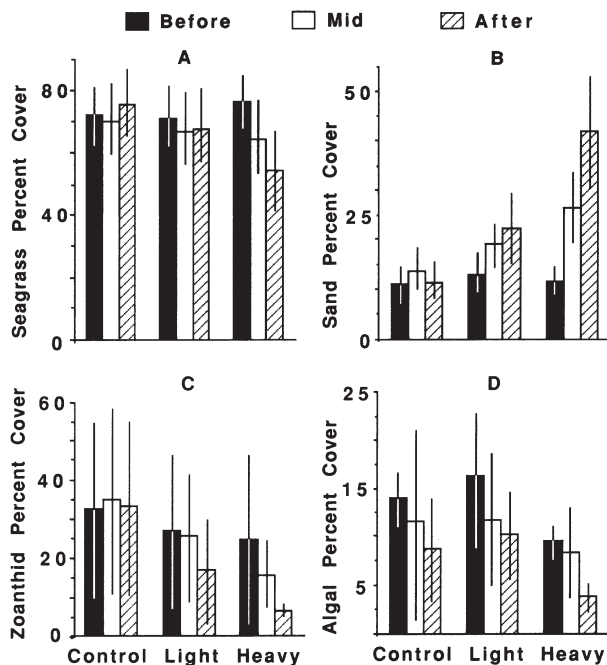

Fig. 4. Percentage cover of seagrass, sand, zoanthids, and macroalgae before (Before), after 2 mo (Mid), and after 4 mo (After) trampling for controls, lightly-trampled lanes (20 passes mo^{-1}), and heavily-trampled lanes (50 passes mo^{-1}). Zoanthids were present at 3 sites, and algae were present at 5 sites. Data are means ±95% confidence intervals

Table 1. Changes in seagrass meadows as a function of trampling intensity. Each p-value is result of 1-tailed Student's *t*-test comparing changes during a certain time interval in a given measure for a pair of treatments (C: control lanes; L: lightly-trampled lanes; H: heavily-trampled lanes): e.g. first p-value in table indicates that change in leaf-area index during first 2 mo of study differed between control and heavily-trampled plots *Significant at per-contrast error rate [alpha = 0.05]; **significant after correcting for multiple comparisons. See Figs. 3 to 8 for details of changes. na: not applicable

| Comparison	0–2 mo	2–4 mo	0–4 mo	4–11 mo
Leaf-area index				
C vs H	0.003**	0.008**	0.001**	0.118**
C vs L	0.005**	0.134	0.002**	0.420**
L vs H	0.047*	0.077	0.001**	0.169**
Short-shoot density				
C vs H	0.015*	0.082	0.003**	0.023*
C vs L	0.036*	0.411	0.046*	0.345*
L vs H	0.375	0.149	0.126	0.021
Canopy height				
C vs H	0.009*	0.010*	0.001**	0.067
C vs L	0.023*	0.431	0.002**	0.159
L vs H	0.338	0.043*	0.001**	0.363
Standing crop				
C vs H	0.012*	0.072	0.002**	na
C vs L	0.160	0.031*	0.023*	na
L vs H	0.059	0.145	0.019*	na
Seagrass cover				
C vs H	0.006**	0.003**	0.001**	na
C vs L	0.041*	0.001**	0.007**	na
L vs H	0.018*	0.027*	0.009**	na
Sand cover				
C vs H	0.011*	0.003**	0.002**	na
C vs L	0.025*	0.019*	0.010*	na
L vs H	0.017*	0.004**	0.009*	na
Zoanthid cover				
C vs H	0.137	0.051	0.055	na
C vs L	0.137	0.034*	0.034*	na
L vs H	0.137	0.446	0.233	na
Algal cover				
C vs H	0.272	0.072	0.342	na
C vs L	0.433	0.459	0.232	na
L vs H	0.433	0.233	0.173	na
Rhizome biomass				
C vs H	na	na	0.046*	na
C vs L	na	na	0.142	na
L vs H	na	na	0.069	na
No. of shrimps				
C vs H	0.100	0.073	0.001**	na
C vs L	0.162	0.015*	0.039*	na
L vs H	0.406	0.453	0.351	na
No. of fishes				
C vs H	0.058	0.183	0.332	na
C vs L	0.099	0.228	0.263	na
L vs H	0.269	0.320	0.220	na
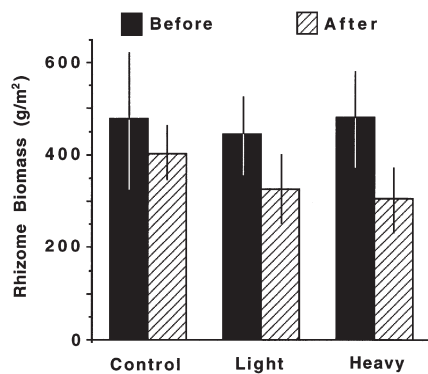
Fig. 5. *Thalassia testudinum.* Rhizome biomass before (Before) and after 4 mo (After) trampling for controls, lightly-trampled lanes (20 passes mo^{-1}), and heavily-trampled lanes (50 passes mo^{-1}). Data are means ±95% confidence intervals

Rhizome biomass decreased in the heavily-trampled lanes (Fig. 5, Table 1). Study sites lost between 0 and 72% of rhizome biomass (except one site with a 5% increase) and between 0 and 81% of standing crop (one increased by 23%) in the heavily-trampled lanes.

The plots did not completely recover to pre-experiment conditions in the 7 mo following the last trampling treatment. Leaf area index, short-shoot density, and canopy height of the trampled lanes were still below the levels of the controls and the pre-trampling levels of the treatment lanes. At several of the study sites, the reduced seagrass cover in the heavily-trampled lanes was visually distinguishable from the surrounding seagrass 14 mo after trampling ended.

Fauna

A total of 2614 shrimps composed of 18 species, and 175 fishes composed of 11 or more genera (sygnathids were not identified to genus level) were collected across all treatment categories. Ninety-seven percent of the total abundance of shrimps was accounted for by 7 species: *Hippolyte zostericola/pleuracanthus* (40%), *Thor manningi* (23%), *Latreutes fucorum* (11%), *Alpheus normanni* (10%), *Periclimenes americanus* (8%), *Processa bermudensis* (3%), *Metapenaeopsis goodei* (2%). Ninety-five percent of the total abundance of fishes was accounted for by 4 genera and the sygnathids: *Malacoctenus* (31.5%), *Sparisoma* (31.5%), *Bathygobius* (16.4%), Sygnathidae (12.1%), and *Haemulon* (3.6%).

After 4 mo of trampling, shrimp abundances (before-after) decreased in both the heavily- and lightly-trampled lanes (Fig. 6, Tables 2 & 3), but there were no seasonal effects in trampling response (F = 0.786, p =

0.384). Compared with the other shrimp species, the abundance of *Thor manningi* decreased after 4 mo in the heavily-trampled lanes (χ^2 = 21.1, df = 1, p < 0.001; Tables 2 & 3). However, the abundance of *Processa bermudensis* increased in comparison with the other shrimp species after 4 mo in the heavily-trampled lanes (χ^2 = 24.8, df = 1, p < 0.001; Tables 2 & 3). Variance in fish abundance was high, and overall abundances did not change after 4 mo of trampling (Fig. 6, Table 1), nor were there seasonal effects (F = 0.007, p = 0.936). In addition, the abundances and percentage composition of individual fish species did not differ significantly among treatments or time intervals (Tables 2, 3). In the controls, shrimp abundances decreased from an average of 72 shrimp m^{-2} to an average of 41 shrimp m^{-2} and fish abundances increased from an average of 1.8 fishes m^{-2} to 3.3 fishes m^{-2} during the 4 mo of trampling. There was an up to 75% reduction in zoanthid cover, although variance was high (Fig. 4, Table 1).

Substrate characteristics

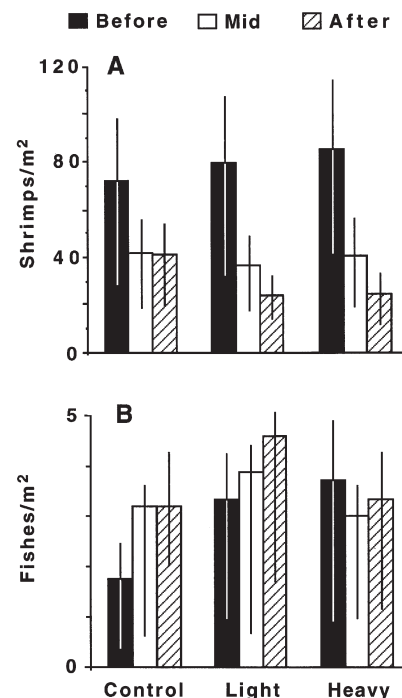The percentage composition of mud ranged from 4.7 to 33.2%, of sand from 58.4 to 88.4%, and of gravel

Fig. 6. Shrimp, and fish abundances per square meter seagrass meadow before (Before), after 2 mo (Mid), and after 4 mo (After) trampling for controls, lightly-trampled lanes (20 passes mo^{-1}), and heavily-trampled lanes (50 passes mo^{-1}). Data are means ±95% confidence intervals

Table 2. Mean (SE) abundances of shrimps and fishes per square meter seagrass meadow before and after trampling

Species	Control	Light	Heavy
Shrimps			
Hippolyte zost/pleur [a]			
Before	34.7 (7.1)	26.5 (5.5)	31.7 (5.7)
After	15.7 (2.4)	10.5 (1.6)	9.8 (2.0)
Thor manningi			
Before	11.9 (2.1)	21.4 (5.5)	23.9 (4.3)
After	10.1 (2.2)	2.5 (0.6)	1.4 (0.5)
Latreutes fucorum			
Before	13.9 (3.5)	14.2 (4.7)	8.9 (2.2)
After	3.2 (0.9)	1.8 (0.4)	1.4 (0.4)
Alpheus normanni			
Before	3.0 (0.6)	4.1 (0.7)	4.6 (1.2)
After	5.5 (1.1)	4.6 (0.8)	3.9 (1.0)
Periclimenes americanus			
Before	4.1 (0.6)	5.3 (1.1)	6.1 (1.4)
After	3.2 (0.6)	1.2 (0.3)	1.1 (0.4)
Processa bermudensis			
Before	1.1 (0.3)	0.5 (0.2)	1.1 (0.3)
After	0.2 (0.1)	1.2 (0.5)	2.8 (0.9)
Metapenaeopsis goodei			
Before	0.7 (0.4)	0.2 (0.1)	2.5 (1.1)
After	0.4 (0.2)	0.5 (0.2)	0.9 (0.4)
Other			
Before	3.0 (0.9)	5.0 (1.6)	4.8 (0.9)
After	3.0 (1.0)	3.4 (0.4)	2.1 (0.1)
Fishes			
Malacoctenus spp.			
Before	0.7 (0.2)	1.3 (0.4)	2.3 (0.5)
After	1.6 (0.4)	1.4 (0.4)	1.3 (0.3)
Sparisoma spp.			
Before	2.1 (0.2)	1.8 (0.7)	1.4 (0.3)
After	1.1 (0.2)	0.9 (0.3)	1.4 (0.3)
Bathygobius spp.			
Before	0.0 (0.0)	0.5 (0.2)	0.4 (0.2)
After	0.5 (0.2)	1.1 (0.4)	0.7 (0.2)
Other			
Before	1.1 (0.4)	0.7 (0.2)	1.4 (0.5)
After	0.7 (0.2)	1.1 (0.2)	0.4 (0.1)

[a]Treated as a complex (*zost* = *zostericola*; *pleur* = *pleuracanthus*)

Table 3. Mean percentage (SE) composition of shrimp and fish assemblages in seagrass meadows before and after trampling

Species	Control	Light	Heavy
Shrimps			
Hippolyte zost/pleur [a]			
Before	27.6 (8.2)	29.3 (7.6)	30.1 (8.4)
After	36.4 (9.6)	39.3 (7.8)	39.3 (11.4)
Thor manningi			
Before	29.4 (7.7)	24.5 (6.7)	35.4 (10.6)
After	17.1 (6.6)	7.6 (2.7)	4.1 (2.0)
Latreutes fucorum			
Before	26.6 (9.3)	23.5 (9.9)	10.8 (4.7)
After	13.5 (6.5)	16.0 (7.5)	8.2 (4.5)
Alpheus normanni			
Before	2.3 (0.9)	7.4 (4.2)	4.6 (2.1)
After	20.3 (9.6)	17.5 (5.8)	12.1 (4.0)
Periclimenes americanus			
Before	5.1 (1.4)	7.3 (3.3)	4.6 (1.9)
After	5.4 (1.6)	3.3 (1.5)	3.0 (1.7)
Processa bermudensis			
Before	1.2 (0.8)	0.6 (0.4)	1.9 (1.4)
After	0.3 (0.3)	2.5 (1.7)	9.4 (5.8)
Metapenaeopsis goodei			
Before	0 (0)	0.8 (0.8)	3.5 (2.4)
After	0 (0)	0 (0)	3.5 (3.1)
Other			
Before	7.8 (2.4)	6.6 (2.0)	9.1 (2.9)
After	7.1 (3.6)	13.8 (2.2)	20.4 (9.7)
Fishes			
Malacoctenus spp.			
Before	11.6 (7.2)	26.9 (15.3)	38.3 (15.4)
After	29.6 (13.3)	29.0 (13.2)	25.9 (13.4)
Sparisoma spp.			
Before	71.6 (17.4)	26.9 (14.7)	35.8 (15.3)
After	30.6 (14.3)	21.0 (11.4)	32.3 (12.3)
Bathygobius spp.			
Before	0 (0)	15.9 (14.1)	8.3 (8.3)
After	9.3 (4.7)	25.0 (13.4)	27.8 (14.7)
Other			
Before	16.6 (10.5)	30.1 (18.1)	17.5 (8.5)
After	30.6 (14.3)	25.0 (11.2)	13.9 (11.1)

[a]Treated as a complex (*zost* = *zostericola*; *pleur* = *pleuracanthus*)

from 2.5 to 22.6% at the 10 study sites (Fig. 7). None of the 3 categories of sediment (mud, sand, gravel) were significantly related to any of the seagrass parameters (p-value ranged from 0.15, for standing crop/gravel, to 0.99 for LAI/mud).

Impact penetration averaged between 95 and 435 mm. This measure accounted for 51.1% of the variability in the percentage change of rhizome biomass (p = 0.01; Fig. 8) but only 1% of the variability in the percent change of standing crop (p = 0.39). Pressure penetration averaged between 15 and 497 mm, and explained

54.1% of the variability in the percentage change of rhizome biomass (p = 0.0075; Fig. 8), but explained only 12.5% of the variability in the percentage change of standing crop (p = 0.16).

DISCUSSION

Human trampling negatively affects terrestrial plants, and we found that trampling similarly reduced the leaf area index, short-shoot density, canopy height, stand-
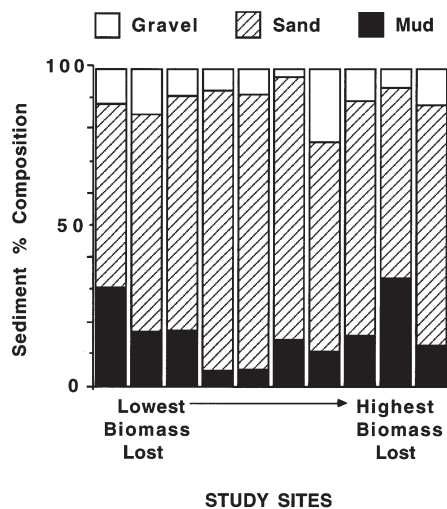
Fig. 7. Percentage composition of gravel, sand, and mud across sites relative to spectrum of seagrass (*Thalassia testudinum*) biomass lost

ing crop, and cover of marine meadows. Intense levels of trampling also resulted in reduced rhizome biomass, a measure that, to our knowledge has not been examined in previous human trampling studies. The amount of damage to *Thalassia testudinum* from trampling is relatively proportional to the intensity and duration of
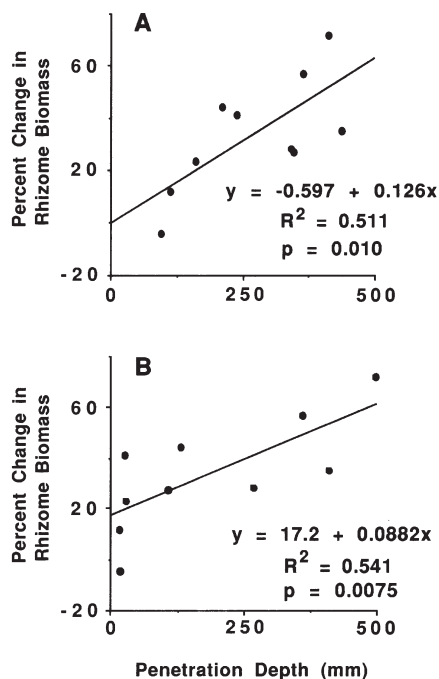

Fig. 8. *Thalassia testudinum.* Percent change in rhizome biomass as a function of substrate penetrability, measured with impact (A) and pressure (B) penetrometers

foot traffic, which is also true for some plants in both marine and terrestrial assemblages (Taylor et al. 1993, Schiel & Taylor 1999).

Seagrasses may be less resistant to trampling than terrestrial grasses. Although *Thalassia testudinum* is grazed by manatees, sea turtles, fishes, and urchins (Thayer et al. 1984, Valentine & Heck 1999), this seagrass has not been subjected to the trampling pressure associated with grazing in terrestrial grasslands. Unlike most terrestrial grasses, *T. testudinum* does not have sclerenchyma tissue, which helps prevent breakage of rhizomes, roots, and leaves (Cronquist 1981, Raven et al. 1981). In addition, being submerged, *T. testudinum* grows in saturated sediment, which may lead to less resistance to trampling relative to terrestrial grasses growing in relatively dry soils. Susceptibility of grasslands to livestock-trampling is greater in wet soil conditions than in dry soil conditions (Robinson & Alderfer 1952, Edmond 1966). Substrates saturated with water are generally more easily penetrated than dry substrates, and trampling in saturated substrates is more likely to lead to substrate breakthroughs and subsequent rhizome damage than trampling in dry substrates. Rhizome density may also influence the probability of substrate break-throughs, although we did not collect sufficient data to test this relationship. It has been suggested that very soft sandflats may be more sensitive to the impacts associated with trampling than more compact sandflats (Wynberg & Branch 1997). In our study, sites that had softer substrates had greater losses in rhizome biomass as a result of trampling. Substrate hardness influences the susceptibility of seagrass to trampling and perhaps other disturbance sources such as propellers and anchors. Habitat factors may also influence the time necessary for recovery of plant assemblages (Harrison 1980/1981, Hylgaard 1980/1981). The present study supports the contention that environmental factors, such as substrate quality, play a role in an organism's response to perturbation (see also e.g. Jans et al. 1993).

The depth of trampling or wading may also be an important factor, perhaps as important as substrate quality, in determining the amount of damage suffered by *Thalassia testudinum*. Depth is a potentially useful mitigating factor not present in terrestrial assemblages. A person would exert less force on the substrate in 1 m of seawater than in 50 cm of seawater because of the buoyancy of the water. Unfortunately, most wading occurs in the shallowest, and probably most vulnerable, areas.

The maximum intensity of use that an area can continue to support under a particular management regime without inducing a major change in the managed area has been termed the 'recreational carrying capacity' (Goldsmith 1974, Sun & Walsh 1998). Our

study suggests that even relatively low intensities of trampling may be non-sustainable and therefore exceed the recreational carrying capacity of *Thalassia testudinum* seagrass beds because of long-lasting negative effects. Although our experiment reproduced the human-disturbance regime observed in Puerto Rico in terms of intensity, area affected, and frequency, each of these parameters can be greater in certain outdoor education settings. For instance, some grassbeds in the Florida Keys receive daily usage by multiple groups (Holmquist pers. obs.). Pickett & White (1985) suggest that root-biased systems, such as *T. testudinum* meadows (Williams 1990), are resistant to above-substrate disturbances and that damage to below-ground components is necessary for substantial changes to these systems. Our experimental treatments caused moderate opening of the rhizome mat. Continued trampling, even at low intensities, may increasingly damage the seagrass and result in sparse seagrass or bare sand. In temperate and sub-tropical regions, where seagrasses experience a shorter growing season and even annual defoliation, the effect of human trampling may be more pronounced than reported in this study. For instance, Valentine & Heck (1991) and Heck & Valentine (1995) found that winter defoliation of north Florida *T. testudinum* was achieved with half the grazing pressure required for summer defoliation (see also Wittmann & Ott 1982). This differential effect has been attributed to seasonally-insufficient rhizome reserves (Valentine & Heck 1991, Heck & Valentine 1995, Valentine et al. 1997 and references therein). Further, effects are likely to vary among species of seagrasses as has been demonstrated for terrestrial plants (Cole 1995b). As an example, *Halodule wrightii* has much smaller rhizomes and is often associated with shorelines and sediments with large proportions of silt-clay. This species may be more susceptible to trampling damage than *Thalassia testudinum*.

Unlike most previous trampling studies, this study has evaluated the response of mobile fauna to trampling disturbance. Direct trampling effects have been implicated in reductions of sessile invertebrate abundances and cover (Kay & Liddle 1989, Brosnan & Crumrine 1994), but indirect effects, via damage to the seagrass canopy, may best explain the observed shifts in the mobile invertebrate assemblage. Epifaunal abundances generally decrease with decreasing structural complexity of seagrasses (Leber 1985, Connolly & Butler 1996). Decreased grass-shrimp abundances in response to trampling, particularly for *Thor manningi*, were probably the result of the decrease in seagrass physical complexity. As trampling slowly thinned the seagrass, shrimps probably emigrated to denser seagrass outside the trampling lanes, or failed to immigrate into the trampling lanes rather than suffering

direct mortality (see also Holmquist 1997, Keough & Quinn 1998, Brown & Taylor 1999). Conversely, shrimps of the family Processidae are often associated with bare patches in seagrass meadows (Holmquist pers. obs.), and this habitat preference may account for the increased abundance and percent composition of *Processa bermudensis* in response to trampling. Trampling effects on the fish assemblage were not as pronounced. Organisms that are more mobile may be less likely to be sensitive to boundary and patch structure at a given spatial scale (Kareiva 1983, Wiens et al. 1985), and this generalization appears to hold for at least some grassbed fauna (Holmquist 1998). The comparatively mobile fishes using these grassbeds may not respond to the patch scale (2.5 × 5 m lanes) produced by trampling in this study.

The sessile zoanthids lie at the opposite extreme of faunal mobility, and these fauna suffered substantial, though variable, reductions in percent cover. Zoanthid colonies often form a dense matrix of sand bound by closely-spaced body columns, and zoanthid mortality could lead to increased sediment instability.

Human trampling damaged *Thalassia testudinum* standing crop and rhizomes, and also decreased seagrass-associated shrimp abundances. Importantly, the *T. testudinum* beds recovered very slowly after trampling, and many trampled lanes were still distinguishable from surrounding seagrass 14 mo after trampling ended. Such a slow recovery has also been noted as a result of other severe disturbance to *T. testudinum*-dominated meadows (e.g. Heck & Valentine 1995, Holmquist 1997) although small gaps in *Halodule wrightii* and *Zostera capricorni* meadows can recover more quickly (Creed & Amado Filho 1999, Rasheed 1999). Educators and managers can minimize impact with alternatives such as underwater viewers, snorkeling, and interpretive aquaria. If group-wading is unavoidable, we recommend concentrating activities in small areas of thigh-deep seagrass with firm substrate. Recommendations for terrestrial systems include minimizing concentrated trampling in relatively pristine areas (Graydon & Hanson 1997, Sun & Walsh 1998). However, given that seagrass beds have a relatively low threshold for damage and long recovery time, concentration of use may be a better strategy. A combination of a short disturbance interval and long recovery time is likely to lead to unstable systems, particularly if such a disturbance regime is of broad spatial extent (Turner et al. 1993).

Although the emphasis of our work was on an evaluation of impact by educational and recreation groups, the results constitute a caveat to researchers. For instance, trampling during emergent throw trapping (versus underwater drop-trapping; Holmquist 1997) in soft sediment can result in 'doughnuts' composed of a

core of relatively intact seagrass surrounded by a ring of denuded substrate (Holmquist pers. obs. during work reported by Sogard et al. 1987, 1989, Holmquist et al. 1989a,b). Given the slow recovery of *Thalassia testudinum* from trampling, researchers should try to minimize wading in study areas, in an effort to reduce artifacts, particularly when plots are to be sampled repeatedly.

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