The Effect of Excavation Depth and Filling on Seagrass Recovery in Experimental Injuries in the Florida Keys National Marine Sanctuary

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Project Description
Greater understanding of the factors affecting seagrass recovery in propeller scars and small injuries is necessary to begin to restore damage to Florida Keys National Marine Sanctuary (FKNMS) resources. This project used experimental manipulation to assess effects of excavation depth and filling/regrading with carbonate pea rock on seagrass recovery into simulated propeller scars. We followed replicate experimental treatments for three years to track changes in *Thalassia testudinum* and *Syringodium filiforme* short-shoot density and macroalgal cover. Results will be used by resource managers to take appropriate measures for planning and implementing restoration of damaged tropical seagrass communities.

Introduction
Propeller scars and vessel groundings excavate sediments and disrupt seagrass rhizomes, leaving behind unvegetated trenches that may be up to 1- 2 m deep, several meters wide, and hundreds of meters long. In addition to the loss of fine sediments and organic material, *Thalassia testudinum* is not well adapted to growing at the steep injury margins created by vessel groundings (Zieman 1976; Kenworthy et al. 2002; Whitfield et al. 2002). *Thalassia testudinum* has thick, relatively inflexible horizontal and vertical rhizomes with meristems that normally remain buried beneath the sediment surface. *Thalassia* vertical rhizome apical meristems are organized to grow upward, ensuring that leaves are exposed to light. Exposure of apical meristems to light diminishes their activity, ensuring the correct position of photosynthetic leaves without exposing meristems. This rhizome morphology and the physiological response of meristems to light exposure is not conducive to vertical downward growth at steep topographical features like those created along the margins of vessel excavations. Furthermore, when sediment excavation and damage to rhizomes occurs, wind, wave, and current-induced erosion may further enlarge trenches, creating injuries that heal very slowly or are periodically reinjured by storms (Zieman 1976; Durako et al. 1992; Dawes et al. 1997; Kenworthy et al. 2002; Whitfield et al. 2002). In some cases the injuries may actually expand. The resulting habitat fragmentation may negatively impact macrofauna that utilize seagrass beds (Bell et al. 2001; Uhrin and Holmquist 2003), thereby compounding the damage to seagrass ecosystems.

Increased population density along United States coastlines and subsequent growth of boating activity will place additional burdens on seagrass resources. Natural resource managers therefore require restoration tools that can be implemented in a timely fashion and at reasonable cost to repair damage to seagrass communities.

This study was designed to address several factors impacting seagrass recovery in propeller scars and other small-scale disturbances. First is the question of excavation depth. Propeller scar depths vary widely depending on the vessel creating the injury as well as environmental characteristics of seagrass beds. The wide range of recovery times reported for propeller scars might be caused, in part, by differences in scar depth (Kenworthy et al. 2002). To this end, we designed an experiment to test the effect of excavation depth on seagrass recovery in simulated propeller scars. We created injuries 10, 20, and 40 cm deep and examined changes in injury depth as well as seagrass short-shoot density and macroalgal recovery as a function of time. As mentioned previously, injuries are vulnerable to expansion by erosion, so a second experiment was designed to test the effect of filling on recovery in simulated propeller scars. Using native limestone pea rock (6-7 mm diameter), we filled 30 cm excavations and compared their recovery to same-sized, but unfilled excavations. These two experiments addressed the following questions: 1) Is there a critical depth beyond which seagrasses would benefit from some sort of intervention to decrease recovery time (increase recovery rate)? 2) Does filling an injury with pea rock enhance or delay seagrass growth into the disturbed area, while protecting the injury from further erosion?

Study Site

Two experiments were deployed on a shallow seagrass-*Porites* sp. coral bank on the Gulf of Mexico side of Marathon Key in the Florida Keys National Marine Sanctuary (24.76^{o} N, 81.16^{o} W, Fig. 1). The bank system intercepts the flow of water through Moser Channel, one of the main

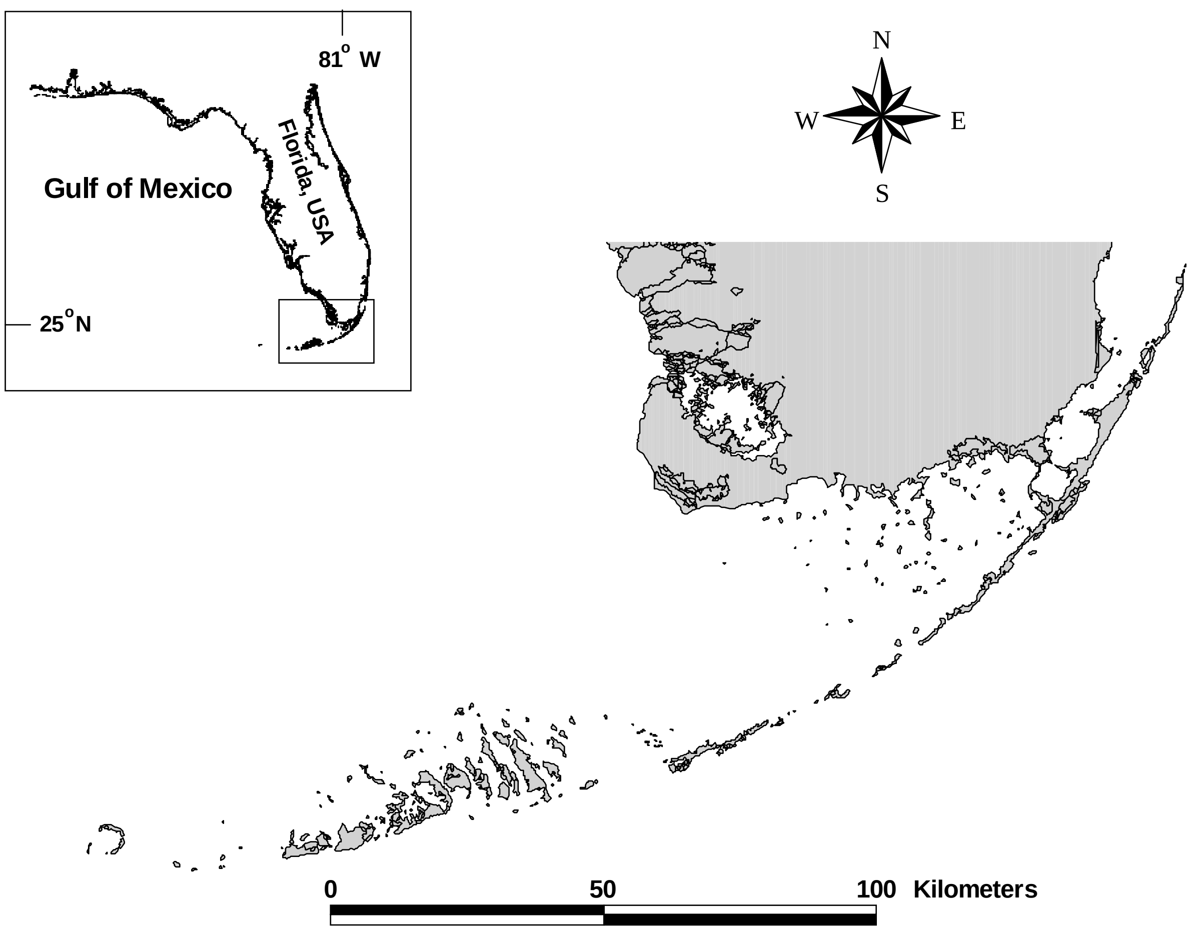

Figure 1. Study site. The area delineated by the box is enlarged in the lower right. The location of the excavation and fill experiments is labeled.

conduits connecting the Gulf of Mexico with the Florida Straits. The banks are raised 2 to 5 m above the surrounding bottom and were formed over several hundred years when the biotic communities physically stabilized a large volume of unconsolidated sediment. Because there is a net long-term transport of water from the Gulf of Mexico to the Florida Straits through Moser Channel (Smith 1994), these banks intercept sediments that are resuspended on the shallow shelf in the southeastern Gulf of Mexico. The large volume of material trapped and stored on these banks minimizes the southerly transport of suspended sediments and affords some protection for the coral reef tract to the south. Water depth on the bank top ranges from 10-15 cm at low tide to 1-1.5 m at high tide. Temperatures range from 9-23^{o}C in the winter months (December-February) to 28-34^{o}C in the summer months (June-August).

Experimental Design

Excavation Experiment

The excavation experiment was deployed in June 2000. Experimental plots were laid out haphazardly in an area of approximately 1,200 m^2 along a northwest-southeast axis, parallel to prevailing winds and perpendicular to tidal currents. Distance between plots ranged from 2 to 10 m, and most plots were approximately 5 m apart. Plots were surveyed seven times: September 2000, January 2001, May 2001, September 2001, January 2002, August 2002, and May 2003.

Five replicates each of four depth treatments (n = 20 replicates total) were deployed: (1) control (no sediment disturbance), (2) 10 cm, (3) 20 cm, and (4) 40 cm. Plot dimensions measured 50 x 150 cm. Positions of the plots were marked with polyvinyl chloride (PVC) and mapped using a differential global positioning system (DGPS). Control treatments were left undisturbed. The three other depth treatments were created by excavating above- and belowground biomass and sediments to the target depth using shovels and hoes (Fig. 2 and 3).

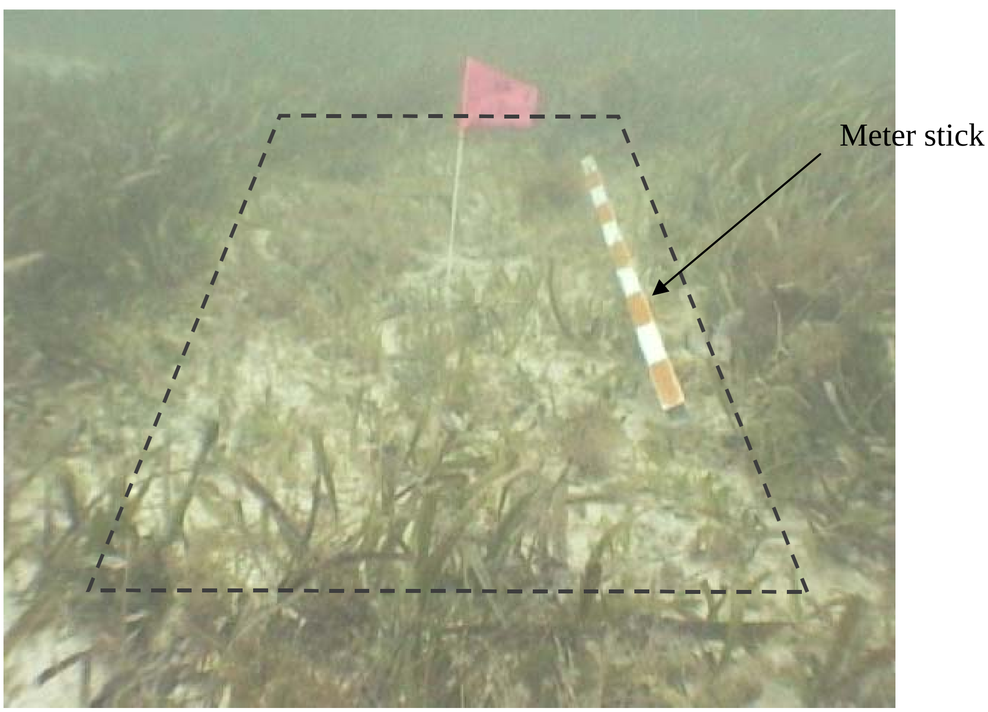

Figure 2. 10-cm treatment in June 2000, a few days after initiation. This depth treatment was created using hoes to scrape away the surface seagrass, macroalgae, and invertebrate biomass.

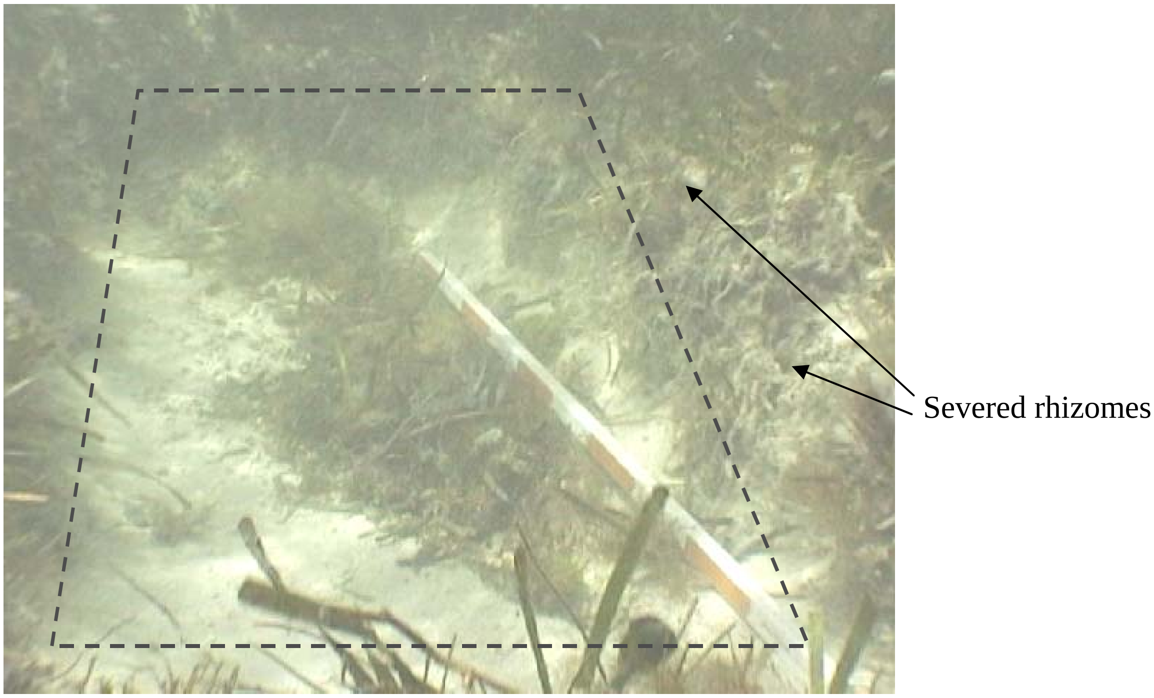

Figure 3. 40-cm treatment in June 2000, a few days after excavation. The 20- and 40-cm treatments were created with shovels. Excavated materials were removed in buckets. Injury margins have already started to collapse into the excavation. Drift algae has collected at the bottom.

During each survey period we collected the following data in each experimental treatment: (1) short-shoot counts of each seagrass species, (2) cover of seagrass and total macroalgae, (3) depth, and (4) video documentation. We evaluated cover of seagrasses and macroalgae using the Braun-Blanquet visual assessment method (Fourqurean et al. 2001). In this method, a numerical value is assigned based on the proportion of the total quadrat that is obscured by a species or functional group when observed from above (Table 1). Total macroalgae cover estimates encompassed all morphologies: upright fleshy, upright calcareous, and turf (Table 2).

Table 1. Braun-Blanquet cover scores. Each seagrass species and macroalgal functional group was scored in each quadrat according to this scale.

Score	Cover
0	Species/functional group absent from quadrat
0.1	Solitary short shoot or individual, < 5% cover
0.5	5 or fewer short shoots or individuals, < 5% cover
1	> 5 short shoots or individuals, < 5% cover
2	> 5 short shoots or individuals, 5-25% cover
3	> 5 short shoots or individuals, 25-50% cover
4	> 5 short shoots or individuals, 50-75% cover
5	> 5 short shoots or individuals, > 75% cover

Table 2. Species list of common macroalgae included in the total macroalgae Braun-Blanquet assessment.

Algal species	Morphology
Acanthophora sp., *Anadyomene stellata*, *Caulerpa* spp., *Dictyosphaeria cavernosa*, *Dictyota* spp., *Gracilaria* spp., *Halymenia* sp., *Hypnea cervicornis*, *Laurencia* spp.	upright fleshy
Acetabularia crenulata, *Avrainvillea nigricans*, *Halimeda* spp., *Penicillus* spp., *Rhizocephalus phoenix*, *Udotea flabellum*	upright calcareous
Amphiroa sp., *Batophera oerstedii*, *Chaetomorpha aerea*, *Dasycladus vermicularis*, turf form of *Halimeda opuntia*, *Neomeris annulata*	turf

Three 50 x 50 cm quadrats were placed end to end to evaluate the entire plot using the Braun-Blanquet visual assessment method. Short shoots were counted inside three randomly placed 25 x 25 cm quadrats in each plot. Twelve depths were recorded systematically from each plot. Depth was measured to the surface of the treatment from a reference pole placed across the treatment. Replicate measurements from each experimental plot were averaged and the mean plot value generated for each of these data types was used in further analysis.

Fill Experiment
The fill experiment was deployed in September 2000 about 25 m east of the excavation experiment on the same bank. Experimental plots were laid out along a northwest-southeast axis in a 300 m^2 area and spaced 2-3 m apart. Plots were arranged in a 3 x 6 array with treatments assigned randomly within each row. The experiment was surveyed seven times: January 2001, May 2001, September 2001, January 2002, May 2002, August 2002, and May 2003.

Six replicates of each of three fill treatments (n = 18 replicates total) were assigned to 50 x 150 cm plots: (1) control (no sediment disturbance), (2) fill, and (3) no fill. The fill and no fill treatments were excavated to 30 cm depth as above. Fill treatments were filled with limestone pea gravel (diameter 0.6 cm, Fig. 4) until the sediment level was restored to original grade, while no fill treatments were left unfilled (Fig. 5). At each survey, short-shoot counts of seagrass species, Braun-Blanquet visual assessment of macroalgae and seagrass cover, depth, and video documentation were collected as above.

Data Analysis
Excavation Experiment
Thalassia testudinum and *Syringodium filiforme* short-shoot counts were square root transformed to meet assumptions of variance homogeneity and residual normality. Short-shoot count data from three survey dates, chosen to roughly coincide with one, two, and three years after deployment of the experiment (May 2001, August 2002, May 2003), were analyzed by species. One-way analysis of variance was conducted on each date’s data and a Bonferroni correction

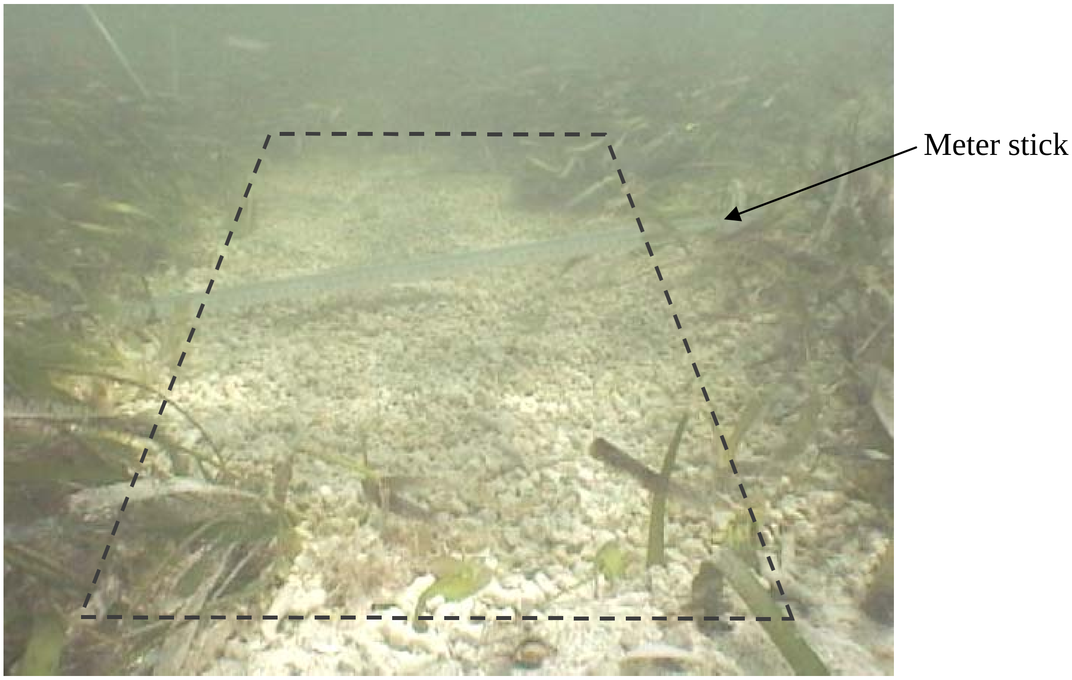

Figure 4. Fill treatment in September 2000, a few days after deployment. Pea gravel was added to restore the excavation to grade.

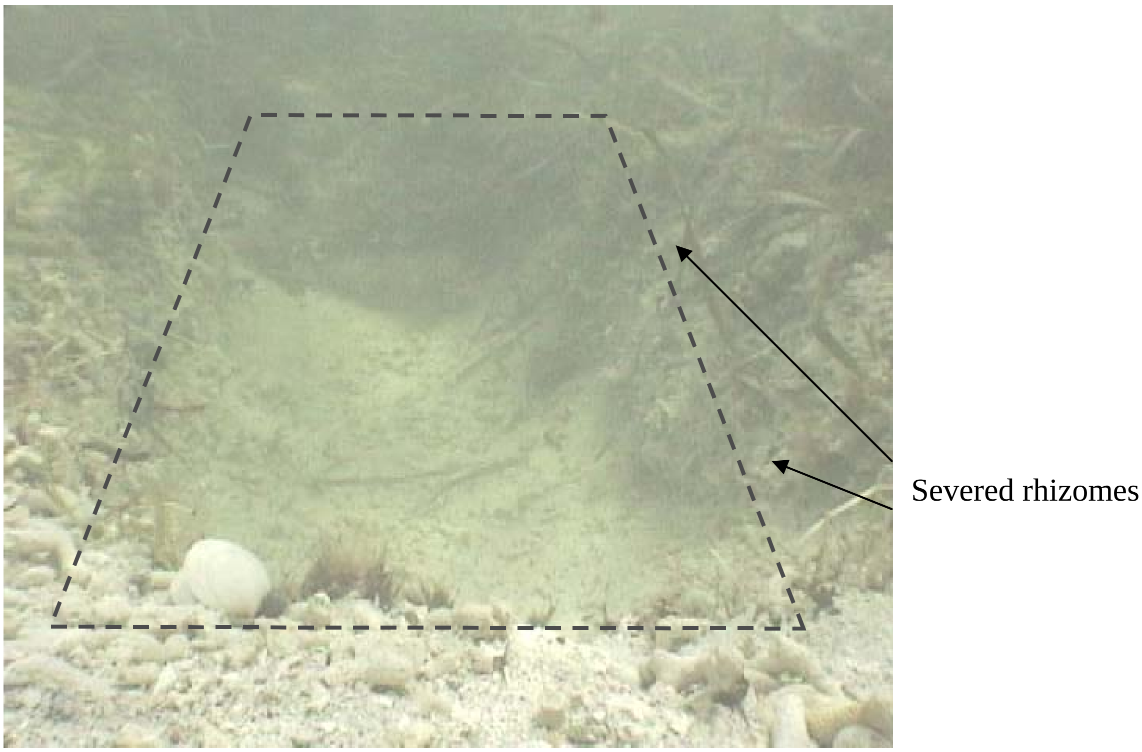

Figure 5. No Fill treatment in September 2000, a few hours after deployment.

was applied to the ANOVA F-test to account for repeated analyses (Underwood 1997). Tukey's studentized range test was used to conduct pair-wise comparisons among treatments when the overall ANOVA was significant at the $\alpha' = 0.017$ level ($\alpha = 0.05$ corrected for 3 ANOVAs).

Excavation experiment treatment depths were analyzed for two survey dates, May 2001 and August 2002. May 2001 data were natural-log transformed to meet assumptions of variance homogeneity and residual normality. While not all treatment residuals were distributed normally for August 2002 data, untransformed variances were homogeneous and transformation failed to resolve residual non-normality. One-way analysis of variance was conducted on transformed May 2001 data and untransformed August 2002 data. Tukey's studentized range test was used to conduct pair-wise comparisons among treatments when the overall ANOVA was significant at the $\alpha' = 0.025$ level (Bonferroni correction as above for 2 ANOVAs).

Fill Experiment
Syringodium filiforme short-shoot counts were square root transformed to meet assumptions of variance homogeneity and residual normality. Transformation was not necessary for *Thalassia testudinum* short-shoot counts. Short-shoot count data from three survey dates, chosen to roughly coincide with one, two, and three years after deployment of the experiment (May 2001, May 2002, May 2003), were analyzed by species. Analyses and corrections were applied as above.

No transformation was necessary for fill experiment treatment depths to meet assumptions of variance homogeneity and residual normality. Depths were analyzed for two survey dates, September 2001 and August 2002, roughly one and two years after deployment. Analyses and corrections were conducted as in the excavation experiment depth analyses.

Results
For both experiments the following system was used in the graphed results. Short-shoot data collected during all surveys is shown in a line and scatter plot, with arrows designating the survey dates that were selected for statistical analysis. Data in the line and scatter plots are displayed at the collection density of short shoots per 0.0625 m^2 quadrat. Data that were used in statistical analysis are plotted in bar graphs, presented in the form in which they were analyzed, including transformation if necessary. Equivalent short-shoot densities per square meter are given in the discussion of the results.

Excavation Experiment
Thalassia testudinum short-shoot counts for all the survey dates are shown in Figure 6. Short-shoot counts were significantly affected by treatment in May 2001 and August 2002 (Table 3). On both survey dates, there were no differences between the control and 10-cm treatment short-shoot counts, but both were significantly greater than the 20- and 40-cm treatments, which were not different from each other (Fig. 7). By May 2003, almost three years (1,077 days) after deployment of the experiment, there were no longer any significant differences in short-shoot counts among the four treatments (Table 3, Fig. 7). Although analyses were not conducted for all dates, it is apparent that the 10-cm treatments showed a rapid increase in short-shoot counts following initiation of the experiment, probably because the treatment involved minimal disturbance of belowground biomass, particularly to seagrass apical meristems. The 10-cm treatment resulted in removal of the aboveground short shoots, which quickly regenerated and

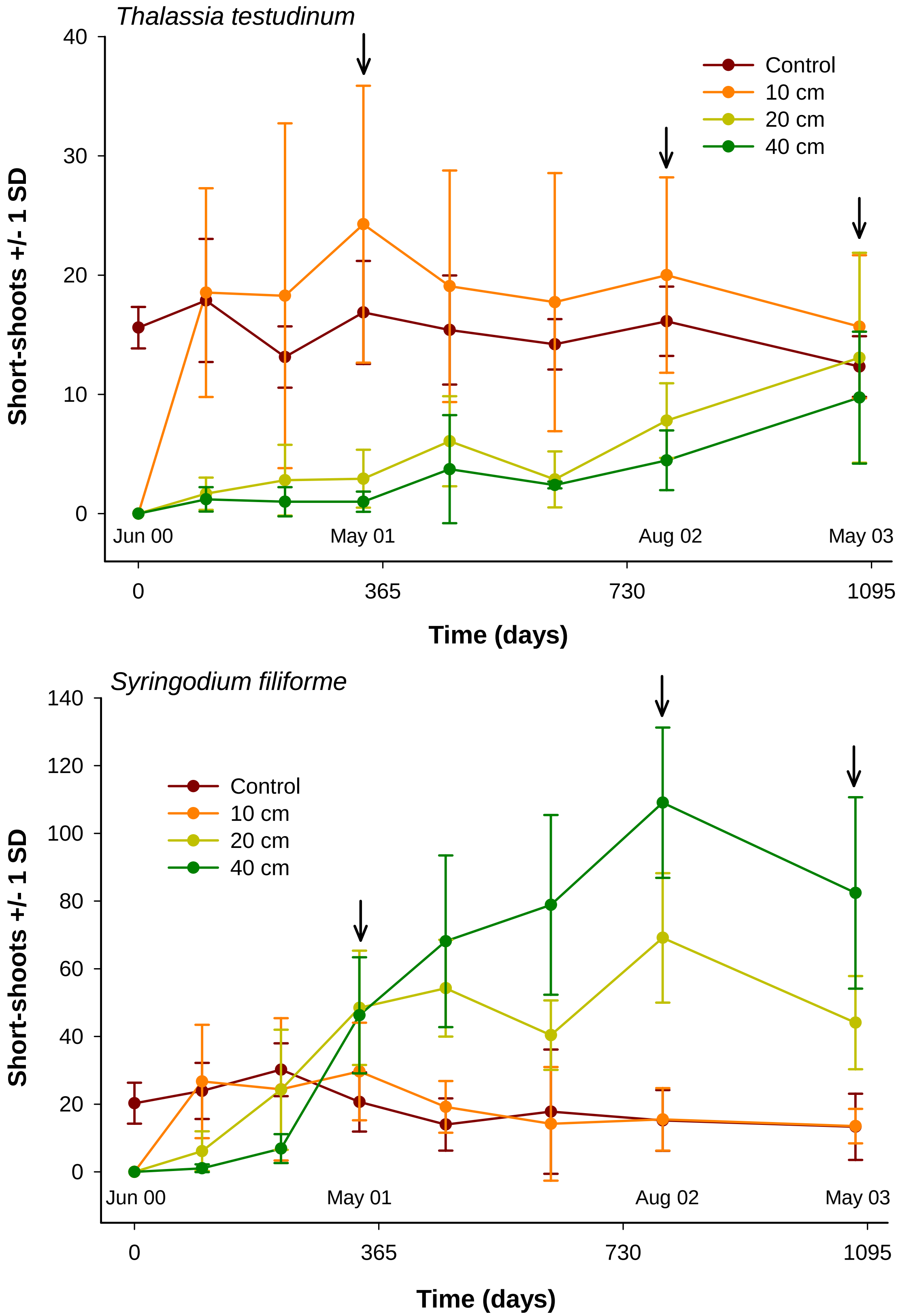

Figure 6. Excavation experiment short-shoot counts in 0.0625 m^2 quadrats for *Thalassia testudinum* and *Syringodium filiforme*. Survey dates used in statistical analysis are indicated by arrows. SD = standard deviation.

Table 3. Analysis of variance results for excavation experiment short-shoot counts. Tests significant at the α = 0.0167 level are indicated by asterisks. SQRT TT and SQRT SF are square-root transformed *Thalassia testudinum* and *Syringodium filiforme* short-shoot counts, respectively, in 0.0625 m^2 quadrats.

Dependent Variable	Date	Independent Variable	SS	MS	F-value	P-value
	May 2001	treatment	54.52	18.17	27.58	< 0.0001 *
SQRT TT	August 2002	treatment	18.22	15.03	15.03	< 0.0001 *
	May 2003	treatment	1.92	0.64	1.01	0.4131
	May 2001	treatment	20.31	6.77	3.97	0.0273
SQRT SF	August 2002	treatment	167.50	55.83	36.79	< 0.0001 *
	May 2003	treatment	104.48	34.83	24.70	< 0.0001 *

were probably no different than control density in September 2000, 90 days after deployment (Fig. 6). Twenty- and 40-cm treatment short-shoot counts continued to be significantly lower than 10-cm and controls through August 2002, 780 days after deployment, although the short-shoot counts were greater than the same treatments in May 2001 (Fig. 7). Between 10 and 20 cm appears to be a critical depth beyond which damage to *T. testudinum* is such that recovery takes much longer. In May 2003, short-shoot densities ranged from 155.7 (standard deviation = 88.5) to 250.7 (SD = 95.9) short shoots m^{-2}, with an overall mean in control treatments for the survey periods of 242 short shoots m^{-2}.

Figure 6 shows the recovery pattern of *Syringodium filiforme* through time, with 10-cm treatments returning quickly to pre-injury conditions, while 20- and 40-cm treatments responded more slowly. *Syringodium filiforme* short-shoot counts responded differently to depth treatments than *Thalassia testudinum*. In May 2001, 11 months after deployment, *S. filiforme* short-shoot counts were not significantly different among treatments (Table 3, Fig. 7). In August 2002, 20- and 40-cm treatment short-shoot counts were not significantly different, but were significantly greater than counts in 10-cm and control treatments. By May 2003, while counts in the two deepest treatments had dropped, they were still significantly greater than 10-cm and control counts, and significantly different from each other (Fig. 7). Unlike *T. testudinum*, however, *S. filiforme* in the deepest treatments showed a compensatory recovery in which counts began to increase in the first year after deployment and were still significantly higher than controls almost three years (1,095 days) later (Fig. 6 and 7). By May 2003, short-shoot counts in 20- and 40-cm treatments had begun to decline, possibly in response to increasing *T. testudinum* short-shoot counts. Control *S. filiforme* short-shoot counts ranged from 213.3 (SD = 156.3) to 330.7 (SD = 140.4) m^{-2} during the study, with a mean of 262 short shoots m^{-2}. The maximum density was 1,745.1 (SD = 355.2) short shoots m^{-2} in the 40-cm treatment in August 2002.

Excavation treatment depths changed dramatically over time, with a roughly 50% decrease in depth in the three experimental treatments three months after deployment (Fig. 8). In May 2001, 330 days after deployment, treatment still significantly affected depth, although only the 40-cm treatment was different from the control and other depths (Table 4). In August 2002, 26 months (780 days) after deployment, the treatment depths were not significantly different (Table 4).

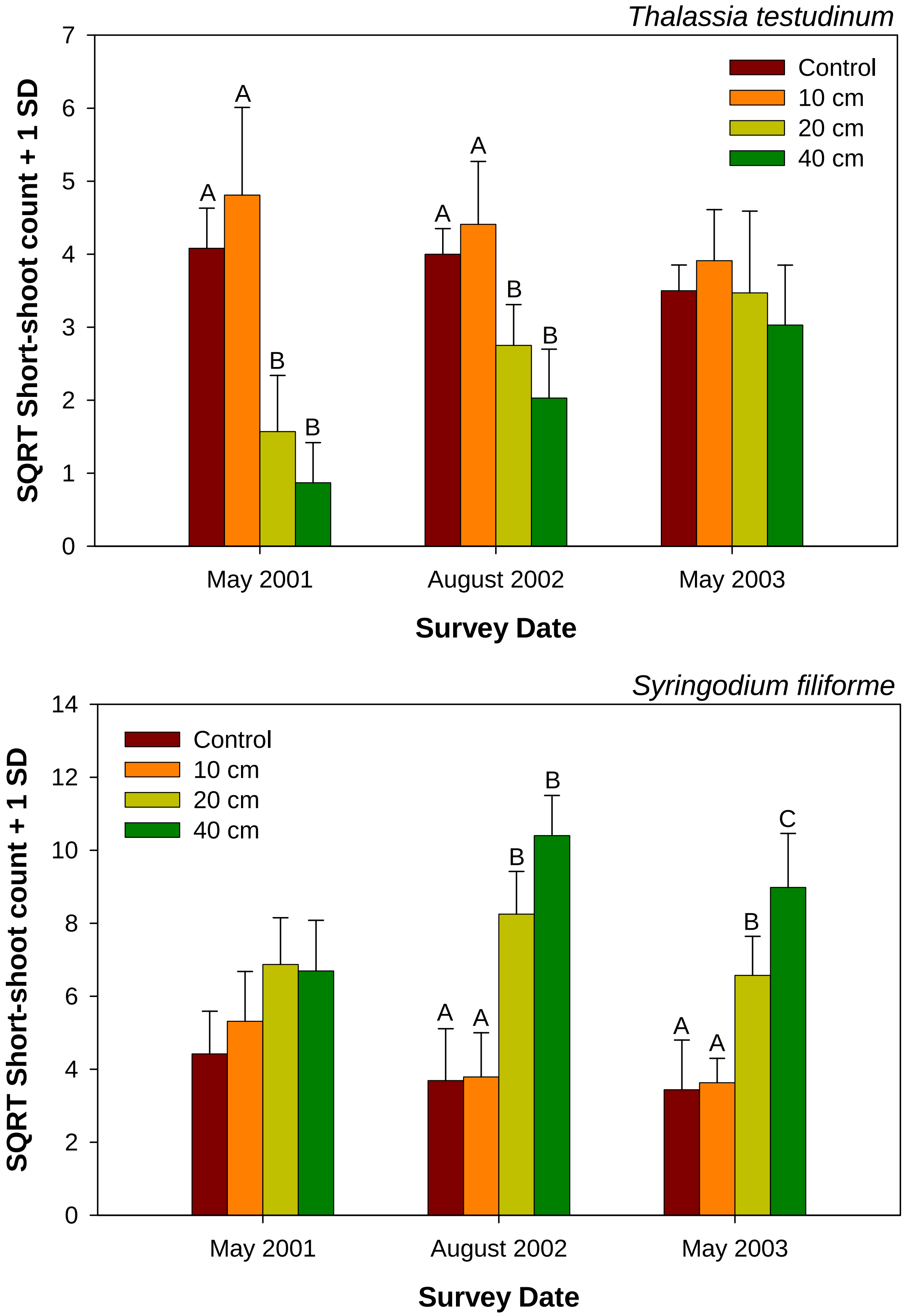

Figure 7. Excavation experiment square-root transformed short-shoot counts used in pair-wise comparisons. Letters indicate significant differences within a survey date. *Thalassia testudinum* counts were not significantly different in May 2003 and *Syringodium filiforme* counts were not significantly different in May 2001. SD = standard deviation.

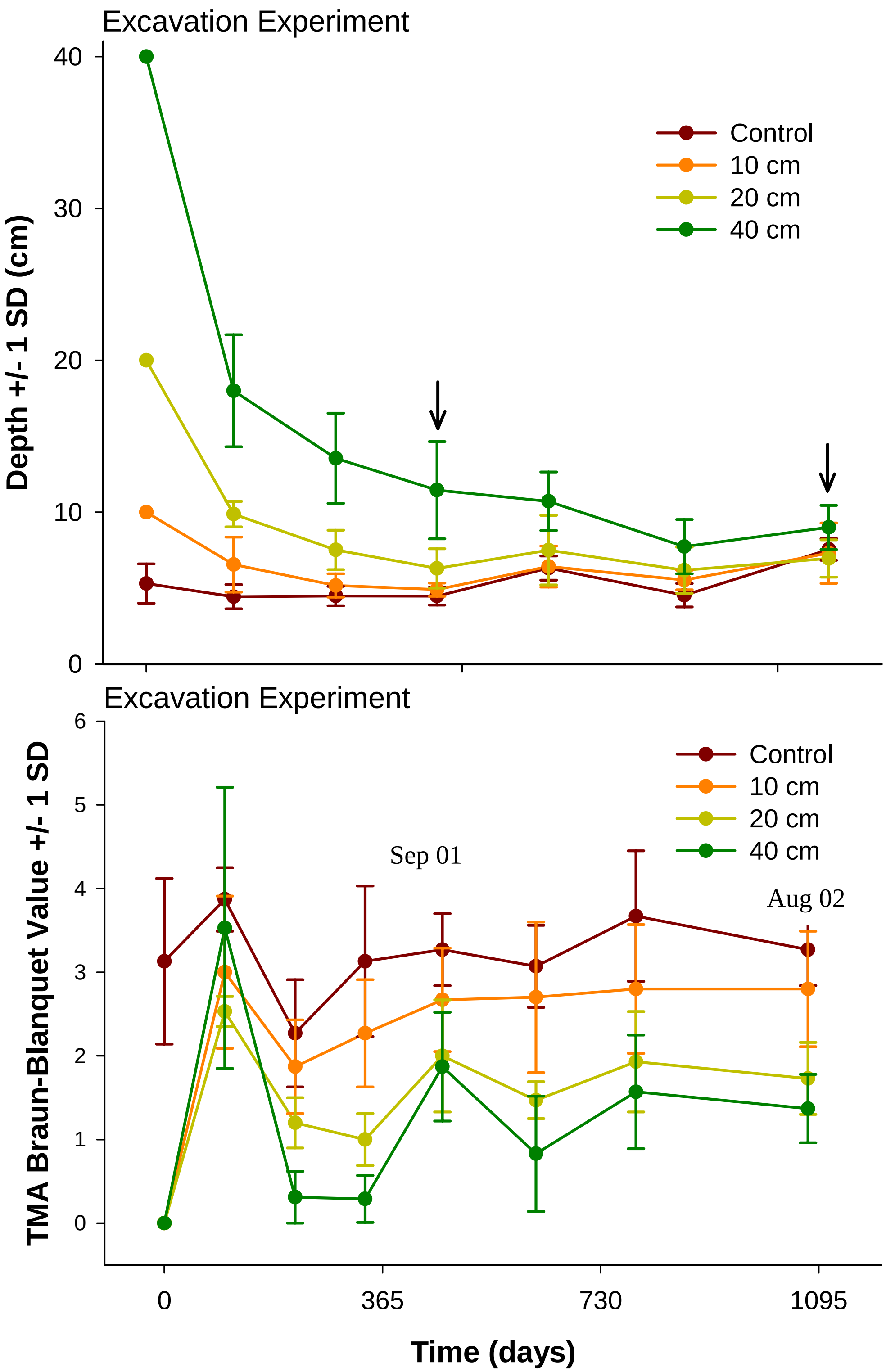

Figure 8. Excavation experiment depth and macroalgal cover. Depths used in statistical analysis are indicated by arrows. SD = standard deviation.

Table 4. Analysis of variance results for excavation experiment depths. Tests significant at the α = 0.025 level are indicated by asterisks. May 2001 depths were natural-log transformed (LN depth) prior to analysis, while August 2002 depths were not.

Dependent Variable	Date	Independent Variable	SS	MS	F-value	P-value
LN depth	May 2001	treatment	2.49	0.83	17.77 `	< 0.0001 *
depth	August 2002	treatment	12.18	4.06	2.00	0.1540

Total macroalgal cover is presented for descriptive purposes only in the excavation experiment (Fig. 8). During creation of the 10-, 20-, and 40-cm treatments all macroalgae was removed. There was a very quick rebound in cover, with an increase from zero coverage in June 2000 to a range of 25-75% cover (Braun-Blanquet values > 2-4) 90 days later. Some of this cover was attributable to drift rather than attached macroalgae (Fig. 3). Then there was a decrease in cover for all treatments that coincided with a cold winter; temperatures on bank tops reached 10-11^{o}C. Although macroalgal cover increased after 330 days, it appears that there was a negative effect on macroalgae in the deeper treatments that persisted through May 2003 (1,077 days).

Fill Experiment

Thalassia testudinum short-shoot counts varied significantly among treatments in the fill experiment (Table 5, Fig. 9). As with the excavation experiment, *T. testudinum* fill and no fill short-shoot counts were significantly lower than control counts during the May 2001 and May 2002 surveys, 270 and 630 days after deployment (Fig. 10). By May 2003, there was no longer a significant difference in short-shoot count (Table 5, Fig. 10). Figure 9 shows a steady increase in *T. testudinum* short-shoot count in the two experimental treatments, and although not tested, the treatments appear to have recovered at the same rate, reaching control levels 990 days (33 months) after deployment. Control short-shoot counts ranged from 202.7 (SD = 88.4) to 262.2 (SD = 90.2) short shoots m^{-2} over the course of the experiment, with an overall mean of 234 short shoots m^{-2} in the control treatments. In fill and no fill treatments, short-shoot densities reached 24.0 and 28.4 (SD = 53.7 and 26.1) short shoots m^{-2} in May 2001 and 160.9 and 210.7 (SD = 59.5 and 80.2) short shoots m^{-2} by May 2003, respectively.

Syringodium filiforme short-shoot counts were also significantly affected by treatment (Table 5, Fig. 9). In May 2001, 270 days after deployment, there were no differences among treatments in short-shoot counts (Table 5, Fig. 9). By May 2002, 630 days after the experiment was initiated, all treatments were significantly different from one another, with the no fill treatment having the highest short-shoot counts and the control treatment having the lowest short-shoot counts (Fig. 10). This condition continued through May 2003, with treatments remaining significantly different from each other 990 days after deployment (Fig. 9). Figure 9 shows that *S. filiforme* in the no fill treatment demonstrated the same compensatory recovery that was exhibited in the 20- and 40-cm treatments in the excavation experiment. Short-shoot counts of *S. filiforme* in the fill treatment also showed an increase over time, but not as dramatic an increase as that of the no fill treatments (Fig. 9 and 10). Interestingly, *S. filiforme* short-shoot counts in control treatments of the fill experiment were lower than control treatments of the excavation experiment. Densities in the fill experiment controls ranged from 96.0 to 148.4 (SD = 102.8 and 99.3) short shoots m^{-2}, with a mean of 117 short shoots m^{-2}. No fill densities peaked at 1,162.7 (SD = 420.5) short shoots m^{-2}, about 10 times higher than control densities, in May 2002. Fill treatment densities also peaked in May 2002, with 493.3 (SD = 233.5) short shoots m^{-2}.

Table 5. Analysis of variance results for fill experiment short-shoot counts. Tests significant at the α = 0.0167 level are indicated by asterisks. TT and SQRT SF are *Thalassia testudinum* and square-root transformed *Syringodium filiforme* short-shoot counts, respectively, in 0.0625 m^2 quadrats.

Dependent Variable	Date	Independent Variable	SS	MS	F-value	P-value
	May 2001	treatment	429.45	214.72	15.69	0.0003 *
TT	May 2002	treatment	414.90	207.45	11.24	0.0010 *
	May 2003	treatment	67.75	33.88	1.60	0.2344
	May 2001	treatment	7.02	3.51	2.94	0.0861
SQRT SF	May 2002	treatment	90.66	45.33	26.32	< 0.0001 *
	May 2003	treatment	120.97	60.49	22.15	< 0.0001 *

The depth of no fill treatments in the fill experiment changed markedly in the first 120 days following deployment in September 2000, declining from a mean depth of 27.6 cm to 12.2 cm. At no time did the fill treatment depths differ from controls (Table 6, Fig. 11), which demonstrate that the fill material was not eroded away by water flow. In fact, by August 2002, 690 days after deployment, there were no significant differences in depth among any treatments (Table 6). As with the 20- and 40-cm treatments in the excavation experiment, some time during the second year following deployment the no fill treatment filled in because the margins collapsed into injuries and suspended sediments settled into them.

Total macroalgal cover was variable in all treatments of the fill experiment (Fig. 11). Over time there was a moderate increase in macroalgal cover, from values much less than 5% (Braun-Blanquet value $\leq$ 1) to values greater than 25% (Braun-Blanquet value $\geq$ 2). As in the excavation experiment, although no analyses were conducted, it appears that macroalgal cover in the no fill treatment continued to be lower than cover in controls through the last survey date 33 months after deployment. Dips in cover in controls correspond to the January sampling dates, suggesting that macroalgal cover is influenced by some seasonal factor, such as water temperature or light (Fig. 11).

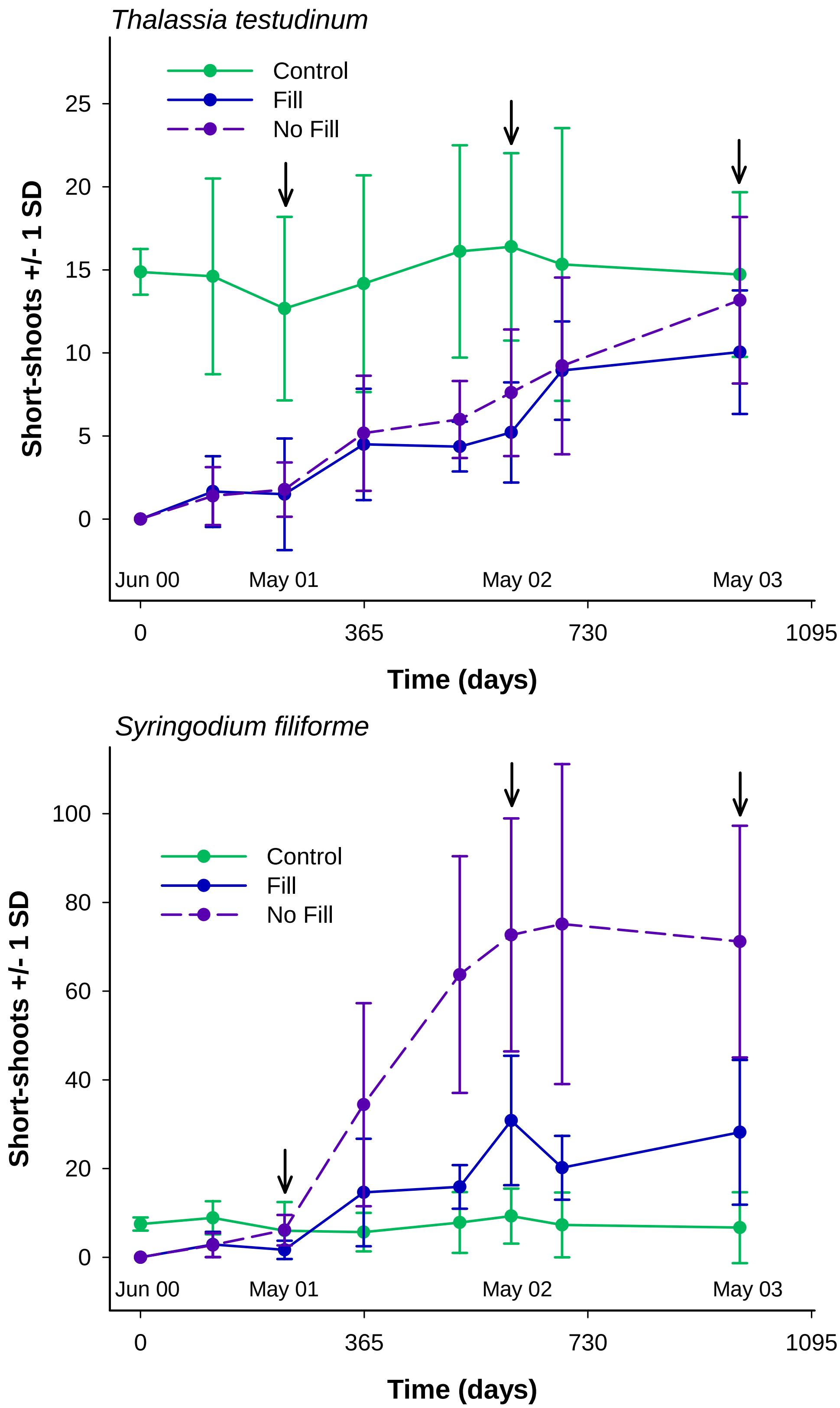

Figure 9. Fill experiment short-shoot counts in 0.0625 m^2 quadrats for *Thalassia testudinum* and *Syringodium filiforme*. Survey dates used in statistical analysis are indicated by arrows. SD = standard deviation.

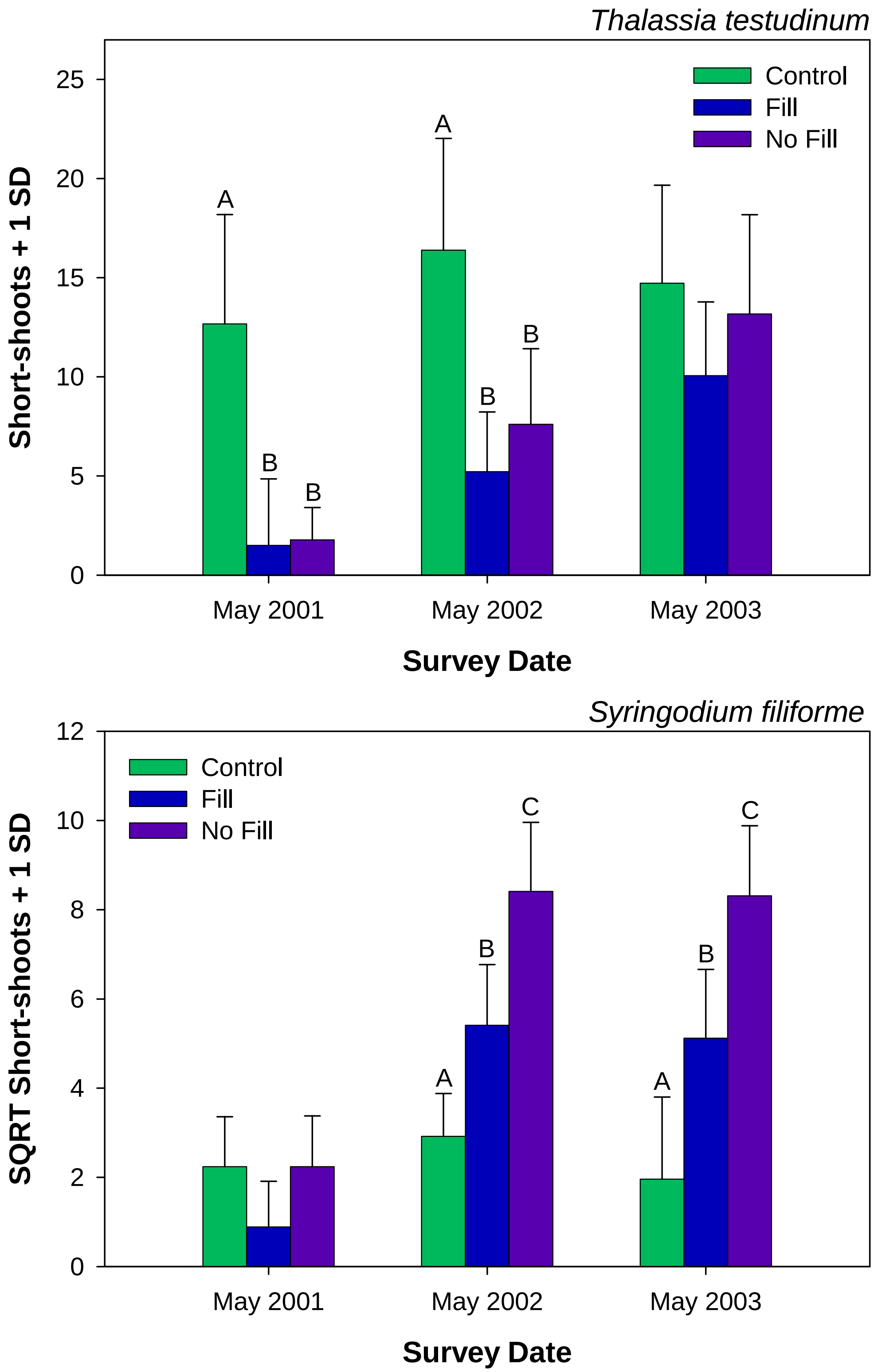

Figure 10. Fill experiment short-shoot counts used in pairwise comparisons. Letters indicate significant differences within a survey date. Thalassia testudinum counts were not significantly different in May 2003 and square-root transformed Syringodium filiforme counts were not significantly different in May 2001. SD = standard deviation.

Table 6. Analysis of variance results for fill experiment depths. Tests significant at the α = 0.025 level are indicated by asterisks.

Dependent Variable	Date	Independent Variable	SS	MS	F-value	P-value
depth	May 2001	treatment	33.47	16.73	9.92 `	0.0018*
depth	May 2002	treatment	7.19	3.60	1.92	0.1815

Discussion

Results of the excavation and fill experiments demonstrated that injuries to seagrass banks that exceeded 10 cm in depth had significant impacts on short-shoot counts of *Thalassia testudinum* and *Syringodium filiforme*, and in some treatments those impacts persisted three years after initiation. In both experiments, *T. testudinum* short-shoot density in all treatments returned to control levels between the second and third year following injury. *Syringodium filiforme* short-shoot densities, however, remained elevated in most deep (> 20 cm) treatments through the May 2003 survey (Fig. 12). Total macroalgal cover also tended to be lower in more disturbed treatments. Although *T. testudinum* short-shoot densities and treatment depths had returned to pre-injury levels in roughly two to three years, treatments continued to impact *S. filiforme* short-shoot counts and macroalgal cover.

The response of *Thalassia testudinum* to these treatments may be explained in part by its morphological characteristics. As much as 80 to 90% of the dry weight of *T. testudinum* is belowground biomass (van Tussenbroek 1998; Kaldy and Dunton 2000), and the belowground fraction may extend deeper than 1 m into the sediment (Marba et al. 1993). Shallow injuries (≤ 10 cm) probably disturb very little of the belowground biomass and apical meristems. Experimental plots may recover quickly because of regrowth of intact short shoots, which were "shaved" by the treatment while no rhizomes were severed. Deeper injuries, however, disturb more of the belowground biomass, thereby severing rhizomes, damaging apical meristems, and removing the root-rhizome-sediment matrix that underlies the visible meadow. Regrowth into deeper injuries (≥ 20 cm) can be slow because it requires vegetative growth from the injury margins and/or recruitment of seedlings, processes dependent on low densities of horizontal meristems and seedlings (van Tussenbroek et al. 2000; Whitfield et al. in press) and the slow rate of clonal growth of *T. testudinum*. Additionally, the excavation of sediment may expose *T. testudinum* apical meristems to light, and there is some evidence to suggest that light inhibits meristematic tissue growth (Terrados 1997). Finally, there appeared to be no significant effect of fill material on the growth of *T. testudinum* into the experimental plots, as demonstrated by the responses in the fill and no fill treatments (Fig. 9).

The response of *Syringodium filiforme* to experimental manipulation was quite different than the response of *Thalassia testudinum*. Once all seagrass above- and belowground biomass was removed, the fast growth of *S. filiforme* conferred a short-term competitive advantage, and *S. filiforme* short-shoot densities quickly exceeded those of the surrounding, undisturbed seagrass bed. In some cases a 10-fold increase in short-shoot density of *S. filiforme* occurred in the deeper, unfilled treatments (≥ 20 cm) (Fig. 13). Williams (1987) reported a doubling of *S. filiforme* short-shoot density after clipping the aboveground biomass of *T. testudinum* in a mixed species seagrass bed in the Caribbean. In our study, an even greater increase in short-shoot

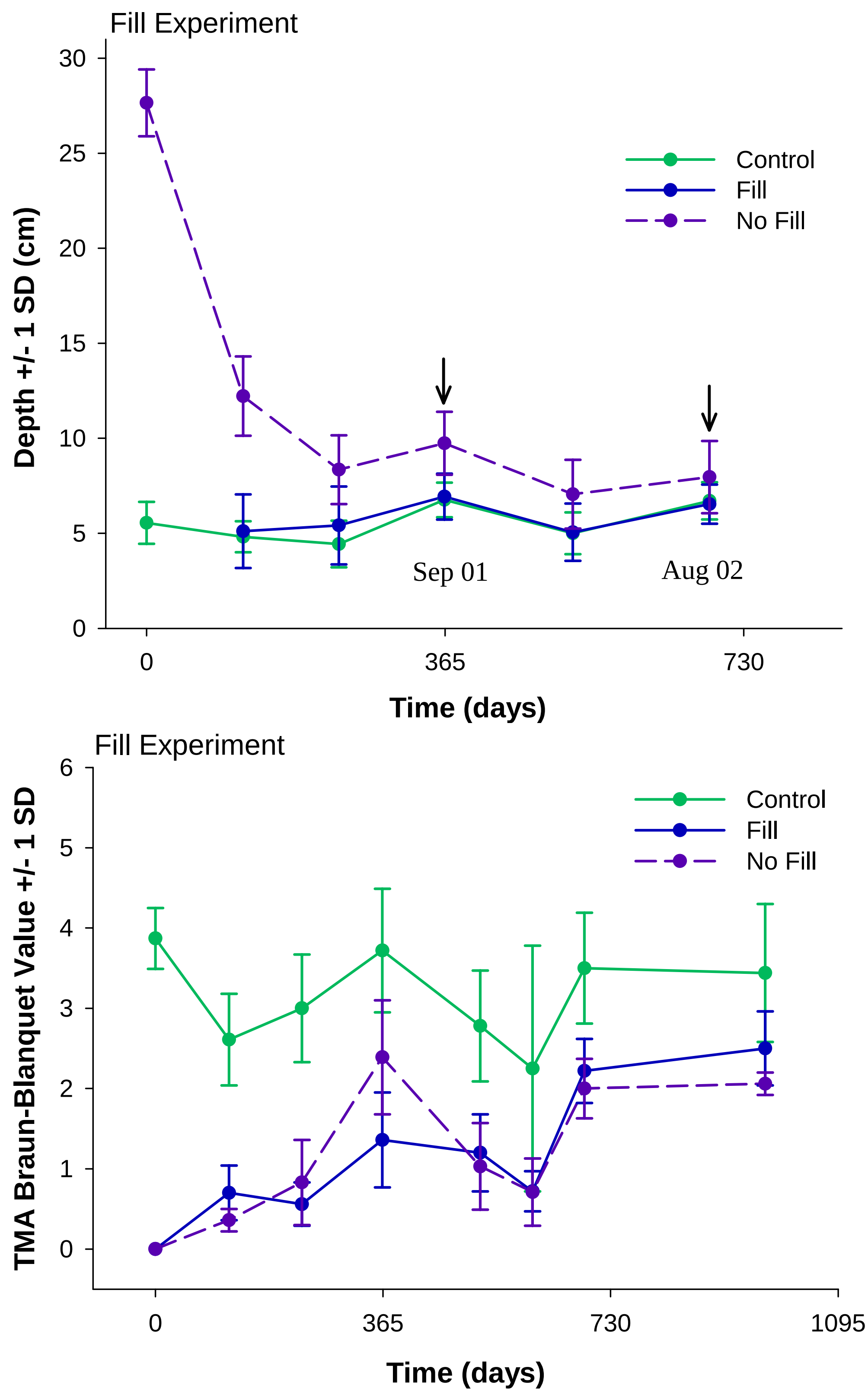

Figure 11. Fill experiment depth and macroalgal cover. Depths used in statistical analysis are indicated by arrows. SD = standard deviation.

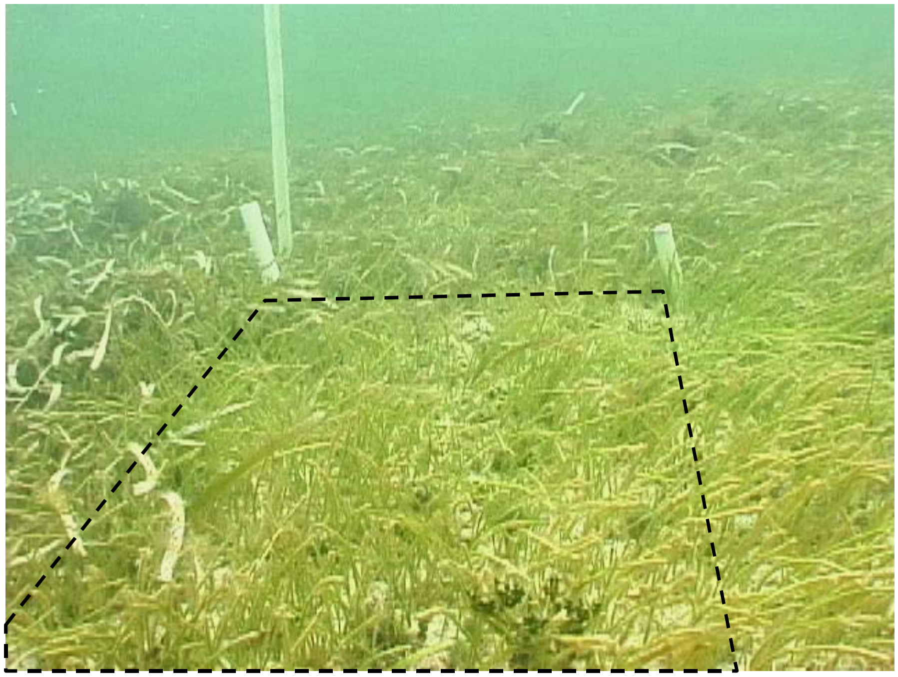

Figure 12. A 40-cm excavation treatment in August 2002, 780 days after deployment. The dominant seagrass inside the treatment is *Syringodium filiforme*. The injury increased in size to include the area to the right of the dotted line, where more *S. filiforme* is present.

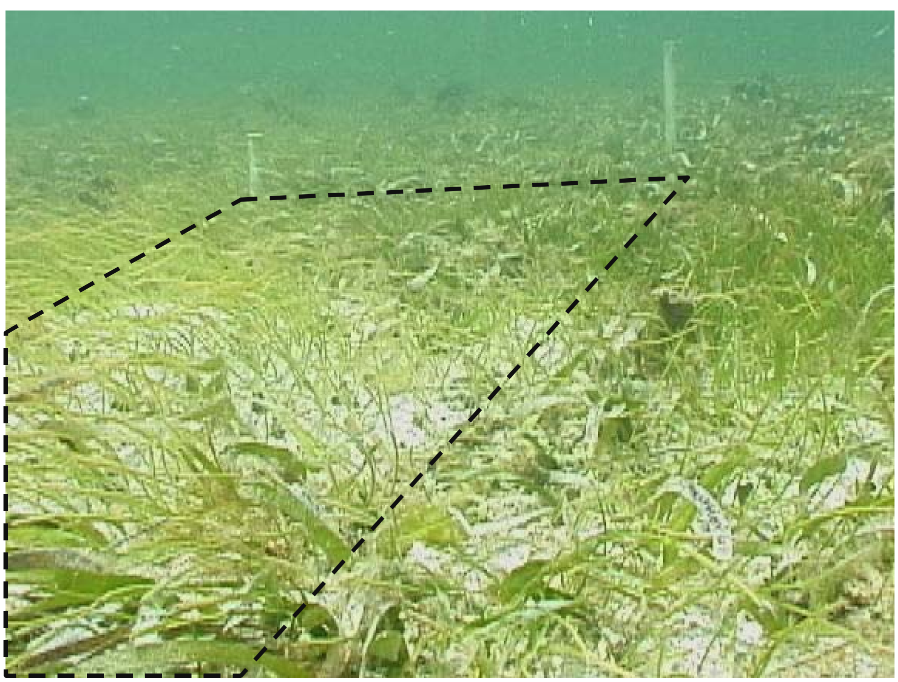

Figure 13. No fill treatment in August 2002, 690 days after deployment. The dominant seagrass inside the treatment is *Syringodium filiforme*.

density was probably a result of not only increased light from above, but decreased competition for space in the substrate (Williams 1988; Duarte et al. 1998, Duarte et al. 2000). During the second year of the study we started to see a leveling off or decrease of *S. filiforme* short-shoot density, and we predict that as *T. testudinum* becomes more established in the deeper experimental plots, *S. filiforme* will decline further (Williams 1988; Williams 1990; Kenworthy et al. 2002).

The results from the fill treatment suggest that pea gravel may have physically inhibited *Syringodium filiforme* recovery along the injury margins. Fill treatment *S. filiforme* short-shoot densities nine months after initiation of the experiment were about 25% of the densities in the control and no fill treatments (26.7 versus 96.0 short shoots m^{-2}). One year later, in May 2002, *S. filiforme* fill treatment short-shoot counts had reached levels about 3.5-times higher than controls, but were still less than half that of no fill plots (Fig. 6). The only difference between the fill and no fill treatments was the presence of pea gravel and probably the much greater proportion of fine sediment that accumulated in no fill plots (Fig. 11). Also, there may have been less organic matter, and therefore less nutrient availability in the pea gravel.

Results of the excavation and fill experiments have implications for seagrass restoration. Without intervention, our experimental treatment *Thalassia testudinum* short-shoot counts reached control levels in 33 to 36 months. This recovery estimate agrees with previous studies on *T. testudinum* recovery in narrow propeller scars. Zieman (1976) reported recovery times of 2-5 years in southern Florida and the Florida Keys, while Dawes et al. (1997) predicted recovery in 2-7 years in Tampa Bay *T. testudinum* beds. A third study found recovery rates of 7-10 years in the Florida Keys (Kenworthy et al. 2002). In these studies, recovery was defined as scar disappearance or recovery was predicted from a regression of short-shoot density change over time. Our results demonstrate that injury effects such as increased *Syringodium filiforme* short-shoot counts and decreased macroalgal cover may persist even though *T. testudinum* short-shoot counts have reached ambient densities. Thus, how recovery is defined is very important.

One factor that was not addressed in this study is the vulnerability of injuries to further erosion. There were no major storms during the three years after deployment of these experiments, but we know from previous studies that storms can have dramatic and lasting impacts on seagrass beds (Preen et al. 1995), especially when there is existing motor vessel damage (Whitfield et al. 2002). Although not tested, we predict that filling of injuries would leave them less susceptible to storm-induced erosion. In the fill experiment, depths of fill treatments were not significantly different than controls one and two years after deployment of the fill material. This fact demonstrates that there was very little erosion of fill material from injuries. Had a storm occurred, unfilled treatments from both experiments would probably have experienced erosion, especially if the storm occurred early in the recovery process. Sedimentation into unfilled treatments begins with the collapse of injury margins into the injury itself and continues with deposition of sediment trapped by seagrass in surrounding beds. Until a new root-rhizome-sediment matrix is established by the regrowth of seagrass into the unvegetated area, the unconsolidated sediment is susceptible to erosion (Zieman 1976; Sargent et al. 1995; Whitfield et al. 2002). Filling of injuries with pea gravel provides protection from erosion, does not inhibit growth of *Thalassia testudinum*, and might minimize stress of competition from *Syringodium filiforme*. The placement of fill into larger blowhole injuries that take decades to recover

(Fonseca et al. 2002) should diminish the probability of further erosion and enhance recovery by allowing regrowth of seagrasses.

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