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Analysis of Seagrass Recovery in Experimental Excavations and Propeller-Scar Disturbances in the Florida Keys National Marine Sanctuary

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ABSTRACT

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We investigated recovery of seagrasses in two types of mechanical sediment disturbances associated with motor vessel injuries: (1) artificial excavations where we removed all seagrasses in three size categories, 0.25 m^2, 1.0 m^2, and 2.25 m^2; and (2) propeller scars of known age. We simulated mechanical sediment disturbance in the three excavation sizes in *Thalassia testudinum, Syringodium filiforme,* and *Halodule wrightii* meadows growing on soft, carbonate mud banks in the Florida Keys National Marine Sanctuary. After 700 days, results confirmed the long-standing paradigm that *H. wrightii* and *S. filiforme* recover significantly faster than *T. testudinum.* Results from the experimental excavations in monotypic seagrass meadows indicate that there were no significant differences in recovery rates between size categories for each of the species. In monotypic *T. testudinum, H. wrightii,* and *S. filiforme* excavations, recovery was predicted to be 1.9, 1.5 and 10.5 years, respectively. Adjusted for a typical scar width of 0.45 m, recovery in propeller scars is estimated to be 9.5 years for *T. testudinum,* 1.7 years for *H. wrightii,* and 1.4 years for *S. filiforme.* In mixed species seagrass communities the subdominant, but pioneering and opportunistic species, *H. wrightii* or *S. filiforme,* sometimes colonized the artifical gaps as fast or faster than *T. testudinum,* suggesting that physical disturbance from motor vessels can alter the relative abundance of seagrass species on a bank. For the 15 existing propeller scar injuries, the rate of recovery predicted for *T. testudinum* was faster than in the excavations, 6.9 years versus 9.5 years. These results suggest that injury recovery models and restoration strategies for vessel injuries should consider species composition of the injured site as well as the physical dimensions of the injury, including the excavation depth.

ADDITIONAL INDEX WORDS: *Tropical, seagrass, recovery, disturbance, propeller scars.*

INTRODUCTION

Background

Seagrass meadows form the basis of highly productive and ecologically valuable marine communities throughout subtropical and tropical waters of the Atlantic, Caribbean, and Gulf of Mexico (ZIEMAN, 1982; ZIEMAN and ZIEMAN, 1989). Because they are widely distributed in shallow water, seagrasses are exposed to many natural and anthropogenic stress factors derived from extreme weather events, land-use patterns, watershed modification, and commercial development (SHORT and WYLLIE-ECHEVERRIA, 1996). Recently, the operation of commercial and recreational motor vessels in shallow water has attracted public and scientific attention to the potential consequences of propeller dredging in seagrass meadows (ZIEMAN, 1976; DURAKO *et al.,* 1992; SARGENT *et al.,* 1995; DAWES *et al.,* 1997). Propeller damage ranges from mowing the canopy and shearing leaves, similar to the cropping behavior of large herbivores, to the most serious form of damage when a vessel's propeller excavates the underlying sediments, injuring the rhizomes and roots. Frequently referred to as propeller dredging, sediment excavation tears the leaves, roots, and rhizomes and redistributes sediments onto adjacent benthic communities, causing further injuries (Figure 1). Excavating the sediments removes organic matter, eliminating one of the primary sources of nutrients for the plants (WILLIAMS,

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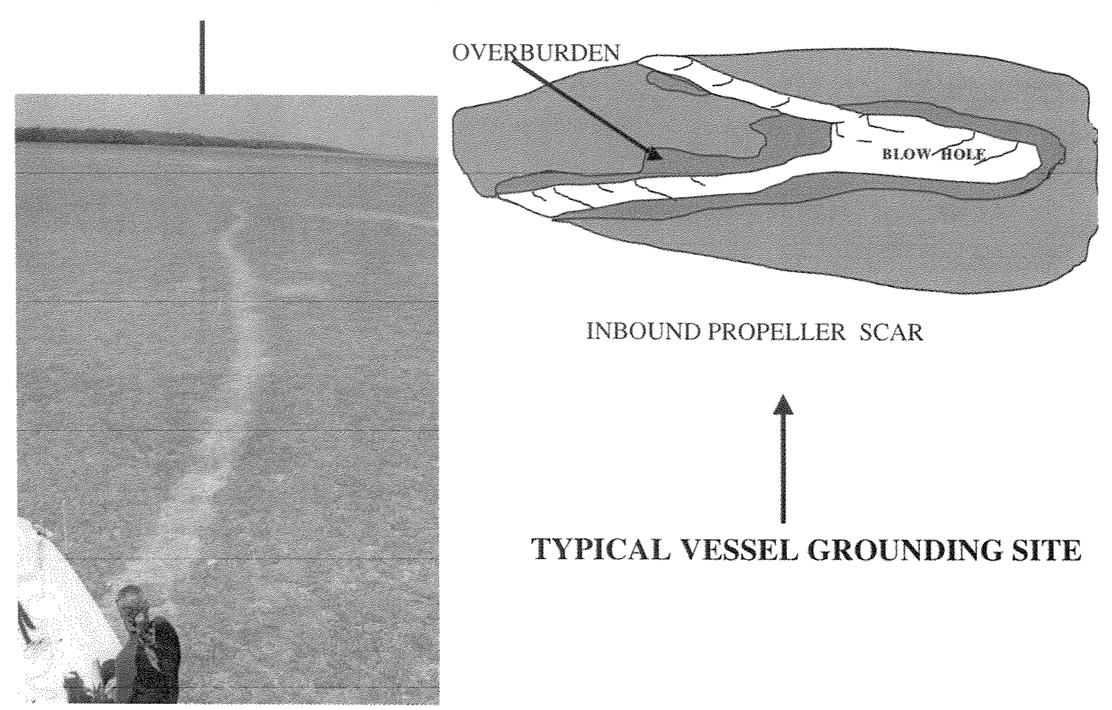

Figure 1. Photograph of a propeller scar (left panel) and illustration of a typical vessel grounding site with an inbound propeller scar, a blowhole, an outbound propeller scar, and overburden (right panel).

1990). The most severe cases of propeller dredging occur when unconsolidated sediments are removed down to the underlying bedrock, severely inhibiting recovery. When the stabilizing capacity of the roots and rhizomes is removed, the injury margins are likely to become more unstable and difficult to restore (see WHITFIELD *et al.,* 2002).

Seagrass Recovery in Propeller Scars

Experimental studies of seagrass regrowth into propeller scars in Tampa Bay, Florida indicate that recovery of disturbed *Thalassia testudinum* (Banks ex Konig) is much slower than *Halodule wrightii* (Ascherson) (DURAKO *et al.,* 1992; DAWES *et al.,* 1997). DURAKO *et al.* (1992) reported that *H. wrightii* recovered about twice as fast as *T. testudinum,* while DAWES *et al.* (1997) reported a range of recovery rates for *T. testudinum* in Tampa Bay, from approximately 3.5 years in scars formed by vessels operating in shallow water to as long as 7.6 years in artificially created scars. Previous studies of seagrass recovery in Florida Bay (ZIEMAN, 1976) and elsewhere in the Gulf of Mexico (WOODBURN *et al.,* 1957; PHILLIPS, 1960; ELUTERIUS, 1987; FONSECA *et al.,* 1987; LEWIS and ESTEVEZ, 1988) suggest that the long-standing paradigm of tropical seagrass species succession (DEN HARTOG, 1971; ZIEMAN, 1982; WILLIAMS, 1990) is applicable to propeller scar recovery. Generally, the paradigm predicts that *T. testudinum* recovers significantly slower than either *H. wrightii* or *S. filiforme.* Therefore, differences in growth rates among species must be considered when predicting recovery in propeller scar disturbances.

Despite agreement between the studies in Tampa Bay, it may not be appropriate to assume that recovery rates are similar from one geographic or climatic region to another. For example, there are differences in the physical and geochemical properties between the clastic sediments of Tampa Bay and the carbonate sediments in the Florida Keys National Marine Sanctuary (FKNMS) (DURAKO *et al.,* 1992). Seagrass growth is nitrogen limited in clastic sediments (Tampa Bay), but phosphorus limited in the softer, shallow carbonate mud banks in the Florida Keys (SHORT *et al.,* 1985; FOURQUREAN *et al.,* 1995). These differences may lead to greater reduction of the sediment nutrient reservoir, a higher frequency of deeper excavations, and consequently, more propeller damage to the root-rhizome structure in the Florida Keys environment. Other differences in recovery may arise from the degree of seasonality in the more northern geographic region of Tampa Bay.

Nearly 1.4 million acres (more than 550,000 ha) of seagrasses are growing within the boundaries of the FKNMS. A large portion of this natural resource is located in shallow water and is vulnerable to propeller dredging (SARGENT *et al.,* 1995). The Florida Marine Patrol (FMP) estimates that there are at least 500 vessel grounding incidents each year where there is measurable damage to benthic resources in the Sanctuary (Bob Currul, Florida Marine Patrol, Marathon, Florida, personal communication, 2001). Based on a recent analysis of aerial photography and detailed benthic surveys of the FKNMS, it was determined that the most widespread injuries result from mechanical damage due to propeller dredging (SARGENT *et al.,* 1995), while more acute damage occurs from large vessels running aground on seagrass banks (WHITFIELD *et al.,* 2002).

Study Objectives

Five species of seagrass occur throughout the FKNMS; however, only three are vulnerable to a high incidence of disturbance due to propeller dredging: *T. testudinum, S. filiforme* (Kutzing), and *H. wrightii.* All three species occur in a wide range of environments, but the shallow water climax communities most frequently encountered by motor vessels are dominated by *T. testudinum.* This dominance pattern is partly due to *T. testudinum*'s robust dimorphic rhizome system (TOMLINSON, 1974) and the unique ability to grow vertically upward (MARBA *et al.,* 1994). Thus, *T. testudinum* beds are able to form stable, elevated mud banks, effectively creating shallow water. Shallow banks are frequently encountered by vessels operating along the margins and outside of navigation channels.

The two main objectives of this paper are: (1) to compare and quantify the recovery rates of *T. testudinum, H. wrightii,* and *S. filiforme* in propeller scar disturbances in the FKNMS; and (2) to gain a better understanding of disturbance and recovery dynamics in tropical seagrass systems. Two approaches were followed. First, excavations of three different sizes and perimeter to area ratios (P/A) in all three species were experimentally simulated at sites across the range of shallow water environments in the FKNMS (seagrass excavation experiments). Second, recovery rates of *T. testudinum* were measured in 15 propeller scars created by motor vessels operating in the Lignumvitae State Management Area (propeller scar recovery experiments).

METHODS

Experimental Design: Seagrass Excavation Experiments

The study was carried out in the Florida Keys at 10 sites widely distributed throughout the Sanctuary between Cross Bank in Florida Bay (25°00′25″N, 80°34′28″W) and Garrison Bight in Key West (24°34′14″N, 81°47′39″W) (Figure 2). Seven of the sites had nearly monotypic *T. testudinum,* six had *S. filiforme,* and six had *H. wrightii.* With the exception of one *S. filiforme* site where the water depth was 2.5 m, water depths were all between 0.5 m and 2.0 m.

The experimental treatments were established at seven of the 10 sites in August 1995 and at three additional sites in May 1996. The excavations were intended to: (1) simulate the most severe form of propeller damage where 100% of the seagrass was lost, including the regenerative capacity of the rhizome apical meristems; and (2) examine the effect of perimeter to area ratio and the geometry of the injury shape on recovery. For each species at a site, the treatments consisted of three excavation sizes with different perimeter to area ratios (P/A): (1) 0.25 m^2 (0.5 by 0.5 m; P/A = 8); (2) 1.0 m^2 (1.0 by 1.0 m; P/A = 4); and (3) 2.25 m^2 (1.5 by 1.5 m; P/A = 2.66). In each plot, the sediments were excavated with a shovel and by hand down to a depth of ~10–25 cm, removing all of the seagrass short-shoots, roots, rhizomes, and apical meristems. The sediments were shaken from the plant material and every effort was made to return as much sediment as possible back into the excavation.

Periodically, for 700 days following the initial excavations, we monitored the recovery of sea-

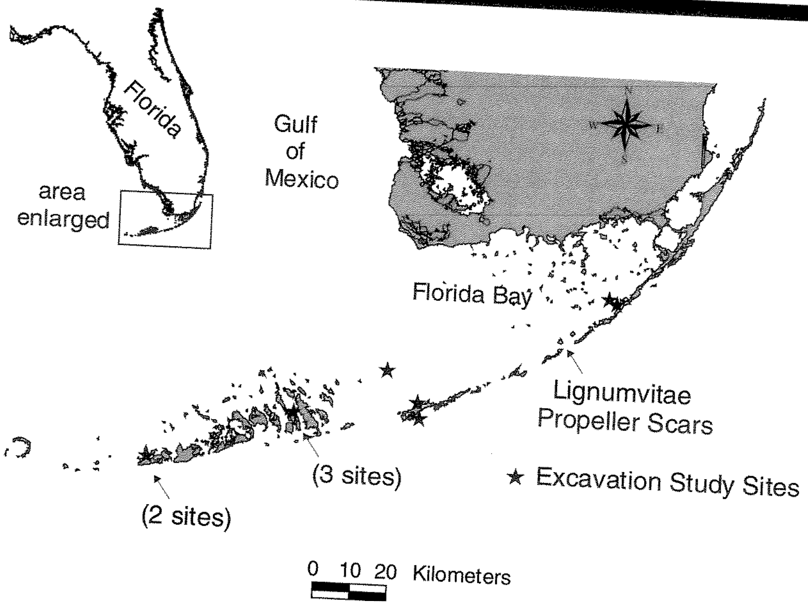

Figure 2. Map of South Florida and the Florida Keys showing the geographic location of the 10 experimental excavation sites (★) and the general location of the 15 propeller scars at the Lignumvitae State Management Area.

grasses in the individual treatments with a nondestructive method. Monitoring events occurred at 158, 190, 250, 340, 442, 502, 624, and 684 days after the initial excavations. To estimate percent cover of seagrasses in each treatment, we positioned a PVC quadrat subdivided into either 100 ($0.25\ m^2$ treatment plots), 400 ($1.0\ m^2$ treatment plots), or 900 ($2.25\ m^2$ treatment plots) 0.05 m by 0.05 m blocks on the sediment surface. The recovery of seagrasses in each plot was measured by counting the number of blocks occupied by seagrass. For each monitoring period, recovery of seagrass was calculated as percent cover by the formula:

$$\%\ \text{cover} = \frac{\text{no. of } 0.0025\ \text{m}^2 \text{ blocks occupied plot}^{-1}}{\text{total number of } 0.0025\ \text{m}^2 \text{ blocks plot}^{-1}} \times 100$$

Prior to examining the relationship between the recovery of each species and the time elapsed as a function of excavation size, we computed linear regressions of percent recovery (dependent variable) as a function of elapsed time (independent variable). We forced the model to pass through zero, under the assumptions that there was no recovery at time zero and that recovery was linear. The slope of the recovery function for each species × excavation size × site combination was treated as a new variable. We tested the residuals of each species slope for normality (SAS PROC UNIVARIATE, SAS™ version 6.12) and calculated F_{max} to test for homogeneity of variances. Where necessary, the data were transformed to meet assumptions of parametric statistics. Either an ANOVA (parametric test) or, when transformation failed to normalize the data, a Kruskal-Wallis procedure (non-parametric test) was used to test for excavation size effects using sites as replicates. After all excavation sizes and sites were grouped within species, an analysis of covariance (ANCOVA) was used to test for differences between the slopes of the regression of percent recovery for each species (dependent variable) as a function of time (independent variable).

Experimental Design: Propeller Scar Recovery

This portion of the study was located in the Lignumvitae State Management Area (LV), which lies within the boundaries of the FKNMS but under the jurisdiction of the Florida Park Service (Figure

2). The Lignumvitae area is typical of the upper and middle Florida Keys environment, consisting of extensive shallow seagrass flats dominated by *T. testudinum* with patchy, sparsely distributed *H. wrightii* interspersed among mangrove islands and deep passes which connect Hawk Channel with Florida Bay. Tides are semi-diurnal with a range of ~0.5 m.

Fifteen propeller scars which formed 1–2 years prior to the study were identified in successive color vertical aerial photographs (1:24,000) and verified by on-site inspection. The scars were located on two shallow banks: (1) the south end of Lignumvitae Key Bank (24°53.2780′N, 80°41.2960′W); and (2) the southwest corner of Shell Key Bank adjacent to Race Channel (24°54.8210′N, 80°41.3632′W). Within each of the 15 scars, we arbitrarily delineated a 10 m long interval and recorded the beginning, mid point, and ending positions of this interval with a Differential Global Positioning System (DGPS, Trimble Pro XL, ≤ 0.5 m accuracy) and permanent PVC stakes. All scars were located in water depths between 0.5 m and 1.0 m.

In April 1998, December 1998 (240 d), and again in November 1999 (570 d), we surveyed each experimental scar by selecting five random locations along the 10 m length of each scar. At each random point within the scar and 1 m outside the scar, we recorded: (1) the number of seagrass short-shoots in a 0.2 m by 0.2 m quadrat placed in the center of the scar; (2) the presence and species composition of macroalgae; (3) the excavation depth at the center of the scar (nearest 0.01 m); and (4) the scar width (nearest 0.01 m). The experimental design created a sample pair (within scar and outside scar) at each randomly selected distance along the 10 m section.

The five point counts of short-shoot density, scar depth, and scar width within each scar were averaged, and a mean short-shoot count for the treatments (within scars) and controls (outside scars) were used to represent each scar in all analyses. To meet unconfirmed assumptions of heteroscedacity, all *T. testudinum* short-shoot counts were transformed $\ln(x + 1)$ (SOKAL and ROHLF, 1969). To predict the time to 100% recovery for *T. testudinum,* mean short-shoot count data from the 15 scars (dependent variable) were regressed on time (independent variable). The model assumed that recovery would be linear throughout the estimated time period.

RESULTS

Seagrass Excavation Experiments

Percent recovery varied as a function of species in all three size categories (Table 1). For *H. wrightii,* the slopes for percent recovery as a function of elapsed time using sites as replicates were nonnormal (neither square-root nor natural log transformations resolved this). Therefore, a Kruskal-Wallis procedure was used to test for the effect of excavation size on percent recovery. There were no significant differences between excavation size ($p = 0.75$). For both *T. testudinum* and *S. filiforme,* the slopes were normal and homogeneous, and excavation size was also not significant (ANOVA, $p = 0.83$ and $p = 0.52$, respectively). For this analysis, we did not include the *S. filiforme* and *H. wrightii* plots, which reached 100% between sampling dates. After determining that excavation size did not significantly affect percent recovery for any of the three species, all excavation sizes within species and sites were grouped together and regressions for the recovery of each of the three species were developed (Figure 3). There was a significant difference between the slopes of the regressions for the individual species (ANCOVA, $p = 0.0001$) (Table 2). The regression models predicted that *S. filiforme* and *H. wrightii* recovery will take < 2.6 years, whereas *T. testudinum* recovery would take 8.5 to 13.5 years, or approximately five times slower than either of the other two species.

There were several *T. testudinum* treatment plots invaded by *H. wrightii* and *S. filiforme,* and several *S. filiforme* plots invaded by *H. wrightii.* Based on the recovery rates measured in these plots where a non-target species invaded, the estimated time to 100% recovery of *H. wrightii* in *S. filiforme* and *T. testudinum* was 10.04 years and 10.58 years, respectively (95% CI = 4.37–19.81 years). The estimated time to recovery of *S. filiforme* in *T. testudinum* was 17.1 years (95% CI = 11.4–34.2).

Propeller Scar Recovery

Thalassia testudinum short-shoot counts inside and outside the 15 scars at the beginning of the monitoring period were 0.17 (SD = 0.22) and 22.10 (SD = 6.41), respectively (Figure 4). Variances were not homogeneous ($F = 0.2$, $df = 14$, $p = 0.002$); therefore, a two-sample t-test was performed on square-root transformed short-shoot

Table 1. *Mean percent cover of each species at each sampling period and in each excavation size. Sample size for each mean computation is given. Not all species were sampled during each sampling period. 100% cover data points were eliminated from the analysis for* S. filiforme *($N = 14$ points) and* H. wrightii *($N = 15$ points).*

		Thalassia		*Syringodium*		*Halodule*	
Elapsed Time	Excavation Size (m²)	Mean ± 1 SD (% Cover)	N	Mean ± 1 SD (% Cover)	N	Mean ± 1 SD (% Cover)	N
158	0.25	1	1	42 ± 28.3	2		
	1	1.7	1	14.7 ± 10.6	2		
	2.25	6.3	1	10.7 ± 10.3	2		
190	0.25			41	1		
	1			32.5	1		
	2.25			25.3	1		
250	0.25	1 ± 1.4	5	59.5 ± 31.8	2	49 ± 24.7	4
	1	2.5 ± 1.5	5	34.1 ± 14.3	2	48.4 ± 31.5	6
	2.25	1.5 ± 1.6	5	53.7 ± 24.2	2	60.7 ± 41.7	6
340	0.25	11	1	7	1		
	1	5.7	1	67.9 ± 43.3	2		
	2.25	18.7	1	77.2 ± 10.5	2		
442	0.25						
	1			99.7	1		
	2.25			96.6	1		
502	0.25	10 ± 8.3	5			86 ± 15.5	2
	1	8.3 ± 8.1	5	90.7	1	44.7 ± 36.8	4
	2.25	6.9 ± 8.5	5			76.5 ± 28.1	3
624	0.25			96	1		
	1			99.2	1		
	2.25						
684	0.25	22.8 ± 14.7	5			2	1
	1	21.5 ± 14.9	5			98.7 ± 1.4	2
	2.25	25.3 ± 18.1	5			99	1

counts. There were significant differences between short-shoot counts inside and outside the propeller scars (t Stat $= -22.58$, df $= 19$, $p < 0.0001$).

To assess the recovery of scars 18 months after the beginning of the monitoring period, we again performed a two-sample t-test on short-shoot counts inside and outside the propeller scars. These data were also log-transformed to meet the assumptions of homogeneity of variance and normality. A two-sample t-test for equal variances was performed on square-root transformed *T. testudinum* short-shoot counts inside the scars and outside in the adjacent undisturbed seagrass beds. The results indicate that *T. testudinum* short-shoot counts outside the scars were significantly greater than counts inside the scars (18.51 versus 4.79; t Stat $= -10.6$, df $= 26$, $p < 0.0001$) (Figure 4).

To avoid concerns that the short-shoot population outside the scars may have declined during the monitoring period and possibly influenced the estimates of recovery, we tested whether or not there were changes between the beginning and the end of the experiment. *Thalassia testudinum* short-shoot counts declined slightly from 22.1 (SD $= 6.4$) $\times\ 0.04\ \text{m}^{-2}$ in April 1998 to 18.51 (SD $=$ 3.9) $\times\ 0.04\ \text{m}^{-2}$ in November 1999. The variances were equal ($F = 2.1$, df $= 14$, $p = 0.09$) and a t-test indicated that there was no significant difference between the initial counts and short-shoot counts at the end of the monitoring period (t Stat $= 1.72$, df $= 27$, $p = 0.0961$). Using the average of these two short-shoot counts (20.7 short-shoots $\times\ 0.04\ \text{m}^{-2}$), the density of *T. testudinum* in the adjacent seagrass beds was ~518 short-shoots m^{-2} throughout the study period.

We regressed *T. testudinum* short-shoot number over time to examine the predicted time to reach the undisturbed *T. testudinum* density of 20.7 short-shoots $\times\ 400\ \text{cm}^{-2}$. This regression was significant (short-shoot count $(0.04\ \text{m}^{-2}) = 0.0082 \times$ days $+\ 0.0040$; 95% CI $= 0.0059 \leq \beta_1 \leq 0.0105$, $r^2 = 0.52$, df $= 1$, $p < 0.0001$) (Figure 5). Assuming a linear model throughout the time period, the estimated time to 100% recovery for the propeller scars was predicted to be at least 6.9 years with a 95% confidence interval of 5.4 to 9.6 years.

Scar depths varied both within a time period and over time (Figure 6). Mean scar depth in-

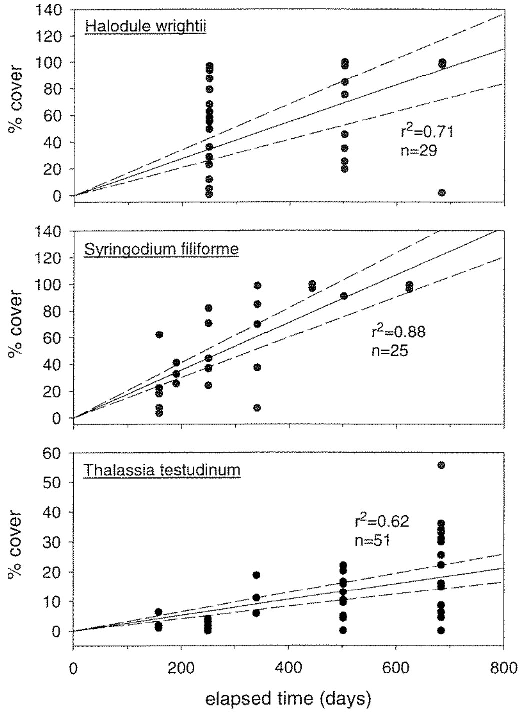

Figure 3. Three panel recovery graph of *Halodule wrightii* (top), *Syringodium filiforme* (middle), and *Thalassia testudinum* (bottom) showing the percent cover as a function of elapsed time in the experimental excavation plots. Dashed lines = 95% confidence interval about the regression line.

creased between April 1998 and December 1998, but decreased slightly in November 1999 (Figure 6). The scar depths averaged $\leq$ 5 cm, while the average scar width was 0.44 m.

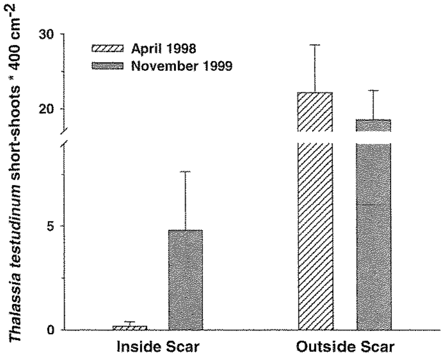

Figure 4. Bar graph of the mean number of *Thalassia testudinum* short-shoots × 400 cm^{-2} (± SD) inside and outside of the 15 propeller scars at the Lignumvitae State Management Area at the start of the survey in April 1998 and 19 months later in November 1999.

DISCUSSION

Recovery in Experimental Excavations

The relative recovery rates of the three seagrass species in our experimental excavations were similar to previous excavation studies reported in Tampa Bay (Durako *et al.,* 1992) and in the Caribbean (Williams, 1990), as well as the results of transplant experiments in the Florida Keys (Fonseca *et al.,* 1987, 1998) and Tampa Bay (Fonseca *et al.,* 1994). Generally, *H. wrightii* and *S. filiforme* recovered at similar rates, and both species recovered faster than *T. testudinum,* conforming to the long-standing paradigm of seagrass succession in tropical communities (den Hartog, 1971; Zieman, 1982; Williams, 1990). In our excavation study in the FKNMS, *H. wrightii* recovered about 5 times faster than predicted for *T. testudinum* (1.9 years vs. 10.5 years, Table 2), but in Tampa Bay the differences between these two species were not nearly as large, ranging between 3.6 to 6.4 years for *T. testudinum* and 0.9 to 4.6 years for *H. wrightii* (Table 1 in Durako *et al.,* 1992). Even though a previous study used fertilizer treatments in an examination of tropical seagrass recovery conducted by Williams (1990), the relative differences in the recovery rates between *S. filiforme* and *T. testudinum* in the Caribbean were still similar to our study in the FKNMS; *S. filiforme*

Table 2. *Regression equations and estimated years to 100% recovery of* Thalassia testudinum, Syringodium filiforme, *and* Halodule wrightii *in experimental excavation plots in the Florida Keys National Marine Sanctuary.*

Species	Time to 100% Recovery $\bar{x}$ (± 95% CI)	Equation	N	r^2	p Value
Thalassia testudinum	10.5 (8.5–13.5)	$y = 0.026x$	54	0.62	0.0001
Syringodium filiforme	1.5 (1.3–1.7)	$y = 0.182x$	27	0.88	0.0001
Halodule wrightii	1.9 (1.6–2.6)	$y = 0.138x$	29	0.71	0.0001

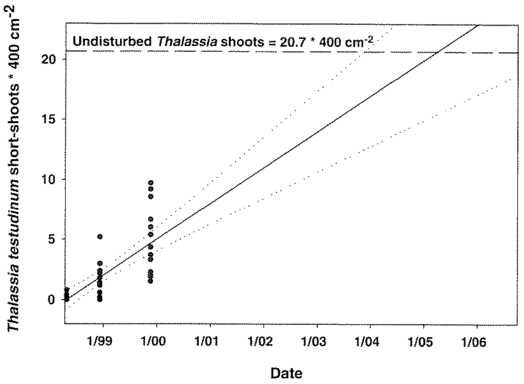

Figure 5. Regression of *Thalassia testudinum* short-shoot density × 400 cm^{-2} (± 95% CI) versus time in the 15 propeller scars at the Lignumvitae State Management Area. Also shown on the horizontal dashed line is the short-shoot density in the adjacent undisturbed seagrass bed and the extrapolation of the regression out to 100% recovery.

recovered to undisturbed control densities 5 times faster than *T. testudinum.*

Previous studies comparing the responses of *T. testudinum, H. wrightii,* and *S. filiforme* to disturbance (WILLIAMS, 1987, 1988, 1990; FOURQUREAN *et al.,* 1995) suggest that recovery rates for these seagrass communities are strongly dependent on the species composition of the disturbed meadows. The pattern of colonization observed in all of these studies and our excavations supports the utilization of recovery models consistent with the succession paradigm (FONSECA *et al.,* 2000) and also indicates that when gaps are formed in climax communities, opportunistic subdominant species can temporarily replace the dominant species (RASHEED, 1999).

The mechanism for recruitment of seagrasses into small gaps formed in seagrass beds is generally thought to be by vegetative propagation from the adjacent beds; however, the relative importance of seed recruitment versus vegetative propagation is still not well understood (WILLIAMS, 1988, 1990; RASHEED, 1999; FONSECA *et al.,* 2000; INGLIS, 2000; KENWORTHY, 2000). Some evidence suggests that seed recruitment may be more important in the recovery of large disturbances (INGLIS, 2000; KENWORTHY, 2000). Even though we did not observe seedling recruitment in our experiments, this does not rule out the possibility that under some conditions seedlings may contribute to recovery (INGLIS, 2000; KENWORTHY, 2000). We should have been able to detect seedlings in the earlier stages of recovery, but this would have become more difficult as the seagrass canopies formed inside the disturbances. If seedling recruitment is important, we may have altered its contribution by physically disturbing the sediment seed bank. Despite this caveat, we still think that our excavations simulated the type of sediment disturbance in propeller scars which would also affect the buried seed bank.

Vegetative propagation includes both rhizome growth from the adjacent undisturbed plots as well as the recruitment of viable vegetative fragments dispersed from surrounding meadows into the gaps (TOMLINSON, 1974; PATRIQUIN, 1975; WILLIAMS, 1988, 1990; RASHEED, 1999). In some plots, we observed a subdominant component of the community colonize a gap nearly as fast as the dominant species. For example, in several of our apparently monotypic *T. testudinum* plots, we observed *H. wrightii* and *S. filiforme* colonizing the excavations at a rate predicted to be within the range of values for *T. testudinum.* This substitution of species also occurred in the experiments in the Caribbean (WILLIAMS, 1990), but eventually *T. testudinum* recovered to become the dominant component of the community. The voluntary recruitment of a faster growing opportunistic species prior to recolonization of the slower growing climax seagrass shows that propeller scar disturbances can result in a patchy mosaic of species diversity on shallow seagrass banks, even though it may only be temporary. These observations also suggest that the restoration of propeller scars may be accelerated by enhancing the growth of the opportunistic species (KENWORTHY *et al.,* 2000).

Comparison of Experimental Excavations With Propeller Scars

In contrast to the linear propeller scars commonly made by motor vessels (Figure 1) (DURAKO *et al.,* 1992; SARGENT *et al.,* 1995; DAWES *et al.,* 1997), our experimental plots were discrete squares. In order to make the recovery rates in the 4-sided excavations comparable to recovery in two-sided propeller scars (DURAKO *et al.,* 1992; DAWES *et al.,* 1997), the measured rates should be halved (slowed by 50%) to eliminate the influence of the two additional recruiting sides. Based on this adjustment, the corrected 2-sided recovery rates, which are comparable to propeller scars, were between 17 to 26 years for *T. testudinum,* 3.2 to 5.2

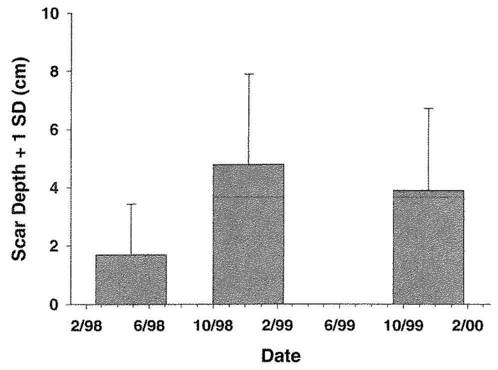

Figure 6. Mean (± SD) propeller scar depths (cm) measured at the 15 propeller scars in the Lignumvitae State Management Area on three different dates.

years for *H. wrightii,* and 2.6 to 3.4 years for *S. filiforme*. All of these recovery periods are longer than previously suggested for these three species recovering in propeller scars in Florida Bay (ZIEMAN, 1976) and Tampa Bay (DURAKO *et al.,* 1992; DAWES *et al.,* 1997). Also, for *T. testudinum,* the adjusted recovery time in the excavation experiments was substantially longer than the estimated recovery time extrapolated from the 15 propeller scars at Lignumvitae (5.4 to 9.6 years) (Figure 5).

The differences between recovery estimates made from our excavations and the other examples may be due to the fact that all of the widths in our excavation experiments (0.5 m, 1.0 m, and 1.5 m) were at least twice as large as the widths of the experimental treatments and propeller scars reported in DURAKO *et al.* (1992) and DAWES *et al.* (1997). In both of these previous studies in Tampa Bay, the scar widths were 0.25 m, while the average width of our treatments was 1.0 m. To directly compare recovery times, we normalized our estimates to an average scar width of 0.25 m. Based on this adjustment, recovery for *T. testudinum, H. wrightii,* and *S. filiforme* in our excavations was 4.25 to 6.75 years, 0.8 to 1.3 years, and 0.65 to 0.85 years, respectively. Using these adjusted times, the apparent differences between our study and the previous work in Tampa Bay diminish. Taking the same approach for the fifteen *T. testudinum* scars at Lignumvitae (average width = 0.44 m) and adjusting our excavation recovery times to this width, the adjusted recovery for *T. testudinum* in the excavations ranges from 8.5 to 13.5 years, or slightly slower than extrapolated from the 15 propeller scars.

Despite a threefold range in excavation widths (0.5 m, 1.0 m, and 1.5 m) and sizes (0.25 m^2, 1.0 m^2, and 2.25 m^2), we did not detect a significant effect of excavation size on the recovery of the three species in our experiments (Table 1). This result was unexpected and difficult to explain. Failure to detect a size effect may be partly due to our experimental design. Rather than attempt to capture the variability within a site, we designed our study to develop a model of recovery rates across the entire Sanctuary. This included a large range of environments and, evidently, a large amount of variation in the response of the seagrasses.

The absence of a size effect may also provide a clue to an important variable affecting seagrass response to mechanical disturbance, especially the recovery of *T. testudinum.* Even though we attempted to replace as much of the sediment we excavated as possible, we were not able to restore the original volume, since we were also removing root and rhizome material and altering the compaction of the sediment. We may have left depressions with margins having steep vertical walls that affected recovery, regardless of the plot size or perimeter to area ratio. Seagrasses, especially *T. testudinum,* are programmed to grow vertically upward rather than downward, according to the branching architecture of their dimorphic rhizomes (TOMLINSON, 1974; DUARTE *et al.,* 1994; MARBA *et al.,* 1994). Vegetative growth of *T. testudinum* is maintained by horizontal rhizome apicals buried in the sediment. These apicals divide and form vertical short-shoots which grow upward at 90° angles from the main horizontal axis, maintaining the leafy shoots above the sediment surface where they are exposed to light and can photosynthesize. This enables seagrasses to form elevated banks with deep rhizome layers, and because of this growth architecture, *T. testudinum* may be limited in its capacity to rapidly propagate across steep topographical gradients where it is necessary to grow downward. With some exceptions (MIKE DURAKO, University of North Carolina at Wilmington, Wilmington, NC, personal communication, 2001), the apical meristems associated with either the vertical or horizontal axes show very little tendency to actively reorient their rhizome apicals to grow downward along steeply graded disturbance margins (WHITFIELD *et al.,* 2002). Occasionally, we have observed *T. testudin-*

um rhizomes oriented or bent downward along the margins of a propeller scar or blowhole, but this is not very common. Usually these rhizomes were associated with eroding margins of scars and blowholes where the vertical walls were collapsing or filling in with sediment and forming margins that were not as steep as the original injury.

In retrospect, we may have created long-lasting depressions in the plots that affected recovery rates. This does not necessarily compromise the use of these data to predict recovery of these seagrasses in propeller scars or similar disturbances, since our excavation technique was very similar to what occurs when a propeller dredges sediment in a seagrass bed. Excavation depth alone could have other effects on recovery. For example, we often observe large accumulations of drift macroalgae and organic matter in deep scars. Once the organic matter is trapped in the scar, the accumulations may cause anoxic conditions and stimulate the production of high concentrations of H_2S at the sediment-water interface. Both of these conditions could inhibit the regrowth of seagrasses into a scar.

Future studies should focus on the effect of excavation depth on *T. testudinum,* given that this species is potentially more vulnerable to deep scars and depressions formed by large vessel groundings. Deep excavations are a common feature on many of the shallow *T. testudinum* banks in the FKNMS (SARGENT *et al.,* 1994; WHITFIELD *et al.,* 2002) and elsewhere throughout the Gulf of Mexico and Caribbean (WILLIAMS, 1988). Susceptibility to excavation depth may be especially important in high energy environments where propeller scars and blowholes formed by vessel groundings can be chronically disturbed by the erosional forces of tides, wind waves, and severe storms (WHITFIELD *et al.,* 2002).

SUMMARY AND CONCLUSIONS

Mechanical sediment disturbances similar to propeller dredging can have long-lasting impacts in tropical seagrass meadows, depending on the species injured. In typical propeller scars commonly formed on shallow carbonate sediments in the FKNMS dominated by *T. testudinum,* full recovery may take as long as 8–10 years. When injured by an excavation, *H. wrightii* and *S. filiforme* both recover at nearly the same rate and significantly faster than *T. testudinum.* Given that we presently equate the ecological services provided by these three species, but their recovery rates are significantly different, the development and refinement of accurate recovery models for injury assessment of propeller scars (FONSECA *et al.,* 2000) should account for: (1) the species composition of the disturbed meadow; (2) the recovery potential of subdominant species which opportunistically colonize gaps formed in other species canopies; and (3) the depth of excavation. In general, models predicting the recovery of seagrasses in disturbances similar to propeller scars in the FKNMS can be formulated from the long-standing paradigm of species succession in tropical seagrass ecosystems.

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