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Regrowth of the seagrass *Thalassia testudinum* into propeller scars

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Abstract

Regrowth of turtle grass, *Thalassia testudinum* Banks *ex* Konig, into existing propeller scars and artificial cuts was studied in a mangal estuary located in Tampa Bay, Florida. Sediments from scars and cuts and adjacent grass beds were not significantly different in relation to particle size distribution and levels of calcium carbonate. Significantly lower concentrations of total organic matter and extractable ammonium but not phosphate were detected in scars. Increases in ammonium levels coincided with the expansion of *T. testudinum* into a propeller scar. Seagrass blade morphology and productivity did not significantly differ in short shoots growing along the edges of scars or cuts relative to those in adjacent seagrass beds. Rhizome architectural studies revealed that apical meristems were few in number (19 to 38% of rhizomes) and randomly orientated in undisturbed grass beds (31 to 53% oriented toward center). In contrast, a greater percentage of apical meristems (78 to 88%) along the edges and in scars or cuts were directed towards the center. Full regrowth required an average of 3.5 to 4.1 years in existing propeller scars and could take up to 7.6 years in artificial cuts. The lack of changes in shoot productivity and limited production of rhizome meristems in *T. testudinum* result in slow regrowth in propeller cuts. The management implication is that turtle grass meadows will show long-term damage from propeller scars if not protected.

Keywords: Rhizome meristem; Seagrass sediment; Extractable ammonium; Blade productivity

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1. Introduction

Declines in seagrass communities can be linked to natural (geological, meteorological, biological) and human-induced (reduction in water clarity, mechanical damage, toxic compounds) disturbances (Short and Wyllie-Echeverria, 1996). Information on declining seagrass beds began with reports of wide-spread reduction of *Zostera marina* L. communities in northern Europe and along the northeastern United States in the 1930's due to the 'wasting disease' (Dexter, 1944; den Hartog, 1987). Reports of seagrass declines include studies in western Australia (Cambridge et al., 1986), in Chesapeake Bay, USA (Orth and Moore, 1983), and more recently, widespread seagrass die backs in Florida Bay (Roblee et al., 1991; Durako, 1994). Natural disturbances to seagrass communities range from volcanic activity (Fortes, 1991), meteorological events such as storms and subsequent high wave energy (Patriquin, 1975; Pulich and White, 1991; van Tussenbroek, 1994), to biological interactions including grazing, competition, bioturbidation and disease (Short and Wyllie-Echeverria, 1996). However, most studies have focused on anthropogenic effects as these can be controlled and are important to management decisions regarding estuaries and coastal habitats.

Localized seagrass die-backs have resulted from oil spills (Zieman and Zieman, 1989; Durako, 1994) and warm-water discharges from the cooling systems of power plants (Thorhaug et al., 1973). Dredging of navigation channels and creation of waterfront property (Zieman and Zieman, 1989; Lewis and Estevez, 1988) and the presence of boat moorings (Walker et al., 1989), all directly affect seagrass beds by removing plant biomass and altering the physical environment. Nutrient enrichment and freshwater run-off, in conjunction with altered substrate surfaces from past dredge and fill operations, have increased light attenuation and decreased the quantity of photosynthetically active radiation (PAR) available to submerged aquatic macrophytes and other aquatic plants (Lewis and Estevez, 1988; Dawes et al., 1995; Tomasko et al., 1996). Reduced PAR can result from increased phytoplankton biomass in the water column, greater epiphyte loads on seagrass blades, and resuspension of sediment. The effect of reduced PAR is decreased productivity (Cambridge et al., 1986; Silberstein et al., 1986; Walker and McComb, 1992; Lapointe et al., 1994) and reduced depth distribution of seagrasses (Cambridge et al., 1986; Dixon and Leverone, 1995). Losses in the Indian River Lagoon (on the east coast of Florida) have reached 100% in some areas (Dawes et al., 1995), with an overall loss of 30% to the entire lagoon (Haddad and Harris, 1985). Extensive loss of seagrass beds has also been reported in Florida Bay (4000 to 23 000 ha; Roblee et al., 1991) and Tampa Bay (ca. 25 000 ha; Lewis and Estevez, 1988). Livingston (1984) reviewed the status of seagrass meadows along the Florida coasts and reported that seagrasses were declining in 7 of the 12 bay systems studied.

In addition to the above stresses placed on seagrass meadows, damage from propeller scars by motor boats has been identified in Florida Bay (Zieman, 1976), the Florida Keys (Matthews et al., 1991), Sarasota Bay (Folit and Morris, 1992) and Tampa Bay (Durako et al., 1992). A recent aerial survey of Florida's coasts indicated that more than 70 000 ha of the 1.1 million ha of seagrass meadows showed some level of scaring (Sargent et al., 1994). In this review, the west coast (Tampa Bay and Charlotte Harbor), the Florida Keys, and Florida's east coast (the northern part of the Indian River Lagoon),

exhibited moderate to severe scarring. Regrowth in propellor scars by *Thalassia testudinum* Banks ex König (turtle grass)is slow with recovery rates estimated to be 2 to 5 years in the Florida Keys (Zieman, 1976) and 3.6 to 6.4 years in Tampa Bay (Durako et al., 1992).

The slow recovery of *Thalassia testudinum* is linked to the highly ordered proliferation of its rhizome (Tomlinson, 1974). The apical rhizome meristem dominates branch proliferation, thus production of short shoots from the rhizome apex is highly regular and is always from a lateral position (Tomlinson and Bailey, 1972). Being a clonal species (Dawes, 1981), production of the leaf-producing short shoots is dependent on a continually active rhizome meristem. If the rhizome is severed, the portion of the genet lacking a rhizome meristem cannot continue to grow until a new apex is generated. Formation of new turtle grass rhizome apices may take as long as 10 months (Kelly et al., 1971), which would partially explain the slow rhizome regrowth and short shoot production in scars. In contrast, proliferation of rhizomes in the seagrass *Halodule wrightii* Ascherson does not require a lengthy period because the short shoot apical meristem can be converted to a rhizome apex (Tomlinson, 1974).

The present study reports recovery rates of *Thalassia testudinum* into boat propeller scars. In an attempt to elucidate the reasons behind the slow recovery rates, three hypotheses were examined. (1) Sediment edaphic factors (particle size, calcium carbonate levels, organic content, and ammonium, phosphate levels) would be altered by the disturbance, and thus would be significantly different than adjacent *T. testudinum* grass beds. In Florida Bay, sediment phosphorous is a controlling factor in the successional sequence between *Halodule wrightii* and *T. testudinum* (Fourqurean et al., 1995) with the latter species having a lower nutrient requirement. Disruption of the sediment may result in distinct physical and nutrient differences that would affect regrowth of turtle grass. (2) Blade production in short shoots (ramets) growing along the edges of scars would be significantly lower than shoots growing in adjacent turtle grass beds. Growth rates of turtle grass blades vary widely according to species and habitat (Dawes, 1981), thus the effect of rhizome damage and subsequent loss of reserve nutrients may reduce the ability to produce new blade tissue (Dawes and Lawrence, 1979). The lower production of blades on damaged genets may negatively affect rhizome expansion. (3) Damage to the rhizome will not result in production of new apical merstems and recovery depends on new apices. Morphological studies suggest that *T. testudinum* rhizomes do not proliferate through production of new apices even when damaged (Tomlinson, 1974).

2. Methods

2.1. Study area

Cockroach Bay (CRB) is a 790 ha mangal estuary located on the southeastern portion of Tampa Bay on the west coast of Florida, USA (27°41′N, 82°30′W). The estuary has been designated a State Aquatic Preserve due to its highly developed mangal and seagrass communities. The estuary is shallow, averaging 0.5 m (MLW) in depth except

for tidal channels and is influenced by seasonal weather patterns. Terrestrial runoff is limited to three sources: a seasonal creek (Cockroach Creek), a canal that drains local farmland (Cockroach Canal), and seepage from shallow water wells. The three Caribbean species of mangroves, *Rhizophora mangle* L., *Avicennia germinans* (L.) Stearn, and *Laguncularia racemosa* Gaertner, form over 30 mangal islands as well as fringing forests throughout the estuary. There are about 164 ha of seagrass beds, consisting mostly of monospecific stands of *Thalassia testudinum* (Dawes and Ehringer, 1995). *Halodule wrightii* (shoal grass) is found in shallower regions and intermixed with *T. testudinum*. Small patches of *Syringodium filiforme* Kützing and *Halophila engelmannii* Ascherson are occasionally found along the fringing mangals that connect with Tampa Bay (Dawes, 1974).

The overall study was initiated in December 1992 and continued through June 1996. Seven sites were selected within CRB; four along the channels connecting the estuary to Tampa Bay and two interior areas. The seventh site was added in 1993 to carry out sediment nutrient studies. All sites contained monospecific beds of *Thalassia testudinum* and had existing propeller scars. An existing scar was haphazardly (without using random number tables) selected for study at each site. Two artificial cuts were created at each of the first six sites in February 1993, by digging 5×0.25 m trenches in seagrass beds, one being parallel and the other perpendicular to local tidal currents.

2.2. Edaphic features

Sediment samples for particle size distribution and calcium carbonate determination were collected from seagrass beds, existing propeller scars and artificial cuts, at sites 3 and 6 every three months between February 1993 and 1995. Five samples were haphazardly collected from each area with a small hand-corer (10 cm deep, 3 cm diameter), transported back to the laboratory in coolers, and air-dried. Samples were dry-sieved to determine the particle size distribution (Ingram, 1971). Calcium carbonate ($CaCO_3$) content was measured by adding 10% HCl to dried subsamples (2.5 g) until all of the $CaCO_3$ was dissolved. Samples were rinsed 5 times with deionized water, dried to a constant mass (2 d at 100°C), and reweighed.

Total organic matter (TOM), pore water content, and nutrient levels (extractable ammonium and phosphate) were measured bimonthly at sites 6 and 7, from April 1994 to July 1995. Sediment cores (10 cm deep, 3 cm diameter) were collected every 20 cm along haphazardly placed 2 m transect lines in existing propeller scars, adjacent grass beds, and adjacent bare areas. Cores were immediately transferred to polyethylene bags, placed on ice for transport to the laboratory, homogenized, and stored at −15°C until analyzed. Pore water content was determined from subsamples (ca. 20–30 g) dried for 24 h at 105°C (Allen et al., 1974). Dried subsamples were then ashed for 4 h at 500°C to determine total organic matter (Dawes, 1981). Ammonium was extracted from subsamples (5 g) with 2 M KCl (Bremner, 1965), and concentrations were measured colorimetrically according to the procedures of Kempers and Zweers (1986). Phosphate was extracted from subsamples (5 g) with 0.5 M Na_2CO_3, and measured with a spectrophotometer (Olsen and Sommers, 1982).

2.3. Seagrass blade features

Additional artificial propeller cuts 2 m in length by 0.25 m wide were made at sites 3 and 6 in February 1994. Blade productivity in short shoots growing within or along the edges of artificial and existing propeller cuts was compared to shoots growing in adjacent *Thalassia testudinum* beds (2 m away). In situ blade productivity was determined by puncturing the base of 20 short shoots with a syringe needle similar to the staple technique of Zieman (1974). Plants were harvested 9 to 14 d later and stored on ice until analyzed. Epiphytes were gently scraped from the blades with a razor blade, dried to a constant mass, and weighed. General blade morphometrics were recorded (i.e. number, length, and width) and the leaf area determined. New and old blade material was separated, dried, and weighed. Productivity was calculated as *shoot production* (weight of new blade material divided by number of days growth = percent d^{-1}) and *leaf turnover* (weight of new blade divided by weight of old and new blade, divided by number of days growth = mg dwt $shoot^{-1} day^{-1}$).

2.4. Rhizome architecture

The subterranean rhizome organization of *Thalassia testudinum* was studied in two ways. Cores (0.0184 m^2; $n = 3$) were taken haphazardly from seagrass beds in June, September and December 1994 in sites 3 and 6. Additional pairs of cores were taken in October 1994 from beds fringing the edge of existing scars and within adjacent seagrass beds ($n = 8$ each) in site 3. After gently removing the sediment, the number of apical meristems, mean total length and mass of the rhizome segments were measured.

The regrowth of *Thalassia testudinum* rhizomes into scars was also examined in two existing scars and one artificial 29 month old cut. A 1 m × 25 cm section of each scar was studied. For comparison, three 1.0×0.25 m^2 strip quadrats were haphazardly placed within adjacent *T. testudinum* beds and also studied. The rhizomes in each section were exposed intact in their original positions by gently removing the sediment with an underwater suction device. Once uncovered, the orientation and length, presence of an apical meristem, and number of short shoots for each rhizome was determined. The rhizome architecture of the intact seagrass beds was so dense and tangled that only the number of short shoots, apical meristems and orientation of the apicals could be determined.

2.5. Predicted recovery in scars

Recovery of *Thalassia testudinum* was monitored in existing scars and artificial cuts throughout the 7 sites in Cockroach Bay. Existing scars were haphazardly selected in 4 sites and 5×1.25 m^2 quadrats were staked out using PVC pipe with the scar running though the center. A strip quadrat, divided into 5 rows of 25 cm^2 quadrats (exterior, interior, central rows) was placed over the stakes every two months. The short shoot densities were counted in randomly (use of random numbers table) chosen 25 cm^2 quadrats ($n = 5$) in the exterior, interior and central (scar) rows. Counts were begun in June 1993 and continued bimonthly through October 1994. In addition, 1.0×0.25 m^2 strip quadrats were established in 17 existing scars and artificial cuts and short shoot densities counted quarterly in the entire strip for the same period.

2.6. Data analysis

All data were tested for normality and homogeneity of variance, and transformed if necessary to satisfy the assumptions of nonparametric statistics. Analyses of variance (ANOVA) were conducted to test for significant differences between the sampling areas for particle size, organic content, pore water content, calcium carbonate levels, extractable ammonium and phosphate, blade growth and blade area. Multiple comparisons were made using Dunn's and the Student–Newman–Keuls methods.

3. Results

3.1. Abiotic data

From September 1992 through June 1996, the lowest and highest water temperature and salinities observed were 17°C (November 1992, December 1993) and 33°C (August 1994, June 1995), and 17 ppt (September 1994, July 1995) and 34 ppt (April 1995) respectively (Fig. 1). Salinities in August through October 1994 and in July 1995 were lower than measured in the previous two years (1992: 27 to 30 ppt; 1993: 31 to 33 ppt) reflecting an increase in rain in the summers of 1994 and 1995.

Sediment particle size did not exhibit any significant patterns in three February samplings (1993, '94, '95) between the reference bed, existing scars, and artificial cuts parallel and perpendicular to tidal currents within sites 3 and 6 in CRB (Fig. 2). The largest variation between the sampling areas was in the amount of granules or coarse material. The primary size class for all areas sampled in sites 3 and 6 was sand with low levels of silts and clays.

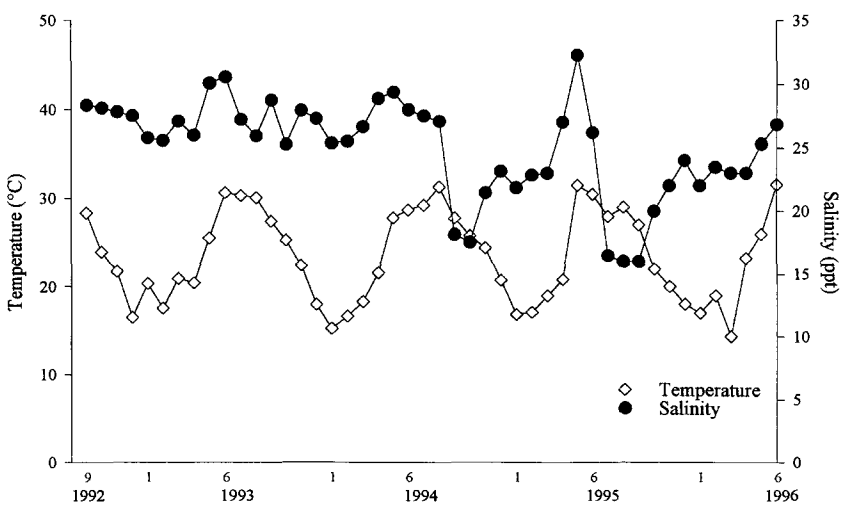

Fig. 1. Mean temperatures and salinities for Cockroach Bay, Florida between September 1992 and June 1996.

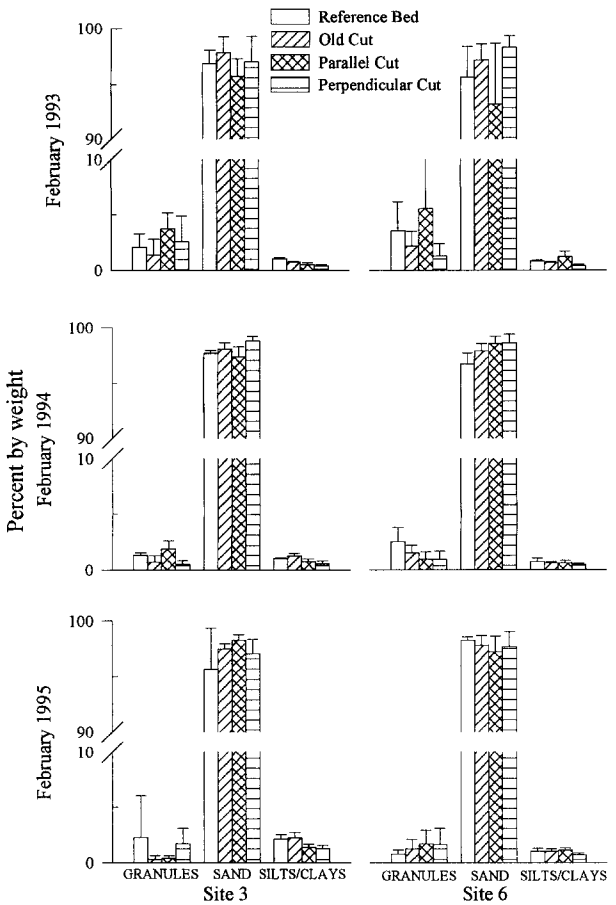

Fig. 2. Sediment particle size (±1 S.D.) distribution for sites 3 and 6 at Cockroach Bay, Florida in February 1993, 94, 95. Samplings were taken in a nearby seagrass bed (Reference Bed), an existing propeller scar (Old Cut), and artificial cuts made in February 1993 parallel (Parallel Cut) and at right angles (Perpendicular Cut) to the tidal currents.

Organic content was significantly higher ($P < 0.05$) in seagrass beds when compared with either bare sediment or scars in site 6 but not in site 7 (Fig. 3). There was a non-significant increase in organic content in the scar at site 7 over time suggesting modification of the sediments.

Sediment pore water content for bare areas and propeller scars were not significantly different in sites 6 and 7 but were significantly lower ($P < 0.05$) compared with the seagrass beds for the 12 months from April 1994 to 1995 (Fig. 3).

Ammonium levels showed a possible seasonal peak in sites 6 and 7 in April (Fig. 4) and increased in the scar at site 7, coinciding with the regrowth of *Thalassia testudinum* into the scar. Ammonium and phosphate levels were lowest in bare areas in both sites (Fig. 4).

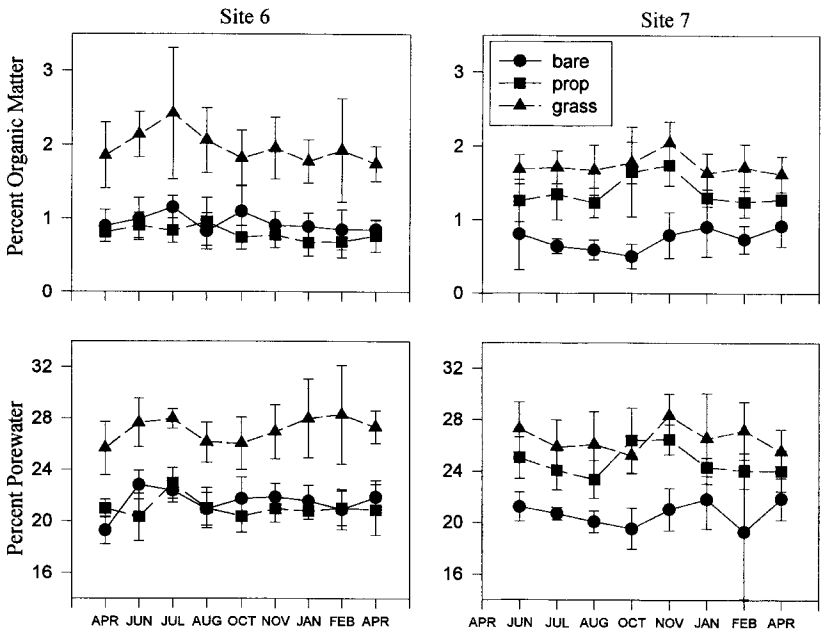

Fig. 3. Percent organic matter and pore water (±1 S.D.) in the sediment of a nearby seagrass bed (Grass), an existing propeller scar (Prop) and an unvegetated area (Bare) in Cockroach Bay, Florida. Samples were taken between April 1994 and 1995.

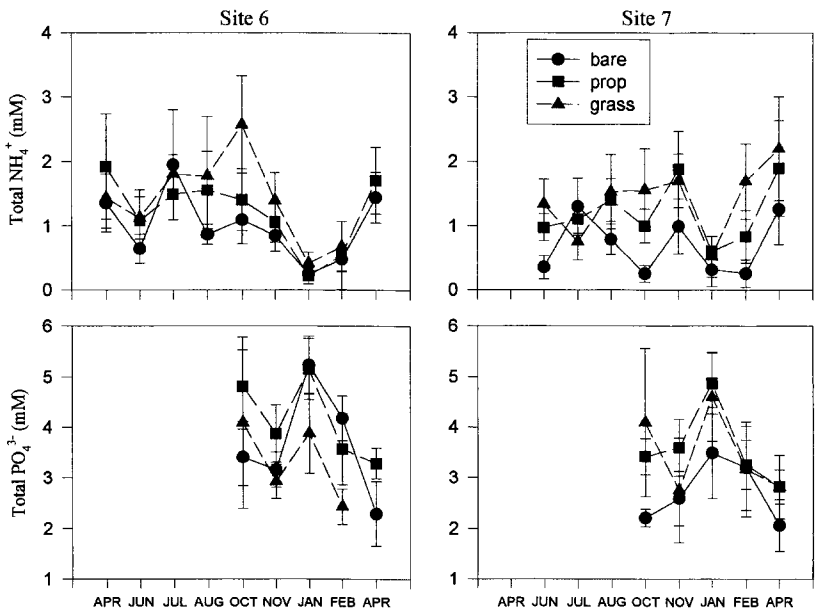

Fig. 4. Total extractable NH_4^+ and PO_4^{3-} (±1 S.D.) from sediment samples at sites 6 and 7, Cockroach Bay Florida between April 1994 and 1995.

Table 1
Leaf area (cm^2) of *Thalassia testudinum* sampled from within and along the edges of boat propeller cuts (prop cut), and within adjacent *T. testudinum* grassbeds (seagrass) from 2 sites in Cockroach Bay. Values are means ± S.D. Superscripts denote significant differences between sampling areas, within each site ($P < 0.05$; Student's t-test and Mann Whitney Rank Sum Test)

Date	Leaf area (cm^2)			
	Site 3		Site 6	
	Seagrass	Prop cut	Seagrass	Prop cut
March 94	25.8 ± 8.6	22.9 ± 3.8	25.3 ± 6.4	22.7 ± 5.2
May 94	46.2 ± 20.1	42.8 ± 11.7	62.6 ± 15.5	56.5 ± 24.2
August 94	25.8 ± 11.0	28.1 ± 10.7	25.6 ± 7.5	25.4 ± 13.0
October 94	27.4 ± 11.1	25.7 ± 11.0	26.9 ± 8.2[a]	19.1 ± 11.1[b]
December 94	17.5 ± 3.6	20.0 ± 7.9	18.9 ± 5.1	16.2 ± 5.0
February 95	16.5 ± 6.9	18.4 ± 7.2	12.8 ± 5.4	14.0 ± 5.2
May 95	41.6 ± 15.9	50.6 ± 20.9	48.6 ± 20.3	50.5 ± 22.3
October 95	30.3 ± 12.8	27.4 ± 10.5	15.5 ± 4.6	14.7 ± 5.4

3.2. Blade dynamics

Although there were some significant differences, no consistent patterns were evident in blade areas (Table 1), epiphyte load (Table 2), and blade productivity (Fig. 5) collected from a propeller scar and an adjacent *Thalassia testudinum* bed at sites 3 and 6. The data for the other sites studied (1, 2, 4, 5) are not shown and were similar to sites 3 and 6 in all respects. Leaf areas were significantly higher ($P < 0.05$) in May, averaging between 42.8 to 62.6 cm^2 (1994) and 41.6 to 50.6 cm^2 (1995). Epiphyte load was high in March and December 1994, and again in February 1995, while it was low in May through October in both years at site 3. Thus, the epiphyte load of blades at site 3

Table 2
Epiphyte load (g dry weight) on short shoots of *Thalassia testudinum* sampled from within and along the edges of boat propeller cuts (prop cut), and within adjacent *T. testudinum* grassbeds (seagrass) from 2 sites in Cockroach Bay. Values are means ± S.D. Superscripts denote significant differences between sampling areas, within each site ($P < 0.05$; Student's t-test and Mann Whitney Rank Sum Test)

Date	Epiphyte load (g dry weight)			
	Site 3		Site 6	
	Seagrass	Prop cut	Seagrass	Prop cut
March 94	0.3 ± 0.2	0.5 ± 0.3	0.2 ± 0.1	0.2 ± 0.2
May 94	0.1 ± 0.1[a]	0.1 ± 0.0[b]	0.1 ± 0.1	0.1 ± 0.1
August 94	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1[a]	0.0 ± 0.1[b]
October 94	0.1 ± 0.0	0.1 ± 0.1	0.2 ± 0.1	0.2 ± 0.1
December 94	0.2 ± 0.2	0.2 ± 0.2	0.1 ± 0.0[a]	0.1 ± 0.1[b]
February 95	0.7 ± 0.5	0.3 ± 0.2	0.1 ± 0.3	0.1 ± 0.1
May 95	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.1
October 95	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

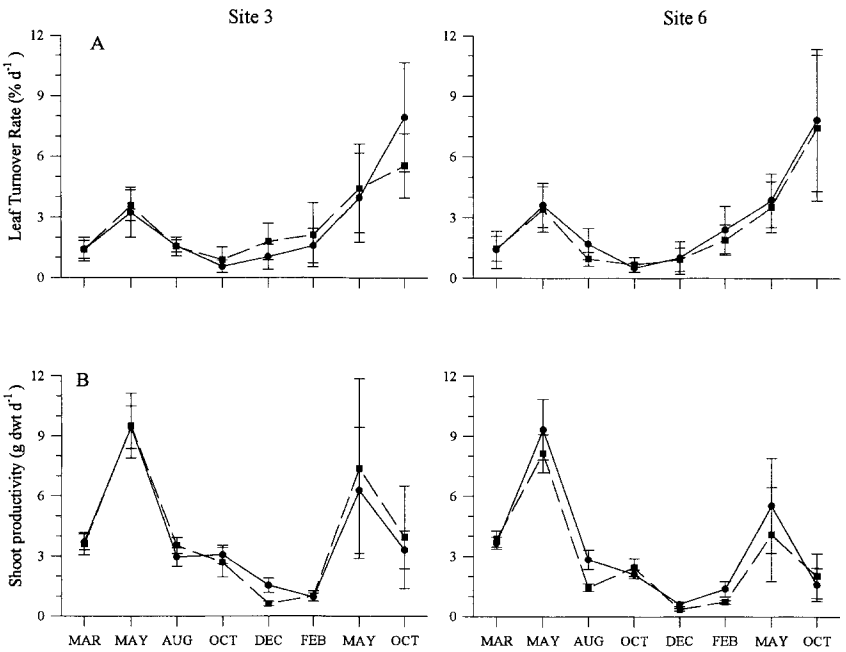

Fig. 5. Leaf productivity (±1 S.D.) of *Thalassia testudinum* at sites 3 and 6 in Cockroach Bay, Florida between March 1994 and October 1995. Leaf turnover rates are the new leaf d^{-1}, while shoot productivity is the new leaf total leaf biomass$^{-1}d^{-1}$. Circles: plants in propeller scar; squares: plants in reference grass bed.

showed an inverse relationship with macroalgal biomass and water clarity (not shown). A seasonal pattern was not evident at site 6 as epiphyte biomass was low throughout both years although blades collected in October and March of 1994 did have higher concentrations.

Shoots collected within and along scars at sites 3 and 6 showed no significant reduction in leaf turnover when compared with plants in reference grass beds (Fig. 5). Shoot productivity (blade production) of plants growing along scars was significantly lower than for plants in reference beds only in August and December 1994 in site 6 ($P < 0.002$, $P < 0.02$) and in October 1995 for site 3 ($P < 0.02$).

3.3. Rhizome architecture

Rhizomes of *Thalassia testudinum* growing at the edge of a scar showed large variations in number of apices and rhizomes and in biomass between sites 3 and 6 in CRB and between sampling dates using 15.1 cm diameter cores (Table 3). The number of apical meristems averaged between 0 and 7.0 core^{-1}. The total length of live rhizome segments averaged 50.2 to 83.0 cm core^{-1}. Total dry weight of below ground biomass ranged from 2.0 to 2.4 and above ground biomass from 2.0 to 3.3 g dwt core^{-1}. Short shoot density ranged from 4.7 to 13 core^{-1}.

Table 3
Rhizome and short shoot growth morphology in *Thalassia testudinum* collected in 0.0184 m^2 cores from 2 sites in Cockroach Bay, 1994. Values are means ± S.D.; $n = 2$ (September); 3 (June and December); 8 (October). [a] = data not collected

Date	Location	Rhizomes			Short shoots	
		Apices (No.)	Total length (cm)	Mass (g)	No.	Mass (g)
June	site 3	1.0 ± 1.7	63.4 ± 18.8	2.4 ± 0.9	7.0 ± 2.0	3.3 ± 0.6
	site 6	1.0 ± 1.0	63.8 ± 38.5	2.0 ± 0.9	8.0 ± 5.3	2.7 ± 0.8
September	site 3	[a]	[a]	[a]	[a]	[a]
	site 6	1.7 ± 1.2	83.0 ± 12.2	2.1 ± 0.9	13.0 ± 6.0	3.1 ± 0.8
December	site 3	0	50.2 ± 28.0	[a]	4.7 ± 2.3	2.0 ± 0.8
	site 6	7.0 ± 4.6	54.4 ± 9.4	1.7 ± 0.4	10.0 ± 0.6	2.8 ± 0.3
October	grassbed	2.3 ± 1.7	63.2 ± 19.4	[a]	8.4 ± 2.9	[a]
	prop cut	1.1 ± 1.1	60.6 ± 17.1	[a]	8.0 ± 3.2	[a]

There were no significant differences between *Thalassia testudinum* occurring along a scar and in an adjacent undisturbed seagrass bed with regard to the number of rhizome apices ($P < 0.14$), total rhizome length ($P < 0.88$), or number of short shoots ($P < 0.81$) (October 1994; Table 3). The number of rhizome apices in the undisturbed bed and the propeller scar were also not significantly different.

In situ examination after sediment removal showed a significantly higher ($P < 0.05$) number of short shoots and apical meristems of *Thalassia testudinum* rhizomes in three undisturbed seagrass beds (samples 1, 2, 3) when compared with two existing propeller scars (cuts A, B) and one artificial cut (cut C; Table 4). The number of rhizome apices pointing toward the center of the seagrass bed were significantly lower than the number pointing toward the center of the propeller cut in samples A and B. In contrast, there

Table 4
Summary of the below-ground characteristics of three beds of *Thalassia testudinum* and three propeller cuts through other beds. Each sampling was conducted using a 100 cm × 25 cm^2 strip quadrat that was haphazardly placed within different seagrass beds (units 1, 2, 3) and over existing (cuts A, B) or artificial (cut C, 29 months old) propeller cuts. After suctioning of the covering sediment, the short shoot number, the number and percent (%) having apical meristems, and the number and percent (%) of the apical meristems pointing into the center of the quadrats were determined

	Short shoots	Apices		Apices pointing toward center	
	(No.)	(No.)	(%)	(No.)	(%)
Propeller cuts					
A	27	8	30	7	88
B	29	9	31	7	78
C	25	11	44	4	36
Seagrass bed units					
1	88	33	38	14	42
2	84	16	19	5	31
3	90	19	21	10	53

Table 5
Regression equations for mean changes in short shoot densities of *Thalassia testudinum* sampled from large permanent strip quadrats (5×1.25 m^2) with a 25 cm^2 quadrat. Random samples were taken 25 cm from the propeller cut (exterior), adjacent to the cut (interior), and directly inside the cut (prop cut)

Site	Quadrats sampled	Linear regression equations for changes in short shoot densities (October 1993–October 1994)
3	exterior	Short shoot density = 10.42 + (0.2450 × Months)
	interior	Short shoot density = 8.099 + (0.3604 × Months)
	prop cut	Short shoot density = 4.073 + (0.3371 × Months)
4	exterior	Short shoot density = 6.021 + (0.2751 × Months)
	interior	Short shoot density = 6.903 + (0.1496 × Months)
	prop cut	Short shoot density = 3.392 + (0.1909 × Months)
5	exterior	Short shoot density = 11.09 − (0.1231 × Months)
	interior	Short shoot density = 9.495 − (0.1010 × Months)
	prop cut	Short shoot density = 2.833 + (0.2206 × Months)
6	exterior	Short shoot density = 18.28 − (0.2888 × Months)
	interior	Short shoot density = 19.47 − (0.3848 × Months)
	prop cut	Short shoot density = 6.538 + (0.1181 × Months)

was no pattern of rhizome orientation in the artificial cut C (Table 4). The artificial cut (cut C, Table 4) was created in a seagrass bed 29 months before sampling while the scars in A and B were existing and thus, their age is unknown.

3.4. Predicted recovery

Short shoot densities of exterior and interior rows in the 5×1.25 m^2 strip quadrats positioned over 4 scars were highest in the summer and lowest in the winter and were not significantly different ($P > 0.05$). As expected, the short shoot density in both the exterior and interior rows showed significantly higher densities ($P < 0.01$) than in the scars (Table 5). The grand mean of short shoot densities in the exterior and interior 25

Table 6
Total changes in short shoot densities of *Thalassia testudinum* in 1×0.25 m^2 strip quadrats in existing and artificial propeller cuts at 6 sites in Cockroach Bay. Total change in short shoot densities and linear regression models are calculated for October 1993 to October 1994

Site	Existing propeller cuts		Artificial propeller cuts	
	Total change	Linear regression equations	Total change	Linear regression equations
1	–	–	+11	No. SS = 24.93 + (1.14 × Time)
2	+6	No. SS = 14.71 + (0.54 × Time)	−1	No. SS = 10.07 − (0.04 × Time)
3	–	–	+3	No. SS = 30.14 + (0.28 × Time)
4	+7	No. SS = 6.86 + (0.62 × Time)	–	–
5	+7	No. SS = 0.64 + (0.73 × Time)	–	–
6	−9	No. SS = 21.14 − (0.57 × Time)	+2	No. SS = 10.07 + (0.26 × Time)

cm^2 rows of the 5×1.25 m^2 strip quadrats were compared with those obtained from short shoot densities in the propeller cuts (Table 5). Using regression analyses, the total recovery was calculated to be 1.7 (site 3) to 7.3 yr (site 6) with a mean of 3.5 yr based on short shoot densities in the adjacent seagrass beds.

The grand mean of short shoot densities in the exterior and interior quadrats at sites 3 and 4 showed an increase over the 12 month study while the opposite was true for sites 5 and 6. The decline in short shoot density at sites 5 and 6 may reflect the drop in salinities (< 18 ppt; Fig. 1) during August and September 1995. Sites 3 and 4 were near channels connecting with Tampa Bay while the other two sites were in the interior of CRB, the area of lowest salinities.

Recovery rates were also determined using 1×0.25 m^2 strip quadrats laid directly over 10 propeller scars and 7 artificial cuts (Table 6). Recovery rates in scars ranged from 2.3 to 8.5 yr with a mean recovery period of 4.3 yr. Rates of regrowth in artificial cuts ranged from 2.3 to 10 yr with a mean of 7.6 yr.

4. Discussion

Reports of seagrass decline worldwide are increasing with losses of over 90 000 ha documented and the actual level probably being much higher (Short and Wyllie-Echeverria, 1996). Although natural events can be responsible for large and small scale damage to seagrass habitats, human affairs now account for a majority of seagrass losses. The most common anthropogenic factor in the continuing decline of seagrass habitats is pollution that results in nutrient loading and a subsequent reduction in water quality (Short et al., 1996). However, mechanical damage through dredge-fill operations will directly (burial) and indirectly (increased turbidity) remove entire communities as seen in Tampa Bay (Lewis et al., 1985). Increased fishing pressure in coastal habitats has resulted in direct propeller damage to shallow water seagrass communities, but this has been poorly documented. The basis of the slow recovery of seagrasses from this form of mechanical damage is also poorly understood. Without restrictions on use of power craft in shallow waters, propeller damage will probably replace the historical losses of seagrass beds by dredge-fill in the near future.

The present study considered recovery rates of *Thalassia testudinum* in terms of its growth habit as well as influences of abiotic factors. The extensive seagrass meadows in Cockroach Bay are occasionally stressed as shown by the ranges in salinity and temperature. Stressful periods occur when water temperatures drop below 15°C in the winter or salinities are depressed due to increased rainfall in the summer. The temperature and salinity stresses can cause blade die-back as described by Phillips (1960) for Tampa Bay. The effect of depressed salinities was seen in this study as well (Table 5). These stresses must influence the growth of *T. testudinum* into propeller cuts and be a partial cause of the wide ranges in rates of recovery (1.7 to 10 yr) from propeller damage.

The first and second hypotheses dealing with edaphic factors and shoot productivity were not supported by the data. Although the grass beds did appear to contain a higher level of smaller sized particles, there were no significant differences when compared

with existing propeller scars and artificial cuts. Scars and bare areas did have slightly lower levels of TOM, percent pore water, and total ammonium than the seagrass beds. These differences were small and the levels fluctuated. Based on this study, it is unlikely that the variations in edaphic factors account for the slow recovery of turtle grass in propeller scars. It does appear that turtle grass meadows in Tampa Bay control the shift in organics and ammonia without colonization by green siphonaceous macroalgae such as that reported by Williams (1990) in the Virgin Islands.

Leaf turnover and short shoot production showed a strong single growth peak in the spring (see Fig. 5B) unlike the bimodal growth reported for *Thalassia testudinum* in Indian River on the east coast of Florida (Dawes et al., 1995). Further, there was no pattern in blade growth between short shoots occurring at the edge and in a propeller cut and plants within adjacent seagrass meadows. These results support the earlier studies demonstrating the advantage of physiological integration of a clonal plant such as *Thalassia testudinum* (Tomasko and Dawes, 1989a,b). The short shoots of damaged turtle grass rhizomes are supported by other ramets within the adjacent bed.

The importance of the rhizome in recovery of turtle grass is demonstrated and the third hypothesis is supported. Because rhizome growth is dependent on the apical meristem (Tomlinson, 1974), damage to the below ground portion of *Thalassia testudinum* would require development of new meristems. In this study, rhizomes damaged by propellers had fewer apical meristems than those in undisturbed seagrass beds. The number of apical meristems oriented toward the center of an older scar suggest that there may be some directional growth into the damaged area, but the present data is limited.

The production of seagrass cultivars for transplantation has not been successful in contrast to nurseries for mangrove and salt marsh plants. Restoration efforts require damaging other natural beds to obtain donors and so a need exists for seagrass nurseries if seagrass beds are to be created or enhanced. Further, *Thalassia testudinum* is a late stage species showing poor survivorship unless two or more ramets are present on the rhizome (Tomasko et al., 1991). In the field, it is not uncommon to find a turtle grass rhizome apex that has developed from a short shoot meristem, perhaps due to wounding of the ramet. In this study we found that rhizome meristems were not induced after damage, thus regrowth must depend on existing apical meristems, the only ones being those of the short shoots. Thus, induction of rhizome meristematic activity in *T. testudinum*, a common practice in horticulture, may be possible via stimulation of short shoot apices. For example, earlier studies reported success in the use of nutrients and growth regulators for induction of growth in turtle grass (Kelly et al., 1971; van Breedveld, 1975). However, these reports did not include statistical analyses, did not examine the rhizome, or have proper controls.

Recovery of *Thalassia testudinum* in propeller scars in Cockroach Bay is similar to, or slower (existing: 3.5 and 4.3 yr; artificial: 7.6 yr) than estimates for the Florida Keys (Zieman, 1976; 2 to 5 yr) and Weedon Island in Tampa Bay (Durako et al., 1992; 6.4 yr). The slow recovery must be related to production of new apical meristems on damaged rhizomes and the level of stress in the estuary. If the seagrass is already under stress from abiotic conditions, production and growth of new rhizome meristems may be further slowed. Thus, propeller damage can have a long lasting effect in the turtle grass meadows so that shallow seagrass beds need protection if they are to recover.

Propeller scarring is severely damaging shallower seagrass beds worldwide, as seen in Florida (Sargent et al., 1994), but losses can be controlled. Aerial mapping of the seagrass beds in Cockroach Bay (Dawes and Ehringer, 1995) found 163.7 ha of seagrass meadows with 11 783 m of propeller scars between December 1992 and January 1995. Of the total, 8120 m were found in December 1992, before motor boat traffic was restricted in March 1993 in the Preserve. By January 1995 only 2105 m of new scars were found and no new ones have been found through July 1996 (Ehringer, personal communication). Thus, boat restrictions and a ban on commercial net fishing that began July 1995 stopped propeller scaring. The slow response by *Thalassia testudinum* suggests that motor boat restrictions will continue to be needed to prevent long term losses and allow sufficient time for recovery.

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