

Development of planted seagrass beds in Tampa Bay, Florida, USA.

I. Plant components

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ABSTRACT: In this study we evaluated the floral attributes of planted seagrass beds as they developed over time. The seagrasses *Halodule wrightii* and *Syringodium filiforme* were planted on 0.5 m centers at several sites within Tampa Bay, Florida, USA. Planting unit (PU) survival, change in areal shoot density, plant morphometrics and associated macroalgae were monitored over a 3 yr period. These parameters were compared with nearby, natural beds as a reference. Comparisons were not limited to the same species, but included *Thalassia testudinum* in order to address management issues regarding the substitution of one habitat type for another. Despite use of experienced personnel, in some plantings, an average 47 % loss of PU was sustained, apparently due to seasonal bioturbation. Depending on the spatial distribution of loss, persistent cover at equivalent densities was still attained within 1.8 yr (for plantings on 0.5 m centers) over portions of some planted sites. Seagrass recovery rate and recommended monitoring times have a positive, linear relationship to spacing of plantings. Although moderately variable, areal shoot density clearly defined trends in bed development over time. Many plantings exhibited little spread in the first year after planting, and then expanded rapidly in the second year. Seagrass surface area, length or biomass, as well as macroalgal biomass, proved to be weak indicators of system development for most seagrass species. Although substantial PU losses were experienced, the subsequent survival, spread and persistence of seagrasses indicate that large areas of Tampa Bay, which historically had supported seagrass, are now suitable for restoration. For remaining seagrass habitat however, conservation provides a more certain basis for maintaining the resource than attempting to mitigate through planting.

KEY WORDS: Seagrass · Restoration · Macroalgae · Mitigation · Density · Biomass

INTRODUCTION

The study of seagrass planting for purposes of restoration and mitigation may best be described as a series of disjunct experiments (Zieman & Zieman 1989). Phillips (1976) and later Backman (1984) began using planting methods as a means of examining phenological characteristics of *Zostera marina*, but for the most part attention has been given to technique development (Addy 1947, Churchill et al. 1978, Fonseca et al. 1982, 1985) in response to the need to

restore losses of the past and mitigate ongoing losses (definitions based on Lewis 1989). Few studies of planted seagrass beds collected quantitative floral data for comparison with reference beds (reviews by Fonseca et al. 1988, 1992, Fonseca 1989, Thom 1990). This lack of comparative data has inhibited development of criteria for defining successful seagrass mitigation.

In this study, we investigated whether planted seagrass beds provided habitat functions similar to those of the natural meadows. We attempted to evaluate the rate of floristic development in planted beds of *Halodule wrightii*, *Syringodium filiforme* and mix-

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tures of these 2 species relative to naturally occurring beds. We extended the natural bed comparison to *Thalassia testudinum* to determine under what conditions one might consider substituting one of the faster-spreading seagrass species (above) for this relatively slow-spreading species (Fonseca et al. 1987) during mitigation.

Our goal was to use these data to determine which aspects of the seagrass itself would be the most useful in assessing planting projects (Fonseca 1989, 1992, 1994) while exploring the dynamics of seagrass beds in Tampa Bay, Florida, USA. We measured several attributes of seagrass beds commonly reported on in the literature (e.g. density, biomass, surface area, associated macroalgal biomass) and compared them to natural seagrass beds over time. The ability of these attributes to represent changes in planted beds over time (as compared to baseline, natural beds) across a wide variety of sites was used to assess their usefulness in evaluating seagrass planting projects.

METHODS

Experimental design. Five 9.5 × 19.5 m experimental *Halodule wrightii* plots (800 planting units composed of 15 to 25 shoots each and attached to metal staples planted on 0.5 m centers) were established at 5 different locations in Tampa Bay in July 1987 (Fig. 1). In May 1988, 3 additional plots of *H. wrightii* and *Syringodium filiforme* planted on alternating rows of each species, and 3 plots of *S. filiforme*, were added to 2 existing sites and 1 new site for a total of 6 sites (Table 1, Fig. 1). Replanting was required within 3 mo at 3 sites, only 1 of which survived to be sampled throughout the study (Table 2). Because some relic seagrass could still be found at replanting, the initiation time for all planted beds was recorded as the first, not subsequent, replanting time. This made for a conservative estimate of transplant development in the 1 surviving bed.

Seagrass (and faunal) sampling was conducted 3 times yr⁻¹ (May, August, November) for the first 2 yr of the study, after which no further August samples were taken (Table 1) in order to extend the overall sampling time within funding constraints. Sampling of the seagrass community was performed together with macroepibenthic faunal sampling for the entire 3 yr study (see companion paper; Fonseca et al. 1996, this issue).

Table 1. Sampling effort by sampling time and treatment. Each number represents the number of replicate dropnet samples. BA: bare area, HT: *Halodule wrightii* transplant; ST: *Syringodium filiforme* transplant; HS: mixed bed transplant; SF: natural *S. filiforme*; HW: natural *H. wrightii*; TT: natural *Thalassia testudinum*; RM: *Ruppia maritima*; CP: *Caulerpa prolifera*. Number of replicate sites for each time × treatment combination may be computed by dividing the number of dropnets by 3

Treatment	Sampling time								Total
	Aug 87	Nov 87	May 88	Aug 88	Nov 88	May 89	Nov 89	May 90	
BA	15	15	15	9	9	9	9	9	90
HT	15	15	15	15	15	15	15	15	120
ST				9	6	6	3	3	27
HS				9	6	6	3	3	27
SF	9	9	9	9	9	9	9	9	72
HW	6	6	6	6	6	6	6	6	48
TT	12	12	12	9	9	9	9	9	81
Total	57	57	57	66	60	60	54	54	465

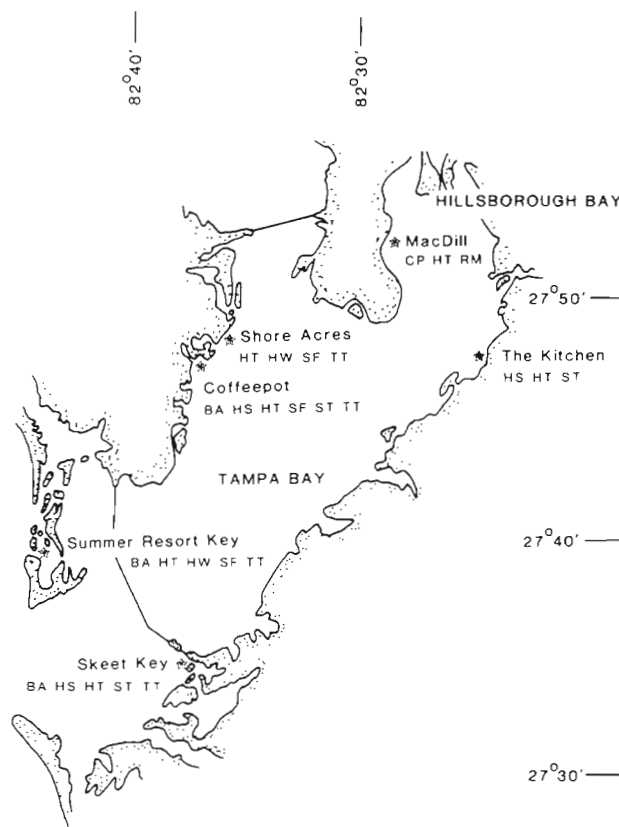


Fig. 1 Map of 1988–1989 planted and reference bed sites in Tampa Bay, Florida, USA. Treatments: BA: bare (unvegetated); CP: *Caulerpa prolifera*; HW: *Halodule wrightii* natural bed; HT: *Halodule wrightii* transplant; SF: *Syringodium filiforme* natural bed; ST: *Syringodium filiforme* transplant; TT: *Thalassia testudinum* natural bed; HS: mixed *H. wrightii*/*S. filiforme* transplant

A site was loosely defined as a collection of 9.5×19.5 m plots composed of different seagrass species (treatments), either natural or planted, within ~ 300 m of one another. Sites were separated by a minimum of 3 km but no sites were found which could contain all natural seagrass bed comparison treatments (Fig. 1). Therefore we resolved to sample along the north-south axis of the Bay, using sites as replicates and excluding within-site comparisons. Some sites (Skeet Key, Coffeepot Bayou, and Shore Acres) appeared to be on areas that may have experienced dredged material deposition in the past (>10 yr), based on proximity to man-made channels. Other sites were among existing meadows or, in the case of The Kitchen, had supported seagrass in the past. Temperature, salinity, water depth, tidal current velocity, wind speed and direction, sediment particle size, and sediment organic content (latter two taken from the top 3 cm of the sediment) were collected from each plot at each sampling time to determine if fauna in beds may have been affected by gradients of these factors as opposed to the grass alone.

Seagrass. Natural (reference) treatments: Two *Halodule wrightii*, 3 *Thalassia testudinum*, 3 *Syringodium filiforme*, and 4 unvegetated bottom plots were arbitrarily selected as reference sites. In natural seagrass treatments, the percentage composition by seagrass species, shoot density, percentage bottom covered, and average shoot length (sheath + leaf) were recorded from 3 randomly located 1 m^2 sampling locations within each plot prior to faunal sampling (see companion paper, Fonseca et al. 1996). If no seagrass was found at that location, a new random location was selected. In each of the three 1 m^2 areas selected for sampling within a natural plot, subsampling ($n = 3$) for coverage and shoot density was conducted at the 0.0625 m^2 scale as described by Fonseca et al. (1990), but using 1.0 m^2 , not 2.25 m^2 , quadrats. Shoot density subsamples were averaged within a quadrat location ($n = 3$) as well as among the 3 replicate sampling locations per plot ($n = 3$). Shoot density was computed as areal density by multiplying m^2 density values by the percentage bottom covered within a quadrat. Previously sampled coordinates were rejected.

Transplanted treatments: At 3 randomly selected 1 m^2 locations in each planted bed, a 1 m^2 quadrat was placed on the bottom as in natural beds (fauna were subsequently sampled at this precise location; see companion paper). Out of a maximum of 9 planting units (PU) contacting the corners and center of each quadrat, the number of surviving PUs, the number that were completely inside or outside the 1 m^2 quadrat, and the proportion of PU partially within the 1 m^2 quadrat were recorded. Numbers inside were used for correlation with fauna while total counts (inside + outside) were used for seagrass population growth model-

ing. If no PUs were encountered at the location, a new location was randomly selected. As in natural plots, previously sampled coordinates were also rejected.

The average percentage of PUs that survived per treatment (grand mean) was computed from these quadrat locations. Bottom coverage and number of shoots for each surviving PU ($n \leq 9$) were surveyed by seagrass species. Coverage by a PU was obtained by placing a 0.5 m^2 quadrat divided into 100 sections of 25 cm^2 over it and counting the number of sections that contained seagrass shoots. Each 25 cm^2 section was recorded as whether it was inside or outside the 1 m^2 quadrat area for individual PUs. Areal shoot density was evaluated by summing the total number of shoots in the portions of the surviving PU within the quadrat. Areal coverage was similarly computed; area per PU was summed for the portions of all PUs within the quadrat. Upon coalescence of PUs, surveys were conducted using natural bed methods.

Area covered and number of shoots per PU prior to coalescence of the individual PUs were regressed on time for subsequent computations on planting spacing and estimated time to achieve complete coverage. Areal shoot density was regressed on time using a quadratic function (chosen over linear, cubic, exponential based on r^2) to estimate time to achieve maximum density. Natural and planted seagrass bed shoot densities were plotted and compared using a 1-way ANOVA for each sampling date after transformation [$\ln(\text{areal shoot density} + 1)$] dealt satisfactorily with heteroscedasticity. Duncan's Multiple Range test was used for comparisons of treatment means when an F -test indicated significant treatment effects. ANOVA could not be performed on the *Syringodium filiforme* and mixed bed plantings because only 1 site survived, providing no independent replicates.

Within the plantings which survived, percentage survival was surveyed only where planting units were encountered in the 1 m^2 random location. Thus, all data on plant growth are based on areas where at least 1 out of 9 possible PUs within the 1 m^2 location survived to that point in time. Because we selected only grassed locations, these estimates of PU survival do not represent samples with equal probability of selection within the plot and cannot be extrapolated to the entire $\sim 2000 \text{ m}^2$ planting area. We took this approach because much PU loss was due to apparent bioturbation, a source of PU loss external to anchoring technique efficacy. By not attempting to extrapolate densities over the entire site, and not weighting by the number of PUs contributing to the total number of shoots, our data underestimate how quickly a m^2 of planted bottom could develop should all of the PUs survive. We allowed this latter bias to be included and recognize the conservative influence on our conclusions.

Morphology. Approximately 30 shoots of each species present were collected from next to one of the 1 m² quadrat locations for morphometric analysis, making sure to collect shoots still attached to their associated rhizome. Sampling of planted beds began when plantings coalesced. In all treatments, 10 shoots of each species were randomly selected from the collected seagrass, and leaf lengths and widths and stem lengths (sediment surface to leaf branching point) were recorded to 0.1 mm for each leaf on the shoot. Shoots were then dried to a constant weight at 80°C and an average weight computed. Seagrass surface area (m²) per unit area of seafloor (m²) was computed for each seagrass species for each sampling time, as were canopy height (mean leaf length) and aboveground biomass (g dry wt m⁻²).

Macroalgae. Three additional 1 m² locations were randomly selected (independent of the 1 m² areas for seagrass surveys and subsequent faunal sampling) within each plot at each site. One 0.0625 m² subsection was randomly chosen from within a 1 m² quadrat; all the drift algae in that subsection was collected. Algae were dried at 80°C to a constant weight by genus. The 3 samples from each plot were averaged for a treatment mean after extrapolation to a m² basis. During the May 1988 sampling, macroalgae from all the 1 m² faunal samples also were saved for comparison with the less time-consuming collection of the 3 random 0.0625 m² samples to determine the accuracy of the extrapolation to a 1 m² basis. There was no significant difference ($p > 0.05$, 1-way ANOVA) between values obtained by the 2 methods on a plot basis ($n = 3$).

Macroalgal aboveground biomass was treated similarly to areal shoot density and plotted over time by treatment. Aboveground biomass data were transformed [$\ln(\text{g dry wt m}^{-2} + 1)$], satisfactorily addressing heteroscedasticity. Identical tests and replication constraints were applied as with areal seagrass shoot density.

Plant species composition. Seagrass and macroalgal species composition was compared pairwise among natural treatments, and planted versus natural treatments of the same species, by computing their percentage similarity at each sampling time (Whittaker & Fairbanks 1958), as used by Holmquist et al. (1989) and Fonseca et al. (1990) for seagrass-associated fauna.

RESULTS

Environmental conditions

Temperature and salinity (19 to 30°C, 18 to 37‰, respectively) displayed typical ranges observed in seagrass beds of these species. Temperature displayed no study-wide pattern whereas salinity increased signifi-

cantly ($F_{23,14}$, $p < 0.001$, $r^2 = 0.573$) over the course of the study, largely due to an increase during the last 3 sampling periods from ~25 to ~32‰ for all treatments combined. Study-wide salinity increase over time was slightly more pronounced in planted treatments ($F_{58,86}$, $p < 0.001$, $r^2 = 0.786$). Wind speeds during sampling were relatively low because dropnets could not be reliably used at wind speeds over 20 knots. Tidal current velocity evidenced quiescent settings (0 to 13 cm s⁻¹). Natural beds exhibited a sediment organic matter content of 2.5% versus ~1% at bare areas and plantings at planting time; sediment organic content displayed no study-wide pattern of change in any treatment. There was no significant difference in surficial sediment silt-clay content among treatments ($F_{0,42}$, $p > 0.79$).

Seagrass beds

Natural/reference beds: shoot density

Areal shoot densities [$\ln(\text{areal shoot density} + 1)$] were compared among dates within treatments using Duncan's Multiple Range test in PC SAS (SAS Procedures Guide 1990). *Halodule wrightii* and *Thalassia testudinum* had no significant changes ($F_{1,45}$, $p > 0.30$; $F_{0,42}$, $p > 0.90$) over the study period while *Syringodium filiforme* had moderate ($F_{1,80}$, $p > 0.15$, $r^2 = 0.44$) among-sampling-time changes but with no consistent temporal pattern (Fig. 2A). Unvegetated plots adjacent to planted areas did not develop any seagrass cover, suggesting there was little natural seed recruitment or vegetative encroachment during the course of the study; therefore, unvegetated plots were not included in ANOVA of shoot density.

Transplanted beds: survival

Of the fourteen 9.5 × 19.5 m plots planted during the course of the study, 6 lost either all or over 95% of their PUs and were subsequently either replanted or abandoned (Table 2). Except for 2 plots at The Kitchen in Hillsborough Bay, the other 5 sites were lost shortly after planting (observations indicated heavy bioturbation, possibly by rays). This occurred during both spring and fall replanting times. Loss of the plots at The Kitchen may have been caused by bioturbation, a localized, rainfall-induced reduction of salinity, or some combination thereof. Of the 3 replanted plots, only one *Halodule wrightii* plot at Coffeeport Bayou survived to coalesce. *Syringodium filiforme* and mixed bed plots replanted at Coffeeport Bayou did not survive, again apparently due to heavy bioturbation by rays.

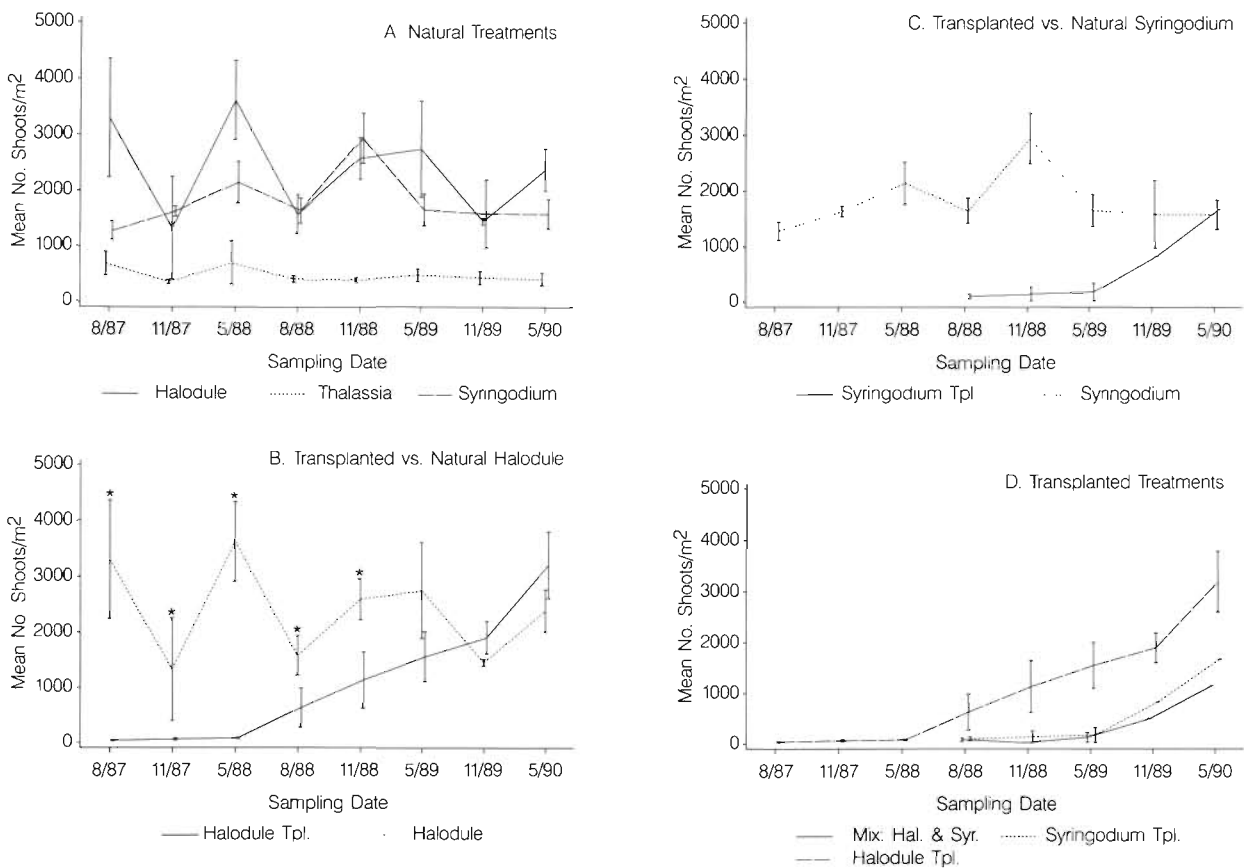


Fig. 2. Mean number of shoots m^{-2} by treatment over time. Note unequal times between sampling dates. (A) Natural treatments: *Halodule wrightii*, *Syringodium filiforme*, *Thalassia testudinum*; (B) natural *H. wrightii* versus planted *H. wrightii*. *Significantly different ($p < 0.05$); (C) natural versus planted *S. filiforme*; and (D) planted *H. wrightii*, *S. filiforme*, and mixed *H. wrightii*/*S. filiforme* plantings. Error bars = 1 SE

Halodule wrightii PU survival (m^2 locations that had >1 surviving PU) within the quadrat location ranged from 49 to 75% (mean = 61, SD = 10.02, $n = 5$). Our estimates based on visual surveys of all the 9.5×19.5 m *H. wrightii* planting areas prior to PU coalescence revealed no pattern of survival within the Bay.

Transplanted beds: coverage and areal shoot density

We observed no obvious pattern of plot coverage within the Bay by the end of the study. Starting in Hillsborough Bay, the MacDill site contained ~80% coverage; mid-Bay locations: Shore Acres ~20%, Coffeeport Bayou ~50%; entrance to the Bay locations: Summer Resort Key ~30% and Skeet Key >100% (spread outside of original study area).

A comparison of natural versus planted *Halodule wrightii* (Fig. 2B) showed that the areal densities of the 2 treatments became similar over time, and no significant difference ($F_{3,58}$, $p > 0.05$) was detected 1.8 yr

(May 1989) after planting. Although there was insufficient replication to test natural versus planted *Syringodium filiforme* or mixed bed areal densities, those plantings moved into the range of natural beds in a similar time frame (Fig. 2C). After an initial lag time, all surviving planted treatments added shoots at similar rates (Fig. 2D). No significant relationship was found when areal shoot density was regressed on distance up the Bay either by time (typical $F_{1,06}$, $p > 0.3$) or across time ($F_{1,0}$, $p > 0.30$, maximum r^2 among times = 0.14). Examination of residuals revealed no discernible pattern of change in areal shoot density with location in the Bay.

The rate of areal shoot density [$\ln(\text{shoot density} + 1)$] development was plotted for each planting treatment in Fig. 3A–D. Both *Halodule wrightii* and *Syringodium filiforme* performed similarly and could be combined into 1 model (Fig. 3D) without a reduction in fit. The estimated time to achieve maximum shoot (computed by solving the derivative of the combined regression for both seagrass species) was 1235 d (~3.4 yr) which was

Table 2. Percentage survival of planting units within the 1 m² quadrat location, with a selection criterion requiring a minimum of 1 planting unit within the quadrat location for a sample to be taken. n: coalesced; subsequently sampled using natural bed survey methods. 0: no subsequent survival; sampling discontinued. RPL: replanted; all PUs had been lost. nd: no data collected at this site (only survival data were collected in the February survey)

Treatment/site	Sampling time				
	Nov 87	Feb 88	May 88	Aug 88	Nov 88
<i>Halodule wrightii</i>					
Skeet Key	66	70	56 (n)		
Summer Resort Key	59	nd	49 (n)		
Coffeepot Bayou	93	81 RPL	52 (n)		
Shore Acres	55	62	44 (n)		
MacDill AFB	70	55	63 (n)		
<i>Syringodium filiforme</i>					
Skeet Key				88 (n)	
Coffeepot Bayou				33 RPL	0
The Kitchen				70	59 (0)
Mixed <i>H. wrightii</i> and <i>S. filiforme</i>					
Skeet Key				36 RPL	0
Coffeepot Bayou				70 (0)	
The Kitchen				81	29 (0)

only slightly beyond our study period. Table 3 shows predicted times to achieve natural bed areal density and maximum areal density, based on the quadratic model in Fig. 3D for various time 0 PU spacings. A 2-fold increase in spacing distance effectively doubled time to achieve goals of equivalent and maximum density.

All beds: seagrass species composition

Although the natural beds studied were typically monospecific, *Ruppia maritima* was periodically found, especially in natural *Halodule wrightii* plots (~15% of the shoots in November 1988), and was occasionally present in *Thalassia testudinum* and *Syringodium filiforme* plots. *H. wrightii* was also found in association with all other species, comprising nearly 50% of the shoots in

1 *T. testudinum* plot in May 1988, which prompted selection of a new, monospecific *T. testudinum* plot in the same vicinity. As mentioned previously, unvegetated controls developed no seagrass cover during the study.

Transplanted *Halodule wrightii* beds sometimes developed with volunteer *Ruppia maritima* representing as much as ~15% of the short shoots, but comprising only ~7% by the end of the study, largely due to a relative increase in *H. wrightii* density. Transplanted *Syringodium filiforme* remained monospecific while the remaining mixed planting was comprised of a 40/60% mix of *H. wrightii* and *S. filiforme*, respectively, based on shoot counts by the end of the study. Shoot density (irrespective of species) in the mixed bed was ~70% and ~40% of the adjacent planted monospecific *S. filiforme* and *H. wrightii* plots, respectively, at the end of the study.

Seagrass morphometrics

Data collection in planted beds did not start until 1 yr after project initiation when plantings coalesced. Surface area per shoot was relatively constant over the course of the study for natural *Halodule wrightii* and *Syringodium filiforme*. Turtlegrass *Thalassia testudinum* showed an increase in per-shoot surface area (Fig. 4A) until August 1988, after which it slowly declined. Average leaf length (Fig. 4B) and surface area (Fig. 4A) did not appear to be coupled consistently over time. Per-shoot surface area tended to higher in natural *T. testudinum* beds than other natural beds (Fig. 4A). Except for August 1988, planted *H. wrightii* per-shoot surface area and leaf length were nearly identical to natural beds over time and displayed no developmental trend (Fig. 4A, B). In contrast, the remaining planted *S. filiforme* linearly increased per-shoot surface area (Fig. 4A), apparently through increased shoot length (Fig. 4B). When average shoot surface area was multiplied by the total number of shoots in the quadrat to obtain a per m² surface area, no obvious differences among natural beds could be detected and no clear temporal trends emerged (Fig. 4C). Areal surface area of both planted *H. wrightii* and *S. filiforme* rose steadily from the time sampling began (Fig. 4C). Areal surface area of planted *H. wrightii* became similar to natural beds apparently as the result of shoot addition (Fig. 2B) rather than change in individual shoot morphology. The re-

Table 3. Predicted effect of planting unit spacing on development of planted seagrass beds

Spacing among planting units (m)	0.5	1.0	2.0
Number of planting units ha ⁻¹	40000	10000	2500
Estimated time to reach natural bed areal density (yr)	1.8	3.6	7.2
Estimated time to reach maximum areal density (yr)	3.4	6.8	13.6

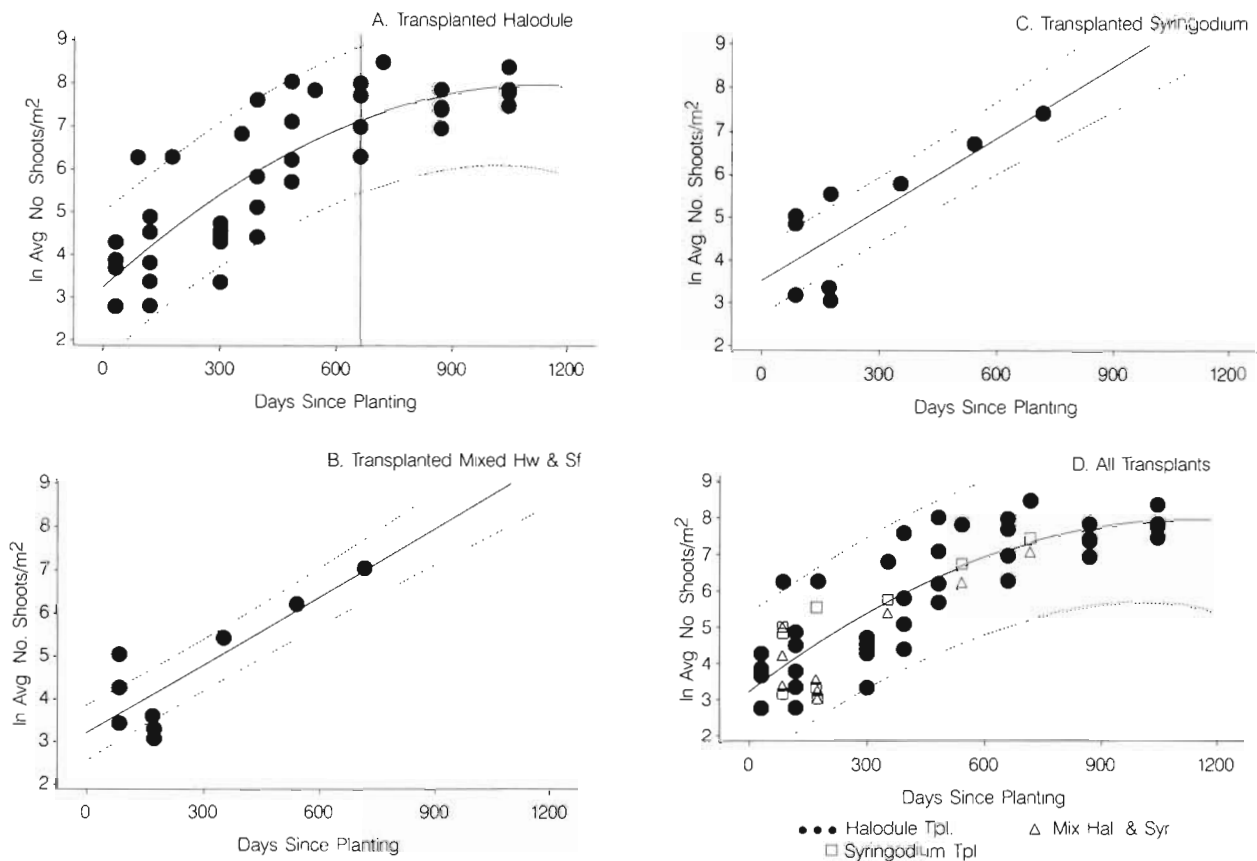


Fig. 3. Regressions (ln-transformed + 1) for mean number of shoots m^{-2} for planted seagrass treatments. (A) *Halodule wrightii* transplant, $r^2 = 0.70$, slope formula is $y = 0.0083x - 0.0000036x^2 + 3.254$, $n = 39$. Vertical line indicates point at which shoot density was not significantly different ($p < 0.05$) from natural beds; (B) *H. wrightii*/*Syringodium filiforme* mix, $r^2 = 0.72$, slope formula is $y = 0.0053x + 3.199$, $n = 9$; (C) *S. filiforme* transplant, $r^2 = 0.64$, slope formula is $y = 0.0055x + 3.541$, $n = 9$; and (D) *H. wrightii*, *S. filiforme* and *H. wrightii*/*S. filiforme* mixed planting, $r^2 = 0.71$, slope formula is $y = 0.0079x - 0.0000032x^2 + 3.217$, $n = 55$. Dashed lines: 95% confidence limits

maining planted *S. filiforme* developed areal surface area higher than the average of any natural bed over the course of the study, apparently as the result of both shoot addition (Fig. 2C) and an increase in individual shoot length (Fig. 4B, C).

Macroalgal biomass

Macroalgal biomass (MAB) was generally greater in natural *Syringodium filiforme* and *Thalassia testudinum* than in planted and unplanted *Halodule wrightii* (Fig. 5A, Table 4) at any given sampling time. Similarly, MAB in unvegetated (bare) treatments was often not significantly different (e.g. $F_{42,55}$, $p < 0.001$) from other treatments, with the exception of *S. filiforme*, which always supported greater MAB (Table 4). MAB was never significantly different among natural and planted *H. wrightii* at any time (Table 4, Fig. 5B) or irrespective of time ($F_{0,32}$, $p > 0.50$). Moreover, *S. fili-*

forme natural beds always had significantly more MAB than planted *S. filiforme* irrespective of time ($F_{15,13}$, $p < 0.01$). Because animal densities apparently did not increase in response to the presence of macroalgae in bare areas (see companion paper, Fonseca et al. 1996), bare areas are not included in the remainder of these results. The remaining *S. filiforme* and mixed bed plantings did not develop MAB equal to the Bay-wide average of natural *S. filiforme* (Fig. 5C). Mean MAB never exceeded ~ 19 g dry wt m^{-2} for seagrass beds (ln back-transformation; Fig. 5A–D).

Macroalgal species composition and similarity

Fourteen genera of macroalgae were encountered in the study, with 10 accounting for 99% of the biomass (Table 5). All genera varied substantially in their relative contribution to overall standing biomass over the 3 yr study period.

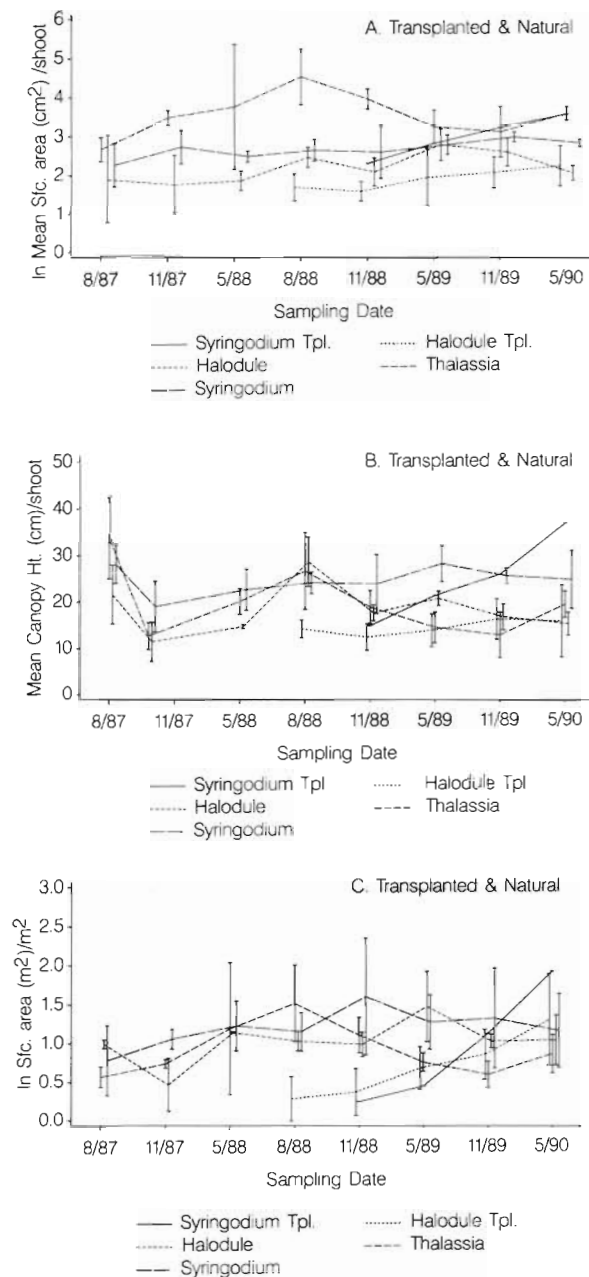


Fig. 4. Comparisons of seagrass morphometrics among natural and planted treatments. Note unequal times between sampling dates. (A) Two-dimensional aboveground seagrass surface area, $(\ln + 1) \text{ cm}^2 \text{ shoot}^{-1}$. Halodule Tpl.: planted *Halodule wrightii*; Halodule: natural *H. wrightii*; Syringodium: natural *Syringodium filiforme*; Syringodium Tpl.: planted *S. filiforme*. (B) Canopy height as computed from average individual shoot length over time. (C) Two-dimensional aboveground seagrass surface area, $(\ln + 1) (\text{m}^2) \text{ m}^{-2}$ seafloor. Error bars: 1 SE

Comparisons among natural beds displayed substantial seasonal variation in percentage similarity (PS) (Fig. 6A). No consistent among-season pattern was

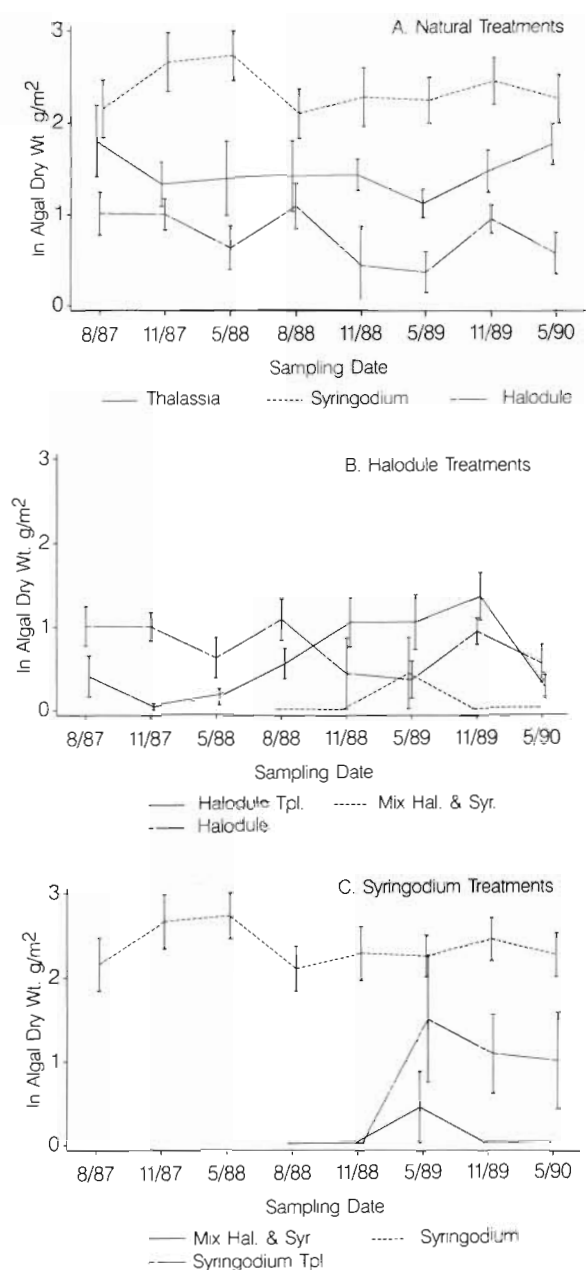


Fig. 5. Mean algal dry weight biomass, $\text{g m}^{-2} (\ln + 1)$, by date and treatment. Note unequal times between sampling dates. (A) Natural, reference bed treatments. Thalassia: *T. testudinum*; Syringodium: *Syringodium filiforme*; Halodule: *Halodule wrightii*. (B) Treatments with *H. wrightii*. Halodule Tpl.: planted *H. wrightii*; Mix Hal. & Syr.: mixed *H. wrightii* and *S. filiforme*; Halodule: *H. wrightii*. (C) Treatments with *S. filiforme*. Mix Hal. & Syr.: mixed *H. wrightii* and *S. filiforme*; Syringodium: *Syringodium filiforme*; Syringodium Tpl.: planted *S. filiforme*. Error bars: 1 SE

evident. Planted beds (*Halodule wrightii* vs *Syringodium filiforme* plantings; Fig. 6B) were more similar to each other in contrast to comparisons with natural beds

Table 4. ANOVA (Duncan's Multiple Range test) of macroalgal dry weight biomass (m^{-2}) to detect significant difference ($F < 0.05$) between natural and planted *Halodule wrightii* treatments, at the site treatment level (natural log transformed data). HW: *Halodule wrightii* ($n = 2$); SF: *Syringodium filiforme* ($n = 3$); HT: *Halodule wrightii* transplant ($n = 5$); TT: *Thalassia testudinum* ($n = 3$); BA: bare area ($n = 5$ during Aug 1987 to May 1988 and $n = 3$ during Aug 1988 to May 1990). Those treatments connected by solid lines or those with solid lines are not significantly different from one another. Dashed lines join like treatments when bridging unlike treatments

Date	Treatment				
	SF	TT	HW	HT	BA
Aug 87	-----	-----	-----	-----	-----
Nov 87	-----	-----	-----	-----	-----
May 88	-----	-----	-----	-----	-----
Aug 88	-----	-----	-----	-----	-----
Nov 88	-----	-----	-----	-----	-----
May 89	-----	-----	-----	-----	-----
Nov 89	-----	-----	-----	-----	-----
May 90	-----	-----	-----	-----	-----

Table 5. Macroalgal genera encountered in the study and their percentages of the total biomass (all treatments combined)

Genus (and species where identified)	Percent of total
<i>Caulerpa prolifera</i>	37
<i>Gracilaria</i>	18
<i>Hypnea</i>	16
<i>Acanthophora</i>	15
Blue-green (mostly unidentified: some <i>Microcoleus</i>)	5
<i>Spyridia</i>	3
<i>Laurencia</i>	2
<i>Ulva</i>	2
<i>Ectocarpus</i>	1
Remaining genera (<5% of total, in descending order):	
<i>Chaetomorpha</i> , <i>Chondria</i> , <i>Soleria</i> , <i>Champia</i> , <i>Enteromorpha</i>	
Total number of macroalgal genera by treatment over the study period:	
Treatment	No. of genera
Bare sand	7
Natural <i>Halodule wrightii</i>	6
Natural <i>Syringodium filiforme</i>	9
Natural <i>Thalassia testudinum</i>	9
Planted <i>H. wrightii</i>	11
Planted <i>S. filiforme</i>	5
Mixed <i>H. wrightii</i> and <i>S. filiforme</i>	1

(Fig. 6B). An unexplained, midstudy increase in similarity among planted and natural beds (Fig. 6B) temporarily produced PS values similar to those of comparisons among natural beds. Values then dropped for the remainder of the study period to values lower than those seen for comparisons among natural beds.

DISCUSSION

Low survival of the planted plots supports the conclusions of previous studies regarding the difficulty of seagrass planting (Fonseca et al. 1987, Fonseca 1989, 1992), a finding that made analysis of some treatments

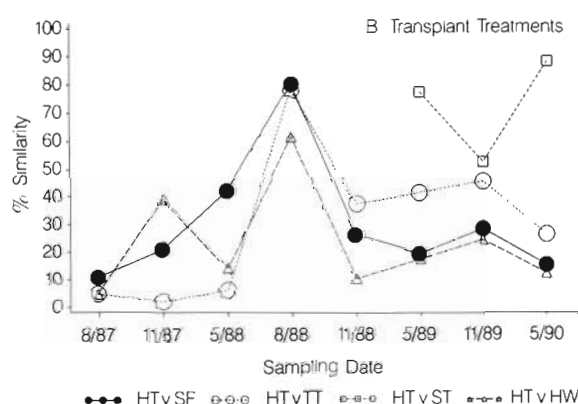
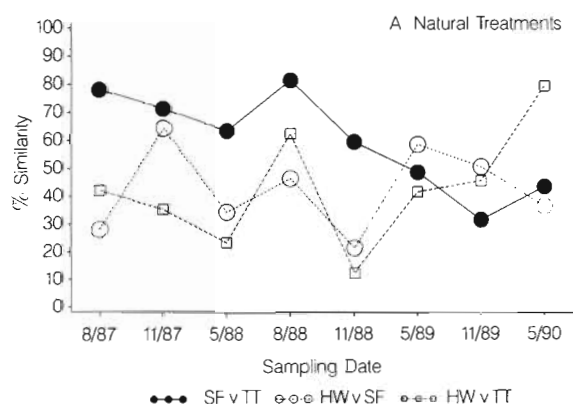


Fig. 6. Comparison of percentage similarity of drift macroalgae in seagrass treatments over time. Note unequal times between sampling dates. v: comparison among (A) natural reference beds (SF: *Syringodium filiforme*; TT: *Thalassia testudinum*; HW: *Halodule wrightii*) and among (B) planted and natural reference beds (HT: planted *H. wrightii*; ST: planted *S. filiforme*)

difficult. In evaluating the overall performance of the planting operation, losses of PUs could be ascribed to several factors. Some losses were site-specific and were possibly related to short-term salinity fluctuations (e.g. The Kitchen site) or worker inexperience. However, one agent of loss commonly observed across most sites was bioturbation. The loss of plantings was often accompanied by the presence of large (0.5 to 1.5 m diameter) pits, likely produced by ray feeding with subsequent modification by decapod crustaceans. However, we found that at some sites replanting later in the year (September–November) established persistent cover. Late season plantings, although not the optimal period of seagrass growth, may be outside the peak in bioturbation, thereby enhancing survival and persistence of plantings. Similarly, Fonseca et al. (1994) found that bioturbation exclosure cages greatly improved springtime planting survival at our most disturbance-prone site, Coffeepot Bayou.

Our surveys of PU survival based on averages among randomly located 1 m² plots revealed that for plots which eventually established persistent cover, 66% PU survival occurred (Table 2). In plots which eventually failed, survival ranged from 29 to 59% in surveys taken 6 mo prior to complete PU loss, indicating that wholesale losses could occur in a short period despite having almost two-thirds of the PUs present. We found that, on the average, ~47% loss of PUs could be sustained yet still produce areas of coalescence later, suggesting that a 47% loss is a sustainable impact to a planting effort. But to predict sustainable impacts, information on the spatial distribution of PU loss would be required. For example, in our 9.5 × 19.5 m plots, if the first ~9 m on the long axis of the plot experienced wholesale loss of PUs (i.e. ~47% loss), the potential for eventual coverage of that portion of the plot would not be the same as if, for example, alternating PUs were lost evenly over the site. In our plots, losses tended not to be evenly spaced but rather occurred in patches several meters on a side (pers. obs.).

The overall loss of half of the planted plots, together with a tolerance of 47% loss on a m² basis when planting on 0.5 m centers (based on surviving plots), demonstrates that planners should anticipate significant replanting efforts to initiate a bed in this area. We conclude that in future seagrass restoration/creation projects in Tampa Bay, even if planted at high PU densities as here (0.5 m centers), a given planting has an approximately 50% chance of initial survival due most likely to bioturbation (unless steps are taken to reduce bioturbation; *sensu* Fonseca et al. 1994). Similarly, without bioturbation exclusion a 50% chance of requiring replanting can be expected in order to establish persistent cover. Performance of the plantings was

assessed also by comparison to natural bed shoot densities. Comparisons of planted beds with natural beds were straightforward because of the low temporal variation in areal shoot density of the natural beds over the course of the study. Areal shoot densities in surviving portions of planted *Halodule wrightii* beds did not differ ($p > 0.05$) from natural *H. wrightii* after 1.8 yr (Fig. 2B). The remaining *Syringodium filiforme* planting showed similar results, although this could not be tested due to a lack of replication from planting failures (Fig. 2C).

By following areal shoot density over time, we expected to be able to evaluate a seagrass species' population growth rate. Similar data have been useful elsewhere in guiding mitigation efforts (Fonseca et al. 1987). However, planting seagrass 0.5 m apart prevented collection of these data because, within 3 sampling times, rhizome extension had overlapped among individual plantings. When this occurred it was impossible to determine from which PU individual shoots originated, precluding independent sampling of PUs for population growth. Even based on changes in areal density alone, the similarity among *Halodule wrightii* and *Syringodium filiforme* in this study (Fig. 3D) was not anticipated: geographically bracketing data sets from the Florida Keys and the Florida Panhandle (Fonseca et al. 1987) showed *H. wrightii* rather than *S. filiforme* to have a higher population growth rate. Our ability to compare population growth rates among seagrass species was further compromised by the lack of site replication with *S. filiforme* plantings due to whole site failures. In contrast, the remaining *S. filiforme* site at the entrance to the Bay did not demonstrate the postplanting lag in shoot addition observed for *H. wrightii* plantings (Fig. 2B). But by modeling areal shoot density over time, we determined that, for all planted species combined, 3.4 yr was required to produce a maximum density (Fig. 3D). Because of high among-site variance no significant differences in density were detected among natural and planted *H. wrightii* after approximately half that time. For *H. wrightii* a minimum of 1.8 yr of postplanting monitoring of plant population growth and coverage would be required to evaluate project success (in terms of the plant community) for plantings on 0.5 m intersections in this area. Longer periods will be required if spacing is increased (Table 3); and, the broad error bars (Fig. 3D) surrounding the regression of areal density over time (a combination of among-site variation in shoot density and PU loss) made this variable a weak indicator of planting success. Areal density is, however, only one indication of planting development.

We also considered morphological attributes as potential measures of planted-bed development given its relevance to trophic transfer (Heck & Crowder

1991) and a host of other ecological factors (see Bell et al. 1991). Aboveground biomass in natural beds was in the low to mid range of values reported for Tampa Bay by Lewis et al. (1985): *Halodule wrightii* aboveground biomass ranged from 38 to 50 g dry wt m⁻² and *Syringodium filiforme* ranged from 50 to 170 g dry wt m⁻². The final high value of the planted *S. filiforme* bed we observed was ~150 g dry wt m⁻². Planted *H. wrightii* developed areal densities equivalent to those of natural beds 6 mo before either planted bed areal surface area or aboveground biomass values overlapped with those observed in natural beds (Fig. 4C). Because *H. wrightii* plants did not change average length (Fig. 4A), it appears that areal surface area and biomass increased solely through shoot addition (population growth). Conversely, the *S. filiforme* planting increased surface area and biomass by both changes in population and individual size (Figs. 2C & 4A–C). We do not have relative water depths among sites, so it is possible that a slightly greater water depth at the planting site as compared to the harvest site could have been responsible for this difference in length. Because areal biomass and surface area varied not only by changes in shoot size but also with the number of individuals in the population on a site-by-site basis, we conclude that morphometric data should not be utilized to evaluate planting development.

A potentially critical evaluation of seagrass restoration projects that has historically been ignored is that of the status of the associated macroalgae. This has occurred despite wide acknowledgement of the role of seagrass-associated macroalgae in supporting indigenous fauna (Nelson 1979, Orth et al. 1984, Stoner & Lewis 1985, Virnstein & Howard 1987). Macroalgal biomass (MAB) was often significantly different among the natural seagrass treatments (Table 4), with a general trend of *Syringodium filiforme* beds > *Thalassia testudinum* > *Halodule wrightii*. Therefore we hypothesized that MAB may be a more influential factor in our subsequent investigations of associated fauna in *S. filiforme* and *T. testudinum* beds than in *H. wrightii* beds. Although MAB in planted beds tended to increase with time (Fig. 5), it was highly variable without any clear pattern of development over time (Table 5) and was often not significantly different from MAB in unvegetated areas. Moreover, low PS values (Fig. 6) among natural and planted seagrass indicated that despite its importance to associated fauna, MAB would not be a reliable diagnostic factor in evaluating planted bed development in the time frame (3 yr) that might be expected to occur with many mitigation projects. However, the rapid increase in MAB followed by sustained MAB levels in the remaining, unreplicated *S. filiforme* planting suggested that, for this seagrass species, MAB should be further evaluated as a poten-

tial diagnostic parameter, especially among beds in close proximity to one another that may have similar physical settings. Once again the lack of site replication for planted *S. filiforme* prevents us from reaching a firm conclusion regarding these findings.

The survival and persistence of seagrass plantings apart from suspected bioturbation-induced losses indicate that much of Tampa Bay may again be capable of supporting seagrass. These data corroborate similar findings by Johansson & Lewis (1993) in Hillsborough Bay where ~3 ha (as of 1991) of natural recruitment by *Halodule wrightii* and some *Thalassia testudinum* has occurred. Diagnostic plantings by Johansson & Avery (unpubl. data) and plantings for this study also show environmental conditions in Hillsborough Bay to be conducive to seagrass growth. Natural recolonization by *H. wrightii* and *Ruppia maritima* is taking place in parts of Hillsborough Bay, but at a slow rate which is likely due to geographic isolation from propagule sources (*sensu* Orth et al. 1994). Acceleration of this process could be accomplished by planting in areas currently remote from propagule invasion and should include not only *H. wrightii* but also less invasive species such as *Syringodium filiforme* and *T. testudinum* that were likely part of the historical composition of seagrasses in Hillsborough Bay.

We also sought to evaluate the development of mixed bed plantings because many natural seagrass beds are not monospecific. Based on our limited data it appears that mixed bed plantings may not develop shoot densities as rapidly as monospecific plantings. Areal shoot density (either both species combined or singly) in the remaining mixed bed treatment at Skeet Key was much lower than the adjacent monospecific plantings, similar to the findings of Williams (1987) which indicated competition among the seagrasses *Syringodium filiforme* and *Thalassia testudinum*. In this case, the close proximity of *S. filiforme* and *Halodule wrightii* appeared to be to the detriment of both species. Broader geographic replication of this treatment is required to advance this hypothesis.

We conclude that few of the parameters measured here provide useful guidance to assessing seagrass planting success (e.g. biomass, surface area, macroalgal biomass). Areal shoot density in comparison with natural beds displayed the clearest temporal pattern of bed development of all the parameters, even though moderate variation occurred. It is important though to differentiate the term 'areal density' from many literature values of shoot density. Our areal density values were computed from replicate samples at the 1 m² scale as opposed to isolated, small diameter cores and can incorporate moderate patchiness in the density estimate, a sensitivity that is useful for monitoring plantings that have begun to coalesce but have not yet

uniformly covered the seafloor. We recommend that within a 3 yr period after planting, sampling at the m² scale be conducted. Measures of aboveground biomass, shoot surface area, or associated macroalgae are currently not likely to provide defensible criteria for assessing seagrass planting success because of inherent high among-site variability. We conclude that previous intuitive, but largely unsupported, recommendations for requiring only coverage and persistence measurements for assessing seagrass mitigation projects (Fonseca 1989, 1992, 1994) were largely correct; but, together with more exacting definitions of coverage, more detailed data collection in the form of areal shoot density measurements is warranted.

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