

# Development of planted seagrass beds in Tampa Bay, Florida, USA. II. Faunal components

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**ABSTRACT:** In this paper we report on changes in shrimp, fish and crab abundance, composition and size in planted *Halodule wrightii* and *Syringodium filiforme* beds as compared to unvegetated, and natural, *H. wrightii*, *S. filiforme*, and *Thalassia testudinum* habitats in Tampa Bay, Florida, USA, over a 3 yr period (1987 to 1990). Using a gear type selective for small resident macroepibenthic fauna (1 m<sup>2</sup> dropnets), we found that in 1.8 yr *H. wrightii* planted on 0.5 m centers developed an animal density, number of taxa, and species composition equivalent to that found in natural beds. Animals tended to be larger in planted beds over the course of the study. Comparison of planted *S. filiforme* and mixed *H. wrightii* and *S. filiforme* with natural beds was impaired due to failure of several planting areas but exhibited a pattern of development similar in some ways to that of planted *H. wrightii*. Macroepibenthic animal density in planted beds displayed an asymptotic relationship with areal shoot density, where animal densities became equal to natural beds at shoot densities only a third of the average density for natural beds. This pattern corroborates the existence of threshold values of habitat structure in seagrass beds influencing numerical abundance of some associated animal communities. Macroepibenthic faunal abundance and composition in planted beds could be inferred from the amount of areal coverage of seagrass and its persistence over time, while measurement of areal shoot density may provide an important first check point on the road to functional restoration of seagrass habitat.

**KEY WORDS:** Seagrass · Fauna · Threshold response · Mitigation

## INTRODUCTION

Seagrass restoration is an inherently complicated process which has not yet been shown to offset net habitat losses due to coastal development (Fonseca et al. 1987, Fonseca 1989, 1992, Kirkman 1992). We do not know how continued loss of seagrass ecosystems will affect our ability to maintain fishery resources, but there is evidence that losses of specific fisheries have been associated with declines in seagrass habitat (Stevenson & Confer 1978). Effective restoration of these habitats depends on answering the question: does planting of seagrass beds provide living marine

resource values similar to the natural beds they are intended to replace?

The resource value of natural seagrass beds has been well documented (Zieman 1982, Phillips 1984, Thayer et al. 1984, Hoffman 1986, Larkum et al. 1989), however there have been few studies to evaluate the assumption that restoring or creating seagrass beds provides a concomitant recovery of commercially and recreationally valuable animal species and/or their food sources (Nessmith 1980, Homziak et al. 1982, McLaughlin et al. 1983, Smith et al. 1989, Fonseca et al. 1990). These studies generally conclude that some functions of seagrass beds can be restored as the result of planting operations (but see Smith et al. 1989). These few studies, some of which experienced poor

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planting success (Fonseca et al. 1990) or lacked control comparisons (McLaughlin et al. 1983), do not constitute sufficient data upon which to make many management decisions regarding the efficacy of seagrass restoration or mitigation. In addition, requiring data collection of a wide variety of seagrass bed functions as success criteria under mitigation can be difficult to enforce except in very large, expensive projects (pers. obs.). Therefore low-cost yet diagnostic success criteria are much needed to provide guidance for evaluating the performance of relatively small seagrass mitigation projects or public interest projects where habitat mitigation often does not receive the scrutiny of larger projects. If consistent restoration of faunal abundance and composition occurs in a predictable manner with growth of planted seagrass beds, we should be able to recommend only monitoring of seagrass recovery to infer faunal recovery in some instances.

In this paper, we compare the development of the faunal component of planted sites with the status of natural seagrass beds. Within-seagrass species comparisons were made for purposes of evaluating functional equivalency of the planted beds with their natural counterparts. Among-seagrass species comparisons were made to address the issue of habitat substitution of seagrass species, a tactic which is recommended for rapid stabilization of a planting area when slow-growing climax species (i.e. *Thalassia testudinum*) are lost (Fonseca et al. 1987). To determine how macroepibenthic fauna and planted seagrass developed together, we assessed the development of shrimp, fish and crab densities, composition, and size in planted *Halodule wrightii* and *Syringodium filiforme* beds over a 3 yr period after planting in comparison to the status of natural beds. A wide range of other highly relevant functions of seagrass beds were not assessed (e.g. primary production, secondary production, nutrient cycling, epiphytic community development, genetic diversity) and await additional study in the context of seagrass habitat restoration.

## METHODS

**Dropnet configuration and deployment.** Environmental conditions, site layout and distribution of the study sites are described in Fonseca et al. (1996, this issue). In summary, 5 permanent locations were arbitrarily selected to represent a range of positions along the axis of Tampa Bay, Florida, USA (Fig. 1 in Fonseca et al. 1996). At each site, a 9.5 × 19.5 m plot of *Halodule wrightii* was planted on 0.5 m centers using the staple method (Fonseca et al. 1987). Of those sites, 3 also received plantings of *Syringodium filiforme*; 3 sites received mixed plantings of *H. wrightii* and *S. filiforme*

by installation of alternating rows of each species during planting. At each site, natural seagrass beds and adjacent, unvegetated sand bottom were sampled seasonally from permanent, arbitrarily placed plots equal to that of planted plots. Comparisons with natural beds and unvegetated bottom constituted baseline values for comparing development of planted beds and controlling for nonplanted seagrass recruitment. Not all of the 3 natural seagrass species under study in Tampa Bay (*H. wrightii*, *S. filiforme*, and *Thalassia testudinum*) were present at each site. Because planting failures occurred (Fonseca et al. 1996), replanting was required for several plots, with variable success in establishing persistent cover, resulting in unequal replication (Table 1 in Fonseca et al. 1996).

Sampling began in August 1987, and was repeated November 1987, May, August and November 1988, May and November 1989, and May 1990. Three randomly selected 1 m<sup>2</sup> locations (replicates) were chosen for plant and animal sampling within each plot at each sample time. Upon completion of shoot counts at each location, 1 × 1 m dropnets similar to those used by Fonseca et al. (1990) were deployed directly over each of the replicate areas. The nets were supported by 4 poles with release pins which were triggered from ~10 m away.

All dropnets were left in place for a minimum of 12 h prior to release. When possible all 3 dropnets within a given treatment were released at the same time. After the traps were dropped, water height measurements were taken from the center of each dropnet. Other physical measurements were taken on each site to assess if these variables were correlated with animal distribution; these included tidal current velocity, water temperature, salinity, time of day, and tidal stage along with an estimation of wind speed and direction.

**Faunal collection.** The order in which dropped nets were collected at a site was randomly determined. Fauna were collected from dropnets using a 1.5 × 1.0 m seine and 0.46 × 0.36 m dip nets, both with 0.16 mm mesh. Faunal sampling was discontinued when 3 consecutive seines and 5 consecutive dip nets contained no fish or shrimp. Crabs were not used as a criterion because of time constraints (some individuals were deeply buried within the seagrass root mat). Animals were placed in 100% ethyl alcohol in the field for later sorting, identification and measurement unless they were large enough to be processed in the field and released. All fish and decapod crustaceans were identified to lowest possible taxon and total numbers of individuals recorded. Body size measurements for all fish (SL), shrimp (short carapace length) and crabs (carapace width: distance between tips of antrolateral spines) were made to the nearest mm.

**Data analysis. Environmental effects:** The relationship of canopy height, macroalgal biomass (MAB), salinity, temperature, and water depth to animal density was determined using stepwise multiple linear regression (MULREG) in PC-SAS (SAS 1989) while blocking for season. Analysis was conducted separately for planted and natural beds by faunal category (fish, shrimp, crabs). Sediment organic content and silt-clay content were also analyzed (Fonseca et al. 1996).

**Numbers of taxa and individuals:** The total catch over the course of the study was summed by species and the top 95% within each faunal category was used for subsequent analysis. Number of species and number of individuals within the faunal categories were plotted over time by seagrass treatment. Number of taxa and individuals were analyzed for differences among natural beds and natural and planted *Halodule wrightii* treatments using a 1-way ANOVA by sampling date. Examination of the taxa data under  $F_{max}$  revealed no need for transformation. However, analyses of variance for testing hypotheses concerning among-treatment differences in shrimp, fish, and crab density were based upon the  $\ln(x+1)$ -transformed density values which met the conditions of the  $F_{max}$  test. Tukey's studentized range test was used to compare treatment means when an  $F$ -test indicated significant treatment effects (SAS 1989). ANOVA could not be performed on data collected from the *Syringodium filiforme* and mixed species plantings because only 1 replicate plot of each treatment survived. Because animal densities were always significantly lower in bare (control) areas, those results are not reported in the remainder of the paper.

**Faunal composition:** Animal composition was compared among pairs of treatments by computing percentage similarity (Whittaker & Fairbanks 1958), as used by Holmquist et al. (1989) and Fonseca et al. (1990) in seagrass systems.

**Body size ratio:** The average size of a species in planted beds was divided by the average size of the same species in natural beds at each sampling time over all sites. These size ratios were then averaged among all species within each faunal category.

**Plant/animal density:** The relationship between animal density and areal shoot density in planted seagrass beds was evaluated by regressing both the arithmetic and  $\ln$ -trans-

formed animal density as a function of areal shoot density. Because areal shoot density was increasing due to spread of plantings over time, these data represented a temporal developmental sequence as well.

## RESULTS

### Environmental effects

When blocking for seasonal effects using MULREG in planted beds, significant ( $p < 0.05$ ) relationships of animal density to environmental cues were found within shrimp and crab categories, but not within fish (Table 1). Most variables accounted for  $<5\%$  of the variation in animal density, with salinity, water depth, macroalgal biomass (MAB) and water temperature being significant most frequently. Similar results were found for natural beds (Table 1); significant relationships were found with some variables in all faunal categories but, again, generally accounted for little variation in animal density. This multiple regression was repeated by sampling date (not shown) with very similar results, in that a differential response of faunal categories to each variable was observed with similarly low  $r^2$  values.

Sediment organic content was slightly greater in natural as opposed to planted beds while no significant difference in sediment silt-clay content was found among treatments (Fonseca et al. 1996).

Table 1. Stepwise multiple linear regression of fish, shrimp, and crab abundance (numbers  $m^{-2}$ ) on environmental variables for both planted beds and natural beds. Regressions were blocked for year and season with shoot density, area covered, algal biomass (all on a  $m^{-2}$  basis), salinity, temperature and water depth as independent variables. Entry level = 0.05 and retention = 0.10 ( $p$  values). Only variables that were retained are shown

Species category	Variable	Partial $r^2$	Blocked total $r^2$	Total model $r^2$
<b>Planted beds only</b>				
Shrimp	Salinity	0.102	0.124	0.242
	Temperature	0.016		
Fish	None			
Crabs	MAB	0.092	0.029	0.200
	Salinity	0.042		
	Canopy height	0.021		
	Water depth	0.017		
<b>Natural beds only</b>				
Shrimp	MAB	0.038	0.009	0.070
	Salinity	0.015		
	Water depth	0.008		
Fish	Temperature	0.020	0.096	0.115
Crabs	Water depth	0.127	0.031	0.170
	MAB	0.013		

### Number of taxa

**Shrimp.** Over the course of the study, 10 taxa accounted for 95% of the shrimp catch (Table 2). The numbers of taxa  $m^{-2}$  in all treatments are shown in Fig. 1A-C. During the first 3 sampling times, numbers of taxa in planted *Halodule wrightii* were significantly different from those in natural *H. wrightii* treatments, but not after August 1988 (~1.1 yr since planting; Fig. 1A) except during May 1989. Although there was insufficient replication to test natural versus planted *Syringodium filiforme* and mixed-species bed (alternating rows of *H. wrightii* and *S. filiforme*) transplants (Fig. 1B), the planted treatments appeared to be similar to natural *H. wrightii* and *S. filiforme* after ~9 mo (May 1989). Except for August 1987, when *H. wrightii* had significantly more taxa than the other 2 natural bed treatments ( $F_{7,03}$ ,  $p <$

0.03), the 3 primary natural seagrass bed treatments had similar numbers of taxa during the study (*H. wrightii* averaged 7.2 species, *S. filiforme* 7.4 species, and *T. testudinum* 5.9 species  $m^{-2}$  over the course of the study; Fig. 1C).

**Fish.** Over the course of the study, 14 fish taxa which are generally considered seagrass bed residents accounted for 95% of the catch (Table 2). The number of fish taxa in planted *Halodule wrightii* was not significantly different from that in natural *H. wrightii* beds 1.8 yr after planting (Fig. 2A). Although there was insufficient replication for statistical tests with planted *Syringodium filiforme* and mixed-species bed treatments (Fig. 2B), mean numbers of species in each remaining treatment replicate were consistently lower than in natural beds (Fig. 2B). There were no significant ( $p < 0.05$ ) differences among natural treatments at any sampling time, although numbers of fish taxa  $m^{-2}$  tended to be

higher in natural *S. filiforme* beds (Fig. 2C) than in natural beds of the other seagrass species. (5.7 vs 4.7 and 3.6 species  $m^{-2}$  for *H. wrightii* and *Thalassia testudinum*, respectively).

**Crabs.** Over the course of the study, 4 crab taxa accounted for 95% of the catch (Table 2). Numbers of taxa in planted *Halodule wrightii* did not differ from those in natural *H. wrightii* beds in August 1988 (1.1 yr after planting) and were significantly different again only in May 1989. Numbers of crab taxa in planted *Syringodium filiforme* and mixed-species bed treatments (Fig. 3B) were similar to those in the natural beds by May 1989 (0.97 yr), much like the pattern observed for shrimp (Fig. 1B) but not fish taxa (Fig. 2B). Although numbers of taxa among natural and planted beds were nearly equal early in the study, the number of crab taxa in mixed-species beds did not follow seasonal fluctuations of *S. filiforme* treatments toward the end of the study period. As with fish, there were no significant differences ( $p < 0.05$ ) among natural bed treatments at any sampling time (Fig. 2C); numbers of taxa displayed only slight seasonal variation (study-wide averages of 3.7, 3.0, and 3.8 species  $m^{-2}$  for *H. wrightii*, *S. filiforme* and *Thalassia testudinum*, respectively). This was in contrast to shrimp and fish collections which had shown some seasonal variation in number of species.

Table 2. Fauna composing the top 95% of the species captured during the entire 3 yr period (combined catch from natural and planted beds) are shown by total numbers and percentage they constituted within each of the general faunal categories, shrimp, fish, and crabs

Species	Common	Total	%
<b>Shrimp</b>			
<i>Hippolyte</i> sp.	Grass shrimp	29440	51.6
<i>Periclimenes longicaudatus</i>	Cleaning shrimp	4903	8.6
<i>Palaemonetes intermedius</i>	Grass shrimp	4441	7.8
<i>Palaemonetes pugio</i>	Grass shrimp	4000	7.0
<i>Tozeuma carolinense</i>	Arrow shrimp	2958	5.2
<i>Processa hemphilli</i>	Grass shrimp	2636	4.6
<i>Periclimenes americanus</i>	Grass shrimp	2531	4.4
<i>Penaeus duorarum</i>	Pink shrimp	1620	2.8
<i>Alpheus normanni</i>	Green snapping shrimp	1352	2.4
<i>Latreutes fucorum</i>	Grass shrimp	1075	1.9
<b>Fish</b>			
<i>Gobiosoma robustum</i>	Code goby	2723	44.9
<i>Eucinostomus</i> sp.	Mojarra	517	8.5
<i>Lagodon rhomboides</i>	Pinfish	468	7.7
<i>Syngnathus scovelli</i>	Gulf pipefish	430	7.1
<i>Symphurus plagiatus</i>	Blackcheek tonguefish	408	6.7
<i>Microgobius gulosus</i>	Clown goby	317	5.2
<i>Hippocampus zosterae</i>	Dwarf seahorse	196	3.2
<i>Opsanus beta</i>	Gulf toadfish	141	2.3
<i>Orthopristis chrysoptera</i>	Pigfish	115	1.9
<i>Anchoa mitchilli</i>	Bay anchovy	113	1.9
<i>Chasmodes saburrae</i>	Florida blenny	112	1.8
<i>Bairdiella chrysoura</i>	Silver perch	110	1.8
<i>Harengula jaguara</i>	Scaled sardine	72	1.2
<i>Lucania parva</i>	Rainwater killifish	56	0.9
<b>Crabs</b>			
<i>Neopanope</i> sp.	Mud crab	10931	83.0
<i>Portunus gibbesii</i>	Portunid crab	795	6.0
<i>Libinia dubia</i>	Spider crab	542	4.1
<i>Callinectes sapidus</i>	Blue crab	358	2.7

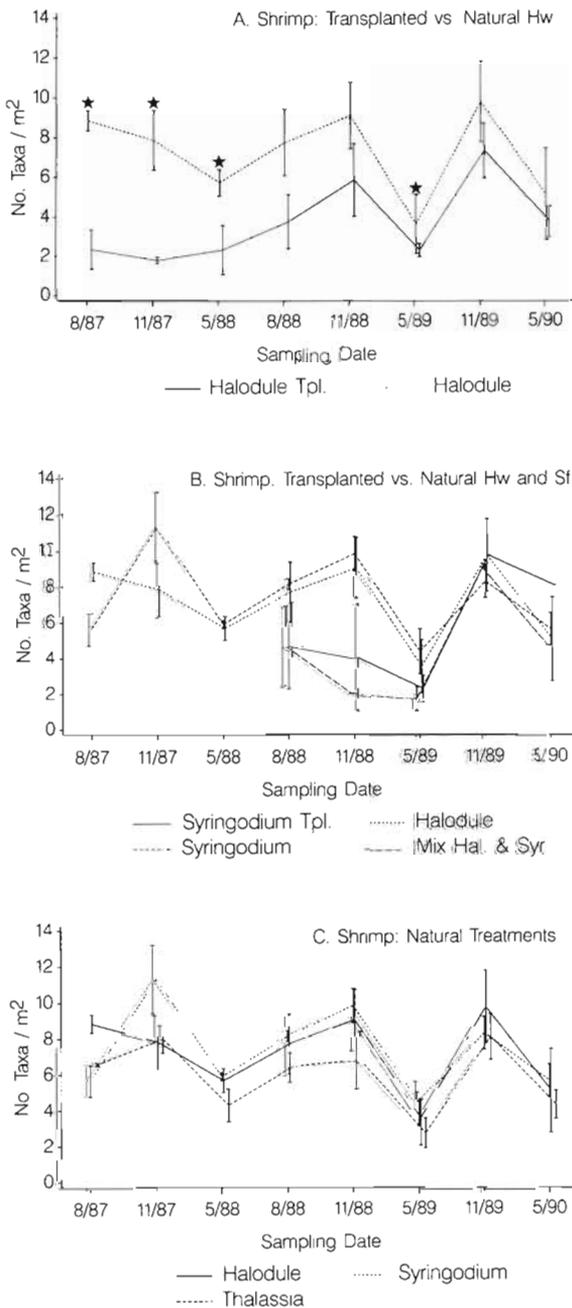


Fig. 1 Number of taxa m<sup>-2</sup> for shrimp species by sampling date. Note unequal times between sampling dates. (A) Natural and planted *Halodule wrightii*, (B) natural and planted *Syringodium filiforme*, (C) naturally occurring seagrass. Error bars: 1 SE. (★) Significantly different ( $p < 0.05$ )

**Number of individuals**

**Shrimp.** By November 1988 (1.2 yr), ln-transformed shrimp density in planted *Halodule wrightii* was not significantly different  $F_{1,02}$ ,  $p > 0.35$ ) from that in natural *H. wrightii* (Fig. 4A). Because there was insuffi-

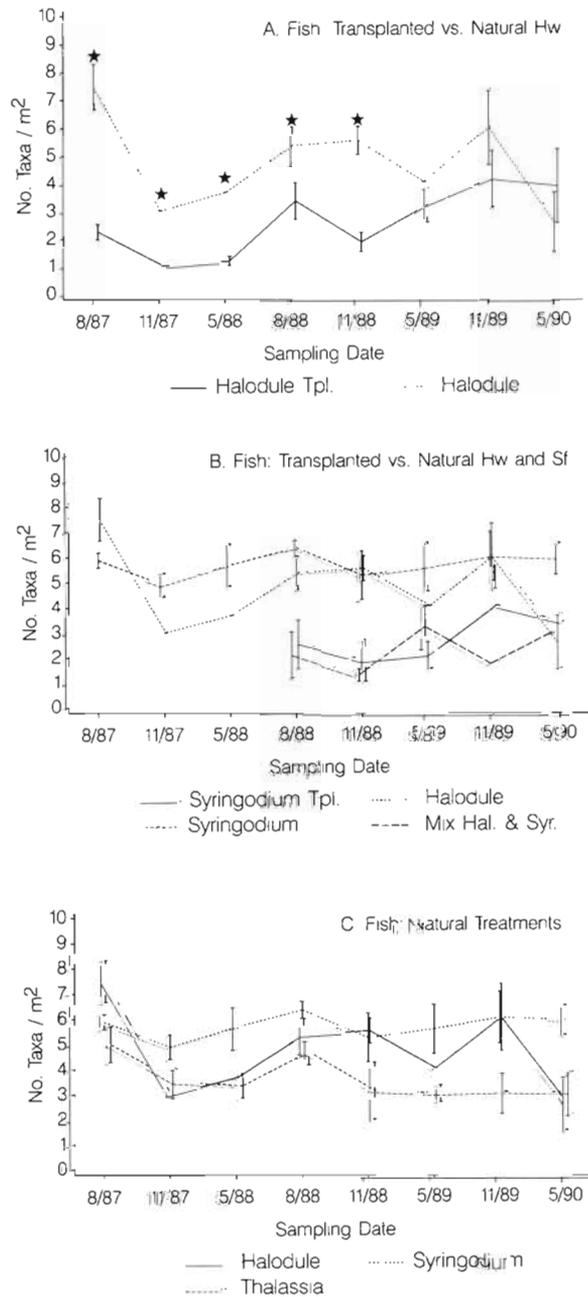


Fig. 2 Number of taxa m<sup>-2</sup> for fish species by sampling date. Note unequal times between sampling dates. (A) Natural and planted *Halodule wrightii*, (B) natural and planted *Syringodium filiforme*, (C) naturally occurring seagrass. Error bars: 1 SE. (★) Significantly different ( $p < 0.05$ )

cient replication for statistical tests of shrimp density in natural versus planted *Syringodium filiforme* and mixed-species bed treatments, only a graphical comparison was made. Trends in shrimp density in the planted *S. filiforme* and mixed-species bed treatments were similar to natural beds, but abundance in plan-

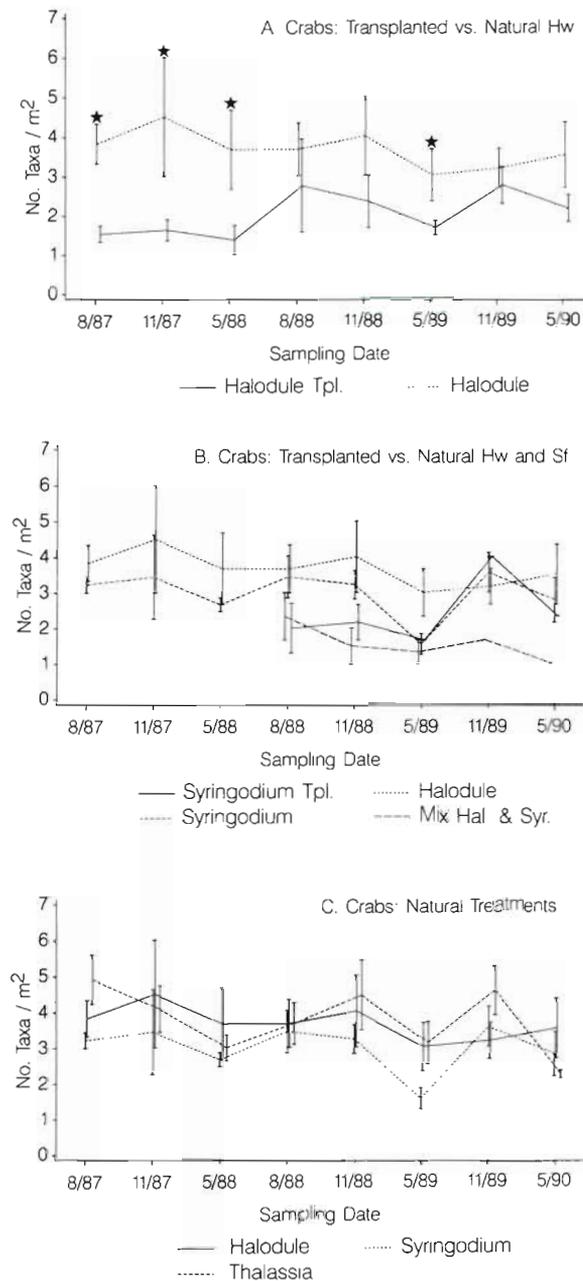


Fig. 3. Number of taxa  $m^{-2}$  for crab species by sampling date. Note unequal times between sampling dates. (A) Natural and planted *Halodule wrightii*, (B) natural and planted *Syringodium filiforme*, (C) naturally occurring seagrass. Error bars: 1 SE. (★) Significantly different ( $p < 0.05$ )

ted beds was much lower than in natural beds ( $\sim 200$  ind.  $m^{-2}$  less; Fig. 4B).

Numbers of individuals in natural *Halodule wrightii*, *Thalassia testudinum* and *Syringodium filiforme* beds were similar to each other (Fig. 4C). Significant differences ( $F_{4,95}$ ,  $p = 0.05$ ) were found among natural bed treatments on only 1 occasion (May 1988), when *H.*

*wrightii* had the highest density. Over the course of the study, the *T. testudinum* bed averaged 111, *H. wrightii* 151, and *S. filiforme* 383 ind.  $m^{-2}$ . November peaks of shrimp density in *S. filiforme* set that treatment apart from the others. Shrimp density in bare areas (mean 3.02  $m^{-2}$ , maximum 8.67  $m^{-2}$ , not shown) was always substantially lower than in any natural bed.

**Fish.** Fish density in both natural and planted *Halodule wrightii* decreased from August 1987 until May 1988 but remained significantly different through May ( $F_{162,43}$ ,  $p < 0.01$ ). By August 1988 ( $\sim 1.1$  yr), no further significant differences (August:  $F_{1,46}$ ,  $p > 0.2$ ) were observed in mean fish densities among planted and natural seagrass beds (Fig. 5A). Trends in fish density in planted *Syringodium filiforme* and mixed-species bed treatments were markedly different from those in planted *H. wrightii*. By the end of the study, the remaining *S. filiforme* and mixed-species bed transplants had a fish density only  $\sim 20\%$  that of natural *S. filiforme* beds (Fig. 5B).

Among natural beds, estimates of fish densities were similar ( $\sim 20$   $m^{-2}$ ) although mean density in *Thalassia testudinum* beds tended to be lower than other seagrass species (Fig. 5C). Significant differences in fish densities were detected only once among natural beds (May 1988:  $F_{10,67}$ ,  $p < 0.01$ ) with higher densities in *Syringodium filiforme* than *T. testudinum* (but not *Halodule wrightii*) beds. Fish densities in bare areas averaged 1.74  $m^{-2}$  with a maximum of 5.92  $m^{-2}$  (not shown).

**Crabs.** All planted treatments showed little or no increase in crab density over time (Fig. 6A, B). Crab density in planted *Halodule wrightii* was not different from natural *H. wrightii* from November 1988 to November 1989 (e.g. November 1989:  $F_{2,37}$ ,  $p > 0.2$ ) (Fig. 6A). Any similarity in crab density between natural and planted *H. wrightii* appeared to have resulted from a decline in the natural crab density bed (Fig. 6A). A similar pattern was observed among crab densities from planted *Syringodium filiforme* and mixed-species beds (Fig. 6B).

Unlike shrimp and fish, crab densities in natural *Halodule wrightii* and *Thalassia testudinum* beds declined gradually from August 1987 to May 1989, followed by a slight increase to the end of the study (Fig. 6C). With the exception of peaks in crab densities in natural *Syringodium filiforme* beds in May 1988 and 1990, crab densities were very similar among natural beds. In May 1988, the only significant difference among natural bed treatments was detected with *S. filiforme* having higher densities than *T. testudinum* (but not different from *H. wrightii*:  $F_{2,37}$ ,  $p > 0.15$ ). Crab densities in bare areas averaged 1.91  $m^{-2}$  with a maximum of 6.60  $m^{-2}$  (not shown).

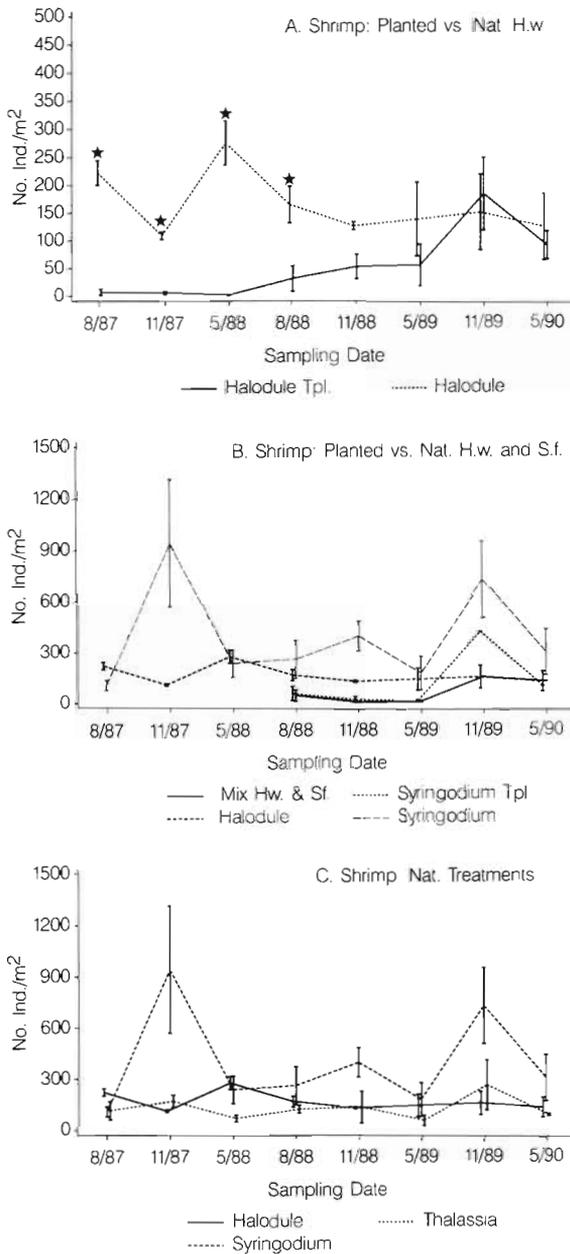


Fig. 4. Number of ind.  $m^{-2}$  for shrimp species by sampling date. Note unequal times between sampling dates. (A) Natural and planted *Halodule wrightii*, (B) natural and planted *Syringodium filiforme*, (C) naturally occurring seagrass. Error bars: 1 SE. (★) Significantly different ( $p < 0.05$ )

**Faunal composition**

Contrasts of taxonomic composition between natural *Halodule wrightii*, *Syringodium filiforme* and *Thalassia testudinum* illustrated marked similarity over the course of the study for all taxonomic groups (shrimp, fish, crabs) (Table 3). In contrast, on the first date of collection, planted and natural bed taxonomic

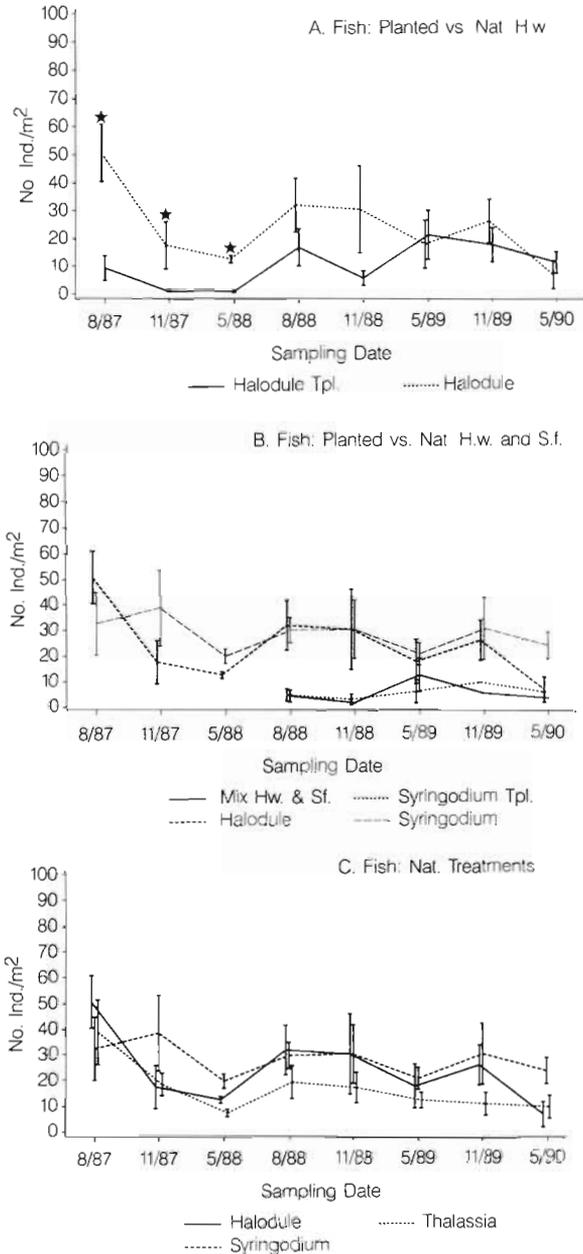


Fig. 5. Number of ind.  $m^{-2}$  for fish species by sampling date. Note unequal times between sampling dates. (A) Natural and planted *Halodule wrightii*, (B) natural and planted *Syringodium filiforme*, (C) naturally occurring seagrass. Error bars: 1 SE. (★) Significantly different ( $p < 0.05$ )

composition were alike, but the similarity then declined during the following 3 to 5 sampling dates for all taxonomic groups (Table 4). Species composition in planted beds then converged with natural beds at slightly different rates for each of the 3 taxonomic groups: ~1.8 yr for shrimp, ~2.3 yr for fish and ~1 yr for crabs for most seagrass treatment comparisons.

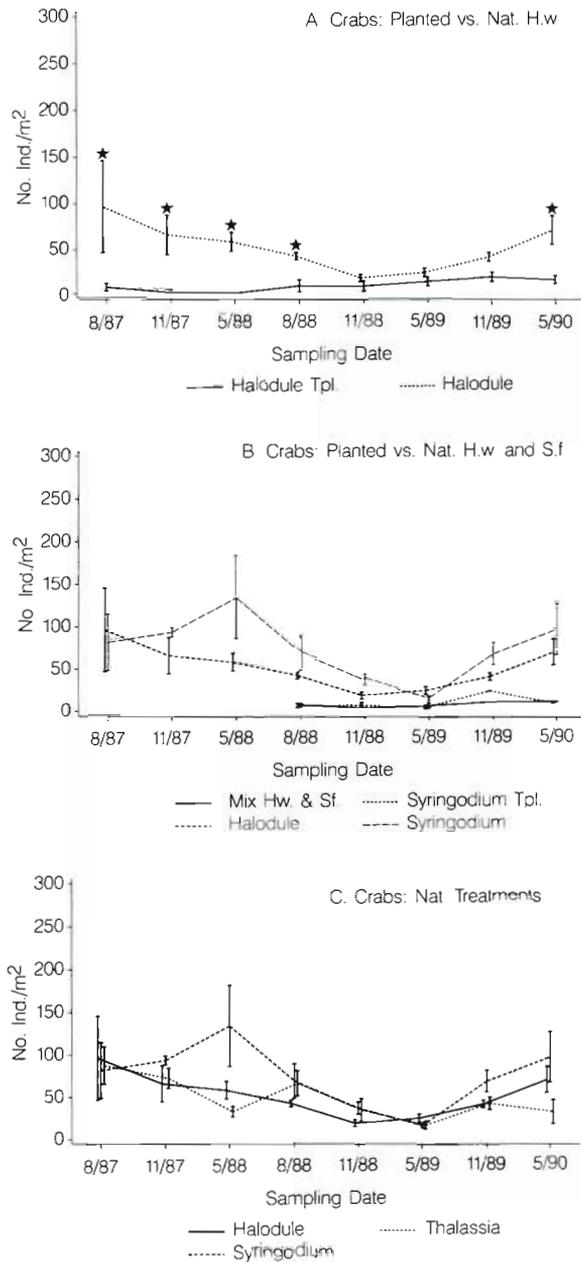


Fig. 6. Number of ind.  $m^{-2}$  for crab species by sampling date. Note unequal times between sampling dates. (A) Natural and planted *Halodule wrightii*, (B) natural and planted *Syringodium filiforme*, (C) naturally occurring seagrass. Error bars: 1 SE. (★) Significantly different ( $p < 0.05$ )

Convergence of planted *Syringodium filiforme* faunal composition with that of natural seagrass species occurred much more rapidly for shrimp and crabs (with the exception of 1 unexplained divergence with fish in November 1989) than observed for *Halodule wrightii* (Table 4). Only crabs from planted *S. filiforme* displayed an initial similarity with natural beds, followed

by a drop, with gradual reconvergence over time, as seen with *H. wrightii* comparisons. Taxonomic similarity among planted and natural *S. filiforme* tended to lag behind similarities among planted *S. filiforme* contrasted with other natural seagrass species.

When species composition in mixed seagrass species plantings and natural *Halodule wrightii* and *Syringodium filiforme* was compared, a very different similarity pattern emerged (Table 4). Similarity values comparing mixed beds and natural beds were lower than similarity values comparing monospecific planted beds with natural beds (Table 4). Similarity among mixed planted beds converged only once (May 1989) for the taxonomic groups shrimp and crabs. Fish showed a peak at this same time but did not approach the similarity of comparisons among natural beds (Table 4).

### Size comparisons

The average body size of species in planted *Halodule wrightii* beds was divided by that of the same species found in natural beds (Fig. 7). This inspection was somewhat confounded by lack of data where a certain species might occur in planted but not natural beds or vice versa, leaving no basis for computing an individual species' ratio for a particular sampling time. Therefore, ratios were averaged among species within categories of fish, shrimp, and crabs (Fig. 7). No consistent pattern of this ratio was visually recognizable within any species composing the top 95% of the catch, either seasonally or over time (not shown). Therefore, there was no suggestion of a temporal sequence of development for any species group. However, on 5 of the 8 sampling dates, mean fish and crab sizes were larger in planted beds and, on 7 of the 8 sampling dates, mean shrimp sizes were larger in planted beds. More than half of the time, fauna encountered in planted *H. wrightii* beds were larger than in natural beds.

### Seagrass-animal relationships

Significant ( $p < 0.05$ ) least squares regressions resulted when natural-log-transformed numbers of taxa and individuals were regressed on areal shoot density (not shown). Although most observations were made after the plantings had coalesced (reached 100% cover), a significant ( $p < 0.001$ ) positive, linear regression was found for number of taxa and number of individuals ( $r^2 = 0.67$  and  $0.65$ , respectively), suggesting a positive influence of seagrass areal shoot density. However, even with the  $\ln$  transformation, a visual inspection of the data suggested a nonlinear relationship.

Table 3. Percentage similarity comparisons (Comp) by category, over time among natural beds. hw: natural *Halodule wrightii*; sf: natural *Syringodium filiforme*; tt: natural *Thalassia testudinum*

Category	Comp	Date							
		Aug 87	Nov 87	May 88	Aug 88	Nov 88	May 89	Nov 88	May 90
<b>Fish</b>	hwsf	87	41	68	85	79	64	74	61
	hwtt	80	50	57	80	48	68	59	67
	sftt	77	65	74	57	48	59	61	50
<b>Shrimp</b>	hwsf	70	34	94	68	59	99	47	78
	hwtt	87	58	88	74	50	93	78	91
	sftt	75	78	87	56	37	92	38	77
<b>Crabs</b>	hwsf	95	87	93	74	63	87	90	99
	hwtt	94	95	90	74	68	88	76	88
	sftt	92	88	84	85	81	80	72	88

Therefore,  $\ln(\text{faunal density} + 1)$  was regressed on areal shoot density using an asymptotic function. The points in time at which fish and shrimp density were no longer significantly different among natural and planted *Halodule wrightii*, *Syringodium filiforme*, and mixed-species beds was noted from Figs. 4 & 5, and the estimated areal shoot density for that time was computed based on a regression presented in Fonseca et al. (1996). The  $\ln$ -transformed animal densities were graphed as a

function of areal shoot density (Fig. 8A–C) for *H. wrightii*, *S. filiforme*, and mixed-species bed planted treatments, respectively. The predictions of faunal densities based on areal shoot densities using the asymptotic model closely matched the distribution of the observed data. A close fit to the asymptotic model indicated that the density of animals in all planted treatments became similar to that of natural bed treatments at areal shoot densities corresponding to early stages of planted bed

Table 4. Percentage similarity comparisons (Comp) by category, over time for planted beds versus natural beds. ht: *Halodule wrightii* transplant; hw: natural *H. wrightii*; sf: natural *Syringodium filiforme*; tt: natural *Thalassia testudinum*; st: *S. filiforme* transplant; hs: mixed *H. wrightii* and *S. filiforme* planting

Category	Comp	Date							
		Aug 87	Nov 87	May 88	Aug 88	Nov 88	May 89	Nov 89	May 90
<b>Fish</b>	hthw	57	51	29	21	47	68	71	62
	htsf	58	1	31	19	39	39	66	76
	httt	48	34	29	24	75	64	57	61
	sthw				47	49	51	23	59
	stsf				43	39	48	23	53
	sttt				57	80	43	41	62
	hshw				30	23	30	5	8
	hssf				30	20	48	1	24
	<b>Shrimp</b>	hthw	69	35	17	68	50	81	81
htsf		58	8	15	37	30	82	49	83
httt		67	24	26	69	73	76	62	81
sthw					34	39	73	65	83
stsf					13	18	72	22	84
sttt					31	49	78	63	77
hshw					35	13	83	51	21
hssf					21	3	83	14	13
<b>Crabs</b>		hthw	90	67	54	77	70	92	87
	htsf	92	61	47	62	63	82	80	7
	httt	87	66	63	72	68	83	96	9
	sthw				73	55	55	58	4
	stsf				70	18	46	50	4
	sttt				78	29	52	71	6
	hshw				59	43	89	25	
	hssf				56	11	89	20	6

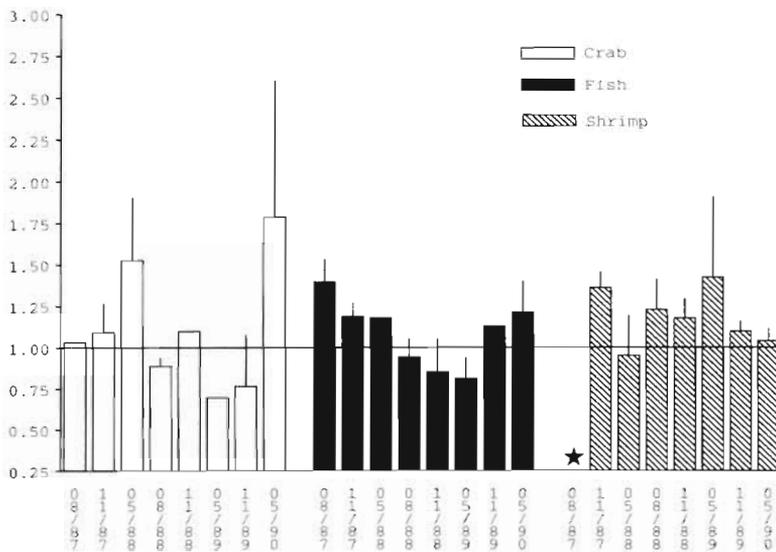


Fig. 7. Average ratio of body size in planted versus natural beds. Ratios were computed on a by-species basis and averaged by class categories of crabs, fish and shrimp for each sampling time. Note unequal times between sampling dates. Error bars: 1 SE. (★) No matching species

development, and well below the average areal shoot densities for natural seagrass beds of the same species (Fig. 8A, B). Because there were no naturally occurring mixed seagrass species sampled, no corresponding natural bed areal shoot densities were computed (Fig. 8C).

Based on the rate of development of planted beds (Table 4 in Fonseca et al. 1996) and the relation of animal density to plant density as computed in Fig. 8, we applied simple ratios and computed the approximate time to expect animal densities in planted beds to equal that of natural beds as the result of varying initial planting density (Table 5). We estimate that doubling spacing between plantings will extend the period to animal density equivalency among planted and natural beds by a factor of ~2.

**DISCUSSION**

**Environmental effects and control comparisons**

Much has been written about the relationship of seagrass bed fauna to a wide variety of ecological factors (e.g. plant morphology: Bell & Westoby 1986a, b, c, Virnstein & Howard 1987, Edgar 1990, Schneider & Mann 1991; biomass: Stoner 1979, 1980; structural complexity in general: Heck & Whetstone 1977), but in this study performance of seagrass transplants could not be ascribed to gradients of environmental conditions. Significant relationships were found among faunal categories and environmental variables

(canopy height, macroalgal biomass, salinity, temperature, and water depth; Table 1). However, only 2 out of 12 of these relations accounted for >5% of the variation in animal density. Variation due to seasonal effects was often approximately equal to or greater than any individual variable effect. Moreover, because comparisons were only made among treatments at each survey time, and planted and natural treatments occurred adjacent to each other, any trends in environmental conditions were likely to act simultaneously, if not equally, on the treatments under comparison. The lack of consistent pattern in variation and low partial  $r^2$  for most variables in accounting for variation in animal density among treatments leads us to conclude that interactions of animals with any systematic (study-wide) changes in environmental conditions were not responsible for the observed, systematic increase in animal density

within planted beds during the study. Therefore increased animal density in transplanted beds and similarity among planted and natural beds over time most likely resulted from the persistence and spread of the planted beds over that time.

To further control for effects of planted bed development on animal numbers and composition we conducted surveys of adjacent, unvegetated areas simultaneous with those of planted and natural areas. Macroepibenthic animal densities in bare areas remained very low throughout the study and always significantly lower than in planted or natural beds, indicating that colonization of planted beds by fauna was the result of the presence of the beds themselves and not changes in baseline animal densities throughout the Bay during our study.

Table 5. *Halodule wrightii*. Estimated effects of planting unit spacing on development of planted seagrass beds in Tampa Bay, Florida. Calculations for plant and animal (shrimp only) equivalency times based on simple ratios of planting spacings applied to empirical findings from this study

Spacing among planting units (m)	0.5	1.0	2.0
Time to equivalent shoot density (planted vs natural beds) (yr)	1.8	3.6	7.2
Time to equivalent faunal density (planted vs natural beds) (yr)	1.2	2.5	5.0

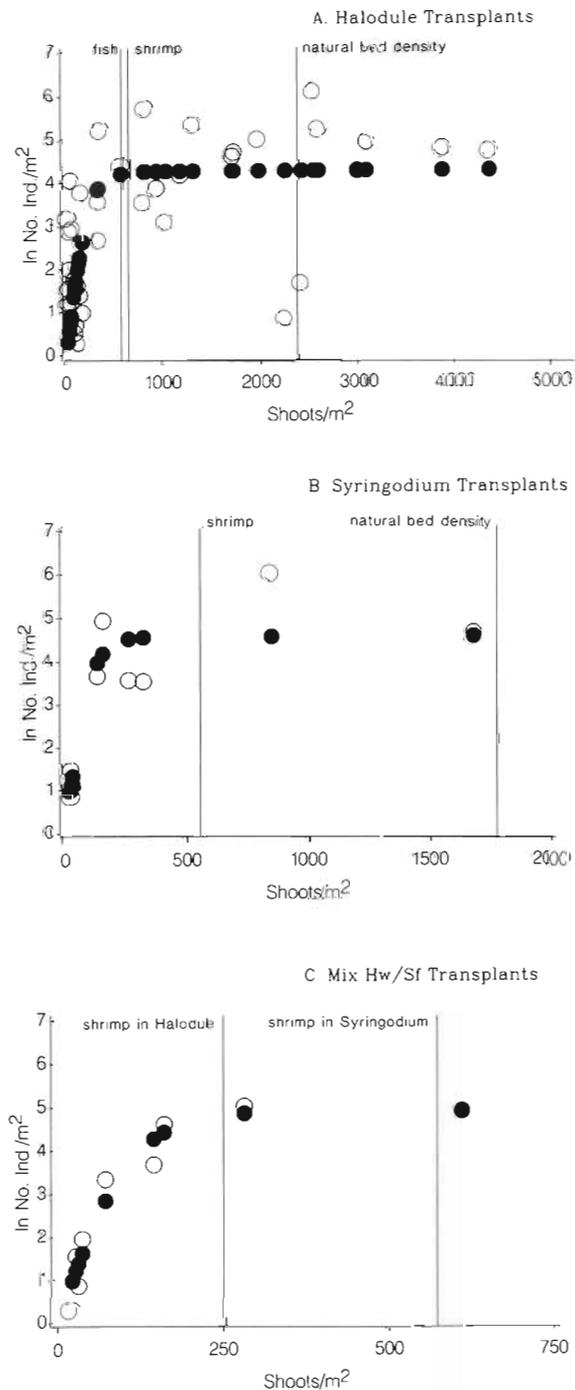


Fig. 8. Natural-log-transformed faunal density plotted against areal shoot density. (O) Observed points, (●) predicted points using an asymptotic function. (A, B) Vertical line for 'shrimp' or 'fish' shows areal shoot density at which densities of these animals first became not significantly different among planted and natural versions of that seagrass species; natural bed density: the study-wide average areal shoot density of natural beds of that seagrass species. (C) Same as (A) only specified by seagrass species due to mixed planting of both seagrass species. Note different areal shoot density scales

### Monitoring for mitigation: selection of parameters and monitoring duration

Rapid development of equivalent numbers and species of fish and shrimp among planted and natural beds was the norm based on beds planted on 0.5 m centers. This equivalency occurred within 2 yr, a period well within that recommended for monitoring a planting project (Fonseca 1989, 1992, 1994). However, changes in crab density over the course of the study did not follow this pattern, demonstrating a potentially critical flaw in evaluation of seagrass restoration projects. Crab numbers in natural beds declined and then rose again to early study levels. Most of this decline appeared to be the result of a reduction in density of *Neopanope* spp. The timing of the natural bed decline in crab density (Fig. 6A) coincided with the time frame when numbers of shrimp and fish in planted beds became equivalent to natural beds (not significant,  $p > 0.05$ ). We speculate that whatever mechanism was responsible for the decline in natural bed crab densities may have also influenced crab densities in the planted beds. Had the study lasted only 1 or 2 yr, it is likely this background fluctuation would not have been detected, possibly leading to a very different interpretation of the data. These results lend credence to a requirement of extended monitoring periods for the holistic evaluation of faunal recovery in planted seagrass beds, particularly if low species richness is found in control areas.

Another result arguing for an extended monitoring period arose from the similarity data. The planted seagrass was colonized in the early stage of the study and then, over many weeks, was apparently not able to support a taxonomic similarity equal to that of natural beds. One reason may be that the fragmented seagrass pattern as formed by the discrete planting units did not provide suitable habitat (as compared to the final, coalesced form of the beds). Planted beds displayed an initial similarity to natural beds for fish, shrimp and crabs, followed by a decline in similarity to natural beds with a subsequent rebound, indicating not only that more species were shared over time, but also that the species being shared were present in similar proportions (i.e. species evenness increased over time). In many instances, similarities between planted and natural treatments at the first sampling time (either for fish, shrimp or crabs) were comparable in magnitude both to values seen later in the study and to among-natural-bed comparisons. Because animals found early after planting tended to be larger than those in natural beds, we attribute the initially high taxonomic similarity to immigration from nearby natural beds in response to the structure provided by the newly planted seagrass (*sensu* Virnstein & Curran

1986, Sogard 1989), perhaps as part of an ongoing habitat search strategy by fauna (*sensu* Virnstein & Curran 1986, Sogard 1989). Thus, early in the study, colonization apparently relied on adults rather than recruitment at early life history stages (settle and stay strategy: *sensu* Bell & Westoby 1986a, b, c, Bell et al. 1987). The list of possible reasons for the early drop in similarity however is all-inclusive, including higher predation rates in the early stage of planted bed development where the seagrass existed as small, isolated patches. Other explanations might include insufficient food resources in these patches precipitating subsequent emigration. Overall our 3 yr pattern of eventual compositional similarity (at least for fish and shrimp) corroborates Smith et al. (1989), who determined that short-term monitoring was not sufficient to demonstrate functional development of restored seagrass beds. In this study 3 yr of natural bed sampling was barely adequate to effectively compare these planted beds with natural beds even though they were planted at a high density (0.5 m centers).

The early, rapid changes in faunal composition of planted beds may have meaning for other experimental approaches. Initially high similarity among planted and natural beds and a subsequent rapid decline suggests potential problems in using short-term studies (days to weeks) to infer transplant performance. Here planted beds were studied over a much longer period than artificial seagrass units (ASU) used in other studies (e.g. Bell & Westoby 1986c, Sogard 1989), largely because ASU have limited deployment periods due to fouling. Here a short-term ASU type experiment (here >~90 d and <~1 yr) could not have observed the eventual recovery of faunal similarity. Thus the observations of change in crab density and the fluctuation in composition of the planted beds over time provide 2 reasons for using caution when interpreting short-term experiments or surveys to infer faunal community structure in seagrass beds without concomitant surveys of nearby natural beds.

While early colonization may be rapid, longer-term experiments are needed to better assess the animal communities within seagrass habitats. Recently Brown-Peterson et al. (1993) suggested that seagrass beds 31 yr old may sustain differences in fish assemblages from that of even older beds. However their samples of 31 yr old and older beds were from different sides of a barrier island lagoon, which in itself could impose gradients on fish communities apart from those of site age alone. Their study points out the gap in our knowledge about the long-term replacement value of created seagrass beds and that without long-term data we can only assume that our findings, including those presented here, will extrapolate across greater temporal scales.

### Constraints imposed by initial conditions

The initial spacing of the planting units also sets bounds on interpreting the rate at which planted beds take on functions of natural beds. If plantings are made on 0.5 m centers (as done here), the number of planting units required to complete a project can be very high and for larger areas, 0.5 m spacing may not be economically feasible. But we expect wider spacing to substantially increase the time to achieve functional equivalency among planted and natural beds (Table 3 in Fonseca et al. 1996). This indicates that the monitoring period for direct faunal assessments of planted beds should be scaled in direct inverse proportion to initial planting density. These conclusions are based on numerical abundance alone; relative faunal composition among planted and natural beds is another consideration for assessing functional equivalency.

### Consistency of results among seagrass species

Testing the consistency of the similarity and animal density response among different species of planted seagrass was compromised due to loss of treatment replicates. Because several planted areas failed, replication of *Syringodium filiforme* and mixed *Halodule wrightii* and *S. filiforme* transplant treatment beds fell to 1 each; thus, statistical testing was not possible, and only qualitative conclusions can be drawn from the *S. filiforme* and mixed-species bed treatments. Subsequently a more detailed examination of animal density and composition on a site-by-site basis (not shown) indicated that the adjacent planted *H. wrightii* at this site (Skeet Key) supported fauna very similar to the other planted *H. wrightii* sites around Tampa Bay. This suggests that the animal composition and abundance data from the remaining *S. filiforme* and mixed species planting may have been representative of Tampa Bay as well. But it remains that the relatively rapid faunal colonization of *H. wrightii* transplants cannot be quantitatively contrasted with what appeared to be a slower colonization of *S. filiforme* and mixed-species bed transplants. We also could not quantitatively contrast faunal composition in planted *S. filiforme* with other treatments, which otherwise showed trends like that observed in *H. wrightii* (initially large, rapid increase of similarity with natural beds followed by declines). The lack of compositional similarity of the remaining mixed species planting after 21 mo raises the possibility that if these seagrass species are in competition, as suggested by Williams (1990), suboptimal fishery habitat may result for some indeterminate period. But without replication we can-

not determine whether the development at that particular location in Tampa Bay was arrested due to local peculiarities or if mixed species plantings require additional time to develop equivalent animal communities.

### Seagrass species substitution (out-of-kind mitigation)

Besides comparisons of faunal development among natural and planted beds of the same seagrass species, comparisons with other seagrass species afforded the opportunity to partially evaluate the consequences of out-of-kind mitigation (Lewis 1989). We conclude that the animal density and composition (composed of species able to be harvested with this gear type) among the different natural seagrass species studied in Tampa Bay were generally similar over the course of the study, although *Syringodium filiforme* beds tended to have seasonally higher animal densities. Although differences in faunal density and composition have been reported among beds composed of different seagrass species (e.g. Stoner 1980, 1983, Virnstein & Howard 1987), those differences were detected when data were (1) collected from geographically distinct areas, introducing the potential for site-to-site variation (Thayer & Chester 1989) or (2) normalized to various plant parameters such as standing stock, which indicated that even certain algal species would support similar animal densities. In contrast, our study reports findings on a unit area basis, irrespective of the structure of the seagrass, and attempts to generalize on the relative roles of the different seagrass species, with consideration given to the importance of temporal variability. We recognize the value of correcting for the influence of habitat attributes, such as algal biomass or complexity (e.g. degree of bifurcation of algae) on animal abundance. But in the context of the decision framework that is imposed on managers in dealing with habitat restoration and mitigation issues, comparing seagrass beds on a unit area basis more closely addresses the aspects of the plant community where managers can effect change: the unit area of habitat generated by a given planting project. Therefore if animal densities stabilize at relatively low shoot densities (as discussed below), then simple measures such as area of seafloor colonized and not complexity per unit area of seafloor (e.g. shoot density, biomass, seagrass surface area) may infer recovery of certain fishery resources.

Are these data sufficient to recommend allowing substitution of one seagrass species for another as a mitigation practice? Having said that animal densities were equivalent among the natural seagrass beds, we

caution strongly against attempting to extrapolate these data to mean that one natural seagrass bed is or is not the functional equivalent of another. Our data on faunal attributes define a very narrow aspect of seagrass habitat function. First, the gear used in this study imposed limitations on the size of the animals that can be caught; most animals caught by dropnets and similar gear are small, resident fauna (Kushlan 1981). Second, other critical attributes of seagrass habitats which may serve to differentiate among seagrass species' functions, such as primary production, nutrient cycling rates, sediment erosion control, epiphytic development, associated macroalgae, and predator-prey interactions, were not measured. In the absence of such holistic evaluations, it is logical that goals for restoration projects should ultimately be the development of the seagrass species which were present consistently over time (where time is the period of available, objective records). We feel that our data should be used only to point out the homology in response by fauna to developing seagrass beds and should not be interpreted as supporting seagrass species substitution.

### Threshold responses of animals to seagrass bed development

Questions of species substitution aside, the eventual equivalency of fish and shrimp among planted (especially *Halodule wrightii*) and natural beds was clear, as indicated by the significant correlation between areal shoot density and faunal density. This correlation is congruent with findings of numerous other investigators (Heck & Whetstone 1977, Heck & Orth 1980, Stoner 1980, 1983, Lewis 1984, Orth et al. 1984, Stoner & Lewis 1985, Bell & Westoby 1986a, b, c, Bell et al. 1987, Sogard et al. 1987, Sogard 1989, Orth 1992), but had not been demonstrated in the case of planted seagrass beds as they developed. Here the seagrass density at which animal density in planted beds became arguably equal ( $p < 0.05$ ) to natural beds was only a third of the average, natural bed shoot density. Although linear models could account for 67 and 65% of the variability, respectively, in numbers of taxa and faunal density in planted treatments over time, a non-linear, asymptotic relationship between  $\ln(\text{animal density} + 1)$  and seagrass areal shoot density was apparent (Fig. 8). The congruence of animals and areal shoot density in the asymptotic model implies that monitoring areal shoot density development and persistence may be an acceptable (and much less costly) diagnostic parameter for determining a threshold planting success than direct measures of faunal abundance, composition, and size. From a management perspective, it would be useful to know if this ratio (1 to 3

planted: natural bed shoot density for generating equivalent animal densities) holds for predicting faunal recovery across a wide range of shoot densities in other geographic locations.

As with the similarity data, there are several ecological factors that could explain the apparent threshold response of animal density to plant density. None can be rejected because we cannot provide evidence that any processes were or were not additive, or in fact even whether they occurred at all (*sensu* Quinn & Dunham 1983). However, by relying on studies where changes in habitat structure were experimentally imposed, we can theorize some potential causes that bear further investigation. There is some suggestion of competitive exclusion or selection for predation resistance, given that animals in planted beds tended to be larger than those in natural beds (Fig. 7). If larger animals were able to differentially exploit the low initial areal shoot density of the early planted beds, this could have resulted in establishment of equivalent animal densities among natural and planted beds at a lower seagrass density than might be encountered in a natural bed; shifting the threshold response to seagrass densities lower than normally encountered in mature, natural beds (Fig. 8). But if occurrence of larger individuals is an indication of competition, we must ask how any competitive tactics could be maintained (maintenance of larger body sizes; Fig. 7) after the beds coalesced and structural similarity was reached among planted and natural beds. Other potential mechanisms accounting for size discrepancies include reluctance on the part of small animals to move across unvegetated gaps to the planted beds, creating the observed size disparity and yielding the same effect as high predation rates. Moreover if some larger animals could survive transit of the unvegetated gaps among planted and natural beds, they may have initially found little in the way of necessary food resources in the newly planted beds to induce them to stay. In the absence of more detailed manipulative experiments yielding information on predation and animal movement, competition and food resources, we do not know which of these ecological conditions, or if some other unrecognized factor, may be the root cause of the observed threshold.

Other studies (Crowder & Cooper 1979, Heck & Orth 1980, Heck & Thoman 1981, Savino & Stein 1982) have observed similar asymptotic or threshold responses of animals to habitat complexity (i.e. plant surface area, biomass, shoot density). Predation efficiency has been shown to drop substantially in response to small changes in habitat complexity (Savino & Stein 1982, James 1989). Release from predation could account for the rapid increase in animal

density in the planted beds if some seagrass habitat threshold were reached. However, these responses have not been consistent among studies. Stoner (1979) found that high sea-grass surface area/unit weight did not afford the best protection from predators. Stoner (1989) attributed this higher predation to enhanced detection by the predator when the prey were in a *Halodule wrightii* bed, where spaces among the shoots were small in comparison to the prey's size. Such discrepancies are the basis for Heck & Crowder's (1991) caution against generalizations regarding animal responses to changes in habitat complexity without understanding the specifics of predator strategy, habitat complexity and prey behavior.

Heck & Crowder (1991) contrast 2 models relating energy gain by predators at different levels of habitat complexity in aquatic ecosystems. In order to compare our findings with these models, we will assume for the moment that our observations of low initial animal densities and rapid reduction in compositional similarity in planted beds (*Halodule wrightii* at least) as compared with natural beds were the result of predation. Given this assumption, our results do not agree well with a model proposed by Crowder & Cooper (1979) in which net energy gained by predators was described as a normal distribution, with peak energy gain at intermediate levels and suppression at both low and high extremes of the habitat complexity scale. Rather, our asymptotic relationship of animal numbers with seagrass density may be more supportive of the model proposed by Heck & Orth (1980), in that high net gain by predators would have occurred at low levels of habitat complexity; net gain diminished markedly at low to intermediate, rather than high, levels of habitat complexity, if the observed animal densities were the result of predation.

We also recognize the substantial differences in experimental approach between this study and previous ones. Here we followed changes in seagrass density (one form of habitat complexity) over time from very low, essentially colonizing densities to that of natural beds, therefore sampling across a range of habitat complexity approached by few other studies. Moreover most past work has measured changes in animal density, behavior and/or composition in response to an abrupt encounter with changes in habitat complexity, such as the deployment of artificial seagrass (Sogard 1989). Similar experimental protocol using abrupt changes in complexity have been employed in closed systems such as ponds (Crowder & Cooper 1979, 1982). Here the experiment was composed of gradual changes in habitat complexity over time as the planted seagrass coalesced in an open system. Thus changes in seagrass surface area and/or biomass were conflated with changes in areal shoot

density over time (Fonseca et al. 1996). By comparison natural bed structural complexity (surface area, biomass, density) was relatively constant over time or at least varied in proportion to planted beds over seasons within a given seagrass species. Despite these differences in spatial and temporal effort, our findings of an asymptotic relationship between animal and seagrass density are remarkably congruent with observations of threshold densities in studies that either imposed immediate, static variations in habitat complexity, or utilized closed systems, or both (e.g. Crowder & Cooper 1979, 1982, Heck & Orth 1980) despite our ignorance of the mechanism.

### Summary

Whatever the mechanisms, it is apparent that once a certain level of habitat complexity was reached, additional complexity in the form of shoot density (and thus, biomass and surface area) or macroalgal biomass did not significantly alter the numerical abundance or composition of animals in the planted beds (narrowly defined as dropnet-derived measures of macroepibenthic fauna, i.e. residents) once that threshold had been reached during our study. These data provide a novel corroboration of previous studies employing temporally static, as opposed to temporally dynamic, seagrass structure. From a management perspective, measures of areal shoot density may provide an important first check point on the road to functional restoration of seagrass habitat. However, there are many other ecological functions that seagrass beds perform that we did not study and that may not exhibit a similar threshold response. Thus, measures of total coverage and persistence of planted beds (Fonseca 1989, 1992, 1994) remain a crucial component of data collection to infer long-term restoration success.

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