Fauna of Natural Seagrass and Transplanted *Halodule wrightii* (Shoalgrass) Beds in Galveston Bay, Texas

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Abstract

We compared nekton and benthos densities and community compositions in a natural mixed seagrass bed dominated by *Halodule wrightii* (shoalgrass) with those found in three shoalgrass transplant sites and adjoining sand habitats in western Galveston Bay, Texas, U.S.A. Quantitative drop traps and cores were used to compare communities up to seven times over 36 months post-transplant where transplant beds survived. Total densities of fishes, decapods, annelids, benthic crustaceans, and most dominant species were significantly higher in natural seagrass than in transplanted shoalgrass or sand habitats during most sampling periods. On occasion, fish and decapod densities were significantly higher in transplanted shoalgrass than in adjoining sand habitats. No consistent faunal differences were found among transplant sites before two of three sites failed. Taxonomic comparison of community compositions indicated that nekton and benthos communities in natural seagrass beds were usually distinct from those in transplanted beds or sand habitats, which were similar. We conclude that reestablishing a shoalgrass bed that resembles a natural seagrass bed and its faunal communities in the Galveston Bay system will take longer than 3 years, provided that transplants persist.

Key words: seagrass, transplant, nekton, fishes, decapods, benthos, community structure, shoalgrass, *Halodule wrightii*, habitat restoration.

Introduction

Significant losses of seagrasses have been reported from many areas of the world (Short & Wyllie-Echeverria 1996). Coincident with, or subsequent to, the disappearance of seagrasses are declines or alterations of local faunal communities and loss of many habitat functions such as provision of shelter and food, habitat complexity, and sediment stabilization (Kirkman 1992; Sheridan et al. 1997; Fonseca et al. 1998). Many reported losses are due to direct or indirect human impacts like dredging or eutrophication (Pulich & White 1991; Gordon et al. 1996; Pergent-Martini & Pergent 1996; Short & Wyllie-Echeverria 1996; Short et al. 1996). The human response often has been to restore degraded or lost seagrass beds or to create new ones, although planting seagrasses is not always successful (Lewis 1987; Fonseca et al. 1998).

The usual goal of restoration activities is to develop a minimum seagrass coverage within a certain time period (Fonseca et al. 1998), for example 70% coverage within 1–3 years, with provision for supplemental planting if the goal is not met. Other success criteria, such as ensuring seagrass shoot densities or faunal densities comparable with those found in natural seagrasses, are rarely examined; thus, it has been difficult to determine the relative values of natural and transplanted seagrass beds (Fonseca et al. 1996, 1998).

Transplanted seagrass beds appear to provide at least some of the structural and functional attributes of natural seagrass beds. Benthic faunal densities in transplanted *Zostera marina* (eelgrass) and *Halodule wrightii* (shoalgrass) beds have been shown to exceed those of adjacent bare substrates in relatively short order (203 days; Homziak et al. 1982) and, for polychaetes, to equal or exceed those of natural beds at 2–4 years of age (Bell et al. 1993). Therefore, enhanced prey densities for upper trophic levels and potential for detrital and nutrient cycling by burrowers seem to occur quickly. Fish and shrimp densities and species richness in newly transplanted eelgrass beds exceeded those in unplanted substrates in less than 1 year, and 1.9-year-old eelgrass beds harbored shrimp densities similar to those in adjoining natural beds although fish densities remained low (Fonseca et al. 1990). Nekton (fishes and decapod crustaceans) densities and species composition in densely transplanted shoalgrass beds were similar to those of adjacent natural beds within 1–2 years (Fonseca et al. 1996). Thus, the mobile macrofauna responds quickly to the provision of habitat complexity, provided that the new habitat persists. The refuge function of

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newly transplanted seagrasses remains questionable: *Argopecten irradians* (bay scallop) disappeared more rapidly from 6-month-old transplanted eelgrass beds than from natural beds, most likely due to more successful seabird predation in the patchy new habitat (Smith et al. 1988).

Seagrass restoration is a prominent feature of the Galveston Bay Comprehensive Conservation and Management Plan, wherein restoration of 567 ha of submerged aquatic vegetation has been proposed (Galveston Bay National Estuary Program 1995). Seagrasses were lost from western Galveston Bay between 1975 and 1982 as direct and indirect responses to hurricane damage, subsidence, and waterfront development of western Galveston Island (Pulich & White 1991; Hammerstrom et al. 1998). Pilot restorations of shoalgrass were conducted in western Galveston Bay during 1994, and shoalgrass survival and growth were monitored over 16 months post-transplant (Sheridan et al. 1998). In the present study, we compared nekton and benthos densities and species composition in those transplanted shoalgrass beds, in adjoining nonplanted sand substrata, and within a nearby mixed seagrass meadow seven times over the 36 months post-transplant. The goal of this project was to estimate the increase in local density of fishery and forage organisms that could be expected with successful seagrass restoration, in advance of the planned large-scale restoration of seagrasses to Galveston Bay.

Methods

Site Descriptions

Shoalgrass transplanting was completed in May 1994 at two sites on western Galveston Island (Fig. 1) as described by Sheridan et al. (1998). Restored beds (one at Redfish Cove and two at Snake Island Cove) each contained all combinations of four different planting densities (0.25-, 0.5-, and 1.0-m centers and nonplanted controls) at three arbitrary depth ranges (shallow, medium, and deep). A total of 3,492 plants was placed in 1,296 m^2 at each site. On any given sampling date, actual depth differences were 15–20 cm between shallow and deep areas at each site. During May–September 1994, the perimeter of each planted bed was surrounded by a fence (10 × 16-mm mesh × 1.2-m high black plastic) to reduce bioturbation by crabs and rays.

Transplants at Snake Island Cove maintained 40–50% survival and 30–40% coverage until 16 months post-planting, when very few live plants were found (Sheridan et al. 1998). During the present study we observed no live plants in these two beds at 27 and 36 months post-transplant (October 1996 and May 1997). Transplants at Redfish Cove maintained at least 70% survival and 70% coverage for the first 16 months (Sheridan et al. 1998) and persisted through 36 months. Floral and faunal monitoring at Snake Island Cove was thus limited to the first 16 months. We did not measure shoalgrass survival, coverage, or shoot densities at Redfish Cove during the final two sampling periods because shoalgrass coverage was patchy. Faunal samples were not taken randomly at the transplant site but were targeted to visible shoalgrass coverage only.

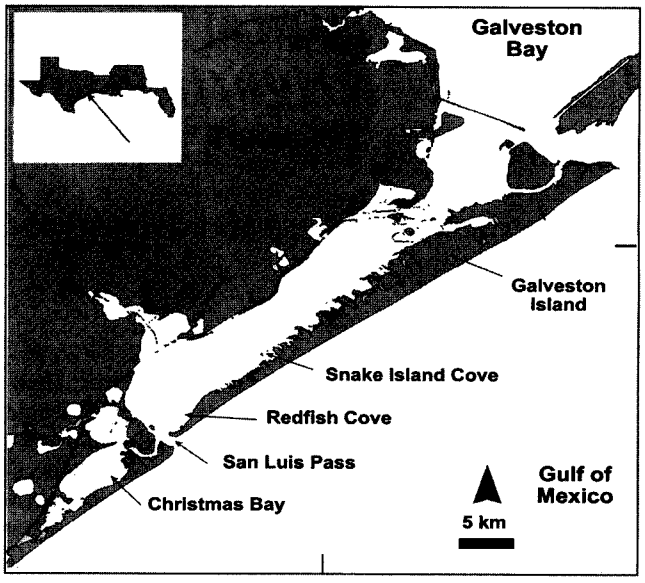

Figure 1. Location of sampling sites in western Galveston Bay, Texas.

Transplanted beds were compared with a reference seagrass bed in nearby Christmas Bay (Fig. 1). All sites were within 20 km of each other. Crotwell (1997) found shoalgrass and *Halophila engelmannii* (clovergrass) occurred more frequently in Christmas Bay than *Ruppia maritima* (wigeongrass) and *Thalassia testudinum* (turtlegrass) (100% and 75% vs. 23% and 5% frequency of occurrence, respectively) and that shoalgrass was biomass dominant (exceeding 50 g dry weight/m^2 in 10 of 12 months vs. 1–2 months for other species). We did not record seagrass species composition when sampling Christmas Bay, other than to note visually that shoalgrass was dominant. The Christmas Bay bed has been present at least since 1956 (Hammerstrom et al. 1998) and was the closest natural bed to the transplant sites. Although choosing the closest bed as a reference site may not have been optimum, the next closest beds positioned near a tidal pass were more than 150 km southwest in Matagorda Bay. This distance increased the potential for variations in biotic and abiotic factors to confound any observed community differences between sites. Water temperature, salinity, and light transmittance were similar among the chosen sites (Sheridan et al. 1998).

Sampling Design

Designs for sampling nekton and benthos were derived from a series of 25 throw trap samples and 25 cores collected haphazardly along a longitudinal transect through

the Christmas Bay seagrass bed in October 1993. Densities of fishes and decapod crustaceans were estimated by clearing a 1.0 $m^2 \times 0.8$-m deep throw trap constructed of solid aluminum sheets and bars (modified from Kushlan 1981). The throw trap was deployed and swept repeatedly with a rigid, form-fitting, 3-mm mesh seine until no targeted organisms were recovered in three consecutive sweeps (six sweeps minimum). Fishes and decapods were frozen or preserved in 10% formalin-seawater. Densities of benthic organisms were estimated using a 78.6 cm^2 (10 cm diameter) corer taken to a depth of 5 cm adjacent to each throw trap. Each core was sieved through a 0.5-mm mesh screen, and retained materials were preserved in 10% formalin-seawater with rose bengal stain added to assist sorting. Organisms were enumerated and identified to the lowest practical taxon.

Each data set was subjected to a power analysis after $\log(x + 1)$ transformation of densities (Sokal & Rohlf 1981). Power analyses indicated a minimum of nine samples would permit detection of a 100% difference in means between any two habitats with $\alpha = 0.10$ and $1\text{-}\beta$ = power = 0.90 for densities of annelids, amphipods, total benthos, 10 of 11 dominant species of fishes and decapods (those averaging more than $1/m^2$), total fishes, and total decapods. We then collected nine nekton and benthos samples per habitat and site for pretransplant and the first 5 post-transplant sampling periods, followed by 10 samples per site for the last two periods.

Nekton Sampling

In April 1994 before planting shoalgrass, nekton samples were collected haphazardly across the future transplant bed at Redfish Cove and along a transect perpendicular to shore in Christmas Bay to compare pretransplant faunal densities. After transplanting, samples were collected in July and September 1994; April, June, and September 1995; October 1996; and May 1997. For the first five sampling periods post-transplant, nekton samples were collected as follows: (1) one sample randomly placed in each of the nine plant density $\times$ depth combinations at each site ($n = 27$); (2) nine samples randomly placed in unplanted sand within the fence post perimeter at each site ($n = 27$); and (3) nine samples along each of three transects in Christmas Bay ($n = 27$). During July and September 1994, an additional nine samples were collected in sand habitat outside each transplant bed perimeter ($n = 27$) to determine whether the fencing altered nekton densities.

Nekton sampling in natural seagrass was conducted along three transects established in Christmas Bay to mimic the relative distances between Redfish Cove (RC) and Snake Island Cove (9 km apart) and between Snake Island Cove east and west (SE and SW, 20 m apart). One transect (Christmas Bay East, CBE) lay on the northeastern end of the bed and two transects (Christmas Bay west 1 and west 2, CB1 and CB2) lay 2 km southwest and 20 m apart. Each transect was a grid 60 m long and 10 m wide, and nekton samples came from randomly chosen 1-m^2 plots within the grid. For the final two sampling periods, collections were limited to seagrass habitats only at RC and CBE ($n = 10$). A minimum of 5 m was maintained between all throw trap samples to minimize faunal disturbance.

Benthos Sampling

After transplanting, benthic organisms were sampled from planted sections only of each restored bed using the same design as for nekton ($n = 9$ per site). In Christmas Bay, benthic organisms were sampled along transects differing from the nekton sampling transects. Three transects 20 m long, 9 m wide, and approximately 1 km apart were spaced along the length of the seagrass bed. Two benthic sampling transects were located near nekton transects CBE and CB2, and the third benthic transect was 1 km west of CB2. One randomly placed benthic sample was collected from inner, middle, and outer thirds of each transect each month except July 1994 ($n = 9$). Densities of benthic organisms were estimated using a 78.6 cm^2 (10 cm diameter) corer to 5-cm depths, except in 1996 and 1997 when a 176.8-cm^2 (15 cm diameter) corer was used. Data from the latter collections were standardized to 78.6 cm^2 for statistical analysis and tabular comparison of densities (numbers of taxa were not adjusted). Nematodes and harpacticoid copepods were included in benthic samples because they were relatively abundant, although they were probably undersampled given the large sieve mesh.

Shoalgrass transplanting was conducted using intact plugs of plant material and surrounding sediments (Sheridan et al. 1998). We were concerned about introducing nonindigenous animals to the transplant sites. For the purpose of detecting any introductions, benthic cores were collected at all seagrass donor locations and transplant sites in April and May 1994 (before transplanting). Ten cores were collected at 6-m intervals along transects perpendicular to the shoreline at each site. Species compositions were compared before and after planting.

Statistical Analysis

Habitat-related faunal differences during each sampling period were examined by one-way analysis of variance (ANOVA) with balanced cell sizes. We tested for differences in the following: (1) densities of total fishes, decapods, annelids, and non-decapod benthic crustaceans; (2) densities of regularly occurring abundant taxa; and (3) total number of nekton and benthos taxa (Table 1). The main effect of habitat type in the nekton ANOVA consisted of three transects in the natural seagrass bed (CB1, CB2, CBE), three transplanted shoalgrass beds (RCT, SET, SWT), and three sand habitats (RCS, SES, SWS). ANOVA for benthos was conducted among the four seagrass beds (CB [= pooled CB1, CB2, and CBE], RCT, SET, and SWT) because sand habitats were not sampled.

For total fishes, decapods, annelids, benthic crusta-

Table 1. Example of analysis of variance (ANOVA) tables for comparison of nekton and benthos densities by habitat.

Taxon	*Date*	*Source*	df	*SS*	*MS*	*F*	p
Fishes	Apr 1994	Habitat (sand and natural seagrass only)	1	3.799	3.799	40.072	<0.001
		Residual error	16	1.520	0.095		
	Jul 1994	Habitat	8	12.464	1.558	16.004	<0.001
		Contrasts					
		Natural seagrass vs. transplanted shoalgrass	1	5.950	5.950	61.127	<0.001
		Transplanted shoalgrass vs. sand	1	0.891	0.891	9.152	0.003
		Transplant sites RCT vs. SET	1	0.001	0.001	0.146	0.904
		Transplant sites RCT vs. SWT	1	0.077	0.077	0.787	0.378
		Transplant sites SET vs. SWT	1	0.057	0.057	0.587	0.446
		Residual error	72	7.009	0.097		
	Oct 1996	Habitat (natural seagrass, transplant site RCT)	1	0.349	0.349	7.055	<0.001
		Residual error	18	0.891	0.050		
Annelids	Jul 1994	Habitat (transplant sites only)	2	0.162	0.081	1.654	0.212
		Contrasts					
		Transplant sites RCT vs. SET	1	0.136	0.136	2.805	0.107
		Transplant sites RCT vs. SWT	1	0.002	0.002	0.050	0.826
		Transplant sites SET vs. SWT	1	0.102	0.102	2.108	0.159
		Residual error	24	1.165	0.046		
	Oct 1994	Habitat (no sand)	3	4.521	1.507	26.244	<0.001
		Contrasts					
		Natural seagrass vs transplanted shoalgrass	1	0.429	0.429	7.468	<0.001
		Transplant sites RCT vs. SET	1	0.175	0.175	3.040	0.091
		Transplant sites RCT vs. SWT	1	2.559	2.559	44.554	<0.001
		Transplant sites SET vs. SWT	1	1.397	1.397	24.317	<0.001
		Residual error	32	1.838	0.057		
	Oct 1996	Habitat (natural seagrass, transplant site RCT)	1	3.488	3.488	77.773	<0.001
		Residual error	18	8.190	0.455		

Models include tests for the main effect of habitat (natural seagrass, sand, transplanted shoalgrass) and for *a priori* contrasts between specific habitat types. The examples present data for total fishes and total annelids as sample collection changed. Some examples apply to several sampling dates: for nekton, July 1994 = September 1994 and April, June, and September 1995; for benthos, October 1994 = April, June, and September 1995; and for nekton and benthos, October 1996 = May 1997. df, degrees of freedom; SS, sums of squares; MS, mean square.

ceans, and nekton and benthos taxa, we also examined five a priori contrasts within the main effect to test for specific differences of interest in habitat utilization: (1) natural seagrass versus transplanted shoalgrass, (2) transplanted shoalgrass versus sand (nekton only) and between transplant site pairs, (3) RCT versus SET, (4) RCT versus SWT, and (5) SET versus SWT (Table 1). Multiple comparison of treatment means used Scheffé's test (Day & Quinn 1989). Similarity of community compositions during each sampling period was compared using pooled samples, unweighted pair-group average cluster analysis of Euclidean distances, and nonmetric multidimensional scaling (MDS) of the resultant distance matrices. Stress values less than 0.2 were maintained in MDS to ensure valid representation of sample relationships (Clarke 1993). We used simple linear regression to examine the relationships of fish, decapod, and nekton species densities to seagrass coverage or shoot density at the transplant sites (seagrass data from Sheridan et al. 1998). We were unable to do similar analyses with benthos data because benthos and seagrass collections were not made at the same times and places.

Examination of the distribution of error terms for abundant macrofauna and for seagrass characteristics before analysis indicated no gross violations of assumed normality (Shapiro-Wilk test statistic). Data were also tested for homogeneity of variance using Levene's test and were log(x + 1) transformed where necessary to meet this assumption (percent seagrass coverage was always arcsine transformed). Transformation was not always successful in achieving homogeneity of variances before ANOVA. Therefore, we conducted analyses using a lower probability level for significance ($p \leq 0.01$) as suggested by Underwood (1981). Tabular data are untransformed means, but ANOVA and multiple comparison results are from transformed data. Analyses were conducted using STATISTICA personal computer software (StatSoft, Inc. 1997).

Results

Fence Effects

Comparison of fenced versus nonfenced sand during July 1994 and September 1994 indicated no significant differences in densities of total fishes, decapods, nekton taxa, or dominant species, with one exception. In July 1994, *Farfantepenaeus aztecus* (brown shrimp) were significantly more abundant inside fences than outside (10.4 ± 0.9/m^2 SE vs. 3.7 ± 0.6/m^2 SE; one-way ANOVA, $p < 0.01$).

Table 2. Densities (mean number per m^2 and, in parentheses, standard error) of total fishes, decapods, and nekton species recorded in three transects of a natural mixed seagrass bed (CBE, CB1, CB2), three transplanted shoalgrass beds (RCT, SET, SWT), and three sand flats (RCS, SES, SWS) in western Galveston Bay, Texas over time.

	CB1	*CB2*	*CBE*	*RCT*	*SET*	*SWT*	*RCS*	*SES*	*SWS*	*ANOVA* p	*Contrast* p *values* 1	2	3	4	5
Fishes															
Apr 94	—	—	16.2 (2.0)	—	—	—	2.6 (1.9)	—	—	<0.001	—	—	—	—	—
Jul 94	13.1 (2.2)	17.3 (2.5)	14.8 (2.3)	2.0 (0.4)	4.3 (2.7)	5.1 (2.2)	0.7 (0.2)	0.6 (0.2)	1.9 (0.8)	<0.001	<0.001	0.003	0.904	0.378	0.446
Sep 94	19.1 (2.6)	14.0 (3.5)	16.3 (2.1)	41.0 (12.9)	5.6 (2.8)	4.6 (2.6)	10.1 (6.0)	10.8 (6.8)	10.0 (6.2)	<0.001	0.004	0.096	<0.001	<0.001	0.442
Apr 95	126.6 (47.8)	47.1 (18.6)	121.3 (32.3)	3.0 (2.0)	6.6 (3.4)	3.8 (1.9)	0.4 (0.2)	0.8 (0.4)	0.3 (0.2)	<0.001	<0.001	0.005	0.150	0.501	0.440
Jun 95	6.4 (1.1)	7.8 (0.5)	8.4 (1.1)	3.7 (1.2)	0.6 (0.3)	1.0 (0.8)	1.3 (0.5)	0.2 (0.1)	0.9 (0.4)	<0.001	<0.001	0.120	<0.001	<0.001	0.754
Sep 95	22.0 (3.2)	7.6 (1.5)	22.7 (1.5)	0.1 (0.1)	4.1 (1.8)	1.3 (0.5)	0.1 (0.1)	1.8 (0.8)	0.3 (0.2)	<0.001	<0.001	0.124	0.001	0.049	0.165
Oct 96	—	—	17.7 (2.2)	9.9 (1.7)	—	—	—	—	—	<0.001	—	—	—	—	—
May 97	—	—	11.6 (2.3)	8.5 (2.2)	—	—	—	—	—	0.197	—	—	—	—	—
Decapods															
Apr 94	—	—	45.6 (5.3)	—	—	—	7.1 (1.4)	—	—	<0.001	—	—	—	—	—
Jul 94	60.2 (4.0)	79.6 (11.4)	88.6 (31.6)	10.4 (2.2)	40.8 (26.2)	38.0 (11.8)	10.8 (1.7)	12.4 (1.2)	14.6 (1.5)	<0.001	<0.001	0.105	0.129	<0.001	0.085
Sep 94	79.6 (5.3)	61.1 (6.7)	141.8 (31.7)	100.9 (55.9)	40.3 (22.8)	26.1 (17.5)	0.7 (0.3)	2.0 (0.8)	1.0 (0.4)	<0.001	<0.001	<0.001	0.169	<0.001	0.026
Apr 95	50.1 (4.6)	43.0 (2.8)	40.6 (8.1)	7.4 (2.9)	4.0 (1.5)	2.1 (1.1)	0.9 (0.2)	0.2 (0.1)	0.2 (0.1)	<0.001	<0.001	<0.001	0.296	0.016	0.161
Jun 95	80.4 (6.0)	86.6 (6.2)	99.1 (5.4)	1.0 (0.3)	0.6 (0.2)	2.0 (1.3)	0.6 (0.3)	0.1 (0.1)	0.2 (0.1)	<0.001	<0.001	0.012	0.291	0.964	0.311
Sep 95	127.8 (10.3)	101.7 (13.1)	120.3 (20.8)	0.6 (0.2)	0.3 (0.2)	0.1 (0.1)	0.3 (0.2)	0.6 (0.2)	0.4 (0.2)	<0.001	<0.001	0.649	0.564	0.194	0.467
Oct 96	—	—	97.3 (15.2)	17.4 (2.6)	—	—	—	—	—	<0.001	—	—	—	—	—
May 97	—	—	40.1 (7.5)	9.2 (0.2)	—	—	—	—	—	<0.001	—	—	—	—	—
Nekton species															
Apr 94	—	—	8.4 (0.5)	—	—	—	2.1 (0.3)	—	—	<0.001	—	—	—	—	—
Jul 94	10.2 (0.8)	11.2 (1.2)	11.3 (0.8)	4.6 (0.4)	4.6 (1.5)	4.2 (0.4)	4.0 (0.4)	2.1 (0.3)	2.7 (0.3)	<0.001	<0.001	0.006	0.165	0.675	0.330
Sep 94	13.6 (0.6)	12.2 (1.0)	12.8 (1.0)	9.2 (1.1)	6.1 (1.6)	3.4 (1.1)	2.1 (0.4)	1.9 (0.4)	1.8 (0.4)	<0.001	<0.001	<0.001	0.029	<0.001	0.013
Apr 95	10.7 (0.6)	10.4 (0.5)	7.9 (1.0)	3.0 (0.9)	2.9 (0.7)	2.3 (0.7)	1.2 (0.3)	1.0 (0.4)	0.6 (0.2)	<0.001	<0.001	<0.001	0.766	0.563	0.382
Jun 95	10.1 (0.6)	10.3 (0.5)	10.2 (0.6)	2.4 (0.4)	1.0 (0.5)	1.3 (0.7)	1.3 (0.3)	0.3 (0.2)	0.9 (0.4)	<0.001	<0.001	0.040	0.003	0.005	0.820
Sep 95	12.0 (0.6)	10.6 (0.9)	12.0 (1.0)	0.6 (0.2)	1.0 (0.3)	0.9 (0.3)	0.4 (0.3)	1.0 (0.3)	0.7 (0.2)	<0.001	<0.001	0.484	0.270	0.354	0.859
Oct 96	—	—	13.7 (0.8)	7.8 (0.8)	—	—	—	—	—	<0.001	—	—	—	—	—
May 97	—	—	7.3 (0.9)	5.2 (0.9)	—	—	—	—	—	0.072	—	—	—	—	—

Transplanting was completed in May 1994. Results of ANOVA comparisons among sites and for *a priori* contrasts are indicated as *p* values. Contrasts include (1) natural vs. transplant, (2) transplant vs. sand and between transplant site pairs, (3) RCT vs. SET, (4) RCT vs. SWT, and (5) SET vs. SWT. See Table 1 for ANOVA models. —, no data.

Nekton Communities

Total densities of fishes and nekton species were significantly higher in natural seagrass than in transplanted shoalgrass or sand habitats during most sampling periods, with the exception of May 1997 when fish densities and nekton species in natural and transplanted shoalgrass were similar (Table 2). Total decapod densities were always significantly higher in natural seagrass (Table 2). There were several occasions when fish and decapod densities in transplanted shoalgrass were significantly higher than densities in adjoining sand habitats, although these differences did not always co-occur. Nekton species in transplanted shoalgrass were always significantly more numerous than in sand habitats (Table 2). There were occasional differences in densities of fishes, decapods, and nekton species among transplant sites, mostly associated with higher densities at Redfish Cove, but there were no consistent trends.

A total of 5,961 fishes representing 48 taxa and 16,339 decapods representing 29 taxa were collected over all habitats. Proportional contributions of fishes and decapods to the total nekton collections were similar between natural seagrass and transplanted shoalgrass, although total catch was five times higher in natural seagrass (Table 3). Fishes made up a greater proportion of the total catch from sand, which itself was only 25% of the catch from transplanted shoalgrass (Table 3). Fourteen fish taxa (each ≥1% of all fish taxa) composed 94.3% of the total fish catch, and 11 decapod species (each ≥1% of all decapod species) represented 98.3% of the total decapod catch (Table 3). Most of the species that occurred regularly in natural seagrass were absent from sand, and several were observed in transplanted shoalgrass only at low overall densities. Several of the abundant but irregularly occurring species were collected primarily during one sampling period, including *Brevoortia patronus* (gulf menhaden) during April 1995, larval Clupeidae (which may have been gulf menhaden but were too small to identify with certainty) during April 1994, *Farfantepenaeus duorarum* (pink shrimp) in September 1995, *Litopenaeus setiferus* (white shrimp) in September 1994, and *Tozeuma carolinense* (arrow shrimp) in September 1994. Other irregularly occurring species were collected primarily during fall months, including *Anchoa mitchilli* (bay anchovy), *Sciaenops ocellatus* (red drum), *Syngnathus scovelli* (gulf pipefish), and *Alpheus heterochaelis* (bigclaw

Table 3. Nekton comprising ≥ 1% of either fishes or decapods captured in natural seagrasses, sand, or transplanted shoalgrass in Galveston Bay, Texas, shown as grand mean density/m^2 and percent of total individuals, fishes, or decapods.

	Natural (n = 164)		*Sand (n = 144)*		*Transplant (n = 155)*	
Group or Taxon	*Density*	*%*	*Density*	*%*	*Density*	*%*
Fishes	28.2	26.0	2.6	44.4	6.2	26.0
Decapods	80.0	74.0	3.3	55.6	17.7	74.0
Total individuals	17746		852		3702	
Total species	57		41		62	
Collected regularly (during seven or eight sampling periods)						
Gobionellus boleosoma	2.6	9.1	<0.1	1.0	1.1	17.1
Gobiosoma robustum	2.4	8.5	<0.1	0.5	<0.1	0.6
Lagodon rhomboides	1.3	4.7	0.1	2.3	0.4	6.0
Symphurus plagiusa	2.8	9.9	<0.1	0.8	0.7	10.6
Callinectes sapidus	24.1	30.2	0.1	3.0	1.6	9.1
Farfantepenaeus aztecus	22.0	27.5	2.7	81.9	8.6	48.6
Hippolyte zostericola	9.1	11.4	<0.1	0.2	<0.1	0.3
Palaemonetes vulgaris	7.7	9.6	0.0	0.0	0.2	0.9
Palaemonetes pugio	7.5	9.3	<0.1	0.2	3.4	19.1
Palaemonetes intermedius	2.5	3.2	0.0	0.0	<0.1	0.1
Collected irregularly (primarily during one or two sampling periods)						
Brevoortia patronus	14.2	50.4	0.0	0.0	0.2	2.7
Anchoa mitchilli	1.1	4.0	2.0	74.6	1.5	24.6
Syngnathus scovelli	0.7	2.5	0.0	0.0	<0.1	0.1
Clupeidae (larval)	0.6	2.1	0.0	0.0	<0.1	0.2
Sciaenops ocellatus	0.5	1.8	0.0	0.0	0.5	7.4
Eucinostomus argenteus	0.2	0.7	0.1	2.3	0.3	4.3
Leiostomus xanthurus	0.2	0.7	0.1	3.6	0.2	3.0
Cynoscion nebulosus	0.2	0.6	<0.1	0.8	0.3	4.6
Menidia beryllina	0.2	0.6	<0.1	1.3	0.2	3.7
Orthopristis chrysoptera	0.2	0.5	<0.1	0.3	0.2	3.5
Farfantepenaeus duorarum	2.0	2.5	<0.1	0.4	0.2	0.9
Alpheus heterochaelis	2.0	2.5	0.0	0.0	0.1	0.8
Litopenaeus setiferus	1.3	1.7	0.1	1.7	0.3	1.9
Callinectes similis	0.9	1.1	0.1	3.0	0.7	4.1
Tozeuma carolinense	0.1	0.1	0.0	0.0	1.7	9.8

snapping shrimp). Gulf menhaden, larval clupeids, gulf pipefish, pink shrimp, white shrimp, and bigclaw snapping shrimp were collected mainly in natural seagrass, whereas arrow shrimp were almost exclusively found in transplanted shoalgrass. Bay anchovy was found over all habitat types. Still other species were scattered over time and habitat at low overall densities, including *Eucinostomus argenteus* (silver jenny), *Leiostomus xanthurus* (spot), *Cynoscion nebulosus* (spotted seatrout), *Menidia beryllina* (inland silverside), *Orthopristis chrysoptera* (pigfish), and *Callinectes similis* (lesser blue crab).

Four fish species and six decapod species were collected regularly (Table 4). When densities exceeded 1/m^2, these nekton species were usually significantly more abundant in natural seagrass than in transplanted shoalgrass or sand habitats (Table 4). There were two occasions when densities in transplanted shoalgrass equaled or exceeded those in natural seagrass: *Gobionellus boleosoma* (darter goby) and *Palaemonetes pugio* (daggerblade grass shrimp) in September 1994. There were also indications that the presence of transplanted shoalgrass supported significantly higher densities of some dominant species than did sand habitat, including *Callinectes sapidus* (blue crab) in July and September 1994, *Symphurus plagiusa* (blackcheek

Table 4. Densities (mean number per m^2 and, in parentheses, SE) of regularly occurring nekton in natural mixed seagrasses, sand, and transplanted shoalgrass in Galveston Bay, Texas.

	Sampling date							
Species and Habitat	*Apr 94*	*Jul 94*	*Sep 94*	*Apr 95*	*Jun 95*	*Sep 95*	*Oct 96*	*May 97*
Gobionellus boleosoma								
Natural	0.2 (0.2)	0.9 (0.3)	1.9 (0.3)	6.4 (1.2)*	1.3 (0.3)*	0.8 (0.2)	6.6 (1.0)*	4.8 (1.6)
Sand	0	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0	0	—	—
Transplant	—	0.3 (0.2)	4.7 (1.3)*	0.1 (0.1)	0.4 (0.2)	0	0	1.7 (0.8)
Gobiosoma robustum								
Natural	0	5.0 (0.6)*	3.3 (0.6)*	0.6 (0.2)	0.7 (0.2)	3.4 (0.4)*	4.1 (0.9)*	0.1 (0.1)
Sand	0	0.1 (0.1)	0	0	0	0	—	—
Transplant	—	0.1 (0.1)	0.1 (0.1)	0	0	0	0	0
Lagodon rhomboides								
Natural	0	2.4 (0.6)*	0.2 (0.1)	2.3 (0.4)*	2.0 (0.3)*	0.3 (0.1)	0.1 (0.1)	2.3 (0.5)
Sand	0	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)	—	—
Transplant	—	0	0.1 (0.1)	1.7 (0.9)*	0.1 (0.1)	0	0	0.3 (0.2)
Symphurus plagiusa								
Natural	0	3.5 (0.6)*	3.0 (0.4)*	0.1 (0.1)	1.2 (0.2)*	8.4 (1.3)*	1.6 (0.5)	0
Sand	0	0	0.1 (0.1)	0	0	0	—	—
Transplant	—	0.5 (0.3)	2.0 (0.7)*	0	0.3 (0.2)	0	2.1 (0.5)	0.3 (0.2)
Callinectes sapidus								
Natural	11.4 (0.8)*	41.4 (7.1)*	32.7 (4.1)*	2.2 (0.3)*	20.1 (1.0)*	33.9 (3.5)*	32.2 (9.5)*	1.8 (0.6)*
Sand	0	0.3 (0.2)	0.1 (0.1)	0	0	0.1 (0.1)	—	—
Transplant	—	1.4 (0.4)*	5.4 (2.4)*	0.2 (0.1)	0.7 (0.3)	0	3.9 (1.3)	0.2 (0.2)
Hippolyte zostericola								
Natural	1.6 (0.7)*	2.2 (0.4)*	7.7 (1.1)*	1.8 (0.4)*	1.0 (0.2)*	32.8 (3.5)*	24.3 (5.8)*	0.4 (0.3)
Sand	0	0	0	0	0	0	—	—
Transplant	—	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)	0	0	0	0
Palaemonetes intermedius								
Natural	1.0 (0.5)	0.9 (0.4)	3.6 (1.9)*	1.0 (0.3)	3.5 (0.8)*	0.9 (0.3)	2.5 (0.9)*	11.4 (3.5)*
Sand	0	0	0	0	0	0	—	—
Transplant	—	0	0	0	0	0	0.1 (0.1)	0
Palaemonetes pugio								
Natural	2.8 (0.8)*	6.3 (3.2)*	11.8 (5.5)*	0	16.3 (2.1)*	8.4 (1.7)*	0.9 (0.6)	3.1 (1.5)
Sand	0.1 (0.1)	0	0	0	0	0	—	—
Transplant	—	0.5 (0.5)	18.8 (14.3)*	0	0	0	0.3 (0.2)	0
Palaemonetes vulgaris								
Natural	1.4 (0.5)*	3.7 (1.0)*	4.8 (1.4)*	1.8 (0.3)*	34.1 (2.8)*	0.6 (0.2)	2.8 (1.0)*	0.3 (0.3)
Sand	0	0	0	0	0	0	—	—
Transplant	—	0.1(0.1)	0.4 (0.2)	0.4 (0.3)	0	0	0	0
Farfantepenaeus aztecus								
Natural	27.2 (4.6)*	18.2 (2.1)	23.7 (1.8)*	34.0 (2.5)*	11.8 (0.8)*	19.7 (1.7)*	24.8 (3.3)*	21.8 (3.6)*
Sand	6.1 (1.2)	10.4 (0.9)	0.9 (0.2)	0.4 (0.1)	0.1 (0.1)	0.3 (0.1)	—	—
Transplant	—	23.2 (7.5)	20.0 (5.3)*	3.2 (0.7)*	0.5 (0.2)	0.3 (0.1)	1.1 (0.5)	4.6 (1.3)

Transplanting was completed in May 1994. *Significant ANOVA main effects at $p < 0.01$. See Table 1 for ANOVA models. Means indicated with different underlining were significantly different (Scheffé's test). —, no data.

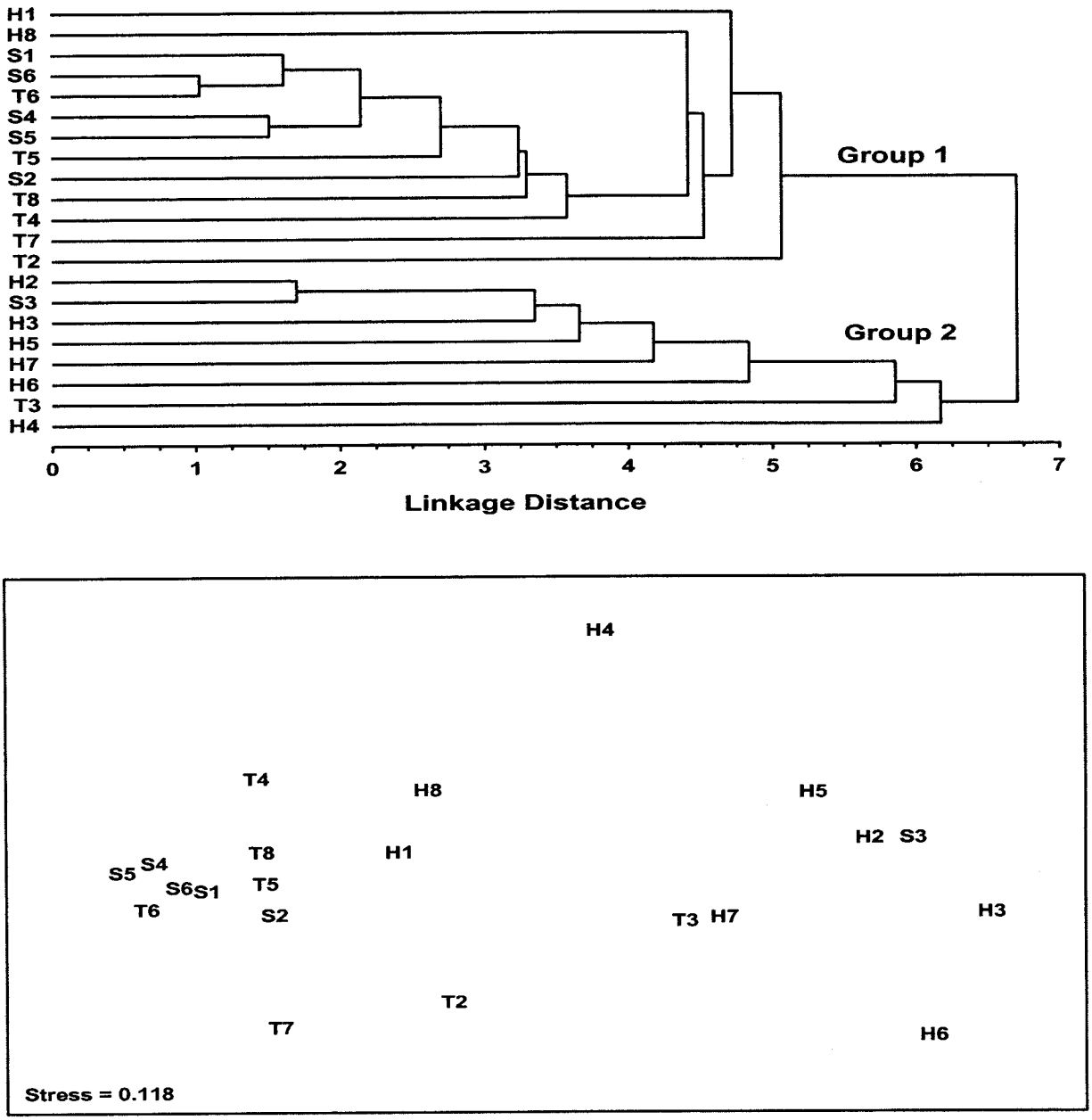

Figure 2. Cluster analysis (upper) and MDS ordination (lower) of nekton communities by habitat type and sampling date using UPGMA linkage of a Euclidian distance matrix. H, natural mixed seagrasses; S, sand; T, transplanted shoalgrass. Sampling dates are sequentially numbered (1, April 1994 to 8, May 1997).

tonguefish) in September 1994, brown shrimp in September 1994 and April 1995, and *Lagodon rhomboides* (pinfish) in April 1995. All of these instances occurred during the first 13 months after transplanting.

Two assemblages of nekton communities were identified through classification and ordination of the pooled temporal data (Fig. 2). Nekton group 1 encompassed all but one each of the sand and transplanted shoalgrass communities, as well as the initial and final natural seagrass communities. Nekton group 2 included all other natural seagrass communities and the distinctive sand and transplant communities. Group 1 communities were characterized by low densities of most species, as well as fewer taxa overall, typical of sand and transplanted shoalgrass. The April 1994 and May 1997 natural seagrass communities (sampling dates 1 and 8) were placed in group 1 because they had relatively low densities of usually abundant taxa such as *Gobiosoma robustum* (code goby), darter goby, blackcheek tonguefish, bigclaw snapping shrimp, blue crab, *Hippolyte zostericola* (zostera shrimp), and *Palae-*

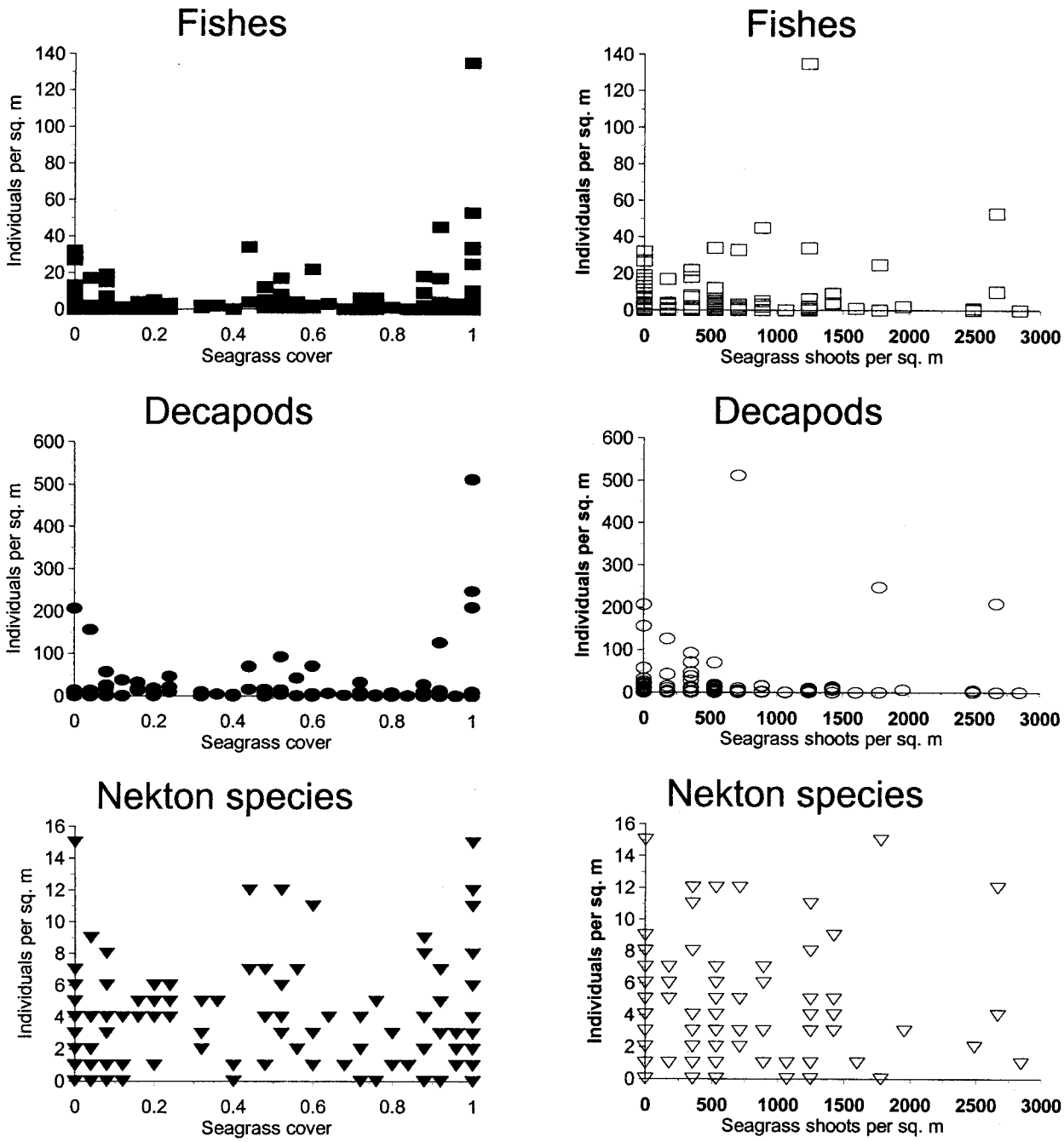

Figure 3. Nekton densities plotted against seagrass coverage and shoot density at transplanted shoalgrass beds.

monetes vulgaris (marsh grass shrimp). In contrast, the usually depauperate sand and transplanted shoalgrass communities were placed in Nekton group 2 during September 1994 (sampling date 3) by virtue of relatively high densities of many of the aforementioned species, as well as bay anchovy, *Lagodon rhomboides* (pinfish), brown shrimp, and daggerblade grass shrimp, which typified natural seagrass for most of the sampling periods. There were no obvious patterns in density change attributable to minor species that would have led to separation of the two groups.

We detected no relationships between densities of total fishes, total decapods, or nekton species and either seagrass coverage or shoot density in the transplanted shoalgrass beds (regression adjusted R^2 values of 0.016 to 0.038; Fig. 3).

Introduction of Nonindigenous Benthic Taxa

Transport of live plants and sediments from donor sites to transplant sites potentially involves transport of nonindige-

Table 5. Densities (mean number per 78.6 cm^2 and, in parentheses, SE) of total annelids, non-decapod crustaceans, and benthic taxa recorded in a natural mixed seagrass bed (CB) and three transplanted shoalgrass beds (RCT, SET, SWT) in Galveston Bay, Texas over time.

	CB	*RCT*	*SET*	*SWT*	*ANOVA* p	*Contrast* p *Values* 1	2	3	4
Annelids									
Jul 94	—	28.8 (2.7)	54.9 (15.4)	30.7 (3.1)	0.212	—	0.107	0.826	0.159
Oct 94	103.4 (16.1)	66.6 (10.9)	46.1 (9.9)	12.0 (2.6)	<0.001	<0.001	0.091	<0.001	<0.001
Apr 95	188.4 (20.7)	35.2 (4.0)	20.4 (2.2)	31.7 (11.0)	<0.001	<0.001	0.030	0.110	0.535
Jun 95	160.9 (22.9)	38.2 (7.2)	39.0 (6.0)	37.3 (7.3)	<0.001	<0.001	0.741	0.973	0.716
Sep 95	181.4 (36.7)	46.7 (7.1)	26.9 (2.5)	20.1 (2.8)	<0.001	<0.001	0.070	0.002	0.137
Oct 96	450.5 (62.9)	68.2 (11.7)	—	—	<0.001	—	—	—	—
May 97	360.4 (36.7)	147.6 (14.7)	—	—	<0.001	—	—	—	—
Non-decapod crustaceans									
Jul 94	—	0.0 (0.0)	1.6 (0.6)	1.0 (0.4)	0.004	—	0.001	0.014	0.348
Oct 94	29.2 (6.6)	2.4 (1.3)	2.6 (0.5)	0.8 (0.3)	<0.001	<0.001	0.285	0.291	0.038
Apr 95	48.4 (11.6)	0.6 (0.4)	1.3 (0.6)	11.9 (8.8)	<0.001	<0.001	0.476	0.008	0.042
Jun 95	76.2 (21.3)	0.2 (0.1)	5.4 (2.6)	4.7 (2.3)	<0.001	<0.001	0.012	0.040	0.596
Sep 95	24.4 (3.6)	1.1 (0.7)	1.2 (0.6)	2.2 (0.6)	<0.001	<0.001	0.793	0.076	0.127
Oct 96	44.9 (6.7)	1.0 (0.5)	—	—	<0.001	—	—	—	—
May 97	202.3 (45.2)	1.6 (0.5)	—	—	<0.001	—	—	—	—
Benthic taxa									
Jul 94	—	12.7 (0.8)	20.2 (2.0)	15.2 (0.9)	0.002	—	<0.001	0.114	0.028
Oct 94	23.1 (2.1)	14.7 (1.5)	13.4 (1.5)	9.2 (1.2)	<0.001	<0.001	0.601	0.007	0.026
Apr 95	31.0 (1.8)	14.0 (0.7)	12.2 (0.6)	15.1 (2.2)	<0.001	<0.001	0.263	0.877	0.205
Jun 95	30.6 (3.2)	15.2 (1.3)	16.2 (1.7)	16.9 (2.5)	<0.001	<0.001	0.727	0.729	0.997
Sep 95	27.6 (1.4)	12.0 (1.3)	9.0 (0.9)	6.9 (1.1)	<0.001	<0.001	0.122	0.001	0.069
Oct 96	22.8 (1.9)	14.0 (1.5)	—	—	0.001	—	—	—	—
May 97	34.7 (1.6)	21.2 (1.3)	—	—	<0.001	—	—	—	—

Transplanting was completed in May 1994. Results of ANOVA comparisons among sites and for *a priori* contrasts are indicated as *p* values. Contrasts include (1) natural vs. transplanted and between transplant site pairs, (2) RCT vs. SET, (3) RCT vs. SWT, and (4) SET vs. SWT. See Table 1 for ANOVA models. Numbers of benthic taxa during October 1996 and May 1997 are per 176.8 cm^2. —, no data.

nous benthic taxa living on or around seagrasses. Examination of pretransplant benthic communities at seagrass donor and transplant sites indicated 75 species or taxonomic groups, of which 25 taxa were held in common and 26 taxa were found only at donor sites. Species or groups that composed ≥1% of the total benthos at each donor site were considered in terms of introduction to, or enhancement at, the transplant sites. *Odostomia* sp. (gastropod) and *Capitella capitata* and *Neanthes succinea* (annelids) were present only at donor sites prior to transplant activities. After 13 months (June 1995), all three taxa were present at the transplant sites in relatively low numbers (≤1% of the total fauna), but all have been reported previously from the Galveston Bay system (Harry 1976; White et al. 1985). No other taxa native to the donor sites were found at transplant sites. Abundance of *Streblospio benedicti*, *Aphelochaeta marioni*, *Heteromastus filiformis*, and *Mediomastus californiensis* (annelids), which were already at the transplant sites, may have been slightly enhanced (mean densities of these species had increased less than 2/core by June 1995). From this information, there appeared to be neither crucial introductions of nonindigenous taxa nor any enhancement of local populations in the seagrass transplanting process.

Benthic Communities

Total densities of annelids, non-decapod crustaceans, and benthic taxa were significantly higher in natural seagrass than in transplanted shoalgrass in all sampling periods (Table 5). There were no consistent differences in densities among transplant sites, although Redfish Cove tended to support higher annelid densities and lower crustacean densities than either Snake Island Cove bed.

A total of 29,027 individuals representing 192 taxa of benthic organisms was found in seagrass habitats over all collecting periods (Table 6). Annelids and crustaceans were the most numerous taxa. Many organisms were rare, as 102 taxa yielded no more than 10 individuals each. Transplanted shoalgrass had higher overall proportions of annelids, bivalves, and gastropods and a lower proportion of crustaceans than did natural seagrass. However, overall densities of all major taxa except bivalves were higher in natural seagrass than in transplanted shoalgrass (Table 6). Twenty taxa each comprised more than 1% of the total number of organisms collected and summed to 81.2% of the total benthos. Eleven of those taxa were collected irregularly in time or by habitat (Table 6). Six taxa were found almost entirely in natural seagrass, including *Xenanthura brevitelson* (isopod) in most months, unidentified harpacticoid copepods and *Ampelisca abdita* (amphipod)

Table 6. Major phylogenetic groups and dominant taxa comprising ≥ 1% of the total benthos captured in natural mixed seagrass and transplanted shoalgrass beds in Galveston Bay, Texas shown as grand mean density per 78.6 cm^2 core and percent of total individuals.

	Natural (n = *56*)		*Transplanted* (n = *155*)	
Group or Taxon	*Density*	*%*	*Density*	*%*
Phylum Annelida (A)	246.7	67.4	45.0	81.6
Class Crustacea (C)	72.8	19.9	2.3	4.2
Class Bivalvia (B)	2.7	0.8	2.9	5.2
Class Gastropoda	2.4	0.7	1.1	2.0
Miscellaneous taxa (M)	41.2	11.3	3.8	7.0
Total individuals	20491		8536	
Total taxa	141		138	
Collected regularly (during at least five of seven sampling periods)				
Aricidea philbinae (A)	11.8	3.2	0.3	<0.1
Capitella capitata (A)	12.4	3.4	1.1	1.9
Chone cf. americana (A)	16.4	4.5	0.2	<0.1
Hargeria rapax (C)	12.5	3.4	0.7	1.3
Heteromastus filiformis (A)	21.3	5.8	6.5	11.8
Mediomastus ambiseta (A)	4.3	1.2	4.0	7.2
Nematoda (M)	38.1	10.4	2.0	3.6
Oligochaeta (A)	25.3	6.9	0.6	1.1
Streblospio benedicti (A)	113.8	31.1	14.5	26.4
Collected irregularly (primarily during one or two sampling periods)				
Ampelisca abdita (C)	5.3	1.4	0.1	<0.1
Ampelisca vadorum (C)	9.4	2.6	<0.1	<0.1
Ampelisca sp. (C)	7.4	2.0	0.0	0.0
Aphelochaeta marioni (A)	0.4	0.1	1.8	3.3
Aphelochaeta sp. (A)	4.1	1.1	1.4	2.6
Aricidea sp. (A)	0.1	0.1	3.1	5.6
Axiothella sp. (A)	4.3	1.2	0.5	<0.1
Harpacticoid copepods (C)	8.9	2.4	0.1	<0.1
Mediomastus californiensis (A)	3.7	1.0	2.2	3.9
Mulinia lateralis (B)	0.5	0.1	1.7	3.2
Xenanthura brevitelson (C)	7.5	2.1	0.2	<0.1

mainly in April and June 1995, *Axiothella* sp. (annelid) in June 1995, and *Ampelisca vadorum* and *Ampelisca* sp. (probably juvenile *A. vadorum*; amphipods) in May 1997. Three taxa were collected mainly in transplanted shoalgrass, including *Mulinia lateralis* (bivalve) in July 1994, *Aphelochaeta marioni* (annelid) between July 1994 and June 1995, and *Aricidea* sp. (near *A. bryani*; annelid) in October 1994 and September 1995. Both *Aphelochaeta* sp. (near *A. marioni*) and *Mediomastus californiensis* (annelids) were common to natural seagrass and transplanted shoalgrass, exhibiting abundance peaks in May 1997 and October 1996, respectively.

The remaining nine dominant taxa were regularly collected from natural seagrass or transplanted shoalgrass or both during most months (Table 7). Six taxa, including unidentified oligochaetes, unidentified nematodes, *Hargeria rapax* (tanaid), and *Chone* cf. *americana*, *Aricidea philbinae*, and *Capitella capitata* (annelids), were always significantly more abundant in natural seagrass than in transplanted shoalgrass. Densities of *Streblospio benedicti* and *Heteromastus filiformis* (annelids) were always more abundant in natural seagrass but not always significantly so. Densities of *Mediomastus ambiseta* (annelid) were usually similar in both types of seagrass beds.

Three assemblages of benthic communities were identified through classification and ordination of the pooled temporal data (Fig. 4). Benthos group 1 encompassed natural seagrass communities from the first four sampling periods, benthos group 2 included all transplanted shoalgrass communities, and benthos group 3 comprised communities found on the final two natural seagrass dates. MDS ordination indicated that group 2 probably included a distinctive subgroup composed of transplant communities on the last two sampling dates. Distinguishing characteristics of benthos group 3 included pronounced declines in densities of *Ampelisca abdita*, harpacticoid copepods, *Xenanthura brevitelson*, nematodes, *Aphelochaeta marioni*, *Aricidea* sp., and *Axiothella* sp. and increases in *Aphelochaeta* sp., *Ampelisca vadorum*, and *Ampelisca* sp. relative to densities characterizing group 1. The subgroup within benthos group 2 was characterized by these same trends as well as by declines in *Mulinia lateralis*, *Aricidea philbinae*, and total taxa recorded. In addition, some of the minor taxa exhibited relatively large changes in abundance between members of group 1 and group 3, as well as between

Table 7. Densities (mean number per 78.6 cm^2 and, in parentheses, SE) of dominant benthos in natural mixed seagrass and transplanted shoalgrass beds in Galveston Bay, Texas.

	Sampling Date						
Taxa and Habitat	*Jul 94*	*Oct 94*	*Apr 95*	*Jun 95*	*Sep 95*	*Oct 96*	*May 97*
Streblospio benedict							
Natural	—	49.1 (19.9)	82.2 (16.9)*	38.3 (7.0)*	106.3 (31.3)*	146.5 (24.5)*	30.3 (2.6)
Transplant	5.8 (1.1)	24.0 (4.7)	4.9 (0.9)	6.9 (2.2)	15.1 (1.3)	12.8 (2.3)	20.2 (2.4)
Heteromastus filiformis							
Natural	—	3.6 (0.7)*	10.4 (1.6)	6.8 (1.1)	6.1 (1.9)*	4.8 (1.0)	38.5 (7.1)
Transplant	1.9 (0.4)	1.1 (0.3)	9.3 (1.9)	3.3 (0.7)	1.5 (0.4)	2.2 (0.6)	22.6 (2.1)
Oligochaeta							
Natural	—	14.1 (2.5)*	11.2 (3.0)*	24.0 (6.9)*	15.3 (4.8)*	23.9 (5.1)*	14.1 (4.0)*
Transplant	0.9 (0.9)	0.5 (0.4)	0.2 (0.1)	0.3 (0.1)	0.1 (0.1)	1.0 (0.3)	0.6 (0.2)
Chone cf. *americana*							
Natural	—	8.0 (2.6)*	22.9 (4.9)*	9.1 (2.7)*	7.2 (1.3)*	3.5 (0.7)*	19.0 (3.0)*
Transplant	0.4 (0.3)	0.1 (0.1)	0.1 (0.1)	0.6 (0.1)	0	0	0.1 (0.1)
Aricidea philbinae							
Natural	—	2.8 (0.7)*	6.3 (1.3)*	8.8 (1.8)*	12.2 (3.2)*	5.0 (2.1)*	12.8 (1.9)*
Transplant	0.4 (0.1)	0.4 (0.2)	0.4 (0.1)	0.3 (0.1)	0.2 (0.1)	0	0.1 (0.1)
Nematoda							
Natural	—	35.3 (9.6)*	106.7 (32.3)*	65.1 (24.4)*	29.8 (5.2)*	—	—
Transplant	2.4 (1.3)	1.9 (0.7)	3.0 (2.7)	3.4 (1.4)	0.8 (0.2)	—	—
Hargeria rapax							
Natural	—	2.6 (1.0)*	7.1 (2.6)*	18.1 (5.3)*	1.7 (0.8)*	2.1 (0.6)*	17.8 (3.8)*
Transplant	0.2 (0.1)	0	2.2 (1.6)	1.4 (0.6)	0	0	0.3 (0.1)
Capitella capitata							
Natural	—	2.7 (1.0)*	12.1 (2.6)*	6.2 (2.8)*	2.3 (1.0)*	7.4 (1.0)*	14.5 (2.3)*
Transplant	0.3 (0.2)	0.4 (0.2)	0.3 (0.2)	0.4 (0.2)	0.2 (0.1)	3.1 (0.7)	2.3 (0.4)
Mediomastus ambiseta							
Natural	—	2.0 (0.7)	3.8 (0.6)*	6.6 (2.6)	5.7 (1.3)*	0	3.6 (0.8)
Transplant	9.3 (1.7)	1.4 (0.3)	1.2 (0.4)	9.3 (1.9)	0.6 (0.2)	0	1.2 (0.2)

Transplanting was completed in May 1994. *Significant ANOVA differences at $p < 0.01$. See Table 1 for ANOVA models. —, no data.

the subgroup and the main cluster in group 2. These included increases in *Rictaxis punctostriatus* (gastropod), *Amygdalum papyria* (bivalve), and *Polydora cornuta* (annelid) and decreases in *Capitella jonesi*, *Capitella* sp., *Micropthalmus* sp. C (of Uebelacker & Johnson 1984), *Polydora ligni*, and *Polydora socialis* (annelids), *Phoronis architecta* (phoronid), and *Sayella* sp. (gastropod). These changes may have been due to cessation of sampling at Snake Island Cove after shoalgrass transplants failed.

Discussion

Successful seagrass restoration includes not only persistence of the new beds but also attracting and supporting fauna at higher densities than would otherwise be found in nonvegetated subtidal habitats (Fonseca et al. 1996, 1998). In our study, transplanted shoalgrass habitats occasionally supported higher densities of fishes and decapods than did adjacent sand habitats. At times, some nekton species were equally abundant in transplanted shoalgrass and natural seagrass, but this was rarely true for total fishes, decapods, and nekton species. Our data indicated increased densities of darter goby, pinfish, blackcheek tonguefish, blue crab, brown shrimp, and daggerblade grass shrimp in transplanted shoalgrass versus nonvegetated sand within 2–5 months of planting, although these densities did not persist. This rapid colonization of transplanted seagrass has been reported previously for nekton (Worthington et al. 1991, 6 weeks; Fonseca et al. 1996, 4 weeks). Faster colonization, on the order of a week, has been demonstrated for fishes with sampling on a finer time scale (Sogard 1989). Progression of the total faunal community in transplanted seagrasses toward that of reference beds usually takes longer. Our study indicated that, in the Galveston Bay system, nekton and benthos densities, numbers of taxa, and species composition in transplanted shoalgrass would take more than 3 years to reach equivalence with natural seagrass. Studies in Florida demonstrated that transplant beds reached densities and species compositions similar to those of reference sites in 1–2.3 years for nekton (Fonseca et al. 1996) and in 2–4 years for annelids (Bell et al. 1993). Benthic communities elsewhere also seem to reach equivalence faster than in Galveston Bay, for example, after 7 months in North Carolina (Homziak et al. 1982) and after 9 months in Oregon (Posey 1988).

This temporal sequence is most likely due first to the provision of structure in an otherwise unstructured sand habitat and later to the progressive increase in areal shoot density and thus potential for food and refuge. Worthington et al. (1991) indicated that the presence of as few as 25

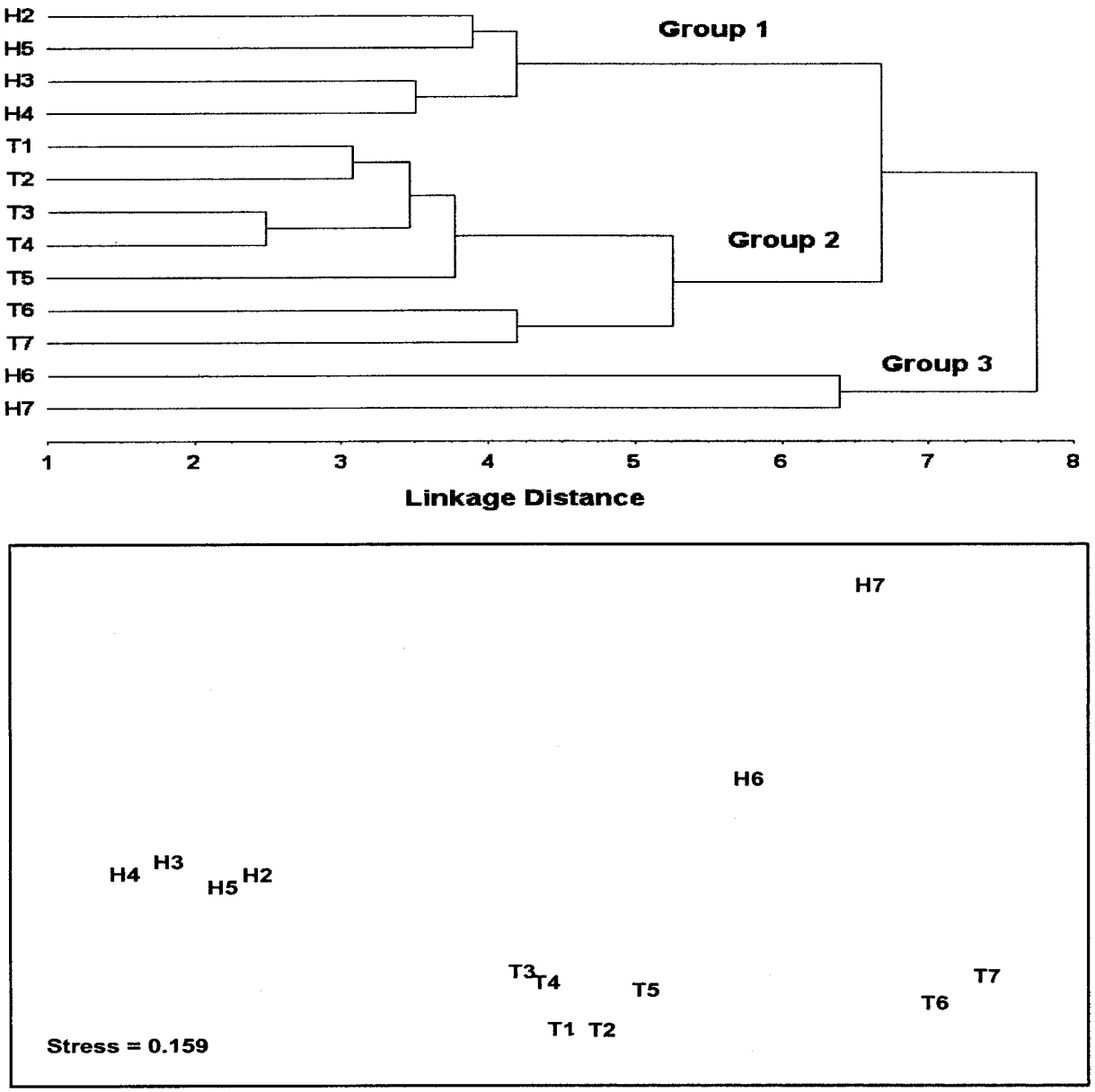

Figure 4. Cluster analysis (upper) and MDS ordination (lower) of benthic communities by habitat type and sampling date using UPGMA linkage of a Euclidian distance matrix. H, natural mixed seagrasses; T, transplanted shoalgrass. Sampling dates are sequentially numbered (1, April 1994 to 8, May 1997).

artificial seagrass shoots per m^2 was enough to effect significantly increased settlement of larval fishes over that observed in bare sand. Homziak et al. (1982) found enhanced benthic faunal densities in transplanted eelgrass and shoalgrass beds relative to adjacent bare habitats when shoot densities reached 200 shoots/m^2. We noted significant increases by some faunal components in transplanted beds over those in sand habitat during the first year of our study, when the average shoalgrass density was about 500 shoots/m^2 (Sheridan et al. 1998). However, we found no significant relationships between seagrass coverage or shoot density and nekton densities in our transplanted beds, even when shoalgrass densities approached 3,000 shoots/m^2 (about 75% of that found in the natural seagrass bed). This was surprising, because Fonseca et al. (1996) demonstrated an asymptotic increase of nekton density with increasing shoot density of transplanted seagrasses. In their study, nekton densities were similar in transplanted and natural beds when shoot densities of transplanted beds reached 700–800 shoots/m^2 (about 33% of natural bed densities). Potential reasons for depressed nekton densities are discussed below. It is interesting to note that, even after reaching parity in shoot and faunal densities, macrofaunal species compositions in restored or

created seagrass beds may remain or become distinctive from those of natural beds over longer time spans (e.g., decades; Brown-Peterson et al. 1993).

The proximity of transplanted and reference sites may also affect patterns in faunal density and species composition. Our sites were placed in potentially different hydrographic settings on either side of a tidal inlet, although water temperature, salinity, and light transmittance were similar (Sheridan et al. 1998). Proximity to sources of planktonic recruits (Bell et al. 1988) and to mobile juveniles and adults (Sogard 1989) have been found to influence faunal densities and species compositions in artificial seagrass beds. Our reference transects were located in a relatively small protected embayment, and our planted sites lay along the open shoreline of a relatively large bay; thus, we might expect persistent differences in communities. Such might be the reason for numerically similar but taxonomically distinct fish communities observed 30 years after seagrass restoration in Florida by Brown-Peterson et al. (1993). In that case, restored and reference sites were on opposite sides of a lagoon bisected by a dredged navigation channel, albeit no more than 600 m apart. Hydrographic variation may not always impede equivalence, however, because less than 3 years was needed to reach similarity in both nekton density and community structure where reference and planted sites were up to 20 km distant either across a large inlet or along an estuarine gradient (Fonseca et al. 1996). So, it is not always possible to predict or expect a given trajectory for structural equivalence of transplanted and natural seagrass beds.

As transplanted beds age, they should begin to provide the refuge and food services long attributed to natural seagrass beds. The value of a transplanted seagrass bed versus an adjacent sand habitat as a source of greater refuge from predators (e.g., small nekton from large nekton) or more food (e.g., benthos or epiphytes) is expected to increase as shoot density increases, most likely as a series of thresholds rather than a linear increase (reviewed by Orth 1992). Our study did not address refuge functions directly, but our data at times indicated higher densities of fishes and decapods and of nekton species in transplanted seagrasses than over sand substrates. Summerson and Peterson (1984) demonstrated that seagrasses acted as a daytime refuge for mobile nekton that foraged in adjacent sand flats at night when the risk of detection by higher order carnivores was reduced. However, nekton densities in our transplanted seagrass were usually lower than in natural seagrass; thus, one or more seagrass density thresholds had not been overcome with respect to provision of refuge. To our knowledge, the refuge function of transplanted seagrass relative to natural seagrass has only been examined once. Smith et al. (1988) found that 6-month-old transplanted eelgrass beds with less than 30% of the shoot density of natural beds provided little refuge for bay scallops from avian and aquatic predators. There is therefore a need to test the refuge function of transplanted seagrasses as they age.

With respect to provision of greater concentrations of food, our transplanted beds remained depleted (relative to natural seagrasses) in nematodes, annelids, and nondecapod crustaceans, which are the primary foods of resident and transient juvenile nekton (Virnstein 1987; Edgar & Shaw 1995). We do not know whether this was due to high predation in a sparse seagrass habitat, variation in habitat preferences among benthic organisms, or low benthic recruitment (Bell & Westoby 1986; Bell et al. 1987). It is also possible that food resources for these benthic herbivores and omnivores, such as epiphytic algae, benthic diatoms, or organic deposits, were also limited. Although we did not measure benthos densities in sands adjacent to transplant sites, Harper (1992) examined the benthos of nonvegetated habitat 15 km east of our transplant sites and reported total densities of 3,000–5,000/m^2 during May–October 1977 (23.6–39.3/core using the size of our corer). Such densities are similar to those we typically observed in transplant beds. Thus, there was little indication that transplanted shoalgrass increased local abundances of benthos, except at the end of our monitoring period. A shortage of preferred food items may have been the primary reason for lower densities of nekton in general, and decapods in particular, in transplanted shoalgrass versus natural seagrass beds (Connolly 1994).

Seagrass species composition could have affected our observations on density and composition of nekton and benthos. Our reference site was a mixture of four plant species, and we transplanted only the dominant seagrass. Thus we created a habitat with potentially reduced complexity of biotic and abiotic conditions. However, the magnitude and direction of change in faunal densities and communities as seagrass species composition changes are by no means consistent. Some studies report differences in faunal densities in adjoining beds with differing seagrass species (O'Gowar & Wacasey 1967; Stoner 1983; Virnstein & Howard 1987; Rooker & Holt 1997; Jernakoff & Nielsen 1998), others do not (Worthington et al. 1992; Zupo & Nelsen 1999), and still others show mixed results (Lewis 1984; Kenyon et al. 1995; Sheridan et al. 1997; Loneragan et al. 1998). In addition, these studies compared relatively pure stands of each seagrass species and not mixed versus single-species seagrass beds. A comparison of mixed versus single-species seagrass transplants would be informative for future restoration projects.

One of the end points of habitat restoration is (or should be) demonstration of enhanced structural attributes or functional processes in restored habitats above the prerestoration levels as a measure of progress toward a natural reference habitat (Kentula 2000; Zedler & Calloway 2000). Most of the previously cited assessments of seagrass restoration documented achievement of structural equivalence, for example, in shoot density or faunal standing stock, within 3 years. We found some enhancement of faunal communities while transplanted beds survived, but we saw scant progress toward structural equivalence with reference beds after 3 years. Functional equivalence in processes such as nutrient cycling, primary and secondary

productivity, predation, or growth rates has rarely been addressed, perhaps because it is more costly and time-consuming to test. To our knowledge, Bell et al. (1993) provided the only published comparison of secondary production rates in restored and natural seagrasses, and this was for only a single species of polychaete. The database necessary to predict structural equivalence of restored and natural seagrass systems remains small (only a few sites around the world), and if the literature we cite herein is any indication, variation in restoration response and success criteria is large. The pace of this progress has ramifications for coastal permitting agencies that might recommend seagrass restoration as compensatory mitigation for habitat damage, as well as for local resource managers attempting large-scale restoration projects such as that proposed for Galveston Bay. Both groups must be prepared for protracted floral and faunal monitoring, and potential replanting of seagrass, beyond the typical 1- to 3-year vegetation check to ensure at least persistence and structural enhancement of both flora and fauna. Assessment of functional equivalence should become a scientific focus until enough data are available for sound management decisions.

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