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A Comparison of Macroepifauna Among Vegetated and Unvegetated Habitats in a South Florida Estuary Using a Passive Sampling Gear

PAUL J. RUDERSHAUSEN, JAMES V. LOCASCIO, AND LOURDES M. ROJAS

We compared abundance, richness, diversity, and community structure of macroepifauna among the seagrasses *Halodule wrightii, Thalassia testudinum,* and *Syringodium filiforme,* and unvegetated substrate in Tarpon Bay, Caloosahatchee River estuary, Florida. Sampling was conducted using wire-mesh minnow traps deployed over fifty-six 24-h periods from Jan. 1999 to Jan. 2000. A total of 36, 35, 28, and 28 species were identified from *Halodule, Thalassia, Syringodium,* and unvegetated samples, respectively. The gastropod *Nassarius vibex* was the most abundant species from *Halodule* and unvegetated substrate, whereas the pinfish (*Lagodon rhomboides*) was the most abundant species from *Thalassia* and *Syringodium.* Abundance of these codominant species varied seasonally throughout the study. For all taxa combined and for codominants, each seagrass contained greater averages than unvegetated substrate in each season. Seagrasses typically had higher average species richness and diversity than unvegetated substrate in each season. Results indicate that Tarpon Bay typifies subtropical estuaries in that its epifaunal community is dominated by few species, faunal abundances vary seasonally, and more organisms are found in seagrasses than in unvegetated areas. Our results serve as a foundation to compare against future research in an understudied system.

Seagrasses are important components of healthy estuaries, sources of refuge and food, and nursery for an array of invertebrates and fishes (Thayer et al., 1975; McRoy, 1977). Comparisons of epifauna found in seagrass meadows and adjacent bare substrates have shown that diversity and abundance is higher (Thayer et al., 1975; Orth, 1977; Virnstein et al., 1983; Bell et al., 1984; Lewis, 1984; Orth et al., 1984; Sogard, 1992; Jordan et al., 1997a; Arrivillaga and Baltz, 1999) and predation lower (Virnstein et al., 1983; Summerson and Peterson, 1984) in vegetated habitats. Arrivillaga and Baltz (1999), for example, found that crustacean and fish abundances were 7 and 20 times higher, respectively, in meadows of turtle grass (*Thalassia testudinum*) than over sand. Between 70 and 90% of the harvested species in the Gulf of Mexico depend on coastal wetlands and seagrass meadows of bays and estuaries for at least part of their life cycles (Lindall and Saloman, 1977). Fauna in Florida seagrasses are characterized by transients, whose young use this habitat (Livingston, 1975; Weinstein et al., 1977).

Seagrasses are affected by increases in turbidity and nutrients and, as such, are threatened directly by development and indirectly by changing patterns of land use (Shephard et al., 1989). In southwest Florida, seagrass declines are associated with decreases in light due to increased phytoplankton, epiphytic, or macroalgal growth (Tomasko et al., 1996). The Caloosahatchee River estuary is heavily influenced by discharges of fresh water (Doering and Chamberlain, 1999) through Franklin Lock and Dam (S-79), located roughly 40 km above the river mouth. The impression of local residents is that seagrass coverage has declined in the lower estuary (Wilzbach et al., 1999). Variations in salinity may be greater in magnitude and different in seasonality at present than before completion of the dam in the mid-1960s. To our knowledge no previous studies have discussed how anthropogenic and natural events have influenced changes in seagrass distribution in the estuary.

Although the lower Caloosahatchee River watershed is being developed rapidly, little quantitative data has been collected to document the use of seagrasses by small fishes and invertebrates. Effects of seagrass loss on fauna cannot be quantitatively predicted for unstudied areas: the only prediction that can be made based on seagrass mortality is that the abundance and richness of benthic invertebrates and fishes will decline (Howard et al., 1989). One method of assessing the importance of seagrasses to fauna in these understudied areas is to compare them with unvegetated substrates (Ferrell and Bell, 1991).

Our objective was to establish baseline estimates of the relative abundance of small fishes and epifaunal invertebrates in seagrasses and unvegetated substrate in an embayment in the lower estuary. Specifically, we compared abundance, species richness, diversity, and community structure of epifauna among the seagrasses *Halodule wrightii, T. testudinum,* and *Syringodium filiforme,* and unvegetated substrate in the estuary, with a null hypothesis that no difference in these parameters would be found among habitats.

MATERIALS AND METHODS

All sampling took place in Tarpon Bay, a 13-km^2, generally polyhaline, embayment of the lower Caloosahatchee River estuary in the J.N. 'Ding' Darling National Wildlife Refuge, Sanibel, FL. Tarpon Bay lies roughly 8 km southwest of the mouth of the Caloosahatchee River and, as such, is influenced by river discharges of freshwater. With the exception of minor bulkheading, Tarpon Bay is fringed by red mangrove, *Rhizophora mangle.* Much of its shallow bottom is covered by *Halodule, Thalassia,* and *Syringodium. Halodule*'s flat blades are narrower and shorter than those of the flat-bladed *Thalassia,* whereas *Syringodium* has narrow, cylindrical blades.

In Tarpon Bay, seagrasses are segregated by depth, with *Halodule* shallowest, *Thalassia* at intermediate depths, and *Syringodium* in the deepest locations inhabited by seagrasses (Wilzbach et al., 1999). Fringing areas of the bay tend to exhibit alternating bands of vegetated and unvegetated substrate. As with other locations in Florida (e.g., Phillips, 1960), in Tarpon Bay *Halodule* and *Thalassia* grow in sandy substrate, whereas *Syringodium* grows in softer, more organic substrate. *Halodule* and *Thalassia* beds in Tarpon Bay are typically long and narrow (<4 m wide) and are either contiguous or separated by thin bands of sand. Additionally, at least five species of drift algae occur in Tarpon Bay during winter, including *Gracilaria tikvahiae, G. caudata, Acanthophora spicifera, Solieria filiformis,* and *Caulerpa fistigiata* (C. J. Dawes, pers. comm.). Windrows of drift algae are common from Dec. through April, when they often cover beds of *Thalassia* and *Syringodium* (pers. obs.).

Sampling was conducted 56 times, roughly on a weekly basis, from 10 Jan. 1999 to 19 Jan. 2000. We used minnow traps 42 cm long and 21.6 cm in diameter at their widest point. Traps were constructed of 0.7-cm square steel wire mesh and had two circular openings, each 2.2 cm in diameter. When traps lay on the bottom, the base of each opening was roughly 9.5 cm above the sediment.

Each week, three traps were deployed for 24 hr in each of four habitats: *Halodule, Thalassia, Syringodium,* and unvegetated sandy mud, for a total of 168 traps deployed in each habitat during the study. We took care to deploy the traps in monospecific beds of seagrass largely void of other species. We rated macrophyte coverage surrounding each trap by using the Braun–Blanquet criteria, which assigns a numerical code to percent cover (1, 0–5%; 2, 5–25%; 3, 25–50%; 4, 50–75%; and 5, 75–100%). With few exceptions, traps were deployed in 75–100% macrophyte cover. Depth, measured with deployment of each trap, ranged from 20 to 110 cm for *Halodule,* 25 to 130 cm for *Thalassia,* 65 to 175 cm for *Syringodium,* and 90 to 200 cm for unvegetated substrate. *Halodule* and *Thalassia* beds are found in shallow waters in Tarpon Bay; occasionally, throughout the study these traps became exposed at low tide. Water temperature (C) and salinity [parts per thousand (ppt)] were measured immediately after deployment of all 12 traps. We assumed that differences in water quality parameters among habitats were slight compared with the direct and indirect differences caused by vegetation. Except for mojarras (*Eucinostomus* spp.), hermit crabs (*Pagurus* spp.), sea hares (*Aplysia* spp.), and grass shrimps (*Palaemonetes* spp.), we identified organisms to the species level. After enumeration, organisms were released with the exception of those that required further identification.

Comparison of average abundance per trap for all taxa combined and for common taxa was first made with analysis of covariance (ANCOVA). Habitat was the independent variable and season (winter, spring, summer, and fall) the covariate. Data were logarithmically transformed ($\ln(x + 1)$) to correct for heteroscedasticity before stastistical testing. Outcomes of ANCOVAs that displayed significant interaction were then analyzed by season and differences in average abundance among habitats subsequently tested by single-factor analysis of variance (ANOVA). When necessary, the Tukey post hoc procedure was used to test for significant differences ($P \leq 0.05$) among pairs of means.

Species richness and diversity was also measured for each trap. Diversity was calculated using Simpson's index, a distribution-free measure (Krebs, 1989). Simpson's index is given as $1 - D = 1 - \Sigma (p_i)^2$, where $1 - D$ is the index of diversity and p is the proportion of individuals of species i. Simpson's index ranges from 0 (no diversity) to almost 1. Average species richness [$\ln(x + 1)$] and diversity were also compared among the four habitats with ANCOVA, using season as a covariate. When nec-

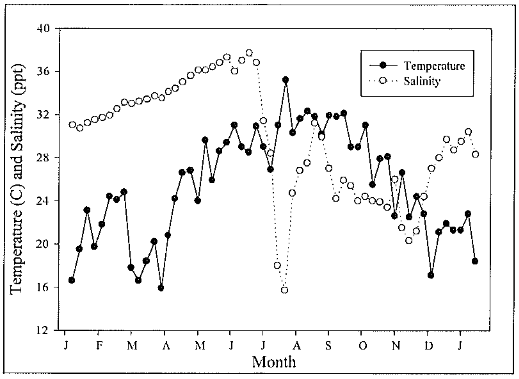

Fig. 1. Temperature and salinity measurements in Tarpon Bay, Jan. 1999 through Jan. 2000.

essary, we used ANOVA and the Tukey post hoc test.

The Kolmogorov–Smirnov (K-S) two-sample test was used to compare the taxonomic composition of samples collected from the four habitats. The test analyzes whether two overall samples are drawn from populations having the same distribution by using differences between cumulative percentages to determine a test statistic (Tate and Clelland, 1957). The critical value for the K-S statistic, D, is defined as $D_\alpha = K_\alpha\{[(n_1 + n_2)/n_1n_2]^{1/2}\}$, where $K_\alpha = \{\frac{1}{2}[-\ln(\alpha/2)]\}^{1/2}$. For K-S comparisons between bottom types, we set $\alpha = 0.05$. Using this K-S test, one can compare general taxonomic compositions among habitats (Brook, 1978).

RESULTS

Temperature ranged from 15.9 to 35.2 C, and salinity ranged from 15.7 to 37.7 ppt throughout the study period (Fig. 1). We observed dramatic spring and summer growth, fall exfoliation, and winter dormancy of seagrass blades, particularly in *Halodule* and *Thalassia.*

A total of 2,897, 3,043, 2,374, and 952 organisms were captured from *Halodule, Thalassia, Syringodium,* and unvegetated samples, respectively. A total of 36, 35, 28, and 28 genera and species were captured from *Halodule, Thalassia, Syringodium,* and unvegetated samples, respectively (Table 1). The pinfish (*Lagodon rhomboides*) was the most abundant species from *Thalassia* and *Syringodium* and the most abundant fish from each seagrass. Mojarras, (*Eucinostomus* spp.) were the most abundant fish taxa from unvegetated substrate. The basket shell (*Nassarius vibex*) was the most abundant species from *Halodule* and unvegetated substrate and the most abundant invertebrate from all four habitats. The pink shrimp (*Farfantopenaeus duorarum*) was the most abundant decapod from *Halodule, Thalassia,* and unvegetated substrate. The mud crab (*Rhithropanopeus harrisii*) was the most abundant decapod from *Syringodium* and the only xanthid captured in the study. Seven common taxa (Table 1, underlined) accounted for 93.4% of the catch from *Halodule,* 89.9% of the catch from *Thalassia,* 92.8% of the catch from *Syringodium,* and 85.0% of the catch from unvegetated substrate. A total of 24, 21, 15, and 18 taxa from *Halodule, Thalassia, Syringodium,* and unvegetated substrate, respectively, were represented by 10 individuals or less.

Combining all taxa, average abundance per trap was highest in May for *Halodule, Thalassia,* and *Syringodium* and in June for unvegetated substrate (Fig. 2A). Average abundance was lowest in Jan. 2000 for *Halodule, Thalassia,* and *Syringodium* and in Jan. 1999 for unvegetated substrate. With the exception of *C. sapidus,* the seven major taxa (Table 1, underlined) were captured in greater average abundance from each seagrass than from unvegetated substrate (Figs. 2, 3; Table 2).

Richness and diversity were generally highest in summer and lowest in winter (Fig. 4). Average monthly richness was highest in Aug. for *Halodule,* in July for *Thalassia* and *Syringodium,* and in June and July (equally) for unvegetated substrate. Richness was lowest in Dec. for *Halodule* and *Syringodium* and in Jan. 2000 for *Thalassia* and unvegetated substrate. Average monthly diversity was highest in Sep. for *Halodule,* in Oct. for *Thalassia,* in June for *Syringodium,* and in July for unvegetated substrate. Diversity was lowest in Dec. for *Halodule* and *Syringodium,* in May for *Thalassia,* and in Jan. 2000 for unvegetated substrate.

We conducted ANCOVA on average trap abundance of all taxa combined, the numerically dominant fish (pinfish), and the numerically dominant invertebrate (basket shell). For each ANCOVA (except that comparing the abundance of basket shells among habitats), factor, covariate, and interaction effects were significant ($P < 0.001$) (Table 3). Interaction accounted for only a small percentage (<13%) of the overall variability in each model (Table 3). However, because of significant interaction effects in each model, we tested for differences of means among habitat by using single-factor ANOVA for each season.

In general, the average abundance of all taxa combined, pinfish, and the basket shell was significantly greater for at least two of the seagrasses than for unvegetated substrate (Ta-

TABLE 1. Abundance summary of species collected from Tarpon Bay. Underlined taxa were used for Kolmogorov–Smirnov testing.

	Halodule		*Thalassia*		*Syringodium*		Unvegetated	
	No.	Percentage	No.	Percentage	No.	Percentage	No.	Percentage
Callinectes sapidus	67	2.3	51	1.7	15	0.6	40	4.2
Eucinostomus spp.	130	4.5	158	5.2	223	9.4	108	11.3
Farfantepenaeus duorarum	196	6.8	298	9.8	188	7.9	146	15.3
Lagodon rhomboides	927	32.0	1,348	44.3	852	35.9	75	7.9
Nassarius vibex	1,070	36.9	348	11.4	451	19.0	240	25.2
Pagurus spp.	123	4.2	265	8.7	139	5.9	80	8.4
Rhithropanopeus harrisii	193	6.7	269	8.8	336	14.2	120	12.6
Miscellaneous taxa	191	6.6	306	10.1	170	7.2	143	15.0
Alpheus normanni	6		4		3		8	
Anachis translirata			1					
Anarchopterus criniger	3							
Anchoa mitchilli	1							
Aplysia spp.			2		13		21	
Archosargus probatocephalus	3		2		2			
Bairdiella chrysoura	2		9		17		8	
Bulla striata	24		5					
Cerithium muscarum	13		15		12		8	
Chasmodes saburrae	5		18		1		2	
Chilomycterus schoepfi							1	
Coryphopterus glaucofraenum			1		1		2	
Cynoscion nebulosus	4		5		5		1	
Echinaster sentus	12		29		47		51	
Fasciolaria lilium	1		1		1			
Gobiosoma robustum	1		1		1		1	
Hippocampus zosterae	1							
Hypsoblennius hentzi	1		9		6		1	
Libinia dubia	3		5					
Lucania parva	47		108		4		2	
Lutjanus griseus	1		3					
L. synagris							1	
Marginella apicina	35		12		13		19	
Menidia peninsulae	1							
Modulus modulus	1							
Monacanthus hispidus							1	
Ophichthus gomesi	1		3		2		1	
Ophidion holbrooki	1							
Ophioderma brevispinum	1		1		1		2	
Ophionephthys limicola	1		1		1		1	
Opsanus beta	5		17		7		4	
Orthopristis chrysoptera	10		44		31		7	
Palaemonetes spp.	2		1		1		1	
Prionotus tribulus			1					
Symphurus plagiusa	3		3		1			
Synodus foetens			1					
Trinectes maculatus	1		4					
Total	2,897		3,043		2,374		952	

ble 4). The only seasonal exception to this was in the fall, when virtually no pinfish were captured. During each season, at least two seagrasses had significantly higher average levels of richness than unvegetated substrate. Because of the influence of dominant species, average species diversity among habitats exhibited no consistent statistical trends among habitats. The results of ANOVA and Tukey tests are summarized in Table 4.

To compare taxonomic composition among habitats using the K-S test, we subdivided col-

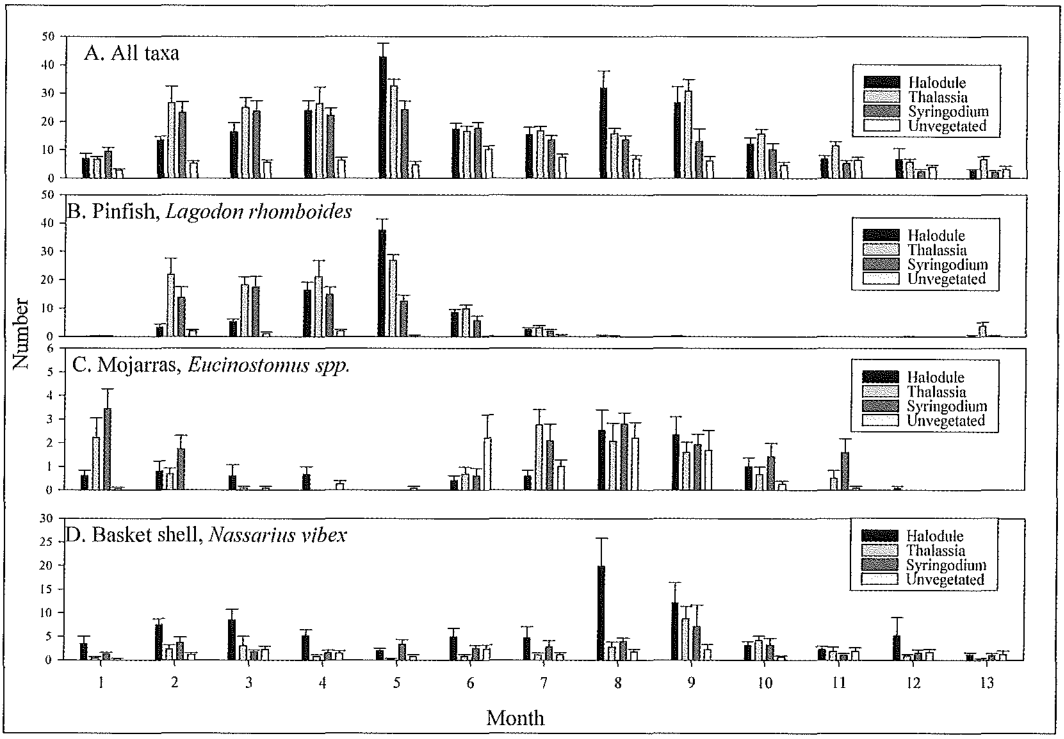

Fig. 2. Average abundance per trap by habitat and month of all taxa and major taxa of fish and mollusks. Note variation of y-axis among panels.

lections into eight groups (Table 1, underlined). In each of the six pairwise comparisons among habitats, the maximum cumulative percentage difference in taxonomic composition was highly significant ($P < 0.001$). In each of these pairwise comparisons the maximum percentage difference between habitats was due to the relative presence or absence of pinfish or basket shells.

Discussion

Temperate estuaries exhibit great variability in physicochemical factors (Hooks et al., 1976), and their biota consists of a large number of individuals of few species (Livingston, 1976). Several taxa in our study, pinfish, mojarras, and the basket shell, dominated collections from all four habitats. As was seasonally the case in our study, populations of these seagrass-associated faunal dominants may increase and decrease rapidly (Hoese and Jones, 1963). Although minnow traps do have upper and lower size limits for entry and exit, our results suggest that Caloosahatchee River estuary seagrasses serve as important seasonal habitat for small fishes and invertebrates. Pinfish, overall the most abundant species (34.6% of all the specimens collected), typified the seasonal fluctuations in common taxa. Our results also suggest that habitat is temporally partitioned by abundant fishes (Huh, 1984) and that habitat-related differences in abundance of common taxa reach a minimum during winter (Gourley, 1989) (Figs. 2, 3).

Like seasonal trends in abundance, richness and diversity were generally higher in warmer months. Diversity values for *Thalassia,* in particular, were influenced by the abundance of pinfish (Table 2). Adams (1976) and Heck (1979) surmised that seasonal fluctuations in abundance and species richness result from predation and changes in seagrass architecture, which are brought about by water temperature. We observed dramatic intra-annual changes in seagrass biomass throughout the study and believe that this directly influenced richness. Concurrent with changes in seagrass biomass, the abundance of common taxa was also generally higher in warmer months and lower in winter (Table 2; Figs. 2, 3).

This study constituted part of an initial effort to describe seagrass-associated epifauna in the Caloosahatchee River estuary. Our findings that seagrasses support greater overall abundance, richness, and diversity relative to unve-

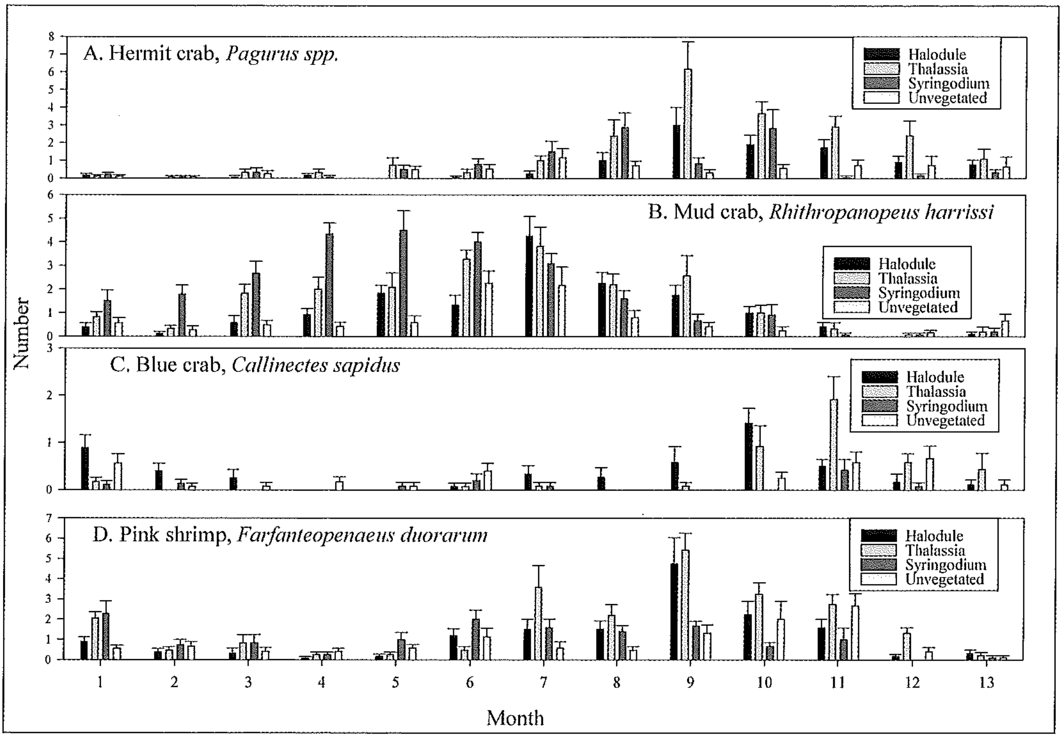

Fig. 3. Average abundance per trap by habitat and month of major taxa of decapods. Note variation of y-axis among panels.

getated substrate are consistent with earlier reports that structurally complex habitats support more individuals and species (Lewis, 1984; Jordan et al., 1997a). The basket shell, pinfish, and rainwater killifish (*Lucania parva*), for example, displayed dramatic preferences for seagrass over unvegetated substrate, and this contributed to these differences. The average number of organisms per trap from each seagrass was greater than that for unvegetated substrate for all seven common taxa (Table 1, underlined) except blue crabs. Taxa captured more equitably between seagrass and bare substrate included two trophically general species of crabs, *R. harrisii* and *Pagurus longicarpus* (Odum and Heald, 1972; Caine, 1975).

Seagrass biomass, blade density, and blade height all appear to influence abundance and diversity of epifauna that use seagrasses (Orth et al., 1984). Differences in nekton exist between *Thalassia* and *Halodule* (Springer and McErlean, 1962; O'Gower and Wacasey, 1967; Stoner, 1983) because of biomass differences and perhaps because wide-bladed *Thalassia* is more structurally complex than narrow-bladed *Halodule* and *Syringodium* (Virnstein et al., 1987; Brown-Peterson et al., 1993). Stoner (1983) and Lewis (1984) found that for monospecific seagrass beds, fish and crustacean abundance were explained by aboveground seagrass biomass. Stoner (1983) found that in such areas blade density predicted fish abundance better than seagrass biomass, and reported that blade-dense *Halodule* beds held greater numbers of small fishes than either *Thalassia* or *Syringodium*. He suggested that for a Florida seagrass dominant, the pinfish, the low biomass and high blade density of *Halodule* beds offered greater predatory success and protection compared with the other two species.

Independent of faunal collections, we measured several aboveground structural components of monospecific seagrass beds in Tarpon Bay (Table 5). Measurements made along randomly chosen transects included summer biomass (g dry weight/m^2), shoot density (SD; shoots/m^2), leaves per shoot (LS), and blade length (BL). From this we modified an index given by Tolan et al. (1997) to compute a complexity index (CI) for monospecific seagrass beds: CI = (SD × LS × BL)/1,000. Because macrophyte structural components were sampled in Tarpon Bay, we believe that these data are representative of sites where traps were deployed.

TABLE 2. Average richness, diversity, and abundance of dominant taxa (per trap) by season and habitat.

	Winter	Spring	Summer	Fall
All taxa				
Halodule	8.39	28.21	22.05	13.03
Thalassia	13.88	26.95	18.28	14.41
Syringodium	12.73	23.41	13.97	6.95
Unvegetated	4.04	6.74	7.15	5.28
Pinfish				
Halodule	1.49	19.56	2.23	0.03
Thalassia	8.76	20.82	0.76	0.00
Syringodium	5.39	13.95	0.85	0.00
Unvegetated	0.63	0.95	0.15	0.00
Nassa				
Halodule	4.24	5.62	10.49	5.80
Thalassia	1.14	1.23	2.92	3.28
Syringodium	1.88	2.44	4.28	2.39
Unvegetated	1.14	1.69	1.21	1.77
Richness				
Halodule	2.90	3.74	5.44	3.87
Thalassia	3.24	4.03	5.82	4.69
Syringodium	3.45	4.62	4.72	2.87
Unvegetated	2.24	3.23	3.56	2.56
Diversity				
Halodule	0.44	0.39	0.63	0.53
Thalassia	0.44	0.40	0.69	0.66
Syringodium	0.46	0.55	0.68	0.43
Unvegetated	0.37	0.51	0.56	0.44

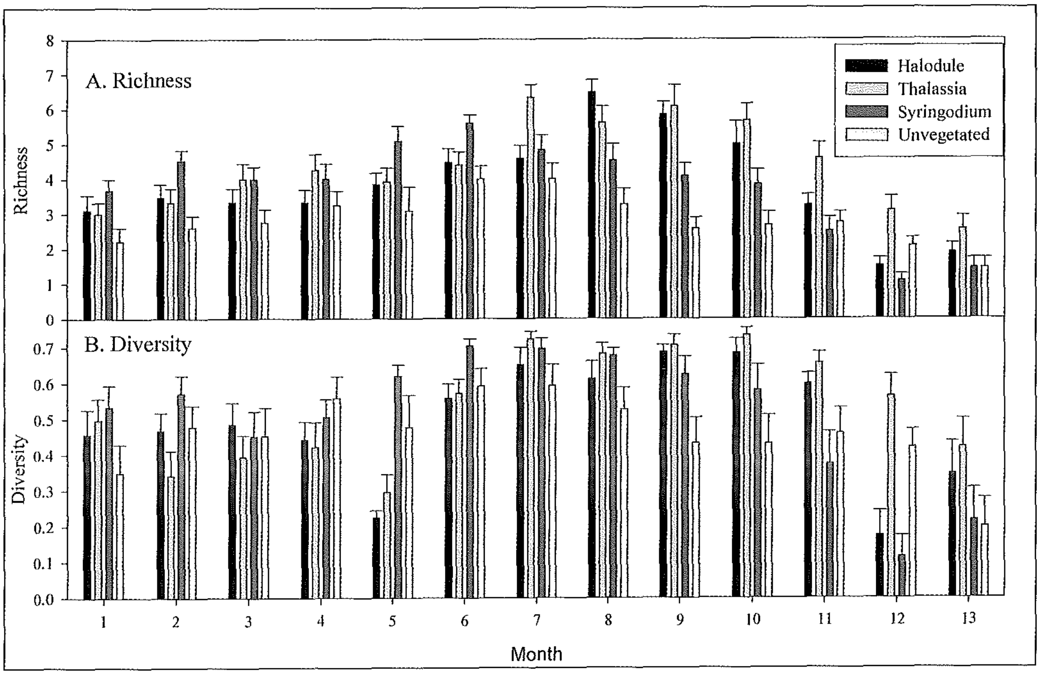

Fig. 4. Average richness and diversity per trap by habitat and month.

TABLE 3. Summary of ANCOVA.

Comparison	Source	F	P
All taxa	Habitat	62.38	0.000
	Season	57.62	0.000
	Habitat × season	4.26	0.000
Pinfish	Habitat	53.26	0.000
	Season	216.51	0.000
	Habitat × season	17.63	0.000
Nassa	Habitat	28.88	0.000
	Season	6.90	0.000
	Habitat × season	1.77	0.070
Richness	Habitat	24.02	0.000
	Season	38.87	0.000
	Habitat × season	2.70	0.004
Diversity	Habitat	3.63	0.000
	Season	27.13	0.013
	Habitat × season	4.58	0.000

In south Florida, seagrass biomass has been correlated with epifaunal abundance (Brook, 1978) and diversity (Heck and Wetstone, 1977). Although significant differences were found in faunal community structure among habitats, our results do not necessarily support the idea that greater biomass (*Thalassia*) will support more individuals than greater blade density (*Halodule*). Long-bladed *Thalassia* had roughly a sevenfold greater average dry weight biomass than either *Halodule* or *Syringodium* (Table 5). On the other hand, *Halodule* had a greater blade density than the other two species. The complexity index incorporates elements of blade length and blade density. Assuming that common taxa displayed some fidelity to the seagrass species in which they were captured as opposed to migrating among seagrasses, this measure may help define the relative abundance of major taxa in Tarpon Bay. *Halodule* and *Thalassia* had almost equally high complexity indices and total abundances in each season. *Syringodium,* with the lowest complexity index, had the lowest total abundance in each season. Components of the complexity index may indicate faunal preferences. For example, the basket shell was captured in significantly greater abundance from blade-dense *Halodule,* whereas the rainwater killifish was far more abundant in high-biomass *Thalassia.* The pinfish was only slightly more abundant in *Thalassia* than in *Halodule,* and it may be that divergent qualities of monospecific beds offset each other when this common species has a choice of seagrass species, each having a unique structural character. Although we found roughly equal numbers of pinfish between *Halodule* and *Thalassia,* previous results in which pinfish preferred blade density rather than biomass (Stoner, 1983) may have become apparent over shorter (<24 hr) deployments.

Characteristics other than those of the

TABLE 4. Summary of ANOVA and significant Tukey multiple comparisons.[a]

				Significant multiple comparisons			
Comparison	Season	F	P	*Halodule*	*Thalassia*	*Syringodium*	Unvegetated
All taxa	Winter	9.43	0.000	H > U	T > U	S > U	U < H,T,S
	Spring	43.86	0.000	H > U	T > U	S > U	U < H,T,S
	Summer	32.63	0.000	H > S,U	T > U	S < H, S > U	U < H,T,S
	Fall	10.01	0.000	H > U	T > S	S < T, S > U	U < H,S
Pinfish	Winter	8.10	0.000	H < T	T > H,U	S > U	U < T,S
	Spring	86.84	0.000	H > U	T > U	S > U	U < H,T,S
	Summer	8.17	0.000	H > U	T > U	—	U < H,T
	Fall	1.00	0.395	—	—	—	—
Nassa	Winter	7.89	0.000	H > T,S,U	T < H	S < H	U < H
	Spring	11.08	0.000	H > T,S,U	T < H,S	S < H, S > T	U < H
	Summer	12.76	0.000	H > T,S,U	T < H	S < H, S > U	U < H,S
	Fall	2.27	0.082	H > U	—	—	U < H
Richness	Winter	4.97	0.000	—	T > U	S > U	U < T,S
	Spring	6.32	0.000	—	T > U	S > U	U < T,S
	Summer	15.40	0.000	H > U	T > U	S > U	U < H,T,S
	Fall	9.43	0.000	H > U	T > S,U	S < T	U < H,T
Diversity	Winter	1.10	0.350	—	—	—	—
	Spring	5.72	0.001	H < S	T < S	S > H,T	—
	Summer	4.78	0.003	—	T > U	S > U	U < T,S
	Fall	7.47	0.000	—	T > S,U	S < T	U < T

[a] Abbreviations: H, *Halodule*; T, *Thalassia*; S, *Syringodium*; U, unvegetated.

TABLE 5. Averages for components of structural complexity from pure stands of *Halodule*, *Thalassia*, and *Syringodium* sampled in Tarpon Bay.

	Biomass (g dry weight/m^2)	Shoot density (shoots/m^2)	Blades per shoot	Blade density (blades/m^2)	Blade length (cm)	Complexity index
Halodule	19.3	1,248	2.52	2,144	12.2	38.3
Thalassia	172.2	565	2.96	1,671	23.4	39.1
Syringodium	26.3	472	1.85	874	21.1	18.4

aboveground portion of seagrass beds may also determine relative abundance of some common fauna we captured. Differences in faunal assemblages among seagrasses may be explained by substrate. *Halodule* colonizes bare, sandy substrate, whereas *Syringodium* is more common in silty areas (Phillips, 1960). Thayer and Chester (1989) suggested that sediment organic content is an important determinant of abundance and composition of fishes in nearby Florida Bay. We found mud crabs in greater numbers in *Syringodium* than in the other two seagrasses. Xanthids associate with decaying vegetation (Ryan, 1956), a characteristic of the organic-rich substrate where *Syringodium* grows (Phillips, 1960).

Assemblages of fishes found among seagrasses may reflect sampling technique (Gray and Bell, 1986). Minnow trapping represents an efficient means to compare use of seagrass by a variety of epifauna. Our data suggest that traps bias collections toward mobile organisms such as pinfish but are largely ineffective at capturing small or sedentary species. For example, we collected only four syngnathids and eight gobiids in the study despite several species of these families being found in Tarpon Bay seagrasses (pers. obs.). Minnow trap catches may not accurately represent habitat-use patterns by species that aggregate or grow too large to enter traps. Catches may have been skewed by pinfish and blue crabs consuming other organisms that entered the traps. However, our passive sampling technique may be a more effective means of capturing some taxa. Xanthids and pagurids, for example, are ineffectively sampled with throw traps because of their burrowing habits (Sogard and Able, 1991). Jordan et al. (1997b) found that with throw traps 17% of fishes were not counted because of burrowing or accidental discard. As passive samplers, minnow traps may eliminate biases in the quality of the 'surprise' element while deploying throw traps in various depths, substrates, and water clarities.

The relatively extended deployment of each trap (24 hr) might have tended to mask interhabitat differences in abundance of fauna at certain times of the day. Overall differences in abundance of fauna among seagrasses may have become even more apparent over shorter time periods. Greening and Livingston (1982), for example, found significant differences in the number of invertebrates captured between day and night in seagrass beds in northern Gulf of Mexico. Thus, our results may provide a conservative estimate of habitat preferences.

Seagrasses in Tarpon Bay are mostly zonated by depth, with the bulk of the seagrass biomass fringing the bay as small, narrow strips alternating with sand. Two different species of seagrass in Tarpon Bay invariably lie adjacent to each other. It is reasonable to assume with this small bed size that fidelity to one seagrass species may be low, particularly for mobile fauna. Brook (1978) found that the composition of invertebrates can vary significantly even in structurally similar, geographically close meadows of the same macrophyte. This may explain the high numeric differences among collections within habitat, season, and taxa. More transient species are taken from small habitat patches than from large patches because of the former having a greater proportion of edge (Heck, 1979). Although Stoner (1979) found that young of pinfish rarely venture beyond seagrass-covered habitats into sand patches, Bell et al. (2002) found that boat propeller scarring in *Thalassia* meadows did not reduce the observed numbers of pinfish or syngnathids. Although fauna restricted in mobility and smaller in size may be more affected by scarring of grass beds (Bell et al., 2002), increase of edge in natural seagrass beds may aid migrations among and utilization of structurally distinct beds.

Nutrient loading to Florida estuarine waters has been linked to degradation of seagrasses (Tomasko et al., 1996). Despite anthropogenic impact to the Caloosahatchee River estuary, no censuses of levels of dissolved nutrients, abundance of seagrass-associated fauna, or coverage of seagrasses are conducted on a regular basis. The abundance of *Thalassia* may decline as nutrient loading increases and ranges of salinity widen in the lower estuary. *Thalassia* has an optimum salinity range between 17 and 36 ppt and is found upriver to Shell Point (Doering and Chamberlain, 1999), 9 km northeast of Tarpon Bay. It is at this upriver boundary that salinity sometimes falls to less than 12 ppt (Doering and Chamberlain, 1999), a level below which Doering and Chamberlain (1999) suggested that, given even unlimited light, parameters of growth in *Thalassia* are negatively affected. Whereas *Halodule* can withstand eutrophic conditions (Lapointe et al., 1994), *Thalassia* is a relatively oligotrophic species (Tomasko et al., 1996) that cannot do well in areas of elevated nutrient loading.

Because densities of benthic invertebrates and fishes that inhabit seagrass meadows are positively correlated with seagrass density and productivity (Stoner, 1983; Sogard et al., 1987), eutrophication of estuarine seagrass meadows will tend to reduce faunal production (Lapointe et al., 1994). In nearby Sarasota Bay, for example, degraded water quality from nonpoint sources has stressed fish habitat by stimulating nutrient-driven phytoplankton production and epiphytic algal growth (Tomasko et al., 1996). The South Florida Water Management District is formulating management plans to meet surface water demands in the Caloosahatchee River watershed through 2020. It is reasonable to expect that increases in human growth and the number of impervious surfaces in the watershed will increase nutrient-driven stressors of seagrasses. Future studies should examine how seagrasses and associated fauna respond to changes in the quality and volume of regulated flows so that managers can ensure the needs of keystone estuarine species.

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