

Gulf of Mexico Science

Volume 20
Number 2 *Number 2*

Article 6

2002

Assessment of Seagrass Plant Demography Within and Among Beds of Turtle Grass (*Thalassia testudinum*), Manatee Grass (*Syringodium filiforme*), and Shoal Grass (*Halodule wrightii*) From the Northern Gulf of Mexico

Paul A.X. Bologna
Dauphin Island Sea Lab

Doug Haywick
University of South Alabama

DOI: 10.18785/goms.2002.06

Follow this and additional works at: <https://aquila.usm.edu/goms>

Recommended Citation

Bologna, P. A. and D. Haywick. 2002. Assessment of Seagrass Plant Demography Within and Among Beds of Turtle Grass (*Thalassia testudinum*), Manatee Grass (*Syringodium filiforme*), and Shoal Grass (*Halodule wrightii*) From the Northern Gulf of Mexico. *Gulf of Mexico Science* 20 (2).

Retrieved from <https://aquila.usm.edu/goms/vol20/iss2/6>

This Article is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in *Gulf of Mexico Science* by an authorized editor of The Aquila Digital Community. For more information, please contact Joshua.Cromwell@usm.edu.

Assessment of Seagrass Plant Demography Within and Among Beds of Turtle Grass (*Thalassia testudinum*), Manatee Grass (*Syringodium filiforme*), and Shoal Grass (*Halodule wrightii*) From the Northern Gulf of Mexico

PAUL A. X. BOLOGNA AND DOUG HAYWICK

Variability in the demographic patterns of seagrasses may affect a variety of physical and biological processes in aquatic communities. We investigated seasonal seagrass demography, sediment size structure, and sediment organic carbon from two sites (north and south) in St. Joseph Bay, Florida, for *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*. Geologically, sands dominated both sites, but the south site had significantly greater proportions of fine and very fine sands, whereas the north site was dominated by coarse and medium sands. Within each site, demographic parameters were assessed for edge (<1 m) and interior portions (>10 m) of grass beds. The objective was to quantify within-habitat demographic characteristics and assess whether differences in plant biomass and shoot density existed between edge and interior portions. Results for *T. testudinum* showed significantly greater shoot density ($P < 0.05$) and plant biomass ($P < 0.001$) from interior portions of the bed than from the edge for the north site, but there were no significant differences for the south site. *Syringodium filiforme* showed significantly greater shoot density from bed interiors than from edges for both the north and south sites ($P < 0.0001$, $P < 0.001$, respectively) as well as plant biomass ($P < 0.0001$, $P < 0.01$, respectively). *Halodule wrightii* showed a similar response, with greater shoot densities from the north interior ($P < 0.008$) and significantly greater plant biomass from interior portions of beds for both the north and south sites ($P < 0.003$, $P < 0.01$, respectively). Within-bay comparisons showed that plant biomass and shoot density were generally greater from the north site than from the south site for *T. testudinum* and *H. wrightii*, but the reverse was true for *S. filiforme*. Although sands dominated both sites, the south site showed greater percentages of finer sediments, and *S. filiforme* biomass has been shown to be inversely related to sediment size. Although we were unable to resolve within-habitat differences in sediment size structure, which may suggest sediment baffling and water velocity changes, we surmise that physical and sedimentary differences exist between edge and interior portions of seagrass beds. These differences may have dramatic effects on processes such as larval settlement, predator-prey interactions, and per unit area primary production. As such, further investigations into within-habitat variability and edge effects in plant demography and associated biological and physical processes are needed.

The overall structure of seagrasses communities covers a broad spectrum of plant species, composition, and areal coverage. In general, seagrass habitats are often distributed as a mosaic of vegetated cover interspersed with varying degrees of unvegetated sediments (see Larkum and den Hartog, 1989; Robbins and Bell, 1994; Marba and Duarte, 1995). These habitat mosaics, coupled with succession, often create ecosystems of variable shoot density, species composition, canopy height, and biomass (Bell and Westoby, 1986; Irlandi, 1994). Therefore, seagrass habitat architecture can be defined at many spatial and temporal scales (Robbins and Bell, 1994), and defining the extent and physical arrangement of the

landscape may be essential for addressing ecological questions (Holling, 1992; Levin, 1992).

Seagrass structure is important in coastal regions because they dampen wave energy and reduce water velocity (Fonseca et al., 1982; Gambi et al., 1990). The reduction of flow associated with grass beds increases particle deposition (Almasi et al., 1987), and the extensive root-rhizome mat may bind particles, thereby stabilizing sediments (Thayer et al., 1984; Fonseca and Fisher, 1986). Seagrass beds, therefore, act as sediment traps and may retain finer sediments than do the unvegetated regions around them (Orth, 1977). The change in physical regime is often most extreme at the edge of a given grass bed. Consequently, edges

are where current baffling would first occur and where coarser-grained sediments should first be deposited. Ideally, finer-grained sediment would be carried under conditions of lower flow further into bed interiors. Particle size gradients should, therefore, occur from the edge into the interior of seagrass beds (Orth, 1977), thus creating settlement shadows (Bologna and Heck, 2000). Consequently, because of the potential differences in physical regime and sediment composition, two different subhabitats may exist within seagrass beds: "edge" and "interior."

It might be surmised that physical and biological regimes would affect seagrass bed structure. For instance, sand dune migration can affect coverage and growth patterns of some species (Marba and Duarte, 1995), whereas consumption by herbivores can greatly reduce standing stock (Camp et al., 1973) and create grazing halos (Ogden et al., 1973). Bioturbation (e.g., stingray feeding) can also contribute significantly to the destruction of local grass beds (Orth, 1975), and in some areas, decapod burrowing creates favorable conditions for storm events to tear rhizome mats (Valentine et al., 1994). Consequently, the distribution of seagrass biomass within a region may vary greatly, and areas most prone to disturbance may be affected the greatest. Under these circumstances, edge habitats might be the most dynamic because of potential differences in physical regimes (e.g., water velocity, turbulence). Few detailed studies, however, have investigated edge effects in marine seagrass communities. As such, our intent was to examine both small-scale within-habitat variability in plant demography and sediment structure among seagrass species and, on a larger spatial scale, potential differences in plant and sediment characteristics within a region, varying in physical exposure. Specifically, the objectives of this study were to assess the seasonal and within-habitat differences in plant demography and biomass in *Thalassia testudinum* ex Banks König, *Syringodium filiforme* Kuetz., and *Halodule wrightii* Aschers. Additionally, we assessed the potential effect these seagrasses have on structuring sediment composition and organic carbon.

STUDY SITE

Research was conducted in St. Joseph Bay, Florida, which lies in the Northeastern Gulf of Mexico (29°N 85.5°W; Fig. 1). It is a shallow semienclosed lagoonal system open to the Gulf of Mexico at the north and has little freshwater

input. Consequently, salinity is normally high and ranges from 25 to 35‰ annually. However, large storm events (e.g., Tropical Storm Alberto) can reduce salinity by as much as 20‰ during short periods of time (Bologna, 1998). Shallow portions of St. Joseph Bay are vegetated by a mosaic of seagrass species covering 2,300–2,400 ha of the benthos (Savastano et al., 1984). Two principal study sites in St. Joseph Bay were investigated: the north site was chosen to represent a more exposed, oceanic habitat, whereas the south site was chosen to represent a physically protected habitat (Koch and Gust, 1999). The southern portion of St. Joseph Bay was more heavily used for recreational activities (e.g., fishing, boating, snorkeling) than was the northern region (pers. obs.). Both sites were shallow (<1.2 m deep mean low water) and comprised a mosaic containing *T. testudinum*, *S. filiforme*, *H. wrightii*, and open sediment.

METHODS

Plant demography.—To determine seasonal and spatial differences in shoot density and plant biomass, 15.24-cm-diameter cores (0.01824 m²) were collected from edge and interior portions of *T. testudinum*, *S. filiforme*, and *H. wrightii* seagrass beds at each site. Edge was operationally defined as vegetation within 1 m of a seagrass-sand interface. Interior was defined to be at least 10 m from any seagrass-sand interface (Bologna, 1998). These distinctions were chosen to represent relative extremes within each habitat. Replicate cores (n = 2, sensu Livingston et al., 1976) were collected in Oct. 1995 and in Jan., April, Aug., and Oct. 1996. Samples were processed in the field, and plant material was frozen and returned to the laboratory. In the laboratory, seagrasses were separated into shoots (aboveground), rhizomes, and roots. Shoots were separated and counted. Shoots, roots, and rhizomes were dried to constant weight at 80 C and then ashed at 500 C for 8–10 hr to determine ash-free dry weight (AFDW). Shoot density and total plant biomass were compared among seasons (e.g., dates of collection) and within habitats (e.g., edge vs interior) using two-way ANOVA. Data were square-root transformed before analysis to normalize data, and analyses were performed on individual seagrass species for a given location (i.e., north or south). Significance testing was performed with $\alpha = 0.05$. Additionally, the individual plant biomass components (e.g., root, rhizome, and aboveground) were compared

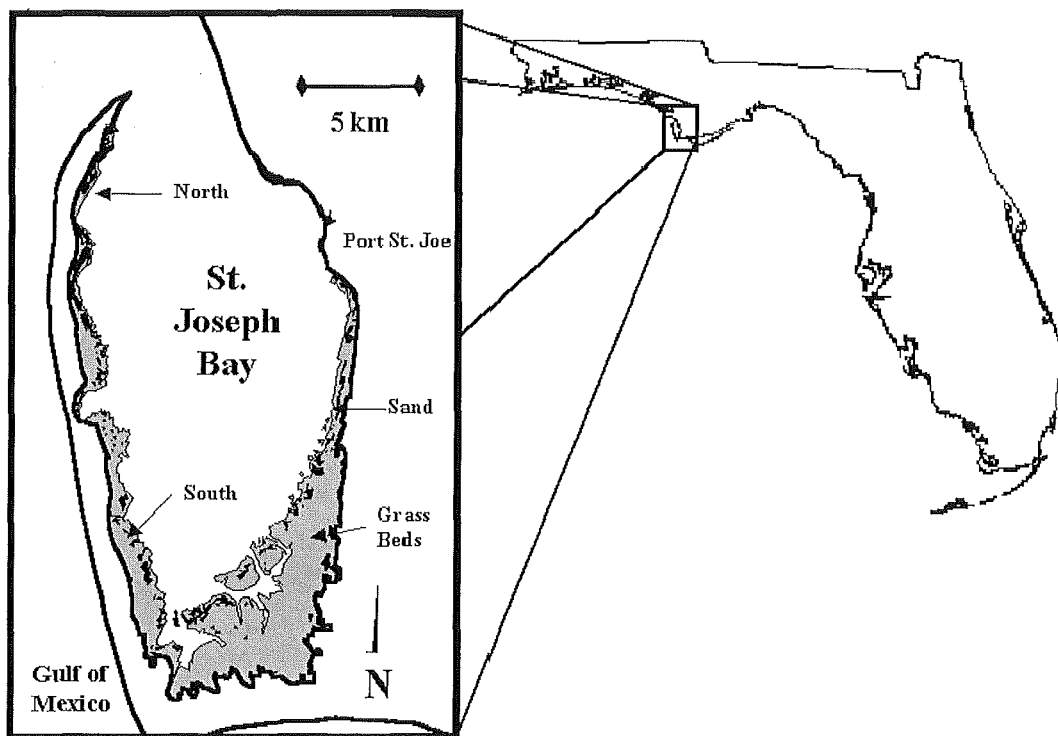


Fig. 1. St. Joseph Bay, Florida. Research was conducted on the western side of the bay in a shallow seagrass mosaic containing *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*. Specific study regions are indicated as north and south.

within habitats for each species at each site following the same protocol.

Sediment size fractionation analysis.—Sediment analysis was undertaken to assess potential differences in sediment type and organic content between sites and among habitats. Replicate 5.1-cm sediment cores were taken to a depth of 10 cm at edge and interior portions of *T. testudinum*, *S. filiforme*, and *H. wrightii* seagrass beds from both north and south sites. Sediment cores were also collected from unvegetated regions adjacent to the seagrass habitats. A total of 31 samples was collected and transported to the Sedimentology and Thin-Sectioning Laboratory at the University of South Alabama. Each sample was soaked overnight in distilled water to remove salts, decanted, and dried in a low-temperature oven (50 C) until dry. Fractions from each sample (25–40 g) were extracted using a sediment splitter for grain size analysis. Percentages of gravel (particle size >2 mm; Folk, 1980), sand (particle size 2 mm to 63 μm), and “fines” (silt + clay) were determined by dry sieving. We opted not to distinguish between silt (particle size: 63–4

μm) and clay (particle size <4 μm) because initial analyses using the pipette and sieve method of Coventry and Fett (1979) demonstrated little clay-sized content within the samples (<0.1%). Sediment composition was compared between sites and among habitats using arcsin-transformed proportion data. Between-site comparisons were analyzed using an unpaired t-test ($\alpha = 0.05$).

Sediment organic carbon content.—Sediment samples were collected before the onset of summer growth (May) and at the end of the growing season (Oct.) in 1996 to determine potential effects of seagrass habitat on organic carbon concentration. Sediment cores of 2.5-cm diameter ($n = 58$) were collected to a depth of 3 cm from unvegetated and edge and interior portions of *T. testudinum*, *S. filiforme*, and *H. wrightii* from each site. Samples were transported to the laboratory, dried to constant weight at 80 C, and ashed at 500 C for 8 hr. The difference in weight between dry weight and AFDW was calculated and used as a percentage of total weight to determine percent organic carbon. Data were arcsin transformed

and compared by seagrass species and analyzed as a three-way ANOVA with date of collection, site, and habitat location as independent factors and organic carbon as the dependent variable ($\alpha = 0.05$).

RESULTS

Plant demography.—*Thalassia testudinum*: Analyses from square-root transformed data collected from the north site showed significantly greater shoot density from interior portions of the bed than from the edge ($F_{1,10} = 5.1$; $P < 0.05$; Fig. 2a). Additionally, there was a seasonal component with significantly fewer shoots from samples collected in winter ($F_{4,10} = 4.5$; $P < 0.02$; Fig. 2a). However, no spatial or temporal pattern was evident from samples collected at the south site (Fig. 2b). When biomass was analyzed, data collected from the north site showed consistent differences in plant biomass. Specifically, leaf ($F_{1,10} = 7.6$; $P < 0.02$), rhizome ($F = 37.1$; $P < 0.00001$), and root biomass ($F = 72.4$; $P < 0.0001$) were significantly greater from interior portions of the bed than from edges. The summed total biomass, consequently, was also significantly greater ($F_{1,10} = 62.0$; $P < 0.0001$; Fig. 3a). Biomass also showed significant seasonal variability, with reduced biomass in Jan. compared with other seasonal samples. When biomass was analyzed for samples collected at the south site, no significant biomass patterns were evident, but samples collected in 1996 showed a consistent pattern of greater total biomass from interior samples than from edges (Fig. 3b).

Syringodium filiforme: Results showed that shoot density was significantly greater from interior portions of the bed than from edges for both north ($F_{1,10} = 45.7$; $P < 0.0001$; Fig. 4a) and south sites ($F_{1,10} = 9.14$; $P < 0.013$; Fig. 4b). Additionally, the north site showed a temporal effect with significantly fewer shoots in Aug. compared with other sampling dates ($F_{4,10} = 11.1$; $P < 0.002$). When sites were compared, shoot density was greater from samples gathered from the south than from those from the north, with the exception of Jan. 1996, when very low shoot densities occurred from south interior samples (Fig. 4b). When biomass was analyzed for *S. filiforme*, data from the north site showed that leaf ($F_{1,10} = 65.6$; $P < 0.0001$), rhizome ($F = 20.1$; $P < 0.001$), and root biomass ($F = 28.7$; $P < 0.003$) were significantly greater from interior portions of the bed than from edges (Fig. 5a). Similar results were seen for data collected at the south site, with leaf

($F = 16.6$; $P < 0.002$) and rhizome biomass ($F = 12.3$; $P < 0.006$) significantly greater from interior sites than from edges (Fig. 5b), but there were no differences in root biomass ($F = 0.4$; $P > 0.5$). In both cases, the resultant total biomass was significantly greater from interior portions of the bed than from edges (north, $F = 48.8$; $P < 0.0001$; south, $F = 9.5$; $P < 0.01$; Fig. 5).

Halodule wrightii: Results showed significantly greater shoot density from interior north *H. wrightii* beds ($F_{1,10} = 10.8$; $P < 0.008$; Fig. 6a); however, no pattern was evident from samples gathered at the south site (Fig. 6b). When plant biomass was analyzed, north and south sites showed the same pattern for plant biomass with significantly greater leaf ($F_{1,10} = 6.8$; $P < 0.02$; $F = 4.5$; $P < 0.06$; north and south, respectively), root ($F = 21.3$; $P < 0.001$; $F = 24.9$; $P < 0.0005$, respectively), and total biomass ($F = 15.1$; $P < 0.003$; $F = 10.3$; $P < 0.01$, respectively) from samples gathered at interior portions of the bed than from edges (Fig. 7). However, both showed no significant differences in rhizome biomass, possibly because rhizomes comprised a relatively small portion of total biomass (Fig. 7).

Sediment size structure analysis.—Sediment analysis showed that samples were primarily composed of sand (mean 98.69%, range 90–100% sand by weight), with minimal amounts of fines and gravel (gravel components consisted of broken shell fragments). There was no significant variation in grain size among edge, interior, and unvegetated samples; however, there were significant differences in grain size between the two study sites. The north site was dominated by medium-grained sands (>50%, 250–500 μm), whereas the south site was dominated by fine sands (>70%, 125–250 μm ; Fig. 8). Additionally, the north site had significantly greater proportions of coarse sand (500 μm to 1 mm) than did the south ($t_{31} = 8.9$; $P < 0.0001$), whereas the south had a significantly greater proportion of very fine sand (63–125 μm , $t_{31} = 3.7$; $P < 0.001$; Fig. 8). There was generally no intrahabitat difference in sediment size distribution within the north sample site. Both edge and interior were dominated by medium to fine sand. However, the south site did show a difference in particle size from edge to interior. Both edge and interior were dominated by fine sand, but there were significantly greater percentages of very fine sands from interior *T. testudinum* ($t_2 = 4.4$; $P < 0.05$),

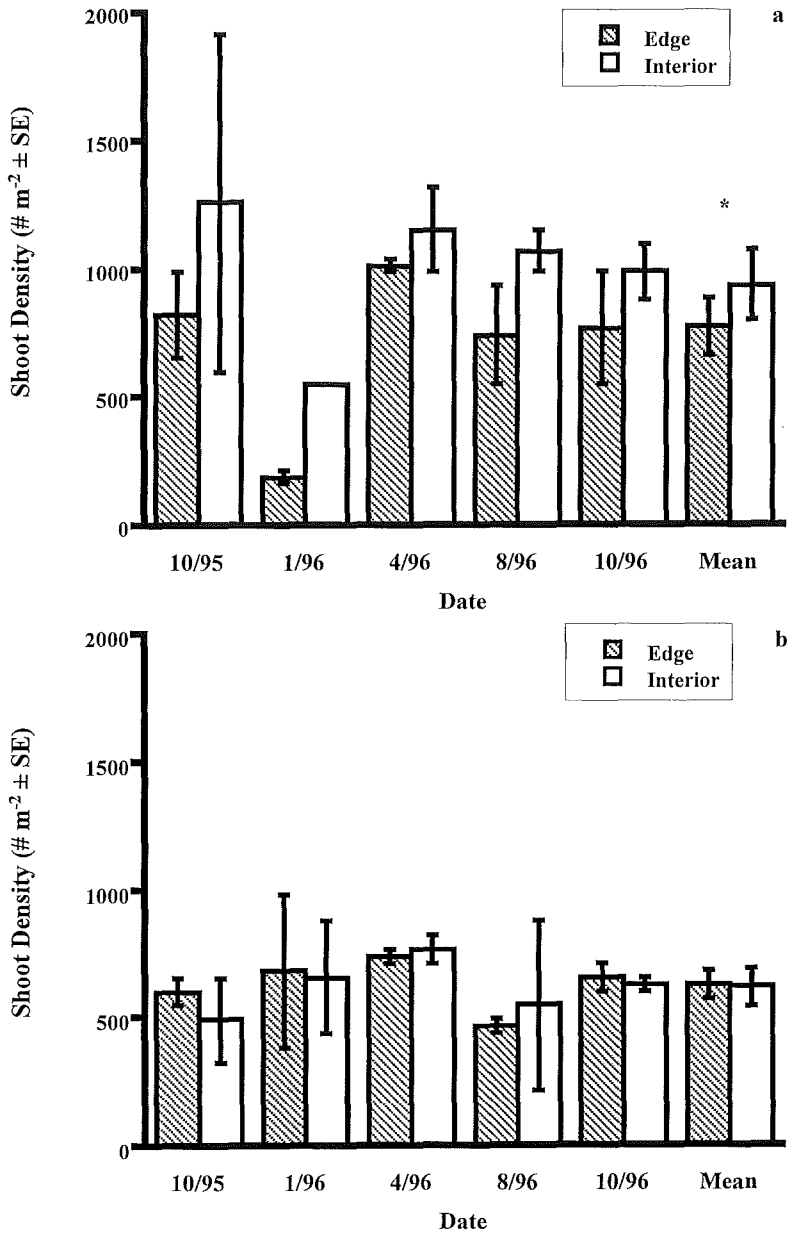


Fig. 2. Comparison of *Thalassia testudinum* shoot density among dates of collection. Data presented represent mean shoot densities expressed as number of shoots per square meter \pm SE for dates of collection, with the addition of the composite mean value. Asterisk above composite value represents significant differences in mean shoot densities between edge and interior portions of the habitat. (a) North *T. testudinum* site. (b) South *T. testudinum* site.

S. filiforme ($t_2 = 4.6$; $P < 0.05$), and *H. wrightii* ($t_2 = 24.7$; $P < 0.002$) than from edges.

Organic carbon content.—Generally, sediment organic carbon was greater from samples gathered in May than from samples gathered in Oct. (Table 1). Only the north *H. wrightii* in-

terior site did not show this pattern. These results suggest that during winter, accumulation of detritus occurred, creating differences in organic carbon concentrations in the sediments. When percent carbon was compared between vegetated and unvegetated habitats (i.e., sand; Table 1), data showed greater content in veg-

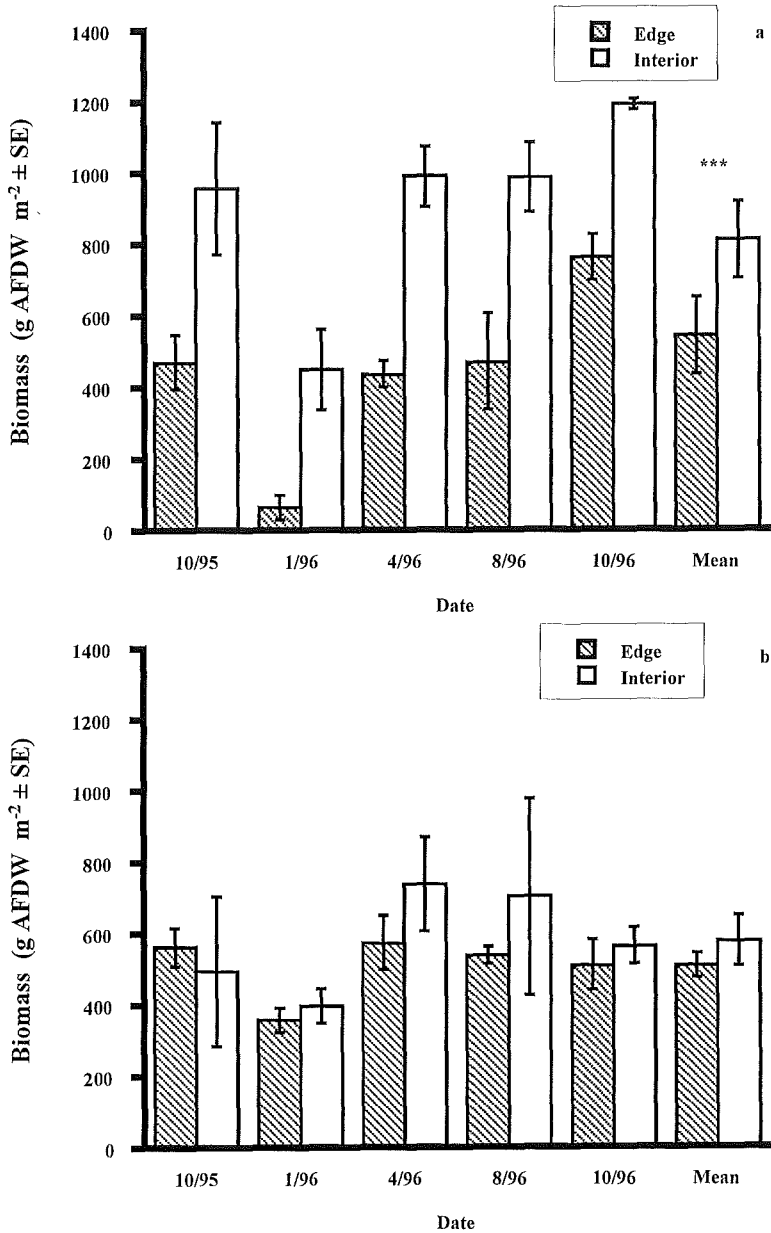


Fig. 3. Comparison of *Thalassia testudinum* plant biomass among dates of collection. Data presented represent mean total biomass for dates of collection expressed as grams AFDW per square meter \pm SE, with the addition of the composite mean value. Asterisk above composite mean value represents significant differences in mean plant biomass between edge and interior portions of the habitat. (a) North *T. testudinum* site. (b.) South *T. testudinum* site.

etated vs unvegetated habitats for both north and south sites and between sampling dates.

DISCUSSION

Understanding the distributional aspects of seagrass biomass may be essential for assessing

processes within and among seagrass communities (Turner et al., 1999). Because these habitats are often vital to the survival of species (Rasmussen, 1973; Thayer and Stuart, 1974) and processes such as recruitment (Peterson, 1986), predation (Heck and Crowder, 1991), and growth (Bologna and Heck, 1999a) may

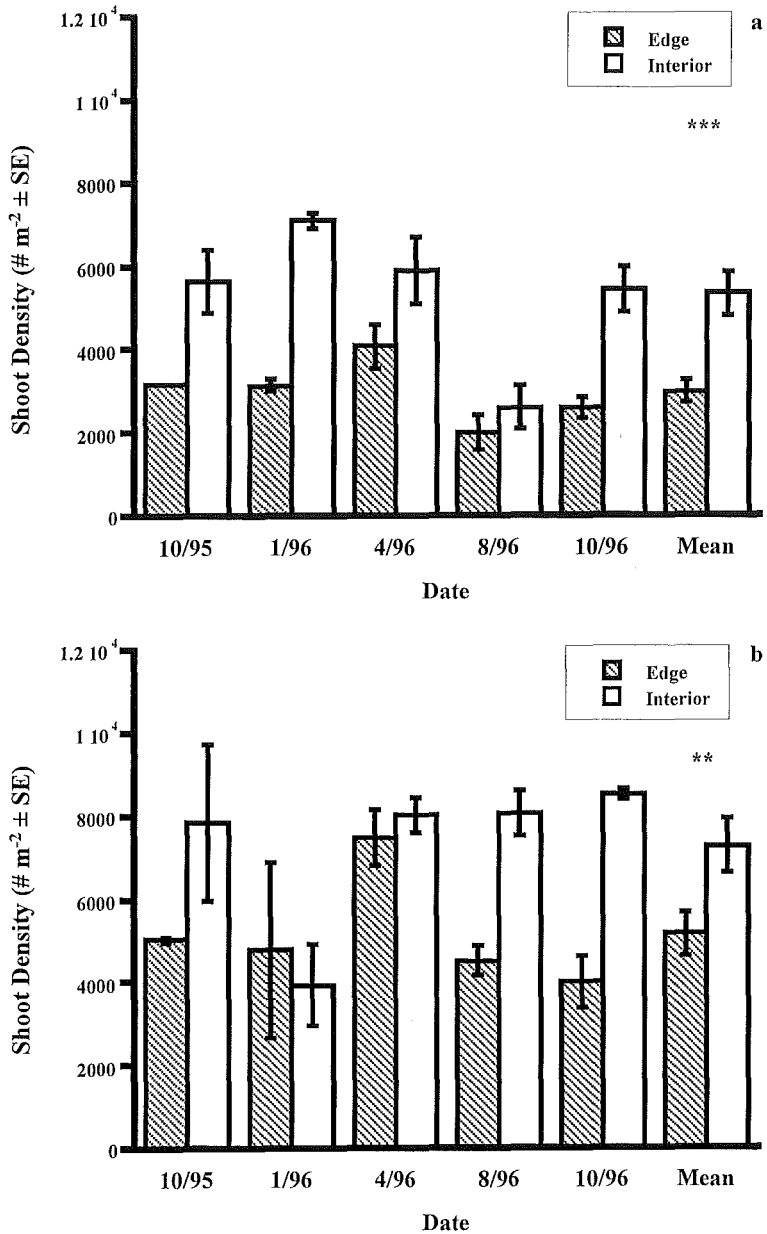


Fig. 4. Comparison of *Syringodium filiforme* shoot density among dates of collection. Data presented represent mean shoot densities expressed as number of shoots per square meter \pm SE for dates of collection, with the addition of the composite mean value. Asterisk above composite value represents significant differences in mean shoot densities between edge and interior portions of the habitat. (a) North *S. filiforme* site. (b) South *S. filiforme* site.

act differently between vegetated and unvegetated habitats, the essential structure of seagrass beds may, to a large degree, determine the productivity (Robertson, 1979; Edgar, 1990a, 1990b; Bologna and Heck, 2002) and trophic transfer within a system (Bologna, unpubl. data). Results from this research indicate

that seagrass demography had not only strong seasonal variability, but also significant within-habitat spatial variability. Shoot density and seagrass biomass were greater from interior portions of continuous seagrass beds than from edges for *T. testudinum* (Figs. 2, 3), *S. filiforme* (Figs. 4, 5), and *H. wrightii* (Figs. 6, 7),

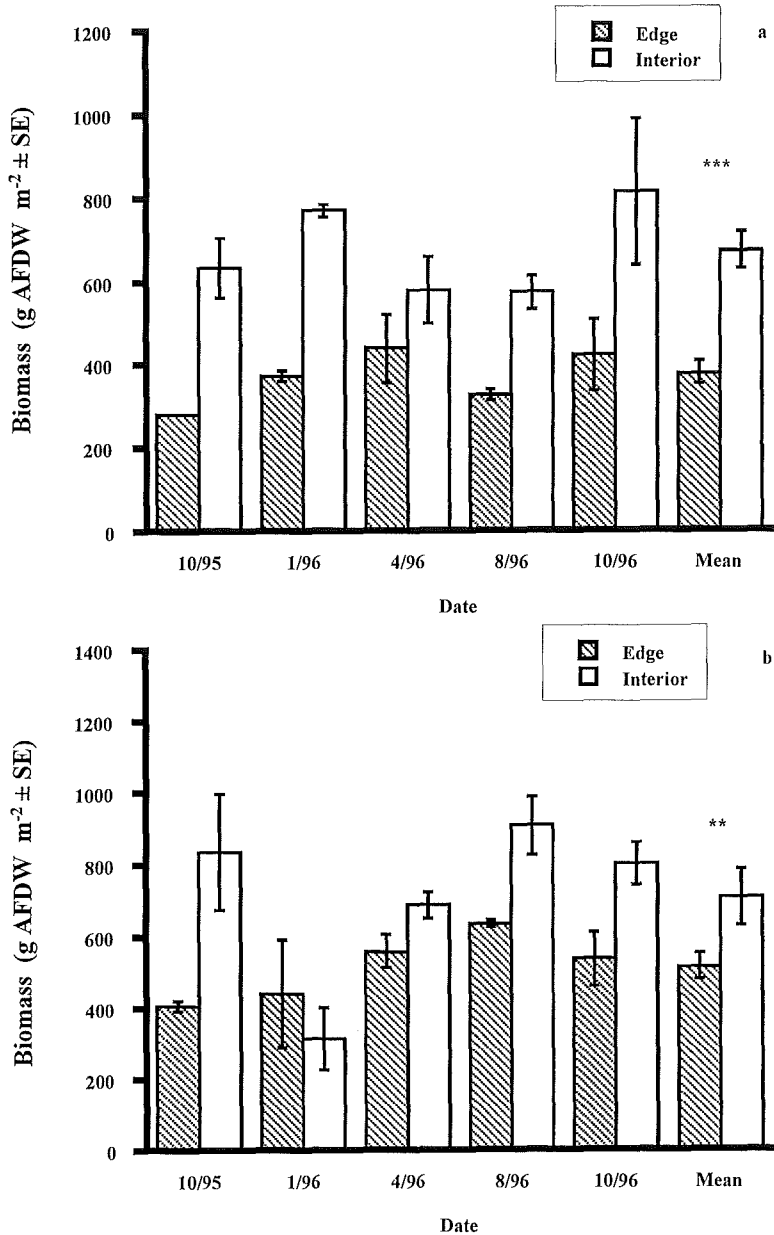


Fig. 5. Comparison of *Syringodium filiforme* plant biomass among dates of collection. Data presented represent mean total biomass for dates of collection expressed as grams AFDW per square meter \pm SE, with the addition of the composite mean value. Asterisk above composite value represents significant differences in mean plant biomass between edge and interior portions of the habitat. (a) North *S. filiforme* site. (b) South *S. filiforme* site.

and this response has also been reported for other systems as well (e.g., *T. testudinum*, Ziemann, 1972; *Zostera marina*, Orth, 1977; *Cymodocea nodosa*, Duarte and Sand-Jensen 1990a, 1990b). However, other investigators have not identified significant edge effects or simply assumed that among-habitat differences were

more important than within-habitat differences. Our results show that shoot density for all species showed high variability, with greater shoot density occasionally occurring at edges but averaged greater at interior sites (Figs. 2, 4, 6). On the other hand, only once was the biomass greater from an edge sampling date

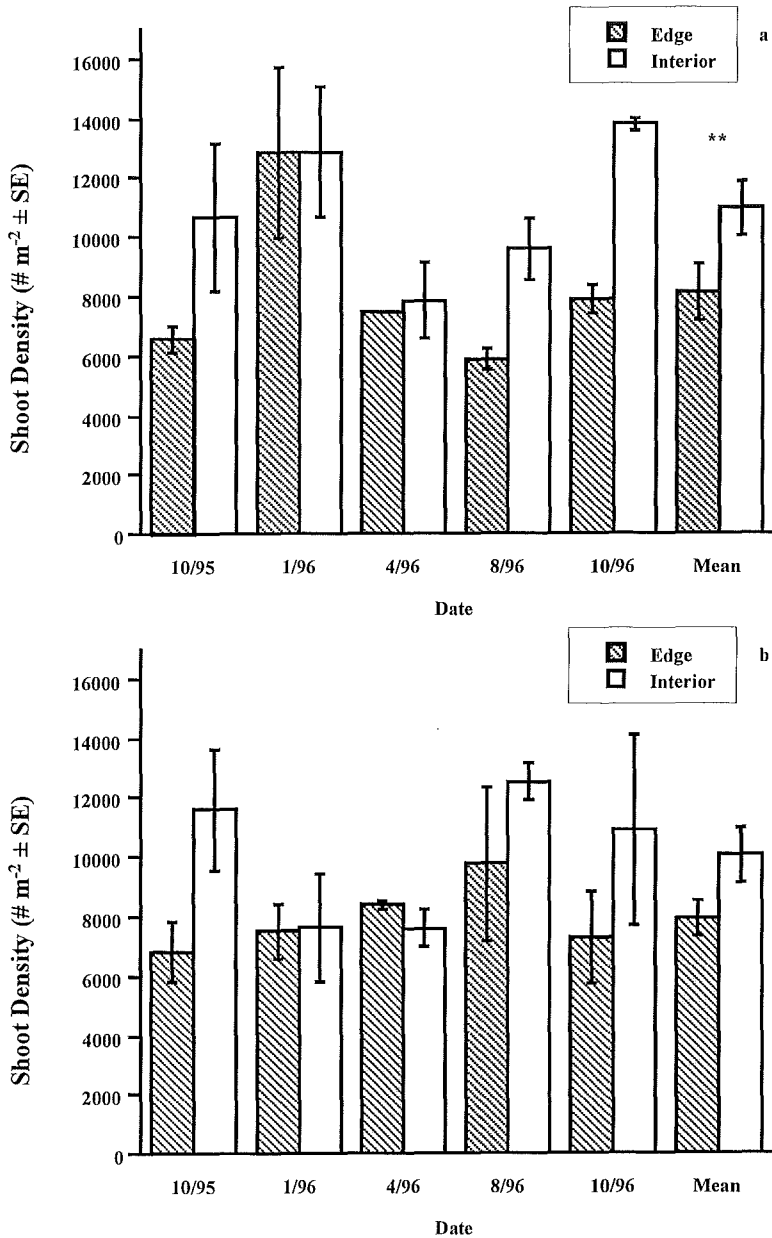


Fig. 6. Comparison of *Halodule wrightii* shoot density among dates of collection. Data presented represent mean shoot densities expressed as number of shoots per square meter \pm SE for dates of collection, with the addition of the composite mean value. Asterisk above composite value represents significant differences in mean shoot densities between edge and interior portions of the habitat. (a) North *H. wrightii* site. (b) South *H. wrightii* site.

(Fig. 3b), and this corresponded to winter biomass minima. These results may have significant implications on our assessment of edge communities in marine systems.

Several factors may make edge habitats more productive. At edges, competition for light and nutrients may be reduced. Edges, with greater

turbulent flow (Fonseca et al., 1982), may see increases in light through reflection from the sand, incident from the side, and increased flashing to the lower portions of the canopy. The greater turbulence may also decrease diffusive boundaries for plants (Koch, 1994), thereby increasing the transfer of nutrients

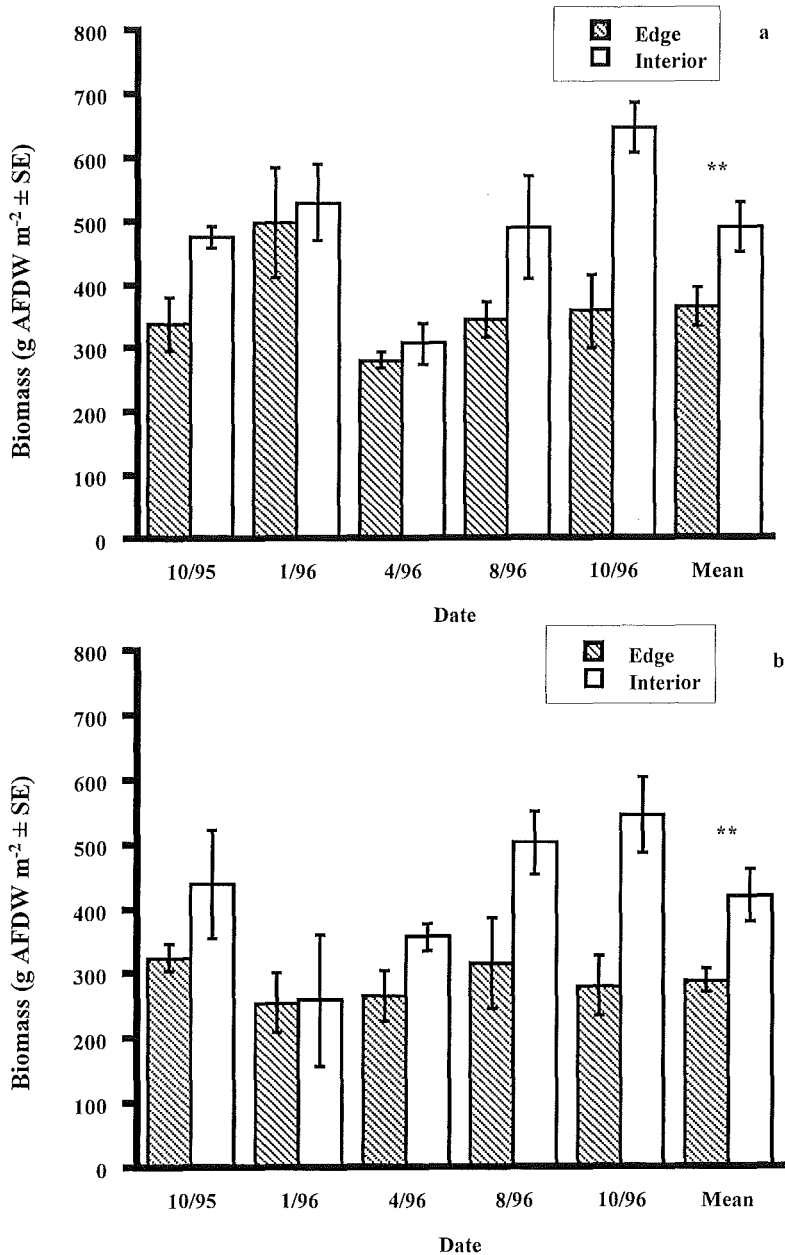


Fig. 7. Comparison of *Halodule wrightii* plant biomass among dates of collection. Data presented represent mean total biomass for dates of collection expressed as grams AFDW per square meter \pm SE, with the addition of the composite mean value. Asterisk above composite value represents significant differences in mean plant biomass between edge and interior portions of the habitat. (a) North *H. wrightii* site. (b) South *H. wrightii* site.

and wastes (Wheeler, 1980), which may lead to increased primary production (Fonseca and Kenworthy, 1987). Because interior portions of the bed are relatively quiescent, nutrients and dissolved inorganic carbon may have to travel through relatively thick diffusive boundaries, possibly limiting primary production (Koch,

1994) compared with the more turbulent boundaries encountered at edges (Fonseca et al., 1982). Edges may also encounter greater water-column nutrient potential because water entering the meadow may become relatively depleted in nutrients as it continues to interior portions of a bed. Additionally, there may be

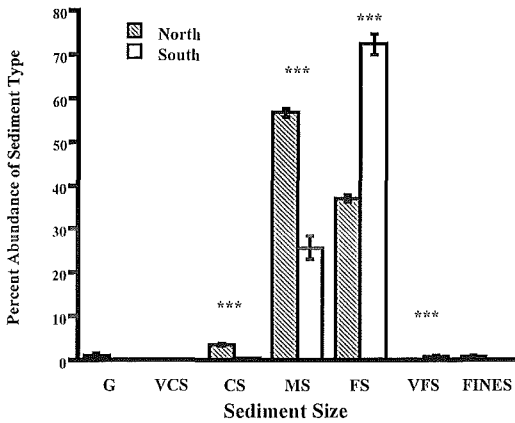


Fig. 8. Comparisons of sediment characteristics between north and south sites. Values expressed as percent total for each given size class \pm SE. Abbreviations: G, gravel; VCS, very coarse sand; CS, coarse sand; MS, medium sand; FS, fine sand; VFS, very fine sand; FINES, fine particulate material (e.g., silt and clay combined $< 63 \mu\text{m}$). Asterisks above bars indicate significant differences in percent abundance between north and south sites.

reduced competition for sediment nutrients at seagrass bed edges because of the lower shoot density and plant biomass there, and this constitutes a major source of nutrients for submerged vegetation (see reviews by Short, 1987; Barko et al., 1991). This may be of great importance for relatively pristine regions such as St. Joseph Bay, Florida (Rutkowski et al., 1999), but less so for regions undergoing eutrophication (Lapointe et al., 1994; Short and Burdick, 1996).

Because there are intimate relationships between seagrass flora and fauna, understanding the distributional aspects of the flora provides essential evidence in the functioning of seagrasses as habitat. Clearly, our results show significant differences in shoot density (Figs. 2, 4, 6) and biomass (Figs. 3, 5, 7) between edge and interior regions for all species investigated. These differences in plant demography may have important effects on growth, predation, and recruitment of associated organisms (Edgar and Robertson, 1992). It has been shown that the density and species richness of seagrass-associated fauna are often related to the biomass and plant surface area (Stoner and Lewis, 1985). However, recent evidence has shown that although biomass and shoot density may be lower at edges, faunal density may be significantly greater (Bologna, 1998). In some cases, organisms may show a settlement shadow (sensu Orth, 1992) elevating densities at edges (Bologna and Heck, 2000), but evidence

TABLE 1. Sediment organic carbon comparisons. Values represent mean percent sediment carbon \pm standard deviation. Collections were made in May and Oct. of 1996 from each of the seven habitats from both north and south sites. * Indicates significantly greater % organic carbon for samples collected in May than for those collected in Oct. † Indicates a significant location effect with % organic carbon greater from interior portions of the habitat than from the edge.

	Sand	<i>Thalassia testudinum</i>		<i>Syringodium filiforme</i>		<i>Halodule wrightii</i>	
		Edge	Interior	Edge	Interior	Edge	Interior
North							
May	0.38 \pm 0.05	0.75 \pm 0.09	1.19 \pm 0.11	0.58 \pm 0.08	0.66 \pm 0.04	1.29 \pm 0.02	0.75 \pm 0.06
Oct.	0.51 \pm 0.07	0.52 \pm 0.12*†	0.59 \pm 0.04*†	0.51 \pm 0.15	0.62 \pm 0.07	0.52 \pm 0.08	0.98 \pm 0.05
South							
May	0.48 \pm 0.01	0.84 \pm 0.06	0.56 \pm 0.14	0.68 \pm 0.003	0.64 \pm 0.07	0.98 \pm 0.21	1.93 \pm 0.29
Oct.	0.39 \pm 0.08	0.48 \pm 0.02*	0.47 \pm 0.02*	0.45 \pm 0.005*	0.49 \pm 0.03*	0.84 \pm 0.28†	1.03 \pm 0.21†

exists that for brooding organisms like amphipods, increased faunal density at edge habitat must confer some benefit to them (Bologna, 1998) and may be related to increases in secondary production (Bologna and Heck, 2002).

Although within-bay differences in plant demography existed in St. Joseph Bay, seagrass biomass in this region is among the highest seen in the Caribbean and Gulf of Mexico (Table 2). Regional comparisons indicate that plant biomass for all seagrass species from St. Joseph Bay more closely resembles biomass patterns from tropical regions rather than from subtropical ones (Table 2). In fact, biomass values for both *S. filiforme* and *H. wrightii* are among the highest values ever recorded for these species. These results are even more striking because our comparisons are made based on AFDW as opposed to dry weight alone (Table 2). It is interesting to note that only *S. filiforme* had greater biomass at the south site than at the north site (Fig. 5). This may relate to the sediment size in the south (Fig. 8), as Iverson and Bittaker (1986) showed an inverse relationship between mean sediment size and *S. filiforme* biomass and shoot density in the eastern Gulf of Mexico, and our results concur.

The differences in grain size characteristics between the north and south site could be attributed to energy regime. The north site is in a more open (higher energy) area of St. Joseph's Bay and consequently, contained coarser sediment than did the south site (Fig. 8). It should be noted, however, that both sites were characterized by relatively well-sorted sand. The lack of fine sediment (e.g., silt and clay) within our study region is significant but not overly surprising. Because there is relatively little riverine input to the system (Wolfe et al., 1988), there may be limited amounts of fine material being deposited from terrestrial sources within St. Joseph Bay. Additionally, both sites may have been situated in relatively high-energy regions and consequently, any fine material that might have been carried over the seagrass beds may have stayed in suspension regardless of baffling effect provided by the seagrasses. Our south site did indicate that finer sediment occurred within the interior portion of beds for all seagrass species (Fig. 8), but as our data were not consistent across the study area, we are forced to conclude that if sediment baffling was occurring within these habitats, it was not resolvable using grain size criteria alone. Seagrass beds in St. Joseph Bay may show a slight positive relief (e.g., 10–30 cm; Bologna, 1998), which suggests that they are sites

of increased sedimentation (cf. Almasi et al., 1987), or sediment retention (Fonseca and Fisher, 1986), and both are indicative of sediment baffling. However, it still may be possible to identify and quantify the importance of sediment baffling by seagrasses in sand-dominated environments through more intensive sampling. It is both desirable and ultimately necessary to assess the role of sediment baffling in seagrass beds because sediments may be a major source of nutrients (Short et al., 1990; Barako et al., 1991), and sediment baffling by various organisms (sea grasses, solitary corals, crinoids etc.) has been suggested as a means of stabilizing sediments before colonization by metazoans (e.g., Walker and Alberstadt, 1975; James and Bourque, 1992). Additionally, seagrasses provide surface area for coralline algal epiphytes (Bologna and Heck, 1999b), and this has been shown to increase the concentrations of CaCO_3 in the sediments (Land, 1970). These changes in sediment composition in relatively pristine regions may then lead to phosphate limitation (Short et al., 1990; Duarte et al., 1995).

Although a great deal of information exists regarding seagrass demography and distribution, we have a very limited understanding of edge dynamics. Because edges are regions in which beds are either expanding or are being destroyed through mechanical disturbance (e.g., boat moorings, crab burrows), we need to understand their community dynamics. This is especially true in regards to plant–animal interactions occurring at edges because the distribution of fauna, as well as the processes affecting their distribution, may be substantially different compared with interior regions of vegetated habitat. Continuing research into edge effects is needed to assess habitat value, as well as per unit primary and secondary production in coastal ecosystems. This will become increasingly important because loss and fragmentation of seagrass beds continue worldwide.

ACKNOWLEDGMENTS

We thank the University of South Alabama Departments of Marine Science and Geology for institutional support. We thank the Dauphin Island Sea Lab for providing laboratory space and access to research equipment. Funding for this project was provided by a grant from the Society of Wetland Scientist (PAXB) and a grant from the Conchologists of America (PAXB). We thank J. Harper and G. Eisel for

TABLE 2. Seagrass Biomass comparisons among regions of the Gulf of Mexico and adjacent areas. Biomass expressed as grams dry weight m⁻² for both above ground biomass (i.e., shoot biomass) and below ground biomass (i.e., rhizome and root biomass). * Indicates values are Ash Free Dry Weight.

Site	<i>Thalassia testudinum</i>		<i>Syringodium filiforme</i>		<i>Halodule wrightii</i>		Reference
	Above	Below	Above	Below	Above	Below	
St. Joseph Bay, FL	64–359*	65–830*	44–210*	199–696*	63–213*	172–460*	This study
St. Joseph Bay, FL	50–450	400–875					Heck and Valentine 1995
St. Joseph Bay, FL	137*						Iverson and Bittaker 1986
NE Gulf of Mexico	50*		5–50*		3–10		Iverson and Bittaker 1986
SE Gulf of Mexico	75–275*		25–250*		10–50		Iverson and Bittaker 1986
Pensacola, FL	20–130						Macauley et al. 1988
Tampa Bay, FL	25–180	600–900	50–170	160–400	38–50	60–140	Lewis and Phillips 1980
Florida Bay	58–267	321–2346	28–102	31–521	5–54	10–200	Zieman 1982
Florida Bay	0–215		0–107		0–87.5		Zieman et al. 1989
Florida Keys	120–180				10–60		Lapointe et al. 1994
Mississippi Sound, MS					42–166		Moncreiff et al. 1992
Chandeleur Sound, LA	52.3	314.9	53.2	150.7	4–42	35–119	Michot and Chadwick 1994
Guadeloupe Estuary, TX					20–70	50–210	Dunton 1990
Laguna Madre, TX	77.8 ± 26.2*		37.8 ± 5.6*		17.5–29*		Onuf 1996
St. Croix, US Virgin Islands	207 ± 52	1092 ± 209	24.5 ± 24.4	57.7 ± 46.2			Williams 1987
Yucatan Peninsula, Mexico	222–693	261–467					Gallegos et al. 1993
Cabelo Gordo de Dentro, Brazil					4–33	16–55	Oliveira et al. 1997

assistance in the laboratory. This is contribution # 344 to the Dauphin Island Sea Lab.

LITERATURE CITED

- ALMASI, M., C. HOSKIN, J. REED, AND J. MILO. 1987. Effects of natural and artificial *Thalassia* on rates of sedimentation. *J. Sedimentol. Petrol.* 57:901-906.
- BARKO, J., D. GUNNISON, AND S. CARPENTER. 1991. Sediment interaction with submerged macrophyte growth and community dynamics. *Aquat. Bot.* 41: 41-65.
- BELL, J., AND M. WESTOBY. 1986. Variation in seagrass height and density over a wide spatial scale: effects on fish and decapods. *J. Exp. Mar. Biol. Ecol.* 104: 275-295.
- BOLOGNA, P. A. X. 1998. The effects of seagrass habitat architecture on associated fauna. Ph.D. diss., Univ. South Alabama, Mobile, AL.
- , AND K. L. HECK. 1999a. Differential predation and growth rates of bay scallops within a seagrass habitat. *J. Exp. Mar. Biol. Ecol.* 239:299-314.
- , AND ———. 1999b. Macrofaunal associations with seagrass epiphytes: relative importance of trophic and structural characteristics. *J. Exp. Mar. Biol. Ecol.* 242:21-39.
- , AND ———. 2000. Impacts of seagrass habitat architecture on bivalve settlement. *Estuaries* 23:449-457.
- , AND ———. 2002. Impact of habitat edges on density and secondary production of seagrass associated fauna. *Estuaries* 25:1033-1044.
- CAMP, D. K., S. P. COBB, AND J. F. VAN BREEDVELD. 1973. Overgrazing of seagrasses by a regular urchin, *Lyttechinus variegatus*. *Bioscience* 23:37-38.
- COVENTRY, R. J., AND D. FETT. 1979. A pipette and sieve method of particle-size analysis and some observations on its efficacy. CSIRO Report No.38, 26 pp.
- DUARTE, C., M. MERINO, AND M. GALLEGOS. 1995. Evidence of iron deficiency in seagrass growing above carbonate sediments. *Limnol. Oceanogr.* 40:1153-1158.
- , AND K. SAND-JENSEN. 1990a. Seagrass colonization: patch formation and patch growth in *Cymodocea nodosa*. *Mar. Ecol. Prog. Ser.* 65:193-200.
- , AND ———. 1990b. Seagrass colonization: biomass development and shoot demography in *Cymodocea nodosa* patches. *Mar. Ecol. Prog. Ser.* 67: 97-103.
- DUNTON, K. 1990. Production ecology of *Ruppia maritima* L. s.l. and *Halodule wrightii* Aschers. in two subtropical estuaries. *J. Exp. Mar. Biol. Ecol.* 143: 147-164.
- EDGAR, G. 1990a. The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *J. Exp. Mar. Biol. Ecol.* 137:195-214.
- . 1990b. Population regulation, population dynamics and competition amongst mobile epifauna associated with seagrass. *J. Exp. Mar. Biol. Ecol.* 144:205-234.
- , AND A. ROBERTSON. 1992. The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and process in a Western Australia *Amphibolis* bed. *J. Exp. Mar. Biol. Ecol.* 160:13-31.
- FOLK, R. L. 1980. Petrology of sedimentary rocks. Hemphill Publishing Co., Austin, TX.
- FONSECA, M. S., AND J. S. FISHER. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Mar. Ecol. Prog. Ser.* 29:15-22.
- , AND W. KENWORTHY. 1987. Effect of current on photosynthesis and distribution of seagrasses. *Aquat. Bot.* 27:59-78.
- , J. C. ZEIMAN, G. W. THAYER, AND J. S. FISHER. 1982. Influence of the seagrass *Zostera marina*, on current flow. *Estuar. Coast. Shelf Sci.* 15:351-364.
- GALLEGOS, M., M. MERINO, N. MARBA, AND C. DUARTE. 1993. Biomass and dynamics of *Thalassia testudinum* in the Mexican Caribbean: elucidation rhizome growth. *Mar. Ecol. Prog. Ser.* 95:185-192.
- GAMBI, M. C., A. NOWELL, AND P. JUMARS. 1990. Flume observations on flow dynamics in *Zostera marina* (eelgrass) beds. *Mar. Ecol. Prog. Ser.* 61:159-169.
- HECK, K., AND J. VALENTINE. 1995. Sea urchin herbivory: evidence for long-lasting effects in subtropical seagrass meadows. *J. Exp. Mar. Biol. Ecol.* 189: 205-217.
- HECK, K. L., AND L. B. CROWDER. 1991. Habitat structure and predator-prey interactions, p. 281-299. *In: Habitat structure: the physical arrangement of objects in space.* S. Bell, E. McCoy, and H. Mushinsky (eds.). Chapman and Hall, New York.
- HOLLING, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.* 62:447-502.
- IRLANDI, E. A. 1994. Large- and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* 98:176-183.
- IVERSON, R. L., AND H. F. BITTAKER. 1986. Seagrass distribution in the eastern Gulf of Mexico. *Estuar. Coast. Shelf Sci.* 22:577-602.
- JAMES, N. P., AND P. BOURQUE. 1992. Reefs and mounds, p. 409. *In: Facies models: response to sea level change.* R. G. Walker and N. P. James (eds.). Geological Society of Canada, St. John's, Canada.
- KOCH, E., AND G. GUST. 1999. Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. *Mar. Ecol. Prog. Ser.* 184:63-72.
- KOCH, E. W. 1994. Hydrodynamics, diffusion-boundary layers and photosynthesis of the seagrasses *Thalassia testudinum* and *Cymodocea nodosa*. *Mar. Biol.* 118:767-776.
- LAND, L. S. 1970. Carbonate mud: production by epibiont growth on *Thalassia testudinum*. *J. Sedimentol. Petrol.* 40:1361-1363.
- LAPOINTE, B., D. TOMASKO, AND W. MATZIE. 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. *Bull. Mar. Sci.* 54:696-717.
- LARKUM, A. W., AND C. DEN HARTOG. 1989. Evolution

- and biogeography of seagrasses, p. 112–156. *In*: Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australia region. A. W. Larkum, A. J. McComb, and S. A. Shepherd (eds.). Elsevier Science Publishers, Amsterdam.
- LEVIN, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- LEWIS, R., AND R. PHILLIPS. 1980. Seagrass mapping project. Tampa Port Authority, Hillborough County, FL.
- LIVINGSTON, R. J., R. S. BOYD, AND M. S. ZIMMERMAN. 1976. Determination of sampling strategy for benthic macrophytes in polluted and unpolluted coastal areas. *Bull. Mar. Sci.* 26:669–575.
- MARBA, N., AND C. DUARTE. 1995. Coupling of seagrass (*Cymodocea nodosa*) patch dynamics to subaqueous dune migration. *J. Ecol.* 83:381–389.
- MCCAULEY, J., J. CLARK, AND W. PRICE. 1988. Seasonal changes in the standing crop and chlorophyll content of *Thalassia testudinum* Banks ex König and its epiphytes in the northern Gulf of Mexico. *Aquat. Bot.* 31:277–287.
- MICHOT, T., AND P. CHADWICK. 1994. Winter biomass and nutrient values of three seagrasses species as potential foods for redheads (*Aythya americana* Eyton) in Chandeleur Sound, Louisiana. *Wetlands* 14:276–283.
- MONCREIFF, C. A., M. SULLIVAN, AND A. E. DAEHNICK. 1992. Primary production dynamics in seagrass beds of Mississippi Sound: the contributions of seagrass, epiphytic algae, sand microflora, and phytoplankton. *Mar. Ecol. Prog. Ser.* 87:161–171.
- OGDEN, J. C., R. A. BROWN, AND N. SALESKY. 1973. Grazing by the echinoid *Diadema antillarum* Philippi: formation of Halos around West Indian patch reefs. *Science* 182:715–717.
- OLIVEIRA, E., T. CROSIER, V. DE ESTON, AND O. AMBRÓSIO. 1997. Phenology of a seagrass (*Halodule wrightii*) bed on the southeast coast of Brazil. *Aquat. Bot.* 56:25–33.
- ONUF, C. 1996. Biomass patterns in seagrass meadows of the Laguna Madre, Texas. *Bull. Mar. Sci.* 58:404–420.
- ORTH, R. J. 1975. Destruction of eelgrass, *Zostera marina*, by the cownose ray, *Rhinoptera bonasus*, in the Chesapeake Bay, Virginia. *Chesapeake Sci.* 16:205–208.
- . 1977. The importance of sediment stability in seagrass communities, p. 281–300. *In*: Ecology of marine benthos. B. C. Coull (ed.). Univ. South Carolina Press, Columbia, SC.
- . 1992. A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance, p. 147–164. *In*: Plant-animal interactions in the marine benthos. D. John, S. Hawkins, and J. Price (eds.). Systematics Association, Clarendon Press, Oxford.
- PETERSON, C. H. 1986. Enhancement of *Mercenaria mercenaria* densities in seagrass beds: is pattern fixed during settlement season or altered by subsequent differential survival? *Limnol. Oceanogr.* 31:200–205.
- RASMUSSEN, E. 1973. Systematics and ecology of the Isleford marine fauna. *Ophelia* 11:1–495.
- ROBBINS, B. D., AND S. S. BELL. 1994. Seagrass landscapes: a terrestrial approach to the marine subtidal environment. *Trends Ecol. Evol.* 9:301–304.
- ROBERTSON, A. I. 1979. The relationship between annual production ratio and life spans for marine macrobenthos. *Oecologia* 38:193–202.
- RŪTKOWSKI, C., W. BURNETT, R. IVERSON, AND J. CHANTON. 1999. The effect of groundwater seepage on nutrient delivery and seagrass distribution in the northeastern Gulf of Mexico. *Estuaries* 22:1033–1040.
- SAVASTANO, K. J., K. H. FALLER, AND R. L. IVERSON. 1984. Estimating vegetation coverage in St. Joseph Bay, Florida, with an airborne multispectral scanner. *Photogrammetric Eng. Remote Sens.* 50:1159–1170.
- SHORT, F. 1987. Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. *Aquat. Bot.* 27:41–57.
- , AND D. BURDICK. 1996. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loadings in Waquoit Bay, Massachusetts. *Estuaries* 19:730–739.
- SHORT, F. T., W. C. DENNISON, AND D. G. CAPONE. 1990. Phosphorus-limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. *Mar. Ecol. Prog. Ser.* 62:169–174.
- STONER, A. W., AND F. LEWIS. 1985. The influence of quantitative and qualitative aspects of habitat complexity in tropical sea-grass meadows. *J. Exp. Mar. Biol. Ecol.* 94:19–40.
- THAYER, G. W., W. KENWORTHY, AND M. FONSECA. 1984. The ecology of eelgrass meadows of the Atlantic coast: a community profile. United States Fisheries and Wildlife Service Biology Series Program. FWS/OBS-84/02, 147 p.
- , AND H. H. STUART. 1974. The bay scallop makes its bed of seagrass. *Mar. Fish. Rev.* 36:27–30.
- TURNER, S., J. HEWITT, M. WILKINSON, D. MORRISEY, S. THRUSH, V. CUMMINGS, AND G. FUNNELL. 1999. Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. *Estuaries* 22:1016–1032.
- VALENTINE, J. F., K. L. HECK, P. HARPER, AND M. BECK. 1994. Effects of bioturbation in controlling turtlegrass (*Thalassia testudinum* Banks ex König) abundance: evidence from field enclosures and observations in the Northern Gulf of Mexico. *J. Exp. Mar. Biol. Ecol.* 178:181–192.
- WALKER, K. R., AND L. P. ALBERSTADT. 1975. Ecological succession as an aspect of structure in fossil communities. *Paleobiology* 1:238–257.
- WHEELER, W. 1980. Effect of boundary layer transport on the fixation of carbon by the giant kelp *Macrocystis pyrifera*. *Mar. Biol.* 56:103–110.
- WILLIAMS, S. 1987. Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. *Mar. Ecol. Prog. Ser.* 35: 91–98.
- WOLFE, S., J. REIDENAUER, AND D. MEANS. 1988. An

ecological characterization of the Florida panhandle. Minerals Management Science Report 88-0063.

ZIEMAN, J. 1972. Origin of circular beds of *Thalassia* (Spermatophyta: Hydrocharitacea) in south Biscayne Bay, Florida, and their relationship to mangrove hummocks. *Bull. Mar. Sci.* 22:671-738.

———. 1982. The ecology of seagrasses of south Florida: a community profile. U.S.F.W.S., Office of Biological Services, Washington, D.C. FWS/OBS-82/25. 158 p.

———, J. FOURQUREAN, AND R. IVERSON. 1989. Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bull. Mar. Sci.* 44:292-311.

(PAXB) DEPARTMENT OF MARINE SCIENCES, UNIVERSITY OF SOUTH ALABAMA, DAUPHIN ISLAND SEA LAB, DAUPHIN ISLAND, AL 36528; AND (DH) DEPARTMENT OF EARTH SCIENCES, UNIVERSITY OF SOUTH ALABAMA, LSCB 136, MOBILE, ALABAMA 36688. PRESENT ADDRESS (PAXB): DEPARTMENT OF BIOLOGICAL AND ALLIED HEALTH SCIENCES, FAIRLEIGH DICKINSON UNIVERSITY, 285 MADISON AVE., M-EC1-01, MADISON, NEW JERSEY 07940. Send reprint requests to PAXB. Date accepted: August 12, 2002.