

BIOMASS PATTERNS IN SEAGRASS MEADOWS OF THE LAGUNA MADRE, TEXAS

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ABSTRACT

The Laguna Madre of Texas supports the most extensive seagrass meadows in the western Gulf of Mexico. In 1988 seagrasses covered 730 km² or about three-quarters of the embayment. *Halodule wrightii* dominated the entire upper laguna, and total biomass was quite uniform near 160 g·m⁻² throughout. Four species shared dominance in the lower laguna. Where present mean biomass of *Thalassia testudinum* was 373 g·m⁻²; *Syringodium filiforme*, 138 g·m⁻²; *Halodule wrightii*, 78 g·m⁻²; and *Halophila engelmannii*, 6 g·m⁻². Macroalgae were widespread, at 71 g·m⁻² where present. *Halodule wrightii* was dominant and biomass was low on sand flats of the barrier island separating the laguna from the gulf. *Halophila engelmannii* was limited to the deep edges of meadows. Biomass >300 g·m⁻² was limited to one extensive *T. testudinum* meadow at the south end of the laguna at all vegetated depths and two small areas with *S. filiforme* dominant at intermediate depths. Laguna Madre was similar in biomass to the two regions of extensive development of seagrasses in the eastern gulf: the Big Bend region of Florida (Iverson and Bittaker, 1986) and Florida Bay (Iverson and Bittaker, 1986; Zieman, et al., 1989). The laguna differed from the eastern gulf sites in more turbid waters and much shallower maximum depths of occurrence of seagrasses (<2 m compared to 8-11 m), higher contribution of *H. wrightii* to system-wide biomass (although *H. wrightii*'s share has rapidly diminished in Laguna Madre as it has been displaced by *S. filiforme* and *T. testudinum* [Quammen and Onuf, 1993]), and much higher macroalgal biomass (limited to the section of the lower laguna receiving agricultural inflows). Similarities in the environments of Laguna Madre and inner Florida Bay suggest that, if cover and biomass of *Thalassia* continue to increase, the laguna may become vulnerable to mass mortalities as are now occurring in Florida Bay.

The Gulf of Mexico region has some of the most extensive seagrass meadows in the world. Recent surveys have documented the occurrence of meadows over 3,000 km² of continental shelf in the Big Bend region of Florida's west coast (28 to 30°N Latitude) (Iverson and Bittaker, 1986), 5,500 km² in Florida Bay (Iverson and Bittaker, 1986, and Zieman et al., 1989), and 2,050 km² off the northwest Cuban coast (Buesa, 1974). The same studies examined patterns in the spatial distribution of biomass for those meadows. Seagrass meadows are relatively minor features along the northern Gulf of Mexico, with fringing meadows on the north side of islands in Mississippi Sound and on the west side of the Chandeleur Islands of Louisiana (Eleuterius, 1987). Along the western shore of the Gulf of Mexico, seagrass meadows are minor features in the north but become increasingly important in embayments behind barrier islands to the south, to the extent that seagrasses cover 730 km² in Laguna Madre, almost three-quarters of the subtidal area of the embayment (Quammen and Onuf, 1993). Major losses of seagrass cover and shifts in species composition from the mid-1960's to 1988 have been documented in this system (McMahan, 1969; Merkord, 1978; Quammen and Onuf, 1993). Here is reported an analysis of the distribution of biomass in this focal area for seagrasses in the western Gulf of Mexico. Seagrasses of the Laguna Madre are of special concern, because Laguna Madre is the primary wintering area for the redhead duck (*Aythya americana*), which feeds almost entirely on one species of seagrass (*Halodule wrightii*) while in residence.

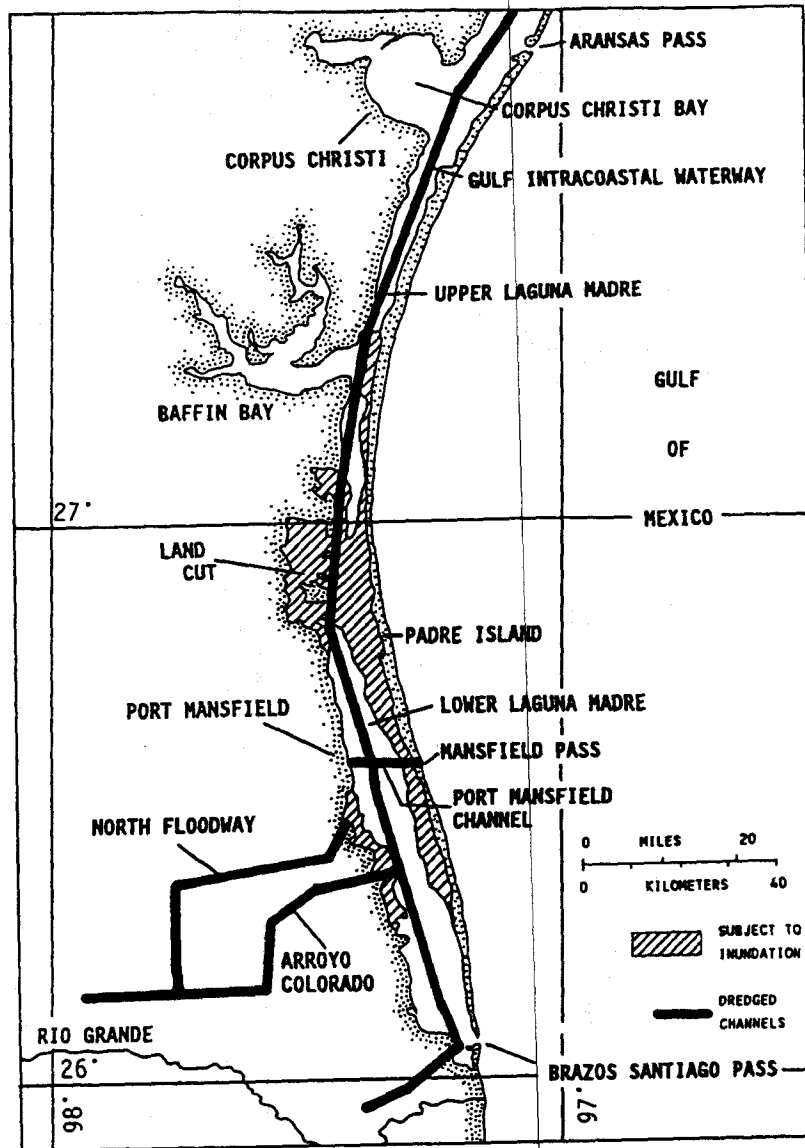


Figure 1. Map of Laguna Madre showing features described in the text.

SITE DESCRIPTION AND METHODS

Laguna Madre is the southernmost embayment along the Texas coast. It extends north from the delta of the Rio Grande some 200 km to Corpus Christi Bay (Fig. 1). The laguna is 12 km across at its widest and has a mean depth of 1 m, with greatest natural depths of 3 m or less generally west of middle along the short axis. The bottom rises quite steeply at the western shore, but for about half its length grades into broad, seldom-inundated flats to the east, the landward side of Padre Island. Padre Island is the coastal barrier that separates Laguna Madre from the Gulf of Mexico. Precipitation in a "normal" year is about 65 cm and evaporation exceeds precipitation by about 60 cm annually (Behrens, 1966). Freshwater inflow is limited in amount and confined to a few flood control and agricultural drains that discharge into the middle reach of the lower laguna on the west side. Consequently, the laguna is hypersaline most of the time, except close to the drains. Lunar tides seldom exceed 10 cm,

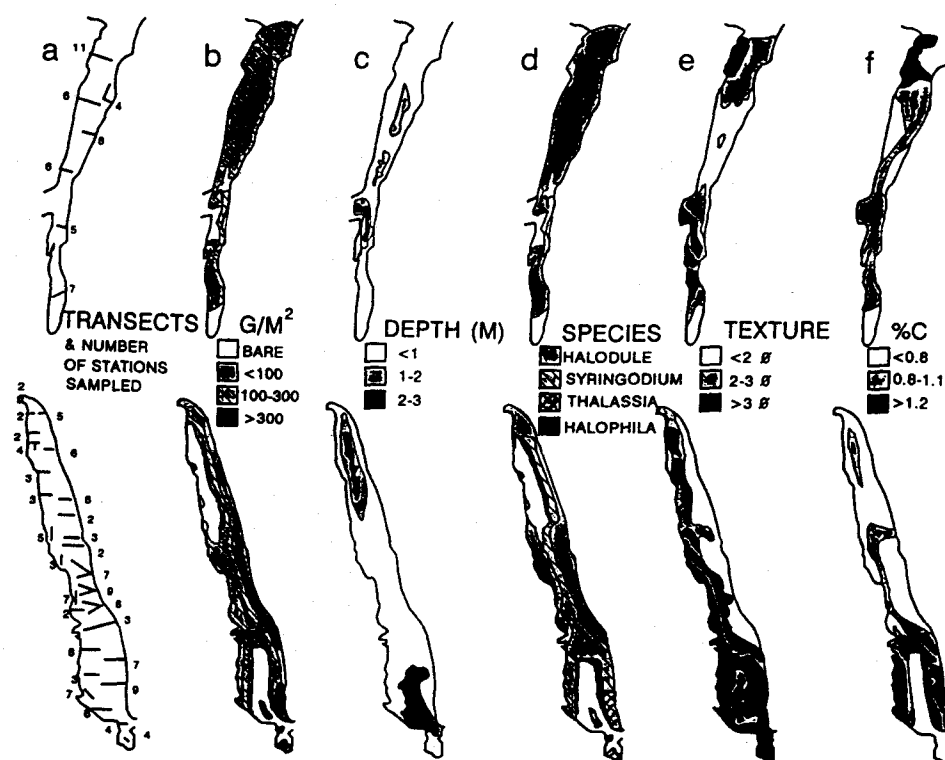


Figure 2. Vegetation and environmental characteristics of Laguna Madre: upper laguna—top, lower laguna—bottom; transects along which biomass samples were collected and number of stations for which biomass determinations were made (a), distribution of biomass (b), depth (c), dominant cover of vegetated areas—blank areas within the bounds of the laguna are bare (d), sediment texture (e), sediment organic content (f). Data for (e) and (f) were extracted from White et al. (1983, 1986, 1989).

while seasonally, water levels may vary as much as 30 cm. Larger changes may be associated with storms or strong northerly winds during frontal passages in the winter. The rest of the time, southeast winds prevail, usually in excess of 10 knots ($19 \text{ km} \cdot \text{h}^{-1}$).

Sampling transects for vegetative cover usually ran perpendicular to shore with approximately 5 km intervals between transects. In some shallow areas, transects were run in a sawtooth pattern, the next transect commencing from the end of the last, or parallel to shore. At each sampling station we collected three or four 80 cm^2 by 15 cm deep sediment cores with associated seagrass and algae and measured water depth, water temperature, salinity (with refractometer), and Secchi depth (20 cm diameter) at stations 100 to 500 m apart, depending on transect and proximity to a boundary. Depths were standardized by adjusting measured depth by the deviation from mean sea level at sampling time for the National Ocean Service tide gauge at Port Mansfield, Texas. Position was determined by loran C. In all, approximately 3,000 cores were collected at 800 stations along 70 transects.

For each core, we recorded all seagrass species, algal presence, and the dominant contributor to vegetative cover. These data were used to determine the extent and composition of seagrass meadows as reported in Quammen and Onuf (1993). Where conditions allowed, we used aerial photography of November 1987 to interpolate boundaries between transects. Too many samples were collected to determine biomass for all. Therefore, samples were retained for further processing only from every third transect and for only two samples per station (three for the middle reach of the lower laguna). Approximately 15% of the samples collected within meadows were kept for later biomass determination. The location of transects and the number of stations from which biomass collections were made are indicated in Figure 2a. All sampling was carried out between July and November 1988. Samples were washed on 1 mm mesh screens. All plant material retained on the screens was placed in plastic bags and stored on ice for transport to the laboratory, where the samples were frozen until processed.

Processing consisted of thawing and separating into live (turgid green, white to beige and pink structures) and dead (flaccid brown to washed-out maroon) fractions. The live fraction was sorted further according to species and into aboveground (green portions of shoots) and belowground (root, rhizome, and unpigmented portions of shoots) fractions. The sample fractions were dried to constant weight at 60°C (72 h), weighed, ashed at 530°C for 1 h, and weighed again. Dry weight and ash-free dry weight were calculated for all plant parts and dead material. Station means were computed on a per m² basis and these in turn were used to compute mean biomass for each species where present and baywide.

Sediment characteristics were obtained from White et al. (1983, 1986, 1989). Light was related to seagrass distribution along a set of transects located between 26°30' and 26°40'N (Onuf, 1991). Approximately 2,000 light vs. depth profiles were obtained on 60 sampling dates between January 1988 and September 1989 using a LI-1000 datalogger (LI-COR, Lincoln, NE) that recorded simultaneous measurements of incident PAR (photosynthetically active radiation) from a flat-plane (2 pi) quantum sensor (LI-190SA) mounted above the boat and a spherical underwater quantum sensor (LI-193SA) mounted on a lowering frame. A mean diffuse attenuation coefficient (*k*) was calculated from each depth profile (Onuf, 1991) and the mean of all diffuse attenuation coefficients within each 0.2' of longitude segment of a transect was computed for the entire study. These values were then related to depth and the occurrence of seagrass as determined from material with live rhizome brought up with the anchor.

RESULTS

Large-scale Biomass Patterns.—The northern (upper) and southern (lower) portions of Laguna Madre differed markedly in spatial distribution of seagrass biomass. Biomass was relatively uniform in the upper laguna. Between 100 and 300 g·m⁻² seagrasses covered almost the entire embayment (Fig. 2b), except for a small area of shallow flats opposite the mouth of Baffin Bay with biomass <100 g·m⁻² (Figs. 1, 2c). The pattern of biomass distribution was much more varied in the lower laguna (Fig. 2b). There was a zone of low biomass (<100 g·m⁻²) along most of the eastern shore and along the outer edge of meadows fringing the two areas of deeper water in the lower laguna (Fig. 2c). High biomass (>300 g·m⁻²) was limited to two elongate areas in the middle reach where seagrass cover was continuous across the laguna and in one area on the east side near the gulf outlet (Fig. 2b). Intermediate biomasses prevailed over most of the middle reach of the lower laguna and in bands at intermediate depth where meadows had an outer edge.

There was some association between biomass (Fig. 2b) and species composition of meadows of the lower laguna (Fig. 2d). *Halodule wrightii* Ascherson always was dominant where there was a nearshore, low biomass band, while *Halophila engelmannii* Ascherson usually was dominant where there was a low biomass band at the outer edge of meadows. Most *Thalassia testudinum* Banks ex König was in the high biomass patch near the south end of the laguna. *Syringodium filiforme* Kützinger also occurred at high biomass but over a much smaller proportion of the area that it dominated than was the case for *T. testudinum*. All species except *H. engelmannii* occurred at intermediate biomasses (100–300 g·m⁻²). Areas dominated by *S. filiforme* often had other species interspersed. The other meadow types or zones tended to be more monotypic. *H. wrightii* dominated all vegetated areas of the upper laguna. The occurrence of a shallow, low biomass band was limited to a short stretch along the eastern shore opposite the mouth of Baffin Bay.

There was no obvious association between biomass (Fig. 2b) and sediment texture (Fig. 2e) or sediment total organic carbon (Fig. 2f). All biomass classes occurred on all sediment types. The area dominated by *T. testudinum* (Fig. 2d) was primarily in the finest sediment texture category (Fig. 2e). Other species occurred over all sediment types.

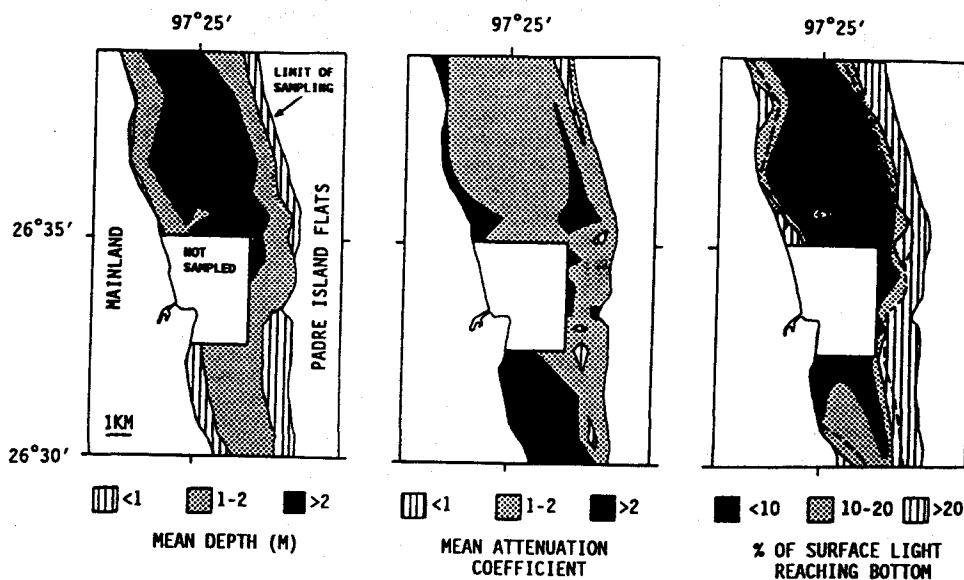


Figure 3. Contour maps of depth (left), mean attenuation coefficient (middle), and percent of surface light reaching the bottom (right) in Laguna Madre near Port Mansfield, Texas. The dashed line in the right panel is the outer limit of seagrass meadow as defined by >50% of anchor samples in a sampling interval having seagrass.

Depth Limits of Seagrasses in Relation to Light.—Detailed observations of the underwater light regime were made only in the vicinity of Port Mansfield (Fig. 1). Waters were least transparent at shallow to intermediate depths along the western shore, and at intermediate depths on the east side, especially in the south (Fig. 3, left, middle). The integrated effect of light attenuation and depth on light reaching the bottom was a central region of low light availability (<10% of surface irradiance [SI]) that extended all the way to the western shore in the south (Fig. 3, right). Elsewhere the central region of low light was bounded by an envelope of intermediate levels of light at the bottom (10–20% SI). The only extensive region of high light at the bottom (>20% SI) was along the eastern edge of the study area (Fig. 3, right), encompassing the areas of clearest water (Fig. 3, middle) and extending from shallow (<1 m) to intermediate (1–2 m) depths (Fig. 3, left).

Based on 0.2' longitude intervals of transects sampled at least 10 times between January 1988 and September 1989, seagrasses were rarely encountered at locations where <10% of surface light reached the bottom (Fig. 4). The mean for all stations in a light interval did not exceed 50% frequency of occurrence until the interval where 20–30% of surface light reached the bottom (Fig. 4). Based on this relationship, >50% frequency of occurrence of seagrass at a station was set as the criterion for continuous meadow. According to this criterion, meadow bounded the entire eastern side of the study area but occurred only at the north and south ends on the western side (Fig. 3, right). The 50% frequency of occurrence isopleth lay in or near the zone where 10–20% of surface light reached the bottom. *Halodule wrightii* tended to be the dominant species at highest and lowest light, *Halophila engelmannii* was only dominant at low light, and *S. filiforme* was almost always the dominant species at intermediate light levels (Fig. 4).

The maximum depth of occurrence of seagrass averaged over all sampling dates

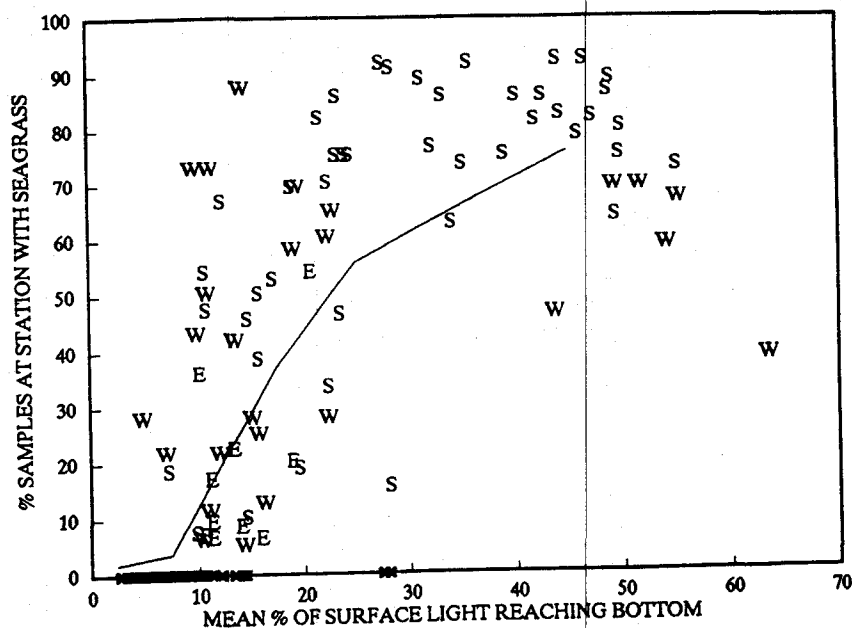


Figure 4. The relationship of seagrass cover to percent of surface light reaching the bottom in a 0.2-min interval of longitude along sampling transects. Means for stations where at least 10 observations of light and cover were made during the 21 months of the study are plotted using a letter to identify the dominant species at the station: E—*Halophila engelmannii*, S—*Syringodium filiforme*, W—*Halodule wrightii*, X—bare. The line connects the means of percent occurrence of seagrasses for 0–5, 5–10, 10–15, 15–20, 20–30, and >30 intervals of percent of surface light reaching the bottom.

was highly variable in the vicinity of Port Mansfield. Seagrasses grew deeper in the northern part of the study area than in the south; however, the north-south trend was much more erratic along the western shore than along the east side of the study area (Fig. 5). In fact, the very occurrence of seagrasses was erratic along the western shore. Twenty-eight percent of the time seagrasses were not encountered at all along transects on the west side, while seagrasses were absent from transects only 6% of the time on the east side. On the transect at 26°35.5'N, an "island" of seagrass was found >30 cm deeper than on either end of the transect (Figs. 3, right; 5). Turbid water extended further toward the middle of the laguna on this transect than elsewhere in the northern half of the study area (Fig. 3, middle). The "island" of seagrass was perched on a rise of the bottom to within 1.5 m of the surface (Fig. 3, left) far enough from the western shore to be in relatively clear water (Fig. 3, middle) and therefore received more light than further in or out on the same transect (Fig. 3, right).

Local Biomass Patterns.—The entire laguna was subdivided to carry out a more refined analysis of biomass distribution. Eastern and western sides were distinguished, because the east side of the laguna is more sheltered from waves generated by the prevailing southeasterly winds than the west side. The difference in exposure between sides of the laguna may influence the development of seagrass meadows. Other distinctions were between upper laguna and lower laguna (monoculture vs. mixed assemblage) and within the lower laguna, between regions with continuous cover across the laguna vs. regions with a bare zone in the middle.

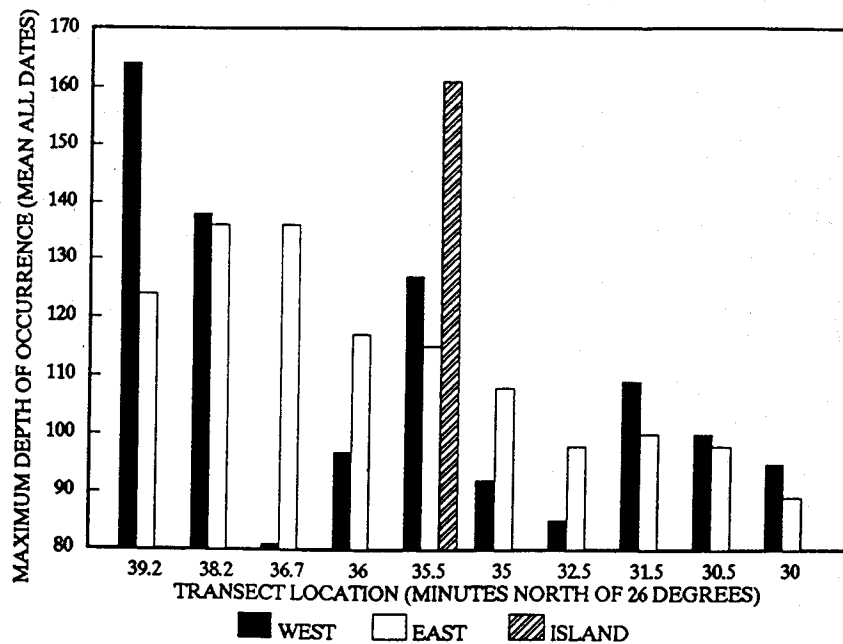


Figure 5. Variation in maximum depth of occurrence of seagrasses with latitude and between east (open bar) and west sides (solid bar) of Laguna Madre near Port Mansfield, Texas. "Island" (diagonal striping) refers to a disjunct patch of seagrass off the western shore on the transect at 26°35.5'N latitude (Fig. 3, right).

Also, extensive areas dominated by *T. testudinum* were treated as a separate meadow type.

Biomass was close to 200 g·m⁻² throughout the upper laguna, except in the shallowest depth zone on the east side, where it was somewhat lower (Fig. 6, top). The lower laguna was much more heterogeneous. In the middle reach where meadow extended across the whole laguna, total biomass was close to 200 g·m⁻² on the west side (lower laguna, west, no deep edge in Fig. 6) with *H. wrightii* dominant in shallow water and *S. filiforme* contributing slightly more than *H. wrightii* in deeper water. On the east side, biomass increased dramatically with depth, from 100 g·m⁻² at 0–39 cm deep to 700 g·m⁻² at 80–119 cm deep (lower laguna, east, no deep edge in Fig. 6). *H. wrightii* contributed most in shallow water, macroalgae in the intermediate zone, and *S. filiforme* deep.

In portions of the laguna with mixed assemblages bordering on deep, bare areas, seagrasses on the west side were barely present in 0–39 cm of water, reached maximal biomass of 160 g·m⁻² evenly distributed among *H. wrightii*, *S. filiforme*, and *T. testudinum* at 40–79 cm, and diminished to 35 g·m⁻² at >120 cm (lower laguna, west, deep edge in Fig. 6). Macroalgae dominated at 80–119 cm, contributing 220 g·m⁻². On the east side, biomass increased from 100 g·m⁻² at 0–39 cm to 230 g·m⁻² at 80–119 cm and decreased to 40 g·m⁻² at >120 cm (lower laguna, east, deep edge in Fig. 6). *H. wrightii* was the only species present at 0–39 cm, *H. wrightii* and macroalgae dominated at 40–79 cm, *S. filiforme* at 80–119 cm, and macroalgae at >120 cm.

Biomass was high at all depths in the *T. testudinum* meadow (lower laguna, east, deep edge, *Thalassia* in Fig. 6), ranging from 300 to 700 g·m⁻². *Thalassia testudinum* dominated across all depths; however, *S. filiforme* contributed >100

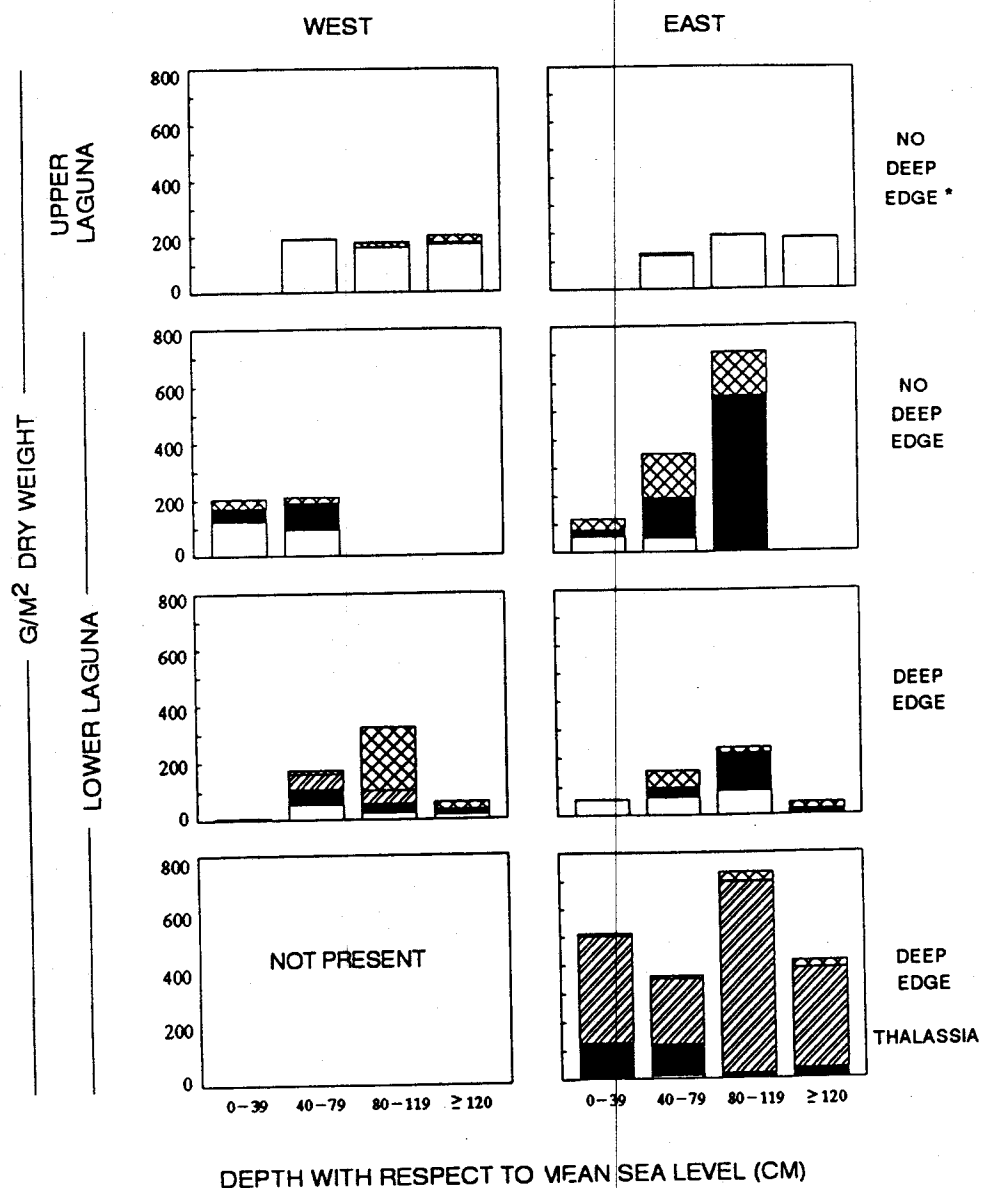


Figure 6. Distribution of biomass according to depth in Laguna Madre: west side of laguna—left; east side of laguna—right; upper laguna—top; lower laguna, continuous cover across laguna—second from top; lower laguna, mixed meadows ending in deep water—third from top; lower laguna, meadows dominated by *Thalassia testudinum*—bottom. *Halodule wrightii*—open bar; *Syringodium filiforme*—black; macroalgae—crosshatch; *Thalassia testudinum*—diagonal striping. The absence of a bar indicates no samples from that depth category. Sample sizes ranged from 3 to 45 for the different bars.

$\text{g}\cdot\text{m}^{-2}$ in the two shallower depth zones. Macroalgae were minor contributors at all depths. Although no obvious relationship between biomass and sediment texture was apparent in the gross patterns of distribution presented above, the apportionment of biomass within *H. wrightii* plants varied in relation to mean grain

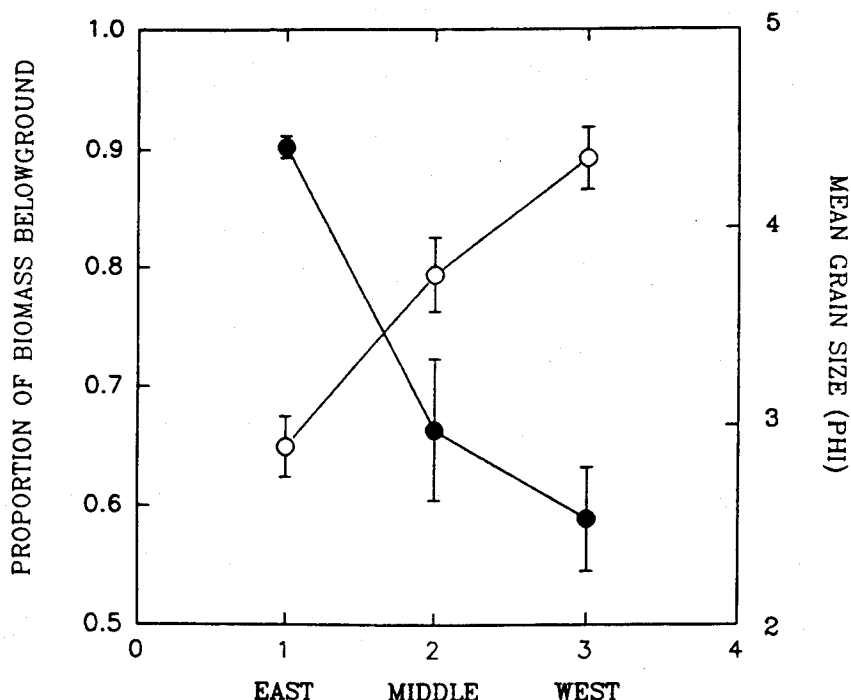


Figure 7. Variation in proportion of *Halodule wrightii* biomass belowground (solid) and sediment grain size (open) across the middle reach of the lower laguna: means and standard errors.

size. In the middle reach of the lower laguna, *H. wrightii* occurred across the whole laguna. The proportion of biomass contained in the belowground fractions increased from the mainland shore in the west to the Padre Island flats in the east, and there was a corresponding increase in sediment grain size (Fig. 7, particles >4 phi are classified as silts and clays).

Bay-wide Biomass.—Overall, in the upper laguna, *H. wrightii* occurred at every station where any vegetation was encountered, macroalgae at 72% of the vegetated stations, *Ruppia maritima* L. and *Halophila engelmannii* at <20% (Table 1). The mean biomass of *H. wrightii* at stations where encountered was almost an order of magnitude higher than macroalgae, the next biggest contributor. When computed over the whole vegetated area of the embayment, *H. wrightii* accounted for 90% of total biomass.

In the lower laguna, macroalgae were most frequently encountered, followed by *H. wrightii* and *S. filiforme*, all occurring at >45% of the vegetated stations, while *T. testudinum* and *Halophila engelmannii* occurred at <20% (Table 1A). Where present, *T. testudinum* occurred at more than twice the biomass that *H. wrightii* achieved in the upper laguna and, in the lower laguna, 2.7 times *S. filiforme*, >4 times *H. wrightii* and macroalgae, and 20 times *Halophila engelmannii*. When adjusted for frequency of occurrence over the entire vegetated area of the lower laguna, *S. filiforme* was the most important contributor of biomass, followed closely by *T. testudinum*, *H. wrightii*, and macroalgae. The contribution of *Halophila engelmannii* and *Ruppia maritima* were negligible. System-wide, biomass was 35% higher in the lower laguna than the upper laguna and distributed among several species rather than concentrated in one. Baywide ash-free dry

Table 1. Percent occurrence and biomass of seagrasses and macroalgae in Laguna Madre (A—Total biomass; B—Ash-free dry weight of aboveground parts)

	% occurrence	Biomass where present (g/m ² ± 1 SE)	Baywide mean biomass (g/m ²)
A. Total biomass (above and belowground dry weight)			
Upper Laguna (N = 47)			
<i>Halodule wrightii</i>	100	158.0 ± 9.0	158.0
<i>Halophila engelmannii</i>	17	4.7 ± 2.1	0.6
<i>Ruppia maritima</i>	15	9.9 ± 3.6	1.5
Macroalgae	72	18.9 ± 5.4	12.4
Total			172.5
Lower Laguna (N = 132)			
<i>Thalassia testudinum</i>	17	373.0 ± 62.4	64.4
<i>Syringodium filiforme</i>	48	138.0 ± 16.0	69.5
<i>Halodule wrightii</i>	66	77.6 ± 7.6	50.8
<i>Halophila engelmannii</i>	13	6.1 ± 1.8	0.8
Macroalgae	73	70.5 ± 12.1	49.8
Total			235.3
B. Aboveground ash-free dry weight			
Upper Laguna (N = 47)			
<i>Halodule wrightii</i>	100	29.2 ± 2.7	29.2
<i>Halophila engelmannii</i>	17	3.2 ± 1.6	0.6
<i>Ruppia maritima</i>	15	8.8 ± 3.8	1.3
Macroalgae	72	12.9 ± 4.0	9.4
Total			40.5
Lower Laguna (N = 132)			
<i>Thalassia testudinum</i>	17	77.8 ± 26.2	13.0
<i>Halodule wrightii</i>	66	17.5 ± 2.5	11.5
<i>Syringodium filiforme</i>	50	37.8 ± 5.6	18.3
<i>Halophila engelmannii</i>	13	1.8 ± 0.4	0.2
Macroalgae	73	35.6 ± 5.5	26.1
Total			69.1

weight of aboveground material was 40 g·m⁻² in the upper laguna and the proportionate contribution of macroalgae was three times greater than to total biomass (Table 1A, B). In the lower laguna, macroalgae were the biggest contributor to aboveground ash-free dry weight (Table 1B), as compared to fourth biggest contributor to total biomass (Table 1A).

DISCUSSION

Biomass patterns in the upper and lower portions of the Laguna Madre of Texas differ in two principal ways. First, one species dominated the upper laguna, whereas three species of seagrass and macroalgae in aggregate contributed roughly equally to total biomass in the lower laguna. Second, biomass was much more uniformly distributed in the upper laguna than the lower.

The difference in species contributions between the two parts of the laguna is a recent phenomenon and may be short-lived. According to surveys conducted in the early 1960's (McMahan, 1969), *H. wrightii* covered 89% of the vegetated area of the lower laguna. By the mid-1970's, *H. wrightii* covered 75% (Merkord, 1978), and by 1988, 45% (Quammen and Onuf, 1993). The probable reason for displacement of *H. wrightii* by *S. filiforme* and *T. testudinum* is moderation of

the salinity regime of the lagoon. Prior to the dredging in 1949 of the Gulf Intra-coastal Waterway through the Land Cut (Fig. 1), a 20 km expanse of emergent flats separating the upper and lower portions of Laguna Madre, salinities exceeding 100 ‰ in the upper lagoon and 60 ‰ in the lower lagoon were not uncommon. Since then, salinities seldom have reached 50 ‰, especially since the mid-1960's (Quammen and Onuf, 1993). The expansion of *S. filiforme* was north from Brazos Santiago Pass, the natural gulf outlet, and had reached the northern end of the lower lagoon by 1988 (Quammen and Onuf, 1993). In the upper lagoon *S. filiforme* was not present at any sampling station in 1988; however, patches were seen in transit, and hundreds have been located in systematic searches for *S. filiforme* patches since 1990 (unpubl. data). Observations at one site suggest that these patches are expanding rapidly. Therefore, it is probable that the composition of seagrass meadows in the upper lagoon will converge toward that of the lower lagoon in the next few decades.

Biomass was remarkably uniform between sides and across depths in the upper lagoon compared to the lower lagoon (Fig. 6). The most likely cause of the uniformity was the morphology and orientation of the basin. Except near the mouth of Baffin Bay, depths ranged from 40 to 180 cm, the basin was narrow, and prevailing winds blew mostly across the basin, rather than along its long axis. Because of relatively small fetch for the wind over deep water, wave development and resuspension of bottom sediments was limited. Consequently, light did not reach limiting levels, and relatively high biomasses were maintained at depths where biomass was reduced or absent over much of the lower lagoon. Conversely, the absence of the 0–39 cm depth class in the upper lagoon meant that the other zone of low biomass of the lower lagoon, broad flats along the east side, had no counterpart in the upper lagoon.

In counterpoint to the uniformity of biomass patterns for the upper lagoon, there is great diversity of pattern in the lower lagoon. At least three factors seem to modify the amount and depth distribution of biomass at a location: side of the lagoon, species, and whether cover is continuous across the lagoon or terminates in a bare middle zone.

The species effect was most obvious for *T. testudinum*. Where it prevailed, high biomass was maintained to its maximum depth of occurrence. *S. filiforme* achieved comparable biomass, but only in a depth class of very limited occurrence (2 stations) in one part of the lagoon (Fig. 6). One possible reason for high *T. testudinum* biomass up to maximum depth of occurrence is that water clarity decreased very sharply from the outermost vegetated station to the first station without vegetation. Across 3.5 km of meadow ranging in depth from 120 to 129 cm, Secchi depth was never less than 120 cm. At the first unvegetated station in 138 cm of water, Secchi depth was 70 cm (unpublished data).

A positive feedback between the filtering action of seagrasses on suspended particulates (Short and Short, 1984) and biomass seems likely. The presence of plants at the margin of a meadow improves the clarity of water in from the margin, allowing proliferation of those plants. The resulting denser canopy will enhance water clarity further. The consequence is a much steeper gradient in biomass at the outer edge of the meadow than would be expected on the basis of depth alone, because the gradient in available light is much steeper than accounted for by depth. Perhaps the lower maximum biomass of other meadow types results in a more gradual improvement in water clarity at the outer edge and consequently a more gradual decrease in biomass.

Prevailing winds and the waves they generate account for east-west differences in meadows having a deep edge. On the east side, wave action was usually neg-

ligible in shallow water and only built to the point of stirring bottom sediments at depths >1 m (personal observations). Consequently, the water usually was clear in shallow water and became turbid in depths of 1 to 2 m. On the west side, waves broke right on shore. The shallowest depth zone was largely unavailable, because the plants were uprooted. Along shore, the water was turbid. Where the bottom dropped steeply, no meadow developed. Where the slope was more gradual, more light reached bottom 0.5 km out from shore than closer, in some cases. This phenomenon was most conspicuous on the transect at $26^{\circ}35.5'N$, where an "island" of seagrass was associated with an offshore area in which 10–20% of surface light reached the bottom (Fig. 3, right). This difference in depth of the most turbid water between sides of the laguna led to the result that seagrasses frequently were encountered deeper along the western shore than on the east side (Fig. 5), even though the east side supported broad meadows and the west side had a narrow fringe or none at all, (Fig. 3, right).

The pattern of dominance by *H. wrightii* at lowest and highest light levels in the lower laguna near Port Mansfield (Fig. 4) is consistent with the depth distribution of biomass across a single bed in north Florida reported by Iverson and Bittaker (1986). The almost complete absence of seagrasses at stations receiving $<10\%$ SI and the low mean frequency of occurrence of seagrasses at stations receiving 10–15% SI (Fig. 4) suggests that $>15\%$ SI is required for the development of continuous meadow. This is consistent with the finding of Kenworthy et al. (1991) that the "ecological light compensation point" was in excess of 10 to 15% SI for the same species in Hobe Sound, Florida, and elsewhere in the Indian River (Morris and Tomasko, 1993).

East–west differences in biomass in the middle reach of the lower laguna where seagrass cover was continuous across the embayment obviously were not driven by light availability and sediment stability. However, differential nutrient supply may contribute to the two and one half times greater biomass of seagrasses in the shallow zone of the west side compared to the east side (Fig. 6, second from top). The two major drains of the lower Rio Grande agricultural district discharge along the western shore (Fig. 1, Arroyo Colorado and North Floodway). Also, prevailing southeast winds and wind-driven currents tend to remove aboveground dead material from the meadows spanning the laguna and deposit great windrows of dead leaves along the western shore. Nutrients regenerated from these deposits would be available first to seagrasses growing in shallow water along the western shore.

The much higher investment of *H. wrightii* in belowground parts on the east side than the west (Fig. 7) also is consistent with the inferred difference in nutrient supplies between sides of the laguna. Similar patterns have been noted in freshwater systems (Barko, et al., 1991), for *Zostera marina* in mesocosms (Short, 1987), and for *T. testudinum* (Burkholder, et al. 1959) grown in sand vs. finer, more highly organic substrates. The alternative hypothesis that increased investment in root and rhizome might be required for anchoring in a high energy environment is not supported. Although coarser sediments usually indicate a higher energy water environment, in this case, the sands are windblown, and waves and currents are negligible, since the wind blows off the land immediately adjacent. The plants on the west side are exposed to larger waves and stronger currents, despite being rooted in finer sediments.

The very high biomass of *S. filiforme* in the 80–119 cm depth range may owe more to history than any special suitability of the depth. There were only two stations in the depth category. The mean of the three samples from one of those stations was $900 \text{ g} \cdot \text{m}^{-2}$. Based on the distributional maps of Merkord (1978, figs. 7–9), that station was the only one sampled in 1988 that also had been dominated

by *S. filiforme* in 1974. *T. testudinum* dominated all other stations in 1988 where *S. filiforme* dominated in 1974. Thus, it is possible that *S. filiforme* had been established too short a time over most of the area it dominated in 1988 to have achieved maximum biomass.

In northeast Florida Bay, nutrient enrichment in the vicinity of roosting birds has led to displacement of *T. testudinum* by *H. wrightii* (Powell et al., 1991; Fourqurean et al., 1992a, 1992b). No such process is evident in lower Laguna Madre. *Halodule wrightii* is dominant where the supply of nutrients probably is least on the east side. Elsewhere, *H. wrightii* is being displaced by *S. filiforme* and *T. testudinum*. Apparently, the more diffuse supply of nutrients in the lagoon does not produce the conditions necessary to favor *H. wrightii*.

In addition to reducing the area of cover by *H. wrightii*, the establishment of *S. filiforme* and *T. testudinum* in the lower lagoon has led to a reduction in mean biomass where *H. wrightii* remained. In 1974, the mean biomass of *H. wrightii* where present was $127 \text{ g}\cdot\text{m}^{-2}$ (Merkord, 1978). In 1988, the mean was $78 \text{ g}\cdot\text{m}^{-2}$ (Table 1), because *H. wrightii* was displaced from depths where it was capable of achieving high biomass in the absence of other species, as was the case in the upper lagoon (Fig. 6, top), and continued dominant only in shallow water on the east side where it occurred at low biomass (Fig. 6, right, second and third from top). In turn, *T. testudinum* may be displacing *S. filiforme* from its optimal sites. Mean biomass of *S. filiforme* at the 9 biomass stations where it was present in 1974 was $218 \text{ g}\cdot\text{m}^{-2}$ (Merkord, 1978), compared to $138 \text{ g}\cdot\text{m}^{-2}$ in 1988 (Table 1). Because of the higher biomasses achieved by the displacing species, baywide mean biomass of seagrasses in vegetated areas was somewhat higher in 1988: $185 \text{ g}\cdot\text{m}^{-2}$ (Table 1), than in 1974: $160 \text{ g}\cdot\text{m}^{-2}$ (Merkord, 1978).

Comparable assessments of biomass are available for two other large seagrass tracts in the Gulf of Mexico: the Big Bend region of Florida, from 28 to 30° north latitude (Iverson and Bittaker, 1986), and Florida Bay (Iverson and Bittaker, 1986; Zieman, et al., 1989). The systems from opposite sides of the gulf differ most strikingly in the depth range of seagrasses. Along the broad, shallow continental shelf of the eastern gulf, the outer limit of seagrass meadow was about 8 m in the north and 11 m in the south (Iverson and Bittaker, 1986). In Laguna Madre on the western side of the gulf, the maximum depth of occurrence of seagrasses was <2 m in this study. Water clarity accounts for the difference in depth penetration across the gulf. In Florida from St. Marks to Crystal River the mean extinction coefficient (k) was 0.5; from Crystal River to Tarpon Springs, 0.32; and in outer Florida Bay, 0.25 (Iverson and Bittaker, 1986). Within Laguna Madre, mean k values were 1.59 within meadows ($N = 62$) and 1.84 in deeper, bare areas ($N = 119$). Presumably, the seagrasses cannot establish offshore along the western gulf because the continental shelf is narrow, and its shore fringe is subject to too much wave action for seagrasses to maintain themselves. In contrast, the Florida Gulf Coast is a relatively low-energy shoreline (Iverson and Bittaker, 1986). Although the lagoon is a protected environment compared to that on the gulf side of Padre Island, wind-generated wave action within the lagoon is strong enough to stir bottom deposits and create turbid conditions much of the time in and adjacent to areas exceeding 2 m in depth.

Aboveground biomass values have been reported for the two great expanses of seagrass meadow in Florida. For the Big Bend region and outer Florida Bay, mean ash-free dry weight of leaves were computed using data extracted from Iverson and Bittaker (1986: figs. 8–10 for *T. testudinum*, *S. filiforme*, and *H. wrightii*). These values were multiplied by the proportion of samples in which each species occurred (Iverson and Bittaker, 1986, figs. 1 and 2) to give system-

Table 2. Aboveground ash-free biomass (g/m^2) and percent frequency of occurrence of seagrasses and macroalgae in large seagrass systems of the Gulf of Mexico. Data for Laguna Madre from this study, Big Bend and Outer Florida Bay from Iverson and Bittaker (1986), and Inner Florida Bay from Zieman et al. (1989). See text for conversion factors to convert Inner Florida Bay dry weights to ash-free dry weights.

	<i>Thalassia</i>	<i>Syringodium</i>	<i>Halodule</i>	<i>Ruppia</i>	<i>Halophila</i>	Macroalgae	Total (seagrass only)
Mean biomass where present							
Upper Laguna Madre			29	9	3	13	
Lower Laguna Madre	78	38	18		2	36	
Big Bend	33	20	10				
Inner Florida Bay	58	30	7				
Outer Florida Bay	140	85	7				
Mean biomass system-wide							
Upper Laguna Madre			29	1	1	9	40 (31)
Lower Laguna Madre	13	18	12			26	69 (43)
Big Bend	28	12	4				(44)
Inner Florida Bay	56	5	3			10	73 (64)
Outer Florida Bay	84	38	2				(124)
% frequency of occurrence							
Upper Laguna Madre, N = 47			100	13	17	72	
Lower Laguna Madre, N = 132	17	48	66		13	73	
Big Bend, N = 106	85	58	60				
Inner Florida Bay, N = 106	95	13	48			?	
Outer Florida Bay, N = 136	60	45	29				

wide means. Ash-free dry weight to dry weight ratios (Iverson and Bittaker, 1986: 586) were used to convert dry weight values for inner Florida Bay (Zieman et al., 1989) to ash-free dry weight. Ratios computed from this study were used to estimate ash-free dry weight of macroalgae from dry weight in inner Florida Bay: *Laurencia* spp.—0.71, *Acetabularia crenulata*—0.40. The value for *A. crenulata* was assumed representative for *Penicillus* spp. (J. Fourqurean, Florida International University, pers. comm.), and the aggregate ratio for all macroalgae collected in Laguna Madre—0.63—was used for *Batophora oerstedii*.

The composition of Laguna Madre seagrass meadows differed from those of the eastern gulf in the much greater contribution of *H. wrightii* (Table 2). In all likelihood, this difference is transitory. Given the trend toward increasing cover of *S. filiforme* and *T. testudinum* between 1965 and 1988 and the occurrence of tolerable salinities throughout the laguna currently (Quammen and Onuf, 1993), the contributions of *S. filiforme* and *T. testudinum* probably will continue to converge toward conditions in the eastern gulf. The low biomass of *H. wrightii* compared to the other species that dominate large areas of bottom probably accounts for low system-wide mean biomass of the upper laguna and the relatively low system-wide mean biomass of the lower laguna compared to locations in the eastern gulf (Table 2, middle). Since the biomass of all species where present in Laguna Madre is within the range of values for locations in the eastern gulf (Table 2, top), system-wide mean biomass should approach that of Florida Bay as *S. filiforme* and *T. testudinum* become more prevalent.

The other difference in biomass among systems was the much higher contribution of macroalgae to total aboveground biomass in the lower laguna than the upper laguna or inner Florida Bay (Table 2). The high standing crop of macroalgae may be the consequence of inflows from a large irrigated agricultural district that the lower laguna receives, unlike the other systems. This speculation is supported

by the observation that algal biomass was three times higher in the middle reach of the lower lagoon ($62 \text{ g}\cdot\text{m}^{-2}$), where the agricultural drains discharge, than the northern section ($17 \text{ g}\cdot\text{m}^{-2}$) or southern ($19 \text{ g}\cdot\text{m}^{-2}$), where drains do not discharge. Associations between high nutrient supply and high biomass of macroalgae have been widely observed in lakes (Cattaneo, 1987), estuaries (Sand-Jensen and Borum, 1991) and coastal lagoons (Harlin and Thorne-Miller, 1981).

Florida Bay has changed dramatically from the summary given here, based on sampling conducted in 1984 (Zieman et al., 1989). *T. testudinum* has died off over large expanses. Dense patches were most severely affected. Abnormally high water temperature, recent reduced frequency of hurricanes, a pathogenic slime mold, and chronic hypoxia of roots and rhizomes are potential causes (Robblee et al., 1991). Leading up to the die-off, biomass had increased greatly (J. Zieman, University of Virginia, pers. comm.). One hypothesis to account for the die-off is that the combined stresses of high salinity and temperature, operating on high biomass and large accumulations of dead material, resulted in extended periods of hypoxia in dense patches that the plants could not withstand (Zieman, pers. comm.). Phytoplankton blooms resulting from nutrient additions to the western part of the bay may also be involved by reducing available light and increasing night-time hypoxia (B. LaPointe, Harbor Branch Foundation, pers. comm.).

Laguna Madre and Florida Bay share much in common. Both have restricted circulation, receive limited freshwater inflow, have higher rates of evaporation than precipitation, experience long periods of high water temperature, and are subject to episodes of hypersalinity. The conditions that allowed *T. testudinum* to flourish have been in effect longer in Florida Bay than Laguna Madre; however, a trend toward dominance by *T. testudinum* and increasing biomass is clearly underway in Laguna Madre. Although the two systems arrived at commonality by opposite hydrological shifts (Florida Bay by interruption of sheet flow through the Everglades and a shift toward higher salinity, Laguna Madre by improved circulation, increased inflow, and lower salinity), seagrasses in Laguna Madre may be on a similar trajectory to those of Florida Bay. If cover of *T. testudinum* continues to expand and biomass increases where it is already established, Laguna Madre may become increasingly vulnerable to the mass mortalities already seen in Florida Bay. Assuming that the rate of expansion of *T. testudinum* evident between 1974 and 1988 continues into the future, *T. testudinum* should not dominate the lower lagoon for another 50 years. Probably the most feasible way to minimize the risk of mass mortalities in the future is to promote practices that will limit inputs of nutrients from the agricultural drains. The development of two large shrimp farms on one of the drainage channels since 1988 points up the immediate need for nutrient input management.

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