

DISTRIBUTION, ABUNDANCE AND PRODUCTIVITY OF SEAGRASSES AND MACROALGAE IN FLORIDA BAY

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ABSTRACT

The distribution, abundance, and productivity of submerged macrophytes were measured in Florida Bay to determine the total productivity and seagrass habitat distribution throughout the region. *Thalassia testudinum* was widely distributed and was the dominant macrophyte species in the 1,660 km² of seagrass beds contained in the bay. *Halodule wrightii* was also common, but had standing crop significantly less than *Thalassia* at all sample locations. *Syringodium filiforme* grew mainly in areas with strong oceanic influence, especially along the south and west margins of the bay. Macroalgae were a small percentage of the total macrophyte biomass. Gradients in environmental and biological variables extended from southwest to northeast Florida Bay. Water clarity, water exchange, and sediment depth were all greatest in the south and west portion of the bay and decreased towards the northeast corner of the bay. The seagrass standing crop varied from between 60 and 125 g dw·m⁻² in the southwest to between 0 and 30 g dw·m⁻² in the northeast. Total seagrass leaf standing crop was 8·10¹⁰ g dw in Florida Bay, 90% of which was *Thalassia* leaf material. *Thalassia* mean leaf productivity was 0.97 g dw·m⁻²·d⁻¹, with higher values in the southwest and lower values in the northeast portions of the bay. Approximately 1.7·10⁹ g dw·d⁻¹ of *Thalassia* leaf tissue was produced in Florida Bay during the summer. *Thalassia* had about the same leaf productivity on a per gram leaf dry weight basis throughout the different environments of Florida Bay, therefore variations in areal leaf productivity were caused by variations in leaf standing crop and not by variations in leaf specific productivity. Distribution, abundance, and productivity data were used to divide the bay into six community types.

A variety of terrestrial and marine habitats form extremely productive, extensive vegetation coverage in south Florida. Seagrass beds, mangrove forests and islands, and coral reefs form the major photoautotrophically-dominated communities which inhabit brackish and salt water environments of the region (Zieman, 1982). The portion of Florida Bay within the Everglades National Park boundaries is about 1,800 km², most of which is covered with seagrasses (Fig. 1). Mangroves covered about 7% of that area (McNulty et al., 1972). Areal seagrass coverage in Hawk Channel, in the portion of the bay within the Everglades National Park, and in the area outside of the Park boundary between the Florida keys and the Everglades which extends to the Dry Tortugas, is approximately 5,500 km² (Iverson and Bittaker, 1986). Seagrasses grow in many shallow coastal areas of the world ocean (den Hartog, 1970), however there are only a few locations where seagrass areal coverage as large as in Florida Bay has been reported (Iverson and Bittaker, 1986).

Estuarine, lagoon, and coastal habitats are extremely important for the productivity of fisheries and wildlife in south Florida. Extensive submarine seagrass meadows bridge the distances between coral reefs and mangroves, which have widely different physical requirements (Zieman, 1982). Early studies emphasized the role of mangrove habitats as a food source and nursery (Odum and Heald, 1972). The results of more recent investigations suggested that seagrass beds in open water environments and within mangrove-lined bays contained the densest populations of organisms such as the commercially important pink shrimp, *Penaeus duorarum* (Carter et al., 1973; Yokel, 1975).

A clear association was obtained between organism catch and seagrass cover

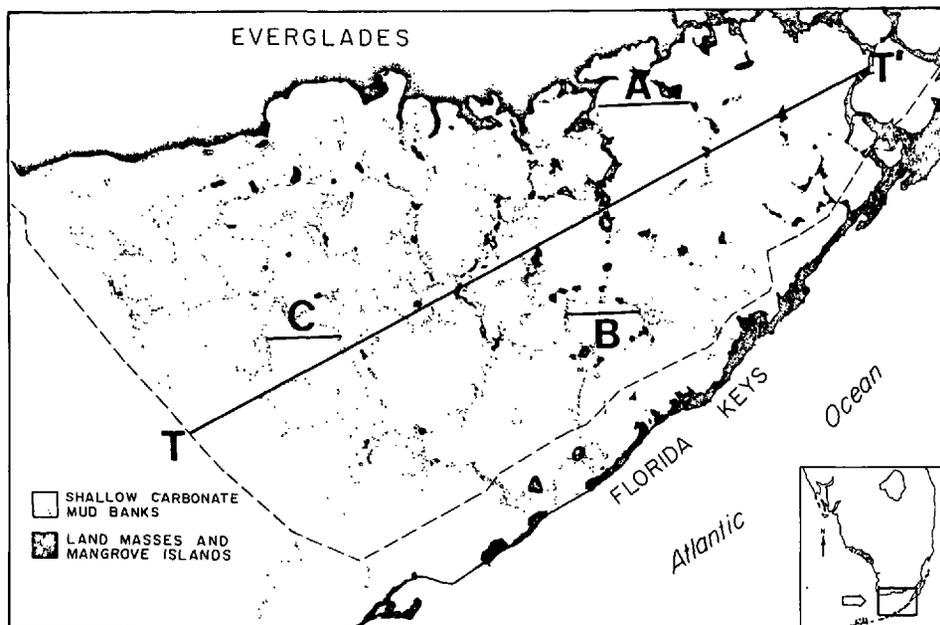


Figure 1. Location map of Florida Bay. The broken line in the figure indicates the boundary of Everglades National Park. The solid lines represent study transects A, B, C and T-T'.

in Rookery Bay, where two stations located in seagrass accounted for 82% of the total pink shrimp catch and 77% of the total catch of fish, crustacea, and mollusks (Yokel, 1975). Seagrass habitat, limited to water depths less than 1 m due to turbid conditions, comprised only 20% of the bay area. A large proportion of the annual animal crop in Rookery Bay depended on seagrass habitat, which covered a relatively small part of the total benthic area (Yokel, 1975). While seagrasses cover a small part of the Rookery Bay benthos, they form the major benthic feature of Florida Bay, offering proportionately greater habitat values. Seagrasses are probably the most productive of marine photoautotrophic communities of south Florida, but until recently they have been least studied (Odum et al., 1973).

MATERIALS AND METHODS

Identification of Benthic Communities.—Aerial photography was initially used to estimate the areal coverage of different benthic communities in Florida Bay. Field verification of the extent and species composition of these communities was performed by visually censusing the bottom at selected stations. Community boundaries were determined by driving boats along previously determined transects, where changes in bottom cover were observed and recorded.

Macrophyte Standing Crop Sampling.—Macrophyte biomass was sampled at 108 stations during the summer of 1984 (Figs. 2, 3). Macrophyte material was collected from within at least three replicate quadrats placed on the bottom at each sample site. Quadrats 10·10 cm in dimension were used for biomass sampling in areas where seagrass leaf density was greater than 6,000 blades·m⁻². When average seagrass leaf density was between 1,500 and 6,000 blades·m⁻², quadrat size was 10·20 cm. Quadrats as large as 50·50 cm were used to obtain samples in areas of low seagrass abundance and in most areas where macroalgae was present. Plant material collected from the quadrats was identified, separated by species, acid washed in 10% HCl to remove calcium carbonate, and oven dried. Sediment depth was measured at all sites using a stainless steel probing rod. Water depth was measured with a marked, weighted line at each station at the time of sampling.

Productivity Measurement.—*Thalassia* leaf production was measured with the leaf marking method at three stations during summer, 1983 and at 13 stations during summer, 1984 (Fig. 4). using 16

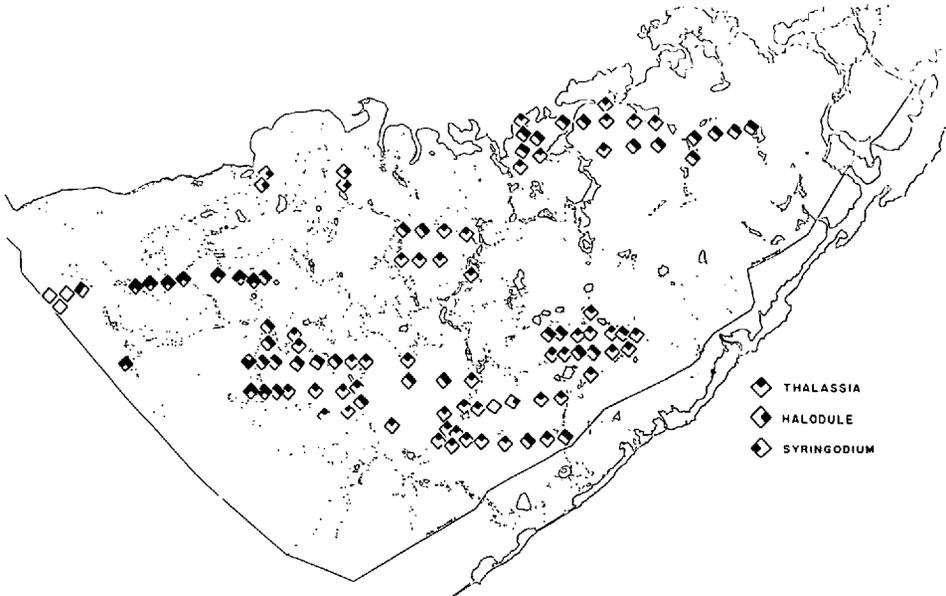


Figure 2. Distribution of the three dominant seagrass species (*Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme*) at stations sampled for macrophyte standing crop across Florida Bay.

replicate 10·20 cm quadrats at each station. The number of short shoots and leaves in each quadrat were counted, and each blade was marked with a staple at the sediment-water interface at the beginning of each sample period. The marked leaves were allowed to grow for approximately 2 weeks, after which the plant material in each quadrat was harvested at the sediment-water interface. Unmarked blades and portions of the blades below the staples, considered to be new growth, were separated from

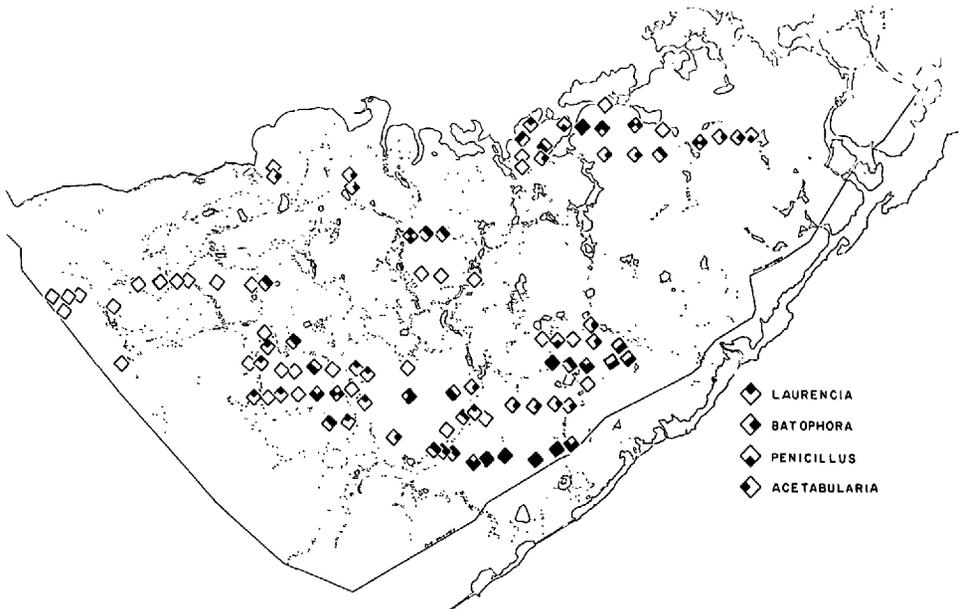


Figure 3. Distribution of the four dominant microalgae (*Laurencia* spp., *Batophora* spp., *Penicillus* spp. and *Acetabularia* spp.) at stations sampled for macrophyte standing crop across Florida Bay.

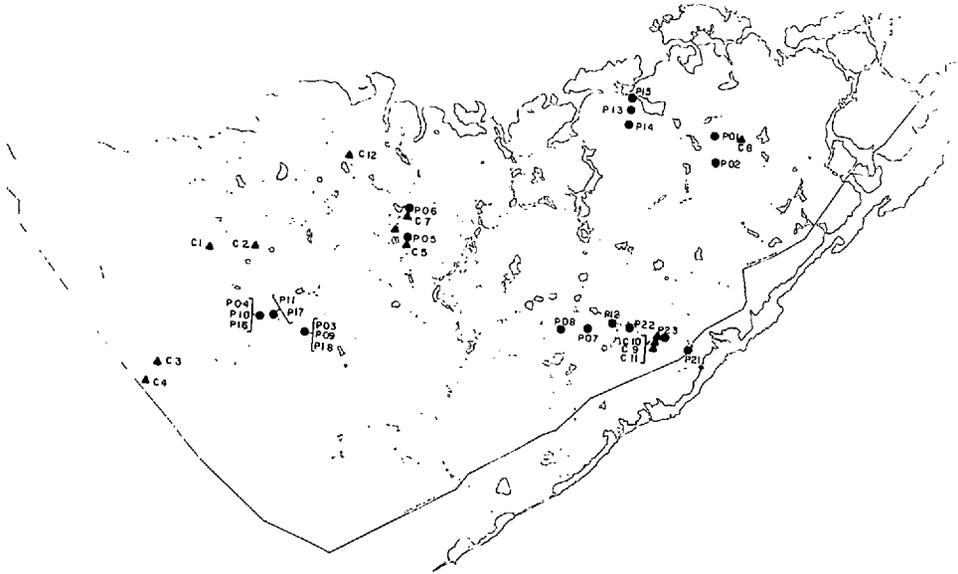


Figure 4. Locations of macrophyte productivity stations. Leaf-mark productivity measurements were made at stations marked with circles, and ^{14}C productivity measurements were made at stations marked with triangles.

the rest of the leaf material. Both leaf subsamples were then washed in 10% v/v HCl and oven dried at 50°C (Zieman, 1974; 1975).

Algal and seagrass leaf ^{14}C uptake measurements were performed with the method of Bittaker and Iverson (1976) at 12 stations during the summer of 1984 (Fig. 4). Samples were incubated in situ for 3 h inside plexiglass cylinders equipped with battery powered stirring motors. Leaves were then collected and frozen on dry ice for transport to a shore facility where most were oven dried at 45°C. A subset of samples was kept frozen and was freeze-dried at a later time. Comparison of ^{14}C activity in lyophilized leaf samples with activity in oven dried samples revealed no significant differences in ^{14}C content. Carbon-14 standardization was performed with the method of Iverson, et al. (1976). Total carbon dioxide was determined with the single point titration alkalinity method given in Parsons, et al. (1984). Light energy extinction coefficients were estimated from submarine light energy measured at each sample site with a LiCor, Inc. quanta sensor. Surface light energy was measured with a LiCor, Inc. quanta sensor throughout each sample day. Dried leaf material was processed with the dimethylsulfoxide extraction method of Filbin and Hough (1984) to solubilize ^{14}C in particulate material before counting ^{14}C activity with a liquid scintillation spectrometer. Extraction efficiency was determined using radioactive, dried *Thalassia* leaf material which had been oxidized with a Packard 306 sample oxidizer. The method used for daily leaf carbon productivity calculation was a modification of the method for calculation of phytoplankton daily productivity developed by Ryther (1956), Ryther and Yentsch (1957), and Small et al. (1972). Average sea surface photosynthetically active radiation (PAR) was determined for each hour of the day from quanta sensor data. Photosynthetically active radiation at the top of the seagrass leaf canopy was obtained by correcting sea surface PAR for water column extinction at each station. Photosynthesis vs. light curves were used to obtain in situ photosynthesis for each hour of the day for each species. The hourly photosynthetic rates were integrated to provide daily seagrass leaf carbon production per unit dry weight. Conversion from carbon fixation to dry weight was made assuming a leaf carbon content of 40% (Zieman, 1982).

Drift Material Sampling.—Surface drift organic material was sampled during October 1979 from the R/V LONGHORN in a rectangle of approximately 78 by 1,850 km (42 by 100 nautical miles), which covered the productive Tortugas shrimp grounds west of Florida Bay. Cape Sable and the Dry Tortugas formed two of the diagonal corners of the rectangle, which was divided into 18.5- by 18.5-km (10·10 nautical mile) squares. Samples were taken at each of 42 stations located in the centers of the squares. Nets used for sampling surface drifting material had a 30 cm by 1 m opening and 0.5-mm mesh Nitex netting (Zieman et al., 1979). Three nets, equipped with floats to keep them at the surface, were towed for 10 min at each station. One of the nets was equipped with a General Oceanics

Table 1. Percent occurrence and standing crop of seagrasses and macroalgae in Florida Bay

Species	Occurrence (N = 108) (%)	Standing crop where present	(gdw·m ⁻² ± 1 SE) baywide average
Seagrasses:			
<i>Thalassia testudinum</i>	95	66.9 ± 5.6	63.6
<i>Halodule wrightii</i>	48	7.9 ± 2.0	3.8
<i>Syringodium filiforme</i>	13	36.7 ± 11.3	4.1
Macroalgae:			
<i>Batophora oerstedii</i>	51	9.2 ± 3.1	4.6
<i>Acetabularia crenulata</i>	19	0.6 ± 0.4	0.1
<i>Laurencia</i> spp.	37	24.1 ± 13.3	8.9
<i>Penicillus</i> spp.	25	6.7 ± 5.8	1.7
Litter (dead plant material)	95	96.7 ± 10.6	91.9

model 2030 current meter to provide data for use in calculating the water volume filtered. The drift material was removed from the nets, sorted into material type, and dried at 100°C after collection.

RESULTS

Macrophyte Distribution and Abundance.—Seagrass and benthic macroalgae species were not all distributed evenly across the bay. *Thalassia testudinum* was the dominant seagrass species in Florida Bay and occurred at 95% of all stations. *Halodule* occurred at 48% of the stations, while *Syringodium* was found at 13% of the stations (Fig. 2). Seagrass standing crop varied greatly across the bay. The standing crop of *Thalassia* ranged from 0.00 to 215.00 g dw·m⁻², with a mean of 66.93 ± 5.60 g dw·m⁻² (± 1 SE, N = 105). *Halodule* and *Syringodium* were more patchy in their distribution than was *Thalassia*. The ranges in standing crop were 0.00 to 87.50 g dw·m⁻² for *Halodule* and 0.00 to 107.00 g dw·m⁻² for *Syringodium*. The mean standing crops of those species for sites where they occurred were 7.93 ± 2.02 g dw·m⁻² (N = 52) for *Halodule* and 36.73 ± 11.34 g dw·m⁻² (N = 12) for *Syringodium*. The standing crops of *Halodule* and *Syringodium* averaged for all stations in the bay were 3.82 ± 1.07 g dw·m⁻² (N = 108) and 4.08 ± 1.69 g dw·m⁻² (N = 108), respectively (Table 1). Neither *Halodule* nor *Syringodium* surpassed *Thalassia* in standing crop at any station at which *Thalassia* occurred. Total seagrass leaf biomass increased from the north-east to the southwest portion of the bay.

Four macroalgal genera, *Batophora*, *Laurencia*, *Penicillus* and *Acetabularia*, occurred at greater than 10% of the stations sampled for standing crop (Fig. 3). *Batophora* was the most widely distributed of the four macroalgae genera, occurring at 51% of the stations. *Laurencia* was the second most common, appearing at 37% of the stations, while *Penicillus* and *Acetabularia* occurred at 25% and 19%, respectively. Only two macroalgae genera had mean standing crops greater than 1 g dw·m⁻². *Laurencia* was the most abundant macroalga, averaging over 24 g dw·m⁻² at the stations where it occurs and averaging 8.9 g dw·m⁻² for all stations in Florida Bay (Table 1).

Macrophyte Productivity.—Macrophyte productivity was measured with the leaf mark and ¹⁴C uptake methods at a subset of the stations where biomass samples were collected (Fig. 4). Areal leaf productivity of *Thalassia*, as determined by the leaf marking method, ranged from 0.05 to 3.42 g dw·m⁻²·d⁻¹, with a mean of 0.97 ± 0.19 g dw·m⁻²·d⁻¹ for all stations sampled in Florida Bay (Table 2). The

Table 2. Daily production rate of *Thalassia testudinum* in Florida Bay as measured by the leaf-mark technique

Station	Standing crop (g·m ⁻²)	Productivity (g·m ⁻² ·d ⁻¹)	Turn over rate (%·d ⁻¹)
P01	5.85	0.16	2.72
P02	2.28	0.06	3.03
P03	142.88	3.42	2.40
P04	89.22	1.80	2.00
P05	33.44	0.83	2.35
P06	56.10	1.48	2.86
P07	7.25	0.10	1.52
P08	11.19	0.21	2.02
P09	131.75	2.19	1.67
P10	101.38	1.46	1.44
P11	42.88	0.73	1.70
P12	38.00	0.77	2.03
P13	1.79	0.06	3.55
P14	1.91	0.05	2.91
P15	10.19	0.23	2.37
P16	87.88	1.62	1.85
P17	39.44	0.81	2.06
P18	122.69	2.03	1.67
P21	68.32	1.06	1.60
P22	22.37	0.66	2.93
P23	22.52	0.62	2.77
\bar{x}	49.49	0.97	2.19
SE	9.81	0.19	0.12
CV	91%	89%	24%

patterns in productivity variation across the bay were similar to patterns in standing crop variation. Seagrass leaf productivity was low on the banks and in the basins of the northeastern portion of the bay, with rates between 0.1 and 0.2 g dw·m⁻²·d⁻¹. Leaf productivity increased to the south and west with rates of between 1.1 and 1.5 g dw·m⁻²·d⁻¹ observed. Productivity increased to between 1.5 and 3.4 g dw·m⁻²·d⁻¹ in the western portion of the bay. These rates are comparable to published seagrass productivity rates for south Florida and comparable areas (Zieman, 1982).

Seagrass leaf productivity and macroalgal productivity were also measured with the ¹⁴C uptake technique. Seagrass ¹⁴C leaf uptake rates were between 1.5 and 3.3 mg C g·dw⁻¹·h⁻¹, while macroalgal ¹⁴C uptake rates were between 0.4 and 1.6 mg C g·dw⁻¹·h⁻¹. The ¹⁴C uptake rates of the seagrasses, in mg C g·dw⁻¹·h⁻¹ ranged from between 1.52 and 3.32 (mean = 2.33 ± 0.28, N = 7) for *Halodule*, between 1.51 and 2.93 with a mean of 2.02 ± 0.12 (N = 12) for *Thalassia*, and between 1.22 and 2.40 (mean = 1.74 ± 0.26, N = 4) for *Syringodium*. Table 3 lists the ¹⁴C productivities of the seagrasses at the various stations as integrated daily rates. ¹⁴C uptake by *Laurencia* spp. ranged between 0.37 and 0.40 mg C g·dw⁻¹·h⁻¹ (mean = 0.39 ± 0.01, N = 3). *Batophora oerstedii* had ¹⁴C uptake rates of between 0.48 and 1.62 mg C·g dw⁻¹·h⁻¹ (mean = 0.92 ± 0.35, N = 3).

Sediment and Water Depth.—The characteristics of basins and sediment banks changed along a gradient from northeast to southwest in Florida Bay. Narrow banks separated relatively large basins in the northeast, while banks dominated the area of the southwest portion of the bay where basins were smaller (Fig. 1).

Table 3. Daily production rates (in $\text{g dw} (\text{g dw})^{-1} \text{d}^{-1}$) of *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme* calculated from ^{14}C uptake measurements

Station	Water depth (m)	Productivity		
		<i>Thalassia</i>	<i>Syringodium</i>	<i>Halodule</i>
C1	1.5	0.052	0.052	0.078
C2	1.3	0.052	0.052	0.078
C3	1.7	0.051	0.051	—
C4	0.75	0.052	0.052	0.068
C5	0.75	0.052	—	0.068
C6	0.75	0.052	—	0.068
C7	1.5	0.051	—	0.071
C8	1.8	0.047	—	0.074
C9	1.75	0.049	—	—
C10	1.75	0.049	—	—
C11	1.75	0.049	—	—
C12	0.6	0.052	—	0.070
\bar{x}		0.051	0.052	0.072
SE		0.001	0.0004	0.001
CV		3.3%	1.6%	5.5%

A thin veneer of sediment covered the basin bedrock in the northeast. The banks become broader and the amount of basin sediment increased towards the southwest. Despite sediment accumulation in the southwest, the general slope of the bedrock caused a deepening of the water column in basins from the northeast to the southwest (Fig. 5).

There is a positive correlation between *Thalassia* standing crop and sediment depth ($r = 0.64$, Fig. 6), but a negative correlation between standing crop and water depth ($r = -0.41$, Fig. 6). These two predictors of standing crop are themselves highly negatively correlated ($r = -0.80$) due to the planar, almost horizontal nature of the bedrock floor. Shallow areas with deep sediment support more grass than deep areas with shallow sediment. The relative contributions of these two correlated predictors in controlling standing crop were examined using stepwise multiple linear regression analysis. Due to heteroscedasticity, the regression analysis was done on square-root transformed data.

The regression equation from this analysis (standing crop^{0.5} = 4.15(sediment depth) + 1.80(water depth) + 0.11) explains 53% of the variation in the standing crop data. Sediment depth alone accounts for 49% of the variation and is statistically significant ($F = 94.4$, $P < 0.001$). The inclusion of water depth to the model explains an additional small but statistically significant portion of the variation (partial $F = 8.78$, $P < 0.005$). The addition of water depth to the equation increases the R^2 from 0.49 to 0.53. These results indicate that water depth has some control over standing crop, independent of the correlation with sediment depth. It is interesting to note that the regression coefficient for water depth in the regression equation is positive, even though the simple correlation between water depth and standing crop is negative. This seems to be caused by the decreased standing crop in very shallow as well as very deep water, as is evident in Figure 6.

Benthic Communities in Florida Bay.—Macrophyte distribution, standing crop, and productivity together with sediment type, sediment depth, and water depth, were used to divide Florida Bay into areas which contained similar biological and physical characteristics (Fig. 7). Since macrophytes were the dominant biological

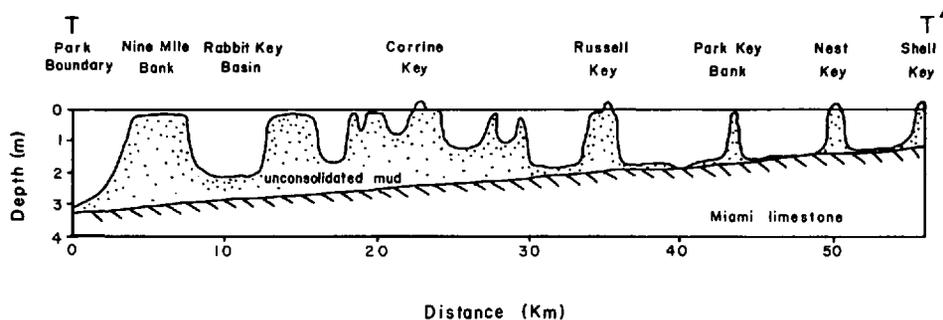


Figure 5. The variation in water depth and sediment accumulation along a southwest to northeast transect in Florida Bay. The location of this transect is given in Figure 1 as T-T'.

characteristic of the Florida Bay benthos, the areas were mainly characterized by photoautotrophic community composition. The characteristics of the communities were distinctly different; however, transitions in characteristics from one community to another were gradual.

The Northeast community was characterized by sparse, patchy *Thalassia* (0 to 10 g dw·m⁻²) growing in shallow basin sediments to 5 cm and in water depths to 1.5 m (Fig. 8A). *Halodule* was found throughout the area with leaf biomass less than 1 g dw·m⁻², although it was locally dominant in recently disturbed areas. the rhizophytic, calcareous alga *Penicillus*, which is responsible for high rates of calcium carbonate deposition in northeast Florida Bay (Stockman, et al., 1967), was an important macrophyte in this community. Bedrock outcrops were common and were colonized by *Batophora* and *Acetabularia*. Heavily epiphytized *Thalassia* occurred in moderate density (around 30 g dw·m⁻²) on the top of banks.

The East-Central community was also dominated by sparse, patchy *Thalassia* (Fig. 8B). Bedrock outcrops were less frequent since basin sediment was generally deeper in the portion of the bay occupied by this community. This resulted in less suitable substrate for the attachment of *Acetabularia* and *Batophora* than that which occurred in the northeast portion of the bay. Sparse *Thalassia* (0 to 20 g dw·m⁻²) was found throughout the basins, however localized increases in sediment depth supported denser standing crops. *Halodule* was present, but in such low biomass that it was of minor importance except in disturbance areas. Banks were covered with medium to dense *Thalassia* with little evidence of leaf epiphytism. The drift alga *Laurencia* was locally abundant in this community, especially on the lee sides of banks.

The Interior community was characterized by dense, monospecific stands of *Thalassia*. Sediments were generally deep enough to allow dense seagrass growth to the center of the basins. *Thalassia* standing crop differed only slightly from 60 g dw·m⁻² on the banks to 50 g dw·m⁻² in basin waters as deep as 2.4 m. *Halodule* was found in isolated patches in areas of recent disturbance. The drift alga *Laurencia* was the dominant macroalga of this community and was distributed throughout the area as a consequence of low wind speeds and low water column mixing.

The Mainland community had the most heterogenous vegetation patterns and showed the most terrestrial influence. Water was generally quite shallow, and turbid conditions were common. *Thalassia* was the dominant benthic macrophyte, with leaf standing crop similar to that found in the Interior community. Nearly

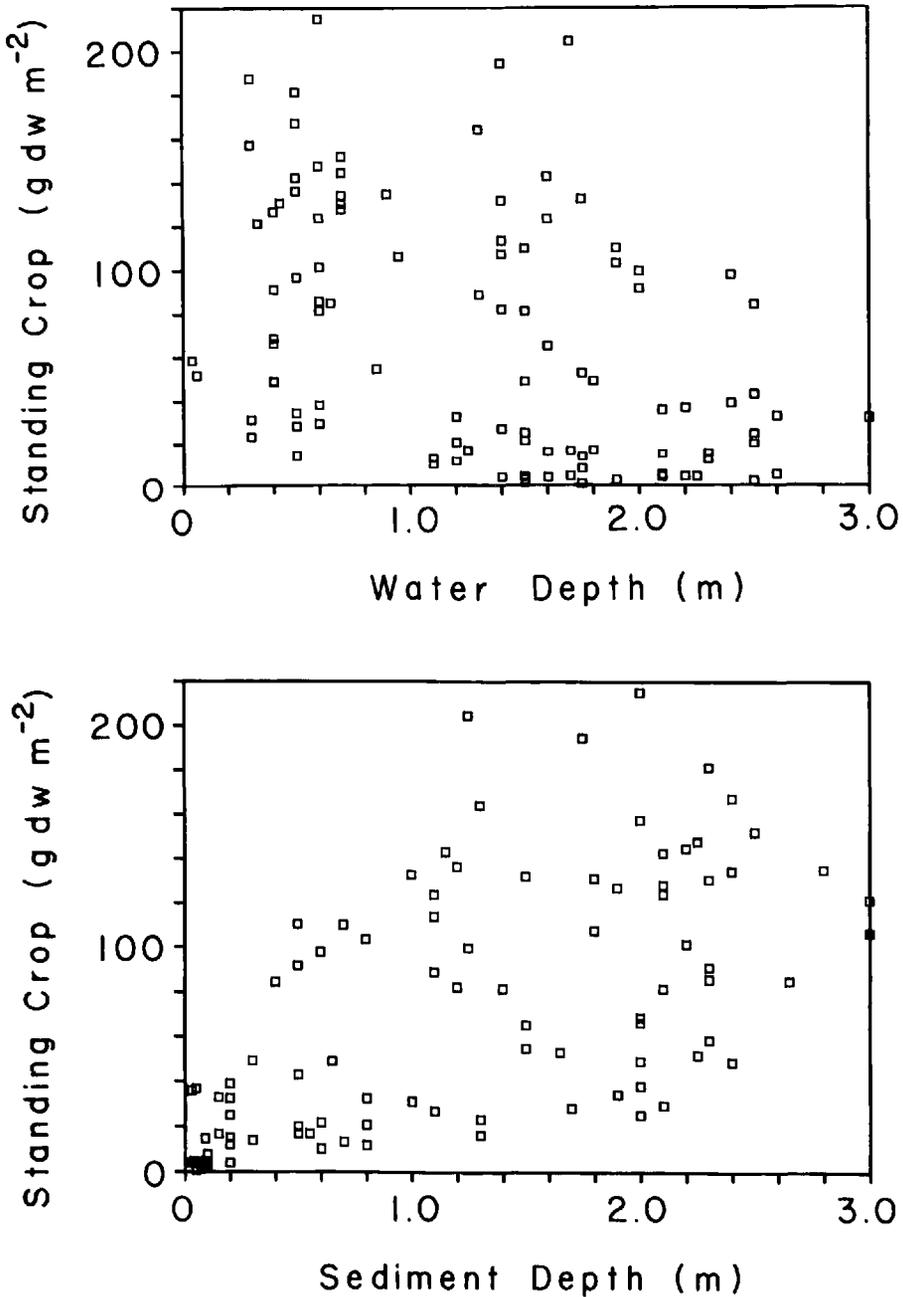


Figure 6. Scatterplots showing the effect of water depth and sediment depth on *Thalassia testudinum* standing crop.

monotypic stands of *Halodule* were found in this area with standing crop reaching $90 \text{ g dw} \cdot \text{m}^{-2}$. *Ruppia maritima* was found along the margins of the mangrove stands which fringed the mainland in the easternmost part of this area. *Ruppia* occurs only in portions of the marine environment where salinity is less than

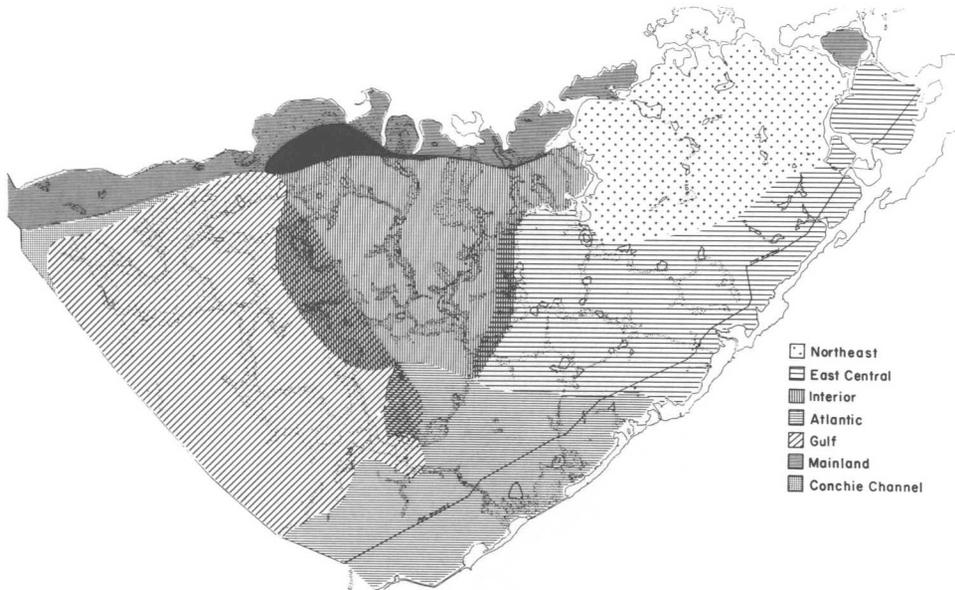


Figure 7. Location and extent of the benthic communities of Florida Bay.

normal seawater values (Verhoeven, 1975). *Syringodium* grew in deeper waters at the western end of the area covered by this community. Leaves of all the seagrass species were highly epiphytized in this area. *Batophora* was common and grew attached to hard substrate.

The Gulf community was the most diverse in Florida Bay. Sediments were deep enough to support lush seagrass growth throughout the area covered by this community. Extensive, lush beds of *Thalassia* (75 to 125 $\text{g dw} \cdot \text{m}^{-2}$) were interspersed with *Halodule* and *Syringodium* both on the banks and in the basins (Fig. 8C). *Syringodium* was present in greatest leaf biomass in water depths of around 3 m. Local outcrops of bedrock in the middle of the basins provided attachment for gorgonians, alcyonarians, sponges, several algal species, and for some hardy hermatypic corals such as *Siderastrea*. The drift alga *Laurencia* was abundant in low energy areas within the community.

The Atlantic community was characterized by very sparse *Thalassia* (20 $\text{g dw} \cdot \text{m}^{-2}$) growing in deep water basins and very lush *Thalassia*, up to 400 $\text{g dw} \cdot \text{m}^{-2}$, growing on firm banks. The basin floors had shallow accumulations of coarse sediment which supported very sparse *Thalassia* except in localized areas of increased sediment depth. Occasional bedrock outcrops were colonized by dense stands of gorgonians, as well as by the hardy hermatypic corals *Porites* and *Siderastrea*. Calcareous algae more typical of reef-tract flora, such as *Halimeda* and *Penicillus*, dominated the macroalgal biomass. The deep bottoms of well-flushed, clear-water tidal channels which cut through the banks were covered with dense stands of *Syringodium*.

Conchie Channel is a deep, highly turbid tidal channel just south of Cape Sable that drains the basins to the south and east of Flamingo. The Conchie Channel community was characterized by hard packed mud or muddy shell and sand bottom with infrequent bedrock outcrops, which coincides with the hard-shell, sand zone described by Tabb et al. (1962). Very sparse *Thalassia* and *Halodule*

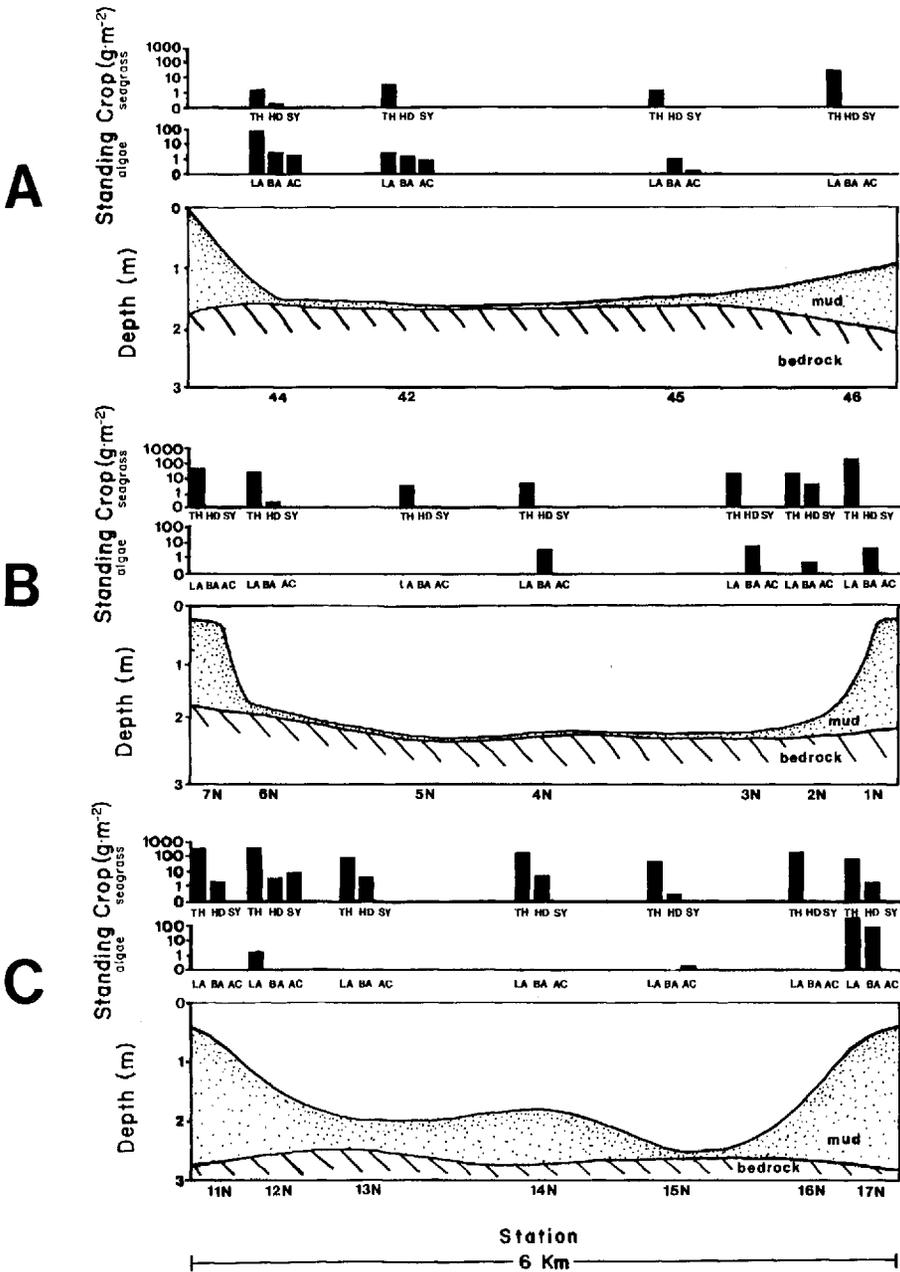


Figure 8. Comparisons of macrophyte standing crop, water depth and sediment depth from three basins in Florida Bay. The locations of these three transects are given on Figure 1. The macrophyte names have been abbreviated as follows: *Thalassia testudinum* = TH, *Halodule wrightii* = HD, *Syringodium filiforme* = SY, *Laurencia* spp. = LA, *Batophora* spp. = BA, and *Acetabularia* spp. = AC. Numbers on the X-axis are station numbers.

Table 4. Summary of the area and *Thalassia testudinum* standing crop and productivity for the benthic communities of Florida Bay

Community		Area (*10 ⁶ m ²)	Basin/Bank ratio	Standing crop (*10 ⁶ g)	Productivity (10 ⁶ g·d ⁻¹)
Northeast	Bank	10.6	23.8	350	3*
	Basin	252.8		2,528	25*
	Total	263.4		2,878	28
Atlantic	Bank	15.9	10.6	1,431	26†
	Basin	168.9		3,378	61†
	Total	184.8		4,809	87
East-Central	Bank	54.9	4.3	3,294	41*
	Basin	168.9		4,684	47*
	Total	289.1		7,978	88
Interior	Bank	95.6	1.7	5,736	103†
	Basin	234.2		6,664	120†
	Total	262.2		12,400	223
Mainland	Bank	65.3	1.4	3,918	71†
	Basin	94.6		3,700	67†
	Total	159.9		7,618	138
Gulf	Bank	223.1	1.3	26,722	558*
	Basin	280.6		18,239	589*
	Total	503.7		45,011	1,147
Total for Florida Bay	Bank	465.5	2.6	41,501	802
	Basin	1,197.7		39,193	909
	Total	1,663.2		80,694	1,711

* Areal productivity measured.

† Areal productivity estimated as 0.018* standing crop (see text).

plants occurred over the entire bottom in densities not exceeding 1 short-shoot·m⁻². Sponges and bryozoans were widely scattered over the bottom.

Areal coverages of the different communities were obtained by planimetry from a map of Florida Bay (Fig. 7). The areas of the Atlantic and Gulf communities were estimated using the Everglades National Park boundary as the western and southern extent of these communities. The transition zone was divided equally between coincident communities where the transition zone was broad, such as between the Interior and Gulf communities (Fig. 7). The Gulf community occupied the largest area, with the Northeast, East-Central, and Interior communities approximately the same size (Table 4). The Atlantic and Mainland communities had the smallest area, which reflects their transitional position between the main part of Florida Bay and oceanic and terrestrial environments, respectively.

Drift Material Distribution.—A gradient was evident in all categories of drift particulate matter with larger values found near Florida Bay and smaller values offshore to the west, driven by the predominately easterly winds (Fig. 9). Seagrasses comprised by far the greatest quantity of the drift material. Mangrove material, which is much denser and floats only a very short time, was present in very small amounts, and even then, was never found far from shore, except for the occasional propagule. What was perhaps more surprising was that drift macroalgae, primarily *Sargassum*, constituted only about 11% of the total drift material. The area sampled for drift material totaled 14,400 km², which contained 4,450 metric tons (mt) of seagrass drift material in 5,025 mt of total drift material, using the average densities given in Table 5.

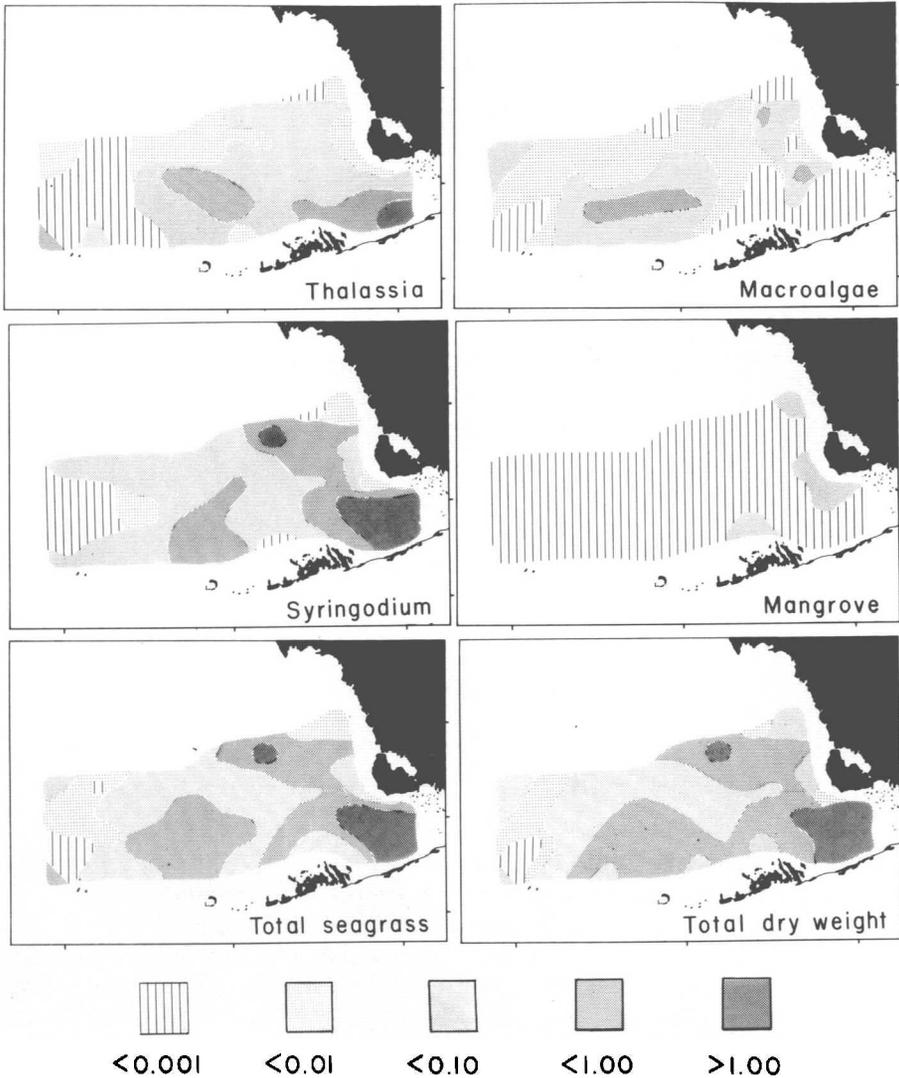


Figure 9. Density of macrophyte surface drift material collected west of Florida Bay in October, 1979. Density units are g m^{-2} .

DISCUSSION

Macrophyte Distribution.—*Thalassia testudinum* was the dominant submerged macrophyte in Florida Bay both in areal distribution and in biomass. *Halodule wrightii* and *Syringodium filiforme* dominated macrophyte community biomass only in limited areas of the bay where physical conditions precluded dense stands of *Thalassia*. *Syringodium* thrives in lower light energy conditions where growth of *Thalassia* is light-limited (Buesa, 1975). This condition occurred in some of the deeper cuts and channels throughout the bay, and was particularly evident in the south and west (Fig. 2). *Halodule* was locally dominant in areas subject to temperature and salinity extremes, such as the crests of the shallower banks and in stagnant areas with low water flushing rates.

Seagrass standing crop had two major patterns in Florida Bay. First, leaf biomass

Table 5. Average density of drift material (g m^{-2}) collected west of Florida Bay in October 1979

	Density	% of total
<i>Syringodium filiforme</i>	0.250	72
<i>Thalassia testudinum</i>	0.054	15
Macroalgae	0.037	11
<i>Halodule wrightii</i>	0.005	1
Mangrove	0.003	1
Terrestrial material	0.000	0
Total seagrass	0.309	88
Total drift material	0.349	100

was directly correlated with sediment depth, especially in the northeastern section of the bay, and second, total leaf biomass increased from northeast to southwest (Fig. 10). Seagrass leaf biomass was much greater in the thick sediments of the banks compared to the thinner sediments of the basins. Sediment depth and water depth have been recognized as important factors which control seagrass standing crop (Zieman, 1972; Buesa, 1975).

Macroalgal biomass was less than seagrass leaf biomass throughout most of Florida Bay; however *Laurencia* spp. was observed in large quantities at a few stations. *Laurencia* was most abundant on the low-energy sides of banks and was almost absent from high energy areas, which is explained by its free-drifting mode of life. *Acetabularia* and *Batophora* require hard substrate for attachment, which was generally provided by dead *Thalassia* rhizomes or empty mollusc shells in Florida Bay. *Penicillus* was sparse with patchy distribution throughout the bay, although it occurred in significant biomass where localized conditions, such as shallow and frequently unstable sediments, prohibited dense seagrass cover.

Macrophyte Productivity.—Specific leaf productivity is defined as $\text{g leaf mass produced (g standing crop)}^{-1} \cdot \text{day}^{-1}$, and is synonymous with leaf turnover rate, which is expressed as percent leaf increase $\cdot \text{day}^{-1}$. The within-species variation in specific leaf productivity, measured by ^{14}C uptake and by the leaf mark method, was very low in Florida Bay. The coefficient of variation (CV) of specific leaf productivity obtained from ^{14}C uptake measurements was 3.3% for *Thalassia*, 5.5% for *Halodule*, and 1.6% for *Syringodium* (Table 3). *Thalassia* and *Syringodium* had similar leaf productivity rates, however *Halodule* leaf productivity was much greater in Florida Bay. Williams and McRoy (1982) found a similar pattern in leaf productivity for these seagrasses growing in Puerto Rican and in Texas waters. The leaf specific productivity rates obtained in this study for each species in Florida Bay were intermediate between the rates obtained for each species in Texas and Puerto Rican waters with the exception of *Halodule*, which showed similar rates in Texas and Florida (Williams and McRoy, 1982). Greater leaf specific productivity of *Halodule*, compared to *Thalassia* and *Syringodium*, at all three locations is an example of the pioneering nature of *Halodule*. *Halodule* colonizes denuded areas and inhabits areas with extreme ranges in physical variables such as periodically exposed banks. *Halodule* is rapidly growing with a small root and rhizome system and with relatively little structural tissue associated with the leaf-bearing short-shoot. The lower specific productivity rates of the successional climax species, *Thalassia*, and the sub-climax species *Syringodium*, reflect the respiration demands of greater amounts of non-photosynthetic tissue in the roots, rhizomes, and short-shoots of these physically larger and more robust plants.

Productivity measurements were made in water depths ranging from 0.6 to 1.8

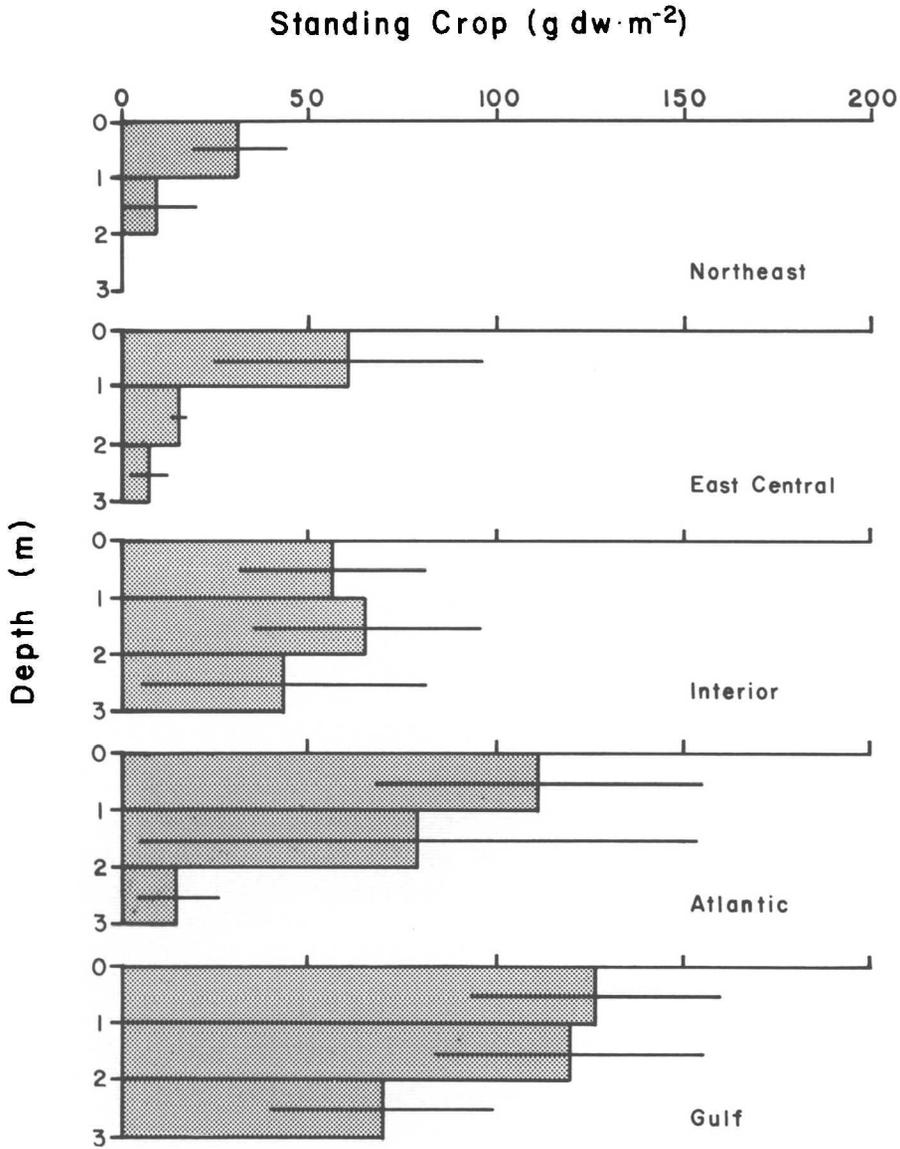


Figure 10. Comparison of *Thalassia testudinum* standing crop in the Northeast, East-Central, Interior, Atlantic and Gulf communities, and the stratification of the standing crop with depth.

m, at locations where leaf standing crops ranged from 1.8 to 142.9 g dw · m⁻² with a 90% coefficient of variation. Areal leaf productivity varied over two orders of magnitude, with an 82.5% coefficient of variation (Table 2). Figure 11 shows the increasing productivity of *Thalassia* on a northeast to southwest transect across the bay. Despite the large variations in standing crop and areal productivity, the variation in specific leaf productivity obtained with the leaf mark method (range of 1.44 to 3.55 g dw · (g dw)⁻¹ · d⁻¹, CV = 24.2%) was much less than the variation in areal leaf production or in standing crop. *Thalassia* areal leaf productivity in Florida Bay showed a direct and consistent relationship to leaf standing crop (Fig. 12). This relationship held for data collected across a wide variety of sediment

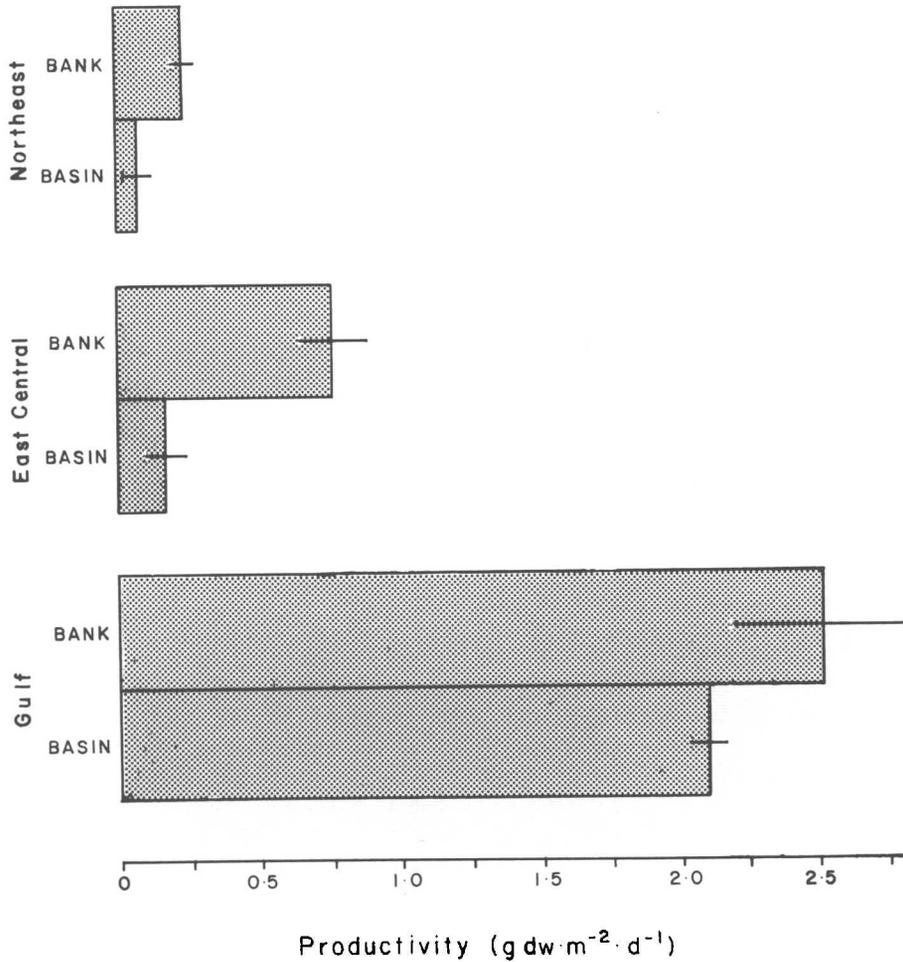


Figure 11. Comparison of areal *Thalassia testudinum* productivity in the Northeast, East-Central and Gulf communities and the differences between bank and basin productivity.

textures, sediment depths and water depths. Florida Bay locations with large *Thalassia* areal leaf productivity were more productive because there was greater leaf biomass in those areas, not because the plants grew faster than plants in other areas.

The relationship between productivity and standing crop can be used to estimate seagrass leaf production within a region from standing crop measurements, which are much easier to acquire than productivity data. Turnover rate, defined as the specific leaf productivity rate times 100%, is commonly used to describe seagrass leaf growth. The mean turnover rate calculated from Florida Bay data was 2.19, while the slope of the regression line (Fig. 12) gave a turnover rate of 1.85. This difference was caused by data from several locations with relatively high productivity rates but with relatively low biomass which increased the grand mean rate proportionately more than they contributed to the regression line slope. Measurements of *Thalassia* leaf productivity and standing crop at several localities in Biscayne Bay and just offshore of Soldier Key in the period 1966–1970 (Zieman,

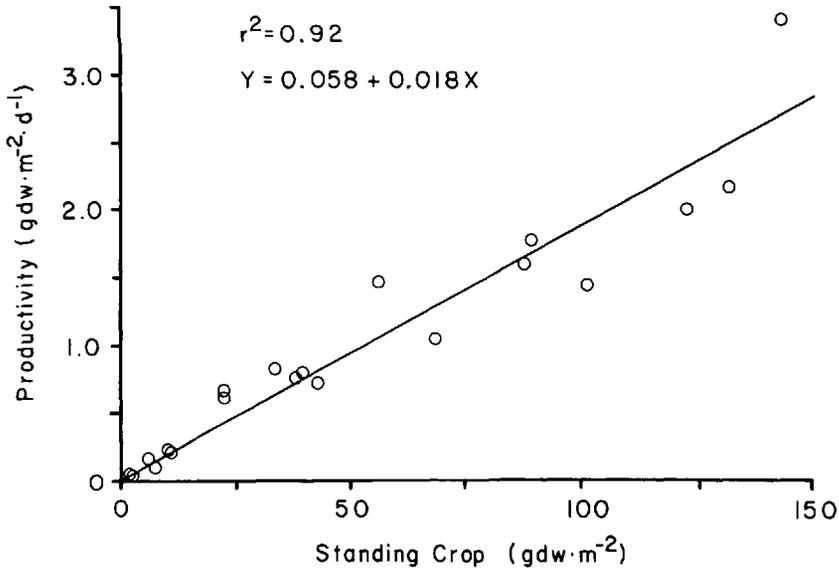


Figure 12. The relationship between *Thalassia testudinum* standing crop and areal productivity. The line is the linear regression equation $\text{Productivity} = 0.058 \pm 0.018(\text{Standing crop})$. This regression is highly significant ($P < 0.001$), and explains 92% of the variation in productivity.

1968; 1975), and more recently near Looe Key and in Pine Channel in the lower Keys (J. C. Zieman, unpubl.) gave leaf turnover rates which averaged between 1.85–2.4% per day. The consistency of these turnover rate values over a distance gradient of 100 km, a time period of 20 years, and a variation in standing crop of over two orders of magnitude, indicates a strong regional regulation of this growth factor.

Community Analysis.—The ratio of basin area to bank area changes greatly across Florida Bay, decreasing from 23.8:1 in the Northeast community to 1.3:1 in the Gulf community, and was an average of 2.6:1 for the entire Bay (Table 4). *Thalassia* was the dominant seagrass in all the communities, both in distribution and in standing crop. Seagrass leaf standing crop increased from northeast to southwest in the bay (Fig. 10; Table 4). The difference between seagrass leaf standing crop on near-surface banks and at the basin bottoms was greater in the Northeast and East Central communities compared to the other communities. The lower seagrass standing crops in these communities were related to shallower sediment depth and to greater light attenuation in the more turbid waters of these areas. Turbid water had a large attenuation effect, greatly reducing photosynthetically active radiation available to benthic macrophytes growing in deeper basin waters. The difference in leaf standing crop between shallow banks and basin bottoms was not as pronounced in the Interior and Gulf communities where sediments were deeper and where the water was much clearer. The patterns in seagrass leaf productivity followed the pattern in the leaf standing crop data. Since seagrass areal leaf productivity was directly proportional to leaf standing crop, leaf productivity could be estimated for all of the biomass stations in Figure 2 with the regression equation obtained for the data in Figure 12. Total seagrass leaf standing crop was $8 \cdot 10^5$ metric tons dry weight, while daily seagrass leaf production was 1,700 mt dry weight in Florida Bay during the summer (Table 4).

Export.—Most seagrass leaf material in tropical environments is retained, and fuels the detrital food web, within the system where it is produced (Zieman, et al., 1979). However a large and unknown portion is exported from Florida Bay and from the lower keys carrying particulate organic matter and large quantities of carbonate epiphytic material out of the areas where they are produced (Fig. 9). The prevailing easterly winds drive surface currents which carry the drift material westward from the shallow waters of the bay. Seagrasses comprised an average 89 % of the material trapped by the nets, with the bulk of the contribution coming from *Syringodium*. Because *Syringodium* is so buoyant, it floats much longer than either *Thalassia* or *Halodule* (Zieman et al., 1979), allowing it to be transported much greater distances, and contribute to distant food webs. However, because it does float off so readily, it makes much less of a contribution to the local food webs than the other seagrasses. The macrophyte drift material provides a substantial subsidy to the detrital food-webs which support the commercial pink shrimp, *Penaeus duorarum*, in the Tortugas region as this material drifts westward at the surface, sinks, and decays.

Changes in Florida Bay Macrophyte Communities.—Changes in the temperature, salinity or light regimes may alter the composition of the benthic macrophyte community of Florida Bay. Reports of local residents suggest *Halodule* biomass has decreased in the northeastern part of the bay now compared to 30 years ago. In the late 1970's, some Florida Bay fishing guides blamed decreased fish catches in the northeastern and north-central portion of the bay on the replacement of mud bottoms previously covered with sparse *Halodule* by *Thalassia* meadows. The *Thalassia* meadows trapped sediment which caused decreased water depth, and were less useful as feeding areas to mullet and sea trout. Since *Halodule* is a pioneering species which occurs under disturbance conditions not tolerated by *Thalassia*, environmental conditions may be more stable now than 30 years ago in the northeastern part of Florida Bay. This condition may have been caused by decreased freshwater drainage from the Everglades and Taylor Slough into the northern reaches of Florida Bay after construction of the C-111 canal and the Aerojet-General canal to the north of Florida Bay (Zieman, 1982). The extension of the Gulf community into Florida Bay, which local residents report to have occurred since the late 1950's, suggests that the western bay experiences more typically oceanic conditions now compared to 30 or more years ago as a consequence of reduced freshwater input to the bay.

The most important factors which control the distribution and development of seagrass and mangrove communities in Florida Bay may be changes in freshwater input and in the frequency of large storm passage through the bay. Tropical storms can devastate mangrove stands and can remove large amounts of sediments from unvegetated basins; however, their effect on seagrass biomass appears to be minimal. Hurricane Donna had little effect on seagrass biomass or on the topography of the shallow seagrass-stabilized carbonate-mud banks in Florida Bay. However, the hurricane splintered and uprooted large expanses of mangroves in the bay (Ball et al., 1967). Most of the hurricane Donna damage to *Thalassia* beds in Biscayne Bay was attributed to low salinity stress. Removal of plants from sediments by hurricane-induced mechanical processes were negligible (Thomas et al., 1961).

Mangroves can replace any of the species in the submerged communities if shallow, protected banks become colonized by *Rhizophora* propagules. New mangrove islands form and existing islands are extended in the bay today. Well established mangrove stands are resilient. Mangroves can lose leaves and branch-

es, however mangrove stands are usually not eradicated during hurricanes. The expansion of existing mangrove islands and the formation of new islands require long inter-storm intervals during which mangrove seedlings can become established. The average recurrence interval for hurricanes in the south Florida region is 7 to 8 years (Simpson and Riehl, 1981). Mangrove seedlings can colonize shallow banks during this time interval, but rarely become well established and can be easily uprooted by a major storm event within that time period. Florida Bay has not experienced the full effects of a large hurricane since Hurricane Betsy in 1965. Numerous changes are apparent in Florida Bay and throughout the lower keys as a consequence of this long hurricane hiatus. Many channels used by small boats are becoming shallow and many subtidal banks are now exposed on moderately low tides in the lower Florida Keys. Sediment has accumulated in many basins as a consequence of the lack of flushing normally caused by hurricane winds and rains. The protracted interval between storms has allowed mangrove seedlings to develop into robust young mangroves in many areas, while simultaneously allowing increased sediment deposition on banks. These new mangrove stands are relatively well anchored and will be difficult to dislodge. Changing patterns in natural events such as the frequency of hurricane passage through the bay, and in freshwater input from terrestrial sources caused by man's activities, appear to have resulted in Florida Bay macrophyte succession away from communities dominated by pioneering species and toward communities dominated by the submergent climax species *Thalassia testudinum* and the emergent *Rhizophora*.

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