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SEAGRASS MEADOWS OF TAMPA BAY - A REVIEW

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ABSTRACT

Seagrass meadows presently cover approximately 5,750 ha of the bottom of Tampa Bay, an 81% reduction from the historical coverage of approximately 30,970 ha. Five of the seven species of seagrass occurring in Florida are found in the estuary, typically in less than 2 m of water. These are: Thalassia testudinum Banks ex Konig (turtle grass); Syringodium filiforme Kutzing (manatee grass); Halodule wrightii Ascherson (shoal grass); Ruppia maritima L. (widgeon grass), and Halophila engelmannii Ascherson. The dominant species are turtle grass and shoal grass. The meadows are subdivided into five types: 1) mid-bay shoal perennial; 2) healthy fringe perennial; 3) stressed fringe perennial; 4) ephemeral; and 5) colonizing perennial. The general characteristics of these meadow types are discussed. In addition, the habitat values, physiological ecology, reproductive biology and on-going research work are summarized. Seagrasses in Tampa Bay reproduce primarily vegetatively. Sexual reproduction occurs in T. testudinum and R. maritima. Thalassia seed production is low, however, and confined to the southern part of the Bay. Seed quantities may be insufficient for significant colonization and restoration projects.

INTRODUCTION

Seagrass beds have long been recognized as a food source and habitat for benthic invertebrates and fish (Phillips 1960a; Randall 1965; Wood et al. 1969). Hutton et al. (1956) were among the first researchers to recognize the importance of seagrass beds as fish and wildlife habitats in Tampa Bay. They also recognized that development activities along the shore and associated effects on these areas conflicted with conservation, fishing and recreational interests. Indeed, the destruction of 1,100 metric tons of seagrasses by dredging and filling in Boca Ciega Bay resulted in the immediate loss of 1,800 metric tons of infauna, and the annual loss of approximately 73 metric tons of fisheries products and 1,100 metric tons of infauna (Taylor and Saloman 1968). The loss of this habitat represented an annual monetary loss of $1.4 million. Godcharles (1971) found that the use of a commercial hydraulic clam dredge in seagrass beds uprooted all vegetation and that no recolonization had occurred after more than a year. He recommended that

the use of these harvesters be prohibited in grassy areas because of the importance of such areas as nursery grounds for the majority of Florida's sport and commercial species. In this regard, Lewis and Phillips (1980) found that the loss of seagrass habitat in Tampa Bay coincided with a reduction in commercial landings of spotted seatrout.

Seagrass habitat value is best summarized by the scheme of Wood et al. (1969):

1. Seagrasses have high growth and production rates;
2. The leaves support large numbers of epiphytic organisms with biomass approaching that of the seagrasses themselves;
3. Although few organisms feed directly on them, seagrasses produce large quantities of detritus which serves as a major food source for many species;
4. Seagrasses bind sediments and prevent erosion, in turn providing a quiescent environment in which a great variety of organisms can grow;
5. Seagrasses provide organic matter which encourages sulfate reduction and an active sulfur cycle; and,
6. Seagrasses act as nutrient sinks and sources.

In addition, Ketchum (cited in Phillips 1978) has estimated that 80-90% of the commercial and sport fish species depend on estuaries during all or part of their life cycle, and estuaries typically support large seagrass beds.

Dense populations of bacteria and fungi are associated with seagrass beds (Burkholder et al. 1959; Klug 1980). These microorganisms form a major source of nutrition for detritus feeders including various polychaetes, crustaceans, mollusks and fish (Brook 1975; O'Gower and Wacasey 1967). Seagrass-derived detrital material is important in food webs within beds, and also in detrital food webs based on material exported from the system (Zieman 1981). Direct herbivory forms the basis for the third type of food web based on seagrasses. However, most of the productivity of seagrasses is believed to be channeled through detrital pathways (Fig. 1 in Ogden 1980).

Several studies dealing with Florida seagrass beds and their associated animal communities have included species lists and population densities (Voss and Voss 1955; Tabb and Manning 1961; Dragovich and Kelly 1964; Santos and Simon 1974; Brook 1975; Stoner 1980; Livingston 1982). These studies show that diversity and abundance of fish and invertebrates are usually higher in grass beds than in unvegetated habitats. Stoner (1980) found that abundances of epifauna, suspension feeders and carnivorous polychaetes were correlated with seagrass biomass. The increase in abundance of epifauna was related to increased surface area of leaf blades. Taylor et al. (1973) reported that for each square meter of bed area, Thalassia leaf blades have a total surface area of up to 18 m^2. This large surface area provides a correspondingly large amount of substrate for epiphytes.

Mobile invertebrate epifauna, including several species of echinoids, asteroids and gastropods, feed upon the seagrasses and epiphytes (Ogden 1980). Other invertebrates such as some crabs, shrimp and gastropods are carnivorous, feeding on smaller herbivores and detritus feeders. Some fish species within seagrass beds may follow developmental sequences that encompass various trophic levels from herbivory to carnivory (Livingston 1982). Many commercially important fish are present in grass beds as juveniles obtaining both food and shelter (Ogden 1980). The major vertebrate consumers of seagrasses are sea turtles and manatees (Zieman 1981). These animals "mow" or "root" when feeding and can have substantial localized impacts on grass beds (Packard 1981; Zieman 1981). Waterfowl also feed on seagrasses which can constitute a major food source for some species (McRoy 1966).

OCCURRENCE AND DISTRIBUTION

Eiseman (1980) notes the occurrence of seven species of

seagrasses in Florida:

1. Thalassia testudinum Banks ex Konig (turtle grass)
2. Syringodium filiforme Kutzing (manatee grass)
3. Halodule wrightii Ascherson (shoal grass)
4. Ruppia maritima Linnaeus (widgeon grass)
5. Halophila engelmannii Ascherson
6. Halophila decipiens Ostenfeld
7. Halophila johnsonii Eiseman

The last species is newly described (Eiseman and McMillan 1980) and historically has probably been confused with H. decipiens (Eiseman 1980).

Thorne (1954) mentioned the occurrence of five of these species in Tampa Bay: Thalassia testudinum, Syringodium filiforme, Halodule wrightii, Halophila engelmannii, and Ruppia maritima. Phillips (1962) conducted the first comprehensive field sampling for seagrasses in Tampa Bay during 1959-60 and reported the occurrence of all of these species except H. engelmannii. Taylor and Saloman (1969) summarized data for 773 benthic samples taken during 1961-65 along 18 transects within Tampa Bay and noted the occurrence of seagrasses in 217 (34%) of the samples. No R. maritima was reported, probably due to difficulty in distinguishing it from H. wrightii without close examination. H. engelmannii was reported at only 2 stations, both in Boca Ciega Bay. Taylor (1973) also reported its occurrence behind Egmont Key. More recently, it has been observed around Cockroach Bay in Middle Tampa Bay by Lewis and Phillips (1980) and Moffler and Durako (unpublished data). Thus five of the seven Florida species of seagrasses have been reported to occur in Tampa Bay.

Phillips (1962, p. 8), sampling at 98 stations between Pinellas Point and Terra Ceia Bay during 1959-60 (Fig. 1), noted that "all attached plants were limited to waters inshore of the one fathom curve". Also, "... Diplanthera (Halodule) is dominant in the southern portions of the bay while Ruppia is dominant in the most northerly portions".

Lewis and Phillips (1980) reported the results of 226 samples collected seasonally at 18 inshore stations during 1980-81, and found 42.5% of the samples contained Thalassia testudinum, 40.7% Halodule wrightii, 19.0% Syringodium filiforme, 15.5% Ruppia maritima, and none contained Halophila engelmannii (Table 1). Table 2 lists the seagrass associations found during the same sampling program. Single species were found in 83.3% of the samples. Four species associations occurred in the remainder of the samples, with H. wrightii/R. maritima being the most common (8.8%), followed by T. testudinum/S. filiforme (5.3%), T. testudinum/H. wrightii (2.2%) and T. testudinum/H. wrightii/S. filiforme (0.5%).

Based on the currently available aerial photography of Tampa Bay (1981), Figure 2 was prepared. It shows 5,750 ha (14,203 acres) of seagrass meadows in Tampa Bay. Similar working maps were prepared using vertical black and white aerial photography of Tampa Bay (secured from the National Archives, Washington, DC) that had been taken by

Table 1. Percent species occurrence, Tampa Bay (Lewis and Phillips 1980). Percent of samples in which species was collected, n = 226.

SPECIES	PERCENT
Thalassia testudinum	42.5
Halodule wrightii	40.7
Syringodium filiforme	19.0
Ruppia maritima	15.5
Halophila engelmannii	0.0

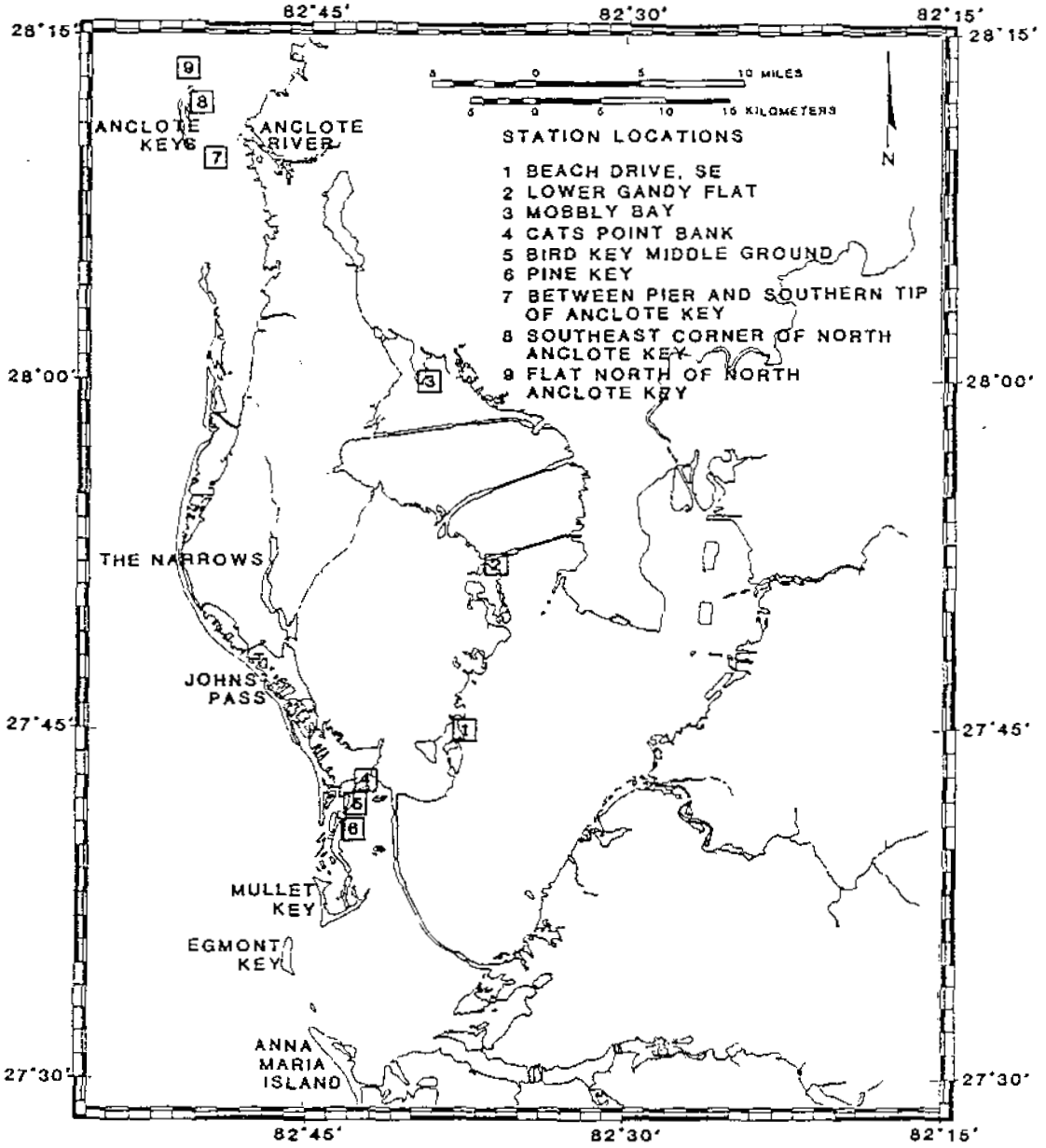

Figure 1. Location of station sites in Tampa Bay, Boca Ciega Bay, and at Tarpon Springs (from Phillips 1960a).

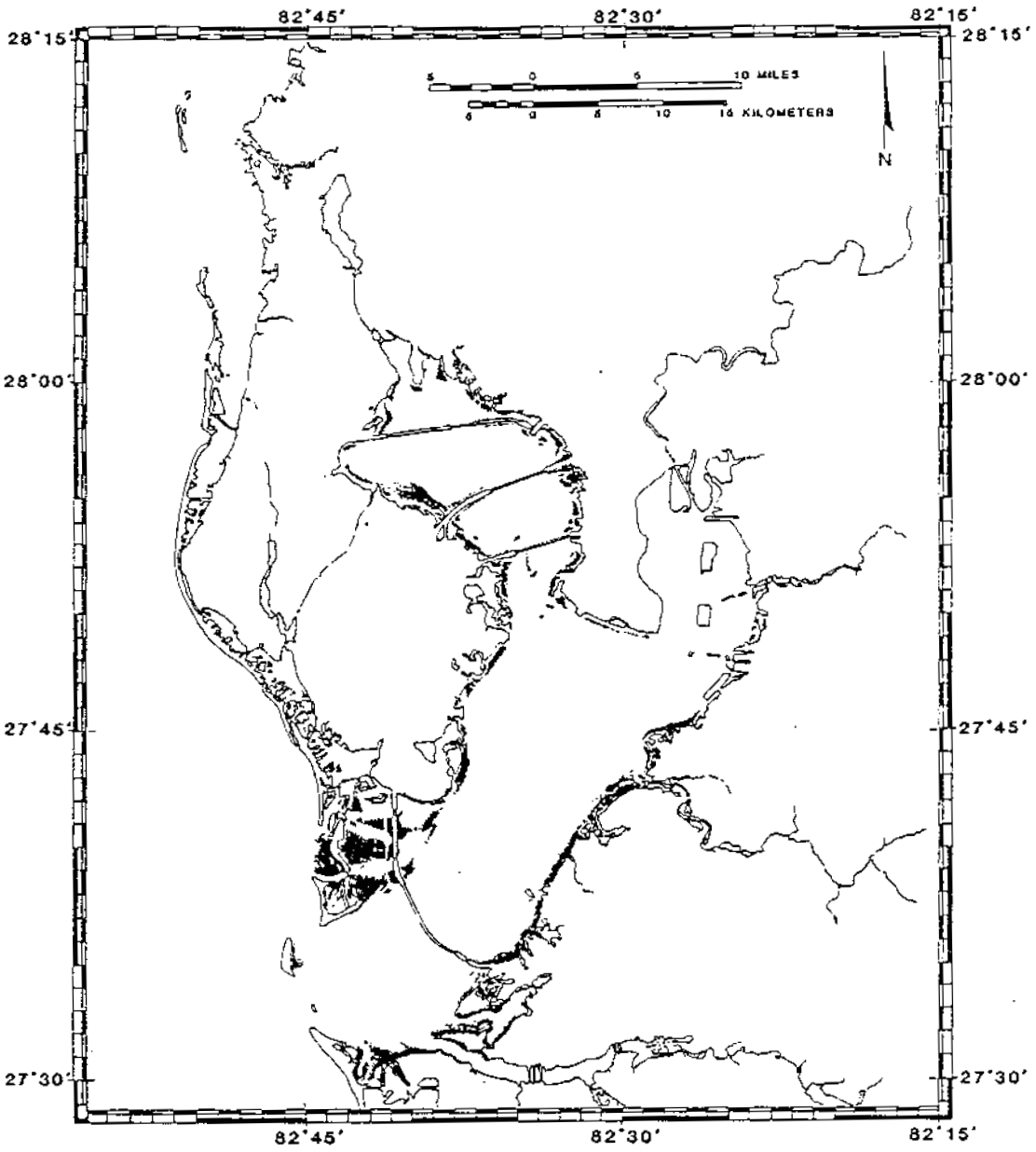

Figure 2. Extent of seagrass meadows in Tampa Bay - 1982.

Table 2. Seagrass species associations, Tampa Bay (Lewis and Phillips 1980). 226 samples.

ASSOCIATION	PERCENT OCCURRENCE	STATIONS
Halodule wrightii Ruppia maritima	8.8	5, 7, 10, 12
Thalassia testudinum Syringodium filiforme	5.3	1, 6, 10
Thalassia testudinum Halodule wrightii	2.2	2
Thalassia testudinum Halodule wrightii Syringodium filiforme	0.5	2

the Soil Conservation Service between 1938 and 1942. These were used in conjunction with maps dating back to 1848 to prepare maps of historical seagrass coverage in Tampa Bay (Fig. 3). It is estimated that seagrass meadows covered 30,970 ha (76,496 acres) prior to man's major impacts upon the bay (c. 1876).

TYPES OF SEAGRASS MEADOWS

Figure 4 illustrates five types of seagrass meadows found in Tampa Bay. These are:

1. Mid-bay shoal perennial - MBS(P)
2. Healthy fringe perennial - HF(P)
3. Stressed fringe perennial - SF(P)
4. Ephemeral - E
5. Colonizing perennial - C(P)

The idealized cross-sections in Figure 4 are derived from actual transects established during 1979-80 (Lewis and Phillips 1980). It is hypothesized that types 2-4 are stages in the eventual disappearance of a seagrass meadow due to man-induced stress, as illustrated by the arrows in Figure 4. A brief description of each seagrass meadow type follows.

Mid-bay Shoal Perennial. These meadows are generally composed of Halodule, Thalassia and Syringodium. Ruppia is rarely observed, which may be attributed to the generally high current regime and/or higher salinities not typically found in meadows closer to shore. These meadows are located on natural shoals existing in the middle portion of the bay. They are present year round (perennial), although variations in cover by the different species occur seasonally.

Healthy Fringe Perennial. These meadows are the most common meadow type in the bay and extend from approximately the mean low water mark into water depths of approximately -2 m MSL. All five species of seagrasses found in the bay occur in this meadow type. Zonation begins with Ruppia in the shallowest water close to shore, and grades with increasing depth through nearly pure patches of Halodule, followed by Thalassia and then Syringodium. Unlike the generalized meadow cross-section from McNulty et al. (1972; Fig. 5), healthy fringe meadows in Tampa Bay normally have an offshore, unvegetated sand bar separating the main portion of the meadow from open bay waters and creating a "basin" behind the bar. This basin was described by Phillips (1960a) as a "central declivity" (Fig. 6). Similar sand bars have been observed offshore of seagrass meadows in Charlotte Harbor and are plainly visible in aerial and satellite photography of that area (Allen Huff, Florida

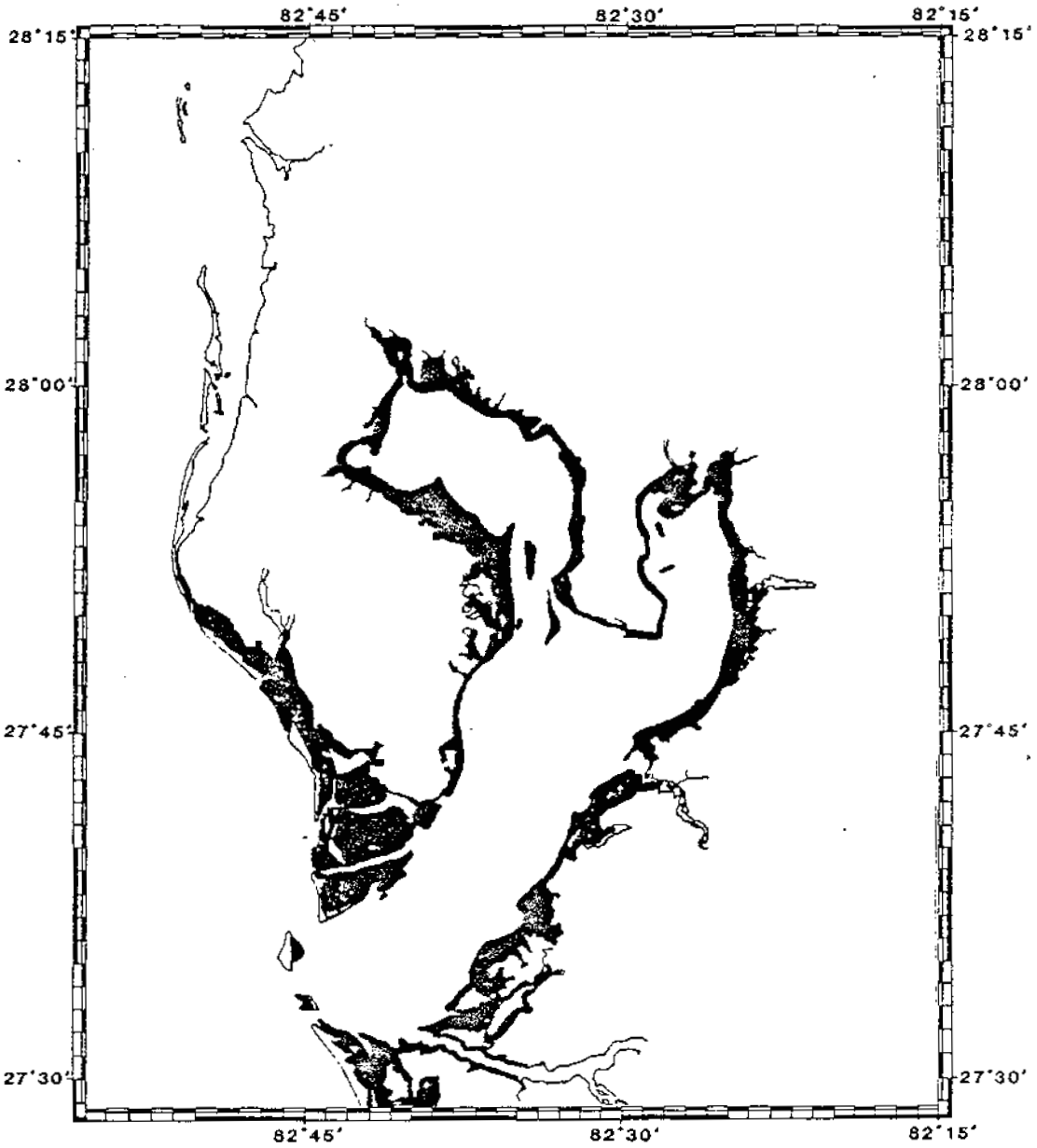

Figure 3. Estimated extent of seagrass meadows in Tampa Bay - 1879.

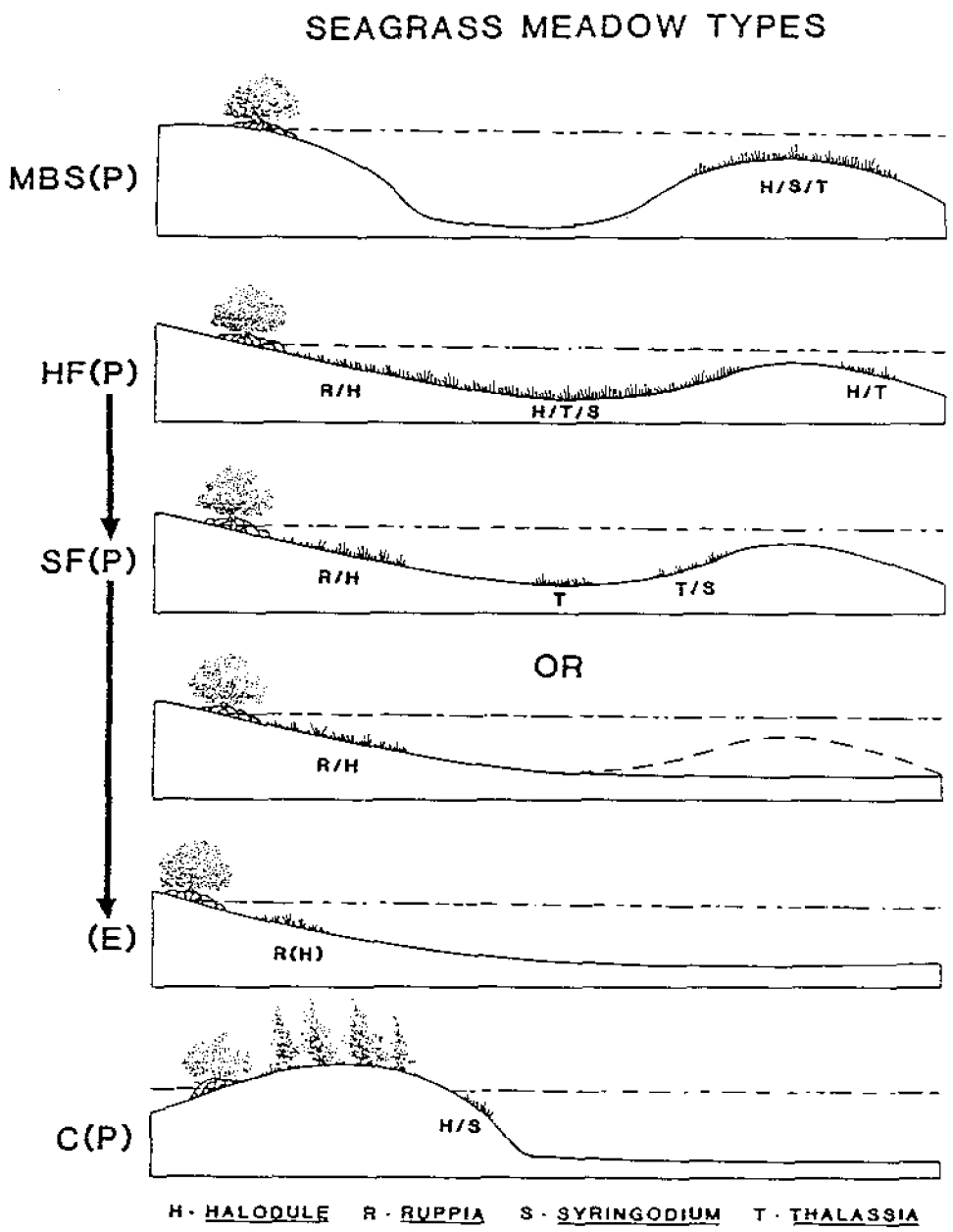

Figure 4. Seagrass meadow types. MBS(P) - mid-bay shoal perennial; HF(P) - healthy fringe perennial; SF(P) - stressed fringe perennial; (E) - ephemeral; C(P) - colonizing perennial.

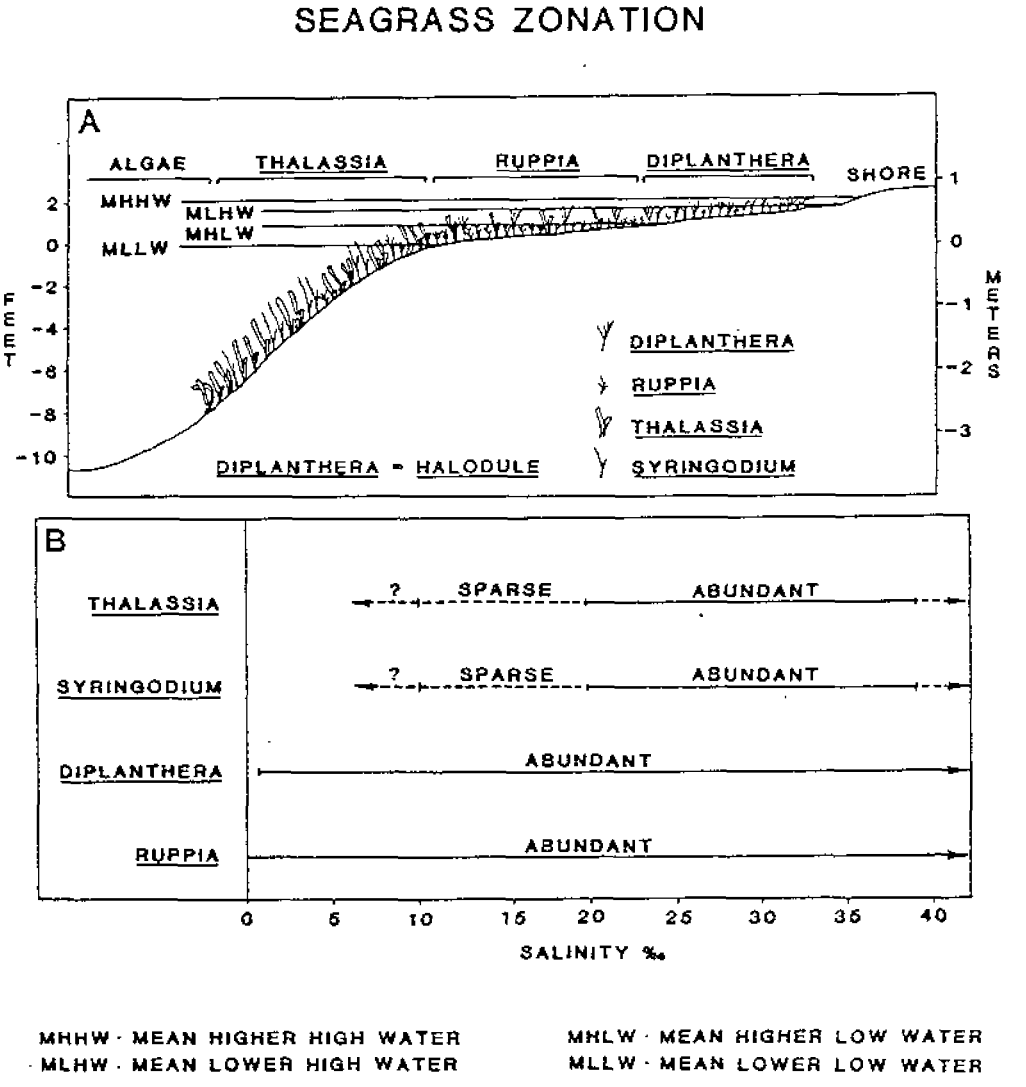

Figure 5. Seagrass zonation (McNulty et al. 1972). A - the zonation of seagrasses in shallow water in Boca Ciega Bay just north of the Bayway to St. Petersburg Beach and in Tampa Bay just south of Bayboro Harbor, St. Petersburg. B - salinity preferences and tolerances of seagrasses (modified from Phillips 1960a and Moore 1963).

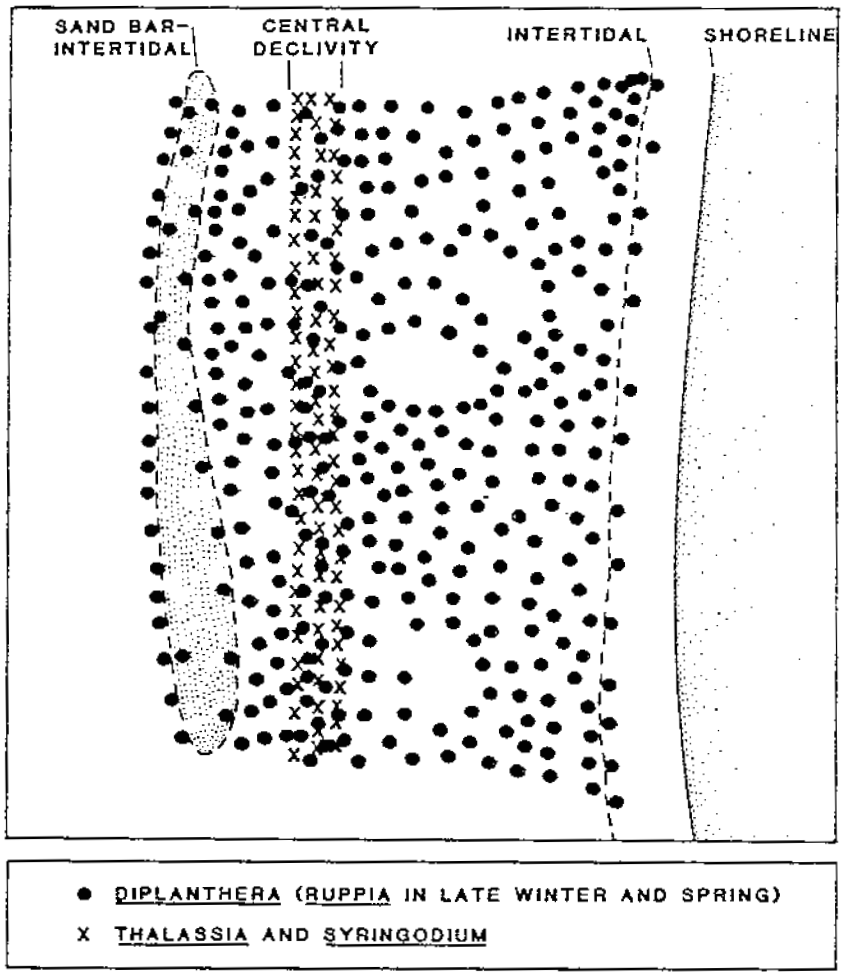

Figure 6. Schematic drawing of Beach Drive station showing intertidal zones and maximum depth declivity with location of grasses (from Phillips 1960b). Diplanthera = Halodule.

Table 3. Chlorophyll a amounts for stations in various parts of Tampa Bay, 1969-1971 (mg/m^3) (from Turner and Hopkins 1974).

SUBDIVISION	FALL	WINTER	SPRING	SUMMER	MEAN
Old Tampa Bay	16.5	3.6	5.4	26.6	13.0
Hillsborough Bay	31.6	56.5	22.0	41.7	40.0
Middle Tampa Bay	21.8	19.3	2.8	21.1	16.3
Lower Tampa Bay	4.8	5.6	11.4	16.1	9.5
Tampa Bay entrance	3.8	3.1	1.6	6.1	3.7
Boca Ciega Bay	12.5	6.7	7.4	16.4	10.8
Terra Ceia Bay	19.7	2.5	13.7	16.7	13.2

Department of Natural Resources, personal communication). A typical cross-section through a healthy fringe perennial seagrass meadow is diagrammed in Figure 7.

Stressed Fringe Perennial. These meadows are similar to healthy fringe perennial meadows except that total cover is reduced within the basin behind the offshore bar. Destabilization of the offshore sand bar apparently leads to its inshore migration and eventual disappearance (Fig. 4). This type of meadows generally occurs in areas closer to Hillsborough Bay with its typical tenfold increase in average chlorophyll a values (Table 3) and over areas closer to the mouth of Tampa Bay. Although there are no experimental data documenting competition between phytoplankton and seagrasses in Tampa Bay, such competition has been theorized to occur in the shallows of other estuaries where nutrient enrichment has been followed by increases in microalgae (phytoplankton) and macroalgae and decreases in seagrass meadows (Cambridge 1975, 1979; Davis and Brinson 1980; Harlin and Thorne-Miller 1981).

Ephemeral. These meadows are composed almost entirely of Ruppia with occasional sprigs of Halodule. They are not present year round and their locations often vary from year to year. Phillips (1962) noted the unusual appearance of Ruppia patches in Hillsborough Bay along Bayshore Boulevard and at the mouth of Delaney Creek in the winter of 1961. No other seagrass species were seen in these areas. Mangrove Systems, Inc. (1978) also noted the cyclic appearance and disappearance of a monospecific Ruppia meadow near the Big Bend power plant in Hillsborough Bay during 1976-78. These meadows probably represent the final stage of seagrass meadow degradation in Tampa Bay and would be followed by the complete absence of meadows as presently seen in most of Hillsborough Bay.

Colonizing Perennial. This meadow type is commonly found in a narrow band in the euphotic zone of man-made fills such as Courtney Campbell Causeway, Howard Frankland Bridge Causeway, and the Picnic Island fill. It is believed to represent a meadow type dominated by those species that can produce abundant propagules that disperse and colonize appropriate shallow substrates. As noted below, only Ruppia shows large scale sexual reproduction and seed production in Tampa Bay. Seed production of the other four species is rare to non-existent and therefore, these seagrasses colonize by dispersal of shoots/rhizomes produced asexually through fragmentation. Due to the exposed nature of the man-made fills and their generally coarser sediments, Ruppia is not as common as in the inshore portions of the fringe meadows. Both Halodule and Syringodium produce large amounts of detached rhizomes, particularly during storms, and it is theorized that these float into unvegetated areas, attach through new root formation, and establish new meadows. Thalassia produces relatively

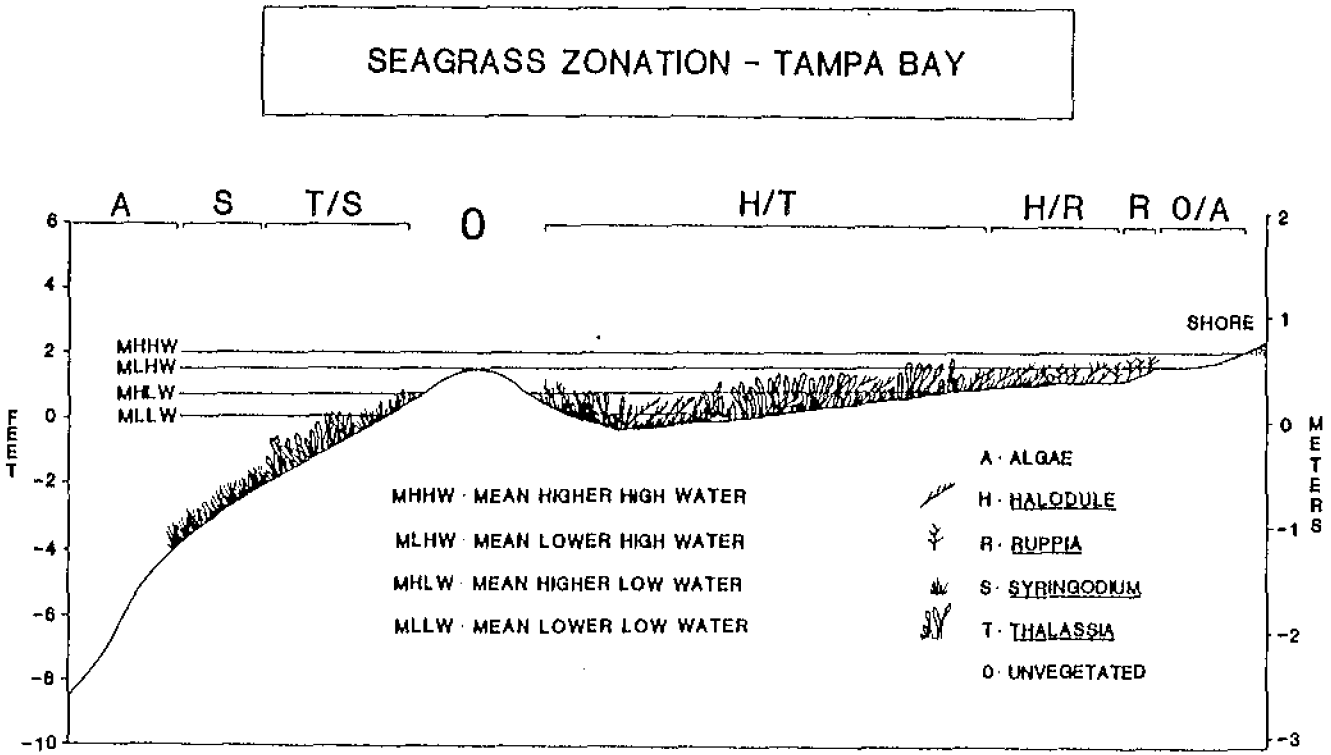

Figure 7. Zonation in a healthy fringe perennial seagrass meadow, Tampa Bay.

fewer detached shoot/rhizomes and, due to their increased buoyancy, these are less likely to sink into an area appropriate for meadow establishment. Even if sinking and attachment do occur, slower root and rhizome growth rates would make establishment of a new meadow by asexual means less likely. This may explain why Halodule and Syringodium are the dominant species in this meadow type.

PHYSIOLOGICAL ECOLOGY

Tidal Zonation. Physiological and morphological differences between seagrass species result in characteristic zonation patterns relative to tidal exposure (Fig. 8). Halodule wrightii is the most abundant species between neap high and neap low tide lines (Phillips 1960a, 1962). This seems to be related to the ability of Halodule to tolerate higher water temperatures and longer air exposures than other species in the bay (Humm 1956). Halodule also can be the dominant species subtidally in lower salinity areas where Thalassia and Syringodium are not found, such as the more turbid parts of upper Old Tampa Bay. Thus zonation of Halodule is not restricted entirely by physical factors; rather it may be out-competed by Thalassia and Syringodium in less turbid, high salinity areas. Ruppia maritima is commonly mixed with Halodule in intertidal areas where the salinity is low (Phillips 1960a, 1962; Earle 1972). Halodule is usually most abundant between the neap low and spring low tide lines in higher salinities (Phillips 1960a).

All four of these species occur subtidally in Tampa Bay. Syringodium filiforme becomes dominant at the spring low tide line, and frequently grows interspersed with Thalassia in deeper water (Humm 1956; Phillips 1960a, 1962; Woodburn 1961b). Although Thalassia is the dominant subtidal species in the Gulf of Mexico (Humm 1956; Earle 1972), Phillips (1962) noted that it occurs in relatively sparse amounts in Tampa Bay. This is probably because salinities in the bay are lower than optimum for this species. However, Thalassia is the dominant species in Boca Ciega Bay (Hutton et al. 1956; Pomeroy 1960; Taylor and Saloman 1968) and in the seagrass beds surrounding Mullet Key. In both of these areas salinity typically exceeds 30 ppt. Halophila engelmannii occurs subtidally mixed with Thalassia and Syringodium.

Phillips (1960b) found that Halodule exhibited three growth forms in Tampa Bay which were related to the tidal zone where they occurred. In areas exposed at both neap and spring low tides plants were dwarfed. Subtidal areas characteristically had more robust plants. Leaf length and width, rhizome thickness, and internode length were all affected by the degree of tidal exposure. Leaf apex features and internal cellular anatomy, features which had been used to distinguish two species of Halodule (H. wrightii and H. beaudetii), were found to vary according to the tidal zone in which the plants were found.

Seagrass growth in the bay has been reported to be limited to bottom areas less than 2 meters (6 feet) deep (Phillips 1962). High turbidity, and consequently low light penetration, seems to be responsible for the relatively shallow depth restriction, whereas desiccation and wave action limit the shoreward edge of seagrass beds.

Salinity. Tidal zonation of Ruppia in Tampa Bay may actually be a secondary effect due to this species' preference for brackish water (Phillips 1962). Of all seagrasses, Ruppia tolerates the broadest range of salinity, occurring in freshwater and in areas with salinities in excess of 35 ppt (although it does seem that somewhat reduced salinity is required for it to set seed). Thorne (1954) and Humm (1973) considered Ruppia primarily a freshwater species that can invade brackish waters and the latter author did not consider it to be a true seagrass. This apparent preference for lower salinites seems to be responsible for its dominance north of the Courtney Campbell Causeway in Old Tampa Bay (Phillips 1962).

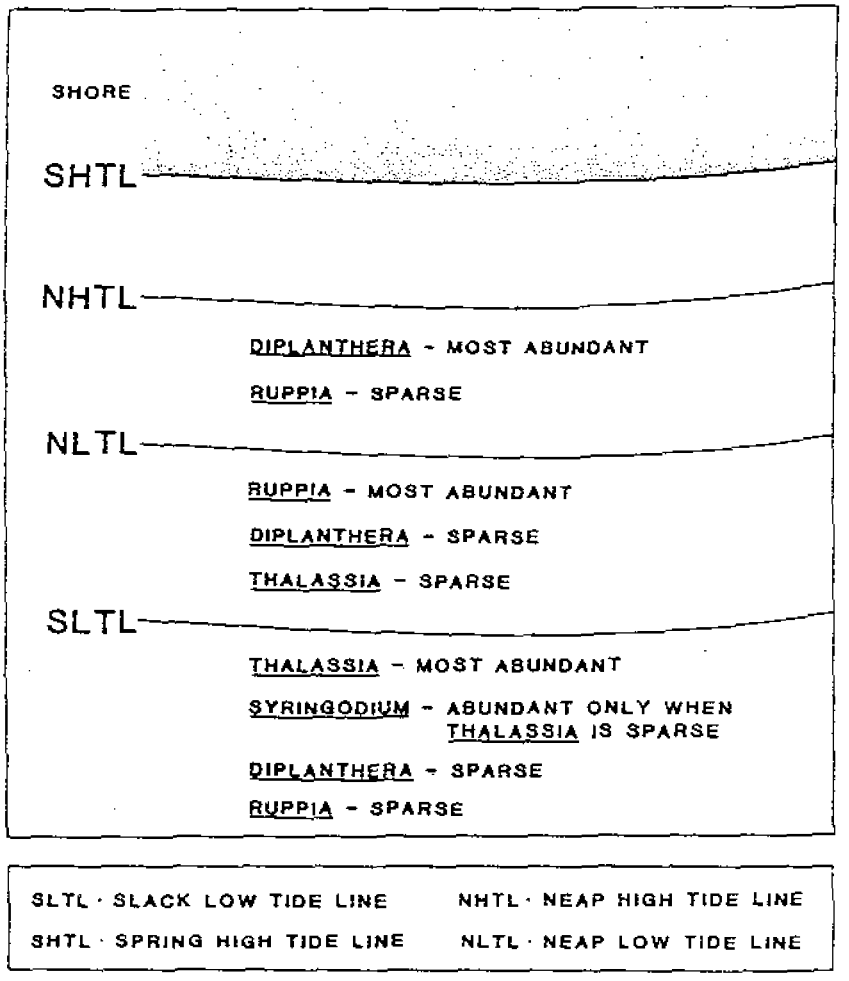

Figure 8. Schematic drawing of seagrass zonation in shallow water. Valid only in areas with salinity over 25.0 ppt. From Phillips 1960a. Diplanthera = Halodule.

Thalassia, by contrast, is relatively stenohaline (Moore 1963) and seems to be restricted to areas with salinity over 25 ppt (Phillips 1960a). Salinity also has been observed to modify the morphology and growth of this species. Phillips (1960a) reported shorter, narrower leaves at low salinities and wider, longer leaves at salinities near those of normal sea water. McMillan (1978) reported similar trends in leaf width of Thalassia cultured at 20, 25 and 30 ppt.

Halodule and Syringodium exhibit maximum growth in moderately brackish water (Phillips 1960a, 1962). Halodule is found throughout Tampa Bay while Syringodium is rarely found where salinities are below 20 ppt, reflecting the broader salinity tolerance of the former (Taylor 1973). Halophila engelmannii has been reported to require relatively high salinities (Taylor 1973), which may partially account for its low abundance in the bay.

Temperature. The distribution of marine plants is largely controlled by temperature (Earle 1972). Optimal temperatures for all 5 seagrass species in Tampa Bay range between 20-30°C (Phillips 1960a; Woodburn 1961b). Temperatures above or below this range can result in leaf damage or dieback (Phillips 1960a; McMillan 1979).

The rate of leaf growth in Thalassia seems to be controlled by water temperature, while ultimate leaf length is related to water depth (Phillips 1960a; Taylor et al. 1972; Durako and Moffler 1982). When water temperatures approach summer maxima in Tampa Bay, Thalassia leaves become soft and flaccid, then break off due to protoplasmic breakdown and accelerated bacterial activity (Phillips 1960b; Durako and Moffler unpub.) Leaf kills also occur during winter when short shoots become desiccated during the extremely low tides associated with the passage of cold fronts. Recovery is slow because the plants are relatively dormant at this time. Unfortunately, leaf growth measurements relative to water temperature are not available for the other species.

McMillan (1978) reported that narrow-leafed variants of Thalassia, Halodule and Syringodium were characteristic of shallow bays with fluctuating temperatures, while broad-leafed variants occurred in water of relatively constant temperature. Chilling tolerances of these three species were also shown to correlate with their geographic distribution; Tampa Bay populations exhibit lower chill tolerances than northern Gulf plants, but higher tolerances than Biscayne Bay or Florida Keys populations (McMillan 1978).

Water temperature is important in modifying floral expression in Thalassia (Phillips 1960a; Moffler et al. 1981; Phillips et al. 1981). Reproductive buds are present as early as October in Tampa Bay populations (Moffler and Durako unpub.) but visible buds are not evident until water temperatures start to increase in spring (May - June).

Vegetative growth, flowering and fruiting of Ruppia coincide with the rise of water temperature from winter to spring and end when high summer water temperatures begin (Phillips 1960a). Fruits seem to remain dormant until winter and germinate when water temperatures again begin to rise.

Substrate. Seagrass-substrate relationships represent a complex cyclical phenomenon. Substrate characteristics are important factors in determining which species of seagrass will be present (Phillips 1960a; Patriquin 1972; Van Breedveld 1975). The presence of a seagrass bed subsequently influences sediment dynamics (Scoffin 1970; Orth 1977; Fonseca 1981), granulometry (Grady 1981) and chemistry (Patriquin 1972; Kenworthy 1981). Sediment, detritus trapping by leaves, and the stabilization of this material by the dense rhizome-root mats are paramount in considering seagrass-substrate relationships (Phillips 1960a; Humm 1975). The mechanisms of sedimentation are related to current flow dynamics in seagrass beds and result in a characteristic bedform raised above the original sediment level (Scoffin 1970; Fonseca 1981).

Thorne (1954) reported that seagrasses in the Gulf of Mexico are limited to soft marl, mud or sand substrates. Dense Thalassia beds in Tampa Bay occur on muddy sand substrates with silt and clay fractions dominating the mud (Phillips 1960a). The substrate also contains calcium carbonate in varying amounts; this may be important in determining phosphate and sulfate availability (Patriquin 1972). The depth of rhizomes and roots in the sediments seems to depend on the depth of the redox potential discontinuity (RPD) layer, as Thalassia requires reducing conditions for normal development. This requirement is related to the nutrient requirements of Thalassia (Patriquin 1972). Anaerobic nitrogen fixation in the sediments seems to be the source of nitrogen for this species' growth. This activity has been shown to be much greater in Thalassia rhizosphere sediments than in non-rhizosphere sediments in Tampa Bay (Babiarz 1976). Fixed nitrogen is taken up in a reduced form as ammonium (Patriquin 1972) while sulfur seems to be taken up as the reduced sulfide (Fry and Parker 1982).

Halodule occurs on the same substrate types as Thalassia, as well as on extremely coarse muddy sands (Phillips 1960a; Grady 1981). However, Halodule is more prevalent on oxidized substrates. Substrate type does not seem to directly influence the distribution of Syringodium (Phillips 1960a). The depth of the RPD layer also seems inconsequential as Syringodium roots occur in both oxidized and reduced substrates (Patriquin and Knowles 1972). This ability to grow in both types of substrates reflects the intermediate successional nature of Syringodium, which is thought to follow Halodule and precede Thalassia in the temporal development of a seagrass bed.

Ruppia is found on predominately mud and silt substrates containing finer textured sand than substrates associated with the other three species (Phillips 1960a). Halophila has been observed to grow on substrates ranging from soft muddy sand (Phillips 1960a) to limestone bottoms and even the prop roots of mangroves (Earle 1972).

The predominance of fine sediments in seagrass beds indicates that once this material reaches the rhizome-root mat it is usually not easily resuspended. Transects across seagrass beds have shown that sediment sorting and mean particle size decrease and percent organic matter increases as one proceeds from bare sand to the interior of the bed (Fig. 8; Orth 1977). Water depth also decreases from fringe to mid-bed regions (Zieman 1972; Durako and Moffler 1982). Intertidal seagrass sediments have almost twice the organic and carbonate carbon content of unvegetated sand flats (Grady 1981).

Growth. It is somewhat paradoxical that rhizome branching and growth are recognized as being largely responsible for the building of seagrass meadows (Tomlinson 1974), yet most of the information on seagrass growth deals with leaf blade growth. This is due to the ease with which leaf growth can be monitored and the importance of leaves as a substrate and food for many organisms. Until recently it was not possible to directly measure growth rates for below-ground structures in a nondestructive manner. In this regard, Fuss and Kelly (1969) measured Thalassia root growth by systematically sacrificing transplants over a 12-month period and comparing root lengths to native plant samples in Boca Ciega Bay. Durako and Moffler (1981) developed a laboratory culture technique in which both leaf blade and root growth of individual Thalassia seedlings could be directly measured. Their results revealed morphogeographic variations in growth patterns for seedlings from Tampa Bay, Biscayne Bay, and the Florida Keys. Tampa Bay seedlings exhibited the lowest leaf blade and root growth rates (Tables 4 and 5), and generally had the narrowest leaf blades of the three populations under a variety of conditions. McMillan (1978) also found the same pattern for leaf blade widths and suggested that the ecoplastic limits

Table 4. Root and leaf blade growth of Thalassia testudinum seedlings in agar/seawater cultures after three months. I.O. = Instant Ocean; N.A. = nutrient agar; NH-15 = nutrient enriched seawater; M.A. = marine agar. Values represent the mean of four replicates.

	Total Root Length (cm)			Leaf Area (cm^2)		
Treatment	Tampa Bay	Biscayne Bay	Florida Keys	Tampa Bay	Biscayne Bay	Florida Keys
60 ml tubes						
NH-15/N.A.	0.95	5.65	4.03	4.32	4.03	6.42
I.O./N.A.	2.48	7.00	6.35	4.48	4.05	6.27
NH-15/M.A.	2.52	6.40	4.75	4.29	4.13	4.58
I.O./M.A.	2.75	5.52	6.00	3.63	5.20	7.00
Mean	2.18	6.14	5.37	4.18	4.35	6.04
Root #/ Seedling	2.50	3.81	2.47			
Length/root	0.87	1.61	2.21			
80 ml tubes						
I.O./N.A.	3.27	12.10	14.98	3.18	4.21	4.50

Table 5. Leaf growth rates of Thalassia testudinum seedlings in laboratory cultures. Numbers in parentheses indicate a growth index where: growth index = (mean leaf area/seedling)/(mean leaf #/seedling).

	Growth Interval (months)	Shoot Growth Rates (cm^2/mo)		
Treatment		Tampa Bay	Biscayne Bay	Florida Keys
Tube Cultures				
60 ml tubes	3	1.38	1.47	2.07
80 ml tubes	3	1.08	1.40	1.50
Pot Cultures				
Instant Ocean	5	0.72	1.04	1.78
von Stosch's	5	1.76	2.53	2.94
Peat Pellets	3	0.93 (1.70)	1.78 (2.52)	1.72 (2.80)

of populations are genetically controlled.

Several authors have measured leaf lengths of Thalassia to monitor its growth in Tampa Bay (Phillips 1960a; Taylor et al. 1973; Durako and Moffler unpub.) These measurements have revealed a bimodal seasonal growth pattern (Fig. 9). Leaf lengths increase from winter minimums to a peak in early summer. There is a summer dieback related to high water temperatures, decreasing salinity, and flowering. This is followed by an increase to a typically lower peak in early fall. Leaf lengths increase at a rate of 5 cm/month during the period of maximum growth and can reach lengths exceeding 30 cm. Taylor et al. (1973) showed that Thalassia can withstand periodic leaf cutting and harvesting without apparent damage. The authors qualified their findings, stating that they did not study the long term effects of harvesting, and suggested that this might be detrimental to both the plants and the associated communities.

Leaf growth of Thalassia near the Anclote River is lower than that in Tampa Bay, with an average growth rate of 1.3 cm/leaf/month and a maximum rate of 2.5 cm/leaf/month (Ford et al. 1974). Syringodium had higher leaf growth rates, averaging 6.7 cm/leaf/month, and a maximum rate of 17.4 cm/leaf/month during the fall. Halodule leaf growth was the highest and ranged from 12.9 to 19.5 cm/leaf/month.

Biomass and Productivity. Humm (1964) suggested that Thalassia is probably the most important plant species in the shallow marine waters of the Gulf of Mexico. In terms of biomass, Burkholder et al. (1959) estimated the standing crop of Thalassia in Puerto Rico to be 2,809 g dry weight/m^2 (g dwt/m^2), of which 23% was leaf biomass. Phillips (1960a) determined standing crop values of Thalassia blades in Boca Ciega Bay (Table 6), which ranged from 98 to 325 g dwt/m^2. However, Bauersfeld et al. (1969) reported much higher leaf values (636 g dwt/m^2) for this area. These values would more than double if roots, rhizomes and below-ground portions of shoots were included (Pomeroy 1960).

Biomass values reported for leaves of Thalassia from Tarpon Springs are higher (601-819 g dwt/m^2) than most previous studies because samples were taken in dense grass beds rather than at random (Table 6; Dawes et al. 1979). By contrast, values in Tampa Bay are much lower, ranging from 0.41-52.7 g dwt/m^2 (Heffernan and Gibson, pers. comm.) to 25-180 g dwt/m^2 (Lewis and Phillips 1980), reflecting suboptimal conditions for this species within the bay. The latter study also reported root biomass values of 600-900 g dwt/m^2 (Table 6).

Below-ground biomass exceeds shoot biomass in Halodule and Syringodium within the Bay as well (Table 6). Lewis and Phillips (1980) reported root and rhizome biomass ranges from 60-140 g dwt/m^2 for Halodule and from 160-400 g dwt/m^2 for Syringodium. The comparatively lower shoot biomass values were 38-50 g dwt/m^2 and 50-170 g dwt/m^2 respectively. These values are much higher than those reported by Heffernan and Gibson (pers. comm.), 4-27 g dwt/m^2 and 5-11 g dwt/m^2 for Halodule and Syringodium respectively. Ruppia biomass is almost equally divided between above- and below-ground structures, being approximately 48 g dwt/m^2 for each component during the spring (Lewis and Phillips 1980). Shoot biomass then decreases to almost zero in the winter while root biomass decreases to a low level of 18-20 g dwt/m^2 in the fall and levels off. The higher biomass values generally reported for Thalassia compared to the other species are a result of the larger size of all three major plant parts (Dawes and Lawrence 1980).

The productivity of seagrass systems is regarded as high for marine communities (Earle 1972). Pomeroy (1960) reported that at depths of less than 2 meters, which constituted 75% of Boca Ciega Bay, Thalassia and Syringodium leaves were as important as phytoplankton and benthic microflora in terms of primary production, fixing 500 g C/m^2/yr. Indeed, values for annual

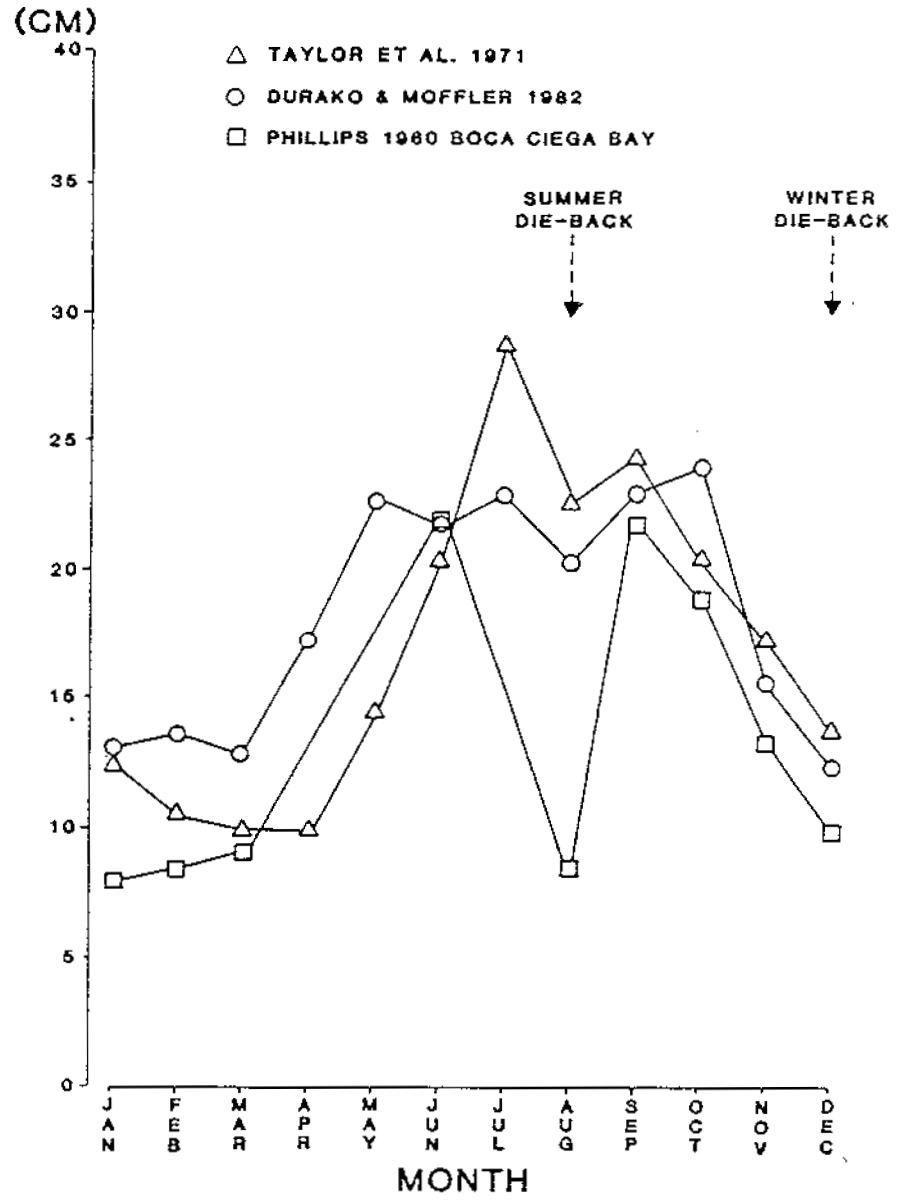

Figure 9. Monthly leaf length of Thalassia testudinum in Tampa Bay.

Table 6. Biomass values for seagrasses in the Tampa Bay area.

SPECIES	Biomass (g dwt/m^2) ABOVE-GROUND	BELOW-GROUND	REFERENCE
Thalassia testudinum			
Boca Ciega Bay	32.4	48.6	Pomeroy 1960
Bird Key	325	-	Phillips 1960a
Cat's Point	98	-	Phillips 1960a
Boca Ciega Bay	636	-	Bauersfeld 1969
	320-1,198	-	Taylor and Saloman 1968
Tarpon Springs	601-819	-	Dawes et al. 1979.
Tampa Bay	0.41-52.7	-	Heffernan and Gibson 1982
Tampa Bay	25-180	600-900	Lewis and Phillips 1980
Syringodium filiforme			
Tampa Bay	5-11	-	Heffernan and Gibson 1982
Tampa Bay	50-170	160-400	Lewis and Phillips 1980
Halodule wrightii			
Tampa Bay	4-27	-	Heffernan and Gibson 1982
Tampa Bay	38-50	60-140	Lewis and Phillips 1980
Ruppia maritima			
Tampa Bay	1.48	18-48	Lewis and Phillips 1980

production of Thalassia range from 200-4,650 g C/m^2 (Odum 1957; Phillips 1974). The higher values exceed the productivity of all agricultural crops (Odum 1959) on a m^2 basis and are also greater than phytoplankton production in upwelling areas off Peru, which are considered some of the most productive in the world (Ryther 1969). Recent work in Tampa Bay using ^{14}C techniques has estimated production rates of Thalassia, Syringodium and Halodule during the fall to be an order of magnitude higher than previously reported: 95, 72.6 and 81.2 mg C/g dwt/h respectively (Heffernan and Gibson, pers. comm.). Areal production rates were calculated to be 0.05, 0.12 and 0.05 g C/m^2/day for Thalassia, Syringodium and Halodule using the radiocarbon techniques. Production values based on leaf growth range from 2-15 mg C/m^2/h for Thalassia, from 2-37 mg C/m^2/h for Syringodium, and from 0.9-1.4 mg C/m^2/h for Halodule near the Anclote River (Ford et al. 1974; Ford and Humm 1975).

The variation in productivity levels determined using oxygen, ^{14}C and leaf growth techniques demonstrates the difficulty involved in accurately measuring this parameter in seagrasses. Storage and recycling of O_2 and CO_2 in the internal lacunar spaces of these macrophytes can cause considerable errors when measuring production rates via O_2 and ^{14}C techniques (Hartman and Brown 1967). Stapling techniques for measuring leaf growth can be traumatic to the leaf and may affect basal growth (Ford and Humm 1975). Therefore, the values obtained should be viewed as estimates of relative rates rather than as absolute values. Also, most seagrass productivity rates are expressed as per m^2 without consideration of total area and production to a system.

Chemical Composition. Because of their high productivity and organic matter production, the chemical composition of the seagrasses has been analyzed by numerous investigators (Burkholder et al. 1959; Bauersfeld et al. 1969; Walsh and Grow 1972; Dawes et al. 1979; Dawes and Lawrence 1979, 1980; Durako and Moffler unpub.) These studies have revealed the presence of annual cycles in the levels of proximate constituents. These seasonal variations in the levels and the changes in allocation of the constituents within the plants are important energetic considerations because many animal communities depend either directly on the plants or on detritus derived from them (Fenchel 1970; Buesa 1974; Greenway 1974).

The chemical composition of Thalassia has been studied in more detail than the other locally occurring species (Tables 7 and 8). Walsh and Grow (1972), and Dawes and Lawrence (1980) reported that protein levels generally are highest during the spring and late summer, while carbohydrate, ash and dry weight levels peak in the fall. Durako and Moffler (unpub.) found slightly different seasonal patterns; protein and carbohydrate levels were low in spring and highest during fall and winter. Ash levels were lowest during the fall and late winter, and highest in mid-winter and summer. Dry weight levels of shoots and rhizomes decreased during the spring, a period of high growth, and increased to high levels in late summer and early fall. Dry weight of roots decreased from a peak in the spring to fall, then increased during the winter. The importance of spatial influences on seasonal patterns of chemical constituents was also demonstrated in this study. Distinctions between fringe and mid-bed samples were significant and of sufficient magnitude to alter apparent seasonal cycles. These spatial differences may represent successional gradients in which colonization occurs on the fringe and maturity is approached in the interior of the bed.

Protein levels in Thalassia are highest in leaves, shoots and roots, reflecting biosynthetic activities. Carbohydrate levels are greatest in rhizomes, which function as storage organs (Tables 7 and 8). In this regard, leaf cropping results in decreased carbohydrate levels as the reserves are utilized in blade regeneration (Dawes et

Table 7. A comparison of proximate constituent values of Thalassia testudinum in the Tampa Bay area.

Dry weight (% fresh wt)	Ash (% dwt)	Protein (% dwt)	Carbohydrate (% dwt)	Lipid (% dwt)	Reference
Leaves					
-	24.8	13.0	35.6	0.5	Burkholder et al. 1959
8-19	46-50	9-12	38.0	0.7	Bauersfeld et al. 1969
15-20	30-40	3-12	3-12	-	Dawes et al. 1979
15-22	33-43	5-15	5-10	-	Dawes and Lawrence 1979
15-20	29-44	8-22	6-9	0.9-4	Dawes and Lawrence 1980
Short Shoots					
12-12.9	47-56	3-10	8-12	-	Dawes and Lawrence 1979
9-12	24-42	2-5	9-16	-	Durako and Moffler 1982
Rhizomes					
6	50	9.6	-	-	Bauersfeld et al. 1969
14-21	21-37	5-12	21-51	-	Dawes and Lawrence 1979
14-18	24-36	7-16	12-36	0.2-1.6	Dawes and Lawrence 1980
15-17	19-27	1-3	19-32	-	Durako and Moffler 1982
Roots					
11-15	26-36	2-5	9-16	-	Durako and Moffler 1982

Table 8. Chemical composition of Syringodium filiforme, Halodule wrightii, and Ruppia maritima in Florida.

Dry weight (% fresh wt)	Ash (% dwt)	Protein (% dwt)	Carbohydrate (% dwt)	Lipid (% dwt)	Reference
S. filiforme					
leaves:					
17-21	28-33	8-13	16-22	1.7-6.2	Dawes and Lawrence 1980
short shoots:					
13-18	27-41	10-14	13-27	0.9-3.6	
rhizomes:					
14-26	16-19	5-12	36-50	0.1-4.7	
H. wrightii					
leaves:					
16-27	25-32	14-19	13-19	1.0-3.2	Dawes and Lawrence 1980
short shoots:					
13-19	25-36	5-9	16-31	0.8-3.5	
rhizomes:					
20-30	14-22	7-9	40-54	0.1-1.6	
R. maritima					
leaves:					
-	16-24	11-26	20-28	-	Walsh and Crow 1972
rhizomes:					
19-25	19-25	11-21	40-57	-	

al. 1979; Dawes and Lawrence 1979). Protein levels are higher and ash levels lower in the regenerated blades due to the presence of new growth and the absence of epiphytes (Dawes and Lawrence 1979).

Caloric (i.e. energy) values are similar for all four species, averaging approximately 3.5 kcal/g dwt for leaves and 3.7 kcal/g dwt for rhizomes (Walsh and Grow 1972; Dawes and Lawrence 1980). These values are comparable to those of other seagrasses (McRoy 1970; Birch 1975; Harrison and Mann 1975). No seasonal patterns have been reported for energy levels, indicating that although proximate composition varies seasonally, the energy contents of the plants remain unchanged.

REPRODUCTIVE ECOLOGY

Seagrasses exhibit two modes of propagation, vegetative and sexual. Thalassia testudinum, Syringodium filiforme, Halodule wrightii and Halophila spp. are hydrophilous, producing flowers under the water surface with submarine pollination. Ruppia maritima produces flowers which anthese at the water surface and has hydroanemophilous pollination.

The majority of the past work on Florida seagrass reproductive biology has principally concerned descriptive floral morphology and anatomy (Phillips 1960a; Orput and Boral 1964; Tomlinson 1969; Tomlinson and Posluszny 1978), reproductive physiology (Marmelstein et al. 1968; McMillan 1980; Phillips et al. 1981), and seed occurrence and seed reserves (Lewis and Phillips 1981; McMillan 1981). Except for brief commentaries in Phillips' 1960 publication on seagrass ecology and distribution, research on seagrass reproductive ecology has only recently been published for Florida populations (Grey and Moffler 1978; Moffler et al. 1981; Phillips et al. 1981).

Studies on the reproductive biology of Tampa Bay seagrasses have primarily been confined to Thalassia testudinum. Phillips (1960a) did not find reproductive Halodule, Syringodium or Halophila in the Tampa Bay system. We (Moffler and Durako) have collected several male specimens of Halodule in June at Sister Key off Bunces' Pass. However, Phillips et al. (1974) and McMillan (1976) found abundant reproductive Halodule in Texas during the summer. Intensive collection efforts are needed in order to determine the reproductive dynamics of Halodule in Tampa Bay.

With regard to the other species, McMillan (1981) suggested that Syringodium filiforme floral initiation occurs during late fall or early spring in Gulf of Mexico and Caribbean populations, with fruits occurring from January through June. Although reproductive material was rare, we (Moffler, Durako and Lewis) have collected female specimens of Syringodium during May at Lassing Park and Egmont Key. McMillan (1981) speculated that the rare flowering of Gulf and Caribbean Syringodium may be related in part to nutrient conditions. He observed highest fecundity in populations in coarse sediments at St. Croix, U.S. Virgin Islands, and Texas, and lowest flowering in areas with high silt accumulations.

Although reproductive Halophila has not been found in the isolated populations of Tampa Bay, McMillan (1976) has documented extensive flowering in Redfish Bay, Texas. He indicated that a coincidence of day length, salinity and temperature were critical for reproduction.

Phillips (1960a) reported the occurrence of abundant flowering Ruppia in Tampa Bay. Flowering and fruiting typically occur in May and disappear in June in these populations. Although Phillips did not observe Ruppia seedling germination and development, he speculated that because flowers and fruits are so abundant, colonization of new areas and expansion of existing beds are quite likely. We (Moffler and Durako) have observed apparent expansion of the Ruppia population at Lassing Park, but do not have quantitative data for documentation. The growth habit of Ruppia with its

profusely branched rhizomes, and its ability to rise off the bottom toward the surface (reaching better light conditions and allowing sexual reproduction), are conducive to survival in Tampa Bay. Since Ruppia is the major component of an ephemeral meadow, areal expansion of this species in Tampa Bay may occur if seagrass meadow degradation continues.

The majority of the literature concerning seagrass reproductive biology in Tampa Bay concerns the dioecious Thalassia testudinum. Phillips (1960a) was the first to publish such information. He found flowering Thalassia on several occasions during his survey of Tampa Bay seagrasses and reported that ten percent of the plants collected in Boca Ciega Bay on May 22, 1958 were flowering. In a large grass flat off Lassing Park, he observed only a very restricted patch of flowering plants. He further pointed out that when Thalassia was in flower, only one sex was observed and no mixing of sexes occurred, which might explain the lack of fruits and seeds in this population. Phillips (1960a) was also the first to report the occurrence of Thalassia seedlings at our latitude at Anclote Key.

In 1976, Grey and Moffler (1978) conducted the first quantitative study of flowering Thalassia populations in Tampa Bay and surrounding waters. Nine sites were surveyed in the Tampa Bay area (Fig. 10); six of these were in the bay proper. Flowering occurred at all sites with females predominating over males at a ratio of 3:1. In addition, they found flowering density to vary independently of short shoot density. Patchiness in the spatial distribution of reproductive short shoots was also noted.

In January 1979, Durako collected Thalassia testudinum short shoots with immature fruits at Lassing Park (Moffler et al. 1981). The presence of fruits at this time of year represented a possible phenological inversion for this species, since fruits of this size are normally found in June. In addition to the early fruits, Moffler et al. (1981) also reported the presence of early immature reproductive buds in January. This was the first report of flower buds of Thalassia occurring in mid-winter. These early buds continued to develop and anthesis occurred during May and June, the typical time for the species.

Phillips et al. (1981) conducted a phenological investigation of Thalassia from selected sites in the western tropical Atlantic, including Tampa Bay, from February 1976 to April 1979. Based on field and laboratory studies, they indicated nearly synchronous flowering of Thalassia at different latitudes which was related to an indigenous temperature regime and natural photoperiod. They suggested that flowering was primarily related to temperature progressions following winter minima. These temperature responses may be genotypically different, thereby accounting for a nearly synchronous anthesis at different latitudes.

Work is continuing on Thalassia testudinum reproductive ecology in Tampa Bay (FDNR, Marine Research Laboratory, St. Petersburg). Investigations to date have indicated the following:

- Unpublished data collected by Moffler and Durako indicates that floral initiation in Tampa Bay populations of Thalassia may occur in late summer or early fall. Inflorescence growth is slow over winter and increases logarithmically during March and April with anthesis occurring during May and June. However, throughout this time period early developmental stages of inflorescences occur which may indicate genetic diversity for floral induction, and that T. testudinum may be a day neutral plant.

- The distribution of sexually reproductive Thalassia shoots within populations is typically patchy or clustered. The Lassing Park population, however, has one of the highest percentages of reproductive short shoot density reported for this species (average 23.05%, range 0-92.31%). One of the Lassing Park

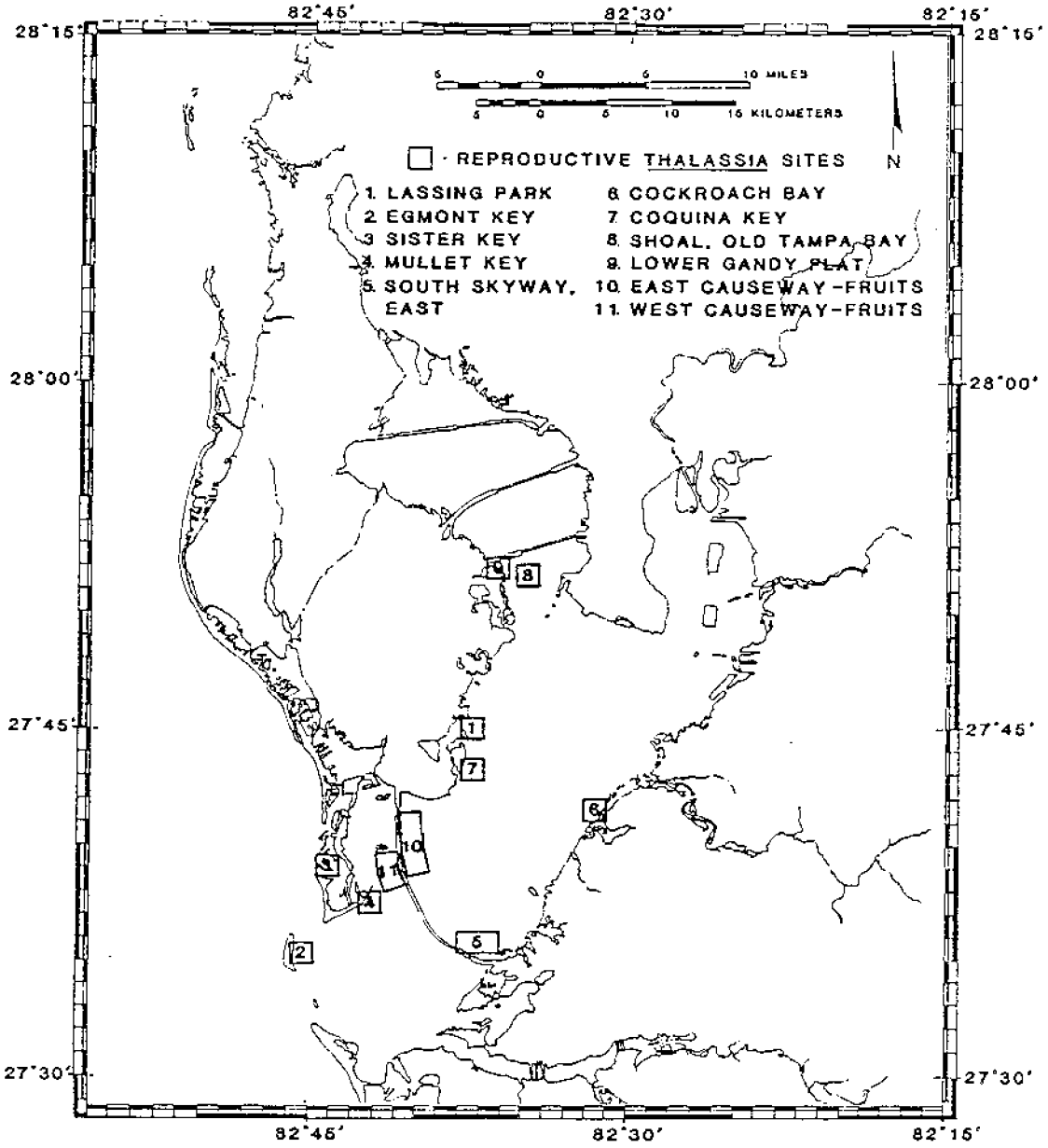

Figure 10. Reproductive Thalassia sites in Tampa Bay.

Thalassia meadows studied (circular bed) was comprised of all female shoots, while surrounding Thalassia beds contained both males and females. Yet, a puzzling phenomenon at the Lassing Park site is the lack of fruit and seed production. When looking at percentages of male and female short shoots in anthesis over time we find females in anthesis first, followed by male anthesis. Percentage of females and males in anthesis peaks at the same time and females are in anthesis past the time of male anthesis; therefore, there should be ample opportunity for pollination and fertilization to occur. The seagrass meadows at Lassing Park are shallow and during low tides water temperature becomes high (35°C). These conditions may inactivate the pollination process or possibly lead to fruit abortion due to pathogens; a high percentage of decaying inflorescences has been observed. It is unclear, however, whether decay is a cause or effect phenomenon. On the other hand, Egmont Key populations complete their reproductive cycle and produce viable seed. This population is at a site with good flushing and more stable temperatures and salinity, with perhaps less opportunity for disease.

Thalassia testudinum seed production in Tampa Bay is apparently confined to areas south and west of Pinellas Point. Fruits have been collected in the beach wrack along the Skyway causeway, Mullet Key and Egmont Key. Large numbers of fruits have never been found during the last 5 years of collecting in these areas; typically less than 100 fruit (200-300 seed) are collected in any one year. Seed production in Tampa Bay is apparently quite low compared to that in Biscayne Bay and the Keys (Lewis and Phillips 1981). It appears that quantities are insufficient for restoration efforts.

Further research is needed on seagrass reproductive biology and ecology in Tampa Bay. Information on the role of sexual reproduction in seagrass population maintenance and distribution is critical. These studies should include reproductive phenology and the role of seed reserves. In addition to furthering our knowledge of the reproductive dynamics of Thalassia, information on the reproductive biology and ecology of the other seagrass species is enthusiastically encouraged.

MANAGEMENT PROBLEMS

Documentation of Functional Role. The functional role of seagrass meadows in the Tampa Bay ecosystem is essentially unknown. From 12 box cores taken at four stations (three with seagrass) in Boca Ciega Bay in August 1964 (Taylor and Saloman 1968), infaunal biomass (excluding large molluscs and crustaceans) was estimated to be 137 g/m^2 (dry weight) for well-vegetated bottoms in comparison to 12 g/m^2 for the three replicates taken in an unvegetated area. Sieve size for these samples was 0.701 mm. Santos and Simon (1974) sampled quarterly for one year in a seagrass meadow and adjacent sand areas and found the greatest density of polychaetes (mean = 33,485/m^2) at the Thalassia stations, second highest at the inshore sand stations (mean = 17,220/m^2) and third highest at the Halodule stations (mean = 13,313 g/m^2). The two sets of offshore sand zone stations had much lower densities (means of 4,934 g/m^2 and 3,231 g/m^2). It is quite probable that the high densities at the inshore sand station were due to the seagrass and algal wrack decomposing along the shore and providing a rich detrital food source not available at the two offshore sand stations.

Routine fish sampling in Tampa Bay (Springer and Woodburn 1960; Springer 1961) has resulted in the identification of 271 species. Springer and Woodburn (1960, p. 97) noted that:

> The characteristic ecological features of the shallow bay habitats we studied are the presence of heavy bottom vegetation (seagrass and algae) and moderately high and stable salinities ... The fish fauna decreases also in

numbers and species with the change from summer to winter. The decrease is probably associated as closely with the decrease in flora as temperature, for even in summer the areas over the sandy bottoms contain few fish. The majority of the fish present are either young or small; the adults of most species eluded capture with the equipment used.

Individual species accounts in the same reference indicate the importance of seagrass habitat to certain species. Regarding the sheepshead, Archosargus probatocephalus (Walbaum), "we found them (young to about 50 mm) primarily in Diplanthera (Halodule) beds" (p. 64); the speckled trout, Cynoscion nebulosus (Cuvier), "spends most of its life over the grass flats ... juvenile stomach contents were comprised mainly of crustaceans: mysids, copepods, and especially caridean shrimp" (p. 52); and the pinfish (Lagodon rhomboides L.), "one of the most ubiquitous and plentiful species in the Tampa Bay area ..." (p. 65), they noted was very abundant in seagrass meadows. This species is noted as an important item in the diet of larger predatory fishes such as snook.

Unfortunately, beyond these few studies there have been essentially no quantitative faunal collections in seagrass meadows in Tampa Bay. Work in other parts of Florida (Carr and Adams 1973; Stoner 1979; Zimmerman et al. 1979; Gore et al. 1981; Greening and Livinston 1982; Zieman 1982) has shown the value of seagrass meadows and their associated invertebrate and fish communities; such data is vital to more fully understand the functional role of seagrasses in Tampa Bay.

Current Status. As indicated previously, large declines in seagrasses have occurred in Tampa Bay. Vital questions presently unanswered are the reasons for these losses (beyond actual burial or excavation), and whether they are continuing.

Concerning the first question, a number of hypotheses have been generated. These include biocide accumulations, stingray or manatee feeding damage, erosion due to increased boat wakes, and reduction in downwelling light reaching seagrass leaves due to phytoplankton, algal blooms, and turbidity. Figure 11 shows the relative chlorophyll a concentrations for the major subunits of Tampa Bay measured monthly between 1972 and 1981. It is apparent that there is an order of magnitude difference between those areas at the mouth of Tampa Bay (2-3 mg/l) and Hillsborough Bay (20-30 mg/l). Hillsborough Bay has historically received large amounts of treated and untreated sewage and urban runoff, and presently supports no perennial seagrass meadows. Only scattered ephemeral beds of Ruppia are found there. The lower portions of Tampa Bay, with lower average chlorophyll a levels, presently do support relatively healthy seagrass meadows. In addition, massive blooms of marine macroalgae were documented in the mid-1960s (FWPCA 1969) in Hillsborough Bay and continue to reappear (Lewis et al., in press). These were attributed to high nutrient (nitrogen, phosphorus) levels due to minimal sewage treatment in the 1950s and 1960s, but more advanced sewage treatment begun in 1978 has not apparently reduced the incidence of algal blooms. Competition among several groups of primary producers (microalgae, macroalgae, and seagrasses) has been documented to result in declines in seagrasses in favor of microalgae in the form of phytoplankton or epiphytic algae on seagrass blades (Sand-Jensen 1977; Cambridge 1979).

However, most of the work on eutrophication and the resulting changes in aquatic plant communities has been done on freshwater systems (Davis and Brinson 1980; Spence 1982) and thus much remains to be learned about these problems in marine ecosystems. Guist and Humm (1976, p. 270) reported that the macroalgae Ulva lactuca L., from Tampa Bay, grew progressively faster in increasing concentrations of sewage effluent and noted that as the water temperature rises, "Ulva growth slows

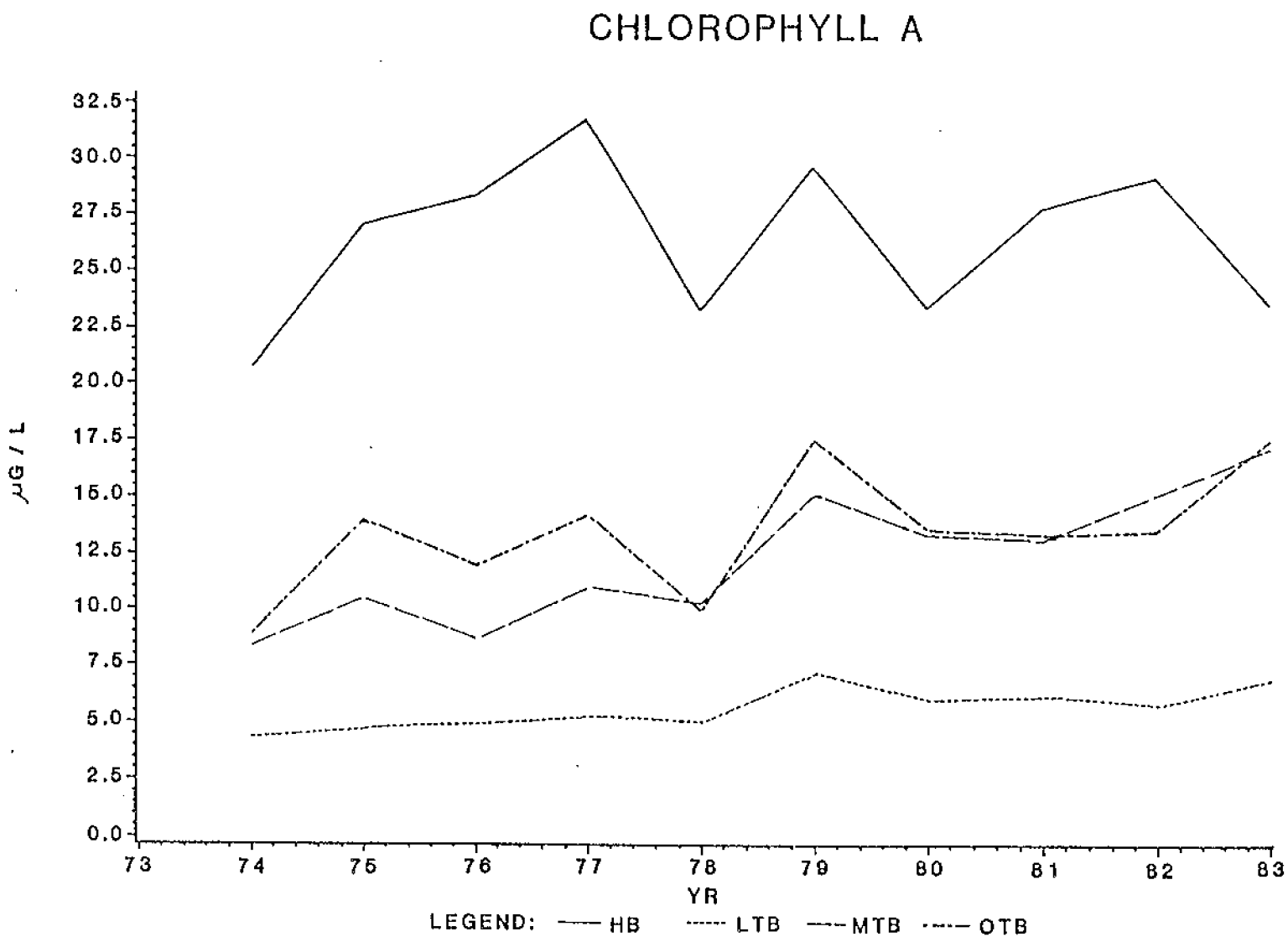

Figure 11. Chlorophyll a concentrations in major portions of Tampa Bay. HB - Hillsborough Bay; LTB - Lower Tampa Bay; MTB - MiddleTampa Bay; OTB - Old Tampa Bay.

and loose masses ... are widely distributed by tidal currents ... these masses remain over seagrass beds long enough to kill seagrass beneath them ... sheets of Ulva up to 10 ft in diameter will develop in early spring."

In light of the lack of research on other factors, progressive eutrophication and reduction in downwelling light reaching seagrass meadows due to absorption by more abundant micro- and macroalgae appears to be the most viable hypothesis concerning declines in seagrasses in Tampa Bay. Research on the other hypotheses should be conducted, but only after the questions of the role of nutrients and algae in Tampa Bay and the contribution of algal by-products and resuspended sediments to "turbidity" are answered.

Concerning the second question, regular monitoring (at least every two years) of the areal extent of seagrass meadows in Tampa Bay should be conducted to determine if their decline is continuing. Thompson (1981) noted the continuing disappearance of meadows of Syringodium in upper middle Tampa Bay in 1979-80. This is not an encouraging sign, particularly since a monitoring program conducted by the U.S. Army Corps of Engineers (Jacksonville District) designed to detect such losses failed to document their disappearance.

Potential for Restoration. Techniques for the replanting of seagrass meadows damaged or eliminated by man's activities have been investigated for 35 years (Phillips 1982). Twelve species of seagrass around the world have been tested for their suitability in restoration projects. Some success has been achieved using the three dominant species in Tampa Bay: T. testudinum, H. wrightii, S. filiforme (Phillips and Lewis, in press). Small scale experimental work on seagrass transplantation has been conducted by a number of researchers in Tampa Bay since 1968 but no large scale attempts to restore significant areas of seagrass in Tampa Bay have been attempted. The reasons for this are twofold. First, no program or agency has any responsibility for "restoring" lost habitat in Tampa Bay and thus no funds are available presently for such work. Secondly, because of the previously discussed problems of water quality degradation, it is not possible to presently identify, with any confidence, areas of barren bay bottom that might now support seagrass meadows. Obviously, if downwelling light has been reduced to the point that seagrasses disappeared and light levels remain low, then it would be a waste of time to try and replant seagrasses in those areas.

On the other hand, due to the low level of successful sexual reproduction of seagrasses in Tampa Bay, few seeds are produced to recolonize barren bay bottoms if downwelling light levels have improved. For this reason, it is recommended that restoration plantings using the latest technological advances in this field be employed to install test plantings along a gradient from relatively clean water at the mouth of the bay to more polluted areas in or near Hillsborough Bay. Such a gradient of installations, properly monitored, could relatively quickly indicate the potential for restoring seagrass meadows in Tampa Bay through active planting efforts.

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