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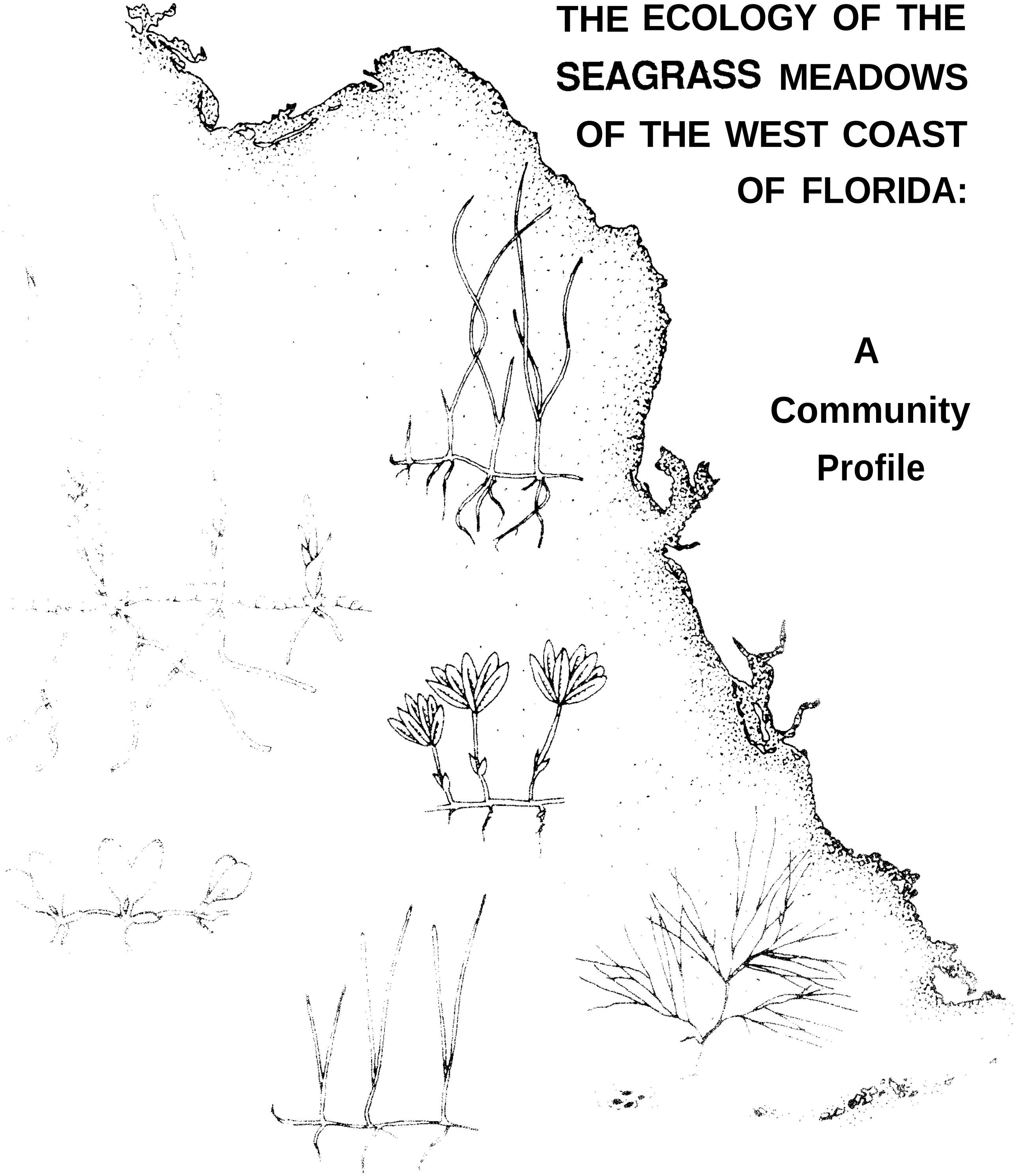
A Community Profile



Minerals Management Service
and
Fish and Wildlife Service

U.S. Department of the Interior

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THE ECOLOGY OF THE SEAGRASS MEADOWS OF THE WEST COAST OF FLORIDA: A COMMUNITY PROFILE

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PREFACE

Seagrass beds have come to be known as extremely productive and valuable coastal wetland resources. They are critical nursery areas for a number of fish, shrimp, and crab species, and support the adults of these and other species that forage around seagrass beds, preying on the rich and varied fauna that occur in these habitats. Seagrass beds support several endangered and threatened species, including sea turtles and manatees along the west coast of Florida, the geographic area covered in this profile.

For these reasons and others, seagrass beds or meadows have been the topic of several of the reports in this community profile series. This report, covering the seagrass community of the Florida Gulf of Mexico coastline from south of Tampa Bay to Pensacola, is the fifth community profile to deal with submerged aquatic vegetation beds; others in the series have synthesized ecologic data on seagrasses of south Florida, eelgrass beds in the Pacific Northwest and along the Atlantic coast, and kelp forests of the central California coastline.

These reports in total represent a major effort toward summarizing and synthesizing what is known of the ecologic structure, functioning, and values of these marine and estuarine communities. This profile in particular builds on the author's earlier profile on the seagrass meadows of south Florida. As will become apparent to the reader, while enough is known to describe the gulf coast seagrass community, there has been little study of the finer points of the structure and function of seagrass beds in this region. To shed light on the ecology of *Thalassia*, *Syringodium*, and *Halodule* meadows on Florida's gulf coast, one is forced to extrapolate a good deal from information from studies conducted on the south and southeast Florida coasts and elsewhere. However, in so doing the author has been able to update his own earlier community profile. Thus, The *Ecology of the Seagrass Meadows of the West Coast of Florida* is not only a synthesis of the topic, but also serves as a state-of-the-art review of subtropical seagrass ecology and a companion volume to *The Ecology of the Seagrasses of South Florida* (Zieman 1982). As with most of the reports in this series, the profile finally highlights how much is still left to learn about these valuable natural habitats.

CONVERSION FACTORS

Metric to U.S. Customary

Multiply	***By***	***To Obtain***
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km’)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (“F)	0.5556 (°F - 32)	Celsius degrees

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The production of this manuscript turned into a much larger project than was envisioned when we began. During that time, many people contributed greatly towards the production of the final product. The authors are especially grateful to Richard L. Iverson who contributed both written material and numerous published and unpublished figures for Chapters 2 and 3.

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Sue Lauritzen did the layout and Daisy Singleton and Joyce Rodberg keyboarded the final draft.

CHAPTER 1. INTRODUCTION

1.1 SEAGRASS ECOSYSTEMS

Seagrass meadows are recognized today as one of the most important communities in shallow coastal waters. Rapidly growing seagrass leaves serve as the basis of a productive grazing and detrital food web, while the canopy structure formed by these leaves offers shelter and protection from predation for innumerable small organisms, many of which are the juveniles of important commercial species. The coastal waters of Florida are especially rich in seagrass resources. The two largest seagrass meadows in Florida have received little human disturbance thus far. The largest, in Florida Bay, is approximately 5,500 km^2, and is protected from large-scale human impact because it is mostly within the boundaries of Everglades National Park. The second largest bed is just off the northwest coast of Florida, between Tarpon Springs and St. Marks, and is approximately 3,000 km^2 (Iverson and Bittaker 1986). Other seagrass meadows, especially those within urbanized estuaries, have not fared as well. Lewis et al. (1985a) found that in 1982, Tampa Bay contained 5,750 ha of seagrass cover. From old maps and aerial photographs they estimated the historical coverage to be nearly 31,000 ha, thus showing a reduction to less than 20% of the historical coverage.

The coastline of western Florida is a major ecocline for the tropical seagrass species. Although the distance is not great, about 650 km from Florida Bay to Apalachicola Bay, it represents a shift from a region in the south where tropical seagrasses reach their highest development, to areas that are the northern limits of distribution for several of the species, notably Thalassia and Syringodium. While this report addresses the west and northwest coast of Florida, the area of central interest for this community profile is the region from Tampa Bay to Apalachicola Bay (Figure 1). This region contains the large offshore beds of the Big Bend area, as well as several representative estuarine systems. It is largely defined by the available data base for the Florida west coast.

Compared with seagrass meadows in southern Florida, communities of western Florida and the northeastern Gulf of Mexico have received little attention from the research community; therefore, this community profile will refer to data from south Florida and the Caribbean when

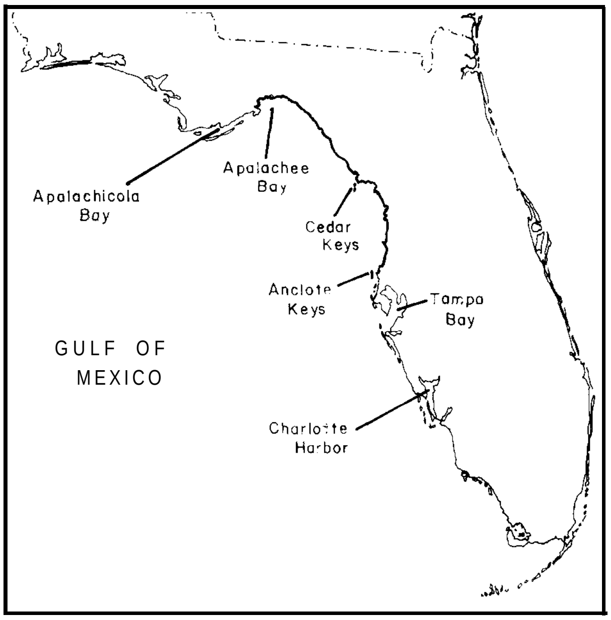


Figure 1. Location map of Florida.

comparable studies from western Florida do not exist. Interestingly, the west coast area was the location of the seminal seagrass studies of Florida, in particular, and the Southeast, in general. This work culminated in the monograph on the seagrasses of Florida by Ronald C. Phillips published in 1960. Within the past 10 years, research on these systems has accelerated in the bays and estuaries of north Florida and in central Florida; however, less work has been done on the large offshore bed between these two regions. This extensive seagrass meadow is unique among Florida's seagrass resources since it is truly offshore, and does not lie behind any form of protective barrier.

Seagrass ecosystems are among the richest, most productive, and most important of all coastal systems. They are also paradoxical in nature--simultaneously simple and complex. They are simple in that there are few species of seagrasses, unique marine angiosperms that live and carry out their life cycle in seawater. Vast and extensive undersea meadows stretching for hundreds of kilometers may be composed of only one to perhaps four species. The ecosystems, however, are complex because there are hundreds to thousands of species of associated flora and fauna that inhabit the seagrass meadows and utilize the food, substrate, and shelter provided by the plants.

The pioneering work of Petersen (1918) in the Baltic region provided the first documentation of the value of seagrass beds to shallow coastal ecosystems. These studies demonstrated how the primary production from these plants was channeled through the detrital food web and supported the rich commercial fisheries of the region. Despite the thoroughness and quality of Petersen's work, only in the past two decades have the richness and value of seagrass ecosystems begun to be realized (Wood et al. 1969; McRoy and McMillan 1977; Zieman and Wetzel 1980). The first conceptualization of the functions of seagrasses was provided by Wood et al. (1969). The generalizations have now been shown to be applicable to a wide variety of systems and situations. The following is an updated version (Zieman 1982) of the earlier conceptual framework.

1. <u>High Production and Growth</u>
   The ability of seagrasses to exert a major influence on the marine seascape is due in large part to their extremely rapid growth and high net productivity. The leaves grow at rates of typically 5 mm per day, but growth rates of over 10 mm per day are not uncommon under favorable circumstances.

2. <u>Food and Feeding Pathways</u>
   The photosynthetically fixed energy from the seagrasses may follow two general pathways: direct grazing of organisms on the living plant material or utilization of detritus from decaying seagrass material, primarily leaves. The export of seagrass material, both living and detrital, to a location some distance from the seagrass bed allows for further distribution of energy away from its original source.

3. <u>Shelter</u>
   Seagrass beds serve as a nursery ground, that is, a place of both food and shelter, for the juveniles of a variety of finfish and shellfish of commercial and sportfishing importance.

4. <u>Habitat Stabilization</u>
   Seagrasses stabilize the sediments in two ways: the leaves slow and retard current flow to reduce water velocity near the sediment-water interface, which promotes sedimentation of particles as well as inhibiting resuspension of both organic and inorganic material. Secondly, roots and rhizomes form a complex, interlocking matrix with which to bind the sediment and retard erosion.

5. <u>Nutrient Effects</u>
   The production of detritus and the promotion of sedimentation by the leaves of seagrasses provide organic matter for the sediments and maintain an active environment for nutrient recycling. Epiphytic algae on the leaves of seagrasses have been shown

to fix nitrogen, thus adding to the nutrient pool of the region. In addition, seagrasses have been shown to take up nutrients from the sediments, transporting them through the plant and releasing the nutrients into the water column through the leaves, thus acting as a nutrient pump.

In addition to providing habitat and shelter, the seagrass leaves are a major food resource in coastal ecosystems, functioning through three major pathways: direct herbivory, detrital food webs, and export to adjacent ecosystems. Direct herbivory on green seagrass leaves is confined to a small number of species and is most prevalent in tropical and subtropical regions, especially in the vicinity of coral reefs. Since the time of Petersen (1918), the detrital food web has been considered the main trophic pathway in seagrass meadows, and current studies continue to support this concept, although direct herbivory can be locally important in some areas (Zieman et al. 1984a; Thayer et al. 1984). In addition to the internal utilization of seagrasses as a food source, many beds, especially those dominated by *Syringodium*, export large quantities of organic material to other distant ecosystems.

In the subtropical waters of south Florida, seagrass meadows often bridge large areas between the mangrove and coral reef communities, while also serving as a primary nursery and feeding ground themselves (Zieman 1982). On the west coast of Florida, they function in a similar manner, as nurseries and feeding grounds, but also serve as an interface between the coastal salt marsh communities and offshore habitats of the eastern Gulf of Mexico.

1.2 THE SEAGRASSES OF THE WEST COAST OF FLORIDA

Seagrasses compose the relatively small group of monocots which have evolved the ability to carry out their life cycle completely submerged in the marine environment. Worldwide, they include 2 families divided into 12 genera and approximately 45 species. The Potamogetonaceae include 9 genera and 34 species and are represented on the west coast of Florida by *Syringodium filiforme* Kutz, whose common name is manatee grass, and *Halodule wrightii* Ascherson, shoal grass; the Hydrocharitaceae contains 3 genera with 11 species (Phillips 1978), of which *Thalassia* testudinum Konig, (turtle grass), and two species of *Halophila*, *H. engelmanni* Acherson and *H. decipiens* Ostenfeld, are found in the waters of the west coast of Florida. *Ruppia* maritima Linneaus (widgeon or ditch grass) euryhaline angiosperm found abundantly in fresh waters and in the marine environment grows primarily in lower salinity areas.

The small number of species occurring in these waters, and their distinctive gross morphologies (Figure 2) preclude the need for a dichotomous key, although systematic works such as den Hartog (1970) and Tomlinson (1980) are available for comparison of seagrasses in other areas. Phillips (1960a) still provides the best treatment of local species.

The three dominant species of the open coastal waters are *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*.

Thalassia is the largest and most robust of the west Florida seaarasses. and the densest growth in the vast" grassded of the Big Bend area is dominated by a mixture of this species and *Syringodium* (Iverson and Bittaker 1986). While this species is not abundant in the lower salinity waters of Tampa Bay (Lewis et al. 1985a), it is the dominant seagrass in the adjacent waters of Boca Ciega Bay (Taylor and Saloman 1968; Bauersfeld et al. 1969), and in the Tarpon Springs area (Phillips 1960a).

Among the local seagrasses, *Syringodium* is distinctive in having cylindrical leaves which are quite brittle and buoyant, and thus are readily broken off and exported from the immediate area by winds and currents. This species is more widely distributed in Tampa Bay than is *Thalassia* (Phillips 1960a; Lewis et al. 1985a), and while it is codominant in the Big Bend grassbed, its biomass is generally lower than that of *Thalassia* in the mixed stands of that area, although

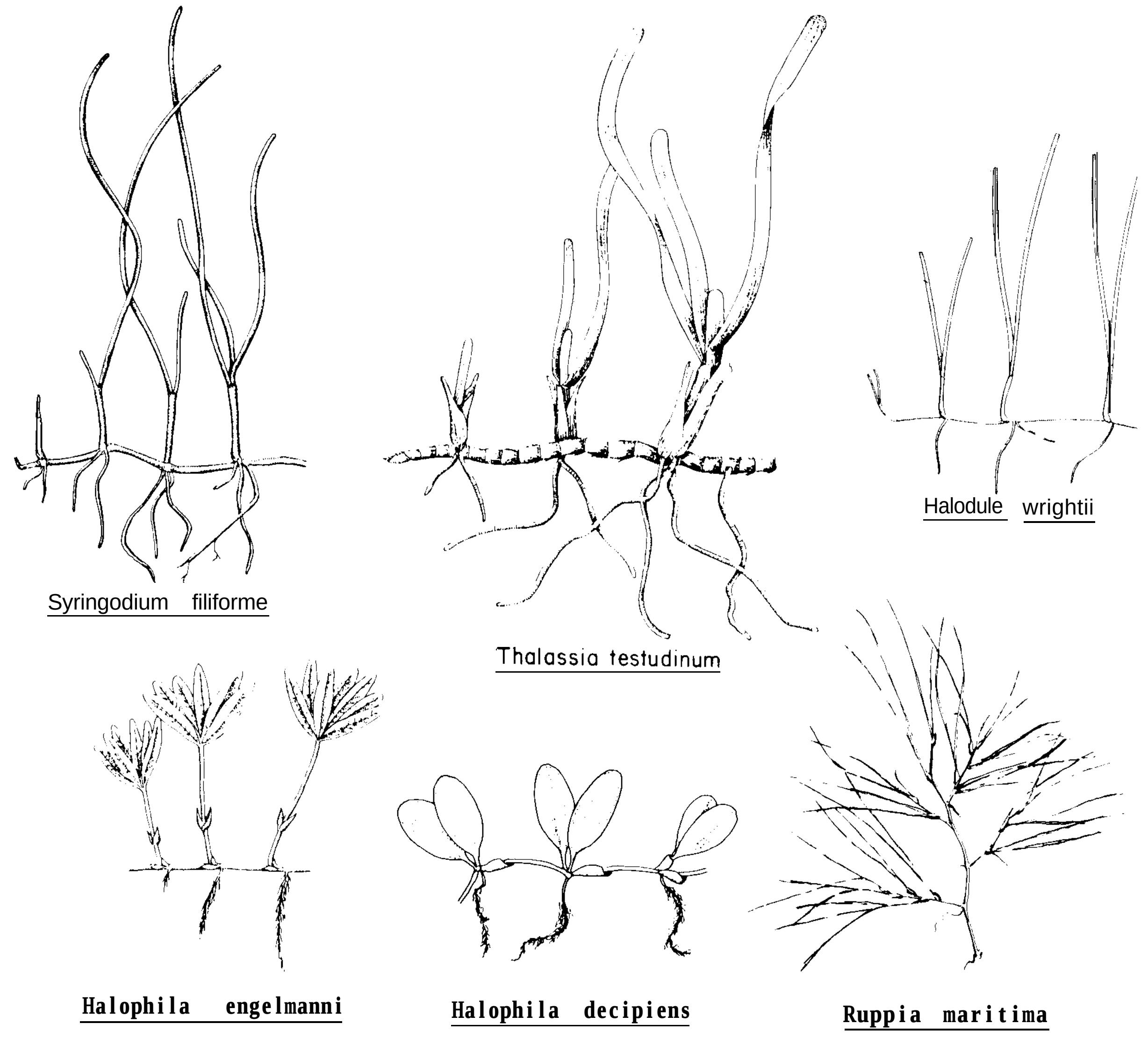


Figure 2. The seagrasses of the west Florida coast.

there are localized areas where it is abundant.

Halodule, which has narrow leaves and a shallow root system, is recognized as the pioneer species in the successional development of grassbeds in the gulf and Caribbean. It is more tolerant of low salinity than both Thalassia and Syringodium, and thus occurs in areas of Tampa Bay where those seagrasses cannot survive (Phillips 1960a; Lewis et al. 1985a). As its common name, shoal grass, indicates, it is often found in shallow waters where it is subjected to repeated exposure to the atmosphere. In the Big Bend grassbed, this plant often forms both the shallowest shoreward fringe of and the deepest, outermost stands of seagrass, and exhibits different morphologies in the two zones (Phillips 1960b; McMillan 1978; R.L. Iverson, unpubl. data).

1.3 PHYSICAL ENVIRONMENT

The west coast of Florida has a mild maritime climate varying from temperate in the north to semitropical in the southernmost regions. For much of the year the southern portion of Florida is dominated by the southeasterly trade winds, while the airflow in the northern and central portion is from the west, under the influence of the westerlies and accompanying cyclones (counterclockwise circulation about a center of low pressure) in the winter, and the western margin of the Bermuda-Azores anticyclone (clockwise circulation about a center of high pressure) in summer.

The resulting differences in temperature patterns are evident in Figure 3, which shows the average monthly water temperatures at several locations from Pensacola to Key West (McNulty et al. 1972). The Cedar Key station is in the center of the region under consideration here. Both the average and maximum summer temperatures vary little among the stations, with highs around 33 °C. Most obvious are the lower winter temperatures and greater seasonal range at the northern stations. Key West has a monthly low average of 22 °C and a range of 14-26 °C during January, while Cedar Key has a January average temperature of 13.5 °C with a range of 4-22 °C.

Earle (1969) found a similar pattern with inshore gulf temperatures of 13-15 °C in the north and 22.6-22.9 °C in the Florida Keys. However, north of Cedar Key, extreme winter lows of 0-5 °C have been recorded. The average winter temperatures in the northern gulf in winter are similar to the summer high temperatures in New England, and Earle (1969) noted that many winter species in the northern gulf are the same as the summer species in New England waters.

Precipitation generally increases northward and westward along the Florida coast from a low of 100 cm annually at Key West to 163 cm at Pensacola (Table 1). However, in the region from Tampa to Apalachicola the precipitation is relatively uniform with a minimum annually of 118 cm at Cedar Key to a maximum of 140 cm at Apalachicola with about half of the annual amount falling between June and September. The average annual and monthly

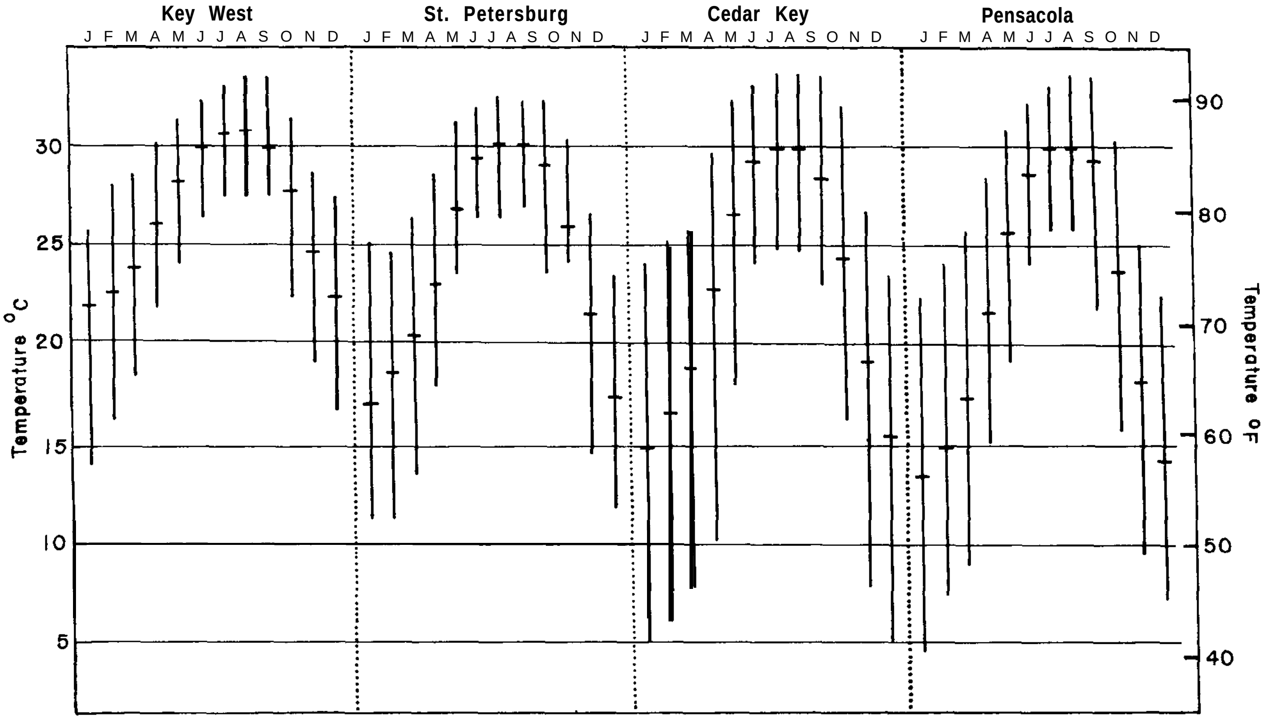


Figure 3. Temperatures at four locations in coastal Florida (from McNulty et al 1972).

Table 1. Precipitation statistics for coastal stations on the eastern Gulf of Mexico (from Jordan 1973).

	Precipitation, Mean Annual (inches)	Precipitation, June-Sept. (%)	Precipitation, Dec.-March (%)
Mobile	65.5	41.4	34.9
Pensacola	63.4	43.3	30.0
Apalachicola	56.2	52.5	25.8
Tallahassee	56.9	47.5	28.5
Cedar Key	46.6	55.9	23.8
Tampa	51.6	60.2	20.6
Fort Meyers	53.3	63.6	14.3
Everglades	54.7	62.5	12.4
Key West	40.0	48.0	17.4

rates show the general patterns, but the extreme months and years are highly variable and can have severe effects on the local biota. For Cedar Key, annual rainfall has varied between 68-208 cm, while monthly values at Apalachicola have varied from a low of 0.03 cm to a high of 57 cm.

In the shallow waters of the estuaries and the inshore gulf, water temperature and salinity are locally affected by both seasonal and isolated storms. The most severe storms are tropical hurricanes with their high winds, heavy rainfall, and often devastating storm surges. Hurricanes occur most frequently in the late summer months when the oceanic surface temperatures are at their highest, but can occur in any month. The probability of encountering hurricane force winds in any one year varies greatly along the Florida coast, being 1 in 8 at Key West and Pensacola, 1 in 17 at Apalachicola and St. Marks, and 1 in 25 at Tampa-St. Petersburg (Bradley 1972). In addition to the immediate local effects of these storms, water quality is affected following their passage by greatly increased runoff from rivers and streams, accompanied by increased turbidity and biochemical oxygen demand.

In most locations, seagrass beds are relatively protected from the surges of large storms. However, in the Big Bend of Florida these beds are subject to the full force of storm waves. In 1985, two hurricanes, "Kate" and "Elena" passed directly through the area causing localized disruption and bottom scouring. Qualitative observations of stations sampled before and after the hurricanes suqqested complete recovery of the denser inshore beds' of Thalassia, Syringodium, and Halodule and the sparse offshore Halophila beds in the vicinity of Tarpon Springs (Continental Shelf Associates 1986). In the vicinity of Cedar Key, where Hurricane "Elena" stalled for about 48 hours, seagrasses appeared to be recovering, but at a slower rate than the other site.

Tidal ranges are low to moderate along most of the Florida west coast. From Florida Bay northward to St. Joseph Bay the tides are predominately semi-diurnal (McNulty et al. 1972), shifting to diurnal west of this point. Throughout the entire area, the mean diurnal range is 0.5-1.1 m. Daily ranges at Tampa Bay are 0.6-0.8 m. Just north of Tampa Bay, the range increases to 1.1 m until Apalachee Bay where it begins to decrease slightly and reaches 0.4-0.7 m at Apalachicola Bay.

Offshore circulation is dominated by two large counter-rotating gyres. The northern one is influenced by coastal estuarine waters, while the southern one is influenced by waters from Florida Bay. In addition, there are periodic incursions of the loop current with waters from the tropical Caribbean and the Yucutan Channel (Chew 1955; Austin 1970).

1.4 GEOLOGIC ENVIRONMENT

The present Florida peninsula is the emergent portion of the Floridan Plateau, consisting of layers of limestone and unconsolidated sediments over a base of sandstone and volcanic rocks (Puri and Vernon 1959; NcNulty et al. 1972). The limestone and ancient sediments are at least 1,000 m in thickness over the entire region. The rivers that. enter the gulf east of Apalachicola Bay drain the coastal plain, carrying small amounts of sediments that are primarily carbonates and anhydrites (McNulty et al. 1972). From Apalachicola Bay westward, the rivers drain areas of the piedmont plateau and the Appalachian highlands, and carry primarily clastic sediments. Table 2 gives the characteristics of sediments for several locations on the west Florida coast.

The coastline of west Florida has been divided and classified (Figure 4) according to several different criteria and schemes, including coastal beach and interface characteristics (Price 1954; Tanner 1960; McNulty et al. 1972), faunal community affinities (Lyons and Collard 1974), and underlying substrates and outcrops (Brooks 1973). The coastal divisions resulting from these differing schemes are very highly correlated, and the divisions used in this paper are a combination of the above schemes.

The coastline west of Lighthouse Point, near Apalachicola Bay, is the northern gulf barrier coastline, with attached sand

Table 2. Sediment characteristics of the west Florida coast (from Folger 1972).

Location	Organic content	Carbonate content	Texture
Florida Bay	Average = 2.1% west	up to 90% (Quartz 3.5% east, up to 30%)	Median size east = 0.025mm west = 0.028mm W = 70% silt, 30% sand
Whitewater Bay		Up to 65% (quartz 5%-10%)	
Gullivan Bay (very open)	1% on shelf 1%-4% in lagoon	10%-40% typically Locally to 60%-80% Quartz 4%-8% near islands maximum = 24%	Non $CaCO_3$ = fine to very fine sand
Port Charlotte Harbor	0.1%-1.0% maximum = 3.1%	--	Very fine to fine sand
Tampa Bay		0.5%-40%	Variable, typically sand sized
Apalachicola Bay	0.5%-2.0%	10%-40%	Variable, very coarse sand to clay
St. Joseph Bay	0.5%-4.5%	10%-80%	Variable, very coarse sand and gravel to clay
Pensacola Bay	—	1.3%-5%	Coarse sand to silt

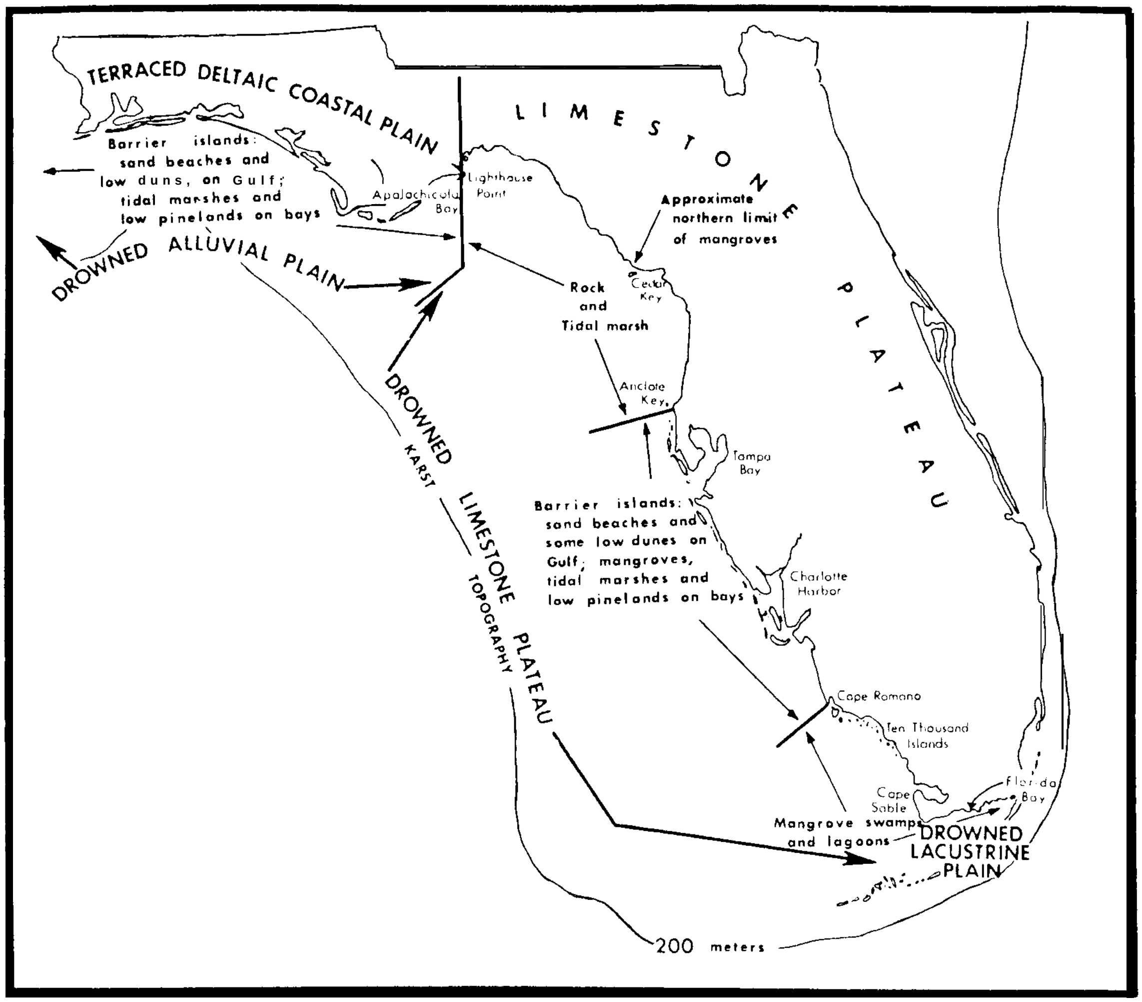


Figure4. Coastalgeologyof the Florida west coast (from McNulty et al. 1972).

beaches alternating with barrier islands. A similar attached beach-barrier island interface exists from Anclote Key southward along the western edge of the central and lower Florida peninsula. Along both the northern gulf and the central and lower peninsula, the barrier beaches and spits enclose the major estuaries and lagoons. However, the Big Bend, the upper coastline of the peninsula, is unique for the region in that it is an extensive area with no offshore barrier, where rivers, creeks, and marshes grade directly into the eastern Gulf of Mexico. A number of physical, geological, and hydrological features interact to produce this effect. The rivers of the Big Bend are notable in that they carry little suspended clastic material to form beaches or barrier islands (Ross 1973) such as those found to the south or to the west.

Of equal or greater importance is that the region between St. Marks and Tarpon Springs is one of the few examples world-wide of a zero-energy coastline (Murali 1982). This is defined as a coast where "the average breaker heights are 3-4 cm or less, and there is no significant littoral transport of sand" (Murali 1982). The major factors that contribute to this phenomenon include the wide, gently sloping shelf; the divergence of approaching wave trains into the large, expanding coastal concavity; the location of the coast in a generally upwind direction; a small supply of new sediment; and the wave dampening effects of old submerged beaches and the submerged seagrass meadows (Murali 1982). Although the presence of submerged seagrass meadows interfacing directly with salt marshes has been considered to be a contributing factor to the zero-energy coast, it is more likely that their presence in this area is in fact the result of existing low energy conditions, as seagrass beds are rare on open oceanic, unprotected coasts. Once established, the seagrass beds could enhance the effects of those primary factors responsible for reduced energy conditions.

1.5 SUCCESSION AND ECOSYSTEM DEVELOPMENT

Throughout their range, few plants participate in the successional sequence leading to seagrasses because there are so few marine plants that can colonize soft sediments. In general, this sequence consists only of the seagrasses and the rhizophytic green algae. Seagrasses are vital to the coastal ecosystem because they are the only plants capable of providing the basis for a mature, productive ecosystem in these regions. Few other systems are so dominated and controlled by a single species as a climax Thalassia or Zostera meadow.

Odum (1974) classified Thalassia beds as "natural tropical ecosystems with high diversity." Compared to other natural systems, tropical seagrass beds are regions of very high diversity, but this can be misleading. These comparisons were made at a time when high diversity was equated with high biological stability. The prevailing concept was that the multitude of different organisms, with their widely differing requirements and interactions, functioned as a highly intricate web structure that lessened the importance of each link to the maintenance of the total system. There was much natural redundance built into such systems. The problem is that at climax there is one species for which there is no redundancy - the seagrass. If the seagrass disappears, the entire associated community disappears along with it; there is no other organism that can sustain and support the system.

The initial colonizers are typically rhizophytic macroalgae, of which various species of Halimeda and Penicillus are the most common, although species of Caulerpa, Udotea, Rhipocephalus, and Avrainvilla occur also. These algae have some sediment binding capability, but their ability to stabilize the sediments is minimal and their major function in the early successional stage seems to be the contribution of sedimentary particles as they die and decompose.

Halodule wrightii, the local pioneer species of seagrasses, colonizes readily either from seed or rapid vegetative branching. The carpet laid by Halodule further stabilizes the sediment surface; the numerous leaves forming a better buffer to protect the integrity of the sediment surface than the algal communities. In some sequences Syringodium will appear next, intermixed with Halodule at one edge of its distribution and Thalassia at the other. However, it is the least constant member of this sequence and is frequently absent. In areas with consistent disturbance and sediments low in organic content Syringodium may become the most abundant species. It is commonly found lining natural channels with hiqh velocity waters and higher turbidity than Thalassia can tolerate.

As successional development proceeds, Thalassia will begin to colonize the region. Its strong straplike leaves and massive rhizome and root system efficiently trap and retain particles, increasing the organic matter of the sediment. The sediment height rises until the rate of deposition and erosion of sediment particles is in balance. This is a function of the intensity of wave action, current velocity, and leaf density.

In shallow-water successional sequences leading to Thalassia, the early stages are often characterized by low sediment organic matter and open nutrient supply; that is, the community relies on nutrients brought in from adjacent areas by water movement as opposed to in situ regeneration. With the progression from rhizophytic algae to Thalassia, there is a progressive increase in the below ground biomass of the community as well as the portion exposed in the water column. With the progressive increase in leaf area of the plants, the sediment trapping and particle retention increases. This material adds organic matter to further fuel the sedimentary microbial cycles.

In summary, as species succession occurs in these shallow marine systems, important structural changes occur. The most obvious change with community development is the increase in leaf area, which provides an increase in surface area for the colonization of epiphytic algae and fauna, with the surface area of the climax community being many times that of either the pioneer seagrass, Halodule, or the initial algal colonizers. In addition to providing a substrate, the increasing leaf area also increases the leaf baffling and sediment trapping effects. Thus, as the canopy component increases, so does the material in the sediment. Thalassia, the climax species, has the highest leaf area, the highest total biomass, and by far the greatest amount of material in the sediments of any of the successional stages.

CHAPTER 2. AUTECOLOGY OF FLORIDA GULF COAST SEAGRASSES

2.1 PLANT MORPHOLOGY AND GROWTH

Seagrasses worldwide show a remakable similarity in their structure and growth (den Hartog 1970; Zieman and Wetzel 1980). For the seagrasses of the northwest coast of Florida, we shall focus primarily on the growth and morphology of Thalassia, considering this as representative of the local species.

Detailed descriptions of the anatomy and morphology of Thalassia were presented by Tomlinson and Vargo (1966) and Tomlinson (1969a, 1969b, 1972). Flat, straplike leaves with rounded tips emerge from erect short shoots which branch laterally from horizontal rhizomes at regular intervals. In this species rhizomes occur from 1 to 25 cm below the sediment surface, but are typically found in the depth range of 3-10 cm. (The rhizomes of Halodule and Halophila are near the surface and often exposed. While the rhizomes of Syringodium are generally found at an intermediate depth, in strong currents, they may be exposed, even extending up into the water column.) Roots of Thalassia emerge from the rhizomes and the short shoots. Much smaller in cross section than rhizomes, the roots vary in length according to sediment composition and depth.

On a Thalassia short shoot, new leaves grow on alternating sides of a central meristem that is enclosed by old leaf sheaths. New growth on leaves is produced by the basal meristem, thus the base of a leaf is the freshest, youngest portion. Short shoots of this species typically have two to five leaves at a time.

Studies of seagrass growth and morphology have revealed patterns of temporal and spatial variation. Grassbeds in areas of relatively low productivity in Biscayne Bay, Florida, averaged 3.3 leaves per short shoot, while in the more productive meadows of the Florida Keys, plants averaged 3.7 leaves per short shoot (Zieman 1975a). The width of leaves increased with age of the short shoot, reaching maximum width five to seven shoots back from the growing rhizome tip (Figure 5). Leaf width can also reflect morphogeographic variation: in Florida, Durako and Moffler (1981) identified the effects of a latitudinal stress gradient in leaves of Thalassia seedlings, with the greatest widths occurring in the Keys and the narrowest leaves found in northern Florida. In another study, leaf widths did not reflect a latitudinal or stress gradient, but showed sexual differences: female short shoots tended to have narrower leaves than male shoots (Durako and Moffler 1985a). Transplant experiments found that narrow-leaved plants of Thalassia, Syringodium, and Halodule from the north coast of the Gulf of Mexico continued to produce narrow leaves, and broader-leaved plants from the southern gulf and Caribbean likewise continued to produce wider leaves, even when moved to different habitats (McMillan 1978).

Thalassia leaves in Biscayne Bay grew an average of 2.5 mm/day in length, but growth rates as high as 1 cm/day were measured over periods of 15-20 days (Zieman 1975a). Leaf growth rate in Thalassia usually decreases exponentially with leaf age (Patriquin 1973; Zieman 1975a). In contrast, leaf elongation in Syringodium proceeded at a relatively steady rate throughout the growth phase (Fry 1983). The first few leaves produced on a new Thalassia short shoot are reduced in size and are tapered; the regular straplike leaves are produced at a rate of

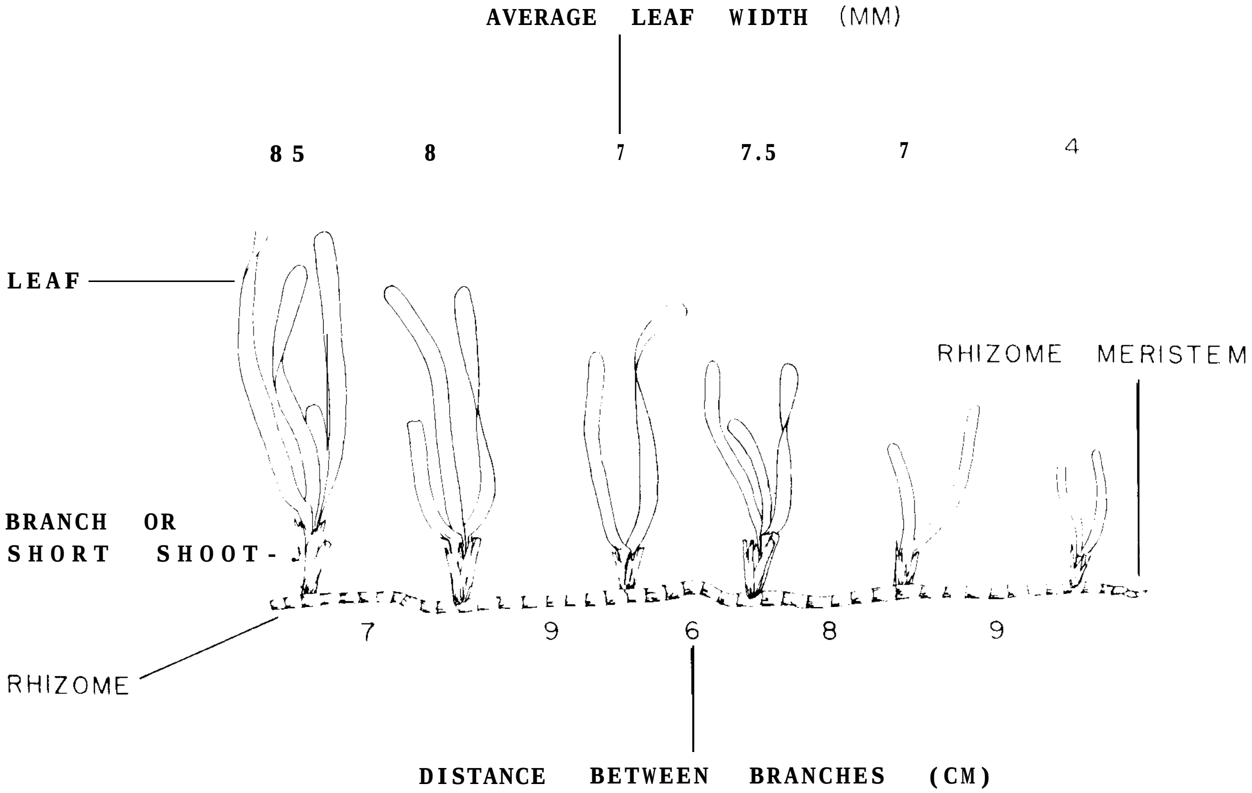


Figure 5. General morphology of a ***Thalassia*** plant.

one-new-leaf-per-short-shoot every 14-16 days. The rate of leaf production in Biscayne Bay was dependent on temperature, with low growth occurring in the cooler winter months (Zieman 1975a). Less seasonal variation was found in the tropical Caribbean waters of Barbados and Jamaica by Patriquin (1973) and Greenway (1974) respectively. Durako and Moffler (1981) found a gradient of root and leaf growth in Thalassia seedlings, from high rates in the Florida Keys to low growth rates in north Florida waters.

In Tampa Bay, Durako and Moffler (1985c) found pronounced seasonal patterns in maximum leaf lengths of Thalassia. There was a slight decrease in the middle of summer, coincident with high temperatures and floral production, but maximum lengths were much less in the cold winter months, reflecting both leaf die-off and depressed growth rates due to exposure to low temperatures. A pattern of spatial variation was evident, with shorter leaves occurring in the middle of the grassbed where the water was shallower.

2.2 REPRODUCTION

Vegetative reproduction in seagrasses accounts for their capacity to produce high biomass and areal cover; however, sexual reproduction is important in providing the genetic plasticity for successful adaptation and competition in the species. Studies of flower production in the seagrasses considered here have focused primarily on Thalassia. This plant is sexually dimorphic, producing separate male and female flowers. Grey and Moffler (1978) found that short shoots occurring on a common rhizome segment produced flowers of the same sex, suggesting that Thalassia is also dioecious, that is, has separate male and female plants.

Flower production in Florida populations of Thalassia occurs from April to August or September, peaking in June (Orpurt and Boral 1964; Grey and Moffler 1978) (Figure 6). While Phillips (1960a) found no flowering north of Tarpon Springs, more recent studies have revealed flowering in the grassbeds of the Florida panhandle (Marmelstein et al. 1968; Phillips et al. 1981). The percent of short shoots in a grassbed bearing reproductive structures varies greatly: less than 1% of plants from north Florida beds reproduced sexually, while reproductive densities in plants from south and central Florida ranged from 1% to 15% (Phillips 1960a; Orpurt and Boral 1964; Zieman 1975). More recently Moffler et al. (1981) found reproductive densities of 44% in Tampa Bay. A later study in Tampa Bay recorded reproductive densities of 11.4%, 20.7%, and 10.0% for 1981, 1982, and 1983, respectively, and found that increased numbers of male flowers accounted for the higher reproductive density of 1982 (Durako and Moffler 1985b). Spatial density distributions showed higher numbers of female plants occurred on the fringes of the bed where short shoots are generally younger, while more male plants were found in the center on presumably older short shoots. This pattern could reflect an age-related sexual expression in the plants, although environmental factors and clonal differences also can influence leaf width (Durako and Moffler 1985b). (Thalassia seed production in Tampa Bay was apparently low compared with south Florida and probably could not provide an adequate supply for restoration projects (Lewis and Phillips 1981).

Phillips (1960a) found flowering Ruppia abundant in Tampa Bay; however, he did not observe seedling germination. Flower and fruit production in Ruppia of this area peak in May and disappear in June (Lewis et al. 1985a). Phillips (1960a) did not find reproductive Halodule, Syringodium, or Halophila in Tampa Bay; however, several reproductive specimens of Halodule were later found in nearby waters (Lewis et al. 1985a). Although reproductive plants are rare in Syringodium, female plants have been collected in the bay (Lewis et al. 1985a). Zimmerman and

Figure 6. Flowers of *Thalassia (left)* and Syringodium (right) (photo by M. J. Durako.)

Livingston (1976b) found a number of flowering Syringodium plants in their Apalachee Bay samples in May, 1972. These authors also found numerous flowering plants of Ruppia in May and June.

In laboratory studies, cultures of Thalassia, Syringodium, Halodule, and Halophila engelmannii flowered under continuous light, suggesting that flowering was independent of day length. The temperature range for flowering in these plants was 22-26 °C (McMillan 1982). Lewis et al. (1985a) also found that flower production in Thalassia was probably controlled by factors other than photoperiod.

2.3 PLANT CONSTITUENTS

Because of their high productivity and wide distribution, seagrasses are recognized as a potentially important food source in shallow coastal marine systems. The fact that this abundant food source is subjected to relatively low levels of direct grazing on the living plant material has prompted studies of the chemical constituents and relative food value of seagrasses. Various authors have performed such constituent analyses for the seagrasses considered here (Burkholder et al. 1959; Bauersfeld et al. 1969; Walsh and Grow 1972; Lowe and Lawrence 1976; Bjorndal 1980; Dawes and Lawrence 1980; Vicente et al. 1980; Dawes and Lawrence 1983). A summary of these results is given in Table 3. Dawes and Lawrence (1980) noted that the differences in sample preparation and chemical analyses employed make direct comparison of the data difficult, and subsequently proposed a procedure to standardize analyses so that future data will be comparable, making it possible to determine the effect of seasonal and other environmental changes on the chemical content of the plants.

The relative amount of protein in the plant tissues has been used as a measure of the potential food value of tropical seagrasses. Comparative studies have shown that turtle grass leaves are roughly equal in percent protein to phytoplankton and Bermuda grass (Burkholder et al. 1959) and 2 to 3 times higher than 10 species of tropical forage grass (Vicente et al. 1980).

Walsh and Grow (1972) found that Thalassia protein content compared favorably with reported values for grain crops: corn contained from 9.8% to 16% protein, sorghum 8.6% to 16.5%, and wheat 8.3% to 12%. Various studies of the protein content of Thalassia leaves have yielded results ranging from a low of 3% of dry weight for unwashed epiphytized leaves (Dawes et al. 1979) to a maximum of 29.7% for leaves rinsed with distilled water (Walsh and Grow 1972). The low value for unwashed leaves reflects the inclusion of sea water salts, and possibly sediment particles which settle on leaves, into the total dry weight. Values more typically range between 10% and 15% of dry weight.

Dawes and Lawrence (1983) and Durako and Moffler (1985c) have reported spatial and temporal variations of protein content. In Tampa Bay values for Thalassia and Syringodium varied from 8% to 22% and from 8% to 13%, respectively, with maximum values occurring in the summer (Table 4). Thalassia leaves collected in July 1979 from Tampa Bay, Key West, and Glovers Reef, Belize, showed a significant increase in protein content from Tampa to Belize, even though the sites were similar in depth, salinity, and temperature (Dawes and Lawrence 1983). If such a latitudinal trend holds, Thalassia from the Big Bend area, for which constituent analyses have not been performed, could have even lower protein content, and thus lower food value. Such a decrease in nutritional value might be reflected in the results of Kitting et al. (1984), who found that several seagrass "detritivores" in the northern gulf actually derived most of their nutrition from epiphytes.

The new growth of the basal portions of leaves of Thalassia are higher in protein and lower in Inorganic content (Cawes and Lawrence 1980). The green turtle has been shown to exploit this fact in its pattern of grazing: a patch of seagrass is initially cropped, with the upper older portions of the leaves left to float away, and such patches are subsequently maintained for a period of time by repeated grazing (Bjorndal 1980). Thus,

Table 3. Constituent analysis of seagrasses (from Zieman 1982).

Species	Component	Season/ date	% as Referenced	Ash	Nitrogen	Protein	Fat	Carbo- hydrates	Energy (kcal/g)	Reference
Thalassia	Leaves	February	%DW	24.8	2.1	(13.1)	0.5	35.6	1.99	Burkholder et al. 1959
		Annual mean	%AFDW		1.6-4.8	25.7		23.6	4.66	Walsh and Grow 1972
			%DW	24.5		(10.3-29.7)				
		January	%DW	29		8	0.9	45	2.4	Dawes and Lawrence 1980
		April		37		9	4.0	50	3.0	
		July		33		22	1.0	44	3.1	
		October		44		13	2.0	41	2.6	
		Mean		36		13	2.0	45	2.8	
		?	%DW (unwashed)	47.3		11.0	0.7	38		Bauersfeld et al. 1969
			%DW (washed)	24.8		13.0	0.5	35.6		
		July-August	%DW	24.7		9.1	2.3	63.9		Lowe and Lawrence 1976
		January August	%DW			16.7				Bjorndal 1980
						17				Vicente et al. 1978

(Continued)

Table 3. (Continued).

Species	Component	Season/ date	% as Referenced	Ash	Protein	Fat	Carbo-hydrates	Energy (kcal/g)	Reference
Thalassia	Rhizomes	Annual mean	%DW	23.8	5.8-12.2			4.88	Walsh and Grow 1972
			%AFDW		11.0		72.1		
	Roots		%DW	50.5	19.6				Bauersfeld et al. 1969
				24.1	15.0				
	Photosynthesis inactive part of short shoot	January	%DW	39	9	1.0	51	2.7	Dawes and Lawrence 1980
		April		51	7	0.5	42	2.2	
		July		48	16	0.7	35	2.5	
		October		56	8	0.8	35	2.0	
		Mean		49	10	0.8	41	2.4	
	Rhizomes	January	%DW	26	9	0.5	65	3.2	
		April		24	8	1.6	66	3.4	
		July		33	16	0.2	51	3.0	
		October		36	7	1.1	56	2.8	
		Mean		30	i-0	0.9	60	3.1	
Syringodium	Leaves	July-August	%DW	27.0	3.10	3.4	66.3		Lowe and Lawrence 1976
	Leaves	January	%DW	30	9	1.7	59	3.1	Dawes and Lawrence 1980
		April		28	8	6.2	58	2.4	
		July		33	13	4.0	50	3.2	
		October		32	13	1.8	53	3.1	
		Mean		31	ii	3.4	55	3.0	
	Short shoots photosynthesis inactive parts	January	%DW	28	10	1.3	61	3.2	
		April		27	11	3.6	58	3.3	
		July		31	14	0.9	54	3.1	
		October		41	11	1.1	47	2.6	
		Mean		32	12	1.7	55	3.1	

(Continued)

Table 3. (Concluded).

Species	Component	Season/ date	% as Referenced	Ash	Protein	Fat	Carbo- hydrates	Energy (kcal/g)	Reference
Syringodium	Rhizomes	January	%DW	16	9	1.0	74	3.6	
		April		18	5	4.7	72	3.7	
		July		17	12	0.1	71	3.6	
		October		19	6	0.5	75	3.5	
		Mean		18	8	1.6	73	3.6	
Halodule	Leaves	January	%DW	32	19	1.0	48	3.1	Dawes and Lawrence 1980
		April		25	18	3.2	54	3.5	
		July		25	19	1.2	55	3.3	
		October		26	14	1.4	59	3.3	
		Mean		27	18	1.7	54	3.3	
	Short shoots photosynthesis inactive part	January	%DW	25	5	1.1	69	3.2	
		April		29	9	3.5	59	3.0	
		July		36	8	0.8	55	2.9	
		October		34	9	1.2	56	2.9	
		Mean		31	8	1.7	60	3.0	
	Rhizomes	January	%DW	14	9	0.7	76	3.7	
		April		17	7	1.6	74	3.7	
		July		22	8	0.1	70	3.4	
		October		17	8	1.1	74	3.6	
		Mean		18	8	0.9	74	3.6	

Table 4. Seasonal content of protein and soluble carbohydrates (% dry weight) in Tampa Bay (after Dawes 1987).

Species	Component	January	April	July	October
Thalassia testudinum					
Leaves	Protein	8	9	22	13
	Carbohydrate	6	9	9	7
Rhizomes	Protein	9	8	16	7
	Carbohydrate	12	21	24	36
Syringodium filiforme					
Leaves	Protein	9	8	13	13
	Carbohydrate	22	16	18	20
Rhizomes	Protein	9	5	12	16
	Carbohydrate	36	38	50	46
Halodule wrightii					
Leaves	Protein	19	18	19	14
	Carbohydrate	14	19	15	13
Rhizomes	Protein	9	7	8	8
	Carbohydrate	43	40	43	54

the turtles create a more energetically and nutritionally rich food source, and, indeed, Zieman et al. (1984) found that the nitrogen content of leaves within turtle patches was similar to the content of the basal portions of ungrazed leaves and higher than the upper portions of those leaves.

The values reported for ash content of Thalassia leaves range from 45% dry weight for unwashed samples to a low of about 25% for samples rinsed in fresh water. Samples washed in ambient seawater contained 29%-44% ash (Dawes and Lawrence 1980). Thalassia rhizomes from the west coast of Florida had ash content significantly lower than did the leaves, with mean values ranging from 21% to 26% dry weight (Dawes and Lawrence 1983). Cell wall carbohydrates (cellulose, hemicellulose, and lignin) accounted for 45%-60% of the dry weight of turtle grass leaves (Bjorndal 1980; Vicente et al. 1980). Dawes and Lawrence (1983) found higher levels of soluble carbohydrates in Thalassia rhizomes compared to the leaves. In Tampa Bay, seasonal variation in soluble carbohydrate content occurred in the rhizomes of both Thalassia and Syringodium, reflecting production and storage of starch during summer and fall (Dawes and Lawrence 1980). Mean values for the lipid content of Thalassia leaves varied from 1.2% to 4.2%, and were comparable to the "fat" content of tropical terrestrial grasses.

2.4 PHYSIOLOGICAL ECOLOGY

2.4.1 Environmental Tolerances and Responses

a. Temperature. The range of thermal tolerance in tropical organisms is often about half that of their temperate counterparts. Although the upper temperature limits are similar, the tropical organisms have reduced cold tolerance. McMillan (1979) found a gradient of chill tolerance in Florida seagrasses, with those from northern Florida most tolerant of low temperatures and those of the Florida Keys least tolerant. After growing in culture for 22 months, Thalassia seedlings maintained their original pattern of chill tolerance: those from Apalachee Bay, Florida, showed less damage than seedlings from the Florida Keys and St. Croix.

In the thermally impacted waters of Anclote Estuary north of Tampa Bay, Barber and Behrens (1985) found that maximal growth in Syringodium occurred between 23 and 29 °C, and between 23 and 31 °C in Thalassia (Figure 7). In the cooler months, thermally impacted stations had higher productivities than did non-impacted areas, but in the summer months, Syringodium productivity was depressed at the warmer stations when the upper thermal tolerance limit of this seagrass was exceeded. In Apalachee Bay, Zimmerman and Livingston (1976b) found that Syringodium tolerated lower temperatures than Thalassia, which suffered leaf kill when temperatures fell below 15 °C. Some defoliation of Thalassia also occurred when summer temperatures rose to 30 °C.

In Texas waters, vigorous growth of Ruppia in the spring correlated with cool temperatures rather than lowered salinities (Pulich 1985). Phillips (1960a) reported a temperature range of 7-35 °C for Ruppia in Tampa Bay; growth and reproduction was highest with spring temperatures, and decreased when high summer temperatures were reached. In Texas, a similar pattern of temperature response was evident for Ruppia in a mixed stand with Halodule; in contrast, Halodule biomass at that site peaked in the warmer summer months and declined in the fall. Phillips (1960a) reported that Halodule in Tampa Bay suffered winter leaf kill, even at sites which were always submerged. However, Halodule suffered little leaf kill in Apalachee Bay, where the minimum winter temperature was 9 °C. This temperature was a new minimum reported for Halophila engelmanni (Zimmerman and Livingston 1976b).

b. Salinity. Although the seagrasses considered here are able to tolerate fluctuations in salinity, the optimum concentration for growth varies among the species. Experiments with transplanted seagrasses showed that, of the species considered here, Halodule had the broadest salinity tolerance,

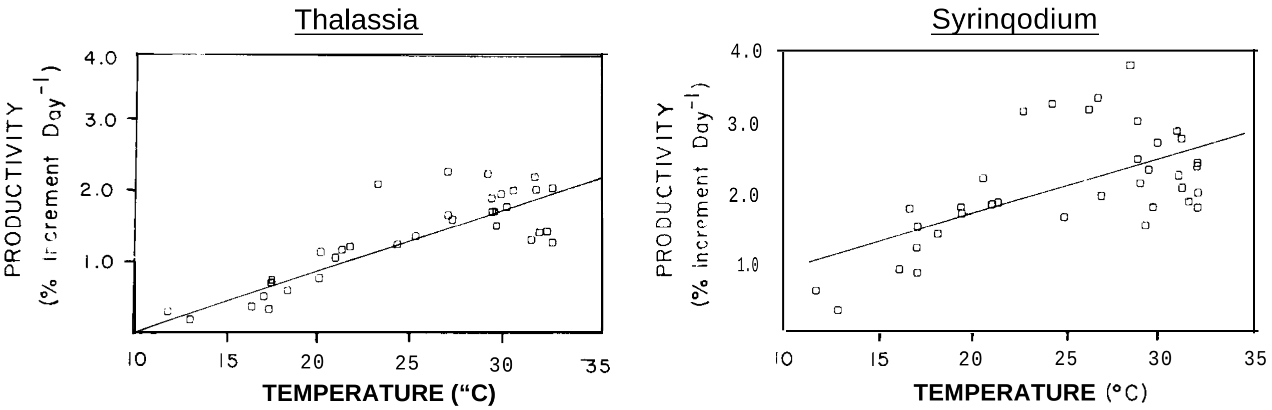


Figure 7. Temperature responses of Thalassia and *Syringodium* on the west Florida coast (after Barber and Behrens 1985).

Thalassia and *Syringodium* (=*Cymodocea*) were intermediate, and *Halophila* the most stenohaline. *Ruppia* showed a wide tolerance ranging from freshwater to hypersaline conditions (McMillan 1974). Evaluating the upper limits of salinity tolerance, McMillan and Mosely (1967) found that *Halodule* (=*Diplanthera*) tolerated the highest salinities, surviving up to 80 ppt, followed, in order, by *Thalassia*, *Ruppia*, and *Syringodium*, with *Halophila*'s relative tolerance apparently somewhere between *Halodule* and *Syringodium* McMillan (1974) reported the order of decreasing tolerance to low salinities was *Ruppia*, followed by *Halodule*, *Thalassia*, *Syringodium* (=*Cymodocea*), and *Halophila*. While both *Ruppia* and *Halodule* exhibit broad ranges of salinity tolerance, the former is the only seagrass species, of this region capable of surviving in freshwater. According to McMahan (1968), *Halodule* does not survive in salinities less than 3.5 ppt and has an optimum salinity of 44 ppt.

Thalassia and *Syringodium* do not grow in areas of low salinity in the eastern Gulf of Mexico (Phillips 1960a), and were not reported in areas with salinities less than about 17 ppt in the northern seagrass bed (Zimmerman and Livingston 1976). Turtle grass can survive short periods of exposure to extremes ranging from a low of 3.5 ppt (Sculthorpe 1967) to a maximum of 60 ppt (McMillan and Mosely 1967); however, significant leaf loss frequently follows exposure to salinity extremes. The optimum salinity reported for this seagrass ranges 24-35 ppt (Phillips 1960; McMillan and Mosely 1967; Zieman 1975a). In turtle grass, maximum photosynthetic activity occurred in fullstrength seawater, and decreased linearly with decreasing salinity (Hammer 1968b). The effect of freshwater runoff following a hurricane was considered more damaging to seagrasses than the effects of high winds and tidal surge (Thomas et al. 1961).

According to Humm (1973), *Halophila* does not tolerate reduced salinities; however, Zimmerman and Livingston (1976b) found a bed of *H. engelmanni* off the mouth of the Econfina River, an area of relatively low salinity. In addition, Earle (1972) reported *Halophila* occurring at depths ranging from intertidal to 13 m, and Strawn (1961) found this species mixed with *Halodule* and *Ruppia* on an old oyster bar. Thus, it appears that *Halophila* may in fact be quite euryhaline.

Ruppia traditionally has been considered a brackish-water species (Verhoeven 1975) and, indeed, among the seagrasses it alone can be maintained in tap water (McMillan 1974). Phillips (1960a) reported that it occurred most frequently in salinities below 25 ppt, which correspond with the findings of Zimmerman and Livingston (1976b). In the Big Bend seagrass bed, *Ruppia* was observed growing near river mouths (R.L. Iverson, Forida State University, Tallahassee; pers. comm.) However, Dawes (1974) found it growing in areas of relatively high but stable salinity in the lower portions of Tampa Bay. *Ruppia* transplants survived in salinities up to 74 ppt (McMillan and Mosely 1967); this species also grew in Texas waters at a site where salinities averaged 25-32 ppt and at another site where hypersaline conditions persisted for several months (Pulich 1985). *Ruppia* also has been observed growing in hypersaline waters in Florida Bay (J. Fourqurean, University of Virginia, Charlottesville; pers. comm.). Thus *Ruppia* also appears to be quite euryhaline.

c. *Oxygen*. The oxygen contained in the water column of seagrass beds generally provides a supply adequate to meet the respiratory demands of the plants themselves and associated organisms. In *Thalassia* beds, photosynthetic oxygen production can be so high that bubbles escape from the leaf margins in the late afternoon. The seagrasses are less susceptible to low oxygen concentrations than the animals of the grassbeds; nevertheless, leaf mortality and increased microbial activity coincided with lowered oxygen levels in Japanese Zostera beds (Kikuchi 1980). Low O_2 levels do slow their rate of respiration, and when internal O_2 concentrations are lowered, the plant's rate of respiration is controlled by diffusion of oxygen from the water column. During the night, the respiratory demand of the seagrasses and associated plant and animal communities can lower concentrations of the surrounding waters (Durako et al. 1982). In Puerto Rico (Odum et al. 1960) and in Florida and Texas (Odum and Wilson 1962) nighttime oxygen concentrations were typically 4-7 mg O_2 L^{-1}, and a low of 2-3 mg O_2 L^{-1} recorded on a calm night in August during an extreme low tide.

d. Light. The fact that well-developed seagrass beds do not occur at depths greater than 10 m has been considered indirect evidence that photosynthesis in seagrasses requires high light intensity, and that light penetration limits the depth to which seagrasses can grow (Humm 1956; Buesa 1975; Wiginton and McMillan 1979). Gessner and Hammer (1961) suggested that increased hydrostatic pressure, as well as decreased light, may limit photosynthesis suggesting that light is probably not the sole factor restricting photosynthesis at depth; however, there were no significant pressure effects on photosynthetic rates of Thalassia and Syringodium for plants collected from various depths near Buck Island, St. Croix, and subjected to 1 and 3 atmospheres of pressure (R.L. Iverson, Department of Oceanography, Florida State University; unpubl. data). It is therefore unlikely that the pressures that exist over the depth gradients where these seagrasses are found can explain the significant decrease in Thalassia biomass at the limit of its depth distribution. However, the maximum depth at which seagrasses occur does indeed correlate with the available light regime. Buesa (1975) reported the following depth maxima for the seagrasses off the northwest coast of Cuba: Thalassia, 14 m; Syringodium, 16.5 m; Halophila decipiens 24.3 m; and Halophila englemanni, 14. 4 m.

Of the visible light spectrum, the longer red wavelengths are absorbed in the first few meters in both clear and turbid waters. The clear tropical waters of the Caribbean Sea are enriched in blue light, while in turbid shallow waters, such as parts of Florida Bay and coastal waters of Texas, enrichment of green wavelength occurs. In a study of the effects of specific wavelengths of light on seagrass photosynthesis, Buesa (1975) found that Thalassia responded best to red light (629 nm) and Syringodium grew best with blue wavelengths (400 nm). Wiginton and McMillan (1979) reported increasing chlorophyll a to chlorophyll b ratios for seagrasses obtained from increasing depths near Buck Island, St. Croix, but concluded that light quantity rather than light quality was the primary environmental determinant of seagrass depth distribution along the Buck Island gradient. Thalassia growing in outer Florida Bay has considerably more non-photosynthetic tissue than Syringodium or Halodule. Iverson (unpubl. data) suggested that the compensation light-energy level (below which annual net increase of total plant biomass cannot occur) for Thalassia growing in tropical habitats is less than the compensation light energy level for Syringodium and for Halodule as a consequence of the respiratory demands created by the greater proportion of nonphotosynthetic tissue mass of Thalassia in those habitats.

Humm (1973) observed that Ruppia occurred in areas of low light and high turbidity. Phillips (1960a) also noted the growth of this species in areas of poor light penetration. Halophila engelmanni, in addition to tolerating the lower light of deeper waters also grows in areas of high turbidity (Zimmerman and Livingston 1976b).

e. Current. Seagrass biomass and production are greatly influenced by current velocity (Conover 1968). The maximum standing crops for both Thalassia and Zostera were found where current velocities averaged 0.5 m sec^{-1}. Rapid currents are thought to disrupt diffusion gradients and increase the availability of CO_2 and nutrients to the plants (Conover 1968). In south Florida, the densest stands of Thalassia and Syringodium are found in the tidal channels separating mangrove islands. Off the coast of Nicaragua, samples from mangrove tidal channels had a leaf standing crop of 262 g dry weight m^{-2} and total biomass of 4,570 g m^{-2}. By comparison, values for samples from a quiescent lagoon were 185 and 1,033 g m^{-2} respectively (McRoy, Zieman, and Ogden, unpubl. data).

Strong currents can affect the structure of seagrass beds. In some areas of high current, lunate features called blowouts occur (Patriquin 1975). These crescent-shaped erosional features migrate through the bed in the direction of the current. Recolonization takes place at the trailing edge of the blowout, and here the successional sequence of seagrass colonization can be observed.

f. Sediment. Seagrasses are found in a variety of substrates, ranging in texture from fine muds to coarse sands. Because they are rooted plants, they do have minimum sediment-depth requirements, which differ among the species. Halodule's shallow surficial root system allows it to colonize thin sediments in areas of minimal hydraulic stability (Fonseca et al. 1981). Thalassia is more robust, reauirina up to 50 cm of sediment for lush-growth, although it occurs in shallower sediments (Zieman 1972). In the Bahamas, Thalassia did not occur in sediments less than 7 cm deep (Scoffin 1970). Phillips (1962) reported that seagrasses in Tampa Bay grew only in muddy sand substrates, and patches of pure sand were unvegetated.

Reduced sediments seem always to be associated with well-developed Thalassia beds and most likely reflect the greater importance of sediment-nutrient content and microbial nutrient recycling in meadows of this species, rather than a specific requirement for reducing conditions. Halodule is generally thought to grow in more aerobic substrates; however, Pulfch (1985), working in Texas waters, postulated that Ruppia normally occurs in low-nutrient sediments while Halodule prefers organic-rich sediments where sulfate reduction is substantial. Phillips (1960a) reported that Syringodium distribution was apparently independent of sediment type and this species is found in both oxidized and reduced sediments (Patriquin and Knowles 1972). Ruppia is generally found in finer substrates than the above species (Phillips 1960a), while Halophila grows in a wide range of substrates from muddy sands to limestone, and even on mangrove roots (Earle 1972).

In the Big Bend area of the west coast of Florida, Iverson and Bittaker (1986) also recorded Thalassia growing in coarser sediments than the other species of that northern grassbed. Syringodium and Halodule biomass were greater in fine sediments (Iverson and Bittaker 1986). Similarly, Buesa (1975) found that Thalassia off the northwest coast of Cuba grew in coarser sediments than Syringodium or Halophila.

g. Exposure. Thalassia and Syringodium are subtidal plants and do not tolerate exposure to the air. While Thalassia does grow on flats that are infrequently exposed, unless such exposure is brief, desiccation will cause leaf kill. Halodule can withstand repeated exposure at low tide, and is most abundant between neap-low and spring-low tide marks in higher salinities (Phillips 1960a). In low-salinity intertidal areas, Ruppia and Halodule often occur in mixed stands (Phillips 1962; Earle 1972). Dawes (1987) noted that Ruppia forms extensive meadows on flats where it can be exposed to intense sun and appears to tolerate a degree of desiccation.

2.4.2 Photosynthetic Carbon Fixation

Three separate biochemical pathways by which plants can fix inorganic carbon photosynthetically have been identified. The majority of terrestrial plants utilize the C_3 pathway, in which CO_2 is initially incorporated into a three-carbon product. In the C_4 pathway, found primarily in plants from tropical and arid areas, a four-carbon product results from the first step of CO_2 incorporation. The third pathway, CAM (crassulacean acid metabolism), by which plants take up CO_2 at night and store it as malic acid until daytime when it is then used in photosynthesis, occurs in water-stressed plants such as desert succulents. A major factor in the differences of photosynthetic physiology between C_3 and C_4 is the greater efficiency of refixation of photorespired CO_2 found in the C_4 plants (Hough 1974; Moffler et al. 1981). High rates of refixation have been detected, however, in some C_3 plants with specialized leaf anatomy and gas lacunae (Sondergaard and Wetzel 1980) and may be implicated in seagrass carbon metabolism (Beer and Wetzel 1982). Seagrass leaves possess large internal lacunar spaces which facilitate gas transport (Zieman and Wetzel 1980). The presence of these lacunae and the absence of stomata provide the plants with a relatively closed pool of carbon dioxide, thus promoting recycling of CO_2.

Seagrasses share with C_4 plants such physiological adaptations as high thermal and light optima for photosynthesis and high productivity rates. Although Thalassia was originally thought to be a C_4 plant, Beer and Wetzel (1982), using radiolabelled HCO^-_3, concluded that both this seagrass and Halodule were intermediaries between C_3 and C_4 in their carbon metabolism. Syringodium and Zostera exhibited the most typically C_3 pattern of the seagrasses studied.

2.4.3 Isotopic Fractionation

A significant result of the differences in carbon metabolic pathways is that imprints are left in the form of characteristic ratios of the stable isotopes of carbon in the plant tissues produced. In biochemical reactions, plants do not utilize ^{12}C and ^{13}C in the exact ratios found in the environment, but discriminate between the two, favoring the lighter isotope. Plants using the C_3 pathway are relatively depleted in ^{13}C, while C_4 plants have higher ratios of ^{13}C to ^{12}C. The relative content of ^{13}C to ^{12}C is compared to the isotopic ratio of a standard and expressed as a "del" value (δ) as follows:

$$\delta^{13}C = \frac{{}^{13}C/{}^{12}C_{\text{sample}}}{{}^{13}C/{}^{12}C_{\text{standard}}} 1x10^3$$

The range of $\delta^{13}C$ values for C_3 plants is -24 to -34 ppt, while C_4 plants vary from -6 to -9 ppt (Smith and Epstein 1971). Seagrass values, particularly those of Thalassia and Syringodium, are similar to those of the C_4 plants. McMillan et al. (1980) reported that 45 of 47 species examined fell within the range of -3 to -19 ppt, with only two species of Halophila having lower values. Samples of Thalassia from the Gulf of Mexico and the Caribbean range from -8.3 to -12.5 ppt, with a mean of -10.4 ppt. Halophila had similar isotopic composition, with means of -10.2 ppt for gulf and -12.6 ppt for Caribbean samples. Syringodium, by comparison, had relatively fewer negative numbers, with a mean of -5 ppt and a range of -3 to -9.5 ppt. This species has a greater proportion of lacunar spaces, and the lacunae are more completely partitioned than those of the other seagrasses considered. This greater lacunar isolation presumably enhances the recycling of CO_2, which occurs in C_4 plants, and thus the similarity in isotopic composition is not unexpected. Tropical seagrasses in general have values less negative than those of temperate species. A study of Zostera showed little seasonal variation in isotopic composition (Thayer et al. 1978). The isotopic composition can vary, however, with habitat (Smith et al. 1976; Zieman et al. 1984c). McMillan and Smith (1982) found that seagrasses grown in laboratory cultures had more negative values, that is, were more depleted in the heavier ^{13}C than samples from the natural environment. They concluded that such results could reflect differences in carbon sources and in recycling of internal carbon.

Since plants have characteristic isotopic compositions, and the animals that consume them retain to within ±2 ppt the same ratio (DeNiro and Epstein 1978; Fry et al 1978), these isotope "signatures" provide a useful tracer for food chain studies (Figure 8). In the marine environment, seagrasses have isotopic ratios distinct from other marine plants. Thus carbon derived from seagrasses (-3 to -15 ppt) is distingished from that of marine macroalgae (-12 to -20 ppt), particulate organic carbon and phytoplankton (-18 to -25 ppt) and mangroves (-24 to -27 ppt) (Fry and Parker 1979). In Texas, sediment organic matter within a seagrass bed was more depleted in ^{13}C compared to sediment organic matter from adjacent bays without seagrasses (Fry et al. 1977), and the same pattern was reflected in the animals (Fry 1981). The $\delta^{13}C$ of the polychaete worm Diapatra cuprea varied from an average of -13 ppt in seagrass-dominated areas to -18 ppt where phytoplankton were the dominant primary producers (Fry and Parker 1979). Similar trends were observed for fish and shrimp.

The utility of this carbon isotope method of food chain analysis is restricted at the present by the high cost of analytical equipment and by the limitations of data interpretation. When a consumer organism has a $\delta^{13}C$ value which falls within a range specific for a particular plant source, the relationship is readily apparent; however, if the animal has a del value falling between two identifiable plant groups, it is unclear whether this represents a food source which itself has a value intermediate between the two known groups or whether the organism is consuming a mixed diet.

2.5 NUTRIENT UPTAKE AND SUPPLY

Seagrasses are highly productive plants that can grow in low-nutrient environments; thus, the manner in which plant nutrient demands are met is of particular interest. Since seagrasses occupy both the water column and the

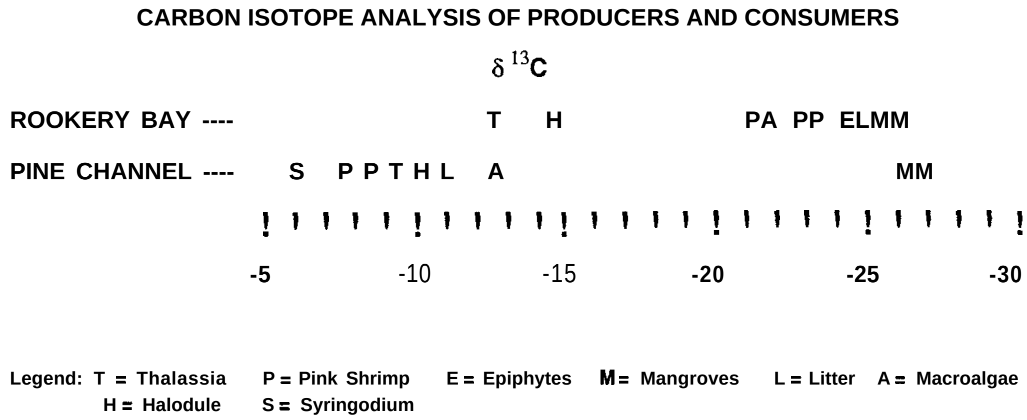


Figure 8. Carbon isotopic variation at two locations in Florida (after Zieman et al. 1984c).

sediments, controversy existed in the past over whether nutrients were taken in through the leaves or the roots. The temperate seagrass *Zostera* is capable of taking in nutrients both from the water column and through the roots (McRoy and Barsdate 1970); however, uptake through the root system was shown to be faster and more efficient (Penhale and Thayer 1980). McRoy and Barsdate (1970) found that *Zostera* could translocate ammonium and phosphate from the sediments to the leaves and excrete these nutrients into surrounding waters. Such nutrient pumping may be important only in sediments with high nutrient concentrations (Penhale and Thayer 1980).

Studies of nutrient supply to seagrasses have concentrated on nitrogen and phosphorus because these, along with carbon, are the primary constituents of plant material. In *Zostera* beds in Chesapeake Bay, the addition of commercial fertilizer containing both nitrogen and phosphorus stimulated leaf growth (Orth 1977a). Harlin and Thorne-Miller (1981) observed similar growth enhancement when inorganic ammonium and phosphate were added to waters overlying *Zostera* beds in a Rhode Island bay. The relative importance of these major nutrients in limiting plant growth has not been determined and probably depends on local nutrient supplies and processes.

Three sources of nitrogen are available to the plants: microbially recycled nitrogen from organic matter in the sediment, dissolved ammonium and nitrate in the water column, and ammonium from the microbial fixation of dissolved N_2. Sources of organic matter for decomposition in the sediment include animal excretions and dead roots and rhizomes, Sediment bacteria convert the organic nitrogen to ammonia in the anoxic zone, which begins only a few millimeters below the surface. Ammonia that is not quickly bound either by biological uptake or chemical adsorption by sediment particles can diffuse upward to the aerobic zone, where it can then diffuse into overlying waters or be converted to nitrate by nitrifying bacteria. Nitrate concentrations are low in the sediments; nitrate is either rapidly assimilated or converted to N_2 by denitrifying bacteria. Patriquin (1972) and Capone and Taylor (1980) identified the recycled organic material as the primary source of nitrogen for leaf growth; however, nitrogen fixed by sediment microbes could supply 20% to 50% of the plants' requirements (Capone and Taylor 1980). In contrast, Capone et al. (1979) found that fixation by phyllosphere microbes contributed primarily to epiphyte growth. The relative importance of the different nitrogen pools to the plants is indicated by such factors as sediment characteristics and water column concentrations.

Inorganic phosphorus, unlike nitrogen, has no gaseous phase and does not change valence state in normal environmental reactions. Thus the source of phosphorus to the seagrasses is dissolved inorganic orthophosphate (PO,), derived either from the breakdown of organic matter or from the weathering of minerals, some of which are biologically precipitated. While water-column concentrations in tropical waters are normally low, phosphate may be quite abundant in the sediments. High levels of HCl-extractable phosphate were found in the carbonate sediments of seagrass beds of Barbados, but pore-water concentrations and concentrations in overlying waters were low (Patriquin 1972). Because the high sediment concentrations probably reflected undissolved phosphate not available for uptake by the plants, Patriquin concluded that the nutrient-poor overlying waters were the primary source of phosphate to the seagrasses. Sediment type influences the dissolution of phosphate, and, therefore, its availability to the plants. Silicious sediments readily exchange phosphate with overlying waters (Nixon et al. 1980), but carbonate sediments tend to absorb phosphate, removing it from solution. Rosenfeld (1979) reported that pore-water phosphate concentrations of Florida Bay sediments were two orders of magnitude lower than concentrations in Long Island Sound pore waters and attributed the difference to calcium carbonate adsorption of phosphate.

Terrestrial runoff also can be an important factor affecting the concentration of dissolved nutrients. In Apalachicola Bay, nutrient concentration peaks coincided with periods of maximum river discharge (Myers and Iverson 1981). The bays and estuaries of the northwest coast of Florida vary widely in sediment composition and terrestrial input; thus, the supply of phosphate and its role in limiting plant growth can be expected to vary accordingly. At this time, the degree to which phosphorous and nitrogen are limiting the growth of Florida's seagrasses is still unknown, and is a timely and important topic for further research.

CHAPTER 3. DISTRIBUTION, BIOMASS, AND PRODUCTIVITY

3.1 DISTRIBUTION

Distribution of seagrasses along the west coast of Florida is unique in that the plants not only occur in protected estuarine grassbeds typically found along the Gulf of Mexico coast (represented in this area by the grassbeds in embayments such as Rookery Bay, Charlotte Harbor, Tampa Bay, and St. Joseph Bay), but also form an extensive offshore bed located along the coastal reach between the St. Marks River and Tampa Bay, known as the Big Bend area.

Seagrass distribution in the eastern Gulf of Mexico has been investigated at several different levels of spatial resolution. Humm (1956) reported seagrasses observed at specific sites along the northern coast of the Gulf of Mexico. Phillips (1960a) described the general location of seagrasses around the Gulf of Mexico based on literature reports and on field surveys. Bauersfeld et al. (1969) and Earle (1972) estimated areal seagrass distribution in the eastern Gulf of Mexico using indirect methods. McNulty et al. (1972) reported seagrass distribution within embayments and estuaries in the eastern Gulf of Mexico based on field observations and on analysis of aerial photography. While the seagrass distribution within embayments adjacent to the northeastern Gulf of Mexico has been reasonably well described, the spatial extent and biomass of seagrasses of the Big Bend area have been only recently investigated (Continental Shelf Associates 1985; Iverson and Bittaker 1986).

3.1.1 Seagrass Distribution in Tampa Bay

Among the estuarine grassbeds of the west coast of Florida, those of Tampa Bay have been studied most extensively (Thorne 1954; Phillips 1962; Taylor and Saloman 1968; Lewis and Phillips 1980; Lewis et al. 1985a). While this estuary has received intense human impact and cannot be considered necessarily typical or representative of west Florida bays, the abundance of information on Tampa Bay seagrasses provides a useful base for comparison with other areas.

Thorne (1954) identified five seagrasses occurring in the bay: *Thalassia*, *Syringodium*, *Halodule*, *Ruppia maritima* and *Halophila engelmannii*. In his survey of seagrasses of Tampa Bay, Phillips (1962) reported the presence of all species but *Halophila*; however, this seagrass was later observed in the bay by Lewis and Phillips (1981) and Moffler and Durako (reported in Lewis et al. 1985a). Phillips (1962) noted that the southern part of the bay was dominated by *Diplanathera* (*Halodule*) and in the northern part *Ruppia* was more abundant, presumably due to a salinity gradient. *Thalassia* is relatively sparse in Tampa Bay, possibly because of low salinities (Phillips 1962), but is the dominant species in the adjacent waters of Boca Ciega Bay (Pomeroy 1960; Phillips 1962; Taylor and Saloman 1968). Lewis et al. (1985a) estimated that the current distribution of seagrasses in the bay, covering 5,750 ha (14,203 acres) represents a reduction of 81% of historical coverage prior to human impact (Figure 9).

a. Seagrass associations. There are five types of seaqrass meadows found in Tampa Bay (Figure 10). Mid-bay shoal perennial beds contain *Thalassia*, *Syringodium*, and *Halodule*, but rarely *Ruppia*, due to either the fast currents or increased salinities found on the shoals where these

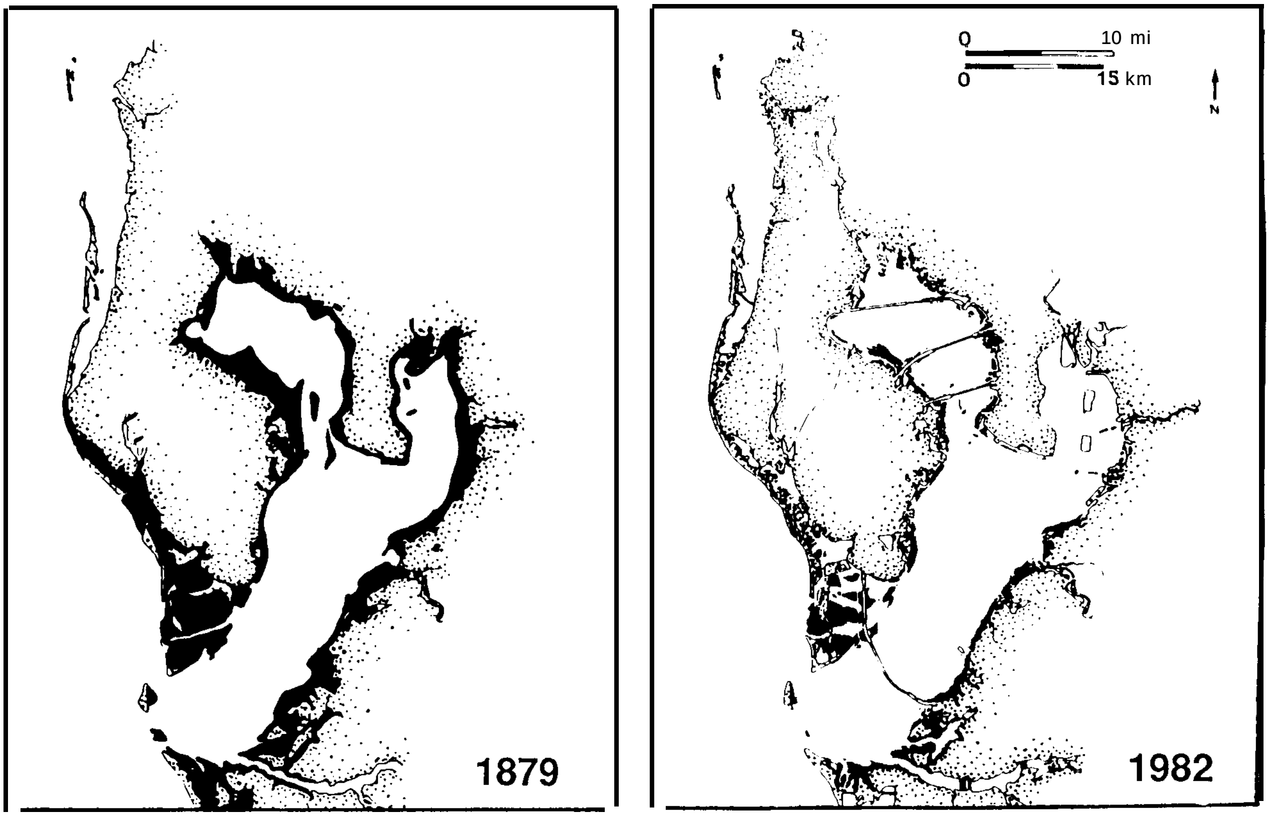


Figure 9. **Seagrass** coverage in Tampa Bay in 1879 and 1982 (after Lewis et al. 1985).

beds grow. Healthy fringe perennial beds contain all five species found in the bay. In these beds, Ruppia is found in the shallowest water close to shore, followed by almost pure stands of Halodule, Thalassia, and Syringodium, respectively, as depth increases. These meadows generally have an unvegetated sand bar separating the seagrasses from the main body of the bay. Stressed-fringe perennial beds are similar to their healthy counterparts except coverage is reduced, and migration of a destabilized sand bar eventually leads to the disappearance of the bed. These beds occur in areas of the bay where phytoplankton are abundant, possibly competing with the benthic macrophytes. Finally, colonizing perennial grassbeds are found in bands in the euphotic zone of man-made fill areas. The dominant species here are Halodule and Syringodium, presumably because their rhizomes are more readily fragmented and dispersed to unvegetated areas.

b. Sediment effects. According to Thorne (1954) seagrass distribution in the Gulf of Mexico was limited to soft marl, mud, or sand substrates. Phillips (1962) found that all seagrasses in Tampa Bay grew in muddy sand, while sandy substrates remained unvegetated. The sediments of the bay contain varying amounts of carbonates, which may be important in determining the availability of essential nutrients.

c. Depth distribution. Phillips (1962) reported that seagrass growth was limited to depths of less than one fathom (2 m) in the turbid waters of Tampa Bay. Syringodium dominates below the spring low-tide mark, and in deeper water frequently occurs in mixed stands with Thalassia (Humm 1956; Phillips 1960a; Phillips 1962). Shallow areas are dominated by Ruppia

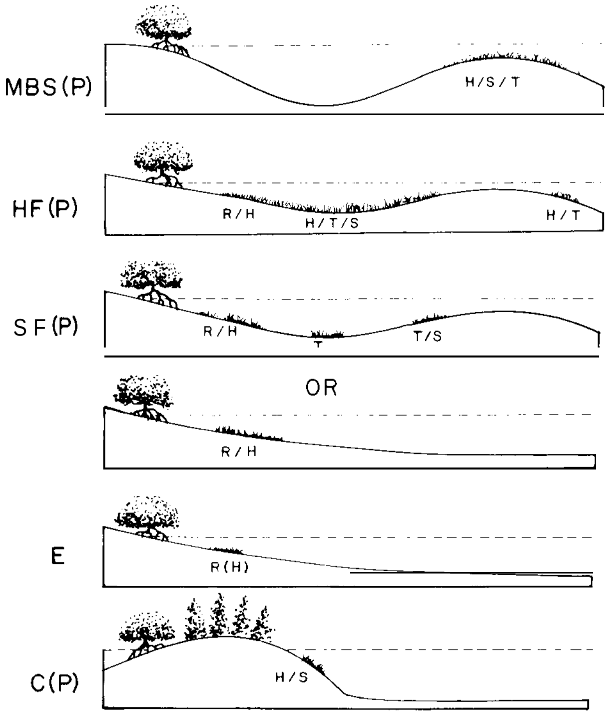


Figure 10. **Seagrass** meadow types in Tampa Bay. **MBS(P)** = mid-bay shoal perennial; HF(P) = healthy fringe perennial; SF(P) = stressed fringe perennial; E = ephemeral; C(P) = colonizing perennial (after Lewis et al. 1985).

and *Halodule* (Phillips 1962). Three morphologically distinct forms of *Halodule* in the bay were identified according to depth distribution Dwarfed plants occurred in areas exposed at neap and spring low tides, while subtidal plants were more robust (Phillips 1960d). Salinity rather than tidal exposure was thought to control the distribution of *Ruppia* in the bay (Phillips 1962).

3.1.2 Seagrass Distribution in the Big Bend Area

The Big Bend seagrass bed overlies drowned karst topography which extends from the town of St. Marks south to Tarpon Springs. The sediments of this low energy region are composed of clay and silicious sand over limestone. Results of recent investigations suggest that seagrasses are the dominant benthic feature of the nearshore environment from St. Marks to Tampa (Iverson and Bittaker 1986; Continental Shelf Associates 1985) Analysis of a photographic composite obtained from aerial photography (Continental Shelf Associates 1985) revealed some broad-scale patterns in seagrass distribution with beds of greatest density in shallow water well removed from river mouths. Beds of lesser density extended as far as 112 km offshore (Figure 11).

Samples for characterization of seagrass distribution in eastern Gulf of Mexico coastal waters were taken by Iverson and Bittaker (1986) from St. Marks to Tampa during the month of October for several years. Visual observations of the presence or absence of different seagrass species were made at each of about 300 stations in the Big Bend area of north Florida (Figure 12). Samples for estimation of seasonal seagrass biomass changes were collected within a 10 m radius of a metal marker stake located in 1 m water depth at stations near the Florida State University Marine Laboratory at Turkey Point, and in St. Joseph Bay.

The line marking the outer limit of the seagrass beds in Figure 12 indicates the maximum depth to which seagrass coverage of about 80% or more of the bottom extended within each major area. Vegetation covered about 3,000 km^2, with seagrasses occurring as a band varying from 11 to 35 km wide between St. Marks and Tarpon Springs, Florida.

All six species of seagrasses presented in Chapter 1 were found in the Big Bend grassbeds. *Halodule* occasionally formed both the innermost and the outermost monospecific stands in this area. Shallow-water *Halodule* growing on shoals often exposed at low tide, generally had short, narrow leaves, and deep-water *Halodule* was tall with wider leaves (Iverson and Bittaker 1986). Shallow-water and deep-water forms of *Halodule* appear to be morphologically different clones (Phillips 1960b; McMillan 1978). Shallow areas not exposed on low tides contained mixtures of *Thalassia*, *Syringodium*, and *Halodule*. Densest portions of the seagrass bed were dominated by *Thalassia* and *Syringodium* in

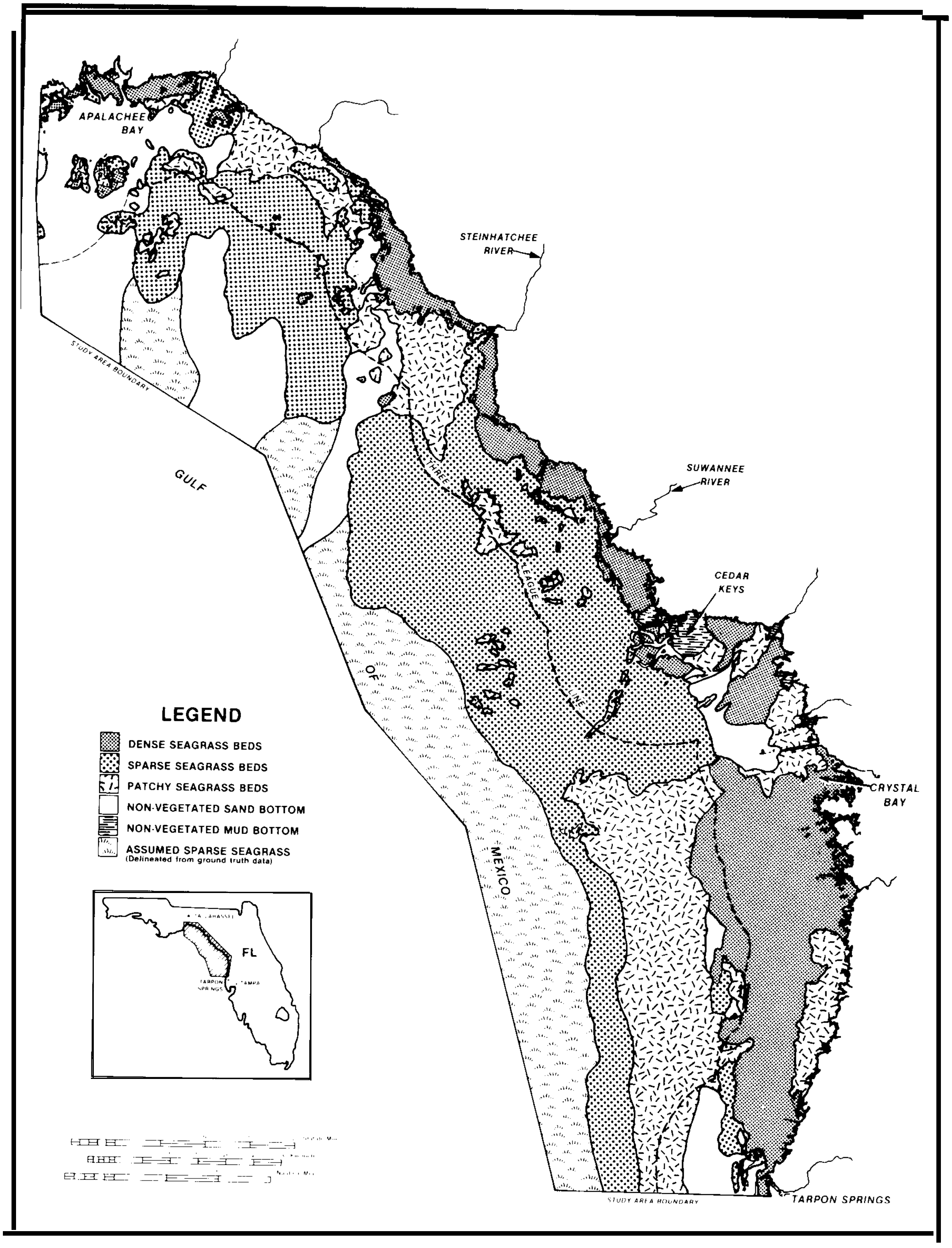


Figure 11. Seagrass distribution and density in the Big Bend area (adapted from Continental Shelf Associates 1985).

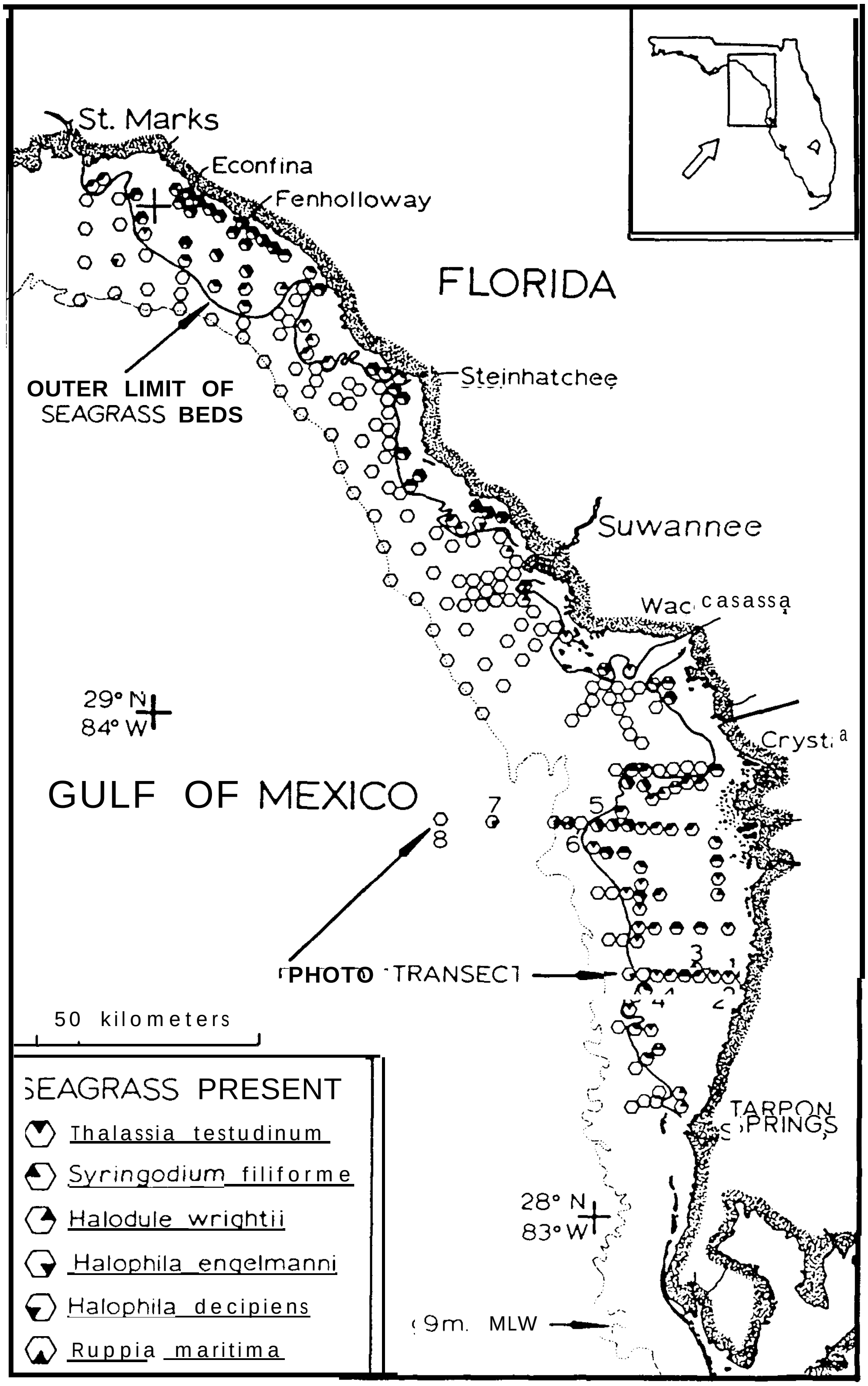


Figure 12. Seagrass species distribution in the Big Bend area (after Iverson and Bittaker 1986).

various mixtures. Halophila engelmanni was common in this grassbed, and was often mixed with Thalassia and Syringodium. Halophila engelmanni was also abundant outside the major seagrass bed to depths of at least 20 m where it occurred in monotypic stands (Continental Shelf Associates. 1985). Halophila decipiens occasionally occurred in small monotypic stands or mixed with sparse Halodule or Caulerpa populations in northern offshore areas deeper than 5 m, as well as in some of the shallowest areas (Continental Shelf Associates 1985). Ruppia was primarily restricted to low salinity areas such as the mouths of the Econfina and Suwannee Rivers.

a. Depth distribution control. Iverson and Bittaker (1986) showed that the major seagrass species were distributed throughout the seagrass beds in mixed associations (Figure 12), in contrast to south Florida, where large monospecific beds are far more common. Thalassia and Syringodium comprised most of the biomass which extended to about 5 m water depth. Halodule wrightii and Halophila engelmanni contributed very little to total seagrass leaf biomass.

A transect taken across a grassbed near the Florida State University Marine Laboratory showed that Thalassia was present in greatest leaf biomass at depths between 0.5 and 2 m, while Syringodium reached greatest leaf biomass at 2.5 m (Figure 13). Halodule occurred at both ends of the transect (Iverson and Bittaker 1986). The general pattern in fine-scale depth distribution of seagrass species appears to be similar among the various American tropical seagrass beds for which observations have been reported. Strawn (1961) described the cross-bed, seagrass distribution near Cedar Key in the northeast Gulf of Mexico. Halodule occurred in monotypic stands on shoals exposed to the atmosphere at low tide and was distributed throughout the seagrass bed. Thalassia grew only in subtidal areas and did not extend to the deepest limits of the bed which contained Syringodium. This depth distribution pattern was evident in several diverse areas: in the grass bed samples in northern Apalachee Bay (Iverson and Bittaker 1986), in the northwest Cuban seagrass bed (Buesa 1974), in a Nicaraguan seagrass bed (Phillips et al. 1982), and in a seagrass bed near Buck Island, St. Croix (Wiginton and McMillan 1979).

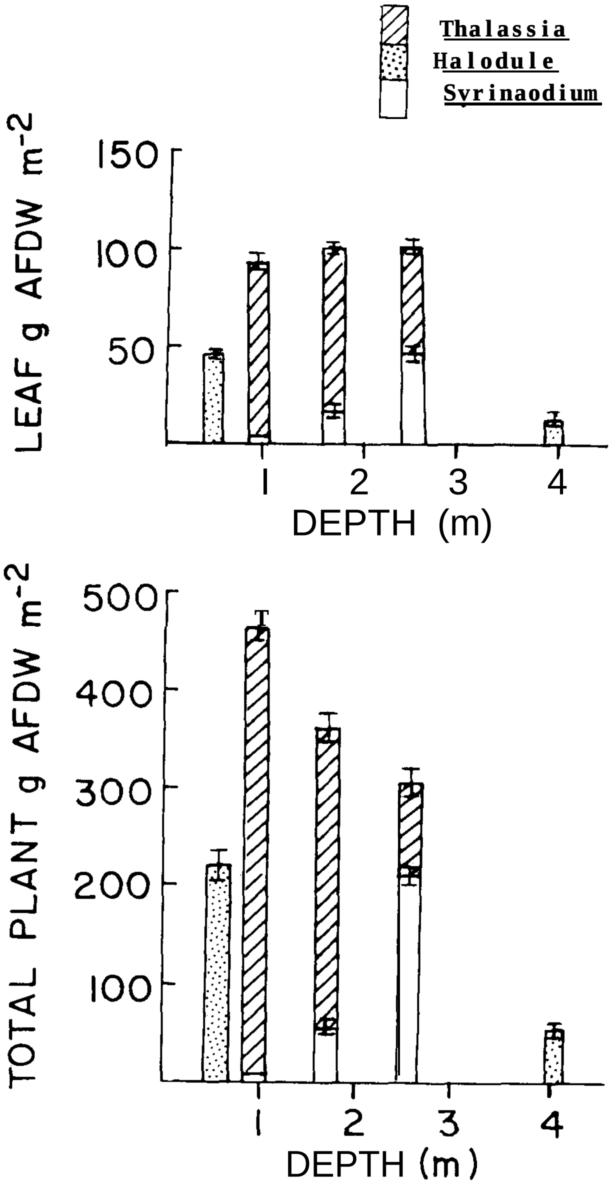


Figure 13. Depth distribution of seagrass biomass in Apalachee Bay (after Iverson and Bittaker 1986).

For many kilometers along the outer limit of the Big Bend seagrass bed between Tarpon Springs and Crystal River, an observer on the waters' surface notices a distinct transition from the dark green outer edge of the seagrass bed and the light sediment bottom seaward of the bed edge. The outer edge of the grassbed is deeper north of Tarpon Springs, in the Big Bend bed, compared with the part between St. Marks and the Crystal River. This variation is a consequence of increased water clarity in the southern part of the Big Bend seagrass bed, as indicated by the extinction coefficients for light energy in the water column measured in those areas. In addition, subjective observations made over a period of years suggest that the relative differences in water clarity from the two areas are consistent (R.L. Iverson, unpubl. data). The nearshore waters of the Big Bend area receive river runoff colored by organic compounds (Bittaker 1975) which, in addition to particulates, contributes to the increased turbidity and higher extinction coefficients observed in that area (Zimmerman and Livingston 1979).

Based on the depth-distribution data obtained in several different investigations, the light-energy compensation level for the annual growth of American tropical seagrass communities dominated by Thalassia appears to be about 10% of sea-surface photosynthetically active light energy. The depths to which 10% of sea-surface light energy penetrated, calculated from measured extinction coefficients, were 7 m for the part of the seagrass bed between Tarpon Springs and Crystal River, and 4.5 m for the portion north of Crystal River. These depths approximate the seaward limit of the major seagrass beds composed of Thalassia, Syringodium, and Halodule in those respective areas of the eastern Gulf of Mexico. Although Thalassia and Syringodium were distributed to greater depths in Cuban coastal waters (Buesa 1974) and in St. Croix waters (Wiginton and McMillan 1979) compared with the Big Bend area and Florida Bay, most of the leaf biomass in the northwest Cuban and the Buck Island, St. Croix, seagrass beds was located shallower than the depth to which 10% of surface light energy penetrated. The maximum possible area in which Thalassia can form well-developed beds appears to be constrained by the slope of the sea floor and the bottom depth of the isolume corresponding to 10% of surface light energy (Iverson and Bittaker 1986).

b. Salinity and temperature effects. The nearshore species composition of seagrass assemblages in the northern bed is influenced by freshwater discharges entering the northeastern Gulf of Mexico from several rivers along the coast. Thalassia testudinum and Syringodium filiforme do not grow in areas of low salinity water in the northeastern Gulf of Mexico (Phillips 1960a) and were not reported in areas with salinities less than about 17 ppt in the northern seagrass bed (Zimmerman and Livingston 1976a).

The seagrasses of the Big Bend area experience a large temperature range (8-33 °C) (Goulet and Haynes 1978). Seagrasses from this bed were more tolerant of very cold temperatures than were seagrasses from Florida bay (McMillan 1979; McMillan and Phillips 1979); however, each winter, leaves of Big Bend seagrasses die back to within several centimeters of the sediment-water interface (Zimmerman and Livingston 1976b), a phenomenon also observed in seagrass beds in Texas waters during cold winters (Phillips 1980).

c. Sediment effects. Thalassia grew in coarser sediments than did the other seagrasses of the Big Bend area (Iverson and Bittaker 1986). Buesa (1975) reported that Thalassia in northwest Cuban grassbeds also grew in coarser sediments than did other seagrasses.

Sediment deposition on leaf surfaces significantly interferes with the growth of both Thalassia testudinum and Halodule wrightii (Phillips 1980). Water turbidity was inversely related to distance from the Econfina River mouth (Bittaker 1975; Zimmerman and Livingston 1979), suggesting that turbidity effects on seagrass growth occur primarily nearshore as proposed by Humm (1956). Moore (1963a) reported that high-water turbidity precluded the growth of Thalassia testudinum in Louisiana coastal waters within the Mississippi River plume.

3.2 BIOMASS

Seagrass biomass can vary greatly depending not only on the species but on such environmental variables as available light, sediment depth, nutrient availability, and circulation. The biomass of Halophila is always low, but Thalassia biomass can reach values greater than 7 kg m^{-2} (Burkholder et al. 1959). Ranges of biomass values for Thalassia, Syringodium, and Halodule are presented in Table 5. The results of many of these studies have been summarized by various authors (McRoy and McMillan 1977; Zieman and Wetzel 1980; Zieman 1982; Thayer et al. 1984b; Lewis et al. 1985a). Since the studies involve a wide range of experimental conditions, including differences in habitat, sampling times and seasons, and sample replication, attempts to compare or generalize based on the cumulative data are of questionable value.

The majority of seagrass biomass, particularly in the larger species, is below the sediment surface. Ordinarily, 15%-20% of Thalassia's biomass is in the leaves (although reported values range from 10% to 45%) with the rest made up by roots, rhizomes, short shoots, and sheathing leaves (Zieman 1975, 1982). Sediment type can affect the relative amount of biomass above and below the surface: the ratio of leaf to root and rhizome biomass in Thalassia increased from 1:3 in fine mud to 1:5 in mud and 1:7 in coarse sand (Burkholder et al. 1959). It is unclear whether this reflects enhanced leaf production in nutrient-richer fine sediments or the need for greater root development for increased nutrient absorption in the generally poorer coarse sediments. Thalassia has the most robust root and rhizome system of the seagrasses of Florida. Halodule and Syringodium have shallower, less well-developed roots and rhizomes, and tend to have a greater portion of their total biomass, 50% to 60%, in leaves (Zieman 1982). However, Pulich (1985) reported that Halodule from Redfish Bay, Texas, had 66% of total biomass below the sediment surface, compared to 31% for Ruppia. Reported values for the relative portions of' above- and below-ground biomass in Florida west coast species are shown in Table 6.

3.2.1 Seagrass Biomass in Tampa Bay

Both above- and below-ground biomass of the seagrasses of the bay were determined by Lewis and Phillips (1980). Ruppia had the lowest biomass, both for standing crop (portion of plant above sediment surface) and root and rhizome (below sediment surface). Thalassia had the highest below-ground biomass, but its leaf standing crop was similar to that of Syringodium.

In nearby Boca Ciega Bay, Thalassia leaf standing crop exhibited seasonal variation, reflecting temperature extremes. Dry weights peaked in spring and early summer, declined during mid-summer temperature maxima, and dropped to the lowest values during winter months (Phillips 1960a). Durako and Moffler (1985c) observed a similar seasonal pattern in maximum leaf lengths of Thalassia in Tampa Bay. Seagrass biomass for the Tampa Bay area, as reported by Lewis et al. (1985a), is given in Table 7.

3.2.2 Seagrass Biomass in the Big Bend Area

Thalassia and Syringodium comprised 84% of total leaf biomass in the Big Bend area; Thalassia alone accounted for 58% of leaf biomass compared to 64% for grassbeds in Florida Bay (Iverson and Bittaker 1986). Thalassia leaf biomass reached a seasonal maximum during August and then declined rapidly at stations located near the Florida State University Marine

Table 5. Representative values of seagrass biomass (g dry weight m^{-2}).

Species	Biomass	Location	Source
Ruppia maritima	60-160	Texas	Pulich 1985
Halodule wrightii	10-400	Texas	McMahan 1968; McRoy 1974; Pulich 1985
	22-208	North Carolina	Kenworthy 1981
	10-300	South Florida	Zieman unpubl.
Syringodium filiforme	15-1100	South Florida	Zieman unpubl.
	30-70	Texas	McMahan 1968
Thalassia testudinum	30-500	Cuba	Buesa 1972,1974; Buesa and Oleachea 1970
	60-718	Puerto Rico	Burkholder et al. 1959; Margalef and Rivero 1958
	60-250	Texas	Odum 1963; MCRoy 1974
	20-1800	Florida (east coast)	Odum 1963; Jones 1968; Zieman 1975b
	57-6,400	Florida (west coast)	Bauersfeld et al. 1969; Phillips 1960a; Taylor et al. 1973a

Laboratory and in St. Joseph Bay (Figure 14). The seasonal effect is related to cycles of light intensity and water temperature (Iverson and Bittaker 1986). The ratios of seasonal maximum to seasonal minimum values at these sites were between 6:1 and 8:1, showing the difficulty of comparing sites on the basis of biomass data, particularly in higher latitudes where seasonal patterns are more pronounced. Continental Shelf Associates (1985) found that for offshore stations with significant blade densities, the density decreased by over 50% at 7 of 11 stations in the winter months. Most stations that showed no difference or a slight increase had only sparse seagrass cover.

The seagrass beds of St. Joseph Bay are primarily composed of Thalassia testudinum growing in monospecific stands. McNulty et al. (1972) estimated 2,560 ha of seagrass coverage within St. Joseph Bay.

Table 6. Biomass partitioning in seagrasses.

Species	Component	Biomass (g dry wt m^{-2})	% of Total	Reference
Ruppia maritima	Above ground	110	69	
	Below ground	50	31	Pulich 1985[a]
	Above ground	48	50	
	Below ground	48	50	Lewis and Phillips 1980
Halodule wrightii	Above ground	150	34	
	Below ground	290	66	Pulich 1985
	Above ground	5-54	11-33	
	Below ground	10-200	67-89	Zieman 1982
Syringodium filiforme	Above ground	28-102	16-47	
	Below ground	31-521	53-84	Zieman 1982
Thalassia testudinum	Above ground	58-267	11-15	
	Below ground	321-2,346	85-90	Zieman 1982

[a] Peak seasonal biomass values.

Table 7. Seagrass biomass of the Tampa Bay area (g dry wt m^{-2}) (from Lewis et al. 1985a).

Species	Location	Biomass		Reference
		Above ground	Below ground	
Ruppia maritima	Tampa Bay	1.48	18-48	Lewis and Phillips 1980
Halodule wrightii	Tampa Bay	38-50	60-140	Lewis and Phillips 1980
Syringodium filiforme	Tampa Bay	50-170	160-400	Lewis and Phillips 1980
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 et al. 1969
		320-1,198		Taylor and Saloman 1969
	Tarpon Springs	601-819		Dawes et al. 1979
	Tampa Bay	25-180	600-900	Lewis and Phillis 1980

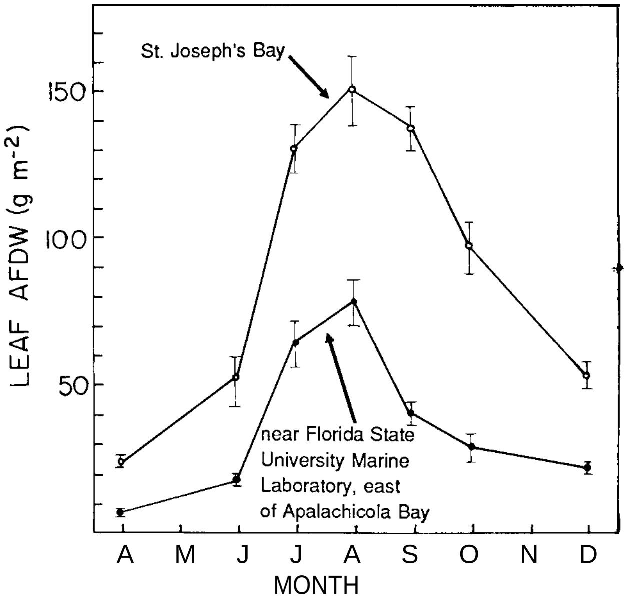


Figure 14. Seasonal cycle of *Thalassia* at two stations in Apalachee Bay(after Iverson and Bittaker 1986).

Another estimate of St. Joseph Bay seagrass coverage obtained during 1978 was 2,300-2,400 ha of coverage, suggesting that seagrass beds are a stable feature of the benthos of St. Joseph Bay and are not markedly affected in spatial coverage by seasonal cycles in leaf biomass density (Savastano et al. 1984). Iverson and Bittaker (1986) found that short-shoot densities did not change significantly throughout the year, and suggested that, during the fall of the year, the use of shoot densities for interbed biomass comparisons would be more appropriate for this area.

3.3 PRODUCTIVITY

The high rates of primary productivity of seagrasses is well recognized. Studies of biomass literature have reported a wide spectrum of productivity measurements (Table 8). Past studies have focused on

Table 8. Seagrass productivity measurements.

Species	Productivity ($g\ C\ m^{-2}\ day^{-1}$)	Site	Reference
Halodule wrightii	0.5- 2.0	North Carolina	Dillon 1971
	1.1	Florida (east coast)	Virnstein 1982[a]
Syringodium filiforme	0.8- 3.0	Florida	Zieman unpubl.
	0.6- 9.0	Texas	Odum and Hoskin 1958; McRoy 1974
Thalassia testudinum	0.6- 7.2	Cuba	Buesa 1972,1974
	2.5- 4.5	Puerto Rico	Odum et al. 1960
	1.9- 3.0	Jamaica	Greenway 1974
	0.5- 3.0	Barbados	Patriquin 1972b; 1973
	0.9-16.0	Florida (east coast	Odum 1957,1963; Jones 1968; Zieman 1975a

[a] Calculated as 38% of reported dry weight.

Thalassia, but more recently Halodule and Syringodium have been studied.

A major problem encountered in attempts to synthesize the results of various productivity studies is that the three major methods of measurement--leaf marking, O$_2$ evolution, and ^{14}C uptake--each yield somewhat different results. In the literature, the highest values are obtained using the O$_2$ method, the lowest values result from leaf marking, while ^{14}C measurements provide intermediate values (Zieman and Wetzel 1980; Kemp et al. 1986). In a carefully developed study, Bittaker and Iverson (1976) found that ^{14}C and leaf marking gave essentially identical results when the ^{14}C results were corrected for inorganic losses, incubation chamber light absorption, and differences in light energy resulting from differences in experimental design. In a study of Thalassia in Bimini, Capone et al. (1979) found, however, that productivity measured by the ^{14}C method was double the rates obtained from the leaf marking technique (Zieman 1974; Fry 1983) which underestimates net productivity since it does not measure below-ground productivity, excreted carbon, or herbivory. The ^{14}C method allows the investigator to determine the partitioning of photosynthate within the plant. Figure 15 shows the location of ^{14}C in Thalassia after a 4-hour incubation period. The leaves contained 49% of the radiocarbon although they made up only 13% of the total biomass.

Despite the methodological differences, studies of the productivity of seagrasses have shown that these are highly productive systems, especially when growing under optimal or near-optimal conditions.

3.3.1 Seagrass Productivity in Tampa Bay

Surprisingly little data exist on the productivity of the seagrasses of this area. In nearby Boca Ciega Bay, Pomeroy (1960) estimated that Thalassia and Syringodium occurring at depths less than 2 m, fixed 500 g C.m^{-2}. yr^{-1}. He concluded that, at these depths, seagrasses, microflora, and phytoplankton were equally important primary producers, whereas

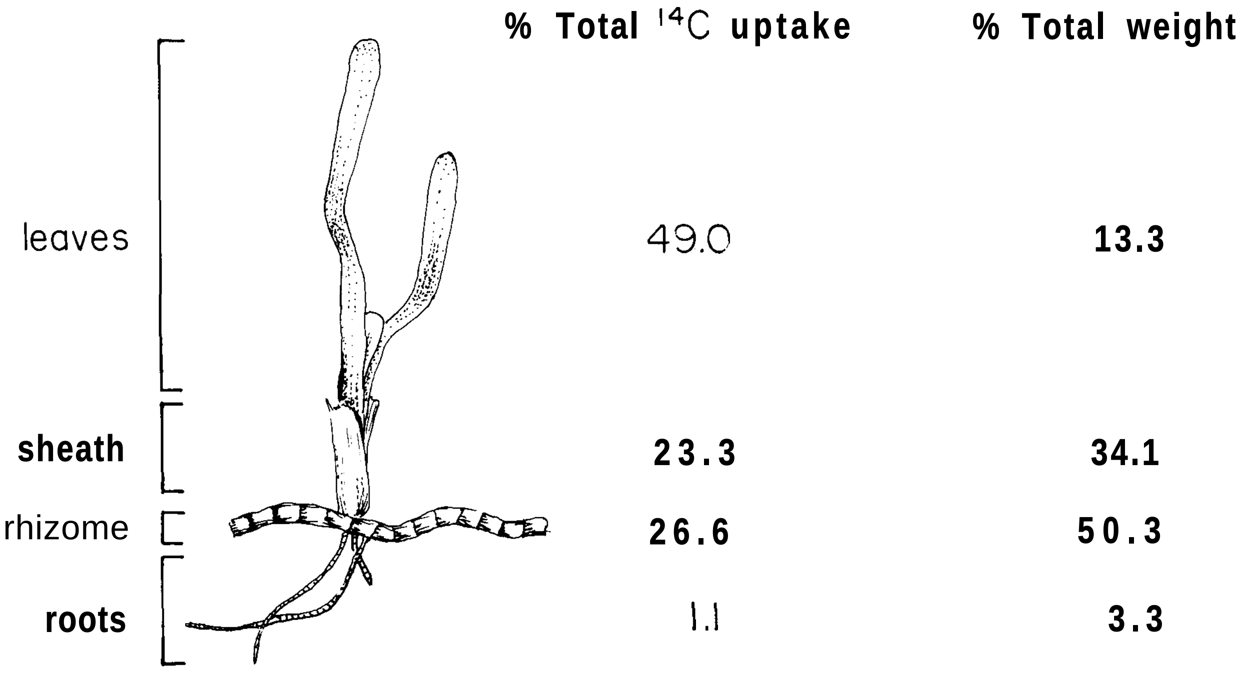


Figure 15. Location of recently fixed carbon photosynthate in *Thalassia* after4 hour incubation. The right hand column shows the typical weight distribution in the plants (after Bittaker and Iverson 1976).

phytoplankton production dominated in deeper waters. Johansson et al. (1985) estimated that phytoplankton productivity in Tampa Bay was higher in deep waters (340 g C.m^{-2}. yr^{-1}) than in shallow waters (50 g C.m^{-2}. yr^{-1}), and concluded that, in contrast to the results of McNulty (1970), phytoplankton production was ten times higher than benthic production in the bay.

Studies of Thalassia leaf growth in Tampa Bay show that leaf lengths can increase at a rate of 5 cm per month during the period of maximum growth in the spring. Maximum leaf length occurs in early summer, before high temperatures cause a mid-summer die-back (Lewis et al. 1985a).

3.3.2 Seagrass Productivity in the Big Bend Area

A seasonal cycle was evident in macrophyte carbon-production data obtained over a period of several years at a station in the northern part of the Big Bend area (Figure 16). Thalassia testudinum contributed most of the carbon production per unit area (up to 2.2 g C.m^{-2}.d^{-1} in July), except for a brief midsummer period when red drift macroalgae were the largest source of photosynthetic carbon fixation. Data from which these composite carbon production figures were made were taken from Bittaker (1975), who showed that the annual carbon production cycle was related to annual variations in solar radiation and water temperature.

Near the Anclote River, seagrass productivity estimated from leaf growth measurements was reported as 2-15 mg C.m^{-2}.h^{-1} for Thalassia, 2-37 mg C.m^{-2}.h^{-1} and 0.9-1.4 mg C m^{-2} h^{-1} for Syringodium and Halodule, respectively (Ford 1974 et al.; Ford and Humm 1975).

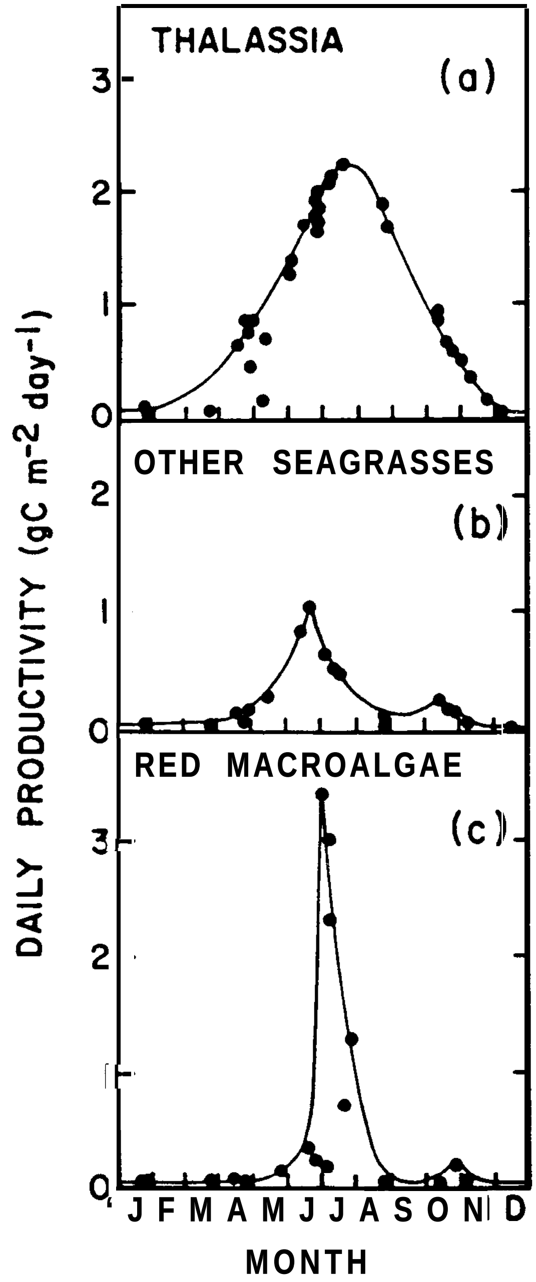


Figure 16. Seasonal changes in productivity of seagrasses and red algae in Apalachee Bay (unpublished data from R. L. Iverson).

CHAPTER 4. COMPONENTS OF THE SEAGRASS COMMUNITY

The distribution and density of seagrass species are dependent on the physical, chemical, and geological environment, while the associated community is the product of this seagrass composition as well as the abiotic variables. Along the west coast of Florida, from Florida Bay to Apalachicola Bay, there are large variations in all of the major physico-chemical parameters. This environmental gradient is reflected in the changes of species associations and community structure within the seagrass system.

Although it is obvious that large changes in abiotic variables and plant composition and density can produce major changes in the community structure, even subtle variations apparently can produce major community differences. At five sample sites in a single south Florida estuary with Thalassia blade densities of over 3,000 m^{-2} the total number of macrofaunal taxa'varied from 38 to 80, and the average density of individuals varied over two orders of magnitude, from 292 to 10,644 individuals m^{-2} (Brook 1978).

Organisms found in seagrass communities can be classified in a number of ways, depending on the objectives of the classification. The biota present in a seagrass ecosystem can be classified in a scheme that recognizes the central role of the seagrass canopy in the organization of the system, and classifies the organisms according to their position relative to the canopy. The principal groups are: (1) epiphytic organisms, (2) epibenthic organisms, (3) infaunal organisms, (4) the planktonic organisms, and (5) the nektonic organisms.

Epiphytic organisms are defined according to the usage of Harlin (1980) and Zieman (1982) as any sessile organism growing on a plant (not just a plant living on a plant). Epibenthic organisms are those that live on the surface of the sediment, and include, in the broadest sense, motile organisms such as large gastropods and sea urchins, as well as sessile forms, such as sponges and sea anemones or macroalgae. Infaunal organisms are those that live buried in the sediments, such as sedentary polychaetes and bivalves, and relatively mobile infauna, such as irregular urchins. Organisms that are buried part-time, for shelter, such as penaeid shrimp or blue crabs, or while waiting for prey, like flounders, are considered epibenthic and not infauna. Planktonic organisms are the minute plants and animals, such as diatoms, dinoflagellates, and many copepods that drift in the water column. They may show local movement, and especially may migrate vertically, but are largely at the mercy of water currents for their lateral movement. By comparison, nektonic organisms are highly mobile organisms living in or above the plant canopy, such as fishes and squids.

Another classification scheme, first proposed by Kikuchi (1980), and slightly modified by Zieman (1982), is based on the mode of utilization of the seagrass beds by the associated fauna. This classification is based on whether organisms are: (1) permanent residents, (2) seasonal residents, (3) temporal migrants, (4) transients, or (5) casual visitors.

4.1 ALGAL ASSOCIATES

The major sources of primary production for coastal and estuarine areas are: (1) macrophytes (seagrasses, macroalgae, salt marsh plants, and mangroves), (2) benthic microalgae (benthic and epiphytic diatoms, dinoflagellates, filamentous green and bluegreen algae), and (3) phytoplankton. In estuarine and coastal regions the relative balance of standing crop and productivity between the major groups of primary producers is a function of many environmental variables, but the major determinants are water column nutrients, turbidity, and substrate. In areas of high water-column nutrients, phytoplankton and microalgal growth will dominate, because these small or single-cell algae rapidly respond to the increased nutrient supply. Because benthic plants take up nutrients from the sediments via their roots, these plants are less able to exploit increased nutrient levels in the water column. The turbidity created by increased algal growth, along with suspended sediments, will cause attenuation of the light reaching the bottom of the water column and thus decrease the light available to benthic plants for photosynthesis. Thus, increased nutrient levels favor suspended and epiphytic plants (both of which derive their nutrients from the water column) at the expense of the benthic attached forms. Turbidity favors phytoplankton primarily since they are capable of moving upward in the water column to intercept the light necessary for photosynthesis. Sediment type is also important in determining benthic communities. Soft sediments favor seagrasses and certain rhizophytic green algae, while rocky substrates favor the development of macroalgal communities.

While portions of the coastal region of west Florida are still miraculously pristine, much of the area is heavily urbanized or otherwise disturbed. Still, as late as 1968, Taylor and Saloman estimated that in Boca Ciega Bay total production, dominated by macrophytes, was six times the annual phytoplankton production.

4.1.1 Phytoplankton

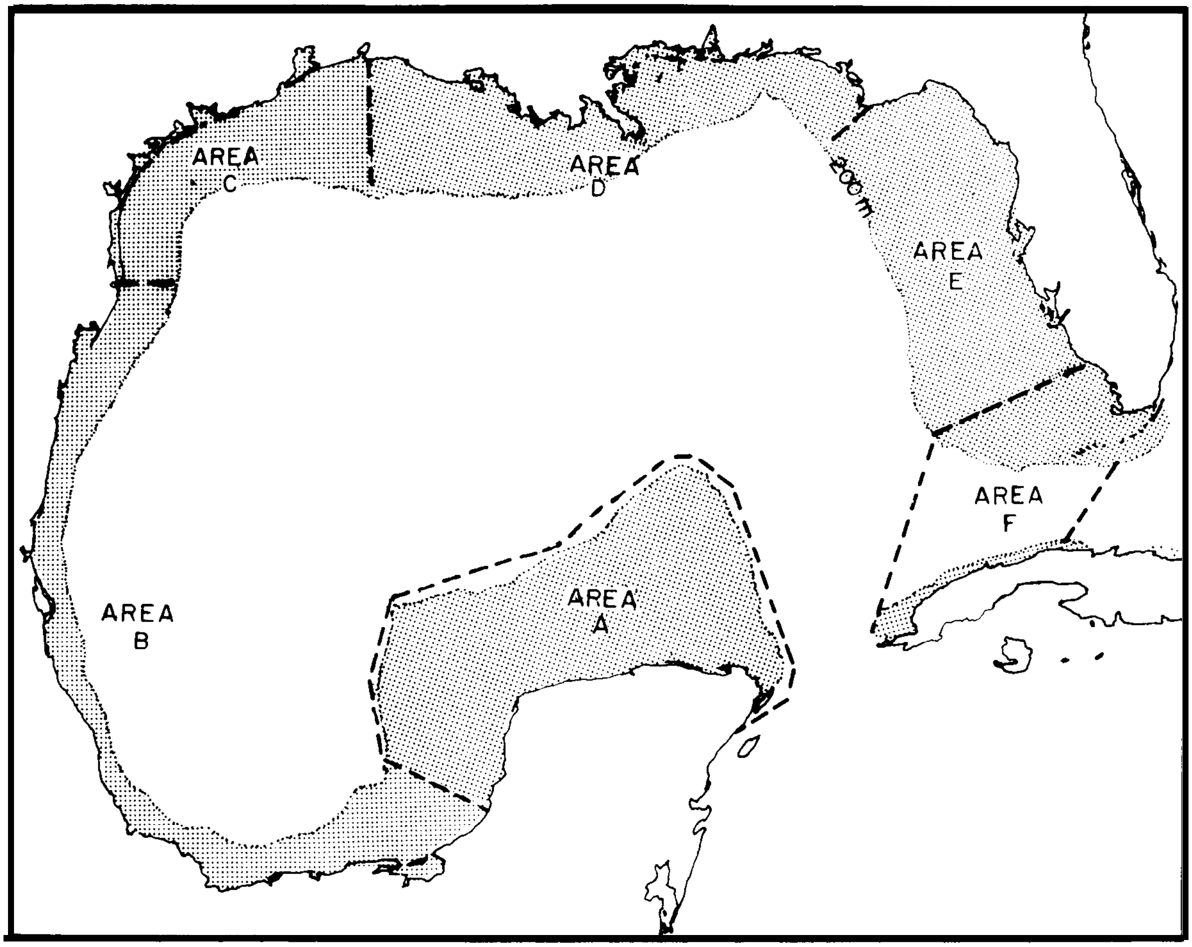
In the coastal and estuarine waters of west Florida, Steidinger (1973) identified four phytoplankton assemblages: estuarine, estuarine-coastal, coastal-open Gulf of Mexico and open gulf. Within these areas, diatoms generally dominate the estuarine and inshore regions, while dinoflagellates are more diverse and abundant in the open gulf and in gulf-influenced areas. The predominant organisms are ubiquitous, cosmopolitan species that are coastal residents, but occasional secondary abundance peaks are attributed to sporadic visitor species. Standing crop and productivity are higher in areas of terrestrial runoff or river mouths, and are lowest offshore in the open gulf, except in areas where divergence or upwelling make more nutrients available (Steidinger 1972, 1973).

The phytoplankton of Tampa Bay are typically dominated by nannoplankton (less than 20 pm), except for periodic blooms of blue-green algae (Schizothrix) or dinoflagellates (Gonyaulax, Gymnodinium nelsonii and others). The dominant species in the bay is the diatom Skeletonema costatum. The red-tide organism Ptychodiscus brevis (= Gymnodinium breve), a toxic coastal species. has invaded the bay 12 times between 1946 and 1982, dominating once for over three months (Steidinger and Gardiner 1985).

Johansson et al. (1985) estimated that phytoplankton in Tampa Bay accounted for 91% of the submerged vegetative production. In deep areas of the bay phytoplankton production was estimated at 340 g $C.m^{-2}.yr^{-1}$; a maximum value of 620 g $C.m^{-2}.yr^{-1}$ was calculated from ^{14}C data (Johansson et al. 1985). In Boca Ciega Bay, Pomeroy (1960) estimated that phytoplankton, benthic microflora, and Thalassia production were of equal importance in depths less than 2 m, which included 75% of the bay. Phytoplankton production dominated in deeper areas.

4.1.2 Benthic Algae

The coastal regions and estuaries of west Florida have a diverse benthic algal flora, occupying several different habitats. Although once regarded as depauperate (Taylor 1954), the flora of the eastern gulf have been shown to be quite diverse in numerous subsequent studies (summarized in Earle 1972; Dawes 1974). In addition to cosmopolitan gulf and Caribbean species, the region also has a pronounced seasonal peak of species with a discontinuous Atlantic-northern gulf distribution (Earle 1972). Figure 17 shows the relative richness and diversity of the algal flora of the region when compared to other areas of the Gulf of Mexico: west Florida waters exhibit less variation in algal flora than the waters of south Florida and northern Cuba but are more diverse in its algal composition than the northern Gulf of Mexico. Table 9



Taxonomic Group	Number of Species in Different Areas						
	A	B	C	D	E	F	Total
Chlorophyta	85	42	45	43	97	151	174
Chrysophyta						1	1
Cryptophyta						1	
Cyanophyta	6	16	21	21	30	20	31
Phaeophyta	41	33	23	24	52	58	82
Rhodophyta	120	121	86	42	171	270	349
Tracheophyta	6	5	4	6	6	6	7
Xanthophyta					1	1	2

Figure 17. Distribution and diversity of benthic marine plants in the Gulf of Mexico. Total is the actual number of species counted in areas A-F (after Earle 1972).

Table 9. Macroalgae of seagrass communities of the west Florida coast.

Location	Total Species	Cyanophyceae	Chlorophyceae	Phaeophyceae	Rhodophyceae
Anclote Anchorage[a]	124	18	39	17	50
Apalachee Bay[b]	34		13	4	17
Seven Sites[c]	30		11	2	17
Crystal River[d]	106		19	24	63
Southwest Coast[e]	148		50	28	70

Table modified from Dawes (1987), with additional material. (a) Hamm and Humm (1976); (b) Zimmerman and Livingston (1976b); (c) Dawes (1985) Dominant species only; (d) Steidinger and van Breedveld (1971); (e) Dawes et al. (1967). Many stations in this survey were offshore of developed seagrass beds.

lists the total number of macroalgal taxa from several sites in Florida and shows the distribution by division at each area.

Because of the combination of protected estuaries on the central and southern portions of the Florida west coast and the gently sloping shelf and moderate wave climate to the north of Tampa Bay, the west coast offers an enormous area for the colonization of either algae or seagrasses. The primary substrates available for algae in the region include: (1) rocky outcrops and hard bottom (2) soft sediments (3) seagrass leaves and mangrove roots and (4) the water column. Much of the shallow region north of Tampa Bay consists of rocky outcrops suitable for algal attachment. Throughout the area, oyster reefs, mangrove prop roots, and scattered rocks or shells offer additional algal substrate, in addition to, human-made structures like pilings, bridge supports, and canal walls.

The only marine and estuarine algae able to consistently utilize sediments as substrate are the mat-forming algae and members of the order Caulerpales of the division Chlorophyta, which possess creeping rhizoids that provide an anchor in sediments (Humm 1973; Dawes 1981). Among the most important genera are Halimeda, Penicillus, Caulerpa, and Udotea, which are primary producers of organic carbon. Halimeda and Penicillus also deposit rigid skeletons of calcium carbonate that become a major component of the sediments upon the death of the plant.

These algae do not have ability to stabilize the sediments as effectively as the seagrasses, although they do buffer currents to some degree, and by their extremely rapid growth can accomodate changes in shifting sediments. Historically, the main utility of their rhizoidal holdfasts was considered to be serving as an anchor for the plant in the substrate, but Williams (1981) has shown that they can take in nutrients through their rhizoids and translocate these throughout the plant in a manner similar to higher plants.

In many tropical and subtropical seas, the calcareous green algae are the major source of sediments. The different genera produce characteristic particles, with Halimeda tending to form sand-grain-sized plates, while Penicillus produces fine-grained aragonitic mud. At current growth rates, Penicillus alone could account for all of the fine mud behind the Florida reef tract and one third of the fine mud in northeastern Florida Bay (Stockman et al. 1967). In addition, the combination of Rhipocephalus, Udotea, and

Acetabularia generates at least as much mud as Penicillus in the same locations.

In the Bight of Abaco, Bahamas, Neumann and Land (1975) calculated that the growth of Penicillus, Rhipocephalus, and Halimeda has produced 1.5 to 3 times the amount of mud and Halimeda sand now in the basin and that in a typical Bahamian Bank lagoon, calcareous green algae alone produce more sediment than can be accomodated. Bach (1979) measured the rates of organic and inorganic production of calcareous green algae in Card Sound, south of Miami. Organic production was low in this lagoon, ranging from 8.6 to 38.4 g ash-free dry weight.m^{-2}.yr^{-1}, and 4.2 to 16.8 g $CaCO_3$.m^{-2}.yr^{-1} for all the species combined.

In areas of western Florida with hard substrate, numerous species of attached algae are found. Among the most common brown algae (Phaeophyta) are Dictyota dichotoma, Sargassum filipendula, S. pteropleuron, and Padina vickersiae (Zimmerman and Livingston 1976a; Dawes 1987). The diversity of the red algae (Rhodophyta) is much greater throughout the area. Some of the more common attached forms include Digenia simplex, Chondria littoralis, and several species of Gracilaria (Dawes 1987). The red algae are the dominant forms in the drift algae of western Florida waters, large mats or algae that have become detached from their anchorages. Rather than floating at the surface-like Sargassum, they tend to roll along on the bottom in clumps or long cylindrical windrows, moved along by tidal currents or wind action. The dominant drift alga is Laurencia, but members of other genera, including Acanthophora, Hypnea, Spyridea, and Gracilaria, are common and may be locally abundant (Dawes 1987).

Although information on the distribution, standing stock, and seasonality of macroalgae on the west coast of Florida is beginning to accumulate, studies on productivity on these plants are still sparse. In a study of seven seagrass communities on the west coast of Florida, macroalgae, both attached and drifting, comprised from 2% to 39% of the total plant standing stock (above ground biomass) (Dawes et al. 1985; Dawes 1987). While Josselyn (1975) estimated the production of Laurencia in Card Sound to average about 8.1 g dry weight.m^{-2}.year^{-1}, which was less than 1% of the production of Thalassia in the area, algal production is undoubtedly much higher in areas where the macroalgae form a substantial portion of the total biomass.

The least studied components of the algal flora continue to be the benthic microalgae. In studies of benthic production performed throughout the Caribbean, Bunt et al. (1972) found the production in Caribbean sediments to average 8.1 mg C.m^{-2}.h^{-1} (range 2.5-13.8) using ^{14}C uptake. By comparison, in the Florida Keys sediment microbes fixed 0.3 to 7.4 mg C.m^{-2}.h^{-1}. These values were found to be equivalent to the production in the water column. Lewis et al. (1985a) have suggested that within areas of excess nutrients and eutrophication, phytoplankton and benthic microalgae increase in abundance at the expense of seagrasses.

4.1.3 Epiphytic Algae

For many species of algae requiring a fixed substrate for colonization and growth (both microalgae and those reaching relatively large size), the seagrasses provide that substrate in a habitat that otherwise consists of inhospitable soft sediments. Although unifying patterns are beginning to emerge, the study of epiphytes has suffered from what Harlin (1980) has described as the "bits and pieces" approach, with most studies consisting of either extended species lists or suggestive but largely observational approaches (Dawes 1987). Literature is currently emerging that focuses on the important role that seagrass epiphytes play as a trophic base in certain seagrass systems.

Humm (1964) compiled an annotated list of 113 species of algae found epiphytic on Thalassia in south Florida. Of these only a few were specific to seagrasses; most were also found on other plants or solid substrate. Later Ballantine and Humm (1975) reported 66 species of benthic algae which were found to be epiphytic on the seagrasses of the west coast of Florida. Table 10, shows the relative distributions of algal epiphytes of sea-

Table 10. Algal epiphytes of the seagrasses of Florida (after Dawes 1987).

Site	Total	Cyanophyceae	Chlorophyceae	Phaeophyceae	Rhodophyceae
Anclote Anchorage[a] (west coast)	66	14	13	8	31
Indian River[b] (east coast)	41	4	10	10	17
All Florida[c]	113	10	15	19	69

[a] Seasonal collections (Ballantine and Humm 1975).

[b] Seasonal collections (Hall and Eiseman 1981).

'Non-seasonal (Humm 1964).

grasses at several locations in Florida. Dawes (1987) further notes that filamentous forms predominate as epiphytes, constituting 73% of the epiphytes from the Indian River and 58% of the epiphytes from Anclote Estuary. Harlin (1980) compiled, from 27 published works, a species list of the microalgae, macroalgae, and animals that have been recorded as epiphytic on seagrasses. The algal lists are quite comprehensive, but none of the reports list the epiphytic invertebrates from Northwest Florida.

Harlin (1975) listed the factors influencing distribution and abundance of epiphytes as:

1. Physical substrate,
2. Access to photic zone,
3. A free ride through moving waters,
4. Nutrient exchange with host, and
5. Organic carbon source.

Providing a relatively stable (if somewhat swaying) substrate seems to be the most fundamental role played by the seagrasses. The majority of the epiphytic species are sessile and need a surface for attachment. The turnover of the epiphytic community is relatively rapid, since the lifetime of a single leaf is quite limited. A typical Thalassia leaf has a lifetime of 30 to 60 days. After a leaf emerges, there is a period of time before epiphytic organisms appear. This may be due to the relatively smooth surface or the production of some antibiotic compound by the leaf. On tropical seagrasses the heaviest coatings of epiphytes occur only after the leaf has been colonized by the coraline red algae, Fosliella or Melobesia. The coral skeleton of these algae may form a protective barrier as well as a suitable roughened and adherent surface.

Expressed in terms of population interactions, the relationship between epiphyte and seagrass host is basically that of an ectoparasite. The relationship is beneficial to the epiphyte ectoparasite, but detrimental to the seagrass host. While the epiphytes enjoy the benefit of being raised higher in the photic zone, the shading effect of the epiphytes has been shown to be detrimental to the seagrass hosts (Orth and van Montfrans 1984), decreasing photosynthesis in Zostera by 31% (Sand-Jensen 1977). In Australia, Bulthis and Woelkling (1983) found that shading from accumulated epiphytes reduced by half the lifespan over which a leaf of Heterozostera tasmanica showed positive net photosynthesis. In areas of high epiphyte growth, the action of epiphyte grazers is extremely important in maintaining seagrass productivity, as well as the longevity of the host seagrasses, without which the system would be nonexistent (Orth and van Montfrans 1984). Epiphyte coverage is limited not only by the activity of grazers, but, to a certain extent, by the growth habit of the seagrass plant, since individual leaves senesce and decay at such a rate that they provide a relatively temporary substrate.

In nutrient-poor waters, the epiphytes can benefit from the nutrients available to the seagrasses in the sediments; several studies have shown that there can be a transfer of nutrients from seagrasses to epiphytes. The upper surfaces of the leaves are subjected to much greater water motion than the lower parts. One effect of the increased water movement is to reduce nutrient gradients produced by biological uptake, thus increasing availability of these nutrients to photosynthetic organisms. In addition, a much greater volume of water containing particulate and dissolved nutrients is delivered to suspension feeding animals. Harlin (1975) described the uptake of PO_4 orthophosphates translocated up the leaves of *Zostera* and *Phyllospadix*. Epiphytic blue-green algae have the capacity to fix molecular nitrogen, but require phosphorus especially in tropical waters. However, Goering and Parker (1972) showed that soluble nitrate fixed by epiphytes could, in return, be utilized by seagrasses.

The standing crop and productivity of seagrass epiphytes and their resultant contribution to the trophic base of the system are highly variable. In some areas, such as immediately behind a coral reef, there are few epiphytes and little contribution, but in other areas, especially those with high external nutrient enrichment, the amount of production is quite high. Jones (1968) estimated that in northern Biscayne Bay, epiphytes contributed from 25% to 33% of the community metabolism. Penhale (1977) found that epiphytes contributed 18% of productivity of *Zostera* meadows in North Carolina. The trophic structure of these leaf communities can be quite complex and important in many areas, such as the shallow, turbid seagrass beds of the Indian River in Florida (Fry 1984) and parts of Redfish and Corpus Christi Bays in Texas (Kitting et al. 1984), and will be discussed later. Much of the epiphytic material, both plant and animal, ultimately becomes part of the litter and detritus as the leaf senesces and detaches.

4.2 INVERTEBRATES

The invertebrate fauna of seagrass beds can at times be exceedingly rich and difficult to characterize, except in very broad terms, unless one is dealing with a defined area or is willing to produce an exhaustive, comprehensive species list since hundreds of species can potentially be represented within a small area. This same fauna can be highly variable, with dramatic changes occurring in the faunal composition and density within relatively small changes of time or distance (Brook 1978).

From south to north along the western coast of Florida, there is a change in the invertebrate fauna of the seagrass beds and associated habitats, beginning as a Caribbean-West Indian fauna at the south and emerging as a predominately temperate fauna in the northern gulf. Collard and D'Asaro (1973) noted that the southerly fauna with West Indian affinities changes to one with Carolinian affinities in the north. They tentatively divide the faunas at the vicinity of Cedar Key but state that the change is gradual and that there are no clear-cut faunal province boundaries in the eastern Gulf of Mexico.

The characteristic species of seagrass beds and associated communities from the west coast of Florida have been described by Collard and D'Asaro (1973) and these associations are listed for the northern (Carolinian) fauna (Figure 18) and for the more southerly (West Indian) fauna (Figure 19). Some of the cosmopolitan fauna that are found in both regions are the sea urchin *Lytechinus variegatus*; the bivalves *Argopecten irradians*, *Modiolus modiolus*, and *Cardita floridana*; and the gastropods *Tegula fasciata* and *Bittium varium*. In the classification of Collard and D'Asaro, the West Indian fauna coincide with the invertebrate fauna described in detail for the seagrass communities of south Florida by Zieman (1982).

In Apalachee Bay, Hooks et al. (1976) found that 6 of the 10 most abundant "trawlable" species (=epibenthic and large epiphytic fauna) in the area were seagrass-associated fauna. Some of the most common organisms found in the bay were the caridean shrimps, especially

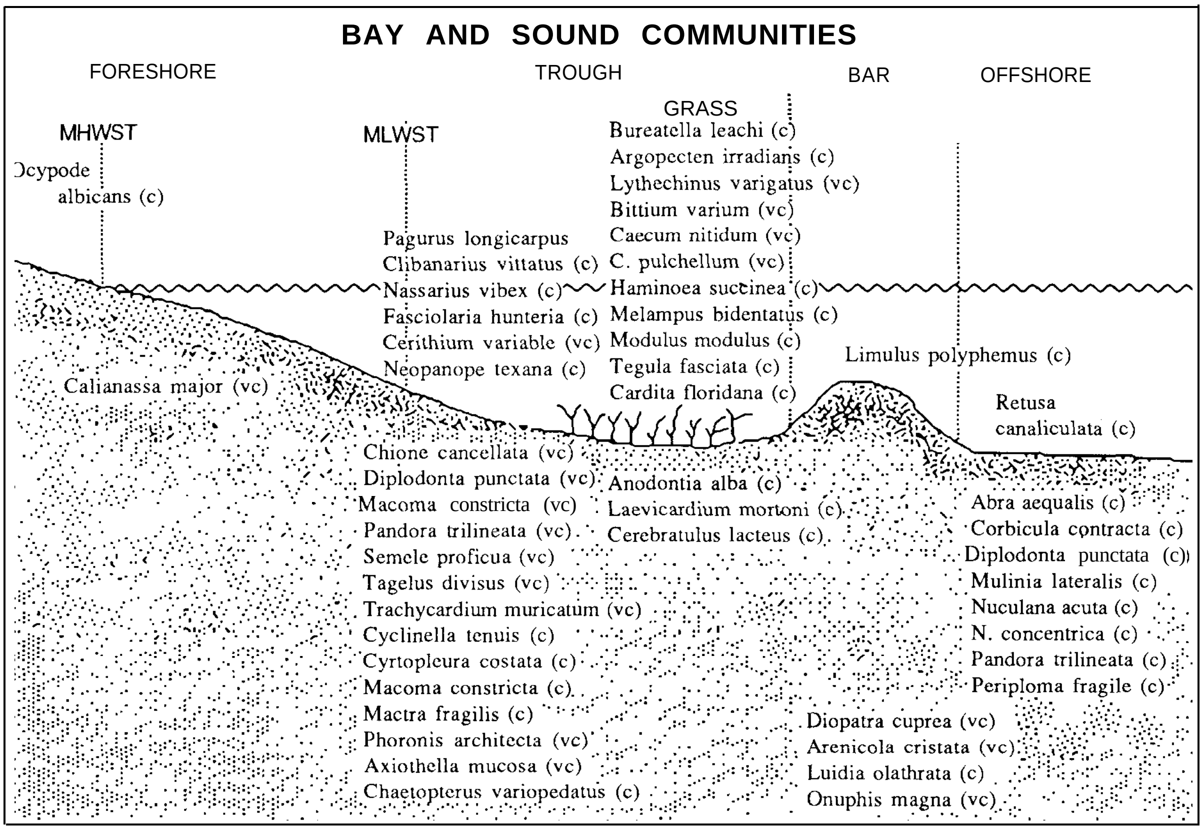


Figure 18. Representative temperate **(Carolinean) invertebrate communities (after Collard and D'Asaro 1973).**

Palaemonetes pugio, Palaemonetes intermedius, Periclimenes longicaudatus, Palaemon floridanus, Tozeuma carolinense, and Hippolyte pleuracantha. Abundant were the scallop Argopecten irradians; the hermit crab bonairensis; the echinoderms Lytechinus variegatus and Echinaster serpentarius; and the majid crabs Libinia dubia, Metoporhaphis calcerata. and Podochela riisei. Workina in the same area, Dugan and Livingston (1982) found similar species associations.

In Tampa Bay, Santos and Simon (1974) found that the Thalassia zone supported the largest number of infaunal polvchaetes of any of the sampled habitats of the bay, although only three of the nine most abundant species showed their highest densities in this zone. In grassbeds offshore from the mouth of the Econfina River in Apalachee Bay, polychaetes made up 35% of macrofaunal numbers, reaching maximum densities of 2,947 polychaetes per square meter (Stoner 1980b). The relative abundances of epifaunal species were directly related to macrophyte density; however, densities of burrowing polychaetes varied inversely with macrophyte density. In this study amphipods made up 47% of the macrofauna and reached densities of 1,578 m^{-2} (Stoner 1980b). Normally, small crustaceans such as amphipods and isopods will be numerically in great abundance; however, the larger penaeid and caridean shrimp often represent a larger biomass within the bed. Data from Brook (1977) for a Card Sound Thalassia grass bed shows that amphipods and caridean shrimp represent respectively 5.8% and 23.3% of estimated biomass of principal taxa collected and 12.4% and 50.3% of crustacean biomass.

The data of Collard and D'Asaro suggest that there is a greater proportion of emergent organisms (those living at or

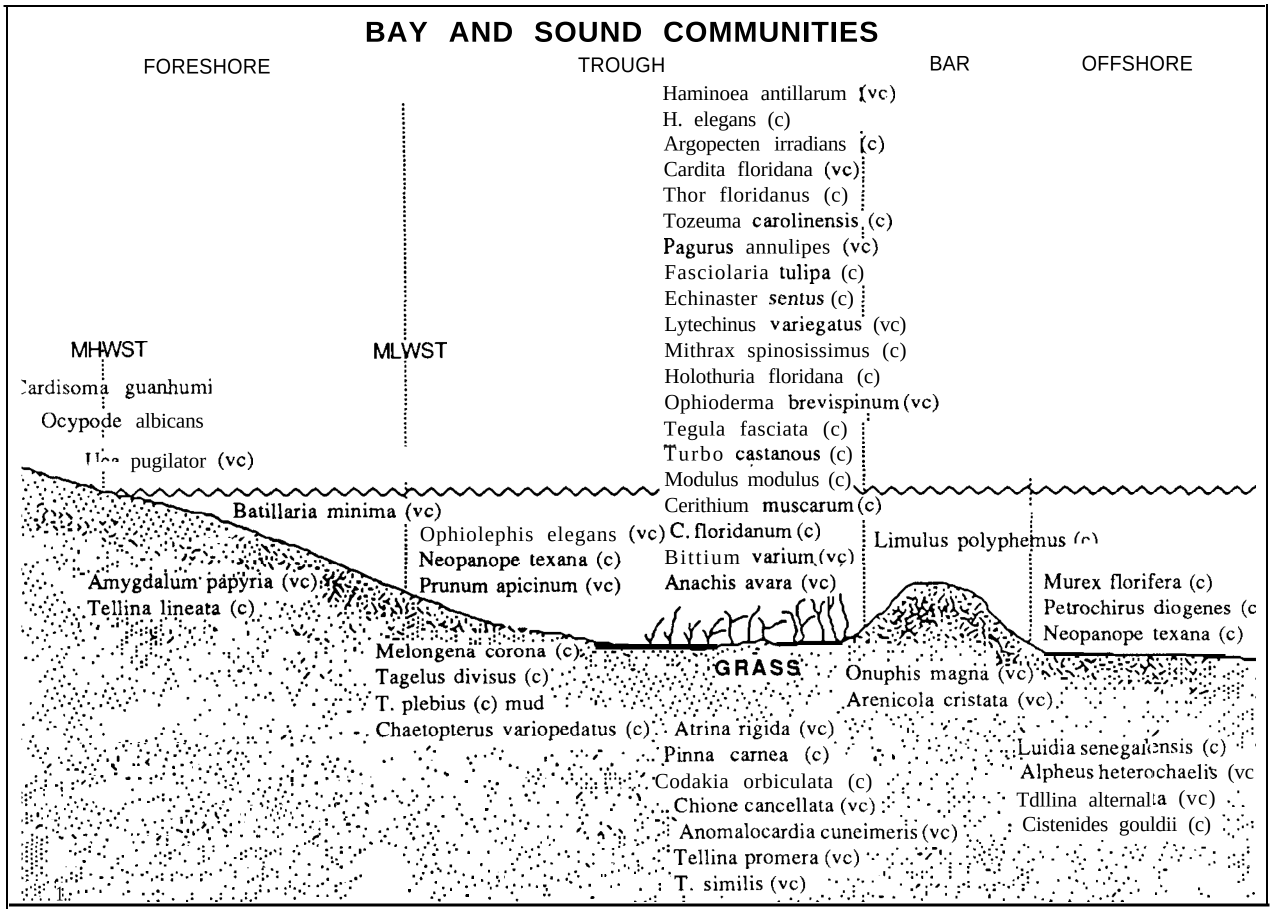


Figure 19. Representative tropical (West Indian) invertebrate communities (after Collard and D'Asaro 1973).

above the sediment surface) than infaunal organisms (those living in the sediment) in the seagrass beds of the southern part of the west Florida coast, changing to a lesser proportion of dominant emergent forms in the north. In addition, they suggest that there are more abundant fauna, both emergent and infaunal, in the surrounding sand and muddy areas in the areas of the Carolinian faunal provinces than in the West Indian provinces.

4.3 FISHES

Seagrass meadows are often populated by diverse and abundant fish faunas. The seagrasses and their attendant epiphytic and benthic fauna and flora provide shelter and food to the fishes in several ways. The grass canopy provides shelter for juvenile fishes and for small permanent residents. These also can feed on the abundant invertebrate fauna of the seagrass meadows, on the microalgae, on the living seagrasses themselves, or on seagrass detritus. In addition, because of the abundance of smaller fishes and large invertebrate predators, such as blue crabs and penaeid shrimps, larger fishes in pursuit of prey organisms transit the meadows, using them as feeding grounds. Numerous surveys have documented the fish faunas of a variety of areas along the west coast of Florida. These have most recently been reviewed and synthesized by Comp (1985).

Fishes that are permanent residents in the seagrass beds are typically small, less mobile, more cryptic species that spend their entire lives there. These species are normally of little or no direct commercial value but are often characteristic organisms of the seagrass habitat and may be highly important as forage for larger fishes, including those of commercial and sportfishing importance. The families and species comprising this category for seagrass meadows on the Florida west coast are nearly identical to those in south Florida (Zieman 1982). Members of families Syngnathidae, Gobiidae, and Clinidae are characteristic of this group. Pipefishes and seahorses, including Syngnathus scovelli, S. floridae, Micrognathus criniger, Hippocampus zosterae and H. erectus, abound in the western Florida seagrass meadows. The gobies and clinids show strong affinities with the south Florida species, and are represented commonly by Gobiosoma robustum, Microgobius gulosus, and Paraclinus fasciatus. Also characteristic of the more cryptic grassbed fauna are the predators that-iurk within the beds or at their edge waiting for mobile prey. Representative of these are the toadfish, Opsanus beta, the batfish Ogcocephalus radiatus, and the lizardfish, Synodus foetens (Mountain 1972; Springer and Woodburn 1960). The most common stingray in the northeast inshore gulf is Dasyatis sabina (Mountain 1972).

A group of resident fishes that are rarely caught with conventional methods are the eels. In St. Croix seagrass beds, Robblee and Zieman (1984) were able to obtain repeatable quantitative samples using an encircling net and rotenone. Capitalizing on a "natural experiment," Springer and Woodburn (1960) observed large numbers of the ophicthid eel, Ophichthus gomesi, following a severe red tide. Mountain (1972) noted that off Crystal River the most common eel in trawl samples was the blackedge moray, Gymnothorax nigromarginatus, a common nocturnal forager in seagrass beds.

Seasonal resident fishes in the grassbeds are those which spend their juvenile or sub-adult stages or their spawning season there. These are abundant fishes that are usually highly visible and are characteristic of grassbed fauna. They include the Sciaenidae, Sparidae, Pomadasyidae, Lutjanidae, and Gerreidae. Some of these species are also found in residence throughout the year.

Comp (1985) found two main spawning times in Tampa Bay. The larger one occurs in the spring and early summer, which enables the juvenile fishes to take advantage of the high summer primary production. The second, smaller spawning occurs in the late summer and early fall months (Comp 1985).

The most abundant fishes in the seagrass beds of Apalachee Bay are listed in Table 11. The most abundant is the pinfish, Lagodon rhomboides, which numerically can often exceed all other fishes combined in abundance (Ryan and Livingston 1980). The pinfish was also observed to be one of the most common fishes in Tampa Bay (Springer and Woodburn 1960; Comp 1985) and the seagrass beds off Crystal River (Mountain 1972). McNulty et al. (1974) found the pinfish to be the most common fish in a composite list from five estuarine areas from St. Marks to Chokoloskee. The most common, the sciaenids, were Leiostomus xanthurus, the spot, and Bairdiella chrysoura, the silver perch. In general, the fishes abundant in the seagrass beds of the Florida west coast are similar to those of south Florida, especially the fauna found in the seagrass beds of Florida Bay (Zieman 1982). Table 12 gives a comparison of the relative

Table 11. Most abundant fish of Apalachee Bay (after Livingston 1984a).

Species	Common name
Lagodon rhomboides	Pinfish
Leiostomus xanthurus	spot
Bairdiella chrysura	Silver perch
Monacanthus ciliatus	Fringed filefish
Diplodus holbrooki	Spottail pinfish
Sygnathus floridae	Disky pipefish
Orthopristis chrysoptera	Pigfish
Eucinostomous gula	Silver jenny
Centropomus melana	Gulf black sea bass
Monacanthus hispidus	Planehead filefish
Eucinostomus argentius	Spotfin mojarra
Paraclinus fasciatus	Banded blenny
Sygnathus scovelli	Gulf pipefish
Anchoa mitchelli	Bay anchovy

Table 12. Relative abundance of fish families in seagrass meadows (Pollard 1984.

State number		7	8	9	10	11	12	13	14
Region		Gulf of Mexico - Florida area							Caribbean
Locality		N.W. Florida	Texas	N.W. Florida	C.W. Florida	S.W. Florida	Texas	S.E. Florida	Panama
Latitude		29°N	28°N	30°N	28°N	26°N	28°N	26°N	9°N
Main seagrass genus		Halodule				Thalassia			
Reference		Carr and Adams (1973)	Hellier (1962)	Livingston (1975)	Springer and Woodburn (1960)	Weinstein and Heck (1979)	Hoese and Jones (1963)	Springer and McErlean (1962)	Weinstein and Heck (1979)
Fish Family	**Rank**								
Syngnathidae	1		+	4	2	4	+	7	15
Gobiidae	2	14	+	8	4	14	+	15	10
Monacanthidae	3	--	--	3	39	8	--	9	4
Sparidae	4	1	+	1	5	5	+	17	13
Labridae	5	—	--	--	--	—	--	29	14
Gerreidae	6	6	+	7	9	3	+	2	3
Scorpaenidae	7			30	--		--	21	8
Sciaenidae	8	2	+	2	1	1	+	37	17
Tetraodontidae	9	13	+	15	16	11	--	19	5
Blenniidae	10	9	—	12	14	19	--	--	31
Clupeidae	11	8	+	25	7	--	--	11	18
Ambassidae	12			--	--	--	--		--
Apogonidae	13	--	--	30	--		--	--	22
Engraulidae	14	5	+	19	6	22	+	1	26
Bothidae	15	—	+	16	24	14	+	10	16
Mugilidae	16	—	+	30	8		+	25	—
Teraponidae	17			--	--	--	--		--
Cyprinodontidae	18	--	+	25	3	--	+	5	
Muliidae	19			--	--		--	37	11
Haemulidae	20	3	+	6	24	2	+	4	6
Clinidae	21	--	--	10	--		--	12	31
Centracanthidae	22			--	--	--	--	--	--
Searidae	23			--	--	13	--	6	2
Serranidae	24	--	--	5	--	7	--	37	7
Diodontidae	25	--	--	11	24	9	--	26	12
Gasterosteidae	26			--	--	--	--		--
Lutjanidae	27	--	--	22	16	6	--	8	1

(Continued)

Table 12. (Continued).

State number		7	8	9	10	11	12	13	14
Region		Gulf of Mexico - Florida area							Caribbean
Locality		N.W. Florida	Texas	N.W. Florida	C.W. Florida	S.W. Florida	Texas	S.E. Florida	Panama
Latitude		29°N	28°N	30°N	28°N	26°N	28°N	26°N	9°N
Main seagrass genus		Halodule		Thalassia					
Reference		Carr and Adams (1973)	Hellier (1962)	Livingston (1975)	Springer and Woodburn (1960)	Weinstein and Heck (1979)	Hoese and Jones (1963)	Springer and McErlean (1962)	Weinstein and Heck (1979)
Fish Family	**Rank**								
Odacidae	28	--	--						
Kyphosadae	29	--	--				--		
Eleotridae	30	--	--	--	--		--	--	
Congiopodidae	31	--	--				--	--	
Belonidae	32	11	+	--	19		+	14	
Batrachoididae	33	--	--	9	24	10	+	24	
Cottidae	34	--	--				--	--	
Atherinidae	35	7	+	--	11	--	+	3	40
Sillaginidae	36	--	--					--	
Arripidae	37	--	--					--	
Aulorhynchidae	38	--	--	--	--				--
Carangidae	39	4	--	22	10	12		30	22
Platycephalidae	40	--	--					--	
Solcidae	41	15	--	20	10	17		41	24
Plotosidae	42	--	--			--	--	--	--
Anguillidae	43	--	--	--	--	--	--	--	--
Gobiesocidae	44	--	--	--	24		--	22	--
Hemiramphidae	45	10	+	--	24	--	--	33	
Callionymidae	46	--	--			--	--	41	
Lethrinidae	47	--	--	--	--		--	--	
Pomacentridae	48	--	--	--	--		--	41	36
Siganidae	49	--	--	--	--	--		--	
Gadidae	50	--	--	14	24			36	--
Scorpididae	51	--	--						--
Cynoglossidae	52	--	--	20	24	--		31	36
Pleuronectidae	53	--	--	--	--	--	--	--	--
Acanthuridae	54	--	--	--	--	--	--	20	20
Muraenidae	55	--	--	--	12	--	--	--	34

(Continued)

Table 12. (Concluded).

State number		7	8	9	10	11	12	13	14
Region		Gulf of Mexico - Florida area							Caribbean
Locality		N.W. Florida	Texas	N.W. Florida	C.W. Florida	S.W. Florida	Texas	S.E. Florida	Panama
Latitude		29°N	28°N	30°N	28°N	26°N	28°N	26°N	9°N
Main seagrass genus		Halodule			Thalassia				
Reference		Carr and Adams (1973)	Hellier (1962)	Livingston (1975)	Springer and Woodburn (1960)	Weinstein and Heck (1979)	Hoese and Jones (1963)	Springer and McErlean (1962)	Weinstein and Heck (1979)
Fish Family	**Rank**								
Chaetodontidae	56	--	--	--	--	--	--	--	9
Aulostomidae	57	--	--	--	--	--	--	--	31
No. fish species		21	31	57	93	49	19	106	106
No. fish families		15	20	36	47	25	13	48	45
Other seagrass genera present		Ruppia	Ruppia	Syringodium	Halodule Syringodium	?	Halodule	Halodule	Syringodium
Depth range (m)		1	1	2	?	?	1	2	1 2
Main coll. method		Seine net	Drop net	Otter trawl	Various	Otter trawl	Drop net	Seine net	Otter trawl

"+"indicates presence.
"--"indicates none found.

abundance of fish families in seagrass meadows in the region.

In addition to the fishes readily caught in trawl surveys, there are numerous seasonal residents and a few permanent residents, that are highly mobile and are quite abundant, but are not easily sampled with this gear. Such fishes include the Atlantic spadefish, Chaetodipterus faber; the sheepshead, Archosargus probatocephalus; the red drum, Sciaenops ocellatus; and the mullets Mugil cephalus, M. trichodon, and M. curema (Springer and Woodburn 1960; Mountain 1972). Many of the fishes in this category are those with significant commercial or sportfisheries importance (Thayer et al. 1978a).

Notable by their absence in northwest Florida grassbeds are the large numbers of juvenile snappers and grunts that use the seagrass meadows of south Florida as nurseries, move to the offshore reefs as adults, and commonly return to the seagrass beds at night to feed (Starck and Schroder 1970). The white grunt Haemulon plumieri seems to be the only lutjanid found through out the region and the gray snapper, Lutjanus griseus has the widest distribution of the serranids (Springer and Woodburn 1960; Mountain 1972; Ryan and Livingston 1980). The spotted sea trout, Cynoscion nebulosus, is a major gamefish during much of the year over seagrass beds, often found following large schools of foraging mullet.

The large roaming predators, or 'occasional migrants" in the classification scheme of Kikuchi (1966), are not normally present, visiting the grass beds to forage only infrequently and (if you are sportsfisherman) unpredictably. On the" Florida west coast, two of the most sought after representatives of this group are the tarpon, Megalops atlanticus, and the king mackerel, Scomberomorus cavalla. Such transient predatory species represent only a small proportion of the biomass present but may be quite important in determining fish community structure.

4.4 REPTILES

The only reptiles that are commonly associated with seagrass meadows are the sea turtles, of which there are several in the eastern Gulf of Mexico. The only herbivorous sea turtle is the green sea turtle, Chelonia mydas. Throughout its range, the primary food of the green turtles is sea grasses and the preferred food is Thalassia (hence its common name, turtle grass). Although not a seagrass feeder, the Atlantic ridley, Lepidochelys kempi, is often caught in commercial nets set for green turtles in seagrass areas on the upper Florida west coast (Carr and Caldwell 1956).

In pre-Columbian times, green turtles were abundant throughout the Gulf and Caribbean, but from very early on were hunted extensively for their succulent meat and calipee (fat), the ingredient that gives turtle soup its unique and delicious flavor. Concern over the reduced populations of green turtles dates back to the previous century (Munroe 1896). Although limited nesting occurs on the small beaches of south Florida, the region has almost certainly been primarily a feeding rather than nesting site. Carr and Caldwell (1956) noted that the green turtle populations of Florida were composed almost entirely of nonbreeding juveniles. The former turtle fishery on the Florida west coast was a seasonal one that began in April and extended until the first cold front of the fall. Most scientists believed that the turtles left the area in mass migrations in the fall, but some local fisherman insisted that the turtles would "bury up" in the mud bottoms and in holes on mud flats and remain there throughout the winter (Carr and Caldwell 1956). Although turtling was carried out to some degree throughout the west coast of Florida from the Florida Keys to Cape San Blas, the greatest activity was in the grass beds near the mouths of the Withlacoochee and Crystal Rivers, an area of superior turtle habitat (Carr and Caldwell 1956).

4.5 BIRDS

Shallow seagrass meadows offer feeding and resting areas for many species of birds, but in most cases the exact relationship between the birds and seagrass meadows is unknown. The embayments of the west coast of Florida are one of the most important areas for many bird species, which either winter in these sheltered bays or use the areas as resting and feeding sites during migration. The ecology of wading birds and their feeding behavior have been reviewed by Kushlan (1976, 1978). Odum et al. (1982) reviewed the avifauna of the mangrove regions of southern Florida, while Woolfenden and Schreiber (1973) gave an extensive review of the birds of marine and brackish-water habitats of the western coast of Florida.

Table 13 lists 81 species of birds that utilize saline habitats in the eastern Gulf of Mexico. This information, based on Christmas bird-count data, shows at least one broad generalization of habitat usage. Nearly all of the 81 species listed occur throughout the coastal waters of western Florida, but there is a variation in the relative abundance, which may be related to habitat usage. In south Florida, with its high concentration of shallow seagrass flats, the most abundant birds are the wading birds that feed in shallow water or on seagrass or mudflats, especially the Ardeidae (herons and egrets) and the Scolopacidae (sandpipers). In contrast, throughout the peninsular and panhandle bays, the most abundant groups were the Anatidae, containing geese and ducks; the Gaviidae, including the common loon; and the Rallidae, including the American coot. Unlike the wading birds, these birds tend to rest on the open water of the bays, commonly in rafts of dozens to hundreds or even thousands of individuals. Many of these species feed in the bays, diving to capture fishes or invertebrates or to forage for grasses, plant tubers, or rhizomes. The most common waterfowl is the lesser scaup, Aythya affinia, which is most abundant in coastal saltwater habitats, often occurring in flocks of over 10,000 individuals. Its primary food is benthic invertebrates, along with some fish and plant material (Woolfenden and Schreiber (1973). Another common swimming bird is the double-crested cormorant, Phalacrocorax auritus, which pursues fish in the water column. Cormorants may be found wherever the water is sufficiently deep for them to swim and clear enough for them to spot their prey.

The groups of birds described above use two of the dominant feeding modes of the marine avifauna. A third group hunts by flying some distance above the water until prey is spotted and then plummeting from the air to seize it. Ospreys, Pandion haliaetus, and bald eagles, Haliaeetus leucocephalus, feed in a similar manner by seizing prey on the surface of the water with their claws, while the brown pelican, Pelicanus occidentalis, plunges from some distance in the air to catch fishes in its pouch. For these birds, the seagrass meadows provide an abundant source of food by concentrating their quarry more than much of the surrounding habitat. Larger birds such as these require great quantities of food for themselves and their young, and are dependent on the local environment not only for protected nesting sites, but for a healthy forage-fish population. Woolfenden and Shreiber (1973) stated that a juvenile brown pelican requires approximately 120 lb of fish to fledge successfully.

4.6 MAMMALS

On the west coast of Florida, Caldwell and Caldwell (1973) reported that 27 species of marine mammals have been observed or reported stranded on beaches. Odell (1979) reported the same number in south Florida. Many of the sightings are rare or of dubious value; only two marine mammals are commonly found in the shallow coastal waters of west Florida: the manatee, Trichechus manatus; and the bottlenose dolphin, Tursiops truncatus. A third species, the spotted dolphin, Stenella plagiodon, is common offshore, and on occasion will venture in close enough to be observed from shore. Numerous sightings of a pinniped, the California sea lion, Zalophus californianus, were reported (Gunter 1968). however. Caldwell and Caldwell (1973) question'that the feral sea lions have established a breeding population.

The bottlenose dolphin is, by a considerable margin, the most common marine mammal in coastal Florida waters,

Table 13. Number of individuals per 10 party hours based on Christmas Bird Count Data, 1957-71, from 17 selected localities grouped in four regions, and for all counts combined (t = trace, less than 0.5 individuals; lines separate the families) (from Woolfenden and Schreiber 1973).

Common name	Scientific name	Panhandle	Peninsula	Coot Bay	Keys	Total[a]
Common Loon	Gavia immer	12	1	t	t	3
Horned Grebe	Podiceps auritus	17	1	3	2	5
Wilson Petrel	Oceanites oceanicus	0	0	0	0	0
White Pelican	Pelecanus erythrorhynchos	t	3	142	2	25
Brown Pelican	Pelecanus occidentalis	t	52	37	54	39
Gannet	Morus bassanus	t	0	0	t	t
Double-crested Cormorant	Phalacrocorax auritus	40	63	98	121	71
Magnificent Frigatebird	Fregata magnificens	0	1	t	6	1
Great White Heron	Ardea occidentalis	0	t	19	12	5
Great Blue Heron	Ardea herodias	5	8	26	6	10
Green Heron	Butorides virescens	t	1	13	2	3
Little Blue Heron	Florida caerulea	5	14	54	14	19
Reddish Egret	Dichromanassa rufescens	0	t	2	3	1
Common Egret	Casmerodius albus	13	15	129	9	32
Snowy Egret	Leucophoyx thula	2	14	132	7	29
Louisiana Heron	Hydranassa tricolor	4	7	40	14	13
Black-crowned Night Heron	Nycticorax nycticorax	1	1	7	t	2
Yellow-crowned Night Heron	Nyctanassa violacea	t	4	3	3	3
Wood Stork	Mycteria americana	t	5	65	1	13
White Ibis	Eudocimus albus	3	34	267	11	62
Roseate Spoonbill	Ajaia ajaja	0	t	19	8	4
Canada Goose	Branta canadensis	114	t	0	0	25
Mallard	Anas platyrhynchos	26	1	t	0	6
Black Duck	Anas rubripes	4	t	0	0	1
Mottled Duck	Anas fulvigula	0	3	7	t	2
Gadwall	Anas strepera	9	1	t	0	3
Pintail	Anas acuta	28	8	170	t	38
Green-winged Teal	Anas carolinensis	4	3	81	1	15
American Widgeon	Mareca americana	49	7	45	1	21
Shoveler	Spatula clypeata	3	1	44	t	8
Redhead	Aythya americana	88	t	t	0	19
Canvasback	Aythya valisineria	2	t	t	0	1
Lesser Scaup	Aythya affinis	203	185	175	t	163
Common Goldeneye	Bucephala clangula	9	t	0	0	2
Bufflehead	Bucephala albeola	26	t	t	0	5
Ruddy Duck	Oxyura jamaicensis	3	t	43	0	8
Red-breasted Merganser	Mergus serrator	26	27	30	33	28

(Continued)

Table 13. (Continued).

Common name	Scientific name	Pan-handle	Penin-sula	Coot Bay	Keys	Total[a]
Bald Eagle	*Haliaeetus leucocephalus*	t	1	2	1	1
Osprey	*Pandion haliaetus*	t	1	7	5	2
Clapper Rail	*Rallus longirostris*	1	t	1	1	1
Sora	*Porzana carolina*	1		t		t
American Coot	*Fulica americana*	159	32 t	241	t 3	89
American Oystercatcher	*Haematopus palliatus*	t	1	0	0	1
Semipalmated Plover	*Charadrius semipalmatus*	1	7	10	19	8
Piping Plover	*Charadrius melodus*	1	1	t	2	1
Snowy Plover	*Charadrius alexandrinus*	t	1	5	0	t
Wilson Plover	*Charadrius wilsonia*	t	4	2	6	3
Black-bellied Plover	*Squatarola squatarola*	7	13	29	42	18
Ruddy Turnstone	*Arenaria interpres*	2	8	6	24	9
Willet	*Catoptrophorus semipalmatus*	11	11	45	6	16
Greater Yellowlegs	*Totanus melanoleucus*	1	1	8	5	3
Lesser Yellowlegs	*Totanus flavipes*	t	26	1	4	13
White-rumped Sandpiper	*Erolia fusiocollis*	0	0	0	0	0
Least Sandpiper	*Erolia minutilla*	2	6	115	35	26
Dunlin	*Erolia alpina*	59	49	211	37	76
Short-billed Dowitcher	*Limnodromus griseus*	5	11	54	134	33
Semipalmated Sandpiper	*Ereunetes pusillus*	12	18	153	54	43
Western Sandpiper	*Ereunetes mauri*	1	6	62	21	59
Marbled Godwit	*Limosa fedoa*	1	1	7	t	2
Sanderling	*Crocethia alba*	10	26	1	12	17
American Avocet	*Recurvirostra americana*	t	t	8	t	1
Black-necked Stilt	*Himantopus mexicanus*	0	t	t	t	t
Parasitic Jaeger	*Stercorarius parasiticus*	t	0	t	t	t
Herring Gull	*Larus argentatus*	39	35	3	15	28
Ring-billed Gull	*Larus delawarensis*	76	316	38	74	183
Laughing Gull	*Larus atricilla*	15	104	92	132	86
Bonaparte Gull	*Larus Philadelphia*	19	1	t		15
Gull-billed Tern	*Gelochelidon nilotica*	t	1	1	t	t
Forster Tern	*Sterna forsteri*	10	8	5	7	8
Roseate Tern	*Sterna dougallii*	0	t	t	1	t
Sooty Tern	*Sterna fuscasa*	0	0	0	t	0
Least Tern	*Sterna albifrons*	t	t	0	0	t
Royal Tern	*Thalasseus maximus*	3	29	12	56	24
Sandwich Tern	*Thalasseus sandvicensis*	t	5	14		3
Caspian Tern	*Hydroprongne caspia*	t	1	7	2	2
Black Tern	*Chlidonias niger*	0	0	0	0	0
Brown Noddy	*Anous stolidus*	0	0	0	0	0

(Continued)

Table 13. (Concluded).

Common name	Scientific name	Pan-handle	Penin-sula	Coot Bay	Keys	Total[a]
Black Skimmer	Rynchops nigra	3	41	161	28	50
Mangrove Cuckoo	Coccyzus minor	0	t	t	t	t
Seaside Sparrow	Ammospiza maritima	2	t	t	0	t

[a] Total represents the average of all birds counted in all areas combined.

although accurate censuses of their abundance and distribution are rare. In the Everglades Park region of south Florida, Ode11 (1976) found that 36% of the animals seen were in open Gulf of Mexico waters, 33% were in Whitewater Bay, 20% were in inland waters and 11% were seen in Florida Bay. The relatively low numbers in Florida Bay were presumed to be due to extremely shallow waters which would inhibit the movement of this large mammal. In a later survey, Irvine et al. (1982) found 700 individuals in 146 herds in the Gulf of Mexico, 491 individuals in 185 herds in bays, and 192 individuals in 100 herds in marsh and river habitats of western peninsular Florida. Bottlenose dolphin are opportunistic feeders, subsisting primarily on fish, squid, and benthic invertebrates (Caldwell and Caldwell 1973). Their diets are not well known, but they are frequently observed pursuing schools of mullet.

The Caribbean manatee or sea cow, Trichechus manatus, is primarily tropical in distribution, but its range formerly extended across the Gulf of Mexico. On the west coast of Florida, it is found in the shallow coastal seagrass meadows or in the coastal rivers. Although its numbers have greatly declined (in recent years) causing it to be placed on the Federal Endangered Species List, recent large increases in populations along the southern Big Bend coast of Florida have been reported (Powell and Rathbun 1984). This coastline provides abundant summer feeding grounds in the coastal grassbeds and winter shelter in the spring-fed rivers of the region, notably the Crystal and Homosassa Rivers, which during the winter are warmer than the coastal waters (Powell and Rathbun 1984). Recently heated effluents of large power plants, especially nuclear plants with their lower thermal efficiency and greatly increased heat output, have provided additional refuges.

Normally, manatees forage singly, or with a mother and calf pair, in the shallow estuarine grassbeds during the warmer months. The major summer feeding grounds are the estuaries and offshore grass beds of the Crystal, Homosassa, Suwanee, Withlacoochee, and Chasshowitzka rivers (Powell and Rathbun 1984). Hartman (1969) reported that they spend a quarter of each day feeding, and will consume at least 10% of their body weight a day in vegetation, a significant amount of seagrass considering adults weigh up to 500 kg.

A survey of western peninsular Florida counted a total of 554 manatees, with the highest percentage sighted in the shallow, brackish waters of Collier and Monroe counties in extreme south and southwest Florida (Irvine et al. 1982). In an earlier study of the Everglades and the south Florida region, Ode11 (1976) found a total of 302 herds with 772 individuals; 46% were sighted within Whitewater Bay, 20% in the Gulf of Mexico, 23% in inland waters, and only I% in Florida Bay.

CHAPTER 5. STRUCTURAL AND FUNCTIONAL RELATIONSHIPS IN SEAGRASS SYSTEMS

The importance of seagrasses to the productivity of shallow coastal waters is well-recognized: they provide shelter and serve as nursery and feeding grounds for diverse assemblages of organisms. The variety observed in community structure in seagrass beds has stimulated efforts to identify the functional relationships within the beds, and thus provide a framework for understanding the interactions and pathways common to these systems.

5.1 THE RELATIONSHIP OF STRUCTURE, SHELTER, AND PREDATION

Seagrasses, with leaf canopies extending into the water column and rhizome systems penetrating the sediment, present a structurally complex habitat where calm water, a stable substrate, and an abundance of detrital and microalgal food support dense populations of motile and sessile organisms. The increased abundance of infaunal and epifaunal organisms which find shelter and protection from predation within the grassbeds promotes, in turn, the value of seagrass habitats as feeding grounds for the predators.

While the faunal richness of seagrass beds was recognized in early studies, more recent works have begun to identify specifically the interactions among component plant and animal species and to define their functional relationships.

5.1.1 Faunal Abundance and Structure

Early ecological surveys of Florida coastal waters included observations of increased densities of fishes and invertebrates within seagrass beds compared to adjacent habitats. Later studies quantified these differences in faunal abundance (Roessler et al. 1974; Yokel 1975a, 1975b; Thorhaug and Roessler 1977; Weinstein et al. 1977). The concise study of Yokel (1975b) reports the findings of this phase of studies. Results from trawls showed that in the Rookery Bay Sanctuary, 3.5 times as many fishes were captured in seagrass as in bare sand and shell substrates (Figure 20), and the standing crop of crustaceans (estimated from trawls) was 3.9 times larger in mixed seagrass and algal flats than on nearby unvegetated bottoms.

The amount of literature demonstrating the increased abundance of organisms in seagrass communities is becoming extensive. Table 14, from Virnstein et al. (1983) summarizes much of the pertinent literature. Numerous studies ranging in area from Florida to Japan to Belize show that in nearly all cases, the ratio of

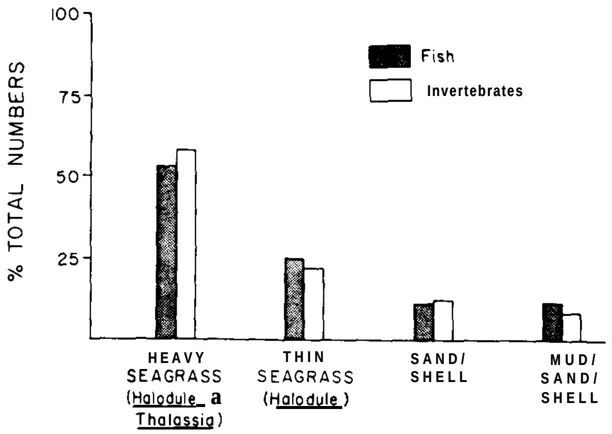


Figure 20. Comparison of faunal abundance between seagrass beds and adjacent habitats (after Yokel 1975a).

Table 14. Comparison of seagrass: sand faunal density ratio (G:S) with other studies. Abundances are per m^2 except those listed in parentheses (from Virnstein et al. 1983).

Area	Seagrass	Faunal group	Coll. gear	Sieve mesh (mm)	Abundance Grass (G)	Sand (S)	G:S ratio	Source
Indian River, FL	Thalassia/Halodule	M	Co	0.5	17,479	5,844	3.0	PS
	"	P	Co	0.5	6,248	3,403	1.8	PS
	"	Cr	Co	0.5	3,152	485	6.5	PS
	"	De	Co	0.5	215	15	14.3	PS
	"	F	Dr	3.2	6.1	0.7	8.8	G (unpubl.)
	Halodule	M	co	1.0	7,460	2,530	2.9	V (1978)
Chesapeake Bay, VA	Zostera	M	co	1.0	39,000	7,850	5.0	V (1978)
	Zostera	M	co	0.5	48,900 13,313	8,462 1,160	42.2 1.6	0 SS (1974) (1977)
Tampa Bay, FL	Halodule	P	co	0.5				
	Thalassia	P	co	0.5	33,485		4.0	SS (1974)
Biscayne Bay, FL	Halodule	M	co	1.0	(1,245)	"	1.6	OW (1967)
	Thalassia	M	co	1.0	(771)	(774)	1.0	OW (1967)
Carrie Bow, BELIZE	Thalassia	Mo+P	co	1.0	6,476	8,000	0.8	YY (1982)
Seto Sea, JAPAN	Zostera	M	Sl	--	(2,755)	(824)	3.3	K (1974)
	"	Cr	Sl	--	(2,054)	(435)	4.7	K (1974)
Chesapeake Bay, VA	Zostera	De	Tr	--	(17,292)	(927)	18.7	HO (1980)
	Zostera	F	Tr	--	(1,090)	(164)	6.7	OH (1980)
Long Is. Sound, NY	Zostera	F	Se	--	(337,677)	(139,264)	2.4	BO (1971)

M = macrobenthos, P = polychaetes, Cr = crustaceans, De = decapods, F = fishes, Mo = mollusks. Collection gear: Co = corer, Dr = dropnet, Sl = sledge, Tr = trawl, Se = seine. References: PS = present study, G = Gilmore (unpubl.), V = Virnstein (1978), 0 = Orth (1977), SS = Santos and Simon (1974), OW = O'Gower and Wacassey (1967), YY = Young and Young (1982), K = Kikuchi (1974), HO = Heck and Orth (1980), OH = Orth and Heck (1980), BO = Briggs and O'Connor (1971).

organisms from seagrasses to organisms from sand is greatly in favor of the seagrass organisms, with ratios of up to 42:1. However, a cautionary note must be added: The ratios are highest in the temperate zone stations and in turbid subtropical areas such as Indian River. The three lowest ratios are from Biscayne Bay, Florida, and Belize, which represent not only the most tropical stations, but also those with the clearest water. It is quite possible, as in other facets of seagrass ecology, that there are distinct differences in functional relationship between temperate and tropical systems. However, studies from the west coast of Florida, which is a transitional area, suggest that here the grassbeds are denser and richer in invertebrate abundance than the adjacent habitats (Santos and Simon 1974; Hooks et al. 1976; Stoner 1980b; Stoner et al. 1983).

Stoner (1980b) found that the density of macrofaunal organisms and the number of species taken was directly related to the density of macrophyte biomass. Here the faunal dominance was different between the vegetated and unvegetated stations. The analysis of sediments showed that the particulate size distribution did not differ and that differences in animal densities could more directly be attributable to macrophyte biomass and not sediment characteristics.

In another study, in the Indian River, Virnstein et al. (1983) surveyed the macrofaunal invertebrates of seagrass beds and nearby bare sand sediments and found that the seagrass beds supported three times the density of invertebrates and 38% more species compared with the adjacent sandy sediments. The abundance of epitaunal organisms was 13 times greater in the seagrass beds compared with the sand flats. In the seagrass beds 54% of the individuals were epifaunal compared to 12% in the sand flats. Virnstein et al. (1983) also found that the epifaunal organisms were much more trophically important, and consequently more heavily preyed upon, than the infauna.

Table 15 summarizes numerous studies on the relationship between the structural complexity of seagrass beds and the distribution and abundance of the associated animal complex. Experimental evidence suggests that grass bed invertebrates actively select vegetated habitat rather than bare sand, indicating that habitat preference is an important force contributing to observed faunal densities in grass beds. Selection often appears to be based on the form or structural characteristics of the seagrass.

While the relative abundance of invertebrates in seagrass is usually high when compared to surrounding habitats, the actual numbers are highly variable. Large changes in abundance and even the species encountered are frequently seen over small changes in space (Brook 1978) and time (Greening and Livingston 1982). When comparing strictly infaunal organisms, a different pattern may appear. Stoner (1983) found that the relative abundances of infaunal organisms in sand decreased in the order, <u>Halodule</u>, <u>Syringodium</u>, <u>Thalassia</u>, as well as from low to higher biomass of the seagrasses.

The least-defined patterns of distribution and abundance are available for seagrass-associated meiofaunal organisms. Bell et al. (1984) reviewed seagrass meiofaunal studies and concluded that while little comparative literature exists that can be directly intercompared, due to both a paucity of studies and the large differences in sampling techniques and sample processing, their studies concluded that nematodes and copepods were the most abundant taxa found in the sediments; that nematode densities were higher in the sediments than on seagrass blades; and that copepod densities on blades were equal or greater than nematode densities in the sediments in winter and spring.

5.1.2 Structure and Predation

With the correlation between the plants and animal abundance established, questions followed addressing the nature of plant-animal interactions and how these relationships shape community structure. Of particular interest is the role of plants in mediating predator-prey interactions. There is abundant indirect evidence that the grass carpet offers protection from predation for the animals

Table 15. Summary of studies describing the influence of seagrass plant architecture on the associated animal distribution and abundance (from Orth et al. 1984).

Feature	Taxa	Function of seagrass	Animal species or community patterns	Reference
Zostera marina roots and rhizomes	macroinvertebrates, infauna only, >0.5 mm	roots and rhizomes protect infauna from predators	more species and individuals in vegetated than in bare sand areas	Orth 1977a,b
Z. noltii roots andrhizomes	macroinvertebrates, epifauna and infauna, >0.25 mm	roots and rhizomes provide spatial refuge from predators	diverse and dense assemblage of fauna associated with vegetation. Greater abundance of epifauna and infauna in dense eelgrass compared to low density eelgrass	Reise 1978
Halodule wrightii leaves	macroinvertebrates, both infauna and epifauna, >1.0 mm	leaves serve as protection against predation	response pattern (increase or decrease) depends on individual macrobenthic species	Young and Young 1977
Z. marina leaves	amphipods as prey; pinfish, *Lagodon rhomboides*, and shrimp, *Palaemonetes vulgaris*, as predators	predation rate decreases with increasing blade density but not in linear function	susceptibility to predators depends on amphipod life style, i.e., infauna or epifauna, tube builders, or epifaunal free-living forms	Nelson 1979a, 1979b, 1980
Thalassia testudinum leaves	ampipods as prey; pinfish, *Lagodon rhomboides*, as predator	degree of species specific selectivity function of macrophyte biomass	amphipod consumption diverged from that predicted by heavy macrophyte cover; epifaunal forms preferred by fish predator more than infaunal forms	Stoner 1979
T. testudinum, *H. wrightii*, *Syringodium filiforme* leaves	amphipods as prey; pinfish, *Lagodon rhomboides*, as predator	blade surface area best estimate of habitat complexity	selection for high seagrass density, i.e., large surface area, based on vulnerability of amphipod to predation by *Lagodon rhomboides*	Stoner 1980a
T. testudinum, *S. filiforme*-leaves	macroinvertebrates, infauna and epifauna, >0.5 mm	biomass of benthic vegetation independent of sediment granulometry, exerts strong influence on abundance, dominance, diversity and trophic organization of macrobenthic infauna and epifauna	abundance of epifaunal amphipods and polychaetes directly related to macrophyte biomass. Infaunal amphipods inversely related to biomass	Stoner 1980b
T. testudinum, *S. filiforme* leaves	amphipods	blade density and plant species composition mediate predation	majority of amphipod species associated with seagrasses	Stoner 1980c
Artificial leaves and rhizomes	shrimp, *Palaemonetes vulgaris* and *Palaemon floridanus*, as prey, pinfish, *Lagodon rhomboides*, as predator	protection from predation	shrimp less vulnerable to predation in vegetated VS nonvegetated habitats. Competitive displacement of *P. vulgaris* by *P. floridanus* made *P. vulgaris* more susceptible to predation	Coen et al. 1981

(Continued)

Table 15. (Continued).

Feature	Taxa	Function of seagrass	Animal species or community patterns	Reference
Artificial leaves and rhizomes	shrimp, Palaemonetes pugio, as prey, killifish, Fundulus heteroclitus as predator	shoot density affects foraging success of predator	significant survival of prey only at high vegetation densities	Heck and Thoman 1981
Z. marina roots and rhizomes	macroinvertebrate burrowers including polychaetes, echinoderms, bivalves, and crustaceans	root-mats prevent hard bodied taxa from burrowing more than soft bodied taxa	size distributions skewed toward small sizes in seagrass bed	Brenchley 1982
Artificial leaves and rhizomes	Mya arenaria as prey, Callinectes sapidus as predator	plant structure prevents digging activities of predator	increased bivalve survival in presence of sparse and dense artificial vegetation	Blundon and Kennedy 1982
Z. marina shoots	macroinvertebrates, both infauna and epifauna, >0.5 mm	shoot density regulates structure of developing community	increasing diversity of faunal assemblage with increasing shoot density	Homriak et al. 1982
Z. marina, artificial leaves and rhizomes	two prey species, juvenile Callinectes sapidus and Mulinia lateralis as prey; adult C. sapidus as predator	leaves reduce predatory efficiency of adult Callinectes sapidus	shallow-dwelling M. lateralis eliminated at all densities of seagrass leaves. Juvenile C. sapidus protected at three different densities of leaves	Orth and van Montfrans 1982
H. wrightii roots and rhizomes	two bivalve species, Chione cancellata and Mercenaria mercenaria	roots and rhizomes function as refuge from predation and bind sediments thus increasing sediment compaction	both clam species less vulnerable to whelk predation but shallower dwelling form more susceptible than deeper dwelling form	Peterson 1982
Z. marina whole plant	two bivalve species, Protothaca staminea and Macoma nasuta	plant serves as protection against siphon nipping by fish. Fish shift feeding to more obvious M. nasuta	bivalve densitities higher compared to clean sand; reduced siphon nipping in vegetation results in greater net growth of P. staminea	Peterson and Quammen 1982
T. testudinum, S. Filiforme. H. wrightii leaves	amphipods as prey, Lagodon rhomboides as predator	leaves reduce foraging efficiency of predator	number of amphipods consumed decreases with increasing seagrass biomass, differences occur among macrophyte species. Predator efficiency function of size	Stoner 1982
T. testudinum shoots	macroinvertebrates, both infauna and epifauna, >1.0 mm	standing crop does not affect species densities	similar densities in bare sand and vegetation	Young and Young 1982
T. testudinum whole plant	macrofauna, infauna and epifauna, >0.5 mm	increased habitat complexity	greater numbers of species and greater faunal densities in close proximity to seagrass shoots	Lewis and Stoner 1983
H. wrightii leaves	juvenile red drum, Sciaenops ocellatus	protection from predators, patchiness more important than plant length and above ground biomass	more red drum along ecotone of seagrass and bare sand than for more homogeneously vegetated sites	Holt et al. 1983

(Continued)

Table 15. (Concluded).

Feature	Taxa	Function of seagrass	Animal species or community patterns	Reference
T. testudinum, H. wrightii, S. filiforme, leaves, roots and rhizomes	amphipods and tanaidaceans	seagrass growth form and biomass mediate distribution and foraging behavior of important predators	relative abundance of crustaceans function of seagrass species and biomass. Significance of seagrass biomass in structuring crustacean assemblages held within, but not across, seagrass species	Stoner 1983
Z. marina and *H. wrightii* leaves, roots and rhizomes	infauna and epifauna >1.2 mm	seagrass growth mediates effects of large epibentic consumers	average density of epibenthos 52x and of infauna 3x the level observed on the sand flat. Epibenthic predators reside in grass bed by day and forage on sand flat at night	Summerson and Peterson 1984
Z. marina whole plant	*Mercenaria mercenaria*	seagrass baffles current, results in higher particulate food concentrations	growth rates of *M. mercencaria* paradoxically higher in seagrass beds than bare sand, but may be consequence of more particulate food	Peterson et al. 1984

living in it, with the dense seagrass blades and rhizomes providing cover for invertebrates and small fishes, while also interfering with the feeding efficiency of their potential predators. Heck and Wetstone (1977) hypothesized that the significant plant biomass, invertebrate abundance relationships observed in Panamanian grass beds largely resulted from predation pressure which is mediated by the structural complexity of the grass carpet. Stoner (1980b) observed that numbers of macrobenthic animals increased noticeably in the fall with emigration of fishes from grass beds in Apalachee Bay. Stoner (1979) also demonstrated that the amphipods consumed most frequently by pinfish were epifaunal. Given the behavioral characteristics of amphipods and the feeding preference of pinfish, it follows (Nelson found) that infaunal amphipods were 1.3 times more abundant than epifaunal tube-dwelling amphipods and 4 times more abundant than free-living epifaunal amphipods with the seasonal influx of pinfish, reiterating the role predators play in controlling both abundances and species composition within the grass carpet (Nelson 1979a; Stoner 1979).

In laboratory experiments, Stoner (1980) found that common epifaunal amphipods were capable of detecting small differences in the density of seagrass and actively selected areas of high blade density. When equal blade biomass of the three common seagrasses--Thalassia testudinum, Syringodium filiforme and Halodule wrightii--were offered in preference tests, Halodule was chosen. When equal surface areas were offered, no preferences were observed, suggesting that surface area was the grass habitat characteristic chosen. In later field studies, Stoner (1983) found that amphipods and tanaidaceans were most abundant in beds of Thalassia or Syringodium, intermediate in Halodule, and least abundant in bare sand, with a superficial correlation related to plant standing crop. However, Thalassia and Halodule supported nearly equal numbers when compared on a unit-biomass or unit-surface area basis. Syringodium was consistently higher than the other two species on a unit-surface area basis.

The shifts in amphipod abundance appeared to be related also to the relative abundance of predators. In Halodule beds where amphipod abundance was low, the number of predatory fish was 2 to 2.5 times the abundance in beds of the other seagrasses. In particular, Stoner (1983) found that pinfish made up 67% of the fish population, and was the major amphipod consumer.

Numerous attempts have been made to assess the role of predation on epifauna in structuring invertebrate populations utilizing exclosure-caging experi-mental manipulations. Excluding fish predators has generally resulted in increases in species richness and density (Young et al. 1976; Orth 1977b; Young and Young 1977), although the results can often be confounding (Virnstein et al. 1983). Where increases did not occur, it was assumed that decapod predators had increased sufficiently in numbers within the cages, presumably due to a release from predation by fishes, that they in turn were capable of significantly reducing faunal numbers within the grass carpet (Young and Young 1977).

Virnstein et al. (1983) attempted to determine the importance of small decapod crustaceans as predators, while also admitting that they were simultaneously demonstrating the problems and difficulties of caging experiments. In both the seagrass and sand communities, nested cages were erected with an outer cage 2 m square with 12 mm mesh, and an inner cage 1.4 m square with 3 mm mesh. Both extended above the surface of the water. It was anticipated that, with the protection afforded by the fine mesh, the smaller organisms in the inner cage would increase in abundance. In fact, the opposite occurred with the numbers of small crustaceans and polychaetes decreasing in the inner cages; large crustaceans and fishes decreased in numbers somewhat, but also increased in size. The conclusion was that the larger crustaceans such as Penaeus duorarum, Palaeomonetes intermedius, and Alpheus heteroclitus, and fishes such as Bairdiella chrysura and Gobiosoma robustum entered the cages as juveniles and grazed heavily on the captive prey as they grew (Virnstein et al. 1983). In turn these intermediate sized organizms were released from predation pressure from larger carnivores. Leber (1985) alleviated such problems associated with caging experiments by documenting predator species, using a smaller mesh size to exclude them, and employing short-term experiments. He concluded that differential predation could account for the strong correlation of amphipods with macrophyte abundance, whereas microhabitat selection was the primary factor determining the strong relationship between the abundance of the caridean shrimp *Latreutes* and plant biomass. The author noted that the refuge value of the seagrass canopy depends on the relationship of prey size to canopy architecture, with smaller organisms afforded more protection from predation. The relative importance of predation avoidance versus microhabitat selection in determining community structure among seagrass prey organisms should vary due to physical and behavioral differences among these populations (Leber 1985).

The above paragraph serves to illustrate the complex interactions between predator and prey populations. Surprisingly little is still known about the interaction of fishes with the structural complexity of the grass canopy. Because of the restricted size of fishes typically inhabiting seagrass beds, Ogden and Zieman (1977) suggested that large predators such as barracudas, jacks, and mackerels may be responsible for restricting permanent residents to those small enough to hide within the grass carpet. For fishes larger than about 20 cm SL the grass bed can be thought of as a two dimensional environment; these fishes are too large to find shelter within the grass carpet. Mid-sized fishes (20-40 cm SL) are thought to be excluded from the majority of the grass beds by the larger predators occasionally present; their activities are limited to brief forays from the shelter of reefs or mangrove roots. Although these fishes are restricted to areas of shelter by day, they may move into the beds at night when predation is less intense (Ogden and Zieman 1977; Ogden 1980).

Heck and Orth (1980a) have hypothesized that both abundance and diversity of fishes should increase with increasing structural complexity until the feeding efficiency of the fishes is reduced due to interference with the grass blades or conditions within the grass canopy become unfavorable, at which point fish densities should decline. Nelson (1979a) demonstrated that the predatory efficiency of the pinfish on amphipods decreased with increasing *Zostera marina* blade densities. Coen (1979) found that with increasing cover of red algae (*Digenia simplex*: *Laurencia* spp., *Gracilaria* spp. and others), the pinfish's foraging efficiency on both *Palaemon floridanum* and *Palaemonetes vulgaris* was reduced. Using artificial seagrass, Heck and Thoman (1981) observed reduced feeding efficiency in the killifish, *Fundulus heteroditus*, on the grass shrimp, *Palaemonetes pugio*, with increasing grass density.

Attempts are being made to sift and synthesize the information contained in the large, and often bewildering, data base now accumulating on the relation between the plant and faunal components of the seagrass community. In a review of the relationships of the plant structure on the predator-prey relationships in seagrass communities, Orth et al. (1984) developed the following "framework" for the assessment of faunal abundance.

1. In general, epifauna are more susceptible to predation by epibenthic predators than infauna. Among the epifauna, tube dwellers and highly mobile species will be less susceptible than free-living and less mobile species. For infaunal species, tube dwellers and burrowers living at or below the rhizome layer will be better protected than those living above it. The depth at which a prey species attains a refuge in the sediments will be shallower in a vegetated habitat thaan in an unvegetated habitat, provided the species can burrow into or beneath the rhizome layer.

2. The density of shoots, the patchiness of the grassbed, plant biomass, individual leaf area, leaf morphology and the thickness, structure and proximity of the rhizome layer to the sediment surface are

the key characteristics of the plant that potentially can mitigate the effects of predation. However, a linear relationship between some of these characteristics and predator success does not appear to exist. Instead, a threshold level of these plant characteristics seems necessary for significant protection from predation to occur. Because of the variety of leaf sizes and shapes present in the diverse seagrass species and the different characteristics of the prey and predator species, this threshold level is variable.

3. Heterogeneous grass beds (bare sand areas interspersed within the bed) should provide more favorable foraging areas for motile fishes or invertebrates, since motile fish or invertebrates can forage over the unvegetated areas while at the same time remaining in close proximity to their protective vegetated habitat. Particularly important to juveniles, seagrass beds may serve as a refuge from which animals may forage in a manner similar to a coral reef (Summerson and Peterson 1984). In addition, it is felt that, in the manner of optimal foraging strategy, prey organisms will "balance predation risk with resource availability in order to maximize energy gain and growth" (Orth et al. 1984).

4. The predator-prey relationships discussed above can be affected by other equally important, yet poorly investigated, biological and physical processes that occur in these multispecies assemblages, such as adult-larval interactions (Woodin 1976), adult-adult competitive interactions (Peterson 1979; Coen et al. 1981), macrofauna-meiofaunal relationships (S.J. Bell, pers. comm. in Orth et al. 1984), and migration patterns due to reproduction and/or feeding, or response to strong physical gradients such as day-night temperature differences (Adams 1976a; Robertson and Howard 1978; Stoner 1980a). The behavioral, physiological, and morphological differences among all the species that utilize the seagrass habitat, coupled with the influence of the plant itself and its variations in shoot density, biomass, and leaf area, all function to determine the structure of faunal communities.

5.1.3 Faunal Sampling: The Problems of Gear and Technique

A major difficulty with studying this abundant fauna is the proper quantitative sampling of the organisms of interest. No one set of gear or techniques samples all segments of the community evenly, and some methods are highly selective, which must be taken into account when comparing different studies that use even slightly different sampling gear or sampling schemes. For instance, the pink shrimp, Penaeus duorarum, is normally buried in the sediments by day and active at night. Sampling schemes that utilized daytime trawling would greatly underestimate the abundance of this and other organisms with similar habits.

When devices are used which yield relatively small quantitative samples, amphipods, isopods, gastropods, and polychaetes are typically found to be most abundant, (Nagle 1968; Carter et al. 1973; Marsh 1973; Kikuchi 1974; Brook 1975, 1977, 1978; Lewis and Stoner 1981). Brook (1975, 1977) used a water-powered suction dredge in a Card Sound Thalassia bed and found that amphipods represented 62.2% of all crustaceans captured. In Apalachee Bay, Lewis and Stoner (1981) compared the sampling results obtained by different-sized corers (5.5 to 10.5 cm diameter) and sieve sizes (0.5 and 1.0 mm) in a northern Florida seagrass meadow. They found that most organisms collected were within the upper 5 cm of sediment, although all sizes of corers captured similar numbers of species and showed very similar species accumulation curves. However, the small corers yielded significantly greater numbers of organisms, and many of the species that were undersampled with the larger corers were those that were closely associated with the seagrass cover. This study also investigated the relative capture efficiency of 2 sieve sizes, and found that the 1.0 mm mesh retained only 51%-57% of the individuals captured on the 0.5 mm mesh. The differences were due to undersampling species with a small terminal size as well as juveniles of the larger species.

While the previously described studies addressed the efficiency 0: different-sized core samplers, the relative efficiency of corers compared with suction samplers was examined by Stoner et al. (1983) for vegetated and unvegetated sites in Pensacola Bay. They found that with similar mesh sizes for sieving of the cores and for the filter bag of the suction sampler (0.5 mm) both samplers collected similar numbers of species. The corers, however, yielded 33% more individuals from a Haloduie bed, and 73% more individuals from a bare sand habitat than the suction sampler when compared on an equal-area basis.

The other major type of sampling device used in sampling fauna in and around seagrass beds is some form of trawl, whether a fixed-frame or beam trawl, or a device such as an otter trawl, which requires a certain velocity through the water column to maintain the trawl in the expanded condition in which it is able to fish. In collections in seagrass beds where these sampling devices have been used, decapods (including penaeid and caridean shrimp and true crabs) and gastropods generally dominate numerically in invertebrate collections (Tabb and Manning 1961; Tabb et al. 1962; Roessler and Tabb 1974; Yokel 1975a, 1975b; Hooks et al. 1976; Thorhaug and Roessler 1977).

Trawl sampling for organisms, especially fishes, in the clear waters of many seagrass beds can yield highly variable results that greatly underestimate the mobile fish fauna within a grassbed. When visibility underwater is 10 to 20 meters, it requires no great effort for highly mobile organisms to evade the trawls that are deployed behind small boats. Drop nets have been used effectively in shallow water environments, but can be difficult to construct and are not useful in deeper waters. For clear waters and deeper seagrass beds, a diver-deployed encircling net has proved highly effective and replicable (Robblee and Zieman 1984).

Somewhat paradoxically, small and intermediate-sized organisms, such as amphipods and caridean shrimp often are captured in large numbers by trawls, whose mesh size is nearly always larger than amphipods. The trawls are usually not directly capturing the animals, however, but instead are efficiently capturing the sessile drift algae which the organisms are utilizing for shelter.

While it is important to recognize that some data will reflect sampling-gear selectivity, it should not obscure the fact that definite patterns of species abundance exist in seagrass meadows when compared to adjacent habitats.

5.2 GENERAL TROPHIC STRUCTURE

Seagrasses and associated epiphytes provide food for trophically higher organisms by means of three distinct routes: (1) direct herbivory, (2) detrital food webs within grass beds, and (3) exported material that is consumed in other systems, either as macroplant material identifiable with the naked eye, or as detritus. Despite the fact that seagrasses have a relatively high protein content (see Section 2.3), they are directly grazed by relatively few animals.

The most vexing questions surrounding seagrass food webs continue to relate to the relative roles of detrital and microalgae-epiphyte grazing pathways, and the functional processes and intermediaries by which the detrital food pathway supplies nutrition to consumers. Most studies continue to show that the primary pathway of energy and nutrient transfer is through the detrital food web, and in many systems it may be the only significant food web. During the past few years, new information has been gathered on the relative role of the other modes of utilization, in particular, the role of active epiphyte grazers, a pathway that has previously been recognized but little studied. The picture emerging is that all of the pathways exist, but find different degrees of expression, depending on local conditions and the consumers present. While the detrital food web appears to be the primary pathway of trophic energy transfer, any of the others may be quantitatively the most important at specific sites.

5.2.1 Seagrass Grazers

Throughout south Florida and in the grassbeds of the Caribbean, often large numbers of direct consumers ingest living seagrass leaves in significant quantities. These include several species of sea urchins, the queen conch, numerous fishes, the green turtle, the Caribbean manatee, and assorted invertebrates, especially crustaceans and gastropods (McRoy and Helfferich 1980; Ogden 1980; and Zieman 1982). In south Florida, grazing on seagrasses is highest in those grassbeds of the Florida Keys and outer margin of Florida Bay which are in relatively close proximity to coral reefs. Major seagrass consumers in that area are parrotfish (Scaridae) (Randall 1965; Ogden and Zieman 1977), surgeonfishes (Randall 1967; Clavijo 1974), porgies and halfbeaks (Randall 1967). With increasing distance from the reef tract or patch reef, the intensity of grazing by large parrotfish and acanthurids decreases. The dominant grazers become the small grassbed-dwelling parrotfish, typified by the bucktooth parrotfish *Sparisoma radians* and sea urchins, the most abundant of which is usually *Lytechinus variegatus*, although *Eucidaris tribuloides*, *Tripneustes venticosus* and juvenile *Diadema antillarum* are also found in seagrass beds (Moore et al. 1963a, 1963b; McPherson 1964, 1968; Randall et al. 1964; Kier and Grant 1965; Moore and McPherson 1965; Ogden et al. 1973; Prim 1973; Greenway 1976; and others).

Assessments of the quantitative importance of direct seagrass consumption have appeared only recently, and for relatively few areas. The tacit assumption is that few organisms consume seagrasses directly, and that herbivory has substantially decreased with the decline of the populations of green sea turtles and manatees. Like many assumptions of tropical and semi-tropical ecosystems, this resulted from too much reliance on analogy from temperate-zone seagrass systems, and a paucity of direct observation. When the widespread use of scuba enabled prolonged underwater observation, the grazing effects of some groups of direct consumers were instantly recognizable, namely the paper-punch, half-moon shaped holes produced by parrotfish grazing on turtle grass. By comparison, the ragged edge produced by urchin grazing is not obvious, and usually resembles a leaf that has been physically torn, until one learns to look carefully for the stepwise nibble marks. The grazing effects of green turtles and manatees are not obvious until one learns what to look for, and are increasingly difficult because of the rarity of the animals and the decreased likelihood of observing them feeding.

The green sea turtle, *Chelonia mydas*, is a diurnal grazer of seagrass meadows. The grazing behavior of the green turtles is similar to some of the large, reef parrotfish in the sense that they graze the seagrass meadows and seek shelter at night, frequently in deep holes or near fringing reefs, surfacing at intervals to breathe. The turtles then swim some unknown distance to the seagrass beds to feed. What is unique is that they return consistently to the same spot and regraze the previously grazed patches, maintaining blade lengths of only a few centimeters (Bjorndal 1980). The persistence of these characteristic patches of neatly cropped leaves provides indirect evidence of turtle grazing. Thayer et al. (1982) have calculated that an intermediate sized *Chelonia* (64 kg) consumes daily about 280 g dry weight of *Thalassia* blades. Turtle consumption of seagrass has been estimated to be 2.2% of body weight per day (Thayer et al. 1980), 1.65% (Bjorndal 1980), and 0.6% (Fenchel et al. 1979).

Turtles do not consume the entire blade on their first graze of an area, but bite only the lower portion and allow the epiphytized upper portion to float away (Bjorndal 1980; Zieman et al. 1984a). Many researchers assumed that the epiphyte complex at the tip of seagrass leaves was of higher food value than the plain seagrass leaf, but other studies have shown that the basal portion of the green leaves is higher in nitrogen concentration than the epiphytized tips (Mortimer 1976; Bjorndal 1980; Zieman et al. 1984a). The nitrogen content of *Thalassia* leaves decrease with age as well as with epiphytization. The basal portion of *Thalassia* leaves from St. Croix contained 1.6% to 2.0% N on a dry weight basis, while the older brown tips of these leaves contained 0.6% to 1.1% N, and the epiphytized tips ranged from 0.5% to 1.7% N (Zieman et al. 1984a). Thus, the current evidence indicates that the green seagrass leaves contain more nitrogen than either the senescent leaves or the leaf-epiphyte complex. By successively recropping leaves from a plot, the turtle maintains a diet that is consistently higher in nitrogen and lower in fiber content than whole leaves (Bjorndal, 1980). The maximum length of grazing time on one distinct patch is not known, but Ogden (West Indies Lab, St. Croix, USVI, pers. comm.) has observed patches that have been repeatedly grazed for up to nine months.

Manatees can weigh over 1000 kg and have been reported to consume up to 20% of their body weight per day in aquatic plants. When feeding on aquatic plants, manatees have been reported to feed indiscriminately on available plants (Hartman 1969). While in marine seagrass meadows, manatees dig into the sediment using their stiff facial bristles, then uproot the plants and shake them free of adhered sediment. A similar mode of feeding has been observed in manatees feeding in Thalassia beds by this author. Feeding patches average from 30 by 50 cm up to about 50 by 50 cm and usually form a conspicuous trail in seagrass beds. The excess sediments from the hole created by plant removal are mounded on the side of the holes as if the manatee had pushed much of it to the side before attempting to uproot the plants.

In the Caribbean and south Florida, the amount of material grazed directly is relatively high. It has been estimated (Odgen 1980) that direct grazing on seagrasses is higher in the Caribbean than in any other marine area. In St. Croix it has been estimated that an amount equivalent to 5%-10% of daily production of Thalassia is directly consumed, primarily by Sparisoma radians and secondarily by the urchins Diadema antillarum and Tripneustes ventricosus and onlv about 1% was exported. while 60% to 100% of the production of Syringodium was exoorted (Zieman et al. 1979). Thus about 70% of the daily production'of seagrasses was available to the detrital system. In Kingston Harbor, Jamaica, 0.3% of the production of Thalassia was consumed by Sparisoma radians, 48.1% was consumed by the urchin, Lytechinus variegatus, 42.1% was deposited on the bottom and available to detritivores, with the remaining 9.5% being exported from the system (Greenway 1976).

The values from St. Croix are similar to other studies in the Caribbean and south Florida (Zieman, unpubl. data), although the Jamaica study may overemphasize the quantity of seagrass material entering the grazing food chain since urchins are not normally found at densities of 20 urchins per square meter as were found in Kingston Harbor (Ogden 1980). While the overall quantitative importance of urchin grazing on the seagrasses of the west coast of Florida has not been determined, several reports indicate that, at times it can be locally significant. A population "explosion" of Lytechinus variegatus off the coast of Dixie County, Florida, resulted in densities of 636 m^{-2} in aggregates of urchins, which denuded approximately 20% of a seagrass bed (Camp et al. 1973). In Apalachee Bay, Zimmerman and Livingston (1976a) reported that this urchin was observed to graze Thalassia leaves down to substrate level, and postulated that this was, at least in part, responsible for low macrophyte biomass at certain stations. Urchins were also present at stations with low seagrass biomass near Florida State Marine Laboratory (R.L. Iverson, pers. comm.). Grazing by the few remaining sea turtles and manatees is very localized and reduced. While the shallow seagrass meadows of south Florida are used by few ducks, geese, and related waterfowl, the shallow bays and estuaries of the upper western coast of Florida offer abundant waterfowl for viewing of hunting, as this area is used extensively as either a resting stop or for wintering. Direct grazing by these birds of the Ruppia commonly found in low-salinity and inshore areas of upper western Florida is a feature of this area not seen further south.

An important by-product of heavy grazing on living seagrasses is an increase in the turnover rate of the standing crop of leaves and the increased production of detrital particles from the fragmentation of living seagrass blades following feeding and passage through the gut (Thayer et al. 1984[a]; Zieman et al. 1984a). In addition, the manner of feeding by green turtles, urchins, and parrotfish results in the release of often large quantities of torn or fragmented living seagrass and its subsequent deposition as litter locally or after export from the bed (Greenway 1976; Zieman et al. 1979).

5.2.2 Epiphyte-Seagrass Complex

Many of the literally hundreds of species of small organisms in grass beds utilize algal epiphytes and detritus as their food sources. Gastropods, polychaetes, as well as amphipods, isopods, crabs, and other crustaceans ingest a mixture of epiphytic and benthic algae as well as detritus (Odum and Heald 1972). As research continues, it is becoming apparent that this represents one of the major energy transfer pathways to higher organisms. As one progresses from the clear, low-nutrient waters of the Caribbean and the Florida keys, to the more turbid and higher nutrient waters on the west coast of Florida, there is an apparent increased dependence on the epiphytic grazing pathway (Fry 1984; Kitting et al. 1984).

In addition to those organisms which feed mainly on the epiphytes of old seagrass leaves, many species that ingest primarily seagrass, such as the parrotfish; will preferentially graze the epiphytized portion of the seagrass blade. As a result, seagrass epiphytes may be quite important in the flow of energy within the grass carpet. Many of the small, mobile epifaunal species so abundant in the grass bed and important as food for fishes, feed at least in part on epiphytes. *Tozeuma carolinense*, a common caridean shrimp, feeds on epiphytic algae attached to seagrass blades; undoubtedly epifauna are consumed coincidentally (Ewald 1969). Three of the four common south Florida seagrass-dwelling amphipods utilize seagrass epiphytes, seagrass detritus and drift algae as food sources, in this order of importance (Zimmerman et al. 1979). Epiphytic algae were eaten at a high rate by' *Cymadusa compta*, *Gammarus mucronatus*, and *Melitanitida*. The algae were also assimilated more efficiently by these amphipods (48%, 43%, and 75% respectively) than other food sources tested, including macrophytic drift algae, live seagrass and seagrass detritus.

Kitting (1984) has used a unique monitoring system to show that grazing of small invertebrates is highest while the invertebrates are on the upper grass blades at night and not while at the base of the leaves among the detritus. It is suggested that these grazers select the rapidly growing ephemeral algae when available, but that detritus may be important when the algae are not available or overgrazed. Kitting et al. (1984) later showed that in Texas estuaries, del ^{13}C ratios suggested a higher assimilation of epiphyte carbon than seagrass carbon. Fry (1984) obtained similar results in a study in the Indian River in Florida, but noted that the dominant seagrass there was *Syringodium* which floats readily and drifts from the bed with little contribution to the local detritus. In the Texas estuaries and the Indian River, the turbidity is very high, and epiphytic growth is very high compared with that in the south Florida estuaries. Epiphytes are thus a higher potential food source than in clearer waters where the epiphytic growths are relatively lower. In highly eutrophic and turbid estuaries, epiphytic grazers can be essential to the health of the seagrasses. Orth and van Montfrans (1984) have shown that in estuaries with excessive nutrient loads, the elimination of epiphytic grazers can cause the death of seagrasses when epiphytes proliferate and block incoming light on the surface of leaves, restricting seagrass photosynthesis.

5.2.3 Oetrital Feeding

Detritus food webs are consistently considered to be the major pathway through which energy flows in seagrass ecosystems. In areas where it is present, *Thalassia* generally forms the predominant fraction of the decaying material, with *Syringodium* and *Halodule* nearly always forming a minor portion of the detritus. Seagrass litter decomposes by being broken down over a period of months by bacteria, fungi and other organisms. In Biscayne Bay, Fenchel (1970) found that *Thalassia* was the principal detrital component present

(87.1%); other portions included: 2.1% other seagrasses, 4.6% algae, 0.4% animal remains, 3.3% mangrove leaves, and 2.5% terrestrial material. The microbial community living in the detritus consisted mainly of bacteria, small zooflagellates, diatoms, unicellular algae and ciliates. These types of organisms form the major source of nutrition for detrital feeders.

Detrital consumers ingest entire particles, but also strip bacteria and other organisms from the detritus. Very frequently detrital feeders are coprophagous, with the recently released fecal pellet being subsequently reingested following a time during which recolonization and regrowth of the microbes occurs (Fenchel 1970).

Mullet and other fishes are abundant and important feeders on detrital particles and benthic microalgae throughout the entire gulf region (Odum 1970). Carr and Adams (1973) found that detritus consumption was of major importance in at least one feeding stage of 15 out of 21 species of juvenile marine fishes, including sparids, hemiramphids, blennies, gobies, atherinids, clupeids and a tetraodontid.

As Stoner (1979) and Livingston (1982a) noted, it can be difficult to impossible to define when an organism is a true detritivore, because many detritivorous organisms are highly omnivorous organisms, consuming many other available substrates, in addition to organic detritus. Most penaeid and caridean shrimp are considered to be omnivores, but they are highly dependent on detritus as juveniles, becoming more omnivorous, or even carnivorous, as adults. Penaeus duorarum, the pink shrimp, in addition to organic detritus, consumes sand, polychaetes, nematodes, caridean shrimp, mysids, copepods, isopods, amphipods, ostracods, mollusks and foraminiferans (Eldred 1958; Eldred et al. 1961). Several of the large and conspicuous invertebrates such as the gastropod, Strombus gigas, and the asteroid, Oreaster reticulatus, while primarily consuming other substrates, will ingest seagrass litter and detritus as a part of their food (Randall 1964; Scheibling 1980). In the seagrass meadows of the upper Florida coast numerous mollusks and polychaetes have been recorded as consuming detritus (Bloom et al. 1972; Santos and Simon 1974; Young and Young 1977).

5.2.4 Carnivory

Typically the infauna in seagrass beds is not as heavily preyed upon as the epifauna (Kikuchi 1974, 1980). The protection from predation afforded the infauna of grass beds by dense leaf canopies and by the fibrous rhizome mats of the more robust species of seagrass like Thalassia, is great enough that few fishes specialize on infauna when feeding (Orth 1977). In the Indian River, Young and Young (1977) found that epifaunal crustaceans such as Cymadusa compta, Melita elongata, and Erichsonella filiformis, which were apparently heavily preyed upon by fish predators, increased in abundance during exclusion experiments, while the infaunal species were not affected. Stoner (1983) noted low abundances and smaller sizes of epifaunal amphipods at Halodule sites, relative to Thalassia and Syringodium sites. By comparison, bottom dwelling and infaunal amphipods showed nearly uniform distribution in both aabundance and size of the organisms among all the seagrasses.

Stoner (1983) believed that the increase in abundance of certain infaunal tanaids and amphipods in Halodule beds was due to the "thick, tough underground mat of roots and rhizomes produced by Halodule," and that "this underground complex may provide a more effective refuge from invertebrate predators than the large diameter rhizomes and sparse roots of Syringodium and Thalassia." While the assumptions described here may be valid, the explanation does not seem consistent with other observations. Halodule beds characteristically have fine-grained sediments which fishes like sea trout (Cynoscion) readily forage, while Thalassia beds are much more stabilized and resistant to penetration, making foraging by infaunal feeders much more difficult (Zieman, 1982). Much work yet remains in determining the controls on abundance of infaunal organisms in seagrass beds and surrounding areas.

Some organisms are quite flexible in their response to prey abundance. The blue crab, Callinectes sapidus, has been observed to shift its feeding from Zostera infauna to epibiota. Because of the protectiveness of the rhizome layer to the infauna, and the accessibility of the epifauna, the impact of blue crab predation may be greatest on epibenthic fauna (Orth 1977b).

Many of the important top carnivores present on the grass flats of south Florida also inhabit the seagrass meadows throughout the western coast of Florida. These include the widely distributed lemon shark (Negaprion brevirostris) and the bonnethead shark (Sphyrna tiburo), the tarpon (Megalops atlanticus), the lizardfish (Synodon foetens), the coronet fish (Fistularia tobacaria), the barracuda (Sphyraena barracuda), carangids, the grey snapper (Lutjanus griesus), and the spotted seatrout (Cynoscion nebulosus). While some of these carnivores are resident, such as the lizardfish and the gray snapper, others, like the tarpon, undergo extensive seasonal migrations.

5.2.5 Trophics and Ontogenetic Development of Grassbed Fishes

Carr and Adams (1973), Stoner (1979), and Livingston (1980b) have all demonstrated ontogenetic changes in the feeding habits of fishes inhabiting seagrass meadows on the west coast of Florida. Much of the work has emphasized the life history changes in the feeding habits of the pinfish, which is one of the most abundant fish throughout the area and is extremely important as a forage fish. Although the pinfish undergoes progressive trophic changes with development, detritus and seagrasses are a component of its diet at all stages (Stoner 1979; Livingston 1980b). As an adult, usually 75% to 90% of its diet consists of seagrasses or detritus and plant debris. Livingston (1982a) investigated the trophic organization of 14 fish species over an eight year period in the shallow grass beds of Apalachee Bay. He divided the fishes into three major trophic groups. The first group was primarily planktivorous forms and included the early life stages of anchovies, spot, mojarras, and pinfish. These juveniles feed primarily on copepods, amphipods, and plant debris and detritus. The earliest stages of the pinfish and spot occur in late winter when they selectively feed on planktonic copepods. With development, all become more omnivorous; the spot and the mojarras become primarily benthic feeders. The second major grouping of Livingston (1982a) is primarily composed of benthic omnivores and carnivores. Included in this group are the intermediate stages of the pinfish, the spotted pinfish Diplodus holbrooki, and the monacanthids. While the monacanthids show similar feeding habits, the two pinfish species showed little dietary overlap despite being both temporally and spacially sympatric (Livingston 1982a). With further development, the pinfish becomes primarily an herbivore. The third group contained the pigfish, Orthopristis chrysoptera, the silver perch, Bairdiella chrysura, and the pipe fish Sygnathus floridae, which may be generalist feeders as juveniles, but specialize on crustaceans such as shrimp, crabs, and amphipods as adults. While some species showed the progressive trophic changes with development, others such as the bay anchovy, Anchoa mitchilli, and the banded blenny, Paraclinus fasciatus, showed more persistent feeding patterns throughout their development.

5.3 DECOMPOSITION AND DETRITAL PROCESSING

Detrital food-web theory in marine and aquatic ecosystems is based on the concept that for the majority of animals that derive all or part of their nutrition from macrophytes, the greatest proportion of fresh plant material is not readily usable as a food source. For these organisms, macrophyte organic matter becomes a food source of nutritional value only after undergoing decomposition to particulate organic detritus, which is defined as dead organic matter along with its associated microorganisms (Heald 1969).

This section will describe only briefly the detrital food-web concept and will then discuss recent work that is pertinent to the understanding of detrital food webs in seagrass ecosystems. Numerous general review papers exist on the subject of detrital processing and detrital food-web theory relating to seagrass systems; among them are Fenchel and Jorgensen (1977), Lee (1980), Tenore and Rice (1980), and Nedwell (1983). Review papers directed more specifically to seagrasses include Fenchel (1977), Klug (1980), Robertson (1982), and Thayer et al. (1984b). Recent and significant work is reported in the Proceedings of the Symposium on Detritus Dynamics in Aquatic Ecosystems (Roman and Tenore 1984). Much of this section has been liberally (and literally) extracted from two previous works (Zieman 1982, 1987).

As plant litter begins to decay, it generally passes through three recognizable phases (Godshalk and Wetzel 1978). The first phase is a rapid weight loss due to leaching and autolysis of plant compounds. This phase is generally very rapid and the materials released are readily utilized by a variety of organisms. In the second phase, decay is slower and weight reduction is due to a combination of fragmentation and the simultaneous degradation of the substrate by microbial activity. At the end of this phase, the remaining substrate is highly refractory and of greatly lowered food value. (Although the material may have a relatively high caloric value, the calories are in the form of structural compounds which most organisms cannot degrade enzymatically.) The third phase of decay involves the relatively slow decomposition and fragmentation of this highly resistant residual material.

Depending on the source material and environmental conditions, this degradation process may take from several weeks to years. Increasing resistance to degradation is roughly in the order: algae, seagrasses, salt marsh plants, and mangroves. The rate of degradation is increased by physical breakdown and fragmentation, alternate wetting and drying (Zieman 1975a), the action of grazers (Fenchel 1970; Morrison and White 1980), and increased nutrients in the medium (Fenchel and Harrison 1976).

During decomposition and detritus formation, the size of the particulate matter is decreased, making it available as food for a wider variety of animals. This size reduction may be the result of simple physical agitation, or of grazing by active detritivores, such as amphipods and isopods. Reduction of particle size increases the surface area available for microbial colonization, thus increasing the decomposition rate. The fine detrital particles, whether utilized locally as suspended or deposited organic matter or transported by the water to distant areas, provide food for trophically important fauna of seagrass beds and adjacent benthic communities, such as polychaete worms, amphipods, isopods, ophiuroids, certain gastropods, and mullet.

The food value of detritus has commonly been considered a function of the nitrogen content of the material (Odum and de la Cruz 1967). However, considering nitrogen content alone can overestimate the nutritional value of the material since up to 30% of the nitrogen can exist in tightly bound non-protein fractions (Harrison and Mann 1975b; Suberkropp et al. 1976; Odum et al. 1979). As decomposition progresses, the non-protein nitrogen fraction can increase proportionally to total nitrogen yielding a food source of lower value as the result of several processes: complexing of proteins in the lignin fraction (Suberkropp et al. 1976); production of chitin, a major cell wall compound of fungi (Odum et al. 1979); and decomposition of bacterial exudates (Lee et al. 1980). However, protein (Thayer et al. 1977) and amino acid (Zieman et al. 1984c) have been shown to increase in some macrophytes during decomposition presumably leading to an enriched food source. Inhibitory compounds found in macrophyte leaves have also been found to decrease in older and decomposing macrophyte leaves and litter (Harrison and Chan 1980), which may increase their palatability to consumers.

Bacteria, fungi, and other microorganisms have the enzymatic capacity that many animals lack to degrade the increasingly refractory macrophyte organic matter! converting a portion of it to microbial protoplasm and mineralizing a large fraction. Whereas nitrogen is typically 2% to 45% dry weight of seagrasses, microflora contain 5% to 10% nitrogen. The microflora may use nitrogen from the macrophyte substrate, but they also have the capacity to incorporate inorganic nitrogen from the surrounding medium (either the sediments or the water column) into their cells during the decomposition process, thus enriching the detritus with proteins and other soluble nitrogen compounds. In addition, carbon compounds of the microflora are much less resistant to digestion than the fibrous components of macrophyte litter. Thus, as decomposition occurs there will be a gradual mineralization of the highly resistant fraction of the seagrass organic matter and corresponding synthesis of microbial biomass that contains a much higher proportion of soluble compounds.

In addition to the refractory material of detritus, the dissolved organic carbon and nitrogen, released by seagrasses (DOC and DON) during both growth and decomposition, provide nutrition for microbes. The DOC-DON fraction released during growth and early decomposition stages is readily utilized, containing much of the soluble carbohydrate and protein of the plants. It is quickly assimilated by microorganisms, but is generally available to consumers as food in significant quantities only after the conversion to microbial biomass. During photosynthesis, living Thalassia leaves were found to release 2% to 10% of recently-fixed material (Wetzel and Penhale 1979). Fresh-dried Thalassia and Syringodium leaves released 13% and 20% respectively of their organic carbon content during leaching under sterile conditions (Robertson et al. 1982). This dissolved fraction was rapidly assimilated by microbial organisms, and in 14 days the DOC released by Thalassia and Syringodium leaves supported 10 times more microbial biomass per unit of carbon than did the particulate fraction (Robertson et al. 1982).

A major tenet of detrital food-web theory has been that microorganisms are a necessary trophic intermediary between the macrophyte litter and detritivorous animals. Much evidence suggests that these consumers derive the largest portion of their nutritional requirements from the microbial component of detritus (Fenchel 1970; Hargrave 1970; Tenore 1977; see also a review in Levinton et al. 1984). Detritivores assimilate microfloral compounds with high efficiencies, ranging from 50% to nearly 100%, often with low corresponding assimilation of detrital plant compounds (Yingst 1976; Lopez et al. 1977; Cammen 1980). Deposit feeding mollusks were found to remove nitrogen from sediment particles by removal of the microorganisms but did not measurably reduce the total organic carbon content of the sediments which was presumably dominated by detrital plant carbon (Newell 1965). When the nitrogen-poor, carbon-rich feces were incubated in seawater, their nitrogen content increased due to the growth of attached microorganisms. A new cycle of ingestion by the animals would again reduce the nitrogen content as the fresh crop of microorganisms was digested. By selective grazing, amphipods and other crustaceans ingested the microbial component on leaf litter without ingesting the substrate (Morrison and White 1980). However, the grazing action of detritivores can also have a positive feedback and enhance the production of microbial populations on the detrital particles. Microbial respiration rates associated with macrophyte detritus were stimulated bv the feedina activities of animals, possibly as a result of physical fragmentation of the detritus (Fenchel 1970; Foulds and Mann 1978) or by the removal of inhibitory decomposition products (Lee 1980).

While the importance of the microbial components of detritus to detritivores is firmly established, other studies have indicated that consumers may be capable of assimilating the plant substrate (Foulds and Mann 1978). In some instances, the high abundance of particulate material compensates for its low assimilation efficiency (Hargrave 1976). Cammen (1980) found that only 26% of the carbon requirements of a population of deposit feeding polychaetes would be met by ingested microbial biomass, although the microbial biomass could supply 90% of the population's nitrogen requirements. Thus while microbial biomass is assimilated at high efficiencies of 50% to 100% (Yingst 1976; Lopez et al. 1977) and can supply proteins and essential growth factors, the large quantities of plant material that are ingested also may be assimilated at low efficiencies (less than 5%) to supply carbon requirements.

In its broadest form, the detrital food web still seems the most applicable to the widest array of seagrass systems. In many areas, undoubtedly detrital and epiphytic food sources are used jointly, based on the relative availability and food value of the material.

The wide variety of information now available permits us to re-examine the role of seagrasses as food sources and the manner in which that food is utilized by consumers. Fundamental to this re-examination is the recognition that the initial composition of macrophyte litter varies widely, and that this variation affects the food value of the initial material, the decomposition rate of the material, and the functioning of the microbial community (Tenore 1977, 1983; Rice 1982). The variation in composition is not only a function of species or type of plant, i.e. Thalassia vs Spartina, but also a function of the source of the material, with Thalassia showing a wide variation in nutritional content as a function of the latitude in which it grew. This variation can affect strongly the apparent trophic role of the seagrasses in individual seagrass beds.

Although seagrasses are marine macrophytes, they are different in many ways from their counterparts, salt-marsh plants and mangroves, with which they are frequently compared. Seagrass leaves, for instance, are initially much higher in nitrogen content than either salt-marsh plants or mangrove leaves, when each enters the system under normal conditions (Rice 1982), and contain up to 4% total nitrogen (Zieman et al. 1984c) and up to 25% protein (Vicente et al. 1980; Dawes and Lawrence 1983). While the senescent leaf tips are low in nitrogen, the bases of recently detached leaves usually retain a significant proportion of living green material.

During decomposition, mangrove and salt-marsh material increases in nitrogen content (Odum and de la Cruz 1967; Heald 1969; Rice 1982), while seagrasses remain relatively constant (Rice 1982), or decrease somewhat (Zieman et al. 1984c). Similarly, the protein and amino acid content of mangroves rise during decomposition but show less or no change for seagrasses (Rice 1982; Zieman et al. 1984b).

When decomposed under similar conditions, the stable isotope ratios of carbon did not change for either seagrasses or mangroves. The stable isotope ratio of nitrogen did not change during seagrass decomposition, but changed markedly for mangrove (Zieman et al. 1984c). The mangrove litter also showed much greater uptake rates of ammonium per gram of plant litter (R.T. Zieman, unpubl. data). From this and other parameters it was concluded that the seagrass decomposition primarily used the internal nitrogen pool while the mangroves required extensive exogenous nitrogen input by the microbes.

In another study, Roger Zimmerman (NMFS, Galveston, TX.; pers. comm.) found that amphipods from seagrass and mangrove habitats survived on seagrass detritus and soon acquired the seagrass carbon isotope signature. When fed on mangrove detritus, the amphipods from the seagrass habitat could not obtain sufficient nutrients and died. Those naturally occurring in the mangrove habitat survived, but never fully acquired the mangrove isotope signature. The conclusion of this study and that of Zieman et al. (1984) is that detrital consumers can obtain more nutritional value from the seagrass substrate than from the mangrove substrate, and that many organisms cannot be sustained solely by the microbial flora of refractory substrates such as mangrove detritus. Findlay and Tenore (1983) and Tenore et al. (1984) found similar patterns between the macroalga Gracilaria containing relatively available nutritive components and the marsh grass Spartina, a refractory substrate similar to mangroves.

In addition to compositional differences between seagrasses and other macrophytes that can lead to different mechanisms of decomposition, the plants themselves vary widely among locales. Dawes and Lawrence (1983) showed a shift in the protein content of Thalassia leaves from 13% in Tampa Bay, to 16% at Key West, to 25% in Belize. Thus, within a single species the mode of decomposition and the quality of the resulting detritus, which affects both initial and ultimate food value of the material, may be quite different depending on regional origin.

Synthesis. From the diverse studies described above, a pattern emerges of the relative utility of the detrital substrate to consumers based on (1) the initial chemical composition of the material, (2) the time of decay, and (3) the external environmental conditions. Mangroves and salt-marsh plants are recalcitrant substrates with low nitrogen content, and require extensive microbial growth and processing growth to become nutritionally useful. For many organisms, macroalgae and epiphytes are useful substrates directly or with little microbial addition. Seagrasses occupy a range from the middle of the spectrum to one overlapping with algae, depending on region and environmental conditions. In the tropics, they are a high-protein source that encourages microbial utilization of the nutrients contained in the seagrass substrate. In more temperate locations, they may be a lower quality protein source and require more extensive microbial processing to become a useful food. In regions of high nutrient loadings, the seagrasses may develop an extensive epiphytic growth that may be more productive and a less refractory food source than the seagrasses themselves, but this level of epiphytism is not seen in clear, nutrient-poor waters.

CHAPTER 6. INTERFACES WITH OTHER SYSTEMS

6.1 SALT MARSH AND MANGROVE

In addition to the seagrass meadows, the west coast of Florida has extensive marsh and mangrove resources. West Florida claims 9% of the 6 million acres of marsh bordering the Gulf of Mexico (Linda11 and Saloman 1977, Thayer and Ustach 1981), but over 85% of the mangroves bordering the gulf (Thayer and Ustach 1981). In some areas, these habitats form only small, narrow fringes around the estuary, while in other areas they extend many kilometers inland.

Like the seagrasses of Florida Bay, a vast quantity of the Florida marsh and mangroves are contained within Everglades National Park (Table 16). Moving northward from the vicinity of Charlotte Harbor on the lower west coast, the amount of mangrove coverage declines with increasing latitude until near Suwannee Sound, north of Tampa, where mangroves are completely replaced by coastal marshes. Salt-marsh development is particularly extensive from Apalachicola Bay eastward. Here, in the Big Bend region, the marshes extend from landward directly into the Gulf of Mexico without any form of protective barrier. In addition to marshes of smooth cordgrass, Spartina alterniflora, the Big Bend area has extensive marshes of black needlerush, Juncus roemerianus. While the typical Florida salt marsh shows Spartina occupying the low marsh, and Juncus the region landward (Figure 21), throughout

Table 16. The areas and major species of submerged vegetation, tidal marsh, and mangrove swamps of estuarine study areas, west coast of Florida (from **McNulty** et al. 1972).

Study area	Submerged vegetation	Emergent vegetation Tidal marsh	Emergent vegetation Mangrove
	Acres	Acres	Acres
Florida bay	256,609	12,148	36,897
Lake Ingraham	1,024	0	891
Whitewater Bay	155	68,757	75,976
Cape Sable to Lostmans River	789	108,644	49,349
Lostmans River to Mormon Key	768	23,840	36,000
Mormon Key to Caxambas Pass	4,319	52,181	92,385
Caxambas Pass to Gordon River	501	7,445	13,387

(Continued)

Table 16. (Concluded).

Study area	Submerged vegetation	Emergent vegetation	
		Tidal marsh	Mangrove
	Acres	Acres	Acres
Doctors Pass to Estero Pass	11	2,959	9,720
Caloosahatchee River	726	1,698	2,973
Pine Island Sound	26,966	7,476	18,657
Charlotte Harbor	23,383	9,087	23,474
Lemon Bay	2,145	331	971
Sarasota Bay System	7,610	235	3,616
Tampa Bay	7,890	843	8,949
Hillsborough Bay	383	203	1,077
Old Tampa Bay	6,809	533	5,024
Boca Ciega Bay	5,800	149	2,464
St. Joseph Sound	8,723	608	1,259
Baileys Bluff to Saddle Key	4,084	16,683	1,301
Saddle Key to S. Mangrove Pt	62,730	32,587	7,915
Waccassa Bay	24,223	30,752	448
Suwannee Sound	5,556	17,643	427
Suwannee Sound to Deadman Bay	2,420	14,763	0
Deadman Bay	1,834	2,549	0
Deadman Bay to St. Marks River	8,110	14,325	0
Apalachee Bay	23,521	55,669	0
St. George Sound	8,641	3,605	0
Apalachicola Bay	737	17,696	0
St. Joseph Bay	6,325	853	0
St. Andrew Sound	373	576	0
East Bay (St. Andrew)	1,146	4,597	0
St. Andrew Bay	2,540	875	0
West Bay	1,542	3,349	0
North Bay	1,030	1,664	0
Choctawatche Bay	3,092	2,816	0
Santa Rosa Sound	4,683	309	0
East Bay (Pensacola)	310	3,307	0
Escambia Bay	43	5,152	0
Pensacola Bay	1,547	213	0
Perdido Bay	1,333	1,408	0
Total	523,431	528,328	392,860

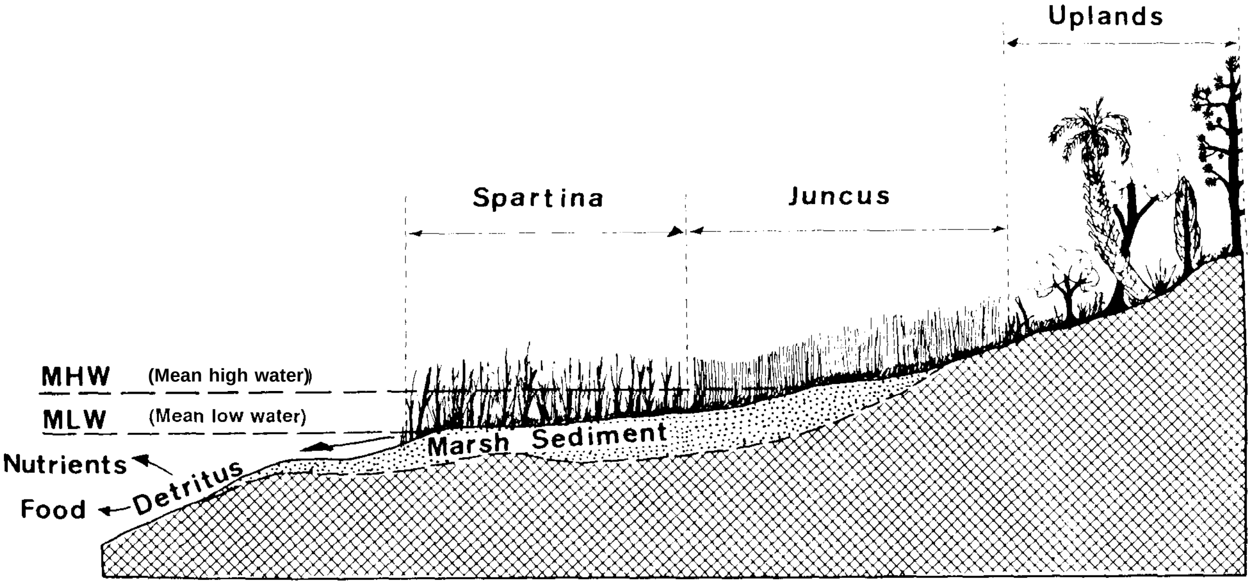


Figure 21. Zonation in Florida salt marsh dominated by *Spartina alterniflora* and *Juncus roemerianus* (from Darovec et al. 1975).

much of the Big Bend area, Juncus will actually form the land-sea interface without an intermediate Spartina zone (Carlton 1977; Stout 1984).

The importance of wetlands habitat to the estuary has been established in a variety of locations (Odum and Heald 1972, 1975; Thayer et al. 1978a; Thayer and Ustach 1981; Odum et al. 1982), but the faunal interactions between these habitats and adjacent seagrass beds are poorly understood. Thayer and Ustach (1981) concluded that "although extensive information exists on tidal marsh and mangrove plant species structure and distribution in the gulf and on commercial species such as shrimp, quantitative studies on the distribution and abundance of submergent plants and on wetland fauna and fishes are scarce."

In particular, it is not known how the faunas of the various areas interact, nor what role the respective habitats play in the life histories of the organisms. Fishes and invertebrates congregate within the mangrove prop roots for protection and shelter similar to the manner in which the seagrass canopy can provide nursery shelter. Gray snapper, Lutjanus griseus, sheepshead, Archosargus probatocephalus, spotted seatrout, Cynoscion nebulasus, and the red drum., Sciaenoes ocellatus. have been found to recruit initially in seagrass habitat but with growth move into the mangrove habitat for the next several years (Heald and Odum 1970). Since both areas serve as nursery grounds for uncounted small organisms, both also provide feeding grounds for larger predators. Some of the game fish that are found both in mangroves and seagrass beds include the tarpon, Megalops atlanticus, the snook, Centropomus undecimalis, the ladyfish, Elops saurus, the crevalle jack, Caranx hippos, the gafftopsail catfish, Bagre marinus, and the jewfish, Epinephelus itajara, (Heald and Odum 1970). While similar interrelationships undoubtedly exist between certain fauna of the seagrass beds and salt marshes, these are not documented. figure 22, from Lewis et al. (1985b), shows the life history of two of the most important fishes on the west Florida coast. For a detailed review of the mangrove ecosystems of Florida, and their necessity to fishery organisms, see Odum et al. (1982) and Lewis et al. (1985b), while Stout (1984) reviews the irregularly flooded marshes of the northeastern Gulf of Mexico.

6.2 GULF REEFS

One of the major influences on the structuring of seagrass communities along

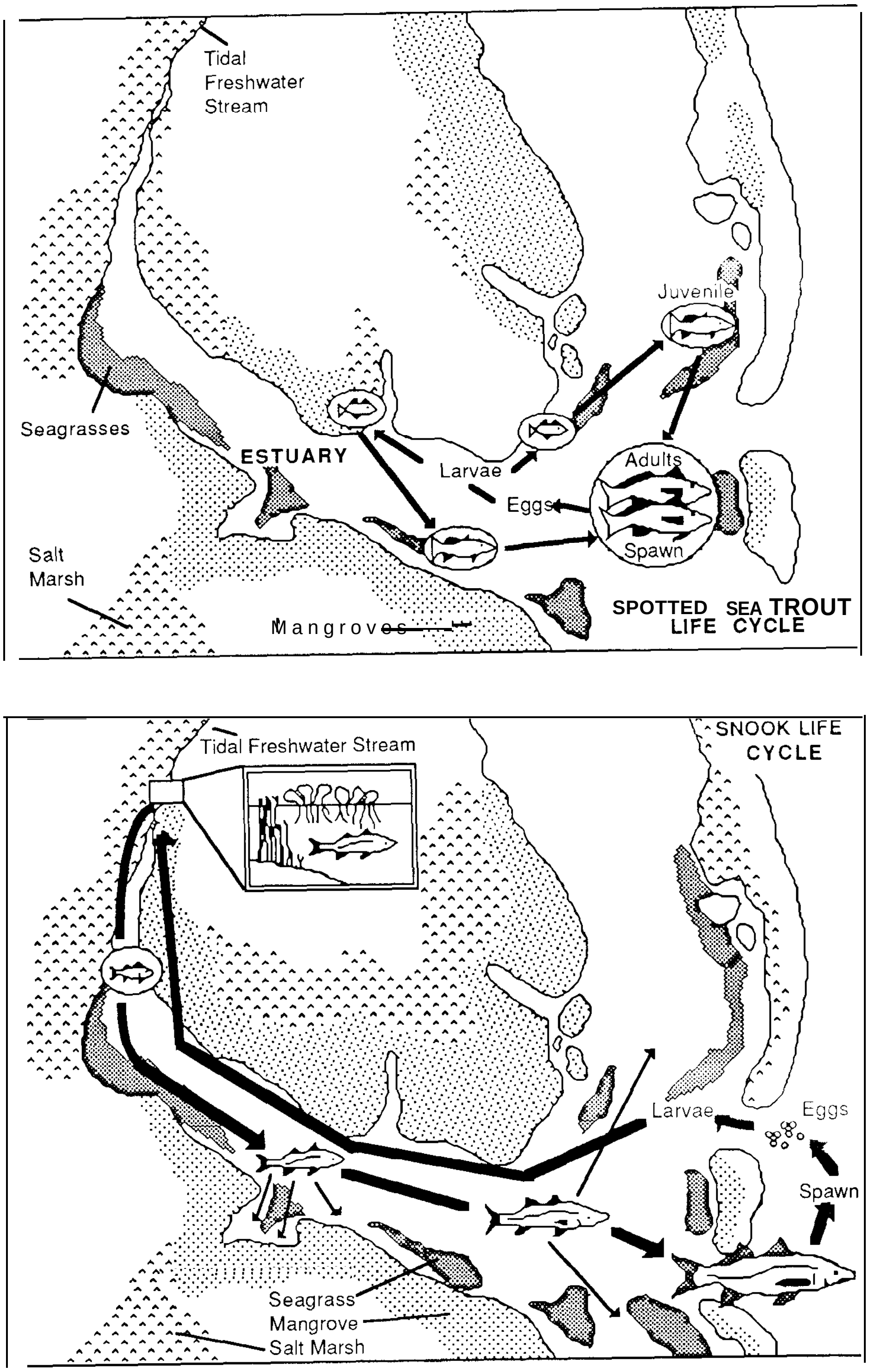


Figure 22. Life histories of spotted sea trout and snook on the west Florida coast (after Lewis et al. 1985b).

the gulf coast of Florida, when compared with the south Florida grass beds, is the lack of shallow coral reefs in close proximity to the seagrasses. While not as intensely studied, the Big Bend area has numerous and extensive limestone outcrops which should function in an analogous manner. In the coral reef areas the most prominent reef-grass bed interaction involves nocturnally active coral reef fishes of several families feeding over grass beds at night. Randall (1963) noted that grunts and snappers were so abundant on some isolated patch reefs in the Florida Keys that it was obvious that the reefs could not possibly provide food or even shelter for all of them. The major groups that shelter on the reef by day and forage into the seagrass beds nocturnally are members of the Pomadasyidae, Lutjanidae, and Holocentridae (Longley and Hildebrand 1941; Starck and Davis 1966). Typically, both juveniles and adults form large heterotypic resting schools over prominent coral heads or find shelter in caves and crevices of the reef. At dusk these fishes migrate (Ogden and Ehrlich 1977; MacFarland et al. 1979) into adjacent seagrass beds and sand flats where they feed on available invertebrates (Randall 1967, 1968), returning to the reef at dawn. These fishes epitomize what Kikuchi and Peres (1977) have defined as "temporal visitors" to the grass bed, utilizing it as a feeding ground (Hobson 1973).

6.3 CONTINENTALSHELF

The ecology of all shallow water communities on the west coast of Florida is strongly influenced by the enormous continental shelf in the region, encompassing more than 78,000 km^2. The extremely low gradient in this region is responsible for seagrasses being found at what would normally be great distances offshore. Throughout the region there are gradual faunal changes that occur both on a north-south gradient along the shore, and along a depth gradient offshore.

Along the latitudinal gradient, the fauna of the shallow water communities changes from a predominantly tropical West Indian fauna in the south to a more warm-temperate continental fauna with Carolinian affinities in the north (Smith 1976; Lyons 1979). This change is primarily related to the decreasing winter temperatures with the northward progression.

Moving from the shoreline to the edge of the shelf, several zones of faunal similarity are recognizable, controlled largely by changes in the physical characteristics of the water column and the substrate. This zonation is based on the classification developed by Lyons and Collard (1974) and Lyons (1979). The nearshore zone extends from the beachline out to 10 m (Figure 23). This area is either carpeted with seagrasses or has a sediment of quartz sand in which the seagrasses are not found. Salinities vary from 31 to 34 ppt and temperatures vary widely over the year due to the shallowness of the water. Lyons (1979) characterized the fauna as being a "rich, warm-temperate fauna with obvious relationship to the estuary."

The next zone seaward, the shallow shelf zone, extends to approximately 30- 40 m in depth, and while salinities are slightly higher and more constant, in the range of 35-36 ppt, the temperatures in the green coastal water are still seasonally variable. Where they exist, the sediments are calcareous, and the area also has numerous scattered outcrops of the limestone bedrock, which provide substrate and shelter for many organisms, especially shallow water tropical species (Lyons 1979). Near the outer edge of this zone, the clear blue offshore waters are found with nearly constant salinities and temperatures that vary only 3 to 4 degrees seasonally. This is the middle shelf zone, extending down to about 140 m, although it has been previously divided into inner and outer subzones at 60-70 m (Lyons and Collard 1974). The sediments in this area are calcareous and the limestone outcrops often extensive. The fauna is primarily tropically derived (Lyons 1979).

Near the junction of the shallow and middle shelf zones southeast of Cape San Blas lies a rich, rocky reef area known as the Florida Middle Ground, a 1500 km^2 area with a mixture of irregular limestone escarpments and knolls that rise as much

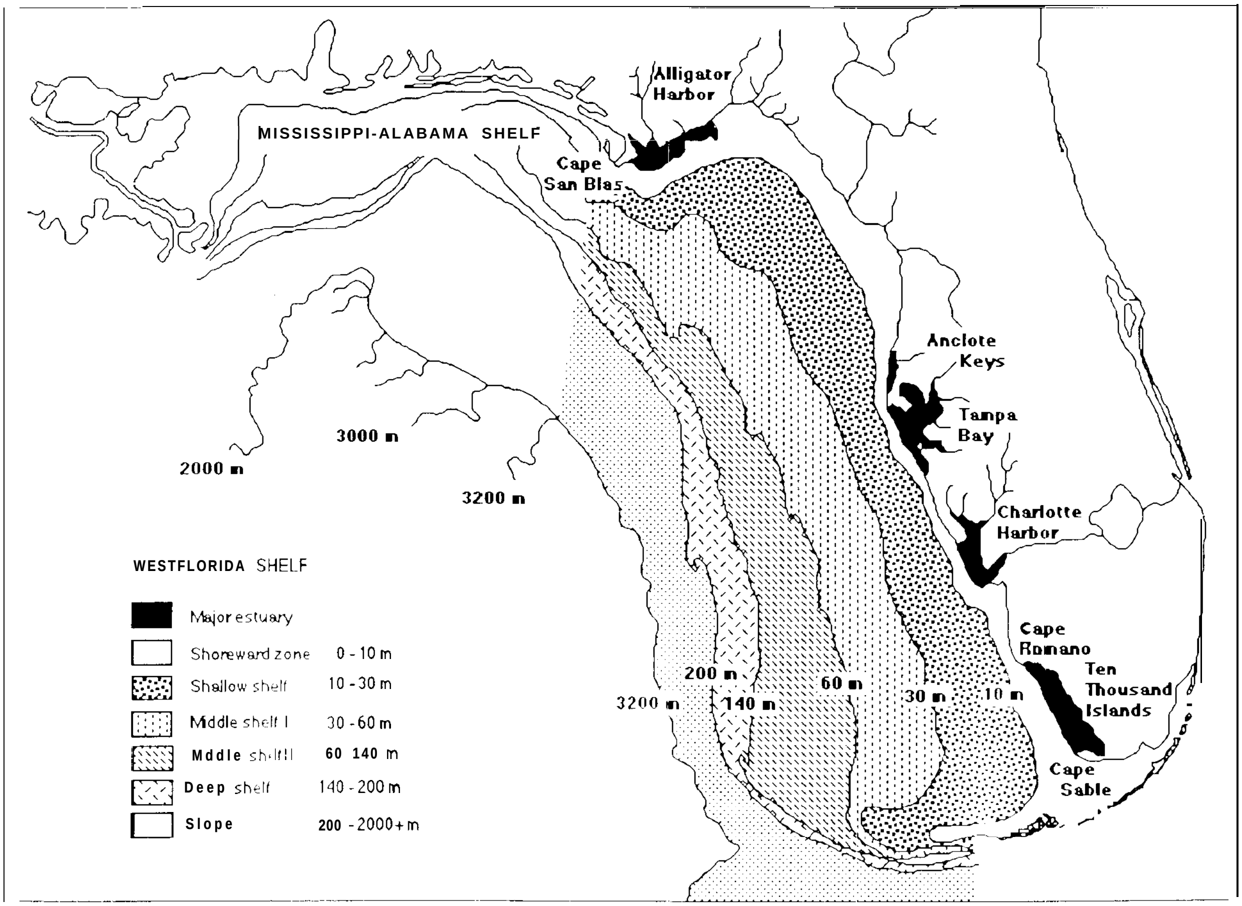


Figure 23. Faunal zonation of the west Florida shelf (after Lyons and Collard 1974).

as 10 to 15 m from the shell and sand substrate (Smith et al. 1975). The highly tropical fauna of the area is characterized by corals of the genera *Porites* and *Oculina*, and the hydrocoral *Millipora*, along with other scleractineans, alcxonarians, actiniarians, and zoantharians (Smith et al. 1975). In addition, benthic algae (Cheney and Dyer 1974), invertebrate (Austin 1970; Smith et al 1975), and fish (Smith et al. 1975) communities have been found to be highly tropical in composition.

The distribution of tropical reef organisms along the northwestern Florida shelf is a function of the highly irregular, shallow shelf-bottom topography and the influence of warm water masses. Inshore circulation is dominated by two large gyres (Figure 24), with elements of Florida estuarine waters in the north, Florida Bay waters in the south, and tropical waters from the Loop Current, brought in from the Yucutan Channel (Chew 1955; Austin 1970), which has the potential for transporting large numbers of tropical larvae into the region (Smith 1976). There is also evidence for seasonal upwelling along the outer edge of the Middle Ground (Austin 1970), which Smith (1976) attributes as the reason for the large numbers of planktivorous fishes in the region.

Throughout south Florida and in other areas, more and more studies are showing the interactions between the faunas of the reefs and the seagrass meadows, as well

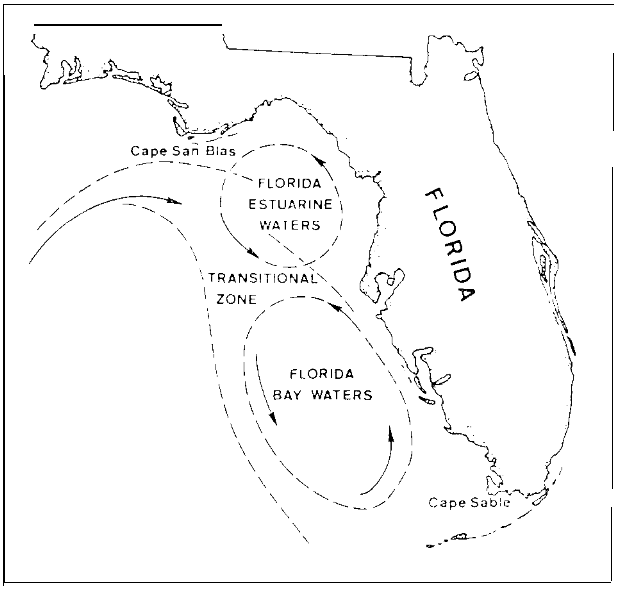


Figure 24. Eastern Gulf of Mexico current patterns during summer (after Chew 1955 and Austin 1970).

as with mangroves and coastal marshes (Ogden and Gladfelter 1983). Such studies for the seagrass meadows and the offshore reef and shelf fauna of the west Florida coast are lacking, but the potential for these faunal interactions is high (Darnell and Soniat 1979).

6.4 EXPORT OF SEAGRASS

One potentially important interaction of the west-coast seagrass beds and the offshore communities is the transport of detached seagrass leaves and particulate material from the highly productive inshore beds to the offshore areas. The material exported from the seagrass meadows can serve as both a carbon and nitrogen source for benthic, midwater, and surface feeding organisms at considerable distances from the original source of its formation (Zieman et al. 1979; Wolff 1980). In south Florida, the prevailing winds move detached blades westward from the shallow grass flats. This material is carried in considerable density over the productive Tortugas shrimping grounds and has been observed nearly 400 km west of the source beds (Zieman, unpubl. data). Incze and Roman (1983) found that particulate organic carbon, largely of benthic macrophyte origin, accumulated in Biscayne Bay during the calm summer months and was then discharged following resuspension by the cold fronts and accompanying turbulence at the onset of the winter season.

Other studies have shown that seagrasses can be transported great distances from their sources. Menzies et al. (1967) collected *Thalassia* leaves and fragments off the coast of North Carolina in 3,160 m of water, although the nearest source of *Thalassia* was 1,000 km south. Roper and Brundage (1972) found blades of *Thalassia* and *Syringodium* in nearly all of 5,000 bottom ohotoaraohs taken in the Virain Islands 'basin-at' depths averaging 3,500-m. Wolff (1976) collected seagrasses, primarily *Thalassia*, from trenches in the Caribbean as deep as 6,740 m. Much of the material showed bite marks of shallow water parrotfish as well as indications of recent consumption.

Grazing by herbivores, mortality caused by low tides on shallow banks, and wave-induced severing of leaves that are becoming senescent are the primary sources of drift material. Sporadic large releases of material occur during major storms, in which both living leaves and rhizomes are uprooted (Thomas et al. 1961).

For all species of seagrasses, blades that are fresh and healthy when detached will float better than senescent leaves. Because of the difference in size and shape of *Thalassia* and *Syringodium* blades, grazing or nibbling by most herbivores will completely sever a *Syringodium* blade and allow it to float off, while the same bite will not sever a *Thalassia* blade (Zieman et al. 1979). In addition. *Syringodium* blades float better than those of *Thalassia*. so that a much higher proportion of' the *Syringodium* production is transported from the source bed. In St. Croix, 60%-100% of the daily production of *Syringodium* was detached and exported, whereas only 1% of *Thalassia* was exported, primarily as bedload (Zieman et al. 1979). In the Indian River, Fry (1984) found that 47% of the *Syringodium* production was transoorted from the system, which, in part,' could account for the absence of seagrass isotopic signature in the consumers there. No studies as yet exist on the export or transport of seagrass material from the meadows of the west Florida coast; however, because of the demonstrated importance in other Florida seagrass beds, it is likely that there is a large amount of material transported from this region. Its destination and fate, however, remain to be quantified.

6.5 NURSERY GROUNDS

One of the most important roles of seagrass beds in the coastal ecosystem is that of a nursery ground in which postlarval stages of fishes and invertebrates concentrate and develop. In addition, important species, such as the spotted seatrout, Cynoscion nebulosus, spawn in, or just adjacent to, seagrass beds (Tabb 1966a,b; Lassuy 1983). Seagrass habitats offer high productivity, surface areas, and blade densities, as well as a rich and varied fauna and flora. Seagrass provides abundant nursery habitat and, based on abundance and size data, many important species prefer it over available alternatives in the estuaries and coastal lagoons (Yokel 1975a). In Apalachicola Bay, Livingston (1984) noted that numerous invertebrates and fishes used the seagrass beds as nurseries. Most of the penaeid shrimp and fishes found in the beds were seasonally abundant during early stages of their reproductive cycles (Livingston 1984b).

Numerous species of fishes and invertebrates have been found to use Florida grass beds as nursery grounds. In Tampa Bay, 23 species of finfish, crab, and shrimp, of major importance in Gulf of Mexico fisheries, were found as immature forms (Sykes and Finucane 1966). Livingston (1984) found Apalachicola Bay to be an important nursery for numerous invertebrates and fishes, and listed the abundance, natural history, and seasonality of 26 of the most important species (Table 17 in Livingston 1984b). A third of the species collected at Matecumbe Key seagrass beds by Springer and McErlean (1962), including all grunts, snappers, filefishes, and parrot fishes, occurred only as young, indicating the nursery value of the seagrass-dominated shoreline habitat sampled.

6.5.1 Blue Crabs

The blue crab, Callinectes sapidus, is an abundant and important resource along the gulf coast for both sport and commercial fisheries, ranking as the third largest food fishery in the Gulf of Mexico (Perry 1975; Oesterling and Evink 1977). Blue crabs are caught throughout Florida, but are in lowest abundance in the Florida Keys and reach their highest abundance in the area between Tampa and Apalachicola Bay (Steele 1979). Like nearly all of the fishery resources of the gulf coast, blue crabs are estuarine dependent throughout much of their life.

Following spawning, the young crab larvae drift with the currents and metamorphose into a megalops stage. The young crabs enter the estuary either as megalopi or as early juveniles, using a form of tidal migration, burying in the sediments on the ebb tide and rising into the water column to be transported into the estuary on the flood tide (Williams 1971; Sulkin 1974), a mechanism first proposed for pink shrimp larval migrations. In the estuary they grow and mature, using the seagrass meadows as nurseries during their juvenile stages. Mature crabs are found throughout the estuary, with many continuing to forage in the seagrass beds. When mature, the females will move into lower salinity waters and protected areas such as tidal creeks, molt a final time, and breed while still soft (Oesterling and Evink 1977). The females cannot molt once fertilized. After hardening and as their egg masses develop, the females begin to migrate offshore to higher salinity waters. The adult males generally remain within the estuary and continue to grow.

The typical patterns described for blue crab spawning indicate that the females move offshore and spawn in the general vicinity of their source estuary. However, tagging studies in Florida have shown that females migrate extensive distances, up to 500 km, to spawn in the Apalachicola Bay region (Oesterling and Evink 1977). Following spawning, the planktonic larvae become entrained in eddy currents related to the Loop Current and the two inshore gyres, and are distributed along the coast of Florida (Figure 25). The losses with this type of reproduction are apparent; it has been estimated that only one millionth of the spawn reach maturity (Van Engel 1958). The migration of the female crabs coincides with the flooding of the Apalachicola and adjacent river systems, which is thought to increase the amount of suspended particulate detritus and aid in providing food for the larvae and juvenile crabs (Oesterling and Evink 1977; Livingston 1984b). Oesterling and Evink (1977) and Livingston (1984b) correctly pointed out that current plans by the Army Corps of Engineers to place additional dams in the Apalachicola drainage basin ostensibly for flood control and navigation, could be disastrous to this vital fishery. Likewise, the diversion of fresh water flow for additional development could have similar deleterious effects.

6.5.2 Shrimp

Penaeid shrimp are an important fishery resource in Florida, especially in the gulf coast region. While the menhaden fishery is the largest in the Gulf of Mexico in terms of pounds landed, the shrimp fishery is the largest in dollar value (Taylor et al. 1973b). The two major shrimping grounds are the Tortugas grounds to the north and west of the Dry Tortugas, and the Sanibel grounds, stretching from just north of Naples to south of Tampa (Saloman et al. 1968). The nurseries for this fishery are in the seagrass beds, mangroves, and marshes of coastal Florida (Tabb et al. 1962, Costello and Allen 1966). The shrimp spawn on the fishing grounds in deeper water throughout much of the year, and the larvae are carried back into the coastal wetlands (Tabb et al. 1962; Munro et al. 1968). Roessler and Rehrer (1971) found post-larval pink shrimp entering the estuaries of Everglades National Park in all months of the year.

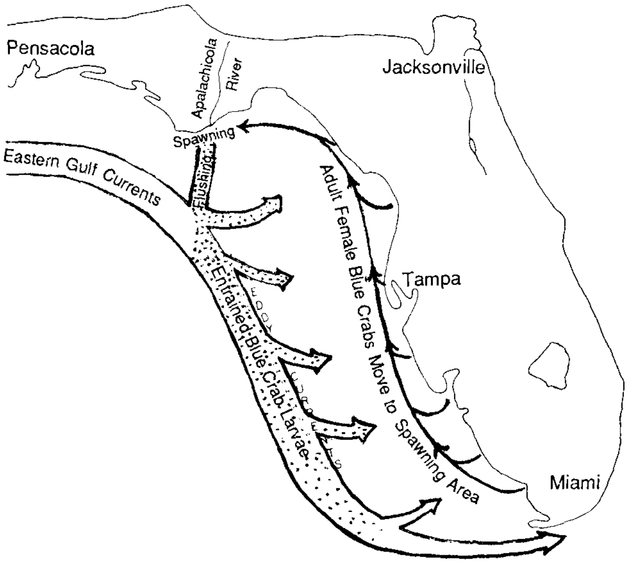


Figure 25. Blue crab spawning migrations and larval transport (after Oesterling and Evink 1977).

Throughout Florida, the most copious penaeid is the pink shrimp, Penaeus duorarum. South of Tampa, individuals of the brown shrimp, Penaeus aztecus, and the Caribbean white shrimp, Penaeus brasieliensis, are found intermixed with the pink shrimp, but are usually not abundant (Saloman et al. 1968). North of Tampa, the pink shrimp is the most plentiful, being the seventh to ninth most abundant invertebrate in Apalachee Bay, while individuals of the white shrimp, Penaeus setiferus, occupy the same habitat but are not numerous in this area (Hooks et al. 1976; Dugan and Livingston 1982). Moving westward from Florida, the pink shrimp catch decreases and the brown and white shrimp catches increase greatly.

Studies throughout south-west Florida estuaries in Rookery Bay, Marco Island, and Fakahatchee Bay have shown that the shrimp were most abundant at stations with seagrass-covered bottoms, and within these stations, where benthic vegetation was dense (Yokel 1975a, 1975b). Post-larval shrimp with carapace lengths less than 3 mm were taken only at stations where Halodule and Thalassia were present in Rookery Bay Sanctuary, while stations without grass always had larger mean sizes. The smallest shrimp are continuously within the seagrass bed. As they increase in size and become too large to burrow between the seagrass short shoots, they tunnel by day in adjacent sand flats and forage in the grass bed at night. As they near maturity, they migrate to the deeper waters offshore, usually at the onset of the first major cold front passage of the season (Hildebrand 1955, Williams 1965). Recent studies using stable isotope tracers have shown populations from two contiguous bodies of water, Rookery Bay and Johnson Bay, to have distinct isotopic signatures which take weeks to months to acquire. This indicates that the populations are staying within their embayment, and are not moving freely throughout the habitat of the region (Zieman et al. 1984c).

6.5.3 Fish

Like those in south Florida (Zieman 1982), the seagrass beds of the west Florida coast are important nursery grounds tor numerous species of commercial and sportfish, and for small forage species that serve as food for larger carnivores. While the composition of the grassbeds of the Florida Keys and portions of Florida Bay are distinct because of the influence of reef-related juveniles, the fauna from northwestern Florida Bay is highly similar to all the inshore regions of the west coast to Apalachicola Bay, both in terms of the important families and the numerically most abundant species. The major families containing predators that are associated with seagrass beds at some stage in their life cycle are the Sparidae, Sciaenidae, Pomadasyidae, Sygnathidae, Balistidae, and Serranidae (Joseph and Yerger 1956; Springer and Woodburn 1960; Tabb and Manning 1961; Wang and Raney 1971; Mountain 1972; Yokel 1975a; Livingston 1984a).

In virtually every survey of fish fauna of the west coast of Florida, the pinfish was the most abundant fish collected, and in nearly all cases was abundant throughout the year. In Rookery Bay (Yokel 1975a) and in Fakahatchee Bay (Yokel 1975b) on the southwest Florida coast, juvenile pinfish showed a strong preference for vegetated areas. The sheepshead, another sparid, initially emigrates to grass beds but quickly moves into mangrove habitats (Heald and Odum 1970) or rocks and pilings (Hildebrand and Cable 1938). The spottail pinfish, Diplodus holbrooki, and'the grass porgy; Calamus arctifrons, are other common but much less numerous sparids that frequent grassbeds in this region.

Several sciaenid species may be found in the grassbeds of west Florida, but the most common are the spotted seatrout, the spot, and the silver perch. The spotted seatrout is one of the few larger carnivorous fishes present in south Florida waters to spawn within the estuary (Tabb 1961, 1966). Its eggs sink to the bottom and hatching takes place in bottom vegetation or debris (Tabb 1966). The silver perch is the most abundant sciaenid (often second to the pinfish) in northern Florida and Whitewater Bays, being taken throughout the year (Tabb and Manning 1961).

The pigfish is the most common pomodasyid, inhabiting areas with grassy or muddy bottoms and turbid water in west Florida estuaries. The white grunt is less abundant, but is common throughout the area, occurring most commonly over Thalassia beds in clear water as juveniles (Tabb and Manning 1961; Roessler 1965; Bader and Roessler 1971; Weinstein and Heck 1979).

The two snappers (Lutjanidae) that are most common throughout the region are the two most often associated with grassbeds, the gray snapper and the Lane snapper. Both occur throughout the range, and are especially common in south Florida. Juvenile gray snappers have been considered the most common snapper in northern Florida and Whitewater Bays, including freshwater regions (Tabb and Manning 1961), while juvenile Lane snappers have been abundant in Thalassia habitat in northern Florida Bay when salinities were above 30 ppt (Tabb et al. 1962) in northern Florida Bay, and were the most common snapper taken in grass habitat of the Ten Thousand Island region of the southwestern Florida coast (Yokel 1975a,b; Weinstein et al. 1977; Weinstein and Heck 1979).

6.5.4 Detached Macrophytes as Nursery Habitat

In the previous chapter, it was noted that even using such a coarse sampling device as a large mesh otter trawl will yield many small organisms, such as amphipods and isopods (see Chapter 5), as well as numerous juveniles which use detached macrophytes as shelter. Although seagrasses may be associated with these materials, it is primarily composed of large balls or amorphous masses of drifting algae (Cowper 1978). While many algae can go into the makeup of the drift algae, the most common ones in western and southern Florida are species of the rhodophyte genus Laurencia.

Currently, there are few studies of this highly important but ephemeral habitat. In western Australia, Lenanton et al. (1982) showed that the concentrations of several important fish were highest in the zone of the drift algae near the shore. The main food of these fishes were amphipods that were profuse in the drift algae. In addition, the arrival of the juveniles appeared to correspond with the greatest accumulations of the drift algae.

While seagrass beds may be important habitat for pre-adult and immature adult spiny lobsters, Panulirus argus, in south Florida, drift algae have been found to be a critical habitat for the newly settled juvenile lobsters (Marx and Herrnkind 1985). The earliest stages of lobsters were found solitarily occupying clumps of Laurencia, using it for shelter and abundant food. After reaching approximately 17 mm in carapace length, the juvenile lobsters leave their solitary existence in the drift algae and begin to accumulate in dens, becoming more gregarious with the transition (Marx and Herrnkind 1985). Although other studies are lacking at this time, drift algae is an associated habitat of potentially great importance as a nursery and needs much more study.

CHAPTER 7. HUMAN IMPACTS AND APPLIED ECOLOGY

The west coast of Florida possesses vast regions of highly productive coastal seagrass, mangrove, and marsh habitats that continue to be relatively undisturbed by human impact. This same region also has areas like Tampa Bay that could serve as case studies on how to rape and plunder a formerly productive natural system with utterly no concern for the future. While some forms of human impact, such as oil spills, have less impact on seagrass meadows than on the emergent interface communities (mangroves and salt marshes), other stresses, especially dredging, filling, and eutrophication are highly destructive to the seagrasses. Heavy population influx and the resulting developmental pressures have severely impacted some areas, but others, such as the Big Bend area, have been less threatened due to their relatively low population density, inacessibility, and recent conservation efforts. In addition, while all of Florida's coastal waters now have increased protection, Rookery Bay, Apalachicola Bay, and much of Charlotte Harbor and Pine Island Sound have now been made estuarine sanctuaries and marine preserves.

Many publications now document the ecological importance of these habitats and the extent of human impact, both potential and realized, upon them (Zieman 1975b, 1982; Thayer et al. 1975, 1984a; Phillips 1978; Ferguson et al. 1980; Livingston 1984a; Zieman et al. 1984c).

In previous reviews (Zieman 1975b, 1982) human impacts were categorized based' on the activity causing the damage. This study adopts a somewhat more functionally based approach. Seagrasses can be killed off by human impacts, or in some cases natural disturbances, either directly or indirectly, by what will be termed acute stress as opposed to chronic stress. Acute stress is stress resulting from direct damage that physically kills or removes the plants. The most common example of this type is the extensive losses that have been caused by direct habitat removal by dredging and filling. By comparison, chronic stress gradually kills the plants over a period of time, creating conditions in which either respiration exceeds production or in which the plants lose their ability to compete with other species for light, nutrients, and space. Two of the major causes of this type of stress are eutrophication, with its excessive algal growth, and the suspended sediments and nutrients from dredging and filling operations. Both of these causes of pollution operate in a similar manner on the seagrasses; that is, they increase turbidity and decrease the light incident on the seagrass leaf, reducing its net production and competitive fitness.

Most of the recorded seagrass losses have been attributed to acute stress effects. However, this may simply be due to the easier accountability when a brief, obvious stress, such as a canal dredging, destroys a grass bed. The great losses that are now being documented for many of Florida's estuaries have been caused by the insidious, continual decline of water quality in these estuaries.

7.1 DREDGING, FILLING, AND OTHER PHYSICAL DAMAGE

7.1.1 Acute Stress

The most common and obvious destructive influence on seagrass beds in Florida has historically been the dredging and filling of estuaries and adjacent wetlands.

Florida ranks third among the gulf coast States, after Texas and Louisiana, in amount of submerged land that has been filled by dredge spoil with 9,520 ha (Lindall and Saloman 1977). In Texas and Louisiana, most of the spoil created came from dredged navigation channels, while in Florida, it accounts for less than 5% of the State total (Figure 26). Not surprisingly, the majority of filling of submerged areas in Florida has been to create land for residential and industrial development.

Studies conducted in Tampa Bay and Boca Ciega Bay were among the first to demonstrate the long-term impact of dredging activities, and remain some of the most definitive. Between 1950 and 1968, an estimated 1,400 ha of the bay were filled during projects involving the construction of causeways and the creation of new waterfront homesites (Figure 27). In undisturbed areas of the bay, luxuriant seagrasses grew in stable sediments averaging 94% sand and shell. At the bottom of dredged canals the unvegetated sediments averaged 92% silt and clay (Taylor and Saloman 1968). While several studies of Boca Ciega Bay collectively described nearly 700 species of plants and animals occurring there, Taylor and Saloman (1968) found only 20% of those same species in the canals. Most of those were fish which are highly mobile and thus not restricted to the canals during extreme conditions. Species numbers were higher in undisturbed areas, but 30% more fish were found in the canals. The most abundant (the bay anchovy, the Cuban anchovy, and the scaled sardine), are planktivorous, and may have benefitted from the higher nutrient levels in the canals and the shelter provided. Recolonization was negligible at the bottom of the canals and it was concluded that the sediments there were unsuitable for most of the bay's benthic invertebrates. Light transmission values were highest in the open bay away from landfills, lowest near the filled areas, and increased somewhat in the quiescent waters of the canals. Due to the depth of the canals, however, light at the bottom was insufficient for seagrass growth. Taylor and Saloman (1968), using conservative and incomplete data, estimated that fill operations in the bay resulted in an annual loss of $1.4 million for fisheries and recreation.

Figure 26. Channel through grassbed with open-water dredge disposal area in Tampa Bay (photo by R. R. Lewis).

At the time these canals were built, developers dredged them as deep as possible to produce cheap fill material locally, frequently to depths of 5-8 m in areas where the original water depth was only 1 m or less. Combined with the easily suspended sediments, this relatively great depth and the shading effects of the vertical canal walls prevented the regrowth of productive seagrasses. The depth and the shallow sill near the opening caused them to become stagnant, organic traps with highly reducing sediments that were easily disturbed. When storm action resuspends these sediments, the water column can quickly become anoxic, causing localized mortality. Many of these problems were alleviated in recent years when permitting of deep canals was curtailed.

Burial of seagrasses can be as destructive as dredging; however, if seagrasses are only lightly covered and the rhizome system is not damaged, regrowth through the sediment is sometimes possible. Thorhaug et al. (1973) found that construction of a canal in Card Sound temporarily covered turtle grass in an

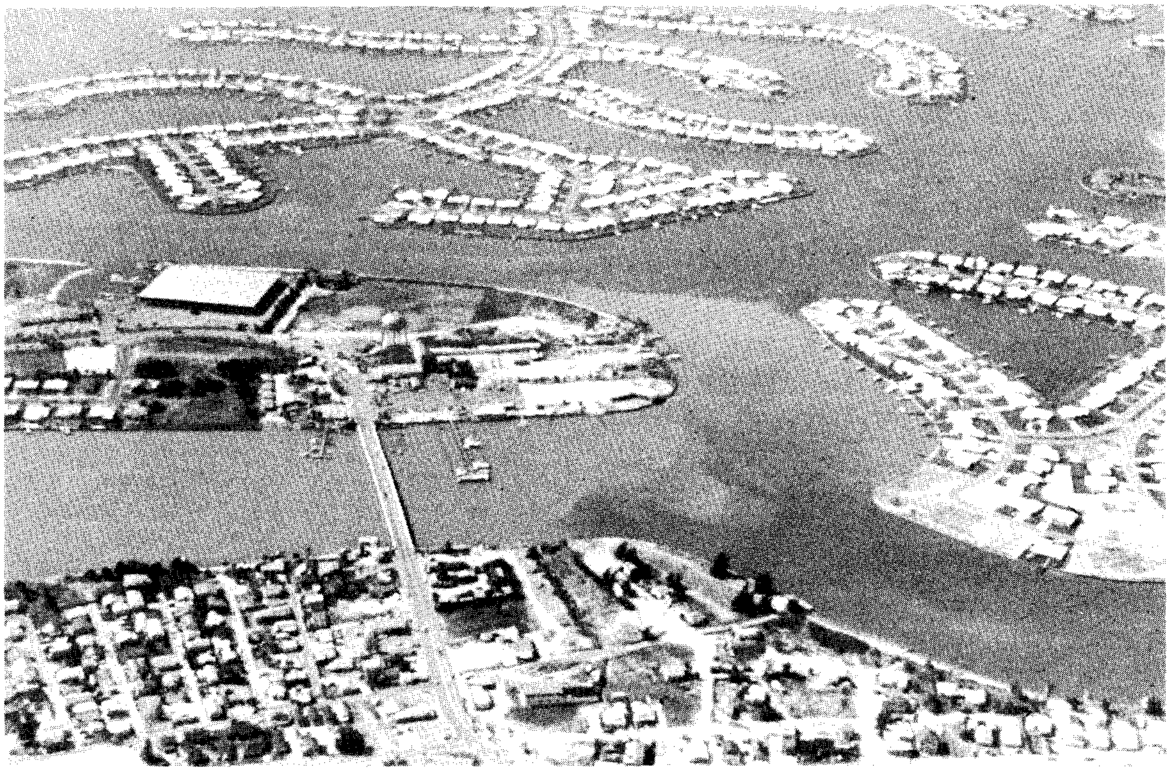


Figure 27. Dredged and filled areas in Boca Ciega Bay (photo by M. J. Durako).

area of 2-3 ha with up to 10 cm of sediment, killing the leaves, but not the rhizome system. Regrowth occurred when the dredging operations ceased and currents carried the sediment away.

7.1.2 Other Physical Damage

Any physical damage to the sediments and rhizome structure of seagrass beds can have long-term effects, no matter how insignificant the damage may seem visually. Small cuts, no more than 10 cm wide and a similar depth in the sediments, from the propellers of the innumerable outboard boats crossing Florida seagrass beds, can take from 3 to 5 years to recover in a Thalassia bed (Zieman 1976).

Damage by larger boats can be vastly more severe and long lasting. During the construction of the new bridges in the Florida Keys, a contractor attempted to cut transit time barging new bridge sections into the Niles Channel bridge. Instead of using the deep water access on the Atlantic side, the contractor used a large tugboat to prop-dredge a new passage through a shallow Thalassia flat. The resulting swath was several hundreds of meters in length, about 10 m in width, and up to 2 m in depth. This, in effect, created a new tidal pass, and with the high water velocities during tidal flow through it, it is doubtful that the cut will ever return to normal. Fortunately, the federal courts determined that such wanton distruction constituted illegal dredging and filling (Zieman, unpubl. data).

In estuaries near Tampa and Tarpon Springs, Godcharles (1971) found no recovery of either Thalassia or Syringodium in areas where commercial hydraulic clam dredges had severed rhizomes or uprooted the plants, although at one station recolonization of Halodule was observed.

7.1.3 Chronic Effects

In addition to the direct effect of burial, secondary effects from turbidity, which restricts nearby productivity, chokes filter feeders by excessive suspended matter, and depletes oxygen by rapid utilization of suspended organic matter, can have serious consequences. The dredged sediments are unconsolidated and readily resuspended. Thus, a spoil bank can serve as a source of excess suspended matter for a protracted time after deposition.

In 1968, lush growths of Thalassia had been recorded at depths up to 10 m in Lindberg Bay, in St. Thomas, U.S.V.I., but by 1971 this species was restricted, by turbidity caused by dredging, to sparse patches usually occurring in water 2.5 m deep or less (Van Eepoel and Grigg 1970). Similar declines were observed by Grigg et al. (1971) in Brewers Bay, St. Thomas.

Odum (1963) found light penetration was reduced in seagrass flats adjacent to the dredging site of an intracoastal waterway in Redfish Bay, Texas. Subsequent decreases in productivity of Thalassia were attributed to the stress caused by suspended silts. Growth increased the following year and Odum attributed this to nutrients released from the dredge material. While dredging altered the 38 m long channel and a 0.5 km zone of spoil island and adjacent beds, in this instance no permanent damage occurred to the seagrasses outside this area beyond this region.

7.2 EUTROPHICATION AND SEWAGE

The greatest losses of seagrass habitat are caused by the effects of physical damage from dredging and the chronic stresses placed on the plants by suspended sediments and eutrophic algal growth, manifested in the form of increased turbidity and resultant light reduction. In many ways it is the most insidious form of pollution, for it usually appears as a slow and gradual worsening of local water quality. With gradually increasing turbidity and decreasing water clarity, it is less noticeable that seagrasses are no longer distributed as deep as they were previously, and the choking growths of epiphytes are also less obvious. Thus, the natural communities are diminished and their valuable functions as habitat and shelter are either decreased or lost entirely.

Seagrass beds subjected to both eutrophication and suspended sediments in Christiansted Harbor, St. Croix, declined and were replaced by the green alga, Enteromorpha, reducing the areal extent of the seagrasses by 66% over a 17-year period (Dong et al. 1972). In Hillsborough Bay, phytoplankton productivity increased due to nutrient enrichment from domestic sewage and phosphate mining discharges (Taylor et al. 1973b). Phytoplankton blooms contributed to the problem of turbidity, which was increased to such a level that seagrasses persisted only in small, sparse patches. The only important macrophyte found in the bay was the red alga, Gracillaria. Soft sediments in combination with low oxygen levels limited diversity and abundance of benthic invertebrates (Taylor et al. 1973b).

In northern Biscayne Bay, McNulty (1970) found few seagrasses in waters that were polluted by sewage discharge in 1956. Within 1 km of the outfall only small patches of Halodule and Halophila were found. Following the construction of an offshore outfall, postabatement studies in 1960 found that the seagrasses had continued to decline, probably due to the persistent resuspension of sediment from a causeway and other nearby construction projects. The fine sediments of this area are highly prone to resuspension when lacking the stabilizing influence of the seagrass canopy.

7.3 OIL

Increased demand for local petroleum supplies has intensified exploration for offshore sources in shallow continental shelf, such as is found off the west Florida coast. The potential for damage to local marine communities, as well as those at some distance, is present at all stages of oil production, including exploration, production, and transportation, although not all of the risks are equal. The National Academy of Sciences (NAS 1975) has found that the greatest risks are associated with shipping accidents, followed by those spills associated with loading and unloading oil. Getter et al. (1980) noted that of 16 oil spills in the Gulf of Mexico and Caribbean 75% were transit accidents. By comparison, NAS (1975) estimates that about 1.3% of the annual input of oil to the oceans is the result of drilling and production losses. On the west coast of Florida, the remaining seagrasses of busy ports like Tampa, as well as the beds of South Florida, would seem to be the most vulnerable to damage from oil spills. The large beds of the Big Bend region are deeper and well removed from major shipping lanes. The known effects of oil spills, cleanup procedures, and restoration on seagrass communities and associated organisms were reviewed by Zieman et al. (1984b).

Petroleum products can damage seagrass ecosystems in a variety of ways. These have been summarized by Blumer (1971), Cintron et al. (1981), and Zieman et al. (1984b) and include:

1. Direct mortality of organisms due to smothering, fouling, and asphyxiation; poisoning by direct contact with oil (especially fresh oil); and absorption of toxic fractions from the water column.

2. Indirect mortality due to the death of food sources or the destruction or removal of habitat.

3. Mortality of sensitive juvenile forms, especially those using the grassbed as a nursery ground.

4. Incorporation of sublethal amounts of petroleum fractions into body tissues, potentially lowering tolerance to other stresses.

5. Reduction or destruction of the food or market value of fisheries due to the tainting of flavor by absorption of hydrocarbons, even though the amounts are sublethal.

6. Incorporation of potentially carcinogenic or mutagenic substances into the food chain.

Although much more laboratory work is needed, the few studies existing that have studied the effects of petroleum products on seagrass community components have shown them to be toxic to the organisms. Seagrasses exposed to low levels of water suspensions of kerosene and toluene showed significantly reduced rates of carbon uptake (McRoy and Williams 1977).

Refined products have consistently been found to be more toxic to marine organisms than crude oils. Larval stages of grass shrimp were slightly more resistant to the oil than the adults, while all forms of the oils were more toxic to the larval and juvenile stages of white and brown shrimp than to adults. Changes in temperature and salinity, which are routine in estuaries, enhanced the toxic effects of the petroleum hydrocarbons (Anderson et al. 1974). The best indicator of oil toxicity is probably the aromatic hydrocarbon content of the oil (Anderson et al. 1974; Tatem et al. 1978).

Numerous studies have indicated that intertidal communities are the most vulnerable of all marine communities; thus, seagrass ecosystems are usually less vulnerable due to their generally subtidal nature. There would seem to be a decreasing likelihood of damage with increasing depth, so that grassbeds several meters or more in depth are possibly better protected from oil spills than intertidal beds.

The impact on marine and estuarine communities, including seagrass communities, of several large-scale oil spills has been investigated but these are after-the-fact damage assessments. The results were highly variable, ranging from heavy destruction to little damage, a factor of the size of the spill and numerous other variables in environmental conditions. The case studies reviewed in Zieman et al. (1984b) are among the best-documented examples of oil spills affecting seagrass beds. In general, seagrasses suffered relatively little damage because of the subtidal nature of the systems; the primary impact was on the associated faunal communities. Those beds that were exposed to oil at low tide did not suffer greatly, due in part to their buried rhizome system.

7.4 TEMPERATURE AND SALINITY

Because of the latitudinal variation along the coast of west Florida, thermal pollution will have different effects along this gradient. At the southern end, the seasonal programming is tropical and many organisms are growing near their thermal maxima in the summer under normal conditions (Mayer 1914, 1918). At the northern end of the gradient, the seagrasses are at the northern limits in their distribution and are more likely to be restrained by winter minima. However, even in this region, summer temperatures are high and areas with shallow water and restricted circulation can become extremely hot in the summer.

The time of exposure to either extreme high or low temperatures is critical in assessing the effect of thermal stress. Many organisms can tolerate large-amplitude temperature changes on a short-term basis, but are intolerant of chronic exposure to smaller changes. Seagrasses have buried rhizome systems that include the meristematic regions for leaf, root, and rhizome growth, and the relatively poor thermal conductivity of the sediments serves as an effective buffer against short-term temperature damage. Therefore, the seagrasses are more resistant to brief high temperature increases than the commonly occurring algae. Continued heating, however, can raise the sediment temperature to levels lethal to the plants (Zieman 1975). The animal components of the seagrass systems show the same ranges of thermal tolerances as the plants. Sessile forms are more affected, being unable to escape either short-term acute effects or long-term chronic stresses.

The primary sources of human-induced thermal stress in estuaries are the cooling systems of electrical power plants (Figure 28). In addition, some industrial plants produce waste heat, and, in some cases, heated wastewater that also contains a variety of waste chemical products.

Damage to communities subjected to these influences has been reported at various study sites in Florida (Zieman and Wood 1975; Thorhaug et al. 1978, Zieman 1982). Effluent from the Bartow power plant near the mouth of Old Tampa Bay, which reached a level of 7.2 °C above ambient temperature, killed 81 ha of seagrasses (Blake et al. 1976). Where temperatures were 2 °C above ambient or less, all of the local seagrass species survived, but at 3 °C above ambient, only sparse Halodule survived. Several parameters of Halodule were measured in the effluent plume and at a control station on the intake side of the plant. At the intake station, the biomass varied from 5 to 10 times greater than on the effluent side, while the length of the leaves and emergent short shoots on the intake side were over twice the length of leaves from the effluent side. During summers, blue-green algal mats covered a large portion of the area where the temperature was greater than 3 °C above ambient (Blake et al. 1976), a condition similar to that found at Turkey Point in south Biscayne Bay (Zieman and Wood 1975).

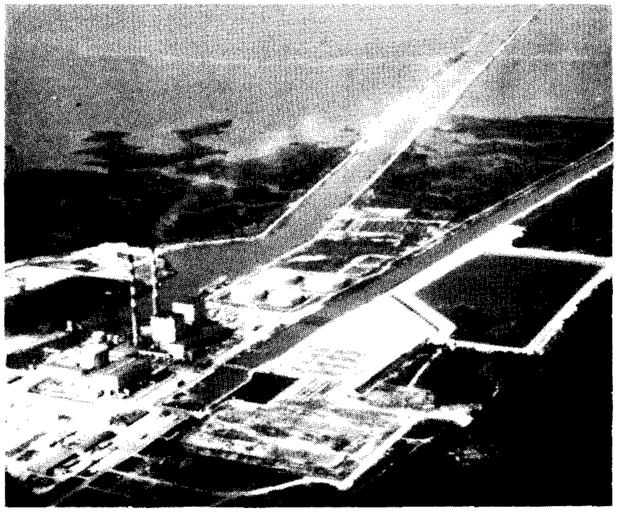


Figure 28. Crystal River power plant (photo by R. R. Lewis).

In addition to the seagrasses, changes were found in the associated animal communities in the effluent of the Bartow power plant. On the intake side of the plant, 104 species of invertebrates were identified, primarily polychaetes, mollusks, crustaceans, and echinoderms, while on the effluent side only 60 species were found (Blake et al. 1976). Numbers of individual polychaetes were greater on the effluent transects, crustacean numbers were greater along the intake transects, and mollusk numbers were similar in both areas (Blake et al. 1976). Virnstein (1977) found a decrease in density and diversity of benthic infauna in the areas where temperatures of 34-37 °C were recorded.

On the west coast of Florida, effluents from the Crystal River power plant impacted shallow-water seagrass and macroalgal communities, but because of the changing nature of the studies over the years, and particularly due to the highly qualitative methods used in the early surveys, full assessment of the impact from thermal effluents is not possible. Numerous studies have shown a reduction in the number of macroalgal species and their abundance in the vicinity of the effluent (Steidinger and Van Breedveld 1971; Van Tine 1981). In the most recent study, stations outside the area of the thermal effects to the south showed greater seagrass species diversity, biomass, and productivity than those associated with the thermal effluent (Stone and Webster 1985). Sample stations north of the thermally-affected area showed patterns similar to those near the effluent, but conditions at these stations proved to be inconsistent with the southern control stations. They were in an area of reduced salinities caused by the Withlacoochee River and the western section of the Cross Florida Barge Canal. Turbidity was high in this region due to the resuspension of sediments from the abandoned barge canal and its spoil islands, thereby limiting its usefulness as a comparison area.

Barber and Behrens (1985) studied the effects of the effluent of an oil-fired power plant near Anclote Key, about 50 km north of Tampa Bay, on the seasonal productivity of Thalassia and Syringodium. Throughout the fall and winter months, both species showed greater productivity in the effluent than at the control station. As temperatures rose in the spring, the productivity increased comparably at all stations, very rapidly in March and April: Thalassia productivity at the thermally stressed station was less than at the control station except for a brief period at the end of the summer, which was not statistically significant. Syringodium productivity at the thermally-effected station exceeded that of the control station in early May, but fell precipitously at the end of the month. Barber and Behrens (1985) concluded that the heated effluents in this central Florida region had a positive effect on seagrass productivity, until it reached the upper optimal growth temperature for each species was reached. Above this upper thermal limit, productivity declined.

The response patterns to thermal effluents seen in these west Florida estuaries are similar to those previously reported in south Florida. As the temperatures in south Biscayne Bay were raised by the effluent of the Turkey Point power plant, the productivity, biomass, and areal distribution of seagrasses decreased along the path of the effluent plume of the power plant (Zieman and Wood 1975). Increases in ambient temperature of 4 °C or more killed nearly all fauna and flora present (Roessler and Zieman 1969). A rise of 3 °C above ambient caused both species numbers and diversity of algae to decrease. The optimal temperature range for maximal species diversity and numbers of individuals for animals was between 26 and 30 °C; temperatures between 30 and 34 °C excluded 50% of the invertebrates and fishes, and temperatures between 35 and 37 °C excluded 75% (Roessler 1971; Zieman and Wood 1975).

Throughout their range, Thalassia communities seem to show similar thermal response patterns. Thorhaug et al. (1978) collated and compared the response of these communities in the Caribbean tropics (Guyanilla Bay, Puerto Rico), subtropics (Biscayne Bay and Card Sound, Florida), and subtropical warm-temperate border (Tampa Bay). The summer mean temperatures in all of the estuaries averaged about 30 °C. Temperature elevations of 5 °C destroyed and denuded the Thalassia meadows; elevations of 4 °C showed severe damage to all components of the communities. With a 3 °C temperature elevation, damage was severe in the higher latitudes and less in the more tropical environments. Data was insufficient to allow intercomparisons of lesser temperature elevations, but it was clearly indicated that temperature elevations of greater than 3 °C above ambient in the warmer months produced severe and sustained damage (Thorhaug et al. 1978).

While all of the local seagrass species are euryhaline to varying degrees, Thalassia and Syringodium show a decrease in photosynthetic rate as salinity drops below full-strenqth seawater, while Halodule is less affected (McMillan and Moseley 1967). The seasonality of seagrasses in Florida is largely explained by temperature and salinity effects (Zieman 1974; Barber and Behrens 1985). The greatest decline in plant populations was found when combinations of high temperature and low salinity occurred simultaneously. The reduction of seagrass biomass and productivity at one set of stations near the Crystal River power plant which were intended to serve as controls, was attributed to reduced salinities emanating from the Cross Florida Barge Canal and the Withlacoochee River (Stone and Webster 1985).

While higher salinities may yield somewhat lusher and more productive seagrass beds compared to those found in mesohaline waters, the intermediate salinities seem to be most important for the nursery function of the seagrass meadows. Tabb et al. (1962) stated: "Most of the effects of man-made changes on plant and animal populations in Florida estuaries (and in many particulars in estuaries in adjacent regions of the Gulf of Mexico and south Atlantic) are a result of alterations in salinity and turbidity . . . . High salinities (30-40 ppt) favor the survival of certain species like sea trout, redfish, and other marine fishes, and therefore improve angling for these species. On the other hand these higher salinities reduce survival of the young stages of such important species as commercial penaeid shrimp, menhaden, oysters, and others. It seems clear that the balance favors the low to moderate salinity situation over the high salinity. Therefore, control in southern estuaries should be in the direction of maintaining the supply of sufficient quantities of fresh water which would result in estuarine salinities of 18 to 30 ppt."

7.5 PAPER MILL EFFLUENTS

Throughout the gulf coast region, with its enormous timber resources, there are numerous paper mills discharging huge quantities of waste materials into rivers, which almost immediately wash this material into the nearby estuaries. Through numerous publications, Livingston (1975, 1984a, 1987) has chronicled the changes in the seagrass communities due to kraft mill effluents, and the subsequent recovery process following a pollution abatement program. Zimmerman and Livingston (1976a) found that a pulp mill on the Fenholloway River dumped from 200,000 to 220,000 m^3 of kraft mill effluents into Apalachee Bay over the 20 year period from 1954 to 1974, at which time a pollution abatement program was enacted. The effluents altered water quality and caused increased turbidity and reduced light penetration, which, in turn, reduced species diversity of macroalgae and reduced productivity in the bay compared with a similar region off the unpolluted Econfina River (Heck 1976; Hooks et al. 1976; Livingston 1984b). The changes in water quality and plant communities caused significant changes in the fishes and macroinvertebrates. Numbers of individuals and species numbers were reduced in areas of severe impact. In areas of moderate but chronic impact, the annual species numbers were equivalent to control stations, but this proved to be the result of the recruitment of a few individuals of rare species (Livingston 1975). Livingston (1987) also noted that although recovery was occurring, the seagrasses, especially Thalassia, were slow to respond following the removal of the stress.

7.6 DISTURBANCE, RECOLONIZATION, AND RESTORATION

7.6.1 Disturbance

While the large offshore seagrass meadows in the Big Bend region of Florida have remained relatively intact and undisturbed, the beds that are found within the enclosed estuaries on the west coast of Florida have suffered tremendously. The greatest losses have occurred in Tampa Bay, where there are only 5,750 ha of seagrasses remaining from an estimated historical coverage of 30,970 ha, a reduction of 81% (Figure 9 from Lewis et al. 1985a). Because of the high turbidity caused in part by the now-unvegetated bottom, seagrass distribution is presently limited to less than 2 m in depth in nearly all cases. The problems and destruction encountered in Tampa Bay are not unique, but are mirrored in nearly all estuaries with heavy urbanization and industrialization (Taylor and Saloman 1968; Simon 1974; Lewis et al. 1985a; Livingston 1987).

Other estuaries on the west Florida coast have shown similar losses (Table 17). In the vicinity of Bayport, seagrasses have declined by 13% (Haddad 1986). St. Joseph Bay, in an area of low population density, has not shown significant changes in seagrass density in 15 years (Savastano et al. 1984), and Apalachicola Bay has shown minimal degradation (Livingston 1987). The coverage of submerged vegetation in Choctawhatchee Bay has declined by 30% since 1949 (Haddad 1986), but the causes are unknown (Burch 1983; Livingston 1987). Within the Pensacola Bay system, occasional beds of Thalassia and Halodule are found in Santa Rosa Sound, but there was a complete loss of seagrass in Escambia Bay, East Bay, and Pensacola Bay between 1949 and 1979 (Olinger et al. 1975; Livingston 1987). Big Lagoon, west of Pensacola, has increased coverage by 55%, one of the few areas in the state to do so (Haddad 1986). In Charlotte Harbor, on the southwest coast, seagrass beds have declined nearly 30% to 9,300 ha remaining (Harris et al. 1983; Haddad and Hoffman 1986).

7.6.2 Recolonization

The natural recolonization of seagrasses is a highly variable process, the rate of which can be affected by local environmental parameters, as well as the species of the seagrass. Halodule is the normal pioneer species in the region and can colonize an area rapidly if sedimentary conditions are favorable and if there is a source of seed or other propagule material. With its surficial rhizome system and smaller investment in belowground biomass than the climax species, it can rapidly cover a damaged area.

Compared to the other seagrasses, Thalassia is much slower to recolonize a disturbed area. At least 10 months are required for Thalassia to begin new short shoot development (Fuss and Kelly 1969), and the initiation of new growth seems to be sensitive to environmental conditions. After 13 months, Kelly et al. (1971) found that 40% of transplanted plants in a control area had initiated new rhizome growth, while only 15% to 18% of the plants transplanted to disturbed sediments had initiated new growth.

It has been well documented that small disturbances in seagrass beds require surprisingly long recovery times. The most common form of disturbance to seagrass beds in the shallow banks and bays of south Florida results from cuts by boat propellers. Although it would seem that these relatively small-scale disturbances would heal rapidly, it typically takes two to five years to recolonize a Thalassia bed (Zieman 1976). The scarred areas rapidly fill in with sediment from the surrounding beds, but the sediment is slightly coarser and has a lower pH and Eh, and probably other physico-chemical differences that the plants can detect (the rhizome apex will frequently grow up to one of these areas and then literally turn back into the parent bed and away from the filled-in cut; Zieman 1976).

Seagrass ecosystems show differential recovery rates from disturbances based on a variety of factors including species involved, the type and magnitude of the disturbance, and especially whether or not the sediments were disturbed. Along the west Florida coast, if the disturbance is great enough, a number of rhizophytic algae act as precursors to the seagrasses. One of the primary determinants of the duration of recovery time is the extent of damage to the sediments. If the sediments and seagrass rhizomes are not severely disturbed, the probability of recovery is greatly increased. Table 18, (1984b), attempts to synthesize and categorize the levels of damage to seagrass ecosystems, system effects, and the likely outcome of the disturbances. Although originally

Table 17. List of data concerning historic anthropogenous impacts on **seagrass** meadows in Florida (from Livingston 1987).

Study area	Location	Status of seagrass meadows	Information source
Indian River	Southeast Florida Atlantic Ocean	Historic declines in number and coverage of seagrass meadows. Declines in Vero Beach area, Fort Pierce Inlet (25%), and Sebastian Inlet (38%) from 1951 through 1984.	Goodwin and Goodwin 1976; Florida Department of Natural Resources, unpubl. data
Biscayne Bay	Southeast Florida Atlantic Ocean	Undetermined deterioration in northern Biscayne Bay. Some damage to *Thalassia-Halodule* beds near power plant (heated effluents) in south Biscayne Bay. Card Sound unaffected by power plant discharge.	McNulty 1961; Rosessler and Zieman 1969; Thorhaug et al. 1973; Zieman 1970, 1982
Florida Keys	South Florida Atlantic Ocean	Few data found. Little effect of Key West desalination plant.	Chesher 1971
Florida Bay	South Florida	Postulated altered species relationships due to increased salinity caused by redirection of freshwater runoff.	Zieman 1982
Tampa Bay system	Southwest Florida Gulf of Mexico	Almost 40% reduction in Boca Ciega Bay due to dredging, filling, and associated activity from 1950 through 1968. Multiple sources (urbanization, storm water runoff, sewage discharge, industrialization, toxic substances). Reduction of seagrass meadows in Tampa Bay, Old Tampa Bay, and Hillsborough Bay from 15,161 to 3,091 acres (1876-1980).	Simon 1974; Taylor 1971; Taylor and Saloman 1968; Lewis and Phillips 1980
Charlotte Harbor	Southwest Florida Gulf of Mexico	Decline of 29% of seagrass beds from 1943 through 1984.	Florida Department of Natural Resources, unpubl. data

(Continued)

Table 17. (Concluded).

Study area	Location	Status of seagrass meadows	Information source
Pensacola Bay System	Northwest Florida Gulf of Mexico	Complete loss of seagrass beds in Escambia Bay, East Bay and Pensacola Bay from 1949-1979. Some fresh-brackish water species extant in delta areas. Some *Thalassia-Halodule* beds still alive in Santa Rosa Sound. Losses due to urbanization, industrial waste discharge dredging and filling, cultural eutrophication.	Livingston et al. 1972; Olinger et al. 1975; Livingston 1979
Choctawhatchee Bay	Northwest Florida Gulf of Mexico	Historical deterioration of seagrass beds from 1949-1983. Causes unknown.	Burch 1983
St. Andrews Bay	Northwest Florida Gulf of Mexico	No data found. Presumed impact due to urbanization, industrialization.	
St. Joseph Bay	Northwest Florida Gulf of Mexico	Extensive coverage unchanged from 1972 through 1983. Relatively unpopulated area.	McNulty et al. 1972; Savastano et al. 1984
Apalachicola Bay System	North Florida Gulf of Mexico	Generally healthy assemblages of seagrasses. Local impact due to dredged opening in associated barrier island. Introduced species spreading in delta areas with as yet undetermined impact. Area under increased pressure from urbanization.	Livingston 1980c, 1983
Apalachee Bay	North Florida Gulf of Mexico	Impacts due to disposal of pulp mill wastes (Fenholloway Estuary) from 1954 to the present. Slow recovery noted in outer portions of impact area (associated with pollution abatement program). Area now threatened by proposed inshore navigation channel and possible offshore oil drilling operations.	Heck 1976; Hooks et al. 1976; Livingston 1975, 1982a, 1984a; Zimmerman and Livingston 1976a,b

Table 18. **Seagrass** damage and restoration assessment (from Zieman et al. 1984b).

Damage level	Plant effects	Associated community effects	System fate	Recovery time	Restoration indicated
1	No visible damage	Possible fauna1 damage	Natural recovery	Weeks-year	No
2	Leaf damage and removal	Fauna1 damage may be extensive	Natural recovery likely	6 months-year	No
3	Severe damage to rhizomes	Fauna1 damage is likely extensive	Natural recovery slow or unlikely	5 years-decades	Yes
4	Severe system damage	System completely altered	Return to same state not possible	?	No

developed for the recommendation of strategy following an oil spill, the results and recommendations are not specific to any particular type of stress and are of general utility. Following a disturbance to the seagrass system, the primary management strategy and objectives should be directed towards minimizing the impact. While all efforts should be directed towards keeping damage at level one or two where recovery may proceed naturally, it is most important to keep level-three damage from becoming level four, where recovery or restoration to a functioning seagrass system is not possible. At this level of transformation, sediment erosion is allowed to proceed to the point where there is insufficient sediment remaining for seagrass colonization.

7.6.3 Restoration

According to the concept of ecological succession, there are two basic ways to restore a mature community: (1) establish the pioneer species and allow succession to take its course, and (2) create the environmental conditions necessary for the survival and growth of the climax species. Van Breedveld (1975) noted that survival of seagrass transplants was greatly enhanced by utilizing a ball of sediment, as in the techniques for terrestrial transplantation of garden plants. He also noted that transplantation should be done when the plants are in a semidormant state (as in winter) to give the plants time to stabilize, another logical outgrowth of terrestrial technique. Where possible, the objective of restoration in general, not just of seagrasses, should be to restore the lost community or some intermediate successional stage. In some cases, restoration of the original community may not be feasible or cost-effective, and it may be necessary to restore to an earlier successional stage and allow natural successional progression to take place.

Transplantation of seagrasses has been attempted since the time of the wasting disease, but there has been a dramatic increase in its use during the past decade (See Phillips 1980; Fonseca et al. 1981, 1987; Zieman et al. 1984b for recent reviews). Darovec et al. (1975) discuss a variety of techniques for restoring coastal regions, including seagrasses, in Florida. This publication is useful because it consolidates a diverse literature, but the seagrass techniques are rudimentary and somewhat dated, and the other reviews mentioned should be consulted. Until recently, most transplant studies reported primarily on transplant technique and survival success, and did not address environmental variables such as sediment type, nutrient conditions, light, turbidity, current velocity, and wave climate, all of which affect the success or failure of the experiment (Fonseca et al. 1981, 1987).

The myriad techniques that have been tried for transplanting seagrass have yielded highly variable results. Those techniques that have shown the most consistent success are plugs, seeds, and shoots--both anchored and unanchored (Phillips 1980). Because of the variety of methods and the different levels of description of these methods in the literature, direct comparison among seemingly similar methods varies from difficult, at best, to impossible. Table 19 summarizes the relative successes recorded in the seagrass transplant literature.

From this diverse literature, a few generalizations stand out. The most obvious is that the plug technique is the only one that has worked with all species upon which it has been tested. This is not ecologically surprising, as the plug minimizes trauma to the roots and rhizomes by taking part of its environment along to the new site. The plug technique provides the highest degree of short-term sediment stabilization of any of the methods. On the negative side, the plug technique is logistically more difficult due to the need to collect the plug intact, move large amounts of sediment, and create sites of disturbance at the donor location.

Methods using bare shoots have shown mixed results, being very successful with pioneer species such as *Halodule wrightii* and *Zostera marina*, but not really successful with *Thalassia*, which is a climax species. Shoot methods require anchoring' to approach the sediment stability of the plug technique (Fonseca et al. 1984). The logistics are somewhat simpler than the plug method since there is no mass of sediment to be transported.

Transplantations utilizing seeds and seedlings have been attempted for several species, but have been successful only with *Thalassia*. If an abundant source of seeds can be readily located, this technique can be very attractive, because of simple transportation and planting logistics. Recently, Lewis and Phillips (1981) have reported on sites of high seed availability in the Florida Keys in late summer. On the negative side, seeds are only seasonally available and newly-planted seeds or seedlings do not offer any sediment stabilization capacity. However, interplanting of *Thalassia* seedlings in beds of recently established

Table 19. Success of seagrass restoration techniques (from Zieman et al. 1984b).

Species	Plug	Shoot (anchored)	Shoot (unanchored)	Seed
Zostera marina	+/+	+/+	+/+	+/-
Halodule wrightii	+/+	+/+	+/-	--
Syringodium filiforme	+/+	+/+	+/-	?
Thalassia testudinum	+/+	+/-	+/-	+/+

Key: attempted/success, -- = not attempted, + = yes, - = no, ? = not sure

Halodule termed a "compressed successional" approach, was tested by Durako and Moffler (1984), and may prove to be a useful mixed-planting technique.

In 1982, Zieman wrote that "transplants of tropical seagrasses may ultimately be a useful restorative technique to reclaim damaged areas, but at this time the results are not consistent or dependable, and the costs seem prohibitive for any effort other than experimental revegetation, especial?; when the relative survival of the plants is considered." In the intervening time, a number of additional projects have been completed, but the situation has not changed significantly. Fonseca et al. (1987) stated that "for the most part, seagrass transplanting as a management tool is not working. Isolated cases of success or partial success can be found, but these are overshadowed by many costly failures. This lack of success is largely due to the general disregard for and the lack of scientific information on environmental requirements of the transplant species." Further, they feel that "the pressure to make management decisions has grown disproportionatelytothe increase regarding seagrass habitat management. With much emphasis having been put on methodology of transplanting and much less on collection of environmental data, we have been at a loss to explain successes and failures in a quantitative fashion."

In the State of Florida, seagrass transplantation and restoration is often treated as if it were a proven-and-fixed technology, capable of producing a product upon specification, when, in fact, it is really a series of loosely coupled experiments. The concept of seagrass transplanting for "mitigation" of environmental damages is becoming an accepted practice in Florida under the assumption that if an environmental disturbance or destruction is "necessary" or "in the public interest," then this perturbation can be "mitigated" by a parallel restoration. As a step toward accepting seagrass transplanting as a viable mitigation method, numerous Federal, State, and local agencies have funded projects aimed at seagrass restoration. However, only recently have any studies been funded to conduct a scientific investigation on the environmental variables causing the success or failure of a particular project. Several recent projects have elegantly tested the viability of different methodologies in a proper scientific manner, but none of these can tell why a particular method succeeded or failed.

One of the major problems in offsite restoration as it is currently practiced, is the selection of a suitable and potentially viable site for restoration, if it is not to be the recently disturbed site. Many times the sites chosen are inappropriate and there are sound ecological reasons why seagrasses are not growing there now, even if there was seagrass coverage at some point in past history (Lewis et al. 1985a; Fonseca et al. 1987). If it can be established that an area meets the environmental conditions to support seagrasses, but has probably not recovered due to lack of natural propagules, then restoration may be indicated. Unfortunately, probably the major problem inhibiting seagrass success today is the deteriorating water quality associated with industrialization and development. If poor water quality increases turbidity and decreases incident light at the sediment level past a certain point, then all the transplanting in the world will not work. In any restored area, the plants must have sufficient light to yield a significantly high positive net photosyntheses to survive and grow. If turbidity is too high, or eutrophication is sufficient to cause a rapid growth of epiphytic algae or phytoplankton, then the effort and money will be wasted.

7.7 FINAL THOUGHTS

The gathering and assimilation of data for this community profile has been highly enlightening. Dozens of studies have shown the importance of submerged vegetation to major commercial and forage organisms (Linda11 and Saloman 1977; Thayer et al. 1978a; Peters et al. 1979; Thayer and Ustach 1981). In the gulf States the recreational saltwater fish catch exceeded $168 million in 1973, representing about 30% of the total U.S. recreational fishery (Linda11 and Saloman 1977). Of the organisms caught, 59% were dependent on wetlands at some state of their life cycles. In the Gulf of Mexico, this estimate was even higher with over 70%

of gulf recreational fisheries of the region being estuarine dependent. The ecological dependence of important commercial fisheries on the estuarine wetlands is even greater. The Gulf of Mexico is the leading region of the United States in terms of both landings (36% of the total U.S. catch) and value (27% of total U.S. fishery value), and 90% of the total Gulf of Mexico and south Atlantic fishery catch is estuarine dependent (Lindall and Saloman 1977).

The west Florida coast contains vast seagrass resources, in the form of offshore beds of the Big Bend region, that have been largely untouched by human activities. However, the seagrass resources within the west Florida estuaries must rank alongside the seagrasses of Chesapeake Bay as some of the most devastated and degraded in the entire country (Lewis et al. 1985a; Livingston 1987). The importance of these losses to both the ecology and the economy of Florida are far out of proportion to the total hectares lost versus those remaining, due to the critical nature of the estuarine seagrass beds as nurseries. While measures must be taken to ensure the continued productivity of the offshore beds, it is most critical that the water quality degradation that has caused the extensive losses in the estuarine grass beds be arrested and reversed. Once the beds are totally destroyed, they are likely to remain lost forever, along with the myriad organisms that they feed and shelter.

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APPENDIX

FISH SPECIES SURVEYS IN SOUTH AND WESTERN FLORIDA

Use these keys to interpret the table that follows.

Key to survey numbers

Survey No.	Location	Reference
1	North Biscayne Bay	Roessler 1965
2	South Biscayne Bay	Bader and Roessler 1971
3	Card Sound	Brook 1975
4	Matecumbe Key	Springer and McErlean 1962
5	Porpoise Lake	Hudson et al. 1970
6	Whitewater Bay	Tabb and Manning 1961
7	Fakahatchee Bay	Carter et al. 1973
8	Marco Island	Weinstein et al. 1971
9	Rookery Bay	Yokel 1975a
10	Charlotte Harbor	Wang and Raney 1971
11	Offshore Tampa	Moe and Martin 1965
12a	Tampa Bay Mouth to Offshore Reefs (Stns. 1 - 3)	Springer and Woodburn 1960
12b	Tampa Bay Grassbed Stations (Stns. 4 - 6)	Springer and Woodburn 1960
13	Crystal Bay Area	Mountain 1972
14	Cedar Key	Reid 1954
15	Alligator Harbor	Joseph and Yerger 1956; Yerger 1961
16	Apalachicola Bay	Livingston 1984

Key to abundance

r = rare
p = present
a = abundant
c = common

Note: Species names are according to Robbins et al. 1980, except where an asterisk (*) indicates that they are given as originally published.

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Orectolobidae/carpet sharks																	
<u>Ginglymostoma cirratum</u> nurse shark	r	r			P							P	P				
Carcharhinidae/requiem sharks																	
<u>Negaprion brevirostris</u> lemon shark						P											
<u>Rhizoprionodon terraenovae</u> Atlantic sharpnose shark																P	
<u>Carcharhinus acronatus</u> blacknose shark													P			P	
<u>Carcharhinus isodon</u> finetoothed shark																P	
<u>Carcharhinus leucas</u> bull shark													P	P		P	
<u>Carcharhinus limbatus</u> blacktip shark													PP			P	
<u>Carcharhinus plumbeus</u> sandbar shark																P	
Sphyrnidae/hammerhead sharks																	
<u>Sphyrna tiburo</u> bonnethead					P								P	PP			P
<u>Sphyrna*</u> ________																P	
<u>Sphyrna</u> <u>mokarran</u> great hammerhead													P				
Pristidae/sawfishes																	
<u>Pristis pectinata</u> smalltooth sawfish					P											P	
Rhinobatidae/guitarfishes																	
<u>Rhinobatus lentiginosus</u> Atlantic guitarfish		r															

(Continued)

Appendix (Continued).

Species	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Torpedinidae/electric rays																	
Narcine brasiliensis lesser electric ray	r					r	r									p	
Rajidae/skates																	
Raja texana roundel skate		r														p	
Raja eglanteria clearnose skate															P		
Dasyatidae/stingrays																	
Urolophus jamaicensis yellow stingray	r	r															
Gymnura micrura smooth butterfly ray							r	r			P	P	P	P		P	P
*Dasyatis americana** southern stingray																P	
Dasyatis sabina Atlantic stingray							r					r		P		P	P
Dasyatis sayi blunt nosed stingray												P				P	
Myliobatidae/eagle rays																	
Aetobates narinari spotted eagle ray																P	
Rhinoptera bonasus cownose ray													a			P	P
Mobulidae/mantas																	
Manta birostis Atlantic manta												P	P				
Lepisosteidae/gars																	
Lepisosteus osseus longnosed gar													p			P	P
Lepisosteus platyrhinchus Florida gar																	

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Elopidae/tarpons																	
Elops saurus ladyfish				p													
Megalops atlanticus tarpon					P							P	P				
Albulidae/bonefishes																	
Albula *vulpes* bonefish					p												
Anguillidae/freshwater eels																	
Anguilla rostrata American eel													p				
Muraenidae/morays																	
Gymnothorax nigromarginatus blackedge moray		r											p				
Gymnothorax saxicola ocellated moray												p					
Ophichthidae/snake eels																	
Myrophis punctatus speckled worm eel			r		r	r		r			p	a				P	P
Ophichthus gomesi shrimp eel					r			r			p		p			P	P
Echiophis intertinctus spotted spoon-nose eel											rr		p			P	
Echiophis mordax snapper eel											r						
Bascanichthys bascanium sooty eel											P	P				p	
Bascanichthys scuticanis whip eel																p	
Clupeidae/herrings																	
Harengula jaguana scaled sardine			r	r		r	r	c			a	a	p	P	P	P	

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Clupeidae/herrings (continued)																	
Harengula humeralis redear sardine		r															
Jenkinsia sp.					r												
Brevoortia smithi yellowfin menhaden																	
Brevoortia patronus gulf menhaden												p	a	p		p	p
*Etrumeus sadina**												P					
Dorosoma petenense threadfin shad																P	P
Opisthonema oglinum Atlantic thread herring				r	r			r				a	P	p		P	
Sardinella auria Spanish sardine				r			r					P	a				P
Engraulidae/anchovies																	
Anchoa cubana Cuban anchovy				r								P	P				
Anchoa lamprotaenia bigeye anchovy				a	P												
Anchoa mitchilli bay anchovy		r		r	p	c	r		r	c		a	a	P	P	P	P
Anchoviella perfasciata flat anchovy				r													
Anchoa hepsetus striped anchovy						r	r	r	c		PP		P		P	P	
Synodontidae/lizardfishes																	
Synodus ______ inshore lizardfish	r	r	r	r	p	c	r	r	r	r	p	p	p	P	P	P	
Synodus intermedius sand diver												P					

(Continued)

Appendix (Continued).

Species	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
	Abundance by survey number																
Ictaluridae/bullhead catfishes																	
Ictalurus catus white catfish																	P
Ictalurus nebulosus brown bullhead													P				
Ariidae/sea catfishes																	
Bagre marinus gafftopsail catfish													P			P	
Arius felis hardhead catfish					p	r		r	r			r	p	P	P	P	P
Batrachoididae/toadfishes																	
Opsanus beta gulf toadfish	c	a	r	r	p	c	c	c	r			P	P	P	P	P	P
Opsanus pardus leopard toadfish												P				P	
Porichthys plectrodon Atlantic midshipman							r					r		p			p
Gobiesocidae/clingfishes																	
Acyrtops beryllinus emerald clingfish	r			r													
Gobiesox strumosus skilletfish		r	p	r								P	P	P		P	
Antennariidae/frogfishes																	
Histrio histrio sargassumfish			r	r													
Antennarius ocellatus ocellated frogfish												p					
Ogcocephalidae/batfishes																	
*Ogcocephalus cubifrons**				r													
Ogcocephalus nasutus shortnose batfish	r														P	P	

(Continued)

Appendix (Continued).

Species	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Ogcocephalidae/batfishes (Continued)																	
Ogcocephalus radiatus polka-dot batfish														P			
Ogcocephalus sp.												P	P				
Halieutichthys aculeatus pancake batfish											P						
Gadidae/codfishes																	
Urophycis floridana southern hake			r														
Ophidiidae/cusk-eels																	
Lepophidium jeannae mottled tusk-eel												p					
Ophidion grayi blotched tusk-eel												p					
Ophidion welshi crested tusk-eel											P					P	
Ophidion holbrooki bank tusk-eel	r												r		P		
Ophidion beani longnose tusk-eel														P			
Ophidion marginatum striped tusk-eel														P			
Bythitidae/viviparous brotulas																	
Ogilbia cayorum key brotula		r	r									P					P
Gunterichthys longipenis gold brotula																	
Carapidae/pearlfishes																	
Carapus bermudensis pearlfish				r													

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Exocoetidae/flying fishes and halfbeaks																	
Hemiramphus brasiliensis ballyhoo				r													
Chriodorus atherinoides hardhead halfbeak					p												
Hyporhamphus unfasciatus halfbeak					p	r				r		PPP				P	
Belonidae/needlefishes																	
Strongylura notata redfin needlefish			r	r	p	r				r		PPP				P	
Strongylura timucu timucu				r		r				r		a	p				
Strongylura marina Atlantic needlefish														P		P	
Tylosuruss ________ houndfish			r														
Tylosorus raphidoma*																p	
Cyprinodontidae/killifishes																	
Flordichthys carpio goldspotted killifish			c	a		r							p		p		
Adinia xenica diamond killifish			r										r			p	
Lucania parva rainwater killifish		a	r	r	p	r			r	r			p	P	P	P	P
Fundulus heteroclitus mummichog			r														
Fundulus grandis gulf killifish													PP			P	
Fundulus similis longnose killifish													r	P	P		
Fundulus confluentus marsh kil'lifish																p	

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Cyprinodontidae/killifishes (continued)																	
Cyprinodon variegatus sheepshead minnow					p					r			p			p	
Rivulus marmoratus rivulus						r											
Poeciliidae/livebearers																	
Poecilia latipinna sailfin molly					p					r				p		p	
Gambusia affinis mosquitofish						r							p				
Heterandria formosa least killifish					r												
Atherinidae/silversides																	
Hypoatherina harringtonensis reef silverside			c	r	p												
Atherinomorus stipes hardhead silverside			a	a													
Menidia beryllina tidewater silverside					r		r	c				a	a	p		P	P
Membras martinica rough silverside					p												
*Membras vagrans**						r				r							
Membras sp.												a	p				
Holocentridae/squirrelfishes																	
Holocentrus ascensionis squirrelfish												a					
Syngnathidae/pipefishes and seahorses																	
Cosmocampus albirostris whitenose pipefish	r	r		r													
Cosmocampus brachycephalus crested pipefish				r													

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Syngnathidae/pipefishes and seahorses (continued)																	
Hippocampus hudsonius*				r								P	P		P	P	
Hippocampus zosterae dwarf seahorse	r	c	r	r	p	r	r	r	r				p				
Hippocampus erectus lined seahorse	r	r	r			r		r	r								
Hippocampus reidi longsnout seahorse								r									
Hippocampus regulus*																p	
Hippocampus sp.														p			
Syngnathus sp.														p			
Syngnathus dunckeri pugnose pipefish				r													
Syngnathus floridae dusky pipefish	c	r	r	r	p	r		r		r		p	p		P	P	P
Syngnathus louisianae chain pipefish	r		r	r		r	r	r	r	r			p		P	P	P
Syngnathus elucens shortfin pipefish												r					
Syngnathus springeri bull pipefish												p					
Syngnathus scovelli gulf pipefish	r	r	c	r	p	c	a	c	c	c		r	p		P	P	P
Micrognathus crinigerus fringed pipefish		a	r		p			r					p		P	P	
Centropomidae/snooks																	
Centropomus undecimalis snook													P			P	
Serranidae/sea basses																	
Centropristis striata black sea bass												r	r	P	P	P	P

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Serranidae/sea basses																	
Centropristis ocyurus bank sea bass												P					
Mycteroperca bonaci black grouper				r												P	
Mycteroperca microlepis gag	r	r			p			rrr				a		P	p		
Mycteroptera falcata*																	
Serraniculus pumilio pygmy sea bass								r			P	P			P		
Serranus subliqarius belted sandfish								r			P	a	r				
Diplectrum bivittatum dwarf sand perch	r																
Diplectrum formosum sand perch	r					r	r	r	r	r	p			P	P	P	P
Epinephalus morio red grouper											P	a				P	
Epinephalus itajara jewfish	P				P						P						
Epinephalus adscensionis rock hind											r						
Grammistidae/soapfishes																	
Rypticus saponaceus greater soapfish											P						
Apogonidae/cardinalfishes																	
Phaeoptyx conklini freckled cardinalfish												r					
Apogon aurolineatus bridle cardinalfish												P					
Astrapogon alutus bronze cardinalfish	r	r										P	R	P			

(Continued)

Appendix (Continued).

Species	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
	Abundance by survey number																
Apogonidae/cardinalfishes (continued)																	
Astrapogon stellatus conchfish		r															
Pomatomidae/bluefishes																	
Pomatomus saltatrix bluefish												P	P	P		P	P
Rachycentridae/cobias																	
Rachycentron canadum cobia												p		P		P	
Echeneidae/remoras																	
Echeneis naucrates sharksucker				r								P	P	P	P	P	
Carangidae/jacks and pompanos																	
Caranx hippos crevalle jack				r	p					r			P	P		P	P
Caranx latus horse-eye jack			r										P				
Caranx ruber bar jack					p												
Caranx bartholomaei yellow jack																	p
Caranx crysos blue runner												r	p			p	
Hemicaranx amblyrhynchus bluntnose jack																p	
Trachinotus falcatus permit			r							c		a					
Trachinotus carolinus Florida pompano										r		p					
Trachinotus sp.														P			
Trachurus lathami rough scad												a					

(Continued)

Appendix (Continued).

Species	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
	Abundance by survey number																
Carangidae/jacks and pompanos (continued)																	
Seriola zonata banded rudderfish												a	a				
Chloroscombrus chrysurus Atlantic bumper												P	P	P		P	P
Oligoplites saurus leatherjacket					p	r				r		P	P	P		P	P
Selene vomer lookdown					r							r	r	P	P	P	P
Vomer setapinnis Atlantic moonfish														P		P	
Lutjanidae/snappers																	
Lutjanus analis mutton snapper		r		r													
Lutjanus apodus schoolmaster		r		a	P												
Lutjanus griseus gray snapper		r	r	c	p	r	r	r	r			P	P	P	P	P	P
Lutjanus jocu dog snapper	r																
Lutjanus synagris lane snapper		r			p	c	r	a	c	r	p		P		P		
Lutjanus campechanus red snapper												P					
Rhomboplites aurorubens vermilion snapper												P					
Ocyurus chrysurus yellowtail snapper	r			r													
Lobotidae/tripletails																	
Lobotes surinamensis tripletails				r									P	P		P	

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Gerreidae/mojarras																	
Eucinostomus argenteus spotfin mojarra	r	c	c	r	p	r	r	r	r	c		p	a	P	P	P	P
Eucinostomus gula silver jenny	r	r	a	a	p	a	a	a	a	a		P	P	P	P	P	P
Eucinostomus lefroyi mottled mojarra				r													
Gerres cinereus yellowfin mojarra																	
Diapterus plumieri striped mojarra													P				
Haemulidae/grunts																	
Haemulon flavolineatum French grunt			r	r													
Haemulon parrai sailors choice	r	r	r	c													
Haemulon sciurus bluestriped grunt			r	c	r	p	r							P		P	
Haemulon aurolineatum tomtate			r	r				r				a	r		p		
Haemulon plumieri white grunt	a	r		a				a	r			P	a	P	P	P	
Haemulon carbonarium caesar grunt	r																
Anisotremus virginicus porkfish	r							r									
Orthopristis chrysoptera pigfish		r		p	c	a	a	a	r		pa		P	P	P	P	
Sparidae/porgies																	
Archosargus probatocephalus sheepshead			r		p	r	r		r			p	a	p		P	P
Archosargus rhomboidalis sea bream		r										P	P				

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Sparidae/porgies (continued)																	
Lagodon boides pinfish	c	c	r	c	p	a	a	a	a	a	p	a	a	P	a	P	P
Calamus arctifrons grass porgy				r					p	r	r	p	p	p			
Calamus calamus saucereye porgy		r															
Diplodus holbrooki spottail pinfish													P	P	P	P	P
Sciaenidae/drums																	
Menticirrhus saxatilis northern kingfish				r						C		P				P	P
Menticirrhus littoralis gulf kingfish												a				p	
Sciaenops ocellatus red drum					p			r	r			P	P	P		P	P
Bairdiella chrysoura silver perch	r	r				C	a	a	c	c	PP	a			pp		P
Cynoscion nebulosus spotted seatrout					p	r	c	r	r	r	p	r	p	P	P	P	P
Equetus acuminatus high-hat	r										P	a					
Equetus lanceolatus Jackknife fish												P					
Bairdiella batabana blue croaker																	
Odontoscion dentex reef croaker	r											p					
Leiostomus xanthurus spot									ca		pa		a	P	P	P	P
Cynoscion arenarius sand seatrout						r		r	rp		p	p	p			P	P
Micropogonias undulatus Atlantic croaker										r	p			P		P	P

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Sciaenidae/drums (continued)																	
Pogonias cromis black drum												a	a			P	
Stellifer lanceolatus star drum																P	P
Larimus fasciatus banded drum														P		P	
Menticirrhus americanus southern kingfish							r		r	c	P	P	p	P	P	P	P
Mullidae/goatfishes																	
Pseudupenueus maculatus spotted goatfish				r													
Ephippidae/spadefishes																	
Chaetodipterus faber Atlantic spadefish				r	p		r	r	r		PP		P	P	P	P	P
Chaetodontidae/butterflyfishes																	
Chaetodon ocellatus spotfin butterflyfish												P					
Pomacanthidae/angelfishes																	
Holacanthus bermudensis blue angelfish												P					
Pomacanthus arcuatus gray angelfish	r																
Pomacentridae/damselfishes																	
Pomacentrus leucostictus beaugregory				r													
Pomacentrus variablis cocoa damselfish												p					
Abudefduf saxatilis sergeant major												p					
Chromis enchrysurus yellowtail reeffish												p					

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Labridae/wrasses																	
Doratonatus megalepis dwarf wrasse	r			r													
Halichoeres bivittatus slippery dick				r	p							a	r		P		
Halichoeres caudalis painted wrasse												r					
Halichoeres radiatus puddingwife																P	
Hemipteronotus martinicensis rosy razorfish				r													
Hemipteronotus novacula pearly razorfish		r															
Lachnolaimus maximus hogfish	C											P		P	P	P	
Scaridae/parrotfishes																	
Nicholsina usta emerald parrotfish		r		r				r									
Scarus coelestinus midnight parrotfish					r												
Scarus croicensis striped parrotfish				r													
Scarus guacamaia rainbow parrotfish				r													
Sparisoma chrysopterum redtail parrotfish				r													
Sparisoma radians bucktooth parrotfish				r													
Sparisoma rubripinne redfin parrotfish	a	r		C													
Sparisoma viride stoplight parrotfish				r													
*Cryptotomus auropunctatus**																	

(Continued)

Appendix (Continued).

Species	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
	Abundance by survey number																
Mugilidae/mullets																	
Mugil halus striped mullet	r		p							a		a	a	P		P	
Mugil curema white mullet			r	r	P					C			P	P		P	
Mugil chodon fantail mullet				r								P	P				
Mugil sp.																	
Sphyraenidae/barracudas																	
Sphyraena barracuda great barracuda	r	r	r	p	r							a	P				
Sphyraena borealis northern sennet												P					P
Sphyraena sp.																P	
Polynemidae/threadfins																	
Polydactylus octonemeus Atlantic threadfin												r	r			P	P
Opistognathidae/jawfishes																	
Opistognathus maxillosus mottled jawfish	r											p					
Opistognathus macrognathus banded jawfish												p					
Dactyloscopidae/sand stargazers																	
Dactyloscopus tridigitatus sand stargazer		r	r														
Uranoscopidae/stargazers																	
Astroscopus y-graecum southern stargazer											PP		P		P		P
Clinidae/clinids																	
Bramerella sp.*																	

(Continued)

Appendix (Continued).

Species	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
	Abundance by survey number																
Clinidae/clinids (Continued)																	
Malacoctenus macropus rosy blenny				r													
*Malacoctenus culebrae**																p	
Emblemaria atlantica banner blenny												r					
Paraclinus fasciatus banded blenny	r	r	c											P	P		
Paraclinus nigripinnis blackfin blenny			r											p			
Paraclinus marmoratus marbled blenny	r	r	r	r	p												
Chaenopsis ocellata bluethroat pikeblenny					p												
Blenniidae/combtooth blennies																	
Chasmodes saburrae Florida blenny		r	r			r	r		r	r			p	P	P	P	
Parablennius marmoreus seaweed blenny					p						p	a					
Lupinoblennius nicholsi highfin blenny														p			
Blennius sp.														p			
Hypleurochilus geminatus crested blenny																p	
Hypsoblennius hentzi feather blenny													p	P	P	P	P
Hypsoblennius ionthas freckled blenny																p	
Callionymidae/dragonets																	
Callionymus pauciradiatus spotted dragonet	r	r	r	r	p												
*Callionymus calliurus**																	

(Continued)

Appendix (Continued).

	Abundance by survey number																
Species	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Gobiidae/gobies																	
Barbulifer ceuthoecus bearded goby				r													
Microgobius microlepis banner goby	r				p												
Microgobius gulosus clown goby					p	c	r		r				P	P		P	P
Microgobius thalassinus green goby						r											
Microgobius carri Seminole goby												a					
Bathygobius curacao notchtongue goby			c														
Bathygobius soporator frillfin goby						r						p				p	
Coryphopterus sp.												p					
Gobionellus hastatus sharptail goby																P	P
Gobionellus bolesoma darter goby					r											P	P
Gobionellus smaragdus emerald goby						r											
Gobionellus shufeldti freshwater goby									r								
Gobionellus stigmaturus spottail goby				r													
Gobiosoma robustum code goby	a	r	r	p	c	c	r	r	r				a	p		p	
Gobiosoma longipala twoscale goby								r									
Gobiosoma macrodon tiger goby		r	r									p				p	
*Gobiosoma longum**	r																

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Gobiidae/gobies (continued)																	
Gobiosoma bosci naked goby													r			P	P
Ioglossus calliurus blue goby												P					
Lophogobius cyprinoides crested goby		r															
Coryphopterus glaucofraenum bridled goby		r															
Acanthuridae/surgeonfishes																	
Acanthurus bahianus ocean surgeon	r																
Acanthurus coeruleus blue tang												P					
Acanthurus chirurgus doctorfish				r													
Trichiuridae/cutlass fishes																	
Trichiurus lepturus Atlantic cutlassfish												P	P	P			
Scombridae/mackerels																	
Scomberomorus maculatus Spanish mackerel												a	p	p		P	P
Scomberomorus cavalla king mackerel												a	P			P	
Euthyhnus alletteratus little tunny												P					
Thunnus atlanticus blackfin tuna												r					
Istiophoridae/billfishes																	
Istiophorus platypterus sailfish												P					

(Continued)

Appendix (Continued).

Species	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Stromateidae/butterfishes																	
Peprilus burti gulf butterfish																	P
Peprilus paru*														P		P	
Peprilus alepidotus harvestfish														P		P	
Peprilus triacanthus butterfish																P	
Nomeus gronovii man-of-war fish			r														
Scorpaenidae/scorpionfishes																	
Scorpaena brasiliensis barbfish	r	r		r								p	r	r		p	
Scorpaena grandicornis piumed scorpionfish	r	r		r													
Scorpaena plumeiri spotted scorpionfish				r													
Triglidae/searobins																	
Bellator militaris horned searobin												p					
Prionotus pectoralis*												p					
Prionotus salmonicolor				r	p												
blackwing searobin																	
Prionotus scitulus leopard searobin	r	r	r			r	r	r	r		P		P	P		P	P
Prionotus tribulus bighead searobin			r	r		r	c		rr		p		P	P		P	P
Prionotus roseus bluespotted searobin											p						

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Bothidae/lefteye flounder																	
Bothus ocellatus eyed flounder	r	r		r							p						
Ancylopsetta quadrocellata ocellated flounder								r			p		r	p		P	P
Cyclopsetta fimbriatta spotfin flounder											p						
Citharichthys macrops spotted whiff		r		r							P			P		P	
Citharichthys spilopterus bay whiff	r	r			r		r		p							p	
Paralichthys albigutta gulf flounder	r	r				r	r	r	r		PP		P	P		P	P
Paralichthys lethostigma southern flounder																P	P
Syacium papillosum dusky flounder											p					p	
Etropus crossotus fringed flounder								r			P	P		P		P	P
Etropus rimosus gray flounder											P			p			
Soleidae/soles																	
Thunnus atlanticus blackfin tuna																	
Istiophoridae/billfishes																	
Istiophorus platypterus sailfish																	
Stromateidae/butterfishes																	
Peprilus burti gulf butterfish																	p
Peprilus paru*														P		P	
Peprilus alepidotus harvestfish														P		P	

(Continued)

Appendix (Continued).

Species	Abundance by survey number																
	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
Stromateidae/butterfishes (continued)																	
Peprilus triacanthus butterfish																p	
Nomeus gronovii man-of-war fish			r														
Trinectes inscriptus scrawled sole		r		r													
Trinectes maculatus hogchoker	r				r	r							PP				PP
Achirus lineatus lined sole		r	r	r	p	c	c		r	r			PP				PP
Cynoglossidae/tonguefishes																	
Symphurus plagiusa blackcheek tonguefish	r	r		r		c	c		r		p		PP				PP
Symphurus diomedianus spottedfin tonguefish											p						
Balistidae/triggerfishes and filefishes																	
Balistes capriscus gray triggerfish				r									p				
Monocanthus ciliatus fringed filefish	c	r	r	c				r	r			a	a	p		P	P
Monocanthus hispidus planehead filefish	c	r	r	c		r	rrrr				PP		P	P		P	
Alutera schoepfi orange filefish		r									p					p	
Ostraciidae/boxfishes																	
Lactophrys quadricornis scrawled cowfish	r	c	r	r	p			r	r		p			p			
Lactophrys trigonus trunkfish	r	r		c				r					p				
Lactophrys triqueter smooth trunkfish		r	r														

(Continued)

Appendix (Continued).

Species	1	2	3	4	5	6	7	8	9	10	11	12a	12b	13	14	15	16
	Abundance by survey number																
Tetraodontidae/puffers																	
Sphoeroides nephelus southern puffer		r		r	p	r	c	r		r	PP		P	P			p
Sphoeroides spengleri bandtail puffer	r	r	r	r				r				r		p			
*Sphoeroides marmoratus**																p	
*Sphoeroides harperi**																p	
Sphoeroides testudineus checkered puffer		r															
Lagcocephalus laevigatus smooth puffer													p				
Diodontidae/porquepinefishes																	
Chilomycterus schoepfi striped burrfish	r	c	r	r	p	r	r	c	r	r	p	p	p	p		P	P
Chilomycterus antennatus bridled burrfish	r																
Diodon holocanthus balloonfish		r		r							p		r				

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This report summarizes information on the ecology of seagrass meadows on the west coast of Florida, from south of Tampa Bay to Pensacola. This area contains more than 3,500 ha of seagrass beds, dominated by three species, Thalassia testudinum (turtle grass), Syringodium filiforme (manatee grass), and Halodule wrightii (shoal grass). Beds occur both on the shallow, zero-energy Continental Shelf and in inshore bays and estuaries. Species ecology, distribution, biomass, and productivity of these dominant seagrass species are discussed.

Seagrass beds support a very diverse and abundant algal flora and fauna, and these organisms and seagrass detritus form the base of a productive food chain. Seagrass beds are important nursery areas providing both cover and food, for a number of commercial and sports fishery species.

Along the west Florida coast, estuarine grass beds are noticeably more stressed and impacted by human activities than the more pristine nearshore beds. Urban development and dredging and filling are the major threates to seagrass beds in this region.

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Thalassia	Halophila

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