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THE ECOLOGY OF THE SEAGRASSES OF SOUTH FLORIDA: A Community Profile

Bureau of Land Management
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THE ECOLOGY OF THE SEAGRASSES OF SOUTH FLORIDA: A COMMUNITY PROFILE

by

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PREFACE

This profile of the seagrass community of south Florida is one in a series of community profiles that treat coastal and marine habitats important to humans. Seagrass meadows are highly productive habitats which provide living space and protection from predation for large populations of invertebrates and fishes, many of which have commercial value. Seagrass also provides an important benefit by stabilizing sediment.

The information in the report can give a basic understanding of the seagrass community and its role in the regional ecosystem of south Florida. The primary geographic area covered lies along the coast between Biscayne Bay on the east and Tampa Bay on the west. References are provided for those seeking indepth treatment of a specific facet of seagrass ecology. The format, style, and level of presentation make this synthesis report adaptable to a variety of needs such as the preparation of environmental assessment reports, supplementary reading in marine science courses, and the education of participants in the democratic process of natural resource management.

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ACKNOWLEDGMENTS

In producing a work such as this profile, it is impossible to catalog fully and accurately the individuals that have provided either factual information or intellectual stimulus. Here much of the credit goes to the mutual stimulation provided by my colleagues in the Seagrass Ecosystem Study of the International Decade of Ocean Exploration. Special recognition must be given to the magus of seagrass idiom during those frantic and memorable years, Peter McRoy.

At one stage or another in its gestation, the manuscript was reviewed and comments provided by Gordon Thayer, Richard Iverson, James Tilmant, Iver Brook, and Polly Penhale. Other information, advice, or welcomed criticism was provided by John Ogden, Ronald Phillips, Patrick Parker, Robin Lewis, Mark Fonseca, Jud Kenworthy, Brian Fry, Stephen Macko, James Kushlan, William Odum, and Aaron Mills.

Two of the sections were written by my students, Michael Robblee and Mark Robertson. To them and other students, present and past, I must give thanks for keeping life and work fresh (if occasionally exasperating). The numerous drafts of this manuscript were typed by Deborah Coble, who also provided much of the editing, Marilyn McLane, and Louise Cruden. Original drafting was done by Rita Zieman, who also aided in the production of Chapter 8, and Betsy Blizard. I cannot thank enough Ken Adams, the project officer, for his patience and help in the production of this work, which went on longer than any of us imagined.

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CHAPTER 1

INTRODUCTION

1.1 SEAGRASS ECOSYSTEMS

Seagrasses are unique for the marine environment as they are the only land plant that has totally returned to the sea. Salt marsh vegetation and mangroves are partially submerged in salt water, but the seagrasses live fully submerged, carrying out their entire life cycle completely and obligately in sea water (Figure 1).

Seagrass meadows are highly productive, faunally rich, and ecologically important habitats within south Florida's estuaries and coastal lagoons (Figure 2) as well as throughout the world. The complex structure of the meadow represents living space and protection from predation for large populations of invertebrates and fishes. The combination of plentiful shelter and food results in seagrass meadows' being perhaps the richest nursery and feeding grounds in south Florida's coastal waters. As such, many commercially and ecologically significant species within mangrove, coral reef, and continental shelf communities are linked with seagrass beds.

Although the importance of seagrass beds to shallow coastal ecosystems was demonstrated over 60 years ago by the pioneering work of Petersen (1918) in the Baltic Sea, it is only in the past 10 to 15 years that seagrasses have become widely recognized as one of the richest of ecosystems, rivaling cultivated tropical agriculture in productivity (Westlake 1963; Wood et al. 1969; McRoy and McMillan 1977; Zieman and Wetzel 1980).

Studies in the south Florida region over the past 20 years have demonstrated the importance of the complex coastal estuarine and lagoon habitats to the productivity of the abundant fisheries and wildlife of the region. Earlier studies describing the link between estuarine systems and life cycles of important species focused on the mangrove regions of the Everglades (W.E. Odum et al. 1982), although the seagrass beds of Florida Bay and the Florida Keys have been identified as habitats for commercially valuable species, as well as for organisms that are important trophic intermediaries. Many species are dependent on the bays, lagoons, and tidal creeks for shelter and food during a critical phase in their life cycle.

Many organisms that are primarily characterized by their presence and abundance over coral reefs, such as the enormous and colorful schools of snappers and grunts, are residents of the reef only by day for the shelter its complex structure provides, foraging in adjacent grass beds at night. These seagrass meadows, often located adjacent to the back reef areas of barrier reefs or surrounding patch reefs, provide a rich feeding ground for diurnal reef residents; many of these organisms may feed throughout their life cycle in the grass bed. The juveniles of many Pomadasyid species are resident in the grass beds. As they grow, however, their increasing size will no longer allow them to seek shelter in the grass and they move on to the more complex structure of the reef for better protection (Ogden and Zieman 1977).

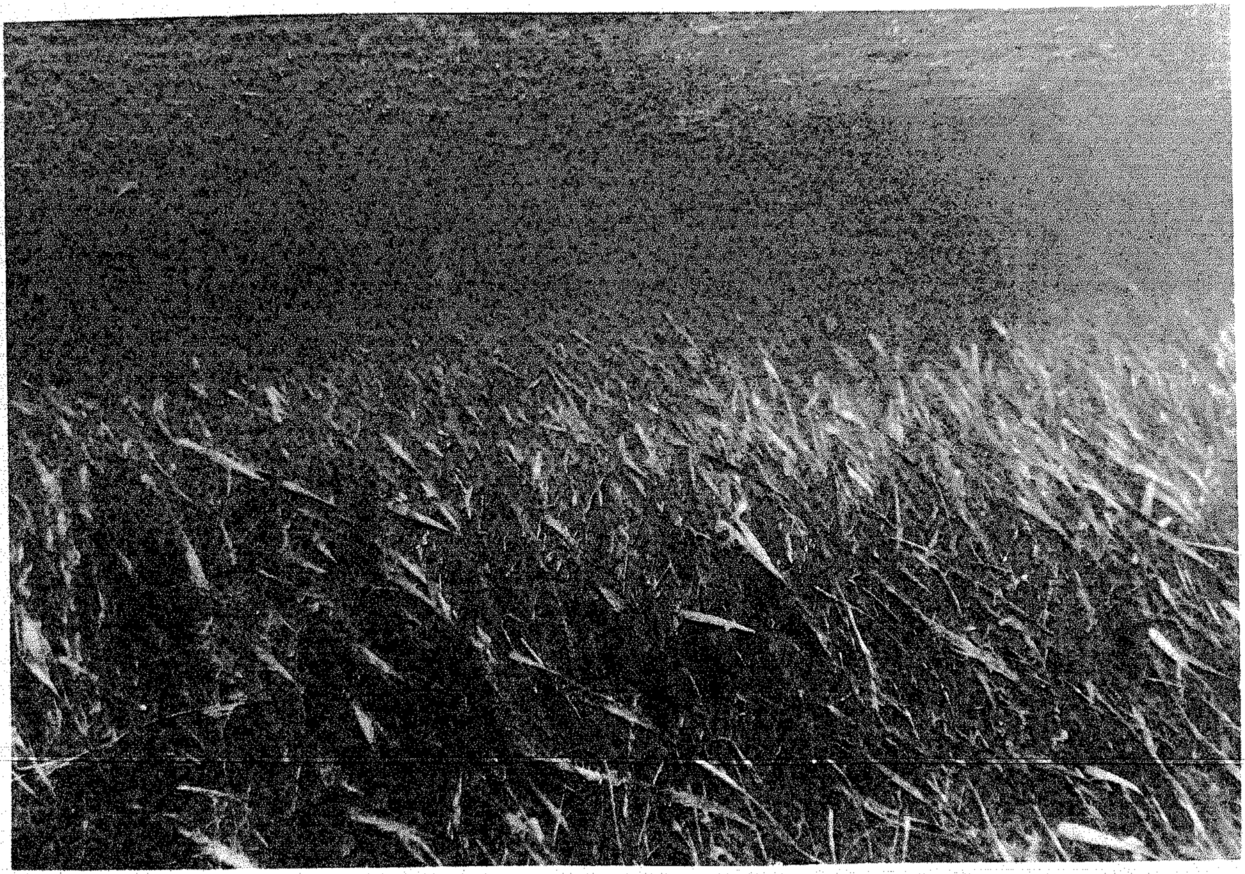


Figure 1. Panoramic view of a south Florida turtle grass bed.

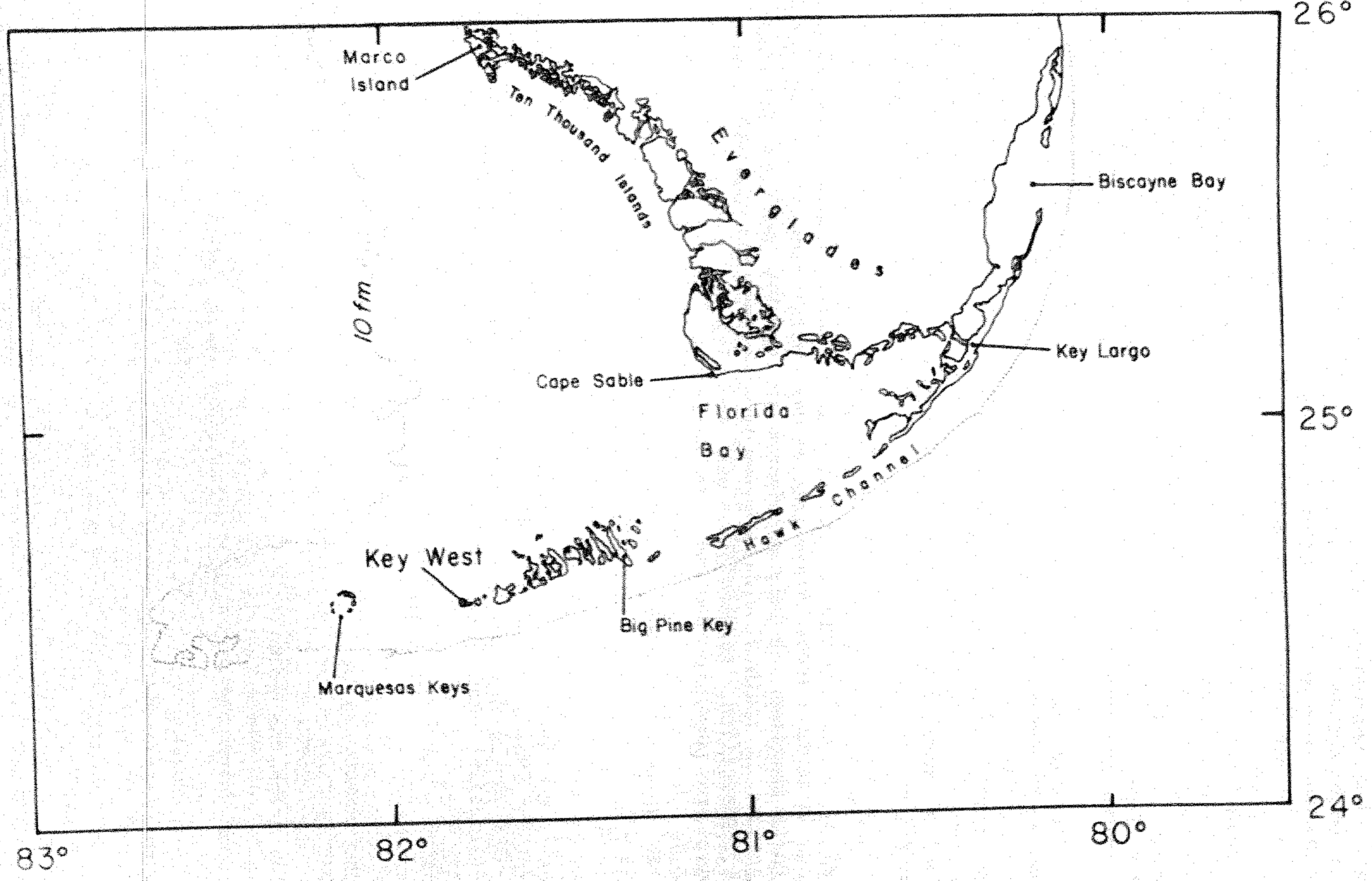


Figure 2. Map of south Florida.

Mangroves and coral reefs are rarely, if ever, in close proximity because of their divergent physio-chemical requirements, but seagrasses freely intermingle with both communities. Seagrasses also form extensive submarine meadows that frequently bridge the distances between reefs and mangroves. Seagrass beds of the larger mangrove-lined bays of the Everglades and Ten Thousand Island region, while being a small proportion of the total bottom coverage of these bays, are the primary zones where important juvenile organisms, such as shrimp, are found.

There are two major internal pathways along which the energy from seagrasses is made available to the community in which they exist: direct herbivory and detrital food webs. In many areas a significant amount of material is exported to adjacent communities.

Direct grazing of seagrasses is confined to a small number of species, although in certain areas, these species may be quite abundant. Primary herbivores of seagrasses in south Florida are sea turtles, parrotfish, surgeonfish, sea urchins, and possibly pinfish. In south Florida the amount of direct grazing varies greatly, as many of these herbivores are at or near the northern limit of their distribution. The greatest quandry concerns the amount of seagrass consumed by the sea turtles. Today turtles are scarce and consume a quantitatively insignificant amount of seagrass. However, in pre-Columbian times the population was vast, being 100 to 1,000 times - if not greater - than the existing population.

Some grazers, such as the queen conch, appear to graze the leaves, but primarily scrape the epiphytic algae on the leaf surface. Parrotfish preferentially graze the epiphytized tips of seagrass leaves, consuming the old portion of the leaf plus the encrusting epiphytes.

The detritus food web has classically been considered the main path by which the energy of seagrasses makes its way through the food web. Although recent studies have pointed to increased importance of grazing in some areas (Ogden and Zieman 1977), this generalization continues to be supported.

When assessing the role of seagrasses, sediment stabilization is also of key importance. Although the seagrasses themselves are only one, or at most three species, in a system that comprises hundreds or thousands of associated plant and animal species, their presence is critical because much, if not all, of the community exists as a result of the seagrasses. In their absence most of the regions that they inhabit would be a seascape of unstable shifting sand and mud. Production and sediment stabilization would then be due to a few species of rhizophytic green algae.

1.2 CLIMATIC ENVIRONMENT

South Florida has a mild, semitropical maritime climate featuring a small daily range of temperatures. The average precipitation, air temperature, surface water temperature, and surface water salinity, for Key West are given in Table 1. Water temperature and salinity vary seasonally and are affected by individual storms and seasonal events. Winds affecting the area are primarily mild southeast to easterly winds bringing moist tropical air. Occasional major storms, usually hurricanes, affect the region on an average of every 7 years, producing high winds and great quantities of rain that lower the salinity of shallow waters. During the winter, cold fronts often push through the area causing rapid drops in temperature and high winds that typically last 4 to 5 days (Warzeski 1977, in Multer 1977). In general, summer high temperatures are no higher than elsewhere in the State, but winter low temperatures are more moderate (Figure 3).

Water temperatures are least affected on the outer reef tract where surface waters are consistently mixed with those from the Florida Current. By contrast the inner regions of Florida Bay are shallow and circulation is restricted. Thus water temperatures here change rapidly with sudden air temperature variations and rain. Water temperatures in Pine Channel dropped from 20° to 12°C (68° to 54°F) in 1 day following the passage of a major winter storm (Zieman, personal observation). These storms cause rapid increases in suspended sediments because of wind-induced

Table 1. Temperature, salinity, and rainfall at Key West (from Zeitschke, in Multer 1977). Precipitation and air temperature data are from 1951 to 1960, water temperatures and salinity are from 1955 to 1962 .

Month	Mean precipitation (mm)	Mean air temp. (°C)	Surface water temp. (°C)		Surface water salinity %	
			range	(mean)	range	(mean)
January	44.0	20.8	13.8-25.0	(19.6)	28.0-37.9	(35.9)
February	54.8	21.7	16.0-27.5	(22.2)	33.1-38.0	(36.0)
March	36.9	23.2	18.2-28.1	(23.5)	33.2-38.2	(36.4)
April	40.7	25.3	21.5-29.7	(25.2)	33.5-38.8	(36.7)
May	85.6	27.0	23.7-30.8	(27.7)	33.3-38.6	(37.0)
June	93.5	28.3	25.9-31.9	(29.4)	32.1-38.8	(36.6)
July	91.8	29.1	27.0-32.5	(30.1)	31.5-38.8	(36.6)
August	101.0	29.4	27.0-33.0	(30.3)	31.5-38.1	(36.6)
September	165.8	28.5	27.0-32.5	(29.4)	33.7-37.6	(36.0)
October	115.9	26.5	22.0-30.8	(27.3)	29.0-38.1	(35.8)
November	99.8	24.1	18.7-28.1	(24.2)	32.5-38.8	(36.3)
December	40.6	21.5	16.5-26.4	(22.1)	32.7-38.4	(36.2)

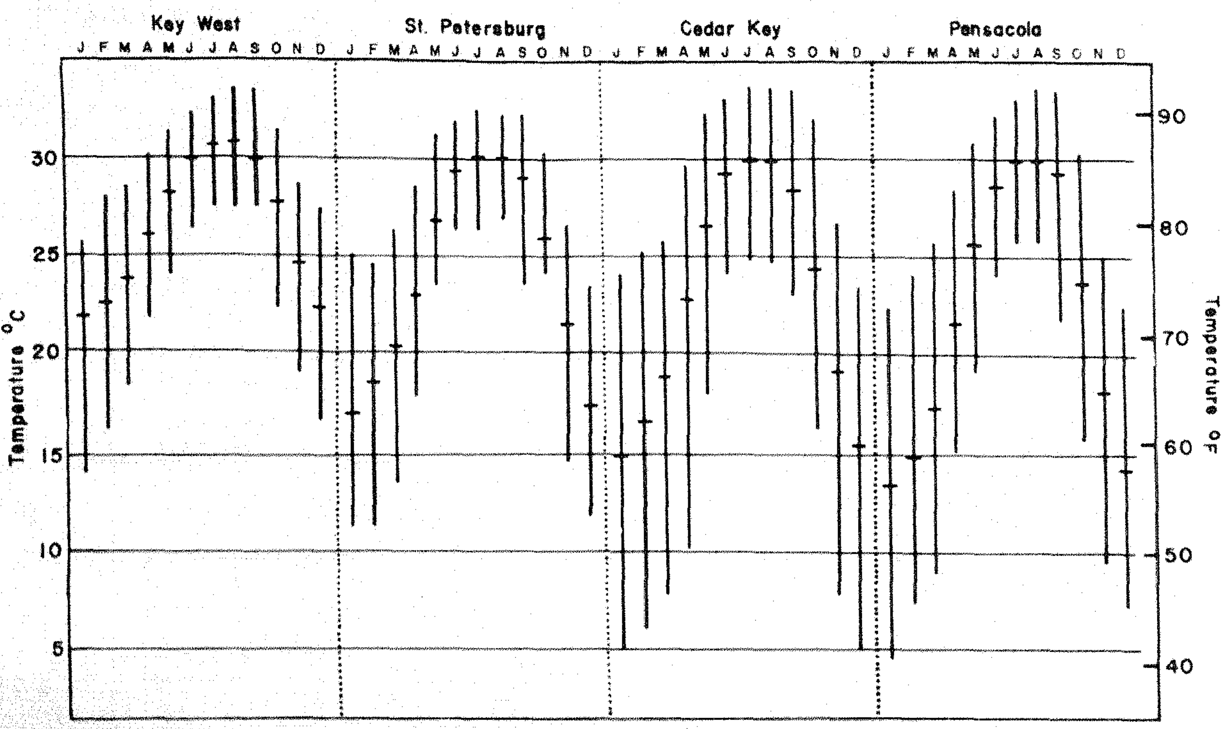


Figure 3. Average monthly temperatures in Florida, 1965 (McNulty et al. 1972).

turbulence and occasionally reduced salinities, all of which stress the local shallow water communities. It is thought that the rapid influx of this type of water from Florida Bay through the relatively open passages of the central Keys, when pushed by strong northwesterly winter winds, is the major factor in the reduced abundance of coral reefs in the central Keys (Marszalek et al. 1977).

Tides are typically about 0.75 m (2.5 ft) at the Miami harbor mouth. This range is reduced to 0.5 m (1.6 ft) in the embayments such as South Biscayne Bay and to 0.3 m (1 ft) in restricted embayments like Card Sound (Van de Kreeke 1976). The mean range decreases to the south and is 0.4 m (1.3 ft) at Key West Harbor. Tidal heights and velocities are extremely complex in south Florida as the Atlantic tides are semidiurnal, the gulf tides tend to be diurnal, and much of this region is between these two regimes. Neither tidal regime is particularly strong, however, and winds frequently overcome the predicted tides. These factors, coupled with the baffling effects of mudbanks, channels, and keys, create an exceedingly complex tidal circulation.

1.3 GEOLOGIC ENVIRONMENT

The south Florida mainland is low-lying limestone rock known as Miami limestone. For descriptive purposes the region can be broken into four sections: the south peninsular mainland (including the Everglades), the sedimentary barrier islands, the Florida Keys and reef tract, and Florida Bay.

The sedimentary barrier islands of north Biscayne Bay, Miami Beach, Virginia Key, and Key Biscayne are unique for the area because they are composed largely of quartz sand. The islands are the southern terminus of the longshore transport of sand that moves down the east coast and ultimately out to sea south of Key Biscayne. All other sediments of the region are primarily biogenic carbonate.

The Florida Keys are a narrow chain of islands extending from tiny Soldier Key, just south of Key Biscayne, in first a southerly and then westerly arc 260 km (163 mi) to Key West and ultimately to the Marquesas and the Dry Tortugas some 110 km (69 mi) further west. The upper keys, from Big Pine northward, are composed of ancient coral known as Key Largo limestone, whereas the lower keys from Big Pine west are composed of oolitic facies of the Miami limestone. (A note to boaters and researchers in these shallow waters: the limestone of the lower keys is much harder than in the upper keys, and occasional brushes with the bottom, which would be minor in the upper keys, will mangle or destroy outboard propellers and lower drive units.)

The Florida reef tract is a shallow barrier-type reef and lagoon extending east and south of the Florida Keys. It averages 6 to 7 km (4 to 4.4 mi) in width with an irregular surface and depths varying from 0 to 17 m (56 ft). The outer reef tract is not continuous, but consists of various reefs, often with wide gaps between them. The development is greatest in the upper keys. The patch reefs are irregular knolls rising from the limestone platform in the area between the outer reef and the keys. Behind the outer reef, the back reef zone or lagoonal area is a mosaic of patchreefs, limestone bedrock, and grass-covered sedimented areas.

Florida Bay is a triangular region lying west of the upper keys and south of the Everglades. This large (226,000 ha or 558,220 acres), extremely shallow basin reaches a maximum depth of only 2 to 3 m (7 to 10 ft), but averages less than 1 m (3.3 ft) over a great area. Surface sediments of fine carbonate mud occur in winding, anastomosing mud banks, seagrass-filled "lakes" or basins, and mangrove islands.

1.4 REGIONAL SEAGRASS DISTRIBUTION

Florida possesses one of the largest seagrass resources on earth. Of the 10,000 km^2 (3,860 mi^2) of seagrasses in the Gulf of Mexico, over 8,500 km^2 (3,280 mi^2) are in Florida waters, primarily in two major areas (Bittaker and Iverson, in press). The southern seagrass bed, which is bounded by Cape Sable, north Biscayne Bay, and the Dry Tortugas, and includes the warm, shallow waters of Florida Bay and the Florida coral reef tract, extends over 5,500 km^2 (2,120 mi^2). Although coverage is broken in numerous places, over 80% of the sea bottom contains seagrass in this area (Bittaker and Iverson, in press). In an inventory of the estuaries of the gulf coast of Florida, McNulty et al. (1972) estimated that over 45% of the total area in the region of Florida Bay west of the Keys and landward to the freshwater line to Cape Sable was submerged vegetation. By comparison, mangrove vegetation comprised less than 7% of the area.

The amount of seagrass coverage drops off rapidly to the north of this area on both coasts. On the Atlantic coast, the shifting sand beaches signal a change to a high-energy coast that is unprotected from waves and has a relatively unstable substrate, coupled with the littoral drift of sand from the north. Throughout this area seagrasses are usually found only in small pockets in protected inlets and lagoons. On the Gulf of Mexico coast north of Cape Sable, seagrasses are virtually eliminated by drainage from the Everglades with its increased turbidity and reduced salinity. Seagrasses are then found only in relatively small beds within bays and estuaries until north of Tarpon Springs, where an extensive (3,000 km^2 or 1,158 mi^2) bed exists on the extremely broad shelf of the northern gulf. Several bays on the gulf coast, including Tampa Bay and Boca Ciega Bay, formerly possessed extensive seagrass resources, but dredge and fill operations and other human perturbations have greatly reduced the extent of these beds.

This profile is primarily directed at the seagrass ecosystem of southern Florida. It is necessary, however, to draw on the pertinent work that has been done in other seagrass systems.

1.5 SEAGRASSES OF SOUTH FLORIDA

Plants needed five properties to successfully colonize the sea, according to Arber (1920) and den Hartog (1970):

(1) The ability to live in a saline medium.

(2) The ability to function while fully submerged.

(3) A well-developed anchoring system.

(4) The ability to complete their reproductive cycle while fully submerged.

(5) The ability to compete with other organisms in the marine environment.

Only a small, closely related group of monocotyledonous angiosperms have evolved all of these characteristics.

Worldwide there are approximately 45 species of seagrasses that are divided between 2 families and 12 genera. The Potamogetonaceae contains 9 genera with 34 species, while the family Hydrocharitaceae has 3 genera and 11 species (Phillips 1978). In south Florida there are four genera and six species of seagrasses (Table 2). The two genera in the family Potamogetonaceae have been reclassified comparatively recently and many of the widely quoted papers on the south Florida seagrasses show *Cymodocea* for *Syringodium* and *Diplanthera* for *Halodule*. Recent discussion in the literature speculates on the possibility of several species of *Halodule* in south Florida (den Hartog 1964, 1970), but the best current evidence (Phillips 1967; Phillips et al. 1974) indicates only one highly variable species.

The small species number (six) and distinctive appearance of south Florida seagrasses make a standard dichotomous key generally unnecessary (Figure 4). General systematic treatments such as den Hartog (1970) and Tomlinson (1980) should be consulted, however, when comparing the seagrasses of other areas. The best descriptions of the local species are still to be found in Phillips (1960).

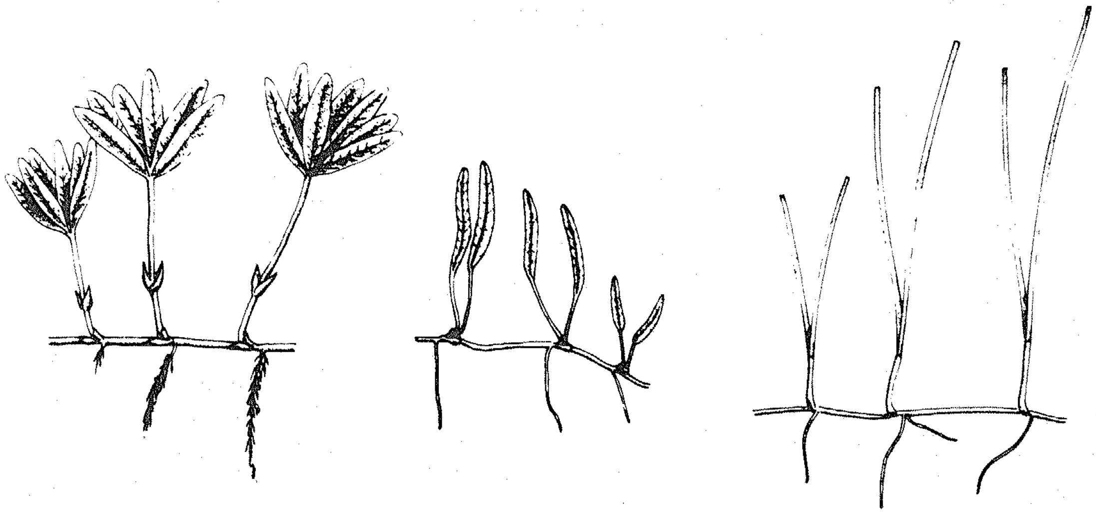
Turtle grass (*Thalassia testudinum*) is the largest and most robust of the south Florida seagrasses. Leaves are ribbon-like, typically 4 to 12 mm wide with rounded tips and are 10 to 35cm in length. There are commonly two to five leaves per short shoot. Rhizomes are typically 3 to 5 mm wide and may be found as deep as 25 cm (10 inches) in the sediment. *Thalassia* forms extensive meadows throughout most of its range.

Manatee grass (*Syringodium filiforme*) is the most unique of the local seagrasses, as the leaves are found in cross section. There are commonly two to four leaves per shoot, and these are 1.0 to 1.5 mm in diameter. Length is highly variable, but can exceed 50 cm (20 inches) in some areas. The rhizome is less robust than that of *Thalassia* and more surficially rooted. *Syringodium* is commonly mixed with the other seagrasses, or in small, dense, monospecific patches. It rarely forms the extensive meadows like *Thalassia*.

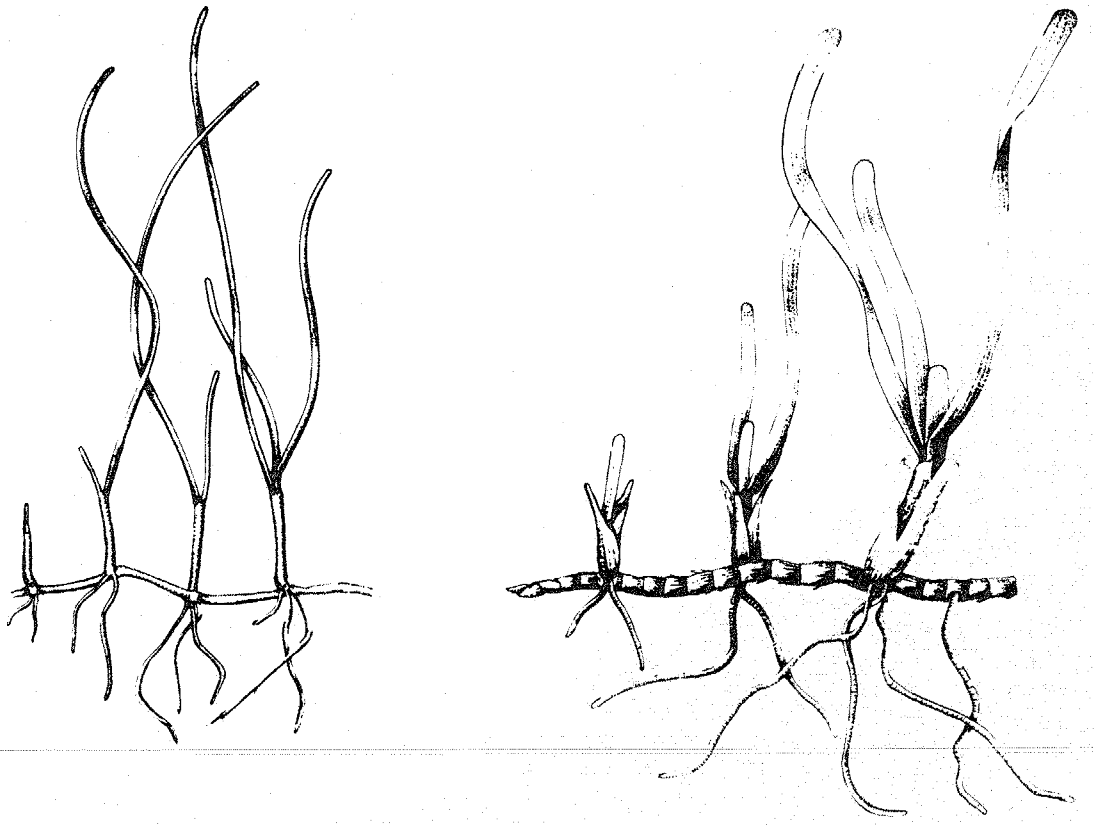
Shoal grass (*Halodule wrightii*) is extremely important as an early colonizer of disturbed areas. It is found primarily

Table 2. Seagrasses of south Florida.

Family and species	Common name
Hydrocharitaceae	
Thalassia testudinum Konig	Turtle grass
Halophila decipiens Ostenfeld	
Halophila engelmanni Ascherson	
Halophila johnsonii Eiseman	
Potamogetonacea	
Syringodium filiforme Kutz	Manatee grass
Halodule wrightii Ascherson	Shoal grass



Halophila engelmanni *Halophila decipiens* *Halodule wrightii*



Syringodium filiforme *Thalassia testudinum*

Figure 4. Seagrasses of south Florida.

in disturbed areas, and in areas where Thalassia or Syringodium are excluded because of the prevailing conditions. Shoal grass grows commonly in water either too shallow or too deep for these seagrasses. Leaves are flat, typically 1 to 3 mm wide and 10 to 20 cm long, and arise from erect shoots. The tips of the leaves are not rounded, but have two or three points, an important recognition character. Halodule is the most tolerant of all the seagrasses to variations in temperature and salinity (Phillips 1960; McMillan and Moseley 1967). In low salinity areas, care must be taken to avoid confusing it with Ruppia.

Three species of Halophila, all small and delicate, are sparsely distributed in south Florida. Halophila engelmanni is the most recognizable with a whorl of four to eight oblong leaves 10 to 30 mm long borne on the end of a stem 2 to 4 cm long. This species has been recorded from as deep as 90 m (295 ft) near the Dry Tortugas. Halophila decipiens has paired oblong-elliptic leaves 10 to 25 mm long and 3 to 6 mm wide arising directly from the node of the rhizome. A new species, H. johnsonii, was described (Eiseman and McMillan 1980) and could be easily confused with H. decipiens. The most obvious differences are that H. johnsonii lacks hairs entirely on the leaf surface and the veins emerge from the midrib at 45° angles instead of 60°. The initial description recorded H. johnsonii from Indian River to Biscayne Bay, but its range could ultimately be much wider.

The major problem in positive identification of seagrasses is between Halodule and Ruppia maritima, commonly known as widgeongrass. Although typically found alongside Halodule, primarily in areas of reduced salinity, Ruppia is not a true seagrass, but rather a freshwater plant that has a pronounced salinity tolerance. It is an extremely important food for waterfowl and is widely distributed. Where it occurs, it functions similarly to the seagrasses. In contrast with Halodule, the leaves are expanded at the base and arise alternately from the sheath, and the leaf tips are tapered to a long point. It should be noted, however, that leaf tips are commonly missing from older leaves of both species.

CHAPTER 2

AUTECOLOGY OF SEAGRASSES

2.1 GROWTH

A remarkable similarity of vegetative appearance, growth, and morphology exists among the seagrasses (den Hartog 1970; Zieman and Wetzel 1980). Of the local species, turtle grass is the most abundant; its growth and morphology provide a typical scheme for seagrasses of the area.

Tomlinson and Vargo (1966) and Tomlinson (1969a, 1969b, 1972) described in detail the morphology and anatomy of turtle grass. The round-tipped, strap-like leaves emanate from vertical short shoots which branch laterally from the horizontal rhizomes at regular intervals. Turtle grass rhizomes are buried in 1 to 25 cm (0.4 to 10 inches) of sediment, although they usually occur 3 to 10 cm (1 to 4 inches) below the sediment. In contrast, rhizomes of shoal grass and Halophila are near the surface and often exposed, while manatee grass rhizomes are most typically found at an intermediate depth. Turtle grass roots originate at the rhizomes or less frequently at the short shoots. They are much smaller in cross section than the rhizomes, and their length varies with sediment type, organic matter, and depth to bedrock.

On a turtle grass short shoot, new leaves grow on alternating sides from a central meristem which is enclosed by old leaf sheaths. Short shoots typically carry two to five leaves at a time; in south Florida, Zieman (1975b) found an average of 3.3 leaves per shoot in the less productive inshore areas of Biscayne Bay, and 3.7 leaves per shoot at stations in the denser grass beds east of the Florida Keys. Short shoots in areas exposed to heavy waves or currents tend to have fewer leaves.

The growth of individual leaves of turtle grass in Biscayne Bay averages 2.5 mm/day, increasing with leaf width and robustness. Rates of up to 1 cm/day were observed for a 15- to 20-day period (Zieman 1975b). Leaf growth decreased exponentially with age of the leaf (Patriquin 1973; Zieman 1975b).

Leaf width increases with short shoot age and thus with distance from the rhizome meristem, reaching the community maximum 5 to 7 short shoots back from the growing tip (Figure 5). The short shoot has an average life of 2 years (Patriquin 1975) and may reach a length of 10 cm (Tomlinson and Vargo 1966). A new short shoot first puts out a few small, tapered leaves about 2 cm wide before producing the regular leaves. New leaves are produced throughout the year at an average rate of one new leaf per short shoot every 14 to 16 days, and times as short as 10 days have been reported. In south Florida the rate of leaf production depended on temperature, with a rate decrease in the cooler winter months (Zieman 1975b). The rate of leaf production varies less throughout the year in the tropical waters of Barbados and Jamaica, according to Patriquin (1973) and Greenway (1974), respectively.

2.2 REPRODUCTIVE STRATEGIES

Seagrasses reproduce vegetatively and sexually, but the information on sexual

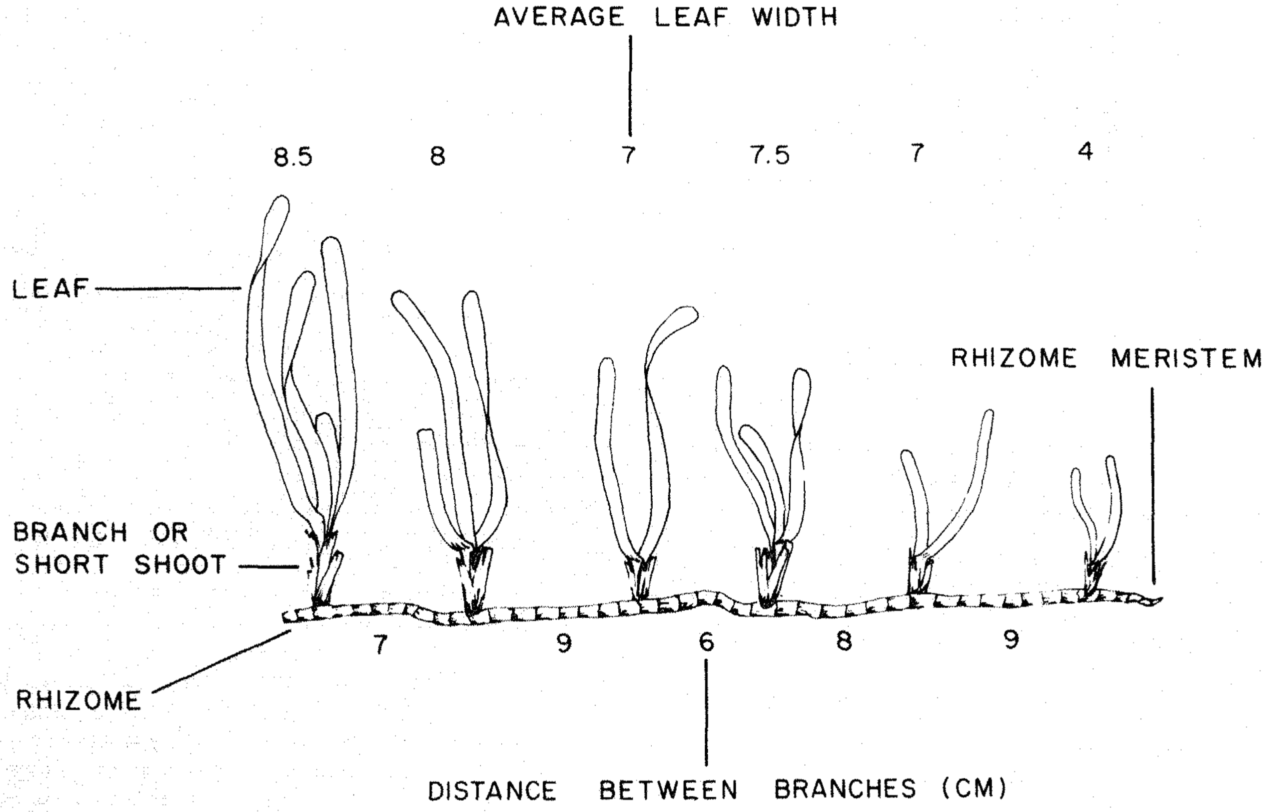


Figure 5. Diagram of a typical Thalassia shoot. Note increasing blade length and width on the older, vertical short shoots.

reproduction of the south Florida seagrasses is sketchy at best. The greatest amount of information exists for turtle grass, because of the extensive beds and because the fruit and seeds are relatively large and easily identified for seagrasses. In south Florida buds develop in January (Moffler et al. 1981); flowers, from mid-April until August or September (Orpurt and Boral 1964; Grey and Moffler 1978). In a study of plant parameters in permanently marked quadrats, Zieman noted that at Biscayne Bay stations flowers appeared during the third week in May and fruits appeared from 2 to 4 weeks later. The fruits persisted until the third week of July, when they detached and floated away.

2.3 TEMPERATURE

One of the first mental images to be conjured up when considering the tropics is that of warm, clear, calm water, abounding with fish and corals. This image is only partially correct. Tropical oceanic water in the Caribbean is typically 26° to 30°C (79° to 86°F), and feels cooler than one would at first suspect. In the past, lack of familiarity with tropical organisms led many otherwise capable scientists to view the tropics and subtropics as simply warmer versions of the temperate zone. Compared with their temperate counterparts, tropical organisms do not have greatly enhanced thermal tolerances; the upper thermal limit of tropical organisms is generally no greater than that of organisms from warm temperate regions (Zieman 1975a). In tropical waters, the range of temperature tolerance is low, often only half that of organisms from equivalent temperate waters (Moore 1963a). This is reflected in the seasonal range of the surrounding waters. At 40° north latitude, the seasonal temperature range of oceanic surface water is approximately 10°C (50°F), while at 20° north, the range is only 3°C, reaching a low of only 1°C (33.8°F) at about 5° north. However, because of the extensive winter cooling and summer heating of shallow coastal water, Moore (1963a) found that the ratio of mean temperature range (30° to 50° N) to mean tropical range (20° N to 20° S) to be 2.5:1 for oceanic waters, but increased to 4.2:1 for shallow coastal waters.

Because of thermal tolerance reduction in the tropics, the biological result is a loss of cold tolerance; that is, the range of thermal tolerance of tropical organisms is about half that of temperate counterparts, whereas the upper tolerance limit is similar (Zieman and Wood 1975).

Turtle grass thrives best in temperatures of 20° to 30°C (68° to 86°F) in south Florida (Phillips 1960). Zieman (1975a, 1975b) found that the optimum temperature for net photosynthesis of turtle grass in Biscayne Bay was 28° to 30°C (82° to 86°F) and that growth rates declined sharply on either side of this range (Figure 6). Turtle grass can tolerate short term emersion in high temperatures (33° to 35°C or 91° to 95°F), but growth rapidly falls off if these temperatures are sustained (Zieman 1975a, 1975b).

In a study of the ecology of tidal flats in Puerto Rico, Glynn (1968) observed that the leaves of turtle grass were killed by temperatures of 35° to 40°C (95° to 104°F), but that the rhizomes of the plants were apparently unaffected. On shallow banks and grass plots, temperatures rise rapidly during low spring tides; high temperatures, coupled with desiccation, kill vast quantities of leaves that are later sloughed off. The process occurs sporadically throughout the year and seems to pose no long-term problem for the plants. Wood and Zieman (1969) warn, however, that prolonged heating of substrate could destroy the root and rhizome system. In this case, recovery could take several years even if the stress were removed.

The most severe mortalities of organisms in the waters of south Florida are usually caused by severe cold rather than heat, as extreme cold water temperatures are more irregular and much wider spaced phenomena than extreme high temperatures. McMillan (1979) tested the chill tolerance of populations of turtle grass, manatee

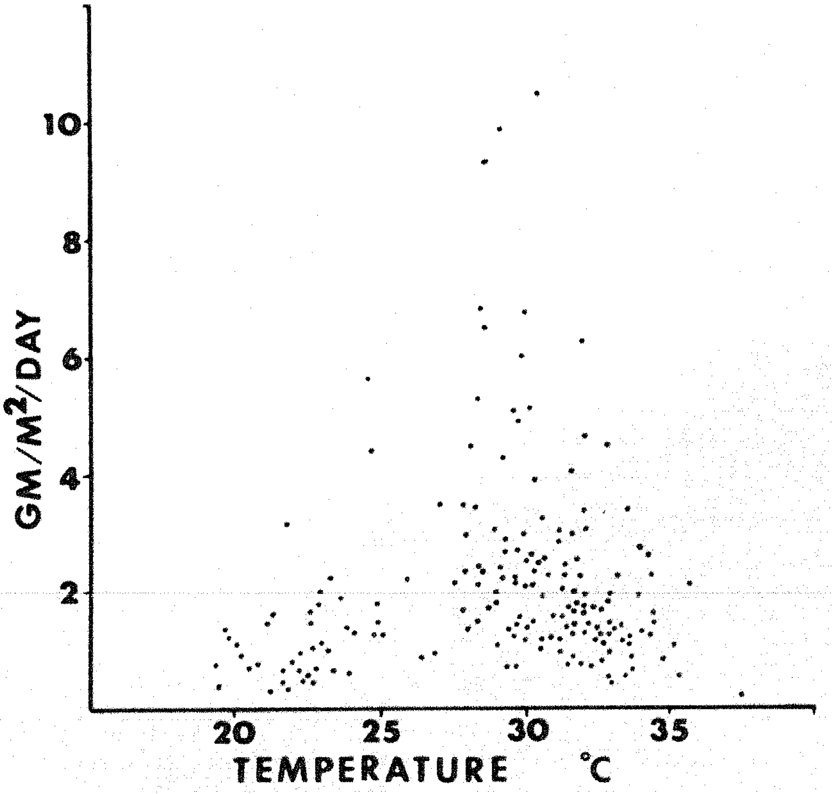


Figure 6. Response of Thalassia production to temperature in south Florida.

grass, and shoal grass in various locations from Texas to St. Croix and Jamaica. Populations from south Florida were intermediate in tolerance between plants from Texas and the northern Florida coast and those from St. Croix and Jamaica in the Caribbean. In south Florida, the most chill-tolerant plants were from the shallow bays, while the populations that were least tolerant of cold temperatures were from coral reef areas, where less fluctuation and greater buffering would be expected. During winter, the cold northern winds quickly cool off the shallow (0.3 to 1 m or 1 to 3.3 ft) waters of Florida Bay. The deeper waters, however, in the area below the Keys and the reef line (up to 15 m or 50 ft) not only have a much greater mass to be cooled, but are also flushed daily with warmer Gulf Stream water which further tends to buffer the environmental fluctuations.

The amount of direct evidence for the temperature ranges of shoal grass and manatee grass is far less than for turtle grass. Phillips (1960) suggested that shoal grass generally prefers temperatures of 20 to 30°C (68° to 86°F), but that it is somewhat more eurythermal than turtle grass. This fits its ecological role as a pioneer or colonizing species. Shoal grass is commonly found in shallower water than either turtle grass or manatee grass, where thermal variation would tend to be greater. McMillan (1979) found that shoal grass had a greater chill tolerance than turtle grass, while manatee grass showed less resistance to chilling.

Seagrasses are partially buffered from temperature extremes in the overlying water because of the sediments covering the roots and rhizomes. Sediments are poorer conductors of heat than seawater and they absorb heat more slowly. In a study by Redfield (1965), changes in the temperature of the water column decrease exponentially with depth in sediments.

Macroalgae associated with grass beds exist totally in the water column, and thus will be affected at a rate that is dependent upon their individual temperature tolerances. Most algae associated with tropical seagrass beds are more sensitive to thermal stress than the seagrasses (Zieman 1975a). In shallow embayments with restricted circulation, such as southwest Biscayne Bay, many algal species are reduced during summer high temperatures and some of the more sensitive types such as Caulerpa, Cladophora and Laurencia may be killed (Zieman 1975a).

2.4 SALINITY

While all of the common south Florida seagrasses can tolerate considerable salinity fluctuations, all have an optimum range near, or just below, the concentration of oceanic water. The dominant seagrass, turtle grass, can survive in salinities from 3.5 ppt (Sculthorpe 1967) to 60 ppt (McMillan and Moseley 1967), but can tolerate these extremes for only short periods. Even then, severe leaf loss is common; turtle grass lost leaves when salinity was reduced below 20 ppt (den Hartog 1970). The optimum salinity for turtle grass ranges from 24 ppt to 35 ppt (Phillips 1960; McMillan and Moseley 1967; Zieman 1975b). Turtle grass showed maximum photosynthetic activity in full-strength seawater and a linear decrease in activity with decreasing salinity (Hammer 1968b). At 50% strength seawater, the photosynthetic rate was only one-third of that in full-strength seawater. Following the passage of a hurricane in south Florida in 1960, Thomas et al. (1961) considered the damage to the turtle grass by freshwater runoff to have been more severe than the physical effects of the high winds and water surge.

The tolerance of local seagrass species to salinity variation is similar to their temperature tolerances. Shoal grass is the most broadly euryhaline, turtle grass is intermediate, and manatee grass and Halophila have the narrowest tolerance ranges, with Halophila being even more stenohaline than manatee grass (McMillan 1979).

2.5 SEDIMENTS

Seagrasses grow in a wide variety of sediments from fine muds to coarse sands, depending on the type of source material, the prevailing physical flow regime, and the density of the seagrass blades. As rooted plants, seagrasses require a sufficient depth of sediment for proper development. The sediment anchors the plant against the effects of water surge and currents, and provides the matrix for regeneration and nutrient supply. Runners occasionally adhere directly to a rock surface, with only a thin veneer of sediment surrounding the roots, but this happens sporadically and is quantitatively insignificant. The single most important sediment characteristic for seagrass growth and development is sufficient sediment depth.

Depth requirements also vary with the different species. Because of its shallow, surficial root system, shoal grass can colonize thin sediments in an area of minimal hydraulic stability (Fonseca et al. 1981). Turtle grass is more robust, requiring 50 cm (20 inches) of sediment to achieve lush growth, although meadow formation can begin with a lesser sediment depth (Zieman 1972). In the Bahamas, Scoffin (1970) found that turtle grass did not appear until sediment depth reached at least 7 cm (3 inches).

The density of turtle grass leaves greatly affected the concentration of fine-grained (less than 63μ) particles in sediments. Compared with bare sediment which showed only 1% to 3% fine-grained material, sparse to medium densities of turtle grass increased the fine percentage from 3% to 6% and dense turtle grass increased this further to over 15%.

The primary effects of the grass blades are the increasing of sedimentation rates in the beds; the concentrating of the finer-sized particles, both inorganic and organic; and the stabilizing of the deposited sediments (Fonseca, in press a, b; Kenworthy 1981). Burrell and Schubel (1977) described three effects produced by these mechanisms:

(1) Direct and indirect extraction and entrapment of fine waterborne particles by the seagrass leaves.

(2) Formation and retention of particles produced within the grass beds.

(3) Binding and stabilizing of the substrate by the seagrass root and rhizome system.

One of the values of the seagrass system is the ability to create a relatively low energy environment in regions of higher energy and turbulence. In addition to the fine particle extraction due to decreased turbulence, the leaves trap and consolidate particles of passing sediment which adhere to the leaf surface or become enmeshed in the tangle of epiphytes of older leaves. As the older portion of the leaves fragment, or as the leaves die and fall to the sediment surface, the organic portions of the leaves decay and the inorganic particles become part of the sediment. The continued presence of the growing leaves reduces the water velocity and increases the retention of these particles, yielding a net increase in sediment.

Key elements in a plant's efficiency of sediment stabilization are plant species and density of leaves. From observational data in Bermuda, researchers found open sand areas had 0.1% to 0.2% fine particles (less than 63μ). In manatee grass beds this increased to 1.9% fines, while turtle grass beds had 4.8% to 5.4% fine material (Wood et al. 1969). In the same study organic matter (% dry weight) was 2.5% to 2.6% in open sand areas with similar values in manatee grass beds; the organic matter in turtle grass beds was 3.5% to 4.9%, demonstrating the increased stabilization and retention power of the more robust turtle grass.

Seagrasses not only affect mean grain size of particles, but other geologically important parameters such as sorting, skewness, and shape (Burrell and Schubel 1977). Swinchatt (1965) found that the mean size of sand fraction particles, the relative abundance of fines, and the standard dimension all increased with an increase in blade density near a Florida reef tract. The quantitative effect of the trapping and bonding was discussed in several studies (Ginsberg and Lowenstam 1958; Wood et al. 1969; Fonseca in press a, b) and is shown graphically in Figure 7 (Zieman 1972).

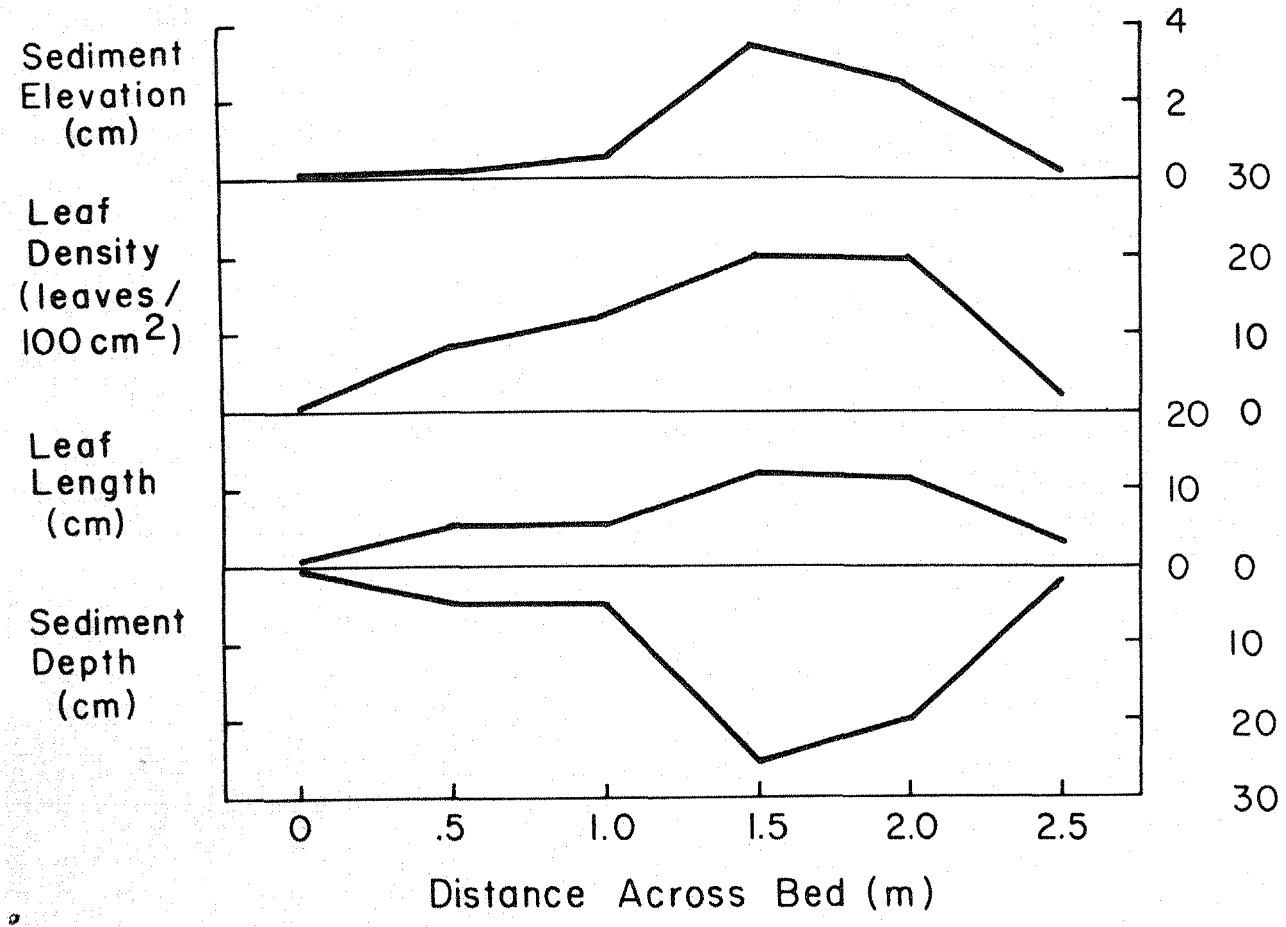


Figure 7. Response of a Thalassia bed to increasing sediment depth. Note increasing blade length and density with increasing depth of sediment. The increase in elevation in the center of the bed is due to the trapping action of the denser blades.

Particles of carbonate are locally produced in seagrass beds and removed from the surrounding water. Older leaves are usually colonized by encrusting coralline algae such as Melobesia or Fosliella. It has been estimated that these encrusting algae produce from 40 to 180 g/m^2/yr of calcium carbonate sediment in Jamaica (Land 1970) and upwards to 2,800 g/m^2/yr in Barbados (Patriquin 1972a).

The high production of seagrasses can affect the production of inorganic particulates also. Cloud (1962) estimated that 75% of aragonitic mud in a region of the Barbados was due to direct precipitation of carbonate when the seagrasses had removed CO_2 from the water during periods of extremely high primary productivity. Zieman (1975b) also noted the ability of seagrasses under calm conditions to overcome the carbonate buffer capacity of seawater and drive the pH up to 9.4.

The microbially mediated chemical processes in marine sediments provide a major source of nutrients for seagrass growth (Capone and Taylor 1980). Bacterial processes convert organic nitrogen compounds to ammonia (Capone and Taylor 1980; Smith et al. 1981b), primarily in the anoxic sediment which usually exists only a few millimeters beneath the sediment surface. The ammonia that is not rapidly utilized will diffuse upward to the aerobic zone where it can either escape to the water column or be converted to nitrate by nitrifying bacteria in the presence of oxygen. Endobacteria were found in the roots of the seagrass Zostera marina (Smith et al. 1981a), and were associated with nitrogen fixation (Smith et al. 1981b). The amount of nitrate is usually low or absent in sediments as it is either rapidly metabolized or converted to dinitrogen (N_2) via denitrifying bacteria.

Sulfur bacteria are primarily responsible for maintaining conditions necessary for the remineralization of nutrients in the sediment. By reducing sulfate to sulfide, these bacteria maintain the environmental conditions (Eh and pH) at a level where the nitrogen mineralization proceeds at a rate greater than its utilization by the microbial community. This produces the available nutrient fractions.

2.6 CURRENT VELOCITY

Little work has been done to determine the response of seagrass communities to different current velocities (Fonseca et al. in press a, b). Seagrass production and biomass are strongly influenced by current velocity (Conover 1968). Both turtle grass and Zostera showed maximum standing crops where current velocities averaged 0.5 m/sec. In south Florida the densest stands of turtle grass and manatee grass with bright, long leaves are observed in the tidal channels separating the mangrove islands. Inferential evidence suggests that the rapid currents break down diffusion gradients and make more CO_2 and inorganic nutrients available to the plants (Conover 1968). In a cruise of the Alpha Helix to Nicaragua in 1977, samples taken from a mangrove-lined tidal channel showed a leaf standing crop of 262 g dry weight (dw)/m^2 and a total biomass of 4,570 gdw/m^2. By comparison, samples from a quiescent lagoon environment were 185 and 1,033 g/m^2 (McRoy, Zieman and Ogden, personal communication).

Where currents are strong and persistent, crescentic features known as blowouts are often formed. These are cusp-shaped holes that actually migrate through grassbeds in the directions of the main current flow, eroding at one edge and colonizing at the other. Their significance is discussed in the section on succession.

2.7 OXYGEN

Most seagrass meadows have sufficient oxygen in the water column for survival of the associated plants and animals. Often the shallow beds can be heard to hiss from the escaping O_2 bubbles in the late afternoon. Dense beds in shallow water with restricted circulation can show extremely reduced O_2 levels or even anoxia late at night on a slack tide. This can be a greater problem if there is a heavy load of suspended organic sediment that would also consume oxygen. Generally the wind required to generate the turbulence necessary to suspend large quantities of sediment offsets this effect by aerating the water.

Low O_2 levels can also slow plant respiration; internal concentrations of O_2 decrease rapidly and CO_2 increases. Respiration then is limited by the ability of oxygen to diffuse from the water. Plants, however, are less affected by low oxygen levels than animals. Although Kikuchi (1980) recorded a marked decrease in oxygen in Japanese Zostera beds coincident with blade die-off and increased microbial activity, apparently it was not lethal. Productivity studies in Puerto Rico (Odum et al. 1960), Florida and Texas (Odum and Wilson 1962) showed nighttime oxygen values that were typically 4 to 7 mg O_2/l; the lowest reported value of 2 to 3 mg O_2/l occurred on a calm, extremely low tide in August.

2.8 SOLAR RADIATION

When one considers the overriding importance of solar energy as the main forcing function on any ecosystem, it is amazing how infrequently values are reported in the scientific literature. Historically there has been a consensus (even without adequate measurement) that seagrasses require high light intensity for photosynthesis (Zieman and Wetzel 1980). This is based on the observation that extensive seagrass beds are not found deeper than 10 m (33 ft). These observations are complicated by evidence that there is also indication of a limitation on productivity due to hydrostatic pressure and not merely light limitation (Gessner and Hammer 1961).

The maximum depth at which seagrasses are found is definitely correlated with the available light regime, provided that suitable sediments are available. Off the northwest coast of Cuba, Buesa (1975) reported maximum depths for tropical sea grasses as follows: turtle grass, 14 m (46 ft); manatee grass, 16.5 m (54 ft); Halophilia decipiens, 24.3 m (80 ft); and H. englemanni, 14.4 m (47 ft). As plant species grow deeper, the quality and quantity of light changes. In clear tropical water such as that near St. Croix, Cuba, and portions of southern waters, the light is relatively enriched in blue wavelengths with depth. By comparison, in highly turbid conditions as in shallow bays in Texas and in Florida Bay, blue light is scattered and the enrichment is in the direction of the green wavelengths. In both clear and turbid waters the longer red wavelengths are absorbed in the first few meters of the water column.

Buesa (1975) studied the effects of specific wavelengths on photosynthesis of turtle grass and manatee grass in Cuba. He found that turtle grass responded best to the red portion of the spectrum (620 nanometers); the blue portion (400 nanometers) was better for manatee grass.

2.9 ZONATION

Although seagrasses have been recorded from as deep as 42 m (138 ft), extensive development of seagrass beds is confined to depths of 10 to 15 m (33 to 49 ft) or less. Principal factors determining seagrass distribution are light and pressure at depth, and exposure at the shallow end of the gradient. A general pattern of seagrass distribution in clear waters of south Florida and the Caribbean was presented by Ferguson et al. (1980). Shoal grass usually grows in the shallowest water and tolerates exposure better than other species. The relatively high flexibility of its leaves allows it to conform to the damp sediment surface during periods of exposure, thus minimizing the leaf surfaces available for desiccation. Turtle grass grows in waters nearly as shallow as that of shoal grass. The shallowest turtle grass flats are commonly exposed on spring low tides, frequently with much leaf mortality. Throughout the range of 1 to 10 m (3 to 33 ft), all of the species may be found, singly or mixed. Turtle grass is the unquestionable dominant in most areas, however, frequently forming extensive meadows that stretch for tens of kilometers. Although the absolute depth limit of the species is deeper, mature meadows of turtle grass are not found below 10 to 12 m (33 to 39 ft). At this depth manatee grass replaces turtle grass and forms meadows down to 15 m (50 ft). Past the maximum depth for manatee grass development, shoal grass will often occur, but it rarely develops extensively. Past the point at which the major species occur, fine carpets of Halophila extend deeper than 40 m (130 ft).

Numerous studies confirmed the pattern described above, or some portion of it. The relative abundance of four species of seagrasses off northwest Cuba, is graphed in Figure 8 (Buesa 1974, 1975). Halophila decipiens was the least abundant with a mean density of 0.14 g/m^2. Halophila engelmanni showed a mean density of 0.25 g/m^2. Manatee grass was nearly 10 times denser than Halophila with an average density of 3.5 g/m^2 down to 16.5 m (54 ft). Turtle grass was the most abundant seagrass, accounting for nearly 97.5% of the total seagrass biomass, with an average of 190 g/m^2 down to its maximum depth of 14 m (46 ft). This area is unique in that there is little or no shoal grass which normally is either the second or third most abundant species in a region.

In St. Croix, turtle grass had the shallowest range, occurring down to 12 m (39 ft) on the west side of Buck Island (Wiginton and McMillen 1979). Shoal grass and manatee grass showed progressively greater depth, occurring to 18 m (59 ft) and 20 m (65 ft), respectively, while Halophila decipiens occurred to 42 m (138 ft). All the species were found in less than 1 m (3.3 ft) of water in St. Croix.

Because of the variety of rocky and sedimentary patterns in the lagoons and

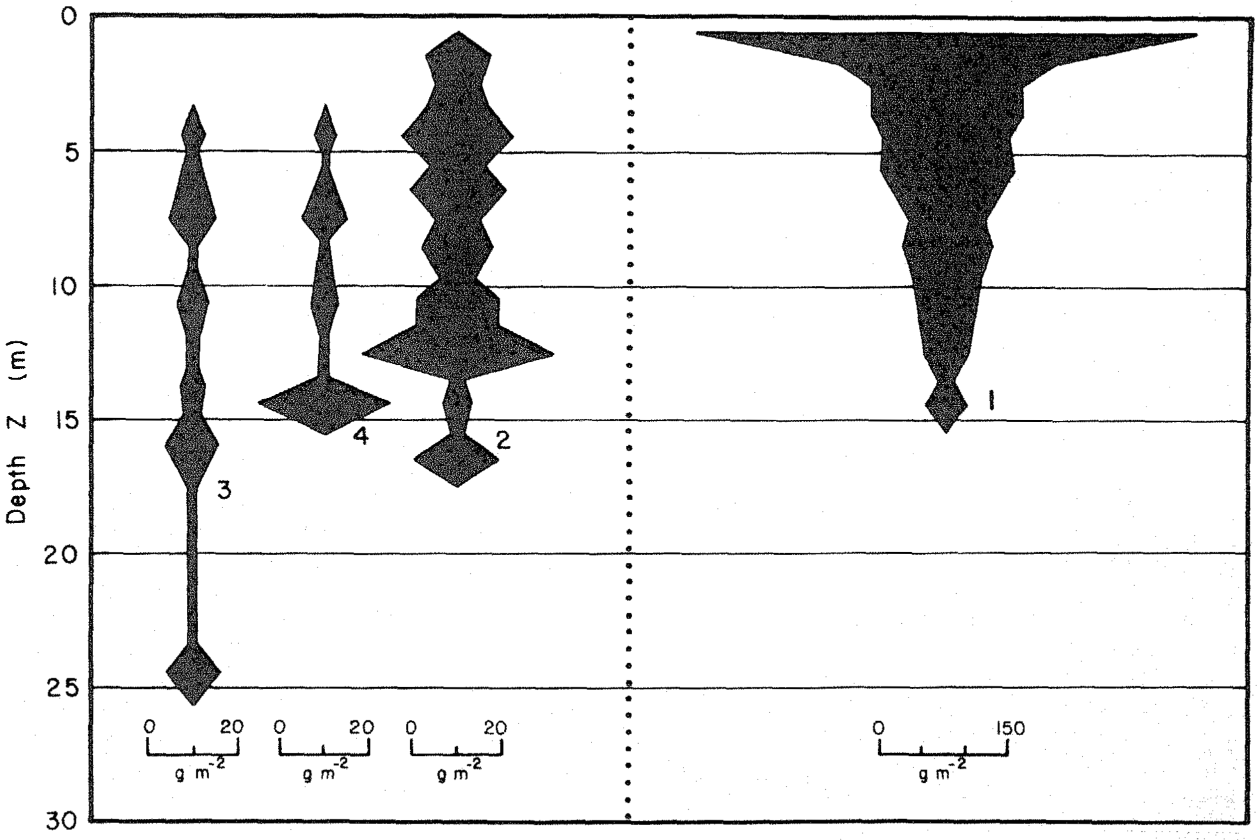


Figure 8. Depth distribution of four seagrasses on the northwest coast of Cuba. 1 = *Thalassia testudinum*, 2 = *Syringodium filiforme*, 3 = *Halophila decipiens*, 4 = *H. engelmanni* (from Busea 1975). Although *Syringodium* is quite abundant in certain localities, note the preponderance of *Thalassia* biomass and the absence of *Halodule* on the Cuban coast.

bays of south Florida, the turbidity and therefore the maximum depth for rooted plants can vary over short distances. Phillips (1960) recorded turtle grass ranging from 10 to 13 m (33 to 43 ft) in depth. In the relatively clear waters of the back reef areas behind the Florida Keys, turtle grass is common to 6 or 7 m (20 or 23 ft) and occurs down to 10 m (33 ft); by contrast, in the relatively turbid portion of the "lakes" of Florida Bay, maximum depths of only 2 m (7 ft) are common.

2.10 EXPOSURE

The seagrasses of south Florida are all subtidal plants that do not tolerate exposure well. Exposed leaf surfaces will lose water constantly until dry, and there is no constraint to water loss that would limit drying (Gessner 1968). Although exposure to the air definitely occurs at certain low tides on shallow turtle grass or shoal grass flats, unless it is extremely brief, the exposed leaf surfaces will be killed.

Following exposure, the dead leaves are commonly lost from the plant. Rafts of dead seagrass leaves may be carried from the shallow flats following the spring low tides. Normally the rhizomes are not damaged and the plants continue to produce new leaves.

CHAPTER 3

PRODUCTION ECOLOGY

The densities of seagrasses can vary widely; under optimum conditions they form vast meadows. The literature is becoming extensive and often bewildering as density values have been reported in many forms. For consistency, the terms used here conform to those of Zieman and Wetzel (1980): standing crop refers to aboveground (above-sediment) material, whereas biomass refers to the weight of all living plant material, including roots and rhizomes. Both quantities should be expressed in terms of mass per unit area. These measurements both have valid uses, but it is sometimes difficult to determine which an author is referring to, because of incomplete or imprecise descriptions. Historically, standing crop has been the primary measure of comparison because of the relative ease of sampling compared with the laborious methods needed to collect and then sort belowground material.

3.1 BIOMASS

Seagrass biomass varies widely depending on the species involved and the local conditions. The biomass of the species Halophila is always small, whereas turtle grass has been recorded at densities exceeding 8 kg dry weight/m^2 (Bauersfeld et al. 1969). Representative ranges of seagrass biomass in south Florida and in neighboring regions are given for comparison in Table 3. Because of the extreme variations found in nature and reflected in the literature, one must be careful not to place too much value on a few measurements. Many of these studies have been summarized by McRoy and McMillan (1977) and Zieman and Wetzel (1980). Because these studies represent a variety of habitats, different sampling times and seasons, wide variation in sample replicates (if any), as well as the diverse reasons for which the investigators collected the samples, it becomes difficult to draw meaningful patterns from these published results.

While the standing crop of leaves is significant, the majority of the biomass of seagrasses is in the sediments, especially for the larger species. Although the relative amounts vary, turtle grass typically has about 15% to 22% of its biomass in emergent leaves and the rest below the sediment surface as roots and rhizomes. The published ranges for turtle grass, however, vary from 10% to 45% for leaf biomass (Zieman 1975b). In central Biscayne Bay, Jones (1968) found a relatively consistent ratio of 3:2:2 for leaves and short shoots: rhizomes: roots. Studies with turtle grass and Zostera have indicated that the ratio of leaves to roots increased with a shift in substrate from course sand substrates to fine muds (Kenworthy 1981). This can be interpreted to indicate either the positive effect of the richer fine muds on more robust plant development, or the need for a better developed nutrient absorptive (root) network in the coarser sediments that tend to be lower in nutrients and organic matter. Thus, substrate may be an important variable when determining phenological indices.

Structurally, turtle grass has the most well-developed root and rhizome system of all the local seagrasses. Table 4

Table 3. Representative seagrass biomass (g dry wt/m^2).

Species	Location	Range	Mean	Source
Halodule wrightii	Florida	10-300	50-250	Zieman, unpubl. data
	Texas	10-250	90	McMahan 1968; McRoy 1974
	North Carolina	22-208		Kenworthy 1981
Syringodium filiforme	Florida	15-1,100	100-300	Zieman, unpubl. data
	Texas	30-70	45	McMahan 1968
Thalassia testudinum	Cuba	30-500	350	Buesa 1972, 1974; Buesa and Olaechea 1970
	Florida (east coast)	20-1,800	125-800	Odum 1963; Jones 1968; Zieman 1975b
	Florida (west coast)	75-8,100	500-3,100	Bauersfeld et al. 1969; Phillips 1960; Taylor et al. 1973
	Puerto Rico	60-560	80-450	Burkholder et al. 1959; Margalef and Rivero 1958
	Texas	60-250	150	Odum 1963; McRoy 1974

lists comparative biomass values from several stations in Pine Channel in the Florida Keys where the three major species coexist. Shoal grass and manatee grass have less well-developed root and rhizome systems and consequently will generally have much more of their total biomass in leaves than does turtle grass. Samples for these two species where the leaf component is 50% to 60% of total weight are not uncommon. Maximum values for the species also vary widely. Biomass measurements for dense stands of shoal grass are typically several hundred grams per square meter; manatee grass reaches maximum development at 1,200 to 1,500 g/m^2, while maximum values for turtle grass are over 8,000 g/m^2.

3.2 PRODUCTIVITY

Seagrasses have the potential for extremely high primary productivity. Recorded values for seagrass productivity vary enormously depending on species, density, season, and measurement techniques. Most studies use turtle grass with only a few scattered values for shoal grass and manatee grass.

For south Florida, turtle grass productivity values of 0.9 to 16 g C/m^2/day have been reported (Table 5). The highest reported values (e.g. Odum 1963) represent community metabolism and reflect the products of the seagrasses, epiphytic algae, and benthic algae. Measurements of seagrass production indicate that the net aboveground production is commonly 1 to 4 g C/m^2/day, although the maximum rates can be several times these values (Zieman and Wetzel 1980). The importance of the high sustained level of production of seagrasses is especially apparent when compared with the production values of the contiguous offshore waters.

3.3 PRODUCTIVITY MEASUREMENT

From the earliest seagrass studies, researchers have continually noted the high productivity of seagrasses, and their ultimate value as food for trophically higher organisms. As a result, much study has been devoted to methods for determining the productivity of seagrass beds.

Three basic methods have been used to study seagrass productivity: marking, ^{14}C, and O$_2$ production. (See Zieman and Wetzel 1980 for a recent review of productivity measurement techniques.)

Many assumptions are made when using the oxygen production method, and all can lead to large and variable errors, primarily because leaves of aquatic vascular plants can store gases produced during photosynthesis for an indefinite period. The largest potential error, however, is related to the storage of metabolically produced oxygen. To use the oxygen production technique, one assumes that oxygen produced in photosynthesis diffuses rapidly into the surrounding water where it can be readily measured. With seagrasses, as with other submerged macrophytes, however, this gas cannot diffuse outward at the rate at which it is produced and so it accumulates in the interstitial lacunae of the leaves (Hartman and Brown 1966). Recent work with freshwater macrophytes has suggested that under well-stirred conditions only a short period is required for equilibration (Westlake 1978; Kelly et al. 1980); however, this has not been verified for seagrasses. As the gas accumulates, seagrass leaves swell up to 250% of their original volume (Zieman 1975b). Some of the oxygen produced is used metabolically, while the remainder either diffuses out slowly or, if production is sufficient, will burst from the leaves in a stream of bubbles.

Measurement of seagrass productivity by radioactive carbon uptake has the advantage of high sensitivity, brief incubation periods, and the ability to partition out the productivity associated with the different morphological parts of the plants as well as productivity of the attendant epiphytes and macroalgae. Although this measurement technique requires sophisticated and expensive laboratory and field equipment, and may have errors associated with CO$_2$ storage, it apparently yields a value near to net productivity and produces values comparable to mark and recovery techniques. The application of the ^{14}C technique to seagrasses is discussed in detail by Penhale (1975), Bittaker and Iverson (1976), and Capone et al. (1979).

Table 4. Comparison of biomass distribution for three species of seagrasses from Pine Channel, June 1980 (Zieman et al. in preparation). MB indicates stations from the central portion of the embayment, while N is from a station at the northern end of the channel.

Species	Component	MB 2		MB 3		N 1	
		g/m^2	%	g/m^2	%	g/m^2	%
Thalassia	Leaves	206	11	58	15	267	10
	Roots and rhizomes	1,669	89	321	85	2,346	90
	Total biomass	1,875		379		2,613	
Syringodium	Leaves	58	24	102	16	28	47
	Roots and rhizomes	182	76	521	84	31	53
	Total biomass	240		623		59	
Halodule	Leaves	54	21	15	11	5	33
	Roots and rhizomes	200	79	120	89	10	67
	Total biomass	254		135		15	
All species	Total biomass	2,369		1,137		2,687	

Table 5. Representative seagrass productivities.

Species	Location	Productivity (g C/m^2/day)	Source
Halodule wrightii	North Carolina	0.5- 2.0	Dillon 1971
Syringodium filiforme	Florida	0.8- 3.0	Zieman, unpubl. data
	Texas	0.6- 9.0	Odum and Hoskin 1958; McRoy 1974
Thalassia testudinum	Florida (east coast)	0.9-16.0	Odum 1957, 1963; Jones 1968; Zieman 1975b
	Cuba	0.6- 7.2	Buesa 1972, 1974
	Puerto Rico	2.5- 4.5	Odum et al. 1960
	Jamaica	1.9- 3.0	Greenway 1974
	Barbados	0.5- 3.0	Patriquin 1972b, 1973

Net production measurements for most seagrasses can be obtained by marking blades and measuring their growth over time (Zieman 1974, 1975b). With this method, the blades in a quadrat are marked at their base, allowed to grow for several weeks, and then harvested. As seagrass leaves have basal growth, the increment added below the marking plus the newly emergent leaves represent the net aboveground production. After collection, the leaves of most tropical species must be gently acidified to remove adhered carbonates before drying and weighing.

Bittaker and Iverson (1976) critically compared the marking method with the measurement of productivity by radioactive carbon uptake. When the ^{14}C method was corrected for inorganic losses (13%), incubation chamber light energy absorption (14%), and difference in light energy resulting from experimental design (8%), the differences in productivity were insignificant. These results reinforce the concept that the ^{14}C method measures a rate near net productivity. In a study of turtle grass productivity near Bimini, however, Capone et al. (1979) found that the ^{14}C measurements yielded values nearly double that of the marking methods.

A method developed by Patriquin (1973) uses statistical estimates based on the length and width of the longest 5% of the leaf population of a given area. Capone et al. (1979) used this method; it agreed +/-15% with the staple marking method. Indications are that this method is very useful for a first order estimate, but more comparative studies are still needed.

Some form of oxygen measurement was used to attain the highest production values recorded in the literature for turtle grass and Zostera. Recently Kemp et al. (1981) surveyed numerous productivity measurements from the literature and confirmed that for seagrasses and several freshwater macrophytes, the oxygen method showed highest productivity values; marking methods, the lowest; and ^{14}C values were intermediate. Although these comparisons required numerous assumptions, the results show the need for further study. The marking method probably gives the least ambiguous answers, showing net aboveground production quite accurately. It underestimates net productivity as it does not account for belowground production, excreted carbon, or herbivory. Modifications of the marking method for Zostera marina have been used to estimate root and rhizome production (Sand-Jensen 1975; Jacobs 1979; Kenworthy 1981) and could be adopted for tropical seagrasses. The generalization that emerges from these various diverse studies is that seagrass systems are highly productive, no matter what method is used for measurement, and under optimum growth conditions production can be enormous.

3.4 NUTRIENT SUPPLY

Seagrasses along with the rhizophytic green algae are unique in the marine environment because they inhabit both the water column and the sediments. There was previously much controversy whether the seagrasses took up nutrients through their roots or their leaves. McRoy and Barsdate (1970) showed that Zostera was capable of absorbing nutrients either with the leaves or roots. McRoy and Barsdate found that Zostera could take up ammonia and phosphate from the sediments through their roots, translocate the nutrients, and pump them out the leaves into the surrounding water. This process could profoundly affect the productivity of nutrient-poor waters.

Sediment depth directly affects seagrass development (Figure 7). The implication is that the deeper sediment is required to allow sufficient root development which would in turn increase the nutrient absorptive capabilities of the roots. Thus to sustain growth, the plants would need greater nutrient absorptive tissue in sediments that contained less nutrients. While studying turtle grass in Puerto Rico, Burkholder et al. (1959) found a change in the leaf to root and rhizome ratios of the plants as the sediment type changed. The ratio of leaf to root and rhizome of turtle grass was 1:3 in fine mud, 1:5 in mud, and 1:7 in coarse sand. Kenworthy (1981) noted a similar change in Zostera in North Carolina. The plants from sandy areas had over twice the root tissue per unit leaf tissue, possibly indicating the need for more nutrient absorptive area or greater anchoring capacity in the coarser sediments. Alternatively, the decrease in root material in fine sediments could result from a negative effect from anaerobiasis or microbial metabolites.

Although seagrasses require a variety of macro- and micronutrients for nutrition, most research effort has been directed to the source and rate of supply of nitrogen. While phosphorous is in very low concentration in tropical waters, it is relatively abundant in the sediments, and estimates on turnover time range from one to two turnovers per year to once every few years (McRoy et al. 1972; Patriquin 1972b). Nitrogen, however, is needed in much greater quantities and its source is more obscure (McRoy and McMillan 1977). Patriquin (1972b) estimates that there was only a 5- to 15-day supply of inorganic nitrogen available in the sediments. This estimate did not account for continuous recycling, however.

Seagrasses have three potential nitrogen sources: recycled nitrogen in the sediments, nitrogen in the water column, and nitrogen fixation. Nitrogen fixation can occur either in the rhizosphere or phyllosphere. Transfers between leaf and epiphyte have also been demonstrated (Harlin 1971; McRoy and Goering 1974). Capone et al. (1979) concluded that nitrogen fixed in the phyllosphere contributed primarily to the epiphytic community while fixation in the rhizosphere contributed mainly to macrophyte production. Indirectly the contribution of nitrogen-fixing epiphytes is important because after the leaves senesce and detach, most of them decay and become part of the litter; some will be incorporated in the sediments. Other sources of nitrogen to the sediments include excretion by plants and animals, particulate matter trapped by the dense leaves, and dead root and rhizome material. Capone and Taylor (1980) agreed with Patriquin (1972b) that the primary source of nitrogen for leaf production is recycled material from sediments, but rhizosphere fixation can supply 20% to 50% of the plant's requirements. Orth (1977a) applied commercial fertilizers directly to a Zostera bed in Chesapeake Bay. After 2 to 3 months the length and density of leaves had increased, the amount of roots and rhizomes was 30% greater than the controls, and the standing crop of leaves had increased by a factor of three to four. Seagrasses seem to be extremely efficient at capturing and utilizing nutrients, and this is a major factor in their ability to maintain high productivity even in a relatively low nutrient environment.

3.5 SEAGRASS PHYSIOLOGY

Seagrasses have evolved a physiology that often distinguishes them from their terrestrial counterparts. Since water has rates of gaseous diffusion that are several orders of magnitude lower than air, much of this physiological modification is a response to the lowered gas concentration and the slower rates of diffusion when compared with the terrestrial environment. It is commonly thought that because of the abundance of inorganic carbon in seawater in the carbonate buffer system, marine plants are not carbon limited. During active photosynthesis, however, in shallow grass beds when tidal currents are slow, the pH may rise from the normal seawater pH of 8.2 to 8.9, at which point the free CO$_2$ is greatly reduced in the water. PH values of 9.4, a point at which biocarbonate is hardly present, have been recorded over grass beds.

The internal structure of seagrasses has been modified to minimize the problems of life in an aquatic environment. Large internal lacunal spaces have developed, often comprising over 70% of the total leaf volume, to facilitate internal gas transport (Arber 1920; Sculthorpe 1967; Zieman and Wetzel 1980). Much of the oxygen produced in photosynthesis is apparently retained in the lacunal system and diffuses throughout the plant to the regions of high respiratory demand in the roots and rhizomes. Similarly, because of the general lack of stomata, the diffusion of CO$_2$ into the seagrasses is slow compared with terrestrial counterparts. In addition, the quiescent water layer next to the leaves does not enhance diffusion of gases.

At normal seawater pH, bicarbonate is much more abundant than CO$_2$. Beer et al. (1977) showed that the major source of carbon for photosynthesis for four species of seagrasses was bicarbonate ion, which could contribute to the calcium carbonate flock frequently observed on seagrass leaves (Zieman and Wetzel 1980). At normal seawater pH, CO_2 concentrations were so low that the high photosynthetic potential was limited by bicarbonate uptake (Beer and Waisel 1979). Increasing the proportion of CO_2 by lowering pH greatly increased photosynthetic rates in Cymodocea nodosa, a large seagrass with high potential production.

Much recent controversy has concerned whether the metabolic pathway of seagrass photosynthesis utilizes the conventional Calvin cycle (called C_3 as the initial fixed sugars are 3 carbon chains) or the C_4 B-carboxylative pathway. C_4 plants refix CO_2 efficiently and little respired CO_2 is lost in the light (Hough 1974; Moffler et al. 1981). C_4 plants are difficult to saturate with light and have high temperature optimums. This photosynthetic system would seem to be of benefit in regions of high temperature and light intensities, as well as marine waters (Hatch et al. 1971). Seagrasses, however, are exposed to lower relative temperatures, light levels, and oxygen concentrations than are terrestrial counterparts; and as the diffusion capacity of CO_2 from leaves is much slower, metabolic CO_2 is available for refixation regardless of the photosynthetic pathway. After much literary controversy, recent evidence has shown that most seagrasses, including turtle grass, manatee grass, and shoal grass are C_3 plants (Andrews and Abel 1979; Benedict et al. 1980).

What makes the photosynthetic pathway of interest to those other than the plant physiologist is that during photosynthesis plants do not use the ^{12}C and ^{13}C isotopes in the ratios found in nature, but tend to differentiate in favor of the ^{12}C isotope which is lighter and more mobile. All plants and photosynthetic cycles are not alike, however, and those using the conventional C_3 Calvin cycle are relatively poor in the ^{13}C isotope, while C_4 plants have high ratios of $^{13}C/^{12}C$. The ratios of $^{13}C/^{12}C$ (called $\delta^{13}C$ or del ^{13}C) generally varies between -24 to -36 ppt for C_4 plants (Bender 1971). Seagrasses have relatively high $\delta^{13}C$ values. McMillan et al. (1980) surveyed 47 species of seagrasses from 12 genera and found that 45 species were within the range of -3 to -19 ppt, with only two species of Halophila being lower. The mean values and range for the local species are shown in Table 6. Turtle grass shows a mean value of -10.4 ppt and a total range from -8.3 to -12.5. This variation included samples from Florida, Texas, the Virgin Islands, and Mexico. The mean values and ranges for shoal grass and Halophila from the Gulf of Mexico and Caribbean are also very similar with mean values ranging from -10.2 to -12.6 ppt, respectively. Manatee grass is the only local seagrass of significantly different value with a more diluted mean of -5 ppt and a range of -3.0 to -9.5 ppt. In general, tropical species had higher $\delta^{13}C$ values than species from temperate regions. There also appears to be little seasonal difference in $\delta^{13}C$ values, at least for Zostera marina (Thayer et al. 1978a).

The $\delta^{13}C$ ratio has attracted much attention recently because of its utility as a natural food chain tracer (Fry and Parker 1979). The seagrasses possess a unique $\delta^{13}C$ ratio for marine plants, and thus organisms that consume significant portions of seagrass in their diet will reflect this reduced ratio. The carbon in animals has been shown to be generally isotopically similar to the carbon in their diet to within +/-2 ppt (DeNiro and Epstein 1978; Fry et al. 1978). Careful utilization of this method can distinguish between carbon originating from seagrasses (-3 to -15 ppt), marine algae (12 to -20 ppt), particulate organic carbon and phytoplankton (-18 to -25 ppt), and mangrove (-24 to -27) (Fry and Parker 1979). In Texas, organic matter from sediments of bays that have seagrasses display a significantly reduced $\delta^{13}C$ ratio when compared with adjacent bays lacking seagrass meadows (Fry et al. 1977). The same trends were reported for the animals collected from these bays (Fry 1981). The $\delta^{13}C$ value for one species of worm, Diopatra cuprea, shifted from an average of -13.3 to -18.4 ppt between seagrass- and phytoplankton-dominated systems (Fry and Parker 1979). The average values for fish and shrimp show a similar trend in that the $\delta^{13}C$ ratios are reduced in organisms from the seagrass meadows.

Table 6. ^{13}C values (ppt) for gulf and Caribbean seagrasses (McMillan et al. 1980)

Species	Mean	Range	Collection value	Collection site
Thalassia testudinum	-10.4	4.2	-8.3 to -11.0	Texas (Parker 1964; Calder 1969; Smith and Epstein 1971; Benedict and Scott 1976; Fry 1977)
			-9.9 to -10.0	St. Croix, U.S. Virgin Islands (Fry 1977)
			-10.9	Veracruz, Mexico
			-12.5	Long Key, Florida (Craig 1953)
Halodule wrightii	-10.8	4.8	-8.5 to -12.3	Texas (Parker 1964; Calder 1969; Smith and Epstein 1971; Fry 1977)
			-9.5	Freetown, Sierra Leone
			-10.5	Gibbitt Island, Bermuda
			-13.3	La Pesca, Tamaulipas, Mexico
Syringodium filiforme	-5.0	6.5	-3.0 to -9.5	Texas (Parker and Calder 1970; Smith and Epstein 1971; Fry 1977)
			-4.0 -5.1	St. Croix, U.S. Virgin Isalnds (Fry 1977)
Halophila decipiens	-10.2	4.7	-7.7 to -12.4	St. Croix, U.S. Virgin Islands
Halophila engelmanni	-12.6	2.9	-11.1 to -14.0	Texas (Calder 1969; Fry 1977)
Halophila johnsonii			-9.8	Ft. Pierce, Florida

Currently the main limitations of the carbon isotope method are equipment and interpretation. It requires use of a mass spectrometer which is extremely costly, although today a number of labs will process samples for a reasonable fee. The interpretation can become difficult when an organism has a $\delta^{13}C$ value in the middle ranges. If the $\delta^{13}C$ value is at one extreme or another, then interpretation is straightforward. However, a mid-range value can mean that the animal is feeding on a source that has this $\delta^{13}C$ value or that it is using a mixed food source which averages to this value. Recent studies utilizing both isotopes of carbon and sulfur (Fry and Parker 1982) and nitrogen (Macko 1981) show much promise in determining the origin of detrital material as well as the organic matter of higher organisms. Knowledge of the feeding ecology and natural history of the organism is needed, as is an alternate indicator.

3.6 PLANT CONSTITUENTS

Recognition of the high productivity of seagrasses and the relatively low level of direct grazing has led to questions regarding their value as food sources. Proximate analyses of seagrasses in south Florida, particularly turtle grass, have been performed by many authors (Burkholder et al. 1959; Bauersfeld et al. 1969; Walsh and Grow 1972; Lowe and Lawrence 1976; Vicente et al. 1978; Bjorndal 1980; Dawes and Lawrence 1980); their results are summarized in Table 7. As noted by Dawes and Lawrence (1980), differences in the preparation and analysis of samples, as well as low numbers of samples used in some studies, make data comparison difficult.

The reported ash content of turtle grass leaves ranges from 45% dry weight for unwashed samples down to around 25% for samples washed with fresh water. Leaves washed in seawater contained 29% +/- 3.6% to 44% +/- 6.7% ash (Dawes and Lawrence 1980).

Values for the protein content of leaves vary from a low of 3% of dry weight for unwashed turtle grass leaves with epiphytes (Dawes et al. 1979) to 29.7% for leaves washed in distilled water (Walsh and Grow 1972), although numbers typically fall in the range of 10% to 15% of dry weight. Protein values may be suspect if not measured directly, but calculated by extrapolating from percent nitrogen. In grass beds north of Tampa Bay, Dawes and Lawrence (1980) found that protein levels of turtle grass and manatee grass leaves varied seasonally, ranging from 8% to 22% and 8% to 13%, respectively, with the higher levels occurring in the summer and fall. The protein content of shoal grass ranged from a low of 14% in the fall up to 19% in the winter and summer. Tropical seagrasses, particularly turtle grass, have been compared to other plants as sources of nutrition. The protein content of turtle grass leaves roughly equaled that of phytoplankton and Bermuda grass (Burkholder et al. 1959) and was two to three times higher than 10 species of tropical forage grasses (Vicente et al. 1978). Walsh and Grow (1972) compared turtle grass to grain crops, citing studies in which 114 varieties of corn contained 9.8% to 16% protein; grain sorghum contained between 8.6% and 16.5%; and wheat was lowest at 8.3% to 12%. Although several studies have included measurements of carbohydrates (Table 7), it is impractical to compare much of the data because various analytical methods were employed.

Studies using neutral detergent fiber (NDF) analyses found that cell wall carbohydrates (cellulose, hemicellulose, and lignin) made up about 45% to 60% of the total dry weight of turtle grass leaves (Vicente et al. 1978; Bjorndal 1980). Dawes and Lawrence (1980) reported that insoluble carbohydrate content in the leaves of turtle grass, manatee grass, and shoal grass was 34% to 46%. The rhizomes of seagrasses are generally higher in carbohydrates than are the leaves. Dawes and Lawrence (1980) found that soluble carbohydrates in turtle grass and manatee grass rhizomes varied seasonally, indicating the production and storage of starch in summer and fall. These authors, however, were working in an area north of Tampa Bay, where such seasonal changes would be more pronounced than in the southern part of Florida and the Keys.

Table 7. Constituents of seagrasses.

Species	Component	Season/ date	%/Ref	Ash	Nitrogen	Protein	Fat	Carbohydrates (kcal/g)	Energy	Reference
Thalassia	Leaves	February	%DW	24.8	2.1	(13.1)	0.5	35.6	1.99	Burkholder et al. 1959
		Annual mean	%AFDW %DW	 24.5	1.6-4.8	25.7 (10.3-29.7)		23.6	4.66	Walsh and Grow 1972
		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 7. Continued.

Species	Component	Season/ date	%Ref	Ash	Protein	Fat	Carbohydrates	Energy (kcal/g)	Reference
Thalassia	Rhizome	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				
	Photosyn. 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	10	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	11	3.4	55	3.0	
	Short shoots-photosyn. 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 7. Concluded.

Species	Component	Season/ date	%/Ref	Ash	Protein	Fat	Carbohydrates	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- photosyn. 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	

CHAPTER 4

THE SEAGRASS SYSTEM

4.1 FUNCTIONS OF SEAGRASS ECOSYSTEMS

In addition to being high in net primary production and contributing large quantities of detritus to an ecosystem, seagrasses perform other functions. Because of their roots and rhizomes, they can modify their physical environment to an extent not equaled by any other fully submerged organism. Phillips (1978) stated that, "by their presence on a landscape of relatively uniform relief, seagrasses create a diversity of habitats and substrates, providing a structured habitat from a structureless one." Thus seagrasses also function to enhance environmental stability and provide shelter.

Seagrass ecosystems have numerous important functions in the nearshore marine environment. Wood et al. (1969) originally classified the functions of the seagrass ecosystem. The following is an updated version of the earlier classification scheme.

(1) High production and growth

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

(2) Food and feeding pathways

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) Shelter

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) Habitat stabilization

Seagrasses stabilize the sediments in two ways: the leaves slow and retard current flow to reduce water velocity near the sediment-water interface, a process which promotes sedimentation of particles as well as inhibiting resuspension of both organic and inorganic material. The roots and rhizomes form a complex, interlocking matrix with which to bond the sediment and retard erosion.

(5) Nutrient effects

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 pick 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 from the sediment.

4.2 SUCCESSION AND ECOSYSTEM DEVELOPMENT

In conventional usage, succession refers to the orderly development of a series of communities, or seral stages, which result in a climax stage that is in equilibrium with the prevailing environmental conditions. In more contemporary usage, however, succession is more broadly used to mean the succession of species, structure, and functions within an ecosystem. Odum (1969) stated the contemporary concept as follows:

> (1) Succession is an orderly process of community development that involves changes in species structure and community processes with time; it is reasonable, directional, and therefore predictable.
>
> (2) Succession results from modification of the physical environment by the community; that is, succession is community-controlled even though the physical environment determines the pattern and the role of change, and often sets limits as to how far development can go.
>
> (3) Succession culminates in a stabilized ecosystem in which maximum biomass (or high information content) and symbiotic function between organisms are maintained per unit of available energy flow.

Species succession has received by far the most attention as it is most obvious and easily measured. The study of succession of processes or functions is just beginning, however. It may well prove to be the most important avenue for understanding ecosystem development. Defining these processes is of much greater importance than mere scientific curiosity. It is also the key to restoring damaged or denuded systems.

4.3 SPECIES SUCCESSION

Throughout the south Florida region, and most of the Gulf of Mexico and Caribbean, the species of plants that participate in the successional sequence of seagrasses are remarkably few because there are so few marine plants that can colonize unconsolidated sediments. In addition to the seagrasses, one other group, the rhizophytic green algae, has this capability. These algae, however, have only limited rhizoidal development and never affect an area greater than a few centimeters from their base.

The most common illustration of succession in seagrass systems is the recolonization following a "blowout." This localized disturbance occurs in seagrass beds throughout Florida and the Caribbean where there is sufficient current movement in a dominant direction (Figure 9). Usually a disruption, such as a major storm, overgrazing caused by an outbreak of urchins, or a major ripping of the beds caused by dragging a large anchor, is required to initiate the blowout. Once started, the holes are enlarged by the strong water flow which causes erosion on the down current side. Slowly a crescentic shape a few meters wide to tens of meters wide is formed. A sample cross section in Figure 10 shows a mature turtle grass community that has been disrupted and is recovering. The region at the base of the erosion scarp is highly agitated and contains large chunks of consolidated sediment and occasional rhizome fragments. With increasing distance from the face of the scarp, turbulence decreases and some material is deposited. The area has become colonized with rhizophytic algae; Halimeda and Penicillus are the most abundant, but Caulerpa, Udotea, Rhipocephalus and Avrainvillea are also common. These algae provide a certain amount of sediment-binding capability as illustrated in Figure 11, but they do not stabilize the surface of the sediments very well (Scoffin 1970). A major function of these algae in the early successional stage is the contribution of sedimentary particles (Williams 1981). The generalized pattern and

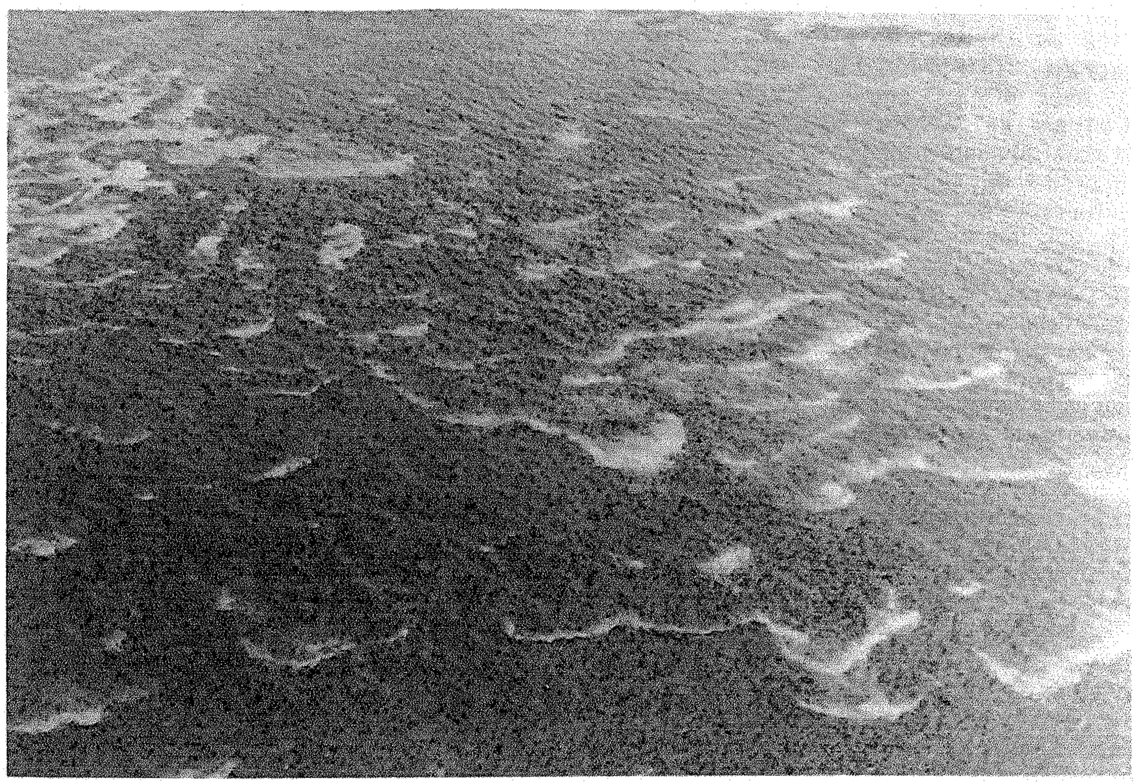


Figure 9. Blowout disturbance and recovery zones.

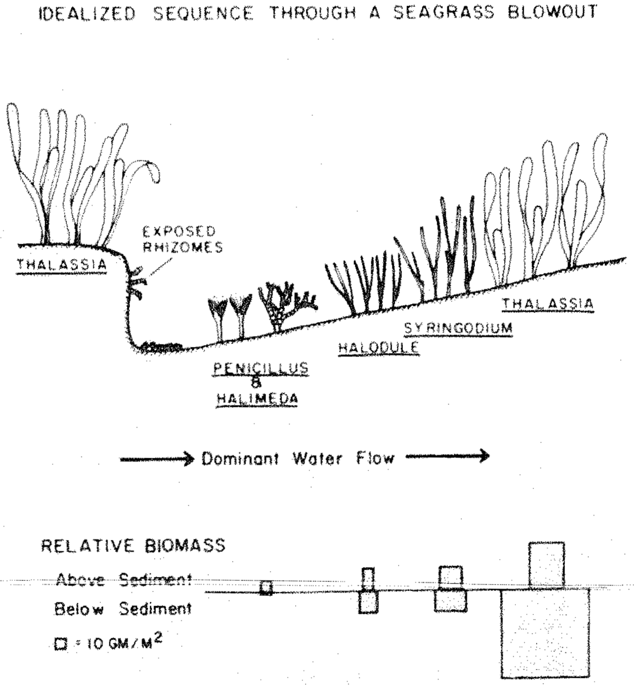


Figure 10. Idealized sequence through a seagrass blowout. Note erosion and recovery zones moving into the dominant water flow.

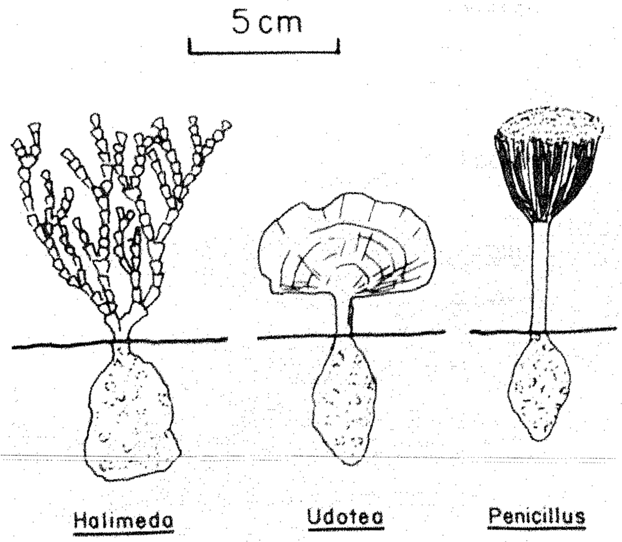


Figure 11. Representative calcareous green algae from seagrass beds. Note the binding action of the rhizoids in forming small consolidated sediment balls.

composition of marine sediments in south Florida as taken from Ginsburg (1956) are illustrated in Figure 12. Behind the reef tract over 40% of the sediment was generated from calcareous algae. Penicillus capitatus produced about 6 crops per year in Florida Bay and 9.6 crops per year on the inner reef tract (Stockman et al. 1976). Based on the standing crops, this would produce 3.2 $g/m^2/yr$ on the reef tract which could account for one-third of the sediment produced in Florida Bay and nearly all of the back-reef sediment. Similarly, Neuman and Land (1975) estimated that Halimeda incrassata produced enough carbonate to supply all the sediment in the Bight of Abaco in the Bahamas.

The pioneer species of the Caribbean seagrasses is shoal grass, which colonizes readily either from seed or rapid vegetative branching. The carpet laid by shoal grass further stabilizes the sediment surface. The leaves form a better buffer than the algal communities and protect the integrity of the sediment surface. In some sequences manatee grass will appear next, intermixed with shoal grass at one edge of its distribution and with turtle grass at the other. Manatee grass, the least constant member of this sequence, is frequently absent, however.

Manatee grass appears more commonly in this developmental sequence in the Caribbean islands and in the lower Florida

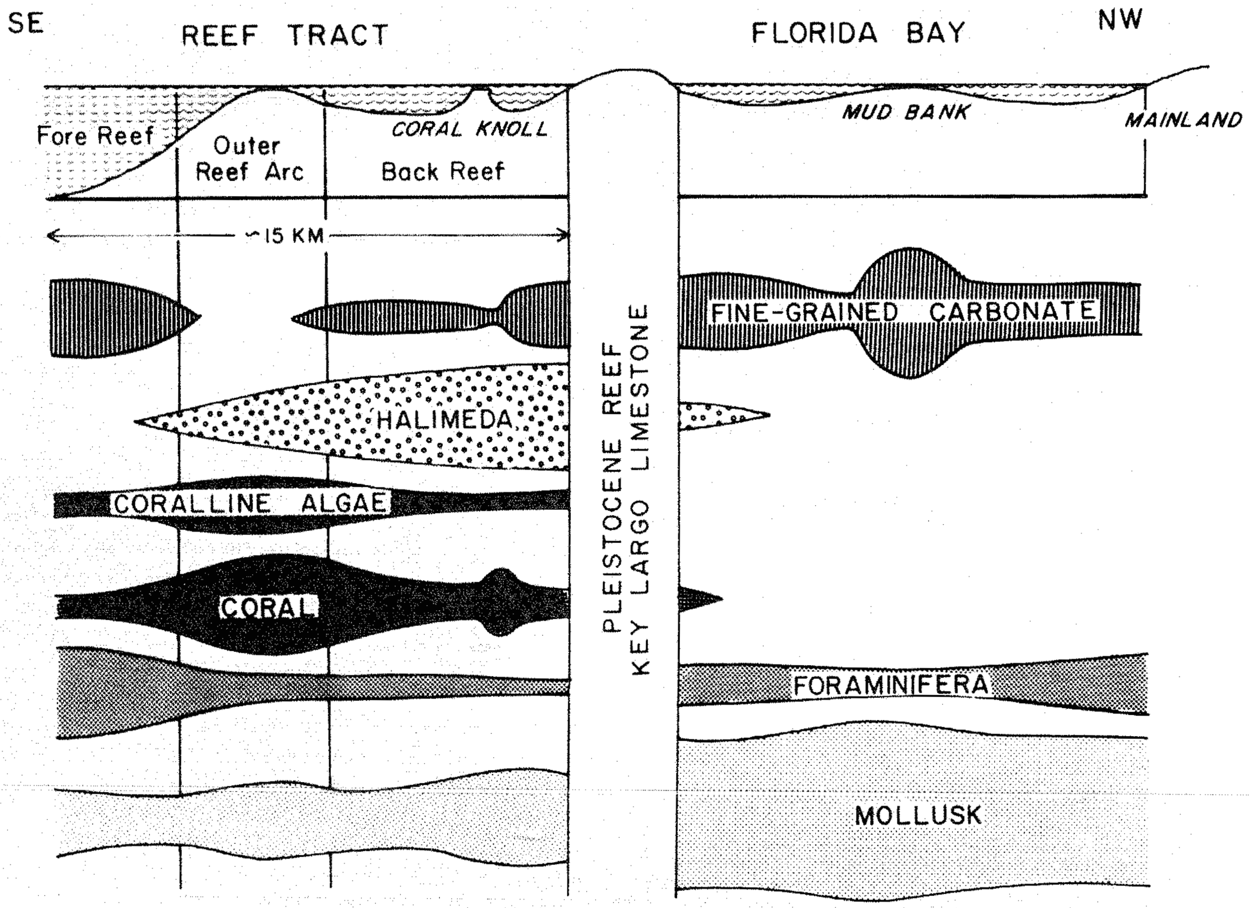


Figure 12. Origin of sedimentary particles in south Florida marine waters (modified from Ginsberg 1956).

Keys waters. Where the continental influence increases the organic matter in the sediments, manatee grass appears to occur less commonly. Lower organic matter in Caribbean sediments, due to the lack of continental effect, may slow the developmental process.

As successional development proceeds in a blowout, turtle grass will begin to colonize the region. Because of stronger, strap-like leaves and massive rhizome and root system of turtle grass, particles are trapped and retained in the sediments with much greater efficiency and the organic matter of the sediment will increase. The sediment height rises (or conversely the water depth above the sediment decreases) until the rate of deposition and erosion of sediment particles is in balance. This process is a function of the intensity of wave action, the current velocity, and the density of leaves.

The time required for this recovery will vary depending on, among other factors, the size of the disturbance and the intensity of the waves and currents in the region. In Barbados, blowouts were restabilized within 5 to 15 years (Patriquin 1975). During the study of Patriquin (1975) the average rate of erosion of the blowout was 3.7 mm/day, while the rate of colonization of the middle of the recovery slope by manatee grass was 5 mm/day. Once recolonization of the rubble layer began, average sediment accretion averaged 3.9 mm/yr.

With the colonization of turtle grass, the normal algal epiphyte and faunal associates begin to increase in abundance and diversity. Patriquin (1975) noted that the most important effect of the instability caused by the blowouts is to "limit the seral development of the community. The change in the region of the blowouts of a well-developed epifauna and flora, which is characteristic of advanced stages of seral development of the seagrass community, is evidence of this phenomenon."

In areas that are subject to continued or repeated disturbances, the successional development may be arrested at any point along the developmental gradient (Figure 13). Many stands of manatee grass

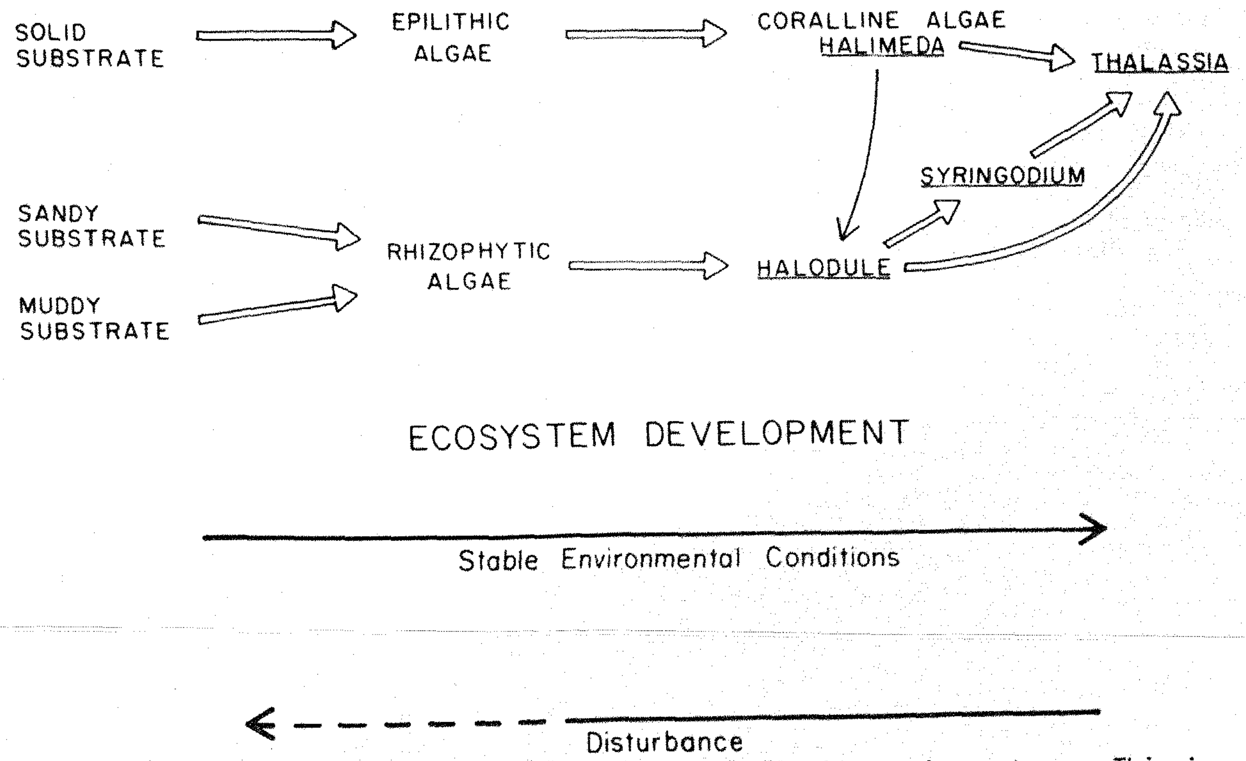


Figure 13. Ecosystem development patterns in south Florida marine waters. This is a generalized pattern, and all stages may not be present. Note that in the absence of disturbance that the tendency is to a Thalassia climax.

are present because of its ability to tolerate aerobic, unstable sediments and to rapidly extend its rhizome system under these conditions. This is especially evident in back-reef areas. Patriquin (1975) attributes the persistence of manatee grass in areas around Barbados to recurrent erosion in areas where the bottom was never stable for a sufficiently long time to allow turtle grass to colonize. Manatee grass can have half of its biomass as leaves (Table 4). Thus, while manatee grass is colonizing aerobic disturbed sediments, which would be areas of low nutrient supply and regeneration, the amount of its root surface available for nutrient uptake would be reduced, and correspondingly leaf uptake would become a major source of nutrients. If this is the case, the higher agitation of the water column would be of benefit by reducing the gradients at the leaf surface.

4.4 THE CENTRAL POSITION OF THE SEAGRASSES TO THE SEAGRASS ECOSYSTEM

Seagrasses are vital to the coastal ecosystem because they form the basis of a three-dimensional, structurally complex habitat. In modern ecology there has been a shift from the autoecological approach of studying individual species independently, to the community or ecosystem approach where the focus is the larger integrated entity. With that realization, one could wonder, "Why spend so much effort on a few species of marine plants, even if they are the most abundant, in a system that has thousands of other species?" The reason is that these plants are critical to most other species of the system, both plant and animal. There are few other systems which are so dominated and controlled by a single species as in the case of a climax turtle grass or Zostera meadow. H.T. Odum (1974) classified turtle grass beds as "natural tropical ecosystems with high diversity." Taken as a total system, tropical seagrass beds are regions of very high diversity, but this can be misleading. Comparisons between tropical and temperate systems 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 made each individual or each link less necessary to the maintenance of the total system. There was much natural redundance built into the system. For certain segments of the community this may be true. The problem is that at climax there is one species for which there is no redundancy : the seagrass. In some cases, if the seagrass disappears, the entire associated community disappears along with it; there is no other organism that can sustain and support the system.

This is shown in a small way when minor disturbances occur as was described with the blowouts. As the grass beds in these areas are eroded away, the entire seagrass system disappears, including the top 1 or 2 m of sediment. These features are small and readily repaired, but give an indication of what could happen if there was widespread damage to the seagrasses.

The largest contribution to the diversity of the system is commonly made by the complex communities that are epiphytic on the seagrass leaves. When defoliation of the seagrasses occurs, most of this community disappears, either by being carried out as drifting leaves or becoming part of the litter layer and ultimately the surface sediments. With the leaves gone, the current baffling effect is lost and the sediment surface begins to erode. Algal mats that may form have minimal stabilizing ability; however, the dead rhizomes and mats will continue to bond the sediments, in some cases for several years (Patriquin 1975; Scoffin 1970).

In south Florida the disappearance of seagrasses would yield a far different seascape. Much of the region would be shifting mud and mud banks, while in many areas the sediments would be eroded to bedrock. Based on the communities found in such areas today, primary production and detrital production would be dramatically decreased to the point that the support base for the abundant commercial fisheries and sport fisheries would shrink if not disappear.

4.5 STRUCTURAL AND PROCESS SUCCESSION IN SEAGRASSES

As species succession occurs in a shallow marine system, important structural changes occur. Because seagrass systems do not have woody structural components and only possess relatively simplistic canopy structure, the main structural features are the leaf area and biomass of the leaves as well as the root and rhizome material in the sediment. The most obvious change with community development is the increase in leaf area. This 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, shoal grass, or the initial algal colonizers. In addition to providing a substrate, the increasing leaf area also increases the current baffling and sediment-trapping effects, thus enhancing internal nitrogen cycling.

As organisms grow and reproduce in the environment, they bring about changes in their surroundings. In doing so these organisms frequently modify the environment in a way that no longer favors their continual growth. McArthur and Connell (1966) stated that this process "gives us a clue to all of the true replacements of succession: each species alters the environment in such a way that it can no longer grow so successfully as others".

In a shallow water successional sequence leading to turtle grass, the early stages are often characterized by a low supply of organic matter in the sediment and open nutrient supply; that is, the community relies on nutrients being brought in from adjacent areas by water movement as opposed to in situ regeneration. With the development from rhizophytic algae to turtle grass, there is a progressive development in the belowground 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 increase. This material adds organic matter to further fuel the sedimentary microbial cycles. Although various segments of this successional sequence have been measured by numerous authors, the most complete set of data has recently been compiled by Williams (1981) in St. Croix (Table 8). In St. Croix, where the data were collected, as on many low, small islands with little rainfall, the climax is commonly a mixture of turtle grass and manatee grass. In south Florida, with its higher rainfall and runoff, the climax more commonly is a pure turtle grass stand. In turtle grass beds in south Florida, Capone and Taylor (1977, 1980) found that nitrification was highest on the developing periphery of the beds and lower in the centers where particulate trapping and retention were greater. Additionally, mature ecosystems, both marine and terrestrial, seem to be based primarily on the detrital food web which aids in conserving both carbon and nitrogen, as direct grazing is quantitatively low in these systems.

Table 8. A gradient of parameters of seagrass succession from Tague Bay Lagoon, St. Croix, U.S.V.I. (Williams 1981). Blank indicates no data; values shown are averages.

Parameters	Bare sediments	Rhizophytic algal community	Colonizing seagrass bed	Immature seagrass bed	*Thalassia* seagrass climax
No. plants/m^2	0	254	981	3,089	1,533
Biomass (g dry wt/m^2)	0	185	89	1,244	2,241
No. *Thalassia*: No. *Syringodium*: No. *Halodule*	0:0:0	0:0:0	1:17:33	1:2:2	1:1:0
Interstitial NH_4 (Micromoles N)	0.0	1.0	304	3-39	6-200
Adsorbed NH_4 (Micromole N/g dry sediment)	-	0.63	2.50	3.05	12.82
Thalassia blade length (cm)	-	-	14.08	16.25	22.37
Thalassia blade width (mm)	-	-	8.33	10.17	10.87
Sediment deposition (g dry wt/m/day)	240	-	2,168	-	2,941
Detrital seagrass (g dry wt/m/week)	-	-	25.21	-	252.10

CHAPTER 5

THE SEAGRASS COMMUNITY - COMPONENTS, STRUCTURE, AND FUNCTION

Seagrass-associated communities are determined by species composition and density of seagrass present, as well as abiotic variables. These communities range from monospecific turtle grass beds in the clear, deep waters behind the reef tract to the shallow, muddy bottoms of upper Florida Bay where varying densities of shoal grass are intermixed with patches of turtle grass.

Turney and Perkins (1972) divided Florida Bay into four regions based largely on temperature, salinity, circulation, and substrate characteristics. Each of these regions proved to have a distinctive molluscan assemblage.

Studies have also shown that great diversity in species number and abundance exists even within communities of similar seagrass composition and density, and within comparatively small geographical regions. Brook (1978) compared the macrofaunal abundance in five turtle grass communities in south Florida, where the blade density was greater than 3,000 blades/m^2. Total taxa represented varied from a low of 38 to a high of 80, and average abundance of individuals varied from 292 to 10,644 individuals/m^2.

The biota present in the seagrass ecosystem can be classified in a scheme that recognizes the central role of the seagrass canopy in the organization of the system. The principal groups are (1) epiphytic organisms, (2) epibenthic organisms, (3) infaunal organisms, and (4) the nektonic organisms.

The term epiphytic organisms is used here the same as that of Harlin (1980) and means any organism growing on a plant and not just a plant living on a plant. Epibenthic organisms are those organisms that live on the surface of the sediment; in its broadest sense, this includes 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 organisms that live buried in the sediments. Organisms such as penaeid shrimp, however, that lie buried part of the day or night in the sediments, but are actively moving on the sediment surface the rest of the time would not be included as part of the infauna. The infauna would include organisms such as the relatively immobile sedentary polychaetes and the relatively mobile irregular urchins. Nektonic organisms, the highly mobile organisms living in or above the plant canopy, are largely fishes and squids.

Kikuchi (1961, 1962, 1966, 1980) originally proposed a functional classification scheme for the utilization of Japanese seagrass beds by fauna that has wide utility. This classification, modified for tropical organisms, would include (1) permanent residents, (2) seasonal residents, (3) temporal migrants, (4) transients, and (5) casual visitors. The third category is added here to include the organisms that daily migrate between seagrass beds and coral reefs. These were not included in the original classification which was based on temperate fauna.

5.1 ASSOCIATED ALGAE

Major sources of primary production for coastal and estuarine areas are the following:

(1) Macrophytes (seagrasses, mangroves, macroalgae, and marsh grasses)

(2) Benthic microalgae (benthic and epiphytic diatoms, dinoflagellates, filamentous green and bluegreen algae)

(3) Phytoplankton

Although in deep, turbid northern estuaries, such as the Chesapeake or Delaware Bays, phytoplankton may be the dominant producer, in most areas that have been investigated the macrophytes are the most important primary producers, often by an overwhelming margin.

Productivities of phytoplankton, marsh grasses, and seagrasses in a North Carolina estuary were compared by Williams (1973); areal production values were 53, 249, and 678 $g/m^2/yr$, respectively. When the total area of the estuarine sound system available to phytoplankton and seagrass was considered, the seagrass production for the entire estuary was still about 2.5 times the annual contribution of the phytoplankton. In the clearer waters of the Florida estuaries and coastal zone, the difference is considerably greater. In Boca Ciega Bay, Taylor and Saloman (1968) estimated that total production, which was primarily macrophytes, was six times the annual phytoplankton production. Thayer and Ustach (1981) have estimated macrophytes to account for about 75% of the plant production in the estuarine-coastal area of the northern Gulf of Mexico.

Benthic Algae

Algal communities on hard substrates can consist of hundreds of species from all of the major macroalgal phyla. The areas inhabited by seagrasses do not offer an optimal habitat for most algae, which require hard substrate for attachment of their holdfast. Primary substrate for algae will include (1) the sediments, (2) the seagrasses themselves, and (3) occasional rocks or outcrops. In addition many macroalgae in south Florida form large unattached masses on the sea bottom, collectively known as drift algae.

Although much of south Florida offers sufficient hard substrate for algal attachment, notably the reef tracts and the shallow zones bordering many of the keys, the dominant substrate type is not solid. In many areas mangrove prop roots, oyster bases, and scattered rocks or shells and to manmade structures such as bridge supports and canal walls offer the primary algal substrates.

The only algae able to consistently use sediments as substrate are (1) the mat-forming algae and (2) members of the order Siphonales (Chlorophyta) which possess creeping rhizoids that provide an anchor in sediments (Humm 1973). Among the most important genera are Halimeda, Penicillus, Caulerpa, Rhipocephalus, and Udotea (Figure 14). These algae are important as primary producers of organic carbon; of even greater importance, all but Caulerpa produce calcium carbonate for their skeleton which, upon death, becomes incorporated in the sediments.

These algae have limited sediment stabilizing properties, the main utility of their rhizoidal holdfasts being to maintain them in place. Because they do not have a large investiture of structure in the sediments, they can more rapidly accommodate changes in shifting sediments, while still maintaining some current buffering capacity. In this capacity they form a prior successional stage for seagrasses (Williams 1981).

Production of lime mud by these algae can be enormous. Halimeda tends to break up into characteristic sand-sized plates, while Penicillus produces fine-grained (less than 15μ) aragonitic mud. Stockman et al. (1967) estimated that at the present rate of production, 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. In addition, the combination

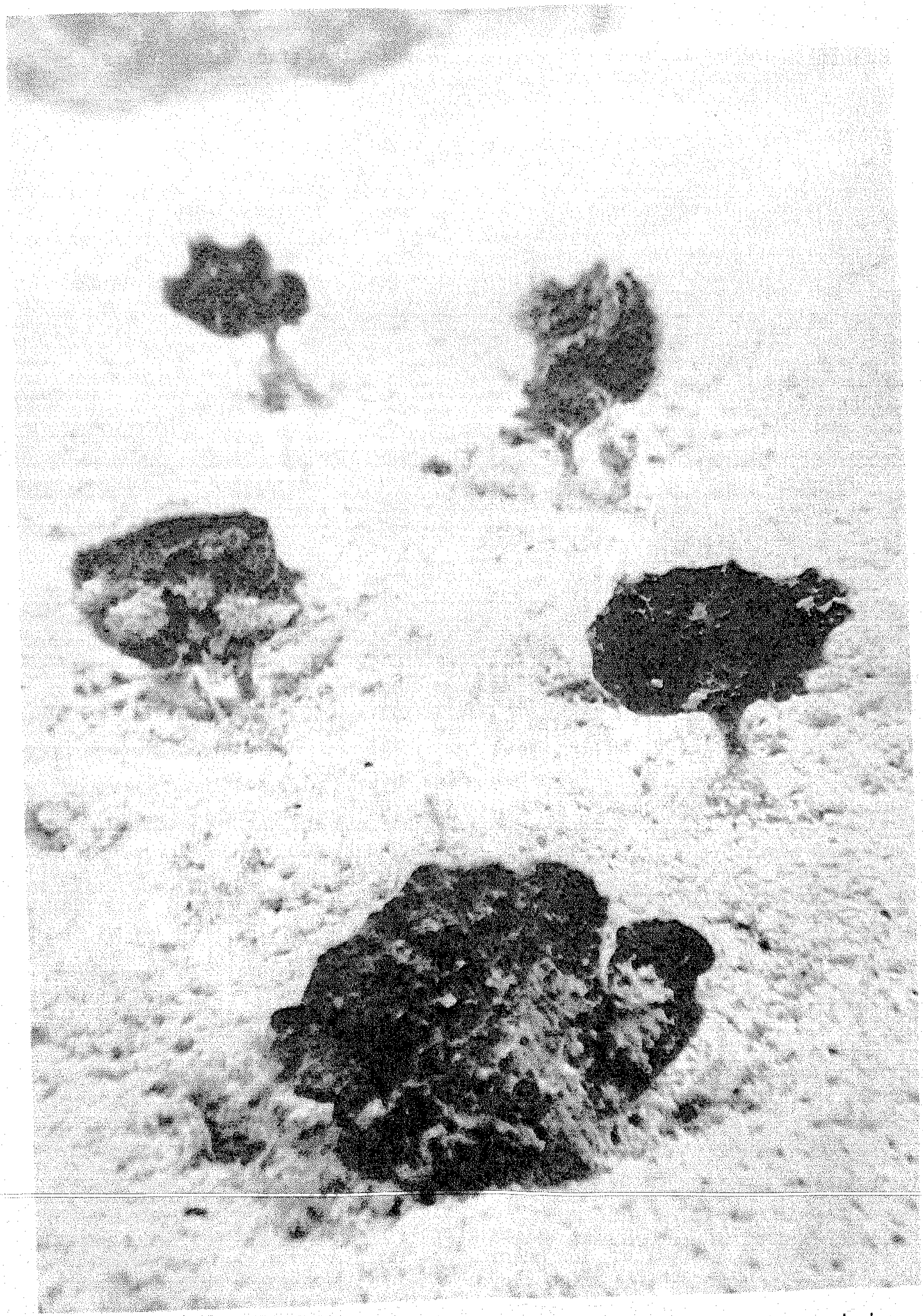


Figure 14. Calcareous algae (Udotea sp.) from the fringes of a seagrass bed.

of *Rhipocephalus*, *Udotea*, and *Acetabularia* produced at least as much mud as *Penicillus* in the same locations.

In the Bight of Abaco, Neumann and Land (1975) calculated that the growth of *Penicillus*, *Rhipocephalus*, and *Halimeda* 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 produced more sediment than could be accommodated. Bach (1979) measured the rates of organic and inorganic production of calcareous siphonates in Card Sound, Florida, using several techniques. Organic production was low in this lagoon, ranging from 8.6 to 38.4 g ash free dry weight /m^2/yr, and 4.2 to 16.8 g CaCO$_3$/m^2/yr for all the species combined.

In addition to the calcareous algae, several algae are present in grass beds as large clumps of detached drift algae; the most abundant belongs to the genus *Laurencia*. The areal production of these algae is low compared with the seagrasses. Joselyn (1975) estimated the production of *Laurencia* in Card Sound to average about 8.1 g dry weight /m^2/yr which was less than 1% of the 1,100 g/m^2/yr estimated by Thorhaug et al. (1973) for turtle grass from the same area.

The least studied components of the algal flora are the benthic microalgae. In studies of benthic production throughout the Caribbean, Bunt et al. (1972) calculated the production in Caribbean sediments to average 8.1 mg C/m^2/hr (range = 2.5 to 13.8 mg) using ^{14}C uptake. By comparison, sediments from the Florida Keys yielded 0.3 to 7.4 mg C/m^2/hr fixation. These values were equivalent to the production in the water column. Ferguson et al. (1980) briefly reviewed microalgal production values and indicated that light and thermal inhibition can occur, particularly in summer.

Epiphytic Algae

One of the main functions for which seagrasses have been recognized has been the ability to provide a substrate for the attachment of epiphytic organisms. Although unifying patterns are beginning to emerge, the study of epiphytes has suffered from what Harlin (1980) described as the "bits and pieces" approach.

An annotated list of 113 species of algae found epiphytic on turtle grass in south Florida was compiled by Humm (1964). 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 epiphytic on the seagrasses of the west coast of Florida. Rhodophyta comprised 45% of the total, Phaeophytas were only 12%, and Chlorophytas and Cyanophytas each represented 21% of the species. 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 comprehensive, but none of the reports surveyed by Humm list the epiphytic invertebrates from south 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
(5) Organic carbon source

The availability of a relatively stable (albeit somewhat swaying) substrate seems to be the most fundamental role played by the seagrasses. The majority of the epiphytic species is sessile and needs a surface for attachment. The turnover of the epiphytic community is relatively rapid since the lifetime of a single leaf is limited. A typical turtle grass leaf has a lifetime of 30 to 60 days (Zieman 1975b). After a leaf emerges there is a period 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 only occur after the leaf has been colonized by the coralline red algae, *Fosliella* or *Melobesia*. The coralline skeleton of these algae may form a protective barrier as well as a suitably roughened and adherent surface for epiphytes (Figure 15).

Figure 15. Thalassia blades showing tips encrusted with calcareous epiphytic algae. Several of the larger blades show the effects of grazing on the leaf tips.

Seagrass leaves are more heavily epiphytized at their tips than their bases for various reasons. For the small algae, being on the leaves has the advantage of raising them higher in the photic zone. The shading effect produced by epiphytic organisms on seagrass leaves decreases photosynthesis by 31% (Sand-Jensen 1975). In addition, the upper leaf surface experiences much greater water motion than the lower surface. This not only provides a much greater volume of water to be swept by suspension-feeding animals, but also reduces the gradients for photosynthetic organisms. Studies have shown that there is transfer of nutrients from seagrasses to epiphytes. Harlin (1975) described the uptake of PO_4 translocated up the leaves of Zostera and Phyllospadix. Epiphytic blue-green algae have the capacity to fix molecular nitrogen, and Goering and Parker (1972) showed that soluble nitrate fixed in this manner was utilized by seagrasses.

Epiphytes also contribute to the primary production of the seagrass ecosystem. In some areas there are few epiphytes and little contribution, but in places the amount of production is high. Jones (1968) estimated that in northern Biscayne Bay epiphytes contributed from 25% to 33% of the community metabolism. Epiphytes contributed 18% of productivity of Zostera meadows in North Carolina (Penhale 1977). The trophic structure of these leaf communities can be quite complex 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.

5.2 INVERTEBRATES

Composition

The invertebrate fauna of seagrass beds is exceedingly rich and can only be characterized in broad terms unless one is dealing with a specific, defined area. This is because the fauna of the grass beds is diverse, with many hundreds of species being represented within a small area, and variable, with dramatic changes occurring in the faunal composition and density within relatively small changes of time or distance. If one does not lose sight of these facts, it is possible to list various organisms that are representative of seagrass meadows over large distances.

The most obvious invertebrates of many of the seagrass beds of south Florida are the large epibenthic organisms (Figure 16). The queen conch (*Strombus gigas*) feeds primarily on epiphytes it scrapes from turtle grass blades, while the Bahamian starfish (*Oreaster reticulata*) and the gastropods *Fasciolaria tulipa* and *Pleuroploca gigantea* prey largely on infauna. Numerous sea urchins, such as *Lytechinus variegatus* and *Tripneustes ventricosus*, are found throughout the beds. Juveniles of the long-spined urchin *Diadema antillarum* are common, but the adults seek the shelter of rocky ledges or coral reefs. The deposit-feeding holothurians *Actinopyga agassizi* and *Holothuria floridana* may be found on the surface, while the large sea-hare, the nudibranch *Aplysia dactylomela*, may be found gracefully gliding over the grass canopy. At night pink shrimp (*Penaeus duorarum*) and spiny lobster (*Panulirus argus*) may be seen foraging in the seagrass along with the predatory *Octopus briareus*.

On shallow turtle grass flats the corals *Manicinia areolata* and *Porites furcata* are common, while in somewhat deeper waters sponges such as *Ircinea*, *Tethya*, and *Spongia* may be found.

The infauna can be diverse, but are not visually obvious. The rigid pen shell (*Atrina rigida*) is a common filter-feeder in many grass beds, along with numerous bivalve molluscs such as *Chione cancellata*, *Codakia orbicularis*, *Tellina radiata*, *Lucina pennsylvanica*, and *Laevicardium laevigatum*. A variety of annelid worms are in the infauna, notably *Arenicola cristata*, *Onuphis magna*, *Terebellides stroemi*, and *Eunice longicerrata*.

The abundance and diversity of epiphytic animals on seagrass blades are dramatic evidence of the effect the seagrass has on increasing bottom surface area and providing a substrate for attachment (Figure 17). The most prominent of these epifaunal organisms in south Florida are the gastropods. *Cerithium mascarum* and *C. eburnum*, *Anachis* sp., *Astrea* spp., *Modulus modulus*, *Mitrella lunata*, and *Bittium varium* are characteristic in turtle grass and shoal grass habitats throughout south Florida, as is the attached bivalve *Cardita floridana*.

Small crustaceans are also common in seagrass beds where they live in tubes attached to the leaf surface, move freely along the blades, or swim freely between the blades, the sediment surface, or the water column above the blades. Common amphipods are *Cymadusa compta*, *Gammarus mucronatus*, *Melita nitida*, and *Grandidierella bonnieroides*, while the caridean shrimps *Palaemonetes pugio*, *P. vulgasis*, and *P. intermedius*, *Periclimenes longicaudatus*, and *P. americanus*, *Thorfloridanus*, *Tozeuma carolinense*, *Hippolyte pleuracantha*, *Alpheus normanni*, and *A. heterochaelis* are abundant within the grass beds. Hermit crabs of the genus *Pagurus* are numerous and at night crawl up the blades to graze on epiphytic material. When they reach the end of the blades, they simply crawl off the end, fall to the sediment, scuttle to another blade, and repeat the process.

Structure and Function

The structure of the grass carpet with its calm water and shaded microhabitats provides living space for a rich epifauna of both mobile and sessile organisms (Harlin 1980). It is these organisms which are of greatest importance to higher consumers within the grass bed, especially the fishes. When relatively small quantitative samples are used in estimating population sizes, gastropods, amphipods, and polychaetes are typically most numerous, while isopods can be important (Nagle 1968; Carter et al. 1973; Marsh 1973; Kikuchi 1974; Brook 1975, 1977, 1978). In a Card Sound turtle grass bed, Brook (1975, 1977) estimated that amphipods represented 62.2% of all crustaceans. When the trawl is employed as a sampling device, decapods, including penaeid and caridean shrimp and true crabs, as well as gastropods, are generally most abundant in invertebrate collections (Thorhaug and Roessler 1977; Yokel 1975a, 1975b;

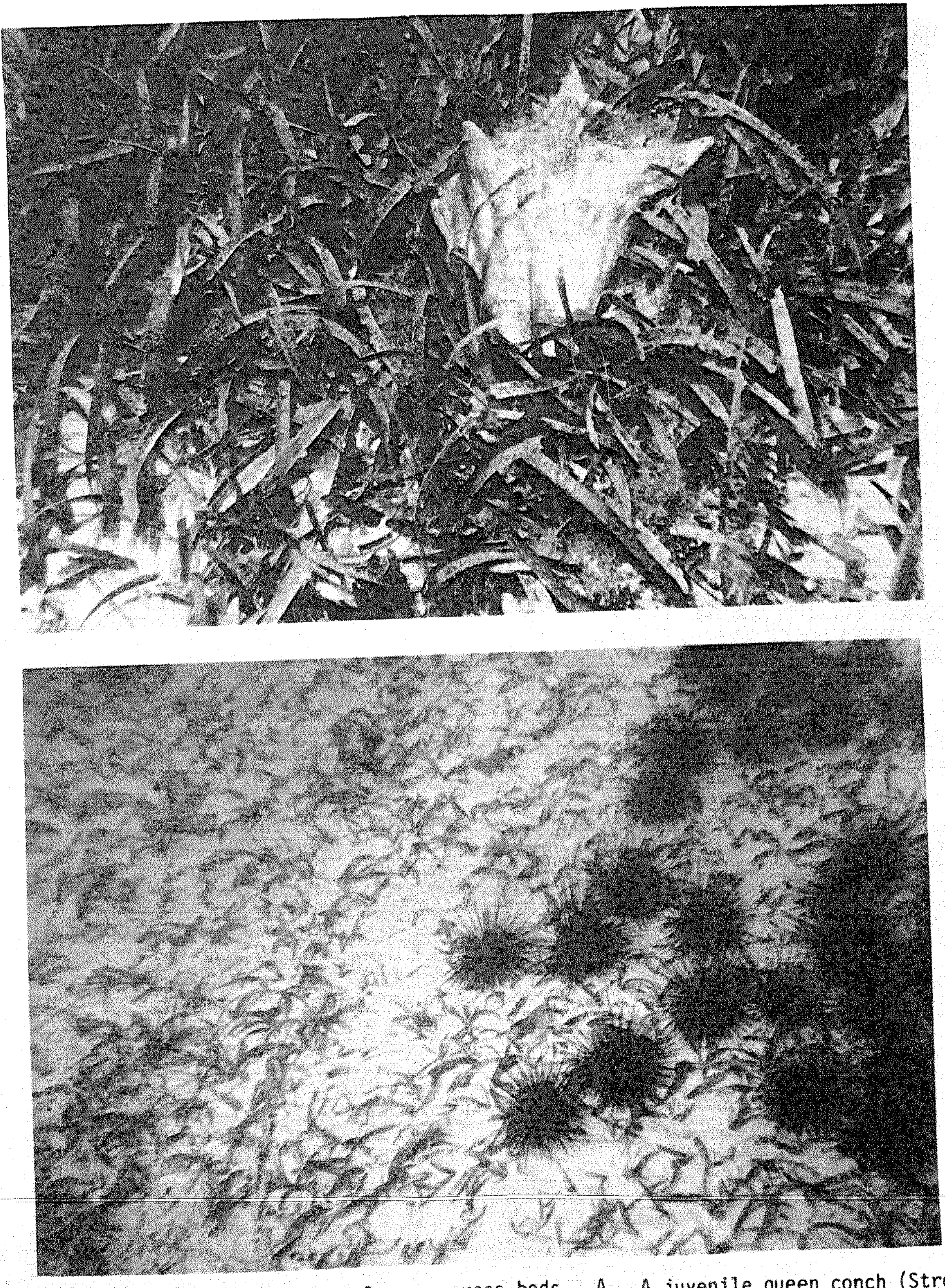


Figure 16. Large invertebrates from seagrass beds. A. A juvenile queen conch (*Strombus gigas*) in a *Thalassia* bed. (Photo by M.B. Robblee). B. A group of the long-spined Caribbean urchin, *Diadema antillarum*, feeding in a *Thalassia* bed near a patch reef.

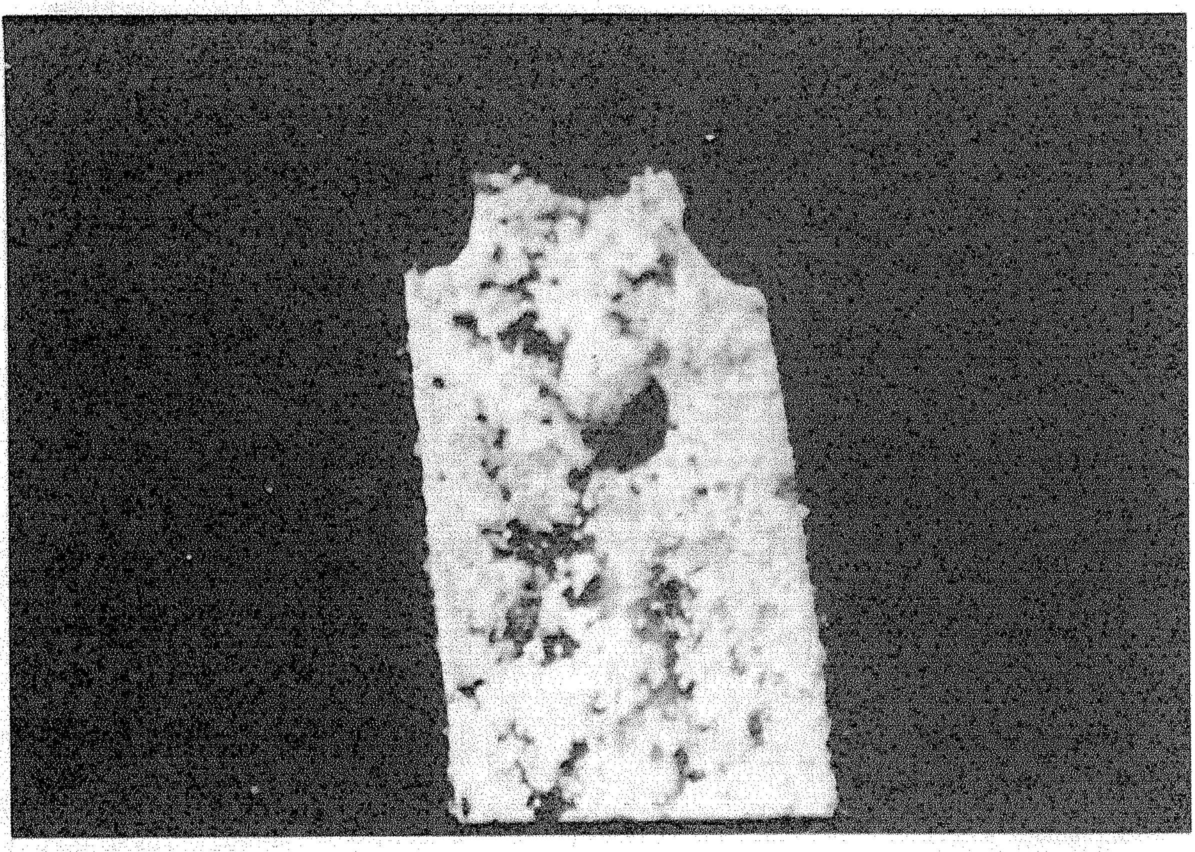


Figure 17. Snail grazing on the tip of an encrusted *Thalassia* leaf. Small snails and hermit crabs are frequently seen grazing the heavily epiphytized portions of seagrass leaves.

Roessler and Tabb 1974; Bader and Roessler 1971; Tabb et al. 1962; Tabb and Manning 1961). Faunal differences among studies reflect sampling gear selectivity, but typically penaeid and caridean shrimp are less numerous than the smaller macrocrustaceans (i.e. amphipods, isopods), yet represent a larger biomass within the bed. For example, data from Brook (1977) for a Card Sound turtle grass grass bed indicated 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. Demonstrating the importance of the physical structure of the grass carpet, Yokel (1975a) reported that the standing crop of crustaceans (estimated using a trawl) was 3.9 times larger in mixed seagrass and algal flats than on nearby unvegetated bottoms (see Figure 18).

It is a long standing assumption that the grass carpet represents protection from predation for the animals living in it. The dense seagrass blades and rhizomes associated with the grass carpet provide cover for invertebrates and small fishes while also interfering with the feeding efficiency of their potential predators. 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 (Heck and Orth 1980). Selection appears to be based on the form or structural characteristics of the seagrass (Stoner 1980a).

It is speculated from experimental work using shapes that the caridean shrimp, *Hippolyte californiensis*, locates its host plant, *Zostera marina*, visually

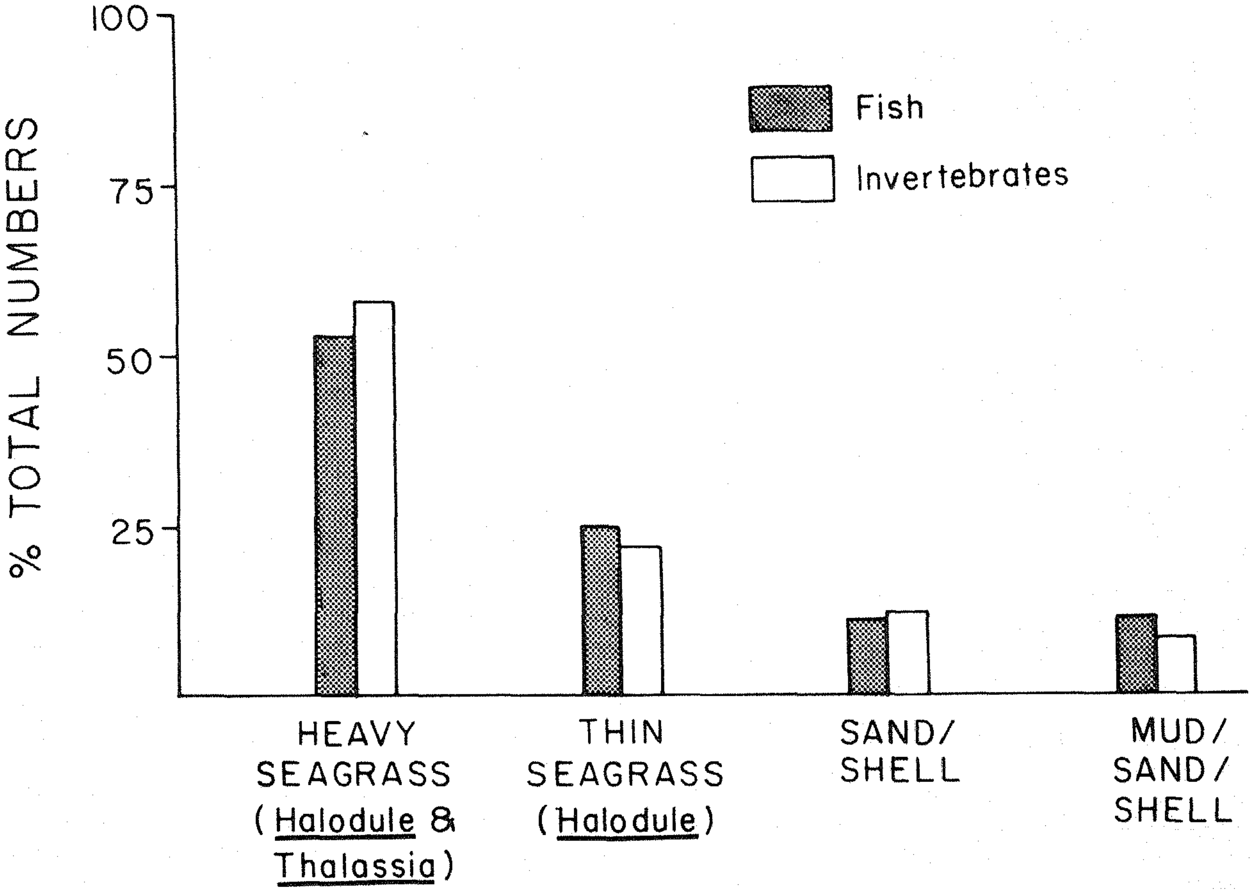


Figure 18. Relative abundance of fishes and invertebrates over seagrass beds and adjacent habitats (after Yokel 1975a).

by discriminating on the basis of form (Barry 1974). Stoner (1980a) demonstrated 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 (turtle grass, manatee grass, and shoal grass) were offered in preference tests, shoal grass was chosen. When equal surface areas were offered no preferences were observed, indicating that surface area was the grass habitat characteristic chosen.

5.3 FISHES

Composition

Seagrass meadows have traditionally been known to be inhabited by diverse and abundant fish faunas. Often the grass bed serves as a nursery or feeding ground for fish species that will ultimately be of commercial or sport fishery value. The classification created by Kikuchi (1961, 1962, 1966) was largely inspired by the fish community found in Japanese Zostera beds and has effectively emphasized the diverse character of seagrass fish and major invertebrates, while also serving to underscore the important ecological functions of seagrass meadows within the estuary as nursery and feeding grounds.

Permanently resident fishes are typically small, less mobile, more cryptic species that spend their entire life within the grass bed. Few, if any, of these species are of direct commercial value but are often characteristic of the seagrass habitat. The emerald clingfish (Acyrtops beryllina) is a tiny epiphytic species found only living on turtle grass blades. In south Florida, members of families Syngnathidae, Gobiidae, and Clinidae may be included in this group.

The pipefishes, *Syngnathus scovilli*, *S. floridae*, *S. louisianae*, and *Micrognatus crinigerus*, as well as the seahorses *Hippocampus zosterae* and *H. erectus* are abundant in seagrass throughout south Florida. The gobies and clinids are diverse groups and well represented in seagrass fish assemblages of southern Florida. The most abundant goby is *Gobisoma robustum*. The clinids appear to be limited to the clearer waters of the Florida Keys and Florida Bay, where *Paraclinus fasciatus* and *P. marmoratus* are most abundant.

Other resident fish species are characteristic of seagrass habitat. The inshore lizardfish (*Synodus foetens*) is a common epibenthic fish predator. The small grass bed parrotfishes -- *Sparisoma rubripinne*, *S. radians*, and *S. chrysopterum* -- are found in the clearer waters of the Florida Keys where they graze directly on seagrass. Eels, including members of families Moringuidae, Xenocongridae, Muraenidae and Ophichtidae (Robblee and Zieman, in preparation), are diverse and abundant in grass beds of St. Croix, U.S. Virgin Islands. These secretive fishes are typically overlooked in fish community surveys. In the grass beds of south Florida, the Ophochtid eels *Myrichthys acuminatus*, the sharptail eel, and *M. oculatus*, the goldspotted eel, can commonly be observed moving through the grass during the day while young moray eels, *Gymnothorax* spp., are not uncommon at night foraging in grass beds for molluscs.

Seasonal residents are animals that spend their juvenile or subadult stages or their spawning season in the grass bed. Sciaenids, sparids, pomadasyids, lutjanids, and gerrids are abundant seasonal residents in south Florida's seagrass communities. Seasonal residents use the seagrass meadow largely as a nursery ground.

At least eight sciaenid species have been found over grass in the variable salinity, high turbidity waters of southwestern Florida's estuaries and coastal lagoons. Not all of these fishes occur abundantly, and only the spotted seatrout (*Cynoscion nebulosus*), the spot (*Leiostomus xanthurus*), and the silver perch (*Bairdiella chrysura*) occur commonly over grass. The pigfish (*Orthopristis chrysoptera*) is the abundant grunt (Pomadasyidae) of muddy bottoms and turbid water associated with grass in Florida's variable salinity regions (Tabb and Manning 1961; Tabb et al. 1962; Yokel 1975a, 1975b; Weinstein et al. 1977; Weinstein and Heck 1979) and is at best rare in the Florida Keys. Other grunts occur over grass only rarely in southwestern Florida and Florida Bay and include *Anisotrenus virginicus*, *Haemulon scirus*, and *H. aurolineatum*. *Lagodon rhomboides*, the pinfish, was the most abundant fish collected in these waters and has demonstrated a strong affinity for seagrass (Gunter 1945; Caldwell 1957; Yokel 1975a, 1975b). *Eucinostomus gula* and *E. argenteus* are seasonally abundant gerrids also most common over grass.

With the exception of the pigfish, the pomadasyids already mentioned are joined by *H. flavolineatum*, *H. parri*, and *H. carbonarium* in the clearer waters of the Florida Keys. Snappers and grunts are more diverse in the clearer waters of the Florida Keys. *Lutjanus griseus* and *L. syngaris*, which are common throughout south Florida, are joined by the schoolmaster (*L. apodus*) the mutton snapper (*L. analis*) the dog snapper (*L. jocu*), and the yellowtail snapper (*Ocyurus chrysurus*). Thayer et al. (1978b) list several seasonally resident fishes that are prominent fishes of sport or commercial fishery value and include the sea bream (*Archosargus rhomboides*), the sheepshead (*A. probatocephalus*), the gap grouper (*Mycteroperca microlepis*), and the redfish (*Sciaenops ocellata*).

The subtropical seagrass system of south Florida appears to differ significantly from more temperate beds by the presence of relatively large numbers of prominent coral reef fishes over grass at night when the bed is located in the vicinity of coral reefs. Fishes from families Pomadasyidae, Lutjanidae, and Holocentridae find shelter on the reef during the day and move into adjacent grass beds at night to feed. This situation is typical of Caribbean seagrass meadows. All of the grunts and snappers mentioned above except *O. chrysurus*, when of appropriate size, will live diurnally on the reef and feed in the grass bed at night. Diel visitors use the grass bed primarily as a feeding ground.

Occasional migrants, as the name implies, are only present infrequently and unpredictably. Representatives include large carnivores of offshore or oceanic origin such as carangids and scrombrids. Organisms of this type represent only a small proportion of the biomass present, but may be important in determining fish community structure.

This system (Kikuchi 1961, 1962, 1966) aids in classifying the fish fauna, but is not exact. For example, the king mackeral could possibly be found over the back reef grass beds much of the year, but during winter large schools move through the region. Thus this fish could be classified as a seasonal resident and as an occasional migrant.

Structure and Function

Because fishes that occupy grass beds are important to commercial fishermen and because the seagrass habitat is apparently important in the life histories of these fishes, it is surprising that relatively little is known concerning the distribution of fishes within the grass bed itself.

Densities of fishes are typically greater in grass bed habitat within south Florida's estuaries and coastal lagoons than in adjacent habitats (Reid 1954; Tabb et al. 1962; Roessler 1965; Yokel 1975a, 1975b; Weinstein et al. 1977). Yokel (1975a, 1975b), using a trawl, reported greatest densities of fishes in seagrass meadows as opposed to bare sand and shell bottoms in the Ten Thousand Island region of south Florida. In the Rookery Bay Sanctuary, 3.5 times as many fishes were captured in grass as in other habitats (Yokel 1975a). Similar results have been reported in Biscayne Bay (Roessler 1965; Roessler et al. 1974; Thorhaug and Roessler 1977). As is true for invertebrates, often highest densities and greatest species richness of fishes are associated with the red algal complex (Roessler et al. 1974; Thorhaug and Roessler 1977), although this is not necessarily an extensive habitat. Clark (1970) in Whitewater Bay observed high densities of fishes associated with patchy shoal grass and the calcareous green alga, Udotea conglutinata.

Although it is well documented that fishes are abundant over grass within south Florida's estuaries and coastal lagoons (Figure 19), knowledge of within-habitat distributional patterns relative to grass bed characteristics (i.e., structural complexity, prey densities) is poor at best. It would seem more often than not that patterns attributable to invertebrates are assumed in principle to also apply to fishes. Fishes are generally larger and more mobile than invertebrates and the extrapolation may not be valid. In Tague Bay, St. Croix, U.S. Virgin Islands, abundance of coral reef fishes feeding over grass at night exhibited a distributional pattern strongly correlated with habitat complexity as measured by plant biomass and bottom topography (Robblee, in prep.). Fish predators may be responding to grass bed characteristics other than just the grass carpet.

Some fish commonly utilize invertebrate fauna found among seagrass (Carr and Adams 1973; Brook 1975, 1977; Adams 1976b; Robertson and Howard 1978). The results of experimental manipulations of predation by exclosure caging have attempted to evaluate the effect predation has in structuring invertebrate populations in seagrass beds. Exclusion of fish predators usually causes increases in species abundance and density (Orth 1977b; Young et al. 1976; Young and Young 1977). If expected increases fail to appear, the abundance of decapod predators probably increased sufficiently to reduce the abundance and composition of the other invertebrates (Young and Young 1977).

Plant biomass and invertebrate abundance relationships observed in Panamanian grass beds are governed largely by predation mediated by the structural complexity of the grasses (Heck and Wetstone 1977). Numbers of macrobenthic animals increased noticeably in the fall with emigration of fishes from grass beds in Apalachee Bay (Stoner 1980b). Amphipods consumed most frequently by the pinfish were epifaunal (Stoner 1979). In studies by Nelson (1979a) infaunal amphipods were 1.3 times more abundant than epifaunal tube-dwelling amphipods and 4 times more abundant than free-living epifaunal amphipods during the seasonal influx of pinfish. These results reiterate the role predators play

Figure 19. Small grouper (Serranidae) foraging in seagrass bed.

in controlling abundances and species composition within sea grass beds (Nelson 1979a; Stoner 1979).

Little is known about how fishes respond to the structural complexity of the grass canopy. Noting the size distribution of fishes typically inhabiting seagrass beds, Ogden and Zieman (1977) speculated 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 (8 inches) 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 to 40 cm or 8 to 16 inches) are probably excluded from the grass bed by occasional large predators. Mid-size fishes are apparently restricted to sheltered areas by day and may move into the beds at night when predation is less intense (Ogden and Zieman 1977; Ogden 1980). The size of the individuals in these groups is a function of the length and density of the grass beds. In Florida, where the seagrasses are typically larger and denser, the grass beds offer shelter for much larger fish than in St. Croix, where the study of Ogden and Zieman (1977) was done.

Heck and Orth (1980a) hypothesized that abundance and diversity of fishes should increase with increasing structural complexity until the feeding efficiency of the fishes is reduced because of interference with the grass blades or because conditions within the grass canopy become unfavorable (i.e., anoxic conditions at night). At this point densities should drop off. Evidence indicates that feeding efficiency does decline with increasing structural complexity.

The pinfish's predatory efficiency on amphipods decreases with increasing density of Zostera marina blades (Nelson 1979a). Coen (1979) found in single-species experiments (one shrimp species at a time) that with increasing cover of red algae (Digenia simplex, Laurencia spp., Gracilaria spp. and others) the pinfish's foraging efficiency on Palaemon floridanum and Palaemonetes vulgaris was reduced. The killifish (Fundulus heteroclitus) fed less efficiently on the grass shrimp (Palaemonetes pugio) in areas of densest artificial seagrass. Virtually nothing is known about the relation of typical grass bed fishes and their predators; research on this topic would be fruitful.

5.4 REPTILES

Although there are several species of sea turtles in the Gulf of Mexico and Caribbean, the green sea turtle (Chelonia mydas) is the only herbivorous sea turtle (Figure 20). In the Caribbean, the main food of the green turtles are sea grasses and the preferred food is Thalassia, hence the name turtle grass (see section 6.2).

Green turtles were formerly abundant throughout the region, but were hunted extensively. Concern over the reduced populations of green turtles dates back to the previous century (Munroe 1897). Although limited nesting occurs on the small beaches of extreme south Florida, the region has almost certainly been primarily a feeding rather than a nesting site. Turtle and manatee feeding behavior are described in Chapter 6.

The American crocodile (Crocodylus acutus) occurs in the shallow water of Florida Bay and the northern Keys.

Figure 20. Seagrass bed following grazing by green sea turtle. Note the short, evenly clipped blades. The scraping on the Thalassia blade in the center is caused by the small emerald green snail, Smaragdia viridis.

Although crocodiles undoubtedly feed in shallow grass beds, little is known of their utilization of this habitat.

5.5 Birds

The seagrass beds of south Florida are used heavily by large numbers of birds, especially the wading birds, as feeding grounds. This heavy utilization is possible because of the relatively high proportion of very shallow grass bed habitat. There are few studies of the utilization of seagrass beds by birds, although there are extensive lists of birds using temperate seagrasses and aquatic plants (McRoy and Helfferich 1980). Birds known to use the seagrass habitat of south Florida and their modes of feeding are listed in Table 9.

Three common methods of feeding in birds are wading, swimming, and plunging from some distance in the air to sieze prey. The most common of the swimming birds is the double-crested cormorant 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 osprey and the bald eagle sieze prey on the surface of the water with their claws, while the brown pelican pluges from some distance in the air to engulf fishes with its pouch. The value of the seagrass meadows to these birds is that prey are more concentrated in the grass bed than in the surrounding habitat, thus providing an abundant food source.

The extensive shallow grass flats are excellent foraging grounds for the larger wading birds (Figure 21). The great white heron is common on the shallow turtle grass flats on the gulf side of the lower Keys. The great blue heron is common

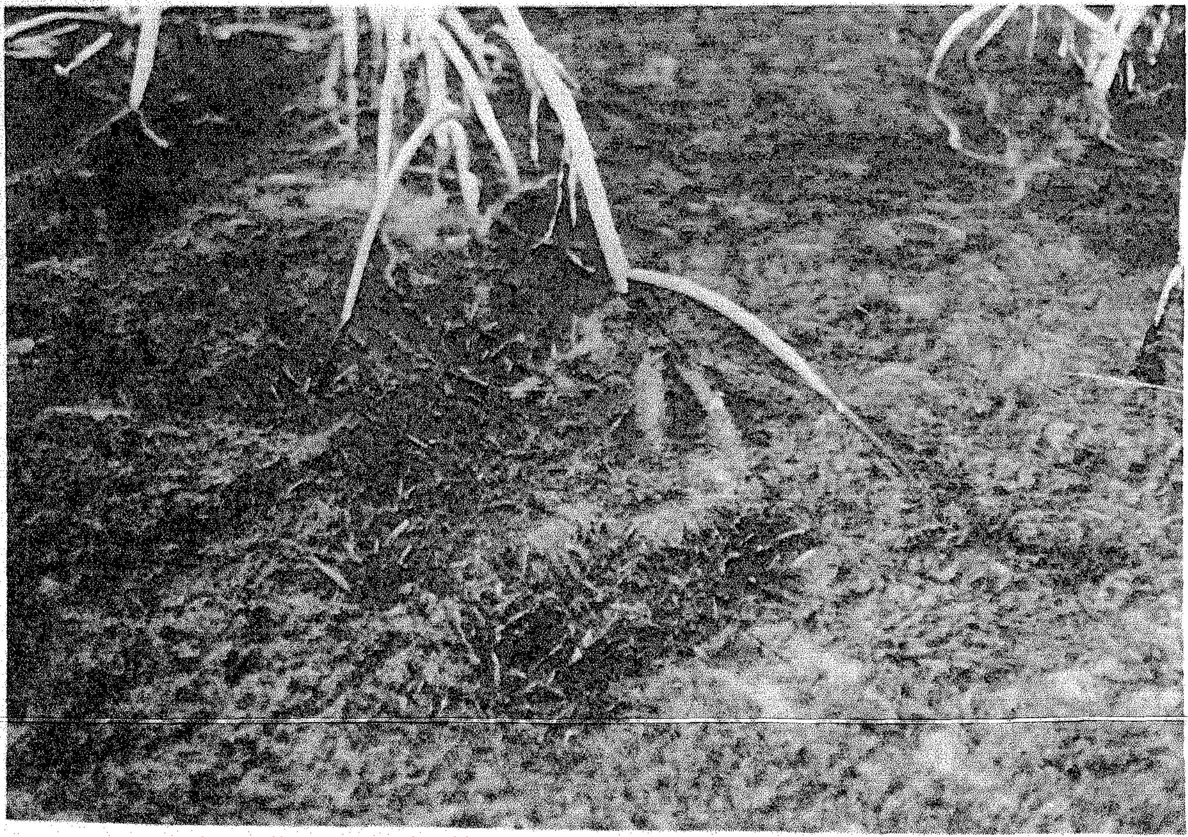


Figure 21. Shallow seagrasses adjacent to red mangrove roots. This is a common feeding area of small and medium sized wading birds.

Table 9. Birds that use seagrass flats in south Florida (data provided by James A. Kushlan, Evergaldes National Park).

Common name	Species name	Preferred feeding tide
Waders-primary		
Great blue heron	*Ardea herodias*	Low
Great white heron	*A. herodias*	Low
Great egret	*Casmerodius albus*	Low
Reddish egret	*Egretta rufescens*	Low
Waders-secondary		
Louisiana heron	*E. tricolor*	Low
Little blue heron	*E. caerulea*	Low
Roseate spoonbill	*Ajaia ajaja*	Low
Willet	*Catoptrophorus semipalmatus*	Low
Swimmers		
Double-crested cormorant	*Phalacrocorax auritus*	High
White pelican (winter only)	*Pelecanus erythrorhynchos*	High
Crested grebe (winter)		
Red-breasted merganser (winter)	*Mergus serrator*	
Flyers-plungers		
Osprey	*Pandion haliaetus*	High
Bald eagle	*Haliaeetus leucocephalus*	High
Brown pelican	*Pelecanus occidentalis*	High

throughout south Florida, but is sometimes found in greatest numbers on the shallow grass flats in Florida Bay. Small egrets and herons probably all feed occasionally on the shallowest, exposed flats, but are generally limited by water too deep for them to wade. The ecology of wading birds and their feeding behavior have been reviewed by Kushlan (1976, 1978). Odum et al. (1981) reviewed the extensive avifauna of the mangrove regions of southern Florida.

5.6 MAMMALS

Some marine mammals also feed in seagrass beds. Odell (1979) reported that although 27 species of marine mammals were either sighted alive or reported stranded on beaches in south Florida in recent years, only 2 were common: the manatee (*Trichechus manatus*) and the bottlenose dolphin (*Tursiops truncatus*).

Although the range of the manatee was formerly much larger, now it seems largely confined to the protected regions of Everglades National Park. Odell (1976) surveyed the manatee distribution in the Everglades region. Of a total of 302 herds with 772 individuals, 46% were sighted in Whitewater Bay, 20% in the Gulf of Mexico, 23% in inland waters, and only 1% in Florida Bay. A later study (Odell 1979) reported no manatee sightings in Biscayne Bay.

The bottlenose dolphin is the most common marine mammal in south Florida waters and feeds over grass flats, even those less than 1 m (3.3 ft) deep. In the Everglades National Park region, Odell (1976) reported that 36% of the animals seen were in the Gulf of Mexico, 33% were in Whitewater Bay, 20% were in inland waters, and 11% in Florida Bay. The relatively low numbers in Florida Bay were probably due to the extreme shallowness which would preclude swimming for this large mammal. Bottlenose dolphin are opportunistic feeders, primarily on fish. Their diets are not well known, but they consume large quantities of mullet in Florida Bay.

By comparison with the Everglades region, Biscayne Bay had a low dolphin density. Odell (1979) found that in aerial surveys of the two regions, 11.4 animals were sighed per flight hour in the Everglades area, while only 1.25 animals per hour were seen in Biscayne Bay.

CHAPTER 6

TROPHIC RELATIONSHIPS IN SEAGRASS SYSTEMS

6.1 GENERAL TROPHIC STRUCTURE

Seagrasses and associated epiphytes provide food for trophically higher organisms by (1) direct herbivory, (2) detrital food webs within grass beds and (3) exported material that is consumed in other systems either as macroplant material or as detritus (Figure 22). Classically the detrital food web within the grass beds has been considered the primary pathway, and in most cases is probably the only significant trophic pathway. During the past few years, new information has been gathered on the relative role of the other modes of utilization. The picture emerging is that in many locations both the direct utilization pathway and the export of material may be of far more importance than previously suspected; however, it still appears that the detrital food web is the primary pathway of trophic energy transfer (Zieman et al. 1979; Kikuchi 1980; Ogden 1980).

Studies have attempted to measure the proportion of daily seagrass production which is directly grazed, added to the litter layer, or exported. Greenway (1976) in Kingston Harbor, Jamaica, estimated that of 42 $g/m^2/wk$ production of turtle grass, 0.3% was consumed by the small bucktooth parrotfish, Sparisoma radians; 48.1% was consumed by the urchin, Lytechinus ariegatus; and 42.1% deposited on the bottom and available to detritivores. The rest of the production was exported from the system. This study may

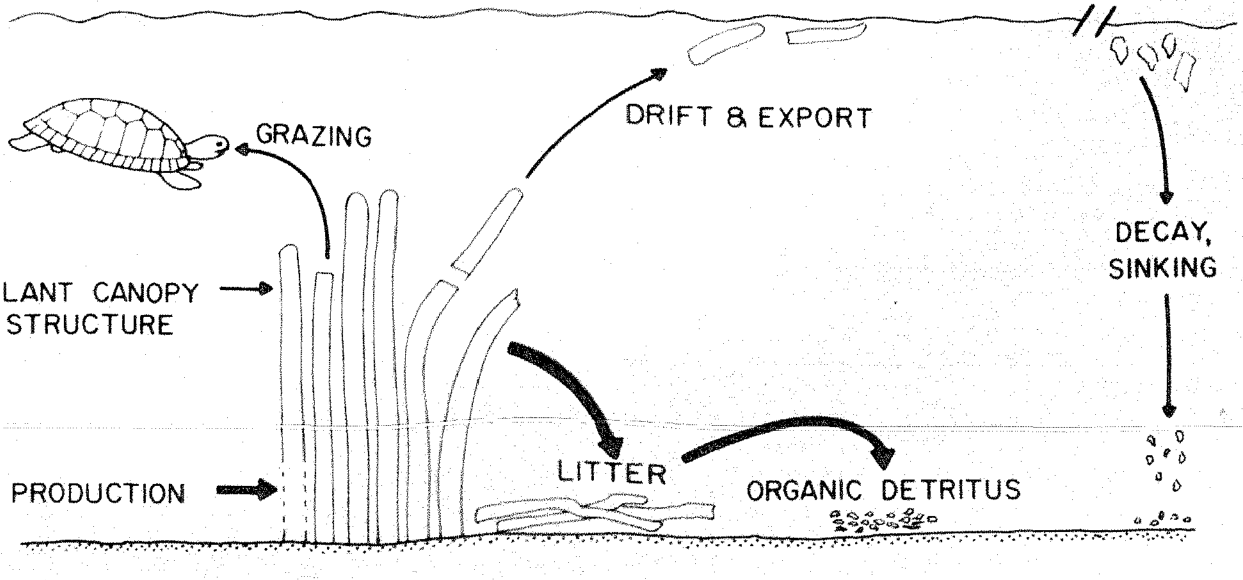


Figure 22. Principal energetic pathways in seagrass beds.

overemphasize the quantity of seagrass material entering the grazing food chain since urchins are not typically found at densities of 20 urchins/m^2 as was the case in Kingston Harbor (Ogden 1980). In St. Croix, it has been estimated that typically between 5% and 10% of daily production of turtle grass is directly consumed, primarily by Sparisoma radians and secondarily by the urchins Diadema antillarum and Tripneustes ventricosus. Averaged over the day, turtle grass production was 2.7 g dw/m^2/day of which only about 1% was exported, while 60% to 100% of the 0.3 g dw/m^2/day production of manatee grass was exported (Zieman et al. 1979). From these figures it is conservatively estimated that about 70% of the daily production of seagrasses was available to the detrital system.

Many of the small organisms in grass beds use algal epiphytes and detritus as their food sources. The gastropods are the most prominent organisms feeding on epiphytic algae in seagrass beds. 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 the utilization of this combination of microalgae and detritus represents one of the major energy transfer pathways to higher organisms.

Notable by their absence are the large flocks of ducks and related waterfowl found on temperate Zostera beds and especially the freshwater Ruppia beds (Jacobs et al. 1981). McRoy and Helfferich (1980) list 43 bird species that consume seagrass primarily in the temperate zone. Relatively few species of birds ingest seagrass species of the tropics or forage for prey in the sediments of shallow grass beds.

Detritus undoubtedly serves as the base of a major pathway of energy flow in seagrass meadows. A significant proportion of net production in the seagrass bed results in detritus either by dying in place and being broken down over a period of months by bacteria, fungi and other organisms (Robertson and Mann 1980) or by being consumed by large herbivores, fragmented, and returned as feces (Ogden 1980). In Biscayne Bay, turtle grass formed the most important constituent of the detritus present (87.1%), while other portions included 2.1% other seagrasses, 4.6% algae, 0.4% animal remains, 3.3% mangrove leaves and 2.5% terrestrial material (Fenchel 1970). The microbial community living in the detritus collected consisted mainly of bacteria, small zooflagellates, diatoms, unicellular algae, and ciliates. It is these types of organisms which form the major source of nutrition for detrital feeders. Bloom et al. (1972), Santos and Simon (1974), and Young and Young (1977) provided species lists annotated with feeding habits for molluscs and polychaetes, many of which ingest detritus.

Typically penaeid and caridean shrimp are considered to be omnivores. The pink shrimp (Penaeus duorarum), in addition to organic detritus and sand, ingests polychaetes, nematodes, caridean shrimp, mysids, copepods, isopods, amphipods, ostracods, molluscs and foraminiferans (Eldred 1958; Eldred et al. 1961). These consumers strip the bacteria and other organisms from the detritus, and the fecal pellets are subsequently reingested following recolonization (Fenchel 1970). Some fishes, notably the mullet (Mugil cephalus), are detrital feeders (Odum 1970). Several large invertebrates such as the gastropod Strombus gigas (Randall 1964) and the asteroid Oreaster reticulatus (Scheibling 1980) take detritus as a part of their food. To emphasize the importance of detritus to higher trophic levels within the grass, the work of Carr and Adams (1973) should be noted. They found that detritus consumers were of major importance in at least one feeding stage of 15 out of 21 species of juvenile marine fishes studied.

It is well documented that fishes feed while occupying grass beds (Carr and Adams 1973; Adams 1976b; Brook 1975, 1977; Robertson and Howard 1978), as opposed to simply using them for shelter. Typically, seagrass-associated fishes are small, generalist feeders, tending to prey upon epifaunal organisms, primarily crustaceans. Infaunal animals are under used in proportion to their abundance as few fishes resident in the grass beds feed on them or on other fishes (Kikuchi 1980).

Numerous fishes ingest some plant material, while relatively few of these species are strict herbivores; exceptions are the Scarids and Acanthurids already mentioned. Most plant and detrital material is probably taken incidentally while feeding on other organisms. Orthopristis chrysoptera and Lagodon rhomboides are two very abundant grass bed fishes in south Florida and apparently during some feeding stages are omnivores, ingesting substantial amounts of epiphytes, detritus and seagrass (Carr and Adams 1973; Adams 1976a, 1976b; Kinch 1979). Other omnivores include some filefishes, porgies, blennies, and gobies.

Gastropods are fed upon by a variety of fishes including wrasses, porcupine fishes, eagle rays, and the permit Trachnotus folcatus. Randall (1967) listed 71 species of fishes that feed on gastropods, 25 ingesting 10% or more by volume. Most species crush the shell while ingesting, but a few swallow the gastropod whole. The white grunt (Haemulon plumeri) appears to snap off the extended head of Cerithium, ignoring the shell. The southern stingray (Dasyatus americana) has been observed turning over the queen conch (Strombus gigas) and wrenching off the conch's extended foot with its jaws as the conch tries to right itself (Randal 1964). The spiny lobster (Panulirus argus) is an active predator on seagrass molluscs.

The southern stingray and the spotted eagle ray (Aetobatis narinari) are two of a relatively few number of fishes that feed on infauna within the grass bed. These fishes excavate the sediments. Other similar feeders are wrasses, goatfishes, and mojarras. Adult yellowtail snapper (Oryhurus chrysurus) have been observed foraging in back reef seagrass sediments (Zieman, personal observation). That the infauna is not heavily preyed upon is typical of seagrass beds (Kikuchi 1974, 1980). Apparently the protection from predation afforded the infauna of grass beds is great enough that few fishes specialize on infauna when feeding (Orth 1977b). The blue crab (Callinectes sapidus) has been observed to shift its feeding from Zostera infauna to epibiota and thus, because of the protective rhizome layer and the accessibility of the epifauna, the impact of blue crab predation may be greatest on epibenthic fauna.

The majority of fishes within the grass bed feeds on small, mobile epifauna including copepods, cumaceans, amphipods, isopods, and shrimp. Fishes feeding in this manner include all the seasonally resident fishes of the south Florida grass beds, such as the Sciaenids, Pomadasyids, Lutjanids, and Gerrids, as well as many of the permanent residents, like Syngnathids, and Clinids. As such, they are deriving much of their nutrition indirectly from seagrass epiphytes and the detrital community present in the grass bed rather than the grasses themselves. Many of these fishes, as adults, will feed on other fishes; however, as juvenile residents in the grass beds, their small size limits them to eating epifauna.

Important piscivores are present in south Florida grass flats. These include the lemon shark (Negaprion brevirostires) and the bonnethead shark (Sphyrna tiburo), the tarpon (Megalops atlantica), 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).

6.2 DIRECT HERBIVORY

Caribbean grass beds may be unique for the numbers and variety of direct consumers of blade tissue (Ogden 1980) as relatively few species ingest green seagrass in significant quantities (Table 10). Prominent herbivores include urchins, conch, fishes, as well as the green turtle, Chelonia mydas, and Caribbean manatee (Trichechus manatus). The elucidation of the role of direct herbivory as a pathway of energy flow in seagrasses has been slow in developing. Until recently, it was assumed that few organisms consumed seagrasses directly, and that herbivory had substantially decreased with the decline of the populations of the green sea turtle. Direct grazing of seagrasses in south Florida is probably of greatest importance in the grass beds of the Florida Keys and outer margin of Florida Bay which are relatively close to coral reefs.

Table 10. Direct consumers of seagrass (adapted from McRoy and Helfferich 1980).

Herbivore scientific name	Common name	Seagrass eaten	Part of seagrass eaten	Seagrass in diet (%)	Location of population	Reference
ANNELIDS						
Arenicola cristata	Lugworm	*Thalassia* *Halodule* *Syringodium*	Detritus	Max. 100	Florida	D'Asaro and Chen 1976
MOLLUSCS						
Strombus gigas	Queen conch	*Thalassia* *Syringodium* *Halodule*	Leaf Leaf Leaf		West Indies	Randall 1964
CRUSTACEANS						
Callinectes sapidus	Blue crab	*Zostera* *Thalassia* *Ruppia*	Leaf Leaf Leaf		U.S. Atlantic Coast Texas	Hay 1904 Pullen 1960
Uca sp.	Fiddler crab	*Thalassia*	Leaf (wrack)		Texas	T. McConnaugher, pers. comm.
ECHINODERMS						
Diadema antillarum	Sea urchin	*Thalassia* *Syringodium*	Leaf Leaf		West Indies	Ogden et al. 1973
Diadema setosum	Sea urchin	*Thalassia*		12	West Indies Zanzibar	Lawrence 1975
Echinometra lacunter	Sea urchin	*Thalassia* *Syringodium* *Halodule*	Leaf Leaf Leaf	10.2 8.9 7.9	Caribbean Alaska Alaska	Abbott et al. 1974
Eucidaris tribuloides	Sea urchin	*Thalassia*	Leaf		Caribbean	McPherson 1964

(continued)

Table 10. Continued.

Herbivore scientific name	Common name	Seagrass eaten	Part of seagrass eaten	Seagrass in diet (%)	Location of population	Reference
ECHINODERMS (continued)						
Lytechinus variegatus	Sea urchin	*Thalassia*	Leaf		Florida	Camp et al. 1973
		Thalassia	Leaf	Max. 100	Jamaica	Greenway 1974
		Thalassia	Leaf		Caribbean	Moore et al. 1963a
		Thalassia	Leaf			Lawrence 1975
		Syringodium	Leaf			
Tripneustes esculentus	Sea urchin	*Thalassia*	Leaf		Florida	Moore et al. 1963b
Smaraydia viridis	Emerald nerite	*Thalassia*	Leaf		Florida West Indies	J. Zieman and R. Zieman per. obs.
Tripneustes ventricosus	Sea urchin	*Thalassia*	Leaf	Max. 100	Florida	Lawerence 1975
			VERTEBRATES			
FISHES						
Acanthostracion quadricornis	Cowfish	*Thalassia*	Leaf	3	West Indies	Randall 1967
Acanthurus bahianus	Ocean surgeon	*Syringodium* *Halophila*	Leaf	8.2	West Indies	Randall 1967
		Thalassia *Syringodium*	Leaf	40-80 (T.)		Randall 1965
Acanthurus chirurgus	Doctor fish	*Thalassia* *Syringodium*	Leaf	5.7	West Indies	Randall 1965
		Thalassia *Syringodium*	Leaf	25	West Indies	Randall 1967
Acanthurus coeruleus	Blue tang	*Halophila* *Syringodium*	Leaf	6.8	West Indies	Randall 1967
Alutera schoepfi	Orange filefish	*Syringodium* *Thalassia*	Leaf	67	West Indies	Randall 1967

(continued)

Table 10. Continued.

Herbivore scientific name	Common name	Seagrass eaten	Part of seagrass eaten	Seagrass in diet (%)	Location of population	Reference
FISHES (continued)						
Alutera scripta	Scrawled filefish	*Syringodium* *Thalassia*	Leaf	9	West Indies	Randall 1967
Archosargus rhomboidalis	Sea bream	*Thalassia* *Syringodium*	Leaf	44.6	West Indies	Randall 1967
Cantherhines pullus	Orange-spotted filefish	*Thalassia* *Halophila*	Leaf	4.6	West Indies	Randall 1967
Canthigaster rostrata	Sharp-nose puffer	*Syringodium* *Halophila*	Leaf	16.1	West Indies	Randall 1967
Chaetodipterus faber	Spadefish	*Syringodium*	Leaf	2.3	West Indies	Randall 1967
Diapterus plumieri (juvenile)	Striped mojarra	*Thalassia*	Leaf	Max. 33	Puerto Rico	Austin and Austin 1971
Diapterus rhombeus	Sand mojarra	*Thalassia* *Ruppia* *Thalassia* *Ruppia* *Halophila*	Leaf Leaf Leaf Leaf Leaf	Max. 16.7 Max. 32.5	Venezuela Puerto Rico Puerto Rico	Cervigon 1966 Austin 1971 Austin and Austin 1971
Diplodus holbrooki	Spottail pinfish				Florida	Hildebrand 1941
Halichoeres bivittatus	Slippery dick	*Thalassia*	Leaf	5	West Indies	Randall 1967
Harengula humerallis	Red-ear sardine	*Thalassia* *Syringodium*	Leaf	2.5	West Indies	Randall 1967
Hemiramphus brasillensis	Halfbeak, ballyhoo	*Thalassia* *Syringodium*	Leaf	81	West Indies	Randall 1967

(continued)

Table 10. Continued.

Herbivore scientific name	Common name	Seagrass eaten	Part of seagrass eaten	Seagrass in diet (%)	Location Reference population	Reference
FISHES (continued)						
Hyporhamphus hildebrandi	Halfbeak	*Halodule*	Leaf		Texas	Carangelo et al. 1975
Hyporhamphus unifasciatus	Halfbeak	*Thalassia*	Leaf	49	Florida	Carr and Adams 1973
Kyphosus incisor	Paddlefish	*Thalassia*	Leaf		West Indies	Randall 1967
Kyphosus sectatrix	Rudderfish, Bermuda chub	*Syringodium*	Leaf	0.5	West Indies	Randall 1967
Lactophrys bicaudalis	Spotted trunkfish	*Syringodium*	Leaf	8	West Indies	Randall 1967
Lactophrys trigonus	Trunkfish	*Syringodium* *Thalassia*	Leaf	3	West Indies	Randall 1967
Lactophrys triquetar	Smooth trunkfish	*Thalassia*	Leaf	1.3	West Indies	Randall 1967
Lagodon rhomboides	Pinfish	*Halophila* *Ruppia* *Halodule*	Leaf		Gulf of Mexico	Carr and Adams 1973; Darnell 1958; Springer and Woodburn 1960
				41	Florida	Hansen 1969
Melichthys niger	Black durgon	*Syringodium*	Leaf	4.4	West Indies	Randall 1967
Melichthys radula	Trigger fish	*Syringodium*	Leaf		West Indies	Randall 1965
Monocanthus ciliatus	Fringed filefish	*Thalassia*	Leaf	15.4	West Indies	Randall 1967
Monocanthus setifera	Speckled filefish	*Thalassia*	Leaf		West Indies	Greenway 1974

(continued)

Table 10. Continued.

Herbivore scientific name	Common name	Seagrass eaten	Part of seagrass eaten	Seagrass in diet (%)	Location of population	Reference
FISHES (continued)						
Mugil curema	White mullet	*Thalassia*	Leaf		West Indies	Randall 1967
Pogonias chromis	Black drum	*Halodule*	Leaf		Texas	Carangelo et al. 1975
Polydactylus virginicus	Threadfish	*Thalassia* *Ruppia*	Leaf	17	Puerto Rico	Austin and Austin 1971
Pomacanthus arcuatus	Grey angelfish	*Syringodium* *Ruppia*	Leaf	 0.1	West Indies West Indies	Earle 1971 Randall 1967
Pomacanthus paru	French angelfish	*Syringodium* *Halophila*	Leaf	0.1	West Indies	Randall 1967
Pomacentrus fuscus	Dusky damselfish	*Syringodium*	Leaf	1.6	West Indies	Randall 1967
Pomacentrus planifrons	Three-spot damselfish	*Thalassia*	Leaf	3.9	West Indies	Randall 1967
Rhinoptera quadriloba	Cownose ray	*Thalassia* *Halodule*	Leaf		Texas	Carangelo et al. 1974
Scarus coelestinus	Midnight parrotfish	*Thalassia*	Leaf	1.3	West Indies	Randall 1967
Scarus guacamaia	Rainbow parrotfish	*Syringodium* *Syringodium* *Thalassia*	Leaf Leaf	95 8	West Indies West Indies	Randall 1967 Randall 1967
Scarus retula	Queen parrotfish	*Thalassia*	Leaf	3.2	West Indies	Randall 1967

(continued)

Table 10. Continued.

Herbivore scientific name	Common name	Seagrass eaten	Part of seagrass eaten	Seagrass in diet (%)	Location of population	Reference
FISHES (continued)						
Scarus taeniopterus	Painted-tail parrotfish	*Thalassia*	Leaf	17.3	West Indies	Randall 1967
Sparisoma aurofrenatum	Redband parrotfish	*Syringodium*	Leaf	1.3	West Indies	Randall 1967
Sparisoma chrysopterum	Redtail parrotfish	*Thalassia*	Leaf	16.8	West Indies	Randall 1967
Sparisoma rubripinne	Redfin parrotfish	*Thalassia*	Leaf	7	West Indies	Randall 1967
Sparisoma radians	Bucktooth parrotfish	*Thalassia*	Leaf	88	West Indies Jamaica	Randall 1967 Greenway, pers. comm.
Sparisoma viride	Spotlight parrotfish	*Thalassia*	Leaf	2.5	West Indies	Randall 1967
Sphaeroides spenglerii	Banded puffertail	*Halophila* *Thalassia*	Leaf	5.3	West Indies	Randall 1967
Strongylura marina	Atlantic neddlefish	*Ruppia*	Leaf			Darnell 1958
Symphurus plagiusa	Blackcheek tonguefish	*Ruppia* *Halodule*	Leaf tips Leaf tips	19	Puerto Rico	Austin and Austin 1971
REPTILES						
Caretta caretta	Loggerhead turtle		Leaf			Rebel 1974

(continued)

Table 10. Concluded.

Herbivore scientific name	Common name	Seagrass eaten	Part of seagrass eaten	Seagrass in diet (%)	Location of population	Reference
REPTILES (continued)						
Chelonia mydas (adult)	Green sea turtle	*Thalassia* *Enhalus* *Posidonia* *Halodule*	Leaf	Max. 100	Indo-Pacific Red Sea	Bustard 1969 Hirth et al. 1973
					Caribbean	Carr 1954
Eretmochelys imbricata (juvenile)	Hawksbill turtle		Leaf	Max. 100		Rebel 1974
MAMMALS						
Trichechus manatus	Manatee	*Ruppia* *Zostera* (captive) *Syringodium*, *Halodule*, *Thalassia* implicated	Leaf		Florida	Hartman 1971

The herbivory of parrotfish and sea urchins may be important in the back reef areas and in Hawk Channel; but, with the exception of sporadic grazing by passing turtles, herbivory is low or non-existent in the areas to the west of the Florida Keys (J.C. Zieman, personal observation).

Parrotfish typically move off the reef and feed during the day (Randall 1965). *Sparisoma radians*, *S. rubripinne*, and *S. chrysopterum* are known to feed on seagrass and associated algae (Randall 1967). The bucktooth parrotfish (*S. radians*) feeds almost exclusively on turtle grass. Other fishes that are important seagrass consumers are surgeonfishes (*Acanthuridae*) (Randall 1967; Clavijo 1974), the porgies (*Sparidae*) (Randall 1967; Adams 1976b), and the halfbeaks (*Hemiramphidae*).

Fishes in the Caribbean seagrass beds tend to be generalist herbivores, selecting plants in approximate relation to their abundance in the field (Ogden 1976; Ogden and Lobel 1978). Some degree of selectivity is evident, however. *Sparisoma chrysopterum* and *S. radians*, when given a choice, will select seagrass with epiphytes (Lobel and Ogden, personal communication). Seagrasses (turtle grass, manatee grass, and shoal grass) ranked highest in preference over common algal seagrass associates.

Urchins that feed on seagrass include *Eucidaris tribuloides*, *Lytechinus variegatus*, *Diadema antillarum* and *Tripneustes ventricosus* (McPherson 1964, 1968; Randall et al. 1964; Kier and Grant 1965; Moore and McPherson 1964; Prim 1973; Abbott et al. 1974; Ogden et al. 1973; Moore et al. 1963a, 1963b; Greenway 1976). The latter two urchins feed in approximate proportion to food abundance in the area. Where present in seagrass beds, *T. ventricosus* and *D. antillarum* feed on seagrasses with epiphytes exclusively (Ogden 1980). *Lytechinus variegatus* is largely a detrital feeder (Ogden 1980), but has denuded large areas in west Florida (Camp et al. 1973).

The queen conch (*Strombus gigas*), once a common inhabitant of Caribbean seagrass beds, has been dramatically reduced in many areas because of its high food value and ease of capture by man. Conchs are found in a variety of grass beds, from dense turtle grass to sparse manatee grass and *Halophila*. When in turtle grass beds conchs primarily feed by rasping the epiphytes from the leaves as opposed to eating the turtle grass. In sparse grass beds, however, conchs consumed large quantities of manatee grass and *Halophila* (Randall 1964). A maximum of 20% of the stomach contents of conchs at St. John, U.S. Virgin Islands, was comprised of turtle grass. In manatee grass (*Cymodocea*) beds, conchs consumed mostly this seagrass along with some algae. The maximum quantity of seagrass found was 80% *Halophila* from the gut of four conchs from Puerto Rico.

The emerald nerite (*Smaragdia viridis*), a small gastropod, commonly 5 to 8 mm long, can be numerous in turtle grass beds although it is difficult to see because its bright green color matches that of the lower portion of the turtle grass blades. It is a direct consumer of turtle grass where it roams about the lower half of the green blades; the snail removes a furrow about 1 mm wide and half the thickness of the blade with its radula (J.C. Zieman and R.T. Zieman, personal observation).

Most studies (for review, see Lawrence 1975) indicate that the majority of seagrass consumers have no enzymes to digest structural carbohydrates and that, with the exception of turtles and possibly manatees, they do not have a gut flora capable of such digestion. Thus, most macroconsumers of seagrasses depend on the cell contents of seagrasses and the attached epiphytes for food and must have a mechanism for the efficient maceration of the material. The recent work of Weinstein et al. (in press), however, demonstrated that the pinfish was capable of digesting the structural cellulose of detrital matter or green seagrasses. Feeding rates are high for urchins and parrotfishes, while absorption efficiency is around 50% (Moore and McPherson 1965; Lowe 1974; Ogden and Lobel 1978). Assimilation efficiencies for *T. ventricosus* and *L. variegatus* are relatively low, 3.8% and 3.0% respectively (Moore et al. 1963a, 1963b).

The result of macroherbivore grazing within the grass bed can be dramatic (Camp et al. 1973). Of greater overall significance, however, is the fragmentation of living seagrass and production of particulate detritus coincident with feeding. Further, the nature of urchin and parrotfish feeding results in the liberation of living seagrass and its subsequent export from the bed (Greenway 1976; Zieman et al. 1979). Zieman et al. (1979) observed that manatee grass blades floated after detachment, whereas turtle grass tended to sink; the result was that turtle grass was the primary component of the litter layer available for subsequent utilization by detritivores.

Many of the macroconsumers, such as Acanthurids, *S. rubripinne* and *S. chrysopterum* (Randall 1967), ingesting living seagrass take in only small amounts, the majority of their diet consisting of epiphytic algae. Species primarily ingesting seagrass (i.e., *S. radians*) typically prefer the epiphytized portion of the seagrass blade. These observations suggest that seagrass epiphytes are important in the flow of energy within the grass carpet. Many of the small, mobile epifaunal species that are so abundant in the grass bed and important as food for fishes feed at least in part on epiphytes. Typically, these animals do not feed on living seagrass, but often ingest significant quantities of organic detritus with its associated flora and fauna. *Tozeuma carolinense*, a common caridean shrimp, feeds on epiphytic algae attached to seagrass blades but undoubtedly consumes coincidentally other animals (Ewald 1969). Three of the four seagrass-dwelling amphipods common in south Florida use seagrass epiphytes, seagrass detritus, and drift algae as food, in this order of importance (Zimmerman et al. 1979). Epiphytic algae were the most important plant food sources tested since they were eaten at a high rate by *Cymadusa compta*, *Gammarus mucronatus*, and *Melita nitida*. Epiphytic 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. Live seagrass had little or no food value to these amphipods.

There is little doubt that the structure of many grass beds was profoundly different in pre-Columbian times when turtle populations were 100 to 1,000 times greater than those now. Rather than randomly cruising the vast submarine meadows, grazing as submarine buffalo, turtles apparently have evolved a distinct feeding behavior. They are not resident in seagrass beds at night, but live in deep holes or near fringing reefs and surface about once an hour to breathe. During morning or evening the turtles will swim some unknown distance to the seagrass beds to feed. What is most 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). Thayer and Engel (MS in preparation) calculated that an intermediate-sized *Chelonia* (64 kg or 141 lb) consumes daily a dry weight of blades equivalent to 0.5 m^2 of an average turtle grass bed (500 g dw of leaves). Since the regrazed areas do not contain as heavy a standing crop as ungrazed grass beds, it is obvious that their grazing plots must be considerably larger. The maximum length of grazing time on one distinct patch is not known, but J.C. Ogden (personal communication) observed patches that persisted for up to 9 months.

The first time turtles graze an area they do not consume the entire blade but bite only the lower portion and allow the epiphytized upper portion to float away. This behavior was recently described in some detail by Bjorndal (1980), but the earliest description was from the Dry Tortugas where John James Audubon observed turtles feeding on seagrass, "which they cut near the roots to procure the most tender and succulent part" (Audubon 1834).

It was previously thought that there was an advantage for grazers to consume the epiphyte complex at the tip of seagrass leaves, as this complex was of higher food value than the plain seagrass leaf. Although this seems logical, it appears not to be so, at least not for nitrogen compounds. While studying the food of turtles, Mortimer (1976) found that entire turtle grass leaves collected at Seashore Key, Florida, averaged 1.7% N on an ash free basis, while turtle grass leaves plus their epiphytes averaged 1.4% N. Bjorndal found that grazed turtle grass leaves averaged 0.35% N (AFDW) higher than ungrazed leaves, and Thayer and Engel (MS. in preparation) found a nitrogen content of 1.55% (DW) in the esophagus of Chelonia. Zieman and Iverson (in preparation) found that there was a decrease in nitrogen content with age and epiphytization of seagrass leaves. The basal portion of turtle grass leaves from St. Croix contained 1.6% to 2.0% N on a dry weight basis, while the brown tips of these leaves contained 0.6% to 1.1% N, and the epiphytized tips ranged from 0.5% to 1.7% N. Thus the current evidence would indicate 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).

Grazing on seagrasses produces another effect on sea turtles. In the Gulf of California (Felger and Moser 1973) and Nicaragua (Mortimer, as reported by Bjorndal 1980), witnesses reported that turtles that had been feeding on seagrasses were considered to be good tasting, while those that were caught in areas where they had fed on algae were considered to be "stinking" turtles with a definite inferior taste.

Thayer and Engel (MS. in preparation) suggested that grazing on seagrasses can short-circuit the time frame of decomposition. They showed that an intermediate-sized green turtle which consumes about 300 g dry weight of leaves and defecates about 70 g dry weight of feces daily, does return nitrogen to the environment at a more rapid rate than occurs for the decomposition of a similar amount of leaves. They point out that this very nutrient-rich and high nutritional quality fecal matter should be readily available to detritivores. It is also pointed out that this matter is probably not produced entirely at the feeding site and thus provides an additional interconnection between grassbeds and adjacent habitats.

Like the turtles, the Caribbean manatee (Trichechus manatus) formerly was common throughout the Caribbean, especially in the mainland areas, but is now greatly reduced in range and population. Manatees live in fresh or marine waters; and in Florida, most manatee studies have focused on the manatee's ability to control aquatic weeds. Manatees, which weigh up to 500 kg (1,102 lb), can consume up to 20% of their body weight per day in aquatic plants.

When in marine waters, the manatee apparently feeds much like its fellow sirenians, the dugongs. The dugongs use their rough facial bristles to dig into the sediment and grasp the plants. These are uprooted and shaken free of adhered sediment. Husar (1975) stated that feeding patches are typically 30 by 60 cm (12 by 24 inches) and that they form a conspicuous trail in seagrass beds. This author has observed manatees feeding in Thalassia beds in much the same manner. The patches cleared were of a similar size as those described for the dugongs, and rhizome removal was nearly complete. The excess sediments from the hole were 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.

Manatees would seem to be more limited in their feeding range because of sediment properties, as they require a sediment which is sufficiently unconsolidated that they may either root down to the rhizome or grasp the short shoot and pull it out of the sediment. Areas where manatee feeding and feeding scars were observed were characterized by soft sediments and lush growth of turtle grass and Halimeda in mounded patches. Nearly all areas in which sediments were more consolidated showed no signs of feeding. In the areas where the manatees were observed, the author found that he could readily shove his fist 30 cm (12 inches) or more into the sediments, while in the adjacent ungrazed areas, maximum penetration was only a few centimeters and it was impossible to remove the rhizomes without a shovel.

6.3 DETRITAL PROCESSING

For the majority of animals that derive all or part of their nutrition from seagrasses, the greatest proportion of fresh plant material is not readily used as a food source. For these animals seagrass 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).

The nonavailability of fresh seagrass material to detritus-consuming animals (detritivores) is due to a complex combination of factors. For turtle grass leaves, direct assays of fiber content have yielded values up to 59% of the dry weight (Vicente et al. 1978). Many animals lack the enzymatic capacity to assimilate this fibrous material. The fibrous components also make fresh seagrass resistant to digestion except by animals (such as parrotfishes and green turtles) with specific morphological or physiological adaptations enabling physical maceration of plant material. Fresh seagrasses also contain phenolic compounds that may deter herbivory by some animals.

During decomposition of seagrasses, numerous changes occur that result in a food source of greater value to many consumers. Bacteria, fungi, and other microorganisms have the enzymatic capacity to degrade the refractile seagrass organic matter that many animals lack. These microorganisms colonize and degrade the seagrass detritus, converting a portion of it to microbial protoplasm and mineralizing a large fraction. Whereas nitrogen is typically 2% to 4% dry weight of seagrasses (Table 7), microflora contain 5% to 10% nitrogen. Microflora incorporate inorganic nitrogen from the surrounding medium--either the sediments or the water column--into their cells during the decomposition process, enriching the detritus with proteins and other soluble nitrogen compounds. In addition, other carbon compounds of the microflora are much less resistant to digestion than the fibrous components of the seagrass matter. 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.

Microorganisms, because of their diverse enzymatic capabilities, are a necessary trophic intermediary between the seagrasses and detritivorous animals. Evidence (Tenore 1977; Ward and Cummins 1979) suggests that these animals derive the largest portion of their nutritional requirements from the microbial component of detritus. Detritivores typically assimilate the microflora compounds with efficiencies of 50% to almost 100%, whereas plant compound assimilation is less than 5% efficient (Yingst 1976; Lopez et al. 1977; Cammen 1980).

During seagrass decomposition, the size of the particulate matter is decreased, making it available as food for a wider variety of animals. The reduced particle size increases the surface area available for microbial colonization, thus increasing the decomposition rate. The abundant and trophically important deposit-feeding fauna of seagrass beds and adjacent benthic communities, such as polychaete worms, amphipods and isopods, ophiuroids, certain gastropods, and mullet, derive much of their nutrition from fine detrital particles.

It is important to note that much of the contribution of seagrasses to higher trophic levels through detrital food webs occurs away from the beds. The more decomposed, fine detrital particles (less than 0.5 mm) are easily resuspended and are widely distributed by currents (Fisher et al. 1979). They contribute to the organic detritus pool in the surrounding waters and sediments where they continue to support an active microbial population and are browsed by deposit feeders.

Physical Breakdown

The physical breakdown and particle size reduction of seagrasses are important for several reasons. First, particle size is an important variable in food selection for a wide range of organisms. Filter feeders and deposit feeders (polychaetes, zooplankton, gastropods) are only able to ingest fine particles (less than 0.5 mm diameter). Second, as the seagrass material is broken up, it has a higher surface area to volume ratio which allows more microbial colonization. This increases the rate of biological breakdown of the seagrass carbon. Physical decomposition rate is an approximate indication of the rate at which the plant material becomes available to the various groups of detritivores and how rapidly it will be subjected to microbial degradation.

Evidence indicates that turtle grass detritus is physically decomposed at a rate faster than the marsh grass, *Spartina alterniflora*, and mangrove leaves. Zieman (1975b) found a 50% loss of original dry weight for turtle grass leaves after 4 weeks using sample bags of 1-mm mesh size (Figure 23).

Seagrass leaves are often transported away from the beds. Large quantities are found among the mangroves, in wrack lines along beaches, floating in large mats, and collected in depressions on unvegetated areas of the bottom. Studies have shown that the differences in the physical and biological conditions in these environments resulted in different rates of physical decomposition (Zieman 1975b). Turtle grass leaves exposed to alternate wetting and drying or wave action breakdown rapidly, although this may inhibit microbial growth (Josselyn and Mathieson 1980).

Biological factors also affect the rate of physical decompositon. Animals grazing on the microflora of detritus disrupt and shred the plant substrate, accelerating its physical breakdown. Fenchel (1970) found that the feeding activities of the amphipod *Parahyella whelpyi* dramatically decreased the particle size of turtle grass detritus.

Microbial Colonization and Activities

Feeding studies performed with various omnivores and detritivores have shown that the nutritional value of macrophyte detritus is limited by the quantity and quality of microbial biomass associated with it. (See Cammen 1980 for other studies of detrital consumption.) The microorganisms' roles in enhancing the food value of seagrass detritus can be divided into two functions. First, they enzymatically convert the fibrous components of the plant material that is not assimilable by many detritivores into microbial biomass which can be assimilated. Second,

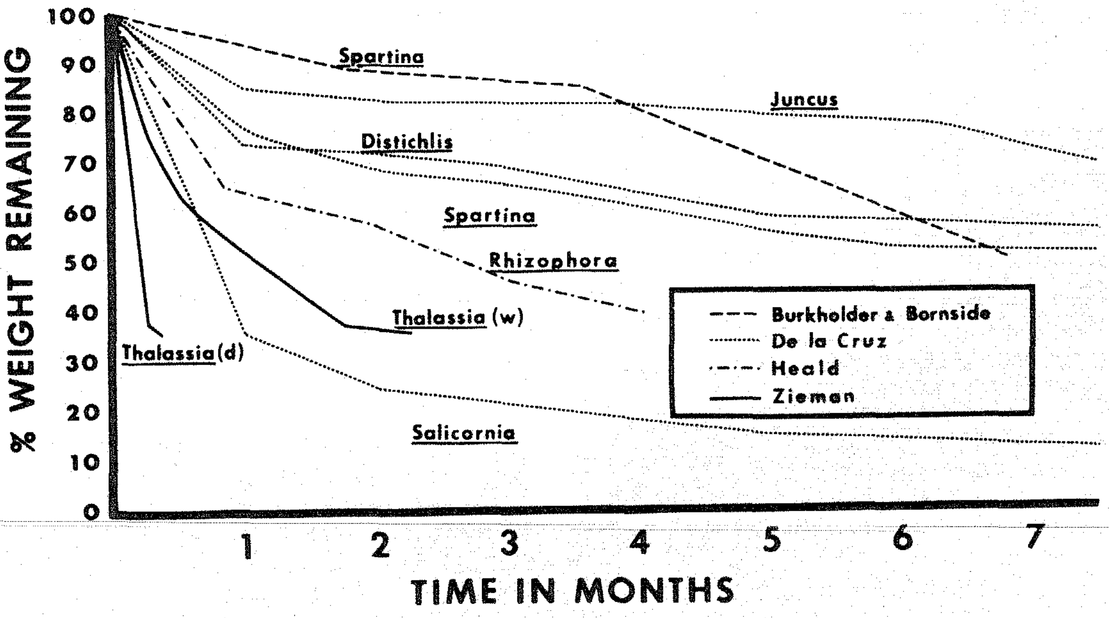


Figure 23. Comparative decay rates showing the rapid decomposition of seagrasses compared with other marine and estuarine plants (references: Burkholder and Bornside 1957; de la Cruz 1965; Heald 1969; Zieman 1975b).

the microorganisms incorporate constituents such as nitrogen, phosphorous, and dissolved organic carbon compounds from the surrounding medium into their cells and thus enrich the detrital complex. The microorganisms also secrete large quantities of extracellular materials that change the chemical nature of detritus and may be nutritionally available to detritivores. After initial leaching and decay, these processes make microorganisms the primary agents in the chemical changes of detritus.

The microbial component of macrophyte detritus is highly complex and contains organisms from many phyla. These various components interact and influence each other to such a high degree that they are best thought of as a "decomposer community" (Lee 1980). The structure and activities of this community are influenced by the feeding activities of detritivorous animals and environmental conditions.

Microflora in Detritivore Nutrition

Microbial carbon constitutes only 10% of the total organic carbon of a typical detrital particle, and microbial nitrogen constitutes no more than 10% of the total nitrogen (Rublee et al. 1978; Lee et al. 1980). Thus, most of the organic components of the detritus are of plant origin and are limited in their availability to detritivores.

Carbon uptake from a macroalga, *Gracilaria*, and the seagrass *Zostera marina* by the deposit-feeding polychaete, *Captella capitata*, was measured by Tenore (1977). Uptake of carbon by the worms was directly proportional to the microbial activity of the detritus (measured as oxidation rate). The maximum oxidation rate occurred after 14 days for *Gracilaria* detritus and after 180 days for *Zostera* detritus. This indicates that the characteristics of the original plant matter affect its availability to the microbes, which in turn limits the assimilation of the detritus by consumers.

Most of the published evidence shows that detritivores do not assimilate significant portions of the non-microbial component of macrophytic detritus. For example, Newell (1965) found that deposit-feeding molluscs removed the 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. When the nitrogen-poor, carbon-rich feces were incubated in seawater, their nitrogen content increased because of the growth of attached microorganisms. A new cycle of ingestion by the animals again reduced the nitrogen content as the fresh crop of microorganisms was digested. In a study of detrital leaf material, Morrison and White (1980) found that the detritivorous amphipod *Mucrogammarus* sp. ingested the microbial component of live oak (*Quercus virginica*) detritus without altering or consuming the leaf matter.

While the importance of the microbial components of detritus to detritivores is established, some results have indicated that consumers may be capable of assimilating the plant carbon also. Cammen (1980) found that only 26% of the carbon requirements of a population of the deposit-feeding polychaete *Nereis succinea* would be met by ingested microbial biomass. The microbial biomass of the ingested sediments could supply 90% of the nitrogen requirements of the studied polychaete population. The mysid *Mysis stenolepsis*, commonly found in *Zostera* beds, was capable of digesting cell-wall compounds of plants (Foulds and Mann 1978). These studies raise the possibility that while microbial biomass is assimilated at high efficiencies of 50% to 100% (Yingst 1976; Lopez et al. 1977) and supplies proteins and essential growth factors, the large quantities of plant material that are ingested may be assimilated at low efficiencies (less than 5%) to supply carbon requirements. Assimilation at this low efficiency would not be readily quantified in most feeding studies (Cammen 1980).

The microbial degradation of seagrass organic matter is greatly accelerated by the feeding activities of detritivores and microfauna, although the exact nature of the effect is not clear. Microbial respiration rates associated with turtle grass and *Zostera* detritus were stimulated by the feeding activities of animals, apparently as a result of physical fragmentation of the detritus (Fenchel 1970; Harrison and Mann 1975a).

Chemical Changes During Decomposition

The two general processes that occur during decomposition, loss of plant compounds and synthesis of microbial biomass, can be incorporated into a generalized model of chemical changes. Initially, the leaves of turtle grass, manatee grass, and shoal grass contain 9% to 22% protein, 6% to 31% soluble carbohydrates, and 25% to 44% ash (dry weight basis), depending on species and season (Dawes and Lawrence 1980). Direct assays of crude fiber by Vicente et al. (1978) yielded values of 59% for turtle grass leaves; Dawes and Lawrence (1980) classified this material as "insoluble carbohydrates" and calculated values of 34% to 41% for this species by difference. Initially, losses through translocation and leaching will lead to a decrease in certain components. Thus, the organic carbon and nitrogen content will be decreased, and the remaining material will consist primarily of the highly refractive cell wall compounds (cellulose, hemicellulose, and lignin) and ash (Harrison and Mann 1975b; Thayer et al. 1977).

As microbial degradation progresses, the nitrogen content will increase through two processes: oxidation of the remaining nitrogen-poor seagrass compounds and synthesis of protein-rich microbial cells (typically 30% to 50% protein) (Thayer et al. 1977; Knauer and Ayers 1977). The accumulation of microbial debris, such as the chitin-containing hyphal walls of fungi, may also contribute to the increased nitrogen content (Suberkropp et al. 1976; Thayer et al. 1977). Nitrogen for this process is provided by adsorption of inorganic and organic nitrogen from the surrounding medium, and fixation of atmospheric N_2. For tropical seagrasses, in particular, there is an increase in ash content during decomposition because of deposition of carbonates during microbial respiration and growth of encrusting algal species, and organic carbon usually continues to decrease (Harrison and Mann 1975a; Knauer and Ayers 1977; Thayer et al. 1977).

Chemical Changes as Indicators of Food Value

Nitrogen content has long been considered a good indicator of the food value of detritus and has been assumed to represent protein content (Odum and de la Cruz 1967). Subsequent analyses of detritus from many vascular plant species, however, have shown that up to 30% of the nitrogen is not in the protein fraction (Harrison and Mann 1975b; Suberkropp et al. 1976; Odum et al. 1979). As decomposition progresses, the non-protein nitrogen fraction as a proportion of the total nitrogen can increase 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. 1979b); and decomposition of bacterial exudates (Lee et al. 1980). As a result, actual protein content may be a better indicator of food value. Thayer et al. (1977) found that the protein content of Zostera leaves increased from standing dead to detrital fractions, presumably due to microbial enrichment. The role of the non-protein and protein nitrogen compounds in detritivore nutrition is not presently well understood.

Like many higher plants, tropical seagrasses contain phenolic acids known as allelochemicals. These compounds are known to deter herbivory in many plant groups (Feeny 1976). Six phenolic acids have been detected in the leaves, roots, and rhizomes of turtle grass, manatee grass, and shoal grass (Zapata and McMillan 1979). In laboratory studies two of these compounds, ferulic acid and p-coumaric acid, when present at concentrations found in fresh leaves, inhibited the feeding activities of detritivorous amphipods and snails grazing on S. alterniflora detritus. During decompositon the concentrations of these compounds decreased to levels that did not significantly inhibit the feeding activities of the animals (Valiela et al. 1979).

Seagrass leaves may also contain compounds that inhibit the growth of microorganisms; this in turn would decrease the usable nutritional value of the detritus. Water soluble extracts of fresh or recently detached Z. marina leaves inhibited the growth of diatoms, phytoflagellates, and bacteria (Harrison and Chan 1980). The inhibitory compounds are not found in older detrital leaves or ones that have been partially desiccated.

Release of Dissolved Organic Matter

Seagrasses release substantial amounts of dissolved organic carbon (DOC) during growth and decomposition. The DOC fraction is the most readily used fraction of the seagrass organic matter for microorganisms and contains much of the soluble carbohydrates and proteins of the plants. It is quickly assimilated by microorganisms, and is available to consumers as food in significant quantities only after this conversion to microbial biomass. Thus, the utilization of seagrass DOC is functionally similar to detrital food webs based on the particulate fraction of seagrass carbon. Both epiphytes and leaves of Zostera are capable of taking up labelled organic compounds (Smith and Penhale 1980).

Experiments designed to quantify the release of DOC from growing seagrasses have yielded a wide range of values. The short-term release of recently synthesized photosynthate from blades of turtle grass was found to be 2% to 10%, using radiolabelled carbon (Wetzel and Penhale 1979; Brylinsky 1977). Losses to the water column from the entire community, including belowground biomass and decomposing portions, may be much higher. Kirkman and Reid (1979) found that 50% of the annual loss of organic carbon from the Posidonia australis seagrass community was in the form of DOC.

Release of DOC from detrital leaves may also be substantial. In freshwater macrophytes, leaching and autolysis of DOC lead to a rapid 50% loss of weight (Otsuki and Wetzel 1974). In laboratory experiments dried turtle grass and manatee grass leaves released 13% and 20%, respectively, of their organic carbon content during leaching under sterile conditions (Robertson et al. 1982).

The carbon released as DOC is extremely labile and is rapidly assimilated by microorganisms (Otsuki and Wetzel 1974; Brylinsky 1977), which leads to its immediate availability as food for secondary consumers. In 14-day laboratory incubations, the DOC released by turtle grass and manatee grass leaves supported 10 times more microbial biomass per unit carbon than did the particulate carbon fraction (Robertson et al. 1982).

DOC may also become available to consumers through incorporation into particulate aggregates. Microorganisms attached to particles will assimilate DOC from the water column, incorporating it into their cells or secreting it into the extracellular materials associated with the particles (Paerl 1974, 1975). This microbially mediated mechanism also makes seagrass DOC available for consumers.

In most marine systems the DOC pool contains 100 times more carbon than the particulate organic carbon pool (Parsons et al. 1977; references therein). The cycling of DOC and its utilization in detrital food webs are complex. The highly labile nature of seagrass DOC suggests that it may play a significant role in supporting secondary productivity.

Role of the Detrital Food Web

The detrital food web theory represents our best understanding of how the major portion of seagrass organic carbon contributes to secondary productivity. The organic matter of fresh seagrasses is not commonly utilized by many animals because of various factors, including their low concentrations of readily available nitrogen, high concentrations of fiber, and the presence of inhibitory compounds. The particulate and dissolved fractions of seagrass carbon seem to become potential food for animals primarily after colonization by microorganisms. During decomposition the chemical nature of the detritus is changed by two processes: loss of plant compounds and synthesis of microbial products.

The decomposer community also has the enzymatic mechanisms and ability to assimilate nutrients from the surrounding medium, leading to the enrichment of the detritus as a food source. As a result, the decomposer community represents a readily usable trophic level between the producers and most animal consumers. In this food web, the consumers derive nutrition largely from the microbial components of the detritus. This decomposer community is influenced by environmental conditions and biological interactions, including the feeding activities of consumers.

CHAPTER 7

INTERFACES WITH OTHER SYSTEMS

7.1 MANGROVE

Mangroves and seagrass beds occur close to one another within the estuaries and coastal lagoons of south Florida, especially in the clear waters of the Florida Keys. While the importance of mangrove habitat to the estuary has been established (Odum and Heald 1972, 1975; Odum et al. 1982), its faunal interactions with adjacent seagrass beds are poorly understood.

Like the seagrass meadow, the mangrove fringe represents shelter; fishes and invertebrates congregate within the protection of mangrove prop roots. Game fish found in mangroves include tarpon (*Megalops atlanticus*), snook (*Centropomus undecimalis*), ladyfish (*Elops saurus*), crevalle jack (*Caranx hippos*), gafftopsail catfish (*Bagre marinus*), and jewfish (*Epinephelus itajara*) (Heald and Odum 1970). Undoubtedly, when mangroves and seagrass meadows are in proximity, these fishes will forage over grass. Grey snapper (*Lutjanus griseus*), sheepshead (*Archosargus probatocephalus*), spotted seatrout (*Cynoscion nebulosus*), and the red drum (*Sciaenops ocellota*) recruit into seagrass habitat initially, but with growth move into the mangrove habitat for the next several years (Heald and Odum 1970). All of these fishes have been collected over grass. Little work has been done, however, to explore the possible interactions between mangroves and seagrass beds. For a detailed review of the mangrove ecosystems of south Florida see Odum et al. (1982).

7.2 CORAL REEF

Coral reefs occur adjacent to extensive turtle grass-dominated grass beds along the full extent of the oceanic margin of the Florida Keys. The most prominent 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 provide food, nor possibly even shelter, for all of them. Longley and Hildebrand (1941) also noted the dependence (for food) of pomadasyids and lutjanids on areas adjacent to reefs in the Tortugas.

Typically, both juveniles and adults form large heterotypic resting schools (Ehrlich and Ehrlich 1973) over prominent coral heads or find shelter in caves and crevices of the reef (Figure 24). 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. Starck and Davis (1966) list species of the Holocentridae, Lutjanidae, and Pomadasyidae families as occurring diurnally on Alligator Reef off Matecumbe Key in the Florida Keys, and feeding nocturnally in adjacent grass beds and sand flats. As such, these fishes epitomize what Kikuchi and Peres (1977) defined as temporal visitors to the grass bed, which serves as a feeding ground (Hobson 1973). Starck (1968) discussed further

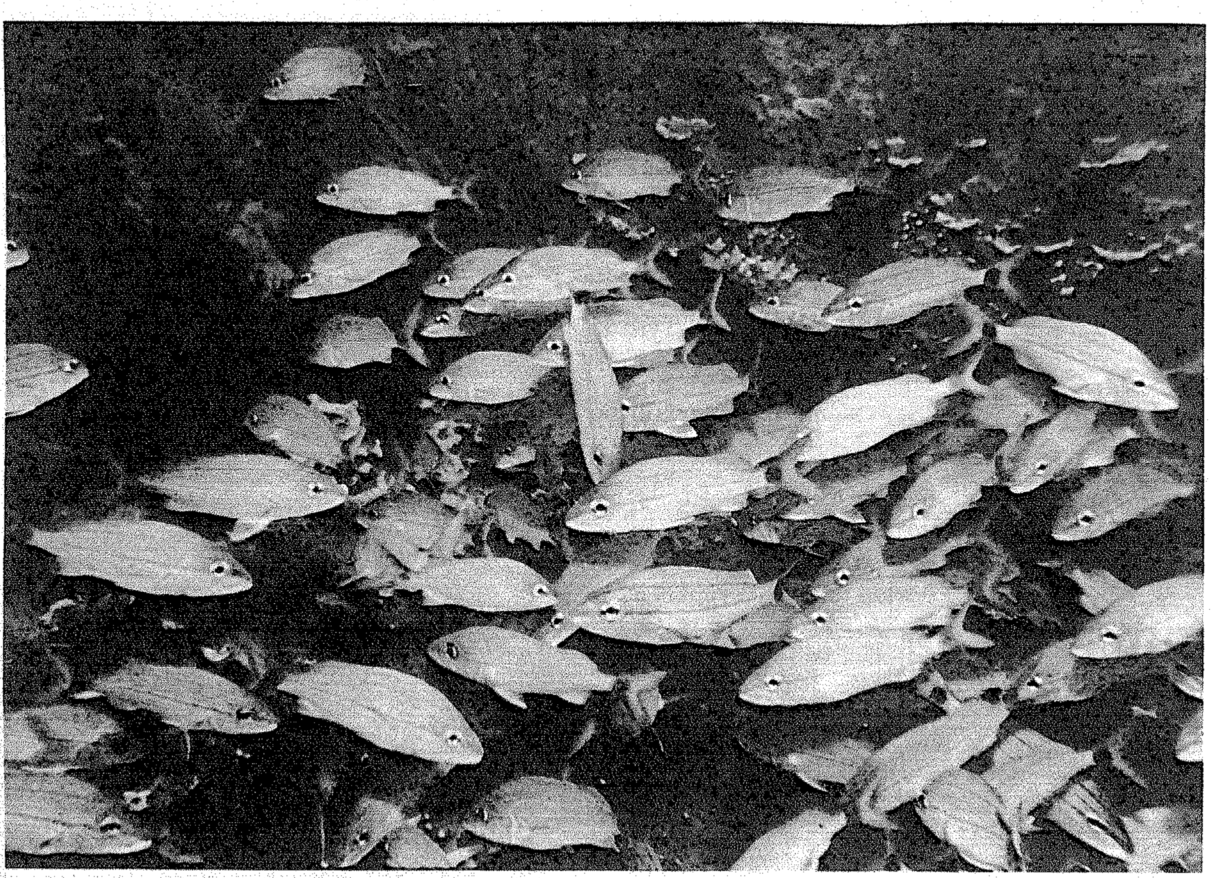


Figure 24. Grunt school over coral reef during daytime. At night these schools will disperse over seagrass beds and adjacent sand flats to feed.

the fishes of Alligator Reef with brief notes on their ecology, while Davis (1967) described the pomadasyids found on this reef and their ecology.

Little is known about the ecology of these nocturnal coral reef fishes while on the feeding ground. These fishes potentially can range far from their diurnal resting sites. Lutjanus griseus and Haemulon flavolineatum range as far as 1.6 km (1 mi) from Alligator Reef (Starck and Davis 1966). Haemulon plumeri and H. flavolineatum typically migrate distances of 300 m (984 ft) to greater than 1 km (0.6 mi) over the grass beds in Tague Bay, St. Croix (Ogden and Ehrlich 1977; Ogden and Zieman 1977). Tagged H. plumeri were repeatedly captured on the same reef and when transplanted exhibited a tendency to home (Springer and McErlean 1962a). Some H. plumeri and H. flavolineatum successfully home to original patch reefs over distances as great as 2.7 km (1.7 mi) in the U.S. Virgin Islands (Ogden and Ehrlich 1977).

It is interesting to speculate on the possible role that habitat partitioning plays in reducing competition for food over the feeding ground. Competition is important in structuring other fish communities, such as Centrachidae (Werner and Hall 1977), Embiotocidae (Hixon 1980) and Scorpaenidae (Larson 1980). Starck and Davis (1966) reported that 11 of 13 pomadasyids found in durnal resting schools on Alligator Reef disperse at night to feed. The lighter colored grunts (seven species) move off the reef and generally distribute themselves along a sand flat-grass bed back reef continuum. Snappers (Lutjanidae) follow a similar pattern with L. griseus and L. synagris moving into mixed sand, grass and rubble back reef habitat. The nocturnal distribution of grunts over the grass beds of Tague Bay, St. Croix, is similar to those reported in the Florida Keys. The French grunt, Haemulon flavolineatum, was most abundant over sparse grass or bare sand bottom, while the white grunt H. plumeri was usually observed in dense grass. Numbers of coral reef fishes (grunts and squirrelfishes) feeding nocturnally over seagrass were positively correlated with a measure of habitat complexity. This correlation implies organization of the fish assemblage while feeding (M.B. Robblee, in preparation). Lutjanids were not found in significant numbers either on the reef or in the grass beds.

These observations on the distribution of fishes over the feeding ground suggest that the nature and quality of grass bed and sand flat habitat adjacent to a coral reef may influence both the composition and abundance of these nocturnal fishes on a reef. Randall (1963) stated that whenever well-developed reefs lie adjacent to flats and these flats are not shared by many other nearby reefs, the grunts and snappers on the reef may be expected to be abundant. Starck and Davis (1966) and Robins (1971) also noted that it is understandable, given the requirement of most pomadasyids and several lutjanid species for back-reef forage area, that these fishes are almost completely absent from certain islands in the Caribbean which have fringing reefs with only narrow shelf and very limited back-reef habitat. Conversely, grunts and snappers form resting schools over characteristic coral heads, most commonly Acropora palamata and Porites porities (Ehrlich and Ehrlich 1973; Ogden and Ehrlich 1977), which also influences their population size. Starck and Davis (1966) commented that these species are excluded from many suitable forage areas by the absence of sheltered locations for diurnal resting sites. When artificial reefs were established in the Virgin Islands (Randall 1963; Ogden, personal communication), rapid colonization by juvenile grunts occurred, indicating the importance of shelter to these fishes near their potential feeding grounds.

Much of the interpretation given above is speculative, but in light of current hypotheses, the structuring of coral reef fish communities is probably largely controlled by their physical requirements for living space. Sale (1978) speaks of a lottery for living space among coral reef fish communities composed of groups of fishes with similar requirements (the representatives on any one particular reef being determined by chance recruitment). Alternatively, Smith (1978) advocated the ordered view that recource-sharing adaptations determine which species can live together. Resources external to the reef influence the species composition and abundances of at least nocturnally feeding, supra-benthic species (grunts and snappers), and perhaps several of the holocentrids.

It has been hypothesized that the diel activity patterns exhibited by these fishes contribute to the energy budget of the coral reef. Billings and Munro (1974) and Ogden and Zieman (1977) suggested, as originally proposed by Johannes (personal communication), that migrating pomadasyids may import significant quantities of organic matter (feces) to the reef. Thayer and Engel (in preparation) have also postulated a similar mechanism for green turtles, whose contribution to reef nutrient budgets may also be important. These assertions are open to investigation.

Temporary visitors from the coral reefs are not limited to fishes. The urchin Diadema antillarum moves off patch reefs at night into the turtle grass-dominated grass bed immediately adjacent in Tague Bay, St. Croix (Ogden et al. 1973). The prominent halo feature associated with many patch reefs is attributed to the nocturnal feeding forays of these longspine urchins. Of greater significance, the spiny lobster (Panulirus argus), is known to move onto offshore reefs as adults in the Florida Keys, seeking shelter in caves and crevices (Simmons 1980). Lobsters remain in their dens during daylight; at or after sunset they move onto adjacent grass beds to feed solitarily, returning to the reef before dawn (Hernkind et al. 1975). While farther from the reef, the spiny lobster ranges over considerable distances, typically several hundred meters.

Use of adjacent grass and sand flats by coral reef creatures is not strictly a nocturnal phenomenon, but seems to be the dominant pattern. Only large herbivores (e.g., Chelonia mydas, Scarus guacamaia) venture far into the grass bed away from the shelter of the reef. Mid-sized herbivores are apparently excluded by predators and feed only near the reef (Ogen and Zieman 1977). Randall (1965) reported parrotfishes (Scarus and Sparisoma) and surgeonfishes (Acanthurus) feeding on seagrasses (Thalassia and manatee grass) closely adjacent to patch reefs in the Virgin Islands during the day. He attributed the formation of halos around patch reefs in St. John to this grazing.

7.3 CONTINENTAL SHELF

Recently interest has been sparked in estuarine-Continental Shelf interactions (Darnell and Soniat 1979). The seagrass meadow represents a highly productive, faunally rich habitat within south Florida's estuaries and coastal lagoons. Many species are dependent on the seagrass bed and estuary. The pink shrimp Penaeus duorarum, the lobster Panulirus argus, and the grey snapper Lutjanus griseus may serve as examples of estuarine or lagoonal dependent fauna which at one life stage or another are found in seagrass meadows.

In south Florida, pink shrimp spawn in the vicinity of the Tortugas Bank, the pelagic larvae returning to the estuary and perhaps the seagrass bed (Yokel 1975a). Eventually mature individuals return to the spawning grounds. Similarly, the lobster matures in inshore seagrass nursery grounds and as a sub-adult resides on inshore reefs while continuing to feed within the grass bed at night. As sexually mature adults, female lobsters move to deep offshore reefs and spawn. The grey snapper initially recruits into grass and with growth moves into mangrove habitat and eventually on to coral reefs and deeper shelf waters. Coming or going, these organisms and others like them serve to transfer energy from the seagrass bed to offshore waters (see section 7.5), as has been shown by Fry (1981) for brown shrimp (P. aztecus) in Texas waters.

7.4 EXPORT OF SEAGRASS

The most recently recognized function of seagrass beds is their ability to export large quantities of organic matter from the seagrass meadows for utilization at some distant location (Zieman et al. 1979; Wolff 1980). This exported material is both a carbon and nitrogen source for benthic, mid-water, and surface-feeding organisms at considerable distances from the original source of its formation. The abundance of drifting seagrass off the west Florida shelf is illustrated in Figure 25 (Zieman et al., in preparation). This material originates on the shallow grass flats and is transported westward by the prevailing winds and tides.

Leaves and fragments of turtle grass were collected by Menzies et al. (1967) off the North Carolina coast in 3,160 m (10,368 ft) of water. Although the nearest source of turtle grass was probably 1,000 km (625 mi) away, blades were found at densities up to 48 blades per photograph. Roper and Brundage (1972) surveyed the Virgin Islands basin photographically and found seagrass blades in most of some 5,000 photographs taken at depths averaging 3,500 m (11,484 ft). Most were clearly recognizable as turtle grass or manatee grass. Seagrasses were collected by trawling in three Caribbean trenches and seagrass material was found in all the trenches sampled (Wolff 1976). Most of the material collected was turtle grass, and there was evidence of consumption by deep-water organisms. Interestingly, some grass blades collected from 6,740 m (22,113 ft) in the Cayman Trench showed the distinctive bite marks of parrotfish which are found only in shallow waters.

The primary causes of detachment are grazing by herbivores, mortality on shallow banks caused by low tides, and wave-induced severing of leaves that are becoming senescent. In addition, major storms will tear out living leaves and rhizomes (Thomas et al. 1961). Which mode of detachment will be most important in a particular area will be largely determined by physical conditions such as depth and wave exposure. Reduced salinity or extreme temperature variation will

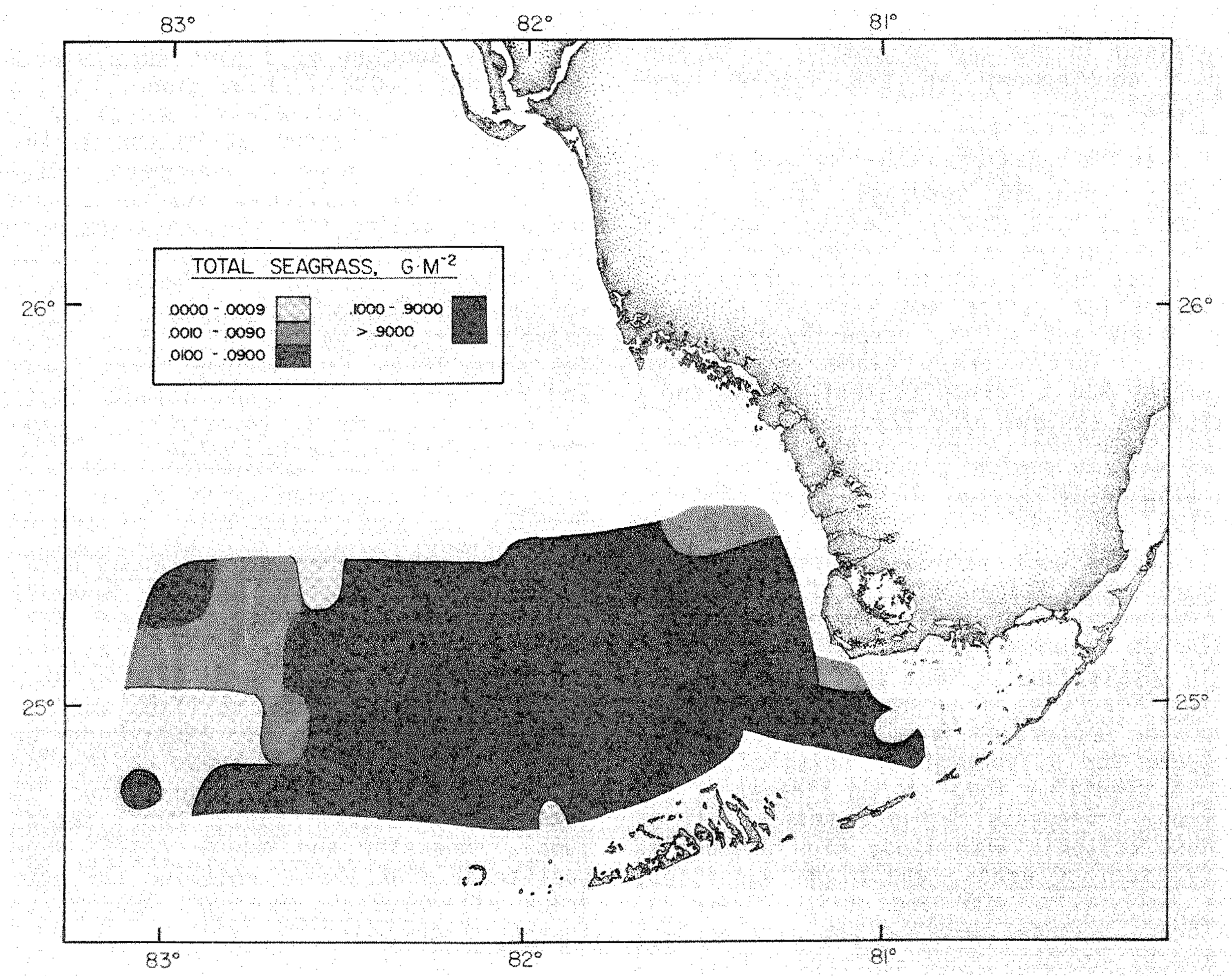


Figure 25. Seagrass export from south Florida to the eastern Gulf of Mexico. In certain areas there is a substantial subsidy to the local carbon and nitrogen budgets by material exported from nearby seagrass beds.

limit the herbivores responsible for detachment (primarily parrotfish, urchins, and turtles).

Freshly detached, healthy blades of all species float better than senescent ones. Because of the difference in size and shape of turtle grass and manatee grass blades, the effect of direct herbivory on the two species is quite different. When a parrotfish or urchin bites a turtle grass blade, it usually removes only a portion of the blade, which remains attached. However, a manatee grass blade is typically only 1 to 1.5 mm wide and one bite severs it, allowing the upper portion to float away (Zieman et al. 1979). Similarly, green turtles sever whole turtle grass blades during initial grazing.

Because of this difference in response to grazing, Zieman et al. (1979) found that in Tague Bay 60% to 100% of the daily production of manatee grass was detached and exported, whereas only 1% of turtle grass was exported, and this was primarily as bedload. This also indicates the relative successional status of these species. Turtle grass retains more of its leaves within the bed, which thus become part of the litter layer, promoting carbon and nitrogen recycling in the seagrass bed and enhancing its performance as a climax species. By contrast, relatively little of the leaf production of manatee grass is retained in the bed to contribute to further development of the little layer (Zieman 1981).

It is possible that in certain regions, exported seagrass could be an important food source. Sediment collected from the bottom of the Tongue of the Ocean that was not associated with turtle grass patches had carbon and nitrogen contents of 0.66% and 0.07%, respectively (Wolff 1980). Turtle grass blade and rhizome samples had a carbon content of 20% and a nitrogen content of 0.77%.

7.5 NURSERY GROUNDS

Grass beds serve as nursery grounds where post larval stages of fishes and invertebrates concentrate and develop and also as spawning grounds for adult breeding populations of some species. To be of significance as a nursery, a habitat must provide protection from predators, a substrate for attachment of sessile stages, or a plentiful food source (Thayer et al. 1978b). Seagrass habitats fulfill all of these criteria with their high productivity, surface areas, and blade densities, as well as a rich and varied fauna and flora. Seagrass provides abundant nursery habitat and is often preferred, based on abundance and size data, over available alternatives, in the estuaries and coastal lagoons, by many commercially or ecologically important species (Yokel 1975a).

The importance of grass bed habitat as a nursery has been historically demonstrated and should not be minimized. Following the decline of Zostera marina along the east coast of the United States in the early 1930's, the sea brant, a variety of goose dependent on eelgrass for food (as are many waterfowl; McRoy and Helffrich 1980), was reduced in numbers to one-fifth its former levels (Moffitt and Cottam 1941). Pronounced decreases in abundance of bay scallops (Argopecten irradians) were also noted following the disappearance of eelgrass (Stauffer 1937; Dreyer and Castle 1941; Marshall 1947). The post-veliger larval stage of the scallop depends on eelgrass to provide an above-sediment surface for attachment. Disruption of eelgrass beds resulted in lowered numbers of bay scallops (Thayer and Stuart 1974).

Many species of fishes and invertebrates use south Florida grass beds as nurseries. Approximately one-third of the species collected at Matecumbe Key, including all grunts, snappers, filefishes, and parrotfishes, occurred only as young, indicating that the grass-dominated shore area was a nursery ground (Springer and McErlean 1962b). 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). Comparatively little is known concerning invertebrates other than those of commercial value.

Shrimp

Pink shrimp (Penaeus duorarum) occupy south Florida grass beds as juveniles (Tabb et al. 1962; Costello and Allen 1966). Penaeus aztecus and P. brasiliensis are also present, but never as abundantly as the pink shrimp (Tabb and Manning 1961; Saloman et al. 1968; Bader and Roessler 1971). Shrimp spawn on the Tortugas grounds, probably throughout the year (Tabb et al. 1962; Munro et al. 1968). Roessler and Rehrer (1971) found postlarval pink shrimp entering the estuaries of Everglades National Park in all months of the year.

Pink shrimp were distributed throughout Rookery Bay Sanctuary in southwestern Florida, but were most abundant at stations with grass-covered bottoms (shoal grass and turtle grass), and within these stations were most abundant where benthic vegetation was dense (Yokel 1975a). Pink shrimp were also abundant in grass habitat at Marco Island and Fakahatchee Bay, also in southwestern Florida (Yokel 1975b). Postlarval pink shrimp with carapace length less than 3 mm were taken only at stations where shoal grass and turtle grass were present in Rookery Bay Sanctuary, while other stations without grass always had larger mean sizes. These observations are in accordance with Hildebrand (1955) and Williams (1965), who noted that very small pink shrimp prefer grassy areas and with increasing size are found in deeper water. In terms of the functioning of the grass bed as a nursery ground, it is interesting to speculate whether this distributional pattern represents a preference on the part of pink shrimp postlarvae for grass bed habitat (associated characteristics) or is the result of differential mortality within the estuary.

Spiny Lobster

Juvenile spiny lobsters (Panulirus argus) are commonly found in nearshore seagrass nursery areas of Biscayne Bay, Florida (Eldred et al. 1972); the Caribbean (Olsen et al. 1975; Peacock 1974); and Brazil (Moura and Costa 1966; Costa et al. 1969). In south Florida these inshore nursery areas are largely limited to clear, near-normal oceanic salinity waters of the outer margin of Florida Bay, the Florida reef tract, and the coastal lagoons. Tabb and Manning (1961) noted that the spiny lobster is rare on the muddy bottoms in northern Florida Bay.

Residence time in shallow grassy areas is estimated at about 9 to 12 months (Eldred et al. 1972; Costa et al. 1969) after which time the small lobsters (carapace length typically less than 60 mm) take up residence on small shallow water patch reefs. On the reefs, the lobsters live gregariously during the day while foraging at night over adjacent grass and sand flats. With maturity (1.5 to 2.0 years, Peacock 1974; up to 3 years in Florida, Simmons 1980) mating occurs and females migrate to deeper offshore reefs to release larvae (Little 1977; Cooper et al. 1975) and then return. Reproductive activity occurs throughout the year in Florida waters, but is concentrated during March through July (Menzies and Kerrigan 1980).

Theories differ about where the larvae which recruit into south Florida inshore nurseries originate. The question is of great importance to the management of this fishery. Once released along Florida's offshore reefs, the larvae (phyllosomes) drift with the current during a planktonic stage of undetermined length; estimates range from 3 months to 1 year (Simmons 1980). Controlled vertical movements in the water column may allow the larvae to remain in the area of hatching via eddies, layered countercurrents or other localized irregularities in the movements of the water (Simmons 1980). Alternatively, larger scale countercurrents and gyres may allow for larval development while still returning the larvae to south Florida waters (Menzies and Kerrigan 1980). It has also been suggested by Sims and Ingle (1966) that larvae recruited to south Florida nursery areas may have been spawned in locations south of the Yucatan Channel, perhaps as distant as the Leser Antilles or Brazil, and deposited ready for settlement by oceanic currents in south Florida waters. Ongoing studies of protein variation as a reflection of genetic variation between adult populations and pueruli postlarvae are designed to determine if Florida spiny lobsters originate within Florida's waters or are recruited from adult population centers elsewhere (Menzies and Kerrigan 1978, 1979, 1980).

Phyllosomes that survive their planktonic existence recruit into the nursery areas as puerulus lobsters (postlarvae) that resemble adults in form, but are transparent. The postlarvae swim toward shore at night and burrow in the bottom by day until they reach inshore seagrass nurseries, where they gradually become pigmented (Johnson 1974; Serfling and Ford 1975; Simmons 1980). Recruitment takes place throughout the year in south Florida with peak influxes usually between February and June and between September and December (Eldred et al. 1972; Witham et al. 1968; Sweat 1968). This pattern may be less pronounced in the lower Florida Keys where high summer influxes have also been noted (Little 1977). A summer peak in abundance was also noted in the Less Antilles (Peacock 1974). Greatest monthly recruitment takes place between new and first quarter moon (Little 1977).

There is some evidence to suggest that pueruli first settle temporarily above the bottom on algal mats, mangrove prop roots, or on floating algal rafts (Smith et al. 1950; Lewis et al. 1952; Witham et al. 1968; Sweat 1968; Little 1977). Peacock (1974), working in Antiqua and Barbados, noted that no pueruli were collected from within the grass bed in the lagoon where juveniles were present, but were collected commonly from the prop roots of mangroves lining its entrance. After the puerulus molts, the body of the young lobster is heavily pigmented. At this time it assumes a demersal behavior in the nursery (Eldred et al.

1972). Similar habitat use by juvenile *P. argus* has been reported in Cuba (Buesa 1969), the Virgin Islands (Olsen et al. 1975), the Lesser Antilles (Peacock 1974), and in Brazil (Costa et al. 1969). Degradation of this habitat would certainly threaten lobster productivity (Little 1977).

Fish

In south Florida it appears that continental fish faunas and insular fish faunas mix. Continental species require changing environments, seasonally shifting estuarine conditions, high turbidities, and muddy bottoms (Robins 1971). Southwestern Florida and northern Florida Bay typify these conditions and their fish assemblages are characterized by many sciaenid species (drums) and the prominent scarid, *Lagodon rhomboides*, which is also the most abundant fish in clearwater seagrass areas of Biscayne Bay and Card Sound (I. Brook, personal communication). Insular species require clear water, buffered environmental conditions, and bottom sediments composed largely of calcium carbonate (Robins 1971). These conditions are found within the grass beds of the Florida Keys and outer margins of Florida Bay. Representative species of families Pomadasyidae, Lutjanidae, and Scaridae are most numerous in these waters. This pattern is most evident among the seasonally resident fishes using seagrass meadows as nurseries.

At least eight sciaenid species (see Appendix) have been associated with the seagrass beds in southwestern Florida coastal lagoons and estuaries. Not all of these fishes occur abundantly, and only the spotted seatrout (*Cynoscion nebulosus*), the spot (*Leiostomus xanthurus*), and the silver perch (*Bairdiella chrysura*) occur commonly over grass as juveniles.

The spotted seatrout is one of the few larger carnivorous fishes present in south Florida waters that spawns within the estuary (Tabb 1961, 1966a, 1966b). Eggs sink to the bottom and hatching takes place in bottom vegetation or debris (Tabb 1966a, 1966b). The spotted seatrout and another sciaenid, the red drum (*Sciaenops oscellata*), spend the first few weeks of their lives in the grass beds of Florida and Whitewater Bays and then move into the mangrove habitat for the next several years (Heald and Odum 1970).

The pinfish (*Lagodon rhomboides*) was the most abundant fish collected and was taken throughout the year in the turtle grass beds of Florida Bay (Tabb et al. 1962), as is generally true for southwestern Florida (Weinstein and Heck 1979; Weinstein et al. 1977; Yokel 1975a, 1975b). Yokel (1975a) in Rookery Bay and Yokel (1975b) in Fakahatchee Bay, both of the Ten Thousand Island region of south Florida, noted a strong preference of juvenile pinfish for vegetated areas. The sheepshead (*Archosargus probatocephalus*), another sparid, initially recruits into grass beds but quickly moves into mangrove habitats (Heald and Odum 1970) or rocks and pilings (Hildebrand and Cable 1938).

The snappers, *Lutjanus griseus* and *L. synagris*, are common throughout south Florida. Juvenile gray snapper (*L. griseus*), are often the most common snapper in Northern Florida and Whitewater Bays, including freshwater regions (Tabb and Manning 1961). The gray snapper is considered to recruit into grass beds and then after several weeks move into mangrove habitat (Heald and Odum 1970). The lane snapper (*L. synagris*), never reaches sufficient size within the bay to enter the fishery significantly. Young lane snappers were abundant in turtle grass habitat when salinities were above 30 ppt (Tabb et al. 1962) in Northern Florida Bay, and were the most abundant snapper taken commonly within grass habitat of the Ten Thousand Island region of the southwestern Florida coast (Weinstein and Heck 1979; Weinstein et al. 1977; Yokel 1975a, 1975b). In Whitewater Bay, *L. griseus* and *L. synagris* were most abundant when associated with benthic vegetation (primarily the calcareous green algae *Udotea flabellum*, but also with some shoal grass.) (Clark 1970).

On the reefs fringing the Florida Keys along their oceanic margin, lane and grey snappers are joined by up to 10 additional lutjanid species (Starck and Davis 1966; Starck 1968; Longley and Hildebrand 1941; U.S. Dept. of Commerce 1980). Of these, the schoolmaster (*L. apodus*), the mutton snapper (*L. analis*), the dog snapper (*L. jocu*), and the yellowtail snapper (*Ocyurus chrysurus*) all occur in low numbers, relative to the grey snapper, as juveniles near shore over grass in the Florida Keys (Springer and McErlean 1962b; Bader and Roessler 1971; Roessler 1965).

Of the Pomadasyidae, juvenile pigfish (*Orthopristic chrysoptera*) are abundant on muddy bottoms and turbid water in Florida's variable salinity regions; adults and juveniles were collected throughout the year in Florida Bay (Tabb and Manning 1961; Tabb et al. 1962) and Rookery Bay (Yokel 1975a). The white grunt (*Haemulon plumeri*) is common throughout south Florida, occurring most often over turtle grass beds in clear water as juveniles (Tabb and Manning 1961; Roessler 1965; Bader and Roessler 1971; Weinstein and Heck 1979). Adults were not found over grass during the day, but were abundant diurnally on coral reefs and at night over grass and sand flats adjacent to coral reefs (Starck and Davis 1966; Davis 1967). Tabb et al. (1962) lists the pigfish and the white grunt as typical residents of the turtle grass community of Florida Bay. Other grunts, including *Anisotremus virginicus*, *Haemulon sciurus*, and *H. aurolineatum*, occur over grass only rarely in southwestern Florida and Florida Bay, (Tabb and Manning 1961; Weinstein and Heck 1979).

Clearer water, higher and less variable oceanic salinities, and the proximity of coral reefs may account for the increased species richness of juvenile pomadasyids in Florida Keys inshore grass beds. In addition to the species already mentioned (except *O. chrysoptera*), *Haemulon flavolineatum*, *H. parrai* and *H. carbonarium* are also present as juveniles in these waters (Springer and McErlean 1962b; Roessler 1965; Bader and Roessler 1971; Brook 1975).

In addition to lutjanids and pomadasyids, other coral reef fishes use seagrass beds as nurseries. Surgeon fishes are found as juveniles in grass beds: most commonly the ocean surgeon (*Acanthurus bahianus*) and the doctorfish (*A. chirurgus*). The spotted goatfish (*Pseudupeneus maculatus*) and the yellow goatfish (*Mulloidicthys martinicus*) occur as juveniles in grass beds (Munro 1976; Randall 1968). The spotted goatfish was taken at Matecumbe Key (Springer and McErlean 1962b). Parrotfish (Scaridae) are often the most abundant fishes on reefs (Randall 1968). Springer and McErlean (1962b), using seines on Matecumbe Key, found eight species of scarids in turtle grass beds. All of these were juveniles; however, *Sparisoma radians* and *S. chrysopterum* are also small fishes which continually reside in seagrasses. The latter is also found on reefs (Randall 1967, 1968). The emerald parrotfish (*Nicholsina usta*), which is most common in seagrass (Randall 1968), was taken on Matecumbe Key, as well as in Biscayne Bay (Bader and Roessler 1971). The remaining species of parrotfishes, *Sparisoma viride* and *S. rubripine* and *Scarus croicensis*, *S. guacamaia*, and *S. coeruleus*, are present on reefs as adults, are less common in Biscayne Bay (Roessler 1965; Bader and Roessler 1971), and are absent in Card Sound (Bader and Roessler 1971; Brook 1975).

CHAPTER 8

HUMAN IMPACTS AND APPLIED ECOLOGY

Since the days when Henry Flagler's railway first exposed the lush subtropical environment of south Florida to an influx of people from outside the region, the area has been subjected to great change at the hands of man. Through the 1950's, booming development precipitated the destruction of many acres of submerged lands as demands for industrial, residential, and recreational uses in this unique part of the Nation increased. While seagrass beds generally have experienced less direct damage than have the mangrove shorelines, seagrasses have not been totally spared the impact of development. Environmental agencies receive permit requests regularly, many of which would directly or indirectly impact seagrass beds. Because of the concern for these biologically important habitats several articles have been published which document their importance and man's impact (e.g. Thayer et al. 1975b; Zieman 1975b, 1975c, 1976; Phillips 1978; Ferguson et al. 1980).

8.1 DREDGING AND FILLING

Probably the greatest amount of destruction of seagrasses in south Florida has resulted from dredging practices. Whether the objective is landfill for causeway and waterfront property construction, or deepening of waters for channels and canals, dredging operations typically involve the burial of portions of an estuary with materials from nearby locations. Such projects therefore can involve the direct destruction of not only the construction site, but also many acres of adjacent habitats. The impact of dredging can be long-lasting since such disturbance creates sediment conditions unsuitable for seagrass recolonization for a protracted period (Zieman 1975c).

Of the Gulf Coast States, Florida ranks third, behind Texas and Louisiana, in amount of submerged land that has been filled by dredge spoil (9,520 ha or 23,524 acres). In Texas and Louisiana, however, most of the spoil created came from dredged navigation channels, while in Florida this accounts for less than 5% of the State total. Not surprisingly, the majority of filling of land in Florida, about 7,500 ha (18,525 acres), has been to create land for residential and industrial development (Figure 26). In addition to the direct effect of burial, secondary effects from turbidity may have serious consequences by restricting nearby productivity, choking filter feeders by excessive suspended matter, and depleting oxygen because of rapid utilization of suspended organic matter. The dredged sediments are unconsolidated and readily suspended. Thus a spoil bank can serve as a source of excess suspended matter for a protracted time after deposition. Zieman (1975b) noted that in the Caribbean dredged areas were not recolonized by turtle grass for many years after operations ceased. Working in estuaries near Tampa and Tarpon Springs, Godcharles (1971) found no recovery of either turtle grass or manatee grass in areas where commercial hydraulic clam dredges had severed rhizomes or uprooted the plants, although at one station recolonization of shoal grass was observed.

Figure 26. Housing development in south Florida . Portions of this development were built over a dredged and filled seagrass bed. This has historically been the most common form of man-induced disturbance to submerged seagrass meadows.

Van Eepoel and Grigg (1970) found that a decrease in the distribution and abundance of seagrasses in Lindbergh Bay, St. Thomas, U.S. Virgin Islands, was related to turbidity caused by dredging. In 1968 lush growths of turtle grass had been recorded at depths up to 10 m (33 ft), but by 1971 this species was restricted to sparse patches usually occurring in water 2.5 m (8 ft) deep or less. A similar pattern of decline was observed by Grigg et al. (1971) in Brewers Bay, St. Thomas. In Christiansted Harbor, St. Croix, U.S. Virgin Islands, removal of material for dredging of a ship channel combined with landfill projects increased the harbor's volume by 14% from 1962 to 1971. Siltation in areas adjacent to the channel caused extensive suffocation; and where deeper water resulted, sediment and light conditions became unsuitable for seagrass growth.

Reduced light penetration was observed in grassflats adjacent to the dredging site of an intracoastal waterway in Redfish Bay, Texas (Odum 1963). Odum suggested that subsequent decreases in productivity of turtle grass reflected 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 (125-ft) long channel and a 400 m (1300 ft) zone of spoil island and adjacent beds, no permanent damage occurred to the seagrasses beyond this region.

Studies of Boca Ciega Bay, Florida, reveal the long-term impact of dredging activities. Between 1950 and 1968 an estimated 1,400 ha (3,458 acres) of the bay were filled during projects involving the construction of causeways and the creation of new waterfront homesites.

Taylor and Saloman (1968) contrasted undisturbed areas of the bay, where luxuriant grass grew in sediments averaging 94% sand and shell, with the bottom of dredge canals, where unvegetated sediments averaged 92% silt and clay. 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 that are highly motile and thus not restricted to the canals during extreme conditions. Interestingly, while species numbers were higher in undisturbed areas, 30% more fish were found in the canals, the most abundant of which were the bay anchovy, the Cuban anchovy, and the scaled sardine. The authors noted that in the few years since the initial disturbance, colonization was negligible at the bottom of the canals and 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. Because of the depth of the canals, however, light at the bottom was insufficient for seagrass growth. Taylor and Saloman (1968), using conservative and incomplete figures, estimated that fill operations in the bay resulted in an annual loss of 1.4 million dollars for fisheries and recreation.

If seagrasses are only lightly covered and the rhizome system is not changed, 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 area of 2 to 3 ha (5 to 7 acres) with up to 10 cm (4 inches) of sediment, killing the leaves, but not the rhizome system. Regrowth occurred when the dredging operations ceased and currents carried the sediment away.

8.2 EUTROPHICATION AND SEWAGE

Seagrass communities are sensitive to additions of nutrients from sewage outfalls or industrial wastes. Because seagrasses have the ability to take up nutrients through the leaves as well as the roots, a moderate amount of enrichment may actually enhance productivity, under certain conditions where waters are well-mixed, as observed by this author in the rich growth of turtle grass and associated epiphytes in the vicinity (within 1 km or 0.6 mi) of Miami's Virginia Key sewage plant. This discharge is on the side of the key open to the ocean. In the immediate area where these wastes are discharged, however, water quality is so reduced that seagrasses cannot grow. Stimulation of excess epiphytic production may adversely affect the seagrasses by persistent light reduction. Often the effects of sewage discharge in such areas are compounded by turbidity from dredging. In Christiansted Harbor, St. Croix, where turtle grass beds were subjected to both forms of pollution, the seagrasses declined and were replaced by the green alga, Enteromorpha. In a 17-year period, the grassbeds in the embayment were reduced by 66% (Dong et al. 1972).

Phytoplankton productivity increased in Hillsborough Bay, near Tampa because of nutrient enrichment for domestic sewage and phosphate mining discharges (Taylor et al. 1973). 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.

Few seagrasses grow in waters of Biscayne Bay that were polluted by sewage discharge in 1956 (McNulty 1970). Only shoal grass and Halophila grew sporadically in small patches within 1 km (0.6 mi) of the outfall. Post-abatement studies in 1960 showed seagrasses in the area had actually declined, probably because of the persistent resuspension of dredge materials resulting from the construction of a causeway.

Physiological studies reveal that seagrasses are not only affected by low levels of light, but also suffer when dissolved oxygen levels are persistently low, a situation encountered where sewage additions cause increased microbial respiration. Hammer (1968a) compared the effects of anaerobiosis on photosynthetic rates of turtle grass and Halophila decipiens. While photosynthesis was depressed in both species, Halophila did not recover after a 24-hour exposure, whereas the recovery of turtle grass was complete, possibly because of its greater ability to store oxygen in the internal lacunar spaces. Such an oxygen reduction, however, will have a far greater impact on the faunal components than on the plants.

8.3 OIL

With the Nation's continued energy demands, the transport of petroleum and the possibility of new offshore drilling operations threaten the coastal zone of south Florida. The impact on marine and estuarine communities of several large-scale oil spills has been investigated; laboratory studies have assessed the toxicity of oil to specific organisms. The effects of oil spills, cleanup procedures, and restoration on seagrass ecosystems have recently been reviewed by Zieman et al. (in press).

Tatem et al. (1978) studied the toxicity of two crude oils and two refined oils on several life stages of estuarine shrimp. Refined Bunker C and number 2 fuel oil were more toxic to all forms than were crude oils from south Louisiana and Kuwait. The larval stages of the grass shrimp (Palaemonetes pugio) were slightly more resistant to the oil than the adults, while all forms of the oils were toxic to the larval and juvenile stages of the white shrimp (Penaeus setiferus) and the brown shrimp (Penaeus aztecus), both common grass bed inhabitants. Changes in temperature and salinity, which are routine in estuaries, enhanced the toxic effects of the petroleum hydrocarbons. The greatest danger to aquatic organisms seems to be the aromatic hydrocarbons as opposed to the paraffins or alkanes. The bicyclic and polycyclic aromatics, especially napthalene, are major sources of the observed mortalities (Tatem et al. 1978). The best indicator of an oil's toxicity is probably its aromatic hydrocarbon content (Anderson et al. 1974; Tatem et al. 1978)).

The effects of oil-in-water dispersions and soluble fractions of crude and refined oils were evaluated for six species of estuarine crustacea and fishes from Galveston Bay, Texas (Anderson et al. 1974). The refined oils were consistently more toxic than the crude oils, and the three invertebrate species studied were more sensitive than were the three fishes.

The effects on seagrass photosynthesis of exposure to sublethal levels of hydrocarbons were studied by McRoy and Williams (1977). Plants exposed to low levels of water suspensions of kerosene and toluene showed significantly reduced rates of carbon uptake. Plants probably are not the most susceptible portion of the community; in boat harbors where seagrasses occur, the associated fauna are often severely affected.

In the vicinity of Roscoff, France, den Hartog and Jacobs (1980) studied the impact of the 1978 "Amoco Cadiz" oil spill on the Zostera marina beds. For a few weeks after the spill, the eelgrass suffered leaf damage, but no long-term effect on the plants was observed. Among the grass bed fauna, filter-feeding amphipods and polychaetes were most effected. The eelgrass leaves were a physical barrier protecting the sediments and infauna from direct contact with the oil, and the rhizome system's sediment-binding capabilities prevented the mixing of oil with the sediment. Diaz-Piferrer (1962) found that turtle grass beds near Guanica, Puerto Rico, suffered greatly when 10,000 tons of crude oil were released into the waters on an incoming tide. Mass mortalities of marine animals occurred, including species commonly found in grass beds. Many months after the incident turtle grass beds continued to decline.

In March of 1973, the tanker Zoe Colocotronis released 37,000 barrels of Venezuelan crude oil in an attempt to free itself from a shoal off the south coast of Puerto Rico. The easterly trade winds moved the oil into Bahia Sucia and contaminated the beaches, seagrasses, and mangroves. Observations were made and samples collected shortly after the spill. By the third day following the release, dead and dying animals were abundant in the turtle grass beds; and large numbers of sea urchins, conchs, polychaetes, prawns, and holothurians were washed up on the beach (Nadeau and Berquist 1977). Although the spilled Venezuelan crude oil is considered to have low toxicity, the strong winds and the wave action in shallow waters combined to produce dissolution and droplet entrainment that yielded an acutely toxic effect. This wave entrainment carried oil down into the turtle grass, killing the vegetation. Lacking the stabilizing influence of the seagrass, extensive areas were eroded, some down to the rhizome layer. Some turtle grass rejuvenation was noted in January 1974, and by 1976 renewed seagrass growth and sediment development were observed. Surveys of the epibenthic communities showed a general decline following the spill, but infaunal sample size proved too small (Nadeau and Berquist 1977) to yield definitive results.

In July 1975 a tanker discharged an estimated 1,500 to 3,000 barrels of an emulsion of crude oil and water into the edge of the Florida current about 40 km (25 mi) south-southwest of the Marquesa Keys. The prevailing winds drove the oil inshore along a 50-km (31-mi) section of the Florida Keys from Boca Chica to Little Pine Key. Chan (1977) observed no direct damage to turtle grass, manatee grass or shoal grass. The natural seagrass drift material apparently acts as an absorbent and concentrator of the oil. This material was deposited in the intertidal zone where the oily deposits persisted at least 1 month longer than the normal seagrass beachwrack, and Chan thought that this reduced detrital input into the dependent ecosystems. The amphipods and crabs typical of this zone did not occur in the polluted material. The author attributed mass mortalities of the pearl oyster (Pinctada radiata) a grass bed inhabitant, to some soluble fraction of petroleum. The severest impacts were in the adjacent mangrove and marsh communities where plants and animals were extensively damaged. Among the effects noted was the increase in temperature above the lethal limit of most intertidal organisms caused by the dark oil coating.

From various studies it is obvious, then, that even when the seagrasses themselves apparently suffer little permanent damage, the associated fauna can be quite sensitive to both the soluble and insoluble fractions of petroleum (Figure 25).

Considering the vast amount of ship traffic that passes through the Florida Straits, it is somewhat surprising that there have not been more reported oil spills. Sampling of beaches throughout the State has shown that a considerable amount of tar washes up on Florida beaches, and that the beaches of the Florida Keys are the most contaminated (Romero et al. 1981). In this study, 26 beaches throughout the State were sampled for recently deposited tar. The density of ship traffic and the prevailing southeasterly winds, result in no tar accumulation on many beaches on the gulf coast, while the largest amounts are found between Elliot Key and Key West. Of the 26 sample stations, 6 were in the Keys between Elliot Key and Key West, and there were 10 on each coast north of this region. The average for the six Keys stations was 17.2 gm tar/m^2 of beach sampled, with the station on Sugarloaf Key showing the highest mean annual amount of 40.5 gm/m^2. By comparison, the average annual amount for the 10 east coast beaches north of Miami was 2.5 gm/m^2, and the average for the west coast beaches north of Cape Sabel was only 0.3 gm/m^2. The implication of this study is quite frightening, for as damaging and unsightly as an oil spill can be on a beach, the potential for damage is inestimably higher in a region such as the Florida Keys with its living, biotic interfaces of mangrove, barely subtidal seagrass flats, and shallow coral reefs.

8.4 TEMPERATURE AND SALINITY

Tropical estuaries are particularly susceptible to damage by increased temperatures since most of the community's organisms normally grow close to their upper thermal limits (Mayer 1914, 1918). The Committee on Inshore and Estuarine Pollution (1969) observed that a wide variety of tropical marine organisms could survive temperatures of 28°C (82°F) but began dying at 33° to 34°C (91° to 93°F). In Puerto Rico, Glynn (1968) reported high mortalities of turtle grass and invertebrates on shallow flats when temperatures reached 35° to 40°C (95° to 104°F). Planktonic species are probably less affected by high temperatures than are sessile populations since larvae can readily be imported from unaffected areas.

Time of exposure is critical in assessing the effect of thermal stress. Many organisms tolerate extreme short-term temperature change, but do not survive chronic exposure to smaller elevation in temperature. For seagrasses that have buried rhizome systems, the poor thermal conductivity of the sediments effectively serves as a buffer against short-term temperature increases. As a result, the seagrasses tend to be more resistant to periodic acute temperature increase than the algae. Continued heating, however, can raise the sediment temperature to levels lethal to plants (Zieman and Wood 1975). The animal components of the seagrass systems show the same ranges of thermal tolerances as the plants. Sessile forms are more affected as they are unable to escape either short-term acute effects or long-term chronic stresses.

The main source of man-induced thermal stress in tropical estuaries probably has been the use of natural waters in cooling systems of power plants. Damage to the communities involved has been reported at various study sites. In Guam characteristic fish and invertebrates of the reef flat community disappeared when heated effluents were discharged in the area (Jones and Randall 1973). Virnstein (1977) found a decrease in density and diversity of benthic infauna in Tampa Bay in the vicinity of a power plant, where temperatures of 34° to 37°C (93° to 99°F) were recorded.

The most thorough investigations of thermal pollution in tropical or semitropical environments have centered around the Miami Turkey Point power plant of Florida Power and Light (see review by Zieman and Wood 1975). Zieman and Wood (1975) found that turtle grass productivity decreased as temperatures rose and showed the relationship between the pattern of turtle grass leaf death and the effluent plume, reporting by late September 1968, that 14 ha (35 acres) of grass beds had been destroyed. Purkerson (1973) estimated that by the fall of 1968, the barren area had increased to 40 ha (99 acres) with a zone of lesser damage extending to include about 120 ha (297 acres). In 1971 the effluents were further diluted by using greater volumes of ambient-temperature bay waters. The net effect, however, was to expand the zone of thermal stress. One station 1,372 m (4500 ft) off the canal had temperatures of 32.2°C (90°F) only 2% of the time in July 1970, but this increased to 78% of the time in July 1971 (Purkerson 1973).

Temperatures of 4°C or more above ambient killed nearly all fauna and flora present (Roessler and Zieman 1969). A rise of 3°C above ambient damaged algae; species numbers and diversity were decreased. The optimum temperature range for maximal species diversity and numbers of individuals was between 26° and 30°C (79° and 86°F) (Roessler 1971). Temperatures between 30° and 34°C (86° and 93°F) excluded 50% of the invertebrates and fishes, and temperatures between 35° and 37°C (95° and 99°F) excluded 75%.

The effects recorded above resulted from operation of two conventional power generators which produced about 12 m^3/sec of cooling water heated about 5°C (41°F). Using this cooling system, the full plant, which was two conventional and two nuclear generators, would produce 40 m^3/sec of water heated 6° to 8°C above ambient. The plant had begun operations in spring 1967 with a single conventional unit, and a year later a second unit was added. Studies at the site began in May 1968 when the area was still relatively undisturbed. Except for a few hectares directly out from the effluent canal, the communities in the vicinity were the same as in adjacent areas to the north and south. As temperatures increased throughout the summer, however, damage to the benthic community expanded rapidly.

Because of the anticipated impact of the nuclear powered units, a new 9-km (5.6-mi) canal emptying to the south in Card Sound was dredged. Fears that this body of water also would be damaged persisted, and as a final solution to the problem a network of 270 km (169 mi) of cooling canals 60 m (197 ft) wide was constructed. Heated water was discharged into Card Sound until the completion of the closed system, however. Thorhaug et al. (1973) found little evidence of damage to the biota of Card Sound, partly because effluent temperatures there were lower than those experienced in Biscayne Bay, and even before the thermal additions, the benthic community of the affected portion of Card Sound was relatively depauperate compared to Biscayne Bay.

The temperatures and salinities of the bays and lagoons of south Florida show much variation, and the fauna and flora must have adequate adaptive capacity to survive. Although the heated brine effluent from the Key West desalination plant caused marked reduction in the diversity in the vicinity of the outfall, nearly all beds of turtle grass were unaffected (Chesher 1975). Shoal grass is the most euryhaline of the local seagrasses (McMillan and Moseley 1967). Turtle grass and manatee grass show a decrease in photosynthetic rate as salinity drops below full strength seawater. The seasonality of seagrasses in south Florida is largely explained by temperature and salinity effects (Zieman 1974). The greatest decline in plant populations was found when combinations of high temperature and low salinity occurred simultaneously. 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."

Perhaps reduced water flow in the Everglades has had unexpected impacts in seagrass beds. The eastern regions of Florida Bay were formerly characterized by low salinity, muddy bays with sparse growths of shoal grass. Fishing here was often excellent as a variety of species such as mullet and sea trout foraged in the heterogenous bottom. One of the mainstays of the fishing guides of this area was the spectacular and consistent fishing for redfish. In recent years the guides have complained that this fish population has become reduced, and it is not worth the effort to bring clients to this area. In January 1979 this author took a trip through this region and found that much of the formerly mud and shoal grass bottom that he had worked on 10 to 12 years prior was now lush, productive turtle grass beds. Where the waters were once muddy, they were now, according to the guide, much clearer and shallower, but provided less sea trout and redfish. Why? The following hypothetical scenario is one explanation.

In the late sixties the infamous C-111 or Aerojet-General canal was built in south Dade County, on which Aerojet hoped to barge rocket motors to a test site in south Dade. The contracts failed to materialize and the canal, although completed, was left plugged and never opened to the sea. Its effect, however, was to intercept a large part of the overland freshwater flow to the eastern Everglades and ultimately to eastern Florida Bay.

The interception of this water is thought to have created pronounced changes in the salinity of eastern Florida Bay, allowing for much greater saltwater penetration. As the salinity increased, turtle grass, which had been held in check by lowered salinity, may have had a competitive advantage over shoal grass and increased its range. The thick anastomosing rhizome mat of turtle grass stabilized sediments and may have made foraging difficult for species that normally grub about in loose mud substrate. Also the greater sediment stabilizing capacity of turtle grass may have caused rapid filling in an environment of high sediment supply and low wave energy.

This scenario has not been proven; thus it is hypothesis and not fact. It points out, however, the conceivability of how a manmade modification at some distance may have pronounced effects on the life history and abundance of organisms.

It is interesting to note that the fishing guides regarded the lush, productive turtle grass beds as a pest and much desired the muddy, sparse shoal grass. What this really illustrates is that quite different habitats may be of vital importance to certain species at specific points in their life cycle. Those features that make the turtle grass beds good nurseries and important to these same carnivores when they are juveniles restrict their foraging ability as adults. It should be noted in passing that while lamenting the encroachment of turtle grass into this area, the guides still hailed the shallow turtle grass beds to be superior bonefish habitat.

8.5 DISTURBANCE AND RECOLONIZATION

The rate at which a disturbed tropical grass bed may recolonize is still largely unknown. Fuss and Kelly (1969) found that at least 10 months were required for a turtle grass rhizome to develop a new apex.

The most common form of disturbance to seagrass beds in south Florida involves cuts from boat propellers. Although it would seem that these relatively small-scale disturbances would heal rapidly, typically it takes 2 to 5 years to recolonize a turtle grass bed (Zieman (1976). Although the scarred areas rapidly fill in with sediment from the surrounding beds, the sediment is slightly coarser and has a lower pH and Eh.

In some regions, disturbances become nearly permanent features. Off the coast of Belize aerial photographs show features in the water that appear as strings of beads. These are holes resulting from seismic detonation; some have persisted for over 17 years (J.C. Ogden, personal communication) with no recolonization. This is not just due to problems associated with explosions, as Zieman has observed blast holes from bombs on a naval bombing range in Puerto Rico where some recolonization occurred within 5 years.

Most cases of restoration in south Florida involve turtle grass because of its value to the ecosystem and its spatial dominance as well as its truculence at recolonizing a disturbed area. Recolonization by shoal grass is not frequently a problem. The plant has a surficial root and rhizome system that spreads rapidly. It grows from remaining fragments or from seed and can recolonize an area in a short time.

By comparison, turtle grass is much slower. Fuss and Kelly (1969) found 10 months were required for turtle grass to show new short shoot development. The short shoots seem to be sensitive to environmental conditions also. Kelly et al. (1971) found that after 13 months 40% of the transplants back into a central area had initiated new rhizome growth, while only 15% to 18% of the plants showed new growth initiation when transplanted to disturbed sediments. Thorhaug (1974) reported success with regeneration from turtle grass seedlings, but unfortunately seeding of turtle grass in quantity is a sporadic event in south Florida.

If one accepts 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 using a "ball" of sediment, similar to techniques in the 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, again a logical outgrowth of terrestrial technique.

Although numerous seagrass transplantings have been performed in south Florida, the recent study by Lewis et al. (1981) is the first to use all major seagrass species in a comprehensive experimental design that tests each of the techniques previously described in the literature. The study site was a 10-ha (25-acre) borrow pit on the southeast side of Craig Key in the central Florida Keys, which was studied from February 1979 to February

1981. The pit was created over 30 years ago as a source of fill material for the overseas highway. The dredged site is 1.3 to 1.7 m (4.3 to 5.6 ft) deep and is covered with fine calcareous sand and silt. The surrounding area is 0.3 to 0.7 m (1 to 2 ft) deep and is well vegetated, primarily with turtle grass, and portions of the borrow pit were gradually being revegetated.

The experimental design used a total of 22 combinations of plant species and transplantation techniques. Bare single short shoots and plugs of seagrass plus sediment (22 x 22 x 10 cm) were used for turtle grass, manatee grass, and shoal grass. Seeds and seedlings of laboratory-raised and field-collected turtle grass were planted, but seeds and seedlings of the other species proved impossible to find in sufficient quantity. Short shoots were attached to small concrete anchors with rubber bands and placed in hand-dug holes 1 to 3 cm deep, which were then filled with sediment. Seeds and seedlings were planted by hand without anchors after it was determined that anchors were detrimental to the survival of the seedlings. The large sediment plugs with seagrass were placed in similar sized holes made with another plugging device. Plugs and short shoots of all species were planted with both 1- and 2-m spacing, while the seeds and seedlings of turtle grass were planted using 0.3-, 1-, and 2-m spacings.

Of the 20 manipulations of species, planting techniques, and spacings, only three groups survived in significant numbers for the full 2 years: manatee grass plugs with 1-m spacing, and turtle grass plugs with both 1- and 2-m spacing. Turtle grass plugs showed the highest survival rate (90% to 98%), but did not expand much, increasing their coverage by a factor of only 1.6 during the 2 years. Manatee grass spread rapidly from plugs under the prevailing conditions and had increased its area by a factor of 11.4 in the 2-year period. The initial planting of shoal grass, however, died out completely after only a few months, and a second planting was made with larger, more robust plants from a different site. This planting survived sufficiently to increase its area by a factor of 3.4 after 1 year.

The transplants using short shoots of the various species were not nearly as successful. Although some of the treatments showed short-term growth and survival, none of the treatments using short shoots survived in significant quantitites. Similarly, the freshly collected seeds and seedlings of turtle grass showed no long-term survival at the barren transplant site, and showed only 4% survival when planted into an existing shoal grass bed. Seeds and seedlings that had been raised in the laboratory showed a modest survival of 29% when transplanted to the field, but even the survivors did not spread significantly.

Although several of the restoration techniques used by Lewis et al. (1981) proved to be technologically feasible, there are still major logistic and economic problems remaining. The plug technique showed the highest survival rate, but the cost estimates ranged from $27,000 to 86,500/ha. Because of the large volume and weight of the plugs, this method requires that large source beds be close to the transplantation site. The removal of large quantities of plugs can represent a major source of disturbance for the source bed, as the plug holes are as slow to recolonize naturally as propeller cuts and other similar disturbances. Despite the spreading recorded at the transplant site, the source holes for the plugs did not show any recolonization at the end of the 2-year period. If source material was required for a large scale revegetation project, the disturbance caused by the acquisition of the plugs could be a major impact itself. For this reason Lewis et al. (1981) suggested that this method be mainly used where there are source beds that are slated for destruction because of some developmental activity.

The only other technique that showed any significant survival was the utilization of laboratory cultivated seeds and seedlings. This method was prohibitively expensive with costs estimated at $182,900/ha, largely due to cultivation costs; survival was still below 30%. Seeds and seedlings are also suitable only in areas where the water motion is relatively quiescent, as their ability to remain rooted at this stage is minimal.

Transplants of tropical seagrasses may ultimately be a useful restoration 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 an experimental revegetation, especially when the relative survival of the plants is considered. Sufficient work has not been done to indicate whether tropical plants are really more recalcitrant than temperate ones. It is likely that continued research will yield more successful and cost-effective techniques.

8.6 THE LESSON OF THE WASTING DISEASE

The information overload that we are subjected to daily as members of modern society has rendered us immune to many of the predictions of doom, destruction, and catastrophe with which we are constantly bombarded. On a global scale, marine scientists recently feared the destruction of a major portion of the reefs and atolls of the Pacific by an unprecedented outbreak of the crown-of-thorns starfish (*Acanthaster planci*). The outbreak spread rapidly and the devastation was intense in the regions in which it occurred. Yet, within a few years *Acanthaster* populations declined. The enormous reef destruction that was feared did not occur and recovery commenced.

In south Florida in 1972-73 there appeared to be an outbreak of the isopod, *Sphaeroma terebrans*, which it was feared would devastate the Florida mangroves. This devastation never materialized, and it now appears that the episode represented a minor population excursion (see Odum et al. 1981 for complete treatment).

These episodic events proved to be short term and probably of little long-range consequence, yet the oceans are not nearly as immune to perturbations as many have come to think. We witness climatic changes having major effects and causing large-scale famine on land, but few think this can happen in the seemingly infinite seas. However, one such catastrophic disturbance has occurred in the seas, and it was in this century and induced by a natural process.

In the early 1930's, *Zostera marina*, a widespread northern temperate seagrass disappeared from a large part of its range. In North America, it virtually vanished from Newfoundland to North Carolina, and in Europe from Norway and Denmark south to Spain and Portugal. The outbreak began on the open marine coasts and spread to the estuarine regions.

Many changes accompanied this disturbance. Sandy beaches eroded and were replaced with rocky rubble. The protective effects of the grass beds were removed. The fisheries changed, although slowly at first, as their detrital base disappeared. Noticeable improvement did not become widespread until after 1945 (Rasmussen 1977), and full recovery required 30 to 40 years. It should be emphasized that this was a large-scale event. In Denmark alone over 6,300 km^2 (2,430 mi^2) of eelgrass beds disappeared (Rasmussen 1977). By comparison, south Florida possesses about 5,000 km^2 (1,930 mi^2) of submerged marine vegetation (Bittaker and Iverson, in press). Originally the wasting disease was attributed to a parasite, *Labyrithula*, but now it is felt that the cause was likely a climatic temperature fluctuation (Rasmussen 1973). As man's role shifts from that of passive observer to one of responsibility for large-scale environmental change, basic understanding of the fundamental processes of ecosystems is necessary to avoid his becoming the cause of associated large-scale disturbance comparable to the wasting disease.

8.7 PRESENT, PAST, AND FUTURE

Increasingly, studies have shown the importance of submerged vegetation to major commercial and forage organisms (Lindall and Saloman 1977; Thayer and Ustach 1981; Peters et al. 1979; Thayer et al. 1978b). Peters et al. (1979) found that in the Gulf States the value of the recreational salt water fish catch exceeded $168 million in 1973, which represents about 30% of the total U.S. recreational fishery (Lindall and Saloman 1977). Of this, 59% of the organisms caught were dependent on wetlands at some stage of their life cycle. Lindall and Saloman (1977) estimated an even higher dependency with over 70% of gulf recreational fisheries of the region being estuarine dependent.

The value of the estuarine regions to important commercial fisheries is even more striking. The Gulf of Mexico is the leading region of the United States in terms of both landings (35% of the U.S. total catch) and value (27% of U.S. total fishery value), according to Lindall and Saloman (1977), who also determined that about 90% of the total Gulf of Mexico and south Atlantic fishery catch is estuarine dependent.

The pink shrimp fishery, largest in the State of Florida, is centered around the Tortugas grounds where 75% of the shrimp caught in Florida waters are taken. Kutkuhn (1966) estimated the annual contribution of the Tortugas grounds to be 10% of the total gulf shrimp fishery, which in 1979 was worth $378 million (Thompson 1981). The vast seagrass and mangrove regions of south Florida are the nursery ground for this vitally important commercial fishery.

In the United States, 98% of the commercial catch of spiny lobsters come from habitats associated with the Florida Keys (Williams and Prochaska 1977; Prochaska and Cato 1980). In terms of ex-vessel value, the spiny lobster fishery is second only to the pink shrimp in the State of Florida (Prochaska 1976). Labisky et al. (1980) reported that the high in lobster landings, 11.4 million lb, was reached in 1972, and the maximum ex-vessel value of $13.4 million recorded in 1974. These figures include lobsters taken by Florida fishermen from international waters which encompass the Bahamian fishing grounds. Since 1975 the Bahamian fishing grounds have been closed to foreign fishing, placing greater pressure on domestic stocks (Labisky et al. 1980).

There is an increasing need for more precise information to first understand and then to manage these resources intelligently. Although south Florida has been late in developing compared with most other regions of the United States, the pressures are becoming overwhelming. The fishery pressure on the two leading commercial species--pink shrimp and lobster--already intense, will inevitably increase. The Bahamian waters, formerly open to U.S. lobstermen, are now closed putting more pressure on the already depleted stocks. In the past about 12% of the shrimp landed on the Florida gulf coast was caught in Mexican waters. Recently the Mexican government announced that the enabling treaty would not be renewed. These actions will put increasing pressure on domestic stocks. As this is happening, development in the region is dramatically escalating. In the eyes of many, the main limitations to further development in the Florida Keys were fresh water availability and deteriorating access highways. All of the bridges in the Keys are now being rebuilt and a referendum was recently passed to construct a 36-inch water pipeline to replace the old Navy line. The price of building lots took a 30% to 50% jump the day after the water referendum passed and in many areas had doubled 6 months after the passage.

It is depressing to read, "Today the mackerel and kingfish are so depleted that they have almost ceased to be an issue with the professional fisherman," or "The luscious crawfish, however, is now in a crucial stage in its career. Largely gone from its more accessible haunts, it has been preserved so far on the reef.... Economic pressure and growing demand however, have developed more intensive and successful methods of catching them, and though a closed season has been put on them, in the open months uncalculable thousands are shipped to market and they are rapidly disappearing." Today we find little surprise in these statements, having come to expect this sort of natural decline with increasing development. What is surprising is that this statement is taken from a chapter entitled, "Botany and Fishing; 1885-6," from the story of the founder of Coconut Grove, Ralph M. Monroe (Munroe and Gilpin 1930).

Today we see south Florida as a tantalizing portion of the lush tropics, tucked away on the far southeast coast of the United States. It is not insignificant in size, and its natural productivity is enormous. Although the waters still abound with fish and shellfish, in quantities that often amaze visitors, it is useful to think back to how productive these waters must have been.

Their future productivity remains to be determined. Present productivity can be maintained, although that will not be easy considering the ever-increasing developmental pressures. A catastrophic decline is certainly possible; merely maintaining the current economic and development growth rates will provide that effect. This point was well made by one of the reviewers of this manuscript whose comments I paraphrase here: Insidious gradual change is the greatest enemy, since the observer is never aware of the magnitude of change over time. A turbidity study in Biscayne Bay showed no significant differences in turbidity between consecutive years during 1972 and 1977, but significant change between 1972 and 1975 (or between 1973 and 1976). In other words, south Biscayne Bay was significantly more turbid in 1977 than 1972, but a 2-year study would not have uncovered it (J. Tilmant, National Park Service, Homestead, Florida; personal communication). To properly manage the region, we must understand how it functions. Decades ago it would have been possible to maintain productivity just by preserving the area and restricting human influence. Now water management decisions a 100 miles away have profound changes on the fisheries. Enlightened multi-use management will require a greater knowledge of the complex ecological interactions than we possess today.

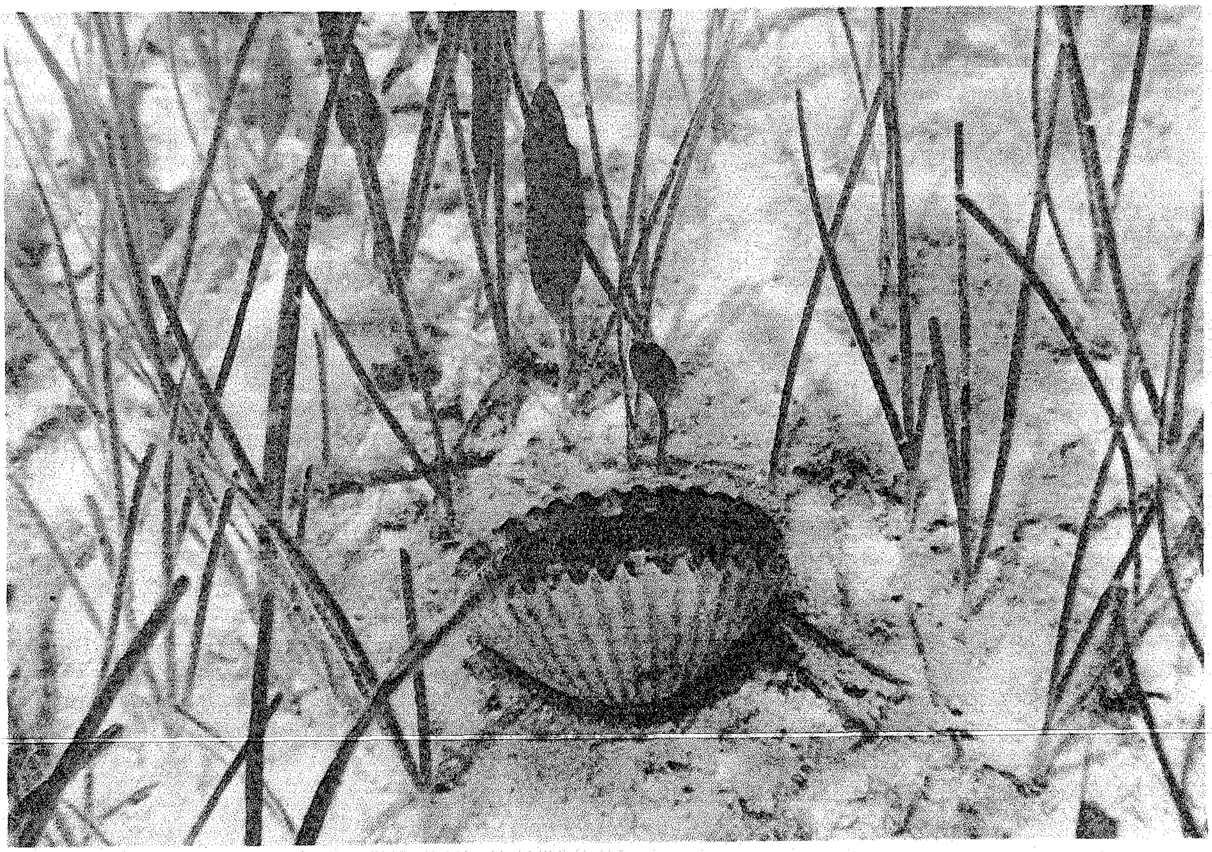


Figure 27. Scallop on the surface of a shallow Halodule bed in Western Florida Bay.

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APPENDIX

KEY TO FISH SURVEYS IN SOUTH FLORIDA

Survey number	Location	Reference
1	North Biscayne Bay	Roessler 1965
2	South Biscayne Bay	Bader and Poessler 1971
3	Card Sound	Brook 1975
4	Metecumbe Key	Springer and McErlean 1962b
5	Porpoise Lake	Hudson et al. 1970
6	Whitewater Bay	Tabb and Manning 1961
7	Fakahatchee Bay	Carter et al. 1973
8	Marco Island	Weinsteain et al. 1971
9	Rookery Bay	Yokel 1975a
10	Charlotte Harbor	Wang and Raney 1971

Key to abundance

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

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Orectolobidae/nurse sharks												
Ginglymostoma cirratum nurse shark	r	r			p						Fish: *Acanthurus* sp., clupeids, scarids *Mugil* sp., *Jenkinsia* sp., *Cantherhines pullus*; molluscs; cephalopods	Randall 1967; Clark and von Schmidt 1965
Carcharhinidae/requiem sharks												
Negeprion brevirostris lemon shark					p						Fish: *Bagre marinus*, *Chilomycterus schoepfi*, *Galeichthys felis*, *Mugil* sp. *Rhinobatos lentiginosus*; octopods	Clark and von Schmidt 1965; Randall 1967
Sphyrnidae/hammerhead sharks												
Sphyrna tiburo bonnethead					p						Crabs: *Callinectes sapidus*, stomatopods; shrimp; isopods; barnacles; bivalves; cephalopods; fish	Bolke and Chaplin 1968 Clark and von schmidt 1965
Pristidae/sawfishes												
Pristis pectinata smalltooth sawfish					p							
Rhinobatidae/guitarfishes												
Rhinobatus lentiginosus atlantic guitarfish	r											
Torpedinidae/electric rays												
Narcine brasiliensis lesser electric ray	r					r	r					
Rajidae/skates												
Raja texana roundel skate		r									Annelids; crustacea; fishes	Reid 1954
Dasyatidae/stingrays												
Urolophus jamaicensis yellow stingray	r	r										
Gymnura micrura smooth butterfly ray							r	r			Fish: *Centropristis striata*, molluscs: *Solemya* sp.; annelids; shrimp; small crustaceans	Peterson and Peterson 1979

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Dasyatidae/stingrays (continued)												
Dasyatis americana southern stingray					p						Fishes; sipunculids; crabs; polychaetes; shrimp; hemichordates; stomatopods	Randall 1967
Dasyatis sabina atlantic stingray								r				
Elopidae/tarpons												
Elops saurus ladyfish					p						Fishes: *Lagodon rhomboides*; shrimp: *Penaeus setiferus*	Gunter 1945; Reid 1954; Austin and Austin 1971; Odum and Heald 1972;
Megalops atlantica tarpon					p						Fishes: *Allanetta harringtonensis*, *Atherinomorus stipes*	Randall 1967; Austin and Austin 1971
Albulidae/bonefishes												
Albula vulpes bonefish					p						Molluscs: *Codakia costata*; crabs; shrimp; fish	Bolke and Chaplin 1968
Muraenidae/morays												
Gymnothorax nigromarginatus blackedge moray			r									
Ophichthidae/snake eels												
Myrophis punctatus speckled worm eel				r		r	r		r		Crabs	Reid 1954; Springer and Woodburn 1960
Ophichthus gomesi shrimp eel						r			r			
Clupeidae/herrings												
Harengula pensacolae scaled sardine			r	r		r			r	c	Juveniles: veligers, crab megalops, amphipods, mysids, copepods, isopods, chironomid larvae	Carr and Adams 1973; Odum and Heald 1972
Harengula humeralis redear sardine			r								Fishes; polychaetes; shrimp larvae; plants: *Enteromorpha* sp., *Thalassia*, *Syringodium*; crab larvae	Randall 1967
Jenkinsia sp.				r							*J. lamprotaenia* - copepods; shrimp larvae; crab larvae; amphipods; fish eggs	Randall 1967

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number										Diet	Source
	1	2	3	4	5	6	7	8	9	10		
Clupeidae/herrings (continued)												
Brevoortia smithi yellowfin menhaden									r			
Opisthonema oglinum atlantic thread herring				r	r					r	Veligers; copepods; detritus; polychaetes; shrimp; fishes; shrimp and crab larvae; mysids; tunicates; stomatopod larvae; eggs; gastropod larvae; other rare items	Randall 1967; Carr and Adams 1973
Sardinella anchovia spanish sardine				r					r			
Engraulidae/anchovies												
Anchoa cubana cuban anchovy				r							Ostracods; copepods	Springer and Woodburn 1960
Anchoa lamprotaenia bigeye anchovy				a	p							
Anchoa mitchilli bay anchovy		r		r	p	c	r		r	c	Less than 23 mm SL veligers, copepods, eggs; 31 to 62 mm SL: amphipods, detritus, ostracods, zooplankton, mysids, harpacticoid copepods, small molluscs, chironomid larvae	Carr and Adams 1973; Reid 1954;
Anchoviella perfasciata flat anchovy				r								
Anchoa hepsetus striped anchovy						r	r		r	c	Veligers; copepods; mysids; zooea; fish; eggs	Carr and Adams 1973; Springer and Woodburn 1960
Synodontidae/lizardfishes												
Synodus foetens inshore lizardfish	r	r	r	r	p	c	r	r	r	r	Fishes: gobies, killifish, silver perch, pipefish, pigfish, juvenile seatrout, puffer; shrimp; plant detritus	Carr and Adams 1973; Reid 1954; Randall 1967
Ariidae/sea catfishes												
Bagre marinus gafftopsail catfish									r		*Callinectes sapidus*; fishes	Odum and Heald 1972
Arius felis sea catfish					p	r		r	r		Crabs; *Rhithropanopeus harrisii*, amphipods; mysids; fishes; copepods; shrimp	Odum and Heald 1972; Reid 1954

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Batrachoididae/toadfishes												
Opsanus beta gulf toadfish	c	a	r	r	p	c	c	c	r		Crabs; penaeid and crangonid shrimp; *Palaemonetes* sp., *Alpheus heterochaelis*; *hermit crabs*; molluscs; amphipods; fish; *Lagodon rhomboides*	Reid 1954; Odum and Heald 1972
Porichthys porosissmus atlantic midshipman						r						
Gobiesocidae/clingfishes												
Acyrtops beryllina emerald clingfish	r			r								
Gobiesox strumosus skilletfish				r	p	r					Amphipods; isopods; chironomid larvae	Odum and Heald 1972
Antennaridae/frogfishes												
Histrio histrio sargassumfish			r	r								
Ogcocephalidae/batfishes												
Ogcocephalus cubifrons				r								
Ogcocephalus nasutus shortnose batfish	r										Pelecypods; gastropods; *Nassarius vivex*; *Cerithium mucarium*; *Urosalphinx tampaensis*; *Bittium* sp.; *Mitrella* sp.; *Modulus modulus*; *Olivella mutica*; *Haminoea elegans*; *Anachris avara*; *polychaetes*	Reid 1954
Ogcocephalus radiatus polka-dot batfish												
Gadidae/codfishes												
Urophysis floridanus southern hake				r							Shrimps; fishes; *Lagodon rhomboides*; amphipods; copepods; crabs; gastropods	Reid 1954; Springer and Woodburn 1960
Ophididae/cusk-eels and brotulas												
Ogilbia cayorum key brotula		r	r			r						
Ophidion holbrooki bank cusk-eel	r											

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number										Diet	Source
	1	2	3	4	5	6	7	8	9	10		
Ophididae/cusk-eels and brotulas (continued)												
Gunterichthys longipenis gold brotula									r			
Carapidae/pearlfishes												
Carapus bermudensis pearlfish				r								
Exocoetidae/flying fishes and halfbeaks												
Hemiramphys brasiliensis ballyhoo				r							Seagrasses: Thalassia, Syringodium, fishes: Jenkinsia sp.	Randall 1967
Chridorus atherinoides hardhead halfbeak					p							
Hyporhamphus unfasciatus halfbeak					p	r				r	Juveniles zooplankton; crab megalops larvae, veligers, copepods, insect remains. Sub-adults and adults epiphytic algae and detritus, seagrasses, occasional microcrustacea	Carr and Adams 1967
Belonidae/needlefishes												
Strongylura notata redfin needlefish			r	r	p	r				r	Shrimp	Reid 1954
Strongylura timucu timucu				r		r				r	Fishes: Anchoa parva, Jenkinsia sp.; shrimp; copepods; insects	Randall 1967; Reid 1954; Srpinger and Woodburn 1960
Tylosurus crocodilus houndfish				r							Fishes: Acanthurus sp., Anchoa sp., Cetengraulis edentulus, Harengula humeralis, Mugil sp.; shrimp	Randall 1967
Cyprinodontidae/killifishes												
Flordichthys carpio goldspotted killifish			c	a		r					Amphipods, copepods, polychaetes, filamentous algae, diatoms, detritus, ostracods, chironomid larvae, isopods, nematodes	Brook 1975; Odum and Heald 1972
Adinia xenica diamond killifish						r					Detritus, diatoms, filamentous algae, amphipods, insects, copepods	Odum and Heald 1972
Lucania parva rainwater killifish		a	r	r	p	r			r	r	Amphipods, musids, chironomid larvae, insects, molluscs, detritus, copepods, cumaceans	Odum and Heald 1972

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number										Diet	Source
	1	2	3	4	5	6	7	8	9	10		
Cyprinodontidae/killifishes (continued)												
Fundulus heteroclitus mummichog			r								Small crustaceans: amphipods, isopods, tanaids, ostracods, copepods; polychaetes, detritus, algae, insects, crabs, fish, gastropods, eggs	Peterson and Peterson 1979
Cyprinodon variegatus sheepshead minnow					p					r	Detritus, filamentous green algae, filamentous blue-green algae, diatoms, crustaceans, nematodes	Odum and Heald 1972
Rivulus marmoratus rivulus						r						
Poeciliidae/livebearers												
Poecilia latipinna sailfin molly					p					r	Detritus; filamentous algae; diatoms	Odum and Heald 1972; Springer and Woodburn 1960
Gambusia affinis mosquitofish						r					Amphipods; algae; hydracarina; chironomid larvae; insects	Odum and Heald 1972
Heterandria formosa least killifish						r					Chironomid larvae; copepods; green algae; diatoms; cladocerans; insects	Odum and Heald 1972
Atherinidae/silversides												
Allanetta harringtonensis reef silverside			c	r	p						Copepods: *Corycaeus* sp., *Labidocera scotti*, *Paracalanus crassirostris*; fish larvae; polychaete larvae	Randall 1967; Brook 1975
Atherinomorus stipes hardhead silverside			a	a							Day. copepods; plants; amphipods; tanaids; insects; polychaetes. night. amphipods; polychaetes; cumacea; copepods; isopods; ostracods; nebalids; insects; plants	Brook 1975; Randall 1967
Menidia beryllina tidewater silverside						r			r	c	Day less than 25 mm SL; veligers; detritus; copepods. Greater than 30 mm; copepods; veligers; insects; chironmid larvae; amphipods; hydracarina; algae; detritus; mysids night greater than 30 mm; mysids, amphipods, copepods, chironomid larvae	Carr and Adams 1973; Odum and Heald 1972

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number										Diet	Source
	1	2	3	4	5	6	7	8	9	10		
Atherinidae/silversides (continued)												
Membras martinica rough silverside					p						Copepods; insects (listed under *Membras martinica vagrans*)	Reid 1954
Membras vagrans					r				r			
Syngnathidae/pipefishes and seahorses												
Corythoichthys albirostris whitenose pipefish	r	r		r								
Corythoichthys brachycephalus crested pipefish				r								
Hippocampus hudsonius			r									
Hippocampus zosterae dwarf seahorse	r	c	r	r	p	r	r	r	r		Shrimp; microcrustaceans	Reid 1954
Hippocampus erectus lined seahorse	r	r	r			r		r	r			
Hippocampus reidi longsnout seahorse								r				
Syngnathus dunckeri pugnose pipefish				r								
Syngnathus floridae dusky pipefish	c	r	r	r	p	r		r		r	Shrimp; amphipods; tanaids; isopods; copepods; nebalids	Reid 1954; Brook 1975; Springer and Woodburn 1960
Syngnathus louisianae chain pipefish	r		r	r		r	r	r	r	r	Copepods; amphipods; shrimp	Reid 1954
Syngnathus scovelli gulf pipefish	r	r	c	r	r	c	a	c	c	c	Amphipods; copepods; tanaids; isopods; shrimp; nebalids	Brook 1975; Reid 1954 Springer and Woodburn 1960
Micrognathus crinigerus fringed pipefish		a	r		p			r			Copepods; microcrustaceans	Reid 1954
Centropomidae/snooks												
Centropomus undecimalis snook					p						Fishes: *Eucinostomus* sp., *Mugil cephalus*, *Lagodon rhomboides*, *Anchoa* sp., *Poecilia latipinna*, and *Gambusia affinis*; caridean and penaeid shrimp; crabs; crayfish	Marshall 1958; Austin and Austin 1971; Odum and Heald 1972

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Serranidae/sea basses												
Mycteroperca bonaci black grouper				r							Fishes: *Fistularia tabacaria*, *Haemulon flavolineatum*	Randall 1967
Mycteroperca microlepis gag	r	r			p		r	r	r		Shrimp; fish	Reid 1954
Serraniculus pumilio pygmy sea bass								r				
Serranus subligarius belted sandfish								r				
Diplectrum bivittatum dwarf sand perch	r											
Diplectrum formosum sand perch	r					r	r	r	r	r	Caridean and palaemonid shrimps; mysids	Reid 1954
Epinephalus morio red grouper	r										Crustaceans; fishes	Randall 1967
Epinephalus itajara jewfish					p						Lobsters; *Panulirus argus*, *Scyllardes aequinoctialis*, fishes; *Dasyatis americana*, *Diodon* sp.; crabs; sea turtles; *Eretmochelys imbricata*	Randall 1967
Apogonidae/cardinalfishes												
Astrapogon alutus bronze cardinalfish	r	r										
Astrapogon stellatus conchfish		r										
Rachycentridae/cobias												
Rachycentron canadum cobia					p						Fishes: *Lactophrys* sp., *Lactophrys triqueter*	Randall 1967
Echeneidae/remoras												
Echeneis naucrates sharksucker				r							Fishes: larval *Catherines pullus*; isopods; crustaceans	Randall 1967

List of fishes and their diets from collections in south Florida.

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Carangidae/jacks and pompanos												
Caranx hippos crevalle jack				r	p					r	Fishes: *Prionotus scitulus*	Randall 1967
Caranx latus horse-eye jack			r								Fishes: atherinids, *Harengula* sp., *Myripristis jacobus*; pteropods; penaeid shrimp; isopods	Randall 1967
Caranx ruber bar jack					p						Fishes: larval *Acanthurus* sp., *Acanthurus coerulus*, *Anchoa hepsetus*, atherinids, engraulids, *Entomarcrodus nigricans*, *Harengula clueola*, *Jenkinsia* sp., *Monocanthus* sp., mullid, *Ophioblennius atlanticus*, *Pomacentrus planifrons*, *Pseudupeneus maculatus*, scarids, *Scarus croicensis*, *Sparisoma aurofrenatus*, *Sparisoma viride*; syngnathid; shrimps; penaeid, *Tozeuma* sp.; mysids; squids; stomatopods; gastropods; crabs	Randall 1967
Trachinotus falcatus permit			r							c	Juvenile fishes; anchovies, tidewater silversides, crabs; *Petrolisthes* sp.; gastropods; shrimp; mysids. adults gastropods; *Astraea longispina*, *Cerithium* sp., *Columbella mercatoria*, *Oliva* sp., *Strombus gigas*, *Tegula lividomaculata*, *Turbo castanea*; echinoids: *Diadema antillarum*, *Echinometera* sp.; pelecypods; *Arca zebra*, *Glycymeris decussata*, *Trachycardium magnum*; hermit crabs: *Pauristes grayi*, crabs: *Albunea gibbesii*, porcellanids.	Carr and Adams 1973; Randall 1967
Trachinotus carolinus florida pompano										r		
Oligoplites saurus leatherjacket					p	r				r	Mysids; shrimp; ectoparasites; copepods	Carr and Adams 1973; Tabb and Manning 1961; Odum and Heald 1972
Selene vomer lookdown						r					Shrimp; other crustaceans, small molluscs	Peterson and Peterson 1979

List of fishes and their diets from collections in south Florida.

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Lutjanidae/snappers												
Lutjanus analis mutton snapper		r		r							Crabs: *Calappa gallus*, calappids, *Cronius ruber*, *majid*, *Parthenope serrata*, *Petrolisthes* sp., portunids, *Portunus* sp., *Portunus sebrae*, *Ranilia muricata*, fishes: *Acanthurus bahianus*, *Diodon* sp., *Fistularia tabacaria*, gobiids, *Haemulon* sp., *Haemulon aurolineatum*, *Halichoeres garnoti aurolineatum*, *Halichoeres garnoti*, *Holocentrus ascensionis*, *Malacanthus plumeri*, *Monocanthus* sp., *Monocanthus setifer*, *Pseudupeneus maculatus*, scarids, *Scorpaena plumeri*, *Sphoeroides spengleri*; gastropods: *Fasciolaria tulipa*, *Murex pomum*, *Strombus* sp., *Strombus gigas*; octopuses; hermit crabs: *Petrochirus diogenes*; penaeid shrimp; lobster: *Panulirus argus*; stomatopods: *Lysiosquilla glabriuscula*	Randall 1967
Lutjanus apodus schoolmaster		r		a	p						Fishes: atherinids, *Aulostomus maculatus*, *Bodianus rufus*, *Cantherhines pullus*, *Chromis multilineata*, *Gymnothorax moringa*, *Haemulon* sp., *Jenkinsia* sp., *Pomcentris fuscus*, scarids, *Scorpaena plumeri*, scorpaenids, serranids, *Sparisoma* sp., *Sparisoma aurofrenatum*; crabs: *Actaea acantha*, calappids, majids, *Mithrax sculptus*, *Pernon gibbesi*, *Portunnus sebrae*, portunids; stomatopods; shrimp; octopuses; gastropods	Randall 1967
Lutjanus griseus gray snapper		r	r	c	p	r	r	r	r		Crabs: *Callinectes* sp., goneplacids, portunids, xanthids; fishes: *Jenkinsia* sp.; penaeid shrimp; gastropods; *Strombus gigas*; scyllarid lobsters	Randall 1967; Reid 1954; Croker 1962; Springer and Woodburn 1960; Odum and Heald 1972

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number										Diet	Source
	1	2	3	4	5	6	7	8	9	10		
Lutjanidae/snappers (continued)												
Lutjanus jocu dog snapper		r									Fishes: atherinids, *Aulostomus maculatus*, *Clepticus parrae*, *Gymnothorax moringa*, *Haemulon* sp., *Haemulon plumeri*, *Haemulon aurolineatum*, *Holocanthus tricolor*, *Holocentrus* sp., *Holocentrus rufus*, *Jenkinsia* sp., *Myrichthys* sp., ophichthids, *Opisthonema oglinum*, *Pseudupeneus maculatus*, scarids, serranids, *Sparisoma* sp., *Sparisoma viride*, *Xanthihthys ringens*; crabs: *Carpilius corallinus*, *Cronius ruber*, *Pitho lherminieri*, portunids, *Portunus* sp.; octopuses: *Octopus vulgaris*; lobsters; *Panulirus argus*, *Panulirus guttatus*, gastropods: *Strombus gigas*; squid; fish eggs; scyllarid lobsters	Randall 1967
Lutjanus synagris lane snapper		r			p	c	r	a	c	r	Crabs: goneplacids, *Leiolambrus nitidus*, portunids; stomatopods: *Lysiosquilla glabriuscula*; fish; shrimp; mysids; copepods	Randall 1967; Reid 1954; Springer and Woodburn 1960
Ocyurus chrysurus yellowtail snapper	r			r							Crabs: *Callappa ocellata*, *Mithax* sp., *Mithax Mithax sculptus*, *Pitho aculeata*; shrimp: caridean, penaeidean, *Sicyonia laevigata*, *Trachycaris restirctus*; fish: *Jenkinsia* sp.; siphonophores; pteropods; *Calvolina* sp.; copepods; cephalopods; mysids; tunicates; ctenophores; gastropods: *Strombus gigas*; stomatopods: *Gonodactylus oerstedii*, *Pseudosquilla ciliata*; scyllarid larvae; heteropods; plecypods; eggs; euphausids; gastropod larvae; amphipods; insects	Randall 1967
Lobotidae/tripletails												
Lobotes surinamensis tripletails				r								
Gerridae/mojarras												
Eucinostomus argenteus spotfin mojarra	r	c	c	r	p	r	r	r	r	c	Less than 63 mm copepods, amphipods, mysids, molluscs, detritus, chironomid larvae.75 to 152 mm amphipods; *Hyale* sp., polychaetes; eunicids, crabs; calappids, majids, raninids, shrimp; alpheids, *Callianassa* sp., tanaids, plecypods; *Tellina* sp., sipunculids, copepods, gastropods	Odum and Heald 1972; Randall 1967; Brook 1975

List of fishes and their diets from collections in south Florida.

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	1	2	3	4	5	6	7	8	9	10		
Gerridae/mojarras (continued)												
Eucinostomus gula silver jenny	r	r	a	a	p	a	a	a	a	a	Less than 60 mm—polychaetes; copepods; amphipods; mysids; small shrimp; small molluscs; detritus	Carr and Adams 1973; Odum and Heald 1972; Reid 1954; Brook 1975
Eucinostomus lefroyi mottled mojarra				r								
Gerres cinereus yellowfin mojarra			r								Crabs: hippids, majids, portunids; pelecypods: Laevicardium sp., Macoma cerina, Solemya occidentalis, Tellina sp., Yoldia perprotracta; gastropods: Acmaea antillarum, Fissurella barbadensis, Hemitoma octoradiata, Olivella sp., Tricolia tessellata; polychaetes; sipunculids; Aspidosiphon sp., shrimps; alpheids; Callianassa sp., stomatopods; Gonodactylus oerstedii, hemichordates; ophiuroids; Ophiothrix sp., amphipods	Randall 1967; Austin and Austin 1971
Pomadasyidae/grunts												
Haemulon flavolineatum french grunt			r	r							Polychaetes: capitellids, Eunice sp., maldanids, terebellids; crabs, sipunculids; Aspidosiphon sp.; chitons; Acanthochitona pygmaea; holothurians; isopods; shrimps; octopuses; pelecypods: Pitar sp., Tellina sp.; ophiuroids: Ophiothrix sp., echinoids: Diadema antillarum, spatangoid; scaphopods: Cadulus sp., Dentalium sp.; hermit crabs; stomatopods; amphipods, gastropods: Arene sp.	Randall 1967; Davis 1967
Haemulon parrai sailors choice	r	r	r	c							Shrimps: alpheids, carideans, penaeids; crabs: majids, portunids; amphipods; gastropods: Olivella sp.; anemones: Phyllactis flosculifera; holothurians; polychaetes; pelecypods: Gouldia cerina, Pecten sp., pitar sp., Solemya occidentalis, Tellina sp.; ophiuroids; isopods; stomatopods; scaphopods: Cadulus sp.	Randall 1967; Davis 1967

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Haemulon sciurus bluestriped grunt		r	c	r	p	r					Crabs: portunids, xanthids; pelecypods: *Macoma cerina*, *Pitar fulminata*, *Tellina caribaea*; shrimps; alpheids, axiids, echinoids: *Diadema antillarum*; ophiuroids: *Ophiothrix* sp.; polychaetes; gastropods: *Acmaea* sp., *Anachis* sp., *Arene* sp., *Bittium varium*, *Cylostremiscus ornatus*, *Diodora* sp., *Hyalina* sp., *Hylina albolineata*, *Mangelia* sp., *Melampus coffeus*, *Mitra barbadensis*, *Modulus modulus*, *Nitidella* sp., *Olivella* sp., *Persicula lavalleeana*, *Rissoina* sp., *Strombus gigas*; ciliatas; sipunclids; fishes; amphipods; octopuses; isopods; tunicates; ostracods; bryozoans; scaphopods; *Cadulus* sp.; tanaids; hermit crabs	Randall 1967; Davis 1967
Haemulon aurolineatum tomtate	r	r						r			Shrimps: larvae; polychetes: *Chloeia* sp.; eggs; hermit crabs; larvae; amphipods: *Ampelisca* sp., *Elasmopus* sp., *Eurystheus* sp., *Megamphopus* sp., *Photis* sp.; copepods: *Undinula vulgaris*; gastropods: *Alvania auberiana*, *Caecum pulchellum*, *Retusa* sp.; pelecypods: *Solemya occidentalis*; barnacle larvae; tanaids; scaphopods: *Cadulus acus*; isopods	Randall 1967; Davis 1967
Haemulon plumeri white grunt	a	r		a				a	r		Less than 40 mm copepods, mysids or shrimp, detritus. 130-279 mm crabs: *Mithrax* sp.; polychaetes; echinoids: *Diadema antillarum*, *Eucidaris tribuloides*; spatangoid, sipunculids: *Aspidosiphon* sp.; gastropods: *Acmaea antillarum*, *Strombus gigas*; shrimps; alpheids, ophiuroids: *Ophiothrix* sp.; fishes; hemichordates; holothurians: *Thyone pseudofusus*; pelecypods: *Cumingia* antillarum, chitons: *Ischnochiton papillosus*, amphipods, tanaids	Carr and Adams 1973; Randall 1967; Reid 1954; Davis 1967

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Pomadasyidae/grunts (continued)												
Haemulon carbonarium ceasar grunt		r									Crabs; majids, *Pisosoma* sp., gastropods; *Acmaea pustulata*, *Columbella mercatoria*, *Diodora* sp., *Emarginula pumila*, *Fissurella* sp., *Fissurella barbadensis*, *Hyalina* sp., *Nitidella* sp., echinoids; *Diadema antillarum*, *Echinometra* sp., *Echinometra viridis*, chitons; *Ischnochiton papillosus*, polychaetes, ophiuroids; *Ophicoma echinata*, *Ophiothrix* sp., sipunculids, shrimp; alpheids, barnacle appendages, fish; blennoid, amphipods, astracods	Randall 1967; Davis 1967
Anisotremus virginicus porkfish	r							r			Ophiuroides; *Ophiothrix* sp., crabs, shrimps; alpheids, carideans, polychaetes; *Eunice* sp., isopods; anthurids, *Asellote* sp., *Cymodoce* sp., excorallanid, sphaeromid, pelecypods; *Americardia guppyi*, *Americardia media*, *Chione* sp., *Chione cancellata*, *Cumingia antillarum*, *Papyridea semisulcata*, *Pecten* sp., stomatopods, gastropods; *Columbella mercatoria*, *Hyalina* sp., *Mitra* sp., *Modulus modulus*, *Olivella* sp., *Zebina browniana*, amphipods; caprellids, gammarids, lysianassids, metopids, copepods; harpacticoids, tunicates; *Tridemnun savignii*, tanaids, ostracods; *Bairdoppilata carinata*, *cypridinine*, chitons, hermit crabs foraminifera, nebaliaceans; *Nebalia* sp., scaphopods: *Dentalium* sp.	Randall 1967; Davis 1967
Orthopristis chrysoptera pigfish		r			p	c	a	a	a	r	Fish of SL 25-50 mm: copepods, ostracods, shrimps, polychaetes; SL 51-150 mm: shrimps, amphipods, copepods, polychaetes, crabs, fishes; SL greater than 150 mm: polychaetes, shrimps, crabs, mollusks, amphipods, insects	Reid 1954; Carr and Adams 1973

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	1	2	3	4	5	6	7	8	9	10		
Sparidae/porgies												
Archosargus probatocephalus sheepshead			r		p	r	r		r		Less than 50 mm amphipods, copepods, polychaetes; larger than 50 mm molluscs, barnacles, algae	Springer and Woodburn 1960; Odum and Heald 1972
Archosargus rhomboides sea bream			r								Seagrass: *Syringodium filiforme*, *Thalassia testudinum*; algae; crabs; gastropods; eggs; pelecypods: *Pinctada ladiata*; polychaetes; amphipods	Randall 1967; Austin and Austin 1971
Lagodon rhomboides pinfish	c	c	r	c	p	a	a	a	a	a	Less than 35 mm copepods; amphipods; mysids; epiphytes; polychaetes; crabs. SL 36-65 mm epiphytes; shrimps; mysids; crabs; fish; amphipods; copepods; detritus. SL greater than 65 mm shrimp, fish; epiphytes; mysids; detritus; crabs; amphipods; copepods	Carr and Adams 1973; Reid 1954; Brook 1975
Calamus arctifrons grass porgy	r								r		Copepods; amphipods; musids; shrimps; pelecypods; gastropods: *Mitrella* sp., *Bittium* sp.; polychaetes	Reid 1954
Calamus calamus saucereye porgy		r									Polychaetes; ophiuroids: *Ophioderma* sp., *Ophiothrix* sp.; pelecypods: *Codakia orbicularis*, *Gouldia cerina*, *Pinna carnea*; hermit crabs; crabs: majid, echinoids: *Diadema antillarum*, gastropods: *Nassarius albus*, *Tegula* sp., *Tegula fasciata*; chitons; sipunculids: *Aspidosiphon* sp.	Randall 1967
Sciaenidae/drums												
Menticirrhus focaliger minkfish				r						c		
Sciaenops ocellata red drum					p				r	r	SL 31-46 mm mysids; polychaetes; amphipods; shrimp: *Palaemonetes intermedius*. SL 59-126 mm fish: *Micropogon undulatus*; shrimp; crabs; insect larvae; mysids. SL 100-500 mm shrimp: penaeids; crabs: xanthids, *Rithropanopeus harrisii*, portunids	Springer and Woodburn 1960; Odum and Heald 1972;
Bairdiella chrysura silver perch	r	r				c	a	a	c	c	SL 25-99 mm shrimp; copepods; amphipods; mollusks; fishes, polychaetes. SL 100-130 mm shrimp, amphipods, crabs, mollusks, fish: *Anchoa mitchilli*	Reid 1954; Odum and Heald 1972; Springer and Woodburn 1960

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Sciaenidae/drums (continued)												
Cynoscion nebulosus spotted seatrout					p	r	c	r	r	r	Juveniles mysids; chironomid larvae; carideans; fishes; *Gobiosoma robustum*. Greater than 150 mm shrimp: *Penaeus duorarum*, fishes: *Anchoa michilli*, *Mugil cephalus*, *lagodon rhomboides*, *Eucinostomus gula*, *E. argenteus*, *Cyprinodon variegatus*, *Gobiosoma robustus*	Odum and Heald 1972; Springer and Woodburn, 1960; Tabb 1966b; Stewart 1961
Equetus acuminatus high-hat	r										Shrimps: alpheids, palemonids, *Periclimenes* sp., *Processa* sp., penaeids, crabs: *Petrolisthes galathinus*; fishes; isopods; stomatopods; copepods; amphipods	Randall 1967
Bairdiella batebana blue croaker								r				
Odontoscion dentex reef croaker	r										Shrimp: larvae, alpheids, carideans, penaeids; fishes: larvae; isopods: *Excorallana antillensis*; crabs; stomatopod larvae	Randall 1967
Leiostomus xanthurus spot									c	a	Less than 40 mm copepods; ostracods; chaetognaths. Greater than 40 mm filamentous algae; desmids; forams; mysids; copepods; amphipods; ostracods; isopods; chaetognaths; insect larvae; pelecypods; gastropods; polychaetes	Springer and Woodburn 1960
Cynoscion arenarius sand seatrout							r		r	r	Fishes; shrimp: *Palaemonetes* sp.; mysids; amphipods; crab zoea	Springer and Woodburn 1960; Reid 1954
Micropogon undulatus atlantic croaker										r	SL 30-107 mm copepods; mysids; caridean shrimp; polychaetes; insect larvae; isopods; pelecypods	Springer and Woodburn 1960
Menticirrhus americanus southern kingfish							r		r	c	Polychaetes; crabs; mysids: *Emerita* sp.	Springer and Woodburn 1960; Reid 1954

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number										Diet	Source
	1	2	3	4	5	6	7	8	9	10		
Mullidae/goatfishes												
Pseudupeneus maculatus spotted goatfish				r							Crabs: calappids, grasoid, majids, portunids, xanthids; shrimps: alpheids, carideans, palaemonid, penaeid, *Tozeuma* sp.; polychaetes; pelecypods; *Pecten* sp., *Tellina* sp., siphunculids; *Aspidosiphon cumingi*, fishes: *Coryphopterus personatus*, syngnathids, stomatopods; *Pseudosquilla ciliata*, *isopods*, *amphipods*, *ophiuroids*, gastropods; *Turbonilla* sp., ostracods, tanaids, eggs	Randall 1967
Ephippidae/spadefishes												
Chaetodipterus faber atlantic spadefish				r	p		r	r	r		Sponges; zoantharians; *Rhodactis sacntithomae*, *Zoanthus* sp., polychaetes; *Sabellastarte magnifica*, tunicates; salps, gorgonians; *Muricea laxa*, algae; gastropod eggs; holothurians; corals; *Oculina diffusa*, *seagrasses*; *Syringodium filiforme*, heteropods; crab larvae; amphipods; hyperiids	Randall 1967
Chaetodontidae/butterflyfishes												
Pomacanthus arcuatus gray angelfish	r										Sponges, tunicates; didemnid; algae; *caulerpa* spp., *Penicillus pyriformis*, *Dictyota* spp., zoantharians; *Zoanthus* sp., *Zoanthus sociatus*, gorgonians; *Pterogorgia* sp., eggs, hydroids, bryozoans, seagrasses; *Ruppia maritima*	Randall 1967
Pomacentridae/damselfishes												
Pomacentrus leucostictus beaugregory				r							Algae, eggs; mulluscs, pomacentrid, polychaetes, fishes, coelenterate polyps, tunicates, crabs, amphipods, corals, foraminifera, hermit crabs, shrimps, copepods, gastropods; *Arene tricarinata*, *Crassispira nigrescens*	Randall 1967
Abudefduf saxatilis sergeant major					p						Anthozoans, copepods, algae, tunicates; appendicularians, opisthobranchs; *Tridachia crispata*, fish eggs, fishes; *Jenkinsia* sp., shrimp larvae, barnacle appendages, ants, polychaetes, siphonophores	Randall 1967

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Labridae/wrasses												
Doratonatus megalepsis dwarf wrasse	r			r								
Halichoeres bivittatus slippery dick				r	p						Crabs: majids, Mithrax sp., Mithrax sculptus, Platypodia spectabilis, portunid, xanthid, echinoid; Diadema antillarum, Lytechinum variegatus, polychaetes; ampharetid, gastropods; Acmaea sp., Acmaea pustulata, acteonid, Arene sp., Arene tricarinata, Bittium varium, Bulla striata, Bullata ovuliformis, Cerithium sp., Modulus modulus, Nassarius sp., Olivella sp., Planaxis lineatus, Pseudostomatella coccinea, Seila adamsi, Smaragdia viridis, Synaptocochlea picta, Tegula lividomaculata, Tricolia bella, Tricolia tessellata, turrid, ophiuroid; Ophioderma sp., Ophiothrix sp., pelecypods; Aequipecten gibbus, Americardia guppyi, Brachidontes exustus, Crassinella sp., Cuminigia antillarum, Ervilia nitens, Isognomon sp., Laevicardium sp., Nuculana sp., Papyridea semisulcata, Tellina listeri, Trachycardium sp., shrimps; alpheid, chitons; Acanthochiton pygmaea, Ischnochiton sp., fishes, stomatopods, hermit crabs; diogenids, pagurids, foraminiferas	Randall 1967
Hemipteronotus martinicensis rosy razorfish				r								
Hemipteronotus novacula pearly razorfish			r								Gastropods: Batilaria sp., Caecum sp., Drillia sp., Litiopa melanostoma, Natica sp., pelecypods; Eryilia nitens, Pitar sp., polychaetes, shrimps, scaphopods; Dentalium sp., isopods; amphipods	Randall 1967
Lachnolaimus maximus hogfish	c										Pelecypods; gastropods; crabs; hermit crabs; echinoids; amphipods; scaphopods; barnacles	Randall 1967; Reid 1954

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number										Diet	Source
	1	2	3	4	5	6	7	8	9	10		
Scarioae/parrotfishes												
Nichlsina usta emerald parrotfish		r		r				r				
Scarus coelestinus midnight parrotfish				r							Algae; seagrass; *Thalassia testudinum*, mollusks; foraminifera; coral; echinoid; sponge	Randall 1967
Scarus croicensis striped parrotfish				r							Algae	Randall 1967
Scarus quacamaia rainbow parrotfish				r							Algae; seagrasses; *Syringodium filiforme*, *Thalassia testudinum*	Randall 1967
Sparisoma chrysopterum redtail parrotfish				r							Algae, seagrasses; *Thalassia testudinum*	Randall 1967
Sparisoma radians bucktooth parrotfish				r							Seagrasses; *Thalassia testundinum*, algae	Randall 1967
Sparisoma rubripinne redfin parrotfish	a	r		c							Algae, seagrasses; *Thalassia testudinum*	Randall 1967
Sparisoma viride stoplight parrotfish				r							Algae, seagrasses; *Thalassia testudinum*	Randall 1967
Mugilidae/mullets												
Mugil cephalus striped mullet			r		p					a	Inorganic sediments, detritus, microalgae	Odum 1968
Mugil curema white mullet			r	r	p					c	Plants, diatoms, *Lyngbya majuscula*, *Rhizoclonium riparium*, *Thalassia testudinum*, *Vaucheria* sp.	Randall 1967
Mugil trichodon fantail mullet				r								
Sphyraenidae/barracudas												
Sphyraena barracuda great barracuda		r	r	r	p	r					Fishes: *Ablennes hians*, *Acanthurus bahianus*, *Allanetta harringtonensis*, atherinids, *Canthigaster rostrata*, carnagids, *Caranx fusus*, clupeids, *Decapterus* sp., *Diodon* sp., *Echidna catenata*, *Haemulon* sp., *Harengula slupeola*, *Jenkinsia* sp., *Ocyurus scarid*, *Sphyraena picudilla*, *Trachinocephalus myops*, octopuses, scyllarid lobsters	Randall 1967; de Sylva 1963

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Opistognathidae/jawfishes												
Opistognathus maxillosus mottled jawfish		r									Shrimps, isopods, fishes, polychaetes, mysids, copepods	Randall 1967
Dactyloscopidae/sand stargazers												
Dactyloscopus tridigitatus sand stargazer		r		r								
Uranoscophidae/stargazers												
Astroscopus y-graecum southern stargazer						r						
Clinidae/clinids												
Malacoctenus macropus rosy blenny				r								
Paraclinus fasciatus banded blenny		r	r	c								
Paraclinus nigripinnis blackfin blenny				r								
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	Amphipods, detritus, polychaetes, crabs, fish, pelecypods; *Crepidula* sp., isopods	Carr and Adams 1973 Reid 1954; Springer and Woodburn 1960
Blennius marmoreus seaweed blenny					p						Algae, detritus, ophiuroides, polychaetes, hydroids	Randall 1967
Hypsoblennius ionthas freckled blenny								r				
Callionymidae/dragonets												
Callionymus pauciradiatus spotted dragonet	r	r	r	r	p							

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number										Diet	Source
	1	2	3	4	5	6	7	8	9	10		
Gobiidae/gobies												
Barbulifer ceuthoecus bearded goby				r								
Microgobius microlepis banner goby	r				p							
Microgobius gulosus clown goby					p	c	r		r		Detritus, copepods, epiphytic algae, amphipods, polychaetes, bivalves, shrimp mysids	Carr and Adams, 1973; Reid 1954; Springer and Woodburn 1960; Odum and Heald 1972
Microgobius thalassinus green goby						r					Small crustaceans; amphipods, other invertebrates	Peterson and Peterson 1979
Bathygobius curacao notchtongue goby				c								
Bathygobius soporator frillfin goby						r					Caridean shrimp; *Palaemonetes intermedius*, chironomids, amphipods	Odum and Heald 1972
Gobionellus boleosoma darter goby				r								
Gobionellus smaragdus emerald goby						r						
Gobionellus shufelti freshwater goby									r			
Gobionellus stigmarturus spottail goby				r								
Gobiosoma robustum code goby		a	r	r	p	c	c	r	r	r	Amphipods, chironomid larvae, mysids, cladocerans, ostracods, small molluscs, algal filaments, detritus, cumaceans	Odum and Heald 1972; Reid 1954
Gobiosoma longipala twoscale goby								r				
Gobiosoma macrodon tiger goby		r	r									
Gobiosoma longum	r											

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Gobiidae/gobies (continued)												
Lophogobius cyprinoides crested goby			r								Amphipods; detritus; filamentous algae; mysids; shrimp; *Neanthes*; ostracods; small bivlaves; chironomid larvae; copepods; *Rithropanopeus harrisii*; snails	Odum and Heald 1972
Coryphopterus glaucofraenum bridled goby	r										Algae and detritus; ostracods; ophiuroids; eggs; pelecypods; copepods	Randall 1967
Acanthuridae/surgeonfishes												
Acanthurus bahianus ocean surgeon	r			r							Algae; organic detritus; diatoms; seagrasses; *Syringodium filiforme*, *Halophila baillonis*, *Thalassia testudinum*	Randall 1967; Clavijo 1974
Acanthurus chirurgus doctorfish				r							Algae; organic detritus; diatoms; seagrasses; *Syringodium filiforme*, *Thalassia testudinum*, worm tubes; gastropods; nudibranch eggs	Randall 1967; Clavijo 1974
Stromateidae/butterfishes												
Nomeus gronovii man-of-war fish			r									
Scorpaenidae/scorpionfishes												
Scorpaena brasiliensis barbfish	r	r		r							Shrimps: penaeid; crustaceans; stomatopods; fishes; *Hippocampus* sp., crabs	Randall 1967
Scorpaena grandicornis plumed scorpionfish	r	r		r							Shrimp: caridean, stenopid; fishes; crustaceans	Randall 1967
Scorpaena plumeri spotted scorpionfish				r							Fishes: *Acanthurus* sp., congrid, *Jenkinsia* sp., crabs; majid, *Mithrax coryphe*, *Pitho* sp., *Portunus anceps*, *Portunus ordwayi*; shrimps; penaeid, *Penaepsis goodei*; octopuses; hermit crabs	Randall 1967
Triglidae/searobins												
Prionotus salmonicolor blackwing searobin				r	p							

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Triglidae/searobins (continued)												
Prionotus scitulus leopard searobin	r	r	r			r	r	r	r		Small molluscs: *Solemya* sp., *Bulla* sp., *Olivia* sp.; shrimp; crabs; fishes	Peterson and Peterson 1979
Prionotus tribulus			r			r	c		r	r	Shrimp; crabs; *Limulus polyphemus*, *Uca* sp.; fishes; amphipods; copepods; annelids; bivalves; echinoids	Peterson and Peterson 1979
Bothidae/lefteye flounder												
Bothus ocellatus eyed flounder	r	r		r							Fishes; *Coryphopterus* sp.; crabs; *Calappa ocellata*; majid; shrimps; amphipods; isaeid; stomatopods: *Pseudosquilla ciliata*	Randall 1967
Ancylopsetta quadrocellata ocellated flounder								r				
Citharichthys macrops spotted wiff		r		r								
Citharichthys spilopterus bay wiff	r	r				r			r		Mysids; shrimp; crabs; copepods; amphipods; fishes; annelids	Peterson and Peterson 1979; Austin and Austin 1971
Paralichthys albigutta gulf flounder	r	r				r	r	r	r		Less than 45 mm SL: amphipods, small crustaceans. Greater than 45 mm: fishes: *Orthopristis chrysopterus*, *Lagodon rhomboides*, *Synodus foetens*, *Anchoa mitchilli*, crustaceans	Reid 1954; Springer and Woodburn 1960
Syacium papillosus dusky flounder		r										
Etropus crossotus fringed flounder								r			Polychaetes; copepods; shrimps; amphipods	Reid 1954
Soleidae/soles												
Trinectes inscriptus scrawled sole		r		r								
Trinectes maculatus hogchoker	r					r	r				Amphipods; mysids; chironomid larvae; polychaetes; *Neris pelagica*; foraminifera	Odum and Heald 1972; Carr and Adams 1973
Achirus lineatus lined sole		r	r	r	p	c	c		r	r	Polychaetes; amphipods; copepods	Springer and Woodburn 1960; Reid 1954

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Cynoglossidae/tonguefishes												
Symphurus plagiusa blackcheek tonguefish	r	r		r		c	c		r		Copepods; amphipods; ostracods; polychaetes; pelecypods;	Reid 1954; Springer and Woodburn 1960 Austin and Austin 1971
Balistidae/triggerfishes and filefishes												
Balistes capriscus gray triggerfish				r								
Monocanthus ciliatus fringed filefish	c	r	r	c				r	r		Algae; detritus; seagrasses: Thalassia testudinum; copepods; shrimp; caridean, amphipods: Colomastix sp.; Leucothoe sp.; tanaids; polychaetes; stomatopod larvae; isopods; shrimps; amphipods	Randall 1967; Reid 1954; Springer and Woodburn 1960
Monocanthus hispidus planehead filefish	c	r	r	c		r	r	r	r	r	Amphipods; pelecypods; polychaetes	Reid 1954; Adams 1976a
Alutera schoepfi orange filefish		r									Seagrasses: Syringodium filiforme, Thalassia testudinum; algae; Halimeda sp.; hermit crabs; Clibanarius tricolor, gastropids; Columbella mercatoria	Randall 1967; Reid 1954
Ostraciidae/boxfishes												
Lactophrys quadricornis scrawled cowfish	r	c	r	r	p			r	r		Sponges; tunicates; zoantharians; Bunodosoma granulifera, Phyllactis flosculifera, Zoanthus pulchellus, hermit crabs; Pagurus bonairensis, algae: bluegreens, Halimeda opuntia; gorgonians: Muricea atlantica; seagrasses: Thalassia testudinum; scyphozoans; polychaetes; eggs; pelecypods; shrimps; amphipods	Randall 1967

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number 1	2	3	4	5	6	7	8	9	10	Diet	Source
Ustraciidae/boxfishes (continued)												
Lactophrys trigonus trunkfish		r	r		c				r		Crabs: calappid, *Emerita* sp., majids, *Mithrax* sp., *Pitho* sp., portunids, xanthids; pelecypods: *Atrina seminuda*, *Codakia costata*, *Musculus lateralis*, *Tellina* sp., *Trachycardium muricatum*, polychaetes: slyerid, pectinariid; echinoids: *Lytechinus variegatus*; algae; tunicates; *Microcosmus exasperatus*; seagrasses: *Syringodium filiforme*, *Thalassia testudinum*; *holothurians*; *Holothuria arenicola*; asteroids; *Oreaster reticulata*; gastropods: *Acmaea pustulata*, *Anachis sparsa*, *Arene* sp., *Bulla* sp., *Haminoea elegans*, *Nassarius* sp., *Elasmopus* sp.; ophiuroids; *Ophioderma brevispinum*, *Ophiothrix* sp., eggs; chitons: *Acanthochitona* sp., hermit crabs, shrimp; alpheid	Randall 1967
Lactophrys triqueter smooth trunkfish		r	r								Polychaetes; onuphid, syllid, sipunculids: *Aspidosiphon spinosscutatus*; crabs: majids, pinotherid, *Upogebia* sp.; shrimps: alpheids, carideans, gnathophyllid; tunicates: *Asidia nigra*, *Trididemnum savignii*, *sponges*, hemichordates; gastropods: *Balcis intermedia*, *Nitidella laevigata*, *Trivia* sp., *Turbo castanea*; *hermit crabs*; *Paguristes* sp.; *Spiropagurus* sp.; echinoids: *Lytechinus variegatus*; pelecypods; *Tellina* sp., amphipods; seagrasses: *Halophila baillonis*, *Thalassia testudinum*; algae: *Halimeda* sp., chitons, eggs, ostracods	Randall 1967
Tetradontidae/puffers												
Sphoeroides nephalus southern puffer		r		r	p	r	c	r		r	Crabs, *Callinectes sapidus*, pelecypods	Reid 1954; Carr and Adams 1973

List of fishes and their diets from collections in south Florida.

Species	Abundance by survey number										Diet	Source
	1	2	3	4	5	6	7	8	9	10		
Tetradontidae/puffers (continued)												
Sphoeroides spengleri bandtail puffer	r	r	r	r				r			Crabs: majids, Microphrys bicorutus, rannid; pelecypods: Musculus lateralis, Pinctada radiata; gastropods: Bullata ovuliformis, polychaetes; echinoids: Diadema antillarum, spatangoid, pohiuroids; Ophiocoma riisei, Ophioderma rubicundum, Ophiothix sp., Ophiothix lineata: amphipods; shrimps; seagrasses: Halophila baillonis, Thalassia testudinum; algae; detritus; hemichordates; eggs; chitons; isopods; copepods; tunciates; hermit crabs; fishes	Randall 1976
Sphoeroides testudineus checkered puffer		r									Crustacea: Portunid megalops; gastropods; Nertina sp.	Austin and Austin 1971
Diodontidae/porcupinefishes												
Chilomycterus schoepfi striped burrfish	r	c	r	r	p	r	r	c	r	r	Molluscs: pelecypods, gastropods, Bittium sp., Mitrella sp.; echinoid; Mellita sp., xanthid crab	Reid 1954; Springer and Woodburn 1960
Chilomycterus antennatus bridled burrfish	r										Gastropods: Anachis sp., Arene sp., Astraea sp., Cerithium sp., Cerithium litteratum, Columbella mercatoria, Crassispira fuscescens, Marginella sp., Mitrella lunata, Modulus modulus, Nitidella ocellata, Pusia sp., Pyramidella candida, Smaragdia viridis, Tegula fasciata, Turbo sp., Turbo castanaea; hermit crabs: diogenids, pagurids; isopods: Paracereis caudata, crabs, shrimps	Randall 1967
Diodon holocanthus balloonfish		r		r							Gastropods: Acmaea leucopleura, Astraea sp., Calliostoma sp., Cerithium algicola, Cerithium litteratum, Crassostrea rhizophorae, Fissurella sp., Modulus modulus, muricids, Nassarius sp., Oliva reticularis, Polinices lacteus, Siphonaria sp., Pusia sp., Pyramidella candida, Smaragdia viridis, Tegula fasciata, Turbo sp., Turbo castanaea; hermit crabs: diogenids, pagurids; isopods: Paracereis caudata, crabs, shrimps	Randall 1967

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16. Abstract (Limit: 200 words)

A detailed description is given of the community structure and ecosystem processes of the seagrass ecosystems of south Florida. This description is based upon a compilation of information from numerous published and unpublished sources.

The material covered includes distribution, systematics, physiology, and growth of the plants, as well as succession and community development. The role of seagrass ecosystems in providing both food and shelter for juveniles as well as foraging grounds for larger organisms is treated in detail. Emphasis is given to the functional role of seagrass communities in the overall coastal marine system.

The final section considers the impacts of human development on seagrass ecosystems and their value to both man and the natural system. Because seagrass systems are fully submerged and less visually obvious, recognition of their value as a natural resource has been slower than that of the emergent coastal communities. They must, however, be treated as a valuable natural resource and preserved from further degradation.

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