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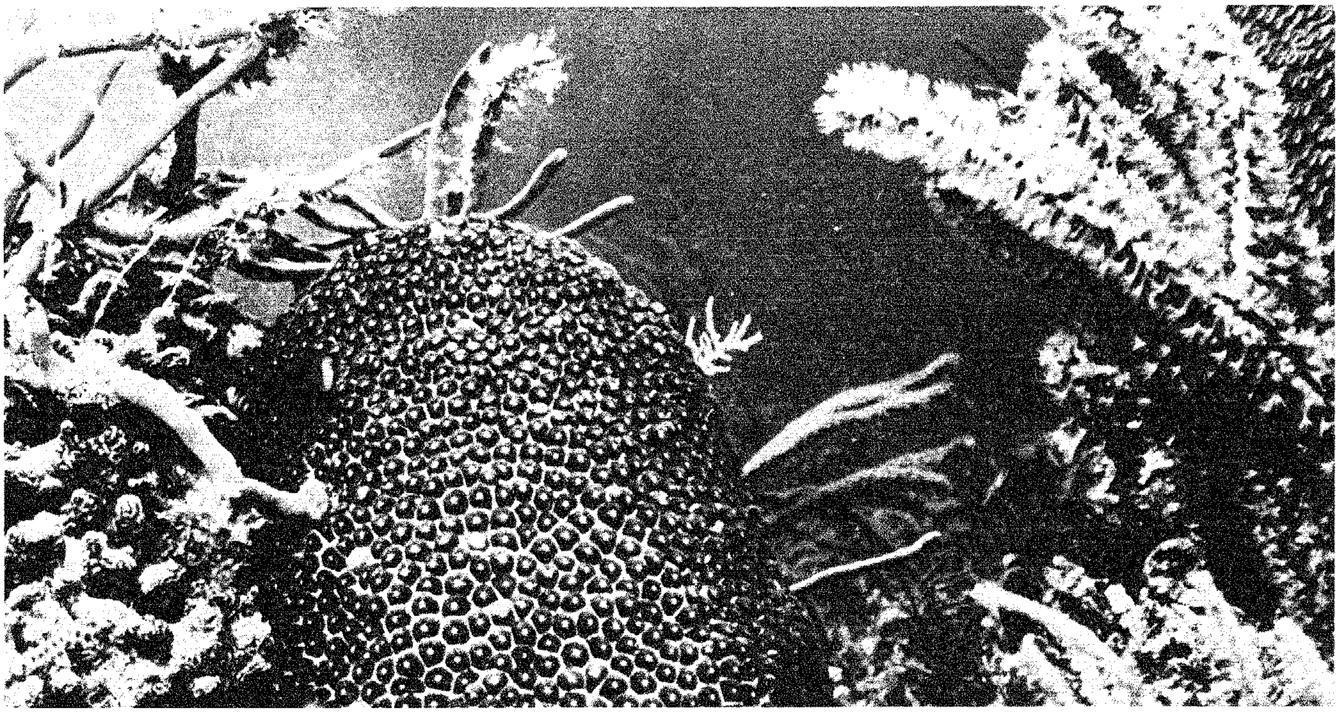
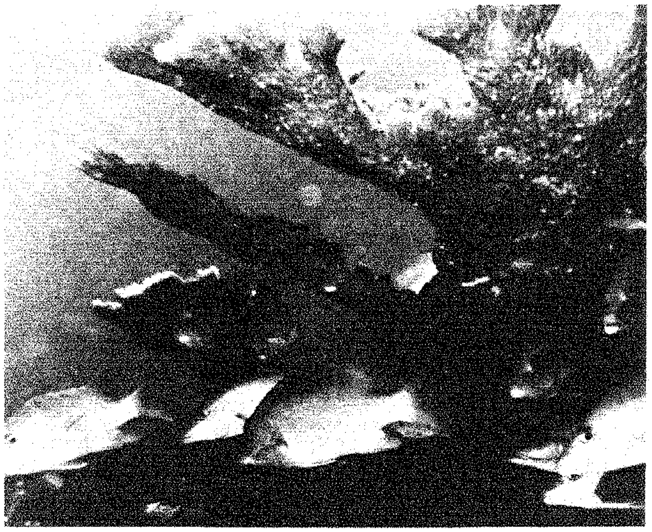
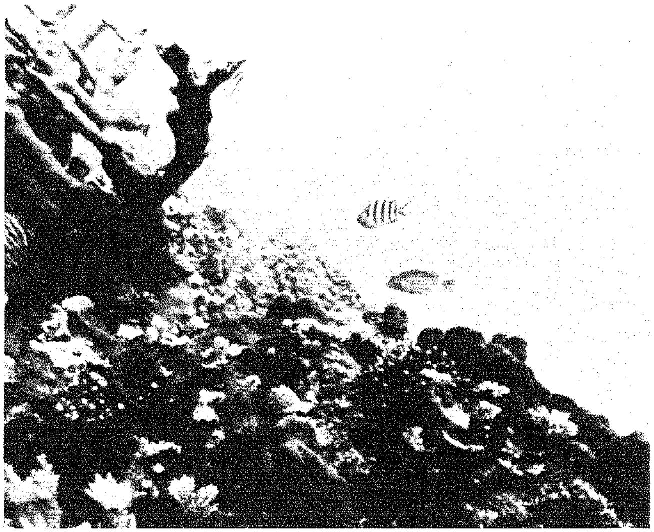
Minerals Management Service
MMS 84-0038

THE ECOLOGY OF THE SOUTH FLORIDA CORAL REEFS: A Community Profile







U.S. Department of the Interior

Fish and Wildlife Service
Minerals Management Service

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THE ECOLOGY OF THE SOUTH FLORIDA CORAL REEFS: A COMMUNITY PROFILE

by

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PREFACE

This profile of the coral reef community of south Florida is one in a series of community profiles that treat coastal and marine habitats important to humans. Coral reefs 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. Coral reefs also provide an important economic benefit by attracting tourists to south Florida.

The information in the report can give a basic understanding of the coral reef community and its role in the regional ecosystem of south Florida. The primary geographic area covered lies seaward of the coast from Miami south and west to the Dry Tortugas. References are provided for those seeking indepth treatment of a specific facet of coral reef 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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ABBREVIATIONS

BNP	Biscayne National Park
CG	(U.S.) Coast Guard
DER	Department of Environmental Regulation (Florida)
DNR	Department of Natural Resources (Florida)
DOA	Department of Administration (Florida)
DOS	Department of State (Florida)
EPA	(U.S.) Environmental Protection Agency
FWS	(U.S.) Fish and Wildlife Service
GS	(U.S.) Geological Survey
JPCRSP	John Pennekamp Coral Reef State Park
KLNMS	Key Largo National Marine Sanctuary (originally referred to as Key Largo Coral Reef Marine Sanctuary in early General Management Plan developed by NOAA)
LKNMS	Looe Key National Marine Sanctuary
MMS	Minerals Management Service
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
NPS	National Park Service
PHC	Petroleum hydrocarbons
Std. Dev. or SD	Standard deviation
USACE	U.S. Army Corps of Engineers
YBP	Years Before Present

CONVERSION FACTORS

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (mt)	2,205.0	pounds
metric tons (mt)	1.102	short tons
kilocalories (kcal)	3.968	BTU
Celsius degrees	$1.8(C^\circ) + 32$	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To Obtain
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1,233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
BTU	0.2520	kilocalories
Fahrenheit degrees	$0.5556 (F^\circ - 32)$	Celsius degrees

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We thank the Minerals Management Service, Gulf of Mexico Regional Office, for printing this document with color plates which increase the scientific usefulness of the report. Larry Handley, Carla Langley, Debbie Miller, Ruth Monical, Cynthia Nicholson, Patricia Thaggard, Cathy Cartwright, Marilyn Parker, and Mimi Griffitt of that office contributed yeoman efforts to the completion of this publication.

This publication is dedicated to all who seek the truth, especially Taylor Alexander; lost friends Lin Brown and Frank Wescott; and especially Karilyn.

CHAPTER 1

CHARACTERIZATION OF THE RESOURCE

1.1 OVERVIEW

Coral reefs are highly complex and diverse communities of biota, a phenomenon of the tropics and subtropics limited by such factors as suitable substratum, temperature, light, and sedimentation. In simplest terms coral reefs are concentrated complexes of corals and other organisms that construct a limestone structure in shallow water. In the initial building process, a set of primary framework builders set down the first structure; later colonizers add to the volume. Skeletal breakdown by physical and biological actions creates carbonate sediments, which are recycled by other biological processes or are cemented to the reef framework through biological or geochemical processes.

The coral reef complex found off southeast Florida represents a mosaic that exhibits extreme variability in all parameters used to evaluate biological communities. Coral reefs provide a wide spectrum of vocational and recreational activities. Many important fisheries are directly tied to these reef communities; a reef's principal resource value (economically) is as a highly productive habitat: it concentrates marine protein in a localized area. Coral reefs also play a significant role in the tourist industry of southeast Florida.

While the level of reef usage is increasing as southeast Florida experiences rapid population growth, management of these reef communities tends to lag or is unresponsive to the problems described herein.

Scientific and lay literature has reported real and potential threats to southeast Florida coral reefs (Straughn 1972; Voss 1973; Davis 1977a; Dustan 1977b; Bright et al. 1981). Impacts have included vessel groundings and sinkings, oil spills, anchor damage, beach renourishment dredging, fishery activities (lobster trap recovery), tropical fish and invertebrate collecting, shipwreck salvage, and diving-related activities. Individually these acts do not greatly affect the resource vitality, but the chronic and synergistic nature of some of these acts is cause for concern.

The goal of this document is to serve as a reference for those interested and concerned individuals responsible for environmental management of the resource, as well as those seeking a better understanding of Florida's coral reefs.

1.2 CORAL REEF DISTRIBUTION

Although the tropical coral reef communities found off southeast Florida (Figure 1) are the emphasis of this report, a brief summary of coral reef distributions throughout Florida will aid in understanding this resource. From the Georgia border to near Fort Pierce on the Atlantic coast, in depths of 15-50 m, *Oculina* (pretzel coral) bank communities are the dominant coral community (Avent et al. 1977; Reed 1980). These are low-diversity coral assemblages, but important fishery habitat. Grouper find refuge, feed, and breed in and near these structures. From Stuart (St. Lucie Inlet) to near Palm Beach is a transitional community of *Oculina* bank flora and fauna and hardier elements of the tropical reef biota. This region is characterized by the convergence of the temperate and subtropical climate zones. From Palm Beach southward to Miami (Cape Florida) elements of the tropical coral reef biota become increasingly important in a north-to-south gradient; however, the building of three-dimensional reef structures does not occur. This area is characterized as an octocoral-dominated hardground community (Goldberg 1973a). The two stony corals most responsible for reef building (*Acropora palmata*, elkhorn coral, and *Montastraea annularis*, star coral) rarely occur here, and currently do not actively build reefs. *Acropora palmata* was once an important reef builder in this area, but it ceased building reefs about 4,000 years before present (YBP) (Lighty 1977; Lighty et al. 1978). Today only a few isolated colonies are found north of Fort Lauderdale.

The region of maximum coral reef development is restricted to south and west of Cape Florida, offshore of the Florida Keys archipelago (Figure 1). This small chain of islands extending from Soldier Key to Dry Tortugas exhibits a diverse pattern of hardgrounds, patch reefs, and bank reefs from 25 m to 13 km offshore. This is the only shallow water (<10 m) tropical coral reef ecosystem found on the Continental Shelf of North America, and has been referred to as "The Florida Reef Tract" (Vaughan 1914a). This discontinuous assemblage of reefs forms an arc paralleling the Keys' coastline in a general southwesterly trend. Landward, the reefs are bounded by the Keys and a series of shallow embayments (Biscayne Bay, Card and Barnes Sounds, and Florida Bay); seaward of the reefs are the Straits of Florida and the Florida Current. The Florida Current, a subsystem of the Gulf Stream, plays an important role in the existence and maintenance of coral reefs off southeast Florida. It modifies the environment by moderating winter temperatures. The current's source is tropical; hence, its waters are significantly warmer than resident shelf water masses during the winter, thereby modifying winter thermal conditions such that offshore reef development is not hindered by extremely cold weather that occasionally occurs when cold fronts intrude into southeast Florida. Inshore patch reefs, however, are more vulnerable to cold extremes caused by winter weather. The current system is dynamic, and eddies or meanders bring considerable volumes of water into the reef environment. This brings plankton, a food source, and new recruitment from nonresident populations to the reefs. The significance of the Florida Current cannot be overestimated when considering coral reef existence off southeast Florida.

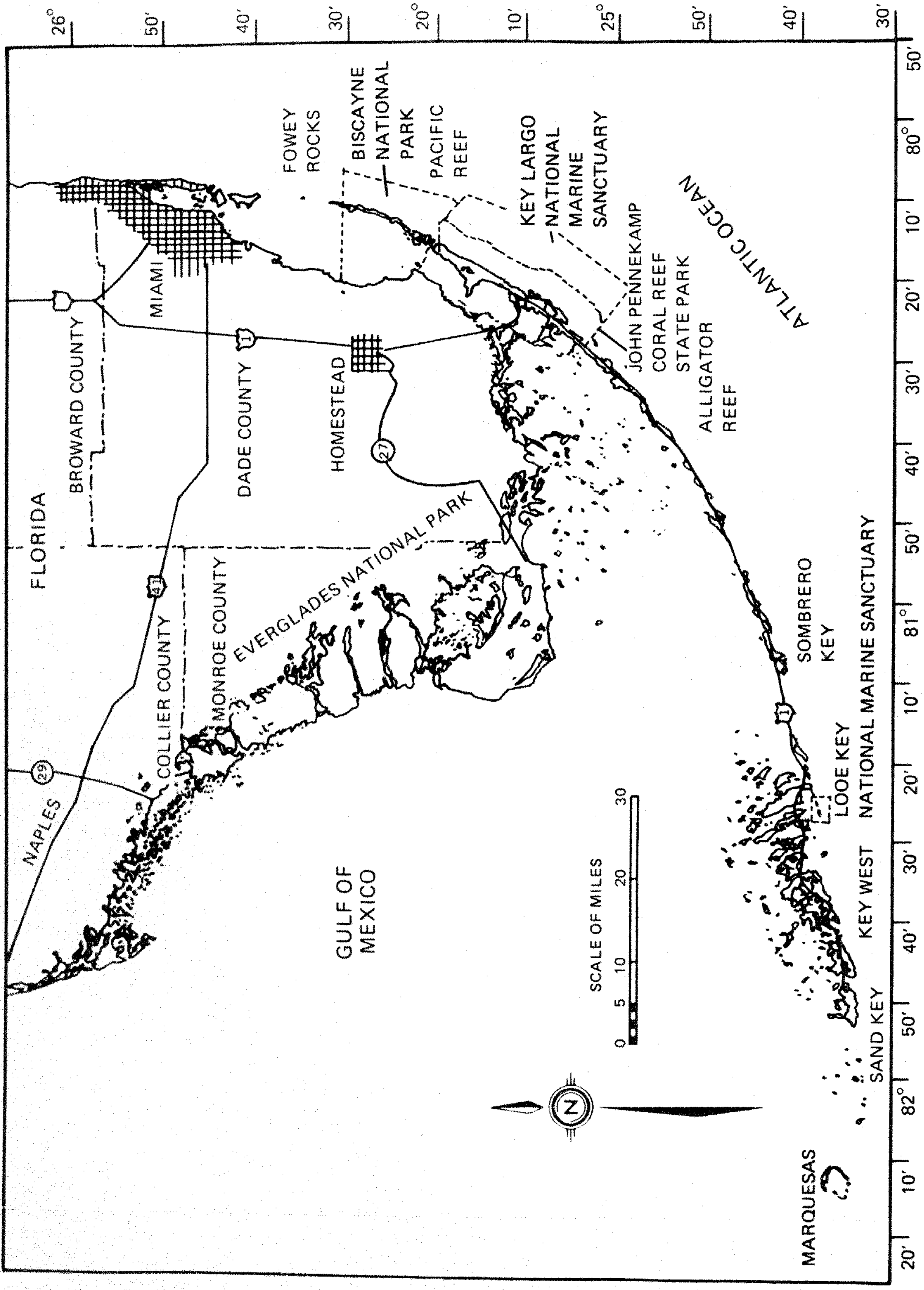

Figure 1. Tropical coral reef communities off south Florida.

The Keys or islands act as barriers to cross shelf water transport from shallower bays and sounds. These bays are very shallow, hence much influenced by meteorological events. Temperature, salinity, and turbidity can be significantly affected. Heavy rainfall, drought, and winter cold fronts are the major influences. Coral reef distribution patterns reflect the extent of water exchange between the bays and sounds and the Atlantic. The larger northern Keys (Elliott and Largo) have extensive reef development off their coasts; the middle Keys, which are smaller and more separated, have numerous channels communicating with Florida Bay (Plate 1a) and exhibit less reef development than the upper or lower Keys. The influence of Florida Bay on water quality negatively affects reef development in the middle Keys area.

Major bank reefs off the Florida Keys include Carysfort, Elbow, Key Largo Dry Docks, Grecian Rocks (Plate 3a), French (Plate 1b), Molasses, Alligator, Tennessee, Sombrero, Looe Key (Plate 2a and b), Eastern, Middle, and Western Sambos, American Shoals, Eastern and Western Dry Rocks, Rock Keys, and Sand Key. Dry Tortugas is studded with various coral reefs (Davis 1979, 1982).

Off the west coast of Florida, tropical reef development is nonexistent. Ledges and outcroppings are a special rocky habitat which supports an association of hardy corals and other biota; however, they do not construct three-dimensional reefs. The Florida Middle Ground (a fossil reef formation about 157 km northwest of Tampa Bay), while exhibiting higher diversity in coral species, is not an active coral reef comparable with those found off southeast Florida. These areas in the eastern Gulf of Mexico, however, are critical habitats that should be provided with rational management, especially since important fisheries are found in association with the gulf live bottom communities.

1.3 COMMUNITY DISTRIBUTION

The Florida Keys possess coral reef communities similar to those found in the Caribbean and other tropical Atlantic areas. The reefs are bathymetrically distributed from less than 1 to 41 m deep. Large-scale synoptic mapping of the Keys' reefs has been recently completed (Marszalek et al. 1977; Marszalek 1981, 1982). Caution should be exercised when interpreting these maps, as they use mapping units based on geological and biological criteria, and in some cases errant interpretation could occur due to their large scale and criteria used.

The basic pattern of marine communities in southeast Florida (where commercial development has not occurred) is one of a shoreline dominated by mangroves, rocky intertidal, or sedimentary environments. From the intertidal zone to Hawk Channel is a mosaic of environments including sediments, seagrass exposed Pleistocene rock, and some patch reefs. Seaward of Hawk Channel, patch reef abundance and frequency increase and bank reefs begin to occur. Seagrass is often abundant and sediment is coarser. Seaward of the bank reefs the sea bottom (where it has been investigated) consists of sediments, sponge habitats, and rubble, with occasional rocky outcrops that generally parallel the basic reefs.

The coral reefs, seagrasses, and mangroves are all integrated into the coastal ecosystem of southeastern Florida. Motile species and trophic energy webs are integrated and interrelated among the three communities.

1.4 HISTORICAL RESUME′ OF FLORIDA CORAL REEF RESEARCH

Arbitrarily, coral reef research can be chronologically placed into three periods: early (to 1900), middle (1900 to 1950), and recent (1950 to present). Early research was descriptive and taxonomic, and was stimulated by the need to provide safe navigation for marine commerce. National security also had some influence in that the Caribbean Sea prior to 1860 was frequented by pirates and European naval powers. During the age of discovery, the Florida coastline was crudely mapped by the Spanish and English. Agassiz (1852, 1869, 1880, 1885, 1888), LeConte (1857), Hunt (1863), and Pourtales (1863-1869, 1871, 1878, 1880) provided the earliest reef descriptions and details about the coast. They also initiated systematic description of the many organisms found in and near the coral reefs.

During the middle period, establishment of the Tortugas Laboratory on Loggerhead Key by the Carnegie Institution was the most significant factor benefiting coral reef studies during the first half of the twentieth century. Alfred G. Mayer and his colleagues conducted much fundamental coral reef research from the Tortugas Laboratory. Mayer (1914, 1916, 1918) determined the thermal tolerances of tropical marine organisms in general and reef coral in particular. T. Wayland Vaughan was the most prolific Carnegie reef researcher, reporting on the geology of Tortugas, south Florida, and the Bahamas (Vaughan 1909, 1910, 1912, 1914a, 1914b, 1914c, 1914e, 1915a; Vaughan and Shaw 1916). He studied the taxonomy and growth rates of scleractinian corals (Vaughan 1911, 1914d, 1915b), summarized seawater temperatures at reef tract lighthouses (1918), and reported on the Tortugas current structure (1935). Other students of scleractinian corals include Duerden (1904), postlarval development in *Siderastrea radians*; Matthai (1916), systematics; Boschma (1925, 1929), postlarval development in *Manicina areolata*; Wells (1932), thermal tolerance knowledge; and Yonge (1935a, 1935b, 1937), *M. areolata* autecology, taxonomy of *Siderastrea* spp., and mucus production in stony corals. Other reef-related research from the Carnegie laboratory includes work by Cary (1914, 1916, 1918a, 1918b), Octocorallia; Taylor (1928), algae; deLaubenfels (1936), Porifera; and Longley and Hildebrand (1941), fish. Another first for the Tortugas laboratory was that the first underwater color photographs of coral reefs were taken by Longley at Tortugas. Dole (1914) and Dole and Chambers (1918) reported on salinity at Tortugas and off Fowey Rocks lighthouse. LeCompte (1937) described some Tortugas reefs. Wells (1933, unpublished) contains considerable information on the Tortugas reefs. A fire destroyed the Tortugas Laboratory in 1937; it was never rebuilt.

Verrill (1902), Smith (1943, 1948, 1971), Vaughan and Wells (1943), and Wells (1956) are the relevant scleractinian taxonomic and systematic references. During the recent period (1950 to present) there has been a great proliferation of scientific literature dealing with Florida coral reefs. Growth rates of coral species were detailed by Broecker and Thurber (1965), Shinn (1966), Jaap (1974), Landon (1975), Emiliani et al. (1978), Dodge (1980), and Hudson (1981). Population dynamics of scleractinian corals were reported by Dustan (1977a). Brooks (1963), Halley (1979), Davis (1982), and Porter et al. (1982) added to Tortugas information.

Ecological studies and reviews include Smith et al. (1950), Voss and Voss (1955), Jones (1963, 1977), Glynn (1973), Hudson et al. (1976), Hudson (1981), Goldberg (1973a, 1973b), Antonius (1974a), Kissling (1975), and Shinn (1975). Coral reef fish studies included Springer and McErlean (1962a, 1962b), Starck (1968), Starck and Davis (1966), Bohlke and Chaplin (1968), Emery (1973), and Jones and Thompson (1978). Reef morphology and physiography were reported by Stephenson and Stephenson (1950), Shinn (1966), Kissling (1965), Starck and Schroeder (1965), Starck (1966), Straughan (1978), Turmel and Swanson (1971), Weeks (1972), Hannau and Mock (1973), and Avent et al. (1977).

Geological literature includes Ginsburg (1956), Brooks (1963), Alt and Brooks (1965), Hoffmeister and Multer (1968), Duane and Meisberger (1969), Enos (1970), Multer (1971), Raymond (1972), Ginsburg (1973), Enos (1974), Gleason (1974), Hoffmeister (1974), Enos (1977), Lighty (1977), Lighty et al. (1978), Shinn (1980), Mitchell-Tapping (1981), and Ghiold and Enos (1982). Geographical research includes work by Ginsburg and Shinn (164), Marszalek et al. (1977), Marszalek (1981, 1982), Reed (1980), and Stoddart and Fosberg (1981).

Guidebooks or general references to Florida reefs include Hoffmeister et al. (1964), Ginsburg (1972a, 1972b), Zeiller (1974), Voss (1976), Greenberg (1977), Colin (1978a), and Kaplan (1982). Hurricane impacts on Florida reefs have been documented by Springer and McErlean (1962a), Ball et al. (1967), Perkins and Enos (1968), and Shinn (1975). The effect on coral reefs by other meteorological phenomena was studied by Jaap (1979), Walker (1981), and Roberts et al. (1982). Physical and chemical oceanography adjacent to the reef tract includes studies by Hela (1952), Chew (1954), Stommel (1959), Wennekens (1959), McCallum and Stockman (1964), Gordon and Dera (1969), Hanson and Poindexter (1972), Lee (1975), Lee and Mayer (1977), Lee and Mooers (1977), and Leming (1979).

The Octocorallia were reported on by Goldberg (1973a, 1973b), Opresko (1973), Cairns (1977), and Wheaton (1981). Underseas parks were reported on by Voss et al. (1969), Spotte (1972), Tzimoulis (1975), and Jameson (1981). Florida Current plankton was reported on by Bsharah (1957). Emery (1968) discussed coral reef plankton. Coral predators and boring and rasping biota were reported by Robertson (1963), Ebbs (1966), Antonius (1974b), Hein and Risk (1975), and Hudson (1977). Physiology of reef corals, particularly the symbiotic relationships of corals with zooxanthellae, was studied by Kanwisher and Wainwright (1967), Kriegel (1972), Chalker (1976, 1977), and Chalker and Taylor (1978). Reports on the impact of human activities include McCloskey and Chesher (1971), Hubbard and Pocock (1972), Straughan (1972), Voss (1973), Antonius (1974b, 1976, 1977), Courtenay et al. (1974), Griffin (1974), Jaap and Wheaton (1975), Manker (1975), Shinn (1975), Chan (1976), Britt and Associates (1977), Davis (1977a), Dustan (1977b), and Bright et al. (1981). Coral reef growth rates in Florida were reported by Hoffmeister and Multer (1964), Shinn et al. (1977), and Shinn (1980).

Echinoid distributions in John Pennekamp Coral Reef State Park were studied by Kier and Grant (1965). Miller et al. (1977) reported on diatoms in the park. Jameson (1981) reported on the biology, geology, and cultural resources in deeper regions of the Key Largo National Marine Sanctuary. Workshop and symposia literature includes Stursa (1974) and Taylor (1977). Shinn (1979) detailed collecting-permit requirements for biological and geological sampling in the Keys' area.

1.5 ECONOMIC SIGNIFICANCE

Exploitation of Florida's reef resources began with the Caloosa Indians, who harvested marine protein (fishes, lobsters, and conchs), shells, and coral for trading. Excavated middens occasionally contain coral artifacts. During the mid-17th to late-19th centuries, the Florida reefs posed a significant navigational hazard to Europeans and Americans. Today, salvagers recover gold, silver, and artifacts from the numerous shipwrecks adjacent to the reefs. Many reefs are named for shipwrecks. Looe Key Reef is named for the 44-gun British Frigate, the HMS *Looe*, which was wrecked on the reef the morning of 5 February 1744. Molasses Reef is named for an unknown vessel laden with molasses that foundered there.

Early Florida Keys' settlers had a thriving enterprise of luring unsuspecting ships onto the reefs with false beacons. They then claimed salvage rights on the wreck, salvaged the cargos, and auctioned them off. Wood from the vessels was also salvaged. Many of the older homes in Key West are constructed with salvaged ship timbers. In an effort to reduce the shipwrecks, early coral reef work was directed toward mitigating the hazards. This resulted in the lighthouse construction between 1825 and 1886 on the most dangerous reefs. These lighthouses significantly changed the nature of the Keys' economy. Fishing, cigar making, sponge harvesting, and agriculture replaced shipwrecking as the major economic endeavor at Key West.

Commercial sale of coral began in Key West around 1830 and remained a poorly organized cottage industry until 1950. During that period collectors used either grappling hooks from boats or hand harvested while reef diving. The industry changed with the advent of scuba diving and the increased interest by the general public in the marine environment. There was increased demand for coral by tourists as well as for export to northern markets. No quantitative data exist on the magnitude or economics of the coral harvest. It is suspected that commercial coral harvest at no time employed more than 20 individuals working on a part-time seasonal basis. In 1973 and 1975 Florida enacted statutes making it illegal to collect, sell, or damage stony corals (Millepora and Scleractinia) and two species of sea fan (*Gorgonia*) within State waters. In 1976, the Federal Government (Bureau of Land Management) wrote regulations under the authority of the Outer Continental Shelf Lands Act to protect corals and reefs in the area under federal jurisdiction (beyond the 3-mi limit in the Atlantic). The Fifth Circuit Court of Appeals, however, ruled that these regulations can only be applied when active mineral or petroleum exploration or production is occurring in the immediate vicinity of the coral. Currently, the Gulf of Mexico and South Atlantic Fishery Management Councils are preparing a management plan for corals and coral reefs in the region between North Carolina and the Texas-Mexican border.

Today, coral being sold is foreign. From 1977 to 1979, 200,000 pieces of coral were imported with a dockside value of $31,500. Retail markup would place the value of imported coral at about $95,000. Most of this coral came from the Philippines, where collecting and selling coral is illegal, but enforcement is difficult because of the thousands of islands belonging to this nation.

Economically, Florida coral reefs directly or indirectly generate an estimated $30 million-$50 million annually within the Monroe County region. These monies come from all aspects of fishing, diving, education, and research. Commercial fishing in particular depends heavily on the coral reef habitats. Most of the sought-after species spend all or part of their lives in the reefs. For some species, the coral reefs are a nursery area where juveniles mature into adults. Many species breed and/or feed within the confines of the coral reef. Resident fish populations may only seek shelter and refuge in the reef and feed in the nearby surrounding grass flats or the open sea. The life history patterns of individual species vary, but the reef is a critical link to the success of these species. Table 1 presents commercial landings of reef-related species in Monroe County for 1980.

Diving as a sport and hobby attracts more than a million people to the Florida Keys annually. These divers rent and purchase equipment, charter tours to the reefs, and purchase food and lodging. Tourists come from as nearby as Homestead and Miami, and as far away as Europe and Canada. A 1979 *Skindiver* magazine survey indicated that the Florida Keys was the most popular diving location in the United States among traveling divers. The survey reported that the average diver spent about $718 per trip. There are 40 businesses in Monroe County devoted entirely to tourist diving. For the most part this activity is a nonconsumptive form of reef usage. Most tourists come to experience the reef environment firsthand and to observe fish. Some divers do spearfish and catch lobsters. Spearfishing is banned in some marine parks and sanctuaries, i.e., John Pennekamp Coral Reef State Park, Key Largo National Marine Sanctuary (JPCRSP–KLNMS), and Ft. Jefferson National Monument. Much of the tourist diving is concentrated offshore of Key Largo in JPCRSP–KLNMS, off Big Pine Key at Looe Key National Marine Sanctuary (LKNMS), and off Key West.

Table 1
Commercial landings of reef-related species in Monroe County, 1980 (NMFS 1981).

Species	Weight (lb)	Value ($)
Ballyhoo	311,724	85,871
Jacks	29,881	2,674
Dolphin	89,977	33,099
Grouper & scamp	509,794	451,014
Hogfish	34,184	17,965
Jewfish	32,646	5,312
Shark	175,643	18,365
Snappers		
Lane	15,526	6,890
Mangrove	240,117	127,530
Mutton	160,469	131,419
Red	15,532	20,820
Vermilion	915	861
Yellowtail	735,104	730,744
Triggerfish	105	19
Warsaw grouper	3,371	1,324
Spiny lobster	4,656,018	10,132,913
Spanish lobster	28,199	67,814
Total	7,039,205	11,834,634

Besides diving, there are glass-bottom boat tours that allow the nondiver to enjoy the reef firsthand without getting wet. Charter airplanes also fly tourists over the reefs. Tourist gift shops market many reef-related souvenirs, from colorful T-shirts to postcards.

All levels of education, from elementary to graduate school (including youth organizations, scouts, sea camps, and diving schools), bring students to the coral reefs to supplement classroom experiences. Special publications, documentaries, and movies about the coral reefs are produced. These are an economic and educational benefit to the Nation.

Economic impacts of applied and basic research on coral reef communities include equipment rentals, air fills, and lodging. Potential commercial applications of this research will benefit pharmacology (anti-cancer compounds from various reef organisms are being tested), medicine (artificial bones), geology, reef fisheries management, aquaria, mariculture techniques, and archaeology.

Revenue from all these activities reenters the south Florida economy and generates employment for many other people in the service sectors. The corals' greatest value, however, is as a living resource, and not as an item of commerce. Their habitat value and attraction to divers are worth far more than as an item of commerce. While coral reefs remain on the seafloor, they are like a good investment: they continue to generate monies through the marine protein harvested there and the divers who come to enjoy them. As curios, they bring a smaller dividend to a fewer number of people.

CHAPTER 2

THE ENVIRONMENT

2.1 CLIMATE

The climate of southeast Florida is characterized as subtropical marine in Miami and tropical maritime in Key West (NOAA 1981). The region is heavily influenced by the adjacent marine environments; the Florida Current, Gulf of Mexico, and Atlantic Ocean affect the terrestrial and marine climates during different seasons. Daily average air temperatures in Key West range from lows of 18.8° C during January to highs of 31.9° C in August (NOAA 1981). Compared to those of Key West, Miami air temperatures are measurably lower in winter and slightly lower during summer (Table 2 and Figures 2 and 3). There is a dry season from November to April in Miami and November to May in Key West. Key West averages 1,007.4 mm of precipitation annually; Miami, 1,518.9 mm (Table 3 and Figure 4). Key West's weather station is within 0.5 km of the coast and is more representative of the reef situation. Throughout most of the year southeast and east-southeast winds prevail, and velocities normally range from 10 to 20 km/hr; wind velocity is less during the summer (Table 4 and Figure 5).

2.2 HURRICANES

Severe hurricanes are common meteorological phenomena in southeast Florida. A formal hurricane

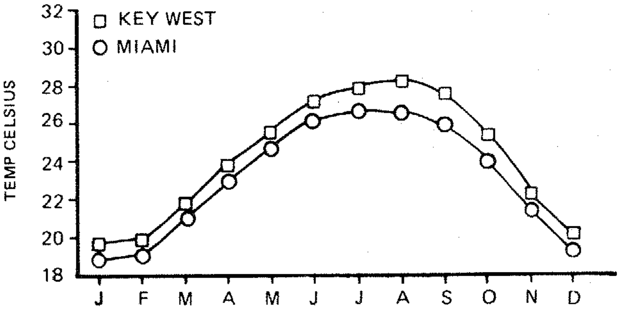

Figure 2. Monthly mean air temperature for Key West and Miami (NOAA 1981). Data base is 29 years for Key West; 38, Miami.

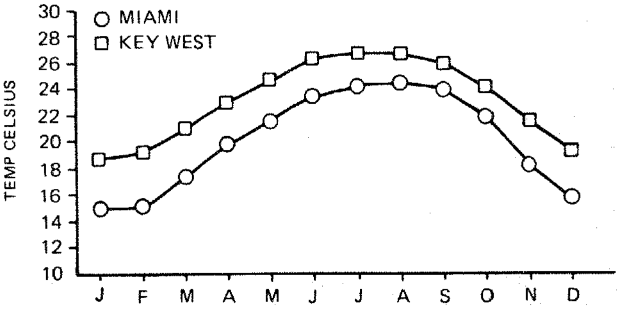

Figure 3. Monthly minimum air temperature for Key West and Miami (NOAA 1981). Data base is 29 years for Key West; 38, Miami.

Table 2

Monthly air temperatures (°C) for Miami and Key West (NOAA 1981).

	Miami		Key West	
Period[a]	Range	Mean	Range	Mean
January	14.8-24.2	19.6	18.8-24.2	21.5
February	15.0-24.8	19.9	19.2-24.8	22.0
March	17.2-26.4	21.8	21.0-26.3	23.7
April	19.6-28.2	23.9	23.1-28.1	25.6
May	21.5-29.6	25.6	24.7-29.6	27.2
June	23.3-31.1	27.2	26.2-31.1	28.6
July	24.2-31.7	27.9	26.7-31.8	29.2
August	24.3-32.2	28.3	26.6-31.9	29.3
September	23.9-31.3	27.6	25.9-31.0	28.4
October	21.7-29.2	25.4	24.0-28.9	26.4
November	18.1-26.6	22.3	21.4-26.4	23.9
December	15.6-24.8	20.2	19.2-24.7	21.9
Yearly	14.8-32.2	24.2	18.8-31.9	25.7

[a] Climate data base for Miami = 38 years; Key West = 29 years.

Table 3

Monthly precipitation (mm) for Miami and Key West (NOAA 1981).

Month[a]	Miami mean	Key West mean
January	54.6	42.4
February	49.5	47.0
March	52.6	39.6
April	91.4	55.1
May	155.4	63.8
June	228.6	115.6
July	175.5	104.4
August	170.7	113.5
September	222.0	186.4
October	207.8	141.5
November	69.1	67.8
December	41.7	38.6
Yearly total	1,518.9	1,015.7

[a] Climate data base for Miami = 38 years; Key West = 29 years.

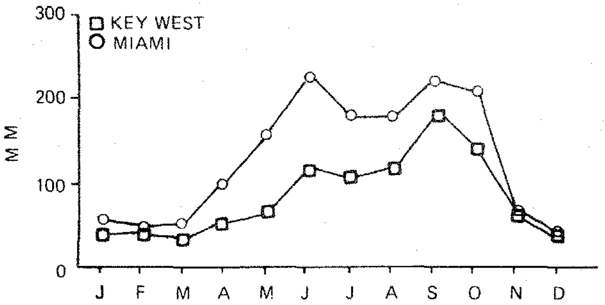

Figure 4. Monthly mean precipitation for Key West and Miami (NOAA 1981). Data base is 29 years for Key West; 38, Miami.

Table 4

Monthly wind speed (km/hr) and direction for Miami and Key West (NOAA 1981).

Month[a]	Miami		Key West	
	Mean speed (km/hr)	Direction	Mean speed (km/hr)	Direction
January	15.3	NNW	19.5	NE
February	16.3	ESE	19.6	SE
March	16.9	SE	20.3	SE
April	17.2	ESE	20.6	ESE
May	15.4	ESE	17.4	ESE
June	13.2	SE	15.6	SE
July	12.7	SE	15.9	ESE
August	12.7	SE	15.4	ESE
September	13.2	ESE	16.3	ESE
October	15.0	ENE	18.2	ENE
November	15.4	N	19.5	ENE
December	14.8	N	19.5	NE
Yearly	14.8	ESE	18.2	ESE

[a] Climate data base for Miami = 38 years; Key West = 29 years.

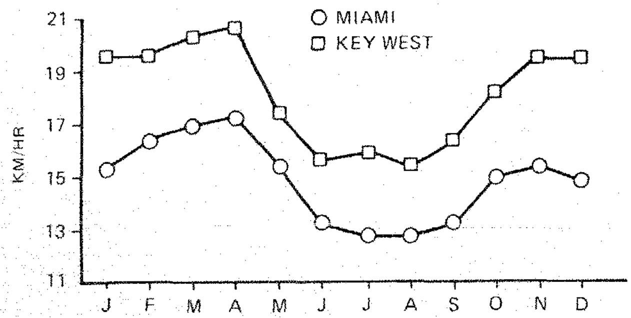

Figure 5. Monthly mean wind velocity for Key West and Miami (NOAA 1981). Data base is 29 years for Key West; 38, Miami.

season exists from 1 June to 30 November. Thirteen major hurricanes have passed across the reef tract and struck the Florida Keys since 1894. Criteria for a major hurricane include one or more of the following: 200-km/hr wind speed; winds reaching out 160 km from the hurricane eye; barometric pressure of 716.28 mm of mercury or less; and/or tide surge of 2.7 m or greater. The Florida Keys has a greater probability of hurricane impact (one in seven) than any other Florida coastal area (Florida Department of Natural Resources 1974). Facts pertaining to hurricane impacts on coral reefs will be detailed in the reef ecology chapter. Table 5 summarizes major hurricanes that have crossed the reef tract since 1873.

2.3 SOLAR RADIATION

Peak solar radiation occurs between 0900 and 1500 hr in Florida (Barnes and Taylor 1973). Transmittance through the water column is greatest at solar noon; albedo (reflection) is significant during early morning and late afternoon. According to Hanson and Poindexter (1972), maximum solar energy was expended at the air-sea interface from 1000 to 1400 hr; most of the energy was expended in heating the water column. Gordon and Dera (1969) studied solar radiation attenuation between Key Largo and Great Abaco Island, Bahamas, and found that in the surface layers (0-5 m) the attenuation (diffusion coefficient) was 0.11-0.57 Kd/m between Miami and the Florida Current. Hanson and Poindexter (1972) reported that the amount of solar radiation impinging on the bottom at 13 m ranged between 5% and 17%; zenith angle, cloud cover, wave action, and turbidity all influenced transmittance. Kanwisher and Wainwright (1967) reported that Florida reef corals required between 200 and 700 footcandles (fc) of solar illumination for autotrophic self-reliance (compensation point). On clear days these values correlated with a depth of about 30 m.

2.4 SEAWATER TEMPERATURE

The most extensive data base for reef seawater temperatures appears in Vaughan (1918). These data came from several lighthouses and Ft. Jefferson, Dry Tortugas, and are summarized in Table 6 and Figures 6-10. More recent data from a patch reef in Biscayne National Park are presented in Table 7 and Figure 11. Temperature extremes are from 14° to 38° C; most annual ranges are from 18° to 30° C. Mean values are above 18° C, the threshold temperature generally accepted for structural reef development by reef building corals (Wells 1956). Temperature variability (range and standard deviation) is greater during the winter. In recent winters (since 1976), polar air masses have cooled coastal waters, causing fish kills and coral mortalities. Areas that have suffered the greatest harm from thermal stresses are off Loggerhead Key, Dry Tortugas (staghorn coral thickets), and patch reefs off Plantation Key (Hens and Chickens and The Rocks). Cold water masses are created in Florida Bay during the winter passage of polar

Table 5

Major hurricanes crossing the coral reefs from 1873 to 1966 (Sugg et al. 1970).

Hurricane name	Date		Wind speed (km/hr)	Tide height (m)
	Day	Year		
	18-30 September	1894	167 (est.)	–
		1896	161 (est.)	–
	27 August	1900	–	–
	11-22 October	1906	–	–
	6-13 October	1909	–	–
	9-23 October	1910	177-201 (est.)	5
	2-15 September	1919	177 (est.)	–
	11-22 September	1926	222	2-4
	22 September-4 October	1929	–	–
	31 August-7 September	1933	201-225	–
	29 August-10 September	1935	322	5-6
	30 October-8 November	1935	121	–
	3-14 October	1941	121-198	–
	12-23 October	1944	193	2-4
	11-20 September	1945	175-315	2-4
	5-14 October	1946	129	5
	9-16 October	1947	–	–
	18-25 September	1948	196	2-6
	3-15 October	1948	161	2
Easy	1-9 September	1950	117	–
King	13-19 October	1950	196-241	2
Donna	29 August-13 September	1960	225-322	4
Cleo	20 August-3 September	1964	177-217	2 (est.)
Betsy	27 August-12 September	1965	266 (gusts)	2-3
Alma	4-14 June	1966	201	–
Inez	21 September-11 October	1966	21-150	2

Table 6

Reef seawater temperatures (°C) (Vaughan 1918).

	Reef							
	Tortugas (1879-1907)		Sand Key (1878-1890)		Carysfort (1878-1899)		Fowey Rocks (1879-1912)	
Month	Range	Mean	Range	Mean	Range	Mean	Range	Mean
January	19.4-24.8	22.1	17.9-24.1	21.8	18.2-25.9	22.5	15.8-26.2	22.2
February	18.7-24.4	22.1	18.3-25.3	22.8	20.6-24.8	23.0	15.6-24.5	22.5
March	19.6-25.4	22.8	20.4-27.3	23.8	21.1-25.6	23.1	18.7-27.4	22.9
April	17.9-25.8	23.6	22.5-28.5	26.1	22.4-26.4	23.9	21.0-29.4	24.4
May	21.9-28.3	25.6	25.8-29.9	28.2	24.0-27.9	25.5	21.4-29.2	26.2
June	23.6-29.3	27.2	27.7-32.2	29.8	25.4-29.4	28.8	21.5-29.6	27.2
July	24.7-31.1	28.8	29.9-31.9	31.1	27.1-30.2	30.0	23.4-30.9	28.3
August	24.2-30.9	29.3	29.2-32.2	30.7	26.5-30.3	30.0	23.5-31.2	28.7
September	24.1-30.5	28.8	28.7-31.2	30.3	27.2-30.1	29.6	22.9-30.7	28.3
October	22.5-29.4	27.3	24.5-30.1	27.6	23.8-29.1	27.6	22.3-29.4	27.0
November	21.4-28.0	25.3	22.3-27.1	25.1	23.0-28.7	25.5	20.0-28.4	25.0
December	21.3-26.4	23.2	18.4-26.0	22.5	21.0-27.3	23.3	15.8-27.9	23.1

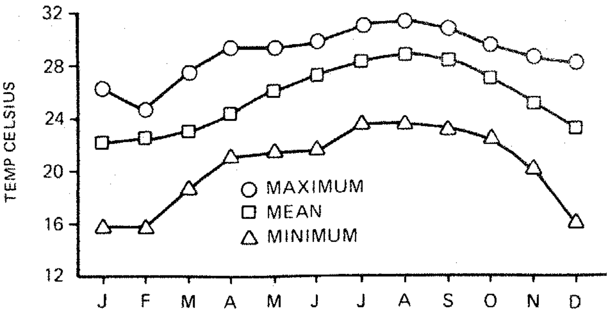

Figure 6. Monthly minimum, mean, and maximum seawater temperature at Fowey Rocks, 1879-1912 (Vaughan 1918).

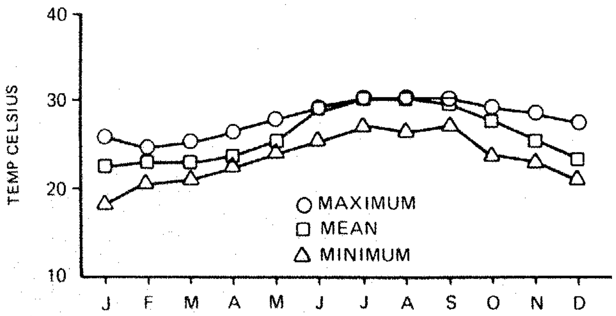

Figure 7. Monthly minimum, mean, and maximum seawater temperature at Carysfort Reef, 1878-1899 (Vaughan 1918).

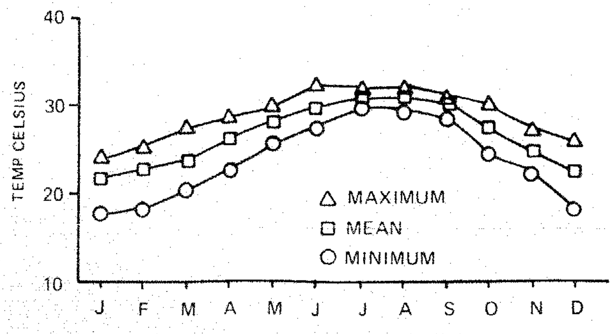

Figure 8. Monthly minimum, mean, and maximum seawater temperature at Sand Key, 1878-1890 (Vaughan 1918).

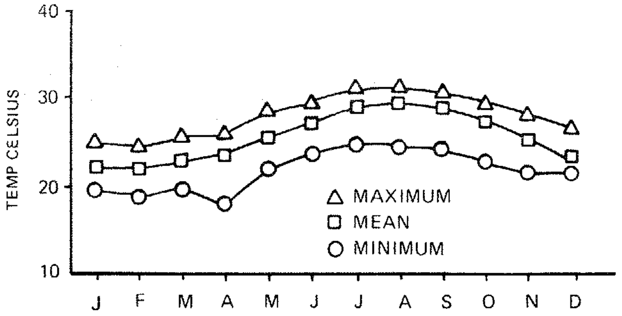

Figure 9. Monthly minimum, mean, and maximum seawater temperature at Dry Tortugas, 1879-1907 (Vaughan 1918).

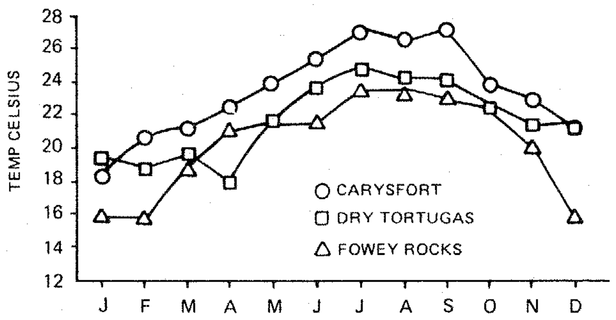

Figure 10. Minimum monthly seawater temperature at Carysfort Reef, Dry Tortugas, and Fowey Rocks.

Table 7

Bottom (3 m) seawater temperature (°C) at Elkhorn Control Reef, Biscayne National Park, 1978 (from daily thermograph data, Biscayne National Park).

Month	Range	Mean	Standard deviation
January	17.5-23.1	20.8	1.3
February	16.7-22.4	20.0	1.4
March	20.4-23.8	22.3	0.9
April	22.3-25.1	24.2	0.7
May	24.5-27.8	26.6	0.7
June	27.2-30.3	28.6	0.8
July	28.5-30.3	29.3	0.4
August	28.7-30.3	29.4	0.4
September	28.4-29.9	29.0	0.4
October	25.2-29.6	28.0	1.3
November	25.1-27.0	25.9	0.4
December	23.8-26.1	24.9	0.8

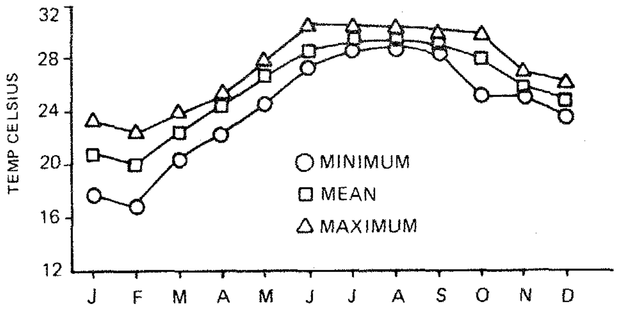

Figure 11. Monthly minimum, mean, and maximum seawater temperature (3m) at Elkhorn Control Reef, Biscayne National Park, 1978 (from thermograph data, Biscayne National Park).

air masses (Roberts et al. 1982). Offshore (into the Atlantic) transport is the effect of tidal pumping, northerly winds, and density gradients. Communities adjacent to tidal channels suffer the greatest impact from this thermal stress. Conversely, during the summer, the Florida Bay water may become hyperthermal (> 31° C) because of solar heating, and communities near tidal passes are more affected.

Seawater temperature reflects the annual climatic cycle: seawater temperatures are lowest from December through March. Temperature peaks in August or early September and cools throughout the fall and winter. A comparison of seawater temperature with air temperature (Tables 2, 6, and 7) for Miami with the recent Biscayne National Park data shows that mean seawater temperature is warmer than mean air temperature throughout the year.

2.5 TIDES

The Atlantic coast from Miami to Key West exhibits a semidiurnal tidal pattern. The area close to Key West is influenced by the Gulf of Mexico, which experiences semidaily or daily tides. Table 8 presents mean and spring tide ranges for several reefs. The major effect of tides on reef communities is the reduction of water depth during spring low tides when shallow reef flats may be near emergent. During the summer, if wind speed is low, heating of the water column may cause hyperthermic conditions such that zooxanthellae (symbiotic algae within the coral tissue) may be expelled (Jaap 1979; Hudson, *in press*). During the winter the reef flat water may be hypothermic, again causing thermal stress (Hudson et al. 1976; Hudson, in press).

A trend of decreasing mean levels and ranges is noted as one approaches the Gulf of Mexico. Tidal currents for the reef area are not presented in the Tide Current Tables prepared by the National Oceanic and Atmospheric Administration. There are significant tidal currents between Florida Bay and the Atlantic.

Table 8

Tidal ranges for several southeast Florida reefs (NOAA 1981).

Location	Mean tide level (m)	Mean tide (m)	Spring range (m)
Fowey Rocks	0.4	0.7	0.7
Molasses Reef	0.3	0.7	0.8
Alligator Reef	0.4	0.6	0.7
Sand Key Reef	0.2	0.4	0.5
Garden Key, Dry Tortugas	0.2	0.3	Not given

2.6 SALINITY

The reef tract area experiences oceanic salinities as summarized in Table 9. The region adjacent to Biscayne Bay is an area where heavy rainfall can reduce salinities for short periods. Dole and Chambers (1918) reported that heavy precipitation in Miami almost always was followed by temporary reduction in chlorinity and salinity at Fowey Rocks 24 hr later. Flat low land, porous soils, and distance offshore minimize the effect of rainfall on salinity in the reef tract areas.

Rarely, entrained Mississippi River spring runoff is carried along the inshore side of the Florida Current. This water mass has salinities of 32-34 ppt, which is within the tolerance limits of reef corals.

Diurnal salinity fluctuations at Margot Fish Shoal ranged from 37.8 to 37.3 ppt because of evaporation and precipitation (Jones 1963).

During hot summer periods, density sinking on shallow reef areas is common. Evaporation creates dense hypersaline surface layers which sink and mix poorly with subsurface cooler waters. Swimmers can feel and see this phenomenon.

2.7 DISSOLVED OXYGEN

Jones (1963) and Jaap and Wheaton (1975) provide limited information on dissolved oxygen. The water column ranges diurnally from 90% to 125% oxygen saturation. Daily maximum values are attained between 1400 and 1600 hr (Jones 1963).

2.8 TURBIDITY

Transparency (equivalent Secchi disc depth) for several stations off the Florida Keys was reported by Williams et al. (1960). They reported that the equivalent Secchi distances ranged from 4.5 to 35 m in this area. Variability of water clarity is considerable. Following storms the water may be nearly opaque. Plankton and suspended matter also affect water clarity.

Water clarity and sedimentation rates for a dredge operation near Basin Hills, Key Largo, were reported by Griffin (1974). Ambient or background suspension concentration in the water column ranged

Table 9

Salinities in the Florida reef tract and vicinity.

Location	Dates	Salinity range (ppt)	Source
Dry Tortugas	1913	35.2 - 36.1	Dole 1914
Fowey Rocks	1914-1916	34.2 - 38.6	Dole and Chambers 1918
Soldier Key	1945-1946	33.1 - 37.1	Smith et al. 1950
Key West area	1953-1954	33.3 - 37.0	Chew 1954
Margot Fish Shoal	1961-1963	36.8 - 37.3	Jones 1963

from 0.5 to 3.7 mg/l at a nearshore patch reef. Suspension concentration within the dredge plume ranged from 18 to 212 mg/l. These levels are probably comparable to the upper limits on the reef tract following a hurricane or major storm.

2.9 CURRENTS

A warm water current (the Florida Current) flows through the Straits of Florida. Wust (1924) calculated that 26 m^3/sec pass through the constricted area between Florida and Cuba. The current's velocity is in the magnitude of 150 cm/sec. It is composed of two water masses in its surface layers. The eastern core is composed of Caribbean water that flows into the Gulf of Mexico through the Straits of Yucatan; the western or nearshore portion of the current is composed of water that flows from the Gulf of Mexico (Wennekens 1959). The Florida Current comes closest to Florida off Palm Beach, where the central axis is about 15 km off the coast. Off Dry Tortugas the current is 124 km south of the islands. The current is very dynamic and meanders a good deal. Generation of eddies off the main body of the current brings current waters onto the shelf and to the reef environments. As noted earlier, the current moderates winter temperature and brings plankton of Caribbean origin into the reefs. Maul (1976) presented the variability of various components of the Gulf Stream system (Figure 12). Schomer and Drew (1982) recently reviewed the physical and chemical environment of southern Florida.

2.10 GEOLOGICAL SETTING

The following information is paraphrased from a field guide to south Florida sediments (Ginsburg 1972a). The Florida-Bahamas region is a carbonate platform part of the Atlantic and Gulf coastal province. The platform is dissected by deep-water channels. The most important consideration here is the Straits of Florida, which is nearly 550 m deep. Marine portions of this platform are generally shallow, less than 16 m deep in most places. Deep test drilling in the area indicates the platform has had a history of continuous subsidence and deposition of shallow-water carbonates and evaporites. Maximum depths of drill penetration (5,486 m at Cay Sal Bank) imply that no near-surface formations older than upper Miocene are extant. The Florida pennisula south of Lake Okeechobee has been a carbonate depositional region during portions of the Mesozoic and throughout the Cenozoic. Recent carbonate sediments are grossly similar to older material. Two major strata dominate the southern Florida coastal areas from Miami southward along the keys. The Key Largo formation is a reef facies formed during the Pleistocene and will be discussed in more detail later. The Miami formation is also a Pleistocene stratum that is composed of oolite and bryozoan skeletons.

2.11 GEOLOGIC HISTORY AND PROCESSES

During the past 20 million years, major change has occurred in western Atlantic coral reefs. Previously, a cosmopolitan reef biota was found throughout the tropics. Twenty million YBP, a land barrier emerged terminating water movement between the Indian Ocean and the Mediterranean Sea. Approximately 7 million YBP, the Central American Isthmus developed, separating the Caribbean Sea and Atlantic Ocean from the Pacific Ocean. What was previously a circum-equatorial tropical zone had thus been isolated into separate biogeographic provinces. During the late Oligocene and early Miocene, 20-30 million YBP, the western Atlantic area experienced its greatest proliferation of reef building. During the Pleistocene (at least 1 million YBP), major environmental change extirpated the Pan Atlantic-Pacific biota. Glacial periods occurred during this time; during each period, sea level was drastically reduced and the marine climate was cooler. Pacific genera of Scleractinia that were eliminated from the western Atlantic include *Stylophora, Pocillopora, Goniastrea, Goniopora, Pavona,* and *Seriatopora* (Newell 1971).

In Florida, a major coral reef community developed during the last major interglacial period, Sangamon, 100,000-112,000 YBP; it was killed during the last glacial advance (Wisconsin) because of the reduction in sea level and the cooler climate. This Pleistocene reef, known as the Key Largo formation, extends from Miami Beach to at least Dry Tortugas and seaward to the Straits of Florida. It varies in thickness from 23 to 61 m or more; the basement has not been reached in several cores. Wherever its base has been lo-

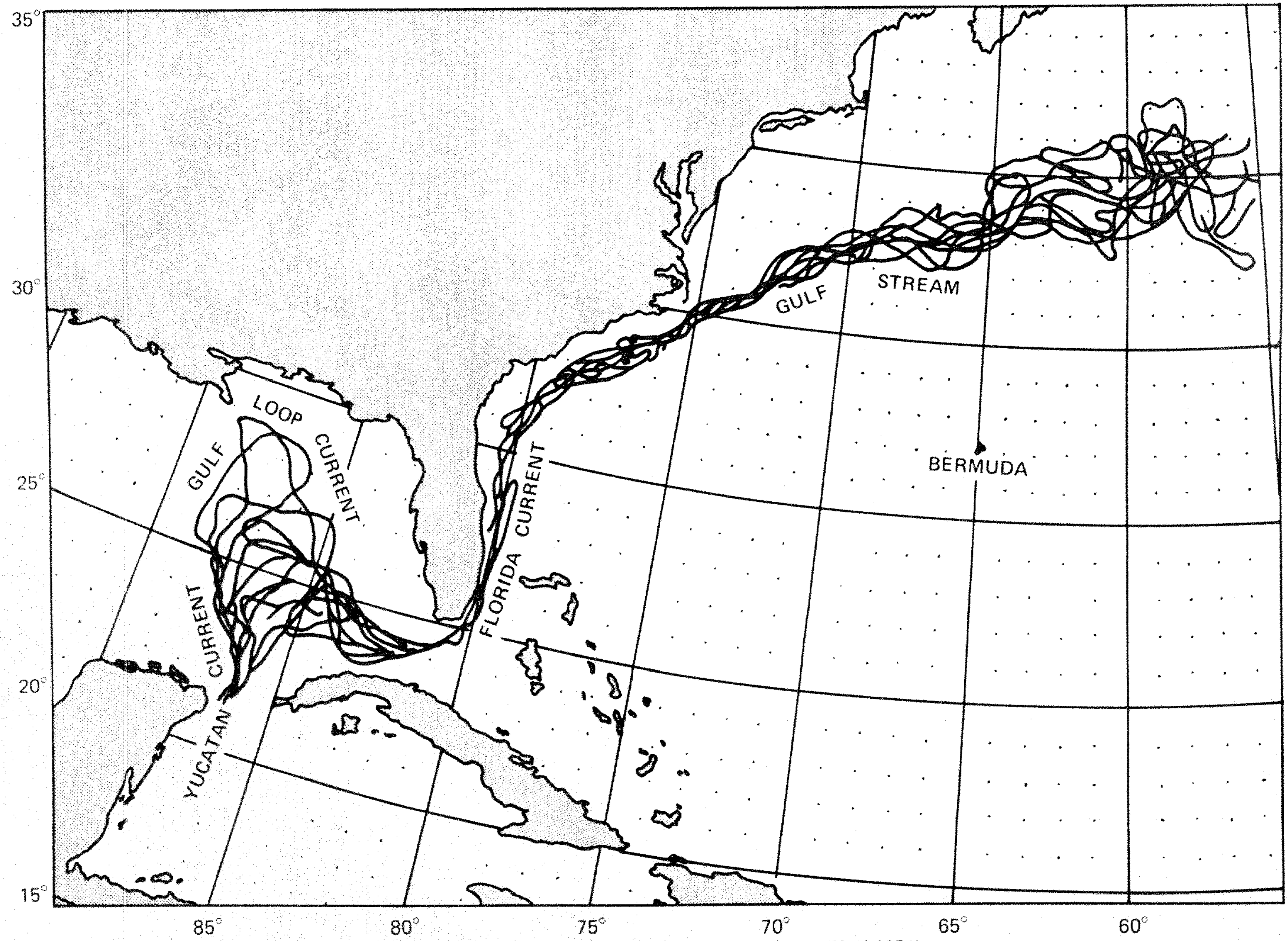

Figure 12. Components of the Gulf Stream System (Maul 1976).

cated, the formation was found to rest atop calcareous-quartz sands. From near Miami to Big Pine Key the Key Largo formation is found near the surface, but from Big Pine Key to Key West it is overlain by the Miami Oolite formation, which may be upwards of 12 m thick (Hoffmeister and Multer 1968). Hoffmeister and Multer (1968) and Hoffmeister (1974) reported that the exposed portion of the Key Largo formation in the Florida Keys is representative of a low-wave-energy patch-reef community. The main evidence for this is that certain scleractinian corals, in particular *Acropora palmata* (elkhorn coral), are absent in the fossil record. Presumably a series of events occurred such that the seaward part of the Key Largo formation did, at one time, possess high wave-energy communities similar to today's reefs; however, as sea level rose during the Holocene transgression, these fossil communities were apparently eroded away by wave action. Hoffmeister (1974) reported that a core made near Looe Key Reef recovered fragments of *A. palmata* from 18 m below the surface.

The Holocene transgression of sea level (Figures 13 and 14) indicates that 10,000 years ago the sea level was about 30 m lower than today (Lighty et al. 1982). Shinn et al. (1977) cored several recent reefs from Miami Beach to Dry Tortugas and dated initial growth from 5,250 to 7,160 YBP. Reef growth or accretion rates ranged from 0.65 to 4.85 m/1,000 years (Table 10; Shinn et al. 1977). For comparison, Adey (1977) reported reef growth off St. Croix, U. S. Virgin Islands, was 15 m/1,000 years (this is the upper limit for Caribbean reef growth). Shinn et al. (1977) reported that the base of recent reefs was Pleistocene Key Largo Reef, fossil mangrove peat, and cross-bedded quartz fossil sand dunes.

More recently, an extensive barrier reef existed off the Ft. Lauderdale area, but it was extirpated about 7,000 YBP (Lighty 1977; Lighty et al. 1978). This reef was a shallow-water *Acropora palmata* community. The demise of this reef was attributed to environmental change caused by increasing sea level (Lighty et al. 1978). Recent coral reef growth off the Florida Keys started from 5,000 to 7,000 years ago.

Development of a coral reef integrates biological, geological, chemical, and physical processes. Soon after the first coral colonies settle and start to grow, the breakdown of organism skeletons by biological and physical agents occurs. Sediments created by these activities become a part of the reef.

Finer sediments filter into voids and borings, and the coarser fractions fill the interstitial space between the reef framework. Reef tract sediments are carbonate and are dominated by algal and coral skeletal material

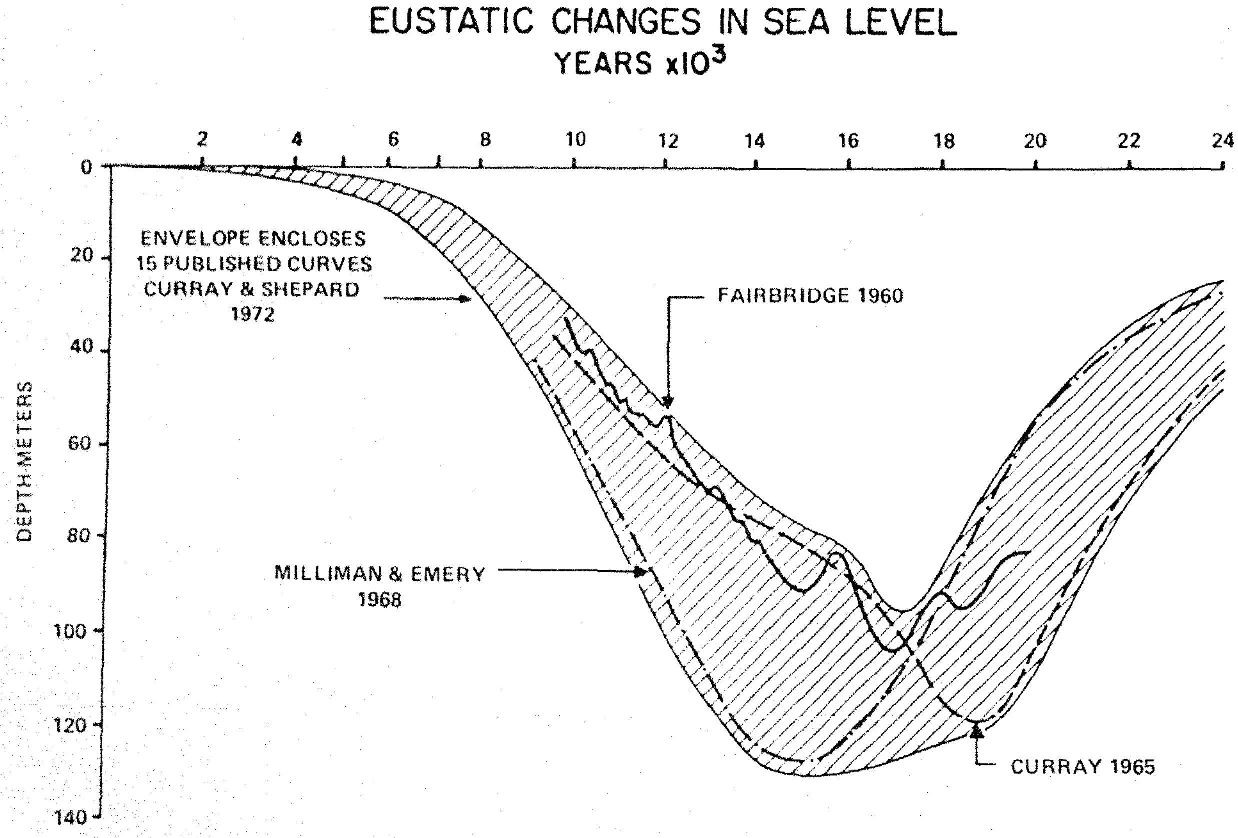

Figure 13. Sea-level change during the Holocene Period (Ginsberg, Comparative Sedimentology Laboratory, University of Miami, Florida).

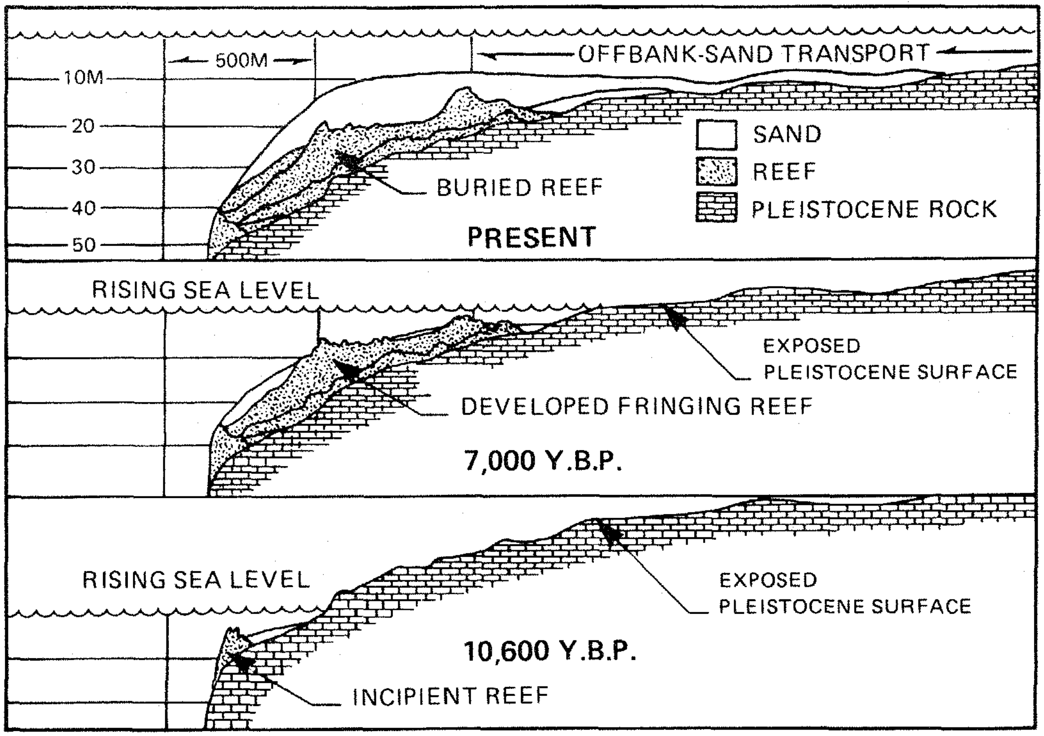

Figure 14. Sea-level change in a Bahamian shelf reef system during the last 10,600 years (Hine and Neuman 1977).

Table 10

Age and growth rate of Recent Florida reefs (Shinn et al. 1977; Shinn 1980).

Reef	Base age (YBP) (with confidence limits)	Accretion (m)	Growth rate (m/1,000 yr)
Long Key	5,630±120	5.0	0.65
Carysfort	5,250±85	7.3	0.86-4.85
Grecian Rocks	5,950±100	9.5	6-8
Bahia Honda	7,160±85	4.6-8.2	1.14
Looe Key	6,580±90	7.3	1.12
Bird Key	6,017±90	13.7	1.36-4.85

(Ginsburg 1956). *Halimeda* and other codiacean algal plates are the most common algal skeletal material. The sedimentary material becomes incorporated into the reef framework through the process of being bound to the platform by crustose coralline algae and through the geochemical processes of *in situ* cementation by high magnesium calcite cements. Ginsburg and Schroeder (1973), among others, detailed the processes of marine cements in coral reefs.

Stearn et al. (1977) presented the most recent quantitative budget of calcium carbonate ($CaCO_3$) within a coral reef ecosystem (Figure 15). This was based on the study of a Barbados fringing reef. While the magnitude of individual components may differ, the concepts are valid and applicable to Florida reefs. Stearn et al. concluded that crustose coralline algae and stony corals (nine species) annually fixed 163 metric tons of $CaCO_3$ on a reef platform with a surface area of 10,800 m^2 (9 kg $CaCO_3/m^2$/year). For comparison, nonreef depositional marine environments in southeastern Florida are reported to produce 0.25-1 kg $CaCO_3/m^2$/year (Stockman et al. 1967; Moore 1972).

Ghiold and Enos (1982) studied $CaCO_3$ production in the brain coral *Diploria labyrinthiformis* from several patch reefs in John Pennekamp Coral Reef State Park (JPCRSP)-Key Largo National Marine Sanctuary (KLNMS). Production ($CaCO_3$) was 11.8±0.3 kg $CaCO_3/m^2$/year of area occupied by the colony. *Porites astreoides* annual $CaCO_3$ production ranged from 13.6±3.5 to 14.0±3.1 kg/m^2/year at Middle Sambo Reef

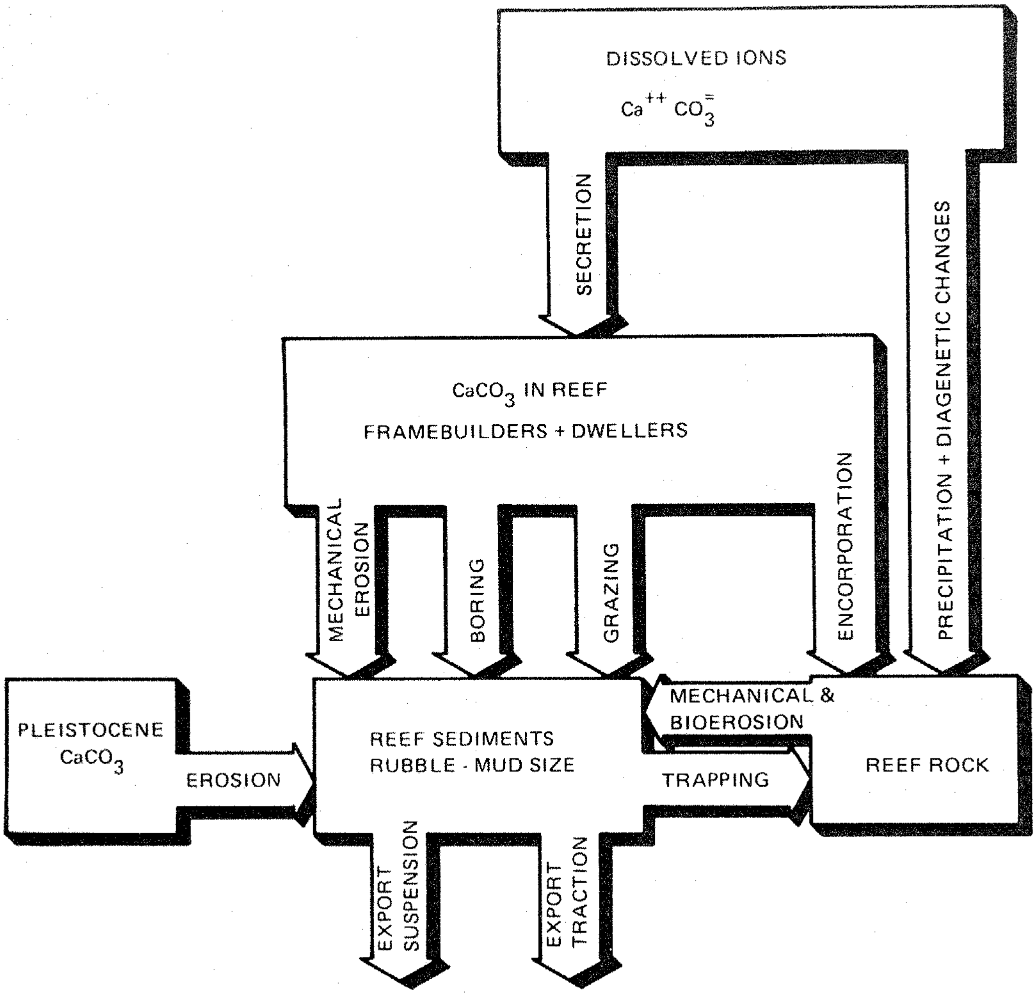

Figure 15. Calcium carbonate flow model based on a Barbados fringing reef (Stearn et al. 1977).

near Key West (Kissling 1977). *Montastraea annularis* has demonstrated annual $CaCO_3$ production of 20 kg $CaCO_3/m^2$/year in Barbados (Stearn et al. 1977).

Ghiold and Enos (1982) extrapolated production values to vertical reef accretion rates of 2.2 m/1,000 years, which is within the magnitude of Holocene reef growth in Florida (Shinn et al. 1977).

Frost et al. (1977) and Taylor (1977) contain many papers about coral reef geology.

CHAPTER 3

CORAL REEF COMMUNITY TYPES

3.1 INTRODUCTION

A biotic community as defined by E.P. Odum (1971) is any assemblage of populations living in a prescribed area of physical habitat. Four discernible coral community types occur off southeast Florida.[1] Generally in a seaward progression are found live bottoms, patch reefs, transitional reefs, and bank reefs. The relief (height above bottom) of these communities and the dominance of stony corals as a structural element increase in a similar progression. All of these communities can be physically characterized as shallow water, wave-resistant, three-dimensional carbonate accretions constructed by limestone-secreting organisms (principally corals, algae, and bryozoans) on a pre-existing hard substrate. This basic structural component is augmented by other community members, sedentary and mobile, permanent and transient.

3.2 LIVE BOTTOM COMMUNITY

The live bottom community, also known as hardground, is generally found closest to shore, e.g., in tidal passes, under bridges, and short distances seaward of the intertidal zone. It usually occupies exposed fossil reef formations, limestone, and other rocky substrates. The faunal and floral elements are not consistent, and the assemblage is usually visually dominated by octocorals, algae, sponges, and smaller hardy stony coral species.

These communities do not actively accrete or build massive structures. They support diverse invertebrate and vertebrate communities and provide an important nursery area for commercial and sport harvested species. Live bottom habitats are scattered from St. Lucie Inlet southward to Dry Tortugas in depths ranging from less than 1 m to beyond 30 m. While these descriptions may imply a single community type, the nearshore and offshore types differ greatly in species composition. In either case the octocorals (soft corals) often dominate in terms of numerical abundance and density. An example of an offshore live bottom community is the reef (Schooner Reef) at number 2 buoy in Biscayne National Park (BNP, Figure 16) off Elliott Key. It exhibits little relief with the exception of a small ballast pile from an old shipwreck on the north side off the reef. The platform is limestone with small ledges, solution holes, and pockets of sediments. It is heavily colonized by octocorals and a sparse number of stony (hard) corals (Table 11). The live bottom community may vary in size from a small area of tens of square meters to one of several hundred square meters. The stony corals most commonly found in the nearshore associations include *Siderastrea radians, Porites porites, P. astreoides, Manicina areolata, Solenastrea hyades,* and *S. bournoni.* Along with these species, *Diploria clivosa, Millepora alcicornis,* and *Dichocoenia stellaris* are commonly found in deeper communities. The region surrounding the live bottom communities is sedimentary, seagrass, rock, or sponge. The seagrass community is treated in detail in Zieman (1982).

Stony coral species are commonly found in the seagrass and sedimentary environments adjacent to the reef communities. These are *Manicina areolata, Porites porites, Cladocora arbuscula,* and *Siderastrea radians,* hardy tolerant species that do not attain great size.

3.3 PATCH REEF COMMUNITY

Patch reefs (Plates 11a, 11b, and 12a) are the second major type of coral community, and they are a most conspicuous element in this region. Their distribution is mostly seaward of Key Largo and Elliott Key; however, they also occur off Big Pine Key, Key West, and Dry Tortugas. They are usually found seaward of Hawk Channel, but a few very nearshore patch reefs exist. Two examples of nearshore patch reefs are (1) an assemblage of patch reefs just to the north of Caesar's Creek (BNP) and (2) a small reef just off Cow Key Channel, Boca Chica Key. Both of these reefs present the general impression of survival under marginal conditions.

A patch reef characteristically has upward of 3 m of relief and is dome-shaped. The surrounding bottom may be sedimentary, seagrass (Plate 12b), or rock. Most patch reefs off southeast Florida are found in 2- to 9-m depths; their upper surface may be nearly emergent at low tide, exemplified by Basin Hill Shoals off Key Largo. Patch reefs are roughly circular in outline and vary in size from about 30-700 m in diameter. Because of different ages of the numerous patch reefs and their local environmental conditions, generalizations fail to adequately characterize them. Jones (1963, 1977) presented information about their physical and chemical environment near Margot Fish Shoal off Elliott Key and the dynamics of developmental stages. Smith and Tyler (1975) and Jones (1977) presented the view that the patch reef community is similar to a super organism, in that it goes through several life stages. The nature of the community reflects the reef's age. While the coral community goes through its cycle of development, the fish assemblages change according to niche availability. An assumed developmental sketch of a patch reef would include the following:

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[1] Darwin (1842), based on his experiences in the Pacific and Indian Oceans, defined three types of coral reefs: fringing, barrier, and atoll. Although many attempts have been made to extrapolate these forms to Atlantic coral reefs, Darwinian-defined reefs do not presently occur in Florida.

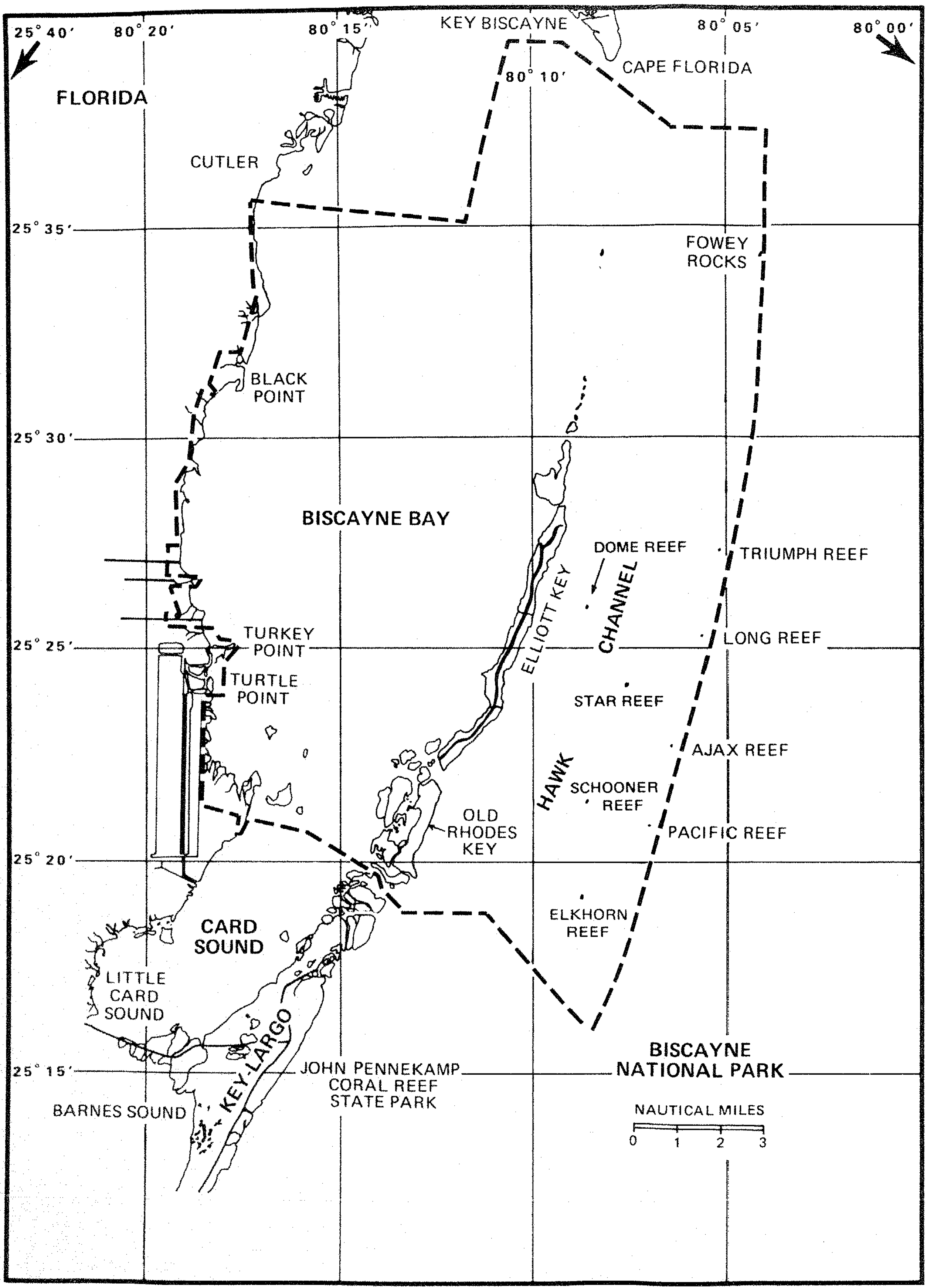

Figure 16. Coral reefs in Biscayne National Park.

Table 11

Live bottom corals from Schooner Reef, Biscayne National Park (four 1-m^2 quadrants; Jaap and Wheaton 1977 MS.).

Species	Type[a]	B.I.[b] (ranking)	Frequency	No. of colonies	Percent of total colonies	Mean no. of colonies/m^2
Plexaura homomalla	O	73	4	18	9.63	4.50
Porites porites	S	73	4	18	9.63	4.50
Gorgonia ventalina	O	70	4	14	7.49	3.50
Pseudopterogorgia americana	O	70	4	14	7.49	3.50
Briareum asbestinum	O	67	4	10	5.35	2.50
Eunicea tourneforti	O	65	4	8	4.28	2.00
Muricea atlantica	O	65	4	8	4.28	2.00
Pseudoplexaura porosa	O	63	4	6	3.21	1.50
Plexaurella fusifera	O	62	4	5	2.67	1.25
Eunicea succinea	O	58	3	25	13.37	6.25
Plexaura flexuosa	O	51	3	11	5.88	2.75
Muriceopsis flavida	O	51	3	10	5.35	2.50
Porites astreoides	S	47	3	6	3.21	1.50
Plexaurella dichotoma	O	47	3	3	1.60	0.75
Millepora alcicornis	S	34	2	7	3.74	1.75
Pseudoplexaura flagellosa	O	32	2	4	2.14	1.00
Eunicea laciniata	O	32	2	2	1.07	0.50
Agaricia agaricites	S	32	2	2	1.07	0.50
Plexaurella grisea	O	31	2	2	1.07	0.50
Eunicea mammosa	O	30	2	2	1.07	0.50
Pseudoplexaura wagenaari	O	29	2	2	1.07	0.50
Dichocoenia stellaris	S	16	1	2	1.07	0.50
Pseudopterogorgia acerosa	O	15	1	1	0.53	0.25
Eunicea calyculata	O	15	1	1	0.53	0.25
Eunicea fusca	O	15	1	1	0.53	0.25
Favia fragum	S	15	1	1	0.53	0.25
Pseudopterogorgia kallos	O	14	1	1	0.53	0.25
Pseudopterogorgia bipinnata	O	14	1	1	0.53	0.25
Siderastrea siderea	S	14	1	1	0.53	0.25
Montastraea cavernosa	S	14	1	1	0.53	0.25
Total				187		

Density

Mean colonies/m^2 = 46.75
Standard deviation = 15.46
Range = 25-61

Mean species/m^2 = 18.50
Standard deviation = 4.53
Range = 13-21

Diversity indices[c]

H' = 4.27
H' max. = 4.91
J' = 0.87

[a] O = octocoral, S = stony coral.
[b] B. I. = Biological Index, McCloskey (1970).
[c] Diversity computed with $\log_2$.

(1) Initial pioneering settlement of coral larvae on appropriate substrates. These species might include *Porites porites, Manicina areolata,* and *Favia fragum.* They would be preparatory colonizers which would eventually die and their skeletons would become the hard substrate that the major framework corals would settle on. If the bottom were rocky, this stage might be unnecessary.

(2) The settlement and growth, both upward and outward, of the primary framework builders. While other coral species are common in the patch reef community, *Siderastrea siderea, Montastraea annularis, Diploria strigosa, D. labyrinthiformis,* and *Colpophyllia natans* build the massive frame or three-dimensional structure of most reefs. Shortly after the framework element has settled, the boring and rasping fauna starts the production of reef sediment. Sediments fill interstitial space and are incorporated into the reef frame. In time, some coral deaths occur providing space for settlement of coral larvae, an essential element for growth of the reef. The newly developing reef is a focal point for attracting the diverse flora and fauna common to the coral reefs. Some of this occurs because of larval settlement, especially for the sessile species. Mobile invertebrates and vertebrates (some residents, some temporary refugees) move to the reef as niches favorable to their requirements become available (Plates 13a and b).

(3) The maturing stage. During this stage the reef grows upward and outward, providing surface area for secondary colonizers. The major framework builders attain 2 m in diameter and greater. The boring and rasping fauna excavate considerable material from the basal surfaces of the corals, creating a labyrinth of caves that become occupied by a cryptic biota. In time, these caves and tunnels are enlarged, and larger fish and invertebrates take refuge in them. The new niches within the interior of the reef are colonized by a wide taxonomic spectrum of shade-loving organisms.

(4) The fully mature stage. Because the primary framework-building corals have approached sea level, upward growth is limited. The undersurface of these corals is cavernous, and in time the framework becomes so weakened that the upper surface may collapse inward forming a rubble or boulderlike surface. This is usually irregularly flat and, in many cases, is dominated by octocorals. Haystacklike colonies of *M. annularis* appear to have large dead areas that are colonized by other species (*Millepora alcicornis* and *Gorgonia ventalina*). If the reef completely collapses from a major storm or vessel grounding, the former major relief patch reef becomes a low-relief pile of rubble that is usually dominated by octocorals and nonframework building stony corals. In this growth and decay of the patch reef community into the live bottom community, geochemical processes play an important role in cementing and binding sediments.

The association of coral found on any particular patch reef is most probably governed by random chance. Some patch reefs have very diverse stony coral faunas while other reefs, only a few meters or kilometers away, have a less diverse, nearly monospecific fauna. Patch reefs exhibit extreme variability in coral abundance, density, and diversity (Table 14). Macrobenthic algae constituted from 0% to 7% of the linear biomass, sponge 0% to 3.6%. Octocorals constituted a numerically dominant element; however, their linear biomass and macrohabitat potential are less than many of the stony corals, especially the massive framework builders. Octocorals do occupy much of the space on the mature older patch reefs. There appears to be a competitive exclusion by octocorals in the interior of older patch reefs. A representative patch reef is the reef at buoy number 4 (Dome Reef) in BNP 16. It is about 250 m in diameter. The greatest relief is about 2 m and is found on the northwest side. Tables 12a and b and 13a and b present the octocoral and stony corals found in this reef based on several transects. Reef organic linear biomass based on line transect surveys from four patch reefs in Biscayne National Park shows that mean stony coral cover was 25.7±10.6% in the stony coral-dominated zones (Table 14). In the interior octocoral-dominated zones the organic linear biomass for stony corals was 14.3% ±9.7% (Table 14). There is usually a halo of barren sand and reef talus (rubble) with sparse grasses and algae surrounding the periphery of most patch reefs (Plates 11a and b). The rubble, composed mostly of dead coral colonies that have been swept away from the reef by storms, is potential substrate for colonization. Outward reef expansion is presumably dependent on the reef talus in sedimentary environments for substrate creation. Halos around some patch reefs resulted from the black sea urchin (*Diadema antillarum*) feeding nocturnally on algae and seagrasses surrounding the reef, according to Sammarco (1972), Ogden et al. (1973), and Sammarco et al. (1974). Randall (1965), however, reported that herbivorous reef fish were responsible for patch reef halos. In either case, the herbivorous consumers graze away the flora adjacent to the reef, creating a barren zone or halo.

Patch reefs are important habitats for many reef fish, permanent and transient (Plate 13a). They provide shelter, food, and breeding ground for mobile fauna. The spiny lobster (*Panulirus argus*) (Plate 19b) utilizes patch reef habitats during part of its life history.

Like most reefs, patch reefs show a temporal change when storms or temperature extremes disturb the communities. Smaller coral colonies are dislodged and transported from their growth positions. If the new position is favorable, they may continue to grow; if not, they may die. This is especially true for octocorals and encrusting colonies of *Millepora* that are on unstable substrates, principally octocoral axes. These colonies may be swept completely off the reef by heavy wave surge. There appears to be high mortality due to this stress; if so, intense recruitment usually prevents large open areas.

3.4 TRANSITIONAL REEF COMMUNITY

The term transitional reef is used to describe those reefs that have the rudiments of bank reefs (see

Table 12a

Octocorals at Dome Reef (two 20-m transects, 1977; Wheaton, in preparation a).

Species	B.I.[a] (ranking)	Frequency	No. of colonies	Percent of total colonies
Plexaura flexuosa	39	2	41	19.33
Plexaura homomalla	36	2	29	13.67
Pseudoplexaura porosa	36	2	28	13.20
Pseudopterogorgia acerosa	34	2	29	13.67
Pseudoplexaura flagellosa	31	2	12	5.66
Gorgonia ventalina	31	2	12	5.66
Pseudopterogorgia americana	30	2	17	8.01
Briareum asbestinum	29	2	10	4.71
Plexaurella fusifera	26	2	7	3.30
Eunicea tourneforti	25	2	6	2.83
Plexaurella nutans	22	2	2	0.94
Eunicea fusca	15	1	4	1.88
Eunicea succinea	14	1	3	1.41
Muricea atlantica	12	1	4	1.88
Eunicea laciniata	12	1	4	1.88
Eunicea calyculata	10	1	1	0.47
Plexaurella grisea	10	1	1	0.47
Muricea elongata	10	1	1	0.47
Eunicea mammosa	10	1	1	0.47
Total			212	

[a] B.I. = Biological Index, McCloskey (1970).

Table 12b

Octocorals at Dome Control Reef (two 20-m transects, 1977; Wheaton, in preparation a).

Species	B.I.[a] (ranking)	Frequency	No. of colonies	Percent of total colonies
Plexaura homomalla	40	2	49	19.76
Pseudoplexaura porosa	36	2	30	12.10
Plexaura flexuosa	35	2	32	12.90
Pseudopterogorgia americana	35	2	26	10.48
Pseudopterogorgia acerosa	34	2	25	10.08
Gorgonia ventalina	27	2	10	4.03
Briareum asbestinum	26	2	12	4.84
Eunicea tourneforti	26	2	9	3.63
Pseudoplexaura flagellosa	26	2	12	4.84
Eunicea calyculata	26	2	12	4.84
Eunicea succinea	22	2	4	1.61
Plexaurella fusifera	22	2	4	1.61
Plexaurella grisea	22	2	4	1.61
Muricea elongata	22	2	4	1.61
Eunicea fusca	21	2	3	1.21
Muricea atlantica	21	2	3	1.21
Muriceopsis flavida	14	1	5	2.02
Eunicea laciniata	11	1	2	0.81
Plexaurella nutans	10	1	1	0.40
Eunicea clavigera	10	1	1	0.40
Total			248	

[a] B.I. = Biological Index, McCloskey (1970).

Table 13a

Stony corals at Dome Reef (two 25-m transects, 1977; Jaap, unpublished).

Species	B.I.[a] (ranking)	Frequency	No. of colonies	Percent of total colonies	Cover (cm)	Percent of total cover	
Montastraea annularis	40	2	21	53.85	880	0.6592	Density
Millepora alcicornis	38	2	8	20.51	140	0.1049	
Siderastrea siderea	36	2	2	5.13	30	0.0225	Mean colonies/trans. = 19.50
Porites porites	36	2	2	5.13	15	0.0112	Standard deviation = 2.12
Colpophyllia natans	19	1	1	2.56	170	0.1273	
Dichocoenia stellaris	19	1	1	2.56	10	0.0075	Diversity indices[b]
Mycetophyllia ferox	19	1	1	2.56	65	0.0487	
Porites astreoides	19	1	1	2.56	5	0.0037	H' = 2.20
Favia fragum	19	1	1	2.56	5	0.0037	H' max. = 2.20
Diploria clivosa	19	1	1	2.56	15	0.0112	J' = 0.66
Total			39		1,335		

[a] B.I. = Biological Index, McCloskey (1970). [b] Diversity computed with $\log_2$.

Table 13b

Stony corals at Dome Control Reef[a] (two 25-m transects, 1977; Jaap, unpublished).

Species	B.I.[b] (ranking)	Frequency	No. of colonies	Percent of total colonies	Cover (cm)	Percent of total cover	
Siderastrea siderea	39	2	10	33.33	290	31.69	Density
Dichocoenia stellaris	38	2	4	13.33	105	11.48	
Agaricia agaricites	36	2	2	6.67	20	2.19	Mean colonies/tran. = 15.00
Millepora alcicornis	20	1	3	10.00	75	8.20	Standard deviation = 11.31
Montastraea annularis	19	1	1	3.33	280	30.60	
Porites astreoides	18	1	2	6.67	25	2.73	Diversity indices[c]
Porites porites	18	1	2	6.67	25	2.73	
Diploria labyrinthiformis	18	1	2	6.67	40	4.73	H' = 2.88
Montastraea cavernosa	18	1	2	6.67	45	4.92	H' max. = 3.32
Favia fragum	17	1	1	3.33	5	0.55	J' = 0.87
Eusmilia fastigiata	17	1	1	3.33	5	0.55	
Total			30		915		

[a] Reef similarity = affinity between Dome experimental and control reefs: Jaccard's coefficient = 0.3333; Morisita's coefficient = 0.5295.
[b] B.I. = Biological Index, McCloskey (1970).
[c] Diversity computed with $\log_2$.

Table 14

Attributes of stony coral associations, Biscayne National Park, based on several line transects at each reef (8 reefs, 18 transects) (Jaap, unpublished).

	Stony coral associations		
Attributes	Transitional bank reefs	Patch reefs	Livebottom
Transects[a] (1977)	E 2, 3; EC 1, 2, 3: 5 transects	St 1, 2; StC 1; D 1, 2; DC 1: 6 transects	E 1; Sc 1, 2; ScC 1, 2; StC 2; DC 2: 7 transects
Dominant species	*Acropora cervicornis* *Acropora palmata* *Porites astreoides*	*Montastraea annularis*	*Porites porites* *Millepora alcicornis*
% of colonies	67.2	44.2	48.2
Unique species	*Millepora complanata* *Siderastrea radians*	*Stephanocoenia michelinii*, *Colpophyllia natans*, *Mycetophyllia ferox*, *Mycetophyllia lamarckiana*	*Diploria labyrinthiformis*
No. of species	12	16	14
No. of colonies	186	124	140
Diversity indices[b]			
H'n	2.79	2.89	2.84
H'c	2.57	2.14	2.91
H' max.	3.58	4.00	3.81
J'n	0.78	0.72	0.75
J'c	0.72	0.54	0.76
% cover ($\bar{x}$ ± SD)			
Algae	0.3 ± 0.3	1.7 ± 2.7	2.0 ± 2.5
Sponge	0.7 ± 0.8	1.1 ± 1.4	2.7 ± 3.3
Octocoral	25.2 ± 12.8	23.2 ± 11.4	38.3 ± 15.3
Stony coral	28.9 ± 15.1	25.7 ± 10.6	14.3 ± 9.7
Abiotic substrate (sand, + rubble + rock)	46.7 ± 9.3	48.4 ± 12.1	42 ± 19.0

[a] E: Elkhorn Reef
D: Dome Reef
Sc: Schooner Reef
St: Star Reef
C: Control Reef, e.g., StC: Star Control Reef.

[b] H'n, J'n computed by abundance.
H'c, J'c computed by cover.

Section 3.5) but are not as fully developed. They can be thought of as embryonic bank reefs, or a series of coalesced patch reefs, or well-developed hardgrounds with relief. The marginal bank reefs found inshore of Pacific Reef and continuing south to Pennekamp Park boundary in BNP are examples of the embryonic bank reefs. They possess a well-developed reef flat with some trend of spur development by *Acropora palmata* on the seaward fringe. The reef at number 1 buoy (Elkhorn Reef) at BNP (Plate 18a) exemplifies these reefs. Elkhorn Reef is about 500 m long in its north/south axis and some 200 m long in its east/west axis. The reef flat is a rocky platform with undercut solution holes and ledges and sedimentary environments seaward and landward. Off the northeast reef flat there are several large haystack colonies of *Montastraea annularis* (Plate 5b), which are extensively excavated on the undersurface. Their upper surfaces are dead, in some cases supporting the sea fan, *Gorgonia ventalina*. The area seaward of the reef flat platform is visually dominated by octocorals and occasional large clusters of *Porites porites*. There is a slight slope to the reef flat that in some places has dense clusters of *Acropora palmata*, elkhorn coral. A summary of coral species, abundance, and density is presented in Tables 15a, 15b, 16a, and 16b.

Acropora palmata colonies on the reef flat interface are situated with major branches oriented into prevailing seas, east/southeast. On the reef flat small, more uniformly oriented colonies in less dense aggregations are common. They are associated with colonies of *Millepora complanata*, *Gorgonia ventalina*, and *Diploria clivosa*. This coral often propagates or spreads by vegetative "fragments" (Plate 10b). Broken fragments settle in the nearby bottom and in a short time are solidly attached. They grow upward forming new colonies. The clustered distribution of this species is probably related to the fact that fragments are not transported great distances from parent colonies. Mergner (1977) reported that *M. complanata* (Plate 3b) is an indicator of heavy wave surge. It is common in the reef flats and spur and groove tract areas where wave surge is greatest. *Acropora cervicornis* (Plate 4b), the other common stony coral, occurs in small patches. It is not firmly attached to the bottom and is moved about a good deal during storms. *Porites astreoides* and *P. porites* are also very common on the reef flat. The former is firmly attached, while the latter is not.

On occasion, dislodged *A. cervicornis* colonies come in contact with *A. palmata* colonies; a gall or fuse is formed by a rejection reaction where the tissues of the two colonies meet. The tapering cylindrical branches of *A. cervicornis* grow upward entwined with the flat frondose branches of *A. palmata*. *A. palmata* overgrows *A. cervicornis* when they are in contact (J. C. Lang, University of Texas, Austin; personal observation).

Another type of transitional reef develops on the artificial substrates found throughout the reef tract. They attract reef biota and in time become very reeflike. They include shipwrecks and other materials. A good example is the *Benwood* wreck in KLNMS. This large steel ship sank during WWII and has numerous corals and other sessile growth. The fish fauna is similar to those of nearby natural reefs. The "French wreck" is a similar phenomenon off Loggerhead Key, Dry Tortugas. Artificial reef substrate is also provided by ballast stone or large blocks of igneous rock that were lost in shipwrecks. These are also colonized by reef organisms, notably *Millepora* sp. A number of large barges and ships have been purposely scuttled in waters of 30 m and greater as fish havens; these also develop natural reef growth.

3.5 MAJOR BANK REEF COMMUNITIES

Bank reefs are typically elongated and form a narrow, linear, discontinuous arc from Miami south and west along the Keys to the Dry Tortugas. They are located near the abrupt change in bottom slope, which marks the seaward edge of the Floridan Plateau and they occur mostly between the 5- and 10-m depth contours.

The distinctive features of these reefs are the occurence of *Acropora palmata*, the coral zonation by depth (Table 18 and Figure 18), and the seaward spur and groove formation.

Major bank reefs vary in morphology and species composition. Some, such as Long and Ajax Reefs (Figure 16 and Table 17), off Elliott Key, are sparsely developed in their shallow zones, but below 12 m there is growth on antecedent reef platforms. Better developed bank reefs exhibit a zonation which varies from reef to reef. Reef age, relative position, hydrodynamics, and underlying topography are the major influences on differences in reef morphology and zonation. The general pattern is presented in Table 18. Specific details for individual reefs are given below.

Carysfort Reef

Carysfort Reef (Figure 17) is the northernmost reef in the KLNMS system. A large lighthouse is near the north end of the reef flat. The reef flat has an extensive concentration of *Acropora palmata* on its seaward flank. The spur and groove formations are in an early stage of development. Seaward portions of the reef flat grade into a nearly barren area that separates the *A. palmata* colonies from the buttress zone. The buttress zone has extensive areas of low relief residual spurs and grooves that have coral development. Haystack size colonies of *Montastraea annularis* and fields of *A. cervicornis* are common. The reef platform terminates at about 27 m. Table 19 presents density and abundance information for the stony corals in the 14- to 15-m depth range. A broad expanse of rock separates the reef platform proper from hard-substrate deep reef communities. These deeper communities were described by Jaap (1981) and Wheaton (1981). Outlying communities continue to a depth of about 41 m. The stony coral composition is similar to that of the deep reef; *Agaricia lamarcki*, *A. fragilis*, and *Helioseris cucullata* are the dominant species on vertical faces, while *Siderastrea siderea*, *M. cavernosa*, and *Madracis mirabilis* are common on the horizontal surfaces.

Table 15a

Elkhorn Reef stony coral fauna (four 4-m^2 plots sampled per reef, 1978; Jaap, unpublished).

Species	B.I.[a] (ranking)	Frequency	No. of colonies	Percent of total colonies	Mean no. colonies/m^2
Porites astreoides	315	16	60	54.05	3.7500
Acropora cervicornis	210	11	15	13.51	0.9375
Diploria clivosa	132	7	11	9.91	0.6875
Porites porites	95	5	7	6.31	0.4375
Acropora palmata	59	3	6	5.41	0.3750
Siderastrea siderea	57	3	4	3.60	0.2500
Millepora alcicornis	38	2	3	2.70	0.1875
Palythoa sp.	19	1	1	0.90	0.6250
Millepora complanata	19	1	1	0.90	0.6250
Favia fragum	18	1	1	0.90	0.6250
Diploria strigosa	18	1	1	0.90	0.6250
Dichocoenia stellaris	18	1	1	0.90	0.6250
Total			111		

Density

Mean colonies/m^2 = 6.94
Standard deviation = 2.35
Range = 3-12

Diversity indices

Mean species/m^2 = 3.31
Standard deviation = 1.54
Range = 1-6

H' = 2.99
H' max. = 3.59
J' = 0.64

[a] B.I. = Biological Index, McCloskey (1970).

Table 15b

Elkhorn Control Reef stony coral fauna (four 4-m^2 plots sampled per reef, 1978; Jaap, unpublished).

Species	B.I.[a] (ranking)	Frequency	No. of colonies	Percent of total colonies	Mean no. colonies/m^2
Porites astreoides	260	14	68	59.65	4.2500
Millepora alcicornis	146	8	9	7.89	0.5625
Diploria clivosa	115	6	7	6.14	0.4375
Acropora cervicornis	96	5	6	5.26	0.3750
Porites porites	94	5	7	6.14	0.4375
Agaricia agaricites	76	4	6	5.26	0.3750
Siderastrea siderea	56	3	5	4.39	0.3125
Palythoa sp.	38	2	2	1.75	0.1250
Dichocoenia stellaris	20	1	1	0.88	0.6250
Millepora complanata	19	1	1	0.88	0.6250
Porites branneri	19	1	1	0.88	0.6250
Favia fragum	19	1	1	0.88	0.6250
Total			114		

Density

Mean colonies/m^2 = 7.13
Standard deviation = 2.35
Range = 3-9

Mean species/m^2 = 3.19
Standard deviation = 1.22
Range = 1-5

Diversity indices

H' = 2.22
H' max. = 3.58
J' = 0.62

[a] B.I. = Biological Index, McCloskey (1970).

Table 16a

Elkhorn Reef octocoral fauna (three 20-m transects, 1977; Wheaton, in preparation b).

Species	B.I.[a]	Frequency	No. of colonies	Percent of total colonies
Gorgonia ventalina	59	3	46	22.01
Eunicea succinea	56	3	31	14.83
Plexaura flexuosa	55	3	28	13.40
Pseudopterogorgia americana	54	3	35	16.75
Plexaura homomalla	48	3	13	6.22
Muricea atlantica	46	3	9	4.31
Pseudoplexaura porosa	45	3	7	3.35
Pseudoplexaura flagellosa	42	3	3	1.44
Eunicea tourneforti	34	2	17	8.13
Plexaurella fusifera	29	2	5	2.39
Pseudopterogorgia acerosa	27	2	3	1.44
Eunicea laciniata	27	2	3	1.44
Pseudopterogorgia kallos	16	1	6	2.87
Muriceopsis flavida	13	1	1	0.48
Eunicea calyculata	13	1	1	0.48
Plexaurella dichotoma	13	1	1	0.48
Total			209	

[a] B.I. = Biological Index, McCloskey (1970).

Table 16b

Elkhorn Control Reef octocoral fauna (three 20-m transects, 1977; Wheaton, in preparation b).

Species	B.I.[a]	Frequency	No. of colonies	Percent of total colonies
Pseudopterogorgia americana	54	3	39	13.27
Eunicea succinea	55	3	50	17.01
Gorgonia ventalina	54	3	49	16.67
Plexaura homomalla	52	3	29	9.86
Pseudoplexaura crucis	52	3	32	10.88
Plexaura flexuosa	51	3	31	10.54
Eunicea tourneforti	43	3	15	5.10
Muricea atlantica	40	3	11	3.74
Pseudoplexaura porosa	39	3	10	3.40
Pterogorgia citrina	37	3	8	2.72
Muriceopsis flavida	35	3	4	1.36
Pseudoplexaura flagellosa	28	2	7	2.38
Plexaurella dichotoma	24	2	3	1.02
Plexaurella fusifera	22	2	3	1.02
Eunicea fusca	13	1	1	0.34
Briareum asbestinum	13	1	1	0.34
Eunicea calyculata	10	1	1	0.34
Total			294	

[a] B.I. = Biological Index, McCloskey (1970).

Table 17
Ajax Reef stony coral fauna at 17 m (fifteen 1-m^2 plots; Jaap, unpublished).

Species	B.I.[a] (ranking)	Abundance	Percent of total colonies	Density Mean	Density Std.dev.	D.I.[b]
Montastraea annularis	32	52	24.19	3.47	2.92	C
Siderastrea siderea	32	50	23.26	4.17	2.86	C
Millepora alcicornis	25	32	14.88	2.13	1.96	R
Montastraea cavernosa	18	21	9.77	1.40	1.55	R
Stephanocoenia michelinii	10	14	6.51	0.93	1.75	C
Madracis decactis	9	9	4.19	0.60	0.74	R
Porites astreoides	8	8	3.72	0.53	0.64	R
Agaricia agaricites	5	5	2.33	0.40	0.51	R
Dichocoenia stellaris	3	3	1.40	0.20	0.56	R
Porites porites	3	3	1.40	0.20	0.77	C
Eusmilia fastigiata	3	3	1.40	0.20	0.41	R
Agaricia lamarcki	2	2	0.93	0.13	0.52	C
Siderastrea radians	2	2	0.93	0.13	0.35	R
Diploria labyrinthiformis	2	2	0.93	0.13	0.52	C
Meandrina meandrites	2	2	0.93	0.13	0.35	R
Acropora cervicornis	2	2	0.93	0.13	0.35	R
Mycetophyllia aliciae	1	1	0.47	0.07	0.26	R
Madracis mirabilis	1	1	0.47	0.07	0.26	R
Mycetophyllia lamarckiana	1	1	0.47	0.07	0.26	R
Helioseris cucullata	1	1	0.47	0.07	0.26	R
Colpophyllia natans	1	1	0.47	0.07	0.26	R
Total species		21				
Total colonies		215				
Density, square meter	Mean	Std. dev.	Range			
Species:	6.13	2.36	1 - 9			
Colonies:	14.33	6.59	1 - 27			

[a] B.I. = Biological Index, McCloskey (1970).
[b] D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

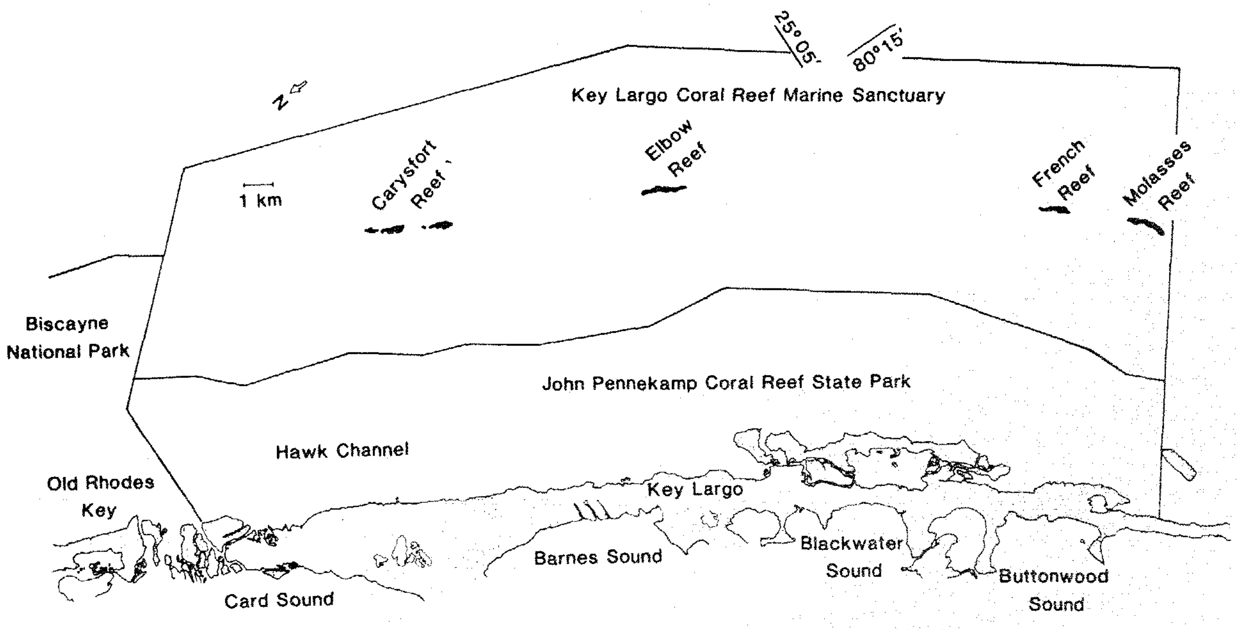

Figure 17. John Pennekamp Coral Reef State Park and Key Largo National Marine Sanctuary.

Table 18

Bank reef zonation patterns.

Zone	Depth (m)	Conspicuous organisms
Back reef/rubble area	0.6 - 1.8	*Porites astreoides, Favia fragum*
Reef flat (Plate 14a)	0.6 - 1.2	*Diploria clivosa, Porites astreoides,* Crustose coralline algae
Shallow spur and groove (Plates 14b and 15a)	1.2 - 2.4	*Millepora complanata, Palythoa* sp.
Deep spur and groove (Plates 15b and 16a)	2.4 - 4.6	*Gorgonia ventalina, Acropora palmata*
Buttress or fore-reef (Plates 16b and 17a)	4.6 - 30.0	*Montastraea annularis, Diploria strigosa, Colpophyllia natans*
Deep reef (Plate 17b)	41.1	*Helioseris cucullata, Agaricia fragilis, Madracis mirabilis*

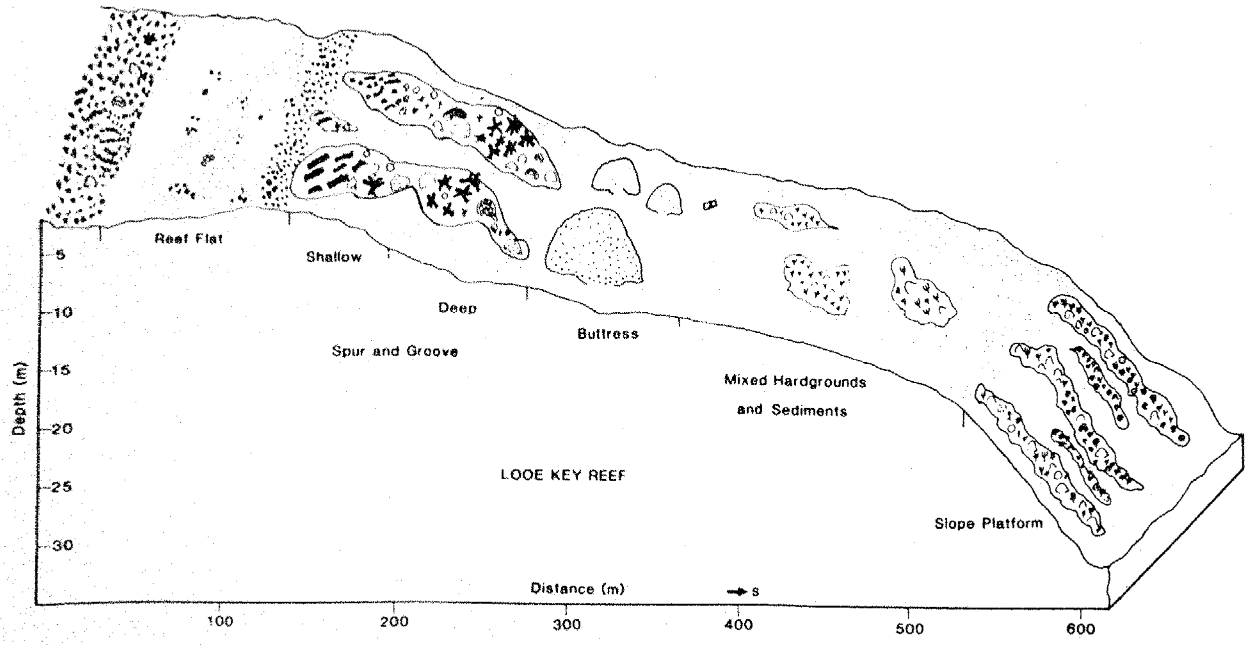

Figure 18. Cross-sectional diagram of Looe Key Reef.

Table 19

Carysfort Reef stony coral fauna at 14 - 15 m (ten 1-m^2 plots; Jaap, unpublished).

Species	B.I.[a] (ranking)	Abundance	Percent of total colonies	Density		D.I.[b]
				Mean	Std.dev.	
Montastraea annularis	18	45	36.00	4.50	3.70	C
Acropora cervicornis	11	26	20.80	2.60	4.60	C
Agaricia agaricites	8	15	12.00	1.50	3.10	C
Siderastrea siderea	6	6	4.80	0.60	0.80	R
Porites porites	5	12	9.60	1.20	3.50	C
Stephanocoenia michelinii	5	7	5.60	0.70	1.90	C
Porites astreoides	5	7	5.60	0.70	1.90	C
Colpophyllia natans	2	2	1.60	0.20	0.40	R
Mycetophyllia aliciae	2	2	1.60	0.20	0.40	R
Mycetophyllia lamarckiana	2	2	1.60	0.20	0.40	R
Millepora alcicornis	2	2	1.60	0.20	0.60	C
Helioseris cucullata	1	1	0.80	0.10	0.30	R
Total species		12				
Total colonies		125				
Density, square meter	Mean	Std. dev.	Range			
Species:	3.70	1.06	2 - 5			
Colonies:	12.50	8.44	4 - 31			

[a] B.I. = Biological Index, McCloskey (1970).
[b] D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

French Reef

French Reef, KLNMS (Figure 17; Plate 1b) is farther south and is a popular reef for dive tours. It has a widely separated reef flat and poorly developed shallow spur and groove zones. The deep spur and groove zone is well developed and has cavernous tunnels through many of the spurs. *Acropora palmata* and *M. annularis* are the dominant stony corals on the spur formations. The spurs are usually 5-6 m deep on their tops; this limits the firecoral *Millepora complanata* and the yellow mat zooanthid *Palythoa* sp. from this reef zone. Table 20 presents information on the abundances and densities of stony corals from the deep spur and groove zone at French Reef. The deep spur and groove zone merges with a well-developed fore-reef buttress zone. Seaward outcrops similar to those at Carysfort Reef are also present seaward of French Reef. A deep-reef survey seaward of about 40 m characterized the bottom as sedimentary with occasional sponges, tilefish burrows, and occasional outcrops of limestone with epibenthic reef biota (Jameson 1981). A few solitary corals (*Paracyathus puchellus*) were collected. Algal nodules were found between 33 and 45 m (Shinn 1981).

Grecian Rocks

Grecian Rocks, KLNMS (Plate 3a), described in detail by Shinn (1963, 1980), is located somewhat inshore of the main reef line of Carysfort, Elbow, French, and Molasses Reefs. Unlike most bank reefs, Grecian Rocks has no fore reef or buttress zone. The zonational pattern includes five zones based on Shinn's (1963) terminology (Table 21). It is about 600 m long and 200 m wide with the long axis in a northeast/southwest trend. The reef is surrounded by sediments and has a narrow bathymetric range of 1.5-7.6 m.

Key Largo Dry Rocks

Key Largo Dry Rocks is near and similar to Grecian Rocks, but has greater depth and more defined spur and groove development. Orientation of *A. palmata* branches are toward the prevailing seas, east to east/southeast.

Key Largo Dry Rocks received much study following Hurricane Donna in 1960 (Ball et al. 1967; Shinn 1975). At that time the charts referred to Grecian Rocks as Key Largo Dry Rocks and vice versa.

Table 20

French Reef stony coral fauna at 6 m (twenty-seven 1-m^2 plots; Jaap, unpublished).

Species	B.I.[a] (ranking)	Abundance	Percent of total colonies	Density Mean	Density Std.dev.	D.I.[b]
Acropora cervicornis	40	172	51.05	6.40	9.10	C
Millepora alcicornis	32	50	14.84	1.90	1.90	R
Acropora palmata	20	42	12.46	1.60	1.60	R
Agaricia agaricites	17	18	5.34	0.74	1.23	C
Montastraea annularis	16	19	5.64	0.72	1.00	R
Siderastrea siderea	13	14	4.15	0.50	0.83	R
Porites astreoides	12	14	4.15	0.50	0.93	R
Dichocoenia stellaris	2	2	0.59	0.11	0.32	R
Mycetophyllia sp.	1	1	0.30	0.03	0.21	R
Colpophyllia natans	1	1	0.30	0.03	0.21	R
Porites porites	1	1	0.30	0.03	0.21	R
Montastraea cavernosa	1	1	0.30	0.03	0.21	R
Favia fragum	1	1	0.30	0.03	0.21	R
Diploria clivosa	1	1	0.30	0.03	0.21	R

Total species		14	
Total colonies		337	
Density, square meter	Mean	Std. dev.	Range
Species:	3.37	1.71	1 - 6
Colonies:	12.48	8.74	1 - 36

[a] B.I. = Biological Index, McCloskey (1970).
[b] D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

Table 21

Grecian Rocks zonation pattern (Shinn 1963, 1980).

Zone	Depth (m)	Conspicuous organisms and remarks
Back reef	0 - 0.9	Nonoriented *Acropora palmata, A. cervicornis*
Reef flat	0 - 0.9	*A. palmata*
Acropora palmata	0 - 1.2	Oriented *A. palmata*
Weak spur and groove	1.2 - 1.8	*Montastraea annularis, M. complanata*
Seaward rubble	1.8 - 2.4	Mostly coral rubble, few *Siderastrea siderea* and *M. annularis*

Since the hurricane, staghorn corals (*A. cervicornis*) have overgrown a great deal of Key Largo Dry Rocks previously unoccupied by reef corals. The slower growing star corals in the reef proper are also being overgrown by the more rapid growing staghorn corals. Shinn (1975) reported on this phenomenon and has followed up the situation with annual inspections of a particular set of colonies that are being encroached upon by *A. cervicornis*.

Molasses Reef

Molasses Reef, KLNMS (Figure 17), is the southernmost of the offshore bank reefs in the park system. It is the most popular reef with scuba diving tourists and has a large lighthouse that makes it very easy to find. This reef fits most of the patterns defined in Table 18; however, its reef flat is located a relatively long distance from the spur and groove zone. The buttress zone is quite narrow, but has large colonies of *M. annularis* just seaward of the deep spur and groove zone. Table 22 provides information on the densities and abundances of stony corals in the spur and groove zone at Molasses Reef. The investigation of seaward zones with a submersible revealed rocky outcrops and sedimentary environments similar to those described for Carysfort and French Reefs (Jaap 1981).

Looe Key Reef

The zonation and morphology of Looe Key Reef, Looe Key National Marine Sanctuary (Plates 2a and b) are presented in Figure 18. Table 23 lists the density and abundance of stony coral fauna on Looe Key Reef. The major significant difference in this reef from others is the wide area between the buttress zone and the deep reef. In the northeastern part of the reef, the deep reef does not exist; however, in the southwestern end, the deep reef community is evident in patches between sedimentary deposits. Shinn et al. (in

Table 22

Molasses Reef stony coral fauna at 5 - 6 m (twenty-five 1-m^2 plots; Jaap, unpublished).

Species	B.I.[a] (ranking)	Abundance	Percent of total colonies	Density		D.I.[b]
				Mean	Std.dev.	
Acropora palmata	43	108	33.23	4.33	3.43	C
Acropora cervicornis	39	125	38.46	5.00	6.31	C
Montastraea annularis	19	38	11.69	1.53	4.11	C
Millepora alcicornis	17	20	6.15	0.82	1.00	R
Siderastrea siderea	6	6	1.85	0.22	0.73	C
Millepora complanata	4	5	1.54	0.21	0.50	R
Agaricia agaricites	4	4	1.23	0.20	0.51	R
Montastraea cavernosa	3	3	0.92	0.10	0.43	R
Porites astreoides	2	2	0.62	0.10	0.32	R
Favia fragum	2	2	0.62	0.10	0.43	R
Diploria labyrinthiformis	2	2	0.62	0.10	0.32	R
Madracis mirabilis	2	3	0.92	0.11	0.60	C
Mycetophyllia lamarckiana	2	2	0.62	0.10	0.30	R
Colophyllia natans	2	2	0.62	0.10	0.41	R
Dichocoenia stokesii	1	1	0.31	0.04	0.21	R
Meandrina meandrites	1	1	0.31	0.04	0.21	R
Mycetophyllia aliciae	1	1	0.31	0.04	0.21	R
Total species		17				
Total colonies		325				
Density, square meter	Mean	Std. dev.	Range			
Species:	3.36	1.55	1 - 7			
Colonies:	13.00	6.71	4 - 29			

[a] B.I. = Biological Index, McCloskey (1970).

[b] D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

Table 23

Looe Key Reef stony coral fauna at 1 - 27 m (fifteen 1-m^2 plots; Jaap, unpublished).

Species	B.I.[a] (ranking)	Abundance	Percent of total colonies	Density Mean	Density Std.dev.	D.I.[b]
Porites astreoides	23	52	26.94	3.51	3.72	C
Millepora complanata	19	47	24.35	3.13	4.61	C
Agaricia agaricites	16	35	18.13	2.32	3.33	C
Porites porites	7	8	4.15	0.51	1.34	R
Favia fragum	6	7	3.63	0.50	0.62	R
Siderastrea siderea	6	8	4.15	0.51	1.13	R
Acropora cervicornis	6	7	3.63	0.50	1.10	C
Madracis decactis	5	9	4.66	0.61	1.63	C
Stephanocoenia michelinii	4	5	2.59	0.32	0.70	R
Siderastrea radians	3	4	2.09	0.30	0.82	C
Montastraea cavernosa	3	3	1.55	0.23	0.83	C
Mycetophyllia lamarckiana	2	2	1.04	0.12	0.42	R
Millepora alcicornis	2	2	1.04	0.12	0.50	C
Acropora palmata	1	1	0.52	0.10	0.30	R
Montastraea annularis	1	2	1.04	0.12	0.42	R
Meandrina meandrites	1	1	0.52	0.10	0.32	R

Total species		16	
Total colonies		193	
Density, square meter	Mean	Std. dev.	Range
Species:	4.06	2.19	1 - 8
Colonies:	12.19	9.29	3 - 34

[a] B.I. = Biological Index, McCloskey (1970).
[b] D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

press) reported that net sediment transport was to the southwest and that sediment was slowly covering the reef's deeper areas.

Eastern and Middle Sambo, Eastern Dry Rocks, Rock Key, and Sand Key Reefs

These reefs follow the general bank reef pattern. They have well-developed seaward platforms that are separated from the main reef structure and that have significant relief. Again, these platforms are separated from the main reef body by sediments.

Bird Key Reef

Bird Key Reef, Dry Tortugas National Monument (Figure 19), is unusual in that it does not have a spur and groove zone in shallow water, and *A. palmata* is not found at all in this reef community. The major coral accretion is in waters deeper than 10 m on an antecedent spur and groove formation that apparently developed during a lower Holocene sea level stand. Shinn et al. (1977) reported that cores bored on the shallow areas of Bird Key Reef revealed that the reef was not founded on a solidified platform but rather on considerable uncon-

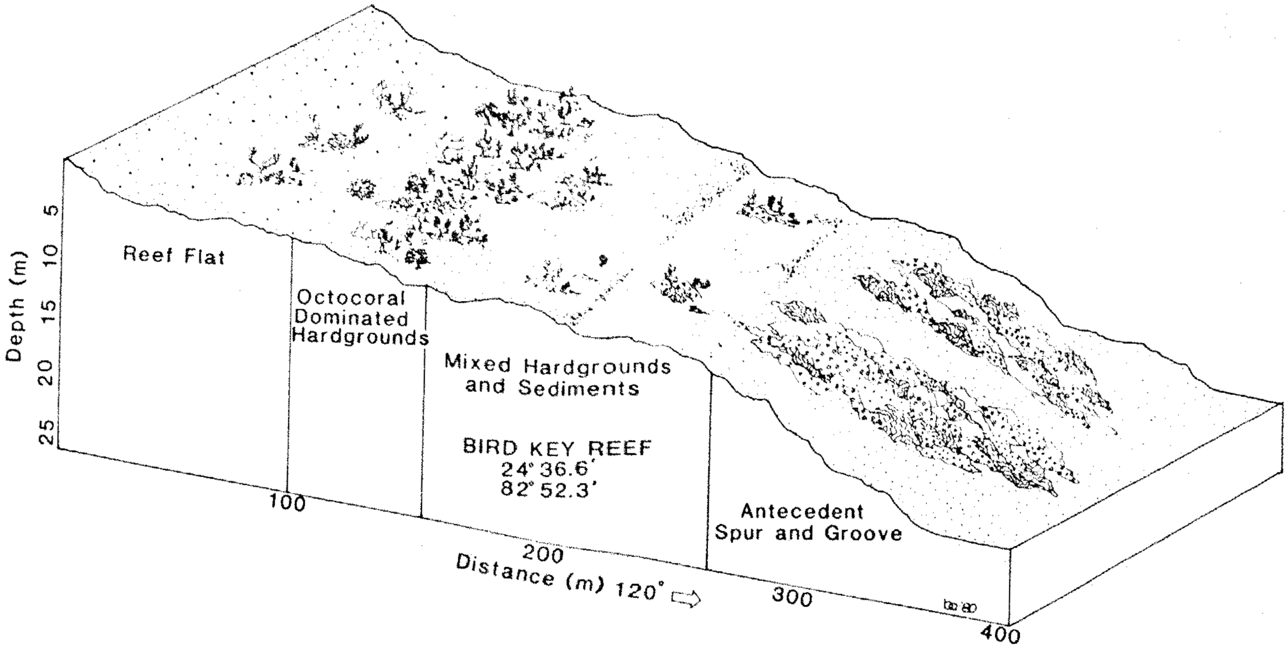

Figure 19. Cross-sectional diagram of Bird Key Reef.

solidated sediments overlying a Pleistocene basement. The shallowness of the reef and severe winter temperatures probably prevent *A. palmata* from occurring on the shallow reef at Bird Key.

Summary

No universal pattern exists; each reef has different features. Major controls include geographic configuration of the Florida Keys archipelago (Ginsburg and Shinn 1964); winter cold fronts chilling Florida Keys water masses (Hudson et al. 1976, Walker et al. 1982); reef age or stage of development (Shinn et al. 1977, 1981); and relationships with sedimentary environments (Ginsburg 1956; Shinn et al. 1981). Community structure patterns reflect the stage of reef development. For example, spur and groove construction requires long term dense aggregations of *Acropora palmata* (Shinn 1963; Shinn et al. 1981). Development of the spur and groove habitat in turn creates microhabitats (niches) that are necessary for the existence of other reef organisms. For example, the *Millepora complanata* association is found in the turbulent shallower portions of the spur and groove habitat (Mergner 1977).

CHAPTER 4

CORAL REEF BENTHOS

4.1 INTRODUCTION

The benthos (bottom-dwelling organisms) within a coral reef is complex, diverse, and for many taxa, poorly known. Benthos in a coral reef constitutes the critical biota or foundation species. In particular, the corals and crustose coralline algae are most significant in niche creation for the other multitudes of species. Complexity is shown by the infaunal boring biota; reports of species within a single coral head ranged from 30 to 220 and the number of individuals ranged from 797 to 8,267 (McCloskey 1970; Gibbs 1971). Most organisms were polychaetes, a group that is poorly understood. Because it would be literally impossible at this time to compile a total benthic community profile, this chapter will cover those groups which are critical to the community: algae, sponges, and Cnidarians (e.g., corals). Since corals are major elements of the reef, emphasis will be on the Milleporina, Octocorallia, and Scleractinia.

Volumes 2 and 3 of *Biology and Geology of Coral Reefs* (Jones and Endean 1973, 1976) contain information on many benthic groups, but the major emphasis is on Indo-Pacific reefs. Although the information can be extrapolated in many cases to Florida, the species are for the most part different. Recently, Rutzler and Macintyre (1982b) published a fine volume on the biota from the barrier reef at Carrie Bow Cay off Stann Creek Town, Belize.

4.2 ALGAE

(by Harold Humm, Department of Marine Science, University of South Florida, St. Petersburg)

Historical

Knowledge of the benthic algae found on coral reefs of southeast Florida is based largely on inference from work done on coral reefs in the West Indies, especially in the Virgin Islands, Puerto Rico, Jamaica, Curacao, Barbados, Guadalupe, and Martinique. There are many seaside research facilities open to visiting scientists in the Caribbean area but only one in southeast Florida, and that with limited facilities for visitors. Thus, for these and other reasons, studies of the benthic algal flora of Florida coral reefs are sparse.

William Randolph Taylor of the University of Michigan was the first to make a significant contribution to the knowledge about the species of benthic algae found on Florida coral reefs, after he spent the summers of 1924-1926 at the Carnegie Laboratory, Dry Tortugas. Taylor's work at Tortugas was a general floristic survey; his field data provided information on species associated with reef environments. These data are included in Taylor (1928) and Taylor (1960), *Marine Algae of the Tropical and Subtropical Coasts of the Americas,* still available from the University of Michigan Press.

Earlier references for the study of benthic algae found on Florida reefs and the western Atlantic in general include Harvey (1852, 1853, 1858); Vicker (1908); Collins (1909); Borgesen (1913-1920); Collins and Harvey (1917); and Howe (1918, 1920).

Contemporary studies of great value include Earle (1969, 1972b), which list virtually all algae known to occur on Florida's coral reefs.

Grazing on algae of coral reefs is discussed by Randall (1961a), Mathieson et al. (1975), Wanders (1977), and Brawley and Adey (1981).

Productivity of algal components within coral reef communities, including those that bore into limestone and the coral symbionts, is treated by Marsh (1970), Littler (1973), and Vooren (1981).

Colonization and succession of reef algae were reported by Adey and Vasser (1975), Wanders (1977), and Brawley and Adey (1981). Algal zonation at Curacao was described by van den Hoek et al. (1975).

Algae that bore into coral and limestone were studied experimentally by Perkins and Tsentas (1976). Coralline algal ridges (Note: these are not found in Florida) are reported by Adey (1975, 1978). The coralline algae were recently treated by Johansen (1981).

The only recent reef algae study from Florida reefs is Eiseman (1981), who made diving observations and collections during the KLNMS deep reef survey using a submersible. The study began at a 30-m depth and reported 60 species from reef and lithothamnion cobble habitats. The algal species from these two habitats were virtually exclusive.

Algae in Coral Reefs

One of the characteristics of coral reefs the world over is the apparent paucity of benthic macroalgae on and around the reefs, at least to the casual observer. "Where are the plants?" might be an immediate question of a biologist who is familiar with temperate or boreal seas and views a coral reef for the first time because rocky substrata in clear, shallow water would normally support a dense stand of large benthic algae.

A significant biological control of algae on coral reefs is the competition for space with other epibenthic sessile organisms. The diversity of organisms on a coral reef probably exceeds that of all other marine ecosystems. The sessile animals occupy space that would otherwise be colonized by benthic algae. On recently exposed limestone substrates, especially following physical impact, benthic algae may be the first colonizers, but they are usually replaced by sponges, tunicates, corals, and bryozoans after a short period. Another major biological control on benthic macroalgae is grazing by the herbivorous invertebrates and fish. Of all shallow-water marine ecosystems, none are more profoundly affected by grazing than coral reefs.

The effects of grazing on coral reefs have been demonstrated experimentally in many reef studies, although apparently not in Florida, by placing a barrier over a selected site and observing the response of the algae that are protected from most grazing. Randall (1961b), working in Hawaii, found a significant difference between the algal cover inside an enclosure and that of areas outside it after 2 months. Inside the enclosure the algae grew to normal height and breadth (to 30 mm); outside the enclosure, the algae averaged 1 mm in height. In Lameshure Bay, St. John, Virgin Islands, Randall excluded fish, but allowed herbivorous sea urchins *(Diadema antillarum)* in the closed area. Results showed that the fish were the major grazers. While the urchins also fed on algae, their action did not affect the algae as severely as did the fish. Randall also showed that parrotfish and surgeonfish graze on seagrass adjacent to the reef, thereby causing the sand halos around patch reefs. Research conducted during the submersible habitat study known as Tektite II at Lameshur Bay, St. John, Virgin Islands, confirmed and expanded Randall's observations on grazing. Fish grazing was found to be a major factor influencing biomass and species diversity of benthic algae on coral reefs. In addition to cage experiments, algae was transplanted from elsewhere to the reef; the algae was rapidly eaten. Grazing pressure was intense to a distance of 30 m; beyond that distance it gradually tapered off (Earle 1972a; Mathieson et al. 1975).

Ogden (1976) reported on algae-grazer relationships on coral reefs and reported those algae that grazers tend to avoid. Prolific algal growth occurred only in areas inaccessible to grazing herbivores, such as wave-washed surfaces and beachrock benches. Ogden and Lobel (1978) summarized the role of herbivorous fish and urchins in coral reef communities with special reference to reefs around St. Croix, Virgin Islands.

A comprehensive study of the effects of elimination or reduction of grazing by means of cages was reported by Wanders (1977), who worked at Curacao. His results are applicable to Florida reefs. He found that crustose coralline algae depend upon grazing for protection from competition by erect fleshy algae. Under a cage that covered a patch of coralline algae, the fleshy algae soon colonized the surface of crustose species, resulting in the death of the crustose species. The crustose forms were penetrated by microscopic species that bored into the limestone. When clean artificial substrates were placed under cages on the reef, a succession was observed as the fleshy algae colonized it. During the first 6-8 weeks the colonizers were principally filamentous brown and green algae of the genera *Griffordia, Cladophora,* and *Enteromorpha.* After 10-15 weeks these were replaced by larger filamentous and parenchymatous species, in particular, the filamentous red algae *Centroceras clavulatum* and *Wrangelia argus;* a small, erect-growing coralline red, *Jania capillacea;* the larger red algae *Spyridia filamentosa, Pterocladia americana,* and *Laurencia microcladia;* and the flat, dichotomous brown algae *Dictyota dichotoma.* All of these are common species on Florida coral reefs and can be found where succession on new substrates would be similar to the experiment at Curacao. Wanders concluded that grazing does not reduce the primary productivity per unit area in Curacao, but only affects species composition.

Brawley and Adey (1981) observed the effects of another category of grazers on coral reefs (other than fish and macroinvertebrates such as urchins) that might be referred to as micrograzers, crustaceans of the Order Amphipoda. In a coral reef microcosm in the Smithsonian Institution, Washington, D.C., they observed that a tube-building amphipod of the genus *Amphithoe* grazed selectively on filamentous algae. They suggested that this micrograzer may help reduce competition for the encrusting coralline algae.

While grazing by fish is a major factor in the paucity of fleshy algae in coral reef habitats, there are a few coral reef fish whose activity has the opposite effect. One of these is the three-spot damselfish, *Pomacentrus planifrons.* It establishes a territory, especially in the proximity of *Acropora cervicornis, A. palmata,* and *Montastraea annularis*, and then bites segments, strips, or patches of the coral, killing the polyps. These dead coral areas are colonized in a few days by a variety of erect -growing fleshy algae. The damselfish, by its unusual aggressive habit of defending its territory, keeps out algal grazers and thus maintains extensive patches of fleshy algae on the reef where normally they would not exist. Detailed observations on the damselfish and their algal lawns were reported in Jamaica by Brawley and Adey (1977) and in other Caribbean localities including Jamaica by Kaufman (1977). The three-spot damselfish occurs on Florida's coral reefs as do all the algae species recorded and listed by Brawley and Adey from Discovery Bay, Jamaica. The exception is *Halimeda goreauii.*

Algal Groups

Benthic algae of tropical coral reefs can be categorized into four major groups, all occupying areas of the reef itself or areas under the influence of grazers inhabiting the reef. They are crustose coralline algae that encrust corals, reef rock, and other limestone skeletal material; filamentous and fleshy algae, which occur as sparse vegetation and dense vegetation; algae on unconsolidated sediments, which are erect macroalgae of the order Siphonales and mats of bluegreen algae; and excavating or boring algae.

Crustose Coralline Algae

The most distinctive and characteristic algal group of the coral reef is the crust-forming coralline red algae Rhodophyceae, order Cryptonemiales, family Corallinaceae, subfamily Melobesieae. These algae form a thin or massive crust with or without erect branches and are calcified throughout. When living, they are usually a shade of red in low light, but may be yellow-brown in surface light. They are chalk-white when dead, but soon become greenish as a result of the establishment of the green and bluegreen algae that bore into limestone and lend color to the upper few to 5 mm of the skeleton.

Crustose corallines form small, scattered colonies or large, distinct patches. On Florida reefs, there may be some degree of development of incipient algal ridges, a formation found extensively on coral reefs in the eastern Caribbean Sea (Adey 1978). Coralline algae are common on the underside of corals such as *Acropora* spp. and colonize dead coral fragments that break off and fall to the seafloor. Large patches are found on the reef platform limestone, the living surface layer covering formerly living veneers of the same species. Minute species that form small, thin crusts are often epiphytic upon larger, fleshy algae, seagrass leaves, octocoral skeletons, mollusk shells, and hydroid colony bases. Crustose corallines are best developed in shallow, turbulent areas where light intensity is high and fish grazers are partially deterred by wave forces.

Colonization, succession, and growth rate of the tropical crustose coralline algae were unknown until the study of Adey and Vassar (1975) in St. Croix. Their results probably apply in Florida, which has fewer species, for April through November. Adey and Vassar (1975) reported that the margins of a crust grow 1-2 mm/month and that accretion rates are 1-5 mm/year, depending on herbivore grazing, especially parrotfish.

Filamentous and Fleshy Algae

Filamentous and fleshy algae are uncalcified coral-reef macroalgae that colonize coral rubble and reef limestones. This group is most adversely affected by grazing. Two subdivisions are recognized: the dense and sparse vegetation. They comprise the same species, although the dense community, if not spatially limited to crevices or small patches, exhibits greater species diversity. The sparse community occurs in areas receiving the heaviest grazing pressure, resulting in cropped forms often 1-2 mm high. There is a transition of sparse community on or near the reef to the dense community located away from the reef, resulting from a gradient in grazing pressure.

Unconsolidated Sediment Algae

Few algae have the functional ability to anchor in unconsolidated sediment. For this reason, the seagrasses, rooted forms that evolved on land and radiated into the marine environment, dominate shallow sedimentary habitats, especially in tropical regions. There are, however, a few specialized algae on loose sedimentary environments; these are especially well represented in coral reef habitats.

There are two major groups capable of colonizing sandy or muddy bottom areas. The bluegreen algae (Cyanobacteria) form mats and penetrate the sediment to some extent. Green algae, belonging to the order Siphonales, erect coenocytic plants (lacking cell walls) having a dense cluster of root-like rhizoids at the base that provides a firm anchorage in unconsolidated sediments. Mathieson et al. (1975) included an underwater photograph of this community.

The mat-forming bluegreen algae community is composed primarily of filamentous species (sensu Drouet 1968), e.g., *Microcoleus lyngbyaceus* and *Schizothrix calcicola*. Other filamentous species, including *Porphyrosiphon notarisii* and *Schizothrix arenaria*, and several coccoid (spherical) species are usually associated with these mats. Ginsburg (1972b) reported that the filaments of mat-forming bluegreens grow upward during the day and selectively trap sediment particles at night; horizontal growth of another species results in binding of trapped sediments.

Erect-growing anchored green algae in sediments are found within the genera *Halimeda, Penicillus, Udotea, Rhizocephalus, Avrainvillea,* and *Caulerpa.* They are usually scattered and scarce immediately around the reefs, but become progressively more abundant away from the reef proper as grazing pressure is reduced. The dense cluster of rhizoids that anchor these plants stabilizes the sediments and absorbs nutrients. Since these algae are coenocytic, transport of nutrients to the tops and of photosynthetic products to the rhizoids is carried on rapidly in conjunction with cytoplasmic streaming. They are a unique group of highly evolved green algae, as advanced among the algae as the flowering plants on land.

Members of this group also contribute significantly to calcium carbonate production and sediment on and around the reef. This is especially notable among the species of *Halimeda.*

Excavating or Boring Algae

Among the least conspicuous and most often overlooked algae are those possessing the ability to bore into limestone by dissolving it as they grow. To the unaided eye they are visible as a greenish tinge or discoloration at the surface of dead coral, mollusk shells, dead coralline algae, and other limestone material. Boring algae belong to three taxonomic groups. Most are bluegreen (Cyanobacteria), some are green (Chlorophyta), and the remaining one (Xanthophyta) has no common name.

Representatives of three families of bluegreen algae are known from Florida coral reefs: *Entophysalis deusta,* family Chamaesiphonaceae; *Schizothrix calcicola,* family Oscillatoriaceae; *Mastigocoleus testarum,* family Stigonemataceae. The green algae *Gomontia ployrhiza* and the xanthophyte *Ostreobium quekettii* are known from Florida.

These algae are collected by dissolving a small sample of greenish limestone in dilute hydrochloric acid and examining isolated filaments. Keys to the species are found in Humm and Wicks (1980). A comprehensive experimental study of limestone-boring algae is found in Perkins and Tsentas (1976); the study was from St. Croix. They reported five bluegreen and three green algae species. One of their bluegreens, *Calothrix* sp. (*Calothrix crustacea*; sensu Drouet 1968), has not been reported as a boring alga in Florida; however, it is abundant on Florida reefs and must be presumed to be a borer. Algae that bore into limestone contribute significantly to the dissolving of limestone, adding calcium and bicarbonate to the mineral pool in the reef environment.

4.3 SPONGES

(by G.P. Schmahl, South Florida Research Center, U.S. National Park Service, Homestead).

Sponges (Porifera) are an important component of the benthic fauna of Florida reef. Although not usually dominant, sponges are common in most reef zones and can be especially abundant in certain situations. Substrate analysis of the benthic fauna on selected upper Florida Keys patch reefs indicated a sponge component ranging from 1.2% to 9.2% of the surface area sampled (Jaap and Wheaton 1977).

Taxonomy

Sponges are grouped into four classes. The largest is the Demospongiae, which account for 95% of all recent species. Virtually all common shallow water reef sponges are demosponges with most of the remainder belonging to the class Calcarea. The Demospongiae are characterized by skeletal components consisting of siliceous spicules that are supplemented or replaced by organic spongin, which forms fibers or acts as a cementing element. The skeleton of the Calcarea, as the name implies, is made up of calcareous, usually triradiate spicules. A third class of sponges, the Sclerospongiae, secrete a compound skeleton of siliceous spicules, spongin fibers, and calcium carbonate. Sclerosponges can be an important structural component of some deep fore reef environments (Lang et al. 1975) but have not been reported from Florida reefs (Dustan et al. 1976). The fourth class of sponges, the Hexactinellida, are mainly deep water species and are characterized by hexactinal (six-rayed) megascleres (type of spicule).

Classification of the sponges is based primarily on the size and shape of the spicules (megascleres and microscleres) and the organization of the skeletal matrix of spicules and organic fibers found within the various species. Gross morphology, surface texture, color, and arrangement of the incurrent and excurrent ostia are also considered important. Recently, studies in the areas of comparative biochemistry (Bergquist and Hartman 1969), reproductive life history characteristics (Levi 1957), structure and function of sponge cells (Simpson 1968), and ecology have contributed much to clarify taxonomic organization. In spite of this, classification of the Porifera is still in a state of change and confusion. However, the widespread use of scuba, *in situ* color photography, and standardized collecting techniques have all helped in the field identification of major sponge species. Field guides are now available (Voss 1976; Colin 1978a; Kaplan 1982) which offer to the nonspecialist some information on Caribbean reef sponges. Of these, the identifications given in Kaplan (1982) are the most up-to-date. Inconsistencies in nomenclature found in these publications reflect the confusion that surrounds sponge systematics. Most common sponge species have characteristic shapes, colors, and habitat preferences which allow them to be identified confidently in the field, at least within a specified geographic area (e.g., Florida).

Of the more technical taxonomic literature on Caribbean sponges, only a few were based on collections primarily from Florida. An early work that described some Florida reef sponges was that of Carter (1885). Later Florida studies on the sponges of the Gulf of Mexico by de Laubenfels (1953) and Little (1963) also included some reef species. The most complete work of sponge taxonomy for Florida reef sponges was made by de Laubenfels (1936) in the Dry Tortugas. Although now somewhat out of date in terms of the present interpretation of sponge classification, this is an important work in that all known Caribbean sponge families were listed and their taxonomic characteristics described. Since the sponge fauna found on Florida reefs is decidedly West Indian, taxonomic works from other areas of the Caribbean are sufficient for most Florida species. Recent studies of this type include those from the Bahamas (de Laubenfels 1949; Wiedenmayer 1977), Bermuda (de Laubenfels 1950), Jamaica (Hechtel 1965), and Curacao (van Soest 1978, 1980). The studies by Wiedenmayer (1977) and van Soest (1980) introduced new classificatory interpretations. Taxonomic works on burrowing sponges likely to be found in Florida include Pang (1973a, 1973b) and Rutzler (1974).

A definitive list of Florida sponge species does not exist. de Laubenfels (1936) described 76 species from the Dry Tortugas, but 5 were dredged from 1,047 m and 9 others were collected from sites ranging from 70 to 90 m, which is out of the range of most typical Florida coral reef growth. Wiedenmayer (1977) described 87 shallow water species from the western Bahamas in a work that reevaluates the validity of scientific names applied to many common reef species. Careful reference to synonymy must be taken into consideration when comparing Wiedenmayer's (1977) lists with those of previous workers. Given the proximity of his study site, it is reasonable to assume that most of the 87 species Wiedenmayer (1977) described can also be found in Florida. Fifty-seven species of sponges have been recorded from Bermuda (de Laubenfels 1950) and Jamaica (Hechtel 1965). Of the species treated by Wiedenmayer (1977), 39 listed are from the Dry Tortugas and 22 from the Florida Keys. These lists were the result of a literature review and not based on field studies, so the actual number of species in these localities is open to question.

A brief survey of sponges of the Dry Tortugas by National Park Service investigators revealed 85 species, only 43 of which were recorded by de Laubenfels (1936), and 57 of which were among the 87 species described by Wiedenmayer (1977). The low overlap of species lists indicates a species pool much larger than reported by any one study; the number of species present is seemingly correlated with the amount of time spent looking. It is important to note that the above studies deal with all sponge species encountered in the area, including those common in lagoonal areas, mangroves, and inshore pilings. Those sponges that dominate in reef areas are a more or less distinct group and, with some overlap, are substantially different from those which are abundant in lagoonal areas (Wiedenmayer 1977). An extensive study of the patch reefs of Biscayne National Park (upper Florida Keys) reported the occurrence of 98 species associated only with inshore reefs in less than 10 m of water (Schmahl and Tilmant 1980). Additional species have been collected from deeper water on the outer bank reefs. From the evidence so far, a conservative estimate of the sponge species occurring on or around Florida reefs must be at least 120.

Autecology

Sponges exhibit both asexual and sexual reproduction. Asexually sponges may be regenerated from fragments, gemmules, and reduction bodies. Sexually, the group has both dioecious and hermaphroditic species. Fertilization is usually internal and both oviparous and viviparous species are common. This fact forms the basis of the division of the Demospongiae into its two main subclasses: Tetractinomorpha (oviparous) and Ceractinomorpha (viviparous), although exceptions are known. Viviparous species usually incubate parenchymula (solid) larvae, while development in oviparous forms is usually external.

Amphiblastula (hollow) larvae are exhibited by a third subclass of Demospongiae, the Homoscleromorpha, and some calcareous forms. A promising method that may be used to access the extent of asexual reproduction in an area is the ability of sponges to recognize tissue of like genetic composition ("self"). Experiments may be carried out whereby strains can be recognized through differential acceptance of tissue from other individuals in an area (Kaye and Ortiz 1981). Reproduction in sponges was reviewed by Fell (1974), but there is much yet that is unknown about that process in most species. A recent review by Simpson (1980) pointed out the many areas open to research.

Larval ecology and behavior is fundamental to the distribution of adult forms. Most sponges have sexually produced larvae that are free-swimming, at least for a short period, although some species have been shown to produce larvae that do not swim but creep over the substrate (Bergquist 1978). Three physical attributes influence the swimming and settlement of sponge larvae: light, gravity, and water turbulence. The comparitive morphology and behavior of some Demosponge larvae have been reviewed by Bergquist et al. (1979).

Sponges are filter feeders and must take in great quantities of water from which they remove plankton, bacteria, organics, and other nutrients from the water column. It has been estimated that the abundance and pumping activity of sponges on the fore reef slope of Discovery Bay, Jamaica, are such that a volume equivalent to the entire water column passes through the population every 24 hours (Reiswig 1974). Sponges are capable of removing extremely small organic particles. In a study by Reiswig (1971b), 80% of the organic carbon removed by three species of sponges could not be seen under an ordinary light microscope and was thus postulated to be of colloidal (quasi-particulate) nature. Many sponges depend on ambient currents to aid in water transport through their tissues and to decrease the amount of energy expended on pumping activities (Vogel 1977). Thus, hydrodynamic regimes are important in shaping sponge distributions. In tropical areas, where reef boundary layers are typically low in nutrients and organic particulate matter, increased water flow by currents can be essential for the survival of many large species.

Light intensity can be important in shaping sponge communities for various reasons. In one respect, reduced light intensity increases sponge abundance due to decreased competition from reef corals that depend on light for survival of symbiotic zooxanthellae. Sponges typically proliferate in deep fore reef areas below the zone of maximum coral growth. Some sponges, however, have been shown to contain species of symbiotic blue-green algae (or Cyanobacteria) which have been implicated in the distribution of those species, restricting them to shallow areas where light is abundant (Wilkinson 1978).

For a good general review of sponge biology, consult Bergquist (1978). Several recent collected works have been compiled as the result of symposia on the biology of sponges or in response to the need for cohesiveness in sponge research. These include Fry (1970), Harrison and Cowden (1976), Levi and Boury-Esnault (1979), and Hartman et al. (1980).

Quantitative ecological studies of sponges on Caribbean reefs are few. The most complete series of studies of Caribbean demosponges to date were those carried out by Reiswig (1971a, 1971b, 1973, 1974) on three common species found on Jamaican reefs. These studies set the standard for ecological methodology of sponges and their information is generally compatible with Florida populations. His findings emphasized the variability displayed by the different species in regard to pumping activities, feeding, life history characteristics, population dynamics, and respiration. Ecological studies on entire sponge communities are rarer still. Alcolado (1979) investigated the ecological structure of sponges on a Cuban reef, and data were given in Wiedenmayer (1977) stressing synecological relationships of sponges in his Bahama sites. The difficulty of carrying out such studies is reviewed by Rutzler (1978) who also gave some methods for quantitative assessment of sponges on coral reefs.

From these studies and from qualitative and incidental observations, sponge communities are known to be partitioned along habitat and depth gradients on coral reefs. Habitat preference, reproductive strategies, growth form, and competitive ability are important biological agents that influence sponge distribution. Abiotic factors, some linked directly or indirectly with depth (e.g., light intensity, temperature, intensity of wave and surge action, and sedimentation) are also major controlling forces in shaping sponge assemblages.

Massive sponges are rare on reef flats where small or low encrusting forms are predominant (Reiswig 1973;

Alcolado 1979), presumably because of the scouring action of waves and the increased sediment load caused by turbulence. Many species cannot tolerate high sediment loads. In *Verongia lacunosa* pumping rate is reduced under increased sediment conditions (Gerrodette and Flechsig 1979). Species with high sediment tolerance, such as *Tethya crypta*, can be common on the reef flat as are encrusting species such as *Spirastrella cunctatrix* and *Thalysias juniperina*. Species of the genus *Cliona* are also common, infesting dead coral skeletons and other suitable substrate. In deeper areas (> 7 m), where conditions are more predictable and favorable, massive sponges increase in abundance. Common species found on the outer reefs of the upper Florida Keys include *Amphimedon compressa, Iotrochota birotulata, Ulosa ruetzleri, Ircinia strobilina, Ectypoplasia ferox, Callyspongia vaginalis, Niphates erecta, N. digitalis, N. amorpha, Cliona deletrix*, and *Xestospongia muta* (name designations after van Soest 1978 and 1980, and Wiedenmayer 1977).

Synecology

Sponges are major competitors with other epibenthic organisms for space and other resources in reef habitats. Sponges have the greatest overgrowth capability of the major groups of organisms encrusting undersurfaces of foliaceous corals (cheilostome ectoprocts, crustose algae, and other algae). Results varied with depth, but sponges were the superior overgrowth competitors in 77% of the interactions monitored (Jackson and Winston 1982). Overgrowth of Caribbean corals by sponges has been observed for *Chondrilla nucula* (Glynn 1973), *Ectyoplasia* sp., and *Plakortis* sp. (Lang 1982), and has been demonstrated for *Anthosigmella* var. f. *incrustans* (Vicente 1978), which was found to have a high level of competitive superiority compared with corals and other sponges. Some sponge species have been shown to exhibit toxicity to corals which they overgrow, causing necrosis of the coral tissue along the line of contact (Bryan 1973). Such a mechanism of competitive interaction presumably concerns the production of species-specific allelochemicals (Jackson and Buss 1975; Buss 1976), which can lead to intricate competitive networks and act to allow high diversity in areas of low disturbance. Sponges have also been shown to enter into complex epizoic relationships (living on one another) with one another (Rutzler 1970) which may be in response to competitive pressures.

Sponges are involved in symbiotic relationships with other reef organisms. Many sponges exist in symbiosis with bluegreen algae (or Cyanobacteria), which are mostly free living within the mesophyll and may constitute up to 52% of the cellular material of the sponge (Rutzler 1981). Nutrient translocation of algal products to coral reef sponges has been demonstrated by Wilkinson (1979). Sponges can, therefore, supplement their energy requirements through this relationship. Goreau and Hartman (1966) noted that the Caribbean sponge *Mycale laevis* has a symbiotic relationship with some stony corals. The sponge benefits from a protected and enlarging coral base to grow on, while the coral is aided by protection from boring organisms that usually gain access through the coral's undersurface. The coral possibly benefits also from greater access to heterotrophic energy sources carried in the sponge-created water currents. An obvious symbiotic relationship in Caribbean sponges involves species of Zoanthidea (Anthozoa) which grow on the surface of some sponges. Taxonomy of the sponge-associated zoanthids has been given by West (1979). Aspects of the ecology of sponge-zoanthid associations have been investigated by Crocker and Reiswig (1981), who found a high specificity between species of host sponges and their associated zoanthids. Lewis (1982) studied some functional aspects of this relationship and suggested that the zoanthid presence may have a deleterious effect by decreasing the host sponge's pumping capabilities.

Another important role of sponges in coral reef ecosystems is that of providing shelter for other reef organisms. Tyler and Bohlke (1972) listed 39 species of fish that associate with sponges, at least 5 of which are obligate sponge dwellers. The interior cavities of certain sponges are inhabited by numerous invertebrates (Pearse 1932; Westinga and Hoetjes 1981), mostly crustaceans, of which the alpheid shrimps are the most prominent. The residents also include polychaete and annelid worms. Reiswig (1973) reported that the sponge *Verongia gigantea* supported large populations of *Haplosyllis spongicola* in the canal system; densities of 50-100 polychaete individuals per ml of sponge were found. *Haplosyllis spongicola* is also a frequent inhabitant of the sponge *Neofibularia nolitangere*.

Sponges serve as a food source for other organisms, predominantly coral reef fish and some marine turtles. In general, however, predation is not intense. Only in 11 of 212 fish species (5%) studied by Randall and Hartman (1968) did sponge remains comprise over 6% of stomach contents. Angelfish of the genera *Holocanthus* and *Pomacanthus* and the whitespotted filefish (*Cantherhines macrocerus*) were the major sponge predators. Abundance of mineralized sclerites, noxious chemical substances, and tough fibrous components have been identified as reasons for low predation pressure on most coral reef sponges. The toxicity to fishes of many common exposed (noncryptic) Caribbean sponges has been shown by Green (1977) through forced feeding experiments. He also noted that, in general, as latitude decreases, the incidence of toxicity in sponges increases, presumably in response to the high diversity and density of associated fishes in the tropics. Predation, therefore, is not usually considered a direct force limiting the distribution of coral reef sponges. This is not true for all sponge ecosystems, as was illustrated by Dayton et al. (1974) in an Antarctic community.

Sponges have been regarded as a major force in the bioerosional process on coral reefs (Goreau and Hartman 1963; Rutzler 1975). The boring sponges are classed mostly in the family Clionidae (genus *Cliona*), but species of the Adocidae *(Siphonodictyon)* and the Spirastrellidae (*Spheciospongia, Anthosigmella*) have also been shown to excavate coral limestone skeletons. They weaken the substrate, causing the collapse and dislodgement of some corals and creating cryptic habitats in the interior of coral skeletons. In a study of *Cliona lampa* in Bermuda, Neumann (1966) found that as much as 6-7 kg of carbonate detritus could be generated from 1 m^2 of sponge-infected substrate in 100 days. Hudson (1977) reported six species of boring sponges that were principal in the bioerosion of *Montastraea annularis* (star coral) at Hens and Chickens Reef in Florida.

In contrast to the erosional effects of the boring species, many other species contribute to the structural integrity of coral reefs by binding unconsolidated reef frame material together and thereby increasing rates of carbonate accretion (Wulff and Buss 1979).

Sponges play a major role in the ecology of Florida coral reefs, but have been greatly neglected in ecological studies. As William Beebe (1928) wrote: ". . .when, in the *Iliad,* Homer described a sponge as 'full of holes,' he expressed about all the knowledge which mankind has possessed until comparatively recent times." Although there have been some advances in knowledge of sponge biology since 1928, there is still much to be learned about the physiology, ecology, and evolution of sponges.

4.4 CNIDARIA

The phylum Cnidaria (Table 24) includes jellyfish, sea anemones, corals, and hydrozoans. Although extremely variable in appearance, all members have a radially symmetrical body plan. The saclike body has a central stomach cavity with a single opening that is usually surrounded by food-capturing tentacles. Stinging

Table 24

Classification of major reef benthic Cnidaria.

PHYLUM CNIDARIA (COELENTERATA)

CLASS HYDROZOA

- ORDER MILLEPORINA: fire corals
- ORDER STYLASTERINA: hydrocorals

CLASS ANTHOZOA

- SUBCLASS OCTOCORALLIA (ALCYONARIA) *sensu* Bayer 1961
  - ORDER STOLONIFERA
  - ORDER TELESTACEA
  - ORDER ALCYONACEA: fleshy soft corals
  - ORDER GORGONACEA: sea whips, sea feathers, sea fans, sea plumes, other gorgonian corals
  - ORDER PENNATULACEA: sea pens
- SUBCLASS ZOANTHARIA (HEXACORALLIA)
  - ORDER ACTINIARIA: anemones
  - ORDER CORALLIMORPHARIA: false coral anemones
  - ORDER ZOANTHIDEA: carpet anemones
  - ORDER CERIANTHARIA: tube anemones, often parasitic in other organisms
  - ORDER SCLERACTINIA (MADREPORARIA): true stony corals
  - ORDER ANTIPATHARIA: black or thorny corals

capsules (nematocysts) on the tentacles narcotize prey before they are drawn into the mouth, and sometimes can inflict powerful stings on humans.

The two classes of Cnidaria in which major colonial reef forms are found are the Hydrozoa and Anthozoa. Within the Hydrozoa class is the order Milleporina, containing the fire corals. The Anthozoa class has two subclasses: (1) Octocorallia or soft corals, including those in the order Gorgonacea (gorgonians), and (2) Zoantharia, containing the order Scleractinia or true stony corals. The following will describe the fire corals; the soft corals, especially the gorgonians; and the stony corals.

Milleporina

On Florida reefs, the Milleporina are represented by a single genus, *Millepora*. These fire corals are quite common throughout the western Atlantic tropical coral reefs. A colony consists of a calcareous skeleton with an internal meshwork and external pores through which the polyps retract and expand. The two kinds of polyps are the dactylozooid and the gastrozooid. The dactylozooid, the defensive and food-collecting polyp, has potent stinging apparatus, the nematocyst. The nematocyst contains a small hypodermiclike structure. This is a capsule with a coiled barb, flagella trigger, and a strong neurotoxin. Upon stimulation the trigger releases the barb that is shot into the prey or predator by hydraulic pressure, and the poison is released. The gastrozooid contains a mouth and digestive enzymes. Dactylozooids and gastrozooids are distributed in cyclosystems of five to seven dactylozooids around each gastrozooid.

Two species of *Millepora* are found in Florida. *M. alcicornis* is a digitate branching form, and *M. complanata* (Plate 3b) is a truncated bladed form. In many cases, it is impossible to render a specific determination. Thin encrusting veneers of reef rubble, the skeletons of other organisms, and jetsam prevent recognition of the specific characters. The western Atlantic species, *M. squarrosa*, is a nominal species. Stearn and Riding (1973) and DeWeerdt (1981) showed that *M. squarrosa* was an ecomorph of *M. complanata*. Boschma (1948, 1956) discussed the systematics and taxonomy of *Millepora*.

Millepora's life history reflects hydroid metagenesis or alternation of polyp and medusa generations. The polyp represents the benthic stage. It asexually produces planktonic medusae, which develop gametes that, when fertilized, produce planktonic larvae. The larvae settle and metamorphose into a juvenile *Millepora* colony. Recruitment can also come from fragment propagules. Following storms or physical impact, the broken pieces have regenerative powers to grow into new daughter colonies.

Millepora is a functional autotroph and heterotroph. It has very dense concentrations of zooxanthellae (microscopic, symbiotic dinoflagellate algae) in its endodermic tissues, discussed in detail in Chapter 7. The zooxanthellae are autotrophic and provide the host animal tissue with carbohydrates and some proteins. Polyp nitrogenous wastes and CO_2 are used by the zooxanthellae in protein synthesis. The calcification rate and colony growth are greatly enhanced by this symbiotic relationship. Plankton, captured by the dactylozooids and digested by the gastrozooids, probably provide the micronutrients to the polyps.

Growth rate data for *Millepora* are limited or nonexistent. After settlement the growth seems to be very rapid, probably upward growth approaches 10 cm annually (author's subjective estimate). Encrusting forms are transitory, instability of substratum usually leads to early mortality for the colony.

Wahle (1980) reported that *Millepora* colonies detect octocoral colonies from stimuli present in surrounding seawater and redirect growth to reach the octocoral colony. *Millepora* then grow over the surface of the octocoral, thus gaining new space.

Millepora complanata has a limited bathymetric distribution. It is generally restricted to the reef flat and shallow spur and groove zones (0-5 m). On Looe Key Reef (Table 23) it was second in abundance and frequency, with a mean density of slightly greater than three colonies per square meter. Mergner (1977) reported that *M. complanata* was an indicator species of photophilic and rheophilic environments; its ecological niche is apparently limited to the shallow, well-illuminated and turbulent waters found in shallow windward reef communities.

Octocorallia (Soft Corals)

The Octocorallia, commonly called soft corals or octocorals, are conspicuous in coral reef communities off southeast Florida (Table 25). They have various shapes ranging from inconspicuous encrusting mats to large sea fans. Nearly all types possess calcareous spicules embedded in an organic matrix. Specific species characteristics include colonial morphology, branching patterns, and morphology and configuration of the spicules. The fundamental morphological character is the polyp, which has eight pinnate tentacles.

The Gorgonacea (gorgonians) are the commonest octocoral in southeast Florida reefs in depths less than 30 m. They include the sea fans, sea plumes, sea feathers, sea whips, and sea rods (Plate 4a), which are all very flexible and attached by a holdfast or base to the reef platform. Branches of gorgonians possess a horny, solid center, while other groups have a solid or calcareous axis.

The taxonomy of the major categories is currently being revised. Bayer (1961) is the most complete single source for identification of the shallow water octocorals found off southeast Florida, and Cairns (1977) is a useful field guide. Deichmann (1936) reported on the deep-water octocorals.

Octocoral autecology, including environmental tolerances summarized by Bayer (1956), is similar to that of the stony corals (see next section, Scleractinia). Octocorals exhibit polytrophism, obtaining energy from multiple sources; planktivory and autotrophism are the two major sources.

Reproduction is generally dioecious. Colonies

Table 25

Octocoral fauna in shallow (<30 m) southeast Florida reef communities (Bayer 1961; Opresko 1973; Wheaton 1981, in preparation b).

Species	Patch reef	Bank reef
Briareum asbestinum	*x*	*x*
Iciligorgia schrammi	*x*	*x*
Erythropodium caribaeorum	*x*	*x*
Plexaura homomalla	*x*	*x*
P. flexuosa	*x*	*x*
Pseudoplexaura porosa	*x*	*x*
P. flagellosa	*x*	*x*
P. wagenaari	*x*	*x*
P. crucis	*x*	*x*
Eunicea palmeri	*x*	*x*
E. pinta	*x*	*x*
E. mammosa	*x*	*x*
E. succinea	*x*	*x*
E. fusca	*x*	*x*
E. laciniata	*x*	*x*
E. tourneforti	*x*	*x*
E. asperula	*x*	*x*
E. clavigera	*x*	*x*
E. knighti	*x*	*x*
E. calyculata	*x*	*x*
Muriceopsis flavida	*x*	*x*
Plexaurella dichotoma	*x*	*x*
P. nutans	*x*	*x*
P. grisea	*x*	*x*
P. fusifera	*x*	*x*
Muricea muricata	*x*	*x*
M. atlantica	*x*	*x*
M. laxa		*x*
M. elongata	*x*	*x*
Lophogorgia hebes	*x*	
Pseudopterogorgia bipinnata	*x*	*x*
P. kallos	*x*	*x*
P. rigida	*x*	*x*
P. acerosa	*x*	*x*
P. americana	*x*	*x*
P. elisabethae	*x*	*x*
P. navia		*x*
Gorgonia ventalina	*x*	*x*
Pterogorgia citrina	*x*	*x*
P. anceps	*x*	*x*
P. guadalupensis	*x*	
Nicella schmitti		*x*

release sperm into the water column; however, fertilization and embryological development are internal. Planula larvae are released through the polyp mouth. Those species studied spawn during the spring, summer, and fall. Recruitment of new colonies results from larval settlement following a brief planktonic period. Metamorphosis occurs after the larvae settle on appropriate (solid) substrate. Juvenile (sexually immature) characteristics are not significantly different from the adult's. Greatest mortality occurs during larval and juvenile stages. Growth proceeds by asexual budding of polyps and is determinant. Octocoral growth rates have not been intensely studied. Kinzie (1974) reported that the black sea rod *(Plexaura homomalla)* exhibited colony growth of 10-40 mm annually. The study also noted that sexually mature colonies were 25-35 mm in height. Kinzie's study was in the Cayman Islands but would generally apply to Florida populations.

Octocorals suffer high mortality from storms when wave surge is too great for the holdfast or the substrate itself becomes dislodged. The colony is often carried off the reef proper and recovery after dislodgement is frequently unsuccessful.

Density of octocorals ranges from very dense to sparse, dependent upon the habitat; variability is quite high. Work at Biscayne National Park, for example, documented a range of 10-50 colonies within a square meter. Both Wheaton (in preparation a) and Opresko (1973) conducted studies in patch reef habitats. Dominant species at Biscayne National Park were *Plexaura flexuosa, P. homomalla, Gorgonia ventalina, Eunicea succinea,* and *Pseudopterogorgia americana.* Opresko reported mean densities of 6.9, 11.3, and 27.1 colonies/m^2 at three reefs.

The octocoral fauna from about Stuart-Palm Beach to Dry Tortugas in depths to near 30 m is typical Caribbean or Tropical Atlantic in species composition. Local environmental conditions (depth, light, substrate, and current) control community structure.

The octocoral fauna is an important component of coral reef communities, principally as shelter and refuge for numerous commensal and epibiotic species important in the trophic structure of the reef community ranging from bacteria to fish. Copepod, decapod, amphipod crustaceans, barnacles, ophiuroids, gastropod and pelecypod molluscs, and often small stony corals attach to the central axis stem or holdfast. The fisheries management plan for coral and coral reefs reported the following predators and parasites of western Atlantic octocorals:

1. Algae in *Pseudoplexaura, Pseudopterogorgia, Plexaurella, Plexaura,* and *Muriceopsis* are manifested in abnormal growth (tumors) in the branches.
2. *Millepora* (fire coral) overgrows the octocoral.
3. The fireworm *Hermodice carunculata* (Plate 18b) preys on many corals including a number of reef octocorals.
4. *Cyphoma* spp. gastropod molluscs feed, sometimes in groups, on octocorals. *Gorgonia ventalina* is a favored prey.

5. Numerous fish have been observed feeding; however, they do not appear to be obligate octocorallivores (Randall 1967).

Octocorals are increasingly harvested for human purposes. Many octocorals contain pharmacologically active compounds within their tissues. Medical-pharmacological research requires harvest of prodigious quantities of octocorals to isolate active compounds. Bayer and Weinheimer (1974) reported on the prostaglandin compounds extracted from *Plexaura homomalla*. Concern has been registered that this might eliminate a species population over a wide area if harvest restrictions were not instituted. Another exploitation of octocorals within the area is for live aquaria. Information provided to the Gulf of Mexico Fishery Management Council reported 5,845 colonies of octocorals belonging to nine species are harvested annually and sold as aquarium specimens; several are nonreef species. Current State and proposed Federal statutes only protect the sea fan, genus *Gorgonia*.

Scleractinia

The Scleractinia (stony corals) are a specialized order of Zoantharia, distinguished by an aragonite calcareous exoskeleton. The skeleton (Plate 9a) is composed of a basal plate, external wall, and specialized internal structures--the septa, pali, and columellae. The group in general expresses radial symmetry set in a hexamerous mode. Yonge (1940, 1973) and Wells (1957b) reviewed scleractinian biology, and Vaughan and Wells (1943) and Wells (1956) provided a glossary of terms and definitions.

The order Scleractinia is divided into five suborders (Table 26)—Astrocoeniina, Fungiina, Faviina, Caryophylliina, and Dendrophylliina. Most shallow-water, reef-building corals are found in the first three suborders, with the greatest number in the Faviina. With few exceptions taxonomic characters are based on the skeleton, especially the septa.

The fundamental unit of the coral colony is the polyp (Plate 7b), a tiny mass of tissue with a set of tentacles and a central mouth. The tentacles and adjacent connecting tissues are covered with cilia and nematocysts. There are three tissue layers: ectoderm, mesoglea, and endoderm or gastroderm. The endoderm of reef Scleractinia is usually filled with dense concentrations of zooxanthellae. The color of coral tissue, a complex of plant and animal tissue, is mostly the result of the plant pigments within the chloroplasts of these zooxanthellae. Coral tissue covers only the very surface of the limestone skeletal mass. McCloskey (in Muscatine and Porter 1977) reported that this tissue complex was 45% plant and 55% animal by weight. Because coral tissues contain the producer, and fixed carbon can be passed directly to the coral animal tissues for utilization without a herbivorous intermediary, the association of coral and zooxanthellae is successful in nutrient-impoverished tropical waters. To augment this ability,

Table 26

Southeast Florida reef Scleractinia.

ORDER SCLERACTINIA

SUBORDER ASTROCOENIINA (Vaughan and Wells 1943)

Family Astrocoeniidae (Koby)

Stephanocoenia michelini (Milne, Edwards, and Haime)

Family Pocilloporidae (Gray)

Madracis decactis (Lyman)
M. formosa (Wells)
M. mirabilis (sensu Wells)

Family Acroporidae (Verrill)

Acropora palmata (Lamarck) (Plate 5a)
A. cervicornis (Lamarck) (Plate 4b)
A. prolifera (Lamarck) (Plate 5a)

SUBORDER FUNGIINA (Verrill)

Family Agariciidae (Gray)

Agaricia agaricites (Linne′)
A. agaricites agaricites (Linne′)
A. agaricites danai (Milne, Edwards, and Haime)
A. agaricites carinata (Wells)
A. agaricites purpurea (LeSueur)
A. lamarcki (Milne, Edwards, and Haime)
A. undata (Ellis and Solander)
A. fragilis (Dana)
Helioseris cucullata (Ellis and Solander)

Family Siderastreidae (Vaughan and Wells 1943)

Siderastrea radians (Pallas)
S. siderea (Ellis and Solander)

Superfamily Poritidae (Gray)

Family Poritidae (Gray)

Porites astreoides (Lamarck)
P. porites (Pallas)
P. porites divaricata (LeSueur)
P. porites furcata (Lamarck)
P. porites clavaria (Lamarck)
P. branneri (Rathbun)

(continued)

Table 26 (continued)

SUBORDER FAVIINA (Vaughan and Wells 1943)

Superfamily Faviidae (Gregory)

Family Faviidae (Gregory)

Favia fragum (Esper)
F. gravida (Verrill)
Diploria labyrinthiformis (Linné)
D. clivosa (Ellis and Solander)
D. strigosa (Dana) (Plate 6a)
Manicina areolata (Linné)
M. areolata mayori (Wells)
Colpophyllia natans (Houttyn)
C. amaranthus (Müller)
C. breviseralis (Milne, Edwards, and Haime)
Cladocora arbuscula (LeSueur)
Montastraea cavernosa (Linné) (Plate 6b)
M. annularis (Ellis and Solander) (Plate 5b)
Solenastrea hyades (Dana)
S. bournoni (Milne, Edwards, and Haime)

Family Rhizangiidae (d'Orbigny)

Astrangia astreiformis (Milne, Edwards, and Haime)
A. solitaria (LeSueur)
Phyllangia americana (Milne, Edwards, and Haime)

Family Oculinidae (Gray)

Oculina diffusa (Lamarck)
O. varicosa (LeSueur)
O. robusta (Pourtales)

Family Meandrinidae (Gray)

Meandrina meandrites (Linné)
M. meandrites braziliensis (Milne, Edwards, and Haime)
Dichocoenia stellaris (Milne, Edwards, and Haime)
D. stokesii (Milne, Edwards, and Haime)
Dendrogyra cylindrus (Ehrenberg) (Plate 7a)

Family Mussidae (Ortmann)

Mussa angulosa (Pallas)
Scolymia lacera (Pallas)
S. cubensis (Milne, Edwards, and Haime)
Isophyllia sinuosa (Ellis and Solander)
I. multiflora (Verrill)
Isophyllastraea rigida (Dana)
Mycetophyllia lamarckiana (Milne, Edwards, and Haime)
M. danaana (Milne, Edwards, and Haime)
M. ferox (Wells)
M. aliciae (Wells) (continued)

Table 26 (continued)

SUBORDER CARYOPHYLLIINA (Vaughan and Wells 1943)

Superfamily Caryophylliidae (Gray)

Family Caryophylliidae (Gray)

Eusmilia fastigiata (Pallas)
Paracyathus pulchellus (Philippi)

SUBORDER DENDROPHYLLIINA (Vaughan and Wells 1943)

Family Dendrophylliidae (Gray)

Balanophyllia floridana (Pourtales)

corals have developed other methods to conserve and recycle limiting resources such that high productivity is maintained. Muscatine and Porter (1977) reported that reef corals are primary producers, primary consumers, secondary and tertiary consumers, deposit feeders, and saprotrophs; different species have perfected different strategies.

The most unusual and probably the most important trophic strategy that is almost universal among the reef-dwelling corals is the primary producer activity. The autotroph or phototroph is carried within the coral tissue as an endosymbiont. Hermatypic scleractinia possess the dinoflagellate *Zooxanthella microadriaticum* (Loeblich and Shirley 1979) (also reported as *Symbiodinium* or *Gymnodinium)* within their endodermic tissues. The zooxanthellae complement the corals by recycling nitrogen and phosphorus, fixing carbon (lipids, amino acids, nonamino organic acids, glycerol, organic phosphates, and glucose), producing oxygen, enhancing calcification, and removing animal metabolic products (CO_2, nitrogenous wastes). Muscatine (1973), Taylor (1973), and Muscatine and Porter (1977) reviewed the coral host zooxanthellae symbiont relationship. Muscatine and Porter (1977) reported that 30% of the carbon fixed by the zooxanthellae on a clear day would satisfy all of the coral's carbon needs.

Corals are suspension feeders. Several techniques are used singularly or in combination to capture zooplankton. The most common technique is to capture drifting zooplankton by stunning the zooplanktors with the nematocysts, a special poison organelle found in the tentacles. (Although most polyp expansion for feeding occurs nocturnally and the tentacles of most species are retracted during the day, *Dendrogyra cylindrus* is an exception (Plate 7a). Porter (1974) reported on polyp expansion.) The captured zooplanktors are delivered to the mouth by the tentacles or by reverse beating of the cilia. In family Agariciidae small polyps generate water currents with the cilia. Food caught in the current is captured by the small tentacles and ingested. Some observations of external digestion via mesenterial filaments have also been reported (Yonge 1973). Plankton can also be caught in mucus nets that are on the coral surface or in the water column. The prey is brought to the mouth for ingestion. Lewis and Price (1975) reviewed coral feeding.

Digestion of animal material occurs in the region of the mesenterial filaments; partially digested material is translocated to the cells for final digestion. Translocation of food and wastes is by diffusion or wandering cells (Yonge 1973). Cellular oxygen and carbon dioxide exchange also occurs via diffusion. Muscatine and Porter (1977) reported that most reef corals cannot receive sufficient energy from planktivory to support their energy requirements; they extrapolated that approximately 20% of energy needs could be met from zooplankton. The role of zooplankton in the diet is suspected to be one of providing critical minerals and nutrients not gained via the autotrophic pathway. Other sources of energy include bacteria, detritus, organics dissolved in seawater, and external mesenterial feeding of animal tissues adjacent to the colony. Wastes are removed through the mouth.

The life history and autecology for many stony coral species are incomplete or totally unknown and are based on hypothesis and conjecture rather than fact. Sexual reproduction includes gametogenesis (Plate 8a) within the polyps near the base of the mesenteries. Some species have separate sexes and some are hermaphroditic. Fertilization occurs internally or externally. Some species such as *Acropora cervicornis* and *A. palmata* appear to be synchronous in development of gametes. Embryology terminates with the development of planktonic larvae, the planula. If there is larval brooding by the species, the planula is released through the mouth and has limited powers of locomotion by cilia. Kojis and Quinn (1981) reported that several species of Pacific Scleractinia had benthic swarming larvae. Lewis (1974) noted that *Favia fragum* in the laboratory were bottom swarming. Fadlallah (1983) reviewed scleractinian reproductive - larval biology. Upon proper stimulation, the larvae settle on appropriate substrates. Negative phototropism is partially responsible for settling. Initial calcification ensues with the forming of the basal plate and the initial protosepta, followed by the theca or wall and axial skeletal members. Buds formed on the initial corallite develop into daughter corallites.

Connell (1973) reviewed the population ecology of reef-building corals. Two generalized contrasting life history strategies are suggested; many species probably fall between the extremes. Opportunistic or R strategists attain small adult size, exhibit determinant growth, reach sexual maturity at an early age, place a great deal of available energies into reproduction, and produce small eggs and sperm that are released into the water column for fertilization. The lifespan of this type of species is short; success is insured by the vast numbers of progeny produced. These species may also be the more eurytopic in environmental tolerances. They are able to invade harsher reef habitats. *Porites astreoides* and *F. fragum* are examples of this form of strategy. Jaap (in progress) studied populations of stony corals at 24 sites (96 m^2) at BNP (1978-81). He found that *P. astreoides* was one of the most commonly recruited species in the patch reef environments. The K strategist exhibits slow growth and a long period before reaching sexual maturity. Most energy is expended toward growth and maintenance. Growth may be indeterminate. Apparently little energy is diverted toward reproduction. These species may live for hundreds or even thousands of years and sexual reproduction may be a very rare event. *Montastraea annularis* is the best example of this type of life history. Some colonies are hundreds of years old. Dustan (1977a) and Bak and Engel (1979) both reported very low or no recruitment for *M. annularis.*

Growth in scleractinian corals involved asexual tissue division and skeletogenesis (skeleton construction) (Barnes 1973). The two processes are highly interdependent; imbalance of either causes change which results in skeletal abnormalities. Growth in branching species such as *A. cervicornis* and *A. palmata* is quite rapid, while growth for the more massive star and brain corals is relatively slow. Table 27 presents growth data for several scleractinian species; many others have not been studied. Hudson (1981) noted that certain cyclic patterns appear over the 75-year growth period of the corals he cored, slabbed, and x-rayed for growth-rate skeletal density patterns. Buddemeir and Kinzie (1976) reviewed coral growth.

Recruitment is critical to perpetuation of the species and ultimately to the vitality of the coral reef communities. Dustan (1977a) reported on stony coral recruitment and mortality at Carysfort Reef (Figure 17) off Key Largo. Because the duration of his study was less than one year, the conclusions are qualified. The study showed that *Agaricia agaricites* was the most commonly recruited species. Bak and Engel (1979) studied recruitment off Bonaire and Curacao, Netherlands Antilles. They also reported that *A. agaricites* was the most commonly recruited species. Again, the one-year time frame of this study is subject to some qualifications. The overall net recruitment comparison of Dustan and Bak and Engel is difficult, since Dustan only considered corals less than 15 cm to be juvenile recruits and Bak and Engel considered colonies in the 2-40 cm range as juveniles. Both of the studies were limited to depths greater than 6.5 m. This is beyond the spur and groove zone, hence it is most representative of the fore reef or buttress zones.

As reported earlier, each reef has its own particular species composition of scleractinian corals. However, certain key framework species are fundamental to the reef-building processes. In patch reefs *M. annularis* (Plate 5b) is usually the most important species. *Diploria strigosa* (Plate 6a), *D. labyrinthiformis, Colpophyllia natans,* and *Siderastrea siderea* are also significant. The remaining species are either in low abundances or frequencies, or their biomass and framework building capacity is low.

In the bank reef communities, different zones manifest different species dominance. On reef flats with

Table 27

Growth rates of scleractinian species from Florida and the Bahamas[a].

Species	Growth rate[b] (mm/yr)	Location	Source
Acropora cervicornis	40.0 H	Dry Tortugas	Vaughan and Shaw 1916[c]
	109.0 H	Key Largo Dry Rocks	Shinn 1966
	115.0 H	Eastern Sambo	Jaap 1974
Acropora palmata	39.5 H	Goulding Cay, Bahamas	Vaughan and Shaw 1916
	105.0 B	Eastern Sambo	Jaap 1974
Acropora prolifera	37.2 H	Goulding Cay, Bahamas	Vaughan and Shaw 1916
Agaricia agaricites	3.5 H	Dry Tortugas	Vaughan and Shaw 1916
Porites porites	17.9 H	Dry Tortugas	Vaughan and Shaw 1916
Porites astreoides	17.6 D	Dry Tortugas	Vaughan and Shaw 1916
Siderastrea radians	4.3 D	Dry Tortugas	Vaughan and Shaw 1916
Siderastrea siderea	6.3 D	Dry Tortugas	Vaughan and Shaw 1916
Favia fragum	4.9 D	Dry Tortugas	Vaughan and Shaw 1916
Diploria labyrinthiformis	7.8 D	Dry Tortugas	Vaughan and Shaw 1916
Diploria clivosa	17.3 D	Dry Tortugas	Vaughan and Shaw 1916
Diploria strigosa	6.9 H	Dry Tortugas	Vaughan and Shaw 1916
	5.0 H	Carysfort	Shinn 1975
Manicina areolata	8.2 D	Dry Tortugas	Vaughan and Shaw 1916
Manicina areolata mayori	14.0 D	Dry Tortugas	Vaughan and Shaw 1916
Montastraea cavernosa	4.4 H	Dry Tortugas	Vaughan and Shaw 1916
Montastraea annularis	9.0 H	Key West	Agassiz 1890
	5.0-6.8 H	Dry Tortugas	Vaughan and Shaw 1916
	10.7 H	Carysfort	Hoffmeister and Multer 1964
	8.4 H	Carysfort	Shinn 1975
	8.0-9.7 H	Key Largo area	Hudson 1981
Oculina diffusa	14.3 H	Dry Tortugas	Vaughan and Shaw 1916
Dichocoenia stokesii	6.7 D	Dry Tortugas	Vaughan and Shaw 1916
Dendrogyra cylindrus	10.4 H	Dry Tortugas	Vaughan and Shaw 1916
Isophyllia sinuosa	5.1 D	Goulding Cay, Bahamas	Vaughan and Shaw 1916
Eusmilia fastigiata	5.8 H	Dry Tortugas	Vaughan and Shaw 1916

[a] Goulding Cay, Bahamas, data were only used when Tortugas information was unavailable.
[b] B = increase in branch length, D = increase in diameter, H = increase in height.
[c] Vaughan and Shaw's multiple values were averaged.

high turbulence *P. astreoides* is dominant with *D. clivosa*. In the spur and grooves, *Acropora palmata* (Plate 5a) is dominant (Table 18). In the buttress zone *M. annularis* is most significant in the reef-building processes. Tables 17, 19, and 20 present the species ranks, abundance, densities, and dispersion patterns for a number of reefs; note the high degree of variability within and between reefs. In deep reef communities (> 30 m) the species that dominate are *Agaricia lamarcki, Madracis mirabilis, Stephanocoenia michelinii, A. fragilis*, and *M. formosa*.

Dynamic population changes affect the nature of coral associations in shallower reef habitats. Colonies are frequently relocated following storms. In many cases, they do not die, but reestablish themselves in the new habitat (Plate 10a). This makes it very difficult to evaluate mortality in a time series within a sampling site. Fragmentation also complicates the issue. During the 4-year BNP study, branching species *(A. palmata, A. cervicornis,* and *P. porites)* were frequently fragmented and scattered throughout the site causing major change in abundance and dominance. What was originally a single colony in some cases was broken into 10 or more living fragments. The great variability over the period of this study points out that shallow patch reefs are dynamic and that physical controls are significant. Table 28 presents a time series of a representative 4-m^2 plot at Elkhorn Reef.

Biological interactions among the Scleractinia are documented by Lang (1971, 1973, 1980); Jackson and Buss (1975); Richardson et al. (1979); Wellington (1980), and Sheppard (1981, 1982). These interactions are mostly involved with maintaining and/or expanding space, "lebensraum" in the reef where spatial resources

Table 28

Time series for abundance, density, and dispersion of stony corals at Elkhorn Reef (one 4-m^2 plot) (Jaap, unpublished).

Species	B. I.[a] (ranking)	Abundance (total no. of colonies)	Percent of total colonies	Density $(\bar{x} \pm s)$	D.I.[b]
1978					
Acropora cervicornis	7	7	24.14	1.75±0.50	R
Acropora palmata	6	6	20.69	1.50±1.29	R
Porites porites	5	5	17.24	1.25±1.26	R
Porites astreoides	4	4	13.79	1.00±0.00	R
Siderastrea siderea	3	3	10.34	0.75±0.96	R
Millepora alcicornis	2	2	6.90	0.50±1.00	R
Favia fragum	1	1	3.45	0.25±0.50	R
Diploria clivosa	1	1	3.45	0.25±0.50	R
Yearly total		29			
1979					
Acropora cervicornis	7	9	36.00	1.75±0.96	R
Acropora palmata	6	6	24.00	1.50±1.29	R
Siderastrea siderea	4	4	16.00	1.00±1.15	R
Porites astreoides	4	4	16.00	1.00±0.82	R
Diploria clivosa	1	1	4.00	0.25±0.50	R
Millepora alcicornis	1	1	4.00	0.25±0.50	R
Yearly total		25			
1980[c]					
Acropora palmata	9	26	74.29	6.50±3.70	R
Acropora cervicornis	4	4	11.43	1.00±1.15	R
Siderastrea siderea	3	3	8.57	0.75±0.96	R
Porites astreoides	2	2	5.71	0.50±0.58	R
Yearly total		35			
1981					
Acropora palmata	10	23	62.16	5.75±1.71	R
Siderastrea siderea	3	3	8.11	0.75±0.96	R
Porites astreoides	3	4	10.81	1.00±0.82	R
Porites porites	3	3	8.11	0.75±1.50	R
Acropora cervicornis	1	1	2.70	0.25±0.50	R
Diploria clivosa	1	2	5.41	0.50±1.00	R
Millepora complanata	1	1	2.70	0.25±0.50	R
Yearly total		37			

[a] B.I. = Biological Index, McCloskey (1970).

[b] D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

[c] Note that a storm during the winter of 1979-80 fragmented a large *A. palmata* colony. Survivors established a new set of colonies, thus changing dominance and density.

are often a limiting factor. Rapid growth among the Acroporid species can shade out other slower growing species (Shinn 1975). Some species have potent external digestive mechanisms whereby the mesenterial filaments are extended and kill the tissues of adjacent corals. Lang (1971, 1973) documented this digestive mechanism as hierarchical among the species of Atlantic Scleractinia. Some species compete with this agressive territorial behavior through sweeper tentacles which keep the mesenterial filaments away from the lower hierarchy species. It is also probable that alleochemicals are important in protecting space. Biological interactions are probably more significant in deeper reef environments where physical events are less frequent and of an intermediate magnitude.

Coral pathology and disease is an infant research area. Phenomena were reported by Preston (1950) and Squires (1965). Laboratory experiments demonstrate that bacteria cause morbidity and mortality in corals (Mitchell and Chet 1975; Ducklow and Mitchell 1979a, 1979b). Antonius (1974b) reported that a blue-green alga, *Oscillatoria,* was capable of killing corals under certain (laboratory and field) conditions (Plate 19a). The alga grew over the coral, killing it in a short period. Gladfelter (1982) reported on an undetermined pathogen that caused epidemic mortality in *A. palmata* on a reef off St. Croix, U.S. Virgin Islands. A similar condition is often seen on Florida reefs; Grecian Rocks appears to be currently infested with this pathogen (Plate 25a). Pathology and band diseases in corals were reviewed by Antonius (1981a, 1981b).

4.5 OTHER BENTHIC GROUPS

The level of insight into many other coral reef benthic groups is poor. Detailed examination will not be attempted here. There are numerous diverse habitats within a coral reef that provide niches to a multitude of species belonging to nearly every phylum (Plate 8b). Sedimentary deposits provide habitat for infaunal organisms. Many mobile forms find refuge under the sedimentary surface and forage for food at night. The reef rock itself is a habitat for both epifauna and boring and cryptic fauna. A single coral head weighing 4.7 kg at Heron Island contained 1,441 polychaete individuals (Grassle 1973); 67% of all organisms from the coral's interior were polychaetes. Vittor and Johnson (1977) studied polychaetes from Grand Bahama Island and reported that 84 species were present. Robertson (1963), Ebbs (1966), Hein and Risk (1975), and Hudson (1977) reported on the boring fauna of Florida corals. Specific references that deal with the other benthos include the proceedings volumes from the past International Coral Reef Symposia, the two volumes from the *Biology and Geology of Coral Reefs*, Volumes 23 (1, 2) of *Bulletin of Marine Science*, Frost et al. (1977), Colin (1978a), and Rutzler and MacIntyre (1982b). Voss et al. (1969) provided a qualitative account of the biota found within BNP prior to its becoming a national monument. The study of most other benthic organisms, save certain commercial species (e.g., spiny lobster), is for taxonomic purposes. Decapod crustaceans were reported on by Gore (1981). Lyons and Kennedy (1981) and Lyons et al. (1981) reported on biological aspects of the spiny lobster *Panulirus argus.* Work (1969) studied West Indian mollusk communities. Kier and Grant (1965) and Kissling and Taylor (1977) discussed echinoderms from Florida reef communities.

CHAPTER 5

PLANKTON

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5.1 INTRODUCTION

Coral reefs are highly productive marine ecosystems with a great abundance and diversity of organisms. They are generally surrounded by waters with small plankton standing stocks. Most studies describing coral reef plankton communities have investigated the importance of zooplankton in coral nutrition. The results of these studies have been somewhat contradictory.

The early studies (Yonge 1930 and others) generally indicated that there was not a sufficient amount of zooplankton in the water column around the reef to support the corals. Recent studies of coral reef zooplankton (Emery 1968; Porter 1974; Sale et al. 1976; Alldredge and King 1977; Porter et al. 1977; Hobson and Chess 1978; Hamner and Carleton 1979; Hobson and Chess 1979; Rutzler et al. 1980; Hamner and Hauri 1981; McWilliams et al. 1981; and Ohlhorst 1982) have shown that methods used in the earlier studies for capturing the reef zooplankton were not adequate to describe the zooplankton community most nutritionally important to the corals. These plankton live in close association with the corals, sometimes within the reef itself.

The earlier collections used nets which were towed or drifted above and sometimes away from the reefs. The recent studies, using an array of different collection and observation methods such as stationary nets, diver-controlled nets, plankton pumps, diver-operated suction devices, emergence traps, light traps, and diver visual and photographic observations (see Porter et al. 1978; Hamner and Carleton 1979; and Youngbluth 1982 for discussion of sampling techniques), have found that coral reefs, worldwide, have an abundant and diverse resident near-reef zooplankton community different from the oceanic forms in the surrounding ocean. Porter et al. (1978), summarizing information from mostly Indo-Pacific reefs, estimated that 75% of the reef zooplankton standing stock was of benthic origin and that 85% of the biomass was of local origin. Parts of this community are, therefore, often not considered as truly planktonic, but rather as epibenthic or demersal. Many organisms in the resident community are only found in the water column at night and spend daylight hours on the sediment or within the reef itself (see Section 5.3).

It is still not clearly demonstrated, however, what importance zooplankton play in coral nutrition. Emery (1968) states that plankton represent a major source of food to the reef, while Muscatine and Porter (1977) suggest that zooplankton feeding does not contribute a majority of either calories or carbon required for reef corals. Hamner and Carleton (1979) summarize and critique studies of reef zooplankton and find that, due to often questionable methodologies used, no conclusive data on the relative importance of zooplankton to coral reef nutrition have yet been published.

Few studies have been conducted describing the free living phytoplankton community in the vicinity of coral reefs. Researchers generally agree that phytoplankton's contribution to the primary productivity of the coral reef ecosystem is small (e.g., Hargraves 1982). Further, Wood (1954) suggested that the waters of the Great Barrier Reef might have a distinctive reef phytoplankton community. Subsequent studies (Jeffrey 1968; Revelante et al. 1982), however, found a reef community similar to the nearby ocean phytoplankton community. The following discussion of coral reef plankton will, therefore, mainly be concerned with the zooplankton community.

5.2 TAXONOMIC COMPOSITION AND SPATIAL DISTRIBUTION

As discussed above, several researchers have described coral reef zooplankton communities in great detail. However, due to geographical considerations, the following discussion will generally be limited to observations of Alligator and Looe Key Reefs in Florida by Emery (1968). The information obtained in these studies is somewhat limited due to the lack of quantitative abundance measurements; however, the report gives a detailed account of the spatial and temporal distribution of the different zooplankton taxa found on the reefs. Emery used several different collection methods, including boat- and swimmer-towed nets, suction devices, light traps, and diver observations, in order to reduce sampling errors of zooplankton living near or within the reefs. Further, he made collections and observations during both day and night. He also subdivided the study areas into several habitats such as grass beds, lagoons, patch reef, reef tops, caves, and deep reefs. Visual observations by divers, swimmer-towed nets, and suction devices produced the most interesting information about the zooplankton on and in close vicinity of the reefs.

Close to the water surface of all areas of the reefs, Emery found a typical offshore zooplankton community, consisting mostly of free living copepods and larvaceans. Visual observations deeper in the water column and just above the bottom often found the reef plankton in close and dense aggregations or swarms. The swarms tended to hold together and move as a unit, and they also maintained their position against the current and the surge. Emery found four species of copepods in these swarms: *Acartia tonsa, A. spinata, Oithona nana,* and *O. oculata*. He estimated that one swarm of *A. spinata* contained 110,000 copepods/m^3. Hamner and Carleton (1979) also reported extremely dense swarms of copepods (max. 3,320,000/m^3) on Australian reefs. Swarming species of copepods, in the Emery study, were most often found on the grass beds and reef tops. Monospecific schools of mysids, of one size class, were also found on the the reef tops often inside caves and along coral faces. Schooling implies a stronger social behavior than swarming since the individuals that belong to one size class are longitudinally aligned and move as a unit. Schooling behavior of mysids has also been reported by other investigators of Alligator Reef (Randall et al. 1964). On the deep reefs and the patch reefs of both Alligator and Looe Key Reefs, close aggregations of the plankton did not appear as important. Copepods and mysids were found individually or in looser aggregations. Emery also observed that the swarming and schooling behavior of these organisms was mostly a daytime phenomenon. They were often found individually at night. Hobson and Chess (1979), reporting on resident reef plankton of Hawaiian atolls, found a similar diurnal pattern for swarms of copepods, mysids, and larval fishes.

Swarming and schooling in dense aggregates are important examples of behavior adaptation by resident reef plankton, which differentiates them from pelagic forms. Hamner and Carleton (1979) stated that at least seven species of copepods, and probably more, engage in swarming behavior at coral reefs in three of the world's oceans. The same authors have suggested that swarming not only reduces predatory pressure, but also facilitates reproduction and permits the plankton to cluster in local eddies to maintain a favorable feeding position with minimum energy cost. In a subsequent paper, Hamner and Hauri (1981) related the resident reef zooplankton distribution to the reef configuration and the local water motion. They found swarms of copepods and chaetognaths directly upcurrent of the reef face in an entrained water mass, which was subject to less removal than downstream waters. This accumulation of biomass and increased primary productivity in areas upstream of reefs is one aspect of the well-known "island mass effect" phenomenon.

5.3 DIURNAL MIGRATIONS

Investigators of coral reef zooplankton who have taken care to sample the populations near the substrate and on a diurnal schedule have found the plankton community undergoes drastic daily changes. Emery (1968) found that nighttime collections contained four times greater volume than daytime collections. A suction device with a light close to its mouth to attract the plankton was used for these collections, and therefore, quantitative comparisons are not in order. Emery did, however, find a very different composition of the plankton at night. Many forms, such as polychaetes, cumaceans, and zoea, which he observed living in caves and crevices during the day, were swimming outside the reef in great abundance at night. Other forms which were most often captured at night included: fish larvae; large copepods; crab larvae; chaetognaths; ostracods; and shrimp larvae. Ohlhorst (1982) found that the zooplankton emerged from the substrate of Discovery Bay, Jamaica, at variable rates throughout the night. The peak activity was usually two hours after sunset. However, smaller species of copepods and juvenile members of large species migrated into the water column during the day and were least abundant in the water column during the night. She suggested that the reasons for diel vertical migration are many and varied. They include: feeding; reproduction; escape from predation; and dispersal. Porter et al. (1977) studied reefs in the Pacific Ocean and found that the volume of emerging plankton was greatest over branching coral and least over sand and rubble. Alldredge and King (1977) and McWilliams et al. (1981), sampling different reefs of the Great Barrier Reef, also found a positive relationship between the structural heterogeneity of the substrate and the amount of epibenthic plankton emerging at dark. The composition of the community Alldredge and King found was similar to the one described by Emery (1968), and they estimated that an average of 2,510 zooplankton emerged per m^2 of the reef substrate. McWilliams et al. (1981), conducting a more detailed study, found not only a greater volume of plankton emerging from the coral than from the sand but also that the composition of the rising communities were different. The reef bases were transitional zones with a mixture of "coral" and "sand" communities. These authors further found that more plankton emerged during the summer than during the winter. The annual range of the "coral" fauna was 5,030-2,350 animals/m^2 and the "sand" fauna 2,720-1,150 animals/m^2. Also, the plankton samples collected during the summer were generally more diverse in taxa than winter samples. Hobson and Chess (1979), collecting emerging plankton from the lagoon substrata of atolls in the Pacific Ocean, found a considerably less abundant plankton community in their traps than reported by Alldrege and King (1977) and McWilliams et al. (1981). Hobson and Chess (1979) suggested that the use of different types of traps may account for some of the variations reported between study areas. Youngbluth (1982) tested three types of emergence traps and found that both density and diversity of the zooplankton collected were affected by the trap design and sampling procedures. He concluded that different mesh size netting in the traps alone could probably account for much of the variability in plankton abundance and diversity between different study areas.

5.4 SUMMARY

The coral reef plankton community can be characterized as follows:

1. A highly abundant and diverse zooplankton community is found on the reefs. It is in striking contrast to the open water community nearby.

2. Most of the reef zooplankton belong to a resident community, which is able to maintain position on the reef.
3. The community consists partly of true planktonic forms living in dense aggregates and using the reef configuration and water currents to maintain position.
4. The major portion of the resident plankton community consists of epibenthic forms. This community generally migrates from the substrate to the water column at dark.
5. Phytoplankton communities found over the reefs appear to be little different from open ocean assemblages.

CHAPTER 6

REEF FISH

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Tropical coral reefs are richer in fish species than any other habitat (Marshal 1965; Emery 1973). The fish fauna of the Florida reef tract is wholly tropical with only seven species that have not been recorded elsewhere in the West Indies. Thus, although the study of coral reef fishes in south Florida has not been extensive, considerable information concerning their biology and ecology has been developed through studies elsewhere in the Caribbean.

The most complete studies conducted in the Florida Keys are those by Longley and Hildebrand (1941) for the Dry Tortugas, and Starck (1968) for Alligator Reef. Field guides to Florida reef fish include Chaplin and Scott (1972); Greenberg (1977); Stokes and Stokes (1980); and Kaplan (1982).

Three major reviews concerning the general ecology of coral reef fish on a worldwide basis are Ehrlich (1975), Goldman and Talbot (1976), and Sale (1980b).

6.1 REPRODUCTION AND RECRUITMENT

Most coral reef fish spawn in the water column above the reef, and their eggs remain in the plankton during development. A few species either lay their eggs demersally and attend to them or they brood them by mouth (Smith 1982; Colin 1982). Breeding aggregations are common to most reef species. These serve to increase egg fertilization and release of egg and sperm in the lee of the reef, thereby increasing dispersion and reducing predation (Colin 1982). Coral reef fishes typically produce large numbers of offspring which are then dispersed by means of a pelagic larval stage (Breder and Rosen 1966; Ehrlich 1975; Johannes 1978; Sale 1980b). The timing of egg release (or hatching for those families with dermersal eggs) is often triggered by dusk, night, or the tides, increasing the ability of newly spawned or hatched eggs to elude predators (Myrberg 1972; Robertson and Choat 1974; Warner et al. 1975; Bell 1976; Colin 1976, 1978b, 1982; Moyer and Bell 1976; Johannes 1978; Lobel 1978; Moyer and Nakazono 1978).

Most species of reef fish spawn several times during their spawning season. Spawning may be daily, biweekly, or monthly (Robertson 1972; Holzberg 1973; Warner et al. 1975; Moyer and Nakazono 1978; Lobel 1978; Ross 1978). These multiple spawnings have been explained as a method of ensuring a wide dispersal of offspring (Sale 1978).

Sex reversal is also common in many reef species. Often the adult populations are largely females (with only a small but sufficient percentage of males). If the number of males in the population becomes reduced, new males are rapidly developed from female stock by some individuals undergoing a protogynous sex reversal. Egg production is maximized by this mechanism and a greater proportion of energy channeled into population maintenance (Goldman and Talbot 1976; Smith 1982). Florida reef species known to undergo sex reversal include most (if not all) parrotfish (Scaridae), many wrasses (Labridae), and some groupers (Serranidae).

A pelagic larval stage is almost universal among coral reef fish species. Little detailed information is known about the life of larval reef fish while in the pelagic phase, although they are frequently taken in offshore plankton tows. Studies in which the time of spawning and time of period of peak recruitment of juveniles from the plankton have been correlated indicate that the larval stage varies from a few weeks to months depending on the species (Randall 1961a; Moran and Sale 1977). Aging of larvae or newly transformed juveniles by counting daily growth increments on the otoliths has revealed that pomacentrids, gobiids, and blenniids have larval lives of about 21 days. The larval stage of siganids, acanthurids, chaetodontids, and labrids is 30 or more days (Sale 1980b). As is common among many marine invertebrates, many species can probably extend their larval life until suitable settlement habitat is found (Randall 1961a; Johannes 1978; Sale 1980b).

The methods by which larval fish are returned to a reef environment have been mostly hypothesized from circumstantial evidence. Generally, it is believed that current gyres that form in the lee of islands and reefs act as traps to prevent the loss of larvae downstream and, through their rotation, return the larvae to the reef (Munro et al. 1973; Leis and Miller 1976; Johannes 1978). Johannes (1978) reported that the spawning migrations, which bring some species to particular sites at precise times, release the gametes into a mass of water that is most likely to return them to the same reef at the end of their pelagic existence. He cited the variability in spawning peaks between various locations, often within the same region, as possible evidence that spawning patterns have arisen as responses to a variable pattern of water circulation. The season in which spawning occurs is not well known for many coral reef species, but it is known some species spawn on a regular basis all year (Colin 1982). For most species that have been studied, spawning peaks in the late afternoon and may last from a few minutes to an hour or more depending on the species (Colin 1982). Present knowledge concerning the reproductive behavior of coral reef fishes in the Caribbean has been summarized in papers by Smith (1982) and Colin (1982).

Seagrass beds are important to the reproduction of coral reef fishes in that they act as nurseries for some species. Ogden and Zieman (1977) reported that at Tague Bay, St. Croix, juvenile spiny puffer (*Diodon*), squirrelfish (*Holocentrus*), yellowtail snapper (*Ocyurus chrysurus*), surgeonfishes (*Acanthurus*), and numerous wrasses (*Halichoeres*) were commonly present within the grassbed. The spotted goatfish (*Pseudupeneus maculatus*) and the yellow goatfish (*Mulloidicthys martinicus*) occur as juveniles in grassbeds off the Florida Keys (Springer and McErlean 1962a; Munro 1976). Springer and McErlean reported capturing eight species of juvenile scarids in *Thalassia* beds off Matecumbe Key; all but one, *Sparisoma radians*, are considered reef species as adults. These fish remain in the seagrass habitat until they become too large (> 20 cm) to hide among the blades (Ogden and Zieman 1977) and presumably migrate to the reef.

6.2 FOOD HABITS AND TROPHIC STRUCTURE

Fish constitute a major portion of the animal biomass on a coral reef, and they are an important component of the overall trophic structure. Most reef fish are carnivores and many studies have shown that carnivorous fishes normally represent three to four times the biomass of herbivorous fishes (Bakus 1969; Goldman and Talbot 1976; Parrish and Zimmerman 1977). This reversal of the "traditional" biomass pyramid results from many carnivorous fishes feeding on invertebrates that form the largest portion of lower trophic levels on reefs. Benthic invertebrates are of considerable importance to reef fish populations as energy assimilators at the planktivore, herbivore, and detrital levels (Vivien and Peyrot-Clausade 1974).

Herbivorous reef fish are sustained primarily by low algal turfs and low-growing filamentous algae and diatoms (Goldman and Talbot 1976). No phytoplankton feeders have been identified in any of the reported studies of reef fish food habits (Hiatt and Strasberg 1960; Randall 1967; Bakus 1969; Hobson 1974; Goldman and Talbot 1976; Parrish and Zimmerman 1977; Hobson and Chess 1978). This is in contrast to fish populations in temperate regions where up to 6% of the species may consume phytoplankton (Davies 1957). Benthic algal feeders include most parrot fish (Scaridae) and surgeonfishes (Acanthuridae) and some blennies (Blennidae), damselfish (Pomacentridae), butterfly fishes (Chaetodontidae), and filefish (Balistidae). A number of studies have shown that the herbivorous reef fish have a marked effect on the distribution and abundance of algae present on a reef. When protected from grazing by exclosures, algal communities will rapidly increase in standing crop (Stephenson and Searles 1960; Randall 1961a; Earle 1972a; Montgomery 1980; Montgomery et al. 1980; Hixon and Brostoff 1981).

The extent to which zooxanthellae is eaten by reef fish has been disputed (Randall 1974). Parrotfishes (Scaridae) have been reported to scrape coral in a feeding manner by Hiatt and Strasberg (1960) in the Marshall Islands; Motoda (1940) in the Palao Islands; Talbot (1965) off East Africa; Al-Hussaini (1947) in the Red Sea; and Bakus (1969) along the Pacific coast of Panama and Costa Rica. This habit was not observed by Randall (1967) during extensive studies in the Caribbean; Finckh (1904) in the Ellice Islands; Wood-Jones (1910) at Cross-Keeling Island; or Choat (1969, cited in Goldman and Talbot 1976) on the Great Barrier Reef. Randall (1974) did observe coral feeding by scarids in some areas of the Pacific, however, and discussed how this habit appears to vary among the same species of fish at different locations. Scraping of massive (head) corals by parrotfish does occur at least occasionally on Florida reefs (W.A. Starck II, personal comment in Randall 1974; J.T. Tilmant, personal observation). The amount of food taken in this way may be insignificant compared to algae ingested by grazing.

There are few true omnivores among most reef fishes. The majority of species tend to be substantially more carnivorous than herbivorous. Most herbivorous fishes have been found to take only a small amount of animal matter. Among the Caribbean species reported as omnivorous are the damselfish (beaugregory and the threespot damselfish); the grey angelfish and French angelfish; the scrawled filefish, orangespotted filefish, and fringed filefish; and the sharpnose puffer (Randall 1967).

Schools of small zooplankton-feeding fishes are common on coral reefs and zooplankton is an important energy source for larval stages of most reef species. Among adult zooplankton feeders commonly schooling on reefs are the herring genera *Harengula, Opisthonema, Sardinella,* and *Jenkinsia*; the anchovies (*Anchoa*); and silversides (*Atherinomorus* and *Allanetta*). Basslets (Grammidae), cardinalfish (Apogonidae), glassy sweepers (Pempheridae), and chromis (*Chromis* spp.) also typically occur in relatively large schools among reef crevices where they feed on plankton. In addition to these adult planktivores, dense schools of minute larval grunts (Haemulidae), snappers (Lutjanidae), and wrasses (Labridae) are often quite common hanging above coral heads or among branches of *Acropora* where plankton and coral mucus are the only available food.

Most of the carnivorous reef fish appear opportunistic, taking whatever is of the right size and is catchable within their habitat (Goldman and Talbot 1976). This conclusion is based primarily on the variety of food items observed within the same species at various locations. Only a few studies of reef fish species have evaluated food consumption in relation to what was actually available: Jones (1968); Vivien and Peyrot-Clausade (1974); and Hobson and Chess (1978).

Some carnivorous reef fish are highly specialized in their feeding habits. Among these are the parasite pickers or cleaners (*Labroides* spp.), juvenile bluehead wrasse, and neon gobies (*Gobiosoma* spp.), and several sponge feeders. Caribbean reef fish reported to feed on sponges include butterfly fish (Chaetodontidae), spadefish (Ephippidae), puffers (Tetraodontidae), and boxfishes (Ostraciidae) (Menzel 1959; Bakus 1964; Randall and Hartman 1968).

Few, if any, reef fish have been classified as detrital feeders and the utilization and turnover of detritus on coral reefs appear to be left primarily to invertebrates. Only a few blennies (none occurring in Florida) have been reported to be primary detritivores (Goldman and Talbot 1976). This number may increase as more food studies for the numerous smaller blennies and gobies become available. Also, much detrital material is ingested by those fish classified as herbivores, and determining actual material being foraged is often difficult (Randall 1967).

Many species utilize the reef only as a refuge. They use adjacent seagrass beds and sand flats as feeding grounds (Longley and Hildebrand 1941; Randall 1963; Starck and Davis 1966; Davis 1967; Ogden and Ehrlich 1977; Ogden and Zieman 1977). Randall (1963) reported that grunts and snappers were so abundant on patch reefs in the Florida Keys that it was obvious that the reefs could not provide food and possibly not even shelter for all of them. Both the abundance and diversity of haemulids and lutjanids have been reported to be reduced on reefs where adequate off-reef forage areas are unavailable (Starck and Davis 1966; Robins 1971; Alevizon and Brooks 1975; Gladfelter et al. 1980). Similarly, when reef shelter is lacking, what appears to be suitable grassbed forage areas may go unused (Starck and Davis 1966; Ogden and Zieman 1977).

In Tague Bay, St. Croix, Virgin Islands, 79.4% of the fishes actively feeding in the grassbeds at night were species that sought shelter on adjacent coral reefs during the day (Robblee and Zieman, in preparation). Starck and Davis (1966) listed species of the Holocentridae, Lutjanidae, and Haemulidae families as occurring diurnally on Alligator Reef and feeding nocturnally in adjacent seagrass beds. Typically both juvenile and adult haemulids and lutjanids form heterotypic resting schools over prominent coral heads (most commonly *Acropora palmata* and *Porites porites*) or in caves or crevices of the reef (Ehrlich and Ehrlich 1973; Ogden and Ehrlich 1977). At dusk these fishes move off the reef into adjacent seagrass beds and sand flats where they feed on available invertebrates (Randall 1967; Ogden and Ehrlich 1977; McFarland et al. 1979). At dawn they return to the reef.

Starck and Davis (1966) reported that 11 of 15 species of haemulids found in diurnal resting schools on Alligator Reef dispersed at night to feed. The lighter colored grunts (seven species) generally distributed themselves along sandy to thin-grass areas of the back reef zone. Snappers (Lutjanidae) followed a similar pattern with *L. griseus* and *L. synagris* in sparse grass to back reef habitat. At Tague Bay, St. Croix, the nocturnal distribution of grunts over the grass beds was quite similar to that reported in the Florida Keys. The French grunt was most abundant over thin grass or bare sand while white grunts were almost always observed by Robblee (in preparation), in thick grass. He also found the number of coral reef fishes feeding nocturnally over a particular area was positively correlated with a measure of habitat complexity, implying some form of organization of the fish assemblage while active over the feeding ground.

It has been hypothesized by Billings and Munro (1974) and Ogden and Zieman (1977) that migrating nocturnal feeders may contribute significantly to the energy budget of the coral reef through the import of organic matter in the form of feces. If so, their contribution to reef nutrient levels and maintenance of more sedentary fish abundance may also be important. Meyer et al. (1983) found what appeared to be higher nutrient levels and coral growth rates associated with diurnal resting schools of grunts. Verification of these links, however, requires further investigation.

Use of adjacent grass and sand flats by reef fish is not strictly a nocturnal phenomenon, but seems to be the dominant pattern. Only quite large herbivores, such as the rainbow parrotfish (*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 (Ogden and Zieman 1977). Randall (1965) reported parrotfishes (*Scarus* and *Sparisoma*) and surgeonfishes (*Acanthurus*) feeding on seagrasses (*Thalassia* and *Syringodium*) closely adjacent to patch reefs in the Virgin Islands during the day. He attributed the formation of halos around patch reefs in St. John, Virgin Islands, to this grazing.

6.3 MOVEMENT

Most reef fish seldom change their residence once they have settled onto a reef and some become quite sedentary (Thresher 1977). Many smaller species, such as gobies (Gobiidae), blennies (Blenniidae), and damselfish (Pomacentridae), maintain relatively small territories which they vigorously defend (Salmon et al. 1968; Rasa 1969; Low 1971; Myrberg 1972; Vine 1974). Tagging studies have shown that even those larger, wider ranging species, such as serranids, lutjanids, haemulids, chaetodontids, and acanthurids, remain, at least diurnally, in a fairly circumscribed place on a reef (Bardach 1958; Randall 1961b, 1962; Springer and McErlean 1962a). Randall (1962) recaptured some serranids and lutjanids at their initial place of capture up to 3 years after their release. Tagged *Haemulon plumieri* were repeatedly captured on the same reef by Springer and McErlean (1962a). When the *H. plumieri* were transplanted, they exhibited a tendency to home (Springer and McErlean 1962a). Ogden and Ehrlich (1977) reported on the sucessful homing of *H. plumieri* and *H. flavolineatum* to original patch reefs over distances as great as 2.7 km in the U.S. Virgin Islands.

Only a small amount of information is available on the usual extent of nocturnal movements of reef fishes that feed on adjacent grass beds. As indicated above, these fishes potentially can range quite far from their diurnal resting sites. *Lutjanus griseus* and *Haemulon flavolineatum* ranged as far as 1.6 km from Alligator Reef (Starck and Davis 1966), while *H. plumieri* and *H. flavolineatum* typically migrated distances greater than 100 m over the grass beds in Tague Bay, St. Croix (Ogden and Ehrlich 1977; Ogden and Zieman 1977). The migrating schools follow a linear path for 20-40 m from the reef, and then begin to break up into smaller and smaller groups in a dendritic pattern (Ogden and Zieman 1977). The distance traveled to feed is undoubtedly related to the abundance and quality of food available within the seagrass bed and can be expected to vary considerably among locations.

6.4 SOCIAL ORGANIZATION

Literature on the social behavior and organization of reef fish assemblages is extensive (see Ehrlich 1975; Goldman and Talbot 1976; Sale 1977, 1980a; Thresher 1977; and Emery 1978 for reviews). It has been conclusively shown that individuals or groups of individuals are not scattered randomly about the reef. Rather, their distribution reflects topographic and biologic features of the environment as well as behavioral adaptations to disperse (Thresher 1977). The interaction of ecologically evolved behavior and the availability of existing resources largely determine the social organization within a given reef fish community.

Most smaller reef species are either herbivorous or planktivorous and are territorial to varying degrees. The size of territory and the extent to which it is defended is a function of resource availability for many species (Low 1971; Thresher 1977; Sale 1980a). Thresher (1976) found that the size of area defended by the threespot damselfish (*Pomacentrus planifrons* = *Eupomancentrus planifrons*) on Florida reefs varied with the type of resource secured and further that the size of the area defended against a given intruder was determined by the threatened severity of the intrusion. The size of territory defended against other families, for example, correlated with the amount of benthic algae in the diet of each species. Thresher (1977) reported that the threespot damselfish in the northern portions of its range generally defended larger territories than those in the southern portion, where thicker algal lawns developed within their territories.

Differences in social structure have been observed within a single species at different locations. Itzkowitz (1978) and Williams (1978), working at different sites in Jamaica, reported different social organizations for *Pomacentrus planifrons*. Itzkowitz found males and females occurring together as neighboring territory holders in the same habitat, while Williams reported the use of different habitats by the sexes. In other regions, Robertson (1972) at Heron Reef (Great Barrier Reef) and Potts (1973) at Aldabra Atoll reported *Labroides dimidiatus* occurring as males with harems and as mated pairs, respectively. Barlow (1974) found a correlation between the social structure exhibited by *Acanthurus triostegus* and the presence or absence of various other territorial acanthurid species. The extent to which the nature and distribution of food resources can predict the form of space and resulting social organization used by territorial species was demonstrated by Thresher (1977) for five species of pomacentrids common on Florida reefs. Invariably, the organization predicted closely matched that observed in the field.

The large reef fish species require a greater food supply and, therefore, tend to range over a larger area of the reef. These species, although often having distinct ranges, are less territorial and frequently form foraging groups (Buckman and Ogden 1973; Ogden and Buckman 1973; Alevizon 1976; Itzkowitz 1977).

6.5 ECOLOGICAL ASPECTS OF REEF FISH DIVERSITY

Only two studies have attempted to fully define the diversity of fish species on selected Florida reefs: Longley and Hildebrand (1941) and Starck (1968). Longley and Hildebrand provided a systematic account of all fishes they captured or observed during 25 years of investigations at the Dry Tortugas, and Starck listed fishes collected and observed during 9 years of study at Alligator Reef. Longley and Hildebrand listed 442 species, 300 of which are closely associated with coral reefs. Starck listed 517 species, 389 of which he considered reef species. The remaining species were either offshore pelagic forms, demersal species from deeper water, or strays from adjacent inshore areas. Both lists are from single reef areas and, therefore, probably underrepresent the actual diversity of fish species on Florida's reefs.

Bohlke and Chaplin (1968) identified 496 fish species within the Bahamas and adjacent waters. About 450 of these species are known to occur on coral reefs and probably approximate Florida's total diversity.

Several less extensive surveys of fish on Florida reefs involved visual census, filming, or limited collecting techniques. One of the earliest surveys was done by Jordan and Thompson (1904), who identified 218 species inhabiting the reefs at the Dry Tortugas by using baited lines and various nets.

The high diversity of fish on Florida's tropical coral reefs is exemplified by a few studies which reported the number of species observed within a given limited area. Bohnsack (1979) recorded a mean number of species ranging from 10 to 23 on isolated natural coral heads less than 330 x 210 x 150 cm in size off Big Pine Key, Florida, and 13 to 20 species on small artificial reefs (160 x 60 x 80 cm) that he established. Alevizon and Brooks (1975) observed an average of 14.7 fish species during 2.75-min samplings during which scuba divers took color movies. During the sample period the diver panned the camera to include most or all fishes sighted within 4-5 m (Alevizon and Brooks 1975).

At present, there appears to be only six or seven species of reef fish that might be considered endemic to the U.S. continental reefs. Two of these, *Lythrypnus phorellus* and *Gobiosoma oceanops*, are small gobies; the latter (neon goby) is common. The purple reef fish (*Chromis scotti*) is also known to occur only within U.S. waters, although the genus is well represented by at least three other species throughout the West Indies. *Ophidion selenops*, the mooneye cusk eel, is a species reported by Starck (1968) to occur occasionally within the area of Alligator Reef (near Matecumbe Key), but has not been reported elsewhere. Cusk eels are curious elongate fishes, highly nocturnal and burrowing into mud during the day. At least five species of cusk eels, representing two genera, are known to occur along the southeastern United States, but the taxonomy of this group is not entirely clear. Two small tropical serranids have also been considered endemic to the continental United States. One of these, the blue hamlet (*Hypoplectrus gemma*), may only be one of many color morphs of a single species, *H. unicolor*, which is common throughout the Caribbean (Thresher 1978; Graves and Rosenblatt 1980). The other serranid is the wrasse bass (*Liopropoma eukrines*), which ranges northward along the continental shelf, but is not known to occur elsewhere in the Caribbean. The remaining possible endemic species is the cubbyu (*Equetus umbrosus*), but its distinction from *E. acuminatus*, found elsewhere in the Caribbean, is questionable (Robins et al. 1980).

The reason for high diversity of fish species on coral reefs is frequently debated and may be related to a number of factors (Sanders 1968; Goldman and Talbot 1976; Smith 1978; Talbot et al. 1978). All biological communities tend to diversify through colonization over time, and coral reefs exist in an environment generally without major perturbations or great temperature change. Most coral reefs have had long and relatively stable periods to develop. Within this overall long-range stability of the tropics, intermittent moderate disturbances from weather events occur. Although we are just beginning to understand the effects of disturbance events (Endean 1976; Bradbury and Young 1981; Pearson 1981; Woodley et al. 1981; Davis 1982; Porter et al. 1982; Roberts et al. 1982), they may help to maintain a higher diversity by preventing a resource-limited equilibrium and the competitive exclusion of some species (Connell 1978).

Coral reefs generally include a variety of microhabitats related to zones of coral growth, wave exposure, and reef structure (Wells 1957a; Maxwell 1968; Stoddart 1969). This diversity of habitat types allows for an increased diversity of fish species. Although habitat relationships have not been extensively studied on Florida reefs, few reef fish have been found to be cosmopolitan over all available habitats. At One Tree Island Reef, Australia, 49% of all species collected were restricted to one or another of five major habitats (Goldman and Talbot 1976). Similar faunal differences among habitats have been reported by Gosline (1965) for the Hawaiian Islands; Chave and Eckert (1974), Fanning Island, South Pacific; Jones and Chase (1975), Guam; Harmelin-Vivien (1977), Tulear Reef, Madagascar; and Williams (1982), the Great Barrier Reef.

The coexistence of a high number of fish species on coral reefs also implies either that these species are highly specialized (occupy finely partitioned niches) or that there is considerable overlap in resource utilization. Predators are generally food limited and tend to have more clearly separated niches (Hairston et al. 1960; Paine 1966). Reef herbivores such as parrotfishes, damselfishes, gobies, and angelfishes are generally believed to use many of the same food resources (Randall 1967; Smith and Tyler 1972; Hobson 1974). Both specialization and resource-sharing appear to occur among various reef fish groups and at various life stages within some species.

Recruitment of juvenile fish to coral reefs may also influence species diversity, although this is hotly contested (Sale 1976, 1980a; Sale and Dybdahl 1978; Smith 1978; Talbot et al. 1978; Brock et al. 1979; Ogden and Ebersole 1981; Sale and Williams 1982). The controversy centers around whether reef communities have an ordered structure with predictable species recruitment to vacant niches or an unpredictable chance species recruitment. An unpredictable larval recruitment would increase local variation in the species present and might well contribute to a higher overall diversity (Goldman and Talbot 1976). Recently some investigators have suggested that differences in recruitment and community structure may be a result of the size of the reef area considered (Ogden and Ebersole 1981) or of the time interval between which samples have been taken (Bohnsack, in preparation).

6.6 COMMUNITY DESCRIPTIONS

Although fish diversity is usually high on coral reefs, fewer number of species will appear abundant or highly obvious to the average reef diver at any one location. Reef fish, like most organisms, have depth and habitat preferences where they can typically be seen. Many are active only nocturnally or diurnally, and some species, such as yellowtail snapper and gag grouper (*Mycteroperca microlepis*), are abundant only seasonally.

A comparison of three Florida reef studies, all of which used the same 50-min visual census technique, shows significant differences in reef fish communities at each study location (Thompson and Schmidt 1977; Jones and Thompson 1978; Tilmant et al. 1979). Although the top six families comprising the fish community in terms of abundance were the same, their relative ranking and individual species members varied (Table 29). Damselfish (Pomacentridae) were the most common family at Tortugas while ranking third at John Pennekamp Coral Reef State Park (JPCRSP) and second at Biscayne National Park (BNP). Parrotfish (Scaridae) were the most common community member at BNP but were second at JPCRSP and the Dry Tortugas. Grunts (Haemulidae) were particularly abundant at JPCRSP (most common family) but were third at BNP and the Tortugas. Of the 165 species observed between JPCRSP and the Dry Tortugas, 115 were shared in common. Thirty-one species were seen only in JPCRSP and 19 were observed only in the Tortugas study areas (Jones and Thompson 1978). Overall, fish communities at John Pennekamp Coral Reef State Park were found to be more diverse and abundant than at the Dry Tortugas.

Seven of the top 10 reef fish species at Biscayne National Park were also within the 10 most common species in John Pennekamp Coral Reef State Park. However, only 10 of BNP's top 20 species were represented in the 20 most common species at JPCRSP.

Three major types of coral reefs are recognized along the Florida reef tracts: patch reefs, hardground live bottom, and bank reefs. Each general reef type supports a characteristic fish fauna (Table 30). General

Table 29

Comparison of the most abundant reef fish families among three Florida coral reef areas as indicated by Jones and Thompson (1978) visual census methods.

Ranking	Pennekamp 1975[a]	Tortugas 1975[a]	Tortugas 1976[b]	Biscayne National Park 1979[c]
1	Haemulidae	Pomacentridae	Pomacentridae	Scaridae
2	Scaridae	Serranidae	Scaridae	Pomacentridae
3	Pomacentridae	Haemulidae	Haemulidae	Haemulidae
4	Labridae	Scaridae	Labridae	Labridae
5	Serranidae	Chaetodontidae	Serranidae	Chaetodontidae
6	Chaetodontidae	Labridae	Chaetodontidae	Serranidae

[a] Jones and Thompson 1978.
[b] Thompson and Schmidt 1977.
[c] Tilmant et al 1979.

Table 30

Coral reef fish most commonly observed by divers on reefs.
The list is based on summary ratings of the average length of time a diver must spend before observing the species.
Species averaging less than 30 minutes to observe are listed
(Thompson and Schmidt 1977; Jones and Thompson 1978; Tilmant et al. in press).

	Reef types and zones				
	Patch		Livebottom	Bank	
Species	Top	Outer Fringe		Shallow	Deep
Ocean surgeon *Acanthurus bahianus*	*	*	*	*	*
Doctorfish *Achirurgus*	*	*	*	*	*
Blue tang *A. coeruleus*	*	*	*	*	*
Barred cardinalfish *Apogon binotatus*		*			
Flamefish *A. maculatus*		*	*		
Belted cardinalfish *A. townsendi*		*			
Trumpetfish *Aulostomus maculatus*	*	*			

(continued)

Table 30 (continued)

Species	Reef types and zones				
	Patch		Livebottom	Bank	
	Top	Outer Fringe		Shallow	Deep
Orangespotted filefish *Cantherhines pullus*	*	*			
Scrawled filefish *Aluterus scriptus*					*
Slender filefish *Monacanthus tuckeri*	*				
Bar jack *Caranx ruber*	*	*		*	*
Queen angelfish *Holacanthus ciliaris*	*	*	*		*
Gray angelfish *Pomacanthus arcuatus*	*	*	*		*
French angelfish *P. paru*			*		*
Rock beauty *Holacanthus tricolor*					*
Reef butterfly *Chaetodon sedentarius*			*		*
Foureye butterfly *C. capistratus*					*
Spotfin butterfly *C. ocellatus*					*
Saddled blenny *Malacoctenus triangulatus*			*		
Roughhead blenny *Acanthemblemaria aspera*	*	*			
Wrasse blenny *Hemiemblemaria simulus*	*	*			
Redlip blenny *Ophioblennius atlanticus*					
Neon goby *Gobiosoma oceanops*	*	*	*		*
Bridled goby *Coryphopterus glaucofraenum*		*	*		*
Masked goby *C. personatus*		*			*
Goldspot goby *Gnatholepis thompsoni*		*	*		*
Hovering goby *Ioglossus helenae*		*			*
Herrings *Clupeidae*		*			
Bermuda chub *Kyphosus sectatrix*	*	*			
Spanish hofish *Bodianus rufus*	*	*	*		*
Slippery dick *Halichoeres bivittatus*	*	*	*	*	*
Yellowhead wrasse *H. garnoti*		*	*		*
Creole wrasse *Clepticus parrai*					*

(continued)

Table 30 (continued)

Species	Reef types and zones				
	Patch		Livebottom	Bank	
	Top	Outer Fringe		Shallow	Deep
Hogfish *Lachnolaimus maximus*		*			*
Clown wrasse *H. maculipinna*	*	*	*	*	*
Blackear wrasse *H. poeyi*			*		
Puddingwife *H. radiatus*	*	*	*		*
Bluehead wrasse *Thalassoma bifasciatum*	*	*	*	*	*
Schoolmaster snapper *Lutjanus apodus*	*	*			*
Mutton snapper *L. anelis*		*			
Gray snapper *L. griseus*	*	*			*
Mahogany snapper *L. mahogoni*					*
Yellowtail snapper *Ocyurus chrysurus*	*	*	*	*	*
Yellow goatfish *Mulloidichthys martinicus*					*
Spotted goatfish *Pseudupeneus maculatus*		*	*		*
Glassy sweeper *Pempheris schomburoki*	*	*	*		*
Sergeant major *Abudefduf saxatilis*	*	*	*		*
Blue chromis *Chromis cyaneus*					*
Brown chromis *C. multilineatus*					*
Yellowtail damselfish *Microspathodon chrysurus*	*	*			*
Dusky damselfish *Pomacentrus fuscus*	*	*	*	*	
Beaugregory *P. leucostictus*		*	*		
Bicolor damselfish *P. partitus*	*	*	*	*	*
Threespot damselfish *P. planifrons*	*	*	*		*
Cocoa damselfish *P. variabilis*	*	*	*	*	*
Black margate *Anisotremus surinamensis*			*		*
Porkfish *A. virginicus*	*	*	*		*
Tomtate *Haemulon aurolineatum*	*	*	*	*	*
Caesar grunt *H. carbonarium*	*	*			*

(continued)

Table 30 (continued)

Species	Reef types and zones				
	Patch		Livebottom	Bank	
	Top	Outer Fringe		Shallow	Deep
Smallmouth grunt *H. chrysargyreum*	*				*
French grunt *H. flavolineatum*	*	*	*	*	*
Spanish grunt *H. macrostomum*	*	*	*		*
White grunt *H. plumieri*	*	*	*	*	*
Bluestriped grunt *H. sciurus*	*	*	*	*	*
Bluelip parrotfish *Cryptotomus roseus*			*		
Midnight parrotfish *Scarus coelestinus*	*	*	*	*	*
Princess parrotfish *S. taeniopterus*					*
Blue parrotfish *S. coeruleus*		*			*
Striped parrotfish *S. croicensis*	*	*	*	*	*
Rainbow parrotfish *S. guacamaia*	*				
Queen parrotfish *S. vetula*	*				*
Redband parrotfish *Sparisoma aurofrenatum*	*	*	*	*	*
Redtail parrotfish *S. chrysopterum*	*	*	*		
Redfin parrotfish *S. rubripinne*	*	*			*
Bucktooth parrotfish *S. radians*		*	*		
Stoplight parrotfish *S. viride*	*	*	*	*	*
Jackknife-fish *Equetus lanceolatus*				*	
Cubbyu *E. umbrosus*		*		*	
Reef croaker *Odontoscion dentex*		*			*
Blue hamlet *Hypoplectrus gemma*			*		*
Barred hamlet *H. puella*		*	*		
Butter hamlet *H. unicolor*		*	*		*
Graysby *Epinephelus cruentatus*		*			*
Red grouper *E. morio*		*			
Nassau grouper *E. atriatus*		*			

(continued)

Table 30 (continued)

Species	Reef types and zones				
	Patch		Livebottom	Bank	
	Top	Outer Fringe		Shallow	Deep
Black grouper *Mycteroperca bonaci*		*			*
Harlequin bass *Serranus tigrinus*		*	*		*
Lantern bass *S. baldwini*			*		
Saucereye porgy *Calamus calamus*		*			
Jolthead porgy *C. bajonado*		*			
Great barracuda *Sphyraena barracuda*		*		*	
Sharpnose puffer *Canthigaster rostrata*		*			*

descriptions of some of the most common fish species follow.

Patch Reefs

On most patch reefs, fish occur in two distinct zones: top and outer. Species commonly seen over the coral rubble substrate of the reef top are bluehead and clown wrasses, the puddingwife, the slippery dick, and bicolor damselfish. The dusky and threespot damselfish staunchly defend small territories of algae-covered rocks. The cocoa damselfish is also abundant at some localities. Resting on coral rubble close to a crevice into which they can dart for cover are redlip blennies, the only species of combtooth blenny (Blenniidae) commonly found on Florida's coral reefs. Also near protective crevices are hamlets (*Hypoplectrus* spp.) of various colors. Scorpion fish (Scorpaenidae) can also be found frequently blending with coral rubble over the top of the patch reefs.

Wider ranging species typically seen moving among the corals within the top zone are the surgeonfish (*Acanthurus* spp.); gray, French, and queen angelfish, white grunts, and striped, stoplight, and redband parrotfish. Frequently blue tang, ocean surgeons, and parrotfish (particularly the midnight parrot) will form large mixed or monospecific schools while ranging about the reef top. Common fish species typically found near coral heads, branching corals, or other outcrops on the top of patch reefs are the bluehead wrasse, sergeant major, tomtate, Caesar grunt, and Spanish grunt. The vertical standing trumpetfish and the slender filefish can usually be seen among the branches of the octocorals.

Around the outer edges of the patch reefs, the water depth is greater (8-10 m), and larger coral heads provide a varied and cavernous habitat. Along this outer zone larger predators such as grouper, particularly black grouper, red grouper, and Nassau grouper, mutton and gray snapper, and hogfish can be found. Close inspection of crevices and holes will commonly reveal sharpnose puffers, squirrelfish (*Holocentrus* spp.), small cardinal and flamefish (*Apogon* spp.), soapfish (*Rypticus* spp.), glassy sweepers, and, possibly, the green moray (*Gymnothorax funebris*). Clinging to coral heads are small neon and masked gobies. The neon goby is noted for its function as a parasite and mucus picker, or "cleaner," on large fish species. Gobies frequently establish "cleaning stations" into which larger fish will move, become quiescent, spread their opercula, and allow the cleaner fish to work freely through the gills and about the head. Juvenile angelfish and the juvenile Spanish hogfish have also been observed functioning as cleaners of larger fish on the reef (Thresher 1980).

Close to the bottom, among the corals along the outer edge of the patch reefs, the puddingwife and yellowhead wrasses become more abundant. Feeding more in the open along the reef edge are typically saucereye and jolthead porgies, spotted and yellow goatfish, redtail parrotfish, and angelfish. Close inspection along grassy areas will frequently reveal the small bucktooth parrotfish, blackear wrasse, and lizardfish (*Synodus* spp.). At the base of the corals on sandy substrate, nearly transparent bridled and goldspot gobies can be seen, as well as the harlequin bass. In open sandy areas immediately adjacent to the patch reef (but not on it), hovering gobies and yellowhead jawfish (*Opistognathus aurifrons*) can usually be seen protruding from their burrows.

The water column over the patch reefs usually does not support a large number of fish, but barracuda, bar jack (*Caranx ruber*), yellow jack (*C. bartholomaei*), and Mojarras (Gerreidae) are among the most commonly observed species. Ballyhoo (*Hemiramphus brasiliensis*) can often be seen moving about just under the surface. In the quieter waters of the back reef, schools of small herring (*Harengula* spp.) are common.

Live Bottom

Live bottom communities are formed on broad areas of limestone outcrops occurring in relatively shallow water (2 m or less) within the protected reef zone. Coral growth may vary greatly in density over the area and often is mixed with seagrasses. The habitat generally has little relief or structure and is composed largely of octocorals, sponges, and small scleractinian corals. Only occasionally are large colonies of stony corals found and these often form an independent cluster.

Fish fauna of the live bottom is generally similar to that found on the top zone of patch reefs. A few notable differences include an increased tendency for tangs and surgeonfish to form large wide-ranging schools, an increased abundance of the large rainbow parrotfish, and frequently larger schools of white, Spanish, and Caesar grunts. An interesting species increase over live bottoms is that of the lantern bass. This small bottom-dwelling bass appears to prefer the broad rocky flats around turtlegrass beds and, occasionally, replaces the similar harlequin bass found more frequently on patch reefs.

Bank Reefs

Bank reefs (Figure 18) form elongated discontinuous structures along the seaward edge of the reef tract. They rise to within a meter or less of the surface and have extensive reef flats supporting only sparse encrusting corals over their shallow zones. Seaward, they slope rapidly to depths exceeding 20 m.

Redlip and saddled blennies, small gobies, and other small bottom-dwelling species dominate the reef flat. Within the shallow spur and groove zone branched and fan octocorals become much more prevalent. Among dense branches of staghorn or elkhorn coral (*Acropora* spp.) are dusky and threespot damselfish, many species of grunts (*Haemulon* spp.), black margates, gray and schoolmaster snapper, sergeant majors, and Bermuda chub. Within the water column over the reef, bar jack, barracuda, and yellowtail snapper are easily seen.

The fish fauna of the deep spur and groove zone can be highly varied depending on depth and the amount of reef structure. Below the *Acropora* coral zone (deep spur and groove zone), however, the following become more prevalent: yellowtail damselfish, the rock beauty, butterfly fish, small groupers (i.e., hamlets, hinds, and graysby), yellowtail and redtail parrotfish, large puddingwives, and large scrawled filefish. With increasing depth, there is a distinct increase in *Chromis* (*Chromis cyaneus* and *C. multilineatus*), the longsnout butterfly fish (*C. aculeatus*), triggerfish (*Balistes* spp. and *Canthidermis sufflamen*), filefish (*Aluterus* spp.), jackknife-fish, schools of creole wrasse, and the blue parrotfish. Along the outer base (mixed hardgrounds) of the bank reefs (usually at depths of 20-30 m), large mutton snapper, grouper, and porgies (Sparidae) become more abundant. The tobaccofish (*Serranus tabacarus*) and sand tilefish (*Malacanthus plumieri*) can easily be found resting openly on the flat calcareous silt bottom in the mixed hardground and sediment zone.

In the deep reef zone the bigeye (*Priacanthus arenatus*) tends to replace the glasseye snapper (*P. cruentatus*) commonly found on the shallower reefs. Similarly, the cubbyu is replaced by the jackknife-fish, and hinds and graysby (*Epinephelus adscensionis, E. guttatus*, and *E. cruentatus*) are replaced by the coney (*E. fulvus*). The snowy grouper (*E. niveatus*) becomes prevalent at depths greater than 30 m. Over these deep reefs, the number of species of jacks (Carangidae) and mackerels (Scombridae) greatly increases. Also commonly seen are the large bar jack (*C. ruber*), rainbow runner (*Elagatis bipinnulata*), amber jack (*Seriola dumerili*), black jack (*Caranx lugubris*), bonita (*Sarda sarda*), and cero mackerel (*Scomberomorus regalis*). Cloud-forming schools of small herrings (*Jenkinsia* and *Sardinella*) are seen over the reefs at depths greater than 20 m during the day. At depths greater than 30 m, a third species of *Serranus*, similar in appearance to the tobaccofish, becomes common. The chalk bass (*S. tortugarum*) is found around small rubble mounds, coral outcrops, and rocks near the base of the reef. At this depth, a short search over the sand plain next to or between reefs will usually reveal a colony of garden eels (*Nystactichtys halis*). They have long, slender bodies and are found in large colonies where, each protruding vertically from its burrow, they form "gardens" of waving heads while feeding on plankton carried by the current.

The number of species described above in no way approximates the total number found within the coral reef habitats of Florida.

6.7 REEF FISH MANAGEMENT

Fish resources on the coral reefs of Florida and elsewhere are highly prized economically and are extensively utilized. Reef-fishing activities commonly include commercial hook-and-line harvest, commercial trapping, sport angling, spearfishing, tropical fish collecting, and scientific collecting. The importance of reef fish resources and their economic potential have been described in a number of summary reports (Camber 1955; Strusaker 1969; Swingle et al. 1970; Stevenson and Marshall 1974; Bullis and Jones 1976; Klima 1976). In addition to descriptive reports of fishing activities, a number of exploratory studies and fishing development projects have been completed for reef fish resources (Brownwell and Rainey 1971; Munro et al. 1971; Kawaguchi 1974; Wolf and Rathjen 1974; Stevenson 1978). Little information, however, is available concerning the impact of commercial or recreational use on reef fish populations or on reef fish management. Fairly substantial sections of Florida's coral reefs are now designated as local, State, or National preserves and are being managed for the protection and conservation of their resources.

The impetus to preserve coral reef resources stems largely from their recognized economic value through tourist attraction and recreational opportunities. But the negative impact of recreational use (i.e., snorkeling, diving, boating, and fishing) on coral reefs has not been extensively investigated. Interestingly, although the taking of tropical fish for aquarium purposes is prohibited in all coral reef preserves, spearfishing is permitted in at least one and hook-and-line fishing is permitted in all. Impacts to fish population through disturbance by boating and diving alone could become significant. On extremely popular reefs, such as Molasses Reef in the Key Largo National Marine Sanctuary, as many as 20-30 boats with divers are often anchored at one time within a 4-5 ha area (NOAA-OCZM 1979). Specific studies at locations with such an extremely high level of use are not available. However, within Biscayne National Park, a 5-year study of eight selected patch reefs revealed little disturbance to fish populations where maximum annual use per reef ranged from 3,400-3,600 persons diving or snorkeling (Tilmant et al., in preparation).

Past research on exploitation of reef fish stocks can best be described as gaining basic information on life histories, food habits, growth rates, and basic biology of important species, and on developing harvest techniques. Only recently have studies evaluating the ecological impacts of fishing activities begun to be reported (Campbell 1977; Davis 1977b; Tilmant 1981; Katnik, in press; Pauly and Ingles, in press; Bohnsack 1982).

The few studies available show that a limited number of reef fish are actually sought and comprise most of the sport and commercial harvest. Austin et al. (1977), after interviewing 4,275 recreational fishermen, reported that only four species groups (grunts, snappers, dolphin, and grouper) constituted almost the entire catch. Within the groups, gray snapper and yellowtail snapper accounted for 85% of the harvested snapper; white and bluestriped grunt, 97% of the grunts; and red and black grouper, 82% of the grouper. Thus, only six species made up about 80% of the total recreational catch. The National Park Service has recorded over 120 species of reef fish caught within Biscayne National Park (Dade County, Florida); however, 10 species accounted for more than 80% of the harvest.

The commercial harvest of fish from coral reef areas is almost entirely directed toward snappers (Lutjanidae) and groupers (Serranidae), although some tilefish (Branchiostegidae), jacks (Carangidae), and triggerfish (Balistidae) are harvested. A complete listing of commercially important reef species can be found in the U.S. Fishery Management Council's management plans for these fish in the Gulf of Mexico (Florida Sea Grant College 1979) and South Atlantic (South Atlantic Fishery Management Council 1982).

Within Biscayne National Park, a limited assessment of fishing impacts on reef fish populations was conducted by underwater visual surveys concurrently with fishermen's creel census (Tilmant 1981). During a 3-year period, fish catch rates varied inversely with the number of fishermen using park waters while reef fish populations remained relatively stable. Katnik (1981) found that of the reef flats surrounding the Pacific island of Guam, those with the highest fishing pressures showed a marked reduction in the large size classes of the most prized species. Also, some fishes of less economic importance were more abundant on heavily fished reefs than on reefs lightly fished (Katnik 1981). Bohnsack (1982) reported that he found significantly smaller piscivorous predator populations on Looe Key Reef (near Big Pine Key, Monroe County, Florida) than on either of the two similar reefs within the Key Largo National Marine Sanctuary. He attributed these differences to spearfishing on Looe Key and believed that the abundance of some remaining species on Looe Key Reef was affected by the larger predator loss.

In 1977 the United States passed the Fishery Conservation and Management Act, which extended jurisdiction over fisheries to 200 mi and called for establishing regional fishery management councils to develop specific long-range management plans for each coastal fishery resource within the Fishery Conservation Zone. In response to this legislation, the coral reef fishery resources within U.S. territorial waters are receiving much greater attention, and management plans for their conservation are being developed. The status of biological knowledge and application of fishery management principles to coral reef fish stocks was reviewed at a workshop on reef fishery management sponsored by the National Marine Fishery Service in October 1980 (Huntsman et al. 1982). The workshop proceedings succinctly summarized the requirements for such management. It is widely recognized that before coral reef ecosystems can be effectively managed, much basic data and many larger-scale multidisciplinary studies are required.

CHAPTER 7

CORAL REEF ECOLOGY

7.1 INTRODUCTION

Wells (1957a) succinctly defined the nature of the coral reef as a "deterministic phenomenon of sedentary organisms with high metabolism living in warm marine waters within the zone of strong illumination. They are constructional physiographic features of tropical seas consisting fundamentally of a rigid calcareous framework made up mainly of interlocked and encrusted skeletons of reef-building (hermatypic) corals and calcareous algae. The framework controls the accumulation of sediments on, in, and around itself. These sediments are derived from organic and physical degradation of the frame and organisms associated with the reef constructors and have bulk ten or more times as great as the frame itself. The coral reef biotope is a facies of the marine tropical biochore, and its essential fauna and flora consists of corals and calcareous algae, which dominate in numbers and volume and provide the ecological niches essential to the existence of all other reef-dwelling animals and plants. In addition, there is an associated fauna and flora of other sedentary organisms which may be represented by relatively few species, and there is also the epifauna and epiflora of associated commensals, symbionts, and parasites living on and within the essential and associated organisms, and finally, the mobile fauna of benthic and nektonic species. Both physically and organically, reefs are complicated structures and are the result of a near balance of constructive and destructive forces. The constructional forces are largely organic, the accumulation of the calcareous skeletons of corals, calcareous algae, foraminifera, mollusks, etc., roughly in that order of importance. . . . Destructive and degradational forces tending to break down the stout framework of reefs are exemplified in the ceaseless breakdown of coral, algal, and molluscan skeletons and reef rock by the normal life activities of a wide variety of perforating, boring, and dissolving algae, sponges, mollusks, worms, and echinoids . . . . A more obvious, but no more important, destructive agency is wave action . . . [including] wind-driven waves, which during hurricanes strike prodigious hammer blows on reefs."

That which Wells (1957a) reported is still valid. Detailed investigations into various ecological functions have increased our understanding and appreciation of the coral reefs in general. Today, Florida's coral reefs are probably one of the most visited reef systems in the world, yet the life history of many species is still poorly understood. The recent increase in coastal development and sport diving has generated concern about the vitality of the coral reefs. Since very little early baseline ecological information is available for comparison, qualitative subjective statements are often offered in support that the reefs are deteriorating. The most significant impacts on the Florida coral reefs are, however, caused by natural events over which man has no control.

7.2 PHYSICAL-CHEMICAL ENVIRONMENT

The substratum for establishment of a coral reef must be rock or consolidated materials. Shinn et al. (1977) reported that the reefs they cored in Florida were established on a basement of Pleistocene reef facies, fossil mangrove, and lithified cross-beaded quartz (old sand dunes). The initial settlement of pioneering species is followed by successional stages during which the genesis for creation of the reef is established. Sheppard (1982) discussed the evolution of reefs based on data from the Red Sea and Hawaii and noted that about a 50-year period was required for a coral reef community to attain the fourth (final stage) or binding-of-sediment phase. Florida reefs are in various phases of development; some have reached considerable development while others are either juvenile or have suffered impacts denying them full development.

Most coral reefs off southeast Florida are found in depths of <43 m. Beyond these depths the substratum and physical environments are unfavorable to the existence of hermatypic reef-building Scleractinia. It should be noted that where the physical environment is favorable in other areas of the Caribbean (Bahamas, Belize, Jamaica), a set of deep reef Scleractinia are found colonizing the escarpment faces. These communities are found as deep as 70-80 m. Off southeast Florida this type of environment is, for the most part, nonexistent. A deep reef was recently found in 60- to 90-m depths west of the Dry Tortugas. Few details are available at this time. Sclerosponges are also a conspicuous element of deep reef communities; these are not reported from Florida reefs. Dustan et al. (1976) discussed the factors limiting sclerosponges from Florida.

Light is probably one of the most significant environmental considerations controlling coral reef development in general. Light is necessary for the symbiotic relationship between the coral and zooxanthellae. Any factor which reduces the amount of solar radiation impinging on the coral surface will affect growth and nutrition. Reef corals are almost universally phototropic. Wells (1957a) reported that species richness at Bikini Atoll was closely controlled by solar illumination and indirectly influenced by temperature and oxygen. General solar radiation characteristics in Florida were discussed in Chapter 2. The nature of light is significant. Jokiel and York (1982) reported that specialized pigments in coral tissues filter the potentially dangerous ultraviolet portions of the spectrum, thus allowing the corals to occupy the shallow waters without being harmed. The zooxanthellae are able to compensate for changes in radiation quality and quantity through changes in their pigments. Wethey and Porter (1967) reported that reef corals were able to compensate to a depth of 25 m without loss of autotrophic efficiency. Kanwisher and Wainwright (1967) reported on respiration and productivity in Florida reef corals from a study at Hens and

Chickens Reef. Wells et al. (1973) reported that some corals were best classified as producers based on P/R (productivity/respiration) ratios being greater than one.

Temperature is related to solar radiation impinging on the water column and the influence of the Gulf Stream or Florida Current. While reef corals have been described as stenothermic (Wells 1957b), many species are very tolerant of temperature variation (Mayer 1914, 1916, 1918). Reef corals flourish (optimum physiological conditions) best between 25° and 29° C. Coral reef development is reported to be limited by low temperatures. This was proposed by Vaughan (1919) for Florida. He reported that corals did not build reefs where temperatures fell below the 18° C minimum for prolonged periods. The growth and demise of staghorn reefs at the Dry Tortugas are related to temperature control. During favorable periods these populations proliferate, but occasionally a cold winter reduces temperature below tolerance levels and mass mortality occurs (Porter et al. 1982). Within a decade, if mild conditions prevail, the populations recover. Temperature data in Figures 6-11 compared recent data with that from the early part of this century. The data imply no major change in climate.

It is apparent that temperature is one of the major controls of reef development off southeast Florida (Roberts et al. 1982). Another source of coldwater stress is from occasional upwelling from sources beneath the Florida Current. These stratified layers occasionally cause localized fish kills. Heat-related stresses in summer usually occur during midday when spring low tides coincide with calm wind conditions (Plate 24b). The shallow reef flats suffer from thermal stresses manifested in zooxanthellae expulsion. Ultraviolet light may also be involved with this phenomenon. As water depth is reduced, the UV light may have sufficient strength to be toxic and physically burn the tissues (Jokiel and York 1982).

Salinity is controlled by precipitation, evaporation, and runoff after major rainfall over adjacent land areas. Salinities are usually in the oceanic range. Table 9 reported ranges from 33.1 to 38.6 ppt. Jones (1963) reported some diurnal changes in a time series from Margot Fish Shoal off Elliott Key. Salinity does not normally pose a threat to the reefs. After hurricane rains, however, there is a potential for dilution due to runoff. The only reported possible salinity-related phenomenon was the 1878 Tortugas "blackwater," which was reported to have killed significant populations of corals. Mayer (1902) reported that a great number of the *Acropora* reefs were devastated by this event. It is suggested that this was a glut of freshwater runoff from the Everglades or a toxic phytoplankton bloom. There is no documented evidence to sustain either hypothesis. In other parts of the Caribbean, particularly the Greater Antilles and other high islands (e.g., Roatan) with mountain ranges, freshwater runoff is a significant threat to nearshore coral reefs. Goreau (1964) reported that freshwater runoff killed corals in Jamaica following a hurricane. Wells (1956, 1957a) reported that reef corals tolerated 27-40 ppt, and that optimal limits were 34-36 ppt.

Tidal conditions off the southeast coast of Florida were presented in Table 8. All ranges are less than 1 m. Tidal conditions only pose a threat to the shallower portions of the reef flat and spur and groove zones. Reef emergence rarely occurs except under synergistic meteorological influences. When spring low tides occur at or near midday during the summer, thermal heating can occur (Plate 24b).

Dissolved oxygen is dependent upon photosynthesis and respiration of benthic organisms. Temperature and salinity control the saturation level of oxygen in the water. Studies by Vaughan (1914d), Mayer (1918), Yonge and Nicholls (1931), Smith et al. (1950), and Jones (1963) reported that oxygen is not truly a limiting factor for corals under most circumstances. Oxygen remains in supersaturation during most of the day. Jones (1963) reported that the diurnal range was from 90% to 125% saturation during the summer.

Water column pH is influenced by organic metabolism. Studies by Jones (1963) and Jaap and Wheaton (1975) reported pH values of near 9. It is not a limiting factor under most circumstances.

7.3 COMMUNITY STRUCTURE

Coral reefs off southeast Florida have developed over the past 5,000-7,000 years. It is presumed that "survival stocks" living in what is now deeper water during the Wisconsin ice age were the seed populations for replenishment of the reefs as the sea level rose during the Holocene transgression. Some evidence for this is found in terraces seaward of some of the major reefs (Middle Sambo and Sand Key Reefs). These were probably active constructional reefs during a lower sea level stand which were drowned as sea level rose rapidly. The fossil barrier reef off Broward and Palm Beach Counties also provides credibility to this theory (Lighty 1977). Since the origin of the recent reefs, organisms have had sufficient time to develop into complex communities. They display all levels of complexity in their structure, diversity, interactions, competition, and trophic relationships.

In terms of abundance, dominance, and diversity, various elements display certain characteristic patterns. The sessile benthos is the most stable and best suited for time series studies. The mobile benthos, plankton, and nekton exhibit properties that make it difficult to make time series comparisons. The significance is that although some organisms are essential to the reef, others may be important, but have not been studied or have such radical seasonal variability that they are not a good indicator of reef vitality. Most of the primary framework coral species have a relatively long lifespan and, once established, are successful in competing for resources. These are keystone species in that they build the reef and create many niches for other biota. Table 29 details abundance measurements conducted at Elkhorn Reef. Additional information on the abundance and densities of stony corals at a number of coral reefs from the reef tract appears in Tables 11, 13-15, 17, and 19. In the patch reef it is apparent that *Montastraea annularis* is a dominant keystone species. *Siderastrea siderea, Diploria* spp., and *Colpophyllia natans* are also important. On the bank reefs, dominance and importance varies among reef zones with great variability between reefs. On reef flats *Porites astreoides* and *Diploria clivosa* are dominant; *Porites porites* and *Acropora cervicornis* are also important. Temporal stability in this zone is poor; hence, the existence of the arborescent species is often transitory. The shallow spur and groove zones are dominated by *Millepora complanata* and the zoanthid *Palythoa* sp. These species thrive in the turbulent conditions around this zone. In deeper spur and groove areas *Acropora palmata* is found to be the dominant and keystone species. Occasionally on some reefs the *A. palmata* zone extends onto the reef flat. This is especially true where the reef flat is deeper than 1-2 m.

On the flanks of the spurs a set of species that favor vertical orientation is conspicuous. This includes several species of *Mycetophyllia* and *Agaricia agaricites*. In the buttress-forereef zone the seaward portion of the spur and groove formation often continues as low relief features into deeper water. *Montastraea annularis* is of prime importance. Other important species include *Acropora cervicornis, Diploria* spp., *Colpophyllia natans, Agaricia agaricites*, and *Meandrina meandrites*. The diversity in this zone is often high. The physical extremes are moderated by depth, and biological interaction is much more significant in affecting community structure.

In the general sense the structure of the entire community can be envisioned, but in fact there is no field study that has quantitatively defined all the biota from a coral reef community. The autotrophic elements are represented by calcareous, crustose coralline, fleshy algae, and the other benthic organisms that contain producer organisms (zooxanthellae) within their tissues: corals, anemones, zoanthids, and sponges. The producers are also represented by a blue-green endolithic algae within the upper levels of living Scleractinia skeletons. All of the above have the function to fix carbon on the reef. The phytoplankton provide limited input; adjacent seagrass and benthic algae add to the carbon budget. Production is portioned into a number of categories. The carbon fixed within the zooxanthellae is conserved within the host or exported as a secretory product: mucus that is an energy source. The herbivore or primary consumer category is complex. Some of the better known herbivores include parrotfish (Scaridae), surgeonfish, tangs (Acanthuridae), and the sea urchins (*Diadema antillarum* and *Eucidaris tribuloides*). Various other organisms also are herbivores. Secondary consumers include those organisms that feed primarily on herbivore consumers. This includes a wide range of fish and invertebrates. There may not be great discrimination by the carnivore on prey selection; they may indiscriminately feed on carnivore, omnivore, and herbivore elements. Some known secondary consumers include the butterfly fish (Chaetodontidae) and fireworm (*Hermodice carunculata*; Plate 18b), which are obligate coral predators. Higher level consumers include larger predatory fishes: grouper (Plate 23b), jewfish, and barracuda. These fishes tend to range widely over numerous reef habitats and forage on prey as opportunity occurs. The omnivores include a number of crustaceans and echinoderms that scavenge plant and animal material. Planktivores include the corals, zoanthids, polychaetes (*Spirobranchus giganteus*; Plate 8b) and basket star (*Astrophyton muricatum*). The corals, as noted in Chapter 4, have a trophic structure that is species dependent. Other organisms are presumably more dependent upon a single resource, e.g., the basket starfish feeds exclusively on plankton.

Community structure of the corals appears to be physically controlled by depth, light, substrate, wave forces, sediment, and temperature. In a dendrogram (Figure 20) of Bird Key Reef (Figure 19), Dry Tortugas, the pattern is consistent with a change of species associations of a few opportunistic species that settle and exploit this region; but the physical extremes often make this area unsuitable for coral habitation. The dendrogram displays low similarity and weak linkage in this portion of the reef. In the moderate depths is a set of species that displays a wide range of distribution, but localized abundance patterns. This is presumably the result of microhabitat preferences, larval settlement, and competition among the other community elements. The similarity found in the dendrogram indicates that these species groups are bound together in a more organized manner than those species found in the shallower portions of the reef. The deepest portion of Bird Key Reef exhibited a unique set of species not found in any other portion of the reef; hence, the dendrogram set this coral association off by itself. The pattern displayed in patch reef communities is much less defined, and depth differences are moderate; hence, the random spatial dispersion usually makes the patch reef a community of greater similarity than that found in the bank reef.

7.4 DIVERSITY

Species diversity of the coral reef communities found off southeast Florida is a difficult parameter to estimate. Coral reefs in general have been described as the most diverse marine biological entities in the biosphere. They have been likened to the tropical rain forest with its multi-canopy of producers: high biomass, rapid turnover, and recycling of limiting nutrients. Physiography is often multilayered, e.g., in the *Acropora palmata* community (Plate 16a) the branches form layers, while smaller corals and other benthos live in the shadow of the elkhorn coral. Numerous other organisms live on, within, or under this coral association. Glynn (1964) reported that six species of crustaceans and echinoderms lived in or around the *A. palmata* community in Puerto Rico (*Gonodactylus oerstedii, Domecia acanthophora, Petrolisthes galathinus, Echinometra lucunter, Holothuria parvula*, and *Ophiothrix angulata*).

The diversity of a community is related to the complexity of the trophic relationships of the habitat (Hutchinson 1959; Paine 1966). Species diversity has developed into polarized theology. Pielou (1966) advo-

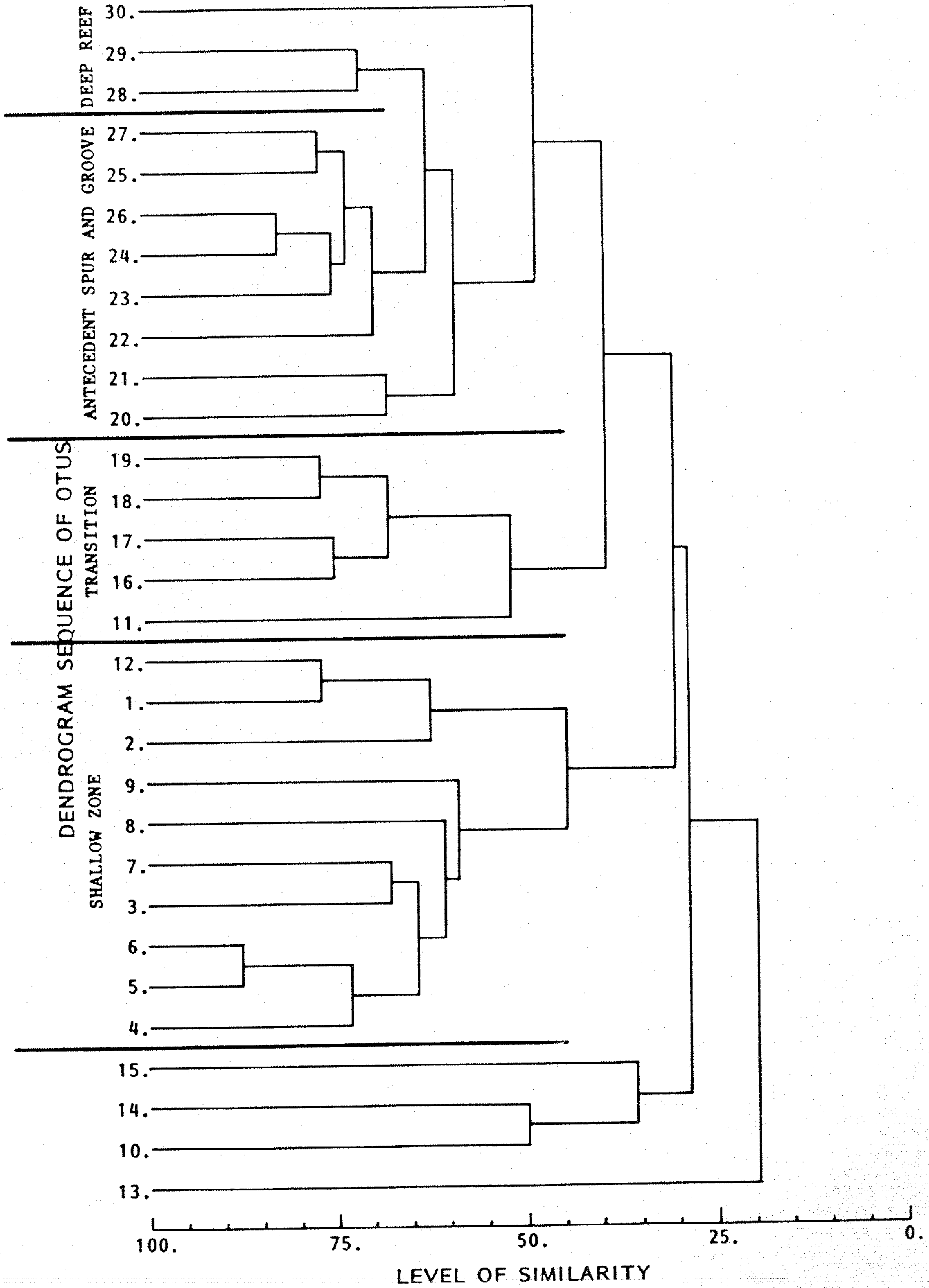

Figure 20. Classification of Bird Key Reef and Dry Tortugas based on abundance of stony corals using group average sorting and Czekanowski's coefficient.

cated use of information theory to study species diversity, and Hurlburt (1971) responded that species diversity was a nonconcept. Species diversity has been measured in many ways. Some reef workers have favored using plotless sampling techniques and computing diversity with the Shannon Wiener Index H' and its evenness component, J', as well as reporting the number of species (species richness). Sampling adequacy is usually determined by the asymptote of a species area curve. The most striking finding in relation to stony corals is the matter of sample size. In the Red Sea (Loya 1972) and Panama (Porter 1972) the minimum acceptable transect length was 10 m; in Florida reef communities, a 25-m length is necessary to insure adequate sampling. This implies that the reefs off southeast Florida are less diverse in their stony coral fauna than those from other more tropical regions. If one studies the species found on any given reef, however, one will find almost all the species reported from other Caribbean areas. They may be quite rare, but present nevertheless. Table 27 presents the Scleractinia found throughout the Florida Reef Tract, and Figure 21 shows similarity of coral fauna at various reefs. Some reefs have received much more intensive study than others; therefore, inter-reef comparisons cannot be drawn. For example, in Table 17 sampling was restricted to a specific site within a narrow depth range; hence, species diversity is limited. On the other hand, work at Bird Key Reef, Dry Tortugas, was intensive over a wide area and more than 50 species were identified (Jaap, in preparation). The same holds true for many other reef taxa. Small-scale studies report fewer species while large-scale (spatial and temporal) studies present long species lists. In some groups the species are so poorly known or so many species remain undescribed that it is truly impossible to evaluate total community species diversity.

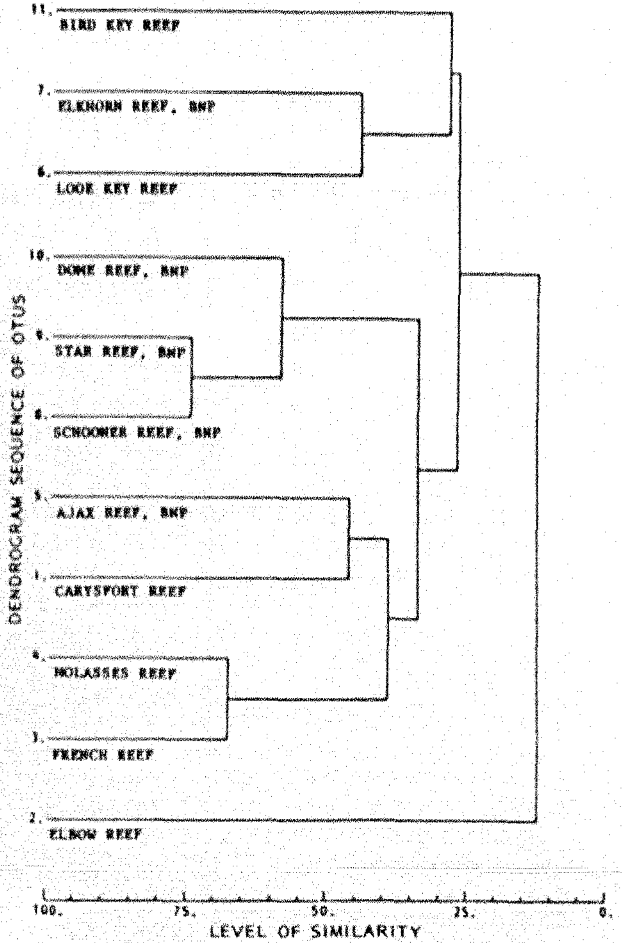

Figure 21. Similarity of coral fauna on Florida reefs using group average sorting and Czekanowski's coefficient.

7.5 SYMBIOSIS

Coral reefs exhibit a high level of species interaction; symbiosis contributes to the high diversity and productivity. There are many scales of symbiosis ranging from the microscopic (zooxanthellae-coral) (Figures 22 and 23) to macroscopic (cleaner shrimp-anemones-fish). It also includes commensalism, mutualism, and parasitism. Numerous organisms display some form of symbiotic relationship in coral reefs. One of the most dramatic forms of symbiosis is the fish-cleaning station. Several associations have developed to take advantage of this resource. One example is the cleaner shrimp, *Periclimenes pedersoni* (Chase). The shrimp lives in a host anemone; various anemones may serve as host, and the shrimp may move from one anemone species to another. *Condylactis gigantea* (Weinland) and *Bartholomea annulata* (LeSueur) are common hosts to *P. pedersoni*. The shrimp attract fish to clean by waving their antennae. The fish come to the anemone, and the shrimp swim to the fish and clean the mouth and gills. Another cleaning relationship involves the cleaning gobies *Elactinus oceanops* and *Gobiosoma genie*. These small gobies establish cleaning stations, usually around a specific coral, but sometimes a few fish form a collective station and cooperate in the cleaning. A fish requesting a cleaning approaches the station and displays a particular behavior to receive cleaning. Upon the displayed signal, the goby swims into the mouth, gill chamber, and around the fish body to remove parasites, fungi, algae, and necrotic tissue. Limbaugh (1961) reported that cleaning symbiosis was very important in coral reef communities. Bruce (1976) and Patton (1976) reported on associations of living corals and crustacean commensalism in coral reefs with most of the emphasis on Pacific reefs.

Organism interactions in a coral reef are also complex and highly developed. Some are obligate while others are mostly by chance. Patton (1976) wrote, "Corals exceed all other invertebrate groups in the diversity of forms and numbers of species to which they play host." Food and shelter are the major factors attractive to associates. The coral skeleton offers an especially good niche for smaller organisms to escape predation. Numerous sponges, polychaetes, bivalves, and sipunculids find habitat in the base of corals. Other

Figure 22. Electron micrograph of *Agaricia fragilis* zooxanthella, 6590 magnification.

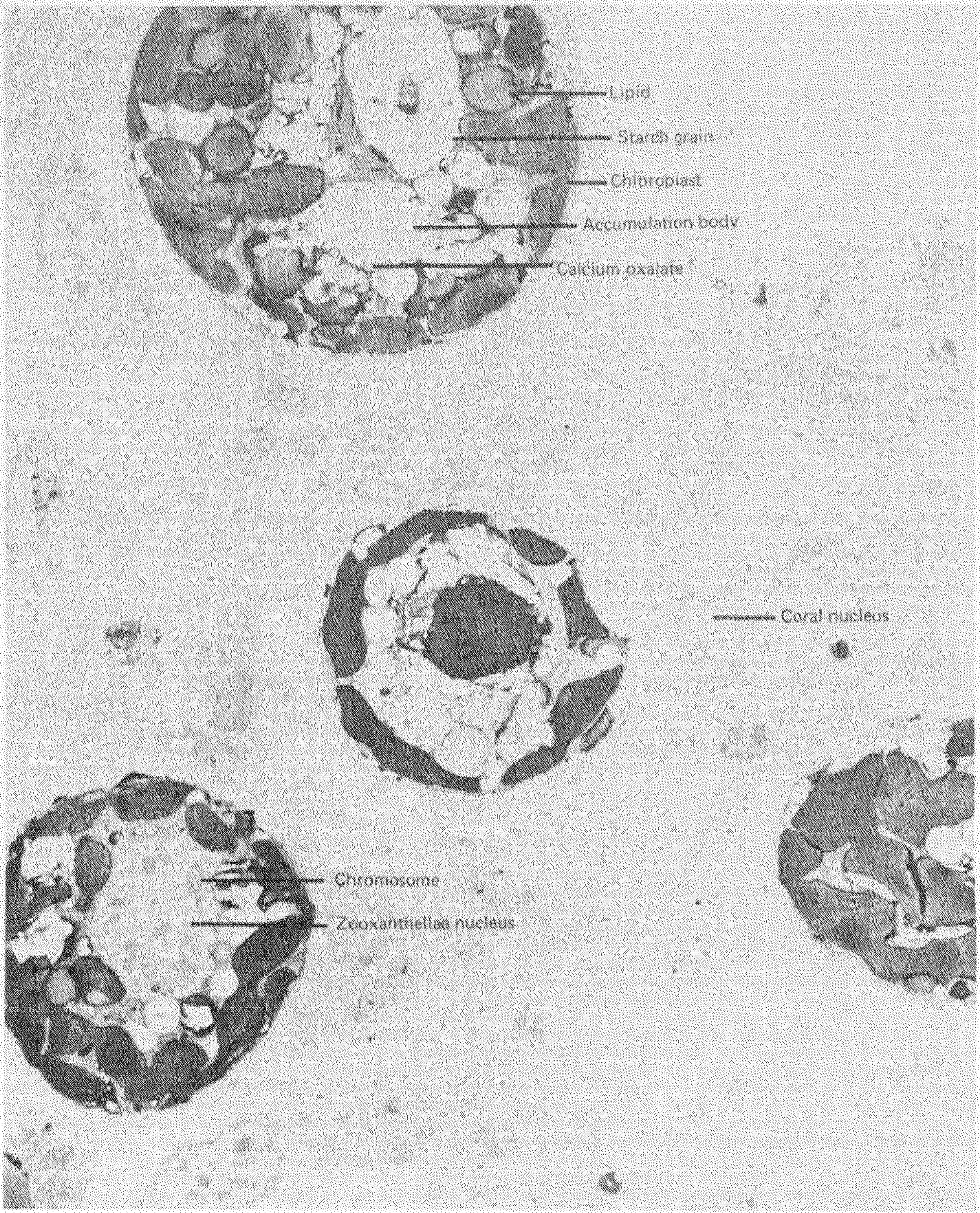

Figure 23. Electron micrograph of *Agaricia fragilis* zooxanthella, 14,660 magnification.

organisms live successfully on the coral's upper surface. Some, such as copepods, have developed specialized forms to live in the coral polyps; they are more wormlike than crustacean (Patton 1976). Some organisms have developed unique ways to modify the coral skeleton. The subfamily Pyrogomatinae (barnacles) and the decapod crustacean *Domecia acanthophora* are able to modify the Scleractinian skeleton. *Domecia acanthophora* lives on *A. palmata* branches (Patton 1967) and is able to influence calcification such that the coral builds a skeletal structure around the crab. The process initiates when a crab seeks a position on the branch margins where bifurcation has begun; the crab maintains its position, and the skeleton grows around its den. In time the area resembles a small pit or cave. *Domecia acanthophora* has modified second maxillipeds that allow the crab to feed on suspended material. In this case, the relationship is both shelter- and food-related. Patton (1976) reported that mobile crustaceans living in close association with corals feed on the sediment and detritus from the water column and that which settles on the coral surface. Corals also release energy sustaining materials that other organisms may utilize, e.g, mucus, fecal detritus, zooxanthellae, and metabolic wastes.

Competitive interactions are important in determining community structure on a coral reef. The major area of interaction is in the competition to acquire spatial territory. Successful organisms can defend their territory against intruders. They are also able to expand into the adjacent region at the expense of organisms that are less able to maintain their territory. An example of local habitat manipulation is the effect of the threespot damselfish (*Pomacentrus planifrons*) on the corals *Acropora cervicornis* and *Montastraea annularis*. Kaufman (1977) and Potts (1977) reported that the threespot damselfish was able to garden small areas of reef by killing the corals and defending the area from herbivorous fish, thus allowing a crop of filamentous algae to grow on the dead corals. These small fish are territorial and defend the area against fish, invertebrates, and divers. As a result, the area has an abnormally high algal cover. This result is short term in *A. cervicornis* habitats. Since this species grows rather rapidly, it can grow away from the damselfish territory and develop a new area. In the case of *M. annularis* where growth is slow and propagation is mostly by larval recruitment, the damselfish may have a more significant negative impact on the affected coral colony.

A number of authors have reported on the effect of the black-spined sea urchin, *Diadema antillarum*, on coral reefs. Sammarco et al. (1974) reported that *D. antillarum* controlled coral community structure; Bak and Van Eys (1975) reported that the urchin fed on coral; and Sammarco (1980) reported that *D. antillarum* was important in providing microhabitats for coral larvae to settle. *Diadema antillarum* is a common resident on most coral reefs; hence, its control is probably significant.

Another form of interaction that has been mentioned earlier is the ability of the corals themselves to maintain or advance territorial superiority by extracoelentric feeding behavior with the extension of mesenterial filaments. The more "aggressive" species have the ability to digest the tissues of less "aggressive" adjacent species. Lang (1973) described this form of interaction. It is not a rapid phenomenon; in some cases it may take months for the interaction to be noticed.

7.6 PREDATOR-PREY RELATIONS

Predator-prey relationships are far too great and complex to detail here. One of the more well-known corallivores is the polychaete *Hermodice carunculata* (Plate 18b), a large marine worm that is documented to feed on a number of coral species (Marsden 1960, 1962; Glynn 1962; Ebbs 1966; Antonius 1974b; Lizama and Blanquet 1975. Glynn (1973) reviewed western Atlantic coral predators. Some organisms such as the gastropods *Coralliophila abbreviata, Calliostoma javanicum*, and *Cyphoma gibbosum* are mobile species that move to and from the coral. They feed on the coral, but apparently do not receive protective shelter. Fish within the families Scaridae, Ephippidae, and Pomacentridae feed on coral (Glynn 1973). They are not obligate to a particular coral species; this major difference between Pacific and Atlantic corallivores (lack of obligate species relationships in the Atlantic) may reflect that the time of development for Atlantic reefs and coral species has been relatively short. (Atlantic Scleractinia are only ca. one million years old; Pacific reefs have a much older fauna.) Predation may directly cause mortality and morbidity. Injury caused by predation may lead to the invasion of boring and rasping biota. When the coral is damaged, recovery may occur by regeneration of tissue; but regeneration may be prevented by successful colonization of the injured area by other organisms (filamentous algae, diatoms, sponges, *Millepora*, and zoanthids). This alien growth is detrimental to the coral, which may succumb to the secondary invasion.

Rapidly growing species may grow over and shade out other organisms, denying them resources. There is also evidence that some reef organisms are able to maintain and advance spatial resources through the secretion of toxic chemicals (Jackson and Buss 1975).

Figures 24-27 show the cumulative effect of these interactions through time for a small area on Elkhorn Reef.

7.7 PRODUCTIVITY

The earliest study of overall productivity of a small coral reef was Odum and Odum (1955) at Eniwetok, a Pacific atoll. The comparability with Florida is poor; however, the concept of high productivity is valid. Odum and Odum (1955) reported that mean annual production was 846 gm dry biomass/m^2. On a 24-hour basis there was a net gain of 2 gm C/m^2. Sournia (1977) reviewed coral reef primary production and concluded that gross production in coral reefs yielded the highest productivity of any ecosystem on earth. The magnitude of gross production ranged from 2-10 gm C/m^2/day; however, net production may, in some cases, be negli-

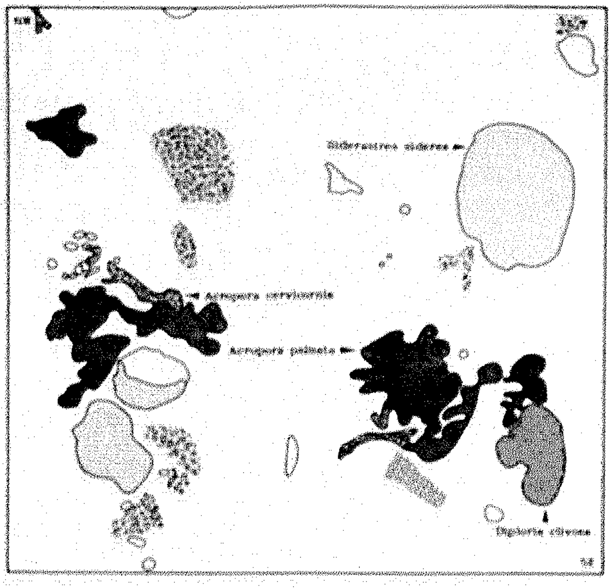

Figure 24. Time series of a 2x2 meter area of Elkhorn Reef, 1978.

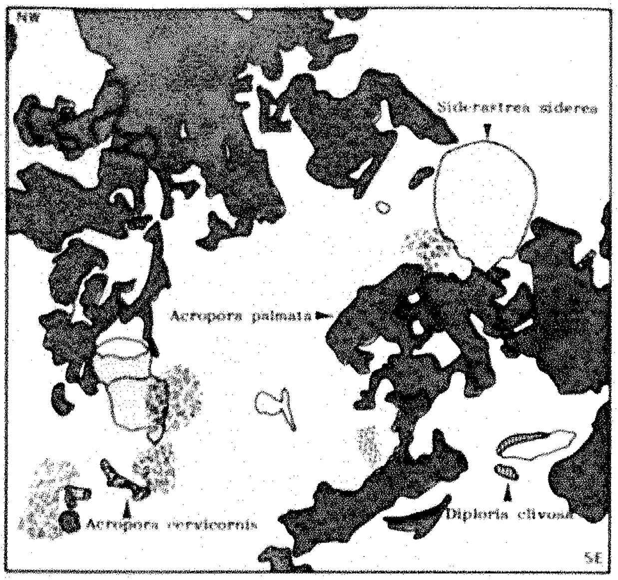

Figure 25. Time series of a 2x2 meter area of Elkhorn Reef, 1979.

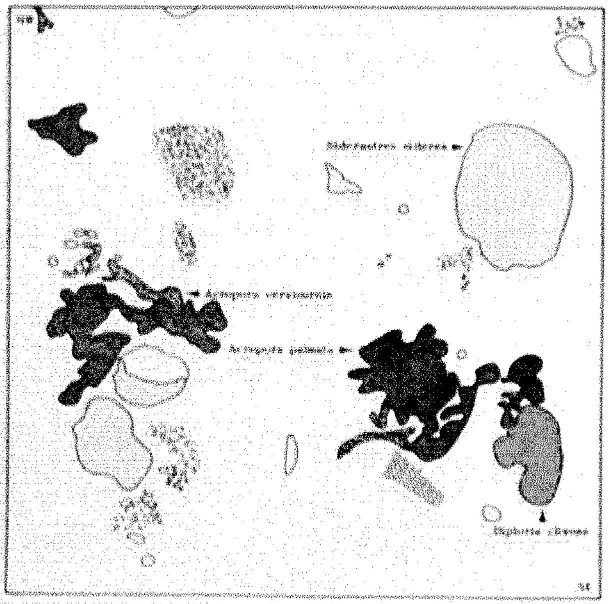

Figure 26. Time series of a 2x2 meter area of Elkhorn Reef, 1980.

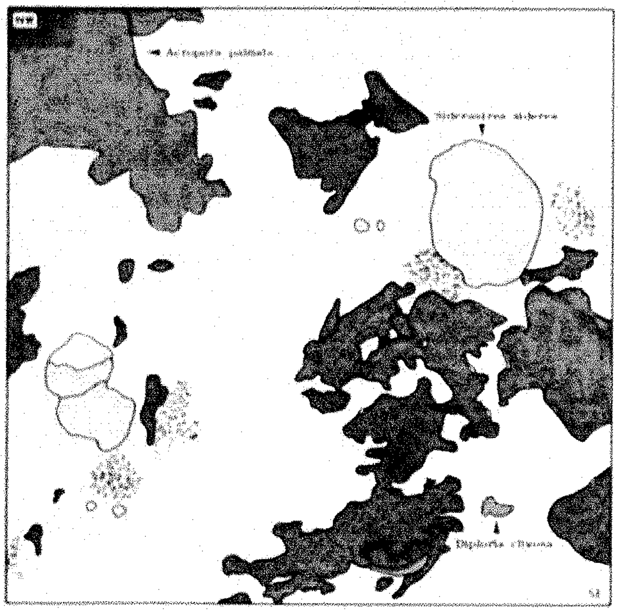

Figure 27. Time series of a 2x2 meter area of Elkhorn Reef, 1981.

gible. Much of this research was accomplished in the Pacific; extrapolation to Florida reefs must be qualified by several facts. The Pacific reefs are usually set in more benign or predictable environments, with negligible seasonal variation in temperature. Because of the difficulty in evaluating community productivity and respiration, few studies have considered total community metabolic budgets. By far, the greatest research emphasis has been on the zooxanthellae and the symbiotic relationship with coral. Trench (1979) and Schoenberg and Trench (1980a, 1980b, 1980c) reviewed the cellular biology of this aspect. Rodgers (1979) studied two 10 x 1 m reef sections at San Cristobal Reef, Puerto Rico; net productivity ranged from 0.03 to 1.85 g $O_2/m^2/hr$. A recent summary-review of coral reef physiology is found in Gladfelter (1983).

7.8 CORAL REEF MODELS

Conceptual models were proposed by Dahl et al. (1974) and improved upon by Smith (1978). The Dahl et al. (1974) model included organism processing units (similar functional elements), pathways, and external driving forces. The following outline is taken from Dahl et al. (1974), with some modification in terminology.

1. *Benthic Plants*
    a. Nitrogen-fixing algae, nutrient recycling function
    b. Crustose coralline algae, framework organism, cementing function
    c. Benthic microalgae, primary producer
    d. Turf algae, <2 cm high, autotroph
    e. Carbonate producing macroalgae, sediment production
    f. Boring algae (Ostreobium), filamentous, within the carbonate frame
    g. Detached macroalgae, Sargassum, floating autotrophs
    h. Marine grasses, blades, adjacent to the reef
    i. Marine grasses, roots, alter sediment characteristics

2. *Plankton*
    a. Heterotrophic phytoplankton, <10 microns
    b. Autotrophic phytoplankton, <10 microns
    c. Autotrophic phytoplankton, 10-100 microns
    d. Autotrophic phytoplankton, >100 microns
    e. Microholoplanktonic omnivores, <200 microns
    f. Mesoholoplanktonic omnivores, 200-500 microns
    g. Macroholoplanktonic omnivores, >500 microns
    h. Neuston omnivores, all sizes
    i. Microepibenthic omnivores, <200 microns
    j. Mesoepibenthic omnivores, 200-500 microns
    k. Macroepibenthic omnivores, >500 microns
    l. Mesoholoplanktonic carnivores, 200-500 microns
    m. Macroholoplanktonic carnivores, >500 microns
    n. Neuston carnivores, all sizes
    o. Mesoepibenthic carnivores, 200-500 microns
    p. Macroepibenthic carnivores, >500 microns
    q. Microholoplanktonic detritivores, <200 microns
    r. Mesoholoplanktonic detritivores, 200-500 microns
    s. Macroholoplanktonic detritivores, >500 microns
    t. Neuston detritivores, all sizes
    u. Microepibenthic detritivores, <200 microns
    v. Mesoepibenthic detritivores, 200-500 microns
    w. Macroepibenthic detritivores, >500 microns

3. *Benthos, Invertebrates*
    a. Animal-plant symbionts, energetic support from autotrophs
    b. Invertebrate "scrapers," remove substratum with food
    c. Invertebrate browsers, do not remove substratum
    d. Passive suspension feeders, collect nutrients from water column without physical action on the part of the organism
    e. Active suspension feeders, actively collect nutrients from the water column by creating currents or selective predation
    f. Microbrowsers (meiofauna), nutrition gained from material in sediments, <2 mm
    g. Macro-deposit feeders, nutrition gained from larger (>2 mm) sedimentary fraction
    h. Sedentary micropredators, selectively capture water column prey
    i. Small predators, motile organisms that harvest invertebrates and vertebrates
    j. Medium predators, mobile organisms that harvest medium-sized invertebrates or vertebrates
    k. Meiofauna predators, live in the sediment, harvest meiofauna
    l. Parasites and pathogens, very selective predator that gains nutrients from a limited number of host organisms
    m. Parasite cleaners, mobile organisms, specializing in removing parasites from other organisms
    n. Attached eggs

4. *Nekton, Vertebrates*
    a. Grazers, also remove a portion of the substrate, i.e., parrotfish
    b. Browsers, do not affect substrate
    c. Bottom feeding planktivores, feed on epibenthic plankton
    d. Midwater feeding planktivores, feed on holoplankton and neuston
    e. Small predators, <50 mm standard length (SL)
    f. Medium predators, 50-250 mm SL
    g. Large predators, 250-500 mm SL
    h. Top predators, >500 mm
    i. Parasite pickers, feed on vertebrate ectoparasites
    j. Detritus feeders
    k. Attached eggs

5. *Detritus/Nutrient*
    a. Nitrate, NO_3 dissolved
    b. Nitrite, NO_2 dissolved
    c. Ammonia, NH_3 dissolved
    d. Organic carbon, C dissolved
    e. Suspended detritus, <10 microns
    f. Suspended detritus, 10-100 microns
    g. Suspended detritus, >100 microns
    h. Trapped detritus
    i. Organic nitrogen, N dissolved
    j. Inorganic phosphate, PO_4
    k. Organic phosphorus, P dissolved
    l. Oxygen, O_2
    m. Interstitial NO_3, dissolved
    n. Interstitial NO_2, dissolved
    o. Interstitial NH_4, dissolved
    p. Interstitial C, dissolved
    q. Interstitial particulate organic C (dead)
    r. Interstitial organic N, dissolved
    s. Interstitial organic P, dissolved
    t. Interstitial PO_4, dissolved
    u. Interstitial O_2, dissolved

6. *Geology*
    a. Dissolved inorganic C (CO_2, HCO_3, and CO_3)
    b. Suspended inorganic C (fine $CaCO_3$)
    c. Bedload inorganic C (coarse $CaCO_3$ sediments on the sea floor)
    d. Frame inorganic C (reef frame)
    e. Organism inorganic C ($CaCO_3$ in living non-frame organisms)
    f. Rubble inorganic C (large talus)
    g. Inorganic C in sand ($CaCO_3$, 62 microns-4 mm)
    h. Inorganic C in mud ($CaCO_3$, <62 microns)
    i. Interstitial dissolved C (CO_2, HCO_3, and CO_3 dissolved in interstitial sediment water)

7. *Input From Outside the Reef Community*
    a. Autotrophic plants, C
    b. Nitrogen-fixing plants, N
    c. Nitrogen-transforming plants, oxidize and reduce N compounds
    d. Decomposing plants, convert organism biomass to simpler organic material, nutrients, CO_2, and water
    e. Birds, remove fish and invertebrates, contribute feces containing N and P compounds
    f. Decomposing organisms, contribute to organic and inorganic chemical pool
    g. Sea turtles, feed on benthos and floating organisms, contribute chemicals from feces
    h. Talus islands adjacent to the reefs, may contribute organic and inorganic chemicals and sediments to the reef.

The Dahl et al. model contained 104 compartments. A matrix of the interrelationships implied about 2,000 of the 10,816 potential interactions were active, and a material and energy flow exists between these categories. In terms of modeling coral reefs, Smith et al. (1978) reported that until the modeling technique advances to the point that it is realistic, the budget analysis method offers better insight into ecosystem dynamics by focusing on an element within the ecosystem (e.g., carbon budget, nitrogen budget). Smith et al. (1978) reported on several budgets from a hypothetical atoll in the Pacific. Figure 15 provided a qualitative graphic representation of a calcium carbonate budget from Barbados.

7.9 NATURAL IMPACTS

Hurricanes are the most severe natural impact faced by coral reef communities. Mega-hurricanes (those with 200-mi/hr or greater winds) have devastated reef areas, and either recovery has been slow or the coral reef community has been replaced by another community. Stoddart (1962, 1963, 1974) reported that Hurricane Hattie destroyed reefs off the coast of British Honduras (Belize) and that recovery was negligible. Woodley et al. (1981) reported that Hurricane David decimated shallow reefs near Discovery Bay, Jamaica, and post-hurricane mortality of damaged organisms was significant (Knowlton et al. 1981).

In considering the effect of hurricanes, two major areas of negative impact are reported. Physical damage occurs as a result of the huge seas generated by the hurricane winds. Shallow reef zones bear the brunt of the wave forces as they are expended on the spur and groove and reef flat. Smaller corals and other attached organisms are often dislodged, fragmented, and abraded by the severe physical pounding. The other major impact concerns dilution of salinity caused by torrential rains. In regions where mountainous terrestrial land masses abut the coral-lined coast, severe runoff may turn coastal waters hyposaline (Goreau 1964). Erosion of soil and transport by the runoff is also credited with causing coral mortality. Goreau (1964) reported shallow reef mortalities due to salinity stress as well as to burial by terrigenous silt. The passage of the storm also causes churning of the bottom sediments increasing turbidity within the water column.

Hurricane damage to Florida reefs reported from the literature are of a lesser magnitude, and in some respects could be considered beneficial. Springer and McErlean (1962a) reported negative impact on patch reefs off Key Largo from Hurricane Donna. The storm crossed the reef tract about 40 km south of Key Largo, 9-10 September 1960. Windspeed was approximately 161 km/hr, with gusts approaching 242 km/hr (Shinn 1975). High seas dislodged and redistributed corals in the adjacent area of Key Largo Dry Rocks (Shinn 1975). Hurricane Betsy passed within 16 km of Key Largo Dry Rocks on 8 September 1967, with a windspeed of approximately 193 km/hr. Shinn reported that hurricane damage was not evident 5 years following Donna and 2 years after the passing of Betsy. Ball et al. (1967) and Perkins and Enos (1968) also discussed the effect Hurricanes Donna and Betsy had on the reefs from a geological standpoint. Jindrich (1972) postulated that hurricanes were one of the controls on reef development at Dry Tortugas.

The nature of hurricane impact has several interesting aspects. First, the hurricane causes considerable physical alteration of habitat. Sessile biota are often dislodged and transported considerable distances from their original growth positions. Fish are dislocated some distance from the resident reefs (Springer and McErlean 1962a). Smaller cryptic organisms are often left homeless, the resident coral or sponge being fragmented or possibly destroyed. When the mobile organism is an obligate commensal (having specialized niche requirements), it is quite likely that it will be difficult for it to locate alternative housing. Following the initial impact, turbidity may remain high for a week or more before water column transparency returns to normal conditions. After several more weeks, those corals that did survive will either exhibit growth over the scars and lesions and reattach to the bottom or they will die. Several recent reports described in detail the process of healing and secondary mortality. Highsmith et al. (1980), Woodley et al. (1981), and Rodgers et al. (1982) reported on the effects of several Caribbean hurricanes. *Acropora cervicornis* and *A. palmata* displayed impressive recovery in Belize and the U.S. Virgin Islands (Highsmith et al. 1980; Rodgers et al. 1982); however, these same species displayed considerable secondary mortality in Jamaica (Woodley et al. 1981). In Florida rapid recovery was reported following Hurricanes Donna and Betsy (Shinn 1975). The differences relate to the magnitude of impact; those reefs exposed to major hurricanes that pass close to the reef will suffer severe impact, while hurricanes that are of lesser magnitude or a greater distance from the reef are a lesser threat. Pearson (1981) reviewed coral reef recovery; he reported that following severe impact, it requires several decades for recovery. Pearson also reported that larval recruitment was much more significant than fragment propagation in the reef recovery process. This finding reflects recovery of Pacific reefs following the plaguelike predation by *Acanthaster planci* (crown-of-thorns starfish) more than recovery from natural physical impacts. It appears that following major storm damage *Acropora palmata* and *A. cervicornis* may benefit from fragment propagation. In Discovery Bay, Jamaica, however, the few fragments of *A. cervicornis* alive 5 months after the storm still suffered heavy mortality from surviving coral predators (Knowlton et al. 1981). Plate 10b shows fragments of an *A. palmata* colony that has been overturned and is now sprouting new branches. Highsmith (1982) reviewed propagation recruitment.

The other major natural impact on coral reefs is thermal stress. This can occur on either end of the spectrum; both heat and cold stress are reported to cause negative impact. Jaap (1979) reported on a zooxanthellae expulsion (Plate 24b) at Middle Sambo Reef (off Boca Chica Key) related to elevated water temperature that was created by synergistic meteorological and tidal conditions. The overall impact was not significant in that recovery took approximately 6 weeks. Vaughan (1911), Mayer (1918), Porter et al. (1982), and Hudson (in press) reported thermal stress damaged or killed reef biota at Dry Tortugas.

Heat-related stress usually occurs in late summer during solar noon to mid-afternoon. It is usually low tide, and the sea state is calm. Under these conditions, shallow reefs heat rather rapidly. Ambient temperatures are already 30°-31° C. Since the upper lethal temperature for *Acropora palmata* is 35.8° C (Mayer 1914), it does not take a great deal of heating to create stressful temperature levels. Shinn (1966) reported that transplanted *A. cervicornis* expelled zooxanthellae at or near 33.8° C. In contrast to cold stress, most heat stress is localized and is not a transported water mass phenomenon.

Cold stress was discussed in Chapter 2 under seawater temperature. The basic geographic configuration lends itself to the creation of cold water masses in shallow embayments, especially Florida Bay during the passage of winter cold fronts. The shallow bay allows the water mass maximum surface exposure to the polar air mass. After cooling, the water is moved to the Atlantic by tidal pumping, density gradients, and winds. The water mass moves through the passes and across the shelf and into the reef communities. Reef development requires no prolonged exposure to 18° C; however, individual species can tolerate significantly lower temperature (Mayer 1914, 1918). Most reef corals are severely stressed at or near 14° C. Shinn (1975), Hudson et al. (1976), and Roberts et al. (1982) reported that cold water masses originating in Florida Bay caused coral mortality to patch reefs adjacent to the passes. Most major offshore reefs do not suffer due to mixing of the cold water with resident water masses and the moderating effect of the Florida Current. Dry Tortugas has suffered significant mortality of staghorn coral populations as reported earlier due to cold stress.

Red tide (toxic phytoplankton blooms) are not common off the east coast, but entrained water masses occasionally carry a red tide into the Atlantic.

Natural events are a major factor controlling coral reef development, community structure, and species diversity. Connell (1978) reported that high diversity in tropical rain forests and coral reefs was related to intermediate frequency and magnitude of interference by natural events. Without negative impact by these agents, dominant organisms outcompete other organisms for resources, and species diversity is reduced. The hurricane or other natural agent opens new spatial habitat to pioneering organisms that can successfully exploit new territories. In a benign environment, one or a few species can potentially dominate, thus reducing diversity and the overall ability of the community to respond to outside stress.

CHAPTER 8

MANAGEMENT

8.1 HUMAN IMPACTS

Coral reefs off southeast Florida are multi-user resources, experiencing increased exploitation that results in some negative human impact on the resource. Although natural events are far more severe than man's individual acts, human impact on the reefs must be multiplied by the number and the frequency of occurrence, which in total may not allow the reef resources sufficient time for recovery. Some negative impact is focused on spatially small areas and is chronic. In recent years a number of publications dealing with coral reef pollution, stress, and death have documented or portrayed these subjects in some detail. Loftas (1970), McCloskey and Chesher (1971), Smith et al. (1973), Johannes (1975), Endean (1976), and Weiss and Goddard (1977) detailed pollution and human impact on coral reef communities. Voss (1973) and Dustan (1977b) reviewed problems in Florida reefs. Currently a number of controls are in force to mitigate human impact. In some cases controls have worked; in others, the negative impact has continued, and increased damage has occurred. Mitigation is difficult because activities are continuous and human impact on coral reefs is controversial. User groups are often polarized, frequently making the possibility of compromise or acceptance of alternative viewpoints difficult.

Dredging and Treasure Salvage

In terms of severity, dredging is the most damaging human activity in and around coral reefs. Poorly planned and managed dredging operations have caused the demise of many reefs. The physical impact of dredge gear (anchors, cables, chains, pipes, suction and cutting heads) dislodge corals or cause lesions or scars that lead to infection and mortality. Reef organisms increase respiration to remove silt resulting in reduced dissolved oxygen levels. Coupled with increased respiration is reduced photosynthesis and oxygen production due to lowered light levels. High turbidity generated by dredging reduces light penetration through the water column (Johannes 1975). Sediments excavated by dredging are often anaerobic and bind up available dissolved oxygen. Silt created by dredging remains in the local area for long periods and is resuspended during storms. Johannes (1975), Levin (1970), Endean (1976), and Bright et al. (1981) reviewed dredging impacts on coral reefs. A coral's ability to remove sediments was reported by Hubbard and Pocock (1972) and Hubbard (1973). Bak (1978) reported on lethal and sublethal effects of dredging on reef corals in Curacao, Netherlands West Indies. Corals that were poor sediment removers expelled zooxanthellae and died. Two species had extremely reduced calcification rates (Bak 1978).

Two types of dredging occur off southeast Florida; most of this activity is located from Miami northward. One kind results in spoil from deepening and maintenance dredging of navigational channels; it is disposed of on land and at sea. When disposed at sea there is potential for reef burial and increased turbidity. Occasionally, dredging operations will cut through living reefs. Sewage outfall pipe burial has also cut through reefs (Shinn et al. 1977). The other form of dredging off the southeast coast is done for beach renourishment. Sedimentary deposits are mined and brought ashore by pipes or barges and deposited on the beach. The material is a slurry; the silty runoff leaches back to sea causing increased sediment loading of the water column. During the fall of 1981, a beach renourishment project on South Miami Beach threatened a small linear hardground community composed of significant numbers of octocorals and stony corals. Dade County Pollution Control, Dade County Marine Institute, U.S. Geological Survey, and Florida DNR personnel transplanted about 200 stony coral colonies that were threatened by burial.

A critical part of all dredging activities should be a coherent field study to insure that reef communities are not endangered by dredging. Occasionally tradeoffs must be made, but should be minimized. Straughan (1972) condemned dredging for the demise of Florida Keys reefs. Courtney et al. (1974) documented reef burial and water quality problems at a beach renourishment dredging project off Hallendale; poor planning resulted in reef burial. Griffin (1974) studied a dredge operation on coastal Key Largo, and reported localized water quality problems. Aller and Dodge (1974), Dodge et al. (1974), and Dodge and Vaisnys (1977) reported that coral growth was retarded by dredge-created sediments. Loya (1976b) reported that Puerto Rican coral reefs impacted naturally by heavy sedimentation had lower species diversity than protected reefs.

Griffin (1974) and Courtney et al. (1974) recommended that all dredge operations in the vicinity of coral reef communities be closely monitored to insure that the community's vitality was not adversely affected. Specifically, Griffin proposed the following guidelines. A buffer zone of at least 0.5 nmi should separate the coral reef community from dredge operations. The magnitude of the buffer zone should be determined by local hydrographic conditions (wave and current patterns). Water column turbidity and sedimentation rates should be closely monitored. The water column sediment load deposition rate should not exceed 200 $mg/cm^2/day$, averaged over a 7-day period; if fall out exceeds this rate, a pause in dredging should be imposed to allow the benthic community to adjust. Because coral transplanting is a time consuming, labor intensive activity, it should not be considered a routine technique for restoration or mitigation. Natural stocks must be used; hence it becomes a matter of removing corals from an existing reef to restore a damaged reef. Survival of transplants may or may not be successful. Insufficient research has been accomplished to rationally judge this.

Another activity affecting reefs that is somewhat similar to dredging is salvaging of ancient shipwrecks for treasure and artifacts. If the activity is near a coral reef, turbidity may increase. Many of these salvage operations employ the "mailbox" technique. A tubular elbow-shaped device surrounding a propeller forces the thrust downward to remove overburden from the shipwreck. Air lifts used to vacuum up material from the bottom for shipboard inspection also increase turbidity. A sufficient buffer zone should be established to protect any reef from the impacts of this activity. Restraints similar to dredging recommendations should be enforced.

Anchor Damage

Anchor damage was a significant negative human impact on coral reefs at Dry Tortugas (Davis 1977a). Carelessly deployed anchors break fragile corals, dislodge reef framework, and scar corals, opening lesions for infection (Plate 27b). Increased visits increase the number of anchorings and the potential for impact. Anchor ground tackle, lines, and chains also are documented as destructive agents (Davis 1977a). Anchor buoys were established at Biscayne National Park in 1977 as a means of mitigating this negative impact on four reefs. During the summer of 1981 anchor buoys were established at French Reef, JPCRSP-KLNMS, as a test (Plate 28b; also see Plate 28a). Anchor buoys, designated anchorages, and better public education are the best way to mitigate this problem. Halas (in preparation) documents the techniques for installing anchorless mooring buoys in the JPCRSP-KLNMS.

Groundings and Shipwrecks

Since the time of the Spanish and English explorations along the Florida coast, shipwrecks and groundings on reefs have been common. As reported in Chapter 1, luring ships onto a reef was a major economic enterprise during the 19th century, a practice that ended with the building of lighthouses. In the recent past small boat shipwrecks and groundings have increased. Table 31 summarizes recent reef shipwrecks. Pleasure and commercial craft of $<$ 100-ft ($<$ 30-m) length have run aground or sunk on many reefs. These occurrences are the result of poor navigational skills, accidents, drug-related incidents, and in some cases, purposeful grounding to avoid sinking. Whatever the reason, the vessels cause physical damage to the reef. In some cases the negative impact is very severe; corals and other organisms are dislodged from the reef platform.

The greatest potential for groundings and shipwrecks is on the reef flat and in barely submerged patch reefs. It would be impossible to buoy all the reefs that are potentially threatened. While conducting research in Biscayne National Park (BNP) during 1979, the author witnessed the grounding of a motor yacht *High Life* on Elkhorn Reef. The vessel captain was confused by the anchor buoy and ran hard aground on the reef flat. The vessel's path was strewn with broken fragments of elkhorn and staghorn coral (Plate 29a). Toxic antifouling paint was driven into several heads of *Siderastrea siderea*. Another patch reef in BNP suffered when a boat struck a large buttress of *Montastraea annularis*, splitting and toppling the coral. Toxic antifouling paint was again driven into the corallites.

Table 31

Recent reef shipwrecks.

Vessel	Size (ft)	Date	Location	Impact
Ice Fog and barge	70	1973	Molasses Reef	Tug sank in deep water; barge grounded on reef; both salvaged.
Capt. Allen (Plate 26a)	60	1973-1974	Middle Sambo	Abandoned on reef flat.
Lola (Plate 26b and 27a)	110	1976	Looe Key	Aground on a spur for 18 days.
Robby Dale	60-75	1977	Looe Key	Aground; spilled fuel.
Morania		1979	Fort Lauderdale	Damaged 5,600 m^2 of live bottom.
2 shrimp boats		November 1982	Looe Key Reef	Extensive damage to a spur.
Wellwood	397	August 1984	Molasses Reef	18.6 acres impacted.

The threat of a major shipwreck is quite real. Much of the ship traffic into and out of the Gulf of Mexico is concentrated just seaward of the reef tract. Traffic into the gulf is between the coral reefs and the Gulf Stream; outbound vessels travel inside the Gulf Stream to take advantage of the current. Large tankers or freighters grounded on a reef because of mechanical difficulties or navigational errors would cause greater damage than small vessels. The 400-ft vessel *MV Wellwood* grounded on Molasses Reef on 5 August 1984, causing severe damage to the reef.

The collisions of large vessels is like a bulldozer blade leveling the top of the reef. Other negative effects of shipwrecks and groundings include fuel leakage and cargo and other materials lost or thrown overboard. An example of a vessel grounding incident was the wreck of the 110-ft motor vessel *Lola* on Looe Key Reef on 5 January 1976 (Plates 26b and 27a). The vessel was loaded with construction steel when it began taking on water. The captain ran the ship aground to avoid sinking. The vessel ended up on a spur and remained aground on the reef for 18 days. Approximately 344 m^2 of reef were impacted. The crew remained aboard ship while the vessel was aground and disposed of garbage, sewage, damaged steel cargo, and other junk including batteries and tools onto the reef. Several weeks after grounding, the ship was lightened by the removal of cargo onto a barge and towed to Key West for repairs. The *Lola* was foreign owned, and no legal action was taken.

Salvage operations pose a threat when they occur around a coral reef. Techniques used to free grounded or sunken vessels are often counter to reef conservation. Explosives, large anchors, and ground tackle pose a threat to the reef. In 1976 the *Robby Dale* carrying contraband drugs was wrecked at Looe Key Reef. A salvager used explosives to remove the ship from the reef, despite warnings by the Bureau of Land Management that unwarranted reef damage would result in legal prosecution under the Outer Continental Shelf Lands Act. The salvage firm of Alexander was brought to court and found guilty on two accounts. However, the Fifth Circuit Court of Appeals ruled that the Outer Continental Shelf Lands Act could only be invoked in cases where mineral or petroleum exploration or production activities were threatening coral reefs.

In cases where tugboats are used to tow the grounded vessel off the reef, care should be exercised to keep towing cables off the bottom. During the *Wellwood* salvage, towing cables caused a great deal of damage to the reef (corals were turned over, broken, and abraded by the towing cables). This could have been avoided. More stringent regulations should be enforced when salvage operations are close to coral reef habitats. Coast Guard cooperation and reef scientists' advice would aid in moderating the severity of negative impacts.

Numerous other incidents could be cited. The results have a general pattern that includes initial damage; sinking or salvaging of vessel; and development of successional communities in the disturbed area. If the structural integrity of the reef platform is not adversely affected, the community will recover; after 5-10 years or more the impact will be unnoticeable (Pearson 1981).

Fishing

Coral reefs concentrate marine protein in a localized area, attracting both commercial and sport fishing interests that use various techniques to harvest fish and invertebrate stocks. Negative impacts occur as a result of gear deployment and harvesting.

Lobster fishing is the largest commercial fishery located in and adjacent to the coral reef habitat area. This fishery was worth over $10 million in 1980 (Table 1). The commercial fishery uses traps or pots to harvest the spiny lobster *Panulirus argus*. Traps are set in waters inshore and offshore of the reefs, and on occasion close to the reefs. Damage occurs when the traps are set on corals, as well as during recovery. Trap recovery takes place while the boat is underway; the hydraulic puller retrieves the trap while the boat motors to the next trap. The trap is pulled along the bottom for a short distance before it clears the bottom. When the lobster trap is on coral, the sliding trap breaks and damages coral and other sessile benthos. Large numbers of traps are lost when buoy lines are cut by boat propellers. Lost lobster traps decompose in time, but cement bottoms do not rapidly degrade. To eliminate this negative impact, fishermen should be required to keep their traps out of the reef environment proper.

Sport divers who harvest lobster damage the reef through their efforts to dislodge lobsters from ledges and caves. The author has seen moderately large (1.5-m diameter) brain coral heads (*D. strigosa*) dislodged and turned over by enthusiastic lobster divers. Smaller fragile corals and other benthic organisms are damaged in the process of lobster hunting. The lobster divers often become so engrossed in their quest to obtain lobster that they break off coral that is in their way to get at the lobster.

Hook-and-line fishing methods are employed by commercial and sportfishermen in the coral reef habitat. There is considerable loss of line, leaders, hooks, sinkers, lures, and other paraphernalia on the reefs. When diving on any reef, it is common to find line, hooks, etc., caught in the coral. The hooks and line impact when the hook is dragged across the coral face, causing lesions or scars. Monofilament line wraps around corals and other organisms, often causing abnormal growth. Net fishing is not common around coral reef habitats; however the author found a net entangled in the coral at Eastern Sambo reef in 1973. Shrimp vessels anchoring at Pulaski Shoal near Dry Tortugas have made a habit of disposing junk on the reef. The area resembles a garbage dump, with all manner of fishing-related gear on the bottom.

Fish traps are a controversial issue with polarized constituents expounding their viewpoint. Traps are not selective, but catch all manner of biota, much of which is not consumed because of cultural biases or lack of a market. The trap is made of steel mesh and is marked with a buoy. If the buoy is lost, the trap continues to harvest fish, many of which die in the trap (Plate 29b). The fish trap, like the lobster trap, can damage the coral by physical impact during setting and recovery. National Marine Fisheries Service laboratory studies show that some reef fish species can enter and escape from fish traps at will.

Spearfishing is the major means divers employ to harvest finfish. Spearpoints damage coral if they are fired into the reef. Some divers use a "bangstick" (explosive head on the end of a spear or a stick) to harvest large fish or for confidence. When exploded on the surface of a stony coral, it creates a concave crater about 0.5 ft in diameter and of equal depth. It is illegal to use spearguns in several of the marine parks, and within much of Monroe County.

Diving Activities

Diving as a sport and hobby has increased and developed into a major industry in the Keys area. As reported earlier, it is a major economic contributor in some parts of Monroe County. With the numbers of persons involved, it is not surprising that negative impacts occur. Unskilled divers grab coral for stabilization. The dive guides try to enforce and instill an axiom of don't touch or collect anything. The efforts are for the most part successful; however, there are so many people to monitor that it is difficult to police everyone. Those persons who visit the reefs in private boats are not governed by similar restraint. A small number of coral collection violations occur within the parks and sanctuaries. Enforcement is spread very thinly; hence many persons probably do collect coral as a souvenir.

Marine collecting as a hobby includes both live and dead material for aquariums. Some individuals harvest mollusk shells and other curio items for collections. For the most part, these specimens are dead; however, some live material is taken. Collection pressure is quite heavy on colorful and distinctive species such as helmet shells (*Cassis* spp.), thorny oyster (*Spondylus* spp.), and the flamingo tongue (*Cyphoma gibbosum*). Queen conch (*Strombus gigas*) is harvested for food and for its shell.

Live marine specimen collecting has developed as a minor industry and popular hobby in southeast Florida. The collection of attractive fish and invertebrates is focused in the coral reef areas primarily between Palm Beach and Key West. Brightly colored fish, crustaceans, mollusks, and other species are collected and sold to pet shops and aquarium stores.

Specimens are collected by divers using various techniques and transported in tanks aboard their boats. Professional collectors use nets, traps, and in some cases narcotizing chemicals to collect target species. Damage is inevitable; in the quest to harvest illusive fish and invertebrates, certain amounts of physical damage are bound to occur. Frequency and magnitude of damage are correlated with the experience and conservation ethic of the collector. Part-time amateur and hobby collectors with limited experience and time pose a greater threat than a professional collector with several years of experience.

Chemical collecting agents threaten corals if used indiscriminately or in strong concentration (Plate 25b). The most frequently employed chemical is Quinaldine (Jaap and Wheaton 1975). The State of Florida requires a permit for its use. When used in a restrained manner, it poses a minimal threat to corals. In strong concentration it may cause zooxanthellae expulsion and stun cryptic microfauna which are rapidly consumed by certain fish (e.g., the bluehead wrasse) that are immune to the chemical. The use of Quinaldine is minimal; hence, it does not pose a great threat. Other chemicals cited as major threats to coral reef communities include a great list of materials (Johannes 1975). The use of commercial laundry bleach (sodium hypochlorite) is a potential threat. It has been cited as a fish and invertebrate collecting chemical, but it also does severe damage (mortality) to sessile benthic invertebrates (Johannes 1975).

Pollution

General reviews of the effects of pollution on coral reefs are Johannes (1975) and Endean (1976). Weiss and Goddard (1977) reviewed a case history of coastal pollution and its effect on coral reefs off the coast of Venezuela. Bright et al. (1981) added additional references on the subject. Loftas (1970), McCloskey and Chesher (1971) and Smith et al. (1973) documented the effects of pollution on coral reefs. Many of the previous studies were either unrealistic field and laboratory experiments or from Kaneeohe Bay, Hawaii. Certainly there is cause for concern in Florida coastal waters as the population continues to grow and municipal sanitary sewage systems use ocean outfalls as an expedient means of disposal of sewage effluent. Kaneeohe Bay, Hawaii, is a classic case of what can go wrong when untreated sewage and siltation from poor land management impact a semi-closed ecosystem. Eutrophication and siltation of the sea bottom extirpated a large number of the reefs (Smith et al. 1973). Florida coral reefs represent an open ecosystem where eutrophication is less likely to occur.

Much of urban Monroe County uses septic tank sewage disposal; therefore, input into the marine environment is likely. Bright et al. (1981) reported that the porous limestone strata in the Florida Keys did not retain the sewage effluent for sufficient time to allow for decompositon. The aforementioned article also reported on the massive amount of liquid wastes pumped into the ocean by southeast Florida coastal communities. As growth in coastal southeast Florida continues, potential for pollution impact on coral reef communities also increases. Dilution in the ocean is not the solution for sewage disposal.

Manker (1975) reported on heavy metal accumulations in the sediments and corals off southeast Florida; he noted higher concentrations of mercury, zinc, lead, and cobalt adjacent to population centers.

Disposal of wastes from existing lighthouse navigational aids may be a minor problem, yet is clearly a cause for concern. Plate 30b shows batteries and other refuse disposed of on the reef flat at Carysfort lighthouse. Coast Guard maintenance crews have, over a period of years, disposed of spent batteries by throwing them into the sea; subsequently, acids are released into the area.

Southeastern Florida is a major truck farm area for vegetables and fruit. Use of agricultural chemicals (fertilizers, herbicides, pesticides, etc.) is intense. Porous soils, canal systems leading to the bays, and rapid runoff of surface materials following rains and irrigation are causes for concern. McCloskey and Chesher (1971) reported that organochloride compounds reduced productivity (photosynthesis:respiration ratios) in *Acropora cervicornis*. The methodology and concentrations of the study were not realistic compared to what is the normal concentration of such compounds in the reef environment. The effect of chronic low level concentrations over a long period has not been studied. Pollution research into chronic low level concentrations of hydrocarbon pollutants documents that reproduction is the most severely affected biological process (Loya and Rinkevich 1980).

Petroleum Hydrocarbons

The effect of petroleum hydrocarbons (PHC) on coral reefs is poorly understood. Reviews summarizing the information include Johannes (1975), Loya and Rinkevich (1980), Ray (1981), and Bright et al. (1981). Gunkel and Gassmann (1980) reviewed oil pollution in the marine environment.

A diversity of methods has been used to evaluate the effects of PHC on corals; many of the procedures used represent exposures or concentrations that are difficult to relate to field conditions. Some situations on a coral reef tend to magnify exposure, while others would lessen impact; laboratory tests often are unrealistic compared with the actual environment. Shallow reef flats, lagoons, and other reef environments with poor circulation expose organisms to higher concentrations than open ocean conditions, while spur and groove formations with high turbulence probably reduce exposure. Experiments have documented response of coral tissue to coating by PHC. Static and flow through bioassay tests are poor because of prolonged exposure, unrealistic concentrations, and unknown real concentration of PHC (detailed as oil added with unknown solubility). Quantitative field research has advanced knowledge on the ecological consequences of PHC in coral reef communities (Loya 1972, 1975, 1976b; Loya and Rinkevich 1980). Quantitative chemical data on uptake, as well as flux between organisms, water column, and sediments are presently the missing links in field studies.

Recent studies documented that detrimental effects of PHC on corals included feeding, reproduction, recruitment, and growth. The environmental parameters make each oil spill a unique ecological problem; temperature, wind, tide, etc., all contribute to overall consequences. Heavier grades of oil that float are less likely to cause negative impact. Jaap (1975, unpublished) and Chan (1976) reported on the 1975 oil spill in the Florida Keys. The spill was of an estimated magnitude of 20,000-50,000 gallons. Diving observations and histopathology revealed little or no damage to the reefs or corals. Lighter fraction PHC that has high solubility poses a greater threat.

Rinkevich and Loya (1977) reported damage to gonadal tissues and no coral recruitment in shallow reef areas off Eilat, Israel, that were chronically polluted by PHC. Other field observations reported that *Acropora* spp. possessed a greater affinity for oil than *Agaricia* (Lewis 1971). Oil mixed with sediments also caused morbidity in corals (Bak and Elgershuzen 1976). Oil dispersant in concentrations of 100-500 ppm was harmful to corals (Lewis 1971). Oil and its effect on reproduction is of prime concern. Recent studies by Rinkevich and Loya (1977) show a strong relationship between reduced coral fecundity and PHC exposure. Lewis (1971) reported reduced feeding responses in corals exposed to PHC.

Corals respond or protect themselves from foreign materials by secretion of mucus, ciliary water currents, and pulsation. Growth and calcification studies indicate various responses to PHC exposure. Neff (1981) tested several species and found both increased and decreased calcification rates.

At this point the evidence indicates that chronic PHC pollution is harmful to coral reef communities. The stenotopic nature of many reef dwelling organisms, and the fact that many are sessile, leads to the conclusion that while most of the research in coral reefs on PHC pollution has dealt with corals, chronic or massive concentrations of PHC would also harm the other organisms. Population dynamics (reproduction, development, larval recruitment, settlement, and juvenile growth) appears to be the biological process most affected by PHC pollution.

Potential oil pollution sources include tanker cleaning and cargo discharge, vessel sinkings and accidents, and accidental discharges from petroleum production and transportation activities. The Minerals Management Service (MMS) (Department of the Interior) controls leasing and operational aspects of offshore oil exploration and development in federal waters.

Although there are numerous reports of other acts that have damaged coral reefs in other areas of the world, they are not germane to Florida at this time; hence, the reader is referred to Johannes (1975) and Bright et al. (1981) for documentation.

Coral Collection

Collection, damage, or sale of stony corals (*Millepora* spp. and Scleractinia) and two species of sea fan (*Gorgonia ventalina* and *G. flabellum*) in Florida waters is prohibited by Florida statute 370.110. Florida waters extend to 3 nmi on the Atlantic and approximately 10.3 nmi on the gulf coast. Corals and other biota within specially designated parks, marine monuments, and sanctuaries are protected by special Federal and State regulations. The area under Federal regulation is currently without protection. However, at the time of this writing the Gulf of Mexico and South Atlantic Fishery Management Councils are developing a fishery management plan for the coral reefs and corals from North Carolina to Texas. The coral reef fishery management plan will be effective as of August 22, 1984. This would extend to all the coral species found within the Federal jurisdiction (the 200-mi zone). Proposed Federal regulations would parallel Florida statutes. There would be allowable bycatch in certain fishing activities. Some areas would receive special considerations as Habitat Areas of Particular Concern (HAPC). Limitations on fishing gear and anchoring are proposed to conserve habitat (Gulf of Mexico and South Atlantic Fishery Management Councils 1981).

8.2 CORAL REEF RESOURCE MANAGEMENT

Coral reef parks and other sanctuaries represent a unique management for subsea resources.

Parks, Sanctuaries, and Monuments

Biscayne National Park (BNP) (70,822 ha; Figure 1). Located off southeast Florida, including nonreef areas in Biscayne Bay. Reef areas are seaward of Elliott and the Ragged Keys to a 60-ft (18.3-m) depth. To the southwest this park adjoins John Pennekamp Coral Reef State Park and Key Largo National Marine Sanctuary. To the north the BNP adjoins Biscayne Bay. The park is administered by the U.S. National Park Service with headquarters at Convoy Point. All coral is protected. Rangers enforce regulations.

John Pennekamp Coral Reef State Park (JPCRSP) (21,741 ha; Figure 1). Located off north and central Key Largo. It includes the mangrove communities to the 3-nmi limit. It is administered by the Florida Department of Natural Resources (FDNR) with headquarters located on Key Largo. Park rangers and the Florida Marine Patrol enforce statutes that protect coral and other living resources.

Key Largo National Marine Sanctuary (KLNMS) (25,901 ha; Figure 1). Continues from the seaward boundary of John Pennekamp Coral Reef State Park to the 300-ft (91-m) isobath. It is administered, by special agreement with the National Oceanic and Atmospheric Administration (NOAA). On site inspection is by the Florida Department of Natural Resources (DNR). Enforcement is by park rangers, U.S. Coast Guard, and Florida Marine Patrol.

Looe Key National Marine Sanctuary (LKNMS) (11,144 ha; Figure 1 and Plate 2). Recently established; located seaward of Big Pine Key. Unlike the previously mentioned parks, it does not include any coastal seafloor in its boundaries but is a discrete area of reef. Administration is by NOAA, with the Florida DNR rangers and Marine Patrol enforcing regulatory statutes on-site.

Dry Tortugas, Ft. Jefferson National Monument (19,021 ha). Located in the Dry Tortugas, 60 mi west of Key West. It is administered by U.S. National Park Service with headquarters on Garden Key, Dry Tortugas. Park rangers enforce regulations.

The following summarizes the various county, State, and Federal regulations governing portions of the resource. Shinn (1979) detailed permitting regulations and agency responsibility for collecting biological and geological specimens. In the coral reef environments a patchwork of regulations and jurisdiction exists that is inefficient and often a duplication of effort. It is beyond the scope of this treatise to review and offer ways to correct this problem. The reader may use the following outline to determine jurisdiction and enforcement responsibilities. Damage mitigation and management recommendations will be presented in 8.3.

Monroe County

Monroe County prohibits use of spearguns for the harvesting of marine protein in and around bridges and piers and in State waters from the Dade County border to Long Key.

State of Florida

Department of Natural Resources (DNR). DNR is responsible for management of all marine fisheries and resources in State waters. In the area of consideration, this includes lobster, snook, snapper, grouper, other commercial and sport species, mangrove, seagrass, and coral reef communities. DNR has specific police powers through the Florida Marine Patrol to enforce State and some Federal statutes. In the area of specific regulations for reef management, the department enforces statute 370.110 (prohibition of harvest, damage, or sale of fire coral, sea fans, and the true stony corals), 370.114 (protection of all corals in John Pennekamp Coral Reef State Park), 370.08 (management of fish collecting chemicals), and 370.15 (fishery gear regulation). The Division of Recreation and Parks manages and operates State parks and Federal marine sanctuaries through agreements with NOAA. The Division of Marine Research conducts scientific research to support management in the areas of coral reef ecology and fisheries.

Department of Environmental Regulation (DER). Within State waters DER has management powers over environmental change caused by human activity. All major engineering projects must be reviewed prior to permitting. Both environmental monitoring and research are conducted. In the area of permitting, DER reviews permits for any human activity that affects the marine environment. Coastal dredging is managed through statute 370.03 and marine pollution under statute 370.09.

Department of Administration (DOA). Under special powers the DOA can enact "State Areas of Critical Concern" and decree special regulations for indefinite periods if growth or other activities overload the capacity of local government to adequately manage the resources.

Department of State (DOS). DOS manages salvage of historical artifacts in State waters. In the Keys area this includes numerous vessels sunk offshore. The activity is managed through the licensing of salvagers and monitoring of operations. Many historical artifacts are recovered for the State. These are archived in museums and displayed for public benefit.

[illegible]

sanctuary and fishery management regulations, managing [illegible] complete an in-depth field study (not a literature survey) in the preparation of an environmental impact statement. Field scientists should have local experience in the area and know the biota. All coral reef communities within 1 nmi of the proposed project should be identified and documented so that monitoring can be accomplished. Dredging operations close to a coral reef should be required to use turbidity curtains. Turbidity and sediment fallout should be monitored; the overall rate should not exceed 200 $g/cm^2/day$ (Griffin 1974). Mechanical dredging equipment should not come in physical contact with the reef. Dredged spoils should not be disposed of on or near reef communities.

Oil spills, vessel groundings, shipwrecks, and sinkings are the responsibility of the Marine Patrol in Florida waters and the Coast Guard in Federal waters. There should be rapid resource evaluation and analysis by competent reef scientists shortly after such accidents. The enforcement agencies should call in reef scientists as soon as possible to evaluate and to offer advice to minimize resource damage in the salvaging efforts.

Each oil spill incident must be evaluated on its own merits. General guidelines are offered here, but local conditions may require taking alternative measures. When major damage occurs, the most expedient way to promote recovery is to let natural recruitment of reef biota recolonize the area. Remedial action should only be taken after it becomes evident that natural recruitment is not occurring or is very slow. Transplanting corals is a slow and costly activity. If it is done, it should be supervised by reef scientists. Hydraulic cement should be used to attach the organisms to the bottom. It will require permits to harvest stock to transplant.

In the case of vessel groundings, if the vessel is afloat or aground it should be removed from the reef as soon as possible in a manner that minimizes reef impact. Explosives should not be used. If the vessel is sunk in depths of less than 5 m, it should be salvaged. Sinkings in deeper water should be evaluated to see what sort of potential harm might occur. They might be left in place if they have no salvage value. In all vessel accidents, care should be taken to minimize fuel and cargo discharge.

Fishing-related problems are the responsibility of DNR in State waters and NMFS in the Federal zone. These agencies should take necessary action to minimize habitat destruction by sport or commercial fishing activities. Action is being taken in some fisheries at the present time. In some areas between Miami and Dry Tortugas it would be beneficial to prohibit the harvest of all fish and invertebrates. This would provide a refuge for those species under intense fishing pressure; in many cases they are harvested before they attain sexual maturity. These refuges would increase reproductive potential and return communities to a more natural state. Several existing marine parks should consider this possibility on an experimental basis for all or portions of their reef areas.

Coral reef communities found off southeast Florida are the northernmost distribution of shallow coral reefs within the tropical Atlantic biogeographical region (exception being Bermuda). Located this far north, they endure natural physical stresses not encountered in more southerly Caribbean areas. Human interferences, as noted, are not individually as harmful to the reef community as natural events (hurricanes); however, it is the chronic and synergistic effect of the human impact that causes problems. These coral reefs are a natural resource similar to California's redwood forests or the Grand Canyon, and they should be viewed as a national treasure worth conserving for future generations. Their fisheries resources are significant and yields could be increased with better management. The economics are very important to southeast Florida. Fishing, diving, boating, and tourism in general are dependent on the vitality of these coral reefs.

LITERATURE CITED

Adey, W. 1975. The algal ridges and coral reefs of St. Croix, their structure and Holocene development. Atoll Res. Bull. 187. 67 pp.

Adey, W. 1977. Shallow water Holocene bioherms of the Caribbean Sea and West Indies. Pages xxi-xxiv, Vol. 2 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Adey, W. 1978. Coral reef morphogenesis: multidimensional model. Science 202:831-837.

Adey, W., and J. Vassar. 1975. Colonization, succession, and growth rates of tropical crustose coralline algae. Phycologia 14:55-69.

Agassiz, A. 1885. The Tortugas and Florida reefs. Mem. Am. Acad. Arts Sci. 11:107-134.

Agassiz, A. 1888. Three cruises of the U.S. Coast and Geodetic Survey steamer *Blake* in the Gulf of Mexico, Caribbean, and along the Atlantic coast of the U.S. from 1877-1880. 2 vols., Boston, Mass., and *in* Bull. Mus. Comp. Zool. 14 and 15.

Agassiz, A. 1890. On the rate of growth of corals. Bull. Mus. Comp. Zool. 20(2):61-64.

Agassiz, L. 1852. Florida reefs, keys and coast. Annu. Rep. Supt. Coast Surv. 1851:107-134.

Agassiz, L. 1869. Florida reefs, keys and coast. Annu. Rep. Supt. Coast Surv. 1866:120-130.

Agassiz, L. 1880. Report on the Florida reefs. Mem. Mus. Comp. Zool. 7(1):1-61.

Alcolado, P. M. 1979. Ecological structure of the sponge fauna in a reef profile of Cuba. Pages 297-301 *in* C. Levi and N. Boury-Esnault, eds. Biologie des spongiaires. Colloq. Int. Cent. Natl. Rech. Sci. 291.

Alevizon, W.S. 1976. Mixed schooling and its possible significance in a tropical western Atlantic parrotfish and surgeonfish. Copeia 1976:796-798.

Alevizon, W.S., and M.G. Brooks. 1975. The comparative structure of two western Atlantic reef-fish assemblages. Bull. Mar. Sci. 25(4):482-490.

Al-Hussaini, A.H. 1947. The feeding habits and the morphology of the alimentary tract of some teleosts living in the neighborhood of the marine biological station, Ghardaqa, Red Sea. Publ. Mar. Biol. Stn. Ghardaqa 5.1-61.

Alldredge, A.L., and J.M. King. 1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar. Biol. 41:317-333.

Aller, R.C., and R.E. Dodge. 1974. Animal sediment relations in a tropical lagoon, Discovery Bay, Jamaica. J. Mar. Res. 32(2):209-232.

Alt, D., and H. Brooks. 1965. Age of the Florida marine terraces. J. Geol. 73(2):406-411.

Antonius, A. 1974a. Final report of the coral reef group of the Florida Keys Project for the project year 1973. Harbor Branch Foundation, Ft. Pierce, Fla. 193 pp.

Antonius, A. 1974b. New observations on coral destruction in reefs. Association of Island Marine Laboratories of the Caribbean, 10th meeting 4-7 September 1973, Mayaguez, Puerto Rico. (Abstr.)

Antonius, A. 1976. Kranke Korallen: Riffzerstorung. Umschan 76:493-494.

Antonius, A. 1977. Coral mortality in reefs: a problem for science and management. Pages 617-623, Vol. 1 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Antonius, A. 1981a. Coral pathology: a review. Pages 3-6, vol. 2 *in* Proceedings 4th Int. Coral Reef Symp., Manila, Philippines.

Antonius, A. 1981b. The "band" diseases in coral reefs. Pages 7-14, vol. 2 *in* Proceedings 4th Int. Coral Reef Symp., Manila, Philippines.

Austin, C.B., R. Brugger, J.C. Davis, and L.D. Siefert. 1977. Recreational boating in Dade County, 1975-76. Contract Rep. to Dade County Dep. of Environ. Res. Manage. 122 pp.

Avent, R.M., M.E. King, and R.H. Gore. 1977. Topographic and faunal studies of shelf edge prominences off the central eastern Florida coast USA. Int. Rev. Gesamten Hydrobiol. 62(2):185-208.

Bagby, M. 1978. The ecology of patch reef gorgonians of the coast of Key Largo, Fla. Rep. Florida International University, Miami, Fla. 28 pp.

Bak, R.P.M. 1978. Lethal and sublethal effects of dredging on reef corals. Mar. Poll. Bull. 9:14-16.

Bak, R.P.M., and J. Elgershulzen. 1976. Patterns of oil sediment rejection in corals. Mar. Biol. (Berl.) 37(2):105-113.

Bak, R.P.M., and M. Engel. 1979. Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar. Biol. (Berl.) 54:341-352.

Bak, R.P.M., and G. Van Eys. 1975. Predation of the sea urchin *Diadema antillarum* Phillippi on living coral. Oecologia (Berl.) 20:111-115.

Bakus, G.J. 1964. The effects of fish grazing on invertebrate evolution in shallow tropical waters. Allan Hancock Found. Publ. Occas. Pap. 27:1-29.

Bakus, G.J. 1969. Feeding and energetics in shallow marine waters. Int. Rev. Gen. Exp. Zool. 4:275-369.

Ball, M.M., E.A. Shinn, and K.W. Stockman. 1967. The geologic effects of Hurrican Donna in south Florida. J. Geol. 75(5):583-597.

Bardach, J.E. 1958. On the movements of certain Bermuda reef fishes. Ecology 39(1):139-146.

Barlow, G.W. 1974. Extraspecific imposition of social grouping among surgeonfishes (Pisces: Acanthuridae). J. Zool. Lond. 174:333-340.

Barnes, D.J. 1973. Growth in colonial scleractinians. Bull. Mar. Sci. 23(2):280-298.

Barnes, D.J., and D.L. Taylor. 1973. In situ studies of calcification and photosynthetic carbon fixation in the coral *Montastrea annularis*. Helgol. Wiss. Meeresunter. 24(1-4):284-291.

Bayer, F. 1956. Octocorallia. Pages F166-223 *in* R. Moore, ed. Treatise on invertebrate paleontology, Vol. F. Geological Society of America and University of Kansas Press, Lawrence.

Bayer, F. 1961. The shallow-water octocorallia of the West Indian region. Martin Nijhoff, The Hague, Netherlands. 373 pp.

Bayer, F., and A. Weinheimer. 1974. Prostaglandins from *Plexaura homomalla*, a symposium. Studies in tropical oceanography 12. University of Miami, Fla. 165 pp.

Beebe, W. 1928. Beneath tropic seas: a record of diving among the coral reefs of Haiti. G.P. Putnam, New York. 234 pp.

Bell, L.J. 1976. Notes on the nesting success and fecundity of the anemone-fish *Amphiprion clarkii* at Miyake-jima, Japan. Jpn. J. Ichthyol. 22:207-211.

Bergquist, P.R. 1978. Sponges. University of California Press, Berkeley and Los Angeles. 268 pp.

Bergquist, P.R., and W.D. Hartman. 1969. Free amino acid patterns and the classification of the Demospongiae. Mar. Biol. (Berl.) 3:247-268.

Bergquist, P.R., M.E. Sinclair, C.R. Green, and H. Silyn-Roberts. 1979. Comparative morphology and behavior of larvae of Demospongiae. Pages 103-112 *in* C. Levi and N. Boury-Esnault, eds. Biologie des spongiares. Colloq. Int. Cent. Natl. Rech. Sci. 291.

Billings, J.C., and J.L. Munro. 1974. The biology, ecology and bionomics of Caribbean reef fishes: Pomadasyidae (Grunts). Res. Rep. 3, Part Ve. Department of Zoology, University of West Indies. 128 pp.

Bohlke, J.E., and C.C.G. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical waters. Livingston Publishing Co., Wynnewood, Pa. 771 pp.

Bohnsack, J.A. 1979. The ecology of reef fishes on isolated coral heads: an experimental approach with emphasis on island biogeographic theory. Ph.D. Dissertation. University of Miami, Coral Gables, Fla. 279 pp.

Bohnsack, J.A. 1982. Effects of piscivorous predator removal on coral reef fish community structure. Pages 258-267 *in* C.M. Caillet and C.A. Simenstad, eds. Gutshop '81: fish food habit studies. Washington Sea Grant Publ., University of Washington, Seattle.

Bohnsack, J.A. (In preparation). Species turnover and the order versus chaos controversy concerning reef fish community structure.

Borgesen, F. 1913-1920. Marine algae of the Danish West Indies. I Chlorophyceae (1913); 1920. II Phacophyceae (1914); III Rhodophyceae (1916-1920). Dansk. Bot. Arkiv. 1(4):1-158, 2(2):1-66, 3(1a-1f):1-498.

Boschma, H. 1925. Studies on anthozoan polyps. Carnegie Inst. Wash. Year Book 24:223.

Boschma, H. 1929. On the post-larval development of the coral *Maeandra areolata*. Carnegie Inst. Wash. Publ. Pap. Dep. Mar. Biol. 391:129.

Boschma, H. 1948. The species problem in *Millepora*. Zool. Verh. (Leiden) 1:1-115.

Boschma, H. 1956. Milleporina and Stylasterina. Pages F90-F96 *in* R. Moore, ed. Treatise on invertebrate paleontology, Vol. F. Geological Society of America and University of Kansas Press, Lawrence.

Bradbury, R.H., and P.C. Young. 1981. The effects of a major forcing function, wave energy, on a coral reef ecosystem. Mar. Ecol. Prog. Ser. 5:229-241.

Brawley, S.H., and W.H. Adey. 1977. Territorial behavior of the three spot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. Environ. Biol. Fish. 2-45-51.

Brawley, S.H., and W.H. Adey. 1981. The effect of micrograzers on algal community structure in a coral reef microcosm. Mar. Biol. (Berl.) 61:167-177.

Breder, C.M., Sr., and D.E. Rosen. 1966. Modes of reproduction in fishes. Natural History Press, Garden City, N.Y.

Bright, T., W. Jaap, and C. Cashman. 1981. Ecology and management of coral reefs and organic banks. Pages 53-160 *in* Proceedings of environmental research needs in the Gulf of Mexico. U.S. Dep. of Commerce, NOAA, E.R.L., Miami, Fla.

Britt, D.E., and Associates Engineers. 1977. Biological monitoring of the John U. Lloyd Beach restoration project. Submitted to the Broward County Erosion Prevention Division Environmental Quality Control Board. Fort Lauderdale, Fla. 41 pp.

Brock, R.E., C. Lewis, and R.C. Wass. 1979. Stability and structure of a fish community on a coral patch reef in Hawaii. Mar. Biol. 54:281-292.

Broecker, W.S., and D.L. Thurber. 1965. Uranium-series dating of corals and oolites from Bahamian and Florida Key limestones. Science 149:58-60.

Brooks, H.K. 1963. Reefs and bioclastic sediments of the Dry Tortugas. Geol. Soc. Am. Spec. Pap. 73:1-2. (Abstr.)

Brownwell, W.N., and W.E. Rainey. 1971. Research and development of deep water commercial and sport fisheries around the Virgin Islands plateau. Virgin Islands Res. Stn. Contrib. 3:1-88.

Bruce, A. 1976. Shrimps and prawns of coral reefs, with special reference to commensalism. Pages 37-94 *in* O. Jones and R. Endean, eds. Biology and geology of coral reefs, Vol. 3. Academic Press, New York.

Bryan, P.G. 1973. Growth rate, toxicity and distribution of the encrusting sponge, *Terpios* sp. (Hadromerida. Suberitides) in Guam, Mariana Islands. Micronesica 9:237-242.

Bsharah, L. 1957. Plankton of the Florida Current, V. Environmental conditions and standing crop, seasonal and diurnal changes at a station forty miles east of Miami. Bull. Mar. Sci. Gulf Caribb. 7(3):201-251.

Buckman, N.S., and J.C. Ogden. 1973. Territorial behavior of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology 54:1377-1382.

Buddemeir, R., and R. Kinzie III. 1976. Coral growth. Oceanogr. Mar. Biol. Annu. Rev. 14:183-225.

Bullis, H.R., and A.C. Jones, eds. 1976. Proceedings: colloquium on snapper-grouper fishery resources of the western central Atlantic Ocean. Mississippi-Alabama Sea Grant Consortium, 17 November 1976.

Buss, L.W. 1976. Better living through chemistry: the relationship between allelochemical interactions and competitive network. Pages 315-327 *in* F.W. Harrison and R.R. Cowden, eds. Aspects of sponge biology. Academic Press, New York.

Cairns, S. 1977. Guide to the commoner shallow-water gorgonians (sea whips, seafeathers, and sea fans of Florida, the Gulf of Mexico, and the Caribbean region). University of Miami Sea Grant Field Guide 6. 74 pp.

Camber, C.I. 1955. A survey of the red snapper fishery of the Gulf of Mexico with special reference to the Campeche Banks. Fla. Board Conserv. Tech. Ser. 12. 64 pp.

Campbell, D.G. 1977. Bahamian chlorine bleach fishing: a survey. Pages 593-596, Vol. 2 *in* D.L. Taylor, ed. Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Carter, H.J. 1885. Catalogue of the marine sponges collected by Mr. Jos. Willcox on the west coast of Florida. Pages 202-209 *in* Proceedings of the Academy of National Sciences of Philadelphia, for 1884.

Cary, L. 1914. Observations upon the growth-rate and oecology of gorgonians. Carnegie Inst. Wash. Publ. 182:79-90.

Cary, L. 1916. Studies of Alcyonaria at Tortugas. Carnegie Inst. Wash. Year Book 15:175-177.

Cary, L. 1918a. The Gorgonacea as a factor in the formation of coral reefs. Carnegie Inst. Wash. Publ. 213:341-362.

Cary, L. 1918b. A study of the respiration in Alcyonaria. Carnegie Inst. Wash. 252(12):185-191.

Cary, L. 1918c. Studies of Alcyonaria at Tortugas. Carnegie Inst. Wash. Year Book 16:175-177.

Chalker, B.E. 1976. Calcium transport during skeletogenesis in hermatypic corals. Comp. Biochem. Physiol. 54a:455-459.

Chalker, B.E. 1977. Daily variation in the calcification capacity of *A. cervicornis*. Pages 417-423, Vol. 2 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Chalker, B.E., and D. Taylor. 1978. Rhythmic variations in calcification and photosynthesis associated with the coral *Acropora cervicornis*. Proc. R. Soc. Lond. B. Biol. Sci. 201:179-190.

Chan, E. 1976. Oil pollution and tropical littoral communities: biological effects of the 1975 Florida Keys oil spill. M.S. Thesis. University of Miami, Miami, Fla. 72 pp.

Chaplin, C., and P. Scott. 1972. Fish watchers' guide to western Atlantic coral reefs. Livingston Publ. Co., Wynnewood, Pa. 65 pp.

Chave, E.H. and D. B. Eckert. 1974. Ecological aspects of the distribution of fishes at Fanning Island. Pac. Sci. 28(3):297-319.

Chew, F. 1954. Physical oceanography of Key West Harbor and approaches. U.S. Navy Hydrographic Office Contract N600-s-x-27065. Part I: 1-37, Part II: Aa-C20. 144 pages.

Choat, J.H. 1966. Parrotfish. Aust. Nat. Hist. 15:265-268.

Colin, P.L. 1976. Filter feeding and predation on the eggs of *Thalassoma* sp. by the scombrid fish *Rastrelliger kanagurta*. Copeia 1976(3):596-597.

Colin, P.L. 1978a. Caribbean reef invertebrates and plants. T.F.H. Publications Inc. Ltd., Neptune City, N.J. 510 pp.

Colin, P.L. 1978b. Daily and summer-winter variation in mass spawning of striped parrotfish, *Scarus croicensis*. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 76:117-124.

Colin, P.L. 1982. Aspects of the spawning of western Atlantic reef fishes. Pages 69-78 *in* G.R. Huntsman, W.R. Nicholson, and W.W. Fox, eds. Proceedings: workshop on the biological basis for reef fishery management. NOAA Tech. Memo. NMFS-SEFC-80.

Collins, F. 1909. The green algae of North America. Tufts Coll. Stud. (Sci. Ser.) 2(3):79-480.

Collins, F., and A. Harvey. 1917. The algae of Bermuda. Proc. Am. Acad. Arts Sci. 53:1-195.

Connell, J. 1973. Population ecology of reef building corals. Pages 205-246, Vol. 1 *in* O. Jones and R. Endean, eds. Biology and geology of coral reefs. Academic Press, New York.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199(4335):1302-1310.

Courtenay, W.R., D.J. Herrema, M.J. Thompson, W.P. Azzinaro, and J. van Montfrans. 1974. Ecological monitoring of beach erosion control projects, Broward County, Florida, and adjacent areas. U.S. Army Corps of Engineers, Coastal Engineering Research Center, Fort Belvoir, Va. Tech. Memo. 41. 88 pp.

Crocker, L.A., and H.M. Reiswig. 1981. Host specificity in sponge encrusting zoanthidea. (Anthozoa: Zoantharia) of Barbados, West Indies. Mar. Biol. (Berl.) 65:231-236.

Dahl, A., B. Patton, S. Smith, and J. Zieman, Jr., eds. 1974. A preliminary coral reef ecosystem model. Atoll Res. Bull. 172:6-36.

Darwin, C. 1842. On the structure and distribution of coral reefs and geological observations on the volcanic islands and parts of South America visited during the voyage of *HMS Beagle*. Ward Lock and Co., London. 549 pp.

Davies, J.H. 1957. The South Africa pilchard (*Sardinops ocellata*). Preliminary report on feeding off the west coast, 1953-1956. Union S. Africa Dep. Commer. Indus. Div. Fish. Invest. Rep. 30. 31 pp.

Davis, G.E. 1977a. Anchor damage to a coral reef on the coast of Florida. Biol. Conserv. 11:29-34.

Davis, G.E. 1977b. Fishery harvest in an underwater park. Pages 605-608, Vol. 2 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Davis, G.E. 1979. Outer continental shelf resource management map coral distribution Fort Jefferson National Monument, the Dry Tortugas. U.S. National Park Service and Bureau of Land Management, New Orleans, La.

Davis, G.E. 1982. A century of natural change in coral distribution at the Dry Tortugas: a comparison of reef maps from 1881 and 1976. Bull. Mar. Sci. 32(2):608-623.

Davis, W.P. 1967. Ecological interactions, comparative biology, and evolutionary trends of thirteen pomadasyid fishes at Alligator Key, Florida Keys. Ph.D. Dissertation. RSMAS, University of Miami, Coral Gables, Fla. 128 pp.

Dayton, P.K., G.A. Robilliard, R.T. Paine, and L.B. Dayton. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol. Monogr. 44:105-128.

de Laubenfels, M.W. 1936. A discussion of the sponge fauna of the Dry Tortugas in particular and the West Indies in general, with material for a revision of the families and orders of the Porifera. Pap. Tortugas Lab. 30, Carnegie Inst. Wash. Publ. 467. Vol. 30: 225 pp.

de Laubenfels, M.W. 1949. Sponges of the western Bahamas. Am. Mus. Novit. no. 1431:1-25.

de Laubenfels, M.W. 1950. The Porifera of the Bermuda Archipelago. Trans. Zool. Soc. Lond. 27:1-154.

de Laubenfels, M.W. 1953. Sponges from the Gulf of Mexico. Bull. Mar. Sci. Gulf Caribb. 2:511-557.

Deichmann, E. 1936. Alcyonaria of the western part of the Atlantic Ocean. Mem. Mus. Comp. Zool. 53. 317 pp.

DeWeerdt, W. 1981. Transplantation experiments with Caribbean *Millepora* species (Hydrozoa, Coelenterata), including some ecological observations on growth forms. Bijdr. Dierkde. 51(1): 1-19.

Dodge, R.E. 1980. Growth characteristics of Broward County, Florida, reef-building corals. Rep. to Broward County Environmental Quality Control Board.

Dodge, R.E., and J.R. Vaisnys. 1977. Coral populations and growth patterns responses to sedimentation and turbidity associated with dredging. J. Mar. Res. 35(4):715-730.

Dodge, R.E., R.C. Aller, and J. Thomson. 1974. Coral growth related to resuspension of bottom sediments. Nature 247(5442):574-577.

Dole, R.B. 1914. Some chemical characteristics of sea-water at Tortugas and around Biscayne Bay, Florida. Pap. Tortugas Lab. 5(5):69-78.

Dole, R.B., and A.A. Chambers. 1918. Salinity of ocean water at Fowey Rocks, Florida. Carnegie Inst. Wash. Publ. 213:299-315.

Drouet, F. 1968. Revision of the classification of the Oscillatoriaceae. Monogr. 15. Academy of Natural Sciences. Philadelphia, Pa. 370 pp.

Duane, D.B., and E.P. Meisburger. 1969. Geomorphology and sediments of the nearshore Continental Shelf, Miami to Palm Beach, FL. U.S. Army Corps of Eng., Coastal Engineering Research Center, Fort Belvoir, Va. Tech. Memo. 29. 47 pp. + appendices.

Ducklow, H.W., and R. Mitchell. 1979a. Observations on naturally and artificially diseased tropical corals: a scanning electron microscope study. Microb. Ecol. 5:215-223.

Ducklow, H.W., and R. Mitchell. 1979b. Bacterial populations and adaptations in the mucus layers on living corals. Limnol. Oceanogr. 24(4):715-725.

Duerden, J. E. 1904. The coral *S. radians* and its postlarval development. Carnegie Inst. Wash. Publ. 20:1-120.

Dustan, P. 1977a. Vitality of reef coral population off Key Largo, Florida: recruitment and mortality. Environ. Geol. 2:51-58.

Dustan, P. 1977b. Besieged reefs of Florida's Keys. Nat. Hist. 86(4):73-76.

Dustan, P., W.C. Jaap, and J. Halas. 1976. The distribution of the class Sclerospongiae. Lethaia 9:419-420.

Earle, S. 1969. Phaeophyta of the eastern Gulf of Mexico. Phycologia 7:71-254.

Earle, S. 1972a. The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. Results of the Tektite Program, B. Collette and S. Earle, eds. Los Ang. Cty. Nat. Hist. Mus. Sci. Bull. 14:17-44.

Earle, S. 1972b. Benthic algae and seagrasses. Pages 15-18, appendix III, pl. 6, and maps 1-4 *in* Chemistry, primary productivity, and benthic algae of the Gulf of Mexico. American Geographical Society, New York.

Ebbs, N.K., Jr. 1966. The coral inhabiting polychaetes of the northern Florida reef tract, Part I. Bull. Mar. Sci. 16(3): 455-485.

Ehrlich, P.R. 1975. The population biology of coral reef fishes. Annu. Rev. Ecol. 6:211-247.

Ehrlich, P.R., and A.H. Ehrlich. 1973. Coevolution: heterotypic schooling in Caribbean reef fishes. Am. Nat. 107(953):157-160.

Eiseman, N. 1981. Algae. Pages 31-35 and 141-144 *in* Key Largo Coral Reef National Marine Sanctuary deep water resource survey. NOAA Tech. Rep. CZ/SP 1, Washington, D.C.

Elliott, J.M. 1971. Some methods for the statistical analysis of samples of 139 benthic invertebrates. Sci. Publ. No. 25. Freshwater Biological Association. 148 pp.

Emery, A.R. 1968. Preliminary observations on coral reef plankton. Limnol. Oceanogr. 13:293-303.

Emery, A.R. 1973. Comparative ecology and functional osteology of fourteen species of damsel fish (Pisces:Pomacentridae) at Alligator Reef, Florida Keys. Bull. Mar. Sci. 23(3):649-770.

Emery, A.R. 1978. The basis of fish community structure: marine and freshwater comparisons. Environ. Biol. Fish. 3:33-47.

Emiliani, C., J. Hudsen, and R. George. 1978. Oxygen and carbon isotopic growth record in a reef coral from the Florida Keys and a deep sea coral from the Blake Plateau. Science 202: 627-629.

Endean, R. 1976. Destruction and recovery of coral reef communities. Pages 215-254, Vol. 3 *in* O. Jones and R. Endean, eds. Biology and geology of coral reefs. Academic Press, New York.

Enos, P. 1970. Carbonate sediment accumulations of the south Florida shelf margin. Tech. Prog. Rep. EPR 29-70-F. Shell Development Co., Houston, Tex. 114 pp.

Enos, P. 1974. Map of surface sediment facies, Florida Bahamas Plateau. Geological Society of America, Boulder, Colo.

Enos, P. 1977. Holocene sediment accumulations of the south Florida shelf margin. *In* P. Enos and R. Perkins, Quarternary sedimentation in south Florida. Geol. Soc. Am. Mem. 147:1-130.

Fadlallah, Y.H. 1983. Sexual reproduction, development and larval biology in scleractinian corals. A review. Coral Reefs 2(3):129-150.

Fell, P.E. 1974. Porifera. Pages 51-132 *in* A.C. Giese and J.S. Pearse, eds. Reproduction of marine invertebrates, Vol. I. Academic Press, New York.

Finks, R.M. 1970. The evolution and ecologic history of sponges during Palaeozoic times. Symp. Zool. Soc. Lond. 25:3-22.

Finckh, A.E. 1904. Biology of the reef-forming organisms at Funafuti Atoll. Rep. Coral Reef Comm., R. Soc. London. Sec. 6:125-150.

Florida Department of Natural Resources, Florida Coastal Coordinating Council. 1974. Florida Keys coastal zone management study. Tallahassee, Fla. 138 pp.

Florida Sea Grant College. 1979. Environmental impact statement and fishery management plan for reef fish resources of the Gulf of Mexico. Gulf Mex. Fish. Manage. Council, Tampa, Fla. 164 pp. + appendices.

Frost, S.H., M. Weiss, and J. Saunders. 1977. Reefs and related carbonates, ecology and sedimentology. Studies in geology 4. American Association of Petroleum Geologists, Tulsa, Okla. 421 pp.

Fry, W.G. 1970. The biology of the Porifera. Zool. Soc. Lond. 25. Academic Press, New York. 512 pp.

Gerrodette, T., and A.O. Flechsig. 1979. Sediment in pumping rate of the tropical sponge *Verongia lacunosa*. Mar. Biol. (Berl.) 55.103-110.

Ghiold, J., and P. Enos. 1982. South Florida patch reefs *in* Carbonate production of the coral *Diploria labyrinthiformis*. Mar. Geol. 45:281-296.

Gibbs, P. 1971. The polychaete fauna of the Solomon Islands. Bull. Br. Mus. (Nat. Hist.) Zool. 21(5): 99-211.

Ginsburg, R.N. 1956. Environmental relationships of grain size and constituent particles in some south Florida carbonate sediments. Bull. Am. Assoc. Petrol. Geol. 40(10):2384-2427.

Ginsburg, R.N. ed. 1972a. Sedimenta II. Guide book for field trip 1, Geological Society of America annual meeting 1964. Comparative Sedimentology Laboratory, University of Miami, Miami, Fla. 72 pp.

Ginsburg, R.N. ed. 1972b. Geology of calcareous algae. Sedimenta I. Comparative Sedimentology Laboratory, Fisher Island Station, Miami, Fla.

Ginsburg, R.N. ed. 1973. Geology of tropical marine environments text notebook. Comparative Sedimentology Laboratory, Division of Marine Geology, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Fla.

Ginsburg, R.N., and J. Schroeder. 1973. Growth and submarine fossilization of algal cup reefs, Bermuda. Sedimentology 20:575-614.

Ginsburg, R.N., and E.A. Shinn. 1964. Distribution of the reef-building community in Florida and the Bahamas. Bull. Mar. Assoc. Petrol. Geol. 48:527. (Abstr.)

Gladfelter, E. 1983. The role of Scleractinian corals in the trophodynamics of the reef ecosystem. Pages 35-50 *in* J. Ogden and E. Gladfelter, eds. Coral reefs, seagrass beds, and mangroves: their interaction in the coastal zones of the Caribbean. UNESCO reports in Marine Science 23. Montevideo, Uruguay.

Gladfelter, W. 1982. White-band disease in *Acropora palmata:* implications for the structure and growth of shallow reefs. Bull. Mar. Sci. 32(2): 639-643.

Gladfelter, W.B., J.C. Ogden, and E.B. Gladfelter. 1980. Similarity and diversity among coral reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. Ecology 61(5): 1156-1168.

Gleason, P.J. 1974. Environments of south Florida: present and past. Memoir 2: Miami Geological Society. 452 pp.

Glynn, P.W. 1962. *Hermodice carunculata* and *Mithraculus sculptus*, two hermatypic coral predators. Association of Island Marine laboratories of the Caribbean 4th Meeting. (Abstr.)

Glynn, P.W. 1964. Common marine invertebrate animals of the shallow waters of Puerto Rico. Pages 12-20 *in* Historia natural de Puerto Rico. University of Puerto Rico, Mayaques, Puerto Rico.

Glynn, P.W. 1973. Aspects of the ecology of coral reefs in the western Atlantic region. Pages 271-324 *in* O.A. Jones and R. Endean, eds. Biology and geology of coral reefs, Vol. 2. Biology 1. Academic Press, New York.

Goldberg, W. 1973a. The ecology of the coral-octocoral communities off the southeast Florida coast: geomorphology, species composition and zonation. Bull. Mar. Sci. 23(3):465-489.

Goldberg, W. 1973b. Ecological aspects of salinity and temperature tolerance of some reef-dwelling gorgonians from Florida. Caribb. J. Sci. 13(3-4): 173-177.

Goldman, B., and F.H. Talbot. 1976. Aspects of the ecology of coral reef fishes. Pages 125-154 *in* O.A. Jones and R. Endean, eds. Biology and geology of coral reefs, Vol. 3. Biology 2. Academic Press, New York.

Gordon, H.R., and J. Dera. 1969. Irradiance attenuation measurements in seawater off southeast Florida. Bull. Mar. Sci. 19(2):279-285.

Gore, R. 1981. Decapoda crustaceans. Pages 49-53 *in* S. Jameson, ed. Key Largo Coral Reef National Marine Sanctuary deep water resource survey. NOAA Tech. Rep. CZ/SP1, Washington, D.C.

Goreau, T. 1964. Mass expulsion of zooxanthellae from Jamaican reef communities after Hurricane Flora. Science 145(3630):383-386.

Goreau, T.F., and W.D. Hartman. 1963. Boring sponges as controlling factors in the formation and maintenance of coral reefs. Am. Assoc. Adv. Sci. Publ. 75:25-54.

Goreau, T.F., and W.D. Hartman. 1966. Sponge: effect on the form of reef corals. Science 151: 343-344.

Gosline, W.A. 1965. Vertical zonation of inshore fishes in the upper water layers of the Hawaiian Islands. Ecology 46:823-831.

Grassle, J. 1973. Variety in coral reef communities. Pages 247-270 *in* O. Jones and R. Endean, eds. Biology and geology of coral reefs, Vol. 2. Academic Press, New York.

Graves, J.E., and R.H. Rosenblatt. 1980. Genetic relationships of the color morphs of the serranid fish *Hypoplectrus unicolor.* Evolution 34(2):240-245.

Green, G. 1977. Ecology of toxicity in marine sponges. Mar. Biol. 40:207-215.

Greenberg, I. 1977. Guide to the corals and fishes of Florida, the Bahamas, and the Caribbean. Seahawk Press, Miami, Fla. 64 pp.

Griffin, G. 1974. Case history of a typical dredge-fill project in the northern Florida Keys - effects on water clarity, sedimentation rates and biota. Publ. 33, Harbor Branch Foundation. 67 pp.

Gulf of Mexico and South Atlantic Fishery Management Councils. 1981. Draft Fishery Management Plan, environmental impact statement, regulatory analysis for coral and coral reef resources. Tampa, Fla. 316 pp.

Gunkel, W., and G. Gassmann. 1980. Oil, oil dispersants and related substances in the marine environment. Helgol. Wiss. Meeresunters. 33:164-181.

Hairston, N.G., F.E. Smith, and L.G. Slobodkin. 1960. Community structure, population control, and competition. Am. Nat. 94:421-425.

Halley, R.B. 1979. Guide to sedimentation for the Dry Tortugas. Southeast. Geol. Soc. 21. 98 pp.

Hamner, W.M., and J.H. Carleton. 1979. Copepod swarms: attributes and role in coral reef ecosystems. Limnol. Oceanogr. 24:1-14.

Hamner, W.M., and J.R. Hauri. 1981. Effects of island mass: water flow and plankton pattern around a reef in the Great Barrier Reef Lagoon, Australia. Limnol. Oceanogr. 26:1084-1102.

Hannau, H.W., and B.H. Mock. 1973. Beneath the seas of the West Indies, Caribbean, Bahamas, Florida, and Bermuda. Hasting House, New York. 104 pp.

Hanson, K.J., and M.F. Poindexter. 1972. The solar irradiance environment of Florida coastal water during FLARE. NOAA Tech. Memo. ERL AOML 16. 32 pp.

Hargraves, P.E. 1982. Plankton diatoms (Bacillariophyceae) from Carrie Bow Cay, Belize. Pages 153-166 *in* K. Rutzler and I.G. MacIntyre, eds. The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. Smithson. Contrib. Mar. Sci. 12. 539 pp.

Harmelin-Vivien, M.L. 1977. Ecological distribution of fishes on the outer slope of Tulear Reef (Madagascar). Pages 289-295 *in* D.L. Taylor, ed. Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Harrison, F.W., and R.R. Cowden. 1976. Aspects of sponge biology. Academic Press, New York. 354 pp.

Hartman, W.D., J.W. Wendt, and F. Wiedenmayer. 1980. Living and fossil sponges: notes for a short course. Sedimenta 8. Comparative Sedimentology Laboratory, University of Miami. 274 pp.

Harvey, W. 1852, 1853, 1858. Nereis Boreali America, Parts I-III. Part I, Melanospermae; Part II, Rhodospermaie; Part III, Chlorospermae. Smithson. Contrib. Knowl. 3(4):1-150; 5(5):1-258; 10:1-140.

Hechtel, G.J. 1965. A systematic study of the Demospongiae of Port Royal, Jamaica. Bull. Peabody Mus. Nat. Hist. 20:1-103.

Hein, F.J., and M.J. Risk. 1975. Bioerosion of coral heads: inner patch reefs, Florida reef tract. Bull. Mar. Sci. 25(1):133-138.

Hela, Ilmo. 1952. The fluctuations of the Florida Current. Bull. Mar. Sci. Gulf Caribb. 1(4):241-248.

Hiatt, R.S., and D.W. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Mongr. 30:65-127.

Highsmith, R.C. 1982. Reproduction by fragmentations in corals. Mar. Ecol. Prog. Ser. 7:207-226.

Highsmith, R.C., A.C. Riggs, and C.M. D'Antonio. 1980. Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. Oecologia 46:322-329.

Hine, A., and A. Neumann. 1977. Shallow carbonate-bank-margin growth and structure, Little Bahama Bank, Bahamas. Am. Assoc. Petrol. Geol. Bull. 61(3):376-406.

Hixon, M.A., and W.N. Brostoff. 1981. Fish grazing and community structure of Hawaiian reef algae. Pages 507-514, Vol. 2 *in* E.D. Gomez, ed. Proceedings: fourth international coral reef symposium. Marine Science Center, University of the Philippines, Diliman, Quezon City.

Hobson, E.S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. U.S. Natl. Mar. Fish. Serv. Bull. 72:915-1031.

Hobson, E.S., and J.R. Chess. 1978. Trophic relationships among fishes and plankton in the lagoon at Eniwetok Atoll, Marshall Islands. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 76: 133-153.

Hobson, E.S., and J.R. Chess. 1979. Zooplankters that emerge from the lagoon floor at night at Kure and Midway Atolls, Hawaii. U.S. Natl. Mar. Fish. Serv. Fish Bull. 77:275-280.

Hoffmeister, J.E. 1974. Land from the sea, the geologic story of south Florida. University of Miami Press, Miami, Fla. 143 pp.

Hoffmeister, J.E., and H.G. Multer. 1964. Growth rate estimates of a Pleistocene coral reef of Florida. Geol. Soc. Am. Bull. 75:353-358.

Hoffmeister, J.E., and H.G. Multer. 1968. Geology and origin of the Florida Keys. Geol. Soc. Am. Bull. 79:1487-1502.

Hoffmeister, J.E., J.E. Jones, H.G. Multer, D.R. Moore, and J.D. Milliman. 1964. Living and fossil reef types of south Florida. Guide book field trip 3. Geological Society of America annual meeting.

Holzberg, S. 1973. Beobachtungen zur Okologie und zum Sozialverhalten des Korallenbarsches *Dascyllus marginatus* Ruppel (Pisces: Pomacentridae). Z. Tierpsychol. 33(5):492-513.

Howe, M. 1918. Algae. Pages 489-540 *in* N.L. Britton, ed. Flora of Bermuda. Charles Scribner's Sons, New York.

Howe, M. 1920. Algae. Pages 553-626 *in* N.L. Britton and C. Millspaugh, eds. The Bahama flora. Private publication.

Hubbard, J.A.E.B. 1973. Sediment-shifting experiments: a guide to functional behavior in colonial corals. Pages 31-42 *in* R.S. Boardman, A.H. Cheetham, and W.A. Oliver, Jr., eds. Animal colonies. Dowden, Hutchinson and Ross Inc., Stroudsburg, Pa.

Hubbard, J., and Y. Pocock. 1972. Sediment rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. Geol. Rundsch. 61:598-626.

Hudson, J.H. 1977. Long-term bioerosion rates on a Florida reef: a new method. Pages 491-497, Vol. 2 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Hudson, J.H. 1981. Growth rates in *Montastraea annularis:* a record of environmental change in Key Largo Coral Reef Marine Sanctuary, Florida. Bull. Mar. Sci. 31(2):444-459.

Hudson, J.H. (In press). Response of *Montastraea annularis* to environmental change in the Florida Keys. Pages 233-240, Vol. 2 *in* Proceedings: fourth international coral reef symposium. Marine Science Center, University of the Philippines, Diliman, Quezon City. (Published 1981.)

Hudson, J.H., E. Shinn, R. Halley, and B. Lidz. 1976. Sclerochronology: a tool for interpreting past environments. Geology 4:361-364.

Humm, H., and S. Wicks. 1980. Introduction and guide to the marine bluegreen algae. John Wiley and Sons, New York. 104 pp.

Hunt, E.B. 1863. On the origin . . . of the Florida reef. Am. J. Sci. New Haven 35:197.

Huntsman, G.R., W.R. Nicholson, and W.W. Fox, Jr., eds. 1982. The biological bases for reef fishery management. Proceedings of a workshop held October 7-10, 1980 at St. Thomas Virgin Islands of the U.S. U.S. Dep. Comm., NOAA Tech. Memo NMFS-SEFC-80. 216 pp.

Hurlbert, S. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577-586.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or Why are there so many animals? Am. Nat. 93 (870):145-159.

Itzkowitz, M. 1977. Spatial organization of the Jamaican damselfish community. J. Exp. Mar. Biol. Ecol. 28:217-241.

Itzkowitz, M. 1978. Group organization of a territorial damselfish, *Eupomacentrus planifrons.* Behaviour 65:125-137.

Jaap, W.C. 1974. Scleractinian growth rate studies. Page 17 *in* Proceedings of the Florida Keys coral reef workshop. Florida Department of Natural Resources, Coastal Coordinating Council. (Abstr.)

Jaap, W.C. 1975. Unpubl. Rep. on the July 1975 Florida Keys oil spill. Florida Department of Natural Resources, Marine Research Laboratory.

Jaap, W.C. 1979. Observations on zooxanthellae expulsion at Middle Sambo Reef, Florida Keys, USA. Bull. Mar. Sci. 29(3):414-422.

Jaap, W.C. 1981. Stony corals (Milleporina and Scleractinia). Pages 7-13 *in* S. Jameson, ed. Key Largo Coral Reef National Marine Sanctuary deep water resource survey. NOAA Tech. Rep. CZ/SP1, Washington, D.C.

Jaap, W.C. (In preparation.) Population dynamics of stony corals in southeast Florida patch reefs.

Jaap, W.C., and J. Wheaton. 1975. Observations of Florida reef corals treated with fish-collecting chemicals. Fla. Mar. Res. Publ. 10. 18 pp.

Jaap, W.C., and J. Wheaton. 1977. Report to National Park Service: Biscayne National Monument reef studies. (MS.)

Jackson, J., and L. Buss. 1975. Alleopathy and spatial competition among coral reef invertebrates. Proc. Natl. Acad. Sci. USA 72:5160-5163.

Jackson, J.B.C., and J.E. Winston. 1982. Ecology of cryptic coral reef communities. I. Distribution and abundance of major groups of encrusting organisms. J. Exp. Mar. Biol. Ecol. 57:135-147.

Jameson, S., ed. 1981. Key Largo Coral Reef National Marine Sanctuary deep water resource survey. NOAA Tech. Rep. CZ/SP1, Washington, D.C. 144 pp.

Jeffrey, S.W. 1968. Photosynthetic pigments of the phytoplankton of some coral reef waters. Limnol. Oceanogr. 13:350-355.

Jindrich, V. 1972. Biogenic buildups and carbonate sedimentation, Dry Tortugas reef complex, Florida. Ph.D. Dissertation. State University of New York at Binghamton. 95 pp.

Johannes, R.E. 1975. Pollution and degradation of coral reef communities. Pages 13-51 *in* R.E. Johannes and E.J. Ferguson Wood, eds. Tropical marine pollution. Elsevier Scientific Publishing Co., Amsterdam, Netherlands.

Johannes, R.E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fish. 3:65-84.

Johansen, H. 1981. Coralline algae, a first synthesis. CRC Press, Boca Raton, Fla. 239 pp.

Jokiel, P., and R.H. York, Jr. 1982. Solar ultraviolet photobiology of the reef coral *Pocillopora damicornis* and symbiotic zooxanthellae. Bull. Mar. Sci. 32(1):301-315.

Jones, J.A. 1963. Ecological studies of the southeastern Florida patch reefs. I: Diurnal and seasonal changes in the environment. Bull. Mar. Sci. Gulf Caribb. 13(2):282-307.

Jones, J.A. 1977. Morphology and development of southeast Florida patch reefs. Pages 231-235, Vol. 2 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Jones, O., and R. Endean, eds. 1973. Biology and geology of coral reefs. Vol. 2: Biology 1. Academic Press, New York. 480 pp.

Jones, O., and R. Endean, eds. 1976. Biology and geology of coral reefs, Vol. 3. Biology 2. Academic Press, New York. 435 pp.

Jones, R.S. 1968. Ecological relationships in Hawaiian and Johnson Island Acanthuridae (surgeonfishes). Micronesica 4:309-361.

Jones, R.S., and J.A. Chase. 1975. Community structure and distribution of fishes in an enclosed high island lagoon in Guam. Micronesica 11:127-148.

Jones, R.S., and M.J. Thompson. 1978. Comparison of Florida reef fish assemblages using a rapid visual technique. Bull. Mar. Sci. 28(1):159-172.

Jordan, D.S., and J.C. Thompson. 1904. The fish fauna of the Tortugas archipelago. Bull. U.S. Bur. Fish. 24:229-256.

Kanwisher, J., and S. Wainwright. 1967. Oxygen balance in some coral reefs. Biol. Bull. (Woods Hole) 133(2):378-390.

Kaplan, E.H. 1982. A field guide to coral reefs of the Caribbean and Florida. Peterson Field Guide Series 27. Houghton, Mifflin Co., Boston, Mass. 289 pp.

Katnik, S. 1981. The effects of fishing pressures on some economically important fishes on Guam's reef flats. Page 111 (abstr.), Vol. 1 *in* E.D. Gomez, ed. Proceedings: fourth international coral reef symposium. Marine Science Center, University of the Philippines, Diliman, Quezon City.

Kaufman, L. 1977. The three spot damsel fish: effects on benthic biota of Caribbean coral reefs. Pages 559-564, Vol. 1 *in* D. Taylor, ed. Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Kawaguchi, K. 1974. Handline and longline fishing exploration for snapper and related species in the Caribbean and adjacent waters. Mar. Fish. Rev. 36(9):8-31.

Kaye, H., and T. Ortiz. 1981. Stain specificity in a tropical marine sponge. Mar. Biol. 63:165-173.

Kier, P.M., and R.E. Grant. 1965. Echinoid distribution and habits, Key Largo Coral Reef Preserve, Florida. Smithson. Misc. Collect. 149(6).68 pp.

Kinzie, R.A., III. 1973. The zonation of West Indian gorgonians. Bull. Mar. Sci. 23:93-155.

Kinzie, R.A. 1974. *Plexaura homomalla:* the biology and ecology of a harvestable marine resource. Pages 22-38 *in* F.M. Bayer and A.J. Weinheimer, eds. Prostaglandins in *Plexaura homomalla,* a symposium. Stud. Trop. Oceanogr. 12. University of Miami, Fla.

Kissling, D.L. 1965. Coral distribution on a shoal in Spanish Harbor, Florida Keys. Bull. Mar. Sci. 15(3):599-611.

Kissling, D.L. 1975. Coral reefs in the lower Florida Keys: a preliminary report. Pages 102E-102J *in* H.G. Multer, ed. Field guide to some carbonate rock environments - Florida Keys and Western Bahamas. Publ. by the editor. Farleigh Dickinson University, Madison, N.J.

Kissling, D., 1977. Population structure characteristics for some Paleozoic and modern corals. Pages 457-507 *in* Proceedings: second international symposium on corals and fossil coral reefs. Bur. Reche. Geolog. Min. 89.

Kissling, D., and G. Taylor. 1977. Habitat factors for reef-dwelling ophiurids in the Florida Keys. Pages 225-231, Vol. I *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Klima, E.F. 1976. Snapper and grouper resources of the western central Atlantic Ocean. Fla. Sea Grant Rep. No. 17.

Kojis, B., and N. Quinn. 1981. Aspects of sexual reproduction and larval development in the shallow-water hermatypic coral *Goniastrea australensis* (Edwards and Haime). Bull. Mar. Sci. 31(3): 558-573.

Knowlton, N., J. Lang, M. Rooney, and P. Clifford. 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. Nature 249(5838):251-252.

Kriegel, R.V. 1972. A study of the correlation between the zooxanthellae/host polyp symbiosis and latitudinal extent of hermatypic coral formation in southern Florida coastal waters. M.S. Thesis. Florida Institute of Technology, Melbourne.

Landon, S. 1975. Environmental controls on growth rates in hermatypic corals from the lower Florida Keys. M.S. Thesis. State University of New York, Binghamton. 80 pp.

Lang, J. 1971. Interspecific aggression by Scleractinian corals. I. The rediscovery of *Scolymia cubensis* (Milne Edwards and Haime). Bull. Mar. Sci. 21(4):952-959.

Lang, J.C. 1973. Interspecific aggression by scleractinian coral 2. Why the race is not to the swift. Bull. Mar. Sci. 23:260-279.

Lang, J. 1980. Are the sweeper tentacles of *Montastraea cavernosa* polyfunctional organs? Assoc. Island Marine Laboratories, Discovery Bay, Jamaica. (Abstr.)

Lang, J.C. 1982. The fore reef. Pages 45-54 *in* E.H. Kaplan. A field guide to coral reefs of the Caribbean and Florida. Peterson Field Guide Ser. 27. Houghton Mifflin Company, Boston, Mass.

Lang, J.C., W.D. Hartman, and L.S. Land. 1975. Sclerosponges: primary framework constructors on the Jamaican deep forereef. J. Mar. Res. 33: 223-231.

LeCompte, M. 1937. Some observations on the coral reefs area of Tortugas. Carnegie Inst. Wash. Annu. Rep. Tortugas Lab., p. 96.

LeConte, J. 1857. On the agency of the Gulf Stream in the formation of the peninsula and Keys of Florida. Am. J. Soc. New Haven 23:46.

Lee, T.N. 1975. Florida current spin-off eddies. Deep Sea Res. 22:753-765.

Lee, T.N., and D.A. Mayer. 1977. Low-frequency current variability and spin-off eddies along the shelf off S.E. Florida. J. Mar. Res. 35:193-220.

Lee, T.N., and C.N.K. Mooers. 1977. Near-bottom temperature and current variability over the Miami slope and terrace. Bull. Mar. Sci. 27:758-775.

Leis, J.M., and J.M. Miller. 1976. Offshore distributional patterns of Hawaiian fish larvae. Mar. Biol. 36:359-367.

Leming, T.D. 1979. Observations of temperature, current, and wind variations off the central eastern coast of Florida during 1970 and 1971. U.S. Dep. Comm. NOAA Tech. Memo. NMFS-SEFC-6. 172 pp.

Levi, C. 1957. Ontogeny and systematics in sponges. Syst. Zool. 6:174-183.

Levi, C., and N. Boury-Esnault, eds. 1979. Biologie des spongiares [Sponge biology]. Colloq. Int. Cent. Natl. Rech. Sci. No. 291. Paris 18-22 Decembre 1978. 533 pp.

Levin, J. 1970. A literature review of the effects of sand removal on a coral reef community. University of Hawaii, Department of Ocean Engineering Publ. 78 pp.

Lewis, J. 1971. The effects of crude oil and oil dispersant on reef corals. Mar. Pollut. Bull. 2:59-62.

Lewis, J.B. 1974. The importance of light and food upon early growth of the reef coral *Favia fragum* Esper. J. Exp. Mar. Biol. Ecol. 15:299-304.

Lewis, J., and W. Price. 1975. Feeding mechanisms and strategies of Atlantic reef-corals. J. Zool. (Lond.) 176:527-545.

Lewis, S.M. 1982. Sponge-zoanthid associations: functional interactions. Smithson. Contrib. Mar. Sci. 12:465-474.

Lighty, R.G. 1977. Relict shelf-edge Holocene coral reef: southeast coast of Florida. Pages 215-222, Vol. 2 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Lighty, R.G., I.G. MacIntyre, and R. Stuckenrath. 1978. Submerged early Holocene barrier reef southeast Florida shelf. Nature (Lond.) 296 (5683):59-60.

Lighty, R.G., I.G. MacIntyre, and R. Stuckenrath. 1982. *Acropora palmata* reef framework: a reliable indicator of sea level in the western Atlantic for the past 10,000 years. Coral Reefs 1:125-130.

Limbaugh, C. 1961. Cleaning symbiosis. Sci. Am. 205 (2):42-49.

Little, F.J., Jr. 1963. The sponge fauna of the St. George's Sound, Apalachee Bay and Panama City regions of the Florida gulf coast. Tulane Stud. Zool. 11:31-71.

Littler, M. 1973. The productivity of Hawaiian fringing-reef crustose Corallinaceae and an experimental evaluation of production methods. Limnol. Oceanogr. 18:946-952.

Lizama, J., and R. Blanquet. 1975. Predation on sea anemones by the amphinomid polychaete *Hermodice carunculata*. Bull. Mar. Sci. 25(3): 442-443.

Lobel, P.S. 1978. Diel, lunar, and seasonal periodicity in the reproductive behavior of the pomacanthid fish, *Centropyge potteri*, and some other reef fishes in Hawaii. Pac. Sci. 32:193-207.

Loeblich, A.R., III, and J.L. Shirley. 1979. Observations on the theca of the motile phase of free-living and symbiotic isolates of *Zooxanthellae microadriatica* (Freudenthal) comb. nov. J. Mar. Biol. Assoc. U.K. 59:195-205.

Loftas, T. 1970. New threats to coral reefs (pollution, algae, sewage). New Sci. (Lond.) 48(731): 559.

Longley, W.H., and S.F. Hildebrand. 1941. Systematic catalogue of the fishes of Tortugas, Fla. with observations on color, habits and local distribution. Pap. Tortugas Lab. 34:1-331.

Low, R.M. 1971. Interspecific territoriality in a pomacentrid reef fish, *Pomacentrus flavicauda* Whitley. Ecology 52:648-654.

Loya, J. 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. Mar. Biol. (Berl.) 13:100-123.

Loya, J. 1975. Possible effects of water pollution on the community structure of Red Sea corals. Mar. Biol. (Berl.) 29(2):177-185.

Loya, Y. 1976a. Sedimentation effects on the community structure of Puerto Rican corals. Bull. Mar. Sci. 26(4):450-466.

Loya, Y. 1976b. Recolonization of Red Sea corals affected by natural catastrophies and man-made perturbations. Ecology 57:278-289.

Loya, Y., and B. Rinkevich. 1980. Effects of oil pollution on coral reef communities. Mar. Ecol. Prog. Ser. 3(2):167-180.

Lyons, W., and F. Kennedy, Jr. 1981. Effects of harvest techniques on sublegal spiny lobsters and on subsequent fishery yield. Proceedings: 33rd Gulf and Caribbean Fishery Institute, San Jose, Costa Rica.

Lyons, W.G., D. Barber, S. Foster, F. Kennedy, and G. Milano. 1981. The spiny lobster, *Panulirus argus*, in the middle and upper Florida Keys: population structure, seasonal dynamics, and reproduction. Fla. Mar. Res. Publ. 38. 38 pp.

MacIntyre, I.G., S.V. Smith, and J.C. Zieman. 1974. Carbon flux through a coral-reef ecosystem: a conceptual model. J. Geol. 82(2):161-171.

Manker, J.P. 1975. Distribution and concentration of mercury, lead, cobalt, zinc, and chromium in suspended particles and bottom sediments - Upper Florida Keys, Florida Bay and Biscayne Bay. Ph.D. Thesis. Rice University, Houston, Tex. 114 pp.

Mapstone, G.N., and E. Wood. 1975. The ethology of *Abudefduf lunidus* and *Chromis chromis* (Pisces: Pomacentridae) from the Azores. J. Zool. 175: 179-199.

Margalef, R. 1968. Perspectives in ecological theory. University of Chicago Press, Ill.

Marsden, J. 1960. Polychaetous annelids from the shallow waters around Barbados and other islands of the West Indies, with notes on larval forms. Can. J. Zool. 38:989-1020.

Marsden, J.R. 1962. A. Coral-eating polychaete. Nature 193(4815):598.

Marsh, J. 1970. Primary productivity of reef building red algae. Ecology 51:255-263.

Marshal, N.B. 1965. The life of fishes. Weidenfeld and Nicholson, London.

Marszalek, D. 1981, 1982. Florida reef tract marine habitat and ecosystems. (Map series) Published in cooperation with the Florida Department of Natural Resources, U.S. Department of the Interior, Bureau of Land Management; and University of Miami, Miami, Fla.

Marszalek, D., G. Babashoff, M. Noel, and P. Worley. 1977. Reef distribution in south Florida. Pages 223-230, Vol. 2 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Mathieson, A.C., R. Fralick, and W. Flashive. 1975. Phycological studies during Tektite II at St. John, U.S.V.I. Results of the Tektite Program: coral reef invertebrates and plants. Nat. Hist. Mus. Los Ang. Cty. Sci. Bull. 20:77-103.

Matthai, G. 1916. Preliminary report on the comparative morphology of recent Madreporaria around Tortugas. Carnegie Inst. Wash. Year Book 14: 209.

Maul, G. 1976. Variability in the Gulf Stream system. Gulfstream 2(10):6, 7.

Maxwell, W.G.H. 1968. Atlas of the Great Barrier Reef. American Elsevier, New York. 258 pp.

Mayer, A.G. 1902. The Tortugas as a station for research in biology. Science 17(422):190-192.

Mayer, A. 1914. The effects of temperature upon tropical marine animals. Pap. Tortugas Lab. Carnegie Inst. Wash. 6:1-24.

Mayer, A.G. 1916. The lower temperature at which reef-corals lose their ability to capture food. Carnegie Inst. Wash. Year Book 14:212.

Mayer, A.G. 1918. Toxic effects due to high temperature. Carnegie Inst. Wash. Publ. Dept. Mar. Biol. 12:175-178.

McCallum, J., and K. Stockman. 1964. Florida Bay. Water circulation. Pages 11-13 *in* R. Ginsburg, ed. South Florida carbonate sediments guidebook. Geological Society of America Convention, Miami, Fla.

McCloskey, L. 1970. The dynamics of the community associated with a marine scleractinia coral. Int. Rev. Gesamten Hydrobiol. 55:13-81.

McCloskey, L.R., and R.H. Chesher. 1971. Effects of man-made pollution on the dynamics of coral reefs. Pages 229-257, Vol. 6 *in* J.W. Miller, J.G. Van Derwalker, and R.A. Waller, eds. Scientist in the sea. U.S. Department of the Interior, Washington, D.C.

McFarland, W.N., J.C. Ogden, and V.N. Lythgoe. 1979. The influence of light on the twilight migration of grunts. Environ. Biol. Fish. 4(1):9-22.

McWilliams, P.S., P.F. Sale, and D.T. Anderson. 1981. Seasonal changes in resident zooplankton sampled by emergence traps in the One Tree Lagoon, Great Barrier Reef. J. Exp. Mar. Biol. Ecol. 52: 185-203.

Menzel, D.W. 1959. Utilization of algae for growth by the angelfish. J. Cons. Perm. Int. Explor. Mer 24: 308-313.

Mergner, H. 1977. Hydroids as indicator species for ecological parameters in Caribbean and Red Sea coral reefs. Pages 119-126, Vol. 2 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Meyer, J.L., E.T. Schulte, and G.S. Helfman. 1983. Fish schools: an asset to corals. Science 220: 1047-1049.

Miller, W., R. Montgomery, and A. Collier. 1977. A taxonomic survey of the diatoms associated with Florida Keys coral reefs. Pages 349-355, Vol. 2 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Mitchell, R., and I. Chet. 1975. Bacterial attack of corals on polluted seawater. Microb. Ecol. 2: 227-233.

Mitchell-Tapping, H.J. 1981. Particle breakdown of recent carbonate sediment in coral reefs. Fla. Sci. 44(1):21-29.

Montgomery, W.L. 1980. The impact of nonselective grazing by the giant blue damselfish, *Microspathodon dorsalis* on algal communities in the Gulf of California, Mexico. Bull. Mar. Sci. 30:290-303.

Montgomery, W.L., T. Gerrodette, and L.D. Marshall. 1980. Effects of grazing by the yellowtail surgeonfish, *Prionurus punctatus*, on algal communities in the Gulf of California, Mexico. Bull. Mar. Sci. 30(4):901-908.

Moore, H. 1972. An estimate of carbonate production by macrobenthos in some tropical, soft bottom communities. Mar. Biol. (Berl.) 17:145-148.

Moran, M.J., and P.F. Sale. 1977. Seasonal variation in territorial response, and other aspects of the ecology of the Australian temperate pomacentrid fish *Parma microlepsis*. Mar. Biol. 39(2): 121-128.

Motoda, S. 1940. The environment and the life of massive reef coral *Goniastrea aspera* Verrill, inhabiting the reef flat in Palao. Stud. Palao Trop. Biol. Stn. 2:61-103.

Moyer, J.T., and L.J. Bell. 1976. Reproductive behavior of the anemonefish *Amphiprion clarkii* at Miyake-jima, Japan. Jpn. J. Ichthyol. 23:23-32.

Moyer, J.T., and A. Nakazono. 1978. Population structure, reproductive behavior, and protogynous hermaphroditism in the angelfish *Centropyge interruptus* at Miyake-jima, Japan. Jpn. J. Ichthyol. 25:25-39.

Multer, G.H. 1971. Field guide to some carbonate rock environments. Florida Keys and western Bahamas. Fairleigh Dickinson University, Madison, N.J., and Miami Geological Society. 158 pp.

Munro, J.L. 1976. Aspects of the biology and ecology of Caribbean reef fishes: Mullidae (goat-fishes). J. Fish. Biol. 9(1):79-97.

Munro, J.L., P.H. Reeson, and V.C. Gaut. 1971. Dynamic factors affecting the performance of the antillean fish trap. Gulf Caribb. Fish. Inst. 23: 184-194.

Munro, J.L., V.C. Gaut, R. Thompson, and P.H. Reeson. 1973. The spawning seasons of Caribbean reef fishes. J. Fish. Biol. 5:69-84.

Muscatine, L. 1973. Nutrition of corals. Pages 77-115, Vol. 2 *in* O.A. Jones and R. Endean, eds. Biology and geology of coral reefs. Biology 1. Academic Press, New York.

Muscatine, L., and J.W. Porter. 1977. Reef corals: mutualistic symbiosis adapted to nutrient-poor environments. Bioscience 27:454-460.

Myrberg, A.A., Jr. 1972. Ecology of the bicolor damselfish *Eupomacentrus partitus* (Pisces: Pomacentridae): a comparative analysis of laboratory and field behavior. Anim. Behav. Monogr. 5 (3): 199-283.

National Marine Fisheries Service (NOAA), and Florida Department of Natural Resources. 1981. Florida landings, annual summary 1975, current fisheries statistics no. 6916. Washington, D.C. 12 pp.

National Oceanic and Atmospheric Administration (NOAA). 1981. Local climatological data, annual summary (1980) with comparative data, Miami and Key West, Florida. NOAA, National Climatic Center, Asheville, N.C. 4 pp.

National Oceanic and Atmospheric Administration, Office of Coastal Zone Management. 1979. Key Largo Coral Reef Marine Sanctuary Management Plan. v.s. Department of Commerce, Washington, D.C. 41 pp.

Neff, J., ed. 1981. Sublethal effects of petroleum on reef corals. American Petroleum Institute, Division of Environmental Affairs, Washington, D.C.

Neumann, A.C. 1966. Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*. Limnol. Oceanogr. 11:92-108.

Newell, N.D. 1971. An outline of history of tropical organic reefs. Am. Mus. Novit. 2465:37 pp.

Odum, E.P. 1971. Fundamentals of ecology. 3rd ed. W.B. Saunders Co., Philadelphia, Pa. 574 pp.

Odum, H.T., and E.P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr. 25: 291-320.

Ogden, J. 1976. Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. Aquat. Bot. 2:103-116.

Ogden, J.C., and N.S. Buckman. 1973. Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology 54:589-596.

Ogden, J.C., and J.P. Ebersole. 1981. Scale and community structure of coral reef fishes: a long-term study of a large artificial reef. Mar. Ecol. Prog. Ser. 4:97-103.

Ogden, J.C., and P.R. Ehrlich. 1977. The behavior of heterotypic resting schools of juvenile grunts (Haemulidae). Mar. Biol. 42:273-280.

Ogden, J., and P. Lobel. 1978. The role of herbivorous fishes and urchins in coral reef communities. Environ. Biol. Fishes 3:49-63.

Ogden, J.C., and J.C. Zieman. 1977. Ecological aspects of coral reef - seagrass bed contacts in the Caribbean. Pages 377-382, Vol. 2 *in* Proceedings: third international coral reef symposium, University of Miami, Miami, Fla.

Ogden, J., R. Brown, and N. Salesky. 1973. Grazing by the Echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. Science 182(413):715-716.

Ohlhorst, S.L. 1982. Diel migration patterns of demersal reef zooplankton. J. Exp. Mar. Biol. Ecol. 60:1-15.

Opresko, D. 1973. Abundance and distribution of shallow-water gorgonians in the area of Miami, Florida. Bull. Mar. Sci. 23(3):535-558.

Paine, R. 1966. Food web complexity and species diversity. Am. Nat. 100:65-75.

Pang, R.K. 1973a. The ecology of some Jamaican excavating sponges. Bull. Mar. Sci. 23(2):227-243.

Pang, R.K. 1973b. The systematics of some Jamaican excavating sponges (Porifera). Postilla 161:1-75.

Parrish, J.D., and R.J. Zimmerman. 1977. Utilization by fishes of space and food resources on an offshore Puerto Rican coral reef and its surroundings. Pages 297-303 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Patton, W.K. 1967. Studies on *Domecia acanthophora*, a commensal crab from Puerto Rico, with particular reference to modifications of the coral host and feeding habits. Biol. Bull. 132(1):56-67.

Patton, W.K. 1976. Animal associates of living reef corals. Pages 1-36, *in* O.A. Jones and R. Endean, eds. Biology and geology of coral reefs, Vol. 3. Academic Press, New York.

Pauly, D., and J. Ingles. (In press). Aspects of the growth and natural mortality of exploited coral fish populations. Pages 89-98, Vol. 1 *in* E.D. Gomez, ed. Proceedings: fourth international coral reef symposium. Marine Science Center, University of the Philippines, Diliman, Quezon City. (Published 1981.)

Pearse, A.S. 1932. Inhabitants of certain sponges at Dry Tortugas. Pap. Tortugas Lab. 28(77):117-124.

Pearson, R. 1981. Recovery and recolonization of coral reefs. Mar. Ecol. Prog. Ser. 4:105-122.

Perkins, R.D., and P. Enos. 1968. Hurricane Betsy in the Florida-Bahama area. Geological effects and comparison with Hurricane Donna. J. Geol. 76: 710-717.

Perkins, R., and I. Tsentas. 1976. Microbial infestation of carbonate substrates planted on the St. Croix shelf, West Indies. Bull. Geol. Soc. Am. 87:1615-1628.

Pielou, E. 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13:131-144.

Porter, J. 1972. Patterns of species diversity in Caribbean reef corals. Ecology 53:745-748.

Porter, J., J. Battey, and G. Smith. 1982. Perturbation and change in coral reef communities. Proc. Natl. Acad. Sci. 79:1678–1681.

Porter, J.W. 1974. Zooplankton feeding by the Caribbean reef-building coral *Montastrea cavernosa.* Pages 111-125, Vol. 1 *in* Proceedings: second international coral reef symposium. Great Barrier Reef Comm., Brisbane, Australia.

Porter, J.W., K.G. Porter, and Z. Bavac-Catalan. 1977. Quantitative sampling of Indo-Pacific demersal reef plankton. Pages 105-112, Vol. 1 *in* Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Porter, K.G., J.W. Porter, and S.L. Ohlhorst. 1978. Resident reef plankton. Pages 499-515 *in* D.R. Stoddart and R.E. Johannes, eds. Coral reefs: research methods. UNESCO Monogr. Oceanogr. Meth. 4. 581 pp.

Potts, D.C. 1977. Suppression of coral populations by filamentous algae within damselfish territories. J. Exp. Mar. Biol. Ecol. 28(3):207-216.

Potts, G.W. 1973. The ethology of *Labroides dimidiatus* (Cuv. & Val.) (Labridae, Pisces) on Aldabra. Anim. Behav. 21:250-291.

Pourtales, L.F. 1863-1869. Contributions to the fauna of the Gulf Stream at great depths. Bull. Mus. Comp. Zool. Harv. Univ. 1(6):103-120; 1(7):121-142.

Pourtales, L.F. 1871. Deep-sea corals. Illustr. Cat. Mus. Comp. Zool. 4:1-93.

Pourtales, L.F. 1878. Reports on the results of dredging in the Gulf of Mexico, by the U.S. Coast Survey Steamer *Blake*. II, Crinoids & corals. Bull. Mus. Comp. Zool. Harv. College.

Pourtales, L.F. 1880. Reports on the results of dredging . . . in the Gulf of Mexico, by the U.S. Coast Survey Steamer *Blake*. VI, Report on the corals and Antipatharia. Bull. Mus. Comp. Zool. Harv. College. 6:95-120.

Preston, F.S. 1950. Coral ulcer. Br. Med. J. (Lond.) 4654:642.

Randall, J.E. 1961a. Overgrazing of algae by herbivorous marine fishes. Ecology 424:812.

Randall, J.E. 1961b. A contribution to the biology of the convict surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sanduicensis*. Pac. Sci. 15:215-272.

Randall, J.E. 1961c. Tagging reef fishes in the Virgin Islands. Proc. Gulf Caribb. Fish. Inst. 14th annu. sess.:201-241.

Randall, J.E. 1962. Additional recoveries of tagged reef fishes from the Virgin Islands. Proc. Gulf Caribb. Fish. Inst. 15th annu. sess.:155-157.

Randall, J.E. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Caribb. J. Sci. 3(1):1-16.

Randall, J.E. 1965. Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. Ecology 46(3):255-260.

Randall, J.E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. 5:665-847.

Randall, J.E. 1974. The effect of fishes on coral reefs. Pages 159-166, Vol. 1 *in* Proceedings: second international coral reef symposium. Great Barrier Reef Comm., Brisbane, Australia.

Randall, J.E., and W.D. Hartman. 1968. Sponge-feeding fishes of the West Indies. Mar. Biol. 1:216-225.

Randall, J.E., R.E. Schroeder, and W.A. Starck II. 1964. Notes on the biology of the echinoid *Diadema antillarum*. Caribb. J. Sci. 4:421-433.

Rasa, O.A.E. 1969. Territoriality and the establishment of dominance by means of visual cues in *Pomacentrus jenkinsi* (Pisces: Pomacentridae). Z. Tierpsychol. 26:825-845.

Ray, J. 1981. The effect of petroleum hydrocarbons on corals. Pages 705-726 *in* Petromat-80. Graham and Trotman Ltd., London. 788 pp.

Raymond, W.F. 1972. A geologic investigation of the offshore sands and reefs of Broward County, Fla. (Supplement supplied species lists.) Masters Thesis. Florida State University, Tallahassee. 95 pp.

Reed, J.K. 1980. Contribution and structure of deep water *Oculina varicosa* coral reefs off central eastern Florida USA. Bull. Mar. Sci. 30(3):667-677.

Reiswig, H.M. 1971a. In situ pumping activities of tropical Demospongiae. Mar. Biol. 9:38-50.

Reiswig, H.M. 1971b. Particle feeding in natural populations of three marine demosponges. Biol. Bull. Mar. Biol. Lab. (Woods Hole) 141:568-591.

Reiswig, H.M. 1973. Population dynamics of three Jamaican Demospongiae. Bull. Mar. Sci. 23(2): 191-226.

Reiswig, H.M. 1974. Water transport, respiration and energetics of three tropical sponges. J. Exp. Mar. Biol. Ecol. 14:231-249.

Revelante, N., W.T. Williams, and J.S. Bunt. 1982. Temporal and spatial distribution of diatoms, dinoflagellates and *Trichodesmium* in waters of the Great Barrier Reef. J. Exp. Mar. Biol. Ecol. 63:27-45.

Richardson, C., P. Dustan, and J. Lang. 1979. Maintenance of living space by sweeper tentacles of *Montastraea cavernosa*, a Caribbean reef coral. Mar. Biol. (Berl.) 55:181-186.

Rinkevich, B., and Y. Loya. 1977. Harmful effects of chronic oil pollution on a Red Sea scleractinian coral population. Pages 585-591, Vol. 2 *in* D. Taylor, ed. Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Robblee, M.B., and J.C. Zieman. (In preparation). Diel variation in the fish fauna of a tropical seagrass feeding ground. (Published 1984 *in* Bull. Mar. Sci. 34(3):335-345.)

Robblee, M.I. (In preparation). The role of habitat preference and competition in structuring the fish assemblage of a tropical seagrass meadow. Ph.D. Dissertation. University of Virginia, Charlottesville.

Roberts, H.H., L.J. Rouse, Jr., N.D. Walker, and H. Hudson. 1982. Cold water stress in Florida Bay and northern Bahamas: a product of winter frontal passages. J. Sed. Petrol. 52(1):145-155.

Robertson, D.R. 1972. Social control of sex reversal in coral reef fish. Science 177:1007-1009.

Robertson, D.R., and J.H. Choat. 1974. Protogynous hermaphroditism and social systems in labrid fish. Pages 217-225, Vol. 6 *in* Proceedings: second international coral reef symposium. Great Barrier Reef Comm., Brisbane, Australia.

Robertson, P.B. 1963. Survey of the marine rock-boring fauna of S.E. Florida. M.S. Thesis. University of Miami, Miami, Fla.

Robins, C.R. 1971. Distributional patterns of fishes from coastal and shallow waters of the tropical western Atlantic. F.A.O. Fisheries Rep. (71.2): 249-255.

Robins, R.C., R.M. Bailey, C.E. Bond, J.R. Brooker, E.A. Lachner, R.N. Lea, and W.B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada. (4th ed.). Am. Fish Soc. Spec. Publ. No. 12. 174 pp.

Rodgers, C.S. 1979. The productivity of San Cristobal Reef, Puerto Rico. Limnol. Oceanogr. 24(2): 342-349.

Rodgers, C., T. Suchanek, and F. Pecra. 1982. Effects of Hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, U.S. Virgin Islands. Bull. Mar. Sci. 32(2): 532-548.

Ross, R.M. 1978. Reproductive behavior of the anemonefish *Amphiprion melanopus* on Guam. Copeia 1978(1):103-107.

Rutzler, K. 1970. Spatial competition among Porifera: solution by epizoism. Oecologia 5:85-95.

Rutzler, K. 1971. Bredin-Archbold Smithsonian biological survey of Dominica: burrowing sponges, genus *Siphonodictyon* Bergquist, from the Caribbean. Smithson. Contrib. Zool. 77. 37 pp.

Rutzler, K. 1974. The burrowing sponges of Bermuda. Smithson. Contrib. Zool. 165:1-32.

Rutzler, K. 1975. The role of burrowing sponges in bioerosion. Oecologia 19:203-216.

Rutzler, K. 1978. Sponges in coral reefs. *In* D.R. Stoddart and R.E. Johannes, eds. Coral reefs: research methods. UNESCO Monographs on Oceanographic Methodology 5:299-313.

Rutzler, K. 1981. An unusual bluegreen alga symbiotic with two species of *Ulosa* (Porifera: Hymeniacidonidae) from Carrie Bow Cay, Belize. Mar. Ecol. 2(1):35-50.

Rutzler, K., and I.G. MacIntyre. 1982a. The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. *In* K. Rutzler and I. MacIntyre, eds. The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities. Smithson. Contrib. Mar. Sci. 12:9-45.

Rutzler, K., and I. MacIntyre, eds. 1982b. The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities. Smithson. Contrib. Mar. Sci. 12. 539 pp.

Rutzler, K., and G. Rieger. 1973. Sponge burrowing: fine structure of *Cliona lampa* penetrating calcareous substrata. Mar. Biol. 21:144-162.

Rutzler, K., J.D. Ferraris, and R.J. Larson. 1980. A new plankton sampler for coral reefs, P.S.Z.N.I. Mar. Ecol. 1:65-71.

Sale, P.F. 1976. Reef fish lottery. Nat. Hist. 85:60-65.

Sale, P.F. 1977. Maintenance of high diversity in coral reef fish communities. A. Nat. 111:337-359.

Sale, P.F. 1978. Co-existence of coral reef fishes - a lottery for living space. Environ. Biol. Fish. 3: 85-102.

Sale, P.F. 1980a. Assemblages of fish on patch reefs - predictable or unpredictable? Environ. Biol. Fish. 5:243-249.

Sale, P.F. 1980b. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Annu. Rev. 18:367-421.

Sale, P.F., and R. Dybdahl. 1978. Determinants of community structure for coral reef fishes in isolated coral heads at lagoonal and reef slope sites. Oecologia 34:57-74.

Sale, P.F., and D. McB. Williams. 1982. Community structure of coral reef fishes: are the patterns more than those expected by chance? Am. Nat. 120:121-127.

Sale, P.F., P.S. McWilliam, and D.T. Anderson. 1976. Composition of the near-reef zooplankton at Heron Reef, Great Barrier Reef. Mar. Biol. 34: 59-66.

Salmon, M., H.E. Winn, and N. Sargente. 1968. Sound production and associated behavior in triggerfishes. Pac. Sci. 22(1):11-20.

Sammarco, P.W. 1972. Some aspects of the ecology of *Diadema antillarum* Philippi: food preference and effect of grazing. Special problem report to the West Indies Laboratory of Fairleigh Dickinson University, Christiansted, St. Croix, USVI. 47 pp.

Sammarco, P.W. 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J. Exp. Mar. Biol. Ecol. 45-245-272.

Sammarco, P.W., J. Levinton, and J. Ogden. 1974. Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. J. Mar. Res. 32(1):47-53.

Sanders, H.L. 1968. Marine benthic diversity: a comparative study. Am. Nat. 102:243-282.

Schmahl, G.P., and J.T. Tilmant. 1980. An initial characterization of macroinvertebrate populations associated with patch reefs of Biscayne National Monument. Fla. Sci. Vol. 43 Suppl. 1. (Abstr.)

Schoenberg, D., and R. Trench. 1980a. Genetic variation in *Symbiodinium (=Gymnodinium) microadriaticum* Freudenthal and specificity in its symbiosis with marine invertebrates. I. Isozyme and soluble protein patterns of azenic cultures of *S. microadriaticum*. Proc. R. Soc. Lond. B207:429-444.

Schoenberg, D., and R. Trench. 1980b. Genetic variation in *Symbiodinium (=Gymnodinium) microadriaticum* Freudenthal and specificity in its symbiosis with marine invertebrates. II. Morphological variation in *S. microadriaticum*. Proc. R. Soc. Lond. B207:445-460.

Schoenberg, D., and R. Trench. 1980c. Genetic variation in *Symbiodinium (=Gymnodinium) microadriaticum* Freudenthal and specificity in its symbiosis with marine invertebrates. III. Specificity of infectivity in *S. microadriaticum*. Proc. R. Soc. Lond. B207:461-474.

Schomer, S.N., and R.D. Drew. 1982. An ecological characterization of the lower Everglades, Florida Bay, and Florida Keys. U.S. Fish Wildl. Serv. Biol. Serv. Program FWS/OBS-82/58.1. 246 pp.

Sheppard, C. 1981. Roles of interspecific and intraspecific competition in coral zonation. Prog. Underwater Sci. 60:57-60.

Sheppard, C. 1982. Coral populations on reef slopes and their major controls. Mar. Ecol. Prog. Ser. 7: 83-115.

Shinn, E.A. 1963. Spur and groove formation on the Florida Reef tract. J. Sediment. Petrol. 33(2): 291-303.

Shinn, E.A. 1966. Coral growth-rate an environmental indicator. J. Paleont. 40(2):233-240.

Shinn, E.A. 1975. Coral reef recovery in Florida and in the Persian Gulf. Shell Oil Environmental Conservation Department and Environ. Geol. 1:241-254.

Shinn, E.A. 1979. Collecting biologic and geologic specimens in south Florida. Atlantic Reef Committee No. 1. 4 pp.

Shinn, E.A. 1980. Geologic history of Grecian Rocks, Key Largo Coral Reef Marine Sanctuary. Bull. Mar. Sci. 30(3):646-656.

Shinn, E. 1981. Geology. Pages 59-64 *in* S. Jameson, ed. Key Largo Coral Reef Marine Sanctuary deep water resource survey. U.S. Dep. of Comm., NOAA Tech. Rep. CZ/SP1.

Shinn, E.A., J.H. Hudson, R.B. Halley, and B. Lidz. 1977. Topographic control and accumulation rate of some Holocene coral reefs: south Florida and Dry Tortugas. Pages 1-7 *in* D. Taylor, ed. Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Shinn, E.A., J.H. Hudson, R.B. Halley, and B. Lidz. (In press). Spur and grooves revisited: construction versus erosion. Pages 475-484, Vol. 1 *in* Proceedings: fourth international coral reef symposium. University of the Philippines, Diliman, Quezon City. (Published 1981).

Simpson, T.L. 1968. The structure and function of sponge cells: new criteria for the taxonomy of poecilosclerid sponges (Demospongiae). Bull. Peabody Mus. Nat. Hist. 25:1-141.

Simpson, T.L. 1980. Reproductive processes in sponges: a critical evaluation of current data and views. Int. J. Invert. Repr. 2:251-269.

Smith, C.L. 1978. Coral reef fish communities: a compromise view. Environ. Biol. Fish. 3:109-128.

Smith, C.L. 1982. Patterns of reproduction in coral reef fishes. Pages 49-66 *in* G.R. Huntsman, W.R. Nicholson, and W.W. Fox, eds. Proceedings of a workshop on the biological basis for reef fishery management. NOAA Tech. Memo. NMFS-SEFC-80.

Smith, C.L., and J.C. Tyler. 1972. Space resource sharing in a coral reef fish community. Bull. Nat. Hist. Mus. Los Ang. 14:125-170.

Smith, C.L., and J.C. Tyler. 1975. Succession and stability in fish communities of dome-shaped patch reefs in the West Indies. Am. Mus. Novit. 2572. 18 pp.

Smith, F.G. 1943. Littoral fauna of the Miami area. I. The Madreporaria. Proc. Fla. Acad. Sci. 6(1): 41-48.

Smith, F.G. 1948. Atlantic reef corals. A handbook of the common reef and shallow-water corals of Bermuda, Florida, the West Indies, and Brazil. University of Miami Press, Coral Gables, Fla. (1971 rev. ed.)

Smith, F.G. 1971. Atlantic reef corals. University of Miami Press, Coral Gables, Fla. 163 pp.

Smith, F.G., R.H. Williams, and C.C. Davis. 1950. An ecological survey of the subtropical inshore waters adjacent to Miami. Ecology 31:119-146.

Smith, S.V. 1978. Symposium on systems modeling and coral reef ecosystems presented at the 13th Pacific Science Congress, Vancouver, British Colombia, Canada. Aug. 18-30, 1975. Atoll Res. Bull. (220):1-110.

Smith, S.V., K. Chave, and D. Kam. 1973. Atlas of Kaneohe Bay: a reef ecosystem under stress. Hawaii University of Honolulu Sea Grant Program Rep. UNIHI SEAGRANT TR-72-01. 119 pp.

Smith, S.V., P. Jokiel, and G. Key. 1978. Bio-geochemical budget in coral reef systems. Atoll Res. Bull. 220:1-11.

Sournia, A. 1977. Primary production in coral reefs: a review of organisms, rates and budget. Ann. Inst. Oceanogr. 53(1):47-74.

South Atlantic Fishery Management Council. 1982. Draft fishery management plan, regulatory impact review, and environmental impact statement for the snapper-grouper complex of the South Atlantic region. S. Atlantic Fish. Manage. Council in coop. with NMFS, Miami, Fla. 65 pp.

Spotte, S. 1972. Pennekamp's wet world. Anim. Kingdom 75(6):2-8.

Springer, V.G., and A. McErlean. 1962a. A study of the behavior of some tagged south Florida coral reef fishes. Am. Midl. Nat. 67(2):386-397.

Springer, V.G., and A. McErlean. 1962b. Seasonality of fishes on a south Florida shore. Bull. Mar. Sci. Gulf Caribb. 12(1):39-60.

Squires, D.R. 1965. Neoplasia in a coral. Science 148 (3669):503-505.

Starck, W.A., II. 1966. Marvels of a coral realm. Natl. Geogr. Mag. 130(5):710-738.

Starck, W.A., II. 1968. List of fishes of Alligator Reef, Florida, with comments on the nature of the Florida reef fauna. Undersea Biology 1(1): 1-40.

Starck, W.A., II, and W.P. Davis. 1966. Night habits of fishes of Alligator Reef, Florida. Ichthyologica 38(4):313-356.

Starck, W.A., II, and R.E. Schroeder. 1965. A coral reef at night. Sea Frontiers 2(2):66-79.

Stearn, C.W., T.P. Scoffin, and W. Martindale. 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part I, Zonation and productivity. Bull. Mar. Sci. 27(3):479-510.

Stearn, C.W., and R. Riding. 1973. Forms of the hydrozoan *Millepora* on a recent coral reef. Lettiaia 6:187-200.

Stephenson, T.A., and A. Stephenson. 1950. Life between tidemarks in North America. I. The Florida Keys. J. Ecol. 38:354-402.

Stephenson, W., and R.B. Searles. 1960. Experimental studies on the ecology of intertidal environments at Heron Island. Aust. J. Mar. Freshw. Res. 11:241-267.

Stevenson, D.K. 1978. Management of tropical fish pot fishery for maximum sustainable yield. Gulf Caribb. Fish. Inst. 30:95-115.

Stevenson, D.K., and N. Marshall. 1974. Generalizations on the fisheries potential of coral reefs and adjacent shallow water environments. Pages 147-158 *in* Proceedings: second international coral reef symposium. Great Barrier Reef Comm., Brisbane, Australia.

Stockman, K.W., R.N. Ginsburg, and G.A. Shinn. 1967. The production of lime mud by algae in south Florida. J. Sediment. Petrol. 37:633-648.

Stoddart, D.R. 1962. Catastrophic storm effects on the British Honduras reefs and cays. Nature 196(4854):512-515.

Stoddart, D.R. 1963. Effects of Hurricane Hattie on the British Honduras reefs and cays. Oct. 30-31, 1961. Atoll Res. Bull. 95:1-142.

Stoddart, D.R. 1969. Ecology and morphology of recent coral reefs. Biol. Rev. Camb. Philos. Soc. 44:433-498.

Stoddart, D.R. 1974. Post-hurricane changes on the British Honduras reefs: re-survey of 1972. Pages 473-483, Vol. 2 *in* Proceedings: second international symposium on coral reefs. Great Barrier Reef Comm., Brisbane, Australia.

Stoddart, D., and F. Fosberg. 1981. Topographic and floristic change, Dry Tortugas, Fla. 1904-1977. Atoll Res. Bull. 253. 55 pp.

Stokes, F. and C. Stokes. 1980. Handguide to the coral reef fishes of the Caribbean and adjacent tropical waters including Florida, Bermuda, and the Bahamas. Lippincott and Crowell Publ., New York. 160 pp.

Stommel, H. 1959. Florida Straits transports June 1956-1958. Bull. Mar. Sci. Gulf Caribb. 9(1): 222-223.

Straughan, R.P.L. 1972. Pollution, dredging decimating Florida's reefs. Natl. Fisherman, Camden, Maine 52(13):46-48.

Straughan, R.P.L. 1978. Exploring the reef. A.S. Barnes & Co., New York. 248 pp.

Strusaker, P. 1969. Demersal fish resources: composition, distribution and commercial potential of the continental shelf stocks off southeastern United States. Fish. Indust. Res. 4:261-300.

Stursa, M., ed. 1974. Proceedings of the Florida Keys Coral Reef Workshop. Florida Department of Natural Resources, Tallahassee, Fla. 38 pp.

Sugg, A.L., L. Pardue, and R.L. Carrodus. 1970. Memorable hurricanes of the United States since 1873. NOAA Tech. Memo. NWS SR-56 U.S. Dep. of Comm., Fort Worth, Tex. 52 pp.

Swingle, W.E., A.E. Dammann, and J.A. Yhterna. 1970. Survey of the commercial fishery of the Virgin Islands of the United States. Gulf Caribb. Fish. Inst. 22:110-121.

Talbot, F.H. 1965. A description of the coral structure of Tutis Reef (Tanganyika Territory, East Africa) and the fish fauna. Proc. Zool. Soc. Lond. 145:431-470.

Talbot, F.H., B.C. Russell, and G.R.V. Anderson. 1978. Coral reef fish communities: unstable, high-diversity systems? Ecol. Monogr. 48:425-440.

Taylor, D.L. 1973. Algal symbionts of invertebrates. Annu. Rev. Microbiol. 27:171-187.

Taylor, D.L., ed. 1977. Proceedings: third international coral reef symposium. Miami, Fla. 2 vols.: 1 Biology, 2 Geology. University of Miami, Miami, Fla.

Taylor, W. 1928. Marine algae of Florida with special reference to the Dry Tortugas. Pap. Tortugas Lab. Carnegie Inst. Wash. 25:1-219.

Taylor, W. 1960. Marine algae of the eastern tropical and subtropical coasts of the Americas. University of Michigan Press, Ann Arbor. 870 pp.

Thompson, M.J., and T.W. Schmidt. 1977. Validation of the species/time random count technique sampling fish assemblages at Dry Tortugas. Pages 283-288 *in* D.L. Taylor, ed. Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Thresher, R.E. 1976. Field analysis of the territoriality of the threespot damselfish, *Eupomacentrus planifrons* (Pomacentridae). Copeia 1976:266-276.

Thresher, R.E. 1977. Ecological determinants of social organization of reef fishes. Pages 551-557, Vol. 1 *in* D.L. Taylor, ed. Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Thresher, R.E., 1978. Polymorphism, mimicry, and the evolution of the hamlets. Bull. Mar. Sci. 28 (2):345-353.

Thresher, R.E. 1980. Reef fish: behavior and ecology on the reef and in the aquarium. Palmetto Pahl. Co., St. Petersburg, Fla.

Tilmant, J.T. 1981. Recreational impacts on coral reef fish populations. Pages 122-138 *in* R.C. Cary, P.S. Markovits, and J.F. Kirkwood, eds. Proceedings: U.S. Fish and Wildlife Service workshop on coastal ecosystems of the southeastern United States. USDI Publ. FWS/OBS-80/59.

Tilmant, J.T., G.P. Schmahl, and D. Morrison. 1979. An ecological assessment of Biscayne National Monument's coral reefs in relation to recreational use. Pages 183-221, Vol. 9 *in* J. Jouge, ed. Proceedings: second conference on scientific research in the national parks. San Francisco, Calif.

Trench, R.K. 1979. The cell biology of plant-animal symbiosis. Annu. Rev. Plant Physiol. 30:485-531.

Turmel, R.J., and R.G. Swanson. 1971. The development of Rodriguez Bank, a recent carbonate mound. Pages 82-86 *in* H.G. Multer, ed. Field guide to some carbonate rock environments: Florida Keys and West Bahamas. Farleigh Dickinson University, Madison, N.J.

Tyler, J.C., and J.E. Bohlke. 1972. Records of sponge-dwelling fishes, primarily of the Caribbean. Bull. Mar. Sci. 22(3):601-642.

Tzimoulis, P. 1975. Key Largo home of Pennekamp Park. Skin Diver Mag. 24(10):58-63.

U.S. National Oceanic and Atmospheric Administration. 1979a. Tide current tables, 1980 Atlantic coast of North America. 214 pp.

U.S. National Oceanic and Atmospheric Administration. 1979b. Tide tables, 1980 high and low water predictions east coast of North and South America including Greenland. 293 pp.

van Soest, R.W.M. 1978. Marine sponges from Curacao and other Caribbean localities. Part I. Keratosa. Stud. Fauna Curacao Caribb. Isl. 56:1-94.

van Soest, R.W.M. 1980. Marine sponges from Curacao and other Caribbean localities. Part II. Haplosclerida. Stud. Fauna Curacao Caribb. Isl. 62 (191):1-173.

van den Hoek, C., A. Cortel-Breeman, and J. Wanders. 1975. Algal zonation in the fringing coral reef of Curacao, Netherlands Antilles, in relation to zonation of corals and gorgonians. Aquat. Bot. 1:269-308.

Vaughan, T.W. 1909. Geology of the Florida Keys and the marine bottom deposits and recent corals of southern Florida. Carnegie Inst. Wash. Year Book (7):131-136.

Vaughan, T.W. 1910. A contribution to the geologic history of the Floridian plateau. Carnegie Inst. Wash. Pap. Tortugas Lab. 4(33):99-185.

Vaughan, T.W. 1911. Recent Madreporaria of southern Florida. Carnegie Inst. Wash. Year Book 8:135-144.

Vaughan, T.W., 1912. Studies of geology of the Madreporaria of the Bahamas of southern Florida. Carnegie Inst. Wash. Year Book 11:153-162.

Vaughan, T.W. 1914a. Investigations of the geology and geologic processes of the reef tracts and adjacent areas in the Bahamas and Florida. Carnegie Inst. Wash. Year Book 12:183.

Vaughan, T.W. 1914b. Building of the Marquesas and Tortugas Atolls and a sketch of the geologic history of the Florida reef tract. Carnegie Inst. Wash. Publ. 182 Pap. Dep. Mar. Biol. 5:55-67.

Vaughan, T.W. 1914c. Preliminary remarks on the geology of the Bahamas with special reference to the origin of the Bahamian and Floridian oolite. Pap. Dep. Mar. Biol. Carnegie Inst. Wash. Publ. 182:47-54.

Vaughan, T.W. 1914d. The reef corals of southern Florida. Carnegie Inst. Wash. Year Book 12: 181-183.

Vaughan, T.W. 1914e. Sketch of the geologic history of the Florida coral reef tract. J. Wash. Acad. Sci. 4:26.

Vaughan, T.W. 1915a. The geological significance of the growth-rate of the Floridian and Bahaman shoal-water corals. J. Wash. Acad. Sci. 5:591-600.

Vaughan, T.W. 1915b. On recent Madreporaria of Florida, the Bahamas, and the West Indies and on collections from Murray Island, Australia. Carnegie Inst. Wash. Year Book 14:220-231.

Vaughan, T.W. 1918. The temperature of the Florida coral reef tract. Carnegie Inst. Wash. Publ. 213: 321-339.

Vaughan, T.W. 1919. Coral and the formation of reefs: Smithson. Inst. Annu. Rep. 1917:189-238.

Vaughan, T.W. 1935. Current measurements along the Florida coral reef tract. Pap. Tortugas Lab. 28:129-141.

Vaughan, T.W., and E.W. Shaw. 1916. Geologic investigations of the Florida coral reef tract. Carnegie Inst. Wash. Year Book 14:232.

Vaughan, T.W., and J.W. Wells. 1943. Revision of the suborders, families, and genera of the Scleractinia. Geol. Soc. Am. Spec. Pap. 44. 363 pp.

Verrill, A.E. 1902. Comparisons of the Bermudian, West Indian and Brazilian coral faunae. Conn. Ac. Art. Sci., Tr., 11, 170-206.

Vicente, V.P. 1978. An ecological evaluation of the West Indian demosponge *Anthosigmella varians* (Hodromerida Spirastrellidae) Bull. Mar. Sci. 28(4):771-779.

Vickeer, A. 1908. Phycologia Barbadensis. Paris, privately printed.

Vine, P.J. 1974. Effects of algal grazing and aggressive behavior of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral reef ecology. Mar. Biol. 24:131-136.

Vittor, B.A., and P.G. Johnson. 1977. Polychaete abundance, diversity, and trophic role in coral reef communities at Grand Bahama Island and the Florida Middle Ground. Pages 163-168 *in* D. Taylor, ed. Proceedings: third international coral reef symposium. University of Miami, Miami, Fla.

Vivien, M.L., and M. Peyrot-Clausade. 1974. A comparative study of the feeding behaviour of three coral reef fishes (Holocentridae), with special reference to the polychaetes of the reef cryptofauna as prey. Pages 179-192 *in* Proceedings: second coral reef symposium. Great Barrier Reef Comm., Brisbane, Australia.

Vogel, S. 1977. Current induced flow through living sponges in nature. Proc. Natl. Acad. Sci. USA 74:2069-2071.

Vooren, C. 1981. Photosynthetic rates of benthic algae from the deep coral reef of Curacao. Aquat. Bot. 10:143-154.

Voss, G.L. 1973. Sickness and death in Florida's coral reefs. Nat. Hist. 82(7):40-47.

Voss, G.L. 1976. Seashore life of Florida and the Caribbean. E.A. Seemann Publ. Co. Inc., Miami, Fla. 168 pp.

Voss, G.L., and N.A. Voss. 1955. An ecological survey of Soldier Key, Biscayne Bay, Fla. Bull. Mar. Sci. Gulf Caribb. 5(3):203-229.

Voss, G.L., F.M. Bayer, C.R. Robins, M. Gomon, and E.T. LaRoe. 1969. The marine ecology of the Biscayne National Monument. Rep. to the National Park Service, Department of the Interior from Institute of Marine and Atmospheric Science. University of Miami, Miami, Fla. 128 pp.

Wahle, C.M. 1980. Detection pursuit and overgrowth of tropical gorgonians by milleporid hydro corals, Perseus and Medusa revisited. Science 209 (4457):689-691.

Walker, N.D. 1981. January water temperatures kill Florida fauna. Coast. Oceanogr. Climatol. News 3(3):30.

Wanders, J. 1976. The role of benthic algae in the shallow reef of Curacao. I. Primary productivity in the coral reef. Aquat. Bot. 2:235-270.

Wanders, J. 1977. The role of benthic algae in the shallow reef of Curacao. II. The significance of grazing. Aquat. Bot. 3:357-390.

Warner, R.R., D.R. Robertson, and E.G. Leigh, Jr. 1975. Sex change and sexual selection. The reproductive biology of a labrid fish is used to illuminate a theory of sex change. Science 190:633-638.

Weeks, A. 1972. Exploring the coral reefs. Reprint. NOAA 3(2):1-8.

Weiss, M., and D. Goddard. 1977. Man's impact on coastal reefs - an example from Venezuela. Pages 11-124 *in* S. Frost, M. Weiss, and J. Saunders, eds. Reefs and related carbonates - ecology and sedimentology. Studies in Biology 4. American Association of Petroleum Geologists, Tulsa, Okla.

Wellington, G.M. 1980. Reversal of digestive interactions between Pacific reef corals: mediation by sweeper tentacles. Oecologia 47(3):340-343.

Wells, J.M., V.A. Wells, and J.G. Van Derwalker. 1973. In situ studies of metabolism in benthic reef communities. Helgol. Wiss. Meeresunters. 24(1-4):78-81.

Wells, J.W. 1932. Study of the reef corals of the Tortugas. Carnegie Inst. Wash. Year Book 31:290.

Wells, J.W. 1933. A study of the reef Madreporaria of the Dry Tortugas and sediments of coral reefs. Unpubl. MS. Cornell University, Ithaca, N.Y. 138 pp.

Wells, J.W. 1956. Scleractinia. Pages F328-F344 *in* R.C. Moore, ed. Treatise on invertebrates. Geological Society of America, University of Kansas Press, Lawrence.

Wells, J.W. 1957a. Coral reefs. Pages 609-631 *in* J. Hedgpeth, ed. Treatise on marine ecology and paleoecology. Vol. I. Ecology. Geol. Soc. Am. Mem. 67.

Wells, J.W. 1957b. Corals. Pages 1087-1104 *in* J. Hedgpeth, ed. Treatise on marine ecology and paleoecology. Vol. I. Ecology. Geol. Soc. Am. Mem. 67.

Wennekens, M.P. 1959. Water mass properties of the Straits of Florida and related waters. Bull. Mar. Sci. Gulf Caribb. 9(1):1-52.

West, D.A. 1979. Symbiotic zoanthids (Anthozoa: Cnidaria) of Puerto Rico. Bull. Mar. Sci. 29(2): 253-271.

Westinga, E., and P.C. Hoetjes. 1981. The intrasponge fauna of *Spheciospongia vesparia* (Porifera, Demospongiae) at Curacao and Bonaire. Mar. Biol. 62:139-150.

Wethey, D., and J. Porter. 1967. Habitat related patterns of productivity of the foliaceous reef coral *Purona praetorta* Dana. Pages 59-66 *in* G. Mackie. Coelenterata ecology and behavior. Plenum Press, New York.

Wheaton, J. 1981. Octocorals (Octocorallia: Gorgonacea). Pages 15-26 *in* S. Jameson, ed. Key Largo Coral Reef National Marine Sanctuary deep water resource survey. NOAA Tech. Rep. CZ/SP 1, Washington, D.C.

Wheaton, J. (In preparation, a.) Report to National Park Service on studies conducted in Biscayne National Park.

Wheaton, J. (In preparation, b.) Gorgonians (Octocorallia. Gorgonacea) of Key Largo Coral Reef Marine Sanctuary.

Wiedenmayer, F. 1977. Shallow-water sponges of the Western Bahamas. Exper. Suppl. (Basel) 28:1-287.

Wilkinson, C.R. 1978. Microbial associations in sponges. I. Ecology, physiology and microbial populations of coral reef sponges. Mar. Biol. 49:161-167.

Wilkinson, C.R. 1979. Nutrient translocation from symbiotic cyanobacteria to coral reef sponges. Pages 373-380 *in* C. Levi and N. Boury-Esnault, eds. Biologie des spongiares. Centre National de la Recherche Scientifique, 291 Paris.

Williams, A.H. 1978. Ecology of the threespot damselfish: social organization, age structure, and populations stability. J. Exp. Mar. Biol. Ecol. 34:197-213.

Williams, D. McB. 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs 1(1):35-44.

Williams, J., E. Johnson, and A. Dyer. 1960. Water transparency observations along the east coast of North America. Smithson. Misc. Collect. 4391. 181 pp.

Wolf, R.J., and W.F. Rathjen. 1974. Exploratory fishing activities of the UNDP/FAO, Caribbean Fishery Development Project, 1965-1971: a summary. Mar. Fish. Rev. 36(9):1-8.

Wood, E.J.F. 1954. Dinoflagellates in the Australian region. Aust. J. Mar. Freshw. Res. 5:172-568.

Wood-Jones, F. 1910. Coral and atolls. Reeve and Co., Ltd., London. 392 pp.

Woodley, J., et al. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science 214(4522):749-755.

Work, P. 1969. Systematics, ecology, and distribution of molluscs of Los Roques, Venezuela. Bull. Mar. Sci. 19(3):614-711.

Wulff, J., and L. Buss. 1979. Do sponges help hold coral reefs together? Nature (Long.) 281:474-475.

Wust, G. 1924. Florida und Antillenstrom. Veroeff. Inst. Meeresk. Meeresforsch. (Univ. of Berl.) 12:1-48.

Yonge, C.M. 1930. Studies on the physiology of corals. I. Feeding mechanisms and food. Sci. Rep. Great Barrier Reef Expd. 1:13-57.

Yonge, C.M. 1935a. Studies on the biology of Tortugas corals. I. Observations on *Macandra areolata*. Linn. Pap. Tortugas Lab. 29:185-198.

Yonge, C.M. 1935b. Studies on the biology of Tortugas corals. II. Variation in the genus *Siderastrea*. Carnegie Inst. Wash. Pap. Tortugas Lab. (452): 201-208.

Yonge, C.M. 1937. Studies on the biology of Tortugas corals. III. The effect of mucus on oxygen consumption. Pap. Dep. Mar. Biol. Carnegie Inst. Wash. Publ. No. 475. 29:207.

Yonge, C.M. 1940. The biology of reef-building corals. Sci. Rep. Great Barrier Reef Expd. 1928-1929 1(13):353-391.

Yonge, C.M. 1973. The nature of reef-building (hermatypic) corals. Bull. Mar. Sci. 23(1):1-15.

Yonge, C.M., and A. Nicholls. 1931. Studies on the physiology of corals. V. The effect of starvation in light and in darkness on the relationship between corals and zooxanthellae. Sci. Rep. Great Barrier Reef Expd. 1928-1929 1(7):177-211.

Youngbluth, M.J. 1982. Sampling demersal zooplankton: a comparison of field collections using three different emergence traps. J. Exp. Mar. Biol. Ecol. 61:111-124.

Zeiller, W. 1974. Tropical marine invertebrates of southern Florida and the Bahamas Islands. John Wiley and Sons, New York. 132 pp.

Zieman, J. 1982. The ecology of the seagrasses of south Florida: a community profile. U.S. Fish Wildl. Serv. Biol. Serv. Program FWS/OBS-82/25. 150 pp.

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An overview of coral reef research in southern Florida is provided as a prelude to a genuine description of the coral reef ecosystem in the Florida Keys and surrounding environments. Coral reef community types, reef benthos, plankton and reef fish are given specific treatment. Coral reef ecology and management are described.

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