

## 4. A Perspective on Florida Keys Coral Reefs

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## Dedication

This chapter is dedicated to Dr. Carl Robert Beaver; a coral reef scientist employed by the Florida Fish and Wildlife Research Institute and formerly by Texas A&M University, Corpus Christi. In the short time he had with us, his heart and soul were passionately devoted to coral reef science and conservation.

## 4.1 Introduction

South Florida is a unique enclave of the Caribbean thanks to the nexus of geography and environmental factors. Tropical mangrove, seagrass, coral reef epifaunal and infaunal sedimentary communities are common from Stuart on the east coast to Tampa Bay on the west coast. Florida is the only state in the continental United States to have such an ecosystem in its coastal waters. Climate and hydrodynamic features support a variety of plants and animals. The Florida Keys are the most Caribbean-like region in Florida. These “islands in the sun” have attracted millions of visitors and residents; some of the more famous include: George Meade (Union General in the Civil War), James Audubon (artist), President Harry Truman (built the Little White House in Key West), Humphrey Bogart and Lauren Bacall (made the movie *Key Largo* in Key Largo), Ted Williams (baseball player and avid fisherman), Tennessee Williams (playwright), Ernest Hemingway (writer), Jimmy Johnson (football coach). Many respected scientists worked their crafts in the coral reefs of the Florida Keys including Louis and Alexander Agassiz, Louis Pourtalès, Alfred G. Mayer, Thomas W. Vaughan, William Longley, Reginald Daly, Lawrence Cary, Walter Stark, Robert Ginsburg, and Eugene Shinn. A significant portion of the foundation of coral reef science is the result of research conducted in the Florida Keys. The first underwater photographs (some in color) of coral reef fish were taken in the Keys. The first coral reef underwater park (John Pennekamp) and marine protected area (Dry Tortugas) were created in the Keys. Coral reefs are important economic, asctic, and natural assets to Florida and the United States (Table 1).

Florida Keys reefs are equivalent to many Caribbean reefs in the biodiversity and richness of coral cover that is present, in the proliferation of benthic algae, and in the scarcity of *Diadema antillarum* (following the post 1983 disease epidemic)

and the apex predator fish species, e.g., grouper and snapper. Unfortunately, also like the Caribbean, pressures associated with coastal development, the heavy extraction of fish and invertebrates, and climate-related incidents have degraded the reefs. Since 2004, the reefs from the Lower Keys to Dry Tortugas have endured five hurricanes (the impact of these hurricanes will be discussed in details later in this chapter). In the twenty-first century, the coral reefs in the Florida Keys continue on; however, their fate is in our hands. Can society control the urge to use more carbon and extract more protein and ornamental species? Are there ways to protect the corals from the virulent diseases that are a relatively recent development? Parks, sanctuaries, wildlife refuges, and marine protected areas have been created in the Florida Keys (Shinn 1979; NOAA 2007); management has reduced physical destruction from anchoring and emphasized education and public awareness. The goal in this chapter is to provide an overview with moderate details and sufficient reference documentation for those wishing to delve deeper into the subjects.

## 4.2 Geography

The Florida peninsula (151, 670 km<sup>2</sup>) is a large carbonate plateau and projects south from the continental land mass of North America into the Atlantic Ocean and Gulf of Mexico (Geology is addressed in chapter X). The Peninsula axis of projection is about 160° and extends approximately 724 km (391 miles) from the northern border to Florida Bay. Distance from the St. Lucie Inlet (Stuart) to Tortugas Banks is 667 km (360 nmi). The Florida Keys archipelago (Figure 1) arcs southwest from Biscayne Bay 253 km (137 nmi) to Key West and 378 km (204 nmi) to the Dry Tortugas.

The islands (keys or cays) from Soldier (25°31.4'N, 80°10.5'W) to Boca Grand (24°32.5'N, 82°00.4'W) are built of Pleistocene marine limestones. The Florida Reef Tract (Vaughan 1914) parallels the Florida Keys archipelago from Fowey Rock (25°35.4'N, 80°05.8'W) to the Dry Tortugas (24°36.9'N, 82°53.6'W), and shallow coral reef communities continue north to the St. Lucie Inlet near Stuart (27°10'N, 80°09'W). Details on temperate-deep reef communities are covered in chapter Y.

The well-developed coral reefs of the Florida Keys are found on the eastern-southern sides of the archipelago (locals say, “ocean side”), parallel to the Florida Current. Biscayne Bay, Card Sound, Little Card Sound, Barnes Sound, Blackwater Sound, and Florida Bay are situated between the Florida Keys and the peninsula. These are shallow bodies of water; average depth in Florida Bay is 1-2 m. Net transport of water is from Florida Bay into the Atlantic Ocean (Smith 1994). Water masses in these bays, particularly Florida Bay, are rapidly altered by environmental events: cold fronts chill the waters, rainstorms reduce salinity, windy weather produces turbid water, hot and dry periods of weather elevate the salinity and temperature, and algal blooms can result in toxic water masses. The Upper Keys, defined here as from the north end of Elliott Key (25°31.4’N, 80°10.6’W) to Upper Matecumbe Key (24°54.1’N, 80°39.6’W), have three narrow channels leading from the bays to the ocean. From Upper Matecumbe to Grassy Key (24°46.5’N, 80° 55.9’W) there are six major channels, some as wide as 4.3 km (2.2 nmi). From Hog Key (24°42.4’N, 81°07.5’) to Cudjoe Key (24°39.8’, 81°28.1’) there are nine major channels, including a 13 km-wide (7nmi) opening into the Atlantic from Florida Bay. This middle portion of the Florida Keys has small islands and wide channels. Reef distribution is influenced by the “inimical waters” generated in Florida Bay (Ginsburg and Shinn 1964). In general, there is poor reef development in those areas where there is unrestricted water movement from Florida Bay into the Atlantic. Wide passes between keys that allow large volumes of Florida Bay water to flow onto the reef tract impede coral reef formation (e.g., the part of the reef tract known as the Middle Keys). Areas isolated from Florida Bay (Key Largo and the area of Key West) have well-developed offshore bank reefs (Ginsburg and Shinn 1964; Jaap 1984; Jaap and Hallock 1990).

### **4.3 History**

Shallow-water coral reefs occurred intermittently during the glacial periods along the east coast of Florida and the Florida Keys (Lighty 1977). Sea level change resulted in a hiatus of coral reefs in some areas and development in others (Lighty 1977; Shinn et al. 1977). The oldest Holocene coral reef (8,000 YBP) is located on the Tortugas Banks (Mallinson et al. 2003). Interestingly, the Tortugas Banks reefs did not keep pace with rising sea levels while Bird Key Reef, a Dry Tortugas

National Park reef did (Shinn et al. 1977). Mallinson et al. (2003) hypothesized that the Wisconsin glacial melt-water flowed across the Tortugas Banks, so that lowered salinity and increased turbidity inhibited reef growth.

Florida and the Florida Keys show evidence of human habitation dating back at least 12,000 years. Florida was discovered by Europeans in 1513 when Spanish conquistador Juan Ponce de Leon came ashore at several locations along the coast he named “La Florida” (from the Spanish *Pascua Florida*, “feast of flowers”) because his first landing occurred during Easter. Among his stops were Biscayne Bay (the northern end of the Florida Keys), Key West, and Dry Tortugas. Florida was in the hands of the Spanish, French, and British until the Spanish sold Florida to the United States in 1819; it subsequently became the 27<sup>th</sup> state in 1845.

The Florida Keys are in Monroe County, established in 1823, with its county seat in Key West. This town has grown from a remote port and fishing (and ship wrecking) settlement in the mid-1500s to a resident population of about 25,000 at present. The Florida Keys are connected to the mainland by the Overseas Highway (US 1), first built in 1912 as a railroad by Henry Flagler. After a severe hurricane destroyed much of the railroad in 1935, bridges and rail bed were converted to a toll road. This is the only land-based transportation corridor into and out of the Keys; it facilitates a lively economy based largely on tourism and commercial and recreational fishing centered in and around coral reefs (Johns et al. 2001; Andrews et al. 2005). The three counties (Miami-Dade, Broward, Palm Beach) to the north of the Keys represent a mass of urban development from Homestead-Florida City to Palm Beach; the 2000 census documented 2.2 million private dwellings and 5.1 million permanent residents in these counties; population increases substantially during the winter tourist season (December – March). The residents are active users of the marine environment; in 2004-2005 fiscal year there were 173,870 boat registrations (167,822 pleasure and 6,048 commercial) (Florida Statistical Abstract 2006) and 173,870 salt water fishing licenses (167,822 recreational and 6,048 commercial) (FWC licenses sales data, personal communication) in Martin, Palm Beach, Broward, Miami-Dade, and Monroe counties alone. Commonly, from spring through early fall, the residents

of the counties north of the Keys will take vacations and extended weekend visits in the Keys, often taking their boats with them.

Miami-Dade and Monroe counties include southern components of the greater Everglades ecosystem. Water resources in south Florida are managed by the South Florida Water Management District and the U.S. Army Corps of Engineers. An extensive canal and dam system is in the process of being redesigned with the goal of reversing the former policy of diverting water resources from the Everglades. Originally, water flowed south from the Lake Okeechobee-Kissimmee River watershed, through the Everglades and Big Cypress Swamp and into Florida Bay and the Ten Thousand Islands. Drainage projects forced the water east (St. Lucie Waterway) and west (Caloosahatchee River), starving the Everglades system of water (Douglas 1947; Sklar et al. 2002; Steinman et al. 2002).

Because of their impact on the economic and social well-being of Floridians and humanity in general, the natural environments of South Florida, including the Everglades and the Florida Reef Tract, have been protected by the establishment of a number of managed areas (Parks, Wildlife Refuges, Reserves, and Marine Sanctuaries). By executive order in 1908, President Theodore Roosevelt designated the Dry Tortugas a wildlife refuge, with the main purpose of protecting bird rookeries. Dry Tortugas National Monument was established in 1935; bird rookeries and cultural resources (Fort Jefferson) were still the principal concerns. In 1980, the enacting language was amended to include coral reefs and resident marine life; in 1992, the area was designated Dry Tortugas National Park (DTNP). The park occupies approximately 25,900 hectares (100<sup>2</sup> miles). Dry Tortugas and Everglades National Parks were designated World Heritage Sites in 1979. Current regulations at DTNP prohibit commercial fishing, although recreational fishing based on Florida and federal regulations is allowed, prohibits taking of lobster, and seasonally closes bird rookeries and turtle nesting islands. Everglades National Park, created in 1947, includes large portions of Florida Bay. John Pennekamp Coral Reef State Park (JPCRSP) was designated in 1963; it was the first park to emphasize underwater resources (coral reefs) in the United States. Pennekamp includes the mangrove and upland hammocks, sea grass beds, and

patch reefs that are within the three nautical mile (5.6 km) limit of state jurisdiction. The rules and regulations in JPCRSP protect coral, allow for recreational and commercial fishing, and close shallow areas to powered boats. Biscayne National Park (previously a National Monument) was created in 1980. It includes portions of Biscayne Bay, Card Sound, the Ragged Keys, Elliott Key, and a dense concentration of patch reefs seaward of Elliott Key (Voss et al. 1969). Regulations protect the benthic resources but allow for recreational and commercial fishing.

The enabling legislation for the Florida Keys National Marine Sanctuary (FKNMS) mandates management of a vast marine area (NOAA 1996): 2,800 nmi<sup>2</sup> from south of Miami (25°17.683'N, 80°13.145'W) to the Tortugas Banks (24°36.703'N, 82°52.212'W). The motivation to designate the entire region as FKNMS was a series of ship groundings in 1989: *Alec Owen Maitland* near Carysfort Reef, *Elpsis* near Elbow Reef, and the *Mavro Vetrican* at Pulaski Shoal. The process included a series of workshops and meetings to establish goals and receive public input. The FKNMS encompasses the water column and seafloor from the coast to 91 m depth. The FKNMS area includes mangroves, sea grasses, sedimentary habitat, hardbottom, and coral reefs (Jaap 1984; Jaap and Hallock 1990; Chiappone 1996). Partial habitat mapping of the region shows that coral reef habitat constitutes 7.79% of the area (Fla. Mar. Res. Inst. 1998). The Tortugas Ecological Reserve (an addition to the FKNMS) was established in 2001 and, at that time, was the largest marine protected area within U.S. waters, a total of 514.5 km<sup>2</sup> (150 nmi<sup>2</sup>). The FKNMS is divided into use zones. Some zones prohibit taking of anything, others are open to recreational harvest, and others are open to commercial and recreational fishers.

The designation of parks and sanctuaries has efficacy in on-site use. One particular success is the reduction of coral injuries at popular reefs through the introduction of mooring systems (Halas, 1985). However, the more subtle and difficult issues (water quality, coastal development, limiting access to certain areas, and region-wide problems such as coral diseases) are not easily managed (fishing issues are discussed in section 4.18 and water quality in section 4.19).

## 4.4 Heritage of Past Research

There is a rich legacy of marine research that focused on Florida Keys and south Florida coral reefs. Louis and Alexander Agassiz (1852, 1869, 1880, 1885, 1888, 1890) and Louis Pourtalès (1863, 1869, 1871, 1878, 1880a, b) were pioneers in studying the reefs and reef organisms. Early studies were, for the most part, exploratory surveys, taxonomic collections, and efforts to see if there were ways to reduce shipping losses along the Florida Reef Tract.

Andrew Carnegie was a wealthy industrialist and wanted to accelerate the United States into the forefront of science. To do this, in 1902, he set up the Carnegie Institution and appointed a board of trustees to guide and fund scientific research. Alfred G. Mayer lobbied the trustees that they should establish a tropical marine laboratory at Dry Tortugas. In December 1903, the trustees awarded Mayer funds to establish a marine laboratory (Colin 1980; Stephens and Calder 2006). In 1904, the Carnegie Institution obtained a lease on the north end of Loggerhead Key, Dry Tortugas, from the U.S. Lighthouse Service for the construction of a research laboratory. Construction began in 1904 under Mayer's direction (Mayer 1902; Stephens and Calder 2006); he had been a student/technician of Alexander Agassiz and was well qualified to pick this site for a tropical research station. The first researchers arrived in the summer of 1905. In spite of remoteness, lack of many amenities, and near destruction of the laboratory by hurricanes in 1910 and 1919, approximately 146 different researchers worked at the laboratory between 1905 and 1939 (Colin 1980; Schmidt and Pikula 1997). The world's first underwater photographs of coral reef fishes were taken by Longley and an assistant at Dry Tortugas; these were published in the *National Geographic* in January 1927. Two well-equipped research vessels were available to Carnegie researchers: the *Physilia*, a 39-foot auxiliary powered ketch served from 1905 until 1910. In 1910, she was replaced by a powered vessel, the *Anton Dohrn*, built in Miami; the *Dohrn* served until the lab closed in 1939. The *Dohrn* supported Vaughan's coral growth rate studies at Golding Cay, Bahamas and other Caribbean cruises (Stephens and Calder 2006). Vaughan's coral growth rates are quite similar to rates reported in modern studies (Jaap 1984). Additionally, the use of surface supplied diving gear (a helmet and hand powered air pump) began in 1920s, another example of the pioneering fieldwork that went



on at Dry Tortugas. Even today, Alfred G. Mayer (Mayor) and Thomas W. Vaughan are recognized for their groundbreaking work on corals and reefs. Mayor studied the physiology of corals, especially their temperature and salinity tolerances. Vaughan was a leading researcher in the origin and formation of coral reefs, a follow-up to the argument between Darwin, Agassiz, and Daley (Dobbs 2005). Articles on the overview of south Florida coral reefs include Jaap (1984); Jones et al. (1985); Jaap and Hallock (1990); Chiappone (1996); NOAA (2002, 2005); and Porter and Porter (2002).

## 4.5 Climate

“The maritime influence of the Caribbean Sea and the Gulf of Mexico transforms Florida’s climate” (Chen and Gerber 1990). Climate is also influenced by the Bermuda high pressure system that reduces precipitation and by northern frontal systems that lower the air temperature (November to April). The “jet stream,” a narrow band of strong winds in the upper atmosphere, steers the cold air masses; it meanders and is influenced by the El Nino Southern Oscillation (ENSO) system. Florida’s climate is superimposed on the ENSO cycles. El Nino results in warmer and wetter winters, fewer hurricanes, and doldrums in late summer that often lead to coral bleaching events. La Nina results in drier and cooler winters, and more frequent hurricanes. Tropical cyclones (hurricanes) force radical changes in the coral reef, sea grass, and mangrove communities; hurricanes are most common in August and September. Climatic data for Key West and Stuart provide a synoptic summary (Figure 2). Variation in seasonal air temperature is greater in Florida than in the more tropical Grand Cayman or Mayaguez, Puerto Rico; and rainfall is less in Florida than in Mayaguez.

Southeast Florida climate ranges from subtropical in Stuart to tropical maritime in Key West (Figure 2). Low air temperatures around 17.6°C occur in January with an average maximum of 32.5°C in August. The temperature in Key West is slightly cooler than Stuart in the summer and warmer in the winter. The dry season is typically November to April-May and the wet season is May-June to October. Total rainfall is around 100 cm a year in Key West and 148 cm in Stuart. Climate data has been summarized from the National Weather Service

Web Page, as well as Schomer and Drew (1982), Chen and Gerber (1990), and McPherson and Halley (1996).

## **4.6 Ocean Temperatures**

Environmental recordkeeping for coastal Florida goes back 125 years (Vaughan 1918); lighthouse keepers [Loggerhead Key, Dry Tortugas (1879 to 1907); Sand Key, Key West (1878-1890); Carysfort Reef, Key Largo (1878-1899); and Fowey Rock, near Cape Florida (1879-1912)] recorded the water temperature using a bucket and a thermometer (Figure 3).

The overall range for these data is 15.6 to 32.2° C (a change of 16.6° C annually); lowest temperatures occurred at Fowey Rock in February and the highest in August at Sand Key. Sand Key water temperature was warmest most of the year. Dry Tortugas was cooler January to May; Fowey Rocks was cooler June to November. Vaughan averaged these temperatures over ten-day periods so the extreme range of temperatures is not in the data set.

The National Oceanographic Atmospheric Administration's (NOAA), National Data Buoy Center operates meteorological-oceanographic data collecting systems off the Florida coast (Table 2). Figures 4 to 8 provide synoptic data on the monthly means, standard deviations, and ranges for air and water temperatures and wind speed for a ten-year period. Data are acquired hourly for each of these parameters. These data confirm the lighthouse keepers' records in the context of general trends. Extreme high temperatures were recorded on occasions in tide pools (Mayer 1914, 1918) and 14°C (a stressful low water temperature) was recorded in 1978 (Davis 1982).

## **4.7 Caribbean-West Indian Connections**

Southern Florida [the region south of an arbitrary line drawn between the St. Lucie inlet (27°12.9'N, 80°12.5'W) and the southern tip of Sanibel Island (26°27.1'N, 82°01.7'W)] displays a greater similarity to the Caribbean and West Indian flora and fauna than to the flora and fauna of northern Florida. The West Indian zoogeographic area is defined as a sub-region of the Neotropical Province. As used here, it includes the Bahamas, Greater and Lesser Antilles, the northern coast of South America, the eastern coast of Central America, and southern

Florida. On land, iconic vegetation providing evidence of Caribbean-West Indian affinity includes the coconut palm (*Cocos nucifera*), sea grape (*Coccoloba uvifera*), red mangrove (*Rhizophora mangle*), Gumbo Limbo (*Bursera simaruba*), and the mahogany tree (*Swietenia mahogani*). In the sea, the alga *Halimeda opuntia*, turtle grass (*Thalassia testudium*), invertebrates such as the horse conch (*Pleuropoca gigantia*), the long-spine, black urchin (*Diadema antillarum*), fire coral (*Millepora complanata*), purple sea fan (*Gorgonia ventalina*), and elkhorn coral (*Acropora palmata*) are typical of this particular ecosystem.

## 4.8 Hydrodynamic Connectivity

The coral reef fauna found in the Bahamas, Cuba, and southern Florida are remarkably similar. The lack of land barriers, connectivity of the water masses, and ocean currents facilitate larval transport of progeny among these areas.

Southern Florida's climate and marine systems are influenced by the large western boundary current (often referred to as the Caribbean Current, Florida Current, or the Gulf Stream). This current enters Lesser Antilles as the Guiana Current flowing northwest of the Venezuelan coast. These waters are forced into the Caribbean Sea north and south of St. Lucia Island; the axis of the current is westward, passing the Aruba Gap and the Columbia Basin before turning north into the Cayman Basin, west to 85-86°W, north through the Yucatan Strait and into the Gulf of Mexico as the "Loop Current" (Fairbridge 1966). The Loop Current is variable in volume and penetration into the Gulf of Mexico (Lee et al. 1992, 1994, 2002); it reverses course in the northern Gulf, returns to the area around the Dry Tortugas, and enters the Straits of Florida, a deep channel between Florida, Cuba, and the Bahamas. The current at this point is typically called the "Florida Current." It meanders offshore-onshore, depending on a multitude of environmental influences. One of the facets of biological significance is that the Florida Current sets up a series of gyres (rotating water masses) that persist for 60 to 100 days at a time (Lee et al. 1994, 2002). The largest of these is the Tortugas Gyre. The Pourtalès Gyre is formed east and north of the Tortugas Gyre; it can extend eastward to Vaca Key. Gyres retain and distribute invertebrate and fish larvae in the Florida reefs (Ingle et al. 1963; Simms and Ingle 1966; Lee et al. 1994; McGowen et al. 1994a,b,c). Upwelling, the other condition resulting from

the current flow, occurs when the boundary current is near the Florida coast. This phenomenon results in cool, nutrient-rich water entering the reef system (Leichter et al. 2003). Short-term pulses of nutrients result in benthic algal blooms (*Dictyota* and *Cladophora*) in the reef system. Beyond the Keys, the Florida Current parallels the coast. Typically it comes closest to the coast in Palm Beach County and tends to stray away from the coast after passing Palm Beach.

The Caribbean Sea and Gulf of Mexico are quite different. The Caribbean is totally tropical in nature and continental land masses enclose it to the south and west. Large and high islands (Hispaniola and Puerto Rico) and smaller islands of the Lesser Antilles form an incomplete barrier to the east. Two large islands, Cuba and Jamaica, are situated in the middle, and volcanic activity is common throughout the area. In contrast, the Gulf of Mexico is a large lake, with no large islands, open to the south, and surrounded by continental land masses. Narrow, sand-barrier islands parallel the west coast of Florida to the Texas-Mexico border. Coral cays are a feature off the Yucatan Peninsula, east coast of Mexico, and the Florida Keys. The climate is temperate in the north and tropical to the south. Tectonic activity is uncommon.

The Bahamas is an extensive area of low islands, carbonate banks, and coral reefs. The Bahamas archipelago is 260,000 km<sup>2</sup> and extends 800 km from SE Florida to northern Hispaniola. The majority of the Bahamas is located on two shallow banks, ideal for coral reef development. Land (2,750 islands and shoals extending above the highest tides) occupies 11,400 km<sup>2</sup> (4.4% of the Bahamas area). The islands are low with few cases of greater than 30 m elevation (Gerace 1988). The northern Bahamas climate is similar to Florida; Little Bahama Bank (Grand Bahama, Walker's Cay, and Abaco) is occasionally impacted by winter cold fronts.

Cuba is the closest high Caribbean island to Florida (167 km [90 mi] south of Key West) with a surface area of 110,860 km<sup>2</sup>. The island has a 5,700 km long estimated coastline; the continental shelf is 100 to 140 km wide; and there are approximately 4,200 islands in four groupings: Los Colorados and Jardines del Rey (northern coast); Los Canarreos and Jardines de la Reina (southern coast)

(Jiménez 1982). Zlatarski and Estalella (1982) and Kühlman (1974a) describe multiple reef types (bank, fringing, cluster, patch, coral canyons, and horst). Jiménez (1984) estimated that the total length of coral reefs on Cuba's north coast was 2,150 km and 1,816 km on the south coast.

## **4.9 Biodiversity and Taxonomic Distinctness of the Scleractinia (Stony Corals)**

The zooxanthellate Scleractinia are representative of the biodiversity and taxonomic character of the region. Order Scleractinia: Phylum Cnidaria: Class Anthozoa is exclusively marine, occurs from the Sub-Arctic to Antarctica, and from near sea level to below 6300 m (Cairns 2001). Physiologically, ecologically (and roughly phylogenetically), the Scleractinia can be divided into two groups: those containing zooxanthellae (dinoflagellate algae of the genus *Symbiodinium*) in their tissues (the zooxanthellate Scleractinia) and those that do not (the azooxanthellate Scleractinia). Zooxanthellate species (ZS) are restricted to the photic zone and are typically found in tropical-subtropical regions in depths that rarely exceed 70 to 80 m. The ZS include species attaining sizes exceeding three meters in diameter and height (e.g., *Colpophyllia natans* and *Montastraea annularis* complex), as well as species that rarely exceed 10 cm in diameter (such as *Cladocora arbuscula* and *Favia fragum*). Most ZS species are colonial (with multiple polyps), and their morphology includes branching, columnar, encrusting, foliaceous, and massive skeletal structures. Within a ZS species, the morphology has great variability, reflecting local environmental conditions, many of which vary with depth, e.g., ambient light, water movement, sedimentation, and temperature. The ZS manifest reticulate evolution, a mechanism that facilitates hybridization and sibling species but confuses and complicates taxonomy (Veron 1995; Medina et al. 1999; Willis et al. 2006). Tissue color (plant pigments) displays large ranges of variability, contributing to the challenge of in situ species determination.

Zooxanthellate corals are sometimes called “hermatypic” corals, because they construct shallow-water reef communities, whereas azooxanthellate corals, sometimes called “ahermatypic” corals, are usually solitary in habit and thus do not form reefs. But there are many exceptions to these generalizations, one being

that deep-water azooxanthellate colonial corals, such as *Lophelia pertusa* and *Madrepora carolina*, may form reefal structures at continental slope depths (Cairns 2001; Cairns and Stanley 1982; Williams et al. 2006). There are also a few species, e.g., *Astrangia poculata* and *Madracis pharensis*, that occasionally have zooxanthellae in their endodermic tissues (Wells 1973; Peters et al. 1988). *Solenastrea hyades* is reported to expel and regain zooxanthellae on a seasonal basis in Onslow Bay, North Carolina (Morgan Wells, personal communication 1983).

The ZS found in Florida were first reported and described in pioneering studies of Louis and Alexander Agassiz (1852, 1869, 1880, 1885), Pourtalés (1880a,b), Vaughan (1901, 1911), and Verrill (1902). Following Smith's 1948 and 1954 publications, understanding of the ZS in Florida area has benefited greatly from studies conducted in the Bahamas, Caribbean, and Mexico using underwater photographs, compiling information on habitat, bathymetric ranges, ecological relationships, and/or paleontological ranges. Relevant publications include: Voss and Voss 1955 (Soldier Key); Voss et al. 1969 (Elliott Key [Upper Keys, Florida]); Squires 1958, Jaap and Olson 2000 (Bahamas); Goreau 1959, Goreau and Wells 1967, Wells 1973, Wells and Lang 1973 (Jamaica); Lewis 1960, Ott 1975, James et al. 1977 (Barbados); Almy and Carrión-Torres 1963 (Puerto Rico); Duarte-Bello 1961, Kühlmann 1971, 1974a, b, Zlatarski and Estalella 1982, González-Ferrer 2004 (Cuba); Roos 1964, 1971, Bak 1975 (Netherlands Antilles); Pfaff 1969, Antonius 1972, Geister 1973, Erhardt and Werding 1975, Werding and Erhardt 1976 (Colombia); Porter 1972 (Panama); Goldberg 1973 (Boca Raton, SE Florida); Scatterday 1974 (Bonaire); Adey et al. 1976 (Martinique); Ogden 1974, Adey et al. 1977 (St. Croix, US Virgin Islands); Roberts 1977 (Grand Cayman); Cairns 1982 (Belize); Horta-Punga and Carricart-Ganivet 1993, Jordán-Dahlgren and Rodríguez-Martínez 2003 (Mexico); Grimm and Hopkins 1977, Jaap et al. 1989, Coleman et al. 2005 (Florida Middle Grounds); Halley et al. 2005 (Pulley Ridge); Brooks 1963, Davis 1979, 1982, Jaap et al. 1989 (Dry Tortugas); Hoffmeister 1974, Jaap 1984, Wheaton and Jaap 1988, Jaap and Hallock 1990 (Florida Keys); Zlatarski and Estella 1982; González-Ferrer 2004 (Cuba).

Field guides to shallow-water stony corals (*Millepora* and Scleractinia) of Florida and the Greater Caribbean include Smith (1948, 1971), Zeiller (1974), Voss (1976), Greenberg (1977), Colin (1978), Kaplan (1982), and Humann and DeLoach (2002). Additionally, Littler and Littler's (2000) field guide of Caribbean algae has numerous plates with ZS species identified.

Smith (1954) reported 40 ZS Scleractinia (Madreporaria) from unidentified Florida records. He misrepresented the following: *Acropora prolifera* is now recognized to be a hybrid and *Astrangia solitaria* is azooxanthelate. *Agarica nobilis* is not recognized; *Porites divaricata* and *P. furcata* are considered forms of *P. porites*; *Colpophyllia amaranthus* is a junior synonym of *C. natans*. *Manicina mayori* is a form of *M. areolata*, *Meandrina brasiliensis* a form of *M. meandrites*, and *Isophyllyia multifora* a form of *I. sinuosa*. Taking these reductions/revisions into account, Smith's reporting in 1954 includes 31 species from Florida. Subsequently, Jaap et al. (1989) listed 43 species for the Dry Tortugas. Smith (1954) missed species that are relatively common in Florida reefs.

The ZS requirements for optimal success were reported by Wells (1956): temperatures greater than 18° C, low turbidity, high solar illumination, stable levels of oceanic salinity, and a solid substratum. Southeastern Florida, Cuba, Bahamas, and southwestern portions of the Gulf of Mexico have more of these conditions in time and space than do the northeastern and northwestern areas of the Gulf. Endemic species are few: *Oculina robusta* is limited to the eastern Gulf of Mexico (Florida Middle Grounds to Dry Tortugas).

The "Florida Reef Tract," as defined by Vaughan (1914), includes the region from south of Soldier Key (25°31.4'N, 80°10.5'W) to Dry Tortugas (24°38.4'N, 82°51.8'W) but excludes the reefs and hardbottom habitats in Miami-Dade (north of Fowey Rock), Broward, Palm Beach, and Martin counties that continue north to the St. Lucie Inlet at a latitude of 27° 10.06'N. There are 47 ZS species at Dry Tortugas, 38 at Looe Key, 28 in Biscayne National Park, 24 in the area north of the Miami harbor channel in Miami-Dade County, 36 off Broward County, 24 off Palm Beach County, and 8 in Martin County on the reefs south of the St. Lucie

Inlet (Herren 2004). North of the St. Lucie Inlet to Cape Hatteras, the ZS fauna is sparse: *Stephanocenia intersepta*, *Leptoseris cucullata*, *Solenastrea hyades*, and *Cladocora arbuscula* are reported. Mexican reefs range from 25 species in the Tuxpan region to 33 at Campeche Bank (Beltrán-Torres and Carricart-Ganivet 1999). For Cuba, (Sancho Pardo to Rio Camarioca) ZS species richness ranges from 19 at Sancho Pardo and Punta Seboruco to 29 offshore of the Oceanographic Institute (Zlataski and Estalella 1982). Banks in the northwestern Gulf are most depauperate in ZS species, e.g., Geyer 2, McGrail 5, Sonnier 7, and Bright 9 (Flower Garden Banks National Marine Sanctuary faunal records). The Flower Garden Banks reports 23 ZS species (Flower Garden Banks National Marine Sanctuary faunal records), and the Florida Middle Grounds is known to have 19 ZS species (Grimm and Hopkins 1977; Jaap et al. 1989; Coleman et al. 2005). Areas in temperate latitudes and deeper depths also have fewer ZS species. The eastern Gulf region from Tampa Bay to Sanibel Island (the “Hourglass” region) includes 14 ZS species. The Florida Bay-Gulf of Mexico side of the Keys is relatively impoverished; in 2000, the FKNMS coral reef monitoring program in the Gulf of Mexico found 12 ZS species at Content Key and 24 at Smith Shoal.

Ubiquitous ZS include *Stephanocenia intersepta*, *Siderastrea radians*, *Agaricia agaricites*, *Porites astreoides*, *P. porites*, *Montastraea annularis* complex, and *M. cavernosa*. Rarer species include *Madracis formosa*, *Oculina robusta*, and *O. valenciennesi*. Species with restricted distribution include *Cladocora arbuscula*, *Dendrogyra cylindrus*, and *Solenastrea* spp.

The Atlantic ZS display a gradient of decreasing similarity based on spatial separation (Figure 9). Areas such as the west coast of Africa and the Azores are most dissimilar to the Gulf and Caribbean, whereas Bermuda and the south Atlantic (Brazil) present a case of intermediate similarity. Brazil has more endemic ZS than any region (Neves et al. 2006). This can largely be explained by current patterns within the Gulf and Caribbean, which provide reasonable connectivity for Bahamas, Cuba, Florida, Mexico, and the Caribbean; however, they are not thought to ordinarily connect the eastern, southern, and western Atlantic in the time frame necessary to transport viable larvae. Interestingly, there are a few species that have managed ampi-Atlantic transit (*Madracis decactis*,



*Siderastrea radians*, *Porites astreoides*, *P. porites*, and *Montastraea cavernosa*) and are found from Brazil to Bermuda.

Average taxonomic distinctness,  $\epsilon^+$ , defined as:  $\epsilon^+ = \{\sum_{i < j} \omega\} / \{S(S-1)/2\}$ ; S is the number of species present, i and j are the range of species observed (Clarke and Warwick 1998; Warwick and Clarke 2001); and variation in taxonomic distinctness,  $\sigma^+$ , defined as  $\sigma^+ = 2(s-m)[m(m-1)(s-2)(s-3)]^{-1}$  (Clarke and Warwick 1998; Warwick and Clarke 2001) were evaluated using regional distribution of ZS, including the regions of the Caribbean, Gulf of Mexico, Florida (Keys, SE Florida), eastern Atlantic, Bermuda, and Brazil (Figure 10). A comprehensive species list of ZS for the region (Table 3) was used to compare the individual locality to an expected taxonomic distinctness based on the comprehensive ZS list (Warwick and Clarke 2001); the null expectation is that any species present at a specific location behaves like a random selection from the regional species pool. If the average taxonomic distinctness for a specific location is outside the confidence limits, the null hypothesis is rejected. Variation in the taxonomic distinctness idea is that, due to habitat heterogeneity, anthropogenic or natural disturbance, some species are over-represented and others are under-represented by comparison with the regional ZS list. Warwick and Clarke proposed that, under disturbance pressure, species with high taxonomic distinctness (species-poor higher taxa; e.g., a genus with one species or a family with two genera) are typically extirpated before species with lower taxonomic distinctness (Warwick and Clarke 1998).

Clustering (Figure 11) showed that ZS distribution at Florida Keys locations was similar to Cuban reefs (75% similarity); Florida Keys reefs also were quite similar to the Mexican Reefs (69% similarity). Ranking by decreasing similarity order is: Cuba, Mexico, Bahamas, SE Florida, E Gulf of Mexico, NW Gulf of Mexico (Figure 11). Martin County was outside the confidence limits of the taxonomic distinctness (Figure 12). The Tuxpan region of Mexico, Dry Tortugas, Looe Key, and Upper Florida Keys in Florida were either on or just outside the confidence limits (Figure 12). The implication is that species assemblages in these areas are slightly reduced in taxonomic distinctness. We suspect that the causes include

thermal extremes, habitat degradation and, perhaps, these areas have less hydro-connectivity to the main body of the Caribbean.

Regional analysis reports that ZS distribution/diversity is highly similar (82% for Colombia, Belize, Panama, Netherland Antilles, Florida Keys, Jamaica, Cuba, and the Bahamas). The Eastern Atlantic, Martin County, Brazil, NW and NE Gulf of Mexico show greater difference, whereas Miami-Dade, Broward, and Palm Beach counties are 70% similar to the Florida Keys and Caribbean (Figure 9). The taxonomic distinctness analysis reported that, regionally, most localities are within the confidence limits (Figure 12); however, the southeastern U.S. and Martin County fell outside the confidence limits. They are both marginal areas for ZS prospering. Bahamas, Florida, Mexico, and Caribbean localities are much alike in taxonomic distinctness (Figure 12). Distinctions for the Eastern Atlantic, Brazil, NW Gulf of Mexico are clearly quite different. Brazil has the greatest number of endemic species and has the greatest Delta+ value, 191.75; Bermuda's ZS fauna is impoverished and has the lowest Delta+ value, 179.05.

#### **4.10 Florida Keys Coral Reefs**

The seaward-most reefs in the Florida Keys are a series of bank reefs separated by expanses that lack coral reef development. In the Holocene reef development, *Acropora palmata* was a principal builder of Florida reefs (Shinn et al. 1977). In the early to mid 1970s, *A. palmata* was common or abundant on most of the outer reefs; however, due to hurricanes and disease, it has become non-extant on many offshore bank reefs.

A prominent feature on many outer reefs (Grecian Rocks, Molasses, Sombrero, Looe Key, Western Sambo, and Rock Key) is a distinct spur and groove system (Shinn 1963; Shinn et al. 1981). These ridges are constructional (Shinn et al. 1981) from coral growth and deposition, while the grooves (surge channels) facilitate water and sediment transport. The seaward margin of the spurs is typically around 10 m below sea level; the spur may be continuous to the reef flat or it may be interrupted by a gap connecting adjacent surge channels. Zonation along the spur follows the depth (light) and wave energy gradients. Seaward, the spur horizontal surface is typically a series of massive corals (*Montastraea* spp,

*Diploria* spp, and *Colpophyllia natans*); the vertical spur walls often have plates of *Agaricia* spp, *Leptoseris cucullata*, and *Mycetophyllia* spp; shallow caverns and shaded overhangs are colonized by *Scolymia* spp, *Agaricia fragilis*, *Mussa angulosa*, and *Madracis pharensis* (Wheaton and Jaap 1988). As the depth decreases, faunal elements change; at approximately 3 m depth, the surface of the spur tops are in a surge zone with the waves breaking and retreating seaward, resulting in turbulent water. Tops of the spurs may be veneered with *Acropora palmata*, *Millepora complanata*, and *Palythoa caribea*; this was described by Geister (1977) as a shallow spur and groove community, common in the Caribbean-Western Atlantic. As the depth decreases to less than 1 m, the surge of water makes it impossible to swim during windy periods. The organisms that characterize this shallowest portion of the spur are *Palythoa caribea*, *Millepora complanata*, *Zoanthus pulchelus*, and *Porites astreoides*. These organisms are very tolerant of heavy wave energy, intense sunlight, and exposure-desiccation during spring low tides. Inshore of the spur and groove system, the spurs coalesce to form a reef flat--a field of rubble material that is loosely held together by calcareous algae and naturally forming marine cements.

The grooves-surge channels usually have a carpet of sediment composed of broken bits of carbonate material and conspicuous plates of *Halimeda*. Following a severe storm, such as a hurricane, the sediment may be completely washed out of the grooves exposing large, sub-recent corals, the foundation of the reef.

The spur and groove system is absent on many outer reefs (Carysfort, Conch, Alligator, Tennessee, Maryland Shoal, Pelican Shoal). These reefs may be too young to have developed such a system or they may have failed to keep pace with sea level rise. A prominent shoal at or near sea level, and a variety of morphological attributes, lacking in a common pattern, characterizes these reefs.

The deeper spur and groove is a prominent feature of some reefs. A good example is Bird Key Reef, Dry Tortugas National Park (Jaap et al. 1989); it is 2 km long, 400 m wide, and the spur and groove system is restricted to 6 to 21 m depth; shallower areas (0 to 5 m) are low-irregular relief, populated with numerous octocorals. Deep spur and groove formations are interpreted as a

situation where the reef growth failed relative to rising sea level. Octocorals are a prominent element in deep spur and groove habitats.

The most common reef type in the Florida Keys is the patch reef. These are widely distributed inshore of the bank reefs. Some are very close to shore; for example, there is a cluster of high relief patch reefs 0.9 km (0.5 nmi) off Big Munson Island, New Found Harbor. Although most of the patch reefs are unnamed, named patch reefs of some notoriety include a cluster of patch reefs at Bache Shoal and Margot Fish Shoal off Elliott Key; two clusters of reefs off Upper Key Largo in John Pennekamp Coral Reef State Park (Mosquito Banks and Basin Hill Shoals); the Rocks and Hen and Chickens (off Plantation Key); the Garden (off Lower Matecumbe Key); Coffins Patch, East and West Turtle Shoal, East Washerwoman Shoal (off Vaca Key); West Washerwoman (off the Saddlebunch Keys); Western Head (off Key West); and Texas Rock, Iowa Rock, Middle Ground (in Dry Tortugas).

Patch reefs have considerable variation in morphology and size. High-relief patch reefs are constructed of massive-framework corals (*Colpophyllia natans*, *Diploria* spp., *Montastraea* spp., and *Siderastrea siderea*). In some patch reefs, the massive corals are on the periphery of the reef and the center of the reef is a dense forest of octocorals and smaller Scleractinian species (*Poites porites*, *Meadrina meandrites*, *Dichocoenia stokesi*). Corals may be in close proximity or widely dispersed. The epitomized patch reef is dome shaped, circular in outline, surrounded by sedimentary-sea grass habitat, and 30 to 700 meters in diameter (Jaap 1984). A good example is the aptly named Dome Reef in Biscayne National Park (Jaap et al. 1989). Here the octocorals tend to be more specious and abundant than the Scleractinian corals (Table 4).

#### **4.11 Tortugas Banks**

A massive complex of reefs (the Tortugas Banks) in 70 to 90 ft (21 to 27 m) is situated west of Loggerhead Key, Dry Tortugas (Jaap et al. 2001). These banks were created during a lower sea level, and it is thought that they were unable to keep pace with rising sea level following the Wisconsin glacial epoch (Mallinson et al. 2003). Growth was retarded after the water became too deep for light

penetration to stimulate vigorous coral activity. A region referred to as Sherwood Forest is characterized by a low relief foundation of Swiss cheese-like karst limestone and moderate sized platy and mushroom-like *Montastraea cavernosa* corals overlying the foundation. Black Coral Rock is a high relief structure with peaks protruding from the seafloor. Multiple peaks and valleys provide a mosaic of horizontal, vertical, and angled surfaces, offering niches to a wide variety of plants and animals, including colonies of *Antipathes* spp. (black coral) that is listed as locally extinct in Florida (Deyrup and Franz 1994). Black corals are moderately abundant in the Tortugas Banks.

#### **4.12 Epibenthic Hardbottom Communities**

Hardbottom habitat was identified by Davis (1982) as major bottom type. He reported 39.65 km<sup>2</sup> of octocoral-covered hardbottom within Dry Tortugas National Park (4.08 percent of the seafloor in the park). Throughout the Keys on both coasts, this is a very abundant and conspicuous habitat type. It is characterized by a great number of sponges and octocorals (sea whips, sea plumes, sea fans), and the topography is rather flat. Octocoral species density at a monitoring station at Pulaski Shoal was 15.50±3.50 species and 92.60±31.74 colonies per m<sup>2</sup>. The area resembles a jungle with the sea floor totally obscured by the octocoral canopy. Octocoral hard grounds have a rich diversity in other species that use the canopy for refuge, to seek prey, and to breed.

#### **4.13 Sedimentary Habitats**

Sedimentary habitat is important to coral reefs; a large portion of the Dry Tortugas sea floor is composed of sediments (silt, sand, gravel); Davis (1982) estimated that sediments made up the largest component (108.92 km<sup>2</sup> or 47.80%) of the benthic habitat in the Dry Tortugas National Park. If sea grasses are included (because they grow in sediments), the sediment benthic contribution in the Tortugas is 78%. Sedimentary habitats provide niches for virtually every marine phyla, thus the biodiversity of these habitats is relatively high. Because the organisms live (for the most part) under the surface of the sediments, there is a misconception that this area is barren (Cahoon et al. 1990; Snelgrove 1999). Diatoms, protozoa, molluscs, crustaceans, echinoderms, polychaetes, gobies, and blennies are examples of taxonomic categories that are found in the sediments.

The sediments are a forage area for larger predators (Cox et al. 1996) and are a pool of recyclable calcium carbonate.

#### **4.14 Status and Trends in Florida Keys Reefs**

The FKNMS Water Quality Protection Plan (initiated by EPA and FKNMS in 1996) monitoring program utilizes repeated sampling; random, stratified protocols were used to select monitoring sites with replicate sampling stations. Data from 1996 through 2004 documents that disturbance events (bleaching, black water, and hurricanes) are a principal cause of change in these coral reef communities. Sampling protocols (quality assurance/quality control plans) were approved by U.S. Environmental Protection Agency in 1996 to generate four annual station level data products:

1. A species list of all stony corals (*Millepora* and *Scleractinia*)
2. A qualitative list of conditions affecting the vitality of the scleractinian corals (bleaching and diseases by coral species)
3. Benthic cover based on video imagery
4. A census of *Diadema antillareum*.

For detailed sampling protocols see Porter et al. (2002, and [www.floridamarine.org](http://www.floridamarine.org)).

From 1996 to 2004 stony coral species number declined in virtually all of the spatial strata. Losses outnumbered the gains and unchanged status. The taxonomic losses for habitat types were 72 to 73%, except for hardbottom (55%). Hardbottom sites generally were taxonomically depressed in species, and those species that are found (e.g., *Stephanocenia intersepta*, *Siderastrea radians*, *Porites astreoides*) in these habitats are often less sensitive to environmental perturbations (temperature and turbidity). Upper Keys stations had a higher percentage loss than Middle and Lower Keys stations. Dry Tortugas taxonomic losses were similar to Upper Keys stations. Gains and unchanged status were greatest for the hardbottom stations.

The confidence interval predicts that the temporal flux of station species richness is described by plus or minus four to five taxa; however, losses were greater than

gains and some stations lost as many as 13 taxa from 1996 to 2003 (Figure 13); very few stations gained species.

Thirty-four species declined in occurrence, 7 increased, and 4 remained unchanged (Figure 14). Decline in taxonomic richness in stony corals was consistent for all habitats (Figure 15).

Sanctuary-wide, the number of stations where *Acropora cervicornis* and *Scolymia lacera* were present decreased significantly ( $\alpha=0.05$ ) while *Copolphyllia natans*, *Madracis mirabilis*, *Porites porites*, *Siderastrea radians*, *Mycetophyllia ferox* and *M. lamarkiana* showed decreases at the  $\alpha=0.1$  level. Only *Siderastrea siderea* was observed at a significantly greater number of stations in 2001 and 2002 than in previous years.

Black band disease (Rützler and Santavy 1983) was the least common of the conditions monitored; the incidence of black band was slightly higher in 1998 and has wavered at low levels in subsequent years (Figure 16). *Colpophyllia natans*, *Montastraea annularis*, *M. cavernosa*, and *Siderastrea siderea* were infected by black band disease. This disease is more active in the summer and is positively correlated with nutrient enrichment (Voss and Richardson 2006).

The category “white disease” includes white plague and white pox which manifest, not surprisingly, a white appearance (Patterson et al. 2002). White plague was first identified in the Florida Keys in 1977. The disease is characterized by an abrupt band of white that separates living coral tissue from exposed skeleton. The disease usually initiates at the base of the colony and travels upward. Three types of white plague been reported. Type I affects 10 species of corals, causing tissue mortality at a rate of about 3 mm/day. Type II plague affects 32 species of corals and can cause up to 2 cm of tissue mortality per day. Plague Type III affects the large reef building corals (*Colpophyllia natans* and *Montastraea* spp.) and can cause tissue loss at a rate much greater than either the Type I or Type II (Richardson 1998). White pox disease affects elkhorn coral (*Acropora palmata*) in the Florida Keys. It was first found in 1996 and is characterized by white circular lesions on the surface of infected colonies. Tissue

loss and mortality may be very rapid and, although the cause of the disease is still unknown.

In 1996, white disease was recorded at 5 stations; in 2002 it was present at 90 stations. *Agaricia agaricites* complex was not infected with white disease in 1996 but was observed at 33 stations in 2002. *Montastraea annularis* complex followed the previous pattern very closely; no reports in 1996 and 32 stations reporting infection in 2002. Other conditions include several suspected diseases; an example is the purple spot on *Siderastrea siderea*. Fourteen species exhibited increased infection by other diseases/conditions: *Agaricia agaricites*, *Colpophyllia natans*, *Dichocoenia stokesii*, *Eusmilia fastigiata*, *Favia fragum*, *Meandrina meandrites*, *Millepora alcicornis*, *M. complanata*, *Montastraea cavernosa*, *M. annularis* complex, *Porites astreoides*, *P. porites*, *Siderastrea sidera*, and *Stephanocenia michelinii*.

A *Diadema antillarum* census recorded a total of 188 urchins between 1996 and 2003, with the greatest number in 2001 and the fewest in 1996. Western Sambo is the site with the greatest cumulative number of *Diadma*: 47 were observed over the seven-year period. Since the *D. antillarum* demise in 1983, recovery has been exasperatingly retarded. Sites in Dry Tortugas, Middle, and Lower Keys had more *Diadema* than the other sites (White Shoal, Western Sambo, Jaap, West Turtle Shoal). *Diadema* numbers testify that recovery is slow with a very slight increase in numbers from 1996 through 2003; densities range from 0.02 to 0.13 m<sup>2</sup>.

Between 1996 and 2002, sampling stations exhibited a 38% decline in stony coral cover. Declines were most noteworthy between 1997 and 1998 (11.3 to 9.6%) and 1998 to 1999 (9.6 to 7.4%). The decline from 1996 to 1999 was significant: p-value of 0.03, Wilcoxon rank-sum test. Since 1999 the mean percentage cover for all stations has wavered between 7.4 and 7.5% and is statistically insignificant. Hypothesis testing by geographic area (Upper, Middle, and Lower Keys) and habitat type (patch reef, shallow and deep reefs) exhibit the same trends (declining coral cover) as observed in the sanctuary-wide analysis.



In 1996, the most cover was contributed by *Montastraea annularis*, *M. cavernosa*, *Acropora palmata*, *Siderastrea siderea*, *Millepora complanata*, and *Porites astreoides*. The average cover per station for *M. annularis* was 4.6% in 1996 and 2.7% in 2002. *Acropora palmata* average cover declined from 1.1% in 1996 to 0.1% in 2002 (91% reduction). The staghorn coral *A. cervicornis* was rare in 1996 (0.2% cover) and had nearly disappeared by 2002 (0.01%).

#### 4.15 Episodic disturbances

Bleaching episodes occurred in summer and fall 1997 and 1998. The areas most influenced were the shallow offshore sites. The water temperature at the Sea Keys C-Man Station at Sand Key peaked near 32°C on August 10, 1997 (unfortunately, the temperature recorder failed on 11 August). Temperatures were high enough to cause zooxanthellae expulsion, discoloring many of the zooanthids, fire coral, stony corals, and some octocorals such as *Briareum* spp. The organisms that were stressed the most by bleaching were *Millepora complanata* and *Palythoa caribea*. These species tend to expel their zooxanthellae at a slightly lower threshold than the other zooxanthellate organisms (Jaap 1979). *Millepora complanata* cover decline was greatest between 1998 and 1999 (Figure 17). There was a slight improvement in percentage cover and frequency of occurrence after 2001. The 1997 bleaching event is suspected to have stressed *M. complanata*, and a second exposure to hyperthermia in 1998 also reduced the population.

The golden sea mat, *Palythoa caribea*, is abundant and conspicuous in shallow reef, high energy communities (Geister 1977). The Coral Reef Environmental Monitoring Program (CREMP) analysis pools all zooanthids (*Zoanthus* spp., *Palythoa* spp., *Ricordia* spp.) as a single category; however, point count experience is that virtually all zoanthids observed in these images are *P. caribea*. Unlike the fire coral, *Millepora complanata*, *P. caribea* showed little change in cover after the bleaching disturbance (Figure 18). There was a slight reduction in the mean percentage cover between 1997 and 1998; however, 2000 and subsequent years, the coverage levels were equal to or exceeded the pre-bleaching period.

Mustard hill coral (*Porites astreoides*) is also common in the shallow reef communities and creates small mounds and encrustations. This coral also was resilient and did not suffer population reduction from the bleaching episode (Figure 19). We are cognizant that *P. astreoides* will expel zooxanthellae, but it has the capacity to recover after hyperthermic conditions dissipate.

Hurricane Georges crossed the Straits of Florida near Key West on 25 September 1998. The Sombrero Key C-MAN buoy (SMKF1) recorded a maximum sustained wind of 82 knots with a peak gust to 92 knots at 1500 UTC 25 September. Hurricane Georges's greatest influence on coral reef communities was between Sombrero Key and Dry Tortugas. The storm's impact was evidenced by the change in *Acropora palmata* cover (Figures 20, 21). All of the descriptive statistics (range, mean, and frequency of occurrence) declined after Hurricane Georges. We sampled before the hurricane struck in 1998, thus the major decline is most noticeable in 1999 and subsequent years.

Western Sambo station two exhibited the greatest *Acropora palmata* cover: 15.28% in 1996 and 16.34% in 1997. The mosaic image (Figure 20) created from video at this station highlights the severity of the loss. From 1996 to 1998, there was a large thicket of *A. palmata* on station two; it disappeared after 1999, and recruitment into the area had not occurred through 2004.

The National Hurricane Center reported that at 2300 UTC on 14 October 1999, Irene reached hurricane status over the Florida Straits. The center moved over Key West at 1300 UTC the next day. The hurricane force winds were concentrated east of Irene's center over the Lower to Middle Florida Keys. Irene made its fourth landfall near Cape Sable and then moved across southeast Florida bringing sustained 39 to 73 mph winds and 10 to 20 inches of rainfall. Irene's sustained and peak wind gusts were less than those of Georges. This second hurricane in a year disturbed the offshore shallow reefs, but, since Hurricane Georges had already reduced the *Acropora palmata* populations, Hurricane Irene's influence was muted.

In early 2002, a body of dark-colored water was reported between Marco Island and Key West (Hu et al. 2003). Hu and colleagues obtained satellite imagery data from the Advanced Very High Resolution Radiometer and the Sea Viewing Wide Field-of-view sensors. Water-leveling radiance and ocean color index were used to create a daily image time series, which documented the water mass anomaly from January through April 2002 (Hu et al. 2003). High concentrations of Rhizosoloniaceae diatoms and the toxic dinoflagellate *Karenia brevis* (red tide) were found in water samples. This phytoplankton bloom extended over two CREMP sampling sites: Content Keys and Smith Shoal. The 2002 and 2003 data for these sites document a reduction in the coral cover at both sites. The Content Key site is a hardbottom site that has had consistently low species richness and cover since 1996. The Smith Shoal site is a high profile patch reef; it exhibited cover losses in all but one species after the black water event, making it probable that the black water anomaly caused the coral decline. Red tide has previously resulted in severe losses in the eastern Gulf of Mexico sponge-octocoral-stony coral communities (Smith 1971, 1976).

## **4.16 Multivariate Analyses**

The 1996 to 2003 Florida Keys National Marine Sanctuary coral reef monitoring database includes files for 1,360 stations, 4,080 transects, and records for 2,400,000 points related to 200,000 images. The multivariate statistical approach (Clarke 1993; Clarke and Green, 1988; Clarke and Gorley 2005; Clarke et al. 2005) exhibits and contrasts the different sources of variation in assemblage structure by strata: hardbottom, shallow, deep and patch reefs; geographical region: Dry Tortugas, Lower, Middle and Upper Keys; site within geographic regions; and across years within each site.

There is a general trend of similarity in assemblage structure from patch reefs through deep reefs to shallow reefs. Hardbottom assemblages tend not to overlap with those on reefs. While some deep reefs, such as Looe Key, Eastern Sambo, Tennessee, and Rock Key, are relatively similar in terms of the community of stony corals inhabiting them, others such as Molasses and Alligator differ from them substantially. Shallow reefs tend to be less similar to each other than deep reefs and exhibit the greatest degree of spatial variability. The major pattern is one

of difference between the strata. Analysis of Similarities (ANOSIM) confirms this observation, as differences between strata are highly significant (Global  $R=0.458$ ,  $p<0.001$ , for all pair-wise comparisons  $p<0.003$ ).

Within shallow reef assemblages (Figure 22a), there is little evidence of a trend in community structure related to each reef's position along the Keys, as assemblages from shallow reefs in the Upper and Lower Keys tend to be more similar to each other than to those from the Middle Keys. A similar lack of geographic pattern is shown for deep reefs (Figure 22b) and patch reefs (Figure 22c). No significant differences were found using ANOSIM tests for differences in average assemblage structure between regions within reef types ( $p>0.167$ ).

Changes through time at each site (Figure 23) reveal the effects of man-made and natural changes in the Florida Reef Tract. It is readily apparent that the changes in some reefs are greater than the changes in others. For example, among shallow reefs in the Lower Keys (Figure 23a), changes over time at Looe Key and Western Sambo are similar in magnitude and direction, but less than changes at Sand Key, Rock Key and Eastern Sambo. Sand Key shows a marked change between 1998 and 1999, which may be related to the passage of Hurricane Georges or the bleaching event, whereas at Rock Key these events did not produce marked changes, but something happened between 2002 and 2003 that changed assemblages at the site substantially. Changes through time at Eastern Sambo are generally larger than changes at Looe Key and Western Sambo, but there is no evidence of a major shift in community structure in any particular year. Among deep reefs in the same areas (Figure 23b), Eastern Sambo, Looe Key, Rock Key and Western Sambo show variations through time, which are similar in magnitude, though essentially random in direction, while changes at Sand Key tend to be greater. Large changes in community structure at Sand Key occurred between 1996 and 1997, between 1998 and 1999, and between 1999 and 2000, as the community returned to a state similar to that observed in most other years. Among patch reefs in the Lower Keys small, essentially random, temporal variation is seen at the Western Head, Cliff Green and West Washerwoman sites (Figure 23c). In contrast, at Smith Shoal and Jaap Reef relatively large changes are seen in some years, especially between 1999 and 2000 and between 2001 and 2002 at Smith Shoal, and between 1996 and 1997, and between 1998 and 1999 at

Jaap Reef. Although changes in some years are greater than in others, assemblages on both these reefs show diverging linear trends such that differences between the two reefs at the start of sampling, in 1996, are very much less than differences between them in 2003.

## **4.17 A Case Study: Dry Tortugas**

The Dry Tortugas is the western terminus of the Florida Reef Tract and lies 100 to 112 km west of Key West, Florida; the geographic coordinates are 24° 33' to 24° 44' N latitude, 82° 46' to 83° 15' W longitude (Figure 24). At the convergence of the Gulf of Mexico, Caribbean Sea, and the Atlantic Ocean, the area is characterized as a mosaic of coral reefs, sedimentary shoals, sea grass meadows, and small islands. A 100 square mile Dry Tortugas National Park is the prominent feature (Figure 24).

### **4.17.1 Environmental setting**

Water temperatures at the Loggerhead Key Lighthouse, recorded between 1879 and 1907, ranged from 17.9 to 31.1°C (Vaughan 1918). The most extreme cold temperature at Dry Tortugas occurred in the winter of 1977-1978, when a cold front chilled the waters to 14°C and caused a massive die off of *Acropora cervicornis* (Davis 1982). Extremely warm temperatures (>32°C) are uncommon but do occur during doldrums (Jaap, unpublished thermograph data, 1988-1996). The National Park Service sponsored a reef-monitoring project at DTNP from 1989 through 1997. At Pulaski Shoal, in a 30 foot (10 m) depth, from 28 August 1993 to 30 August 1994, the temperature ranged from 20.13 to 30.35°C (hourly thermograph data). During a coral bleaching event spanning August 31 to September 13, 1991, the extreme high temperatures ranged from 30.4 to 31.5°C. From December through April, the extreme low temperatures should range from 17.9 to 21.3 based on Vaughan's lighthouse data.

Salinity off the Dry Tortugas typically ranges from 37 to 32 parts per thousand. Lower salinity values result from entrained Mississippi River freshwater runoff (Ortner et al. 1995; Gilbert et al. 1996).

Waves are a function of wind speed, duration, and fetch. During the period of frontal passages, wave heights can exceed 3.1 meters. Currents that influence this area are tidal and episodic gyres from the Loop Current. Tides are semidiurnal or mixed; two tide current stations are listed for Southwest and Southeast Channels, and maximum current speed listed is  $51.44 \text{ cm sec}^{-1}$  (Tide Current Tables, 2002).

Two major currents influence the Tortugas area: the Florida Current in the Straits of Florida and the Loop Current that sweeps into the eastern Gulf of Mexico from the Yucatan Straits and reenters the southern Straits of Florida to join the Florida Current. Lee et al. (1994) report that gyres propagate and move off the Tortugas as the Loop Current reenters the southern Straits of Florida. The gyre is important because of larval transport as well as influencing the thermal regime because of cold water in the gyres. The cooler water can be detected at 20 m; a thermograph positioned at Bird Key Reef detected a cold-water gyre from 7 to 11 August 1988. Water temperature pulsed from  $22.5^{\circ}$  to  $29^{\circ}\text{C}$  (Jaap et al. 1991). Loop Current gyres or eddies routinely occur on the Tortugas Banks. In 2002, (May 9-15) while the FMRI Coral Reef Monitoring Project group was sampling at Black Coral Rock, the current speed was so strong that our research team could not work underwater. During the March 1993 “storm of the century,” current speeds ranged from  $42.2$  to  $50.2 \text{ cm sec}^{-1}$  at an oceanographic buoy in 30 meters of water between Southwest and Southeast Channels. This is similar to maximum tide speeds in SW Channel ( $51.44 \text{ cm sec}^{-1}$ ).

#### **4.17.2 Early Research**

As previously mentioned, natural history expeditions to the area in the nineteenth century include Louis and Alexander Agassiz and Louis Pourtalès. The greatest contribution in documenting marine benthic resources during this era is a map of submerged habitats published by Alexander Agassiz (1882). In 1905, when the Carnegie Institution established a laboratory on Loggerhead Key, Dry Tortugas (Colin 1980; Stephens and Calder 2006) this facility became a leader in early twentieth-century marine research, studying the biology, geology, and environmental conditions of the Dry Tortugas and adjacent area (Davenport 1926; Colin 1980; Stephens and Calder 2006). Papers of the Tortugas Laboratory

published by the Carnegie Institution, Washington, D.C., contain a complete set of the publications resulting from this research. Seminal coral reef work includes: Vaughan (1911, 1914, 1915, 1916), Mayer (1914, 1918), and Wells (1932). Vaughan studied the growth rate of corals and the geologic history of coral reefs; Mayer did extensive studies on the physiology of medusa and temperature tolerance of corals. Subsequent publications on Tortugas coral reefs include Shinn et al. (1977), Thompson and Schmidt (1977), Davis (1979, 1982), Halley (1979), Dustan (1985), Jaap et al. (1989), and Jaap and Sargent (1993). Schmidt and Pikula (1997) published an annotated bibliography of scientific studies within Dry Tortugas National Park. An excellent history of the Dry Tortugas island dynamics is found in Robertson (1964). Robertson reported that Bird Key was a major island with a large rookery of terns (documented by Audubon in 1832). Severe hurricanes in 1910 and 1919 destroyed the vegetation (bay cedars, many reaching eight feet high). This was followed by chronic erosion of the island, and, in 1929, the Audubon warden abandoned his house on Bird Key and moved to Garden Key. It is a possibility that the hurricane and subsequent erosion of Bird Key was partially responsible for the loss of coral in the shallow portions of Bird Key Reef.

#### **4.17.3 Habitat Description**

The major reef types at Dry Tortugas include bank reefs, patch reefs, and thickets of elkhorn and staghorn corals. The elkhorn corals today are situated in the middle of five-foot channel, the sea floor is limestone with virtually no sediment. The staghorn coral thickets are situated on sedimentary rubble at White Shoal and west of Loggerhead Key. Benthic habitat mapping began over a century ago and continues today (Agassiz 1882; Davis 1982; Fla Mar Res Inst 1998; Franklin et al. 2003). In a recent mapping effort, Franklin and his team classified approximately 200 km<sup>2</sup> of previously unmapped habitat. Habitats were classified into nine reef and hardbottom habitats ranging from low-relief hardbottom habitats to high-relief coral pinnacles/reef knolls.

Over the past 30 years, coral communities in the Dry Tortugas have trended downward in coral cover and coral diversity (Jaap et al. 2002). The once abundant elkhorn coral (*Acropora palmata*) assemblages have virtually

disappeared from the area (Davis 1982; Jaap and Sargent 1993). Staghorn (*A. cervicornis*, *A. prolifera*) populations have also declined due to hypothermic stress (Roberts et al. 1982) and a virulent disease of unknown etiology (Peters et al. 1983). More recently the Coral Reef Environmental Monitoring Program (CREMP) has documented a decrease of mean percentage stony coral cover at several Tortugas reefs between 2001 and 2003. This decrease was largely attributed to losses in two stony coral species, *Montastraea annularis* complex and *Colpophylla natans*, and is most likely the result of an unknown disease infecting these two corals.

Bird Key Reef, in the southern portion of the park, was intensely studied during the 1975-1976 TRACTS Program (Shinn et al. 1977; Jaap et al. 1989), including the stony coral fauna community structure. *Montastraea annularis*, *M. cavernosa*, and *Siderastrea siderea* were the principal framework builders on this reef. Coral diversity, cover, and habitat complexity increased with depth. Coral cover (as determined by linear measurement) was highest in depths between 9 and 13 m. If this is used as the baseline for temporal trends, the patterns of change are remarkable. Average coral cover was 47% in 1975, declined to 21 to 28% from 1989 to 2001, and in 2004 ranged from 12 to 14% (Figure 25). The decline was caused by winter cold fronts, bleaching, coral diseases, and hurricanes.

The trends in Florida Keys reefs are disturbing, but they are no different from most other Caribbean and Bahamian reefs. Declines began in the late 1970s to early 1980s; early on, *Acropora cervicornis* and *A. palmata*, particularly, exhibited significant population losses. One hundred years earlier, in 1882, Alexander Agassiz published a map of the marine communities. This map included the spatial coverage of the principal marine community components (Table 5). At that time, the staghorn and elkhorn reefs contributed most of the reef habitat at Dry Tortugas shallow reefs.

These are the earliest qualitative data for any western Atlantic reef system and are significant comparative aids in documenting the downward trend in reef diversity and vitality. Although the Carnegie workers added greatly to the knowledge of corals and reefs, they did not map reefs. John W. Wells studied Tortugas reefs in



1932; his field notes (unpublished 1932) reflect that the *Acropora palmata* reefs were similar to what Agassiz had reported. From the closing of the Carnegie laboratory in 1939 until 1973, there was a hiatus in reef research at Dry Tortugas. In 1982, Davis published a map of Dry Tortugas marine communities (Table 6).

The principal differences between Agassiz's and Davis's evaluations are:

1. Davis included sea grasses and algae, which were not detailed in Agassiz's evaluation.
2. A great increase in the octocorals hardbottom habitat from 1882 to 1982. (Note the actual surveys occurred in 1881 for Agassiz and in 1975-1977 for Davis).
3. The staghorn (*Acropora cervicornis*, *A. prolifera*) reefs had increased slightly while the elkhorn reefs (*A. palmata*) virtually disappeared.

In January 1978, an extreme cold-water disturbance resulted in a 95% or greater loss of *Acropora cervicornis* from the Dry Tortugas (Davis 1982; Porter et al. 1982; Roberts et. al. 1982). Projects at Dry Tortugas have monitored coral abundance and cover at Bird Key Reef, west of Loggerhead Key (*A. cervicornis* thickets prior to the cold water disturbance), Pulaski Shoal, Texas Rock, and White Shoal. Neither *A. cervicornis* nor *A. palmata* populations have recovered (Jaap and Wheaton 1995). In 2002 and 2004, the Dry Tortugas sites were surveyed again and some areas with a few colonies of *A. cervicornis* were found but no general recovery (Jaap et al. 2002).

Jaap and Sargent (1993) published details on mapping of the *Acropora palmata* community in Five Foot Channel. They identified the community as occupying 1,400 m<sup>2</sup> (containing both sparse and dense concentrations of *A. palmata*; however, the dense concentration was confined to within 728 m<sup>2</sup>). The area is slightly larger than what Davis (1982) reported.

In the 2002 expedition to Five Foot Channel, an inspection of the *Acropora palmata* and the *A. prolifera* communities revealed that they had suffered from disease and/or environmental stresses. In 2000, a channel that separated Garden and Bush Keys filled in with sediment thus changing water circulation. The

circulation at flood tide is from the southeast through the Five Foot Channel gap between the Long Key and Bird Key Reef rampart. At ebb tide, the flow reverses and the source of water changes; now water from and around the Garden Key anchorage (possibly including overflow from the Garden Key septic tank field) flows out Five Foot Channel (previously, water entering the channel between Garden and Bush Keys formed the principal volume).

In October 2004, approximately a month after the eye of Hurricane Charlie passed over the Dry Tortugas, another visit was made to Five Foot Channel. It was observed that the storm had fragmented many corals and the pieces had been scattered inshore as far as 100 m from the *Acropora palmata* and *A. prolifera* communities concentrated area. Some fragments had healthy-looking tissue. The patches were reduced in upward relief but did not seem to have suffered catastrophic destruction.

A site off the northeast side of Loggerhead Key (3 m deep) was also impacted by the storm. Dana Williams (National Marine Fisheries Service, personal communication) observed in 2002 a moderate population of *Acropora cervicornis*. Following the hurricane, this site exhibited severe disturbance. There were very few multi-branched colonies; mostly it was small branch fragments, many of which had washed inshore (west) and ended up in a sparse *Thalassia* bed. For the most part, the vitality of the fragments in the *Thalassia* appeared satisfactory (color, few signs of disease, or predation).

Recent disturbances at Dry Tortugas have radically changed the area's shallow coral reef communities, although deeper reefs on the Tortugas Banks were not impacted. Based on the past history of coral reef recovery in Florida (Shinn 1975) after Hurricane Donna, the expectation is that recovery will be decades or longer for the Tortugas shallow reef communities.

## 4.18 Fisheries Issues in the Florida Keys Coral Reef Ecosystem

### 4.18.1 Florida Keys coral reef fisheries

Coral reefs in southeastern Florida and the Florida Keys provide the ecological foundation for vital fisheries and a tourism-based economy that generated an estimated 71,000 jobs and \$6 billion dollars of economic activity in 2001 (Johns et al. 2001). They also contributed to the designation of Florida as the “fishing capital of the world” by the state legislature (FWC 2007; <[www.floridaconservation.org](http://www.floridaconservation.org)>). Coral reef ecosystem goods and services, however, extend beyond fishing to include a range of educational, scientific, aesthetic, and other recreational uses, such as snorkeling, SCUBA diving, and tourism.

Fisheries in southern Florida are complex. Adult reef fishes are caught for food and sport around bridges and on offshore patch and barrier reefs. Commercial and sport fisheries also target spiny lobster, marine aquarium fishes and invertebrates, inshore and offshore. Pink shrimp (*Penaeus duorarum*), a principal prey item of the snapper-grouper complex, are intensively exploited. Offshore, a substantial commercial food fishery targets adult pink shrimp inhabiting sedimentary areas near coral reefs. In coastal bays and near barrier islands, juvenile pink shrimp are commercially targeted as live bait for the recreational fishery. Both food and sport fisheries target pre-spawning sub-adult pink shrimp as they emigrate from coastal bay nursery grounds to offshore spawning grounds. Inshore, sport fisheries pursue highly prized game fishes, including spotted seatrout (*Cynoscion nebulosus*), sheepshead (*Archosargus probatocephalus*), black and red drum (*Sciaenops* spp.), snook (*Centropomus undecimalis*), tarpon (*Megalops atlanticus*), bonefish (*Albula vulpes*), and permit (*Trachinotus falcatus*), while commercial fisheries primarily target sponges and crabs (blue and stone). Offshore of the deep margin of the bank reefs, commercial and sport fisheries capture an assortment of species including amberjack (*Seriola dumerili*), king (*Scomberomorus cavalla*) and Spanish (*S. maculatus*) mackerel, barracuda (*Sphyraena barracuda*), sharks (Class Chondrichthyes), and small bait fishes (e.g., Exocoetidae, Mullidae, Carangidae,

Clupeidae, and Engraulidae). Further offshore (seaward of the 40 m isobath), commercial and sport fisheries catch dolphin-fish (*Corypaena hippurus*), tunas (*Thunnus* spp.), and swordfish (*Xiphias gladius*), and sport fishers target sailfish (*Istiophorus* spp.), wahoo (*Acanthocybium solandri*), and white (*Tetrapterus albidus*) and blue (*Makaira nigricans*) marlin.

#### **4.18.2 Florida Keys fishery management**

Fisheries are managed along the Florida Keys ecosystem (Figure 26) by the Florida Fish and Wildlife Conservation Commission (<[www.myfwc.com](http://www.myfwc.com)>) and two federal fishery management councils (South Atlantic [<[www.safmc.org](http://www.safmc.org)>] and Gulf of Mexico [<[www.gulfcouncil.org](http://www.gulfcouncil.org)>]). Special regulations can also apply in the Florida Keys National Marine Sanctuary (FKNMS, <[www.fknms.noaa.gov](http://www.fknms.noaa.gov)>) under NOAA (Department of Commerce); in three national parks (Biscayne, Everglades, Dry Tortugas, <[www.nps.gov](http://www.nps.gov)>) and four National Fish and Wildlife Refuges (Department of Interior); and in John Pennekamp Coral Reef State Park (Florida Department of Environmental Protection).

##### *4.18.2.1 Biodiversity of the major reef fauna groups*

The Florida Keys has more than 500 fish species, including 389 that are reef associated (Stark 1968), and thousands of invertebrates, including corals, sponges, shrimps, crabs, and lobsters. Snapper-grouper utilize a mosaic of cross-shelf habitats and oceanographic features over their life spans (Ault and Luo 1998; Lindeman et al. 2000). Most adults spawn on the bank reefs and sometimes form large spawning aggregations (Domeier and Colin 1997). The Dry Tortugas region in particular contains numerous known spawning aggregation sites (Schmidt et al. 1999). Pelagic eggs and developing larvae are transported from spawning sites along the barrier reef tract by a combination of seasonal wind-driven currents and unique animal behaviors to eventually settle as early juveniles in a variety of inshore benthic habitats (Lee et al. 1994; Ault et al. 1999). Some of the most important nursery habitats are located in the coastal bays and near barrier islands (Lindeman et al. 2000; Ault et al. 2001). As individuals develop from juveniles to adults, ontogenetic habitat utilization patterns generally shift from coastal bays to offshore reef environments. The frequency of occurrence of the more common

fish species (Table 7) notes that the most common species have similar ranking over time, the less common species are more dynamic in temporal rank.

#### *4.18.2.2 Human impacts and conservation issues*

Coral reefs in the Florida Keys are impacted by fishing and by habitat degradation from other human activities including coastal development, altered freshwater flow, and changes in water quality from pollution, sedimentation, and excess nutrients (CERP 1999; Cowie-Haskell and Delaney 2003). Human impacts have escalated as a result of Florida's tenfold population growth from 1.5 million people in 1930 to 16 million in 2000. In 2000, over 5 million residents, nearly a third of Florida's population, lived in the five southern counties adjacent to coral reefs (Palm Beach, Broward, Miami-Dade, Monroe, and Collier). In addition, over 3 million tourists visit the Keys annually (Leeworthy and Vanasse 1999).

The Florida Keys reef ecosystem is considered one of the nation's most significant, yet most stressed, marine resources and is managed by Florida, NOAA, and the National Park Service. Reef fisheries target the "snapper-grouper complex", which consists of 73 species of mostly groupers and snappers, but also grunts (Pomadasyidae), jacks (Carangidae), porgies (Sparidae), and hogfish (Labridae). The fishery has been intensively exploited over the past 75 years, during which time the local human population has grown exponentially, generating concerns over sustainable fishery productivity. Many reef species are extremely sensitive to exploitation, and coastal development subjects coral reefs to a suite of other stressors that can cumulatively impact reef fish populations by degrading water quality and damaging nursery and adult habitats.

#### **4.18.3 Fishing and fishing intensity**

Extensive recreational and commercial fishing occurs in Florida Keys waters. Recreational fishers emanate either locally (from SE Florida or the Keys) or from more distant venues desiring to experience "The Fishing Capital of the World," as the state of Florida promotes itself (Ault et al. 2005a, b; FWC 2007).

In addition to SE Florida's expanding human population, recreational vessel registrations in south Florida increased more than 100% from 1964 to 2006.

Commercial vessel registrations increased by about 100% from 1964 to 1998 but have since decreased by 37% (Figure 27). Commercial fisheries target reef and pelagic fish species, spiny lobster, stone crabs, blue crabs, shrimp, and ballyhoo. Headboat fisheries, in which customers pay “by the head” to fish from vessels with a typical capacity of from 10 to 20 people, predominantly target reef species. Precise data on fishing effort on coral reefs do not exist but are reflected by statewide and regional fishing statistics. In the five most recent years for which recreational fishery estimates are available (2001-2005) for Florida, more than 6.4 million anglers averaged 27.2 million marine fishing trips annually. An estimated 173.3 million fish were caught annually, of which a little more than 50% were released (86.9 million) (NMFS 2007). Two recent (2000-01, 2003) non-concurrent studies showed that 3.64 million person/days were spent fishing on natural reefs annually in the Florida Keys (Johns et al. 2001; Johns et al. 2004). Concomitant with increasing fishing pressure associated with increasing population, average fishing power (the proportion of stock removed per unit of fishing effort) may have quadrupled in recent decades because of technological advances in fishing tackle, hydroacoustics (depth sounders and fish finders), navigation (charts and global positioning systems), communications, and vessel propulsion (Bohnsack and Ault 1996; Mace 1997).

Fishing can impact coral reefs by removing targeted species and by killing nontarget species as bycatch, both of which may result in cascading ecological effects (Frank et al. 2005). Because fishing is size-selective, concerns exist about ecosystem disruption by removal of ecologically important keystone species, top predators (groupers, snappers, sharks, and jacks), and prey (e.g., shrimps and baitfish).

Fishing can also negatively impact reef ecosystems via fishing-related habitat damage. Commercial fisheries in the Keys for lobsters and stone crabs utilize traps that are deployed in habitats adjacent to reefs. Currents associated with strong storms can move traps onto reefs, where corals and other benthic organisms are damaged or killed (e.g., Sheridan et al. 2005). In 2005, it is estimated that approximately 300,000 lobster traps were lost during a series of hurricanes and strong storms (Clark 2006). Many reefs throughout the Keys are

littered with lost traps and with monofilament line lost by recreational anglers. Reef damage may also occur from anglers anchoring on reefs (Davis 1977). Stress associated with fishing-related removal of species and habitat damage may be compounded when combined with other stressors such as pollution and climate change (Wilkinson 1996).

In response to declining trends in reef fishery catches, a series of regional federal and state management regulations were imposed including recreational bag limits, minimum size limits, commercial quotas and trip limits, seasonal closures, gear restrictions, limited commercial entry, closed fisheries, species moratoria, game fish status, and restrictions on sale and possession. These regulations were implemented to stabilize catches, protect spawning stock biomass, and reduce fishing mortality rates. In general, the history of regional regulations for reef fishes has been complex and has tended to be more restrictive over time. Nonetheless, despite the bevy of regulations imposed in the Florida Keys, recent fishery assessments indicate that, for example, black grouper spawning stock biomass was less than 10% of its historical size (Ault et al. 2005b).

In recent years, new ecosystem-based management measures have been enacted in the Florida Keys, including the 1997 implementation of a network of 23 No Take Marine Reserves (NTMRs) by the Florida Keys National Marine Sanctuary (FKNMS, NOAA, <[www.fknms.noaa.gov](http://www.fknms.noaa.gov)>). These are relatively small (mean area 2 km<sup>2</sup>, range 0.16-31 km<sup>2</sup>), comprising 46 km<sup>2</sup> in total area (U.S. DOC 1996) and have varying levels of protection: four allow catch-and-release surface trolling and four can only be accessed by special permit. In July 2001, the Florida Keys network was expanded to become the largest in North America with the implementation of two NTMRs in the Dry Tortugas region covering about 566 km<sup>2</sup>. The Tortugas region is believed to be extremely important for coral reefs and fisheries as a source of recruitment because of its upstream location in the Florida Current that facilitates advective dispersion and transport of eggs and larvae to the rest of the Keys.

#### 4.18.4 Fisheries history

Native Americans fished for reef fishes on Florida reefs long before the arrival of European settlers (Oppel and Meisel 1871). Reef fishing accelerated in the 1920s. Following growing public conflicts and sharp declines in catches, monitoring programs at the species level began in the early 1980s (Bohnsack et al. 1994; Bohnsack and Ault 1996; Harper et al. 2000; Ault et al. 2005a, b).

Reef fish landings trends for the period 1981 to 1992 were reported for the Florida Keys by Bohnsack et al. (1994). Depending on year, recreational landings comprised between 40% and 66% of total landings. Reef fishes accounted for 58% of total fish landings, 69% of recreational landings, and 16% commercial landings. Commercial landings were dominated by invertebrates (spiny lobster, shrimp, and stone crabs), which comprised 63% of total landings.

In a report to the U.S. Congress, NMFS classified 11 species that are landed in the Keys as overfished (i.e., depleted below minimum standards), and 11 as subject to overfishing (i.e., being fished at a rate that would lead to being overfished), with some overlap between the two categories (NMFS 2005). Included in these totals are reef-associated species such as gag (*Mycteroperca microlepis*), black (*M. bonaci*), red (*Epinephelus morio*), snowy (*E. niveatus*), Warsaw (*E. nigritus*), goliath (*E. itajara*) and Nassau (*E. striatus*) groupers, speckled hind (*E. drummondhayi*), and red (*Lutjanus campechanus*) and vermilion (*Rhomboplites aurorubens*) snappers. Fisheries for goliath and Nassau groupers and for queen conch (*Strombus gigas*) were closed in the 1990s and remain closed today, although the goliath grouper stock continues to indicate signs of recovery (Porch et al. 2003, 2006) to the extent that considerable debate occurs regarding re-opening the fishery.

Ault et al. (1998) assessed the status of multiple reef fish stocks and determined that 13 of 16 groupers (Epinephelinae), seven of 13 snappers (Lutjanidae), one wrasse (hogfish; Labridae), and two of five grunts (Haemulidae) were overfished according to federal (NMFS) standards. It was suggested that some stocks appeared to have been chronically overfished since the 1970s, and that the Florida keys fishery exhibits classic “serial overfishing” in which the largest, most



desirable species are depleted by fishing (Ault et al. 1998). Ault et al. (2001) found that the average size of adult black grouper in the Upper Keys was close to 40% of its 1940 value, and that the spawning stock for this species is now less than 5% of its historical unfished maximum. In subsequent analyses, Ault et al. (2005a, b) determined that, of 34 species within the snapper-grouper complex for which sufficient data were available for analysis, 25 were experiencing overfishing (Figure 28).

Partly in response to concerns about fisheries exploitation, the Florida Keys National Marine Sanctuary (FKNMS) established a series of “Sanctuary Preservation Areas (SPAs)” in 1997. Comparison of fish and benthic communities within versus outside of the SPAs is underway. The FKNMS also created the Tortugas Ecological Reserve in 2001 to protect reef resources and support sustainable reef fisheries. The reserve covered 151 mi<sup>2</sup>; prohibited all anchoring, fishing, and other extractive activities; and, at the time, was the largest marine reserve in North America. Scientists at the University of Miami and NOAA Fisheries Service have studied and reported on responses of coral reef fish populations to this reserve. Based on data collected during over 4,000 research dives, they compared changes in the Dry Tortugas region between 1999 and 2000 before the reserve was established and in 2004, three years after the reserve was established (Ault et al. 2006). As predicted by marine reserve theory, significant regional increases in abundance for several exploited and non-exploited species were detected. Significantly greater abundance and larger fish sizes were found in the Tortugas Ecological Reserve for black grouper (Figure 29), red grouper (Figure 30), and mutton snapper compared to the baseline period. No significant declines were detected for any exploited species in the reserve, while non-exploited species showed both increases and declines. Abundance of exploited species in fished areas on the Tortugas Bank either declined or did not change. A comparison of black grouper size distributions as a function of management zone is given in Figure 31.

On January 19, 2007, the National Park Service established a 46 mi<sup>2</sup> Research Natural Area within Dry Tortugas National Park. This area was contiguous to the FKNMS Ecological Reserve and effectively expanded the marine reserve network

since it also prohibited all anchoring and extraction. Ongoing research and monitoring are planned to ascertain whether patterns observed in protected areas in the Tortugas are due to influences of marine reserves, confounding effects of recent changes in fishing regulations, hurricane disturbances, or random oceanographic and chance recruitment events.

#### **4.19 Human Influences and Water Quality**

The U.S. Environmental Protection Agency Water Quality Protection Plan for the FKNMS includes a quarterly sampling dating from 1995 (Boyer and Briceño 2005). They report trends implying anthropogenic input to coastal waters that include:

- Elevated concentration of dissolved inorganic nitrogen
- Elevated concentration of total organic carbon
- The “back country” (Florida Bay) exhibits trends of elevated concentrations of dissolved inorganic nitrogen, total organic carbon, chlorophyll A, greater turbidity, and greater nitrite concentrations.
- Water quality measurements are consistent from year to year with seasonal fluctuations.

Boyer and Briceño (2005) reported that the water quality in FKNMS is mostly driven by hydrological and meteorological forces that extend beyond the Florida Keys boundaries.

Episodic disturbance events such as hurricanes, bleaching episodes, and harmful algal blooms are most responsible for structuring the coral reef communities. Vessel groundings are a growing concern (Jaap 2000; Jaap et al. 2006) as recovery is frequently impeded by repeated groundings on the same reef sites. Anthropogenic activities add stress to a system that is already under pressure from natural forces, especially the extensive urbanization of the coast and resource utilization that is perceived by many to exceed a reasonable carrying capacity. Florida’s reefs are in crisis. Although the faunal population has shown resilience over the thousands of years of natural change, the speed and variety of man-made pressures on the community are overwhelming the habitat’s ability to recover.

Figures 32-34 document a cross section of Octocorallia and Scleractinia from Florida Keys reefs.

Transport of risky materials into the region has marine, terrestrial, and airborne components. The hydrodynamic system brings both freshwater and pollutants from as far away as Montana and Wisconsin via the Mississippi, Missouri, and Ohio drainage basin (Ortner et al. 1995; Gilbert et al. 1996). Runoff from the urban areas brings nutrients (pet feces and fertilizer), petroleum, trace metals, and chemicals into the marine system. The upper level winds transport dust from Africa (Darwin 1846; Gillette 1981; Prospero et al. 1987; Goudie and Middleton 2001; Garrison et al. 2003) including metals and pathogens that enter directly or indirectly into the marine system (Duce and Tindale 1991; Shinn et al. 2000; Shinn et al. 2003; Jickells 2005).

Anthropogenic alterations of the environment began when the Flagler railroad (1912) built causeways and bridges linking Key West with the mainland. Urbanization and development in the last century radically altered coastlines that were dominated by protective buffers: mangroves and wetlands that filter upland runoff, stabilize sediments, absorb nutrients, and maintain water quality, benefiting seagrass and coral reef communities. Natural coastal habitats have been replaced with concrete seawalls and cul-de-sac canals that have increased water turbidity and nutrient enrichment while decreasing sea grass cover and degrading juvenile fish habitat.

Estimates indicate that approximately 1,000 new residents move to Florida each day, many with dreams of waterfront property and ocean views. The pressure on coastal development is intense; investors purchase developed properties such as shipyards, marinas, and trailer parks and convert them into high-rise condominiums, increasing the population. Historically, Keys homesteads relied on rainwater because there was very limited fresh water; today, homes and businesses import their fresh water from the mainland. Wastewater treatment is a challenge (Kruczynski 1999), since building advanced water treatment plants on multiple islands is very expensive. Experiments funded by US EPA and FDEP (Florida Department of Environmental Protection) indicate that advanced

wastewater treatment systems for each dwelling are not economical or, from a practical standpoint, feasible. The enigma that must be solved is how to deal with millions of gallons of wastewater. The porous nature of the Florida Keys geologic strata and extensive canalization enhances wastewater migration to the marine system (Paul et al. 2000; Griffin et al. 2003) and has generated near shore nutrient loading. Chemicals entering the near shore marine system are the soup of society: human waste (Griffin et al. 2003), household chemicals, residues from medications and health products, and yard and garden chemicals. The biological results include algal blooms, displacement of species that do not tolerate high loads of nutrients, and reproductive failure in some species. The best example of reproductive failure is the queen conch (*Strombus gigas*) an icon of the Florida Keys. In nearshore waters, queen conch no longer produce progeny (Glazer and Quintero 1998; Delgado et al. 2004). If you move the individuals offshore, they resume a reproductive cycle and produce progeny. Individuals from offshore that were sexually functional lose that ability when moved to nearshore locations. Experts speculate that birth control chemicals flushed in the waste water may be involved.

Scientific debate on the transport of nutrient-enriched waters beyond the nearshore zones in the Florida Keys corresponds to the complexity of the hydrodynamic processes and the distance from shore (Szmant and Forrester 1996; Fourqurean and Zieman 2002). Net flow of water is from the Gulf side to the Atlantic (Smith 1994); however, the distance the water moves in a tide cycle is limited. Wind events will drive water far to sea and bring it into contact with patch and bank reefs. Reef corals are typically considered to thrive in oligotrophic conditions; however, the precise tolerances for nutrients are unclear (Szmant 2002). Mosquito spraying is chronic in the Florida Keys, and there is evidence of dibrom residue resulting in impacts to coral physiology (Morgan and Snell 2002).

A Working Group of the Intergovernmental Panel on Climate Change (IPCC) recently released their fourth assessment report titled “Climate Change 2007: The Physical Science Basis” (Intergovernmental Panel on Climate Change 2007). They state, unequivocally, that “global atmospheric concentration of carbon dioxide, methane and nitrous oxide have increased markedly as a result of human

activities since 1750 and now far exceed pre-industrial values.” Fossil fuel burning, land use change, and agriculture are the primary anthropogenic forces in these changing atmospheric conditions. Ocean conditions have also been altered as a result of the intrinsic link that exists between the atmosphere and the ocean. Observations since 1961 show that the average temperature of the global ocean has increased to depths of at least 3000 m and the ocean has been absorbing more than 80% of the heat added to the climate system (Intergovernmental Panel on Climate Change 2007).

Bleaching is strongly associated with elevated seawater temperatures as stressed, overheated organisms expel their zooxanthellae and become pale or white. If thermal stress is severe (greater than 31°C) and prolonged (weeks), most zooxanthellate organisms (fire corals, octocorals, zooanthids, and scleractinian corals) will bleach and many may die. A model by Hoegh-Guldberg (1999) shows an invariant bleaching “threshold” at approximately 1° C above mean summer temperatures. This threshold will be exceeded over the next 50 years as temperatures continue to rise, leading to predictions of massive coral losses. Other abiotic factors, such as increased ultraviolet radiation, salinity extremes, high turbidity, sedimentation, and bacterial infection, have also been implicated in coral bleaching. However, the seven major episodes of bleaching that have occurred since 1979 have been primarily attributed to increased sea water temperatures associated with global climate change and El Niño/La Niña events, with a possible synergistic effect of elevated ultraviolet and visible light (Hoegh-Guldberg 1999). Detrimental physiological and morphological effects on the corals as a result of bleaching include reduced skeletal growth and reproductive activity, lowered mucus production and subsequent decrease in a capacity to shed sediments and resist bacterial/viral invasion (Glynn 1996). Affected colonies can regain their zooxanthellae within weeks to months only if stressful conditions abate and the bleaching is not too severe (Jaap 1979; Glynn 1996).

Thermal expansion of seawater in response to elevated temperatures, combined with melting ice sheets, glaciers, and ice caps, has contributed to a global average rise in sea level of approximately 100 mm (data from 1961 to 2003) with models showing continued rise. If rates of sea level rise exceed the rates of coral growth,

then reefs could essentially be “drowned” as they sink beneath their optimal photic zone. Another consequence of rising sea level are the impacts to aquatic and terrestrial habitats. The saltwater will kill the plants, and the detritus will be washed to sea and add nutrients to system. This is referred to as the reef being shot in the back by the flood of coastal effluents (Neumann and Moore 1975).

Climatic shifts over decades or less have occurred in the past; in the Pleistocene and Holocene, extant coral species underwent dramatic shifts in geographic range in response to periods of warming and cooling (Paulay 1996) and sea level change (Veron 1995). Coral species display a range of adaptive capabilities with certain species able to survive rapid changes much better than others through migration, morphological changes, and expulsion/assimilation of certain zooxanthellae clades. The major difference between today’s climate driven changes in reefs and the recent past is that current reef dwelling species are profoundly affected by people. Human impacts and increased fragmentation of the coral reef habitat has undermined reef resilience, rendering them increasingly susceptible to climate change. Persistently elevated rates of mortality, reduced recruitment of larvae, and slow recovery rates have been observed on a more frequent basis (Hughes et al. 2003).

Ocean acidification accompanied by increased atmospheric CO<sub>2</sub> concentration may have profound effects on calcifying organisms in general, with particular negative implications for coral reefs. In the past 200 years, oceans have absorbed approximately half of the CO<sub>2</sub> produced by fossil fuel burning and cement production (Royal Society 2005). This is a reduction of surface water pH of 0.1 units, or a 30% increase in the concentration of hydrogen ions. If global emissions continue to rise at the current rate, the Royal Society predicts a 0.5 decrease in pH by the year 2100. This hydrogen ion concentration is probably higher than what has been experienced in hundreds of millennia and, more critically, the rate at which it will be achieved will far exceed that of any past records. This is important to corals and other plants and animals that remove calcium from seawater and combine it with the bicarbonate ions to build a limestone shell or skeleton (mollusks and corals).

The carbon cycle provides the needed bicarbonate and carbonate ions for calcium carbonate ( $\text{CaCO}_3$ ) construction. Increased  $\text{CO}_2$  concentrations and the resultant lowered pH reduces the saturation state of  $\text{CaCO}_3$  and raises that saturation horizon in the ocean (the depth at which temperature and pressure effects cause the rate of  $\text{CaCO}_3$  dissolution to exceed  $\text{CaCO}_3$  formation). Calcium carbonate is precipitated by organisms in two forms: calcite (foraminifera and coccolithophores) and aragonite (corals and pteropods); mollusks may have both aragonite and calcite in their shells. Aragonite is the more soluble form and it is postulated that corals and pteropods will be most susceptible to dissolution as oceans continue to acidify.

Increased  $\text{CO}_2$  concentration is lowering the aragonite saturation state of the oceans, further compounding the effects of elevated ocean temperatures, bleaching, disease, and phase shifts. Kleypas et al. (1999) have proposed that the calcification rates of corals would decrease by 10 to 30% under a doubling of atmospheric  $\text{CO}_2$  concentrations. The synergistic interactions of anthropogenic activities will most likely cause a major shift in the distribution, diversity, and abundance of corals. Over longer time scales, reef frameworks will begin to erode and dissolve, leading to a possible reduction in biodiversity and carrying with it severe implications for coastlines, which depend on the presence of reefs for protection from hurricanes, cyclones, and tsunamis.

The long term health and longevity of Florida Keys reefs are analogous to a patient that has suffered major trauma and medical intervention. Unfortunately, the prognosis is fair to poor (Hallock et al. 2003). Wilkinson (2004) ranked the Atlantic coral reefs, including Florida, as a “low C” based on 18 criteria and noted that climate change may inhibit recovery after bleaching events and hurricanes in heavily populated areas (added stress from use and pollution will impact the resilience of the organisms). Local, regional, and global threats are stressing the system. The interactions of the stressors and the unpredictability of the episodic disturbances are challenging. Employing an intermediate disturbance model (Connell 1978) is simplistic but relevant. When the stressing factors are chronic in time and space, long-term longevity of the coral reefs is doubtful. A prognosis that might be reasonable is complete loss of the shallowest (less than 3 m depth)

coral reef communities and marginal survival of corals in depths that exceed 3 m. In special locations, such as Tortugas Banks and Pully Ridge, the buffer of depth and remoteness will provide some protection for the corals. We can only hope that Florida's reefs are up to the challenge.

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Region (county)	Habitat area (hectares)	Capitalized Value (Billions of 2001 \$)	Annual usage (person days, millions)
Palm Beach	12,000	1.4	2.83
Broward	8,300	2.8	5.46
Miami-Dade	7,200	1.6	6.22
Monroe	115,290	1.8	3.64

**Table 1** Coral reef habitat estimates, Florida, east coast (Johns et al. 2001).

Buoy Code	Location	Latitude	Longitude
42036 W Tampa	Near the Florida Middle Grounds	28°30'00"	84°31'00"
DRYF1	Dry Tortugas	24°38'18"	82°51'42"
SANF1	Sand Key	24°27'25"	81°52'42"
SMKF1	Sombrero Key	25°37'36"	81°06'36"
FWYF1	Fowey Rocks	25°35'25"	80°05'48"
LKWF1	Lake Worth	26°36'42"	80°05'48"

**Table 2** Selected Meteorological-Oceanographic Data Buoys off Florida.

**Table 3** Zooxanthellate Scleractinia distribution

<b>Location</b>	<b>A</b>	<b>B</b>	<b>C</b>	<b>D</b>	<b>E</b>	<b>F</b>	<b>G</b>	<b>H</b>	<b>I</b>	<b>J</b>	<b>K</b>	<b>L</b>	<b>M</b>	<b>N</b>	<b>O</b>	<b>P</b>	<b>Q</b>	<b>R</b>	<b>S</b>	<b>T</b>	<b>U</b>	<b>V</b>	<b>W</b>	<b>X</b>
<i>Stephanocoenia intersepta</i>	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Madracis decactis</i>	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	1
<i>Madracis formosa</i>	0	0	0	0	0		1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Madracis mirabilis</i>	0	1	0	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1
<i>Madracis pharensis</i>	0	0	0	1	1	1	1	1	1	0	1	0	1	1	1	0	0	0	1	0	0	0	0	1
<i>Acropora cervicornis</i>	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Acropora palmata</i>	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Acropora prolifera</i>	0	0	0	1	1		1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Agaricia agaricites</i>	0	0	0	1	1	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0
<i>Agaricia fragilis</i>	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0	0	1
<i>Agaricia lamarcki</i>	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	1	1	1
<i>Agaricia tenuifolia</i>	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Agaricia undata</i>	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0
<i>Leptoseris cucullata</i>	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Siderastrea radians</i>	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0
<i>Siderastrea siderea</i>	0	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0	0	0
<i>Porites astreoides</i>	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	0	0	0	0	0
<i>Porites branneri</i>	0	0	0	1	1	0	1	1	1	1	1	0	1	0	1	1	1	0	0	1	0	0	0	0
<i>Porites colonensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Porites porites</i>	1	1	0	1	1	1	1	1	1	0	1	1	1	0	1	1	1	0	1	0	0	0	0	0



AF: Alacran, Mexico  
AG: Campeche Bank, Mexico  
AH: Sancho Pardo, Cuba,  
AI: Buena Vista, Cuba  
AJ: Bajas, Cuba  
AK: Cayo Arenas, Cuba  
AL: Cayo Levisa, Cuba  
AM: Cayo Medano de Casiguas  
AN: Morrillo, Cuba  
AO: Pt. Gobernadora, Cuba  
AP: Ortigosa, Cuba  
AQ: Bahia Cabanas, Cuba  
AR: Inst. Oceano, Cuba  
AS: Patricio Lumumba, Cuba  
AT: Guanabo, Cuba  
AU: Punta Seboruco, Cuba  
AV: Km 14, Cuba  
AW: Rio Camarioca, Cuba

Species	Category	Number of Colonies	Percent abundance	Cumulative abundance
<i>Plexaura homomalla</i>	Octocoral	49	17.63	17.63
<i>Plexaura flexuosa</i>	Octocoral	32	11.51	29.14
<i>Pseudoplexaura porosa</i>	Octocoral	30	10.79	39.93
<i>Pseudopterogorgia americana</i>	Octocoral	26	9.35	49.28
<i>Pseudopterogorgia acerosa</i>	Octocoral	25	8.99	58.27
<i>Pseudoplexaura flagellosa</i>	Octocoral	12	4.32	62.59
<i>Eunicea caliculata</i>	Octocoral	12	4.32	66.91
<i>Briareum asbestinum</i>	Octocoral	12	4.32	71.22
<i>Siderastrea siderea</i>	Scleractinian	10	3.60	74.82
<i>Gorgonia ventalina</i>	Octocoral	10	3.60	78.42
<i>Eunicea tourneforti</i>	Octocoral	9	3.24	81.65
<i>Muriceopsis flavida</i>	Octocoral	5	1.80	83.45
<i>Plexaurella grisea</i>	Octocoral	4	1.44	84.89
<i>Plexaurella fusifera</i>	Octocoral	4	1.44	86.33
<i>Muricea elongata</i>	Octocoral	4	1.44	87.77
<i>Eunicea succinea</i>	Octocoral	4	1.44	89.21
<i>Dichocoenia stokesi</i>	Scleractinian	4	1.44	90.65
<i>Muricea atlantica</i>	Octocoral	3	1.08	91.73
<i>Millepora alcicornis</i>	Hydrozoan	3	1.08	92.81
<i>Eunicea fusca</i>	Octocoral	3	1.08	93.88
<i>Porites porites</i>	Scleractinian	2	0.72	94.60
<i>Porites astreoides</i>	Scleractinian	2	0.72	95.32
<i>Montastraea cavernosa</i>	Scleractinian	2	0.72	96.04
<i>Eunicea laciniata</i>	Octocoral	2	0.72	96.76
<i>Diploria labyrinthiformis</i>	Scleractinian	2	0.72	97.48
<i>Agaricia agaricites</i>	Scleractinian	2	0.72	98.20
<i>Plexaurella nutans</i>	Octocoral	1	0.36	98.56
<i>Montastraea annularis</i>	Scleractinian	1	0.36	98.92
<i>Favia fragum</i>	Scleractinian	1	0.36	99.28
<i>Eusmilia fastigiata</i>	Scleractinian	1	0.36	99.64
<i>Eunicea clavigera</i>	Octocoral	1	0.36	100.00
	Total	278		

**Table 4** Species abundance, Dome Reef, Biscayne National Park, 1977. Source: Above data, from two, 25 m long transects (Jaap 1989).

<b>Habitat</b>	<b>Acres</b>	<b>Hectares</b>	<b>Percent</b>
Land	108.7	44	0.20
<i>Astrea</i> and <i>Meandrina</i> Reefs	380.5	154	2.80
<b>Staghorn reefs</b>	<b>1030.4</b>	<b>417</b>	<b>1.90</b>
<b>Elkhorn reefs</b>	<b>108.7</b>	<b>44</b>	<b>0.20</b>
Broken coral heads	163.1	66	0.30
<b>Total Coral Reef</b>	1682.8	681	3.09
Octocoral-hardbottom	2607.0	1,055	4.80
Sediments	49,952.3	20,215	91.90
Total	54,350.8	21,995	

**Table 5** Terrestrial and marine habitats, Dry Tortugas. Source: Agassiz 1882.

<b>Habitat</b>	<b>Acres</b>	<b>Hectares</b>	<b>Percent</b>
Land	113.7	46	0.20
Bank Reefs	338.5	137	0.60
Coral head buttresses	620.2	251	1.10
<b>Staghorn Reefs</b>	<b>1181.2</b>	<b>478</b>	<b>2.10</b>
<b>Elkhorn corals</b>	<b>1.5</b>	<b>0.6</b>	<b>(.0026)</b>
Total Coral Reef	2140.7	867	3.8
Octocoral hardbottom	9,797.7	3,965	17.40
Benthic algae	281.7	114	0.50
Seagrasses	17,060.1	6,904	30.29
Sediments	26,914.7	10,892	47.80
Total	56,309.3	22,788	

**Table 6** Terrestrial and marine habitats, Dry Tortugas. Source: Davis 1982.



## Figure Legends

Fig. 1 Map displaying the Straits of Florida: Yucatan Peninsula, North Coast of Cuba, Northwestern Bahamas, and Southern Florida.

Fig. 2 Synoptic climate data: Key West and Stuart, Florida, George Town Cayman Islands, and Mayaguez, Puerto Rico. Source: National Weather Service, NOAA, and Grand Cayman Government.

Fig. 3 Seawater temperature (1878-1912, C°), Florida Reef Tract Lighthouses (Vaughan, 1918).

Fig. 4 Air temperature (C°), Dry Tortugas, Sand Key, Sombrero Reef, Fowey Rock ten year average, range, standard deviation. Source: National Data Buoy Center, NOAA.

Fig. 5 Wind Speed (knots), Dry Tortugas, Sand Key, Sombrero Reef, Fowey Rock ten year average, range, standard deviation. Source: National Data Buoy Center, NOAA.

Fig. 6 Seawater temperature (C°), Dry Tortugas, Sand Key, Sombrero Reef, Fowey Rock ten year average, range, standard deviation. Source: National Data Buoy Center, NOAA.

Fig. 7 Air temperature (C°), Seawater temperature (C°), Eastern Gulf of Mexico and Lake Worth (Palm Beach). Source: National Data Buoy Center, NOAA.

Fig. 8 Wind Speed (knots), Eastern Gulf of Mexico and Lake Worth (Palm Beach). Source, National Data Buoy Center, NOAA.

Fig. 9 Dendrogram, classifying 56 locations and presence of ZS species using the Bray Curtis Similarity Coefficient and the dendrogram formed by group average sorting; 75% boundary line inserted on the Y axis.

Fig. 10 Average Taxonomic Distinctness (Delta+) and variation in the taxonomic distinctness (Lambda+), Atlantic Ocean ZS, for 56 locations using 5000 permutations of these data and a master list of 59 ZS species for the Atlantic.

Fig. 11 Dendrogram, classifying 29 Bahamas, Cuba, and Florida locations based presence of ZS species using the Bray Curtis Similarity Coefficient and the dendrogram formed by group average sorting, 75% boundary line inserted on the Y axis.

Fig. 12 Average taxonomic distinctness values, Delta +, plotted against the observed number of species for the Atlantic ZS at 56 locations. Dashed lines indicate the simulated mean Delta+ from 5000 random selections from the master list of 59 ZS species. Intervals (solid lines) within which 95% of the simulated Delta+ lie (the expected range of Delta+ for a given number of species) are constructed for each of the 56 locations and represented as a probability funnel (Warwick and Clarke 2001). seUSA= southeast USA, eATL=eastern Atlantic, neGUL= NE Gulf of Mexico, BRA=Brasil, BER=Bermuda, swGUL= SW Gulf of Mexico, seFLO=SE Florida, BAH=Bahamas, CAR=Caribbean, seGUL=SE Gulf of Mexico.

Fig. 13 Change in number of species observed at CREMP monitoring stations, contrasting 1996 and 2003.

Fig. 14 Number of CREMP stations that lost or gained particular species of corals between 1996 and 2003. A negative number, such as -5, reports that the species occurred at five fewer stations in 2003 than in 1996.

Fig. 15 Trends in species richness, 1996 through 2003 by habitat type, mean and standard error of the mean.

Fig. 16 Trends in coral disease, 1996 through 2003, compiled by the occurrence of the disease at a station.

Fig. 17 *Millepora complanata* cover at shallow offshore stations (N=39) mean, the rectangle is  $\pm$  one standard deviation, and vertical line is the range.

Fig. 18 Zooanthid cover (*Palythoa mammillosa*) at shallow offshore stations (N=39). The mean, the rectangle is  $\pm$  one standard deviation, and vertical line is the range.

Fig. 19 *Porites astreoides* cover at shallow reef stations (N=39). The mean, the rectangle is  $\pm$  one standard deviation, and the vertical line is the range.

Fig. 20 Mosaic image of Western Sambo Shallow Station 2 (approximately 4 m of middle video transect, 4) 1996 and 2002. Image product of Ravenview application software.

Fig. 21 *Acropora palmata* cover, shallow offshore station (N=39). The mean, the rectangle is  $\pm$  one standard deviation, and vertical line is the range.

Fig. 22 Ordination by MDS of Bray-Curtis similarities between fourth-root transformed percentage cover data for stony corals from each site within: a) shallow reefs; b) deep reefs; c) patch reefs. Sites are grouped according to their location along the reef tract (Lower, Middle and Upper Keys). Data from all sampling occasions are averaged for most sites, except for two within each plot for which samples from different times are kept separate in order to illustrate the relative magnitude of changes in time compared to differences between locations.

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Fig. 24 Dry Tortugas, Florida

Fig. 25 Coral cover trends, Bird Key Reef, Dry Tortugas: 1975-2004. Source: Jaap et al. 1989, Jaap unpublished, J. Miller unpublished.

Fig. 26 (a) Topographic and (b) oceanographic complexity along the Florida Keys coral reef ecosystem from Miami to the Dry Tortugas. Circulation gyre exhibited in the proximity of the Dry Tortugas in the lower panel.

Fig. 27 South Florida (Monroe, Collier, Dade, Broward and Palm Beach Counties commercial and recreational vessel registrations by year ( Source: Florida Statistical Abstract 2006, Table 19.45 - State of Florida, Department of Highway Safety and Motor Vehicles, Bureau of Vessel Titles and Registrations; <http://www.hsmv.state.fl.us/dmv/vslfacts.html>).

Fig. 28 Spawning potential ratio (SPR) analysis for 34 exploited species in the snapper-grouper complex from the Florida Keys for the period 2000-2002. Dark bars indicate overfished stocks and open bars indicate stocks above the 30% SPR standard. Source: Ault, J.S. et al. 2005. ICES Journal of Marine Science 62: 417-423.

Fig. 29 Black grouper (*Mycteroperca bonaci*) size distributions from the Tortugas region in 1999-2000 (Top) and 2004 (Bottom), before and after the establishment of the Tortugas Ecological Reserve in 2001. Blue bars represent size classes larger than the minimum legal minimum size. Percentages show the proportion of the population larger than the legal minimum size of capture.

Fig. 30 Red grouper (*Epinephelus morio*) size distributions from the Tortugas region in 1999-2000 (Top) and 2004 (Bottom), before and after the establishment of the Tortugas Ecological Reserve in 2001. Blue bars represent size classes larger than the minimum legal minimum size. Percentages show the proportion of the population larger than the legal minimum size of capture.

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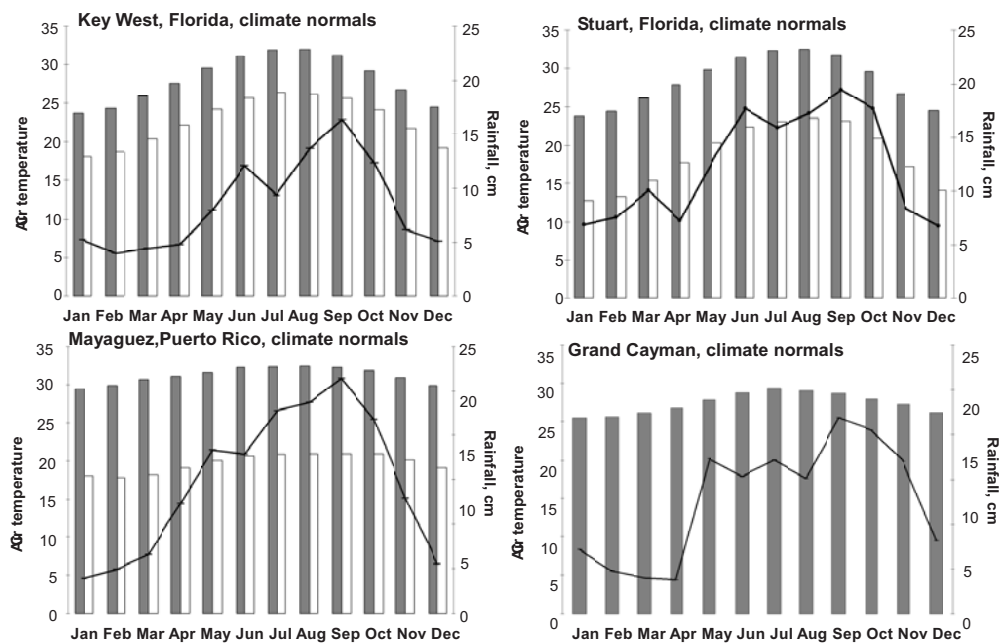
Fig. 32 (a) *Millepora complanata* (Lamarck, 1816) [Bladed Fire Coral], Western Sambo Reef, 3 to 5 m, July 26, 2004. (b) *Gorgonia ventalina* Linnaeus, 1758 [Common sea fan], Western Sambo Reef, 3 to 5 m, July 26, 2004. (c) *Briareum asbestinum* (Pallas, 1766) [Deadman's finders], Western Sambo Reef, 3 to 5 m, July 26, 2004, photo credit W. Jaap. (d) *Siderastrea radians* (Pallas, 1766) [Lesser Starlet Coral], Smith Shoal, 6 to 7 m, July 24, 2004 (photo credits W. Jaap).

Fig. 33 (a) *Madracis mirabilis* sensu Wells, 1973 [Yellow pencil coral], Western Sambo Reef, 3 to 5 m, July 26, 2004. (b) *Acropora palmata* (Lamarck, 1816) [Elkhorn coral], Western Sambo Reef, 3 to 5 m, July 26, 2004. (c) *Acropora cervicornis* (Lamarck, 1816) [Staghorn coral], Western Sambo Reef, 3 to 5 m, July 26, 2004. (d) *Agarica agaricites* (Linnaeus, 1758) [Lettuce coral], Smith Shoal, 6 to 7 m, July 24, 2004 (photo credits W. Jaap).

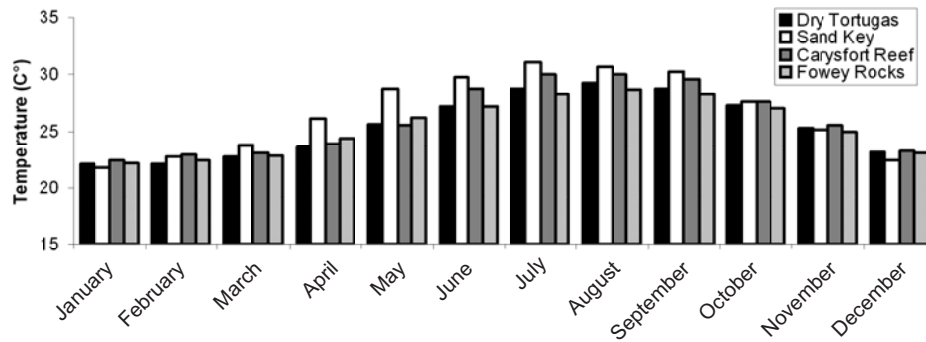
Fig. 34 (a) *Mycetophyllia ferox* Wells, 1973 [Rough cactus coral], Western Sambo Reef, 3 to 5 m, July 26, 2004. (b) *Solenastrea bournoni* Milne Edwards and Haime, 1849 [Smooth star coral], Smith Shoal, 6 to 7 m, July 24, 2004. (c) *Diploria strigosa* (Dana, 1846) [Symmetrical brain coral] and *Spirobranchus giganteus* (Pallas, 1766) [Christmas tree worm], Western Sambo Reef, 3 to 5 m, July 26, 2004. (d) *Mussa angulosa* (Pallas, 1766) [Large flower coral], Western Sambo Reef, 3 to 5 m, July 26, 2004 (photo credits W. Jaap).



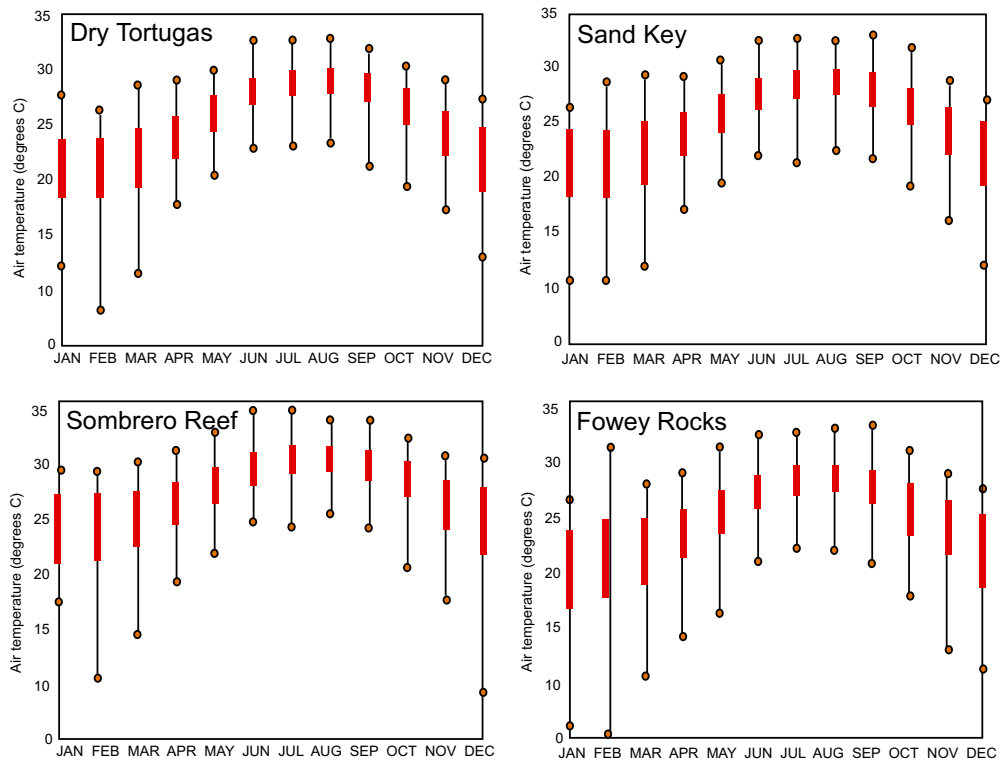
**Fig. 1** Map displaying the Straits of Florida: Yucatan Peninsula, North Coast of Cuba, Northwestern Bahamas, and Southern Florida.



**Fig. 2** Synoptic climate data: Key West and Stuart, Florida, George Town Cayman Islands, and Mayaguez, Puerto Rico. Source: National Weather Service, NOAA, and Grand Cayman Government.

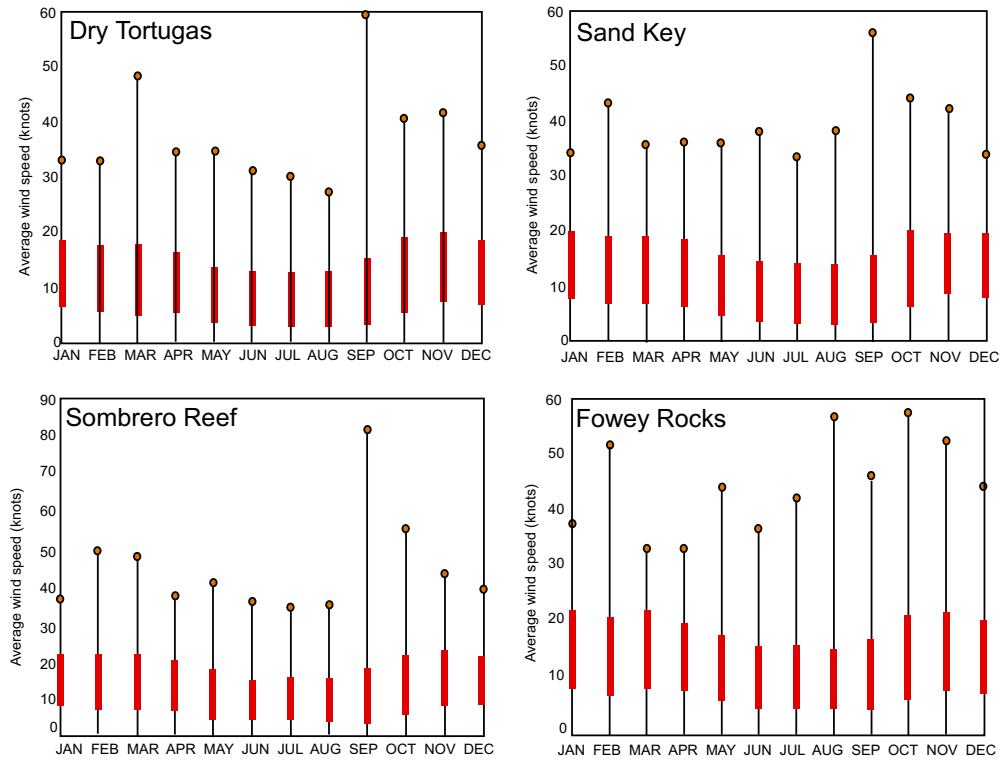


**Fig. 3** Seawater temperature (1878-1912, C°), Florida Reef Tract Lighthouses (data from Vaughan, 1918).

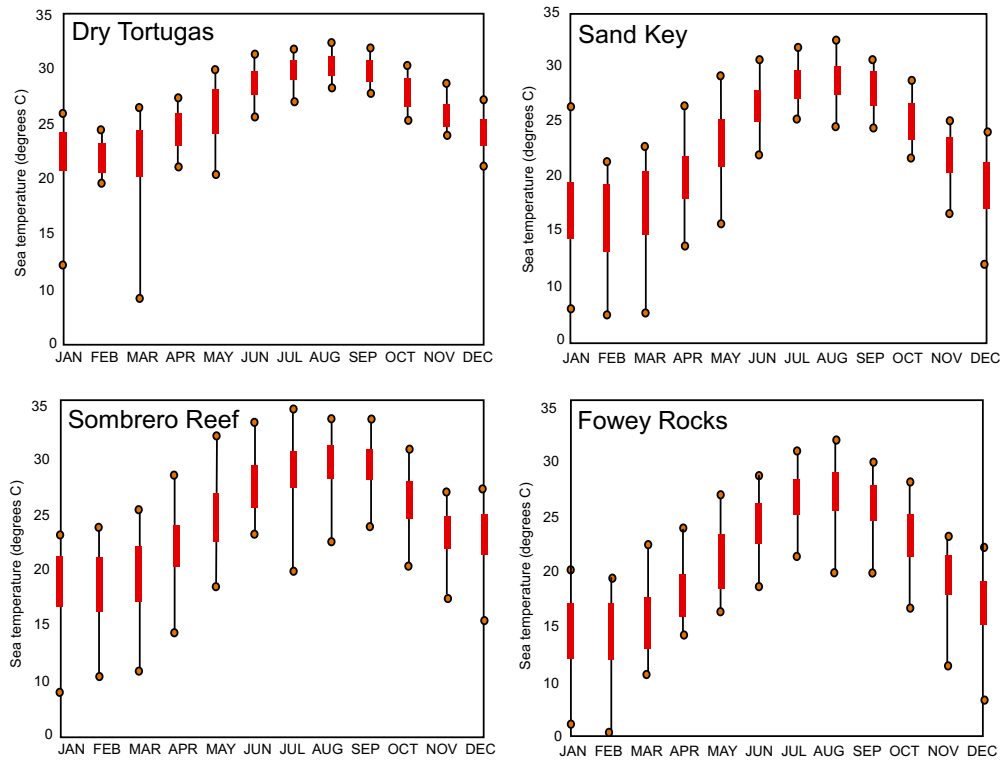


**Fig. 4** Air temperature (C°), Dry Tortugas, Sand Key, Sombrero Reef, Fowey Rock ten year average, range, standard deviation. Source: National Data Buoy Center, NOAA.

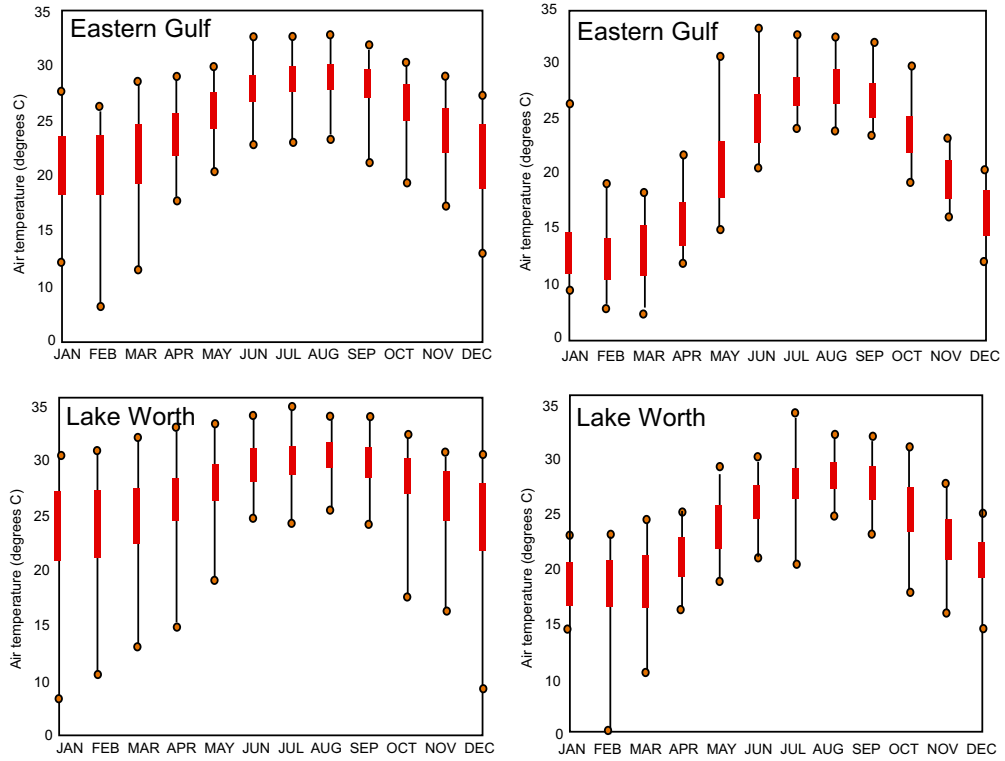
What do the black cu=icles and red bars mean???



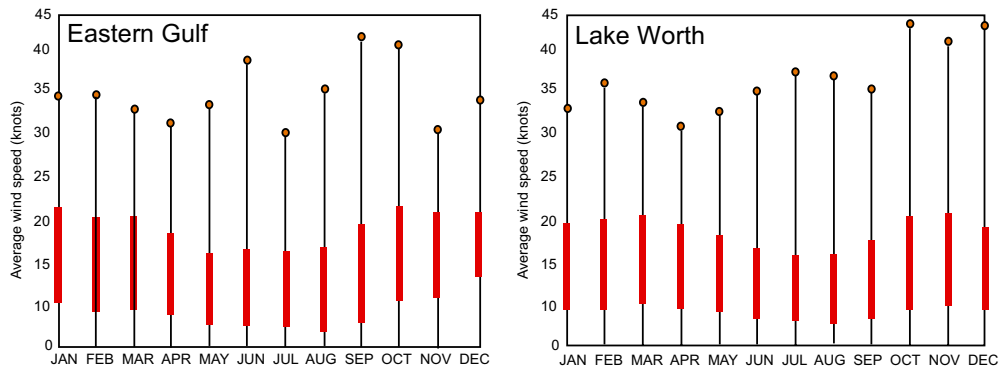
**Fig. 5** Wind Speed (knots), Dry Tortugas, Sand Key, Sombrero Reef, Fowey Rock ten year average, range, standard deviation. Source: National Data Buoy Center, NOAA.



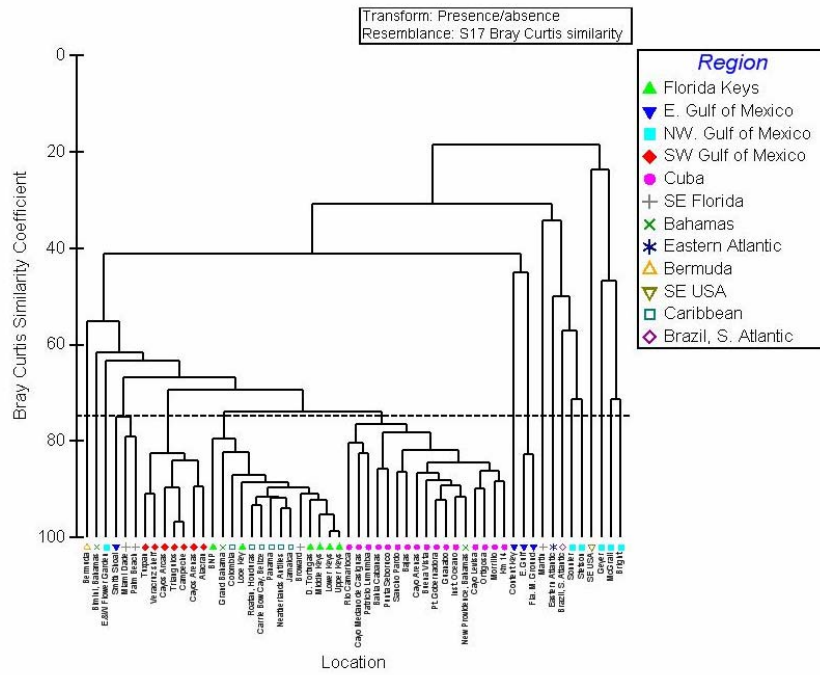
**Fig. 6** Seawater temperature (C°), Dry Tortugas, Sand Key, Sombrero Reef, Fowey Rock ten year average, range, standard deviation. Source: National Data Buoy Center, NOAA.



**Fig. 7** Air temperature (C°), Seawater temperature (C°), Eastern Gulf of Mexico and Lake Worth (Palm Beach). Source: National Data Buoy Center, NOAA.



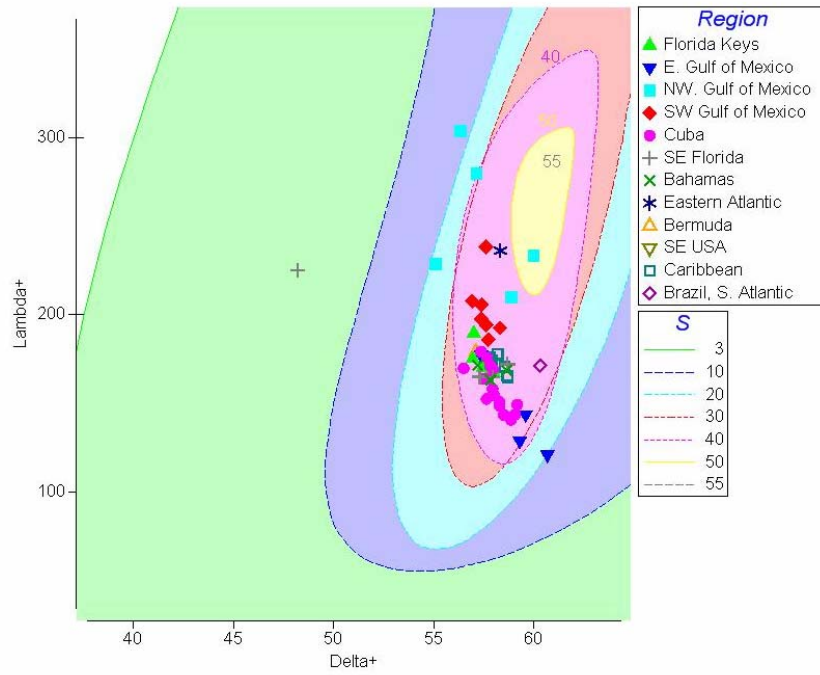
**Fig. 8** Wind Speed (knots), Eastern Gulf of Mexico and Lake Worth (Palm Beach). Source: National Data Buoy Center, NOAA.



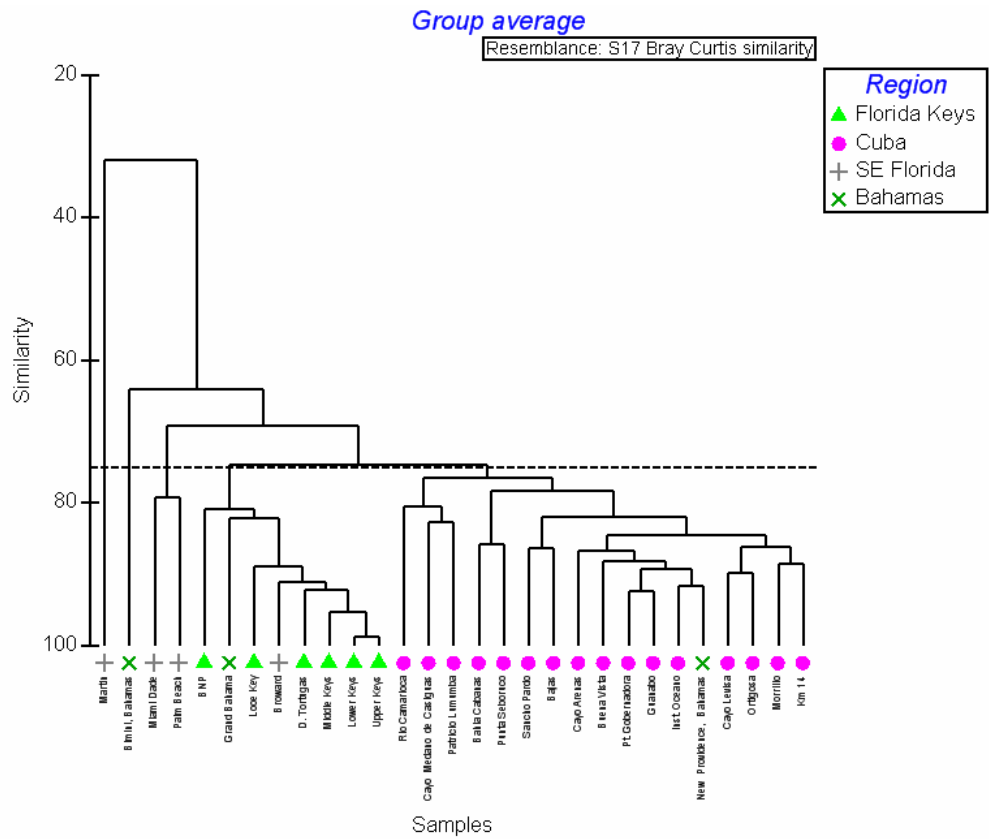
**Fig. 9** Dendrogram, classifying 56 locations and presence of ZS species using the Bray Curtis Similarity Coefficient and the dendrogram formed by group average sorting; 75% boundary line inserted on the Y axis.

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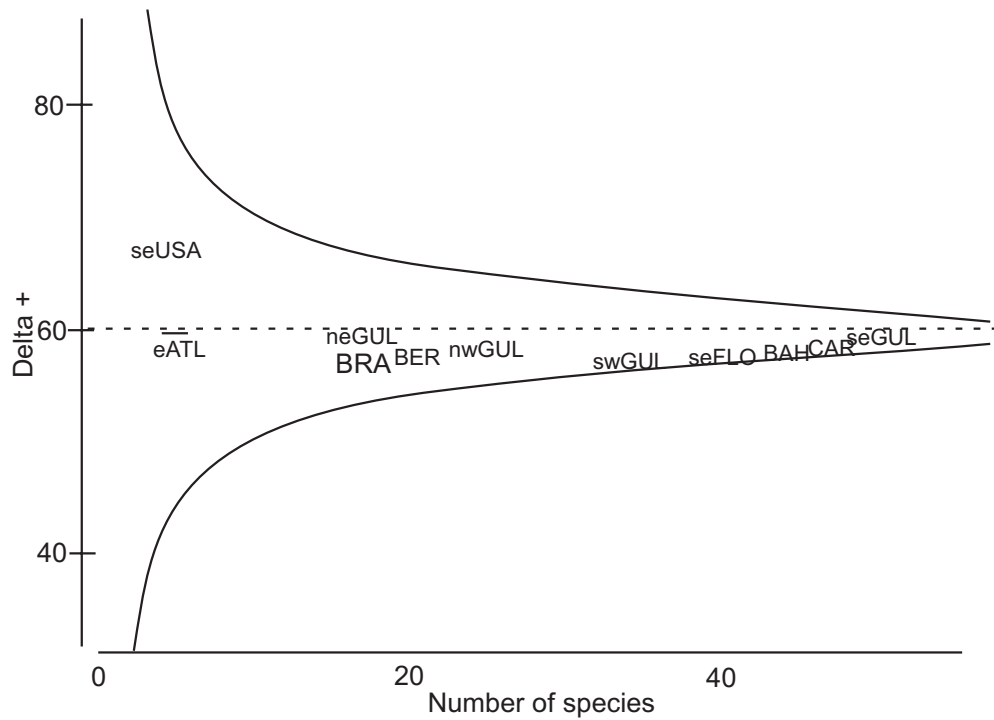


**Fig. 10** Average Taxonomic Distinctness (Delta+) and variation in the taxonomic distinctness (Lambda+), Atlantic Ocean ZS, for 56 locations using 5000 permutations of these data and a master list of 59 ZS species for the Atlantic.

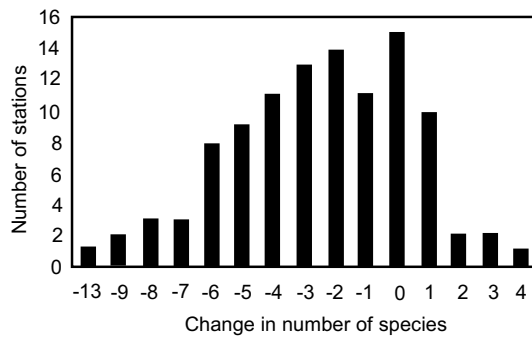


**Fig. 11** Dendrogram, classifying 29 Bahamas, Cuba, and Florida locations based presence of ZS species using the Bray Curtis Similarity Coefficient and the dendrogram formed by group average sorting, 75% boundary line inserted on the Y axis.

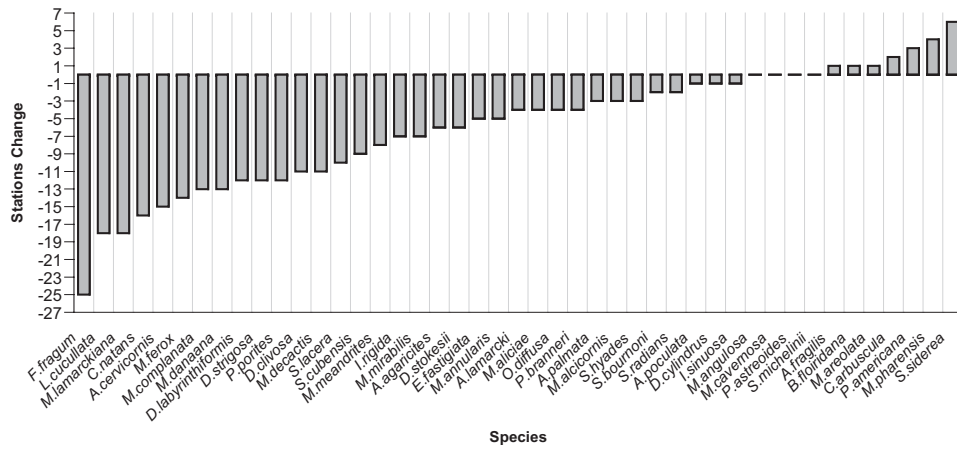
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**Fig. 12** Average taxonomic distinctness values, Delta +, plotted against the observed number of species for the Atlantic ZS at 56 locations. Dashed lines indicate the simulated mean Delta+ from 5000 random selections from the master list of 59 ZS species. Intervals (solid lines) within which 95% of the simulated Delta+ lie (the expected range of Delta+ for a given number of species) are constructed for each of the 56 locations and represented as a probability funnel (Warwick and Clarke 2001). seUSA= southeast USA, eATL=eastern Atlantic, neGUL= NE Gulf of Mexico, BRA=Brasil, BER=Bermuda, swGUL= SW Gulf of Mexico, seFLO=SE Florida, BAH=Bahamas, CAR=Caribbean, seGUL=SE Gulf of Mexico.

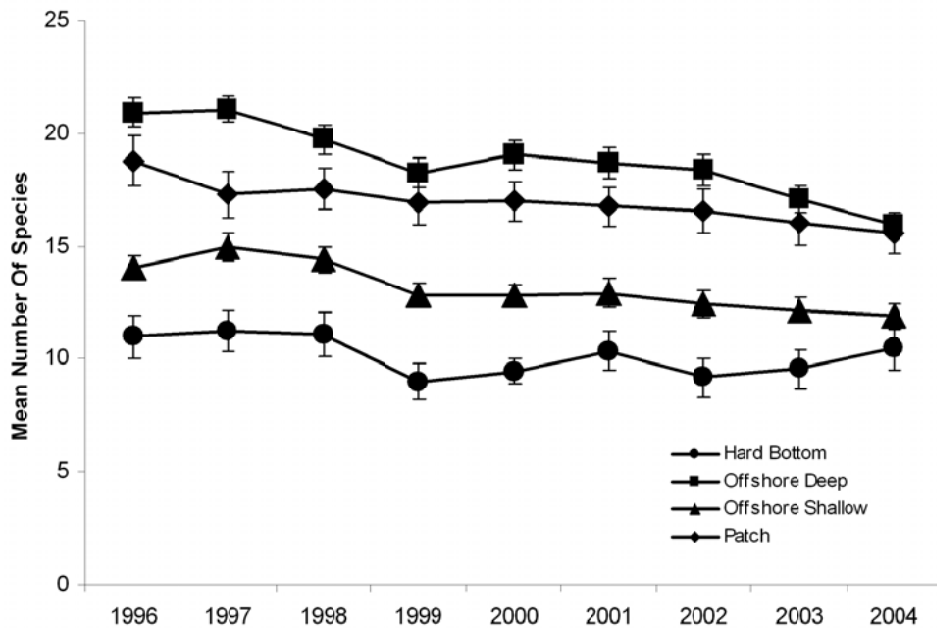


**Fig. 13** Change in number of species observed at CREMP monitoring stations, contrasting 1996 and 2003.

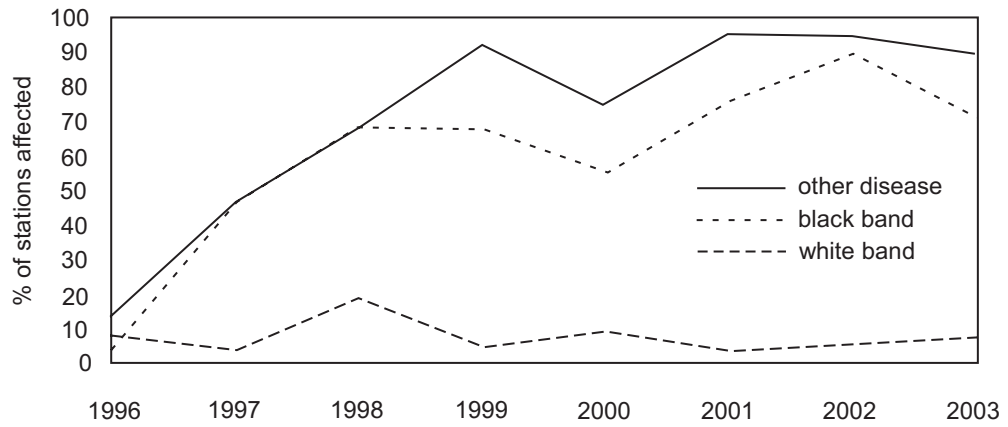


**Fig. 14** Number of CREMP stations that lost or gained particular species of corals between 1996 and 2003. A negative number, such as -5, reports that the species occurred at five fewer stations in 2003 than in 1996.

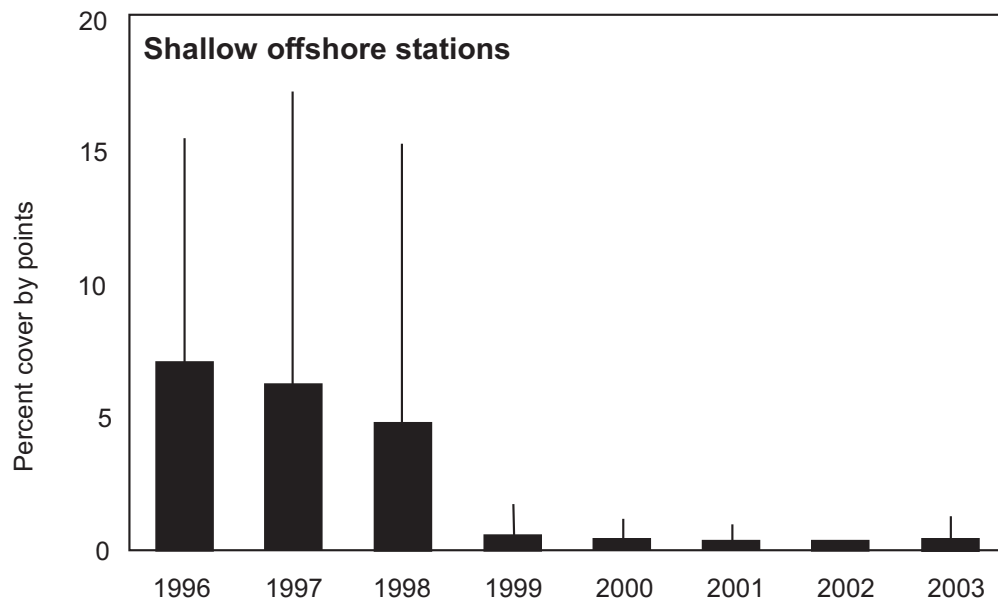
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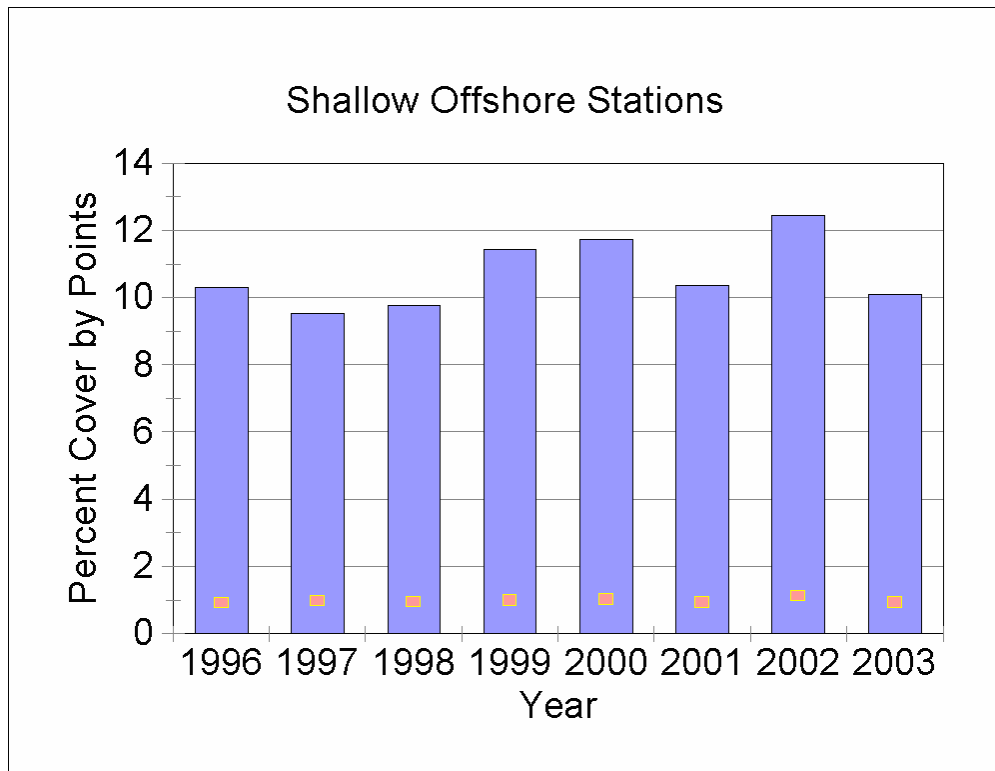
**Fig. 15** Trends in species richness, 1996 through 2003 by habitat type, mean and standard error of the mean.



**Fig. 16** Trends in coral disease, 1996 through 2003, compiled by the occurrence of the disease at a station.

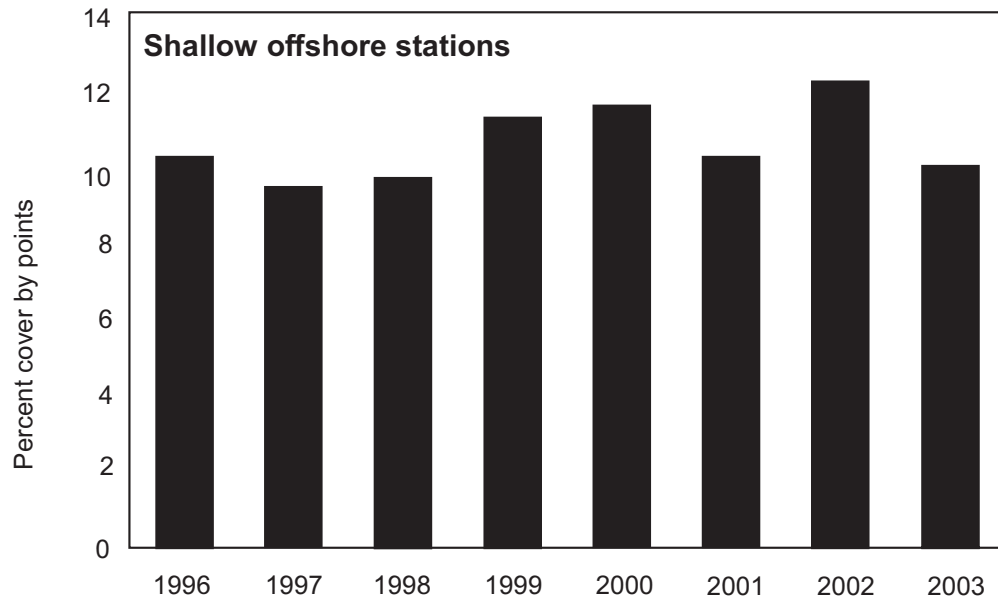


**Fig. 17** *Millepora complanata* cover at shallow offshore stations (N=39) mean, the rectangle is  $\pm$  one standard deviation, and vertical line is the range.

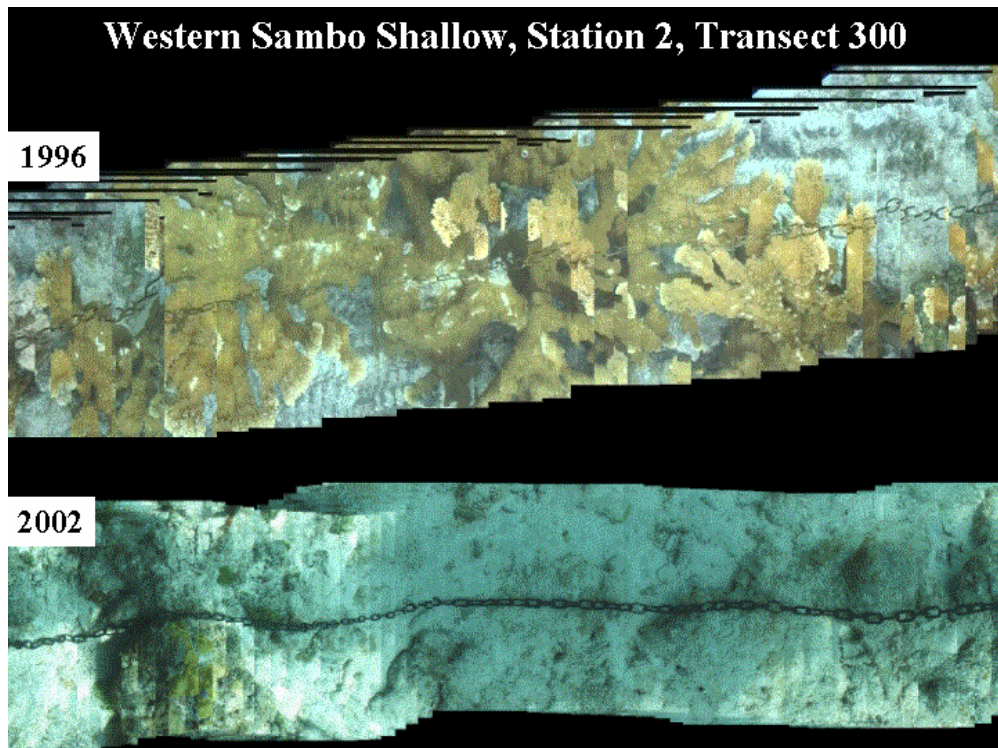


**Fig. 18** Zooanthid cover (*Palythoa mammillosa*) at shallow offshore stations (N=39). The mean, the rectangle is  $\pm$  one standard deviation, and vertical line is the range.

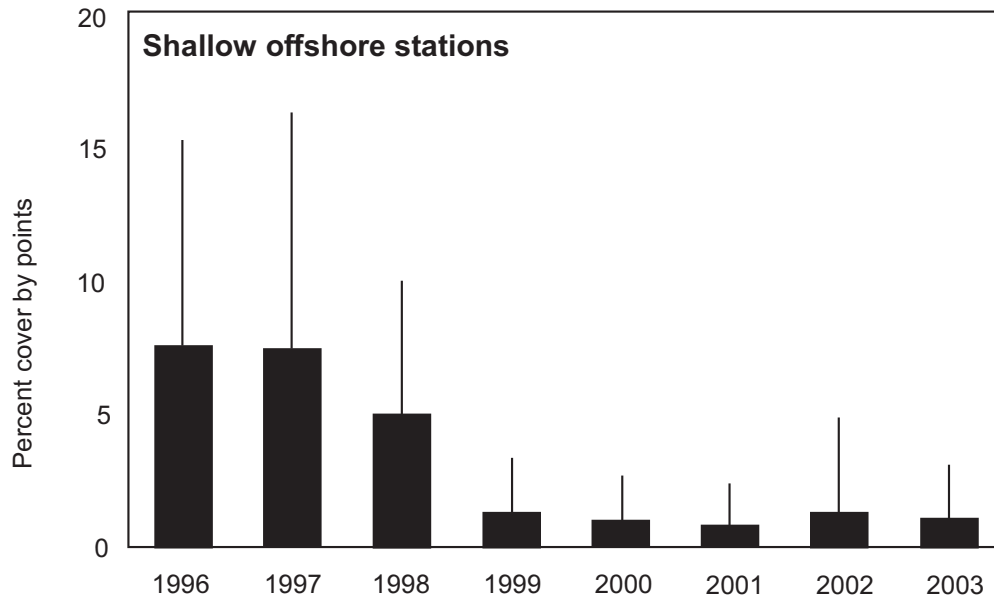
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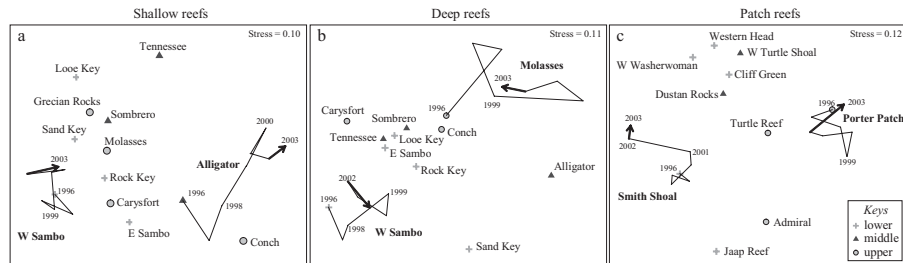
**Fig. 19** *Porites astreoides* cover at shallow reef stations (N=39). The mean, the rectangle is  $\pm$  one standard deviation, and the vertical line is the range.



**Fig. 20** Mosaic image of Western Sambo Shallow Station 2 (approximately 4 m of middle video transect, 4) 1996 and 2002. Image product of Ravenview application software.



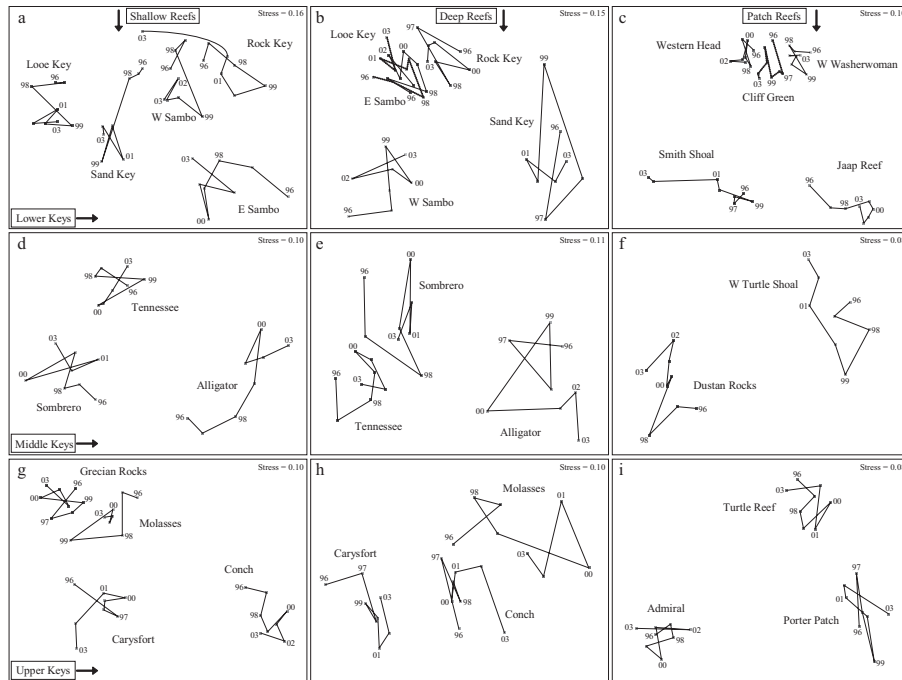
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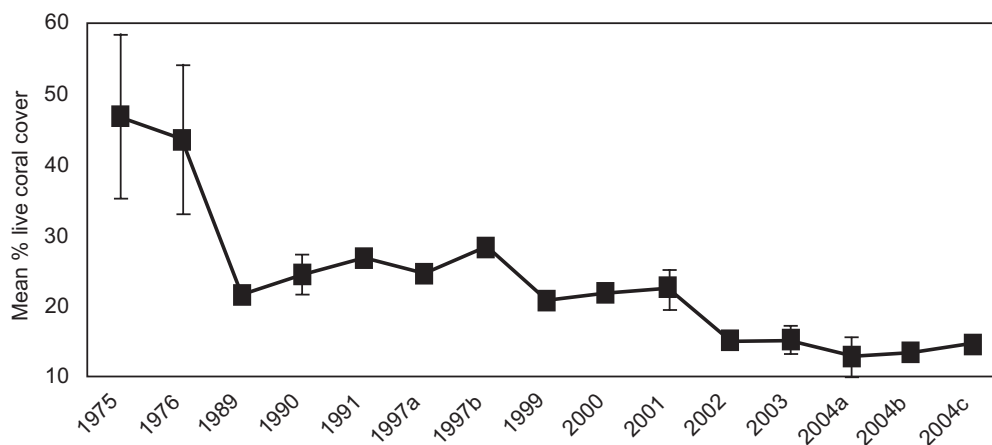


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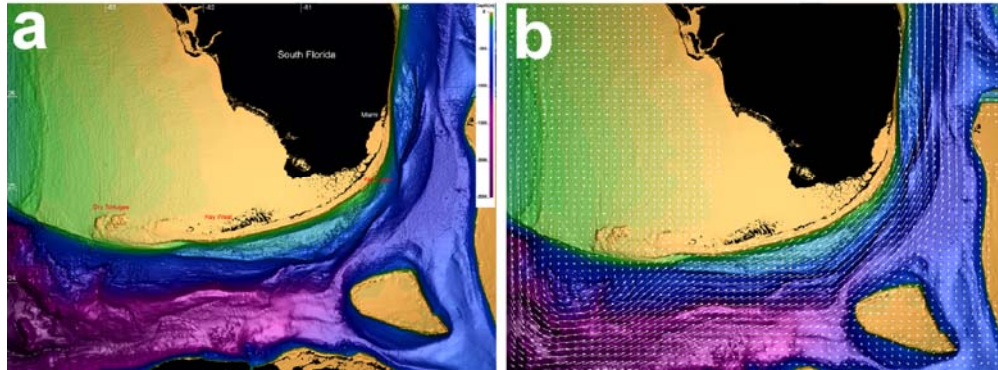
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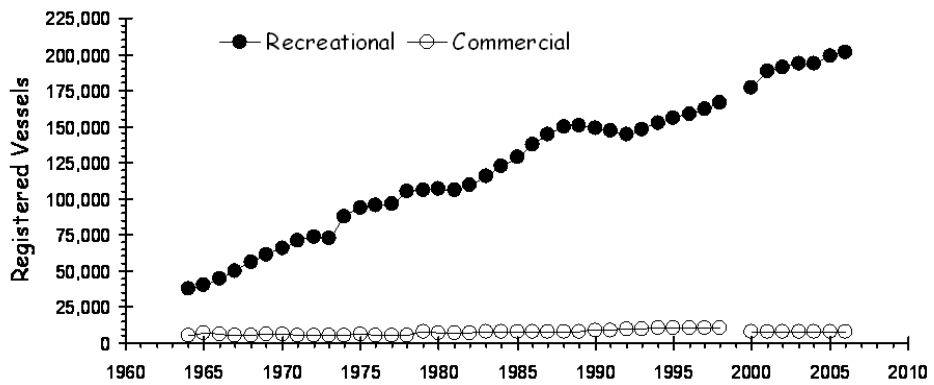
**Fig. 24** The Dry Tortugas, Florida.



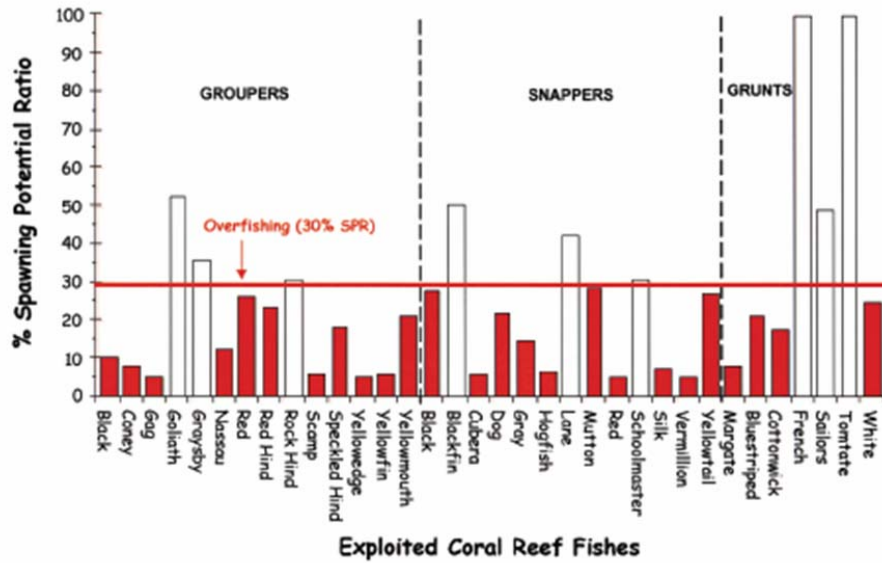
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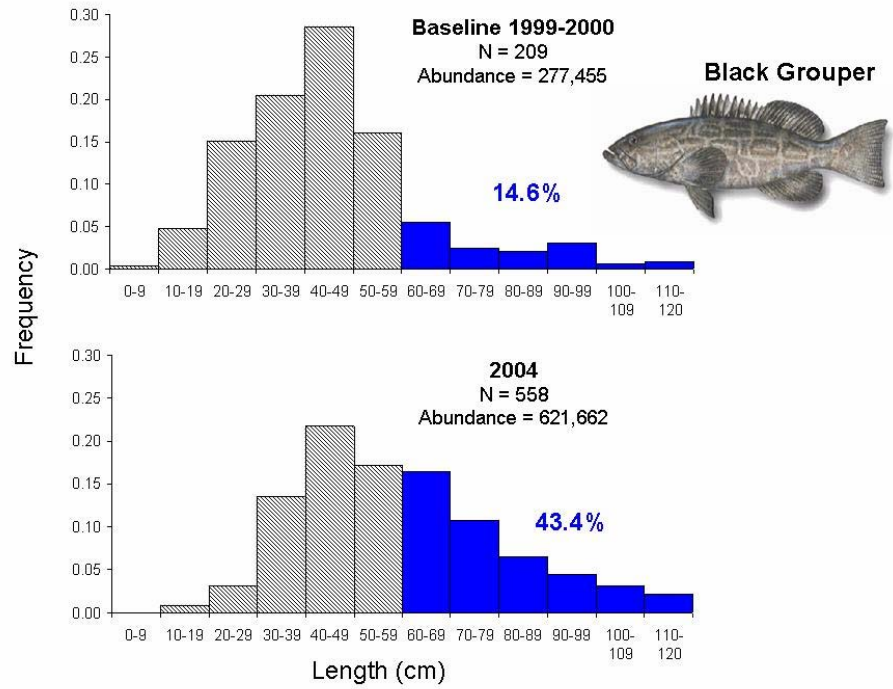


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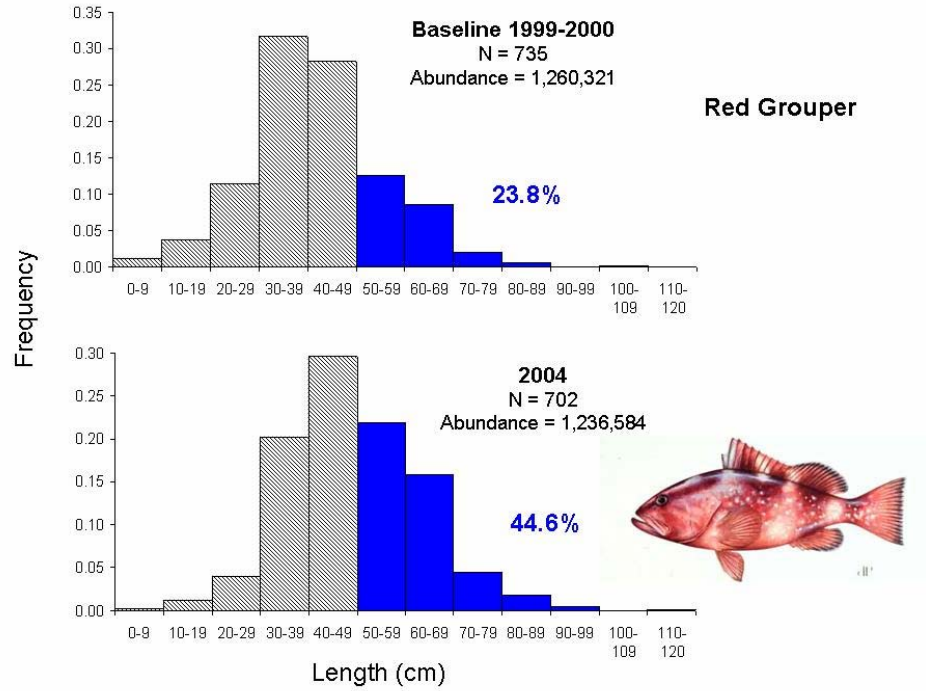


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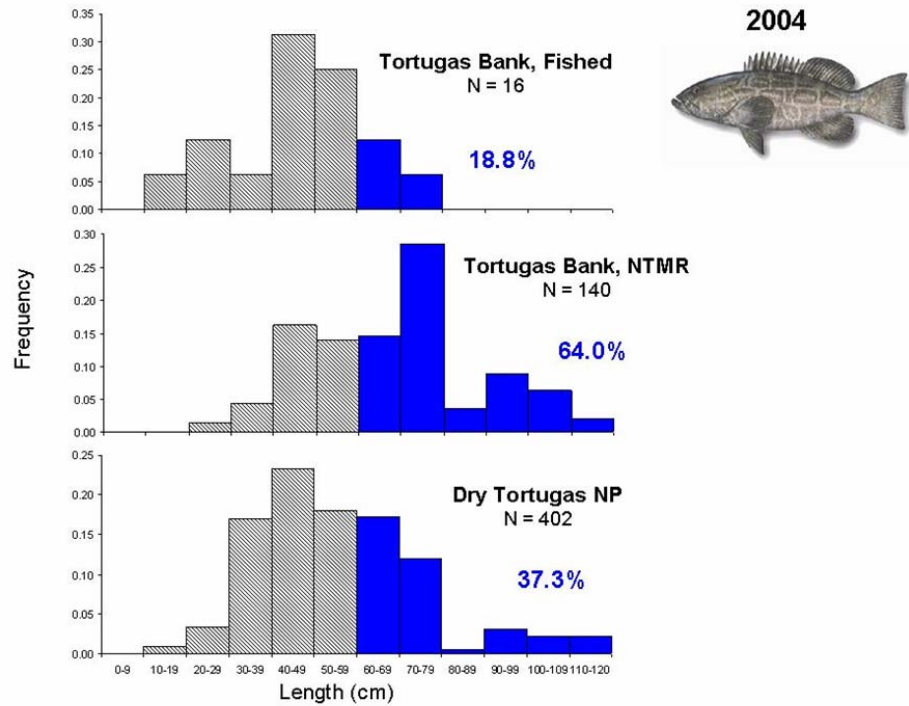
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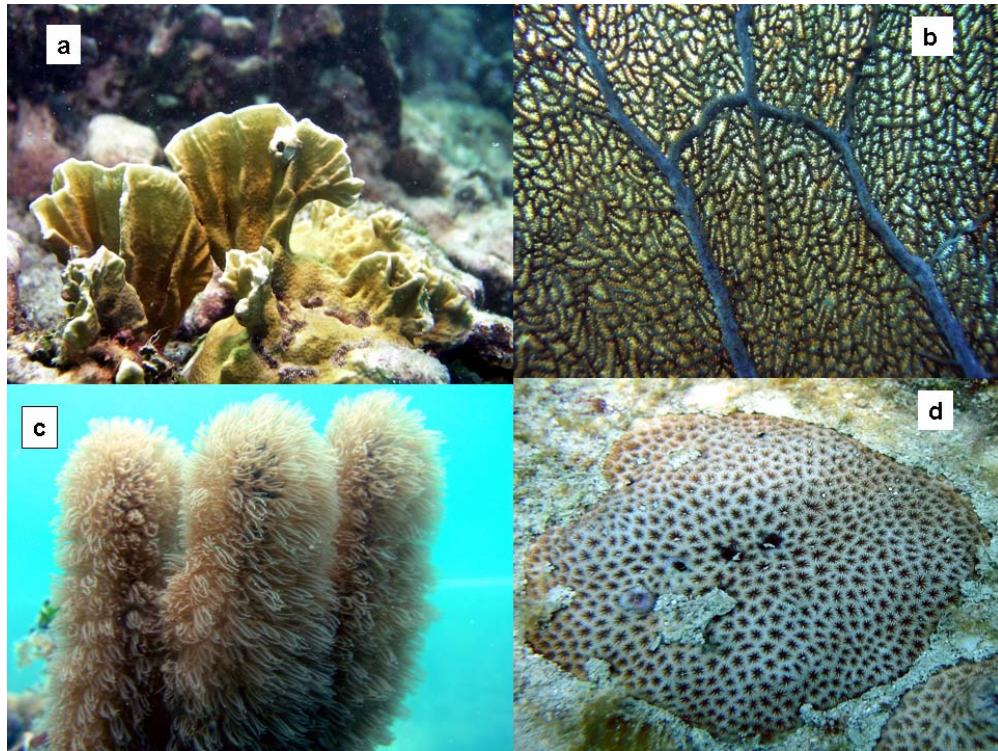
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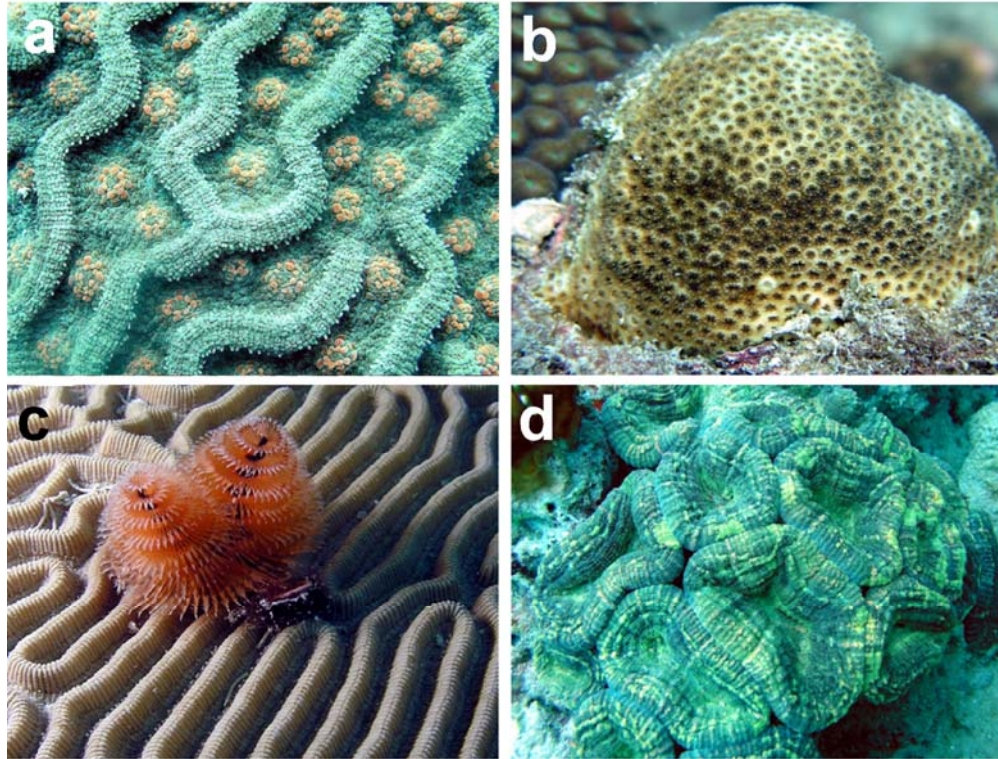
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