Benthic Habitat: Coral and Hardbottom

Diego Lirman
University of Miami/Rosenstiel School of Marine and Atmospheric Science

In a nutshell

- Coral reefs and hardbottom communities are unique ecosystems that support a diverse community of fish and invertebrate species.
- The recreational and commercial fishing and harvesting activities centered around coral reefs provide a multi-billion dollar income to the local economy.
- Coral reefs in Florida and around the world have undergone a dramatic decline in the recent past caused by human (e.g., overfishing, eutrophication, pollution) and natural (e.g., storms, extreme temperatures, diseases) disturbances.
- The protection of reef resources is crucial to southeast Florida where a substantial portion of revenue and jobs are dependent both directly and indirectly on the status of reef resources.

The reef communities of the Florida Reef Tract represent the only living tropical coral reef system in the continental U.S. (Figure 1). Reefs of the Florida Keys, from Key West to Key Biscayne, are commonly divided into two main types: offshore shelf-margin bank reefs and lagoonal patch reefs. Offshore bank reefs with spur and groove habitats are generally oriented perpendicular to the shelf and are found on the seaward face of the shelf margin (Marszalek *et al.,* 1977). Patch reefs are high-relief features (up to 9 m of vertical relief) located within the inner lagoon between the Florida Keys and the shelf-margin reefs. Patch reefs are commonly dome- or linear-shaped and range in diameter from a few meters to up to 700 m (Marszalek *et al.,* 1977; Jaap, 1984). Several interacting factors have contributed to the consideration of this ecologically, economically, and aesthetically unique system as an "ecosystem at risk" (Bryant *et al.,* 1998). Over 40 species of stony corals have been documented on Florida reefs. Other dominant taxa include octocorals, sponges, and zoanthids. Historically, the shallow areas of shelf-margin reefs were dominated by the fast-growing branching genus *Acropora* (*A. palmata* and *A. cervicornis*), but these species have undergone a drastic decline and are now listed as threatened under the U.S. Endangered Species Act (Porter and Meier, 1992; Miller *et al.,* 2002; NMFS, 2006). Dominant coral taxa on offshore reefs include *Porites, Montastraea, Diploria, Dicocoenia,* and *Siderastrea*. Patch reefs are dominated by medium-to-large colonies of boulder corals like *Montastraea, Diploria, and Siderastrea* (Lirman and Fong, 2007).

Low-relief hardbottom communities are another key component of the coastal habitats of South Florida. Hardbottom habitats in the Florida Keys can be found adjacent to the mainland and islands at depths from <1 m to >20 m. Hardbottom communities are characterized by a limestone platform covered by a thin layer of sediment and consist of a sparse mixture of stony corals, soft corals, macroalgae, and sponges (Bertelsen *et al.,* 2009). Many of these communities are found on remnant, low-profile habitats lacking significant zonation and topographical development (<1 m of vertical relief) in areas where sediment accumulation is <5 cm (Blair and Flynn, 1989; Chiappone and Sullivan, 1994; Lirman *et al.,* 2003).

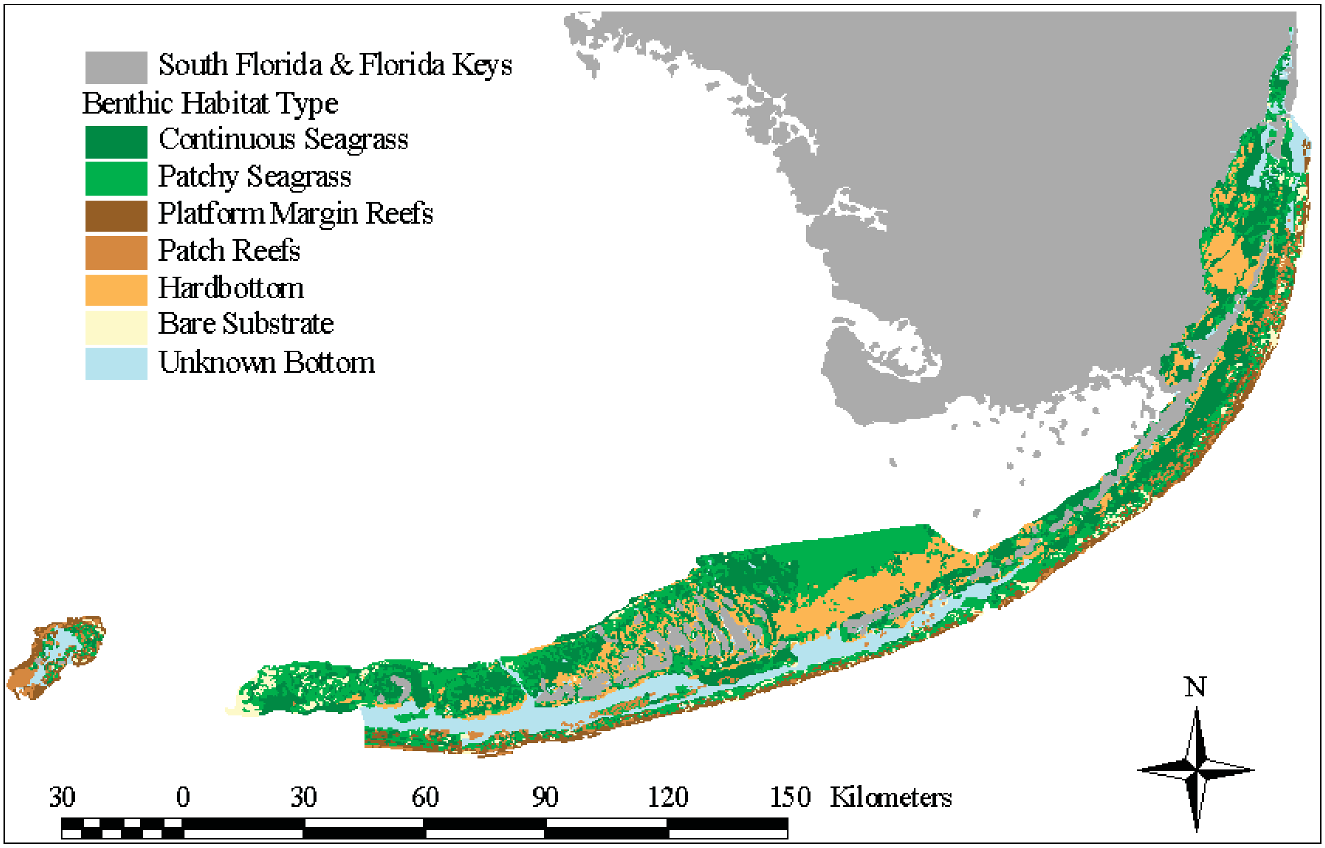

Figure 1. Benthic habitats of the Florida Keys (from Fourqurean *et al.,* http://serc.fiu.edu/seagrass/NearshoreWeb).

Role in the Ecosystem

Healthy reefs are vital to the economy of South Florida. A substantial portion of revenue and jobs in Florida are dependent both directly and indirectly on the status of their reef resources. In addition to the intrinsic value of coral reefs as centers of biodiversity and productivity, these habitats provide important services such as shoreline protection, sand production, building materials, nutrient cycling, carbon sequestration, adult and nursery habitat for fish and invertebrate species, fisheries resources, pharmaceutical and biomedical products, as well as societal services such tourism revenues, education and recreation opportunities, and cultural resources (Conservation International, 2008). Hardbottom communities can be important nursery habitats for shrimp and lobsters (Diaz, 2001; Butler *et al.,* 1995; Hunt, 2001; Bertelsen *et al.,* 2009) and have supported, in the past, commercial sponge fisheries (Cropper *et al.,* 2001).

The importance of coral reef habitats to the economic welfare of southeast Florida was evidenced in a study by Johns *et al.* (2001), which reported that reef-related expenditures generated more than $4 billion in sales and supported over 72,000 full- and part-time jobs in 2000-2001 in Monroe, Miami-Dade, Broward, and Palm Beach counties. On a worldwide basis, recent reports have estimated that the total net benefit of the world's coral reef ecosystems is nearly $30 billion/year (Cesar *et al.,* 2003). Moreover, the average global value of coral reef recreation has been estimated at $184 per visit (Brander *et al.,* 2007). Within the long list of services provided by these habitats, the following have been identified as the most valuable (Conservation International, 2008; Cesar *et al.,* 2003): (1) tourism and recreation (accounting for $9.6 billion of the total $29.8 billion global net benefit of coral reefs); (2) fisheries ($5.7 billion); (3) coastal protection ($9 billion); (4) biodiversity ($5.5 billion); and, more recently, (5) carbon sequestration (contribution to global economy not quantified yet).

Coral Reef Protection in South Florida

The current level of protection of reef resources varies among the counties of southeast Florida and ranges from unrestricted access to no-take and research-only areas with access limited by permitting. In 1990, the Florida Keys National Marine Sanctuary and Protection Act designated 9,950 km^2 of coastal waters in the Florida Keys as a Marine Protected Area to offer protection to over 1,400 km^2 of coral reef habitats found within the Sanctuary (http://floridakeys.noaa.gov) (Figure 2). In 1997, the management plan of the Florida Keys National Marine Sanctuary (FKNMS) created a network of protected zones to achieve biodiversity conservation, wildlife protection, and the separation of incompatible uses. Zone types include: wildlife management areas to minimize disturbance to sensitive wildlife and habitats; ecological reserves to protect large and contiguous habitats; sanctuary preservation areas (SPAs) to protect heavily used reefs; and special-use areas for scientific research, education, restoration, or monitoring.

The original 23 fully protected zones, where extractive and consumptive activities are prohibited, include 65 percent of the shallow coral reef habitats and 10 percent of all reef resources in the FKNMS (Keller and Donahue, 2006). In addition to the SPAs established in 1997, the Tortugas Ecological Reserve was implemented in 2001, increasing the amount of coral reef habitat within no-take zones to 10 percent within the Sanctuary. The Tortugas Ecological Reserve, located in the westernmost portion of the Florida Reef Tract, is the largest (517.9 km^2) of the Sanctuary's fully-protected zones. This reserve is located adjoining to the Dry Tortugas National Park (262 km^2) and its newly designated Research Natural Area (RNA; 129 km^2) where anchoring and fishing activities are not allowed. Together, the Tortugas Ecological Reserve and the Dry Tortugas National Park's RNA fully protect nearshore to deep reef habitats and form the largest marine reserve in the continental U.S.

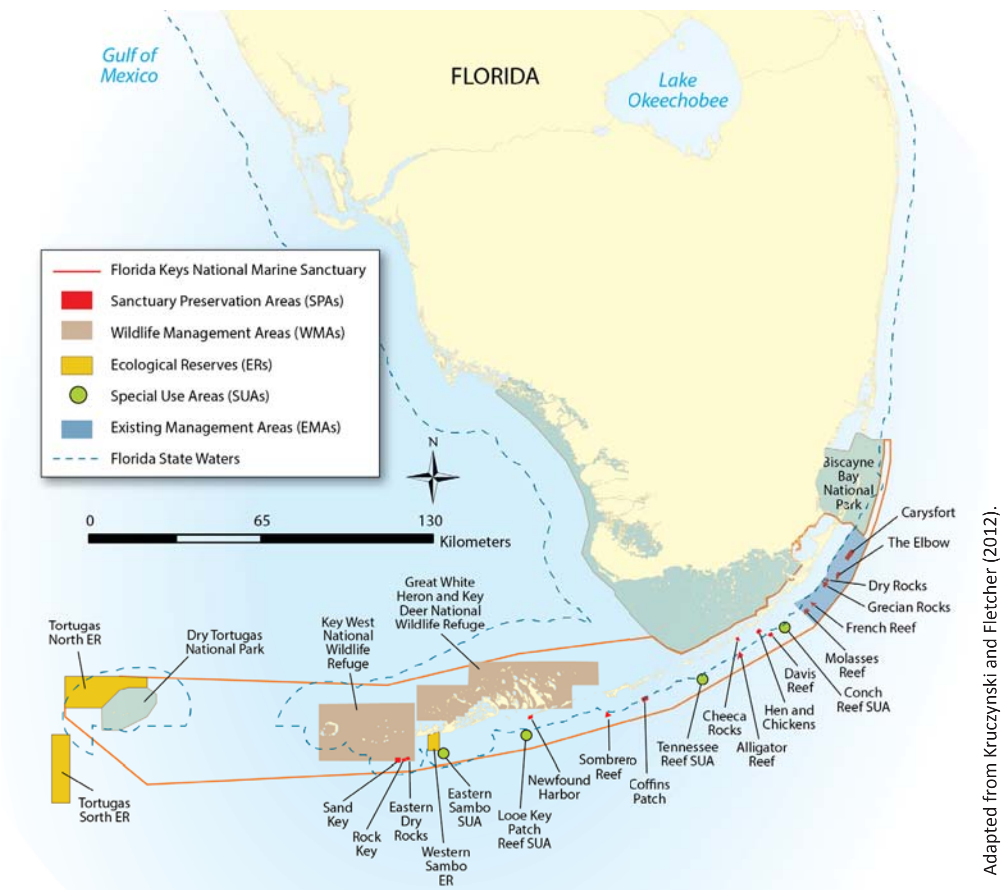

Figure 2. Map of the southeast Florida and the location of Biscayne National Park, Dry Tortugas National Park, and the Florida Keys National Marine Sanctuary.

Just north of the FKNMS boundaries, Biscayne National Park encompasses a large portion of the northern Florida Reef Tract with 291 km^2 of coral reefs and coral-dominated habitats. While extractive activities (e.g., fishing, spearfishing, lobster, and crab collection) are still permitted within Biscayne National Park, a revision of its General Management Plan is underway. Several of the alternatives proposed in this revision include the designation of management zones where fisheries resources and nursery habitats would be protected from fishing and other disturbances (http://www.nps.gov/bisc/parkmgmt/planning.htm). At present, the coral reef resources in the region north of Biscayne National Park (Miami-Dade to Martin counties) do not fall within any marine protected area.

In addition to areas with federal protection, reef resources are also found within a number of state parks and aquatic preserves that presently offer limited protection to corals and reef-associated resources. Examples of these include the Key West National Wildlife Refuge and Great White Heron National Wildlife Refuge, John Pennekamp Coral Reef State Park, Lignumvitae Key Botanical State Park, Biscayne Bay Aquatic Preserve, and the St. Lucie Inlet Preserve State Park. Lastly, the Oculina Bank Habitat Area of Particular Concern (HAPC), established in 1984, runs from Ft. Pierce to Cape Canaveral and protects deep-water populations of the ivory coral (Oculina).

Attributes People Care About

Coral reefs and hardbottom communities of the Florida Keys support attributes of the marine environment that people care about. These attributes are directly related to ecosystem services provided by the Florida Keys marine ecosystem:

- Abundance of healthy coral
- Abundance and large variety of fish and shellfish
- Ecosystem resilience to disturbance
- Protection from erosion and storms
- Critical habitat for protected species
- Aesthetics and recreation

Abundance of Healthy Coral

The essential characteristic of healthy coral reef habitats is the high abundance and diversity of stony and soft corals. Coral reefs are centers of biodiversity and productivity, and the services provided by these ecosystems are directly tied to their biodiversity. A wide range of coral morphologies provides a variety of niches for fish and invertebrates, and coral abundance is directly related to fish biomass. Moreover, the high topography, variety of sub-habitats, and diversity of species are the attributes that attract tourists, snorkelers, and divers to these ecosystems in Florida and elsewhere.

Abundance and Large Variety of Fish and Shellfish

Fish and macroinvertebrates are important ecological components of reef ecosystems and also sustain a productive commercial and recreational fisheries industry worldwide. In addition to their economic value, abundant and diverse fish and invertebrate stocks are an essential component of the "reef experience," and snorkelers and divers enjoy viewing these organisms as much as corals. Finally, a healthy fish and invertebrate trophic structure is essential for the growth and persistence of corals. Fish and invertebrate grazers play a major role in keeping the reef free of macroalgae that can outcompete and kill corals. Fish also play a major role in the recycling of nutrients within reefs.

Ecosystem Resilience to Disturbance

Periodic disturbances are an integral component of coral reef ecology, and coral reefs, like all other natural ecosystems, are in a constant state of damage and recovery. However, under healthy conditions, coral reef organisms are able to withstand and recover from disturbances. This ability to recover quickly from disturbance is an attribute that is highly valued by scientists, managers, and the public (Nyström and Folke, 2001). When disturbance thresholds are exceeded or multiple stressors compromise the recovery capabilities of reef organisms, coral reefs can enter into an alternate state of degradation from which it is increasingly more difficult to recover. Some of the attributes that make a reef community resilient to disturbance include an intact trophic structure, a high diversity of organisms, and good water quality.

Protection from Erosion and Storms

Corals are ecosystem engineers that can create large and complex three-dimensional carbonate structures that provide significant buffering from waves and currents. The presence of healthy, growing reefs provides valuable benefits in terms of storm and shoreline protection. This is especially important in Florida where a big part of the tourism economy is based on beach-related activities. Much like seagrasses that buffer water motion, coral reefs provide cost-effective, natural shore protection that reduces the need for costly beach renourishment and erosion control projects.

Critical Habitat for Protected Species

Florida reefs are essential habitat for the endangered green turtle and support threatened fisheries species like the Nassau grouper and queen conch. Florida reefs are also essential habitat for two species of threatened stony corals, staghorn (*A. cervicornis*) and elkhorn (*A. palmata*) corals.

Aesthetics and Recreation

Coral reefs, often described as the tropical rain forests of the ocean, provide a wonderful mosaic of diverse structures, colors, and even sounds! Healthy coral reefs with lots of fish and associated organisms provide a unique aesthetic experience that create long-lasting memories in those that have the opportunity to experience these magnificent ecosystems. Coral reefs also provide a number of recreational opportunities that are highly valued by visitors. These include fishing, collecting, diving, snorkeling, and glass-bottom viewing.

Attributes We Can Measure

A number of large-scale, long-term monitoring programs have been established in the Florida Keys in recent years to evaluate the status and trends of coral reef communities. These monitoring programs include the NOAA/National Undersea Research Center program (1999-present, http://people.uncw.edu/millers/CoralReef_QuickLooks.htm), the Coral Reef Monitoring Project (CREMP, 1994-present, http://ocean.floridamarine.org/fknms_wqpp/pages/cremp.html), and the more recent Florida Reef Resilience Program (FRRP, 2005-present, http://frrp.org).

In contrast, coordinated efforts to evaluate the status and trends of hardbottom communities are less common or have restricted spatial and temporal coverage. Baseline abundance and distribution of organisms within hardbottom habitats have been documented by Lirman *et al.* (2003), Fourqurean *et al.* (http://serc.fiu.edu/seagrass/NearshoreWeb), and Bertelsen *et al.* (2009). Hardbottom communities within the Florida Reef Tract are also being monitored as part of the National Undersea Research Center program (http://people.uncw.edu/millers/CoralReef_QuickLooks.htm) and the Florida Reef Resilience Program (http://frrp.org/).

The monitoring programs designed to determine regional-scale gradients in the status of coral reefs and hardbottom communities commonly collect information on the following attributes:

- Reef structure
- Diversity
- Species abundance
- Species distribution
- Size of coral colonies
- Partial mortality
- Disease and bleaching prevalence

Reef Structure

Structure and function are closely tied in coral reefs where reef-building stony corals provide the three-dimensional structure that is utilized as essential habitat for associated organisms. Thus, measures of topographical structure or relief are commonly collected in monitoring programs as a proxy for reef condition and habitat value. The close relationships between coral abundance, reef topographical structure, and habitat value for fisheries have been highlighted by recent studies of reef degradation that have shown that declines in coral abundance have resulted in a general "flattening" of reefs (Alvarez-Filip *et al.,* 2009) and a corresponding loss of fisheries resources (Paddack *et al.,* 2009) worldwide. Topographical structure is commonly measured using rugosity-chain measures or coral colony heights (McCormick, 1994; Kramer and Lang, 2003).

Diversity

Coral reefs are known centers of biodiversity, and diversity or species richness are commonly recorded in monitoring programs through cumulative species counts (Rutten *et al.,* 2009). While no recent records of species losses have been recorded in Florida reefs and hardbottom communities, loss of species from certain reefs or areas have been recorded during the recent patterns of reef decline (Porter *et al.,* 2002). Most monitoring programs focus on stony corals; others do collect richness information on soft corals, sponges, and associated macroinvertebrates (NOAA-NURC).

Species Abundance

The abundance of coral colonies is commonly documented as the proportion of the bottom occupied by a give taxon in a two-dimensional view. The abundance of coral taxa provides a good snapshot of the status of a given site and, through repeat surveys, changes in cover can provide information of temporal trends in coral reef or hardbottom status. Coral cover has always been synonymous with coral reef condition, and measurements of percent coral cover are made (either directly or indirectly) by most coral reef monitoring programs using point or line-intercept methods (AGRRA, NOAA-NURC, CREMP) or colony measurements (Lirman and Fong, 2007; FRRP) (Porter *et al.,* 2002; Miller *et al.,* 2002). In addition, the proportion of the bottom occupied by corals, monitoring programs also collect data on the abundance/cover of other key taxa like sponges, zoanthids, and macroalgae.

Species Distribution

Changes in the distribution of coral and associated taxa can often be indicative of changes in environmental conditions. Thus, the spatial distribution of benthic organisms is commonly documented in Florida using habitat-specific and spatially structured monitoring approaches (Miller *et al.,* 2002; Lirman and Fong, 2007; Bertelsen *et al.,* 2009). Spatially structured monitoring approaches maximize survey efficiency and also allow managers to delineate critical habitat for protected species like the genus *Acropora* (Smith *et al.,* 2011; http://www.nmfs.noaa.gov/pr/species/criticalhabitat.htm). Most species of corals have widespread distributions within reef and hardbottom habitats of the Florida Keys, but some species have been lost within specific plots and reefs during the recent declining trends (Porter *et al.,* 2002).

Size of Coral Colonies

Although changes in coral cover and diversity can provide good indicators of reef degradation (Porter *et al.,* 2002), these measures alone can't be used to examine sublethal effects of chronic exposure to stressors. Thus, most monitoring programs have incorporated demographic indicators (e.g., size of colonies, prevalence of fragmentation and fission, recruitment) to supplement measurements of coral cover to reveal more subtle differences among populations that cover and diversity measures alone may miss. Population size structure has been shown to provide good indicators of stress and condition (Bak and Meesters, 1999; Ginsburg *et al.,* 2001; Nugues and Roberts, 2003). All large-scale monitoring programs in the Florida Keys include colony size measurements within their protocols. The abundance of juvenile corals (<4 cm in diameter) is also used as an indicator of recruitment success (Lirman and Fong, 2007). Size measurements of sponges on other benthic organisms are also collected as part of monitoring programs on hardbottom habitats (Cropper *et al.,* 2001; Lirman *et al.,* 2003).

Partial Mortality

The amount of recently dead tissue on coral colonies is being used increasingly as an indicator of the impact of recent disturbances. Recent tissue mortality is described as portions of a coral colony devoid of living tissue where the corallite structure is still present and allows identification to the species level (Kramer and Lang, 2003). This indicator is intended to provide information on the impacts of disturbance with impacts concentrated within the recent past (weeks-months). Percent recent mortality is commonly estimated as the proportion of a coral colony that exhibits recent tissue mortality, and this metric is commonly averaged within and among sites for all colonies present and compared to similar measurements taken immediately after a major disturbance like a bleaching episode (Kramer, 2003; FRRP) or, more recently, a cold-water anomaly (Lirman *et al.,* 2011).

Disease and Bleaching Prevalence

One of the main sources of coral mortality in Florida and the Caribbean in the past decades has been coral diseases (Porter *et al.,* 2001; Richardson and Voss, 2005). In fact, the large-scale demise of *Acroporid* corals in the Florida Keys has been attributed to outbreaks of white-band disease (Precht and Miller, 2007; Patterson *et al.,* 2011). Similarly, warm-water anomalies that cause coral bleaching (i.e., the expulsion of the endosymbiotic zooxanthellae) have been a major source of mortality in Florida and elsewhere (Jaap, 1979, 1985; Baker *et al.,* 2008). All large-scale monitoring programs in place in the Florida Keys include measurements of bleaching and disease prevalence, commonly estimated as the percentage of colonies exhibiting signs of disease or bleaching. In addition to prevalence, the proportion of the colony surface affected by these two types of disturbance can be estimated.

Drivers of Change

The human drivers identified as having a direct influence on the state of coral reefs and hardbottom communities include both near-field (i.e., acting within the region) and far-field (i.e., at global scale) (Figure 3). Near-field drivers include coastal construction, tourism and recreation, industry, agriculture, energy, transportation, waste disposal, recreational and commercial fisheries, and water management. Far-field drivers include global climate change and climatic extremes (e.g., sea-level rise, high and low temperatures, storms, acidification), diseases, and invasive species.

The potential causal factors implicated in the observed decline in coral reefs and hardbottom habitats in Florida are those common to other reef systems around the world (Brown, 1997) and include: hurricanes (Porter and Meier, 1992; Lirman and Fong, 1997); ship groundings (Lirman and Miller, 2003; Gilliam, 2006); the demise of the sea urchin *Diadema antillarum* and increased macroalgal competition (Forcucci, 1994; Lirman, 2001); coral diseases (Porter *et al.,* 2001; Richardson and Voss, 2005); increased nutrients (Lapointe *et al.,* 2002); sedimentation (Dustan, 1999); high temperature and bleaching events (Jaap, 1979, 1985; Manzello *et al.,* 2007); cold-water events (Hudson, 1981; Walker *et al.,* 1982; Lirman *et al.,* 2011); and phytoplankton (Hu *et al.,* 2003) and cyanobacterial (Butler *et al.,* 1995; Paul *et al.,* 2005) blooms.

Mechanisms of Change

Direct impacts to coral reefs and hardbottom communities can be generally grouped into lethal and sublethal impacts. While sublethal impacts (e.g., reduced growth, reduced calcification) may be precursors of lethal impacts if pressures exceed a certain threshold, recovery from sub-lethal impacts can also take place. Impacts can also be grouped into functional (e.g., reduced productivity) and structural (e.g., reduced topographical complexity, reduced diversity). Often, functional and structural impacts are tightly linked. For example, reduced growth can result in reduced topography which, in turn, can result in reduced primary productivity.

The impacts that are directly related to the ecological, economic, and societal services that coral reefs and hardbottom habitats provide include: mortality of key benthic components (hard and soft corals, sponges); reduced water quality (turbidity, eutrophication, sedimentation, low pH, algal blooms); declines in structural attributes (diversity, abundance, distribution, complexity, fragmentation); reductions in key functions or processes (photosynthesis, production, calcification, growth); higher prevalence of bleaching and diseases; and reductions in ecosystem resistance and resilience (i.e., the ability to absorb disturbances and the ability to bounce back after disturbances).

The principal threats to coral reefs and hardbottom communities of the Florida Keys marine waters occur mainly through the following pathways:

Coastal Development

The impacts of coastal development and the stressors created by associated activities (sedimentation, eutrophication, solid and chemical wastes, overexploitation, physical impacts) have been consistently ranked at the top of disturbance rankings with significant negative impacts on coral reefs and other coastal resources (Kleypas and Eakin, 2007; Waycott *et al.,* 2009). In the Florida Keys, impacts of population growth and an expanded need for both coastal and inland development on coral reefs and hardbottom communities are manifested mainly through the pathways or mechanisms listed below.

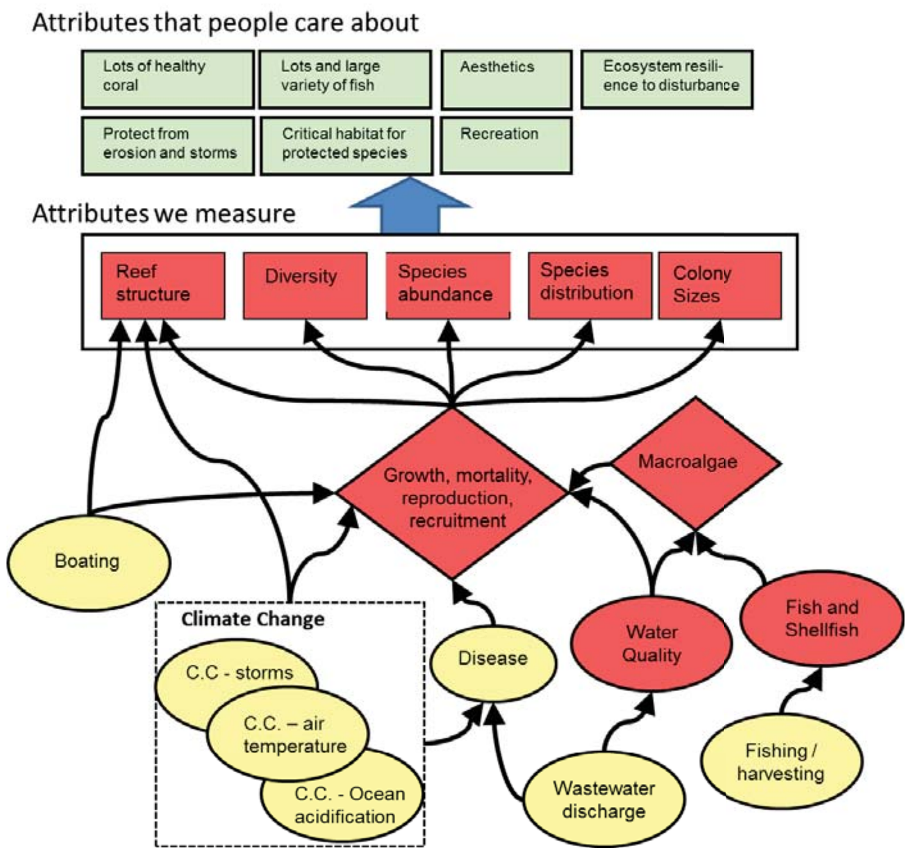

Figure 3. Coral and hardbottom submodel diagram for the Florida Keys/Dry Tortugas.

Fishing and Changes to Trophic Structure

Recreational and commercial fishing activities targeting coral reef and hardbottom communities provide a major economic driver in the Florida Keys. While the impacts of these activities on the fishery stocks are described in more detail in a separate conceptual model in this report, damage to benthic resources as a result of fishing and collection can also be considerable. These impacts generally fall into two categories: (1) changes to the trophic structure; and (2) physical impacts on benthic resources.

Corals and other slow-growing benthic organisms are in competition for limited space by faster growing macroalgae (Birrell *et al.,* 2008). Thus, any factor that favors macroalgal growth directly affects the growth and survivorship of corals (Steneck and Detheir, 1994). Overexploitation of fish stocks in the Caribbean has resulted in significant changes to the trophic structure of reef fish communities and a significant reduction in the abundance and size structure of populations of herbivorous fishes like parrotfishes (Hughes, 1994; Mumby, 2006). The reduction in grazing pressure and other factors like increased nutrients have prompted a phase in shifts on Caribbean reefs away from algal dominance towards algal-dominated states (Mumby, 2009). In Florida, grazing fishes are not targeted and are still abundant on Florida reefs. However, the major changes that have taken place over the last three decades may have limited their influence. The regional demise of the sea urchin, *Diadema antillarum*, as well as potential increased nutrient inputs from human activities, may have resulted in the present conditions of algal overgrowth that may be threatening some reef communities of the Florida Reef Tract (Carpenter, 1990; Lapointe and Clark, 1992; Szmant and Forrester, 1996; Lapointe, 1997; Bryant *et al.,* 1998).

The physical impacts of fishing and harvesting activities include the damage caused by ship groundings and propellers scars, as well as the damage caused by fishing gear such as lines, sinkers, traps, and trawler nets to benthic organisms like corals and sponges. In a study conducted in 2001, Chiappone *et al.* (2005) showed that lost hook-and-line fishing gear accounted for >85 percent of all debris encountered on Florida reefs and hardbottom communities and was responsible for >80 percent of the impacts to sponges and corals. The main impact of this type of gear consisted of tissue abrasion and partial or complete colony mortality. Similarly, considerable damage can be made to benthic resources by fishing gear targeting macroinvertebrates like lobsters and shrimp. Rogue lobster traps are often seen littering reefs after severe storms, and the long lines attached to these traps often cause severe abrasion to large coral colonies. The trawl nets used for the extraction of shrimp can also cause damage to sponges and soft corals on hardbottom habitats as shown in the study by Ault *et al.* (1997).

Changes in Water Quality

Pollutants

The location of Florida reefs adjacent to rapidly growing urban centers makes this unique system especially vulnerable to pollution commonly associated with coastal development and industrial, agricultural, and shipping activities. Contamination by pesticides, heavy metals, hydrocarbons, or other pollutants can significantly affect the health of reefs and other benthic communities. Heavy metals such as copper and zinc and some hydrocarbons have been linked to reduced fertilization, fecundity, and growth in corals and a large number of other reef organisms. Moreover, herbicides are known to cause physiological stress in corals even after short-term exposure at environmentally relevant concentrations. In addition, experiments conducted with fertilizers have shown that infection rates and the spread of coral diseases can be accelerated by increased concentrations of inorganic nutrients. Pathogens may also be introduced into the coastal environment through wastewater and groundwater releases.

Nutrients

At least part of the loss in coral cover recorded for the Florida Reef Tract in the recent past has been attributed to increased nutrient inputs from anthropogenic sources (Dustan and Halas, 1987; Lapointe and Clark, 1992, 1997; Porter *et al.,* 1999). Increased nutrient inputs into coastal habitats of Florida have been associated with activities such as coastal and upland development, water management practices, and stormwater runoff. Higher nutrient concentrations may affect corals directly by reducing calcification, growth, and fertilization rates (Fabricius, 2005) or indirectly favoring macroalgal growth, resulting in coral overgrowth, abrasion, and reduced recruitment (Tomascik and Sander, 1985, 1987; Kuffner *et al.,* 2006). A rapid increase in macroalgal abundance can cause severe degradation to reef communities and establish a persistent phase shift that delays or precludes the recovery of coral-dominated reef communities. Blooms of macroalgae (*Caulerpa brachypus*) and blue-green algae (*Lyngbya spp.*) have already been observed on reefs in South Florida and may, if persistent, result in such community shifts.

Increased nutrient levels can enhance phytoplankton production, increasing turbidity and reducing light penetration. Light reduction results in decreased photosynthetic yields in corals, while increased phytoplankton abundance may influence the activities of filter-feeding organisms such as sponges. Moreover, phytoplankton blooms can create anoxic or toxic conditions that may result in the mortality of both mobile and benthic reef organisms such as bivalves, sponges, and fish. Finally, several studies have documented increased abundances of reef bioeroders such as the boring sponge *Cliona spp.* and the bivalve *Lithophaga spp.* in response to enhanced nutrient availability. The activities of these bioeroders and coral competitors can cause reef communities to be more susceptible to physical disturbances such as storms and ship groundings.

Sedimentation

Around the world, water quality in coastal areas is changing in response to rapidly increasing coastal development and urbanization. Among the coral reef stressors commonly associated with these activities, sedimentation has been shown to be one of the predominant causes of reduced condition, abundance, and spatial extent of corals and other reef-associated organisms (Fabricius, 2005). In Florida, increased sedimentation has been associated with human activities such as port expansion, dredge-and-fill projects, coastal development, shoreline hardening activities, upland development, water management practices, and boating activities. Increased sediment loads can increase water turbidity, cause shading, smothering, and even burial of benthic organisms (Tilmant *et al.,* 1994; Te, 1997). Some of the effects commonly associated with high sedimentation include reductions in coral photosynthesis, growth, recruitment, and survivorship (Rogers, 1990).

Physical Impacts

Boating

The proximity of South Florida's reef resources to major ports, marinas, and shipping lanes, as well as the intense recreational and commercial boating activities that take place in the region, also means that benthic resources are especially vulnerable to physical impacts. The physical damage caused by ship and boat impacts include increased sedimentation, fragmentation of benthic organisms, detachment of sponges and coral colonies and, in the worst cases, the fracture or pulverization of the carbonate framework (Lirman *et al.,* 2010).

Storms

The impacts of storms on coral reefs and hardbottom organisms of the Florida Keys have ranged from minor (Manzello *et al.,* 2007) to severe (Lirman and Fong, 1997). The damage caused by storms includes breakage and fragmentation, abrasion, smothering, and burial (Fong and Lirman, 1995). In the most severe cases, portions of the reef framework can be dislodged during severe hurricanes (Gleason *et al.,* 2007).

Global Climate Change

Temperature Extremes

One of the most worrisome predictions of global climate change scenarios for coral reefs is the projected increase in seawater temperatures over the upcoming decades (IPCC, 2007). For coral reefs that are close to their thermal tolerance, increases in the intensity and frequency of warm-water anomalies can be catastrophic (Baker *et al.,* 2008). The most common response of corals to increased seawater temperature (commonly >30°C for extended periods) is bleaching, or the expulsion of their endosymbiotic dinoflagellates (zooxanthellae). The loss of zooxanthellae represents a serious energetic drain, as these microalgae provide their coral host with both nutrients and energy in the form of reduced carbon compounds. While bleaching is a reversible process, extended bleaching can cause significant coral mortality, as evidenced by the 2005 bleaching event that caused widespread mortality throughout the Caribbean region (Eakin *et al.,* 2010).

Finally, while high temperatures can impact corals directly, increased temperatures have also been correlated with a higher prevalence of diseases that can also cause significant coral mortality and would be an undesirable effect of global climate change in the Florida Keys (Brandt and McManus, 2009; Miller *et al.,* 2009).

Sea-Level Rise

Projected sea-level rise may influence both the condition of present coral reefs, as well as the future distribution of these communities. Changes in water depth can influence species distributions based on their specific light limitations and may limit the abundance of reef or hardbottom species with high light requirements (Hoegh-Guldberg, 1999). Communities and species living at their physiological depth/light limits will be most affected. Similarly, flooding of coastal habitats may increase inputs of sediment and nutrients with associated impacts on benthic organisms (as described in previous sections).

Ocean Acidification

With the realization that rising atmospheric carbon dioxide concentrations will cause changes in the ocean's carbonate chemistry leading to lower pH and lower saturation states of carbonate minerals, there is growing concern for marine organisms like corals that use such materials to build and support their skeletal structures (Kleypas *et al.,* 2006). Under global climate change scenarios, it is predicted that calcification rates will decrease up to 60 percent within the 21st century. The potential negative effects of acidification on corals include reduced fecundity, reduced larval settlement, reduced larval survivorship, reduced coral growth and calcification and, in the most extreme conditions, skeletal dissolution (Albright *et al.,* 2010; Albright and Langdon, 2011). Similar impacts are expected on other calcifying organisms like foraminifera, macroalgae, and macroinvertebrates. Limited information is presently available on the carbon chemistry of seawater on Florida reefs and hardbottom habitats.

Status and Trends

In Florida, documented rates of reef decline are similar to those reported by Gardner *et al.* (2003) for the entire Caribbean region. In the Florida Keys, coral cover has been lost at an average rate of 12.6 percent per year from 1996-1999 (Porter *et al.,* 2002). In addition to these declines in coral cover, declines in species richness of stony corals have also been recorded for the same time period. While patterns of coral decline have been certainly widespread, *Acropora spp.* and *Montastraea spp.*, the main reef-building taxa in Florida, have been especially impacted. For example, Miller *et al.* (2002) reported declines of 93 percent and 97 percent in the total live area of *A. palmata* and *A. cervicornis,* respectively, at Looe Key in the Lower Florida Keys between 1983 and 2000. A similar decline in the abundance of *A. cervicornis* (96 percent reduction) was reported by Jaap *et al.* (1988) at Molasses Reef in the Upper Florida Keys from 1981-1986. Dustan (1999) and Dustan *et al.* (2001) have also shown patterns of long-term declines in coral cover and condition at Carysfort Reef in the Upper Keys starting as far back as 1975. Lastly, steady declines in coral cover, especially on those sites dominated by *A. palmata,* were documented at permanent sites from Biscayne National Park to Looe Reef from 1984-1991 by Porter and Meier (1992) and from 1996 to 2000 by Patterson *et al.* (2002).

While the decline in coral condition may have started at least 20 years ago, more recent studies report a continuing decrease in coral abundance and diversity. For example, Porter *et al.* (2002) reported a decline in coral richness at 67 percent of permanent transects between 1996 and 2000 and a corresponding decline in coral cover of 38 percent over the same period. All sectors showed negative relative percent changes in coral cover between 1996 and 2000, but the Upper Keys experienced the most significant losses, with 72 percent of all stations reporting declines.

When patterns in coral cover from 1996-2009 for the Florida Keys were examined by the Coral Reef Evaluation and Monitoring Project (CREMP, http://ocean.floridamarine.org/fknms_wqpp/pages/cremp.html), consistent year-to-year declines were documented, with the biggest declines coinciding with the 1998 and 2005 coral bleaching events. The mean cover for all sites and habitat types recorded in 1996 was 12.7 percent and reached a minimum of 6.4 percent in 2006. However, since 1999, declines in coral cover have decreased in magnitude, and the first significant increase in coral cover (from 6.6 percent to 7.3 percent) was recorded between 2008 and 2009 (http://conference.ifas.ufl.edu/floridakeys/Presentations/Wednesday/PM/1415%20Ruzzicka%20R.pdf). Unfortunately, these positive trends were completely reversed by the cold-water anomaly that caused significant mortality to coral reefs in the Florida Keys in January 2010 (Lirman *et al.,* 2011).

Detailed information on the long-term condition patterns of hardbottom communities is generally lacking (but see Fourqurean *et al.,* http://serc.fiu.edu/seagrass/NearshoreWeb), and this clearly represents a knowledge gap for the system (Bertelsen *et al.,* 2009). Nevertheless, hardbottom communities have also experienced ecological declines in the recent past. One example is the mass mortality of sponges that was observed in Florida Bay and adjacent habitats in 1991. This decline was likely due to a bloom of cyanobacteria (Butler *et al.,* 1995).

Research and Knowledge Gaps

The coral reefs of the Florida Keys are one of the best studied ecosystems in the world. Long-term monitoring programs and scientific research have provided ample documentation on the status and trends of these resources, especially within the last 20 years. Some future research priorities and gaps include:

Improved Knowledge of Status and Trends of Hardbottom Habitats

Increased understanding of the factors influencing the abundance and distribution of hardbottom organisms. Hardbottom communities have received comparatively less attention than coral reef habitats and thus research and monitoring in these habitats is lagging behind that in offshore coral reefs. Spatial gaps in knowledge are especially evident for hardbottom habitats of north Key Largo and Biscayne National Park.

Genetic Connectivity of Coral Populations

While the connectivity of fish populations in the Florida Keys has received some attention, limited knowledge presently exists on the genetic connectivity of coral populations in the Florida Keys (with the exception of populations of *Acroporid* corals). Information is needed on the connectivity among regions, as well as between shallow and deep habitats that may serve as refuge from thermal anomalies.

Mesophotic Reefs

At present, only limited information is available on the abundance, distribution, diversity, and condition of coral from mesophotic reefs (>30 m in depth and characterized by a low availability of light). These habitats may prove to be important spawning grounds for commercial and recreational reef fish species like groupers and may also play a role as refuges from extreme environmental disturbances like temperature anomalies and storms.

Impacts of Everglades Restoration on Hardbottom and Coral Reef Habitats

While some adverse impacts related to changes in hydrology have been documented for hardbottom habitats (i.e., cyanobacterial blooms that cause sponge mortality), the potential future impacts of the changes in the freshwater delivery patterns into coastal bays are presently unknown. To document and predict such changes, especially those related to changes in salinity and nutrient content, additional research focused on nearshore hardbottom and coral reef habitats is needed.

Impacts of Ocean Acidification

While the impacts of seawater temperature anomalies on corals and other benthic organisms have been well documented, research on the impacts of ocean acidification on coral reefs and hardbottom habitats of the Florida Keys is still in its infancy. Additional research is needed to document present carbonate chemistry on these habitats and potential impacts of reduced calcification scenarios on corals and other calcifying organisms like macroalgae, urchins, and gastropods.

References

Albright, R., and C. Langdon. 2011. Ocean acidification impacts multiple early life history processes of the Caribbean coral *Porites astreoides*. Global Change Biology, 17(7):2478-2487 (doi:10.1111/j.1365-2486.2011.02404.x).

Albright, R., B. Mason, M. Miller, and C. Langdon. 2010. Ocean acidification compromises recruitment success of the threatened Caribbean coral *Acropora palmata*. Proceedings of the National Academy of Sciences USA, 107(47):20,400-20,404.

Alvarez-Filip, L., N.K. Dulvy, J.A. Gill, I.M. Côté, and A.R. Watkinson. 2009. Flattening of Caribbean coral reefs: Region-wide declines in architectural complexity. Proceedings of the Royal Society B, 276:3019-3025.

Ault, J.S., J. Serafy, D. DiResta, and J. Dandelski. 1997. Impacts of commercial fishing on key habitats within Biscayne National Park. University of Miami/Rosenstiel School of Marine and Atmospheric Science, Final Report on Cooperative Agreement No. CA-5250-6-9018, 80 pp.

Bak, R.P.M., and E.H. Meesters. 1999. Population structure as a response of coral communities to global change. American Zoologist, 39:56-65.

Baker, A.C., P.W. Glynn, and B. Riegl. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends, and future outlook. Estuarine, Coastal and Shelf Science, 80(4):435-471.

Bertelsen, R.D., M.J. Butler, IV, W.F. Herrnkind, and J.H. Hunt. 2009. Regional characterization of hardbottom nursery habitat for juvenile Caribbean spiny lobster (*Panulirus argus*) using rapid assessment techniques. New Zealand Journal of Marine and Freshwater Research, 43(1):299-312.

Birrell, C.L., L.J. McCook, B.L. Willis, and G.A. Diaz-Pullido. 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Oceanography and Marine Biology: An Annual Review, 46:25-63.

Blair, S.M., and B.S. Flynn. 1989. Biological monitoring of hard bottom reef communities off Dade County, Florida: Community description. Proceedings, 9th Annual Scientific Diving Symposium, American Academy of Underwater Sciences, September 28-October 1, 1989, Woods Hole, MA, 9-24.

Brander, L.M., P.J.H. Van Beukering, and H.J.S. Cesar. 2007. The recreational value of coral reefs: A meta-analysis. Ecological Economics, 63:209-218.

Brandt, M.E., and J.W. McManus. 2009. Disease incidence is related to bleaching extent in reef-building corals. Ecology, 90:2859-2867.

Bryant, D., L. Burke, J. McManus, and M. Spalding. 1998. Reefs at risk: A map-based indicator of potential threats to the world's coral reefs. World Resources Institute, Washington, DC, 56 pp.

Brown, B.E. 1997. Disturbances to reefs in recent times. In *Life and Death of Coral Reefs,* C. Birkeland (ed.). Chapman and Hall, NY, 354-378.

Butler, M.J., J.H. Hunt, W.F. Herrnkind, M.J. Childress, R. Bertelsen, W. Sharp, T. Matthews, J.M. Field, and H.G. Marshall. 1995. Cascading disturbances in Florida Bay, USA: Cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobsters, *Panulirus argus*. Marine Ecology Progress Series, 129(1-3):119-125.

Carpenter, R.C. 1990. Mass mortality of *Diadema antillarum*, I. Long term effects on sea urchin population-dynamics and coral reef algal communities. Marine Biology, 104:67-77.

Cesar, H.J.S., L. Burke, and L. Pet-Soede. 2003. The economics of worldwide coral reef degradation. Cesar Environmental Economics Consulting, Arnhem, and WWF-Netherlands, Zeist, The Netherlands. 23 pp.

Chiappone, M., and K.M. Sullivan. 1994. Patterns of coral abundance defining nearshore hardbottom communities of the Florida Keys. Florida Scientist, 57:108-125.

Chiappone, M., H. Dienes, D.W. Swanson, and S.L. Miller. 2005. Impacts of lost fishing gear on coral reef sessile invertebrates in the Florida Keys National Marine Sanctuary. Biological Conservation, 121:221-230.

Conservation International. 2008. *Economic Values of Coral Reefs, Mangroves, and Seagrasses: A Global Compilation*. Center for Applied Biodiversity Science, Conservation International, Arlington, VA, 35 pp.

Cropper, W.P., D. Lirman, S.C. Tosini, D. DiResta, J. Luo, and J. Wang. 2001. Sponge population dynamics in Biscayne Bay, Florida. Estuarine, Coastal and Shelf Science, 53:13-23.

Diaz, G.A. 2001. Population dynamics and assessment of pink shrimp (*Farfantepenaeus duorarum*) in subtropical nursery grounds. Ph.D. Dissertation, University of Miami, Coral Gables, 175 pp.

Dustan, P. 1999. Coral reefs under stress: Sources of mortality in the Florida Keys. Natural Resources Forum, 23(2):147-155.

Dustan, P., and J.C. Halas. 1987. Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. Coral Reefs, 6:91-106.

Dustan, P., E. Dobson, and G. Nelson. 2001. Landsat thematic mapper: Detection of shifts in community composition of coral reefs. Conservation Biology, 15(4):892-902.

Eakin, M., J. Morgan, S. Heron, T. Smith, G. Liu, L. Alvarez-Filip, B. Baca, E. Bartels, C. Bastidas, C. Bouchon, M. Brandt, A. Bruckner, L. Bunkley-Williams, A. Cameron, B. Causey, M. Chiappone, T. Christensen, M.J. Crabbe, O. Day, E. de la Guardia, G. Diaz-Pulido, D. DiResta, D. Gil-Agudelo, D. Gilliam, R. Ginsburg, S. Gore, H. Guzman, J. Hendee, E. Hernandez-Delgado, E. Husain, C. Jeffrey, R. Jones, E. Jordán-Dahlgren, L. Kaufman, D. Kline, P. Kramer, J. Lang, D. Lirman, J. Mallela, C. Manfrino, J.-P. Maréchal, K. Marks, J. Mihaly, W.J. Miller, E. Mueller, E. Muller, C. Orozco Toro, H. Oxenford, D. Ponce-Taylor, N. Quinn, K. Ritchie, S. Rodríguez, A. Rodríguez-Ramírez, S. Romano, J. Samhouri, J. Sanchez, G. Schmahl, B Shank, W. Skirving, S. Steiner, E. Villamizar, S. Walsh, C. Walter, E. Weil, E. Williams, K. Woody, and Y. Yusuf. 2010. Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005. PLoS ONE, 5(11):e13969 (doi:10.1371/journal.pone.0013969).

Fabricius, K.E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. Marine Pollution Bulletin, 50:125-146.

Fong, P., and D. Lirman. 1995. Hurricanes cause population expansion of the branching coral *Acropora palmata* (*Scleractinia*): Wound healing and growth patterns of asexual recruits. Marine Ecology, 16:317-335.

Forcucci, D. 1994. Population density, recruitment, and 1991 mortality event of *Diadema antillarum* in the Florida Keys. Bulletin of Marine Science, 54:917-928.

Gardner, T., I.M. Cote´, J.A. Gill, A. Grant, and A.R. Watkinson. 2003. Long term region-wide declines in Caribbean corals. Science, 301: 958-960.

Gardner, T.A., J.A. Gill, A. Grant, A.R. Watkinson, and I.M. Côté. 2005. Hurricanes and Caribbean coral reefs: Immediate impacts, recovery trajectories and contribution to long-term decline. Ecology, 86:174-184.

Gilliam, D.S. 2006. Southeast Florida Coral Reef Evaluation and Monitoring Project. 2005 Year 3 Final Report. Florida Fish and Wildlife Conservation Commission/Fish and Wildlife Research Institute/Florida Department of Environmental Protection, 26 pp.

Gleason, A.C.R., D. Lirman, D. Williams, N.R. Gracias, B.E. Gintert, H. Madjidi , R.P. Reid, G.C. Boynton, S. Negahdaripour, M. Miller, and P. Kramer. 2007. Documenting hurricane impacts on coral reefs using two-dimensional video-mosaic technology. Marine Ecology, 28:254-258.

Ginsburg, R.N., E. Gischler, and W.E. Kiene. 2001. Partial mortality of massive reef-building corals: An index of patch reef condition, Florida Reef Tract. Bulletin of Marine Science, 69(3):1149-1173.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine Freshwater Research, 50:839-866.

Hu, C., K.E. Hackett, M.K. Callahan, S. Andréfouët, J.L. Wheaton, J.W. Porter, and F.E. Muller-Karger. 2003. The 2002 ocean color anomaly in the Florida Bight: A cause of local coral reef decline? Geophysical Research Letters, 30(3):1151 (doi:10.1029/2002GL016479), 4 pp.

Hudson, J.H. 1981. Growth rates in *Montastrea annularis*: A record of environmental change in Key Largo Coral Reef Marine Sanctuary, Florida. Bulletin of Marine Science 3:444-459.

Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral. *Science,* 265(5178):1547-1551.

Hunt, J.H. 2001. Status of the fishery for *Panulirus argus* in Florida. In *Spiny Lobster Management,* B. Phillips, S. Cobb, and J. Kittaka (eds.). Blackwell Press, Oxford, 189-199.

IPCC (Intergovernmental Panel on Climate Change). 2007. Summary for Policymakers. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR4),* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller (eds.). Cambridge University Press, Cambridge, UK and New York, NY, 996 pp.

Jaap, W.C. 1979. Observations on zooxanthellae expulsion at Middle Sambo Reef, Florida Keys. Bulletin of Marine Science, 29:414-422.

Jaap, W.C., 1984. The ecology of the South Florida coral reefs: A community report. U.S. Fish and Wildlife Service/Office of Biological Services, Washington, DC, FWS/OBS-82/08, 138 pp.

Jaap, W.C. 1985. An epidemic zooxanthellae expulsion during 1983 in the Lower Florida Keys coral reefs: Hyperthermic etiology. Proceedings, Fifth International Coral Reef Congress, 6:143-148.

Jaap, W.C., J.C. Halas, and R.G. Muller. 1988. Community dynamics of stony corals (*Milleporina* and *Scleractinia*) at Key Largo National Marine Sanctuary, Florida, during 1981-1986. Proceedings, Sixth International Coral Reef Symposium, 2:237-243.

Johns, G.M., V.R. Leeworthy, F.W. Bell, and M.A. Bonn. 2001. Socioeconomic study of reefs in southeast Florida. Final Report to the Broward County Department of Planning and Environmental Protection (available at http://www.dep.state.fl.us/coastal/programs/coral/pub/Reef_Valuation_DadeBrowardPBMonroe2001.pdf) (Accessed 17 April 2012).

Keller, B.D., and S. Donahue (eds.). 2006. 2002-03 sanctuary science report: An ecosystem report card after five years of marine zoning. National Oceanic and Atmospheric Administration/Florida Keys National Marine Sanctuary, Marathon, FL.

Kinsey, D.W., and P.J. Davies. 1979. Effects of elevated nitrogen and phosphorus on coral growth. Limnology and Oceanography, 24:935-940.

Kleypas, J.A., and C.M. Eakin. 2007. Scientists' perceptions of threats to coral reefs: Results of a survey of coral reef researchers. Bulletin of Marine Science, 80(2):419-436.

Kleypas, J.A., R.A. Feely, V.J. Fabry, C. Langdon, C.L. Sabine, and L.L. Robbins. 2006. Impacts of ocean acidification on coral reefs and other marine calcifiers: A guide for future research. Report of a workshop held 18-20 April 2005, St. Petersburg, FL, sponsored by NSF, NOAA, and the U.S. Geological Survey, 88 pp.

Kramer, P.A. 2003. Synthesis of coral reef health indicators for the Western Atlantic: Results of the AGRRA Program (1997-2000). Atoll Research Bulletin, 496:1-57.

Kramer, P.R., and J.C. Lang. 2003. The Atlantic and Gulf rapid assessment protocols: Former version 2.2. Atoll Research Bulletin, 496:611-624.

Kuffner, I.B., L.J. Walters, M.A. Becerro, V.J. Paul, R. Ritson-Williams, and K.S. Beach. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Marine Ecology Progress Series, 323:107-117.

Lapointe, B.E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography, 42:1119-1131.

Lapointe, B.E., and M.W. Clark. 1992. Nutrient inputs from the watershed and coastal eutrophication in the Florida Keys. Estuaries, 15(4):465-476.

Lapointe, B.E., W.R. Matzie, and P.J. Barile. 2002. Biotic phase-shifts in Florida Bay and fore reef communities of the Florida Keys: Linkages with historical freshwater flows and nitrogen loading from Everglades runoff. In *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook*, J.W. Porter and K.G. Porter (eds.). CRC Press, Boca Raton, FL, 629-648.

Lirman, D. 2001. Competition between macroalgae and corals: Effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs, 19:392-399.

Lirman, D., and P. Fong. 1997. Susceptibility of coral communities to storm intensity, duration, and frequency. Proceedings, Eighth International Coral Reef Symposium, 1:561-566.

Lirman, D., and M. Miller. 2003. Modeling and monitoring tools to assess recovery status and convergence rates between restored and undisturbed coral reef habitats. Restoration Ecology, 11:488-456.

Lirman, D., and P. Fong. 2007. Is proximity to land-based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract. Marine Pollution Bulletin, 54:779-791.

Lirman, D., B. Orlando, S. Maciá, D. Manzello, L. Kaufman, P. Biber, and T. Jones. 2003. Coral communities of Biscayne Bay, Florida and adjacent offshore areas: Diversity, abundance, distribution, and environmental correlates. Aquatic Conservation, 13:121-135.

Lirman, D., N. Gracias, B. Gintert, A. Gleason, G. Deangelo, M. Dick, E. Martinez, and R.P. Reid. 2010. Damage and recovery assessment of vessel grounding injuries on coral reef habitats using georeferenced landscape video mosaics. Limnology and Oceanography: Methods, 8:88-97.

Lirman, D., D.S. Schopmeyer, D. Manzello, L.J. Gramer, W.F. Precht, F. Muller-Karger, K. Banks, B. Barnes, E. Bartels, A. Bourque, J. Byrne, S. Donahue, J. Duquesnel, L. Fisher, D. Gilliam, J. Hendee, M. Johnson, K. Maxwell, E. McDevitt, J. Monty, D. Rueda, R. Ruzicka, and S. Thanner. 2011. Severe 2010 cold-water event caused unprecedented mortality to corals of the Florida Reef Tract and reversed previous survivorship patterns. PLoS ONE, 6(8):e23047 (doi:10.1371/journal.pone.0023047).

Manzello, D.P., M. Brandt, T.B. Smith, D. Lirman, J.C. Hendee, and R.S. Nemeth. 2007. Hurricane-associated cooling benefits bleached corals. Proceedings of the National Academy of Sciences USA, 104:12,035-12,039.

Marszalek, D.D., G. Babashoff, M.R. Noel, and D.R. Worley. 1977. Reef distribution in South Florida. Proceedings, Third International Coral Reef Symposium, 2:223-229.

McCormick, M. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. Marine Ecology Progress Series, 112:87-96.

Miller, J., E. Muller, C. Rogers, R. Waara, A. Atkinson, K.R.T. Whelan, M. Patterson, and B. Witcher. 2009. Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs of the U.S. Virgin Islands. Coral Reefs, 27:191-195.

Miller, S.L., D.W. Swanson, and M. Chiappone. 2002. Multiple spatial scale assessment of coral reef and hard-bottom community structure in the Florida Keys National Marine Sanctuary. Proceedings, Ninth International Coral Reef Symposium, 1:69-74.

Mumby, P.J. 2006. The impact of exploiting grazers (*Scaridae*) on the dynamics of Caribbean coral reefs. Ecological Applications, 16:747-769.

Mumby, P.J. 2009. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. Coral Reefs, 28:683-690.

NMFS (National Marine Fisheries Service). 2006. Endangered and threatened species: Final listing determinations for Elkhorn coral and Staghorn coral. Federal Registrar, 71:26,852-26,861.

Nugues, M.M., and C.M. Roberts. 2003. Coral mortality and interaction with algae in relation to sedimentation. Coral Reefs, 22:507-516.

Nyström, M., and C. Folke. 2001. Spatial resilience of coral reefs. Ecosystems, 4:406-417.

Paddack, M.J., J.D. Reynolds, C. Aguilar, R.S. Appeldoorn, J. Beets, E.W. Burkett, P.M. Chittaro, K. Clarke, R. Esteves, A.C. Fonseca, G.E. Forrester, A.M. Friedlander, J. García-Sais, G. González-Sansón, L.K.B. Jordan, D.B. McClellan, M.W. Miller, P.P. Molloy, P.J. Mumby, I. Nagelkerken, M. Nemeth, R. Navas-Camacho, J. Pitt, N.V.C. Polunin, M.C. Reyes-Nivia, D.R. Robertson, A. Rodríguez-Ramírez, E. Salas, S.R. Smith, R.E. Spieler, M.A. Steele, I.D. Williams, C.L. Wormald, A.R. Watkinson, and I.M. Côté. 2009 Recent region-wide declines in Caribbean reef fish abundance. Current Biology, 19(7):590-595.

Patterson, K.L., J.W. Porter, K.B. Ritchie, S.W. Polson, E. Mueller, E.C. Peters, D.L. Santavy, and G.W. Smith. 2002. The etiology of white pox, a lethal disease of the Caribbean elkhorn coral, *Acropora palmata*. Proceedings of the National Academy of Sciences USA, 99(13):8725-8730.

Patterson, K.L., S. Shaban, L.J. Joyner, J.W. Porter, and E.K. Lipp. 2011. Human pathogen shown to cause disease in the threatened elkhorn coral, *Acropora palmata*. PLoS ONE 6(8):e23468 (doi:10.1371/journal.pone.0023468).

Paul, V.J., R. Thacker, K. Banks, and S. Golubic. 2005. Benthic cyanobacterial bloom impacts the reefs of South Florida (Broward County, USA). Coral Reefs, 24:693-697.

Porter, J.W., and O.W. Meier. 1992. Quantification of loss and change in Floridian reef coral populations. American Zoologist, 32(6):625-640.

Porter, J.W., S.K. Lewis, and K.G. Porter. 1999. The effect of multiple stressors on the Florida Keys coral reef ecosystem: A landscape hypothesis and a physiological test. Limnology and Oceanography, 44:941-949.

Porter, J.W., P. Dustan, W.C. Jaap, K.L. Patterson, V. Kosmynin, O.W. Meier, M.E. Patterson, and M. Parsons. 2001. Patterns of spread of coral disease in the Florida Keys. Hydrobiologia, 460:1-24.

Porter, J.W., V. Kosmynin, K.L. Patterson, W.C. Jaap, J.L. Wheaton, K. Hackett, M. Lybolt, C.P. Tsokos, G. Yanev, D.M. Marcinek, J. Dotten, D. Eaken, M. Patterson, O.W. Meier, M. Brill, and P. Dustan. 2002. Differential coral recruitment patterns in the Florida Keys. In T*he Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook,* J.W. Porter and K.G. Porter (eds.). CRC Press, Boca Raton, FL, 789-811.

Precht, W.F., and S.L. Miller. 2007. Ecological shifts along the Florida Reef Tract: The past is a key to the future. In *Geological Approaches to Coral Reef Ecology,* R.B. Aronson (ed.). Springer, NY, 237-312.

Richardson, L.L., and J.D. Voss. 2005. Changes in a coral population on reefs of the northern Florida Keys following a coral disease epizootic. Marine Ecology Progress Series, 297:147-156.

Rogers, C.S. 1990. Responses of coral reefs and reef organisms to sedimentation. Marine Ecology Progress Series, 62:185-202,

Rutten, L.M., M. Chiappone, D.W. Swanson, and S.L. Miller. 2009. Stony coral species diversity and cover in the Florida Keys using design-based sampling. Proceedings, Eleventh International Coral Reef Symposium, 2:800-804.

Smith, S.G., D.W. Swanson, M. Chiappone, S.L. Miller, and J.S. Ault. 2011. Probability sampling of stony coral populations in the Florida Keys. Environmental Monitoring and Assessment, 183(1-4):121-138 (doi:10.1007/s10661-011-1912-2).

Steneck, R.S., and M.N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. Oikos, 69:476-498.

Szmant, A.M., and A. Forrester. 1996. Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, and potential relationships to past and present coral reef development. Coral Reefs, 15:21-41.

Te, F.T. 1997. Turbidity and its effects on corals: A model using the extinction coefficient (k) of photosynthetic active radiance (PAR). Proceedings, Eighth International Coral Reef Symposium, 2:1899-1904.

Tilmant, J.T., R.W. Curry, R. Jones, A. Szmant, J.C. Zieman, M. Flora, M.B. Robblee, D. Smith, R.W. Snow, and H. Wanless. 1994. Hurricane Andrew's effects on marine resources. Bioscience, 44:230-237.

Tomascik, T., and F. Sander. 1985. Effects of eutrophication on reef-building corals, I. Growth rate of the reef-building coral *Montastrea annularis*. Marine Biology, 87:143-155.

Tomascik, T., and F. Sander. 1987. Effects of eutrophication on reef-building corals: Reproduction of the reef-building coral *Porites porites*. Marine Biology, 94:77-94.

Walker, N.D., H.H. Roberts, L.J. Rouse, and O.K. Huh. 1982. Thermal history of reef-associated environments during a record cold-air outbreak event. Coral Reefs, 1:83-87.

Waycott, M., C.M. Duarte, T.J.B. Carruthers, R.J. Orth, W.C. Dennison, S. Olyarnik, A. Calladine, W.J. Fourqurean, K.L. Heck, A.R. Hughes, G. Kendrick, W.J. Kenworthy, F.T. Short, and S.L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences USA, 106:12,377-12,381.