8 Ecology of Coral Reefs in the US Virgin Islands

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This chapter is dedicated to Judith and Ed Towle

8.1 Introduction

The US Virgin Islands (USVI) in the northeastern Caribbean, consist of St. Croix (207 km²), St. Thomas (83 km²), St. John (52 km²) and numerous smaller islands (Dammann and Nellis 1992). They are part of the Lesser Antilles and Leeward Islands on the eastern boundary of the Caribbean plate (Fig. 8.1). An extensive platform underlies St. Thomas and St. John and connects these islands to Puerto Rico and the British Virgin Islands. This platform extends about 32km north of the islands and then slopes gradually to depths of over 300 m and eventually descends into the 8,000 m deep Puerto Rican Trench. South of the islands, the platform extends about 13km and then abruptly drops off to over 4,000 m. St. Croix, about 60 km to the south, is on a separate platform which is much shallower than the northern Virgin Islands' platform and extends less than 5km from shore except on the east end of the island. The deepest part of the Virgin Islands Trough that separates St. Thomas and St. John from St. Croix is 4,200 m.

Fringing, bank-barrier, patch, spur and groove reefs, algal ridges, and a submarine canyon are all present in the US Virgin Islands (Ogden 1980). Corals are found from the shoreline to depths of about 50 m (Figs. 8.2–8.4). Coral communities, as opposed to true coral reefs, are found growing on boulders and mangrove prop roots in shallow water around most of the island shorelines. St. Croix, St. Thomas, and St. John have 113, 85 and 80km of shoreline, respectively (Dammann and Nellis 1992). Some reefs have grown off of rocky points and across the mouths of bays, creating salt ponds, for example, in Newfound Bay, St. John (Robinson and Feazel 1974). Reefs are absent directly offshore of the mouths of intermittent streams (Hubbard 1987). The most developed reefs in general are found off the eastern, windward ends of the islands. Algal ridges occur off the eastern end of St. Croix (Adey 1975). The steep, lower forereefs of the fringing reefs around the islands tend to have higher coral cover than other habitats at depths less than 20 m around the islands, although high coral cover is found on deeper offshore reefs such as those that are part of the Mid-shelf Reef complex and the Red Hind Bank which lie south of St. Thomas and St. John. Well-developed reefs dominated by Montastraea annularis complex (M. annularis, M. franksi, and M. faveolata) occur at depths of 33-47 m south of St. Thomas (Armstrong et al. 2006; Herzlieb et al. 2006). Sand halos from the grazing of herbivorous fishes and sea urchins, notably Diadema antillarum (zones that separate the reef from nearby seagrass beds), are often seen at the base of the lower forereefs and around patch reefs (Randall 1965; Ogden et al. 1973).

Some reefs are close to seagrass beds and mangroves, e.g., Salt River Submarine Canyon and Tague Bay Reef (St. Croix), reefs in Benner Bay and around Cas Cay (St. Thomas), and reefs in

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FIG. 8.1. Index map shows location of St. Thomas, St. John, and St. Croix relative to other islands in the wider Caribbean region

Great Lameshur Bay (St. John), although mangroves are not extensive in the Virgin Islands.

Many shallow reefs have extensive stands of dead *Acropora palmata* (elkhorn coral), although high density stands of living elkhorn occur in some areas. In general, *Montastraea annularis* complex is dominant on many mid-depth and deeper reefs (Armstrong et al. 2006, Herzlieb et al. 2006, Rogers and Miller 2006), although *Agaricia* species become relatively more abundant with depth. The deepest reefs often have higher coral cover and more plate-like coral growth.

Estimates of total reef area in the USVI (and wider Caribbean) vary widely because of differences in definitions of reefs, depth zones, and mapping approaches (Burke and Maidens 2004). The World Atlas of Coral Reefs (Spalding et al. 2001) estimates a total area for USVI reefs as 200 km², 1%

of the wider Caribbean. They define reefs as "shallow structures built by corals and other hermatypic organisms". Rohmann et al. (2005) included mangroves, seagrass beds, and other habitats in their estimates of potential coral reef ecosystem area (or extent) within the 10-fathom (~18m) depth curve and arrived at a total area of 344 km². Based on detailed mapping from aerial photographs and, like Rohmann et al. (2005), including other associated habitats, Kendall et al. (2001) estimated a total reef area of 485 km² to a depth of 30 m. US Virgin Islands coral reefs also include large areas of mostly unexplored reefs at depths below 30m (Armstrong et al. 2006). In 2005, multibeam and ROV video surveys conducted off the north side of Buck Island, St. Croix, revealed colonies of the deep water coral Lophelia at depths greater than 1,000 m.



FIG. 8.2. Virgin Islands Coral Reef National Monument

8.2 History of Research

Early studies of coral reefs and reef organisms in the USVI, as elsewhere before the development of snorkeling and scuba gear, were restricted to what someone pulled up in a dredge or found in very shallow water near shore. Bayer (1969) reviewed findings from numerous research cruises beginning in the late 1800s, although many focused more on Puerto Rico than the USVI. HMS *Challenger* crossed the Atlantic and reached St. Thomas in 1873. The ship's scientists collected 40 species of fishes, corals, and other organisms, including seven new species. Among these were *Diadema setosum* (presumably *D. antillarum*), *Madrepora palmata* and *Madrepora cervicornis* (*Acropora palmata* and *Acropora cervicornis*). A few references to corals, brittle stars, and other organisms collected in



FIG. 8.3. Map of St. Croix shows location of coral reefs

the 1840s from the USVI appear in Wolff (1967). Early descriptions of fishes from Puerto Rico and the Virgin Islands appear in Evermann and Marsh (1902) and Nichols (1929, 1930). Fiedler and Jarvis (1932) described the VI fishery in 1930, but few other substantive reports on marine resources were written until those by Jack Randall and his associates beginning in the late 1950s and 1960s.

Although some scientists had hoped for the establishment of a permanent biological research station in the Danish West Indies in the early 1900s (Wolff 1967), the first station was established at the Virgin Islands Environmental Resource Station (VIERS) in Lameshur Bay, St. John, in 1966. From 1958 to 1961, Randall and others were based there. A comprehensive review by Dammann (1969) includes studies of St. John reefs in Chocolate Hole and Mary Creek (Stoeckle et al. 1968 cited in Dammann 1969). Some of the early studies done in the USVI included some of the first experimental manipulations such as tagging of fishes (Randall 1962), use of artificial reefs (Randall 1963), and fish exclusion cages (Earle 1972, Mathieson et al. 1975).

The Caribbean Research Institute of the College of the Virgin Islands (now University of the Virgin Islands, UVI) produced many reports in the 1970s and 1980s, primarily focusing on water quality. Island Resources Foundation prepared an inventory of the marine environments in the USVI (IRF 1977) with an emphasis on oceanography, climatology, and marine ecology.

Research increased following the establishment of Fairleigh Dickinson University's West Indies Laboratory (WIL) on St. Croix, in 1971. The faculty and students produced numerous papers (>300 papers plus numerous technical reports) including some which provided a baseline for



FIG. 8.4. Map of St. Thomas shows location of coral reefs

long-term monitoring (see annotated bibliography of papers on research at Buck Island Reef National Monument by Gladfelter 1992). Research conducted at WIL includes a variety of early studies, many of which stimulated subsequent research on key issues in tropical marine ecology including herbivore–plant interactions, coral morphology/physiology/ecology, chemical and mechanical defenses, seagrass ecology, invertebrate ecology, fish community structure, recruitment and dispersal in reef fishes, resource partitioning in reef fishes, behavioral ecology of fishes, microbiology, nutrient dynamics and productivity.

A series of projects (Tektite I and II) was conducted by scientists operating out of an underwater laboratory/"habitat" in Great Lameshur Bay, St. John, in 1969 and 1970 (Collette and Earle, 1972; Earle and Lavenberg 1975; see textbox). Later, from 1977 to 1989, the West Indies Laboratory and the National Oceanic and Atmospheric Administration (NOAA) ran a saturation diving program to support research out of two other underwater laboratories (first Hydrolab and then Aquarius) in Salt River Canyon, St. Croix (see Appendix A in Kendall et al. 2005). There were studies of fishes, fish behavior, corals, squids, octopuses, crinoids and ophiuroids, black corals, gorgonians, sponges, seagrasses, queen conch, and coral metabolism.

In 1981, three dives were made in the *DSRV ALVIN* to 2455–3950m depth along the northern St. Croix slope, and a strong connection between the shallow insular shelf and deep basin was discovered (Hubbard et al. 1981). Shallow-water sediments and detrital seagrasses were collected, along with three species of holothurians and two species of urchins. The analysis of stable carbon C^{13} : C^{12} ratios of seagrass detritus and animal tissue revealed that a significant proportion of the nutrition of both groups is derived from detrital seagrasses either by direct consumption or by feeding on sediments enriched by decomposed seagrasses. One urchin species fed almost exclusively on *Syringodium* (Suchanek et al. 1985).

In 1985, the submersible Johnson Sea-Link II was used to make observations and record video of areas 36–758 m deep off of St. Thomas, St. Croix, and St. John, partly to determine the potential for a deep water commercial fishery and to learn more about the deepwater corals and macroalgae (Nelson and Appeldoorn 1985). In one dive off the 100 fathom contour south of St. John, scientists described "a spectacular wall with ambient light penetrating to ca. 272 m (800')" and provided a list of fishes that were observed.

The Virgin Islands Resource Management Cooperative (VIRMC), established in 1983 with support primarily from the National Park Service and under the direction of Island Resources Foundation, produced a series of reports that established baseline data for the USVI and British Virgin Islands (see Rogers and Teytaud 1988). These included descriptions and maps of bays and fish habitats within Virgin Islands National Park (VINP) and Buck Island Reef National Monument (BIRNM) (Anderson et al. 1986, Beets et al. 1986, Boulon 1986a, b), assessment of fish and shellfish stocks in the VINP and BIRNM (Dammann 1986, Tobias et al. 1988), early fish and reef monitoring efforts (Boulon et al. 1986, Rogers and Zullo 1987), and observations of white band disease on elkhorn coral (Davis et al. 1986).

8.2.1 Mapping of USVI Coral Reef Ecosystems

Mapping of the coral reef ecosystems found around the US Virgin Islands has a long history ranging from simple visual assessments by divers on tow boards to analysis of multispectral imagery. Over time the maps of corals and other benthic habitats, such as seagrass and algae, have increased in spatial resolution and thematic content. The first map of reefs, seagrass beds, and sand bottom to a depth of about 20 m around St. John was produced in 1958 from observations made by scientists towed on a sled behind a boat (Kumpf and Randall 1961). Maps of St. Croix reefs are presented in Ogden et al. (1972). Rosemary Monahan and Betsy Gladfelter made a detailed map of Buck Island in 1977 (Gladfelter et al. 1977). As part of the VIRMC studies, maps of St. John and Buck Island were produced from visual interpretation of aerial photos by Beets et al. (1986), Boulon et al. (1986), and Anderson et al. (1986). In 2000, an extensive seafloor mapping project around all of the USVI was completed by NOAA (Kendall et al. 2001). This project mapped 485 km² of benthic habitats in the USVI to a nominal depth of 30m based on visual interpretation of color aerial photography (Jeffrey et al. 2005). Analyses of these maps revealed that coral reef and hard-bottom habitats make up 61%, submerged aquatic vegetation 33%, and unconsolidated sediments 4% of the shallow water areas (Kendall et al. 2001). Most recently, Harborne et al. (2006) collected 410 km² of multispectral imagery around St. John and St. Thomas and generated benthic habitat maps using unsupervised classification in conjunction with contextual decision rules (Mumby et al. 1998) to classify the digital imagery. Contextual decision rules are defined by the user to aid in classifying the imagery based on features within the imagery, such as dramatic changes in bathymetry and the presence of bright reflectance areas indicating sand habitat.

All of the above mapping studies addressed the shallow water (<30m) coral reef ecosystems surrounding the USVI, but several sonar-based efforts have recently characterized deeper reefs in the USVI (20-1,000m). Sonar is useful for mapping benthic habitats that are too deep or turbid to map using either aerial or satellite based sensors. Side scan sonar has been used by the Caribbean Fishery Management Council to map the Marine Conservation District south of St. Thomas. Recently, the NOAA Biogeography Team (http://ccma.nos.noaa.gov/ecosystems/coralreef/usvi_nps.html) has collected multibeam sonar data and underwater video to define the bathymetry and associated habitats for selected areas of the USVI with emphasis on Virgin Islands Coral Reef National Monument (VICRNM) and Buck Island Reef National Monument. These data are currently being processed into digital bathymetry maps, and analysis of the "backscatter" return signal from

the sonar is being classified into benthic habitats and confirmed by the visual inspection of underwater video. Extensive sidescan sonar data have been collected south of St. John to the shelf edge and in select areas south of St. Thomas. Detailed geo-referenced bathymetric maps exist for most of the marine protected areas and seasonally closed areas along the shelf margin such as the Marine Conservation District (41 km² area), the Grammanik Bank (1.5 km²), and Lang Bank (12 km²). Between 2004 and 2006, NOAA's Research Vessel Nancy Foster conducted extensive sea floor mapping around Buck Island, Salt River Bay, and Lang Bank (St. Croix). In 2006 NOAA collected 143.3 km² of multibeam coverage from 14.7 m water depth to 1,000 m. Total ROV data for the mission included 22 linear km of video transects from 20 to 830m water depth. For St. Croix, approximately 81 km² of multibeam bathymetry and backscatter data were collected from Salt River to the northeast end of Lang Bank north of the island to greater than 1,000 m (Battista 2006).

8.2.2 Long-term Monitoring

Over the last 20 years, there has been an increasing investment in long-term monitoring in the USVI by many different agencies. The National Park Service (NPS), University of the Virgin Islands (UVI), US Geological Survey (USGS), the Division of Fish and Wildlife (DFW), the West Indies Laboratory (until it was closed after Hurricane Hugo in 1989), the National Oceanic and Atmospheric Administration (NOAA), The Nature Conservancy (TNC), The Ocean Conservancy (TOC), the National Science Foundation, the Sea Grant Program of the University of Puerto Rico, and others have conducted or supported research on coral reefs in the USVI. As a result, some of the oldest continuous records of anywhere in the Caribbean on water quality, coral reefs, and reef fishes are available for the USVI. Over the last few decades there has been increasing use of technology, including GPS, digital video cameras, in situ recording stations such as those in the Integrated Coral Observatory Network, Acoustic Doppler Current Profilers, CTD (Conductivity, Temperature, and Depth) sensors, ROVs, and multibeam sonar.

Extensive long-term monitoring of coral reefs has been augmented by experimental research

including studies of ecological processes such as coral and fish recruitment (Edmunds 2000, 2004, 2006; Nemeth 1998, Tolimieri et al. 1998, Rogers et al. 1984, Rogers and Garrison 2001), herbivory (Carpenter 1990a, b; Steneck 1993), calcification and coral growth rates (Gladfelter 1982, 1984, Gladfelter et al. 1978), coral and reef metabolism (Adey et al. 1981, Rogers and Salesky 1981).

The establishment of relatively large marine reserves off St. Thomas in 1999 and St. John and St. Croix in 2001 (see below) has led to efforts to evaluate the effectiveness of these areas in reversing degradation of marine resources in the USVI.

Island Resources Foundation has assembled and maintained a comprehensive library with references pertaining to research and resource management in the USVI and wider Caribbean (IRF 1989, www. irf.org).

8.3 Physical Oceanography/ climate

Easterly trade winds predominate in the USVI. The wind varies in direction and intensity, with maximum winds usually occurring in winter and minimum in the fall. Hurricanes usually occur between the months of June and November, with a peak in August and September (US Naval Oceanographic Office 1963, Hubbard 1989, Kendall et al. 2005). Rainfall is variable with no well-defined wet and dry seasons, although most rainfall occurs between August and December (see NOAA Climatological Bulletin). Rainfall can be very intense, with significant amounts of rain falling during very short time periods. For example, on the north side of St. John, in April 1983, 19 in. (483 mm) of rain fell in 21 h; in November 2003, 11.2 in. (284 mm) fell in 144 h with a total of 23.79 in. (604 mm) for the month, one of the wettest months recorded in the past several decades. Annual totals from 1984 to 2005 for this site ranged from 27.2 (691) to 69.6 in (1768 mm). (R. Boulon, unpublished data 2006). Rainfall can be localized and is often associated with tropical storms and hurricanes. Although there are no permanent streams or rivers, even brief (but intense) rains result in runoff from the intermittent streambeds on the islands.

Coastal currents within the USVI are usually less than 10 cm/s (range: 0–40 cm/s) and are primarily

Tektite Program

As early as 1972, Great Lameshur Bay was referred to as "one of the best known marine communities in the world" (Collette 1972) because it was the focus of a great deal of research by Jack Randall (e.g., Randall 1963, 1965) and the site of the Tektite underwater habitat program (Fig. 8.5).

The Tektite Program took place in Great Lameshur Bay in 1969 and 1970 (Collette and Earle 1972; Earle and Lavenberg 1975). Divers lived in an underwater habitat at a depth of 15 m for up to 60 days. Although the objective of the program was to learn how divers could function safely and effectively under saturation conditions and not to conduct an integrated study of a single coral reef or provide a baseline for future research (Collette 1972), some of the papers provide intriguing insights into changes that have taken place at Tektite Reef in the last 4 decades. One scientist noted "maximum visible range exceeded 30m on exceptionally clear days, and rarely fell short of 10m under the worst conditions" (Clifton and Phillips 1975). Now underwater horizontal visibility rarely exceeds 10-15 m.

Some observations made during Tektite missions show how fish assemblages have changed. For example, Collette and Talbot (1972) noted seven species of groupers, some quite numerous, all of which are now rarely seen. (It is currently rare to see even a single Nassau grouper during an hour dive in most locations). They noted that most of the fishes they saw on their study reefs were benthic carnivores, particularly the larger groupers, whereas now most of the fishes at the Tektite Reef are herbivores. They reported that yellow-tail snappers and bar jacks (schools of several of these up to 20 cm long) were the most common predators near the Habitat. Schools of up to 200 lane snappers were seen. Threespot damselfish (*Stegastes planifrons*) which are now very abundant (J. Beets and A. Friedlander, personal communication 2007) were only "moderately common" when the Tektite missions were conducted.

Some of the projects involved experimental manipulation, such as the use of cages to exclude herbivorous fish from small areas on the reef (Earle 1972; Mathieson et al. 1975). Earle (1972) found 35 species of herbivorous fishes in 14 families, and recorded feeding behavior. She also found 154 species of marine plants, including 26 never reported before from the USVI. Other projects included several on fish behavior, cleaner shrimps, and lobsters (Mahnken 1972; Smith and Tyler 1972; Herrnkind et al. 1975).

Tektite Reef is now the subject of long-term monitoring by NPS and other researchers and has been the focus of intensive research on changes in coral cover resulting from bleaching and disease (see below).



FIG. 8.5. The Tektite underwater habitat on a barge in Great Lameshur Bay (Photo: G. Davis)

driven by wind and tides. Within the semi-enclosed bays of the islands, the currents are dominated by the tides and secondarily by entrainment into the bays from the eastern ends and detrainment at the western ends of the bays. Entrainment and detrainment into and out of the bays are influenced by the easterly trade winds that force surface currents to advect from east to west (Halliwell and Mayer 1996). The complex components of current regimes near the coasts and especially in embayments lead to complex retention/dispersal dynamics of larval transport (Cowen 2002). In offshore waters surface currents (5 m depth) average 23 cm/s but can range from 12 to 65 cm/s whereas near the bottom (30 m depth) current speeds average 16 cm/s and range from 10 to 27 cm/s [from University of the Virgin Islands (UVI) Acoustic Doppler Current Profiler (ADCP) data from November 2005 to March 2006]. During the passage of Hurricane Hugo (1989), the most severe hurricane to ever hit the USVI, currents and water levels were measured in Salt River Submarine Canyon, on the north shore of St. Croix. Currents reached a maximum velocity of 5 m/s (9.7 knots) (Hubbard et al. 1991).

Tides within the region are mixed semi-diurnal, and ranges typically are <20 cm (Hubbard 1989), but can reach 40 cm during spring tides. Circular tidal currents dominate the unidirectional winddriven currents during the full and new moons. At other times, wind-driven currents dominate the tidal influences (http://tidesandcurrents.noaa.gov, N. Idrisi, personal communication 2007).

The University of Miami is developing the HYCOM-ROMS general circulation ocean model for the Interamerican Seas region that includes the Caribbean (see Cowen et al. 2000, 2006; Kourafalou et al. 2006). To ground-truth the model for the Virgin Islands and increase the resolution, the University of the Virgin Islands is using data from ADCPs deployed in 2005–2006 and bathymetry data from the Environmental Protection Agency (EPA) research cruise in 2006 (N. Idrisi, personal communication).

The reefs around the Virgin Islands are influenced by freshwater lenses migrating from the Amazon and Orinoco Rivers as anticyclonic rings. These signals peak in June to August (Hu et al. 2004). UVI conductivity-temperature-depth (CTD) data indicate the salinity signal from the south of St. Thomas and St. John (Caribbean side) is lower (34–35 ppt) than to the north of the islands (Atlantic side: 36 ppt). Along with lower salinity waters, these anticyclonic rings are nutrient-rich with greater ocean color signals as seen from SeaWiFS data (Hu et al. 2004).

In 2002, NOAA installed a Coral Reef Early Warning System Station (CREWS, now referred to as ICON for Integrated Coral Observing Network) near the west wall of Salt River Canyon, St. Croix. This station provides hourly data on wind direction, wind speed, air and water temperature, salinity, photosynthetically active radiation (PAR), and ultraviolet radiation at the water surface and 1 m depth (see www.coral.noaa.gov/prototype). Recently, NOAA installed a tsunami warning system on St. John.

The USVI Government Department of Planning and Natural Resources collects water quality data quarterly from 135 stations around St. Thomas, St. Croix, and St. John. The National Park Service collects data quarterly from 16 stations around St. John. All of these data are entered into the Environmental Protection Agency's database, STORET.

One of the longest in situ water temperature records is from Great Lameshur Bay, a semienclosed bay on the south side of St. John, where data have been collected from 9 and 14 m for almost 20 years. Here mean monthly seawater temperature has increased gradually by 0.6°C/decade since 1989, and the number of days exceeding 29.3°C, the bleaching threshold defined by NOAA for the Virgin Islands, has increased as well (Edmunds 2004). In 2005, sea water temperatures exceeding 30°C were associated with the most severe bleaching event on record in the USVI. Data on subsurface sea water temperature from Saba Island south of St. Thomas have been collected since 1990 and compared to AVHRR satellite records (Quinn and Kojis 1994a, b). Water temperature data from the USVI are available from near the surface to a depth of 40m. Along the shelf edge south of St. Thomas at 40 m depth sea water temperature averaged 27.1°C and ranged from 26°C to 29°C from February 2003 to May 2005 (Nemeth et al. 2007).

Dust from the Sahel/Saharan region in Africa affects the USVI frequently, primarily in the summer months (Prospero and Lamb 2003; Griffin et al. 2003). The possible role of African dust in causing reef degradation is the subject of ongoing research (Shinn et al. 2000; Garrison et al. 2003; Griffin et al. 2003). Large dust clouds can dampen hurricane activity (Dunion and Velden 2004).

Volcanic ash from the active Soufriere Hills volcano on Montserrat periodically reaches the USVI. Effects on marine ecosystems are not known.

8.4 Biodiversity of USVI Coral Reefs

Similar to other Caribbean reefs, reefs in the USVI have over 40 species of scleractinian corals and three species of *Millepora* (Appendix 8.2). A comprehensive inventory of octocorals, sponges, and other invertebrates has not been prepared, but lists from particular locations are found in several papers, including Gladfelter (1993a, b), Kendall et al. (2005), and Idjadi and Edmunds (2006).

Randall's "Caribbean Reef Fishes" (1968) describes 300 fish species, over half of which were collected and photographed from the Virgin Islands. Clavijo et al. (1980) listed 400 species of fishes in 93 families from around St. Croix. NOAA fish surveys from 2001 to 2006 list a total of 215 fish species from St. John and 202 fish species from St. Croix (combined 236 species) from visual censuses (http://www.ccma.nos.noaa.gov/ecosystems/coralreef/reef_fish.html). A recent study of sharks and shark nursery habitats in the USVI lists nine shark species: great hammerhead, scalloped hammerhead, Caribbean reef, tiger, blacktip, lemon, blacknose, Caribbean sharpnose and nurse (DeAngelis 2006). Great white, thresher, white-tip, and mako sharks have also been reported from USVI waters. Several whale sharks were seen south of St. Thomas and St. John in 2006.

Buck Island Reef Sea Turtle Research: Program Summary

There are very few places in the Caribbean where any large numbers of hawksbill turtles (Eretmochelys imbricata) remain today (NMFS/USFWS 1993) (Fig. 8.7). Today throughout their range, hawksbill turtles nest in low density; nesting aggregations consist of a few dozen to at most a few hundred individuals (NMFS/USFWS 1993). Buck Island Reef National Monument (BIRNM) is one of the most significant areas under US jurisdiction where hawksbill sea turtles are still nesting in any numbers (50-75/season) (data as of 2006). The Hawksbill Recovery Plan (NMFS/USFWS 1993) identified BIRNM as an index beach for hawksbill turtle recovery in the Eastern Caribbean. The Monument also provides critical habitat for post-pelagic to subadult sea turtles that shelter in the reefs and feed on zoanthids, sponges, and seagrasses.

Endangered hawksbill sea turtles, threatened green sea turtles, occasional leatherback turtles and most recently loggerheads nest on Buck Island. Throughout the peak summer months a saturation tagging program records nesting behavior and fidelity, remigration period, individual fecundity, size, and hatching and emergence success. Tissue samples are taken for genetic analysis. Threats to hatching success such as predation, poaching, inundation by seawater, and desiccation are monitored and mitigated (Phillips and Hillis-Starr 2002). In the course of 19 years of conducting basic research on hawksbill sea turtle nesting behavior, several other projects have been initiated including radio-, sonar-, and satellite telemetry to determine the movements of nesting hawksbill turtles during their inter-nesting period, and after nesting. Buck Island was the site of a study to develop a non-lethal method of determining the sex of sea turtle hatchlings. Incubation temperature, not X or Y chromosomes, determines the sex of sea turtles, and the results of this study along with records of nesting beach temperatures, enables determination of the sex ratio of hatchlings without sacrificing them.

Buck Island nesting hawksbill turtles are not part of a larger population, but genetically distinct and isolated from hawksbill turtles nesting in Puerto Rico, Antigua, and Barbados. However, they show strong genetic identity with hawksbill turtles sampled in Belize and Nicaragua; additionally, three tag recoveries for Buck Island nesting hawksbill turtles are from Central America and Cuba.

Hawksbill turtles may take 30 years to reach sexual maturity. In light of the increasing number of new recruits encountered from 1996 to 2006, Buck Island may be starting to see the results of 30 years of nesting beach protection and conservation. The genetic analyses indicate that the island's nesting hawksbill population may be distinct in the Caribbean and therefore should be afforded as much protection as possible.



FIG. 8.6. Brokenbar blenny, *Starksia smithvanizi*. This small blenny (15–25 mm total length) was first recognized as a new species as a result of studies conducted at Buck Island Reef National Monument



FIG. 8.7. A hawksbill sea turtle (Photo: C. Rogers)

In a study of cryptic fishes around Buck Island, St. Croix, using controlled rotenone treatments, Smith-Vaniz et al. (2006) found 228 species (in 55 families), with 60 of these documented for the first time from St. Croix. These included 13 additional species in the family Gobiidae, 12 in the Labrisomidae, five each in the Chaenopsidae and Bythitidae, and four each in the Gobiesocidae and Ophidiidae (Fig. 8.6).

Earle (1972) recorded 154 species of algae from Great Lameshur Bay, St. John, including 26 never reported before for the US VI. Gladfelter and Gladfelter (2004) documented 164 species of molluscs (seashells) from Southgate Beach, St. Croix. Four species of sea turtles are found in the USVI, with hawksbills and greens the most abundant (see Side bar).

In 2005, a wide diversity of habitat types was characterized from multibeam and ROV data off of Buck Island. Seafloor features included rock precipices, ledges, limestone caves, boulders, rock outcroppings, and flat expanses of mud. The biota below 200m, never visually characterized before, included *Lophelia* coral, black coral, sea whips, feather stars, sea pens, sea anemones, sea stars, brittlestars, urchins, sponges, isopods, sea cucumbers, albino lobsters, shrimps, crabs, conch, Orange Roughys, roundnose grenadiers, tripod fish, and several types of snappers. Especially useful guides to the identification of marine organisms in the USVI include Gladfelter (1988), Suchanek (1989), and Beets and Lewand (1986), and for the Caribbean in general Warmke and Abbott (1962), Voss (1976), Kaplan (1982), Colin (1978), Humann and DeLoach (2002a, b, c), and Littler and Littler (2000).

8.5 Marine Protected Areas in the Virgin Islands

Many Marine Protected Areas (MPAs), including some marine ("no-take") reserves, are found in the USVI. Buck Island Reef National Monument (BIRNM) was established in 1961 and consisted

Federal Marine Reserves/National Monuments

In 1999, former Secretary of the Department of the Interior Bruce Babbitt conceived of a marine protected area for the Virgin Islands that would encompass all representative ecosystems and provide further protection for the area's marine resources. The original proposal recommended a marine protected area of about one-million acres (404,700 ha). When the Virgin Islands Coral Reef National Monument (VICRNM) was ultimately established in 2001, it included 12,708 acres (1,096 ha) of submerged land. At the same time Buck Island Reef National Monument (BIRNM) was expanded from 880 (356 ha) to 19,015 acres (7,695 ha). The process which resulted in the VICRNM and the expanded BIRNM is complex.

In 1974 the Submerged Lands Act transferred all submerged lands out to three nautical miles (5.6 km) from the US Government to the USVI. However, within the Act, there was an exception for "submerged lands adjacent to US owned above-tideland uplands" out to the extent of the 5.6 km (3 nm) Territorial Sea. As the National Park Service owned coastlines around St. John and Buck Island at that time, this exception applied. The Minerals Management Service was asked in 1999 to determine what this included, and they mapped approximately 37,000 acres (14,974 ha) of submerged lands around St. John, Buck Island and Water Island that met this exception. Only the submerged lands contiguous with NPS lands were considered for monument status.

In 2001 President William Clinton used the Antiquities Act of 1906 which allows for Presidential Proclamation of National Monuments to establish VICRNM and expand BIRNM. These proclamations were challenged twice by the USVI Governor and Delegate to Congress but were upheld both times by the US General Accounting Office in late 2002. Rules and regulations for both monuments were enacted in May 2003. Both BIRNM and VICRNM are no-take/ no-anchoring areas with the exception of regulated harvest of Blue Runner and baitfish (two migratory species) in VICRNM. One result of using the Submerged Lands Act exception to map the monument areas is that the boundaries of these areas are defined politically rather than ecologically. Therefore, some of the essential marine habitats necessary for ecosystem balance are not included in the monuments. This also produced non-contiguous sections of VICRNM on the south side of St. John due to private coastal lands. This issue is being resolved by exchanging an equivalent amount of submerged land within the eastern boundary of VICRNM for the USVI owned strip of submerged lands in the middle of the monument. This will eliminate confusion for users, improve enforcement, and include a significant reef structure within the VICRNM.

The Marine Conservation District (MCD), also referred to as the Red Hind Bank, 10km south west of St. Thomas encompasses deep water (35-50 m) shelfedge habitats and contains extensive well-developed Montastraea spp. dominated coral reefs, patch reefs, colonized hard-bottom, algal plains and sand flats. Two deep-water coral ridges 50-100 m wide and over 15 km long run parallel to the southern edge of the insular platform. The outer ridge is immediately adjacent to the drop-off and varies between coral reef and colonized hard bottom habitats. The inner ridge about 300m from the drop-off is wider and deeper than the outer ridge and is primarily coral reef habitat. The two coral ridges are separated by a deeper 5-100 m wide channel (50 m) composed of sand, patch reef, and rubble (Nemeth et al. 2007). Patch reef and soft bottom habitats extend for several km north of the inner ridge before giving way to extensive Montastraea reefs especially near the northwestern corner of the MCD. The Red Hind Bank was closed seasonally in December 1990 and established as the permanently closed Red Hind Bank Marine Conservation District (MCD) in December 1999 (Federal Registers 55(213), November 2, 1990 and 64(213), November 4, 1999, respectively).



FIG. 8.8. Buck Island Reef National Monument

of 356ha. Virgin Islands National Park (VINP) was established in 1956, with the marine portions (2,286ha) added in 1962. In 1999 the Marine Conservation District (MCD, also known as the Red Hind Bank) was established to protect 41 km² of deep reef habitats south of St. Thomas. The MCD includes an important spawning aggregation site of the red hind grouper. Local and federal fisheries regulations and small marine reserves such as the Marine Garden at BIRNM (188ha) and Trunk Bay (21 ha) were not effective in protecting marine resources in the Virgin Islands (Rogers and Beets 2001; Rogers et al. 2007), and in 2001 President Clinton established the Virgin Islands Coral Reef National Monument (VICRNM) and expanded BIRNM by 7,339 ha (total now is 7,695 ha) (See textbox; Figs. 8.2 and 8.8). Although the boundaries were based on ownership of federal property

and not on ecological considerations, the monuments are relatively large and could play a vital role in reversing marine resource degradation in the USVI (Rogers et al. 2007).

In addition to these federal MPAs, there are several territorial MPAs, most notably the recently established East End Marine Park (Fig. 8.9) and several seasonally closed areas (see textbox).

8.6 Changes in USVI Coral Reefs

Coral reefs in the Virgin Islands have changed dramatically in the last three decades. Insights into these changes come from long-term monitoring of sites ranging in depth from sea level to 40 m. Live coral cover has declined; coral diseases have become more numerous and prevalent; macroalgal cover

East End Marine Park, Marine Reserves and Wildlife Sanctuaries, and Salt River Bay National Historic Park and Ecological Preserve

The East End Marine Park (EEMP) was established by the 24th Legislature of the USVI in 2003 through Act No. 6572 of the VI Code Title 12, Chapter 1. This act not only established the EEMP but also gave the Virgin Islands Department of Planning and Natural Resources (DPNR) the authority to establish other Territorial Marine Parks. The DPNR Coastal Zone Management Division has management responsibility for the EEMP. The legislative authority establishing the park states that its goal is "to protect territorially significant marine resources, promote sustainability of marine ecosystems, including coral reefs, seagrass beds, wildlife habitats and other resources, and to conserve and preserve significant natural areas for the use and benefit of future generations...." The website for the EEMP is www.stxeastendmarinepark.org.

A comprehensive management plan for the park was developed and formally adopted in 2002. The plan was formulated by the Virgin Islands chapter of The Nature Conservancy (TNC) based on a participatory process involving many different stakeholders on St. Croix.

EEMP is comprised of four different types of managed areas or zones. These are: Recreational Management Areas, a Turtle Wildlife Preserve Area, No-take Areas, and Open Areas. Allowable activities in the Recreational Management Areas include snorkeling, diving, catch and release fishing, cast net bait fishing and boating. The primary intention of the Turtle Wildlife Preserve Area is to protect index turtle nesting beaches (as defined in speciesspecific Recovery Plans) for green, hawksbill, and leatherback turtles. A prohibition on the use of gill and trammel nets in this area also offers protection for turtles in the park waters. Approximately 8.6% of the EEMP is made up of No-take Areas established to protect critical habitats for important reef species. All commercial and recreational fishing is prohibited within these areas. Over 80% of the EEMP has been designated as Open Area where existing USVI fishing and other marine activity regulations apply and the removal of coral or live rock is prohibited.

There are five Marine Reserve and Wildlife Sanctuaries (MRWS) in the USVI. Three of these sites are located on the east end of St. Thomas, and St. Croix and St. John each have one. All five sites were authorized by both the Wildlife and Marine Sanctuaries Act of 1980 (Act No. 5229) and the Virgin Islands Code Title 12, Chapter 1, and were officially designated between 1992 and 2000. The Department of Planning and Natural Resources is responsible for the management of these protected areas which have one primary goal in common: the protection of fish and wildlife resources and the habitats on which they depend.

The Compass Point Pond MRWS on St. Thomas was established in 1992 to protect this important wetland area on St. Thomas and prevent any further degradation of its natural resources. The pond is connected to the sea and fringed with mangroves that filter sediment from a large watershed. All plants and animals are protected, and alterations to habitat are prohibited.

The Cas Cay/Mangrove Lagoon MRWS was established in 1994 in Benner Bay, St. Thomas, to protect essential habitat for juvenile reef fish, lobsters, birds and wetland plants and animals and to support the restoration of these populations within the protected area. It is illegal to take any living organism from this protected area with the exception of baitfish within 50 ft of the shoreline of Cas Cay by permit only.

The St. James MRWS, established in 1994 on the southeast coast of St. Thomas, includes all the waters from Cas Cay around Great St. James Island to Cabrita Point. It is closed to all harvest of marine species except for baitfish and fish caught by hook and line.

The Frank Bay MRWS (2000) essentially protects the salt pond at Frank Bay on St. John. It is illegal to harvest or disturb any wildlife or plant species around or in the pond, similar to the Compass Point MRWS.

The Salt River MRWS on St. Croix was established in 1995. Proposed Rules and Regulations were signed in 2002. These regulations make it unlawful to remove any marine or other wildlife from the Salt River MRWS or to anchor outside of designated areas.

Although the regulations, or proposed regulations, that exist for each of these sites are comprehensive and seek to effectively protect marine and wildlife resources, none of these sites has a complete management plan, and no staff is dedicated to education and management of this MRWS system. There is little enforcement of the regulations described above.

The Salt River Bay National Historic Park and Ecological Preserve, established in 1992, is co-managed by the federal and territorial government. It is comprised of 224 acres of land. The NPS area is part of the larger Salt River Marine Reserve and Wildlife Sanctuary established in 1995 and is jointly managed by the NPS and the VI Government. Whereas the NPS has jurisdiction over the land under its ownership, DPNR has jurisdiction over adjacent wetlands and the marine portion of the protected area.

Seasonally Closed Areas

The Grammanik Bank is located east of the MCD and is a relatively small and recent (2005) seasonal closure designed to protect a multi-species spawning aggregation site used by a variety of groupers (yellowfin, Nassau, tiger, yellowmouth) and snappers (cubera, dog and schoolmaster). A similar reef structure to the MCD (i.e., two parallel Montastraea coral ridges) exists at the Grammanik Bank in 35–50 m depth. Below 55 m depth large patch reefs of Agaricia spp. extend beyond scuba diving limits (R. Nemeth, personal observation 2006). East and west of the Gammanik Bank, the ridges transition into a shallower (30m) hard bottom habitat. The Grammanik Bank was closed to all fishing, except for migratory pelagics, from February 1 to April 30 each year, and all bottom fishing gear, including trap fishing, is prohibited year round (Federal Register 70(208), October 28, 2005).

The Lang Bank seasonal closure is composed largely of colonized hard-bottom and patch reef habitats. Near the eastern margin of the shelf and about 16km east of St. Croix, *Montastraea* -dominated coral reef ridges exist on old spur and groove formations in 30–40 m depth. A deep-water basin (50–60 m deep) separates the inner and the outer coral ridges (Nemeth et al. 2007). The eastern end of Lang Bank is closed seasonally from December 1 to February 28 to protect a red hind spawning aggregation. This closure was implemented December 1993 (Federal Register 58(197), October 14, 1993). On October 28, 2005 (Federal Register 70(208)), the Lang Bank seasonally closed area was closed to all bottom fishing gear year-round.

The Mutton Snapper seasonal closure, which was established in 1993 to protect a mutton snapper spawning aggregation, is located off the southwest corner of St. Croix and encompasses 2.5 km^2 of both territorial and federal waters. The habitats within the closure are composed of linear reefs, patch reefs, hardbottom and sand habitats from 20 to 30 m deep. The closed season extends from March 1 to June 30 each year and was designed to protect a mutton snapper spawning aggregation, although enforcement is lacking and poaching prevalent (Federal Register 58(197) October 14, 1993).

To further protect several species during their seasonal spawning aggregations, harvest of yellowfin, tiger and yellowmouth grouper and mutton snapper are prohibited in federal and territorial waters during most or all of the period of the seasonal closures (Federal Register 58(197); VI Rules and Regulations T.12, Chapter 9A). Harvest of Nassau grouper is prohibited year round in federal and territorial waters (VIRR T.12, Chapter 9A).



FIG. 8.9. St. Croix East End Marine Park Zonation (DPNR)

has increased; fish of some species are smaller, less numerous or only rarely seen; and the longspined black sea urchins *Diadema antillarum* are less abundant.

Coral cover has declined on most if not all reefs in the USVI for which there are quantitative data. In the 1970s and 1980s coral cover on some reefs was over 40% and even higher in some shallow elkhorn coral zones (Gladfelter et al. 1977, Gladfelter 1982, Rogers et al. 1983, Edmunds 2002). At that time, algal turf typically made up a large component of the benthic cover, while macroalgae were absent or scarce. Hurricanes caused significant losses in coral cover and changes in the physical structure of many reefs (Hubbard et al. 1991). For example, Hurricane David (1979) caused a reduction in mean coral cover along transects at Flat Cay Reef (St. Thomas) from 65% to 44% (Rogers et al. 1983). In addition, Hurricane Hugo (1989) caused a 30-40% decline in coral cover along transects and within quadrats in Great Lameshur Bay, St. John (Edmunds and Witman 1991, Rogers et al. 1991).

By the 1990s, many long-term monitoring sites had coral cover of about 25% or less, and macroalgal cover, although variable, often reached much higher values than in the past. Coral cover continued to decline or remain stable until the major 2005 bleaching /disease event (described more fully below). Now coral cover is less than 12% on many reefs, including five long term study sites in St. John and St. Croix covering over 10ha of reefs that formerly had high coral cover and diversity. Even deep reefs have been affected by bleaching and disease (Herzlieb et al. 2006). Some deeper reefs still have high coral cover (Herzlieb et al. 2006), averaging over 30% for deep (>30m) mid-shelf and shelf-edge reefs inside and outside protected areas, even after the extensive bleaching in 2005.

In shallow zones (<6 m), physical structure has changed remarkably as elkhorn reefs have been decimated by storms and disease. Dead elkhorn branches litter the bottom and provide less shelter than intact colonies for parrotfishes, octopuses, hawksbill turtles and other organisms. *Porites* patch reefs that have little live coral can be found in many bays around St. John (Rogers 1999) as well as St. Thomas (Magens Bay) and St. Croix (fore reef of Tague Bay).

Overall, the most significant cause of coral mortality on Virgin Islands reefs has been disease

following the bleaching event of fall 2005 (Miller et al., 2006; T. Smith, personal communication 2006). Hurricanes have been very destructive in localized areas, especially in shallow water. White band disease in the 1970s and 1980s affected just two species, Acropora palmata and Acropora cervicornis, but the effects were devastating and widespread, and the losses of these reef-building species have had lasting effects on the USVI coral reefs. In contrast to the effects of storms and white band disease, the bleaching/disease episode in 2005 and 2006 affected most coral species to depths of over 30m. The coral losses from the 2005 bleaching event and subsequent disease outbreak were especially well documented at long-term monitoring sites maintained by NPS and USGS around St. John and St. Croix.

The following discussion provides greater detail on both the shallow (*Acropora palmata*-dominated; mostly <6 m deep) and deeper reefs around the USVI. The term "deeper reefs" refers here to reefs that are not characterized by living or dead *Acropora palmata* (elkhorn coral) and which occur mostly at depths >6 m, although they range all the way to the shoreline in some locations. Many of these reefs are dominated by *Montastraea annularis* complex (Fig. 8.10). These different reef types have somewhat different ecological histories and have been studied using different methods.

8.7 *Acropora palmata* Reefs in the Virgin Islands

No reefs in the USVI currently have densities of *Acropora palmata* as high as those recorded in the 1960s and 1970s (Rogers et al. 2002). Buck Island Reef National Monument off St. Croix was established in 1961 as a unit of the US National Park Service primarily in recognition of the barrier reef that surrounds the eastern end of the island. The reef at that time was characterized by dense, interlocking colonies of living *Acropora palmata* (Fig. 8.11). Some early studies of this species, the most significant reef-building species in the Caribbean and western Atlantic, took place at Buck Island and at Tague Bay Reef, 1.6km to the south off the north shore of St. Croix. These included studies of growth rates (Gladfelter et al. 1978), metabolism (Rogers



FIG. 8.10. Montastraea annularis is the most abundant coral species on many USVI reefs (Photo: J. Miller)



FIG. 8.11. Acropora palmata, Buck Island, 1970 (Photo: W. Gladfelter)

and Salesky 1981), effects of hurricanes (Rogers et al. 1982), and white band disease (Gladfelter 1982, 1991; Davis et al. 1986). Gladfelter et al. (1977) first described white band disease in 1977 and followed its progression through a reef area. This disease had devastating effects at Tague Bay and Buck Island, and it is thought to be the cause of extensive mortality of *A. palmata* throughout the Caribbean (Aronson and Precht 2001; Bruckner 2002). In 2006,

Acropora palmata (and Acropora cervicornis) were listed as threatened under the Endangered Species Act (Acropora Biological Review Team 2005).

Hurricanes also have killed elkhorn corals in the USVI (e.g., Rogers et al. 1982). In surveys of reefs around St. John in 1984, Beets et al. (1986) noted active white band at several sites and large areas with dead *A. palmata* from disease and storm damage. Gladfelter documented a decrease from white

band disease of 85% to 5% elkhorn cover in a 200 m^2 study plot at Buck Island, and then a further decrease to less than 1% after Hurricane Hugo in 1989 (Gladfelter 1991). In the fall of 2005, elkhorn coral bleached for the first time on record in the USVI, causing some mortality.

Informal observations around St. John (and videotape documentation around Buck Island) showed some increase in number of elkhorn colonies in the 1990s although densities were very low.

8.7.1 Acropora palmata Reefs: St. John

Scientists with USGS, UVI, and NPS began intensive monitoring of elkhorn colonies in 2003 on the fringing reef in western Haulover Bay, St. John, in a zone that once had one of the most impressive elkhorn stands in the USVI (Beets et al. 1986). Initial surveys located 67 colonies in the area $(17,627 \text{ m}^2)$, dispersed widely over a distance of about 500 m parallel to the shoreline. These colonies were monitored and photographed every month from February 2003 to December 2006 for signs of disease (primarily white pox and white band), bleaching, physical breakage, and predation (Fig. 8.12). Identification of diseases in the field is problematic, although white pox and white band are relatively well-defined (Fig. 8.13). There is no evidence so far that the bacterium *Serratia marcescens* found in human sewage and elsewhere is associated with white pox around St. John, although it has been reported as the cause of white pox on Florida reefs (Patterson et al. 2002). Other, undescribed "white diseases" which do not resemble either white pox or white band have also been observed.

Randomly selected elkhorn colonies at Hawksnest Bay, St. John (n = 60), were monitored almost monthly from May 2004 to December 2006. During each survey, complete and partial mortality were estimated as well as the cause of any recent mortality, defined as areas of recently exposed skeleton absent of filamentous algae, sediments, and sessile invertebrates. The causes of recent mortality included physical damage, predation, sedimentation, abrasion, bleaching, as well as disease. This location is less than 3 m deep, and 78% of the colonies experienced physical damage, most likely from snorkelers and high wave action. Although fewer colonies suffered from disease (73%), it was the most frequent cause of tissue loss. There were a total of 180 separate disease incidences with over 500 disease-induced lesions, causing much more damage than the number of broken branches (72). The prevalence of disease also showed an increasing trend during times of higher sea surface temperatures (Fig. 8.14). Higher prevalence during



FIG. 8.12. Percent of *Acropora palmata* colonies at Haulover Bay, St. John, affected by disease, physical damage, bleaching, and damselfish territories



FIG. 8.13. White pox (**a**) and white band (**b**) disease affecting *Acropora palmata* colonies [Photo (**a**): C. Rogers; (**b**): P. Mayor]



FIG. 8.14. The relationship of diseases and bleaching of *Acropora palmata* and sea-surface temperature (SST) at Hawksnest Bay

warm water conditions may occur from either a more compromised host or an increase in virulent pathogens within the reef area. Regardless of the cause, as global temperatures rise and the oceans continue to warm, an increase in mortality from disease is likely.

Complete colony mortality was highest during the summer/fall 2005 Caribbean bleaching event.

Bleaching of colonies, from the loss of zooxanthellae or their pigments, began in late July 2005 and peaked in late September 2005 when the monthly temperature averaged 30.4°C. The next survey in late October revealed the highest amount of disease prevalence (33%) recorded during the 32 month study (Fig. 8.14). Approximately half of the colonies showed some sign of thermal stress through paling or bleaching between July and December 2005. A combination of bleaching and/or disease caused 16% (9) of the colonies to completely die and 23% (13) to die partially. All of the colonies that survived had regained full coloration by January 2006.

To complement the monthly surveys at Haulover and Hawksnest, from August 2004 to May 2005, 13 elkhorn zones (11 within Virgin Islands National Park and two outside) with a total of 3,628 colonies were surveyed (Rogers et al. 2005). Densities at these 13 sites ranged from 0.05 to 9.4 elkhorn colonies/10 m². The focus of this work was disease occurrence and size class distribution. White band disease was noted on only one coral. White pox prevalence (number of colonies with this disease divided by the total number of colonies surveyed within the reef area) ranged from less than 1% to 34.7% and was more often found on colonies greater than 50cm in maximum dimension. Saltpond Bay had the highest disease prevalence of any elkhorn site around St. John, with a prevalence of 34.7% during the first survey in September 2004.

Surveys were done almost every month at 2 of the original 13 sites (Saltpond on the south side of St. John and Trunk on the north side) from July 2005 to July 2006 (Rogers et al. 2006). All *A. palmata* colonies were surveyed 17 times over a 22-month period, from September 2004 (Saltpond only) to July 2006. Disease, bleaching, mortality, and predation were documented and photographed for all colonies (including fragments) encountered. A fragment was defined as any coral not attached by tissue to the substrate. Trunk Bay is the site within VINP that receives the greatest number of snorkelers, while few snorkelers go to reefs within Saltpond Bay. No apparent correlation was found between disease prevalence and visitation.

Overall, bleaching associated with high water temperatures in the fall of 2005 (over 30°C) caused more complete mortality at Trunk and Saltpond than disease, predation, physical breakage, and competition. Twenty-one colonies completely died at Saltpond Bay with the majority (11) dying directly from bleaching and only two from disease. Thirteen (13) colonies died at Trunk Bay, with four dying from bleaching and four from disease.

At Saltpond the prevalence of disease increased from approximately 3% before bleaching began, to 4.9% during the month following the height of the bleaching event. This slightly higher level of disease was sustained for 5 months, until March 31, 2006. Although there was a small increase in the amount of disease, the overall prevalence of disease during the 12 months of study was much lower (1.4-4.9%) than the initial survey at Saltpond in September 2004 (34.7%). Disease prevalence at Trunk Bay did not increase during the months following the bleaching event. White pox or recent mortality caused by disease that could not be categorized as either white pox or white band (referred to as "unknown disease") was present during every survey at Saltpond, with prevalence ranging from 1.4% to 4.9%. The highest amount of white pox and unknown disease (4.9%) was found in late October 2005 when water temperatures were approximately 29.6°C. The prevalence of disease at Trunk Bay ranged from 0% to 10.7% with the highest number of A. palmata colonies with disease occurring in February 2006 when water temperatures were relatively low (26.06°C). White band disease affected only 15 colonies at Saltpond and two at Trunk Bay.

Physical damage to elkhorn at Trunk and Saltpond was more from heavy seas than from careless snorkelers. Although broken branches of *A. palmata* can re-attach and grow as separate colonies, research at these sites revealed that about 40–50% of the observed fragments died. The reef at Trunk Bay experiences the heaviest visitation in VINP. Here, 47.4% of the fragments (total n = 19) were alive at the end of the study in July 2006, and no fragments had attached to the substrate.

In comparison, at Saltpond, which has far fewer snorkelers, 59.5% of the fragments (total n = 205) were still alive when the study ended in July 2006, although 33.3% of them had lost over half of their tissue. The causes of mortality included disease and bleaching.

Overall, bleaching caused more mortality than disease, predation, and physical breakage at Saltpond and Trunk. In general, unlike on deeper reefs dominated by *Montastraea* spp. (see below), bleached elkhorn corals regained normal coloration by January 2006, and then only minor outbreaks of disease were observed. Out of a subset of 467 elkhorn colonies being monitored monthly from late 2005 to July 2006 at Saltpond, Trunk, Hawksnest, and Haulover, 48% bleached, 13% died partially, and only 8% died completely. The ability to determine the genotypes of elkhorn coral colonies (Baums et al. 2005a) creates opportunities to explore some interesting research questions. For example, do corals with different genotypes have different susceptibility to bleaching and disease? At Haulover, one elkhorn coral bleached and died while the immediately adjacent colony did not (Fig. 8.15). These colonies had different genotypes although they had the same zooxanthellae clade (data from I. Baums and B. Schill). At Haulover, 43 of 48 colonies had different genotypes.

Although Acropora cervicornis is an important reef-building coral throughout the Caribbean and was listed as a threatened species along with *A. palmata* in 2006, it has received much less attention than *A. palmata*. *A. cervicornis* grows over a much larger depth range and often exists as isolated and widely dispersed colonies in the USVI, unlike *A. palmata* that is often in depths less than 6m and in nearly monospecific stands. In 2005 and 2006, *A. cervicornis* populations were surveyed in a 28,824 m² area at Haulover Bay. Quantifying colony size is difficult in this species. Three-dimensional size measurements were made by measuring the height, length and width to determine a volume for each colony. The total volume decreased by 19.3% from 2005 to 2006. The total number of colonies increased from 358 to 655, for respective densities of 0.012 and 0.023 colonies/m². However, the average volume per colony decreased by 55.9%. The increase in number of colonies coupled with the decrease in colony size, suggests that remnant patches of tissue from the original colonies were isolated from each other by mortality, resulting in several smaller colonies where there was originally one. Alternatively, some colonies may have experienced physical damage that broke an individual colony into several smaller ones. However, no evidence of physical damage was seen on the majority of colonies, and the decrease in total volume suggests considerable mortality occurred between years. Incidence of white band disease did not change substantially, with 27 colonies in 2005 and 30 colonies in 2006 affected. However, the proportion of colonies with white band disease dropped from 7.5% to 4.6%. The number of coral-eating snails found on the colonies more than doubled from 40 in 2005 to 82 in 2006.



FIG. 8.15. Adjacent elkhorn colonies with bleaching of the right colony no bleaching of the left by (Photo: E. Muller)

8.7.2 *Acropora palmata* Reefs: St. Croix

In 2002, nine reef sites around the eastern tip of St. Croix were surveyed that had formerly been dominated by Acropora palmata were surveyed, (Rogers et al. 2002). These included six north shore reefs, of which two had measured planar cover of 62% (Buck Island barrier eastern fore reef; Gladfelter et al. 1977) and 47% (Tague Bay forereef; Gladfelter 1982) and the others an estimated 25-35% during the mid 1970s; the three south shore reefs had measured planar cover of between 7% and 33% (Adey et al. 1981). In 2002, the north shore reefs had between 0.1% and 3.6% cover, while the south shore reefs were between <0.1% and 1% cover. Several sites (with an areal extent of hundreds of square meters), had numerous young, healthy A. palmata colonies, many of which were the result of more than one successful episode of sexual recruitment. These populations were capable of recovery, barring other sources of mortality like storms, bleaching, and disease (E. Gladfelter, personal communication, 2007).

In 2004, 2,492 large elkhorn colonies (greater than 1 m maximum dimension) were recorded along randomly selected transects at depths of 10 m or less within Buck Island Reef National Monument (Mayor et al. 2006). Density ranged from 0.004 to 0.160/m². The overall prevalence of white band disease was 3%, but along transects

with white band disease an average of 15% of the colonies were affected. Gladfelter et al. (1977) found 3% prevalence within the initial boundary of BIRNM but 42% at Tague Bay. White pox disease was not quantified in the 2004 study but appeared more common than white band.

At BIRNM, Acropora palmata experienced extensive bleaching in 2005 (Fig. 8.16). National Park Service staff quantified the extent of the bleaching and the subsequent mortality of Acropora palmata. Shallow Acropora palmata habitat is present on reef crest formations and "haystack" features in addition to the barrier reef surrounding Buck Island. However, the majority of Acropora palmata habitat at BIRNM is found on the Buck Island bar to the north of Buck Island, at a depth of 5–10 m. In general, Acropora palmata colonies located on the shallow barrier reef bleached earlier and suffered greater tissue loss than those in deeper water outside the barrier reef.

The extent of bleaching among *A. palmata* colonies at BIRNM was measured in two ways: (1) by continuing to monitor 44 colonies at three sites ("Selected Sites"); and (2) by a rapid assessment of survey plots (250 m^2) at 62 random sites in suitable habitat throughout the Monument ("Monument-wide Colonies"). Two of the three Selected Sites were located on the barrier reef (referred to as the backreef and south forereef sites), and the other was located on the north bar. The colonies at these sites were



FIG. 8.16. Extensive bleaching of *Acropora palmata* at Buck Island Reef National Monument, November 2005 (Photo: E. Muller)

monitored monthly before, during, and after the bleaching event (beginning in March 2005). The Monument-wide survey based primarily on planar photographs of colonies was initiated in November 2005 and repeated once in February 2006 to augment observations from the Selected Sites. Photographs of a subset (65) of the 277 colonies originally surveyed were analyzed for percent tissue bleached and unbleached, and for percent algal-covered skeleton to assess bleaching and mortality. Since shaded portions (undersides) of Acropora palmata colonies are less likely to bleach, and would not be recorded in planar photographs, these results may overestimate bleaching and may not be comparable to results from studies where bleaching was quantified in situ.

Among the 321 colonies (277 + 44) examined for bleaching, 113 colonies (35%) showed no bleaching. Maximum bleaching on the barrier reef (66.5% of all live tissue for the backreef and forereef sites) occurred in November 2005. At the north bar, outside the barrier reef, 65% of the live tissue was bleached in November 2005. However, colonies in the Monument-wide survey, which also showed a peak in bleaching in November 2005, showed a much lower level of bleaching (an average of 41%).

Interestingly, colonies located on the backreef were impacted before colonies located on both the forereef and on the north bar. Already by August 2005 the backreef site was experiencing bleaching levels of 25%, whereas the forereef site was experiencing only 11% bleaching. It is possible that decreased current and wave action caused colonies located on the backreef to be exposed to higher levels of thermal stress than sites outside the barrier reef. Most of the sea water temperature measurements that exceeded 30°C were recorded in September, with the highest (30.6°C) on September 29, 2005 on the backreef.

Mortality, like bleaching, was higher on the barrier reef than throughout the rest of the Monument, and the backreef experienced more mortality and experienced it sooner than the forereef. The backreef site experienced the highest average mortality (66.4%) during the event, followed by the south forereef (58.1%), and the north bar site (36.4%). The Monument-wide sites experienced 21% average tissue mortality, how-

ever mortality was only recorded from November 2005 to February 2006.

8.7.3 *Acropora palmata* Reefs: St. Thomas

In general, *A. palmata* and *A. cervicornis* reefs have been much less studied on the island of St. Thomas. Six reefs dominated by (living or dead) *Acropora* were surveyed in 2003. Impressive mixed stands of these species (and the hybrid *A. prolifera*) occur around St. Thomas with percent cover of living *Acropora* spp. varying from 11% to 13% at Hans Lollik, Flat Cay, and Coculus Point and 6% to 8% at Botany Bay, Inner Brass Island, and Caret Bay (at Vluck Point). White band disease affected an average of 7% of colonies, but prevalence was highest (28%) for *A. palmata* colonies at Caret Bay, suggesting white band as the cause of substantial recent mortality at this reef (Nemeth et al. 2004).

8.8 Deeper Reefs

8.8.1 St. John

Since 1987 Edmunds (2002, 2006) has monitored photoquadrats along haphazardly selected transects at two sites in Great Lameshur Bay (GLB) (three 10m transects/site), one located just north of the NPS site at Yawzi Point (9m depth), and the other at Tektite Reef (14 m depth) near the mouth of GLB (Fig. 8.17). At the Yawzi site, declines in coral cover, also of Montastraea annularis, were recorded that began with Hurricane Hugo in 1989 and continued throughout the 1990s (Edmunds 2002); these trends are similar to those documented at the nearby site monitored by NPS researchers (Rogers et al. 1991; Rogers and Miller 2006). In contrast, transects on the deeper Tektite reef escaped damage by Hurricane Hugo, and staged a 34% increase in coral cover from 1987 (37% cover) to 1998 (43% cover) that continued at a modest rate until about 2004. The 2005 bleaching /disease event killed >20% of the coral at this deeper site, but the losses at the shallower site at Yawzi Point were barely detectable, largely because the coral cover already had declined to ca. 9.0% by 2005 and fell to 8.6% in 2006 (P.J. Edmunds, unpublished data 2007).



FIG. 8.17. Representative quadrats from the Yawzi Point (9 m depth) and Tektite (14 m depth) study sites that have been monitored with an annual frequency since 1987 (Edmunds 2002; Edmunds and Elahi 2007)

NPS scientists began long-term monitoring of coral, algae, and other benthic substrate on haphazardly selected transects on reefs of high coral cover, diversity and complexity in Great Lameshur Bay (Lameshur Reef) and Newfound Bay in 1989 and 1990, respectively (Rogers et al. 1991; Rogers and Miller 2006). Lameshur Reef is a fringing reef off Yawzi Point, which separates Great and Little Lameshur Bays on the south side of the island and falls within the boundary of Virgin Islands National Park. The reef extends seaward from a nearshore, shallow Acropora palmata zone in to deeper water. The base of the reef occurs at about 15 m where there is a sand halo adjacent to an algal plain. Newfound Reef is on the northeastern side of St. John, outside the boundary of Virgin Islands National Park. Although outside the national park, the watershed associated with this reef has no development. The reef crest is wider and better defined than at Lameshur Reef. It parallels the east and west shores of Newfound Bay and extends partway across the mouth of the bay from either direction, creating a shallow lagoon with a channel to the outer reef. The reef drops to about 14m where it ends abruptly in a sand halo near an algal plain. Haphazardly selected "chain" transects (average depth ca. 12m at Lameshur, 7.6m at Newfound) were supplemented with randomly selected video transects (average depth 13.7–15.0m at Lameshur, 6.5–9.5m at Newfound) from larger areas of the reefs at both sites in 1999 (see below).

Montastraea annularis is the most abundant coral at each reef. Hurricane Hugo in 1989 caused a 40% decline in coral cover (from about 20% to 12%) along the five transects off Yawzi Point,

with a loss of *M. annularis* (from 7.5% to 5.2% cover). No increase in coral cover was noted up through 2002. There was a significant though small increase in coral cover along the single 100 m chain transect at Newfound from 1990 to 2002.

Coral cover (~8%) did not change significantly along the randomly selected video transects at Lameshur from 1999 to 2003. However, at Newfound, coral cover declined significantly from 18% to 14% from 1999 to 2000, with declines seen along each video transect. The suspected cause is disease (Rogers and Miller 2006).

The randomly selected video transects at Newfound and Lameshur were established during pilot studies in protocol development under the NPS/USGS Inventory and Monitoring (I&M) program. Digital video monitoring was used, along with a newly developed Random Sample Selection Protocol (Fig. 8.18, Miller and Rogers 2002; Rogers et al. 2002). This represented a large change in sampling strategy for monitoring within the Virgin Islands, and coral reef monitoring in general (Lewis 2004). Traditionally (including most studies presented within this chapter), coral reef and other marine habitat sampling is conducted with haphazardly selected study plots or sampling units (quadrats or transects) which provide excellent data on the selected units, but those data may not have inference over any area other than the quadrats or transects and can not be said to be representative of the entire reef or other habitat that contains them. The Random Sample Selection Protocol used a sonar mapping system to:

- 1. Accurately define or map the study area
- 2. Identify the entire population (given defined spacing between sample points)
- 3. Randomly select the sample points from within the sample population (origins of transects in the case of using the Video Monitoring Protocol)

This allowed every point within the defined sample area to have an equal chance to be chosen for sampling, thus allowing the results obtained to be inferred over the entire defined area (given a large enough sample size). Results obtained using these methods are identified with the reef "name" and size of the study area from which the samples were chosen (domain) so the area to which the data may be inferred is identified.

The I&M program operating at VINP was absorbed into the South Florida /Caribbean Network (SFCN) in 2002 and additional long-term



FIG. 8.18. Videotaping along randomly selected transects, Newfound Reef (Photo: C. Rogers)

monitoring sites were established at the South Fore Reef (Buck Island 2002), Haulover (2003) and Tektite (2005) (Table 8.1). Note that trends will be provided for data prior to and through the bleaching /disease event in 2005/06. (The data for the South Fore Reef and Western Spur and Groove sites off Buck Island are included here for comparison.)

8.8.2 Effects of Bleaching and Disease

Some of the warmest sea temperatures on record for the Caribbean, with temperatures reaching over 31°C, occurred in 2005, and USVI and Puerto Rico coral reefs were particularly affected by bleaching (Fig. 8.19). More than 90% of the coral cover bleached at five long-term monitoring sites (Miller et al. 2006). In early October 2005, 279 mm of rain fell in St. John. The rainfall and overcast conditions lowered the seawater temperatures, and many corals began to regain their normal coloration. However, a severe outbreak of white plague disease led to significant coral mortality (Fig. 8.20).

Intensive monitoring throughout the bleaching /disease outbreak revealed that at the peak intensity, the number of disease lesions increased an average of 40 fold (range: 16.4 to 72.9) and total

TABLE 8.1. NPS long-term monitoring sites in St. John and Buck Island, St. Croix, and trends in coral cover prior to the bleaching /disease event (NPS, unpublished data).

Site	Location	Study area (m ²)	Annual monitoring began	Pre-bleaching /disease Coral cover trend
Newfound	St. John	13,786	1999	Decrease $(p = 0.0002)$
Yawzi	VINP	7,125	1999	increase $(p = 0.05)$
Mennebeck	VINP	12,495	2000	increase $(p = 0.0432)$
Haulover	VINP	13,568	2003	No change
Tektite	VINP	18,711	2005	Not applicable
S. Fore Reef	BIRNM	40,753	2002	Increase $(p = 0.0006)$
W. Spur and Groove	BIRNM	26,365	2000	No change



FIG. 8.19. Bleached corals off Scott Bay, St. John (Photo: C. Rogers)



FIG. 8.20. A severe outbreak of white plague disease (Photo: E. Muller)

coral tissue area killed increased an average of 25.4 times (range: 2.1 to 80.0) across all sites. Tektite Reef had the highest levels (area killed and number of lesions) of disease, and high levels of disease while corals were bleached so an outbreak may have been underway at Tektite Reef prior to other sites. For more discussion of coral disease findings during this outbreak, see section on coral diseases.

The combination of extremely severe bleaching followed by unprecedented levels of mortality from coral disease caused catastrophic losses in coral cover at all sites averaging 51.3% decline (range 34.1–61.8; data through SFCN annual monitoring for 2006, see Table 8.2).

8.8.3 Coral Species Effects: Changes in Relative Abundance

Montastraea annularis complex was and remains the dominant coral within these reefs but its abundance relative to other coral species dropped during the bleaching/disease event from an initial average cover of 79.2% (SD=7.1) to 71.8% (SD=9.4) (Table 8.3). A reef building species, *Colpophyllia natans*, although a smaller component of the reef community, also decreased relative to other corals. *Agaricia agaricites* declined dramatically in cover and relative abundance, due to mortality from bleaching, as 93% of *A. agaricites* bleached (base on cover), the corals were rarely affected by disease. *Montastraea cavernosa*, *Siderastrea siderea* and poritids which bleached less than *M. annularis* (complex), *C. natans*, and agariciids, had "relatively" moderate disease levels and have increased in abundance compared to other corals.

8.9 The Deepest Reefs

Most information on coral reefs around St. John comes from relatively shallow (0-20 m deep) study sites. Surveys by NOAA and the NPS in 2005 using a remotely operated vehicle expanded the sampling range to deeper waters (200 m). Their data revealed that in general deep zooxanthellate coral reefs are less deteriorated than their shallower counterparts. Coral cover in deep reefs often exceeded 40% and estimates of algae cover were relatively low. However, deep reefs are not categorically invulnerable. NOAA/NPS surveys in early 2005 found a massive coral mortality event on a 30-40 m deep reef. The mortality event was distinguished by a high amount of dead coral covered by turf algae. As much as 50% of the reef within the transect (500 m²) was affected and estimates of coral loss exceeded 30%.

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			Pre-bleaching	g/disease	Pe	ik of disease ou	tbreak	Mean percent (coral cover	
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Island or		coral cover		Total area	Total #	Total area	Month of	Pre-bleaching/	Latest	decrease in
Park	Site	bleached	Total # lesions	(sp. cm.)	lesions	(sp. cm.)	peak disease	disease	2006 data	coral cover
STJ	Newfound	92	17	1162	569	5318.0	Mar. 2006	13.3	6.2	-53.4
VINP	Mennebeck	94	No sampling prior to event		641 ^a	5718.5 ^b	Apr. 2006 and Dec. 2005	26.7	10.2	-61.8
VINP	Haulover	96	8	149.5	583	3968.4	Apr. 2006	22.5	12.4	-44.9
VINP	Tektite	26	No sampling prior to event		1213	26025.5	Nov. 2005	24.7	11.1	-55.1
BIRNM	South Fore Reef	96	10	108.3	627	8635.0	Mar. 2006	19.8	11.4	-42.4
VINP	Yawzi	71						8.5	5.6	-34.1
BIRNM	W. Spur and Groove	4c	Not sa	mpled episodica	lly during bleac	hing/disease outb	eak	5.1	3.1	-39.2
	Average values:	95.0	11.7	473.3	726.6	9933.1		21.4	10.3	-51.5
	Range values:	71 – 97	8 - 17	108.3 - 1162.0	569 - 1213	3968.4 - 26025.5		5.1 - 26.7	3.1 - 12.4	-34.1 to -61.8
^a Peak in n ^b Peak in tc ^b Peak in tc ^c Sampling	umber of lesions stal area disease o occurred in May	observed in April observed in Decen	2006 aber 2005 5; bleaching data not c	comparable with	other sites or us	ed in ranges/aver	ages.			

Initial			Latest 2006 sample			Relative	
Avg.	SD	Rank	Avg.	SD	rank	Loss/gain	
79.2	7.1	1	71.8	9.4	1	-9.3	
1.3	0.8	7	0.9	1.4	5	-30.0	
1.8	1.5	5	2.3	2.1	4	29.3	
1.5	1.8	6	2.4	2.2	3	55.0	
1.9	0.7	4	4.7	1.3	6	143.4	
2.0	0.6	3	0.3	0.5	7	-82.4	
9.5	6.1	2	12.4	3.9	2	30.2	
	Avg. 79.2 1.3 1.8 1.5 1.9 2.0 9.5	Initia Avg. SD 79.2 7.1 1.3 0.8 1.8 1.5 1.5 1.8 1.9 0.7 2.0 0.6 9.5 6.1	Initial Avg. SD Rank 79.2 7.1 1 1.3 0.8 7 1.8 1.5 5 1.5 1.8 6 1.9 0.7 4 2.0 0.6 3 9.5 6.1 2	Initial Late Avg. SD Rank Avg. 79.2 7.1 1 71.8 1.3 0.8 7 0.9 1.8 1.5 5 2.3 1.5 1.8 6 2.4 1.9 0.7 4 4.7 2.0 0.6 3 0.3 9.5 6.1 2 12.4	Initial Latest 2006 s Avg. SD Rank Avg. SD 79.2 7.1 1 71.8 9.4 1.3 0.8 7 0.9 1.4 1.8 1.5 5 2.3 2.1 1.5 1.8 6 2.4 2.2 1.9 0.7 4 4.7 1.3 2.0 0.6 3 0.3 0.5 9.5 6.1 2 12.4 3.9	$\begin{tabular}{ c c c c c c c c c c c c c c c } \hline \hline Initial & Iatest 2006 sample \\ \hline Avg. & SD & Rank & Avg. & SD & rank \\ \hline \hline Avg. & SD & Rank & 0.9 & 1.4 & 5 \\ \hline 1.3 & 0.8 & 7 & 0.9 & 1.4 & 5 \\ \hline 1.8 & 1.5 & 5 & 2.3 & 2.1 & 4 \\ \hline 1.5 & 1.8 & 6 & 2.4 & 2.2 & 3 \\ \hline 1.9 & 0.7 & 4 & 4.7 & 1.3 & 6 \\ \hline 2.0 & 0.6 & 3 & 0.3 & 0.5 & 7 \\ \hline 9.5 & 6.1 & 2 & 12.4 & 3.9 & 2 \\ \hline \end{tabular}$	

TABLE 8.3. Changes in relative abundance of coral species. MACX = *Montastraea annularis* complex (calculated as MA = *Montastraea annularis*, MFAV = *Montastraea faveolata*, MFRA = *Montastraea franksi*), SD = standard deviation.

Monitoring surveys in the summer of 2006 revealed significant degradation at depths of 30 m on reefs that are part of the Mid-shelf Reef complex, 2-8 km south of St. Thomas and St. John. Coral cover varies greatly on these reefs. UVI scientists surveyed transects at one Montastraea dominated site and found that coral cover dropped from 56% during the 2005 bleaching event to 41% following the bleaching and subsequent white plague outbreak (T. Smith et al., personal communication 2006). This was a 26% drop in coral cover on one of the highest coral cover sites known in the USVI. This reef area is less than a kilometer away from the site of the mortality event noted in 2005 and described above. Additionally, random surveys conducted by NOAA and NPS within this reef system, inside the Virgin Islands Coral Reef National Monument (VICRNM), suggested a significant decrease in coral cover between 2005 and 2006. Coral cover decreased from $4.0 \pm 0.4\%$ (range 1–9) in 2005 to $2.3 \pm 0.3\%$ (range 1–5) in 2006 ($\chi^2 = 9.21$, P = 0.0024, n = 20). Interestingly, the decline in coral cover between 2005 (15.0%, range 3-45) and 2006 (12.3%, range 0-25) on the same reef system but outside VICRNM boundaries was not significant ($\chi^2 = 0.19$, P = 0.6609, n = 15).

8.9.1 St. Croix

At Buck Island Reef National Monument, permanent, haphazardly selected transects and individual colonies of *Montastraea annularis*, *Diploria strigosa*, and *Porites astreoides* have been monitored since 1988 (Bythell et al. 1993, 2000a, b). Hurricane Hugo (1989) was responsible for the most significant changes up through 2000. The three sites with permanent transects differed greatly from each other in terms of coral cover and coral species composition. Coral cover increased from 32% to 40% at one site, but decreased from 25% to 15% at another site. Although Hurricane Hugo caused more loss of Porites porites than of the more abundant M. annularis, bleaching in 1998 caused more loss of M. annularis than of other species along the transects. Within 5 years of Hurricane Hugo an increase in coral cover was noted, but bleaching in 1998 and additional hurricanes caused more declines. Bythell et al. (2000a) suggested that in spite of the variations along the transects the reef assemblages over a scale of tens to hundreds of meters were relatively stable, with changes over time being less than differences among sites.

Observations of 303 individual coral colonies from 1988 to 2000 showed that mortality (or removal) of entire colonies was 6% for *Montastraea annularis*, 20% for *Diploria strigosa*, and 49% for *Porites astreoides*. The major reef-building species *M. annularis* sustained greater losses from bleaching in 1998 than from hurricanes while *Porites astreoides* and *D. strigosa* had more severe losses from the storms (Bythell et al. 2000b). Disease incidence was low throughout the entire study period and was associated with bleaching.

Twelve permanent coral reef sites ranging in depth from 4 to 23 m have been monitored on St. Croix by researchers from the University of the Virgin Islands. Of these sites, ten were established in 2001, with the remaining shelf-edge Mutton Snapper site and the nearshore Great Pond site established in 2002 and 2003, respectively. Overall coral cover averaged 15%, with 13% at nearshore sites, similar to the 16% coral cover at nearshore St. Thomas sites. In common with St. Thomas coral cover, there were no apparent trends in coral cover over time prior to the 2005 bleaching (Nemeth et al. 2005; Smith et al., personal communication). With few exceptions, Montastraea spp. (MACX = Montastraea annularis complex) were most abundant (average = 52%) at all sites combined (62% with M. cavernosa). Dead coral with algae (dca) consistently contributed the highest cover ranging from 20% to 80%, while macroalgae ranged from 2% to 40%. Less than 10% of the cover was sponges and gorgonians.

The prevalence of disease on St. Croix reefs prior to the 2005 bleaching event was generally low. However, there were low level (less than 1% prevalence) infections of white plague at the high *Montastrea* spp. cover sites, Sprat Hall and Mutton Snapper. Low-level severity, chronic bleaching was also low, from only a few colonies affected at Mutton Snapper to 6% at Sprat Hall.

8.9.2 St. Thomas

In 2001, University of the Virgin Islands scientists began the monitoring of nearshore (6-20 m depth) reefs and expanded the program in 2003 and again in 2005 to include mid-shelf (5-30 m depth - including reefs which fringe offshore cays and non-emergent reefs on the island platform), and shelf-edge reefs (>30 m depth) (Fig. 8.21). Of the 15 sites monitored before the 2005 bleaching event, coral cover averaged 20% and ranged from 4% to 53%. The lowest coral cover values were typically found on nearshore reefs (average = 14%) with the lowest cover (4%) occurring in a relict coral reef just outside the highly impacted Charlotte Amalie Harbor. Coral cover generally increased with depth and distance from shore and averaged 26% on mid-shelf reefs and 36% on shelf edge reefs (Herzlieb et al. 2006). The highest coral cover was typically found on the deep shelf-edge reefs, attaining a maximum value of 53% at College Shoal. Prior to the 2005 bleaching event, coral cover tended to remain constant at all the monitoring sites sampled over multiple years. Coral species composition varied by reef location with the percent of Montastraea spp. increasing with depth and distance from shore. Nearshore reefs contained an average of 34% M. annularis complex [(MACX) – or 44% with M. cavernosa], 61% MACX (or 79% with M. cavernosa) at mid-shelf sites and 85% MACX (or 88% with M. cavernosa) at shelf-edge sites (Nemeth et al. 2004). Macroalgae cover averaged 33% and ranged from 4% to 60%, with the lowest values corresponding with high coral cover sites and highest values corresponding with exposed areas on the mid-shelf. Macroalgae cover was the most abundant component at all sites except at two of three shelf-edge sites, and trended upward at three nearshore (Benner, Botany, and Magen's Bays) and one 23 m deep mid-shelf site (S. Capella). Dead coral covered with turf algae averaged 30% and ranged from 20% to 50%. Combined sponge and gorgonian cover averaged 8% and ranged from 3% to 12%, with no apparent cross-shelf trends.

One would predict that reefs closer to shore and therefore more likely to be affected by humans would be more degraded than those in deeper water and/or farther from shore. For St. Thomas, evidence of a nearshore to offshore trend in increasing coral cover supports this. In 2003, Herzlieb et al. (2006) assessed a total of eleven reefs within three categories based upon reef position along the insular platform south of St. Thomas: near-shore reefs (5-30 m depth, <1 km from the shoreline of St. Thomas); mid-shelf reefs (5-30m depth, 1-10km from shore); and shelfedge reefs (\geq 30 m depth, 10–15 km from shore). Percent cover of biotic and abiotic substrata, coral species composition, and levels of bleaching and disease were compared among the near-shore, mid-shelf, and shelf-edge reef systems. Nearshore reefs had significantly lower live coral cover and higher cover of dead coral with turf algae than the other two reef systems. In addition, nearshore reefs had a significantly lower relative abundance of a coral species sensitive to terrigenous stress (Montastraea annularis) and significantly higher percent composition of a coral species resistant to terrigenous stress (Siderastrea siderea) than the other reef systems.

Smith et al. (personal communication 2007) found that coral diseases on these St. Thomas reefs



FIG. 8.21. The mean percent cover of benthic categories from 600 transects at 16 coral reefs surveyed off St. Thomas over the years 2001–2006. Bars represent the standard error of the mean. Locations included nearshore reefs (6–13 m), mid-shelf reefs associated with islands (9–15 m), mid-shelf reefs not associated with islands (19–30 m), and shelf-edge reefs (30–40 m)

from 2003 to 2005 (before the bleaching began) were more prevalent at nearshore monitoring sites (8% of colonies affected) as opposed to mid-shelf and shelf edge sites (2-4%). Two coral diseases (dark spots syndrome and yellow blotch disease) were more prevalent at nearshore coral reef sites, independent of coral species competition, and tended to drive the onshore to offshore differences, with a combined average of 7% of colonies affected nearshore and less than 1% at offshore sites. Furthermore, bleaching, predominantly lowlevel partial bleaching potentially associated with chronic stress, was highest nearshore (30% of colonies affected) and trended downward offshore to the shelf-edge sites (12%). The proportion of coral colonies with old partial mortality (i.e., degraded skeleton and algal cover) was highest at nearshore sites (36%), double the average at offshore sites (17%). Distressingly, recent partial mortality was highest at the shelf edge sites around St. Thomas, and, Lang Bank, the deepest and most remote St. Croix site, had the highest incidence of disease at about 17% and the highest bleaching (ca. 22%). This suggests that degradation may have begun in some of the most remote coral reefs in the USVI. Herzlieb et al. (2006) speculated that increased disease of deep coral reefs on the Grammanik Bank might be due to fish traps which act as vectors for pathogens when they are moved from shallow to deep water sites on a seasonal basis.

8.9.3 Benthic Composition of Reefs in St. John and St. Croix: NOAA

Since 2001, NOAA has been using a random sampling design to characterize benthic composition on reef and hardbottom areas around St. John and Buck Island, and along the northeastern shore

of St. Croix including the East End Marine Park. Data from 788 sites indicate that reef and hardbottom areas in both St. Croix and St. John generally are dominated by algae (Fig. 8.22). The most abundant of three algal categories observed was turf and crustose algae with a mean cover of $36\pm$ 1.2% in St. Croix and $30.4\%\pm1.7\%$ in St. John. Macroalgae cover averaged $12.1\pm0.5\%$ and $13.9\pm$ 0.9% in St. Croix and St. John, respectively.

In St. Croix, the macroalgae with the highest observed cover were *Dictyota* spp., *Halimeda* spp., *and Sargassum* spp. In St. John, the most common macroalgae observed were *Dictyota* spp., *Lobophora variegata*, *and Halimeda* spp. Filamentous algae and Cyanobacteria accounted for $5.2\pm0.6\%$ cover in St. Croix and $1.7\pm0.4\%$ cover in St. John (Fig. 8.22).

Live scleractinian coral cover was low and averaged 6.4±0.5% in St. Croix and 5.8±0.5% in St. John (Fig. 8.22). Gorgonians had higher crown cover in St. John when compared with reef and hardbottom areas in St. Croix (Wilcoxon/Kruskall-Wallis One-way χ^2 test, p < 0.0001). Milleporid corals and sponges also had higher cover in St. John than in St. Croix (p < 0.0002).

Patterns in the relative cover of benthic organisms were consistent across reef types (Kendall et al. 2001), with two algal categories (turf/crustose algae and macroalgae) dominating all six reef types (Fig. 8.23). Cyanobacteria and filamentous algae had the highest cover and were most variable on reef rubble and scattered coral and rock sites. The mean percent cover of live scleractinian coral was significantly highest on patch reefs (11.8±1.2%, p<0.05, Dunn's multiple comparison test) and lowest on reef rubble and scattered coral and rock sites (1.59±0.6%, Fig. 8.23). Gorgonians had the lowest cover on reef rubble sites. The percent cover of sponges and fire corals were similar among benthic habitats.

Live scleractinian coral cover in St. Croix and St. John comprised 18 coral genera (Fig. 8.24). The three most abundant genera were *Montastraea* spp., *Porites* spp., and *Diploria* spp. Some significant differences in coral composition on reefs and hardbottom areas were observed between St. Croix



FIG. 8.22. Mean percent cover of benthic organisms on reefs in St. John and St. Croix. Bars represent the standard error of the mean. The number of sites (n) surveyed on each island is shown in parentheses. Sites ranged in depth from 0 to 28 m. In St. John, sites were located around the entire island, whereas in St. Croix, only sites in the north shore of East End Marine Park and the Buck Island Reef National Monument were surveyed. Benthic composition was estimated visually from five replicate 1 m² quadrats within a randomly chosen 100 m² belt transect at each site (NOAA Biogeography Program, http://www8.nos.noaa.gov/biogeo_public/query_main.aspx)



FIG. 8.23. Mean percent cover of benthic organisms found in different reef habitats off St. John and St. Croix. Other sessile invertebrates include anemones, tunicates, zooanthids, and tubeworms. Habitat types were classified based on digital benthic maps (Kendall et al. 2001). Bars represent the standard error of the mean. The number of sites (n) surveyed for each habitat is shown in parentheses. Benthic composition was estimated visually from five replicate 1 m² quadrats within a randomly chosen 100 m² belt transect at each site (NOAA Biogeography Program, http://www8. nos.noaa.gov/biogeo_public/query_main.aspx)



FIG. 8.24. Mean percent live cover of coral genera on randomly selected reef sites between 0 and 28 m deep in St. John and St. Croix. Bars represent the standard error of the mean. The percent cover of live coral was determined visually from five replicate 1 m^2 quadrats at each site (n=768)

and St. John. *Montastraea* spp., *Siderastrea* spp., and *Agaricia* spp. had higher average cover in St.

John compared with St. Croix (p < 0.0001, Wilcoxon/Kruskall Wallis One-way χ^2 test). However, *Diploria* spp. and *Acropora* spp. had higher cover in St. Croix than in St. John, (p < 0.04). The cover of other coral genera was similar between St. Croix and St. John.

8.10 Coral Diseases

All of the coral diseases reported for the Caribbean (Weil et al. 2006, Sutherland et al. 2004) have been seen on reefs in the USVI. White plague and white band disease have been the most severe. In the late 1990s white plague appeared on reefs in St. John. From December 1997 through November 2005, monthly surveys of disease, coral cover, and macroalgal cover were conducted using 1 m² quadrats along eight 10m transects in a portion of Tektite Reef which initially had very high coral cover (ca. 66%) (Miller et al. 2003; NPS, unpublished data 2007). Disease incidence was estimated by percent planar cover within quadrats and by size of disease patches (lesions). The disease had the gross appearance of white plague, and samples confirmed the presence of Aurantimonas coralicida, the reported pathogen (Denner et al. 2003). Disease was present each month and was not correlated with seawater temperature. The mean live coral cover declined significantly over the study period, with significant losses in seven of the eight transects. Especially severe outbreaks were seen in August 2000 and August 2005. Most of the coral in the transects was Montastraea annularis, although other species such as Colpophyllia natans and Diploria labyrinthiformis were present. The dead coral was primarily covered with algae, although some recruits of Agaricia and Porites were observed.

In addition to analysis of digital videotapes for changes in percent coral cover over time (described above), two other approaches have been used to examine the responses of corals at the NPS longterm study sites to the 2005 bleaching /disease event. First, the amount of disease affecting the coral reefs was estimated on each sampling date by measurement of lesions (areas that have recently been killed by disease) on coral colonies one meter on either side of the permanent transects. At all locations, disease was more extensive following the bleaching than before bleaching began (based on videotapes and quantitative data). Second, videotapes from successive time periods at each longterm site have been compared side by side to follow the condition and fate of individual coral colonies. This analysis showed that some coral species, including the larger, major framework building species (Montastraea annularis complex, Colpophyllia natans, and others) exhibited the most severe bleaching. Recovery from bleaching varied by species, with some corals such as those in the M. annularis complex showing significant recovery followed by severe disease and colonies of other species dying directly from bleaching.

A total of 6,061 disease lesions were recorded on 23 coral species from September 2005 to July 2006 at all sites. Five diseases/syndromes were observed including black band disease, dark spots syndrome, white band disease, and yellow blotch, but 99% of the lesions and of the total area killed was due to white plague. Ninety-three percent of the disease occurred on colonies within the genus *Montastraea* (*M. annularis* complex primarily, with *M. cavernosa* to a much lesser extent). Other affected genera included *Colpophyllia*, *Siderastrea*, *Diploria*, and *Porites*.

Samples of healthy and diseased corals are being analyzed to determine if there are shifts in the associated microbial communities that occur when corals become diseased. In August 2005, just before the severe bleaching event, samples of diseased and apparently healthy corals (mostly Montastraea annularis) were taken along transects at Tektite Reef, within Virgin Islands National Park, using a non-destructive swabbing method. Sterile foam swabs were used to sample corals, and material was transferred to Whatman FTA cards for storage and transport to the laboratory. Bacterial 16S ribosomal genes and zooxanthellae ITS-1 genes were readily amplified by polymerase chain reaction (PCR) from card samples. PCR products were further analyzed to examine the diversity of bacteria and zooxanthellae colonizing the corals sampled. No obvious associations between disease status and zooxanthellae clades were noted, however investigations of bacterial associations were informative. Both healthy and diseased corals had Aurantimonas coralicida,

an alphaproteobacterium. Further analysis revealed different communities of alphaproteobacteria in diseased vs healthy *M. annularis* (Pantos and Bythell 2006; USGS, unpublished data 2007).

Members of the alphaproteobacteria are extremely diverse in form, function, and ecological role. The subdivision includes symbionts as well as serious plant and animal pathogens. Several studies from multiple researchers have detected shifts in coralassociated alphaproteobacteria that seem to be associated with heath/disease status. To further study this possible relationship, a set of PCR primers was developed that direct the amplification of a highly variable sequence stretch in the alphaproteobacterial gene that codes for 16S ribosomal RNA. Sixty-four samples taken from the apparently healthy Tektite Reef Montastraea annularis colonies and 31 samples taken from diseased colonies were amplified and examined by melting curve analysis. Of the 64 apparently healthy colonies, 56 harbored a common, single type of alphaproteobacterium, while the remaining eight harbored either distinctly different single types or multiple types of these microbes. This contrasts with the 31 diseased samples that all harbored alphaproteobacterial types that appeared to be different from any of those found in the healthy colony samples. The species identifications of characteristic alphaproteobacteria associated with healthy and diseased coral colonies are currently being determined by genetic sequence analysis. The data suggest that there may be an alphaproteobacterium that forms either a commensal or a symbiotic relationship with Montastraea annularis and that this relationship is disturbed in the disease process. The unusual alphaproteobacterial signatures found in 8 of 64 of the apparently healthy colony samples may represent either rarely occurring normal flora, or alternatively, may be the first representation of the onset of disease in which case these sorts of analyses could be predictive in assessment of reef vulnerability.

Black band disease (BBD) has been seen at low levels on reefs in the USVI for at least 2 decades (Edmunds 1991) and affects fewer species than the more recently appearing white plague (Fig. 8.25). Edmunds (1991) documented the proportion of corals infected on shallow reefs (<10 m deep) in Great Lameshur Bay, St. John, between August 1988 and September 1989. BBD infections were most common on *Diploria strigosa*, *D. labryinthiformis*, *Montastraea annularis*, *Siderastrea siderea*, and *Colpophyllia natans*, but only 0.2% of 6908 colonies were infected in the autumn of 1988. Infection rates were lower in February, when the seawater temperature was the coolest, compared to September and November. Edmunds (1991) estimated that the disease could remove 3.9% of the living tissue of *Diploria strigosa* colonies each year.

Recently a study was carried out to compare the microbial communities in BBD on corals from three regions of the wider Caribbean, including the USVI (Voss et al. 2007). BBD consists of a migrating, cyanobacterial-dominated microbial mat that moves across corals at rates up to 1 cm/ day, completely degrading coral tissue and exposing pure coral skeleton. It can kill an individual coral colony in a matter of months. No primary pathogen has been identified, and the disease may by a polymicrobial infection that requires a specific microbial community. It has been shown that four major physiological groups are always present in BBD – phototrophs, heterotrophs, sulfate reducers, and sulfide oxidizers.

In this study 97 samples were analyzed from 19 reef sites within the three regions. These consisted of three sites at St. John (Haulover Bay, Hawknest, and Watermelon Cay), seven sites at Lee Stocking Island, Bahamas, and nine sites at the northern Florida Keys. Depths ranged from 2 to 6 m at St. John, 3 to 20 m at Lee Stocking Island, and 2 to 6 m on the northern Florida Keys. Five of the 97 samples were from St. John, with individual samples from BBD on *D. stokesi*, *D. labyrinthiformis*, *M. annularis*, *M. cavernosa*, and *S. siderea*.

Data analysis was carried out by profiling the BBD microbial community using molecular techniques that targeted the 16S rRNA gene. The BBD microbial communities were statistically discriminate (p < 0.05) among the three regions and between host species. The variability was driven by differences in cyanobacteria within the community as well as alphaproteobacteria, a heterotrophic group. These results suggest that, if BBD is a true polymicrobial infection, different members of the major physiological groups may be represented by different species that perform the same physiological role within the BBD consortium.



FIG. 8.25. Progression of black band disease on *Diploria strigosa*, St. John, from July 2004 to July 2005 (Photos: C. Rogers)

8.11 Sedimentation

Runoff is recognized as one of the most serious stressors affecting coral reefs in the USVI (Fig. 8.26; Hubbard 1987). Steep slopes, with more than 80% of them on St. Thomas and St. John over 35% grade, drenching rainfall, shallow easily eroded soils, and numerous drainage guts combine to increase the amounts of erosion, sedimentation and non-point source pollution that



FIG. 8.26. Development is leading to increased rates of runoff in the USVI

reach downstream marine communities. Hubbard (1987) reviewed effects of sedimentation on coral reefs and highlighted the potential for reef damage from many development projects in the USVI (see also Hubbard et al. 1987). However, almost 20 years later we still lack quantitative studies that show sedimentation rates before, during, and after upland and coastal construction that can be conclusively linked to reef degradation. Some studies show lower coral cover in areas that have higher sedimentation rates, but these correlations cannot pinpoint sedimentation as a cause of the existing benthic composition or relative abundance of corals. While there is no doubt that increasing amounts of sediment are entering nearshore waters, the effects of chronic sedimentation are harder to document than the more conspicuous results of hurricanes or coral diseases.

Development of steep hillsides in the USVI and cutting of new, unpaved roads has caused severe runoff of silt-laden water into the bays. No permanent streams or rivers occur in the islands, but runoff is a significant problem because the islands slope steeply to the coast and many reefs are so close to shore. [The highest points of land on St. Croix, St. Thomas, and St. John are 355, 472, and 389 m, respectively (Dammann and Nellis 1992)]. Plumes of silt are typically seen after short but intense rains. Runoff of sediments is an increasing concern because of the accelerating pace of development in the USVI and the very steep hillsides. New roads and driveways are being cut in areas with heavy vegetation. Measurement of erosion rates on St. John (in a study from 1998 to 2001) indicated that unpaved roads contribute up to four orders of magnitude more sedimentation than undisturbed hillsides (Ramos-Scharron and MacDonald 2005).

Sediment core testing for terrestrial based sediments deposited in nearshore wetland and coastal embayments from around St. Thomas and St. John, show that over the past 15-25 years, sedimentation rates have increased from 1 to 2 orders of magnitude (Brooks et al. 2004). Unpaved roads and altered drainage contribute the most sediment, but excavation for home and driveway constructions also contribute significantly to the sediment load. While the pace of construction development on heavily populated St. Thomas and St. Croix is moderate, St. John has seen a significant increase in the cutting of new roads and the excavation of home sites on steep inclines. As a result of physical topography and human activities on these islands, downstream marine communities, reefs especially,

are subjected to multiple stressors with unknown long term synergistic impacts.

Sedimentation rates in the Virgin Islands vary considerably among sites and seasons. Nearshore waters adjacent to highly developed watersheds (Fish Bay, Magens Bay) typically average over 10 mg/cm²/d. In contrast reefs adjacent to less developed watersheds (i.e., Lameshur Bay, Sprat Bay) or offshore cays (i.e., Flat Cay, Buck Island) receive less than 4 mg/cm²/d. Offshore reefs not associated with a land mass typically receive less than 0.5 mg/cm²/d (R. Nemeth, unpublished data 2007). Seasonal variation in sedimentation rates are usually highest during the rainy season when sediment load can increase from less than 2 mg/ cm^2/d during the dry season to greater than 30 mg/ cm²/d during a severe rain event (Nemeth and Sladek Nowlis 2001). Sometimes, however when terrigenous sediments are deposited in channels between reefs and become re-suspended during large swells not associated with storm events. For example, sedimentation rates can increase from less than $2 \text{ mg/cm}^2/\text{d}$ to over $15 \text{ mg/cm}^2/\text{d}$ when a north swell hits the north coast of St. Thomas (Nemeth and Sladek Nowlis 2001). During one study coral cover was monitored before, during, and after development in Caret Bay, St. Thomas, from July 1997 to March 1999. A weak correlation between bleaching and sedimentation and decline in coral was found, but the study took place at the time of the October 1998 bleaching event in the USVI and coral losses cannot be conclusively attributed to sedimentation. Coral cover was less than 5% on the study reef and declined along five transects by an average of 14%. This study also found a significant correlation between sedimentation rate and bleaching (Nemeth and Sladek Nowlis 2001).

8.12 Fisheries and Fish Assemblages

Here we present a brief overview of the fisheries in the Virgin Islands to provide a context for subsequent discussion of changes in reef fish assemblages over the last several decades (Fig. 8.27). The area available for fishing around the USVI is relatively small, an estimated 5,180 km² (Dammann 1969). In 1930, the population of the USVI was 22,012 and approximately 405 fishers used about 1,600 traps (Fiedler and Jarvis 1932). In the late 1950s, Idyll and Randall (1959) reported over 500 traps were in use around St. John alone. In 1961, there were 400 fishers using 838 traps (Anonymous 1961 cited in Dammann 1969). In 1968, the estimated number of fishers remained the same, but the population of the USVI had more than doubled to 55,000. In 2003 there were 383 licensed commercial fishers in the USVI, 160 in the St. Thomas /St. John District and 223 in the St. Croix District, and the USVI population had increased to almost 110,000 (Kojis 2004).

In the 1980s and 1990s, the USVI fishery greatly capitalized, and the effort increased offshore to the shelf edge. By 2003, fishers used a wide variety of gear including pots, handlines, a variety of nets, vertical set lines and scuba. Based on a census conducted by the DPNR/Division of Fish and Wildlife in 2003 (Kojis 2004), commercial fishers owned approximately 1,234 fish traps in the St. Croix District and 7,407 fish and lobster traps in the St. Thomas /St. John District. Traps were still an important fishing gear in the St. Thomas/St. John District, but had largely been replaced by other types of fishing equipment on St. Croix where fishers had experienced severe trap loss from hurricanes. Traps are more vulnerable to storm damage on St. Croix because of the narrow, shallower shelf.

Boat size changed little between 1930 and 2003 for the majority of fishers. Most commercial boats in 2003 were between 5 and 8 m long (Kojis 2004) compared to 4.6 to 6 m in 1930 (Fiedler and Jarvis 1932). However, boat ownership increased from 50% of commercial fishers in 1930 (Fiedler and Jarvis 1932) to 99% in 2003 (Kojis 2004). In 1930 very few boats had engines (Fiedler and Jarvis 1932) while by 1968 100% of boats were powered by an engine (Swingle et al. 1970). In 1967, there was a fleet of large vessels with inboard engines in the St. Croix District that ventured up to 100 miles (160 km) to catch and sell seafood (Swingle et al. 1970). This fleet declined as Caribbean countries claimed jurisdiction of their 200nm (370 km) Exclusive Economic Zone. In 2003, only 11 boats (4.4% of the USVI fishing fleet) were >30 ft (9 m) in length (Kojis 2004). However, fishers often used new technology such as GPS, echo sounders, winches and electric or



FIG. 8.27. Fishing with traps off St. John, 1909 (NPS files)

hydraulic reels to increase their fishing efficiency (Kojis 2004).

8.12.1 Changes in Fish Assemblages

Fish assemblages have been characterized and monitored intensively in the USVI. All studies have shown low abundance of fishes that are targeted by the trap fishery in the USVI. There have been losses of shelf-edge spawning aggregations, declines in fish species sizes, and changes in fish assemblage structure (Olsen and LaPlace 1978; Appeldoorn et al. 1992; Beets 1997; Beets and Friedlander 1999). Strong evidence suggests that fishing pressure had already changed the fish assemblage decades before sustained monitoring began in the late 1980s. Reef fish assemblages have changed since the 1950s and 1960s as a result of deterioration or loss of reef, seagrass, and mangrove habitats and intense fishing pressure. Even before the loss of habitats from coastal development, coral diseases, hurricanes, and other stresses, some signs of overfishing were evident (J. Randall's field notes 1958-1961; Olsen et al. 1975). Jack Randall's observations from the late 1950s and early 1960s indicate that the fishes targeted by the fishery were already in decline. He noted: "The trapping of reef fishes in pots is the major commercial fishery of the Virgin Islands. Most fishing takes place over the narrow fringing reef that surrounds much of the islands. The limited fringing reef area receives nearly all of the fishing effort, and as a consequence the effect of overfishing is evident." (Randall 1963). In reference to Lameshur Bay, St. John, he wrote: "Impressed by the lack of food fishes such as groupers and snappers. *Cephalopholis fulvus* are occasional, but I saw only two small Nassau groupers, one tiger rockfish, and no other groupers, a couple of gray snappers and schoolmasters. It would seem that there has been considerable fishing effort".

However, many commercially important fishes, including Nassau groupers, were undoubtedly more abundant in the 1960s than at present. For example, Randall speared over 100 Nassau groupers around St. John over 2.5 years (1958–1961), and this species was the most abundant grouper in his samples. In addition, he tagged 124 adult Nassau groupers in Lameshur Bay during a study between February 1959 and June 1961 (Randall 1962). A major Nassau grouper spawning aggregation site was fished out in the 1970s (Olsen and LaPlace 1978). In 1994–1999 surveys of groupers in 32 sample plots (each 5,000 m²) on four reefs around St. John, only 37 Nassau groupers were observed (Beets and Friedlander, unpublished data 2007).

Randall also mentioned midnight parrotfish as "moderately common" and spadefish as "ubiquitous". Both of these species are very rare around St. John now. No midnight parrotfishes and only a few spadefish have been observed in annual visual point count samples taken from 1988 to 2006 (Beets and Friedlander, unpubublished data). It is also unusual to see rainbow parrotfishes and hogfish. All of these fish are readily caught in fish traps and are attractive to spearfishers.

An experimental trapping study at Yawzi Point Reef over 6 months in 1993-1994 clearly showed that even a small number of traps fished over a relatively short time period caused statistically significant declines in several trophic groups (Beets 1996). Results from this investigation were also compared to records from 6 to 8 traps of similar design set by a fisher in 1982-1983 on the same reef. A comparison of the data from the two time periods 11 years apart suggests alarming changes (Beets 1997). The species composition had changed with large increases in the proportion of herbivorous fishes and decreases in the proportion of groupers and snappers. The average size of fishes in all trophic groups captured was smaller in the 1993–1994 samples. Four species of groupers caught in traps hauled during 1982-1983 were not trapped in 1993-1994. These findings are in stark contrast to the results Randall obtained from poison stations within the same bay, which showed that groupers and other related species (Serranidae) were the second most abundant group of fishes (Randall 1963).

Two studies conducted in the 1990s on St. John offer further evidence of the present scarcity of preferred predatory fish species and the increase in relative abundance of herbivorous fishes. Garrison et al. (1998) recorded the number and sizes of individuals of each species observed in traps set by fishers in 1992, 1993, and 1994 inside and outside VINP waters. Only 6 out of a total of 1,340 fish observed in traps in their study were Nassau groupers. The most abundant family of fishes observed in traps was the Acanthuridae.

In 1994, Wolff (1996) used visual censuses (Bohnsack and Bannerot 1986) and experimental trapping in four habitats (patch reef, rocky reef, gorgonian hardbottom, and seagrass) to compare species composition and vulnerability of fishes to trapping. No Nassau groupers were seen in any of the 159 visual censuses in Wolff's study, and this species comprised less than 1% of the catch when present in trap hauls, with most caught in gorgonian not stony coral habitat. Three herbivorous species, the redband parrotfish (*Sparisoma aurofrenatum*), blue tang (*Acanthurus coeruleus*), and ocean surgeon (*Acanthurus bahianus*) were the most abundant species observed in visual censuses and in traps, accounting for over 50% of the individuals recorded. The scarcity of Nassau groupers, large snappers, and queen triggerfish and the dominance of herbivorous species in these two studies are striking and indicative of overfishing.

Dominance of herbivorous fishes was also found in surveys conducted from 1998 to 2001 on St. John, St. Thomas and St. Croix where herbivore densities represented 70% of the fish on a typical reef in the Virgin Islands (Table 8.4). However, significantly higher densities of carnivores (primarily grunts and snappers) occurred on St. John reefs (p < 0.03) relative to St. Thomas and St. Croix (Table 8.4).

Recruitment of large predatory fishes, such as groupers, is presently very low on St. John reefs. Very few juvenile groupers (<10 cm) were observed in monthly samples of juvenile reef fishes on St. John from July 1997 to July 2000 (Miller et al. 2001). However a survey of shallow shoreline habitats in 2006 found Nassau groupers (n = 46) to be the most numerically abundant grouper species around St. John (search time = 1,388 min) followed by red hind (*Epinephelus gutattus*, n = 36) and rock hind (E. adscensionis, n = 25) (R. Nemeth, unpublished data). Of 11 sites on St. Thomas (search time = 958 min), the three most numerically dominant grouper species were red hind (n = 36), Nassau (n = 31) and graysby (*Cephalapholis cruentatus*, n = 11). On both islands Nassau were most common on rubble covered with macroalgae or rocky reef habitats adjacent to seagrass beds whereas red hind were found on Porites porites coral or coral rubble and patch reef habitats.

Reef fish assemblages within VINP, which is not a marine reserve, do not differ substantially from those outside the park (Rogers and Beets 2001). For example, Garrison et al. (1998) found no significant differences in the species or number of fishes observed in traps inside vs outside the park. Visual point count samples from reefs around St. John from 1989 to 1994 demonstrated no significant differences in the number of fishes, number of species or biomass of fishes per sample and for

TABLE 8.4. Density (#/100 m²) and percent composition of herbivores (Acanthuridae and Scaridae) and carnivores (Serranidae, Lutjanidae, and Haemulidae) on St. John (STJ), St. Thomas (STT) and St. Croix (STX) between 1998 and 2000 (Modified from Nemeth et al. 2003a).

Island	Herbivore density (%)	Carnivore density (%)
STJ	38.9±23.02 (60.9%)	61.1±12.91 (39.1%)
STT	27.3±11.43 (81.7%)	32.8±3.97 (18.3%)
STX	9.8±6.87 (72.6%)	35.8±5.13 (27.4%)
Virgin	14.6±18.10 (69.6%)	47.5±12.20 (30.4%) Islands

mean size of fishes observed inside vs outside park boundaries.

Standardized fish trap samples conducted inside and outside park boundaries during 1993 also documented no significant difference in number of fishes caught per trap haul (n = 145 trap hauls, t-stat: 1.24, P = 0.22; Beets 1996).

All of these studies documented the failure of federal and territorial regulations to protect reef fishes or reverse the declines in abundance of preferred species such as the large groupers and snappers. Lack of enforcement played a role; over 50% of the traps set by fishers observed during 1993–1995 had no functioning biodegradable panels (required by territorial legislation) to allow fish to escape if traps were lost or abandoned (Garrison et al. 1998). Enforcement is difficult since many trap lines are set without buoys, or with buoys located across park boundaries. It is also confounded because park legislation allows traditional fishing with traps, and distinguishing between commercial and traditional fishing is problematic. However, it is unlikely that even full compliance with existing regulations would be adequate to reverse the alarming trends.

8.13 Reef Fish Monitoring Trends at Long-time Sites in St. John: 1989–2006

Trends in reef fish assemblage characteristics in VINP over the past 17 years have been dominated primarily by storm effects. Monitoring of four reference sites (Yawzi Point, Haulover Bay, Tektite Reef, and Newfound Bay, outside the park) began following Hurricane Hugo in 1989, the largest storm to pass the Virgin Islands in decades, which had a large impact on reef substrate, encrusting organisms (especially corals), as well as reef fishes. Similar impacts were documented following the second largest storm that passed the Virgin Islands during the past 20+ years, Hurricane Marilyn (1995). Although these large storms damaged reef structure and decreased coral cover in shallow water, reef fish abundance and species richness recovered within 3–5 years following these impacts (Fig. 8.28).

During the past several years, the most profound changes in the reef fish assemblage have been shifts in trophic structure. From 2000 to 2005, the abundance of planktivorous fishes has increased, along with their proportion of total abundance that has surpassed the previously dominant guild of herbivorous fishes (Fig. 8.29). The plantivorous damselfishes (Chromis spp.) are the dominant species responsible for the increase. Numerous factors may contribute to this shift, but the changes in benthic cover with the large decrease in coral cover and subsequent increase in algal cover are probably large contributors. Additionally, reduction in habitat complexity associated with these biotic changes has likely affected the distribution and abundance of many reef fish taxa.

The massive coral bleaching /disease event in 2005 apparently had an effect on trophic structure, with a decline in planktivorous fishes and increases in herbivorous fishes on all four reference reefs. Abundance increases were noted for small benthic herbivores (benthic damselfishes) and large mobile herbivores (parrotfishes and surgeonfishes). These increases in herbivore abundance are likely correlated with the increase in macroalgae cover as a result of the bleaching and disease mortality.

Predatory fishes provide strong regulatory effects in reef systems (Hixon 1991; Bascompte et al. 2005) and have experienced large changes in abundance over decades throughout the Caribbean (Jackson et al. 2001; Pandolfi et al. 2005). Large fishes, particularly the intensively harvested grouper and snappers, declined in the USVI prior to the establishment of NPS monitoring programs (Beets and Rogers 2002; Beets and Friedlander unpubl. data 2007). During the 17-year monitoring period, the frequency of occurrence of large groupers in



FIG. 8.28. Trends in average reef fish abundance and biomass (+SD) over 17 years of monitoring on four reference reefs, St. John, US Virgin Islands, 1989–2006 (Beets and Friedlander, personal communication)

samples has declined and remained very low since 2000 (Fig. 8.30). A mid-sized grouper, red hind (*Epinephelus guttatus*), has shown an increase during recent years, likely in response to the spawning aggregation closure enacted in 1990. Small groupers have increased during recent years, probably due to ecological release in response to sustained low numbers of larger groupers.

The reef fish assemblage in the USVI has suffered the loss of large predators and declines in abundance across all trophic levels resulting from decades of overfishing, prior to the 2005/06 bleaching and disease mortality. This release from top-down control has likely increased the importance of bottom-up processes such as disturbance events and habitat loss.



FIG. 8.29. Trends in average abundance among reef fish trophic guilds over 17 years of monitoring on four reference reefs, St. John, US Virgin Islands, 1989–2006. Herb = herbivores, Pisc = piscivores, Sec. Consumer = secondary consumers, and Plank = planktivores

8.14 Monitoring Trends for Commercially Important Reef Fish Species: St. Croix and St. Thomas

Nemeth et al. (2004) found at St. Croix that commercially important species (e.g., groupers, snapper, angelfishes, triggerfishes) are rarely seen but are more frequently observed at mid-shelf and shelf-edge sites where average fish size also tends to be larger. Species richness and diversity of fishes did not appear to be correlated with the amount of living coral or algal cover. Wrasses, damselfishes, parrotfishes and surgeonfishes were the most numerically abundant fishes on both St. Croix and St. Thomas with all other families representing less than 2% each. A comparison of relative abundance of eight commercially and ecologically important fish families in St. Croix showed little change (mean = 0.01%, range = -2.75 to 3.05%) between 2001 and 2004 surveys. Average relative abundance for these families between St. Croix and St. Thomas in 2004 were: Scaridae (40% vs 43%), Acanthuridae (25% vs 15%), Haemulidae (10% vs 8%), Serranidae (10% vs 4%), Chaetodontidae

(7% vs 14%), Balistidae (5% vs 1%), Pomacanthidae (2% vs 2%), and Lutjanidae (2% vs 13%).

Between 2001 and 2004, most commercially important species on St. Croix increased an average of 2 cm in length with the exception of parrotfishes and grunts that were smaller by 3.0 and 2.5 cm, respectively. In 2004, commercial species on St. Thomas were, on average, 5 cm larger (range = 0-9 cm) than on St. Croix. This trend in fish size was also found by Nemeth et al. (2006a) for spawning populations of red hind on St. Thomas and St. Croix.

Known grouper spawning sites in the USVI include Red Hind Bank, Grammanik Bank and Lang Bank, and snapper spawning sites include Seahorse Cottage Shoal, Red Hind Bank, Mutton Snapper and Grammanik Bank. The Red Hind Bank, also known as the MCD, prohibits all fishing year round. The Grammanik Bank, which has been seasonally protected since 2005, is a unique multispecies spawning aggregation site that supports at least four species of groupers and three species of snappers. Heavy fishing on the Grammanik Bank spawning aggregation removed about 10,000 pounds of yellowfin grouper in March 2000 and 2001 (USVI DFW, unpublished data 2007) and



FIG. 8.30. Trends in the frequency of occurrence of groupers in samples over 17 years of monitoring on four reference reefs, St. John, US Virgin Islands, 1989–2006

is suspected to have caused the aggregation not to form in 2002 (R. Nemeth, personal observation 2006). Continued fishing on the Grammanik Bank is thought to have caused decreases in yellowfin and Nassau groupers between 2003 and 2004 as well. However, since the seasonal closure was implemented in 2005, spawning population estimates of yellowfin grouper have increased from ca. 600 to over 1,000 fish, and Nassau grouper have increased from ca. 100 to nearly 200 fish in 2006, the first potential recovering spawning aggregation in the Caribbean. Spawning aggregations of tiger grouper, cubera snapper and dog snapper contain up to 100, 800 and 1,000 fish, respectively. All aggregating species use similar sections of the reef and frequently overlap in time (Nemeth et al. 2006b).

8.15 Reef Fish Monitoring at Randomly Selected Sites Among Different Benthic Habitats: St. John and Buck Island

Reef fish data collected by the NOAA Biogeography Program between 2001 and 2005 around St. John and Buck Island showed that community structure and fish assemblages varied considerably among different benthic habitats (Menza et al. 2006). The fish community was defined as the compilation of all observed fish species, community structure as indices of diversity or density for the community, and fish assemblages as components of the fish community categorized by trophic group or taxonomic family. Fish-habitat relationships were identified by grouping spatially explicit fish data according to the benthic habitat type in which the data were collected and examining the mean and variance of samples. Benthic habitat types were differentiated using regional benthic habitat maps (Kendall et al. 2001).

Nonparametric analysis of variance indicated that habitat types significantly explained some of the variance in species richness, species diversity (Shannon-Weaver), grouper density, snapper density, herbivore density and piscivore density (Table 8.5). At Buck Island the highest species richness and assemblage densities were typically found in linear reef, aggregated patch reef, and individual patch reef habitats and were lowest in sand, seagrass, and scattered coral/rock in sand habitats (Fig. 8.31). At St. John, the highest species richness and assemblage densities were not found to be as consistently associated with habitat types as around Buck Island. Species richness, community density and grouper density were highest at midshelf reef sites, but densities of snappers and piscivores (all species combined) were conspicuously low (Fig. 8.32). The distinction among relative densities of piscivores and groupers at Mid-Shelf Reef sites suggests that groupers were not a large component of the piscivore assemblage. Aggregated patch reefs, individual patch reefs, and colonized bedrock habitats also possessed high densities for some of the tested assemblages (e.g., snapper, herbivores, piscivores), but this pattern was not consistent across assemblages (Fig. 8.32). As in the Buck Island study area, sand and seagrass habitats were associated with low assemblage densities and species richness.

Most reef fish community measures, except density, showed little annual change between 2001 and 2005 (Fig. 8.33) (Menza et al. 2006). Multiple comparisons using 95% confidence intervals (with sequential Bonferroni correction) indicated that significant changes occurred in community density at BIRNM (2002>2003; 2002>2004; 2002 >2005) and species richness in VINP (2003> 2005). In 2002, the community density estimate at BIRNM and VINP had an abnormally large confidence interval. The large interval in both parks is an indication that the increase may have been a regional phenomenon (Menza et al. 2006). Metrics for trophic or taxonomic components of the fish community were more variable than for the whole community, yet changes in grouper density (2002>2005), snapper density (2002> 2004), piscivore density (2002>2005) in BIRNM and grouper density and frequency of occurrence (2005>2004) in VINP were found (C.I.=0.95, Menza et al. 2006). Density estimates for grouper, snapper, and piscivore assemblages were all larger in 2002 than in other years, partly explaining high community density in 2002. Grouper, snapper, and piscivore density decreased monotonically from 2002 to 2005 in BIRNM and snapper density in VINP decreased from 2001 to 2005.

Temporal changes were also observed in total number of red hind and Nassau groupers (*Epinephelus guttatus* and *E. striatus*) between 2001 and 2006 (Table 8.6; NOAA Biogeography Program, unpublished data 2007). The observed increase was greater in St. John, where the total number of red hinds (<35 cm) increased steadily from 21 individuals in 2001 to 90 in 2006. There was greater variability in the number of red hinds at Buck Island, with total observed ranging between 42 and 52 individuals during the same period. Very few larger red hind and Nassau groupers (>35 cm) were observed during the 5-year study, but more of them were seen at St. John than at Buck Island (Table 8.6).

TABLE 8.5. The results from a nonparametric analysis of variance (Kruskal-Wallis test) for species richness, community density, and assemblage densities among 12 habitat types in the (A) Buck Island and (B) St. John study areas. (A) Buck Island.

Community or Assemblage (Metric)	Kruskal-Wallis H	P [H] $< \chi^2_{0.05,10}$
Species richness	494.89	< 0.0001
All species (density)	394.21	< 0.0001
Groupers (density)	393.24	< 0.0001
Snappers (density)	81.12	< 0.0001
Herbivores (density)	452.96	< 0.0001
Piscivores (density)	24.36	0.0113
(B) St. John		
Community or assemblage (Metric)	Kruskal-Wallis H	P [H] $< \chi^2_{0.05,10}$
Species richness	318.14	< 0.0001
All species (density)	256.01	< 0.0001
Groupers (density)	168.73	< 0.0001
Snappers (density)	31.65	0.0016
Herbivores (density)	299.47	< 0.0001
Piscivores (density)	22.37	0.0335



FIG. 8.31. Plots of density (fish per unit area) or species richness against variance among distinct habitat types in the Buck Island study area. Benthic habitat types are defined as: 1– colonized bedrock, 2 – colonized pavement, 3 – colonized pavement with sand channels, 4 – linear reef, 5 – macroalgae, 6 – aggregated patch reefs, 7 – individual patch reefs, 9 – sand, 10 – scattered coral/rock in unconsolidated sediment, and 11 – seagrass

8.16 Spawning Aggregations

Research on reproduction in reef fishes has a long history in the Virgin Islands starting with Randall's observations of parrotfish spawning aggregations off St. John in the late 1960s (Randall and Randall 1963; see also Colin 1996). Early work on Nassau grouper spawning aggregations off St. Thomas in the 1970s documented their vulnerability to overfishing and extirpation (Olsen and LaPlace 1978). Extensive studies of bluehead wrasse (*Thalassoma bifasciatum*) by Warner and others on St. Croix in the 1980s and 1990s laid the foundation for theoretical and empirical studies of reproductive strategies in reef fishes (Warner 1988, 1990; Warner and Swearer 1991). Most recently a renewed interest in the importance of spawning aggregations (Fig. 8.34) to sustaining local fisheries has resulted in the use of new techniques (Whiteman et al. 2005) and provided new information on the reproductive



FIG. 8.32. Plots of density (fish per unit area) or species richness against variance among distinct habitat types in the St. John study area. Benthic habitat types are defined as: 1 – colonized bedrock, 2 – colonized pavement, 3 – colonized pavement with sand channels, 4 – linear reef, 5 – macroalgae, 6 – aggregated patch reefs, 7 – individual patch reefs, 9 – sand, 10 – scattered coral/rock in unconsolidated sediment, 11 – seagrass, and 12 – MSR (Mid-Shelf Reef)

characteristics and movement patterns of commercially important grouper and snapper species (Beets and Friedlander 1999; Nemeth 2005; Kadison et al. 2006; Nemeth et al. 2006a, b, 2007).

Since 1999, a long term study of a previously fished red hind spawning aggregation in St. Thomas documented that protection during the spawning season can result in population recovery. Nemeth (2005) found that the average size of red hind increased 10 cm during 12 years of seasonal closure. From 2000 to 2003 average density and biomass of spawning red hind increased over 60% and maximum spawning density more than doubled following permanent closure. Nemeth (2005) estimated that total population size increased dramatically from ca. 11,000 red hind in 1997, to 26,000 in 2000, 38,000 in 2001 to over 84,000 red hind in 2003. Strong recruitment into the spawning population and protection from fishing mortality of resident fish within the Marine Conservation



FIG. 8.33. Annual estimates of the community measures of species richness, biomass, species diversity, and density within (A) BIRNM and (B) VINP during 2001–2005. Error bars are 95% confidence intervals

District most likely contributed to these dramatic increases. Data from St. Thomas port landings show the average length of red hind from the commercial catch has also steadily increased since the season closure was established (Fig. 8.35). Moreover, interviews with commercial and recreational fishermen around St. Thomas during the past several years highlighted a general perception that the red hind being caught now are larger and more abundant than before the MCD was established (Pickert et al. 2006).

However, a seasonally protected area may not have the same effect on every spawning population. For example, a comparative study of two spawning aggregations in the USVI found that 10 years of seasonal protection resulted in significant increases in length and biomass of *E. guttatus* on St. Thomas but little change on St. Croix (Nemeth et al. 2006a).

TABLE 8.6. Number of observed *Epinephelus guttatus* and *E. striatus* individuals for two different size groups observed at Buck Island, St. Croix, and St. John, USVI, between 2001 and 2006 (Data: NOAA Biogeo, http://www8. nos.noaa.gov/biogeo_public/query_fish.aspx).

Region	Size class (cm)	Species	2001	2002	2003	2004	2005	2006
Buck Island, St. Croix	1–35 cm	Epinephelus guttatus	42	56	60	34	87	52
		E. striatus	0	0	0	0	1	2
St. John		E. guttatus	21	57	60	78	68	90
		E. striatus	0	0	0	2	2	2
Buck Island, St. Croix	36–45 cm	E. guttatus	0	0	0	1	3	1
		E. striatus	0	0	0	0	1	0
St. John		E. guttatus	0	1	1	6	0	4
		E. striatus	0	0	0	0	1	0



FIG. 8.34. Red hind length data (±SD) from port sampling (PORT) and spawning aggregation catches (SPAG) from 1975 to 2003. Seasonal closure of aggregation site was in 1990 and permanent closure was in 1999 (From Nemeth 2005)

Although a variety of factors may have influenced these differences, it was found that the Lang Bank, St. Croix, spawning site was only 600 m from the closure boundary while on St. Thomas the closure boundary was over 3km distant (Nemeth et al. 2006a, 2007). The close proximity of the spawning aggregation to the closure boundary may not have been sufficient to protect the aggregation from poaching or fishing activity on the boundary edge during daily or monthly movements of spawning E. guttatus. Tagging studies have shown red hind can migrate 2-30 km to spawning aggregation sites and remain on the spawning site from 1 to 8 weeks. In addition, their spawning is highly synchronized with the lunar cycle (Nemeth 2005; Nemeth et al. 2007). All these factors make them very vulnerable to fishing mortality.

In addition to the two red hind spawning aggregation sites, larger groupers (Nassau, vellowfin, and tiger), snappers (cubera, dog, mutton and schoolmaster) and possibly jacks (black, permit, horse-eye) form spawning aggregations on the Grammanik Bank and within the MCD south of St. Thomas (Nemeth et al. 2006b; Kadison et al. 2006). Mutton snapper also spawn off southwest St. Croix. While these sites typically occur close to the shelf edge other sites on the mid-shelf (i.e., Seahorse Cottage Shoal) host spawning aggregations of lane and gray snapper. Year-round protection exists for the Red Hind Bank while seasonal closures include Lang Bank (December 1-February 28), Grammanik Bank (February 1-April 30) and Mutton Snapper (March 1–June 30).



FIG. 8.35. Aggregation of spawning red hind (*Epinephelus guttatus*) located on Lang Bank, St. Croix, at 30 m depth on old spur-and-groove reef (Photo: R. Nemeth)

8.17 Acoustic Tracking of Reef Fishes

A current project to examine movement of fishes in space and time among management units around St. John uses an array of in situ acoustic receivers to track fishes implanted with "pinging" tags. Results to date show consistent diel movement of grunts off-reef to adjacent seagrass beds just after sunset, returning to the reef just before dawn. Other species such as groupers have shown strong site fidelity and little within reef movement. Such studies provide a better understanding of the linkages between ecosystem components and potential benefits of the new monument (VICRNM) to adjacent areas from enhanced reproductive output and adult spillover into VINP and adjacent harvested areas (Friedlander and Monaco, personal communication 2007).

8.18 Evaluating the Effectiveness of Marine Reserves

Recognition of the changes in the fish assemblages in the USVI was a primary basis for the establishment of the National Park Service national monuments. Evaluation of the effects of these monuments is a primary consideration in recent research. For example, Monaco et al. (2007) sampled fishes and habitats along the mid-shelf reef (17-35 m) within the southern portion of the VICRNM using belt transects in July 2002, 2003 and 2004. They compared benthic habitat and fish assemblage characteristics (species richness, numerical density, biomass density) inside and outside the monument. Rugosity and live coral cover were greater outside the VICRNM than inside. Fish biomass, species richness and fish density were all significantly greater outside the national monument. Of the few economically important groupers that were observed, more were seen outside the monument.

8.19 Conchs and Lobsters

Queen conchs (*Strombus gigas*) support valuable fisheries in the Caribbean (Brownell and Stevely 1981). Historically, queen conchs were extremely abundant around St. John. Randall (1964) and colleagues collected and observed hundreds of queen conchs during investigations of their biology. Schroeder (1965, p. 8) mentioned "conchs by the thousands in Salt Pond Bay", St. John during his work with John Randall. Conch are not abundant today. Concerns over overharvesting of this species led to a moratorium in St. Thomas and St. John from 1988 to 1992. In spite of this moratorium, additional regulations in 1994, and a limit of two conchs per person per day for VINP waters, as of 1996, conch populations in general appeared to be decreasing and density of conchs inside park waters was not significantly higher than outside the park (Friedlander 1997). Conchs were surveyed along transects around St. John and St. Thomas in 1981, 1985, 1990, 1996 and 2001 (Wood and Olsen 1983; Boulon 1987; Friedlander et al. 1994; Friedlander 1997; Quinn and Hanrahan 1996; Gordon 2002). Surveys in 1996 showed that conchs were usually found in seagrass beds. This habitat has been reduced greatly as a result of hurricane and anchor damage.

Transects surveyed in 1996 were re-evaluated in 2001 to compare densities of juvenile and adult conchs around St. Thomas, St. Croix, and St. John at several different depths and in different habitats. A total of only 244 conchs were found in 22 transects (Gordon 2002). Conch abundance and density were examined in 1998/99 in six shallow backreef bays around St. Croix. Most of the conchs were juveniles and were found in seagrass habitats, suggesting these bays are important nursery areas (Tobias 2005).

Because conchs have patchy distributions and move among several habitats and over a gradient of depths, it is difficult to document and interpret changes in their abundance.

Wolff (1998) noted that lobster densities at Fish Bay and Reef Bay in 1996 were similar to those in 1985 (Boulon 1987), and densities in Lameshur Bay and Tektite Reef in 1996 were similar to estimates made in 1970 (Cooper et al. 1975). However, overall data suggest that there has been a large decline in the average size of the lobsters within the park since 1970 (Olsen et al. 1975). Virgin Islands National Park regulations allow only two lobsters to be taken per person per day; however, it is widely known that harvest exceeds this amount.

Tobias (2000) noted that lobsters accounted for 6% of total reported fishery landings for the USVI in 1998–1999. He reported a 10% decrease in mean

size between 1997 and 2000, which suggests that overfishing is occurring (Tobias 2000; Mateo and Tobias 2002; see also Bohnsack et al. 1991). The USVI Division of Fish and Wildlife routinely monitors commercial lobster landings (weight and carapace length) and has periodically monitored lobster recruitment around St. Thomas where recruitment appears to be highly variable but generally low (Gordon and Vasques, personal communication).

Florida Fish and Wildlife Conservation Commission (Florida Marine Research Institute) scientists conducted spiny lobster surveys annually from 2004 to 2006 at BIRNM (unpublished data 2006). Timed lobster surveys were conducted on scuba inside and outside the park boundaries in hardbottom habitat (depth range 3-40 m). On average 150-190 lobsters were found on 35-45 surveys. Sizes ranged from an individual with 10 mm carapace length (CL) found at the base of a linear reef to one with 130 mm CL found on a deep reef west of the park boundary. Most spiny lobsters were found in backreef habitats. The mean size of adult Panulirus argus found inside the park was 99 mm CL (N=64). Juvenile habitat was not found in the park but located inside Tague Bay among near shore patch reefs covered with rubble and algae. Although spiny lobster habitat at BIRNM has been severely degraded by coral disease and hurricanes, the Monument remains an important refuge for this commercially important species. The designation of the East End Marine Park also provides critical habitat protection for juvenile spiny lobsters not found in the Monument (Florida Marine Research Institute, unpubl. data 2006).

8.20 Ecological Relationships and Processes

Coral reefs, mangroves, and seagrass beds in the Caribbean are linked through the movement of larval and adult organisms and the transport of nutrients (Ogden and Gladfelter 1983; Meyer et al. 1983; Ogden 1997). Numerous research projects in the USVI have explored relationships among habitats, among habitats and organisms, and ecological processes such as recruitment, herbivory, and calcification. The West Indies Laboratory on St. Croix was a key study site for the Seagrass Ecosystem Study (SES), one of the programs of the International Decade of Ocean Exploration (IDOE) funded by the US National Science Foundation from 1974 to 1979. The SES put seagrasses on the global map, emphasized the interconnection with coral reefs, and produced a few hundred publications and several books.

At the start of the SES in the early 1970s the prevailing view was that detritus was the primary pathway for seagrass production into higher trophic levels. By the end of the program, however, a large number of grazers had been identified and studied but the percentage of seagrass production going to direct grazers was still estimated to be relatively small. Research interest in seagrass herbivores and their importance has grown steadily (Larkum et al. 2006). The global estimated percentage of production grazed is still < 30%. Recent historical ecology studies have concluded that prior to extensive harvesting of Caribbean marine resources by humans the seagrass fauna was dominated by large herbivores, especially green turtles and fishes (Jackson et al. 2001).

Seagrass beds in the USVI are not as extensive as they once were because of severe anchor damage and hurricane effects (Rogers and Beets 2001). Data on seagrass densities and changes over time appear in Williams (1988) and Muehlstein and Beets (1999). The installation of mooring buoys in VINP has resulted in some increase in density of seagrasses (NPS, unpublished data).

Scientists with the West Indies Laboratory produced some key papers on urchin and fish herbivory and the relationship of different levels of herbivory to productivity (Ogden et al 1973; Carpenter 1990a, b). Carpenter (1990a) showed a dramatic increase in macroalgae after the sea urchin (Diadema antillarum) die-off in 1983/84 (Lessios et al. 1984) and a decrease in rates of primary productivity. He also showed an increase in herbivorous fish population densities and an increase in their grazing intensity after the die-off (Carpenter 1990b). Levitan (1988) showed a 30-fold increase in algal biomass in St. John after the mass mortality of the sea urchins. In an early study, Rogers et al. (1984) showed a decrease in abundance with depth from the surface to 37m on both walls of Salt River Submarine

Canyon, St. Croix (density 2.6 ind/m^2 at 9 m and 0 at 37 m).

Although there are signs of a population recovery of Diadema antillarum in St. Croix (Fig. 8.36) and elsewhere throughout the Caribbean (Miller et al. 2003; Carpenter and Edmunds 2006), population densities generally remain low on shallow reefs, and even lower at greater depths. Between 1998 and 2000, Nemeth et al. (2003b) reported a range of 0.3-11.5 Diadema/100 m² for shallow reefs around St. John, St. Croix, and St. Thomas, while Kuffner (unpublished data 2007) noted an average of 0.86/m² from several shallow sites surveyed around St. John in 2004. In a more recent survey (July–September 2006), densities of 1–3/m² were found from sites about 2m deep around St. Thomas. Although these urchins are becoming more abundant around St. Thomas, their densities are still lower than those reported by Hay and Taylor (1985) for Brewers Bay, St. Thomas before the die-off (Walters et al., unpublished data 2006).

UVI also monitored populations of the important herbivorous urchin *Diadema antillarum* at coral reef monitoring sites and found an average of 2.3 urchins/100 m^2 , with a maximum at Great Pond, St. Croix, of 28.4 urchins/100 m^2 . Most urchins were found in shallower sites and were patchy in distribution as 70% of urchins encountered at 34 sites were at shallow (<12 m) nearshore reefs, and 60% of all urchins were concentrated at only four of 34 sites.

8.20.1 Calcification and Herbivory

By quantifying rates of photosynthesis, respiration, calcification, and dissolution of reef communities under two different levels of Diadema antillarum herbivory (no urchins and high density) Kuffner et al. (personal communication) explored effects of grazing on reef metabolic processes. They used the Submersible Habitat for Analyzing Reef Quality (SHARQ). Biogeochemical measurements were made before and after urchins were transplanted into reef areas (plots) enclosed within the SHARQ (two pairs of plots, one control and one with urchins added). The reef plots where urchins were introduced (at densities similar to those before the Diadema die-off-4.3 urchins/m²) showed statistically significant reductions in the standing crop of algae and reef productivity in one set of plots,



FIG. 8.36. The sea urchin, *Diadema antillarum*, is becoming more abundant in shallow water in the USVI (Photo: P. Mayor)

and reduction in respiration rates in the other set. Though replication was limited due to the large scale of the experiment, this work supports the hypothesis that algal-dominated reefs may experience higher area-specific rates of productivity and/ or respiration compared to reefs that are regularly grazed by herbivores.

8.20.2 Connectivity

The degree of connectivity among the marine reserves and other MPAs in the USVI has significant management implications not only for the USVI but for the entire Caribbean region. Recent papers by Cowen et al. (2000, 2006) present a model of current patterns and potential dispersal of reef fish larvae which demonstrate that St. Croix could be more isolated than many other land masses, indicating that local management could be more significant for this island than "upstream" areas. A finer resolution model for the USVI, with more shallow water bathymetry and current data, is needed. Significantly, although most marine organisms have planktonic larvae that can be dispersed over large distances, evidence to date suggests that most larvae of reef-associated animals come from within tens of kilometers rather than hundreds of kilometers away. This finding suggests the need for more closely linked reserves throughout the region. Cowen's et al. (2000, 2006) models focused on fish larvae. A similar model of the transport of elkhorn coral larvae throughout the Caribbean has been presented by Baums et al. (2005b). It suggests some separation of elkhorn populations in eastern and western regions of the Caribbean, with mixing near Puerto Rico.

If the reserves are largely dependent on local habitats and fish assemblages for larvae for replenishment, local management becomes even more critical. For example, bluehead wrasse are locally retained around St. Croix (Warner et al. 2000; Hamilton et al. 2006). Also further research on movement of adult fishes and patterns of habitats use is needed for a better understanding of connectivity among reefs, reserves, and adjacent exploited areas. NOAA has just begun a tagging and telemetry study of several species of fishes within VINP and VICRNM (see above).

The connections between seagrass ecosystems and reefs have been examined by many scientists working in the USVI, including Randall (1963, 1967), Meyer et al. (1983), Robblee and Zieman (1984), Beets et al. (2003), Kendall et al. (2003), and Grober-Dunsmore et al. (2006). In general, proximity of seagrass beds appears to increase diversity and abundance of reef fishes.

Mangroves in the USVI are little-researched. Mangroves filter sediments from runoff, provide nursery habitat, and have trophic/nutrient links to seagrass beds and coral reefs (Ogden 1988). Mangrove forests are not extensive in the islands, and many have been removed by filling and dredging, or killed by droughts and hurricanes. Most are primarily narrow fringes around sheltered bays and salt ponds, although large mangrove areas are found near Salt River, St. Croix, and Benner Bay/ Cas Cay, St. Thomas. They are important nurseries for grunts, snappers, and other reef fishes (Boulon 1992; Adams and Tobias 1994).

8.20.3 Fish/reef Interactions

In response to the devastating coral losses in the USVI, the National Park Service and USGS have begun censusing fish along randomly selected transects at long-term study sites in St. John. Other, ongoing studies are exploring the correlation between fish assemblage characteristics and the amount of living coral and reef topographical complexity ("rugosity"). NOAA's fish monitoring program suggested that fish community structure on reefs in St. John were influenced by the amount of live coral cover and structural complexity. Total fish abundance and fish species richness increased, whereas fish diversity decreased significantly with an increase in live coral cover and reef rugosity (Figs. 8.37 and 8.38). The decrease in fish diversity as percent live coral cover increased may have resulted from an overwhelming abundance of a few species (e.g., Chromis spp.) at sites with high coral cover, which could have reduced the overall fish diversity of those sites compared with sites having lower coral cover. The percent live coral cover was significantly correlated with reef rugosity ($r^2 = 0.37$,

p = 0.00). Additionally, the overall average percent live coral cover measured at 144 reef sites in St. John was 7.5% and has not changed significantly since 2001, although data on coral cover since the 2005/06 bleaching/disease event have not yet been analyzed ($r^2 = 0.02$, P = 0.09). Thus, fish community structure and reef condition (coral cover) in St. John were spatially rather than temporally correlated, such that reefs with more live coral supported greater numbers of fish individuals and species than did less healthy reefs.

In another study, a positive relationship ($r^2 = 0.85$, P < 0.005) between coral cover and fish density was found (Fig. 8.39) at 16 sites around St. Thomas and St. John, but no relationship between coral cover and fish diversity (H') (R. Nemeth, unpublished data). Also AGRRA (Atlantic and Gulf Rapid Reef Assessment Program) surveys between 1998 and 2000 in the USVI and the British Virgin Islands found a weak relationship between fish species richness and percent live coral cover ($r^2 = 0.30$, p < 0.01) (Nemeth et al. 2003a).

8.20.4 Coral and Fish Recruitment

Research on coral recruitment has taken place on St. John, St. Croix, and St. Thomas. Rogers et al. (1984) examined different recruitment rates at depths from 30' to 120' (9-37 m) at Salt River Submarine Canyon, St. Croix. Rogers and Garrison (2001) showed relatively high recruitment in the scar created on a reef by a cruise ship within VINP but no increase in coral cover over at least 10 years. Many of the studies show similar densities in coral recruits, 15-25 juveniles/m² (Rogers and Garrison 2001; Edmunds 2000, 2004). Juvenile corals in Great Lameshur Bay (GLB), St. John, have been studied extensively by Edmunds (2000, 2004, 2006). Starting in 1994, the density of juvenile corals - defined as colonies <40 mm diameter - has been documented at six sites within and near GLB, and starting in 1996, individual juvenile colonies have been tagged to track their fates (e.g., growth, mortality). These annual surveys are in shallow water (5-9 m deep) and are biased towards the subset of species that are encountered in large numbers as small colonies: Porites, Agaricia, Siderastrea and Favia. Over 14 years, the density of juvenile corals generally has remained high



FIG. 8.37. Comparison of fish abundance, species richness, and diversity among reef sites classified by coral cover in St. John, USVI

(e.g., up to a mean of 22 juveniles/m²) relative to other Caribbean locations (Edmunds 2000, 2004), although there has been a high degree of spatio-temporal variability (Edmunds 2000). Seawater temperature can account for much of the variation in density of juvenile corals among years with, somewhat surprisingly, the density increasing in years characterized by warmer



FIG. 8.38. Results of regression of mean fish species abundance, richness, and diversity against mean reef rugosity for reefs in St. John, USVI

average seawater temperatures (Edmunds 2004). It is unclear, however, to what extent this effect represents the consequence of high temperature on larval development, or post-settlement events that influence the growth and survivorship of juvenile colonies.

While elevated temperatures of extreme magnitude clearly result in coral death, sublethal



FIG. 8.39. The relationship between coral cover and fish density at 16 sites around St. Thomas and St. John. Blue = mid-shelf and shelf-edge reefs, yellow = mid-shelf cays, red = nearshore. BP = Black Point, LB = Long Bay, BB = Benner Bay, FBI = Fish Bay inner, FBO = Fish Bay outer, GLBI = Great Lameshur Bay inner, GLBO = Great Lameshur Bay outer, BOT = Botany Bay, CBV = Caret Bay Vluck, BI = Buck Island, SB = Sprat Bay, FC = Flat Cay, SC = South Capella, SH = Sea Horse, CS = Collage Shoal, RH = Red Hind Bank, GB = Grammanik Bank

increases in temperature would be expected to accelerate the development of coral larvae (Edmunds et al. 2001; O'Conner et al. 2007), and probably also would affect larval settlement, metamorphosis, and post-settlement success. Small increases in temperature could enhance coral recruitment by accelerating larval development, restricting larval dispersal (O'Conner et al. 2007), and promoting larval settlement and metamorphosis, or they could modify postsettlement success by reducing the growth of new recruits and juvenile colonies, and perhaps increasing their mortality rates (Edmunds 2004). Teasing apart the effects of temperature on pre- and post-settlement events will be difficult, but one approach with considerable promise is the use of settlement tiles to sample competent coral larvae in local habitats differing in thermal regimes. One potential mechanism underlying the reduced growth of juvenile corals at higher temperatures in St. John recently was identified by a more detailed analysis, which revealed that warm water favored isometric growth (i.e., growth that is independent of size), while cool water favored positive allometry for growth (i.e., growth rates were accelerated at greater size) (Edmunds 2006).

Kojis (1997) examined annual scleractinian and milleporan recruitment to terracotta tiles at three sites around St. Thomas : Saba Island, Fortuna Bay, and Hans Lollik Island. Twenty terracotta tiles were deployed on PVC arrays at each site and retrieved annually over a 2-year period (mid-1992-mid-1994). The deployment depth ranged from 9 to 12 m at Saba Island and Fortuna Bay and 1-5m at Hans Lollik. Scleractinia comprised 62.3% of the recruits at the two southern sites and 91.8% of the recruits at the northern site, while Millepora comprised 37.9% of the recruits at the southern sites and 8.2% at Hans Lollik. The dominant Scleractinia recruiting to the tiles were the Poritidae, Agariciidae, and Faviidae. Most of the poritid recruits were Porites astreoides and most of the faviid recruits were Favia fragum. The agariciid recruits could not be identified to species. Only one Acropora spat recruited to the tiles, indicating a low recruitment rate for this genus. Recruits from the family Agariciidae were more common at the northern and shallower Hans Lollik site than at the two sites south of St. Thomas, comprising 44-48% of the recruits at Hans Lollik compared to 8.6–13.2% at the Fortuna and Saba sites. Poritids dominated recruitment at the two southern sites, comprising 65–82% of all scleractinian recruits. In contrast, poritids comprised only 38–44% of the recruits at Hans Lollik. Faviid recruitment varied from 8.1% to 22.6% over all sites and showed no difference with locale.

Nemeth et al. (2003b) reported coral recruit densities ranging from 4.4 to $10.3/0.25 \text{ m}^2$ quadrat for shallow reefs in St. John, St. Thomas, and St. Croix. The most abundant species were *Siderastrea* spp, *Agaricia* spp., and *Porites* spp.

Steneck (unpublished data 2005) examined coral recruitment to terracotta tiles in St. John, St. Croix, Belize, Mexico, Bonaire and the Bahamas. The average number of coral recruits per plate was lowest in St. Croix (<1), within Buck Island Reef National Monument, which at the time of the study was not a "no take" zone. Recruitment for the Newfound and Haulover sites in St. John (ca. 2.5) was lower than in Bonaire but higher than all other locations.

Recruits of *Acropora palmata* can be impossible to distinguish from remnants of colonies that have suffered partial mortality from bleaching, disease, and other causes. In general, few recruits of this species or the other major reef-building coral in the USVI, *Montastraea annularis* complex, are found in settling plate studies. Nemeth et al. (2004) found that density of *Acropora* recruits within sampling quadrats ranged from 0.1/m² at Caret Bay and Flat Cay to 0.9/m² at Coculus Point. Spawning of *A. palmata* was observed in 2004 and 2005 in St. John, but not in 2006.

Most of the coral recruits observed in the USVI studies have been from the Poritidae and Agariciidae, as has been shown for other Caribbean locations. *Agaricia* was particularly hard hit by the 2005 bleaching event (NPS, unpublished data), and recruits from these species could possibly decrease in abundance.

Several studies of fish recruitment, in addition to those referred to in this chapter, have been conducted in the USVI (Booth and Beretta 1994; Nemeth 1998; Tolimieri 1995, 1998a, b; Tolimieri et al. 1998; Risk 1997, 1998). Damselfishes, stoplight parrotfishes, and ocean surgeonfishes have been the focus of this research.

8.21 Conclusions

In the last four decades, coral reefs in the USVI have been affected by acute and chronic stressors including hurricanes, high seawater temperatures, coral diseases, elevated sedimentation rates, and fishing pressure. The most conspicuous changes to the physical structure of the reefs have been from: 1) white band disease (affecting A. palmata and A. cervicornis) and hurricanes in the late 1970s through the mid-1990s; and 2) the extreme bleaching/disease episode that began in September 2005. Listed as threatened under the Endangered Species Act in May 2006, A. palmata showed signs of increasing in abundance within the last 10 years but then bleached for the first time on record in 2005 in the USVI with total mortality of some colonies. White band disease is now rare, but white pox and other undescribed diseases are very common, and along with physical damage from storms and boat groundings are hindering the regrowth of this species. Unlike white band disease which affected only two (albeit key reef-building) coral species (A. palmata and A. cervicornis) with most pronounced effects in depths less than 10 m, the 2005 disease outbreak (most likely white plague) affected virtually all coral species to depths over 30 m.

At deeper long-term monitoring sites, most of the (non-acroporid) coral colonies surviving the bleaching and disease that began in September 2005 had begun to regain some of their normal coloration by February/March 2006. However, many coral colonies remained pale as late as December 2006. The severity of disease peaked on the deeper reefs (dominated by M. annularis complex) within 2 to 7 months after the maximum seawater temperatures and associated bleaching. Disease following the severe 2005 bleaching event caused drastic losses (an average of 50% within one year) in living coral, the most substantial declines on these reefs in the last 40 years. Prevalence of active disease varies, but disease now seems to be present on the reefs year-round. Bleaching events (and major storms) are expected to become more frequent in the future. More research is urgently needed on these diseases and their interaction with bleaching, both of which could undermine the benefits of the marine reserves and other protected areas in the USVI; and on the effects of the reef degradation on fishes and other organisms.

Reef fish assemblages in the USVI have changed because of habitat degradation (not only of coral reefs but also of seagrass beds, mangroves, and deeper algal plains) and fishing pressure. Intensive and extensive monitoring of reef fishes, which began after fishing pressure had already caused changes, shows low abundance and reduced size of fish targeted by the fisheries (including Nassau and other groupers), and the absence or scarcity of some fish species.

The coral reefs of the USVI have been the subject of research for 40 years. Intensive and extensive monitoring of reefs, fishes and other reef organisms has been augmented by studies of ecological processes. Future research should focus on the role of the USVI reserves and the recently established Research Natural Area in Dry Tortugas National Park in the overall region (Western Atlantic and Caribbean), as well as the possible links among the three major US Virgin Islands, between VINP and VICRNM, and between BIRNM and the East End Marine Park. Connectivity among mangroves, seagrass beds, and coral reefs inside and outside the marine protected areas is an important area needing further study, along with an evaluation of the effectiveness of the marine reserves. Marine reserves are more likely to support the recovery of reef fish assemblages than the benthic resources. Recovery to previous levels of coral cover and to former relative abundance and diversity of coral and fish species in the USVI seems very unlikely.

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Subject	References
Herbivore-plant interactions	Ogden et al. 1973; Carpenter 1979, 1984a, 1985, 1986, 1988; Robblee 1983; Steneck 1983, 1989; Adey and Steneck 1985
Coral morphology/physiology/ecology	Gladfelter W. 1982; Gladfelter E. 1982; 1983a, b, 1984, 1985; Bythell 1988; Sebens and Miles 1988; Porter and Targett 1988; Patterson et al. 1991; Gleason 1993
Chemical and mechanical defenses	Targett et al. 1986; Hay 1985; Hay et al. 1988; Harvell and Fenical 1989; Harvell et al. 1993, 1996; West et al. 1993
Seagrass ecology	Ogden and Zieman 1977; Thayer et al. 1984
Invertebrate ecology	Gladfelter W 1975, 1978; Scheibling 1979; Suchanek 1983, 1985; Nowlis 1993
Fish community structure	Shulman 1983; Gladfelter and Gladfelter 1978; Gladfelter et al. 1980, Ogden and Ebersole 1981; Clarke 1988, 1996
Recruitment and dispersal in reef fishes	 Shulman et al. 1983, 1984; Shulman 1984, 1985; McFarland and Ogden 1985, McFarland et al. 1985; Shulman and Ogden 1987; Caselle and Warner 1996; Warner 1997; Swearer et al. 1999; Warner et al. 2000; Swearer et al. 2002; Shulman and Bermingham 1995; Shulman 1998
Resource partitioning in reef fishes	Moese 1980; Grippo 1981; Robblee 1983; Gladfelter and Johnson 1983; Clarke 1989, 1992, 1994
Behavioral ecology of fishes	Ogden and Erlich 1977; Quinn and Ogden 1984; Wolf et al. 1983; McFarland et al. 1979; Gladfelter 1979; Fallows 1985; Helfman et al. 1982; Helfman 1983, 1989; Henson and Warner 1997; Petersen and Warner 1998; Warner and Dill 2000
Microbiology	King et al. 1990; Fenchel et al. 1979
Nutrient dynamics and productivity	Adey et al. 1981; Rogers and Salesky 1981; Carpenter 1990a, b; Gladfelter 1977; Bythell 1988; Szmant-Froelich 1983; Meyer et al. 1983; Williams et al. 1985; Williams 1984; Williams and Fisher 1985

APPENDIX 8.1. References pertaining to research at West Indies Laboratory, St. Croix.

APPENDIX 8.2. Stony coral species occurring in the US Virgin Islands.

Stephanocoenia michelinii Madracis decactis Madracis mirabilis Acropora palmata Acropora cervicornis Acropora prolifera (a hybrid) Agaricia agaricites (several different forms)

Agaricia tenuifolia Agaricia undata Agaricia lamarcki Agaricia grahamae Agaricia fragilis Helioseris cucullata (= Leptoseris cucullata)

Siderastrea siderea Siderastrea radians Porites astreoides Porites branneri Porites porites Porites divaricata Porites furcata Isophyllia sinuosa Isophyllastrea rigida Mycetophyllia lamarckiana Mycetophyllia ferox Mycetophyllia aliciae Eusmilia fastigiata Millepora alcicornis Millepora complanata Millepora squarrosa Tubastraea aurea Favia fragum

Colpophyllia natans Colpophyllia breviserialis Cladocora arbuscula Montastraea annularis Montastraea franksi Montastraea faveolata Montastraea cavernosa Solenastrea bournoni Oculina diffusa Meandrina meandrites

Diploria clivosa

Diploria strigosa

Manicina areolata

Diploria labyrinthiformis

Dichocoenia stokesi Dichocoenia stellaris Dendrogyra cylindrus Mussa angulosa Scolymia lacera Scolymia cubensis

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