

Figure 1. AGRRA survey sites in the Virgin Islands. (1) Caret Bay, (2) Brewer's Bay, (3) Flat Cay, (4) Buck Island, (5) Sprat Bay, (6) Cane Bay, (7) Salt River, (8) Long Reef, (9) Fish Bay east outer, (10) Fish Bay west outer, (11) Fish Bay east inner, (12) Great Lameshur Donkey, (13) Great Lameshur VIERS, (14) Fish Bay west inner, (15) Great Lameshur Tektite, (16) Great Lameshur Yawzi, (17) Iguana head, (18) Eustatia Reef, (19) Herman's Reef, (20) Horseshoe Reef, (21) Jack Bay, (22) West Cow Wreck.

A RAPID ASSESSMENT OF CORAL REEFS IN THE VIRGIN ISLANDS (PART 1: STONY CORALS AND ALGAE)

BY

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ABSTRACT

The Atlantic and Gulf Rapid Reef Assessment (AGRRA) benthos protocol was conducted in depths of 3-14 m at 22 coral reef sites in the U.S. Virgin Islands (St. Croix, St. Thomas, St. John) and the British Virgin Islands (Anegada, Guana Island and Virgin Gorda). Live stony coral cover averaged between 10% and 35% in 85% percent of the sites. The size of colonies ≥ 25 cm in diameter averaged 55 cm and their composition was dominated by the genus *Montastraea*. Coral recruitment varied considerably among sites and was dominated by species that brood their larvae. Nearly all sites had stony corals that were affected by disease, bleaching or damaged by fish bites. Mean values for total (recent + old) partial mortality exceeded 40% of colony surfaces in eight sites and were between 20% and 40% for the remainder. The abundance of "standing dead" stony corals was typically less than 1.5%. The relative abundance of macroalgae exceeded 30% in 15 of 22 sites and macroalgae were dominated by *Dictyota*.

INTRODUCTION

The Virgin Islands (18°20' N, 64°50' W) lie between two major island archipelagoes: the Greater Antilles to the west and the Lesser Antilles to the southeast. With the exception of St. Croix, the northern United States Virgin Islands (USVI), together with the British Virgin Islands (BVI) and the islands of Puerto Rico, rise from a geological shelf that is surrounded by deep water (Dammann, 1969). This shelf covers approximately 3,200 km², contains about 500 km of shelf edge and is generally less than 100 m in depth. St. Croix sits on a similar, but smaller, shelf that is separated from the

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northerly Virgin Islands by the 4,685 m deep, 60 km wide Virgin Islands trough.

Upwelling of deep, nutrient-rich waters from the North Equatorial and Caribbean Currents, coupled with the fact that these shelves lie within the photic zone, aid in the development of deep (45 m) and shallow (2 to 20 m) fringing reefs, bank barrier reefs and patch reefs (Dammann, 1969). St. Thomas, St. John and St. Croix, the three main islands of the USVI, are surrounded by more than 90 uninhabited islands, cays, and rocks which provide hard substrata suitable for the growth of coral reefs (Towle, 1970, unpublished report; Dammann and Nellis, 1992). The three main islands of the BVI, Tortola, Virgin Gorda and Anegada, are also surrounded by nearly 50 smaller islands, cays and rocks. With the exception of Anegada and St. Croix, the Virgin Islands are of volcanic origin. Anegada is a low coral island (Dunne and Brown, 1976, unpublished report) and St. Croix has a sedimentary and carbonate origin (Hubbard, 1989; R. Watlington, personal communication). Many of the reefs in the Virgin Islands are associated with mangrove forests, seagrass beds and algal plains, which are important to reef-associated fishes.

Over the past 20 years, eight major hurricanes, numerous outbreaks of disease, and sporadic bleaching events have caused extensive coral mortality to the coral reefs surrounding the Virgin Islands (Gladfelter, 1982; Edmunds and Whitman, 1991; Rogers et al., 1991; Causey et al., 2000). Recovery from these natural disturbances is hindered by a multitude of human impacts that affect coral reefs such as overfishing, ship groundings, anchor damage and non-point source pollution (Roberts, 1993; Sebens, 1994; Rogers and Garrison, 2001). Moreover, rapid development of inland and coastal areas has dramatically increased soil erosion and sedimentation onto many of these coral reefs (Rogers, 1990; MacDonald et al., 1997; Anderson and MacDonald, 1998; Ramos, 1998, unpublished report). The cumulative effects of these human impacts reduce coral abundance, diversity, and larval recruitment and may make corals more susceptible to disease and bleaching (Nemeth and Sladek Nowlis, 2001).

In response to these threats to coral reefs, Ginsburg et al. (1996) initiated a process of rapid reef assessment. After development of the AGRRA protocols, a Caribbean-wide effort to assess the condition of coral reefs throughout the region was launched. The University of the Virgin Islands' Center for Marine and Environmental Studies joined the effort and set out to assess the reefs of the Virgin Islands using the AGRRA protocols. This paper reports on the initial findings of our benthic assessments. Results of the fish surveys are given in Nemeth et al. (this volume).

METHODS

Site-selection criteria in the USVI and the BVI varied among the different islands but most (18/22) choices were made for strategic reasons. In St. Thomas, five sites were selected based on their inclusion in a long-term, sedimentation monitoring project, their proximity to the University of the Virgin Islands McLean Marine Science Center and the presence of historical data (i.e., Rogers, 1982, unpublished report; Nemeth and Sladek Nowlis, 2001). Three popular recreational diving sites were selected in St. Croix, one of which is within the Salt River Bay National Historic Park and Ecological Preserve. The eight sites in St. John were part of a study comparing sedimentation rates between Great

Lameshur Bay, which is within the National Park Boundary, and Fish Bay, which has been experiencing heavy development within its watershed. Four of these sites were shallow reefs (<6 m) located inside the bays and four sites were in deeper (>6 m) reefs located outside the bays. Four of the six sites surveyed in the BVI (Iguana Head in Guana Island, Eustatia Reef in Virgin Gorda, West Cow Wreck Bay and Herman's Reef in Anegada) were selected haphazardly. Eustatia Reef is a heavily visited dive site whereas Guana Island is a privately owned island with a low human population. The other two sites in Anegada (Jack Bay and Horseshoe Reef, a designated protected area) were selected because of historical surveys conducted by Dunne and Brown (1976, unpublished report) and the West Indies Laboratory (1983, unpublished report). The reefs of Anegada were included in the AGRRA survey to provide a remote reference site with low human population and little landmass. A qualitative assessment of human and natural impacts at the 22 sites surveyed in the Virgin Islands is given in Appendix A (this paper).

The AGRRA Version 2.0 benthos protocol (see Appendix One, this volume) was used. Four of us constituted the primary dive team and we were augmented by five alternates. All divers participated in at least one three-day training session of the AGRRA protocol. Training sessions were conducted in the spring of 1998, 1999, and 2000 and consistency training was used for the primary dive team at least once a year. All corals were identified to species except species of *Agaricia*. Although *A. agaricites* was a dominant species, it was not distinguished from other species of *Agaricia*. Coral and algal identification guides included Humann (1993) and Littler et al. (1989). Stony coral sizes were measured to the closest cm. We also recorded the percentage of individually surveyed (≥ 25 cm diameter) colonies with parrotfish or damselfish bites. Fish-bite damage from parrotfish or damselfish was distinguished when possible. Macroalgal heights were measured to the closest 0.5 cm. When scoring the relative abundance of crustose coralline algae, divers typically removed sediment with vigorous handsweeping motions. Algal turfs were omitted from the July 2000 assessment of Anegada and Virgin Gorda sites in accordance with the May 2000 revisions of the AGRRA benthos protocol. Because of these changes, percent relative abundances of macroalgae and crustose coralline algae are not comparable to earlier surveys. Therefore, percent absolute abundance of macroalgae in the quadrats is presented to make comparisons among the sites.

Data were summarized by island groups within three geographic areas to examine general trends in coral reef condition throughout the Virgin Islands. The geographic areas were: 1) Anegada; 2) the shallow and deeper reefs of the remaining islands in the northern Virgin Islands (NVI); and 3) St. Croix. Anegada was considered a geographic unit because of its isolation from the other Virgin Islands and its unique geology (low coral island). St. Croix was considered a geographic unit also because of its isolation from the NVI, its unique geology (sedimentary/carbonate) and because it is completely within the Caribbean Sea. The NVI (USVI = St. Thomas, St. John; BVI = Guana, Virgin Gorda) were grouped because of their close proximity to one another, their similar geologic origins and topographies (high volcanic islands) and their exposure to both Atlantic waters from the north and Caribbean waters from the south. The shallow sites in St. John were analyzed separately from the deeper sites within the NVI archipelago. Comparisons of coral cover among "island/depth groups" (hereafter referred to as island groups) were made using single factor Analysis of Variances (ANOVA). Prior to statistical analysis, residuals of coral cover data were graphically analyzed for normality

using Systat statistical analysis software. Coral cover data were found suitable for statistical analysis at a significance level of $\alpha = 0.05$. Tukey HSD was used for post-hoc multiple comparison analyses.

RESULTS

Site Characteristics

A total of 22 sites in eight islands or cays (Fig. 1) were surveyed during three time periods: May 1998; May to December 1999; and February to October 2000 (Table 1). All of the surveyed sites were in fringing reefs at depths that ranged from 3 to 14 m (Table 1). The fringing reefs in St. Thomas, St. John, Guana Island and Virgin Gorda were all located close to the shoreline and sloped relatively steeply from their crests to their bases where the reefs gave way to sandy substrata. In St. Croix, the reefs were within a few hundred meters of the Virgin Islands trough and dropped off steeply into abyssal depths. In the low island of Anegada, the fringing reefs sloped more gently than in the high volcanic NVI. All of the deeper reef surveys were carried out on their seaward slopes with the exception of Herman's Reef in Anegada which was on the leeward side of the reef crest. Most of the sites that were surveyed were relatively sheltered from the prevailing seas (i.e., from exposure to northeast swells). Sites with direct exposure to northeast swells included Jack Bay, Horseshoe Reef, and West Cow Wreck Bay in Anegada. The three reefs in St. Croix were also exposed to swells although the Virgin Islands archipelago 60 km to the north provided some protection. Reefs with moderate protection from prevailing seas included Herman's Reef in Anegada, Caret Bay in St. Thomas, and Eustatia Reef in Virgin Gorda.

Over 85% of the sites surveyed had between 10% and 35% live stony coral cover (Table 1) with means for the island groups ranging between 12% and 19% (Fig. 2). The lowest cover occurred in Fish Bay, St. John whereas the deeper Tektite site in Great Lameshur Bay, St. John had exceptionally high (nearly 50%) live coral cover (Table 1). Significant differences in percent coral cover occurred among island groups (ANOVA: $F_{3,341} = 12.4$, $P < 0.001$). Anegada and the shallow St. John sites were significantly lower in coral cover than sites in the deeper NVI and St. Croix groups (Fig. 2).

The "large" stony corals that were individually surveyed (i.e., those ≥ 25 cm in diameter) were numerically dominated by the *Montastraea annularis* species complex (*M. annularis*, *M. faveolata*, *M. franksi*) in all island groups except St. Croix which was dominated by *M. cavernosa* (Fig. 3). The deeper NVI and shallow St. John sites were similar in overall composition and quite different from those in St. Croix and Anegada, which also differed from each other (Fig. 3). The second most common taxon was *Siderastrea siderea*, except in Anegada where *Porites astreoides* and *Diploria strigosa* were each twice as common as *S. siderea*. Other individually surveyed taxa that were each less than three percent in abundance in the four island groups are as follows: shallow St. John (*Millepora alcicornis*, *Agaricia*, *Colpophyllia natans*, *Diploria labyrinthiformis*, *D. strigosa*, *Stephanocoenia intersepta*, *Solenastrea bournoni*); deeper NVI (*M. alcicornis*, *Acropora cervicornis*, *A. palmata*, *Dichocoenia stokesi*, *Madracis mirabilis*, *M. decactis*, *S. intersepta*, *Dendrogyra cylindrus*, *Solenastrea bournoni*, *D.*

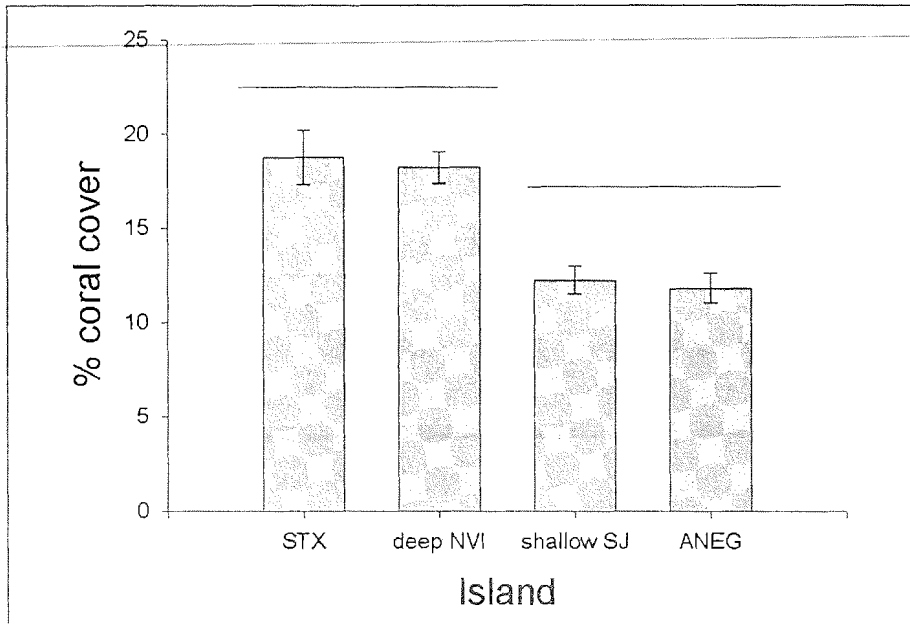


Figure 2. Mean live stony coral cover (percent \pm se) in St. Croix, deeper NVI (St. Thomas, St. John >6 m deep, Guana Is., Virgin Gorda), shallow St. John and Anegada. Lines connecting bars indicate no significant difference ($\alpha = 0.05$).

labyrinthiformis, *D. strigosa*); St. Croix (*D. cylindrus*, *D. labyrinthiformis*, *M. decactis*, *Porites porites*); and Anegada (*P. porites*, *M. franksi*, *A. cervicornis*, *D. stokesi*, *S. intersepta*, *D. clivosa*, *D. cylindrus*, *M. mirabilis*).

The diameter of the individually surveyed corals (Table 2) averaged 55.0 cm with exceptionally large (up to 260 cm) colonies of *M. annularis* occurring off St. John. Within the *Montastraea annularis* species complex, the size frequency distribution in most sites showed a positive skew toward smaller colonies of <50 cm diameter (Fig. 4). The shallow St. John sites were unique in that they showed a platykurtic size-frequency distribution (Fig. 4) even though the local abundance of the *M. annularis* species complex as a whole was similar to that of the deeper NVI sites (Fig. 3). Three of the four shallow sites off St. John had very large coral colonies and so exerted a proportionately greater influence in this group than did the two deeper Great Lameshur sites in the much larger set of the deeper NVI group. The mean sizes of the predominant *Montastraea* varied within and among the island groups (Fig. 5). *M. annularis* and *M. faveolata* were significantly larger than *M. franksi* and *M. cavernosa* in the deeper NVI ($F_{3,678} = 13.72$, $p < 0.001$) whereas, in St. Croix, *M. faveolata* and *M. franksi* were significantly smaller than *M. annularis* and larger than *M. cavernosa* ($F_{3,201} = 22.47$, $p < 0.001$). In the shallow reefs of St. John, *M. cavernosa* was significantly smaller than *M. annularis* ($F_{3,251} = 3.64$, $p < 0.01$) whereas *M. faveolata* and *M. franksi* were intermediate in size. All *Montastraea* on Anegada were similar in size (Fig. 5).

Stony Coral Condition

Coral bleaching was recorded in all sites (Table 2) with the highest average values for large stony corals occurring in St. Croix (48% in October/December 1999, $n=3$

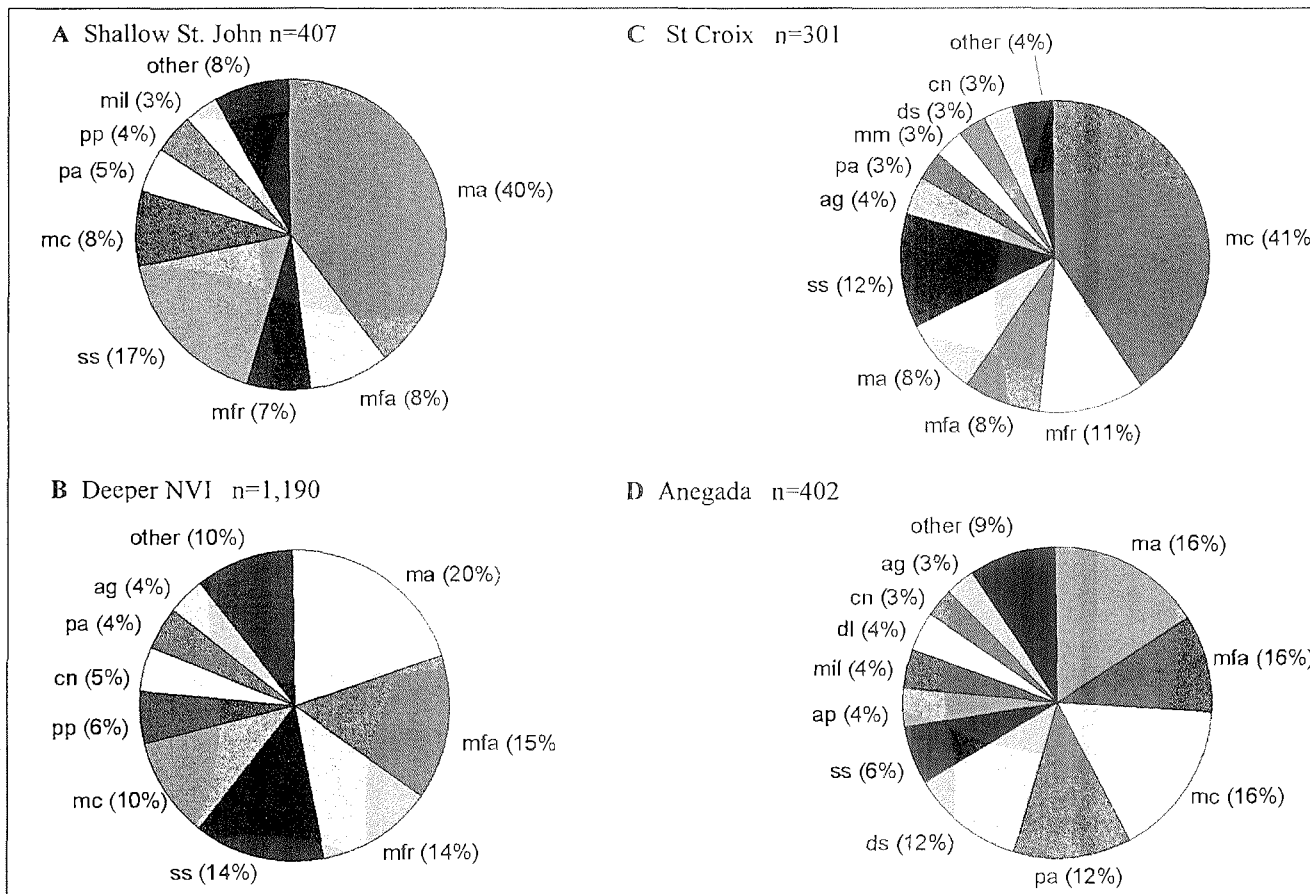


Figure 3. Species composition and mean relative abundance of all stony corals (≥ 25 cm diameter) in (A) shallow St. John, (B) deeper NVI, (C) St. Croix, and (D) Anegada. ap = *Acropora palmata*, ag = *Agaricia*, cn = *Colpophyllia natans*, dl = *Diploria labyrinthiformis*, ds = *D. strigosa*, mm = *Madracis mirabilis*, mil = *Millepora alcicornis*, ma = *Montastraea annularis*, mfa = *M. faveolata*, mfr = *M. franksi*, mc = *M. cavernosa*, pa = *Porites astreoides*, pp = *P. porites*, ss = *Siderastrea siderea*, other = all species with $< 3\%$ abundance.

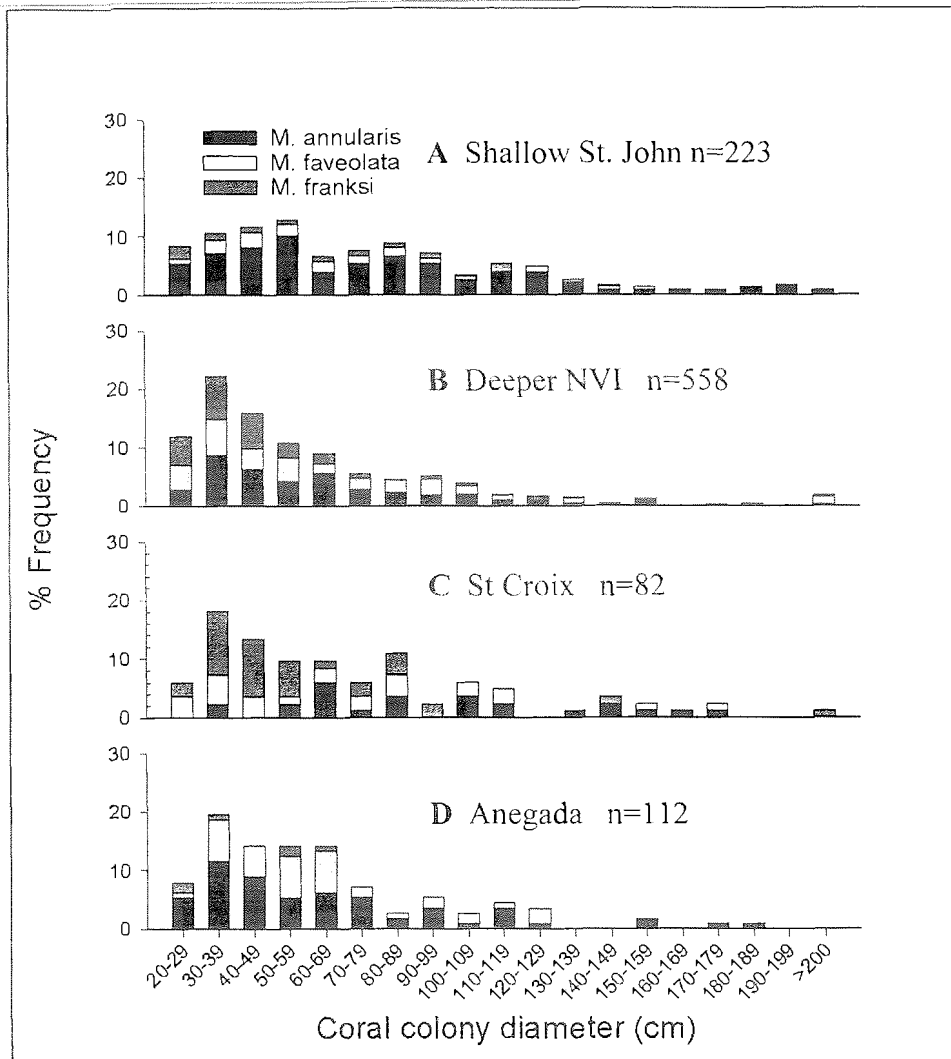


Figure 4. Size-frequency distribution of all colonies (≥ 25 cm diameter) of *Montastraea annularis* (ma), *M. faveolata* (mfa) and *M. franksi* (mfr) in (A) shallow St. John (ma=162, mfa=34, mfr=27), (B) deeper NVI (ma=237, mfa=178, mfr=143), (C) St. Croix (ma=24, mfa=24, mfr=34), and (D) Anegada. (ma=64, mfa=42, mfr=6).

sites), in two shallow St. John sites (~38% in October/November 1999), in St. John's deeper Tektite Reef (36%, in August/November 1999) and in Anegada (28% in July 2000. n=4 sites). Occasional temperature measurements during surveys documented that normal sea-surface temperatures to 10 m depth were coolest in February (25° C), began to warm during June (26° C) and July (27° C), peaked in August (28-29° C), and began to cool during October and November (27° C). Water temperatures deeper than 12 m could be up to 1.5° C cooler than in shallower depths. The Caribbean-wide 1998 bleaching event was first detected in September 1998 in the Virgin Islands when surface sea-water temperatures exceeded 30° C. Bleaching of coral colonies peaked in October 1998 but nearly all signs of bleaching had disappeared by February 1999 (Nemeth and Sladek Nowlis, 2001). Since no surveys were conducted from June 1998 to May 1999, the 1998 bleaching event did not directly influence the results presented in this report.

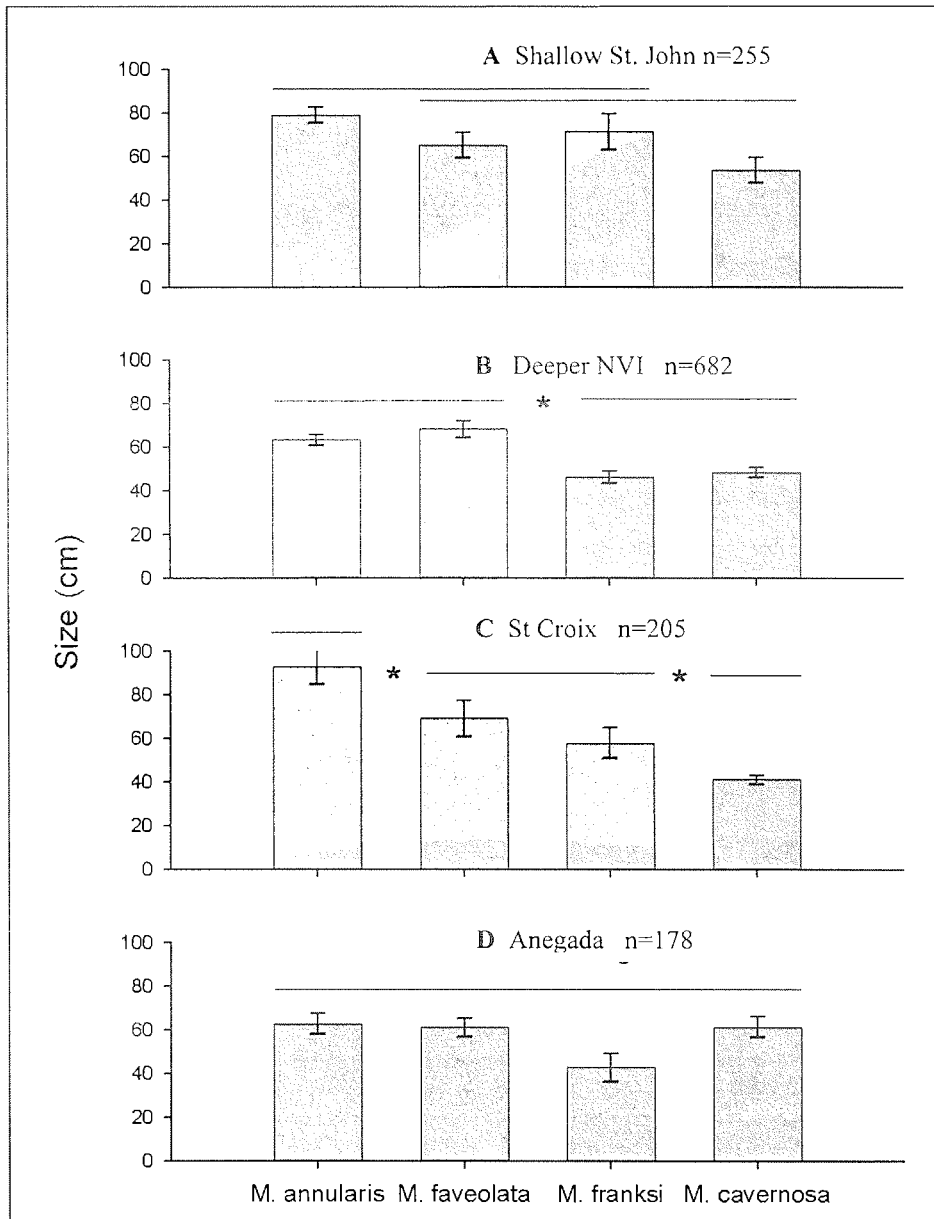


Figure 5. Mean size of *Montastraea annularis* (ma), *M. faveolata* (mfa), *M. franksi* (mfr) and *M. cavernosa* (mc) in **(A)** shallow St. John (ma=162, mfa=34, mfr=27, mc=32), **(B)** deeper NVI (ma=237, mfa=178, mfr=143, mc=124), **(C)** St. Croix (ma=24, mfa=24, mfr=34, mc=123), and **(D)** Anegada (ma=64, mfa=42, mfr=6, mc=66). Lines connecting bars indicate no significant differences ($\alpha=0.05$) in average size among species.

Signs of disease in the individually surveyed stony corals were present in most (20/22) of our assessment sites (Table 2). Divers were able to recognize four general disease types: black band, yellow blotch, white plague, and dark spots (Fig. 6). The species most susceptible to disease included *Montastrea faveolata*, *M. franksi*, *M. cavernosa*, *M. annularis*, *Colpophyllia natans* and *Siderastrea siderea*. Of particular interest, white-band disease was observed in one colony of *Acropora cervicornis* each in Caret Bay, St. Thomas and in Herman Reef, Anegada. The percent of diseased corals

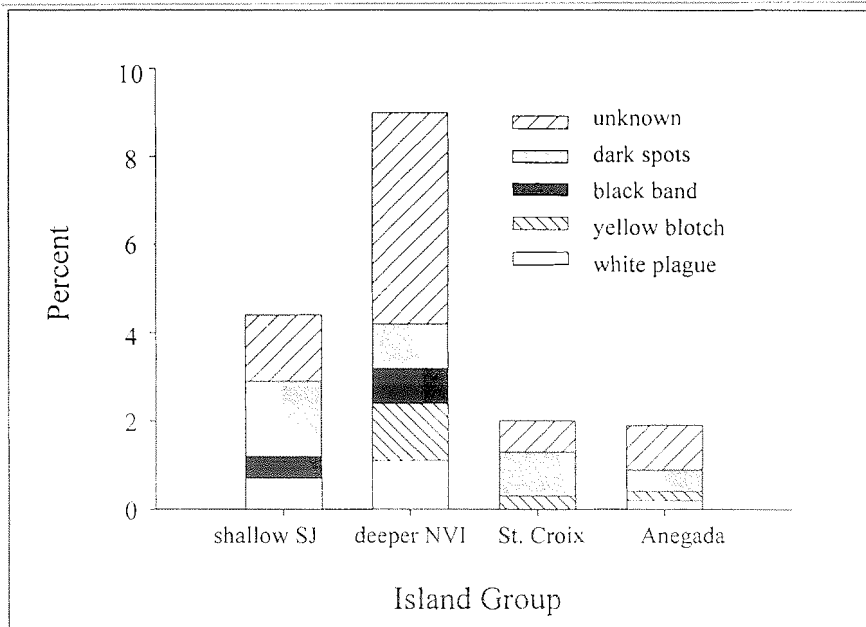


Figure 6. Percent damage to all stony corals (≥ 25 cm diameter) from disease in shallow St. John ($n=18$ infected corals), deeper NVI ($n=106$ infected corals), St. Croix ($n=6$ infected corals), and Anegada ($n=8$ infected corals).

varied among sites within island groups with St. Croix (in October and December 1999) and Anegada (in July 2000) having lower levels of disease than the shallow St. John sites (in October/November 1999 and May/August/October 2000) and deeper NVI sites (various dates between May 1998 and July 2000). Five percent or more of the colonies were affected at 13 sites (maximum being 24% in Guana Island), 9 of which included surveys that had been made between May and November, 1999. At 4 sites in St. Thomas, sampling dates either occurred both in 1998 and 1999 (Buck Island), in 1998 and 2000 (Caret Bay), or in 1999 and 2000 (Brewers Bay, Flat Cay) (Table 1). In the first two cases no diseases were observed in 1998 but they were present in all sites on the other survey dates. The incidence of disease was considerably higher in 1999 than in 2000 for Brewer's Bay.

Damselfish and parrotfish bites were responsible for causing tissue damage to 25% or more of the individually surveyed stony corals in three sites and were present in colonies at all but three sites (Table 2; Fig. 7). The most frequently attacked species included *M. annularis*, *M. faveolata*, *M. franksi*, *C. natans*, *M. cavernosa* and *P. porites*. The shallow sites in Great Lameshur Bay, St. John had the greatest percentage of tissue damage from damselfish. This was largely due to the high density of three-spot damselfish (*Stegastes planifrons*) on colonies of *M. annularis*. Damselfish overall occupied 35.4% of the stony corals in the shallow St. John sites, 7.1% in the deeper NVI, 3.2% in Anegada and 2.0% in St. Croix. Tissue damage by parrotfish was greatest in St. Croix and Anegada (Fig. 7).

Mean values for total (recent and old) partial mortality exceeded 40% of colony surfaces in eight sites and were between 20% and 40% in the remaining sites (Table 2). Recent partial mortality of colony surfaces averaged less than three percent overall in

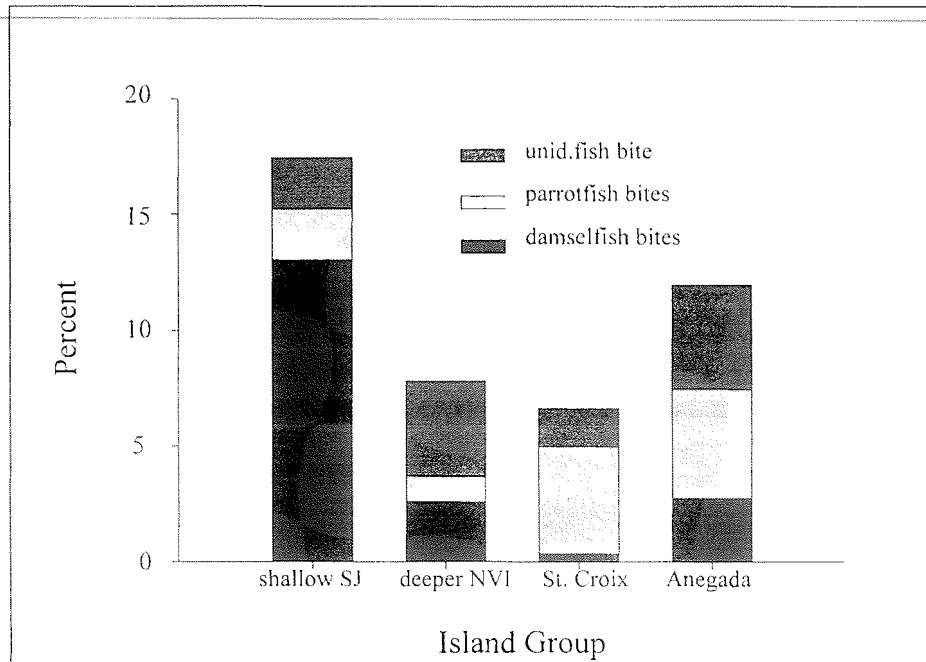


Figure 7. Percent damage to all stony corals (≥ 25 cm diameter) from fish bites in shallow St. John (71 corals with bites), deeper NVI (60 corals with bites), St. Croix (20 corals with bites), and Anegada (48 corals with bites).

most (17/22) sites (Table 2). Although the highest rate of recent partial mortality (5.5%) for an individual reef was in Anegada (Jack Bay, Table 2), the highest rates of recent partial mortality for an island group occurred in the shallow St. John sites where over 50% of the large stony corals were affected during the surveys in 1999 and 2000 (Fig. 8). Fifty-five to 70% percent of the corals throughout the Virgin Islands had signs of old tissue mortality on more than 10% of their upper surface areas (Fig. 8). Average levels of old tissue mortality per coral colony were highest in the shallow St. John sites (43%) followed by Anegada (40%), St. Croix (34%) and the deeper NVI (27%). The percent of large colonies that were “standing dead” (no living tissues and still in growth position) was less than or equal to 1.5% at 17 sites but was relatively high (8% and 12%) in two reefs off Anegada (Table 2). The average frequency of standing dead colonies by island group was as follows: St. Croix (0.3%, $n=1$ coral), deeper NVI (0.3%, $n=4$ corals), shallow St. John (1.7%, $n=7$ corals), and Anegada (9%, $n=36$ corals). Standing dead corals in shallow St. John, deeper NVI and St. Croix consisted of a variety of species: *M. cavernosa*, *M. faveolata*, *M. annularis*, *S. siderea*, *P. astreoides*, *C. natans*, and *A. palmata*. In Anegada, however, all (12/12) of the standing dead colonies at Horseshoe Reef were *A. palmata* and most (11/14) of the standing dead colonies at Jack Bay were *M. cavernosa*. Other standing dead colonies at Anegada included *Agaricia*, *D. labyrinthiformis*, *D. strigosa*, *M. annularis*, *M. franksi*, *P. astreoides*, and *P. porites*.

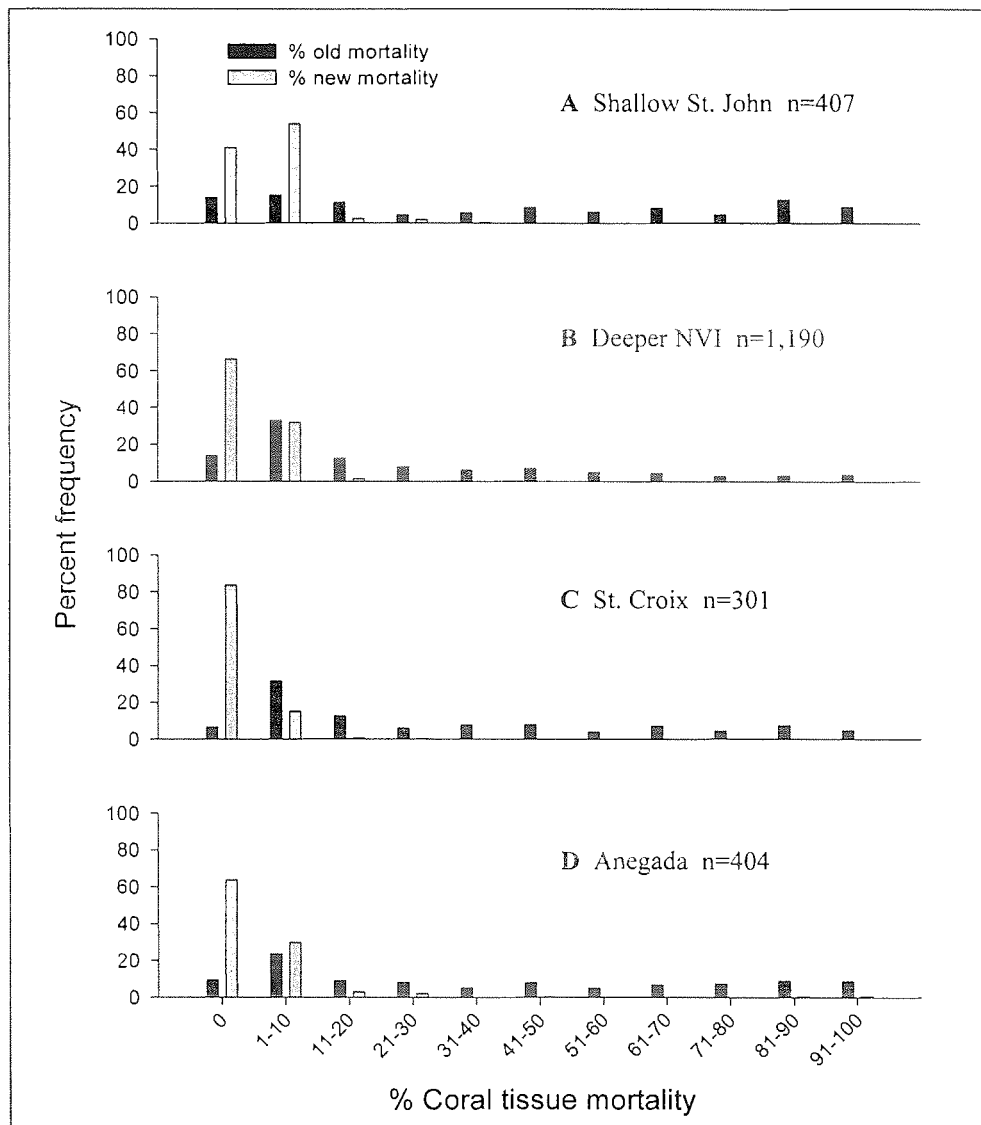


Figure 8. Frequency distribution of recent and of old partial colony mortality of all stony corals (≥ 25 cm diameter) in (A) shallow St. John, (B) deeper NVI, (C) St. Croix, and (D) Anegada.

Stony Coral Recruitment, Macroalgae and *Diadema*

Stony coral recruitment varied considerably from site to site (Table 3). With the exception of *Siderastrea siderea*, coral recruits were dominated by species that brood their larvae. The five most abundant taxa, *Siderastrea siderea* (23%), *Agaricia* (17%), *P. astreoides* (15%), *P. porites* (13%) and *S. radians* (6%) comprised 70% to 80% of the recruits in all island groups (Fig. 9). Other recruits that were each less than three percent in abundance in the four island groups are as follows: shallow St. John (*D. strigosa*, *D. labyrinthiformis*, *M. mirabilis*); deeper NVI (*M. mirabilis*, *S. bournoni*, *M. cavernosa*, *D.*

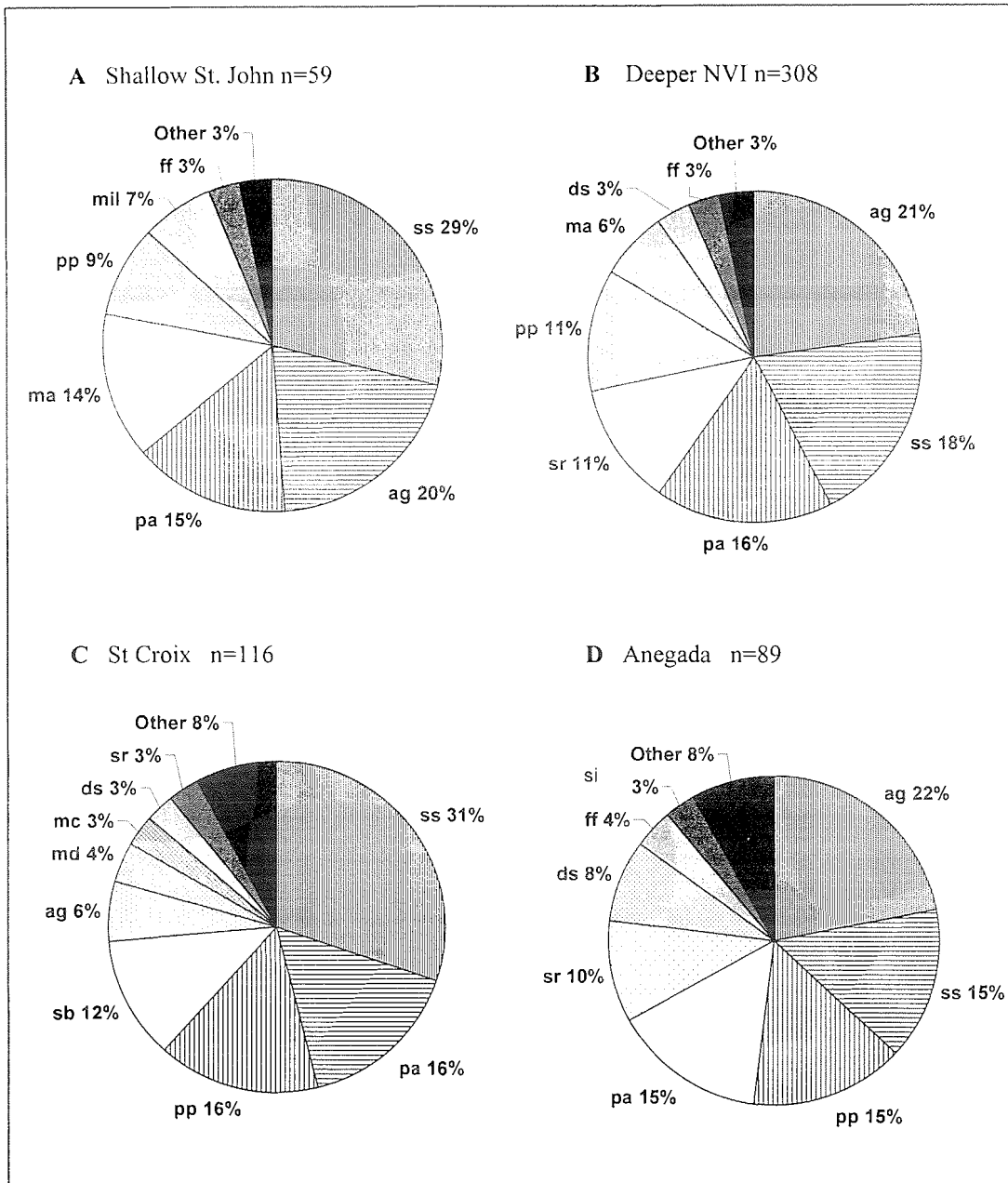


Figure 9. Species composition and mean relative abundance of all stony coral recruits (<2 cm diameter) in (A) St. John shallow, (B) Northern Virgin Islands, (C) St. Croix, (D) Anegada. AG = *Agaricia*, ds = *Diploria strigosa*, ff = *Favia fragum*, md = *Madracis decactis*, mil = *Millepora alcicornis*, ma = *Montastraea annularis* species complex, mc = *Montastraea cavernosa*, pa = *Porites astreoides*, pp = *P. porites*, sr = *Siderastrea radians*, ss = *S. siderea*, sm = *Stephanocoenia intersepta*, sb = *Solenastrea bournoni*, Other = all species with <3% abundance.

labyrinthiformis, *A. cervicornis*, *D. stokesi*, *Eusmillia fastigiata*, *S. intersepta*, *D. clivosa*, *M. alcicornis*); St. Croix (*M. mirabilis*, *S. intersepta*, *D. stokesi*, *E. fastigiata*, *M. alcicornis*, *F. fragum*, *M. annularis*); and Anegada (*D. labyrinthiformis*, *M. alcicornis*, *M. annularis*, *M. cavernosa*).

Of the 16 sites in which relative abundance estimates were made for all three algal functional groups, four were dominated by macroalgae, eight were dominated by turf algae and these two groups were essentially coequals in the remaining four. Crustose coralline algae were the least abundant at all but one site (Caret Bay, St. Thomas) where they were more abundant than turf algae. When comparing absolute abundances of macroalgae within the quadrats, over half (14/22) of the sites ranged from 25% to 45%, two were over 50% and three sites were under 10% (Table 3). *Dictyota* was the dominant macroalga in the Virgin Islands reefs and macroalgae were typically less than 3 cm in height (Table 3). Values for the macroalgal index (as relative macroalgal abundance x macroalgal height) obtained from the 1998-1999 surveys ranged from 3-35 in St. Croix, 6-247 in the deeper NVI and 46-278 in the shallow St. John sites. Corresponding values based on absolute macroalgal abundances for the entire dataset produced a similar pattern with shallow St. John>Anegada>deeper NVI>St. Croix (Table 3).

The density of *Diadema antillarum* was greatest in the shallow St. John sites (i.e., in depths of less than five meters) (Table 3).

DISCUSSION

It was anticipated that coral reefs located near human population centers would be exposed to higher levels of sedimentation, pollution, recreational diving, anchor damage and more intense fishing and thus would be in worse condition than reefs more remote from these human impacts (Appendix A, this paper). Contrary to this assumption, our surveys found that the Anegada sites had the greatest amount of dead stony coral tissue and the lowest live coral cover among the deeper reef systems. Old mortality in Anegada was largely attributed to the fact that its reefs were historically dominated by *Acropora palmata* which was decimated during a white-band disease epizootic in the late 1970's (Dunne and Brown, 1976, unpublished report; Gladfelter, 1982). During our survey, many of these *A. palmata* were broken or severely eroded with other species of corals colonizing their surfaces; thus many did not get categorized as standing dead colonies.

The shallow St. John sites were fairly similar to the deeper NVI sites in the species composition of large corals and in coral recruitment (Figs. 3 and 9). However, the shallow St. John sites had a much higher percentage of old partial-colony mortality than the deeper NVI (43% vs. 27%) and had fewer small (<50 cm diameter) colonies of the *Montastraea annularis* species complex (29% vs. 50%) (Fig 4). The partial death or damage to these shallow-water corals was possibly due to a series of strong hurricanes impacting St. John's reefs during the past 20 years or to possible epizootic events (see below). All else being equal, large storm waves have a greater impact in shallow reefs by breaking branching corals, dislodging or toppling boulder corals, or scouring thin coral tissues (Rogers et al., 1983; Edmonds and Witman, 1991; Rogers et al., 1991; Nemeth and Sladek Nowlis, 2001). The shallow St. John sites also contained higher densities of

Diadema antillarum, a pattern of recolonization that is typical throughout the Caribbean (Nemeth, personal observation) following its die-off in the early 1980's (Lessios, 1988).

The shallow reefs also contained higher densities of damselfish, in particular *Stegastes planifrons*, which is known to inhabit shallow reef areas and to damage and kill living coral tissue for its algal gardens (Itzkowitz, 1977; Kaufman, 1977; Williams, 1979). This resulted in large numbers of coral colonies showing signs of tissue damage from damselfish bites. Bites by parrotfish were also assessed. Since the stoplight parrotfish, *Sparisoma viride*, is known to cause damage to coral colonies (Bruckner and Bruckner, 1998; Bruckner et al., 2000), we examined the AGRRA fish data collected during our surveys (Nemeth et al., this volume) and found that bite damage seemed to be positively associated to the average size of ≥ 5 cm stoplight parrotfish present in reef sites. For example, the St. Croix and Anegada reefs showed the highest incidence of parrotfish bite damage and had the largest stoplight parrotfish observed during the AGRRA fish surveys (29.2 cm and 17.7 cm, respectively). In contrast, the average size of stoplight parrotfish in the deeper NVI and in shallow St. John was 13.1 cm and 9.27 cm, respectively.

Although the 1998 bleaching event did not directly influence the results presented in this report, Nemeth and Sladek Nowlis (2001) found that sedimentation from land development made corals more susceptible to bleaching, especially during the 1998 event. Nemeth and Sladek Nowlis (2001) also documented low-to-moderate levels of seasonal bleaching during July, August and early September, when sea surface temperatures typically reach an annual high, and during the rainy season (October, November, early December) when the influx of terrigenous sediment into the marine environment is greatest. This may explain the moderate levels of bleaching observed for all sites in St. Croix (October, December) and Anegada (July), four of five sites in St. Thomas (July/August) and the deeper St. John sites (July/August), three of four shallow sites in St. John (August/ October/November) and the one site in Virgin Gorda (July). The lowest levels of bleaching typically occurred in sites surveyed from February to June.

Among the island groups, the incidence of disease was lowest in Anegada in July 2000 and in St. Croix during October and December 1999. Although little is known of the mechanisms of transmission of coral diseases, both these islands are remote relative to those in the NVI. Guana Island was unusual in that it was among the highest in live stony coral cover, among the lowest in macroalgal abundance and in the percentage of total partial-colony mortality, but it also had a considerably higher percentage of diseased corals (24% in 1999) than found at any date in any other site (Tables 1-3). Our AGRRA survey may have documented the initial stages of a disease outbreak at this site in which 65% of the affected corals were in the genus *Montastraea*. Unfortunately, most of the signs of disease in the Guana Island corals were unfamiliar to us and classified as "unknown." Alternatively, since Guana Island is privately owned, sparsely populated, and its reefs receive minimal human disturbance, its stony corals may be more capable of resisting or recovering from diseases which may have been present for some time. Outbreaks of white plague type II, which occurred repeatedly in St. John (December 1997, April, May, June; December 1998; August 2000), resulted in considerable mortality to several isolated reefs around St. John including Tektite Reef in Great Lameshur Bay (Miller et al., in press). None of our survey dates in St. John corresponded

with these peak periods in disease outbreaks. However, the percent of diseased colonies in our surveys in Tektite Reef (10% in August/November 1999) was similar to that reported by Miller et al. (in press) who found 5-12% diseased by white plague type II during the same time period. Temporal variability in outbreaks of disease may have contributed to the low percentage of disease detected at sites in Anegada and Virgin Gorda which were all sampled during a three-day period in July 2000.

Based on our comparison of populated islands with remote islands, we conclude that the condition of coral reefs around the Virgin Islands is primarily determined by large-scale natural disturbances such as hurricanes and disease epidemics. Although many reefs in the Caribbean and other parts of the world were severely damaged by the 1998 mass bleaching event, the corals around the Virgin Islands had largely recovered by 1999. The remoteness of Anegada may benefit the ecology of its reefs under certain circumstances but, following disturbances, it is possible that larval recruitment of major, reef-building corals is limited which may slow the recovery of reefs surrounding this island.

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Table 1. Site information for AGRRA stony coral and algal surveys in the Virgin Islands.

Site name	Site code	Reef Type ¹ / Exposure	Latitude (° ' " N)	Longitude (° ' " W)	Survey Date(s)	Depth (m)	Benthic transects (#)	>25 cm stony corals (#/10m)	% live stony coral cover (mean ± sd)
<i>Northern Virgin Islands</i>									
<i>St. John (shallow)</i>									
Great Lameshur, Donkey	12	F/Windward	18 18.853	64 43.312	May 26 00	3	12	8.5	18.5 ± 3.5
Great Lameshur, VIERS	13	F/Windward	18 19.094	64 43.390	Oct 23 99	5.5	25	4	13.5 ± 6.0
Fish Bay East, Inner	11	F/Windward	18 19.073	64 45.808	Nov 14 99	5	27	3.5	10.5 ± 6.0
Fish Bay West, Inner	14	F/Windward	18 19.053	64 45.878	Aug 15 00, Oct 24 00	5	12	8.5	7.0 ± 6.0
<i>St. John (deep)</i>									
Great Lameshur, Tektite	15	F/Windward	18 18.572	64 43.302	Aug 3 99, Nov 29 99	11	10	10.5	48.5 ± 13.5
Great Lameshur, Yawzi	16	F/Windward	18 18.831	64 43.596	July 23 99	13	26	4.5	16.0 ± 8.0
Fish Bay East, Outer	9	F/Windward	18 18.948	64 45.777	Feb 08 00	6.5	23	4.5	12.0 ± 5.0
Fish Bay West, Outer	10	F/Windward	18 18.850	64 45.845	Aug 02 99	7.5	29	4	13.0 ± 6.5
<i>St. Thomas</i>									
Brewer's Bay	2	F/Windward	18 20.670	64 59.157	May 26 99, June 9 00	8.5	16	6.5	19.0 ± 6.5
Buck Island	4	F/Windward	18 19.781	64 57.097	May 19 98, July 14 99	14	38	3.5	11.5 ± 6.0
Caret Bay	1	F/Windward	18 22.421	64 59.371	May 21 98, July 17 00	9.5	17	6	23.5 ± 8.5
Flat Cay	3	F/Windward	18 19.072	64 59.444	July 7 99, June 12 00	12	18	6	21.0 ± 7.5
Sprat Bay	5	F-B/Windward	18 19.718	64 55.630	Aug 31 00	10	8	13	29.5 ± 7.0
<i>Virgin Gorda</i>									
Eustatia Reef	18	F-B/Windward	18 30.50	64 20.250	July 24 00	8.5	11	9.5	17.0 ± 6.0
<i>Guana Is</i>									
Iguana Head	17	F/Windward	18 28.477	64 34.941	Aug 06 99	10	13	8.5	30.0 ± 9.5
<i>St. Croix</i>									
Cane Bay	6	F/Windward	17 46.230	64 48.530	Oct 14 99, Dec 16 99	9.5	13	7.5	30.5 ± 11.0
Long Reef	8	F-B/Windward	17 46.118	64 41.490	Oct 13 99	13.5	13	7.5	16.0 ± 3.5
Salt River East	7	F/Windward	17 47.227	64 45.330	Oct 13 99	10	17	6	14.0 ± 4.0
<i>Anegada</i>									
Herman's Reef	19	B-B /Leeward	18 33.841	64 14.320	July 24 00	13	10	10	19.5 ± 5.5
Horseshoe Reef	20	B-B /Windward	18 39.965	64 13.890	July 22 00	10.5	17	6	14.0 ± 6.5
Jack Bay	21	F-B/Windward	18 44.961	64 19.246	July 22 00	9	23	4.5	8.0 ± 4.5
W. Cow Wreck	22	F-B/Windward	18 45.164	64 24.596	July 23 00	8.5	14	7	11.5 ± 3.5

¹ F = fringing; F-B = fringing-barrier; B-B = bank-barrier

Table 2. Size and condition (mean \pm standard deviation) of all stony corals (>25 cm diameter) by sites in the Virgin Islands.

Site name (Site code)	Stony corals		Partial-colony mortality (%)			Stony corals (%)			
	#	Diameter (cm)	Recent	Old	Total	Standing dead	Bleached	Diseased	With fish bites
<i>Northern Virgin Islands</i>									
<i>St. John (shallow)</i>									
Great Lameshur, Donkey (12)	101	95.0 \pm 46.0	2.5 \pm 3.0	53.5 \pm 31.0	56.0 \pm 31.0	2.0	25.0	0	25.5
Great Lameshur, VIERS (13)	104	53.0 \pm 27.5	4.5 \pm 7.0	28.5 \pm 30.5	33.0 \pm 30.0	0	38.5	6.0	39.5
Fish Bay East, Inner (11)	100	52.0 \pm 28.5	3.5 \pm 6.0	39.5 \pm 32.5	43.0 \pm 31.5	1.0	38.0	10.0	4.0
Fish Bay West, Inner (14)	102	55.0 \pm 36.0	3.0 \pm 5.0	50.5 \pm 37.5	53.0 \pm 36.5	4.0	12.5	2.0	0.0
<i>St. John (deep)</i>									
Great Lameshur, Tektite (15)	103	75.0 \pm 46.5	0.5 \pm 2.5	21.0 \pm 18.5	21.5 \pm 19.0	0	36.0	10.0	3.0
Great Lameshur, Yawzi (16)	112	47.0 \pm 25.0	1.0 \pm 3.5	21.5 \pm 24.0	22.5 \pm 25.0	0	21.5	5.5	2.5
Fish Bay East, Outer (9)	102	58.5 \pm 35.5	0.5 \pm 1.5	44.5 \pm 37.0	45.0 \pm 37.0	1.0	10.0	6.0	4.0
Fish Bay West, Outer (10)	102	54.5 \pm 38.5	1.0 \pm 2.5	21.0 \pm 22.5	22.0 \pm 22.5	0	19.0	11.5	1.5
<i>St. Thomas</i>									
Brewer's Bay (2)	103	50.0 \pm 30.0	1.5 \pm 3.0	37.0 \pm 33.5	38.5 \pm 34.0	0	8.0	9.5	9.5
Buck Island (4)	133	41.0 \pm 22.5	2.0 \pm 9.0	25.5 \pm 30.5	27.5 \pm 30.0	1.5	23.5	4.5	13.5
Caret Bay (1)	105	53.5 \pm 32.5	0.5 \pm 2.0	26.0 \pm 30.5	26.5 \pm 30.5	0	18.0	6.5	8.5
Flat Cay (3)	107	42.0 \pm 20.5	1.0 \pm 2.0	22.0 \pm 30.5	23.0 \pm 28.0	0	18.5	10.5	3.7
Sprat Bay (5)	105	52.5 \pm 30.5	3.5 \pm 5.0	28.5 \pm 24.0	32.5 \pm 23.0	0	15.0	6.0	7.5
<i>Virgin Gorda</i>									
Eustatia Reef (18)	103	56.0 \pm 42.0	2.5 \pm 7.0	30.0 \pm 29.0	32.5 \pm 29.5	0	24.0	5.0	15.5
<i>Guana Is</i>									
Iguana Head (17)	112	55.0 \pm 30.5	1.0 \pm 3.0	17.5 \pm 28.0	22.0 \pm 23.5	0	15.0	24.0	14.5
<i>St. Croix</i>									
Cane Bay (6)	98	63.0 \pm 41.0	1.5 \pm 3.5	23.5 \pm 25.0	24.5 \pm 25.0	0	52.0	5.0	19.5
Long Reef (8)	100	48.5 \pm 26.0	0.5 \pm 1.5	42.0 \pm 31.0	42.5 \pm 31.0	0	46.0	1.0	1.0
Salt River East (7)	103	37.5 \pm 14.5	<0.5 \pm 1.0	35.0 \pm 33.5	35.0 \pm 33.5	1.0	46.5	0	0
<i>Aneгада</i>									
Herman's Reef (19)	100	54.5 \pm 32.0	2.0 \pm 4.0	40.5 \pm 30.0	42.5 \pm 29.5	3.0	25.0	1.0	25.0
Horseshoe Reef (20)	102	64.0 \pm 57.0	1.0 \pm 2.0	38.0 \pm 37.0	39.0 \pm 37.0	12.0	23.5	2.0	9.0
Jack Bay (21)	100	55.5 \pm 34.0	5.5 \pm 20.0	38.0 \pm 36.0	43.5 \pm 37.0	8.0	35.0	2.0	5.0
W. Cow Wreck (22)	100	46.5 \pm 25.0	1.0 \pm 2.0	44.5 \pm 33.5	45.5 \pm 33.5	0	28.0	3.0	9.0

Table 3. Algal characteristics, and density of stony coral recruits and of *Diadema antillarum* (mean \pm standard deviation) by sites in the Virgin Islands.

Site name (Site code)	# quadrats	Macroalgae		% relative abundance turf algae	% relative abundance crustose coralline algae	Macroalgal		Recruits #/0.0625m ²	<i>Diadema</i> #/100m ²
		% relative abundance	% absolute abundance			Height (cm)	Indices Relative (Absolute) ²		
Northern Virgin Islands									
St. John (shallow)									
Great Lameshur, Donkey (12)	52	28.5 \pm 23.0	31.8	68.5 \pm 23.0	3.0 \pm 4.0	2.5 \pm 1.5	71 (80)	5.0 \pm 0.5	26
Great Lameshur, VIERS (13)	50	23.0 \pm 18.0	36.1	59.5 \pm 21.0	17.5 \pm 14.0	2.0 \pm 1.0	46 (72)	7.5 \pm 1.0	5
Fish Bay East, Inner (11)	58	36.0 \pm 26.5	38.8	49.0 \pm 27.4	15.0 \pm 17.0	3.0 \pm 1.0	108 (116)	3.5 \pm 0.5	7
Fish Bay West, Inner (14)	59	79.5 \pm 28.5	51.6	11.0 \pm 27.5	9.0 \pm 15.5	3.5 \pm 1.0	278 (181)	1.5	8
St. John (deep)									
Great Lameshur, Tektite (15)	54	76.0 \pm 30.0	44.6	17.5 \pm 23.5	6.5 \pm 15.5	2.5 \pm 1.5	190 (112)	8.0 \pm 1.0	0
Great Lameshur, Yawzi (16)	50	37.0 \pm 29.5	20.3	49.5 \pm 31.5	14.0 \pm 13.0	1.5 \pm 1.0	55 (31)	10.0 \pm 1.0	1
Fish Bay East, Outer (9)	50	6.0 \pm 7.0	6.8	75.5 \pm 18.0	18.5 \pm 17.0	1.0 \pm 1.0	6 (7)	17.5 \pm 1.5	0
Fish Bay West, Outer (10)	60	51.5 \pm 34.0	30.4	42.5 \pm 35.0	6.0 \pm 9.5	1.0 \pm 0.5	52 (30)	3.5 \pm 0.5	0
St. Thomas									
Brewer's Bay (2)	50	33.0 \pm 17.0	47.1	62.5 \pm 18.5	4.5 \pm 7.5	2.5 \pm 2.0	83 (118)	12.5 \pm 1.0	4
Buck Island (4)	72	69.0 \pm 25.5	38.2	19.0 \pm 22.0	12.0 \pm 15.0	2.5 \pm 1.0	173 (96)	8.5 \pm 1.0	0
Caret Bay (1)	52	55.0 \pm 35.0	40.9	7.0 \pm 20.0	38.0 \pm 30.0	2.0 \pm 1.0	110 (82)	7.5 \pm 1.0	0
Flat Cay (3)	50	46.5 \pm 28.0	26.3	37.0 \pm 30.0	16.5 \pm 19.0	2.0 \pm 1.5	93 (53)	10.5 \pm 1.0	1
Sprat Bay (5)	8	70.5 \pm 28.5	57.6	* ¹	29.5 \pm 28.5	3.5 \pm 2.0	247 (201)	2.0	4
Virgin Gorda									
Eustatia Reef (18)	52	58.0 \pm 31.5	43.2	*	42.0 \pm 31.5	2.0 \pm 1.5	116 (86)	3.0 \pm 0.5	6
Guana Is									
Iguana Head (17)	50	8.0 \pm 14.0	7.7	78.5 \pm 22.5	13.5 \pm 20.0	1.0 \pm 1.0	8 (8)	10.0 \pm 1.0	0
St. Croix									
Cane Bay (6)	50	17.5 \pm 17.0	35.2	67.0 \pm 20.0	15.0 \pm 19.5	2.0 \pm 1.0	35 (70)	6.0 \pm 1.0	4
Long Reef (8)	70	25.0 \pm 21.5	18.9	66.0 \pm 24.6	8.5 \pm 14.5	1.0 \pm 0.5	25 (19)	16.0 \pm 2.0	0
Salt River East (7)	50	5.5 \pm 10.5	3.2	89.0 \pm 15.5	6.0 \pm 9.5	0.5 \pm <0.5	3 (2)	9.0 \pm 1.0	0
Anegada									
Herman's Reef (19)	51	52.0 \pm 33.0	27.3	*	48.0 \pm 33.0	2.0 \pm 1.5	104 (55)	4.5 \pm 0.5	0
Horseshoe Reef (20)	50	73.5 \pm 27.5	35.1	*	26.5 \pm 27.5	2.0 \pm 1.5	147 (70)	10.0 \pm 2.0	0
Jack Bay (21)	70	40.5 \pm 32.8	30.8	*	59.5 \pm 33.0	2.5 \pm 2.0	101 (77)	4.5 \pm 0.5	0
W. Cow Wreck (22)	53	65.7 \pm 28.0	42.8	*	34.3 \pm 28.0	3.5 \pm 4.5	230 (150)	7.5 \pm 1.0	0

¹* = not recorded²Macroalgal index = % relative (or absolute) macroalgal abundance x macroalgal height.

Appendix A. Qualitative assessment of human and natural impacts at 22 sites in the Virgin Islands.

Site name (Site code)	Sediment	Divers	Fishing	Exposure to prevailing seas	Historical hurricane damage	Historical disease epizootics
<i>Northern Virgin Islands</i>						
<i>St. John</i>						
<i>(shallow)</i>						
Great Lameshur, Donkey (12)	low	low	low	low	moderate	moderate
Great Lameshur, VIERS (13)	low	moderate	Moderate?	low	moderate	moderate
Fish Bay East, Inner (11)	moderate	low	low	low	low	moderate
Fish Bay West, Inner (14)	high	low	low	low	low	moderate
<i>St. John (deep)</i>						
Great Lameshur, Tekite (15)	low	moderate	moderate?	low	moderate	high (white plague)
Great Lameshur, Yawzi (16)	moderate	moderate	moderate?	low	high	moderate (white plague)
Fish Bay East, Outer (9)	moderate	low	low	low	high	moderate?
Fish Bay West, Outer (10)	high	low	low	low	high	moderate?
<i>St. Thomas</i>						
Brewer's Bay (2)	moderate	low	moderate	low	low	low
Buck Island (4)	low	high	low	low	low	low
Caret Bay (1)	low	low	low	moderate	low	low
Flat Cay (3)	low	high	moderate	low	low	low
Sprat Bay (5)	low	moderate	moderate	low	low	low
<i>Virgin Gorda</i>						
Eustatia Reef (18)	low?	high	moderate?	moderate	moderate?	moderate? (white band)
<i>Guana Is</i>						
Iguana Head (17)	low?	low?	moderate?	low	low?	low?
<i>St. Croix</i>						
Cane Bay (6)	moderate	high	low	moderate	low	low?
Long Reef (8)	moderate	high	high	moderate	moderate	high (white band)
Salt River East (7)	moderate	high	moderate	moderate	low	low?
<i>Anegada</i>						
Herman's Reef (19)	low	low	low?	moderate	high	high (white band)
Horseshoe Reef (20)	low	low	low?	high	high	high (white band)
Jack Bay (21)	low	moderate?	moderate?	high	high	high (white band)
W. Cow Wreck (22)	low	low	low?	high	high	high (white band)