

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 2: FISHES)

BY

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ABSTRACT

The Atlantic and Gulf Rapid Reef Assessment (AGRRA) fish survey was conducted in depths of 3-14 m at 22 coral reef sites in the U.S. Virgin Islands (St. Croix, St. John, St. Thomas) and the British Virgin Islands (Anegada, Guana Island, Virgin Gorda). Total fish species richness, determined by using the roving diver technique was 72-160 species. A total of 14,441 fish from 54 species of selected families were counted in belt transects. The select fish fauna was dominated by the Scaridae (35%), Acanthuridae (35%) and Haemulidae (16%). Key herbivorous fish densities among sites ranged from ~4-49 fish/100m² for scarids and from 1-60 fish/100m² for acanthurids. Predatory fish densities among sites ranged from 0.2-5.5 fish/100m² for serranids and from 0-11.5 fish/100m² for lutjanids. The density of large herbivorous fishes showed a significant negative relationship with macroalgal index and with the percent of coral colonies occupied by territorial damselfish. Also significant were the positive relationships between total fish species richness and coral cover, between chaetodontid density and total fish species richness, and between pomacanthid density and depth.

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 British Virgin Islands (BVI) and the islands of Puerto Rico, rise from a geological shelf that is surrounded by deep water (Dammann, 1969, unpublished report). 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 northerly Virgin Islands by the 4,685 m-deep and 60 km-wide Virgin Islands trough. The three main U.S. islands of St. Thomas, St. John and St. Croix are

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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). Many of these reefs are adjacent to mangrove forests, seagrass beds and algal plains, which are important nursery habitats for reef-associated fishes (Austin, 1971; Parrish, 1989; Heck and Weinstein, 1989).

The USVI, like other populated regions of the world, have witnessed steady declines in catches of commercially important marine fishes (Caribbean Fisheries Management Council, 1985, unpublished report; Roberts, 1997). Millions of people in developing countries depend upon coral reef fishes for their livelihoods (Roberts, 1993). However, declining fisheries cannot only be attributed to overfishing but to a suite of other factors since evidence suggests that degradation of coral reefs can influence reef fish communities (Bell and Galzin, 1984; Bouchon-Navaro et al., 1985). Over the past 20 years, eight major hurricanes, numerous disease outbreaks, sporadic bleaching events, ship groundings, anchor damage, plus inputs of sediment and pollution have caused excessive damage to the coral reefs surrounding the Virgin Islands (Gladfelter, 1982; Rogers et al., 1991; Rogers and Garrison, 2001).

The USVI fishing community has remained relatively stable since the early 1900's. Licensed fishermen have consistently numbered approximately 400 between 1930 and today, even though the total population of the islands has increased from 22,012 to about 100,000 (Fielder and Jarvis, 1932; Department of Commerce Census, 2000). Since the early 1970's, fish stocks in the near shore USVI have been declining steadily despite government-funded research and development programs for the deep-water fisheries around the Virgin Islands plateau (Brownell and Rainey, 1971, unpublished report). The catch of fishery products fluctuated between 550,000 and 1,650,000 pounds per year between 1930 and 1997 (Fielder and Jarvis, 1932; de Graff and Moore, 1987, unpublished report; Tobias, 1997, unpublished report), but the fishing effort increased dramatically. For example, in the USVI the average number of traps fished per full-time fisherman increased from 4 in 1930, to 8 in 1967, to >100 in 1997 (Fielder and Jarvis, 1932; Dammann, 1969; unpublished report; T. Tobias, USVI Fish and Wildlife, 1998). The maximum number of traps fished by a single fisherman in 1930 was 30 traps whereas today it can be as high as 2000 traps (Fielder and Jarvis, 1932; Downs and Petterson, 1997, unpublished report). The pursuit of declining stocks not only puts fish populations at risk of commercial extinction but often increases reef damage associated with fishing (Sladek Nowlis and Roberts, 1998; Appeldoorn, 2001, unpublished manuscript; Nemeth, unpublished data).

Increased fishing pressure on nearshore and offshore fish populations has already resulted in the collapse of several species. For example, in the 1970's unregulated fishing in spawning aggregations of Nassau grouper (*Epinephelus striatus*) and yellowfin grouper (*Mycteroperca venenosa*) off St. Thomas led to the commercial extinction of these species (Olsen and LaPlace, 1978; Beets and Friedlander, 1992, 1999). In the absence of Nassau grouper, fishermen targeted red hind (*E. guttatus*) spawning aggregations. Within 10 years, the St. Thomas red hind population was on the verge of collapse when a seasonal (December through February) closed area at the red hind spawning aggregation site was implemented in 1990 (Beets and Friedlander, 1992). Within 6 years of the closure, Beets and Friedlander (1999) reported that an increase in

their average size and an improved sex ratio (red hind are protogynous hermaphrodites) were indications of red hind population recovery.

Without proper management tools, sustained fishing mortality can decrease the capacity, productivity and genetic diversity of the fishery (Bohnsack, 1990). Moreover, selective removal of ecologically important species can lead to ecosystem damage and produce major ecological shifts (Hay, 1984; Roberts, 1995; Botsford et al., 1997). 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 and associated fishes throughout the region was launched. The Center for Marine and Environmental Studies of the University of the Virgin Islands (UVI) joined the effort and set out to conduct a broad survey of the fish assemblages of the Virgin Islands with a focus on commercially and ecologically important species using the AGRRA protocol. This paper reports on the initial findings of our assessment. Results of the benthic surveys are given in Nemeth et al. (this volume).

METHODS

An assessment of fish species abundance and diversity was conducted at 22 sites in the Virgin Islands (Fig. 1) between May 1998 and July 2000. 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 long-term sedimentation and reef fish monitoring projects, their proximity to the UVI MacLean 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 off 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 deeper reefs (> 6 m) located outside the bays. Four of the six sites surveyed in the BVI (Iguana Head on Guana Island, Eustatia Reef on Virgin Gorda, West Cow Wreck Bay and Herman's Reef on Anegada) were selected haphazardly. Eustatia Reef, off Virgin Gorda, is a heavily visited dive site whereas Guana Island is a private island with few inhabitants. The other two sites on Anegada (Jack Bay and Horseshoe Reef—a designated protected area) were selected because of historical surveys (Dunne and Brown, 1976; West Indies Laboratory, 1983, unpublished reports). The reefs of Anegada were included in the AGRRA survey to provide a remote reference site with low human population and little landmass. The major difference in fishing regulations between the USVI and the BVI is that spearfishing is prohibited in the BVI. A qualitative assessment of natural and human impacts, including fishing pressure, at each site surveyed in the Virgin Islands is given in Appendix A of Nemeth et al. (this paper).

The AGRRA fish protocol Version 2.0 (see Appendix One, this volume) was used except off St. Croix where Version 2.1 was employed. Three divers (authors) constituted the primary fish survey team with R. Nemeth conducting the majority of surveys on all islands except those off St. Croix. Fish identification guides included Humann (1994), Pp. 566-589 in J.C. Lang (ed.), Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

Stokes (1984) and Robins and Ray (1986). Visual fish counts were conducted along at least ten 30 x 2 m transects, and one 30-minute roving diver survey was conducted at each site except in Brewer's Bay, St. Thomas (n = 2 surveys) and off St. Croix, where longer (60-90 minute) survey were conducted in Cane Bay (n = 3), Long Reef (n = 5) and Salt River (n = 6). During fish transects, transect width and fish lengths (cm) were estimated using a 1 m-wide T-bar constructed of polyvinylchloride pipe marked in 5 cm and 10 cm increments. In all sites except St. Croix, scarids (parrotfish) and haemulids (grunts) less than 5 cm in length were counted and identified to species whenever possible. Using transects as replicates, the average density ($\#/100\text{m}^2$) and size (cm) of each species and family were calculated for each site and island group (see below). The size distributions of herbivores [parrotfish, surgeonfish (acanthurids) and the yellowtail damselfish, *Microspathodon chrysurus*] and of the AGRRA carnivores [select groupers (serranids) and all lutjanids] were also calculated.

Data were summarized by island groups within three geographic areas to examine general trends in reef fish assemblages and to be comparable with the Virgin Islands benthic data which are presented in Nemeth et al. (this volume). The geographic areas were: (1) Anegada; (2) the shallow and deep reefs of the northern USVI and BVI (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. John, St. Thomas; BVI = Guana Island, 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 off St. John were analyzed separately from the deep reefs within the NVI archipelago.

RESULTS

A total of 256 fish transects and 34 roving diver surveys were conducted at 22 sites throughout the USVI and the BVI (Table 1). During visual belt transects of the selected AGRRA fishes (Appendix One), divers recorded 54 species and counted a total of 8,227 fish (n= 14,441 fish when grunts and parrotfishes <5 cm in Anegada and the NVI are included). Fish species richness, based upon the maximum number of species seen during any single roving diver survey, varied between a high of 74 species in Cane Bay (St. Croix) and a low of 40 species in Fish Bay (shallow St. John) with >90% (20/22) having values between 40 and 70 species (Table 1). The average number of fish species by island group was greatest in St. Croix (68 species), followed by the deep NVI reefs (59), Anegada (52) and the shallow St. John sites (47), although these differences were not significant ($F_{3,29} = 2.75$, $p = 0.061$). Total cumulative reef fish richness by island group was 160 species in the NVI (n = 12 surveys at 11 sites), 131 species in St. Croix (n = 14 surveys at 3 sites), 98 species in Anegada (n = 4 surveys at 4 sites) and 72 species in the shallow St. John sites (n = 4 surveys at 4 sites). The additional roving diver surveys conducted in St. Croix and the large number of deeper sites in the NVI most likely contributed to a higher number of fish species seen within these island groups. To

illustrate, divers in St. Croix counted: 58, 68 and 74 fish species during three roving surveys in Cane Bay; 45, 53, 63, 65, and 68 species during five roving surveys in Long Reef; and 37, 49, 54, 58, 60 and 63 species during six roving surveys in Salt River. The cumulative numbers of fish species seen in Cane Bay, Long Reef and Salt River reefs during these multiple surveys were 92, 88 and 117, respectively (Table 1). Based on an analysis of the six roving diver surveys at Salt River where search times averaged 73 minutes per survey, a species accumulation curve showed that at least four such surveys (i.e. 4.8 hours search time) are necessary to record at least 90% of the fish species and at least six surveys (i.e., 7.3 hours search time) to approximate total species diversity at a site. Thus, depending upon the skill level of the diver, species diversity estimates based on a single 60-minute roving diver survey may represent only 40% to 70% of the actual number of species present in a reef. The 25 most commonly seen species during roving diver surveys were represented by 11 fish families (Pomacentridae, Scaridae, Labridae, Serranidae, Acanthuridae, Holocentridae, Haemulidae, Chaetodontidae, Gobiidae, Mullidae, and Tetraodontidae) with *Thalassoma bifasciatum*, *Acanthurus coeruleus*, *Sparisoma aurofrenatum*, *S. viride* and *Haemulon flavolineatum* being ubiquitous in all sites (Table 2).

Of the 54 AGRRA species sighted in belt transects, scarids and haemulids were each represented by 9 species, lutjanids by 7 species, serranids and pomacanthids each by 6 species, balistids by 5 species, chaetodontids by 4 species, acanthurids by 3 species, labrids by 2 species, and pomacentrids, sphyraenids and carangids each by 1 species. The 25 most abundant of these species (Table 3) represented nearly 94% of all fish sighted in the belt transects. Numerically the AGRRA fish fauna in the Virgin Islands was dominated by the families Scaridae (35%, all ≥ 5 cm), Acanthuridae (35%) and Haemulidae (16%, all ≥ 5 cm) (Fig. 2, Table 3). The herbivorous scarids and acanthurids represented 7 of the 10 most abundant species, with the ocean surgeonfish (*Acanthurus bahianus*) ranked first overall. Three carnivores, the French grunt (*Haemulon flavolineatum*), tomtate (*H. aurolineatum*) and yellowtail snapper (*Ocyurus chrysurus*) were also ranked among the top 10 most abundant species (Table 3). Although newly recruited grunts were not included in this analysis, high densities of juvenile haemulids (<5 cm) were observed in the NVI off Guana Island (710.7 grunts/100 m²) and Buck Island, St. Thomas (10.7 grunts/100 m²), as well as in VIERS (8.3 grunts/100m²) and Fish Bay East Inner (3 grunts/100 m²) in shallow St. John. High densities of juvenile scarids were also recorded. Scarids <5 cm comprised 24-77% of parrotfish densities in Anegada and the NVI (Fig. 3). We found a general increase in the density of juvenile scarids off Anegada (the easternmost reefs) through the lower BVI to the shallow St. John sites where they were most abundant (Fig. 3). Juvenile densities dropped in the deep St. John sites and were slightly higher around St. Thomas. A weak negative relationship between the density of juvenile scarids <5cm and depth ($r^2 = 0.18$, $F_{20,1} = 4.48$, $p < 0.05$) was found in a regression analysis.

Herbivorous fish densities (# fish/100 m²) among sites ranged from 3.8 (Fish Bay West Inner, St. John) to 48.8 (Great Lameshur, Yawzi, St. John) for the Scaridae and 1.0 (Brewer's Bay, St. Thomas) to 60.5 (Fish Bay East Outer, St. John) for the Acanthuridae (Table 4). Overall, the abundance of parrotfishes (>5 cm) and surgeonfishes were similar in both shallow (11.6 scarids versus 13.1 acanthurids/100 m²) and deeper (19.4 scarids versus 18.2 acanthurids/100 m²) reefs. Predatory fish densities (# fish/100 m²) among

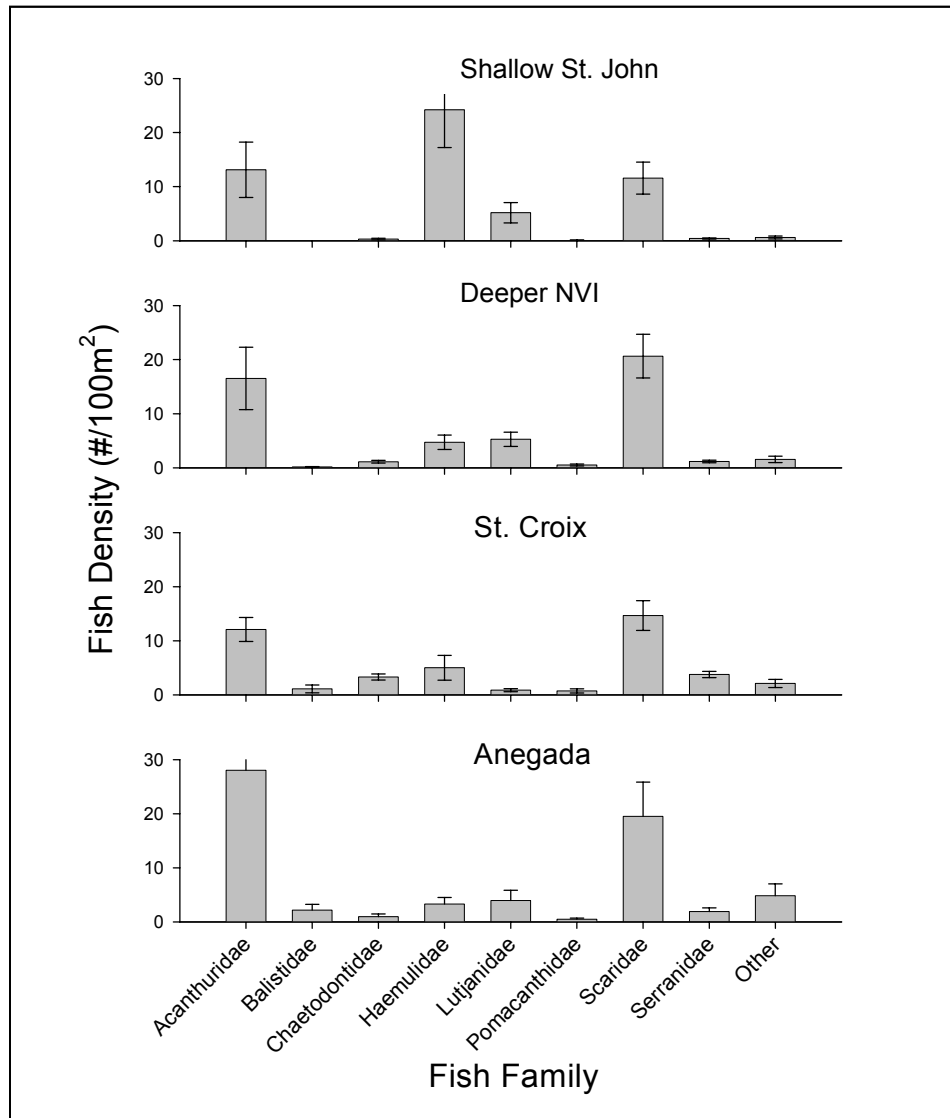


Figure 2. Fish density (mean no. fish/100 m² ± standard error) for AGRRA fishes in shallow St. John, deeper NVI (St. Thomas, St. John >6 m deep, Guana Is., Virgin Gorda), St. Croix and Anegada. Other = *Bodianus rufus*, *Caranx ruber*, *Lachnolaimus maximus*, *Microspathodon chrysurus*, *Sphyraena barracuda*.

sites ranged from 0.2 (Fish Bay East Inner, St. John) to 5.5 (Cane Bay, St. Croix) for the Serranidae, and from 0.0 (Herman's Reef, Anegada) to 11.5 (Sprat Bay, St. Thomas) for the Lutjanidae (Table 4). It is unusual to note that no snappers were seen at Herman's Reef during transects or roving diver surveys and no grunts were counted during transects at Horseshoe Reef (one French grunt was seen during a roving diver survey).

The size distributions of fishes comprising the two major feeding guilds (herbivores and carnivores) were found to be fairly similar among the deeper NVI reefs and those of St. Croix (Fig. 4). Anegada was unique in that it had twice the density of 21-30 cm carnivores and 11-20 cm herbivores as the other sites and an abundance of juvenile acanthurids <5 cm (Fig. 4). Jack Bay was unusual in that it had considerably smaller groupers than other sites in Anegada (Table 5). The shallow St. John sites had

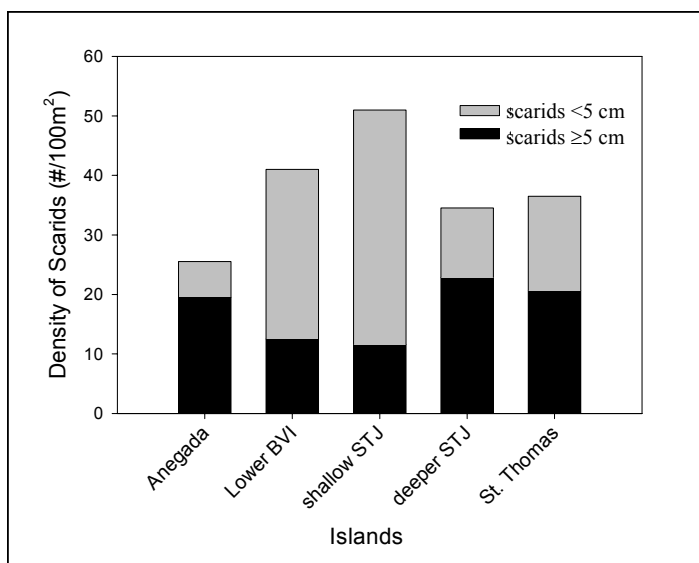


Figure 3. Density (mean no. fish/100 m²) of scarids $< 5 \text{ cm}$ and $\ge 5 \text{ cm}$ in length for Anegada (four reefs), Lower BVI (two reefs), shallow St. John (four reefs), deeper St. John (four reefs) and St. Thomas (five reefs). Scarids $< 5 \text{ cm}$ were not recorded in St. Croix.

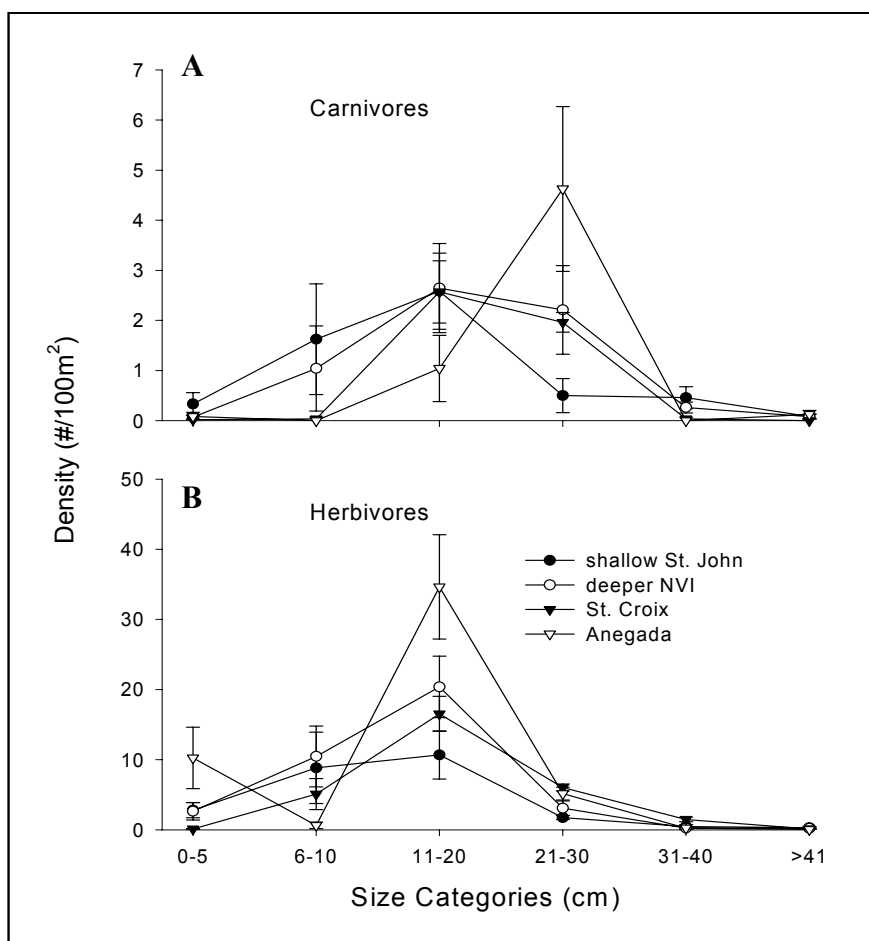


Figure 4. Size composition (mean density \pm standard error) of (A) carnivores (lutjanids, large serranids) and (B) herbivores (acanthurids, scarids $\ge 5 \text{ cm}$, *Microspathodon chrysurus*) in shallow St. John, deeper NVI, St. Croix and Anegada.

substantially fewer groupers and snappers in the 21-30 cm size class (Fig. 4) but over twice as many newly settled (<5 cm) scarids as the other sites (Fig. 3). Within the deeper NVI sites, two reefs in the BVI (Virgin Gorda and Guana Island) and most of the deeper sites around St. John had larger groupers than the reefs around St. Thomas (Table 5). With the exception of Buck Island and Sprat Bay, the reefs off St. Thomas also tended to have smaller snappers and parrotfish relative to the other NVI sites. One site in Great Lameshur Bay (VIERS) had smaller groupers than the other shallow sites off St. John. Similarly, Cane Bay generally had smaller snappers than the other two reefs off St. Croix (Table 5).

A series of multiple regression analyses were conducted between the average fish density or the total fish species richness and each of the following: depth, live stony coral cover and, for “large” (≥ 25 cm diameter) stony corals, mean size and recent partial-colony mortality (Nemeth et al., this volume). Only one of these comparisons was significant. Total fish species richness (using results from a single roving diver survey per site) showed a positive relationship with percent live stony coral cover (Fig 5). Upon further analysis of fish guilds or individual species, some other interesting patterns emerged. A significant negative relationship was found between the density of herbivorous fishes greater than 5 cm in length and macroalgal index calculated from percent absolute abundance of macroalgae (Fig 6). This relationship remained significant even when herbivore density was compared to macroalgal index calculated with percent relative abundance of macroalgae ($r^2 = 0.28$, $p < 0.04$) or when compared directly to absolute macroalgal abundance ($r^2 = 0.64$, $p < 0.001$). Significant positive relationships were also found between the density of butterflyfish (Chaetodontidae) and total fish species richness from either a single roving diver survey per site ($r^2 = 0.19$, $p < 0.04$) or from results of multiple roving diver surveys (Fig. 7). However, no significant relationship was found between the density of chaetodontids and percent live stony coral cover ($p < 0.62$). A significant positive relationship was found between the density of angelfish (Pomacanthidae) and depth (Fig. 8). Finally an interesting negative relationship was found between the density of large herbivores (≥ 10 cm) and the percent of large stony corals occupied by territorial damselfishes (*Stegastes planifrons*, *S. diencaeus* and *S. fuscus*; Fig. 9).

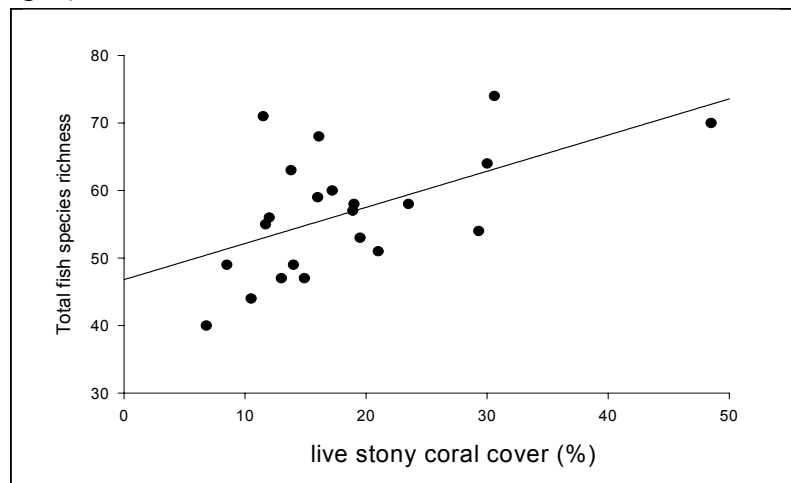


Figure 5. Regression between total fish species richness and percent live stony coral cover ($r^2 = 0.30$, $p < 0.01$), by site in the Virgin Islands.

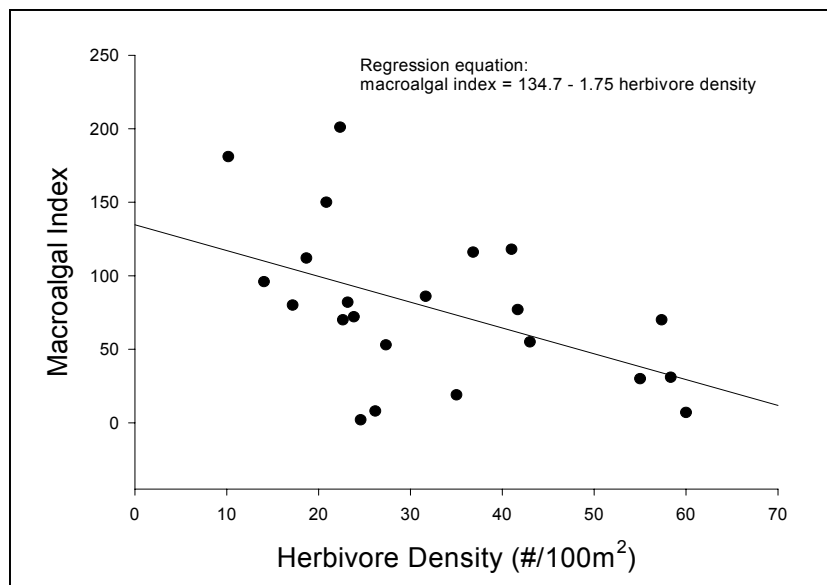


Figure 6. Regression of herbivore (acanthurids, scarids ≥ 5 cm, *Microspathodon chrysurus*) density versus the macroalgal index (absolute abundance of macroalgae x macroalgal height) by site in the Virgin Islands. $r^2 = 0.24$, $F_{20,1} = 6.33$, $p < 0.02$.

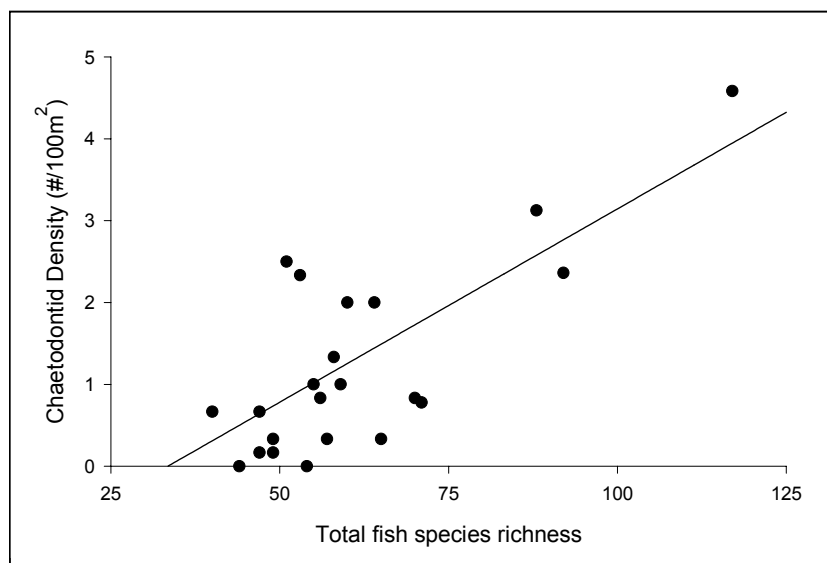


Figure 7. Regressions between chaetodontid density and total fish-species richness ($r^2 = 0.564$, < 0.0001) by site in the Virgin Islands.

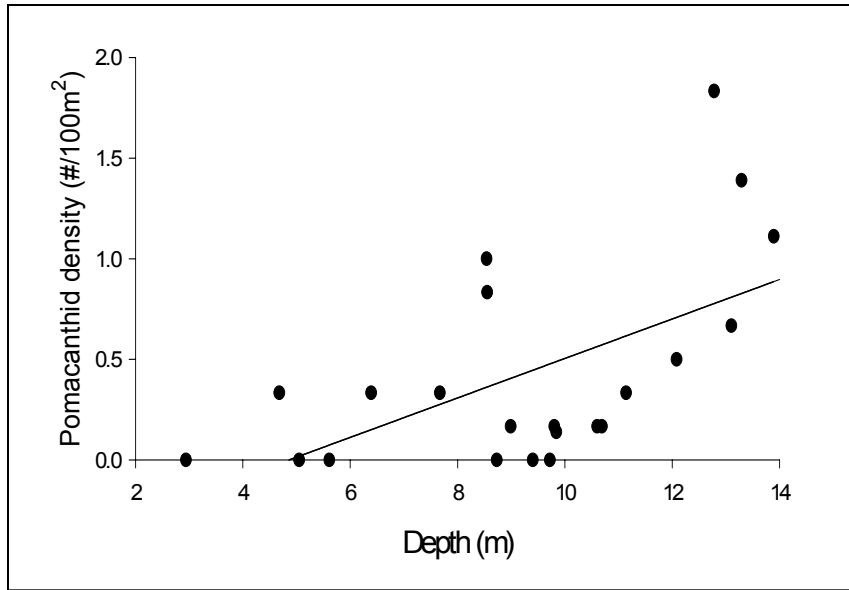


Figure 8. Regression of pomacanthid density and depth ($r^2 = 0.32$, $p < 0.005$) by site in the Virgin Islands.

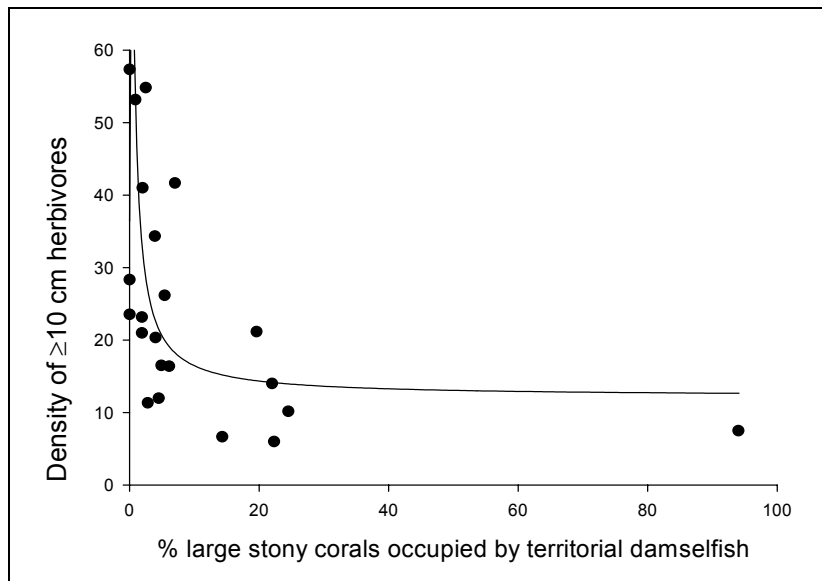


Figure 9. Relationship between the density of adult (≥ 10 cm length) herbivores (acanthurids, scarids, *Microspathodon chrysurus*) and the percent of large (≥ 25 cm) stony corals occupied by territorial damselfish by site in the Virgin Islands. Nonlinear stepwise regression analysis produced a significant fit ($r^2 = 0.97$, $p < 0.0001$) with an inverse second order quadratic equation ($F = y_0 + a/x = b/x^2$).

DISCUSSION

Fish assemblage structure was relatively similar among island groups within the USVI and BVI. Herbivorous fishes, especially the parrotfishes and surgeonfishes, dominated the reefs at all sites and, overall (≥ 5 cm scarids only), comprised 72% of the

fish fauna. The shallow St. John sites deviated from this pattern with the ≥ 5 cm Haemulidae showing a five-fold increase in abundance relative to the deeper reef areas throughout the region. The abundance of haemulids in shallow reefs can be attributed most likely to the proximity of seagrass beds (Parrish, 1989; Muehlstein and Beets, 1992; Nagelkerken et al., 2000a,b,c, 2001), which are prevalent along the south coast of St. John. Juvenile scarids were a major component (24% to 77%) of parrotfish densities in Anegada and the NVI. There was a general increase in density of juvenile parrotfish from the easternmost reefs of Anegada to the shallow reefs of St. John, which may indicate an upstream source of larval fish recruitment (Roberts, 1997). However, a weak negative relationship with depth or the lower number of large carnivores on the shallow reefs of St. John may also explain some of the spatial variation in juvenile scarid densities. Although temporal variation in recruitment patterns may have influenced juvenile scarid densities on the shallow St. John reefs, many of the fish surveys were conducted during similar time periods.

The remaining selected fish families [i.e., snappers, groupers, angelfish, butterflyfish, and triggerfish (balistids)] were similar in abundance among the deep reef areas but much less common in the shallow St. John sites. Total fish species richness was also similar among the island groups, although estimates were greatly influenced by the number of sites visited or the number of roving diver surveys performed at a site. Based on species accumulation curves, a minimum of six roving diving surveys or more than seven hours search time would be needed to approximate the actual species diversity at a site. Although this level of effort would not be practical considering that AGRRA is supposed to be a rapid assessment technique, it is recommended that future AGRRA surveys conduct at least one, but preferably two, 60-minute roving diver surveys.

Multiple regression analyses detected some interesting regional patterns of abundance associated with benthic parameters which accounted for a significant portion of the variability in total fish species richness and in the density of butterflyfish and angelfish. The significant relationship between total fish species richness and percent cover of live stony corals (Fig. 5) suggests that species packing occurs where well-developed reefs provide greater structural complexity (Risk, 1972; Luckhurst and Luckhurst, 1978; Bell and Galzin, 1984; Roberts and Ormond, 1987). In earlier studies of chaetodontid fish assemblages around the world, significant relationships were found between their densities and the percent living coral cover and coral diversity (Bell et al., 1985; Bouchon-Navaro et al., 1985; Bouchon-Navaro and Bouchon, 1989; Roberts et al., 1992). Our analysis differed from these results in that the density of butterflyfishes was not associated with any benthic factor. A positive relationship between butterflyfish density and total fish species richness in the Virgin Islands (Fig. 7) complemented the results of Roberts et al. (1992), who found a positive relationship between the density and total abundance of butterflyfishes and species richness in the Red Sea.

Important differences in fish size distribution patterns were apparent among the island groups. Within the Virgin Islands archipelago, Anegada is the most remote and least populated island, and its reefs probably experience the lowest level of fishing pressure relative to the other islands. Moreover, large portions of the extensive reef system surrounding Anegada, along with 12 other sites in the BVI, are marine conservation parks protected by the BVI National Parks Trust. All commercial and recreational fishing is prohibited within marine park boundaries (BVI National Parks Pp. 566-589 in J.C. Lang (ed.), Status of Coral Reefs in the western Atlantic: Results of initial Surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. Atoll Research Bulletin 496.

Trust, unpublished). These factors probably contributed to a greater abundance of the large-size classes of predators and herbivores in Anegada as well as in the two other BVI reefs (Iguana Head, Guana Island and Eustatia Reef, Virgin Gorda).

Patterns also emerged when the average sizes of several commercially important fish families were compared among islands. In general, most sites off St. Thomas had smaller groupers, snappers, grunts and parrotfishes than deeper reefs off other islands (i.e., St. John, St. Croix, Virgin Gorda and Guana Island). These differences were probably due to a suite of factors specific to each island. For example, St. Thomas has the greatest human population density of all the islands, the largest number of seasonal workers from other Caribbean islands (who often supplement their diet by fishing in near shore waters), and the highest number of tourists who participate in recreational or sport fishing activities (US Department of Commerce, 2000; Virgin Islands Department of Fish and Wildlife, 2001, unpublished report). Fishing regulations, primary target species, and gear types may also influence harvest rates. In a survey of recreational fishers in the Virgin Islands, Jennings (1992) reported that nearly 65% of the fishers targeted groupers and snappers. He also found that up to 8% speared fish in the St. Thomas/St. John area, whereas none spear fished in St. Croix. In contrast, spear fishing is prohibited throughout the BVI and within the Virgin Islands National Park waters surrounding approximately 50% of St. John. In the Florida Keys, sites protected from spear fishing had higher densities and larger sizes of several species especially snappers and grunts (Roberts and Polunin, 1993). Even low levels of protection within an area have resulted in increased biomass of commercially important fishes (Bohnsack, 1996; Roberts and Hawkins, 1997). In a recreational fisher survey conducted in the USVI in 2001 by the Virgin Islands Division of Fish and Wildlife, 67% of the people interviewed indicated that they spear fished or bottom fished less than 3 miles from shore (unpublished report). These and other factors would greatly intensify the fishing pressure on near-shore stocks and result in over-harvest around the St. Thomas area (Jennings, 1992).

By focusing on the variation in fish size within each island or island group, we also observed that some sites had consistently smaller fish across most commercially important families (Table 5). These sites included the VIERS shallow reef and Tektite deep reef (St. John), Brewer's Bay (St. Thomas), Cane Bay (St. Croix) and Jack Bay (Anegada). Although many natural factors may contribute to the impacts on reef fisheries, one of the most important similarities among all of these sites seems to be accessibility to skin or scuba divers. Easy access from shore and popularity of a dive site (i.e., presence of a public mooring) will concentrate fishing activity in these locations. This is especially true when commercial dive charters allow patrons to spear fish. VIERS reef, Brewer's Bay, Cane Bay and Jack Bay are unique among all the sites surveyed since they are easily accessible from shore by skin and scuba divers who may participate in spear fishing (R. Nemeth, personal observation). Brewer's Bay, in particular, is a beach frequently (e.g. weekly) used by local spear fishermen (R. Nemeth, personal observation). Tektite reef is also a popular dive destination, and may experience increased fishing pressure even though it is within the Virgin Islands National Park. The fact that Rogers and Beets (2001) found no apparent difference in fish assemblage structure inside or outside the national park boundaries indicates that fishing pressure is still substantial at some sites within the park.

Further support of the hypothesis that size structure is largely determined by access to divers can be gained by looking at reefs off islands that consistently had larger fish in most commercially important families. Sites such as Caret Bay (St. Thomas) and Fish Bay East Outer (St. John) are rarely, if ever, visited by skin or scuba divers, and Salt River (St. Croix), although a popular dive area, is within the Salt River Bay National Historic Park and Ecological Preserve. Thus fishing pressure at these sites is very low relative to more popular or unprotected sites.

Overall densities of parrotfishes and surgeonfishes in the shallow and deeper reefs of the Virgin Islands were comparable to those reported by Lewis and Wainwright (1985) with the exception that parrotfishes of all sizes in the shallow St. John sites were 7.5 times more abundant than in Belize (50.9 versus 6.7 scarids/100m²). The significant negative relationship between herbivore density and macroalgal index (Fig. 6) suggests that grazing pressure of herbivorous fishes is an important factor in determining the structure of tropical benthic communities (Lewis and Wainwright, 1985; Lewis, 1985, 1986). Grazing pressure was strongly correlated to herbivore density in Belize (Lewis, 1985, 1986). Lewis (1986) showed a nearly 30% increase in the cover of macroalgae (primarily *Padina* and *Dictyota*) relative to controls when herbivorous fishes were excluded from experimental plots in back-reef habitats in Belize. Total macroalgal index calculated from Lewis (1986) was 150 within shallow back-reef exclusion cages compared to an average macroalgal index of 126 on shallow reefs and 99 on deeper reefs of the Virgin Islands archipelago (Nemeth et al., this volume).

In the Virgin Islands, the density of large (≥ 10 cm) herbivores (parrotfishes and surgeonfishes) was negatively related to the percent of large stony corals occupied by territorial damselfishes (Fig. 9). The presence of territorial damselfishes, which aggressively defend their algal turfs, has been shown to have a dramatic effect on the social behavior, abundance, and feeding strategies of other herbivorous competitors (Williams, 1979; Hourigan, 1986). In the Caribbean and Pacific, several studies have shown that parrotfishes and surgeonfishes form large schools to feed in the territories of other species, especially territorial damselfishes (Vine, 1974; Robertson et al., 1976; Hourigan, 1986). Robertson et al. (1976) found that schooling parrotfishes and surgeonfishes, which settled and fed en masse within damselfish territories, had higher feeding rates and fewer aggressive episodes than non-schooling individuals. The experimental removal of territorial damselfish within a defined area typically results in a rapid increase in the abundance of other herbivorous fishes (Robertson et al., 1976; Hourigan, 1986; Nemeth, unpublished data). The negative relationship between the density of large herbivores and the density of territorial damselfish could be due to an actual competitive exclusion of herbivores in the area and/or an artifact of the belt-transect method, which may underestimate the densities of schooling herbivores. By comparing the relative densities of herbivores from fish transects and roving diver surveys, we found that density estimates were comparable in magnitude at 85% (11/13) of the sites where damselfish occupied less than 10% of the coral heads but in only one of the six (17%) sites where damselfish occupied more than 10% of the coral heads. This suggests that, in areas with high densities of territorial damselfishes, the abundance of large herbivores were underestimated using fish transects since roving schools of parrotfishes and surgeonfishes can move unpredictably over large areas of coral reef (Robertson et al. 1976).

Considering the wide range of benthic conditions, human factors, and management regulations that could potentially influence fish assemblage structures, we were surprised to find that the abundance and size structure of commercially and ecologically important species were relatively similar among island groups of the Virgin Islands. Within the island groups, the primary notable differences were the larger size structure of herbivores and carnivores in Anegada and the greater abundance of haemulids in the shallow reefs of St. John. The significant relationships between selected fish families and various benthic parameters generally supported the observations of previous studies within the Caribbean and other tropical regions. Within each island, site-specific differences in fish-size structure may be explained by variations in fishing pressure from recreational fishermen, including spear fishers.

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Table 1. Site information for AGRRA fish surveys in the Virgin Islands.

Site name	Site code	Reef Type ¹ / Exposure	Latitude (° ' " N)	Longitude (° ' " W)	Survey Date(s)	Depth (m)	>25 cm stony corals (#/10m) ²	% live stony coral cover (mean ± sd) ²	# 30 m fish transects (# RDT) ³	Total fish species (#) ⁴
Northern Virgin Islands										
<i>St. John (shallow)</i>										
Great Lameshur, Donkey	12	F/W	18 18.853	64 43.312	May 26 00	3	8.5	18.5 ± 3.5	10 (1)	57
Great Lameshur, VIERS	13	F/W	18 19.094	64 43.390	Oct 23 99	5.5	4	13.5 ± 6.0	10 (1)	47
Fish Bay East, Inner	11	F/W	18 19.073	64 45.808	Nov 14 99	5	3.5	10.5 ± 6.0	10 (1)	44
Fish Bay West, Inner	14	F/W	18 19.053	64 45.878	Aug 15 00, Oct 24 00	5	8.5	7.0 ± 6.0	10 (1)	40
<i>St. John (deep)</i>										
Great Lameshur, Tektite	15	F/W	18 18.572	64 43.302	Aug 3 99, Nov 29 99	11	10.5	48.5 ± 13.5	10 (1)	70
Great Lameshur, Yawzi	16	F/W	18 18.831	64 43.596	July 23 99	12.5	4.5	16.0 ± 8.0	10 (1)	59
Fish Bay East, Outer	9	F/W	18 18.948	64 45.777	Feb 08 00	6.5	4.5	12.0 ± 5.0	10 (1)	56
Fish Bay West, Outer	10	F/W	18 18.850	64 45.845	Aug 02 99	7.5	4	13.0 ± 6.5	10 (1)	47
<i>St. Thomas</i>										
Brewer's Bay	2	F/W	18 20.670	64 59.157	May 26 99, June 9 00	8.5	6.5	19.0 ± 6.5	10 (2)	58 (65) ⁵
Buck Island	4	F/W	18 19.781	64 57.097	May 19 98, July 14 99	14	3.5	11.5 ± 6.0	16 (1)	71
Caret Bay	1	F/W	18 22.421	64 59.371	May 21 98, July 17 00	9.5	6	23.5 ± 8.5	10 (1)	58
Flat Cay	3	F/W	18 19.072	64 59.444	July 7 99, June 12 00	12	6	21.0 ± 7.5	10 (1)	51
Sprat Bay	5	F B/W	18 19.718	64 55.630	Aug 31 00	10.5	13	29.5 ± 7.0	10 (1)	54
<i>Virgin Gorda</i>										
Eustatia Reef	18	F B/W	18 30.50	64 20.250	July 24 00	9	9.5	17.0 ± 6.0	10 (1)	60
<i>Guana Island</i>										
Iguana Head	17	F/W	18 28.477	64 34.941	Aug 06 99	10	8.5	30.0 ± 9.5	10 (1)	64
<i>St. Croix</i>										
Cane Bay	6	F/W	17 46.230	64 48.530	Oct 14 99, Dec 16 99	10	7.5	30.5 ± 11.0	12 (3)	74 (92) ⁵
Long Reef	8	F B/W	17 46.118	64 41.490	Oct 13 99	13.5	7.5	16.0 ± 3.5	24 (5)	68 (88) ⁵
Salt River East	7	F/W	17 47.227	64 45.330	Oct 13 99	10	6	14.0 ± 4.0	24 (6)	63 (117) ⁵
<i>Anegada</i>										
Herman's Reef	19	B B /L	18 33.841	64 14.320	July 24 00	13	10	19.5 ± 5.5	10 (1)	53
Horseshoe Reef	20	B B /W	18 39.965	64 13.890	July 22 00	10.5	6	14.0 ± 6.5	10 (1)	49
Jack Bay	21	F B/W	18 44.961	64 19.246	July 22 00	9	4.5	8.0 ± 4.5	10 (1)	49
W. Cow Wreck	22	F B/W	18 45.164	64 24.596	July 23 00	8.5	7	11.5 ± 3.5	10 (1)	55

¹F = fringing; F B = fringing barrier; B B = bank barrier; W = windward, L = leeward

²From Nemeth et al. (this volume)

³RDT = roving diver technique surveys

⁴Number of fish species based on the maximum number seen on any one RDT survey.

⁵Number in parenthesis = cumulative number of species for multiple RDT surveys.

Table 2. Twenty-five most frequently sighted fish species during roving diver surveys for all sites combined in the Virgin Islands, with density (mean \pm standard deviation) for species in belt transects.

Fish Species	Rank ¹	Sighting Frequency ²	Density (#/100m ²)
<i>Thalassoma bifasciatum</i>	1.	100	-
<i>Acanthurus coeruleus</i>	2.	100	7.0 \pm 6.58
<i>Sparisoma aurofrenatum</i>	3.	100	4.4 \pm 3.03
<i>Sparisoma viride</i>	4.	100	3.6 \pm 2.42
<i>Haemulon flavolineatum</i>	5.	100	3.3 \pm 3.90
<i>Scarus taeniopterus</i>	6.	94.7	4.8 \pm 8.82
<i>Stegastes partitus</i>	7.	89.5	-
<i>Mulloidichthys martinicus</i>	8.	86.8	-
<i>Epinephelus cruentatus</i>	9.	81.6	0.7 \pm 1.04
<i>Serranus tigrinus</i>	10.	81.6	0
<i>Acanthurus bahianus</i>	11.	80.7	7.7 \pm 7.94
<i>Halichoeres garnoti</i>	12.	80.7	-
<i>Chaetodon capistratus</i>	13.	80.7	1.0 \pm 0.95
<i>Scarus croicensis</i>	14.	78.1	3.6 \pm 3.12
<i>Chromis multilineata</i>	15.	75.4	-
<i>Chromis cyanea</i>	16.	75.4	-
<i>Holocentrus rufus</i>	17.	70.2	-
<i>Epinephelus fulvus</i>	18.	68.4	0.7 \pm 1.03
<i>Abudefduf saxatilis</i>	19.	62.3	-
<i>Stegastes diencaeus</i>	20.	59.6	-
<i>Canthigaster rostrata</i>	21.	58.8	-
<i>Coryphopterus glaucofraenum</i>	22.	57.9	-
<i>Myripristis jacobis</i>	23.	57.0	-
<i>Stegastes planifrons</i>	24.	56.1	-
<i>Halichoeres maculipinna</i>	25.	56.1	-

¹Rank of species with the same sighting frequency was determined by calculating the REEF density index for each species based upon the weighted abundance categories: S (single=1), F (few = 2), M (many = 3) and A (abundant = 4). Equation to calculate weighted density average was:

$$\text{Density} = [(S*1) + (F*2) + (M*3) + (A*4)] / (\text{number of surveys in which species was observed})$$

²Sighting frequency (%SF) for each species was calculated using the equation:

$$\%SF = [S + F + M + A] / (\text{number of surveys})$$

Table 3. The total number and density (mean \pm standard deviation) of the twenty-five most common species counted in belt transects for all sites combined in the Virgin Islands.

Fish species	Rank	AGRRA fishes without <5 cm scarids + haemulids		AGRRA fishes with <5 cm scarids + haemulids ¹	
		Sum (#)	Density (#/100 m ²)	Sum (#)	Density (#/100 m ²)
<i>Acanthurus bahianus</i>	1	1176	7.7 \pm 7.94		
<i>Acanthurus coeruleus</i>	2	1070	7.0 \pm 6.58		
<i>Scarus taeniopterus</i>	3	743	4.8 \pm 8.82	1640	10.5
<i>Sparisoma aurofrenatum</i>	4	677	4.4 \pm 3.03	911	6
<i>Scarus croicensis</i>	5	556	3.6 \pm 3.12	869	5.5
<i>Sparisoma viride</i>	6	549	3.6 \pm 2.42	920	6
<i>Haemulon flavolineatum</i>	7	510	3.3 \pm 3.90	4926	32
<i>Haemulon aurolineatum</i>	8	309	2.0 \pm 5.35	311	2
<i>Acanthurus chirurgus</i>	9	294	1.9 \pm 5.05		
<i>Ocyurus chrysurus</i>	10	204	1.3 \pm 2.17		
<i>Microspathodon chrysurus</i>	11	191	1.2 \pm 2.11		
<i>Sparisoma rubripinne</i>	12	153	1.0 \pm 1.82	166	1
<i>Chaetodon capistratus</i>	13	147	1.0 \pm 0.95		
<i>Epinephelus cruentatus</i>	14	113	0.7 \pm 1.04		
<i>Epinephelus fulvus</i>	15	113	0.7 \pm 1.03		
<i>Haemulon plumieri</i>	16	104	0.7 \pm 1.75	108	0.7
<i>Haemulon sciurus</i>	17	100	0.6 \pm 1.94	100	0.6
<i>Lutjanus mahogani</i>	18	93	0.6 \pm 1.56		
<i>Scarus vetula</i>	19	79	0.5 \pm 0.76	285	2.05
<i>Caranx ruber</i>	20	77	0.5 \pm 1.06		
<i>Holocanthus ciliaris</i>	21	74	0.5 \pm 0.95		
<i>Lutjanus apodus</i>	22	74	0.5 \pm 1.03		
<i>Lutjanus griseus</i>	23	59	0.4 \pm 1.40		
<i>Lutjanus jocu</i>	24	57	0.4 \pm 1.91		
<i>Melichthys niger</i>	25	57	0.4 \pm 1.12		

Except St. Croix, where \leq 5 cm scarids and haemulids were not counted.

Table 4. Density (mean \pm standard deviation) of AGRRA fishes by site in the Virgin Islands.

Site name	Site code	Density (#/100 m ²)						Macroalgal index Rel. (Abs.) ³
		Herbivores			Carnivores			
		Acanthuridae	Scaridae (≥ 5 cm)	<i>M. chrysurus</i> ¹	Haemulidae (≥ 5 cm)	Lutjanidae	Serranidae ²	
Northern Virgin Islands								
<i>St. John (shallow)</i>								
Great Lameshu Donkey	12	7.5 \pm 7.0	10.8 \pm 7.3	0	28.5 \pm 25.8	2.5 \pm 5.5	0.6 \pm 1.0	71 (80)
Great Lameshur VIERS	13	8.0 \pm 5.0	17.7 \pm 12.7	0	32.5 \pm 29.4	3.0 \pm 2.5	0.5 \pm 2.0	46 (72)
Fish Bay East Inner	11	28.5 \pm 50.5	14.0 \pm 16.3	0.3 \pm 1.0	32.3 \pm 23.1	10.5 \pm 15.0	0.2 \pm 0.5	108 (116)
Fish Bay West Inner	14	8.5 \pm 13.0	3.8 \pm 4.0	0	3.5 \pm 5.5	4.5 \pm 7.5	0.4 \pm 1.0	278 (181)
<i>St. John (deep)</i>								
Great Lameshur Tektite	15	5.5 \pm 3.0	13.7 \pm 10.8	0.2 \pm 0.5	5.0 \pm 5.5	10.0 \pm 29.5	2.5 \pm 2.0	190 (112)
Great Lameshur Yawzi	16	10.0 \pm 4.5	48.8 \pm 30.1	0.2 \pm 0.5	15 \pm 17.2	2.0 \pm 2.0	1.0 \pm 1.5	55 (31)
Fish Bay East Outer	9	60.5 \pm 78.0	6.8 \pm 5.0	0	8.5 \pm 17.3	3.0 \pm 3.5	0.4 \pm 1.0	6 (7)
Fish Bay West Outer	10	45.0 \pm 57.0	22.2 \pm 17.3	2.3 \pm 1.4	7.0 \pm 18.8	3.6 \pm 3.0	0.7 \pm 1.0	52 (30)
<i>St. Thomas</i>								
Brewer's Bay	2	1.0 \pm 1.5	40.7 \pm 58.2	0	2.0 \pm 4.3	1.0 \pm 2.0	0.5 \pm 0.5	83 (118)
Buck Island	4	3.5 \pm 3.0	9.7 \pm 8.9	0.1 \pm 0.4	7.0 \pm 17.4	3.0 \pm 5.5	2.0 \pm 2.5	173 (96)
Caret Bay	1	9.5 \pm 5.0	14.5 \pm 10.7	1.7 \pm 1.4	0.5 \pm 0.7	0.5 \pm 1.0	1.0 \pm 1.0	110 (82)
Flat Cay	3	8.0 \pm 4.5	28.0 \pm 13.9	0	2.7 \pm 3.5	2.0 \pm 3.0	1.5 \pm 1.0	93 (53)
Sprat Bay	5	4.0 \pm 3.0	17.8 \pm 15.4	0.5 \pm 0.8	1.0 \pm 1.4	11.5 \pm 31.0	1.0 \pm 1.0	247 (201)
<i>Virgin Gorda</i>								
Eustacia Reef	18	21.0 \pm 44.5	12.0 \pm 12.8	4.3 \pm 3.1	1.8 \pm 2.9	5.5 \pm 12.0	0.5 \pm 0.5	116 (86)
<i>Guana Island</i>								
Iguana Head	17	13.0 \pm 15.0	13.0 \pm 5.3	0.7 \pm 1.2	1.5 \pm 2.5	7.0 \pm 7.5	2.5 \pm 2.0	8 (8)
<i>St. Croix</i>								
Cane Bay	6	5.5 \pm 4.0	14.5 \pm 7.5	2.4 \pm 1.9	9.5 \pm 15.0	0.5 \pm 1.0	5.5 \pm 2.5	35 (70)
Long Reef	8	14.0 \pm 6.5	19.5 \pm 13.0	1.6 \pm 1.4	3.5 \pm 3.5	1.5 \pm 1.5	3.5 \pm 2.5	25 (19)
Salt River East	7	14.5 \pm 8.5	10.0 \pm 6.0	0.4 \pm 1.0	2.0 \pm 1.5	0.5 \pm 1.0	3.0 \pm 2.5	3 (2)
<i>Anegada</i>								
Herman's Reef	19	13.5 \pm 6.0	27.7 \pm 10.5	3.5 \pm 2.1	3.2 \pm 2.7	0	2.0 \pm 2.5	104 (55)
Horseshoe Reef	20	40.5 \pm 14.5	32.8 \pm 32.4	1.2 \pm 2.7	0	7.0 \pm 21.0	0.5 \pm 1.0	147 (70)
Jack Bay	21	26.0 \pm 23.5	10.8 \pm 7.6	9.0 \pm 6.7	4.5 \pm 5.2	7.5 \pm 13.5	4.0 \pm 3.0	101 (77)
W. Cow Wreck	22	32.5 \pm 9.5	6.8 \pm 4.5	0	5.5 \pm 10.5	1.5 \pm 3.5	1.5 \pm 2.5	230 (150)

¹*M. chrysurus* = *Microspathodon chrysurus*²*Epinephelus* spp. and *Mycteroperca* spp.³Rel = % relative macroalgal abundance x macroalgal height; Abs. = % absolute macroalgal abundance x macroalgal height; from Nemeth et al. (this volume).

Table 5. Length (mean \pm standard deviation) in cm of AGRRA fishes by site in the Virgin Islands.

Site name	Site code	Acanthuridae	Scaridae (≥ 5 cm)	Haemulidae (≥ 5 cm)	Lutjanidae	Serranidae ¹	Pomacanthidae	Rank ²
Northern Virgin Islands								
<i>St. John (shallow)</i>								
Great Lameshur Donkey	12	10.5 \pm 3.5	19.7 \pm 13.5	16.1 \pm 1.5	22.5 \pm 4.5	24.5 \pm 18.0		++
Great Lameshur VIERS	13	11.0 \pm 4.0	16.0 \pm 1.0	10.0 \pm 2.0	14.0 \pm 7.5	13.0 \pm 0		---- +
Fish Bay East Inner	11	4.5 \pm 2.5	17.9 \pm 8.0	11.5 \pm 6.0	16.5 \pm 8.0	35.5		- +
Fish Bay West Inner	14	9.5 \pm 6.0	18.0 \pm 4.0	16.9 \pm 4.0	20.5 \pm 9.5	19.0 \pm 23.5	25.5 \pm 1.0	+
<i>St. John (deep)</i>								
Great Lameshur Tektite	15	11.0 \pm 3.5	18.0 \pm 4.0	14.0 \pm 4.0	18.0 \pm 14.0	17.0 \pm 6.0	9.0 \pm 9.0	----
Great Lameshur Yawzi	16	11.4 \pm 2.5	17.5 \pm 1.5	14.5 \pm 6.0	20.0 \pm 6.5	23.5 \pm 7.5	13.5 \pm 3.0	
Fish Bay East Outer	9	11.5 \pm 3.5	21 \pm 3.0	17.5 \pm 2.5	21.5 \pm 3.5	30.5 \pm 7.0	15.5 \pm 0	+++++
Fish Bay West Outer	10	10.0 \pm 2.2	20.5 \pm 5.5	17.4 \pm 3.0	20.0 \pm 7.0	24.0 \pm 10.5	9.0 \pm 9.0	-
<i>St. Thomas</i>								
Brewer's Bay	2	4.5 \pm 3.0	10.0 \pm 4.0	15.5 \pm 0	11.0 \pm 4.0	15.5 \pm 0.0		---
Buck Island	4	8.5 \pm 4.5	17.0 \pm 3.0	11.5 \pm 6.5	27.0 \pm 18.5	15 \pm 11.0	12.0 \pm 5.5	-- ++
Caret Bay	1	13.0 \pm 2.0	16.5 \pm 2.0	20.5 \pm 7.0	15.5 \pm 0	19.0 \pm 8.0		+++
Flat Cay	3	11.0 \pm 3.0	12.0 \pm 2.5	16.0 \pm 5.0	15.5 \pm 0	17.0 \pm 4.0	13.5 \pm 2.5	
Sprat Bay	5	10.0 \pm 2.5	18.0 \pm 11.0	14.0 \pm 3.5	22.0 \pm 5.0	18.0 \pm 10.5	25.5	
<i>Virgin Gorda</i>								
Eustacia Reef	18	16.5 \pm 2.5	19.0 \pm 5.0	18.0 \pm 3.0	25.0 \pm 2.5	20.5 \pm 7.0	25.5 \pm 0	
<i>Guana Island</i>								
Iguana Head	17	14.0 \pm 4.0	19.0 \pm 3.0	15.0 \pm 9.0	23.0 \pm 6.0	19.5 \pm 4.5	35.5	
<i>St. Croix</i>								
Cane Bay	6	17.5 \pm 3.5	21.0 \pm 7.5	17.5 \pm 2.5	15.5 \pm 0	19.0 \pm 4.0		--- +
Long Reef	8	15.5 \pm 1.5	19.0 \pm 3.5	18.5 \pm 3.0	22.5 \pm 5.0	20.0 \pm 3.5	18.0 \pm 6.0	-- +
Salt River East	7	16.0 \pm 1.5	22.0 \pm 4.5	21.0 \pm 5.0	20.5 \pm 7.0	21.0 \pm 4.0	12.0 \pm 5.5	+++
<i>Anegada</i>								
Herman's Reef	19	13.7 \pm 2.0	16.8 \pm 2.0	22.0 \pm 5.0		26.0 \pm 2.5	14.0 \pm 16.0	-
Horseshoe Reef	20	10.5 \pm 2.0	17.3 \pm 2.0		33.5 \pm 14.0	30.5 \pm 18.0	15.5	++
Jack Bay	21	14.1 \pm 2.5	20.0 \pm 7.0	19.0 \pm 4.0	25.5 \pm 0	15.0 \pm 5.5	2.5	--- +
W. Cow Wreck	22	8.0 \pm 3.0	21.0 \pm 5.0	23.0 \pm 4.5	25.5 \pm 0	20.5 \pm 4.5	7.0 \pm 6.0	-- ++

¹*Epinephelus* spp. and *Mycteroperca* spp.

²Ranking = number of times a site within an island (i.e. St. Thomas) or group (e.g., St. John shallow) was represented by the smallest (-) or largest (+) value within the size range of a family. Angelfish were excluded due to the number of missing cells and Virgin Gorda and Guana Island were excluded since they only had one site per island.