

Figure 1. Location of the windward Netherlands Antilles.

A POST-HURRICANE, RAPID ASSESSMENT OF REEFS IN THE WINDWARD NETHERLANDS ANTILLES (STONY CORALS, ALGAE AND FISHES)

BY

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ABSTRACT

Reefs of the windward Netherlands Antilles (Saba, Saba Bank, St. Eustatius, St. Maarten) were assessed at 24 sites in late 1999. The Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol was used with modifications to detect recent hurricane impacts. Live coral cover averaged 18%. The assemblage of ≥ 10 cm stony corals was primarily composed of small-sized colonies (mean diameter ≈ 37 cm) of which the *Montastraea annularis* complex was the most abundant (30% of colonies). Overall, $\approx 1\%$ of the individually surveyed colonies had been physically damaged by Hurricane Lenny but injury levels were higher in Saba (2.6%). Bleaching was noted in $>23\%$ of colonies at the time of the assessment with the greatest percentage occurring on St. Maarten (44%) and the lowest on Saba Bank (9%). Total (recent + old) partial mortality of reef-building corals averaged less than 18% although levels were higher (26%) in *Colpophyllia natans*. Coral recruitment densities were relatively consistent (mean ≈ 5 recruits/m²) across sites. Commercially significant fish species (i.e., serranids, lutjanids, haemulids ≥ 5 cm) were present with mean densities of 4.5 individuals/100 m². High biomass (mean ≈ 5.8 kg/100 m²) of grazing, herbivorous fishes (acanthurids, scarids ≥ 5 cm, *Microspathodon chrysurus*) partially explains the relatively low macroalgal cover (mean $\approx 7\%$) throughout this area. Saba's fish community had a greater total biomass than those in the other three geographic areas (mean ≈ 11 kg/100 m² versus 7 kg/100 m²). While the coral reefs of St. Maarten show signs of disturbance (i.e., increased bleaching and sedimentation), those of Saba, Saba Bank, and southern St. Eustatius have been relatively little disturbed by coastal development and remain potential sources of marine life. Nevertheless, reef development in the windward Netherlands Antilles is limited by frequent hurricanes.

INTRODUCTION

The windward Netherlands Antilles (N. A.) are located at the northern arc of the leeward Lesser Antilles in the Caribbean Sea (Fig. 1). Included in the windward N. A.,

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and separated from each other by distances of 20-50 kilometers, are Saba (Fig. 2A), Saba Bank (Fig. 2B), which is totally submerged, St. Eustatius (Fig. 2C), and the southern portion of St. Martin/St. Maarten (Fig. 2D). As each represents a distinctly different area in terms of geophysical aspects and degree of human impact, they are described separately below.

Saba (17°36'N, 63°15'W) is an isolated volcanic island of late Pleistocene to mid-Holocene origin (Westermann and Kiel, 1961). Saba does not rest on a carbonate shelf but a narrow submarine platform fringes the island before sloping steeply to the deep sea floor. Devoid of sandy beaches, Saba's coastline is formed of steep, rocky cliffs. Rapid erosion of this coastline and Saba's constricted shelf do not allow extensive reef development. Coral communities circumfuse the island occurring on granite boulders, pinnacles, and lava formations that extend seaward from the island. Close to shore, scattered coral colonies encrust large boulders that have eroded from the steep, coastal embankments. Extending seaward along Saba's gently sloping (<10°) insular shelf are lava-flow formations aligned perpendicular to the coastline. These volcanic features, often separated from each other by sand channels, provide a basal structure for the development of coral communities. In some areas where corals have, almost contiguously encrusted lava flows, the topography superficially resembles spur-and-groove formations.

Saba's villages are located above 240 m altitude (Buchan, 1998) and coastal development is limited to a small harbor that accommodates the marine-park office, the island's dive operators, and a recently closed rock-crushing plant. While Saba has become a popular dive destination in recent years, there appears to be minimal human impact on its reefs. (Although the authors acknowledge that Saba's coral communities do not fit the narrow definition of coral reefs in the technical sense, we have elected to use the term throughout this paper for the sake of fluidity). However, Saba's corals are physically damaged by hurricanes (most recently Hurricanes Luis in 1995, Georges in 1998, Lenny in 1999), especially the *Acropora palmata* in some shallow, high-surge zones. An area surrounding the island from the high-water mark down to a depth of 60 meters is actively regulated by the Saba National Marine Park which was established in 1987.

Saba Bank (17°25'N, 63°30'W) is a submarine plateau that has been described as a sunken atoll (Vaughan, 1919; Van der Land, 1977). Its eastern edge lies about 3-5 km SW of Saba. Saba Bank is 60 to 65 km long and 30 to 40 km wide and, with a total surface area of about 2200 km, ranks among the largest atolls in the world. Rising about 1000 meters above the surrounding sea floor, it reaches a plateau at a depth of about 15 m. Here aggregations of gorgonians and sparsely spaced, small (< 25 cm diameter) scleractinians are arranged linearly in tracts that are 20-40 m wide and separated by 10-20 m-wide sand channels. Depths vary between 7 and 20 m near its eastern and southeastern rim. The western ridge reportedly is deeper (50 m) and dominated by sand. From the bank's eastern rim at ≈20 m depth, the bottom terrain slopes seaward to meet a terrace before it drops precipitously beyond 35 m depth. Corals are more densely spaced along

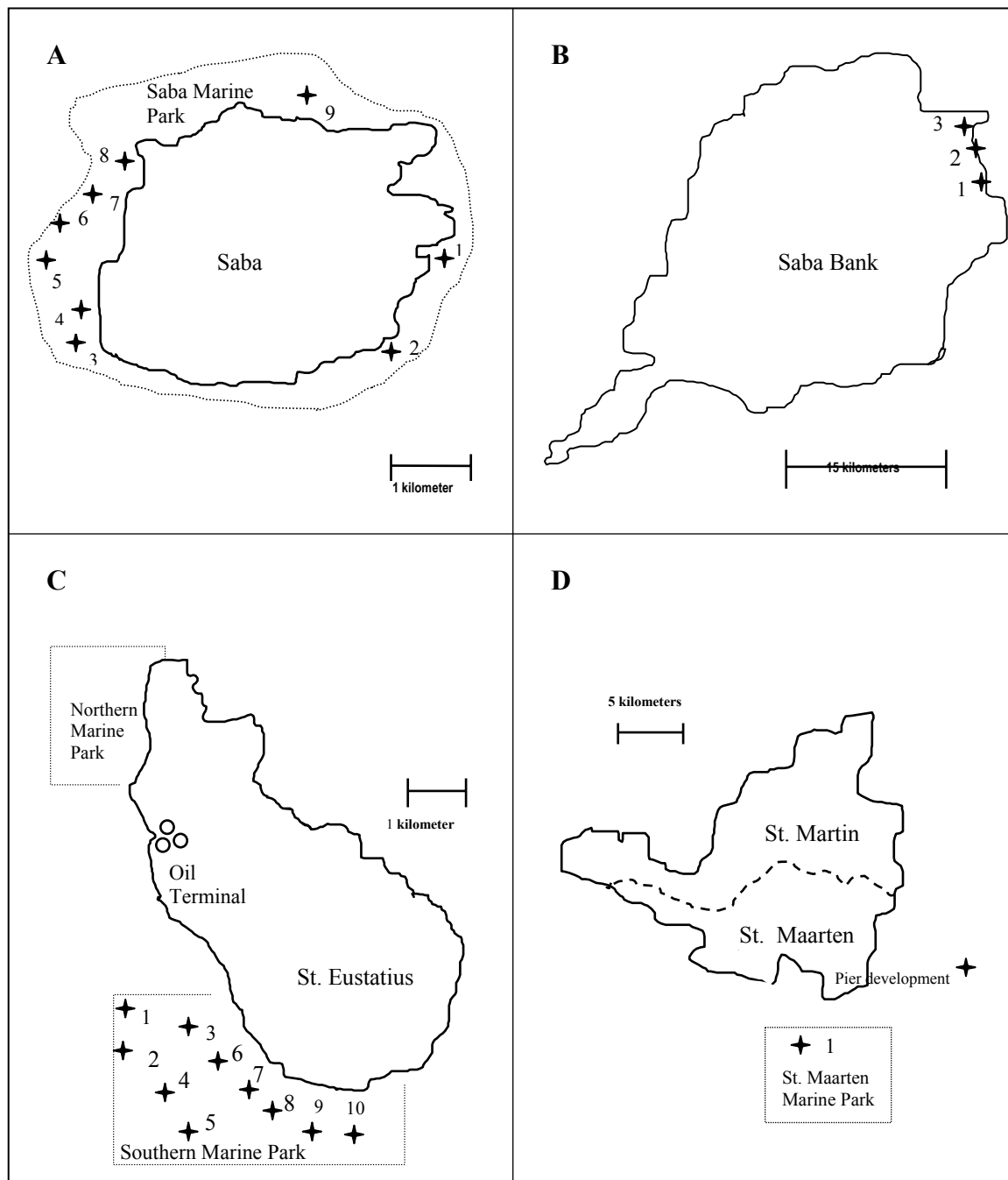


Figure 2. AGRRRA survey sites for (A) Saba, (B) Saba Bank, (C) St. Eustatius, (D) St. Maarten, in the windward Netherlands Antilles. See Table 1 for site codes.

this slope (i.e., between 20-35 m depth) than at our sampling depths of 15-20 m. As depth increases, colonies become progressively larger and, for many of the *Montastraea* and *Agaricia*, increasingly flattened in morphology. Van der Land (1977), who referred to this coral-covered slope as the "front reef," noted that Saba Bank was an island during the last glacial period and until at least about 5,000 years ago. He hypothesized that this windward "front reef" originated, when sea levels were 20-30 m below present, as a fringing reef of Saba Bank's island.

Because a considerable distance separates Saba Bank from land, human impact on its corals is restricted to that imposed by fishing activity, boats and ships. Part of the Bank is within the geographic scope of Saba island's jurisdiction as territorial sea; the larger part falls within the limits of a possible Exclusive Economic Zone (EEZ) within the competency of the Netherlands Antilles. At present, only a limited EEZ has been claimed by the Netherlands Antilles in the form of an Economic Fisheries Zone. Van der Land (1977), Meesters et al. (1996) and Dilrosun (1999) have ascertained that, in isolated areas, Saba Bank's reefs are rich in terms of cover and diversity of reef-building corals but that its fish stocks appeared to be declining. However, its reefs have remained largely unexplored. Hence, Saba Bank provides us with a rare opportunity to study the regional potential for reef development in the absence of coastal processes.

Sint Eustatius (17°29'N, 62°57'W) is situated on a submerged platform shared with the islands of St. Kitts and Nevis. The island consists of two extinct volcanoes, an older (late Pliocene) eroded volcano in the northwest and a younger volcano with evidence of activity as recent as the early Pleistocene epoch (Adey and Burke, 1976) in the south. A narrow platform (<2 km wide) surrounds most of the island. Fringing reefs occur mid-shelf off its southern and northwestern coasts. The remainder of the shelf is a flat, sandy plateau with limited potential for coral development. Lava flow formations from the southern volcano extend seaward and, along with large volcanic boulders, provide a high-relief (≈3-4 m) structural base for reefs on the island's southern side. These reef structures, each about 30-50 m wide, are separated by sand channels of ≈50 m width and frequently occur in a series. St. Eustatius' most robust reefs in terms of coral cover occur mid-shelf near the island's southernmost tip. Here the underlying substrata on which the corals occur is carbonate in nature but it is not apparent from casual observation whether these are entirely of carbonate composition or whether they embody inorganic, pyroclastic fragments. While typically spanning an area similar in size (30-100 m in any direction), they are not as consolidated as lava flows nor do they exhibit the uniform orientation ("seaward") of lava flow. However, these formations are equal in vertical relief (rising 3-4 m from the sand-covered bottom) and, where disjunct, are often cemented together with mature (>100 cm diameter) colonies of *Montastraea*. Corals also fringe the rocky northwestern coast near shore where broken skeletons of *A. palmata* and live stands of *Millepora* occur on boulders in the high-surge zones. Further from shore, scattered coral heads occur along a reef flat, though most are dead and covered with sediment.

The coastline of St. Eustatius is relatively undeveloped with the exception of its capital city, Oranjestad, and a trans-shipment oil terminal, both located on the western coast. The St. Eustatius Marine Park was established in January 1998 and is operated by the St. Eustatius National Park Foundation (STENAPA). Two areas, the Northern Marine Park and the Southern Marine Park, are actively protected by St. Eustatius Marine Park

officials and fishing activity is restricted in these zones. St. Eustatius' reefs have been impacted by hurricanes in recent years and those in the Northern Park have been severely impacted by anthropogenically enhanced sedimentation.

Saint Martin/Saint Maarten (18°N, 63°W) is situated on the Anguilla Bank, a microplate shared by the islands of Anguilla and St. Barthelemy. The Anguilla Bank is comprised of an old (early to mid-Tertiary period) basal rock of fine mudstones and the islands represent an uplifted veneer of young (Pleistocene to Recent) reef limestones and sandstones (Oxenford and Hunte, 1990). A fringing reef flat occurs mid-shelf (\approx 2-3 km) off the southern coast of the island and fringing reefs are found adjacent to small islets located at similar distances from St. Maarten's southeastern coast. The reefs off the southern coast emerge from the surrounding hardbottom at depths of about 8-15 m. Most of this system is characterized by low-relief, scattered corals but a spur-and-groove system of intermediate relief (<2 m) occupies a small area. These reefs are routinely exposed to strong offshore currents. Remnants of *Acropora palmata* are apparent within the spur-and-groove zone but most colonies are either "standing dead" (i.e., entirely dead but still attached to the substratum) or, if still living, have spread horizontally without having attained much height above the substratum. The reefs which fringe the small islets on St. Maarten's southeastern side grow compactly along a slope (<30°) with no lagoonal area separating them from the islets.

Tourism is a primary contributor to St. Maarten's economy. St. Maarten is a major port of call for Caribbean cruise ships and, at the time of this survey, operations were under way to expand harbor capacity to accommodate additional vessels. As the island's infrastructure struggles to meet the demands of development, St. Maarten's reefs are increasingly threatened by devegetation, siltation, sewage input, recreational boating (Nijkamp et al., 1995), and anchor damage (Smith et al., 1997). Additionally, Smith et al. (1997) reported that heavy seas during Hurricane Luis (1995) resulted in resuspended sand, smothering reefs and damaging *A. palmata* in shallow water. The Marine Park of St. Maarten, established in 1997 in conjunction with the Nature Foundation St. Maarten, encompasses a portion of its reefs. At the time of this assessment, the marine park was in its initial stages of devising a management plan. One of our survey sites (SXM01), which lies within the marine park boundaries (Fig. 2D), has been the site of two cruise ship groundings in recent years.

The windward N. A. are frequently impacted by hurricanes. During the previous decade, a succession of severe storms (Hugo in 1989, Luis and Marilyn in 1995, Bertha in 1996, Georges in 1998, José and Lenny in 1999) had come near enough to impose harm to the reefs. Prior to Hurricane Luis in 1995, *Acropora palmata* was the predominant scleractinian on many of Saba's shallow (<10 m) reefs (i.e., at sites 1, 2, 8, 9; Fig. 2A). Although some recovery of *A. palmata* was evident following Hurricane Luis, they sustained further damage during Hurricanes Georges (1998) and Lenny (1999). Hence, at many Saba sites, *A. palmata* has been replaced by gorgonians and *Millepora* spp. (Kooista, personal observations).

Our surveys were conducted less than two weeks after the passage of Hurricane Lenny, a category 4 (Safir/Simpson scale) hurricane, which coursed between St. Maarten and Saba on November 18 and 19, 1999. Coupled with the impact of Hurricane José (category 2), which had earlier passed through the windward N. A. islands in October

1999, we were provided with an opportunity to assess damages associated with recent hurricanes.

METHODS

The surveys were conducted in the windward N. A. (Fig. 1) during November and December 1999. Data were collected from nine sites along the coast of Saba (Fig. 2A), three sites along the eastern rim of Saba Bank (Fig. 2B), 10 sites along St. Eustatius' southwestern shore (Fig. 2C), and two sites along St. Maarten's southern and southeastern shore (Fig. 2D). These sites were among those chosen during a reconnaissance evaluation in October 1999 to be representative of reefs within the area and to strategically accommodate marine park management objectives. Due to reduced visibility associated with storm-induced rainfall and runoff, we omitted sampling where conditions were prohibitive including the reefs in St. Eustatius' Northern Marine Park.

Sites were surveyed using the AGRRA protocols version 2.1 (see Appendix One, (this volume)). The benthic surveys were made by four divers. In quantifying individual stony corals, we modified the method to include all colonies ≥ 10 cm in maximum diameter to ensure adequate sample sizes. Coral sizes were measured to the nearest cm. Additionally, we recorded incidence of recent hurricane damage along each benthic transect as indicated by overturned, broken, or abraded coral colonies. Stony corals were searched for damselfish algal gardens and the numbers of benthic damselfish along the transect line were also counted. The *Montastraea annularis* complex was treated as a single species with three morphologically distinct formae. Sediment in the algal quadrats was wafted away by hand before scoring the relative abundance of crustose coralline algae. Macroalgal heights were measured to the nearest cm. Two divers conducted all the fish surveys between 9:00 a.m. and 4:00 p.m. Counts of serranids (groupers) were restricted to species of *Epinephelus* and *Mycteroperca*; scarids (parrotfishes) and haemulids (grunts) less than 5 cm in length were not tallied. Roving Diver observations averaged 30–45 minutes each. Fish biomass was estimated using length-weight relationships given in Appendix Two (this volume). Species recorded during the roving dives were assigned to trophic guilds developed by Schmitt et al. (1998) based on the major source of food in their diet determined from prior studies (Randall, 1967). Field guides included Humann (1992, 1993, 1994), Goodson (1976), Littler et al. (1989), and Smith (1948).

Parameters were statistically analyzed to detect differences between the four geographical areas using Statistica software, Version 5.1 (StatSoft, Inc., 1998). To reduce heteroscedasticity of variance, a single-factor, Kruskal-Wallis nonparametric Analysis of Variance (ANOVA) by rank was used. Kruskal-Wallis nonparametric ANOVA by rank was also used to detect differences among sites within each of the four geographical areas. The Tukey HSD for unequal N was used, when relevant, as an *ad hoc* multiple comparison test. Significance was tested at $\alpha = 0.05$. Coral species composition and coral size distribution were analyzed using a chi-square analysis to detect proportional differences among the four geographical areas. Where no significant differences were found, the data were combined as a single value for the windward N. A. Fish densities and biomass were calculated for sites within the four areas and collectively for the

windward N. A. A linear regression was performed to examine the relationship between the biomass of herbivorous fishes (i.e., acanthurids, scarids ≥ 5 cm, *Microspathodon chrysurus*) and macroalgal abundance.

RESULTS

Stony Corals at the Reef Sites

The 284 benthic transects were made in depths of 6-20 m at the 24 survey sites (Table 1). Mean live coral cover for the windward N. A. (Fig. 3) was 18% (se = 5.7). Though not significantly different from the other three geographical areas (ANOVA, $p = 0.33$), the lowest live coral cover ($11\% \pm 2.4$ se) was found in St. Maarten. Significant, between-site differences in live coral cover (Table 1) were evident in the three remaining areas (for each ANOVA, $p < 0.001$, Tukey $p < 0.05$). Sites SAB03 and SAB09 in Saba (mean = $8\% \pm 1.1$ se) were significantly lower than the other Saban sites (mean = $20\% \pm 3.9$ se), but comparable in live coral coverage to the St. Maarten sites (ANOVA, $p = 0.12$). All three sites on Saba Bank differed significantly from each other. Sites EUX01 through EUX08 in St. Eustatius were statistically similar (mean = $16\% \pm 1.6$ se) and substantially lower than EUX09 and EUX10 (mean = $46\% \pm 1.5$ se).

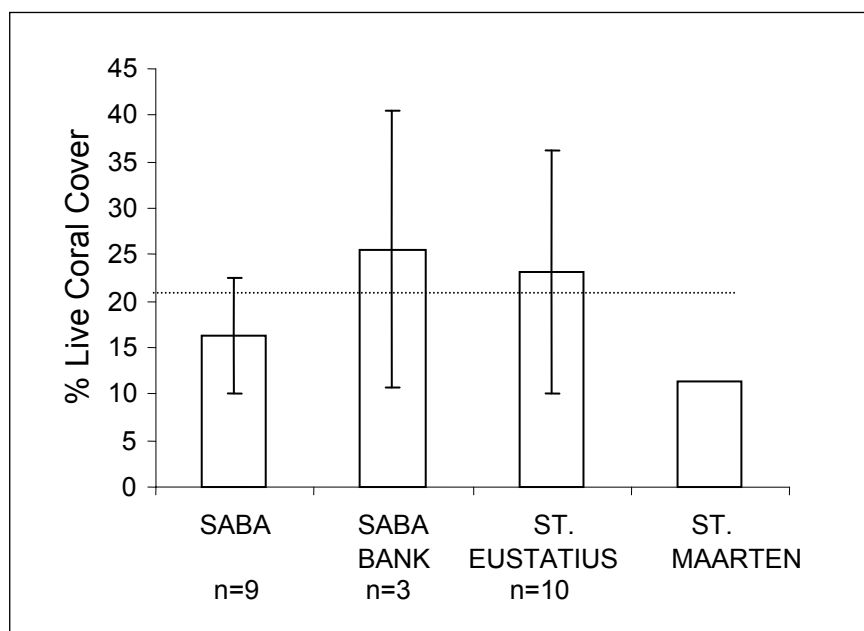


Figure 3. Mean live stony coral cover (percent \pm se) for each geographical area in the windward Netherlands Antilles. Dotted line represents overall mean. n=number of sites.

The 2,930 colonies of stony corals, each at least 10 cm in diameter, that were encountered along the transect lines represented 24 species of stony corals (23 scleractinians and the hydrozoan *Millepora complanata*). *Montastraea* was the most abundant stony coral genus throughout the windward N. A. (40% of all individually surveyed colonies). *Montastraea annularis faveolata* was the predominant taxon (19% Pp. 404-437 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.

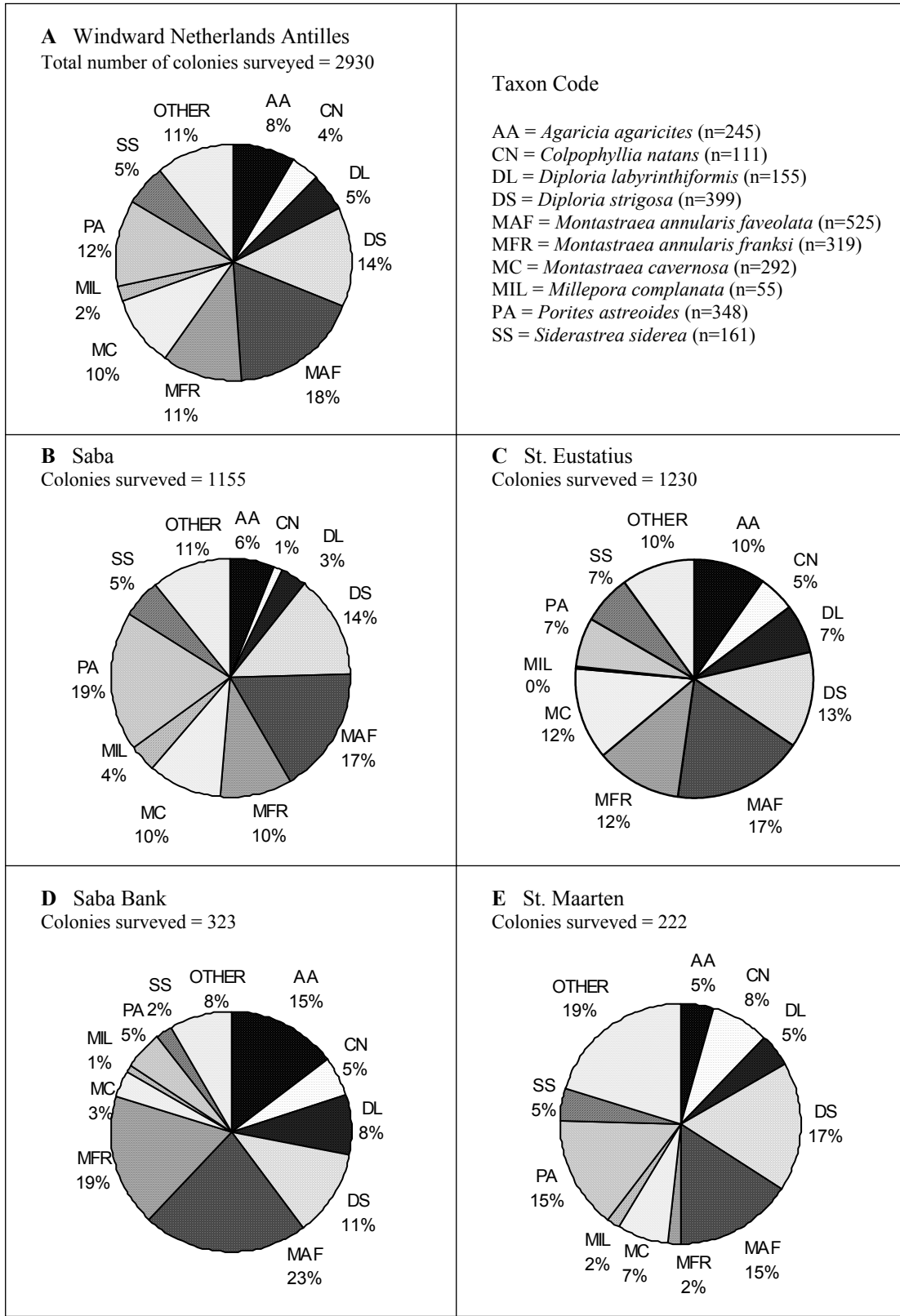


Figure 4. Species composition and mean relative abundance of all stony corals (≥ 10 cm diameter) in (A) windward Netherlands Antilles, (B) Saba, (C) St. Eustatius, (D) Saba Bank, (E) St. Maarten.

of all colonies), and nine species accounted for nearly 90% of the “major reef-building corals” (Fig. 4). *Acropora palmata*, most of which were located near Green Island at SAB09, comprised <1% of these corals. Only two colonies of *A. cervicornis* were encountered during our entire survey.

Results of a chi-square analysis for proportional similarity suggest that the individually surveyed corals in Saba and St. Eustatius are statistically similar in species composition (chi-square, $p = 0.35$). Likewise, those of Saba Bank and St. Eustatius show similar proportions (chi-square, $p = 0.31$). Marginally significant similarities in species composition were detected between Saba and St. Maarten (chi-square, $p = 0.11$). Significant similarities were lacking for the three remaining geographic comparisons (each chi-square, $p < 0.015$).

Coral recruits were observed at all sites with an overall mean density equivalent to 4.7 recruits/m² (Table 3). Recruitment levels were not significantly different between the four areas (ANOVA, $p = 0.10$) and, although variable between transects, were not significantly different among sites at each of the four geographical areas (each ANOVA, $p > 0.12$). Recruits were composed primarily of *Siderastrea* spp., *P. astreoides*, and *Agaricia agaricites* (Fig. 5).

Condition of Individually Surveyed Corals (at least 10 cm in Diameter)

On average, the maximum diameter of the ≥ 10 cm corals in the windward N. A. was 37 cm and their height was 19 cm. In Saba, however, many colonies of *Diploria* spp. and *P. astreoides* form thin crusts (<10 cm high) as they spread over boulders that have eroded from the island. Mean colony size was notably greater (Table 2) at three sites (BNK01, EUX09, EUX10) where the species composition was more heavily dominated (44%, 51%, and 43 %, respectively) by *Montastraea annularis faveolata*. In addition, mean diameters of *Montastraea annularis faveolata* were greater at these three sites (105 cm, 122 cm, 122 cm) than was documented at other sites (*M. annularis faveolata*, mean diameter: BNK = 95 cm; EUX = 83 cm).

Size distributions for the five most common coral taxa (Fig. 6) reveal that *M. annularis faveolata* had the largest colonies (maximum diameter = 610 cm). The remaining corals were considerably smaller, especially the two smallest (*P. astreoides*, *A. agaricites*). Sample sizes were adequate to perform a chi-square analysis of size distribution among three geographical areas for four of the common coral taxa. Significant differences in size distribution were only noted in *M. annularis franksi* (Fig. 7), for which a higher proportion of smaller colonies (< 30 cm diameter) was found at St. Eustatius than in Saba and the Saba Bank ($p < 0.001$, both locations).

The impact of Hurricane Lenny was evident wherever coral colonies or fragments had been freshly dislodged. Recent storm damage was greatest at Saba, particularly at sites 4, 8 and 9 (where 4.5%, 6.5%, and 4.5%, respectively, of the individually surveyed stony corals were affected), but averaged about 1% for the windward N. A. as a whole (Table 2). It is noteworthy to mention that *Millepora complanata*, although it only represented $\approx 2\%$ of the surveyed corals, constituted about 40% of the colonies that were damaged in the storm. While physical damage to corals was less severe in St. Maarten than Saba (Table 2), it was apparent that large quantities of sediment had been transported by currents here, burying some structures and exposing others.

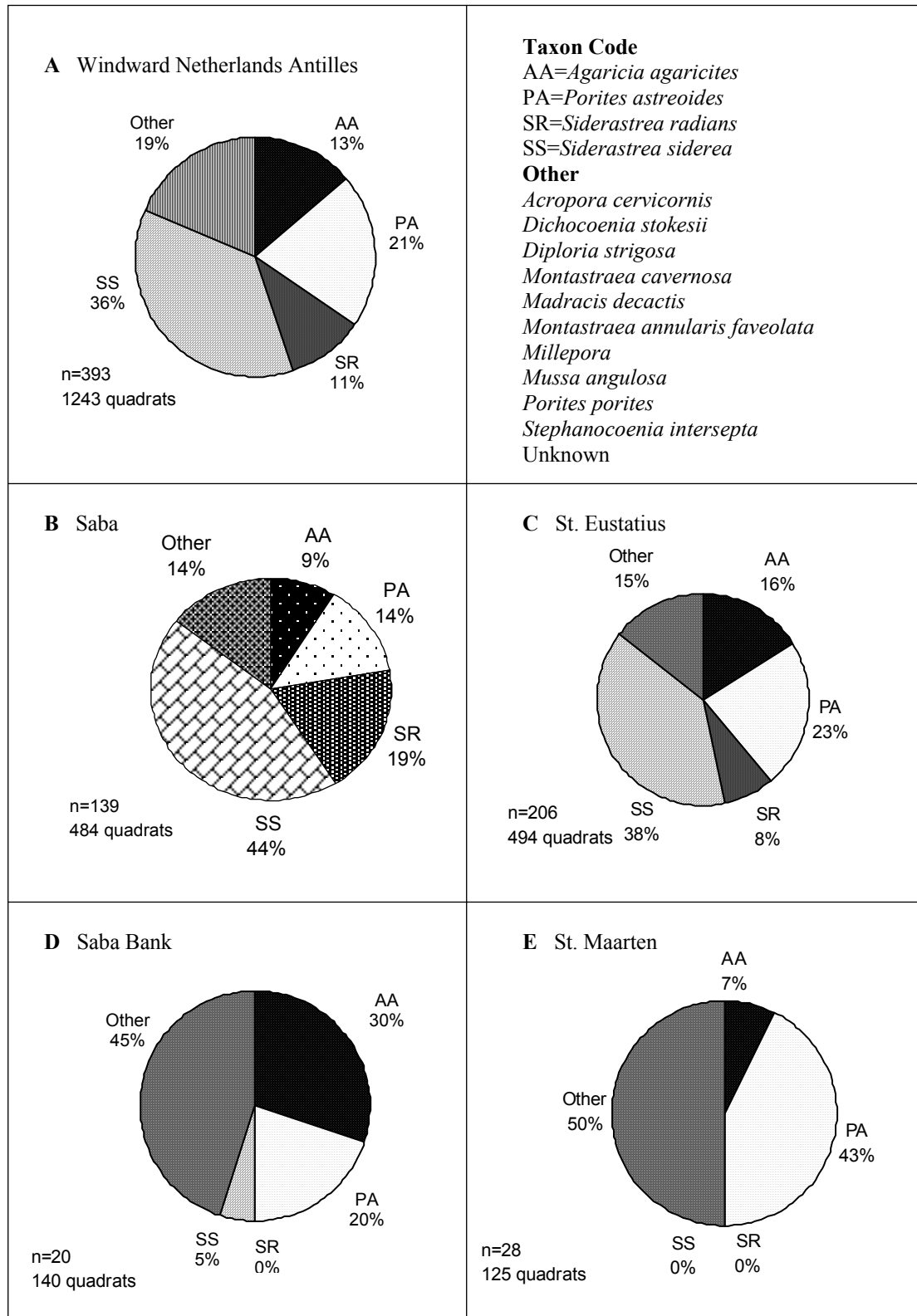


Figure 5. Species composition and mean relative abundance of all stony coral recruits (≤ 2 cm diameter) in (A) windward Netherlands Antilles, (B) Saba, (C) Saba Bank, (D) St. Eustatius, (E) St. Maarten.

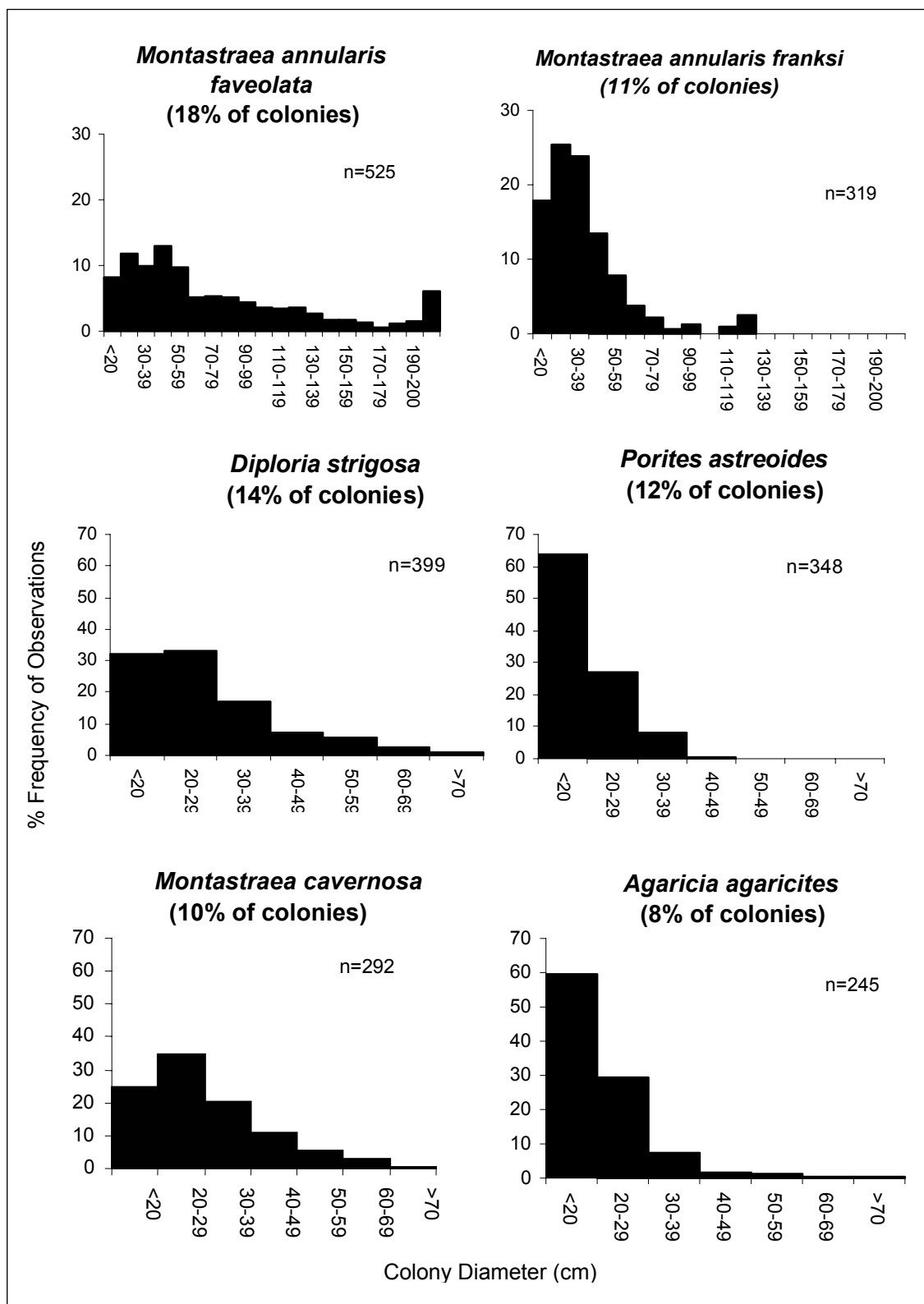


Figure 6. Size-frequency distribution of all colonies (≥ 10 cm diameter) of *Montastraea annularis faveolata*, *M. annularis franksi*, *Diploria strigosa*, *Porites astreoides*, *Montastraea cavernosa*, *Agaricia agaricites* in the windward Netherlands Antilles.

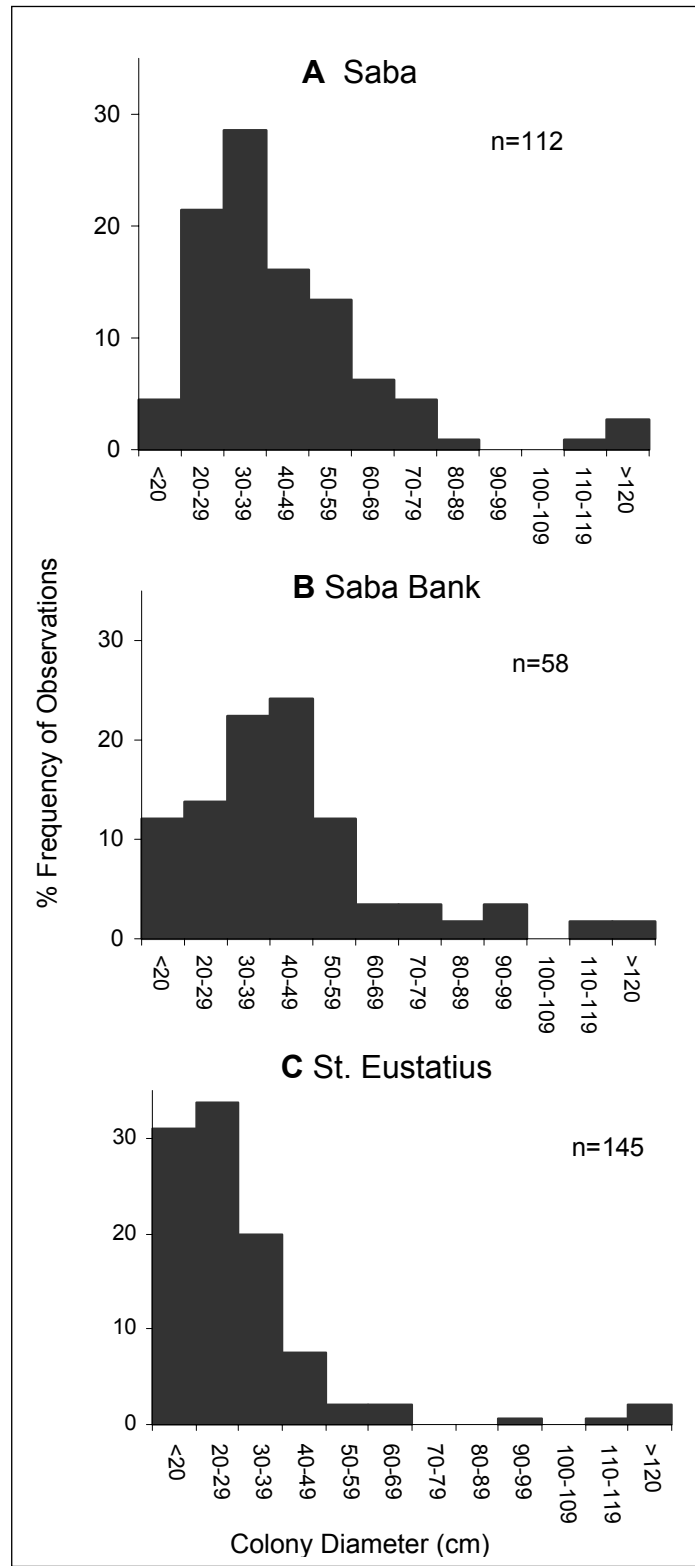


Figure 7. Size-frequency distribution of all *Montastraea annularis faveolata* (≥ 10 cm diameter) for (A) Saba, (B) Saba Bank, (C) St. Eustatius. St. Maarten was not included in the analysis due to insufficient sample size.

Over 23% of the > 10 cm stony corals exhibited some degree of bleaching (Table 2) but only 1% of these colonies were totally bleached. Of the bleached colonies throughout the N. A., more colonies were partly bleached (12%) than uniformly pale (9%). Bleaching was most prevalent in St. Maarten (44% of all colonies) where the percentage of pale colonies exceeded that found in the other three geographical areas (SXM = 25%; SAB = 10%; BNK = 2%; EUX = 9%). The Saba Bank sites were the least bleached (9% of all colonies). Intermediate levels of coral bleaching were found at Saba and St. Eustatius (22% and 24%, respectively).

Diseases were noted in about 0.7% of the individually surveyed corals and showed relatively little geographic variation in abundance (Table 2). Yellow-blotch (yellow-band) disease, primarily in the *Montastraea annularis* complex, was the most prevalent disease affecting about 0.4% of the colonies overall. Black-band disease, occurring in 0.1% of the stony corals, affected *Diploria strigosa*, *Agaricia agaricites*, *M. annularis faveolata*, and *M. cavernosa*. Darkspots disease occurred in 0.1% of the colonies and was only seen in *Siderastrea siderea*. White-band disease was seen in *Acropora palmata* and affected 0.1% of the stony corals. White-plague disease was rare and seen in < 0.1% of the colonies of *Colpophyllia natans*.

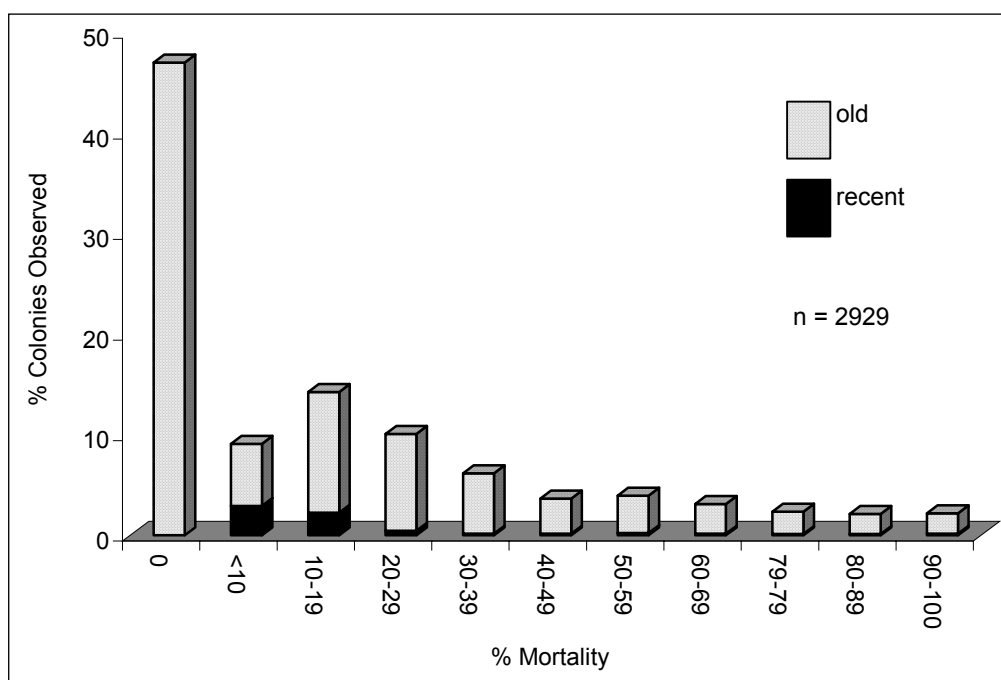


Figure 8. Frequency distribution of total (recent and old) partial colony mortality of all stony corals (≥ 10 cm diameter) in the windward Netherlands Antilles.

Partial-colony mortality of the individually surveyed corals averaged 1.0% for recent mortality and 16% for old mortality (Table 2). Forty-seven percent of these colonies showed no evidence of any kind of mortality and most of the remainder had less than 2% recent and 30% total (recent + old) partial mortality (Fig. 8). Although there were no significant differences among the four areas in recent, old, or total partial mortality (K-W ANOVA, $p \geq 0.35$), partial mortality varied by taxon (Fig. 9). *Porites*

astreoides exhibited the lowest levels of recent and old partial mortality (0.5% and 5.0%, respectively). Recent mortality was highest in *C. natans* (3.5%) and *Diploria strigosa* (3.0%). Old (and total) mortality was also substantially higher in *C. natans* (26%). Overall, 0.7% of all surveyed corals were standing dead (Table 2). However, 45% of the *A. palmata* colonies we surveyed were determined to be standing dead and their skeletons represented 56% of the total standing dead in the windward N. A. survey.

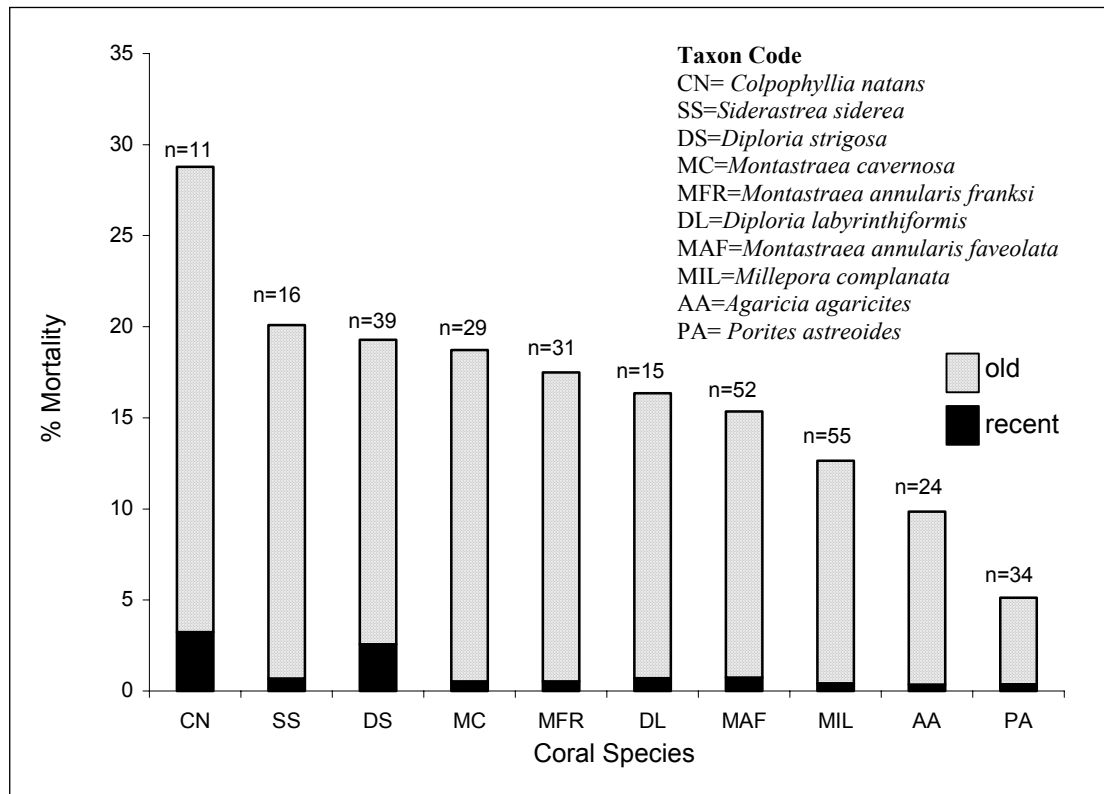


Figure 9. Mean percent total (recent and old) partial colony mortality of common stony corals (≥ 10 cm diameter) in the windward Netherlands Antilles.

Algal Groups, *Diadema*, and Damselfishes

Relative algal coverage was assessed for a total of 1,242 quadrats in the windward N. A. Turf algae were the predominant functional group at 13 sites, and were codominants with crustose coralline algae at a further seven sites. Turf relative abundance overall averaged 53%, while the crustose corallines and macroalgae averaged 42% and 7%, respectively. Where macroalgae were present, they displayed a low vertical profile (< 2 cm at 21/24 sites) so that macroalgal indices (% relative abundance of macroalgae \times macroalgal height—a proxy for macroalgal biomass) everywhere were < 40 (Table 3). Most of the macroalgae we encountered were fleshy species, mainly *Dictyota*, but some calcareous *Halimeda* were also present. No *Diadema antillarum* were found in the benthic belt transects and *Diadema* were only sighted twice during any of our dives.

Benthic damselfish were detected in quantities of ≈ 1.5 individuals per 10 m transect (Table 2) and were represented primarily by the yellowtail damselfish, *Microspathodon chrysurus*. The threespot damselfish, *Stegastes partitus*, was rare as were its algal gardens in the surveyed corals.

Fish Diversity

A total of 142 species of fish were recorded during 25.5 hours of roving diver surveys conducted at the 24 sites of the windward N. A. The fish assemblages were represented by six major trophic guilds with herbivores being dominant (28% of species sighted) and species from planktivorous and piscivorous guilds each representing 24% of the sightings (Table 4; Fig. 10).

Sightings of serranids included *Epinephelus fulvus* (coney, 100% of dives), *E. cruentatus* (graysby, 86% of dives), *E. guttatus* (red hind, 52% of dives), *Mycteroperca venenosa* (yellowfin grouper, 24% of dives), *M. tigris* (tiger grouper, 21% of dives), *E. striatus* (Nassau grouper, 7% of dives), *M. interstitialis* (yellowmouth grouper, 3% of dives), and *E. morio* (red grouper, 3% of dives).

Although no fish kills were noted, many of the fish, especially in St. Maarten and Saba, bore bruises and lacerations presumably resulting from Hurricane Lenny. These were particularly apparent on the pale, smooth skin of acanthurids but also noted on many scarids. Additionally, it appeared that a greater number of fish than normal were spending time at cleaning stations, seemingly having their injuries tended.

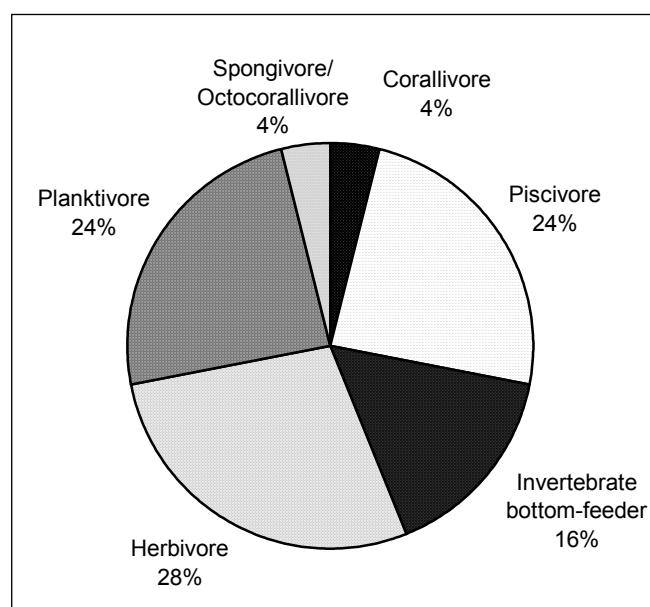


Figure 10. Trophic guild composition of the 25 most commonly sighted fish species during roving diver surveys in the windward Netherlands Antilles.

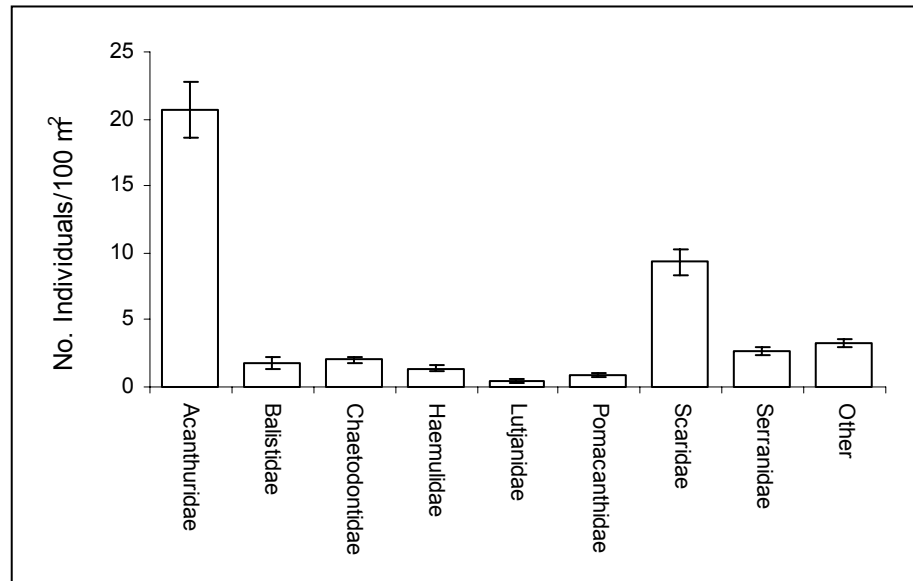


Figure 11. Mean fish density (no. individuals/100m² ± se) for AGRRA fishes in the windward Netherlands Antilles. Other = *Bodianus rufus*, *Caranx ruber*, *Lachnolaimus maximus*, *Microspathodon chrysurus* and *Sphyrna barracuda*.

Ecologically and Commercially Significant Fishes

A total of 6,116 individual fish were counted in 240 belt transects. Acanthurids (surgeonfish) and scarids dominated the selected species surveyed in the belt transects (Fig. 11). The most common species were *Acanthurus bahianus*, *A. coeruleus*, *Sparisoma aurofrenatum*, *S. viride*, *Scarus croicensis* and *S. taeniopterus*. Although variable among sites and areas, acanthurids had the greatest densities (mean = 19 individuals/100 m²) and highest biomass (mean = 3,150 grams/100 m²) overall (Table 5). Total lengths for four common species of parrotfish (counts restricted to ≥5 cm) averaged 19 cm for *Scarus croicensis*, 23 cm for *S. taeniopterus*, 20 cm for *Sparisoma aurofrenatum* and 28 cm for *S. viride*. No significant differences were detected in mean lengths among the four geographical areas for *S. croicensis* (ANOVA, $p = 0.20$) and for *S. viride* (ANOVA, $p = 0.51$). However, *S. aurofrenatum* were significantly larger in Saba (ANOVA, $p = 0.01$) than on the Saba Bank (Tukey, $p = 0.05$) and in St. Eustatius (Tukey, $p = 0.01$), but overlapped with those in St. Maarten where mean lengths were highly variable (Fig. 12). Statistical comparisons for *S. taeniopterus* were not computed since this species was abundant only in St. Eustatius.

The density of herbivorous fishes (i.e., acanthurids, scarids ≥5 cm, *M. chrysurus*) averaged 30.8 individuals/100 m². Acanthurids were predominant with an overall mean density of 19.3 individuals/100 m² followed by scarids and *M. chrysurus* with respective means of 9.3 and 2.2 individuals/100 m². This pattern of dominance was consistent throughout the four geographical areas surveyed with the exception of Saba Bank where densities of acanthurids and scarids were nearly equal. However, mean density of the

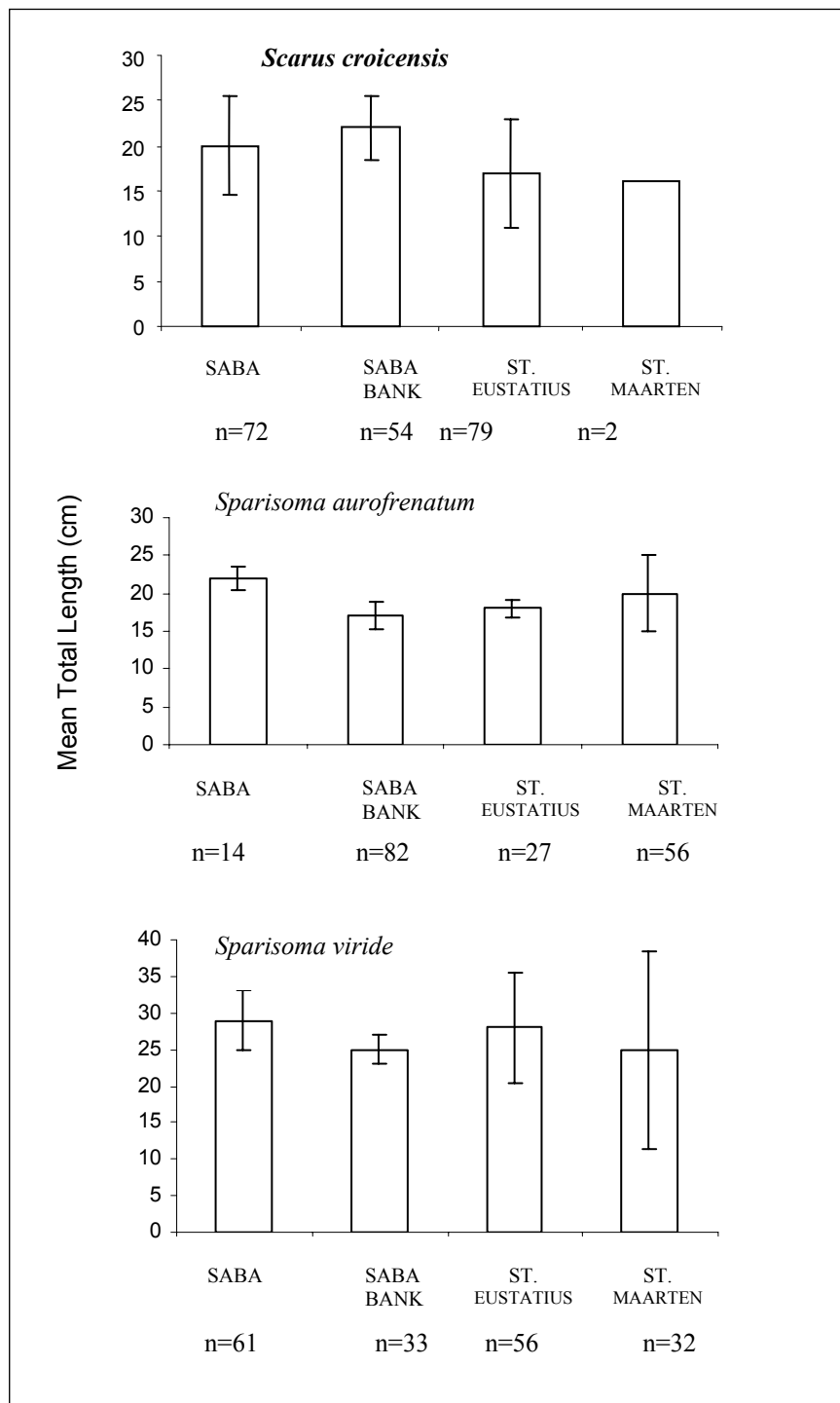


Figure 12. Mean total length (\pm se) for three common scarids (all ≥ 5 cm) for each geographical area in the windward Netherlands Antilles.

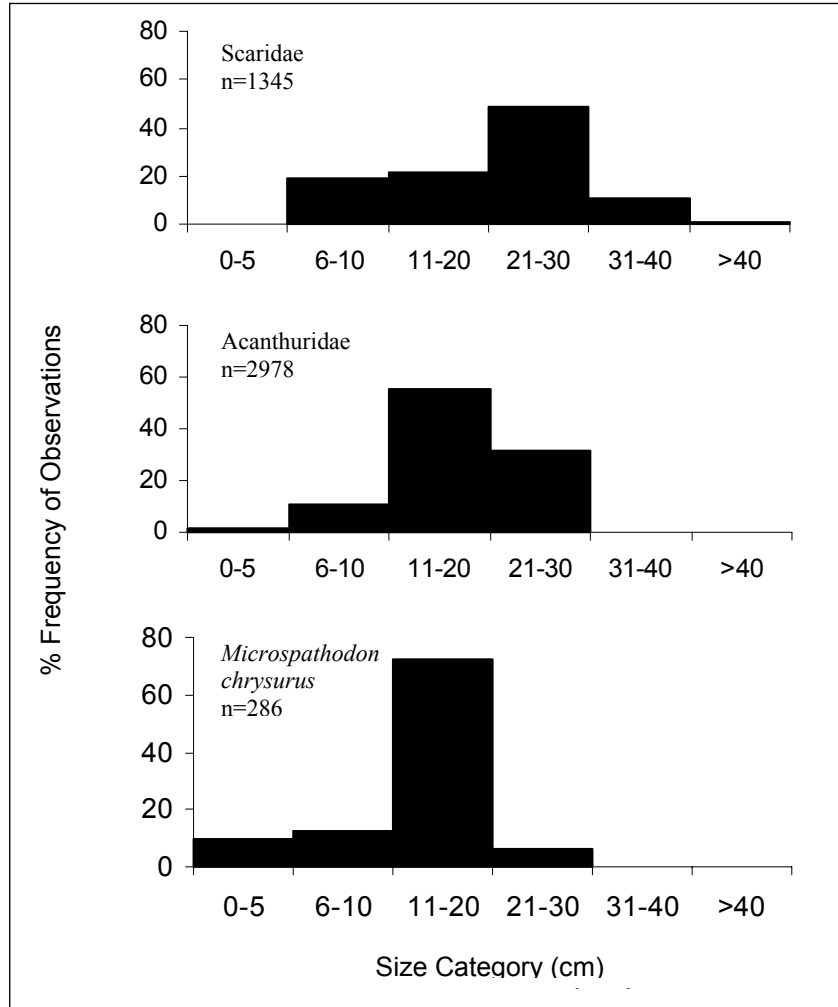


Figure 13. Size frequency distribution of dominant herbivores in the windward Netherlands Antilles.

Acanthuridae was notably greater in Saba than in the other three areas (Table 5). Most of the herbivorous fish we recorded were between 11 and 30 cm in length (Fig. 13).

The mean density of fish species of high commercial value (i.e., large serranids, lutjanids, haemulids ≥ 5 cm) was 4.5 individuals/100 m². The Serranidae, of which the numerical dominant was *Epinephelus fulvus* (with 85% of individuals), was the predominant family with an overall mean of 2.4 individuals/100 m² (Table 5). The most common size class for individual serranids and lutjanids in the windward N. A. was 21-30 cm whereas haemulids were evenly distributed between 11-20 cm and 21-30 cm (Fig. 14).

Total community biomass for the eight fish families included in the AGRRA belt transects averaged 16 kg/100 m² (± 5.1 se). Saba (Fig. 15) had a significantly greater biomass (mean = 11 kg/100 m² ± 3.5 se; $p=0.0003$) than the other geographical areas (combined mean = 7 kg/100 m² ± 2.0 se).

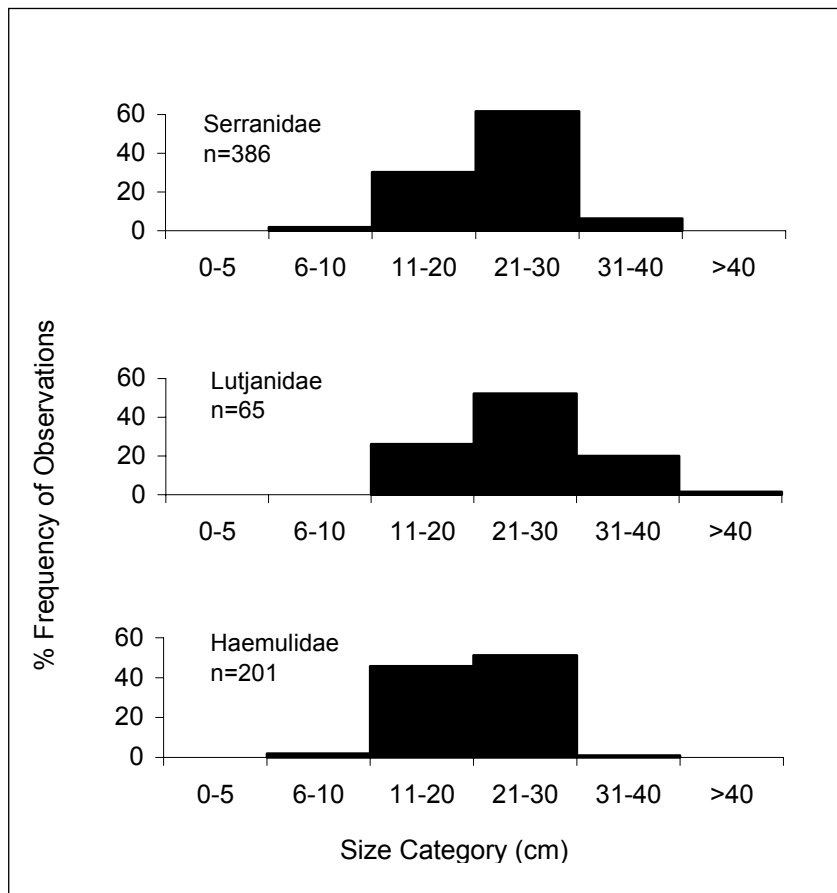


Figure 14. Size frequency distribution of commercially valuable carnivores in the windward Netherlands Antilles.

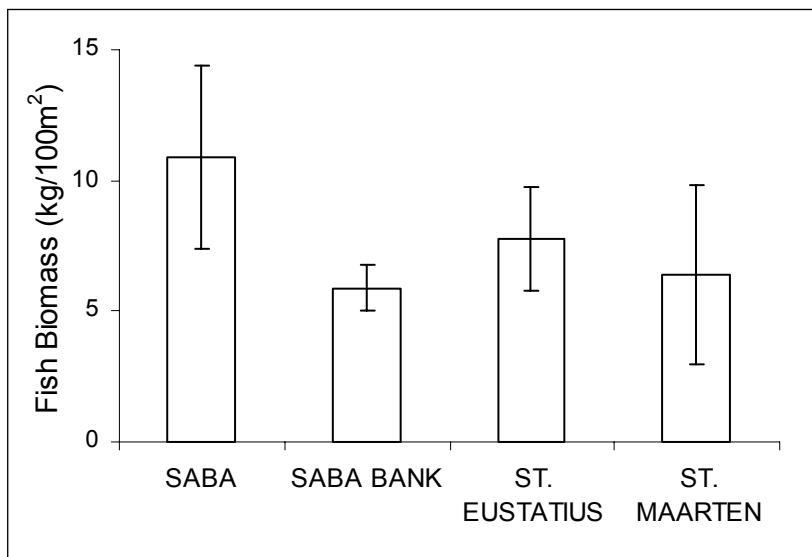


Figure 15. Total mean biomass (kg/100 m² ± se) for the AGRRA fishes in eight families in the windward Netherlands Antilles.

A linear regression revealed a significant inverse relationship ($p = 0.03$; $r^2 = 0.19$) between herbivorous fish biomass and macroalgal index at the windward N. A. survey sites (Fig. 16).

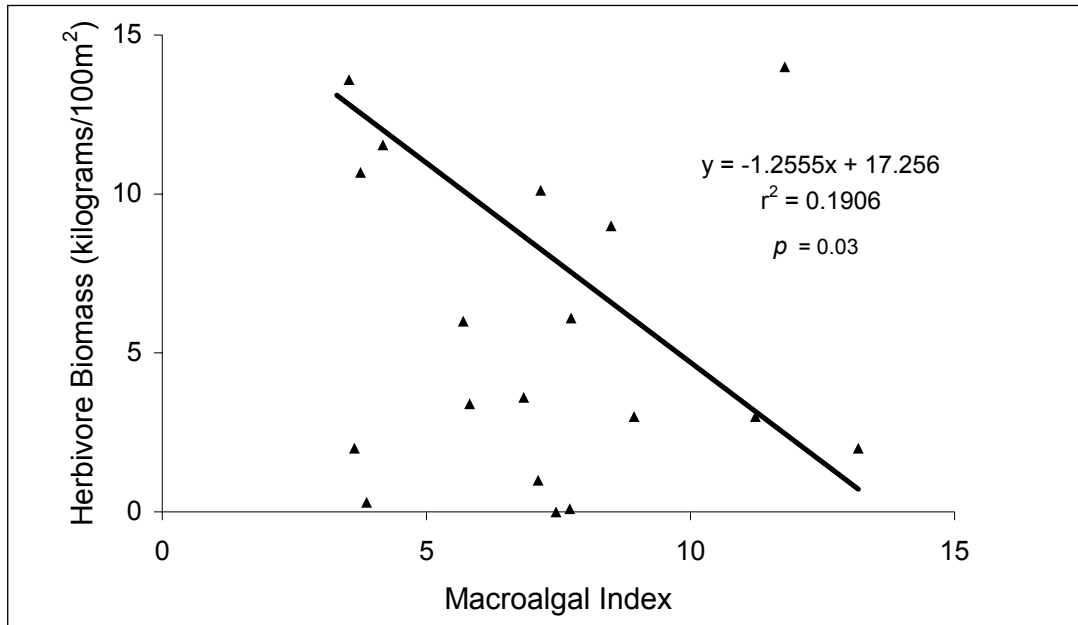


Figure 16. Regression plot between mean herbivore biomass (kg/100m²) and mean macroalgal index, by site in the windward Netherlands Antilles.

DISCUSSION

The condition of reefs in the windward N. A. is largely influenced by their position within the hurricane belt of the Atlantic Ocean. The vulnerability of this region to the impacts of storm forces is evidenced by the disappearance of mature stands of *Acropora palmata* in recent years (Acroporids are particularly susceptible to damaging storm forces due to their fragile, branching nature.). Before Hurricane Luis (1995) *A. palmata* dominated sites SAB1 and SAB2 on Saba's windswept east coast, along with sites SAB8 and SAB9 on the north coast which also frequently experience high waves and strong surges (ENCAMP, 1980a). Although some recovery had been observed since Luis (Kooistra, personal observations), Hurricanes Georges (1998) and Lenny (1999) caused still more damage. We were unable to detect most of the colonies of *A. palmata* which died during earlier storms as the remaining skeletons have been eroded beyond taxon recognition.

The overall small size of the individually surveyed corals at most sites in the windward N. A. (Table 2; Fig. 6) reflects the high abundance of small colonies of *Diploria* spp., *Porites astreoides* and *Agaricia agaricites*. The flattened growth patterns of *Diploria* spp. and *P. astreoides* on many Saban reefs may reflect an adaptation to high surge and frequent hurricanes.

Hurricanes normally develop over the Atlantic and approach the windward N. A. islands from the east. Hurricane Lenny was unusual in that it developed in the southern Caribbean and advanced from west to east. While situated between St. Maarten and Saba, the hurricane stalled in position for nearly 22 hours which may explain why the greatest physical damage to stony corals was experienced in the Saban sites with western exposure (SAB4, SAB8, SAB9).

During our dives, visibility was somewhat restricted (ranging from 4–23 meters) due to increased turbidity from suspended sediments following Hurricane Lenny's passage. The high levels of partial bleaching that we recorded (nearly 25% of the individually surveyed colonies) was likely a response to conditions of reduced light due to the increased turbidity. Bleaching conditions may have been compounded by circumstances (i.e., suspended sediment and turbidity) introduced by Hurricane José in October 1999, although we have no evidence to support this claim. Although some settling of sediment had occurred at the time of our assessment, the full extent of the hurricane's impact on the reefs of the windward N. A. might not be recognizable since delayed mortality due to sedimentation will be difficult to attribute to this storm with any degree of certainty.

Additional damage was noted in large (up to 1 m high) barrel sponges. Some of the *Xestospongia muta*, which were previously abundant on the reefs of Saba and St. Eustatius, disappeared during Hurricane Lenny while others were severely damaged. Regrowth rates of approximately 2.5 cm per month were initially recorded in the surviving sponges (Kooistra, personal observation) although recovery rates slowed after several months.

It remains unclear why *C. natans* displayed a higher incidence of partial mortality (particularly old mortality) than these other species. Incidence of disease in *C. natans* and in *Diploria strigosa* (for which recent partial mortality was also relatively elevated) were no higher than in other taxa. Other potentially aggravating agents such as *Corallophilia abbreviata*, *Palythoa* spp., and burrowing serpulids were noted but *C. natans* and *D. strigosa* were not disproportionately plagued by these factors.

Partial mortality in the ≥ 10 cm corals was low throughout the windward N. A. in late 1999 (Fig. 8). It should be recognized, however, that all of our sites were situated in deeper water (by AGRRA standards) where mortality is normally less prominent. In all likelihood, mortality estimates would have been greater had we been able to document the demise of the *Acropora* that once existed in these waters (see above).

The *Montastraea annularis* complex consists of slow-growing massive corals and, like the acroporids, has been an important primary reef-builder in the Caribbean. If future climate conditions resemble contemporary patterns, it is unlikely that the reefs of the windward N. A. will sustain substantial populations of *Acropora*. Hence, the importance of the massive *Montastraea annularis* complex as a reef-building component is reinforced as it is more resilient to destructive storm forces. *Montastraea* has been a persistent genus on reefs over geologic time (Birkeland, 1997). Westerman and Kiel (1961) reported "plate-like" colonies of fossilized *M. annularis* embedded in St. Eustatius' coastal cliffs (Sugar Loaf) near our sites EUX09 and EUX10. Its presence in this region 20,000 to 70,000 years ago, and as mature living colonies today, suggests that local environmental conditions have been suitable and recruitment successful for this species throughout glacial sea-level oscillations and disturbances during the Recent. The

potential exists for reef development throughout this area if environmental conditions remain favorable and if *M. annularis* continues to proliferate and withstand disturbances.

Notwithstanding its dominance throughout the windward N. A. (the *Montastraea annularis* complex collectively constituted 30% of the individually surveyed corals), none of the various morphs had been a major contributor (< 1%) to coral recruitment (Fig. 5) in late 1999. Our findings are consistent, however, with previous studies of coral recruitment within the Caribbean. Rylaarsdam (1983) reported that *Montastraea annularis* composed $\leq 1\%$ of juveniles recorded at Discovery Bay, Jamaica where its colonies made up 7-32% of the coral cover. Hughes (1985) noted complete failure to detect *M. annularis* recruitment on reefs at Rio Bueno, Jamaica where larger colonies were locally abundant. Similarly, a paucity of juveniles of reef-building taxa from Curacao and Bonaire led Bak and Engel (1979) to conclude that the composition of the adult coral community is not a direct function of juvenile abundance. The low rate of recruitment of *M. annularis* on Caribbean reefs has been explained as a characteristic of its life history strategy. This is in contrast to species which commonly dominate the juvenile community and that display relatively high rates of recruitment followed by high mortality (eg., *Agaricia agaricites* and *Porites astreoides*). *M. annularis* has a relatively high survival rate aided by its moderate ability to clear sediment from its surface, its aggressive nature toward other species, and its ability to regenerate lesions (Bak and Engel, 1979; Wittenberg and Hunte, 1992). However, since it is unknown what threshold level of parental spawning stock is necessary to maintain coral populations at sustainable levels, a decrease in adult spawners, as evidenced by a decline in live coral cover, may indicate a reduced capacity to replenish populations. Long-term monitoring studies in the U.S. Virgin Islands where *M. annularis* is the dominant coral indicated that following a 35% decline in its cover, there had been no substantial recovery (Smith et al., 1997). Subsequent recruitment studies in this area revealed that broadcast spawning species (including the *M. annularis* complex and *Acropora* spp.) composed less than 4% of coral recruits (Kojis and Quinn, 2001). Even if relatively low densities of juvenile *M. annularis* are a natural phenomenon, these levels may not be adequate to offset reduced reproduction associated with high rates of decline in live coral cover. Hence, the importance of *M. annularis* as a major component to reef structure in the N. A. may warrant monitoring to detect future trends.

The rather high relative abundance of crustose coralline algae (Table 3) is suggestive of conditions that should be conducive for the settlement and recruitment of coral larvae. Indeed, while recruitment was highly variable, corals less than 2 cm in diameter were detected at all sites. A low standing stock of macroalgae and low macroalgal indices (Table 3) may indicate a seasonal response to reduced light and water temperatures (Littler et al., 1986). Alternatively, it may imply that algae are routinely nutrient-limited or that algal biomass is kept in check by grazing herbivores. There are no data to support nutrient limitation or enrichment and the grazing echinoid, *D. antillarum*, was not present in our transects. Herbivorous fishes, especially acanthurids, were present in high densities at most sites (Table 5), however, and macroalgal biomass was inversely related to the biomass of herbivorous fishes in late 1999 (Fig. 16). Unfortunately, we have no quantitative data by which to compare algal conditions prior to Hurricane Lenny with those at the time of our assessment. Fleishy macroalgae (e.g., *Dictyota*) were abundant at two sites in St. Eustatius (EUX03, EUX05) during reconnaissance dives in

October 1999 but were not conspicuous elsewhere at that time. Considering that large barrel sponges were displaced by Hurricane Lenny, it is reasonable to believe that many of the macroalgae would also have been dislodged by this storm.

The fish assemblage of the windward N. A. is fairly rich in species and well represented by trophic guilds (Fig. 10). A relatively high density of herbivorous acanthurids and scarids was present at the time of our assessment (Table 5; Fig. 11). That we found greater mean total lengths for *Sparisoma aurofrenatum* in Saba (and possibly St. Maarten) than at Saba Bank and St. Eustatius (Fig. 12) may be an indication of better growth conditions at the former or it could be related to variations in age distribution among the geographic areas. Since these species are not targeted by the fishing community, small deviations in size are not of great concern but may be a point of interest to the dive community, or for future growth or size-related studies.

A number of studies have demonstrated that macroalgae appear to be common only where they are not heavily grazed (Lewis, 1986; Morrison, 1988; Schmitt, 1997). The inverse relationship we detected between herbivorous fish biomass and macroalgal biomass (Fig. 16) may suggest that herbivorous fish biomass increased as a result of effective grazing although this relationship only explains 19% of the variation in herbivore biomass. Even though most reef fish are generally considered “nonmigratory,” foraging groups of scarids and acanthurids are known to cover distances of hundreds of meters to several kilometers from their “home” reef (Reeson, 1983; Risk, 1998; Williams, 1991). Since fish biomass is a consequence of preceding food conditions and may have been attained at a time and locale where algal conditions varied from what we sampled in 1999, caution must be exercised in drawing conclusions based on a “snapshot” algal/fish biomass relationship.

It is noteworthy to recognize that most of the serranids encountered in our belt transects were *Epinepheus fulvus* (coney), a smaller (reaching ≈ 30 cm) less-targeted species. Since many of the larger serranids are wary of divers, it is possible that the belt-transect method did not adequately quantify their abundance. We did not detect many individuals of commercial value less than 10 cm (Fig. 14) which is not unexpected since our assessment took place in relatively deep water and it is recognized that juvenile serranids, lutjanids, and haemulids occupy shallow-water habitats (Thompson and Munro, 1983a; Thompson and Munro, 1983b; Gaut and Munro, 1983). Although lutjanids and serranids are known to feed on a wide range of prey, they are primarily piscivorous (Parrish, 1987). Their relatively low density suggests the possibility of reduced predation pressure on the fish community and may account for the fairly high densities of acanthurids and scarids.

The total biomass for the eight families (Fig. 15) provides an assay of fish community production in the windward N. A. Sites within the N. A. were relatively productive in fish biomass. A comparison of fish biomass from the same eight families from 60 sites along Jamaica’s north coast (Klomp et al. in press), where decades of intense fishing activity has reduced fish abundance and size, indicates that fish biomass is over seven times greater in the windward islands of the N. A. Although not conclusive from this study, the greater biomass in Saba in part may be a result of reduced fishing pressure associated with the long-term protection within the Saba Marine Park since 1987.

The trophic guild classification (Fig. 10) illustrates the functional structure of the fish community as it existed in late 1999. It is important to remember that the forces responsible for shaping this community are a result of past events (e.g., larval recruitment and settlement, predation, environmental conditions) and cannot be identified from a single survey. This assessment does serve, however, as a baseline against which future data can be compared and, collectively with other AGRRA assessments, a point from which current trends in community structure can be detected (see Kramer, this volume).

Being able to detect between-site differences in live coral cover within the four geographical areas allows us to partition sites according to their potential for reef development. For example, *Acropora* has been virtually eliminated from Saban sites SAB01, SAB08, and SAB09 by recent hurricanes (see above). SAB03 is downstream from the only major coastal development on Saba (a man-made harbor and a recently closed rock-crushing facility). Increased sedimentation may be a limiting factor for coral development at SAB03 (Buchan, 1998). The remaining Saban sites offer the greatest potential for reef development and stand to benefit the most by maintaining marine-park protection. Indeed, while the coral assemblages along the west coast are not generally recognized as “true reefs” (Bak, 1977; Nagelkerken, 1981), they have accreted a contiguous, biogenic substratum (e.g., at SAB04, SAB05, and SAB06) and could, arguably, be classified as coral reefs (van’t Hof, 1991). Not surprisingly, the *M. annularis* complex is the dominant coral (41% of all colonies) at these three sites. Our estimates for dominant coral cover (i.e., *M. annularis* complex = 46% of all colonies) and percent coral cover (mean = 23%) at SAB04 and SAB05, agree with estimates reported by Buchan (1998) for the CARICOMP coral reef site which lies between these two AGRRA sites (CARICOMP: *M. annularis* complex = 43% of all colonies; live coral cover = 24%).

Having an area greater than 2,200 km², we did not sample a large enough sector on the Saba Bank to make definitive statements about the condition of its reefs. However, on the basis of our reconnaissance dives in October 1999 and previous reports (Hoetjes et. al., 1999; Macintyre et. al., 1975; Van Der Land, 1977), it is clear that live coral cover in some sectors exceeds that recorded during our December 1999 assessment and elsewhere approximates our lower estimate (\approx 11%). An extensive investigation, with the sole purpose of inventorying Saba Bank, would greatly increase our ability to speculate on the potential for reef development in the absence of coastal processes.

EUX09 and EUX10 had higher than average values for live coral cover (46%), and were dominated by colonies of *Montastraea annularis faveolata* having larger than average sizes. They may also have a positional advantage being the most southerly of our survey sites in St. Eustatius. Since prevailing coastal currents approach this area from the southeast (ENCAMP, 1980b), stony coral growth at EUX9 and EUX10 may be enhanced by currents introducing relatively nutrient-rich water and/or by receiving less coastal runoff.

The two sites surveyed on St. Maarten are routinely exposed to strong currents (SXM01) and high-energy waves (SXM02), their mean live coral cover was low (11%), and they are probably the most threatened reefs we encountered in the windward N. A. Even were hurricanes not a certain hazard, it will be a challenge to afford them enough protection to diffuse the impacts of St. Maarten’s burgeoning coastal development and tourism.

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Table 1. Site information for AGRRA stony coral, algal and fish surveys in the windward Netherlands Antilles.

Site name	Site code	Reef type	Latitude (° N)	Longitude (° W)	Survey date	Depth (m)	Benthic transects (#)	≥25 cm stony corals (#/10 m)	≥10 cm stony corals (#/10 m)	% live stony coral cover (mean ± sd)	30 m fish transects (#)	RDT fish species (#) ¹
Saba												
Core Gut	SAB01	encrusted boulders; high-surge embayment	17 37.85	63 12.90	Dec 3 99	9	13	4	8	14 ± 6	10	58
Hole in the Corner	SAB02	encrusted boulders; gentle slope	17 36.90	63 13.50	Dec 3 99	11	13	6	12	22 ± 8	10	61
Tent Reef	SAB03	encrusted ledge w/ escarpment to sloping flat	17 36.98	63 15.51	Dec 6 99	10	15	3	8	9 ± 4	10	70
Hot Springs	SAB04	encrusted boulders and lava formations	17 37.49	63 15.57	Dec 7 99	11	12	7	11	22 ± 8	10	60
Ladder Labyrinth	SAB05	encrusted rock buttresses & sloping lava flows	17 37.60	63 15.58	Dec 6 99	12	11	6	11	25 ± 12	10	53
Babylon	SAB06	encrusted ridges, sloping lava flows & sand channels	17 37.69	63 15.57	Dec 6 99	13	11	7	13	22 ± 4	10	54
Porites Point	SAB07	encrusted lava & boulders	17 37.76	63 15.53	Dec 9 99	15	13	6	11	19 ± 8	10	67
Torrens Point	SAB08	exposed, encrusted boulders & high-relief buttresses	17 38.60	63 15.19	Dec 9 99	6	14	5	10	15 ± 6	10	40
Green Island	SAB09	encrusted boulder & rocky outcrops extend from islet	17 38.98	63 13.68	Dec 9 99	7	18	4	6	7 ± 4	10	46
All Saba										17 ± 6		113
Saba Bank												
BANK 1	BNK01	submerged atoll/bank rim	17 27.78	63 13.36	Dec 7 99	20	9	9	12	41 ± 12	10	54
BANK 2	BNK02	submerged atoll/bank rim	17 29.21	63 13.90	Dec 8 99	15	12	4	10	11 ± 4	10	47
BANK 3	BNK03	submerged atoll/bank rim	17 29.27	63 13.94	Dec 8 99	17	8	7	13	25 ± 12	10	54
All Saba Bank										26 ± 15		81
St. Eustatius												
Barracuda Reef	EUX01	low profile reef flat bordering sand flat	17 28.08	62 59.50	Dec 14 99	17	8	6	15	16 ± 6	10	52
Anchor Point	EUX02	low profile reef flat	17 27.86	62 59.27	Dec 13 99	14	8	6	15	18 ± 4	10	52
Hangover	EUX03	ridge abutment w. lava flow terminations	17 27.89	62 59.16	Dec 11 99	14	10	5	12	16 ± 6	10	60
The Blocks	EUX04	encrusted ledge; parallel to shoreline	17 27.86	62 59.10	Dec 12 99	15	9	7	13	17 ± 7	10	59
The Ledges	EUX05	encrusted ledge; parallel to shoreline	17 27.80	62 59.08	Dec 11 99	14	10	6	13	17 ± 6	10	66
Five Fingers	EUX06	sloping lava flows separated by sand channels	17 27.89	62 58.00	Dec 13 99	15	10	5	13	16 ± 12	10	64
Valley of the Sponges	EUX07	sloping lava flows separated by sand channels	17 27.84	62 58.95	Dec 12 99	14	11	4	10	12 ± 4	10	45
The Humps	EUX08	boulder corals on rocky outcrops	17 27.81	62 58.69	Dec 13 99	12	11	6	15	16 ± 6	10	61
Mushroom Gardens	EUX09	fringing reef; <i>M. annularis faveolata</i> dominant	17 27.75	62 58.66	Dec 11 99	16	8	10	14	47 ± 12	10	64
Mushroom South	EUX10	fringing reef; <i>M. annularis faveolata</i> dominant	17 27.70	62 58.66	Dec 14 99	16	9	9	14	45 ± 14	10	58
All St. Eustatius										22 ± 13		106
St. Maarten												
Mikes Maze	SXM01	reef flat; midshelf	17 59.74	63 03.60	Nov 30 99	9	20	3	5	10 ± 4	10	77
Hen & Chicks	SXM02	fringing reef off rocky islets	18 00.64	63 00.48	Dec 1 99	11	20	4	6	13 ± 8	10	69
All St. Maarten										11 ± 2		92

¹RDT = Roving Diver Technique

Table 2. Size and condition (mean \pm standard deviation) of all stony corals (≥ 10 cm diameter) and mean damselfish density by site in the windward Netherlands Antilles.

Site name	Stony corals			Partial-colony mortality (%)			Stony corals (%)				Damselfish ¹ (#/10 m)
	#	Diameter (cm)	Height (cm)	Recent	Old	Total	Standing dead	Bleached	Diseased	Hurricane damaged	
<i>Saba</i>											
Core Gut	106	41 \pm 42	17 \pm 24	2.0 \pm 9.5	14 \pm 22	16 \pm 24	0.9	26	1.0	2.0	3.0
Hole in the Corner	151	38 \pm 36	19 \pm 24	<0.5 \pm 1.0	11 \pm 20	12 \pm 20	0.0	30	0.5	0.5	1.5
Tent Reef	115	26 \pm 16	14 \pm 14	2.0 \pm 10.0	16 \pm 22	18 \pm 24	0.9	20	1.0	2.5	0
Hot Springs	132	48 \pm 43	32 \pm 29	2.0 \pm 7.5	18 \pm 26	20 \pm 26	0.0	27	1.0	4.5	5.5
Ladder Labyrinth	120	39 \pm 40	22 \pm 22	1.5 \pm 9.0	17 \pm 24	19 \pm 27	0.8	18	0.0	0.0	0
Babylon	145	31 \pm 25	17 \pm 14	0.5 \pm 2.0	15 \pm 22	15 \pm 23	0.0	28	1.5	2.0	.5
Porites Point	137	40 \pm 44	22 \pm 22	0.5 \pm 2.0	15 \pm 24	16 \pm 24	0.7	25	0.5	0.5	4.5
Torrens Point	136	32 \pm 30	16 \pm 14	1.5 \pm 6.5	18 \pm 27	19 \pm 28	0.0	21	0.0	6.5	0
Green Island	113	40 \pm 47	23 \pm 30	2.5 \pm 13.5	25 \pm 32	27 \pm 33	7.1	3	2.5	4.5	0
All Saba	1155	37 \pm 7	20 \pm 5	1.4 \pm 0.9	17 \pm 4	18 \pm 4	1.2	22	0.9	2.6	1.6 \pm 2.1
<i>Saba Bank</i>											
BANK 1	105	73 \pm 66	23 \pm 24	<0.5 \pm 1.5	15 \pm 18	15 \pm 18	0.0	6	1.0	0	4.0
BANK 2	114	25 \pm 15	12 \pm 10	1.0 \pm 6.0	18 \pm 25	19 \pm 26	0.0	12	0	0	2.0
BANK 3	104	39 \pm 37	26 \pm 26	1.0 \pm 6.5	18 \pm 23	16 \pm 21	1.0	9	0	0	0
All Saba Bank	323	46 \pm 25	20 \pm 7	0.7 \pm 0.4	17 \pm 2	17 \pm 2	0.3	9	0.3	0	1.9 \pm 1.9
<i>St. Eustatius</i>											
Barracuda Reef	119	24 \pm 16	12 \pm 8	0.5 \pm 5.5	17 \pm 24	18 \pm 24	0.0	17	1	0	1.0
Anchor Point	116	23 \pm 12	13 \pm 12	0.5 \pm 4.0	18 \pm 26	19 \pm 28	0.9	12	0	0	0
Hangover	121	27 \pm 19	14 \pm 12	2.5 \pm 10.5	14 \pm 21	17 \pm 24	0.8	26	1	0	0
The Blocks	113	28 \pm 16	15 \pm 13	1.5 \pm 4.0	15 \pm 24	16 \pm 24	0.0	31	1	0	0
The Ledges	126	29 \pm 31	14 \pm 11	<0.5 \pm 1.0	12 \pm 22	12 \pm 22	0.8	18	0	0	0
Five Fingers	125	29 \pm 21	16 \pm 16	1.5 \pm 8.0	16 \pm 24	17 \pm 25	0.0	26	0	0	0
Valley of the Sponges	109	24 \pm 14	15 \pm 14	0.5 \pm 2.0	22 \pm 26	22 \pm 26	0.0	28	0	1	0
The Humps	165	25 \pm 15	14 \pm 12	0.5 \pm 2.0	15 \pm 22	15 \pm 22	0.0	22	0	0	0
Mushroom Gardens	113	80 \pm 90	37 \pm 38	0.5 \pm 1.5	12 \pm 18	12 \pm 18	0.0	28	2.0	0	1.0
Mushroom South	123	73 \pm 88	33 \pm 38	1.0 \pm 7.5	15 \pm 22	16 \pm 22	0.8	34	1.5	1	9.0
All S. Eustatius	1230	36 \pm 21	18 \pm 9	0.9 \pm 0.7	16 \pm 3	17 \pm 3	0.3	24	0.6	0.2	1.1 \pm 2.8
<i>St. Maarten</i>											
Mikes Maze	105	27 \pm 16	12 \pm 12	0.5 \pm 1.5	8 \pm 20	9 \pm 20	1.9	45	0	0	0
Hen & Chicks	117	47 \pm 55	19 \pm 21	2.0 \pm 1.5	18 \pm 27	20 \pm 30	1.7	43	1.0	1.0	1.5
All St. Maarten	222	37 \pm 14	15 \pm 5	1.3 \pm 1.2	13 \pm 7	14 \pm 8	1.8	44	0.5	0.5	0.9 \pm 1.2

¹Primarily *Microspathodon chrysurus*.

Table 3. Algal characteristics, density of stony coral recruits and *Diadema antillarum* (mean \pm standard deviation) by site in the windward Netherlands Antilles.

Site name	Site code	Quadrats (#)	Relative abundance (%)			Macroalgal		Recruits (#/.0625 m ²)	<i>Diadema</i> (#/100 m ²)
			Macroalgae	Turf algae	Crustose coralline algae	Height (cm)	Index ¹		
<i>Saba</i>									
Core Gut	SAB01	60	13 \pm 7	61 \pm 30	26 \pm 30	1.0 \pm 0.5	14	.35	0
Hole in the Corner	SAB02	46	3 \pm 5	49 \pm 31	48 \pm 30	2.0 \pm 1.5	6	.13	0
Tent Reef	SAB03	68	1 \pm 1	75 \pm 30	25 \pm 30	1.0 \pm 0.0	0	.50	0
Hot Springs	SAB04	50	2 \pm 5	57 \pm 32	41 \pm 33	1.0 \pm 0.5	2	.23	0
Ladder Labyrinth	SAB05	50	7 \pm 8	49 \pm 25	44 \pm 27	2.5 \pm 5.5	18	.14	0
Babylon	SAB06	45	4 \pm 7	49 \pm 28	47 \pm 29	1.0 \pm 0.5	3	.18	0
Porites Point	SAB07	55	8 \pm 7	49 \pm 26	43 \pm 27	1.0 \pm 0.5	9	.11	0
Torrens Point	SAB08	55	2 \pm 5	52 \pm 30	46 \pm 30	1.5 \pm 0.5	3	.28	0
Green Island	SAB09	55	1 \pm 2	67 \pm 28	32 \pm 28	1.0 \pm 0.5	1	.16	0
All Saba		484	5 \pm 4	56 \pm 9	39 \pm 9	1.4 \pm 0.6	6 \pm 6	.24 \pm .18	0
<i>Saba Bank</i>									
BANK 1	BNK01	50	14 \pm 15	30 \pm 26	57 \pm 32	1.0 \pm 1.0	18	.18	0
BANK 2	BNK02	50	<1.0 \pm 1	56 \pm 31	44 \pm 31	2.0 \pm 1.0	1	.14	0
BANK 3	BNK03	40	<1.0 \pm 1	34 \pm 28	65 \pm 29	1.0 \pm 0.0	<1	.10	0
All Saba Bank		140	5 \pm 8	40 \pm 14	55 \pm 11	1.4 \pm 0.5	6 \pm 10	.14 \pm .04	0
<i>St. Eustatius</i>									
Barracuda Reef	EUX01	50	17 \pm 18	44 \pm 26	39 \pm 24	1.0 \pm 0.5	19	.34	0
Anchor Point	EUX02	50	15 \pm 15	44 \pm 25	41 \pm 24	1.0 \pm 0.5	18	.46	0
Hangover	EUX03	50	6 \pm 8	35 \pm 23	58 \pm 22	1.0 \pm 0.5	6	.22	0
The Blocks	EUX04	50	9 \pm 10	47 \pm 28	44 \pm 27	1.0 \pm 0.5	10	.68	0
The Ledges	EUX05	50	15 \pm 13	34 \pm 26	51 \pm 29	1.0 \pm 0.5	17	.34	0
Five Fingers	EUX06	50	9 \pm 13	63 \pm 30	28 \pm 26	1.0 \pm 0.5	11	.34	0
Valley of the Sponges	EUX07	50	3 \pm 5	64 \pm 29	32 \pm 27	1.0 \pm 0.0	3	11.2	0
The Humps	EUX08	50	4 \pm 5	64 \pm 24	33 \pm 24	1.0 \pm 0.0	4	.26	0
Mushroom Gardens	EUX09	45	11 \pm 11	59 \pm 31	30 \pm 30	1.0 \pm 0.5	12	.13	0
Mushroom South	EUX10	50	14 \pm 15	63 \pm 25	24 \pm 23	1.0 \pm 0.0	14	.18	0
All St. Eustatius		495	10 \pm 5	52 \pm 12	38 \pm 11	1.1 \pm 0.1	11 \pm 6	.42 \pm .31	0
<i>St. Maarten</i>									
Mikes Maze	SXM01	58	<1.0 \pm 1	62 \pm 28	38 \pm 28	0.5 \pm 0.0	<1	.29	0
Hen & Chicks	SXM02	67	15 \pm 21	51 \pm 31	34 \pm 27	2.0 \pm 1.0	33	.18	0
All St. Maarten		125	8 \pm 10	57 \pm 8	36 \pm 3	1.4 \pm 1.2	16 \pm 23	.24 \pm .08	0

¹Macroalgal index = % relative abundance of macroalgae x macroalgal height

Table 4. Twenty-five most frequently sighted fish species during roving diver surveys in the windward Netherlands Antilles with mean densities for species in belt transects.

Scientific name	Common name	Sighting frequency (%) ¹	Density (# individuals/100 m ²)				
			Saba	Saba Bank	St. Eustatius	St. Maarten	N. A. area
<i>Acanthurus coeruleus</i>	Blue Tang	100.0	12.8	2.4	7.6	7.3	8.9
<i>Thalassoma bifasciatum</i>	Bluehead Wrasse	100.0					
<i>Acanthurus bahianus</i>	Ocean Surgeonfish	100.0	14.5	7.5	9.4	14.5	11.5
<i>Epinephelus fulvus</i>	Coney	100.0	2.3	3.0	2.4	0.3	2.3
<i>Sparisoma viride</i>	Stoplight Parrotfish	100.0	1.1	1.8	1.3	2.7	1.4
<i>Microspathodon chrysurus</i>	Yellowtail Damselfish	100.0	2.4	1.1	1.7	3.0	2.0
<i>Holocentrus rufus</i>	Longspine Squirrelfish	100.0					
<i>Caranx ruber</i>	Bar Jack	100.0	0.6	0.4	0.6	0.1	0.5
<i>Stegastes partitus</i>	Bicolor Damselfish	96.5					
<i>Chromis cyanea</i>	Blue Chromis	96.5					
<i>Halichoeres garnoti</i>	Yellowhead Wrasse	96.5					
<i>Chaetodon capistratus</i>	Foureye Butterflyfish	96.5	2.0	0.8	0.9	1.6	1.3
<i>Bodianus rufus</i>	Spanish Hogfish	96.5	1.1	0.2	0.6	0.3	0.7
<i>Mulloidichthys martinicus</i>	Yellow Goatfish	93.1					
<i>Melichthys niger</i>	Black Durgon	93.1	2.5	0.7	1.1	0.6	1.5
<i>Holacanthus tricolor</i>	Rock Beauty	93.1	0.4	1.0	0.8	0.3	0.7
<i>Serranus tigrinus</i>	Harlequin Bass	93.1					
<i>Aulostomus maculatus</i>	Trumpetfish	93.1					
<i>Chromis multilineata</i>	Brown Chromis	89.6					
<i>Sparisoma aurofrenatum</i>	Redband Parrotfish	89.6	2.7	4.6	4.7	4.7	3.9
<i>Scarus taeniopterus</i>	Princess Parrotfish	89.6	0.7	1.5	4.9	0.3	2.5
<i>Canthigaster rostrata</i>	Sharpnose Puffer	89.6					
<i>Epinephelus cruentatus</i>	Graysby	86.2	0.1	0.4	0.6	0.1	0.3
<i>Haemulon carbonarium</i>	Caesar Grunt	86.2	0.4	0.8	0.2	0.0	0.5
<i>Myripristis jacobus</i>	Blackbar Soldierfish	82.7					

¹Sighting frequency for the AGRRA surveys from the REEF database at <http://www.reef.org/data/twa/surveys/index.shtml>

Table 5. Mean density and biomass of AGRRA fishes by site in the windward Netherlands Antilles.

Site code ¹	Herbivores						Commercially important carnivores					
	Acanthuridae		Scaridae (≥5 cm)		<i>Microspathodon chrysurus</i>		Haemulidae (≥5 cm)		Lutjanidae		Serranidae ²	
	Density (#/100 m ²)	Biomass (g/100 m ²)	Density (#/100 m ²)	Biomass (g/100 m ²)	Density (#/100 m ²)	Biomass (g/100 m ²)	Density (#/100 m ²)	Biomass (g/100 m ²)	Density (#/100 m ²)	Biomass (g/100 m ²)	Density (#/100 m ²)	Biomass (g/100 m ²)
Saba												
SAB01	30.0	9481	3.5	1332	3.5	973	0.0	0	1.0	378	2.0	475
SAB02	27.0	4105	2.5	921	4.5	674	<0.5	59	0.5	155	2.5	415
SAB03	20.0	3272	10.0	3346	1.5	839	2.0	678	0.5	95	4.5	936
SAB04	43.5	10146	7.5	2297	4.0	734	4.5	1138	0.5	130	2.0	505
SAB05	7.0	1154	6.5	2141	1.5	273	1.0	349	0.0	0	2.5	394
SAB06	26.0	5708	8.5	2843	1.5	379	0.5	132	2.0	1294	3.0	579
SAB07	15.5	4623	7.5	3328	0.5	543	1.0	132	1.5	502	2.0	668
SAB08	49.0	10438	1.0	261	3.5	527	1.0	213	0	0	1.0	215
SAB09	31.0	4777	6.0	1393	6.5	945	0.0	0	0	0	2.5	699
All Saba (mean ± standard error)	27.7 ± 13.0	5967 ± 3967	5.9 ± 2.9	1985 ± 1083	3.0 ± 1.8	654 ± 244	1.2 ± 1.4	300 ± 379	0.6 ± 0.7	284 ± 417	2.4 ± 0.9	543 ± 208
Saba Bank												
BNK01	7.5	1181	14.5	2169	1.5	287	<0.5	12	0.5	57	2.5	511
BNK02	13.0	1167	11.0	2299	<0.5	171	0.5	117	0.0	0	5.0	651
BNK03	10.0	1327	7.5	1732	1.5	812	3.0	783	2.0	321	3.0	639
All Saba Bank (mean ± standard error)	10.1 ± 2.8	1225 ± 89	11.0 ± 3.3	2067 ± 297	1.1 ± 0.8	423 ± 341	1.2 ± 1.6	304 ± 418	0.8 ± 1.1	126 ± 171	3.6 ± 1.3	600 ± 78
St. Eustatius												
EUX01	17.0	1663	10.0	1925	1.5	445	3.5	1019	0.5	143	1.5	480
EUX02	14.5	1548	9.5	2125	1.5	217	1.5	329	0	0	3.0	928
EUX03	18.5	2765	22.0	4463	3.0	511	1.0	200	0	0	2.5	763
EUX04	17.3	2793	16.5	3882	1.5	488	1.0	305	0	0	4.0	1577
EUX05	20.5	2466	16.0	4016	2.5	633	0.5	224	0	0	3.5	750
EUX06	14.5	1389	10.5	2089	1.0	276	3.5	466	0.5	85	3.5	868
EUX07	17.5	3341	9.5	2155	1.5	327	0.5	119	0	0	3.5	1160
EUX08	20.5	2823	13.5	3169	3.0	850	1.5	214	<0.5	45	4.0	1005
EUX09	10.0	1794	7.5	2010	1.0	375	1.0	106	0	0	3.0	767
EUX10	24.0	2188	7.0	1169	1.5	177	1.0	144	0.5	229	1.5	407
All St. Eustatius (mean ± standard error)	17.4 ± 3.9	2277 ± 659	12.3 ± 4.7	2700 ± 1099	1.8 ± 0.6	430 ± 204	1.5 ± 1.2	313 ± 271	0.2 ± 0.3	50 ± 80	3.1 ± 0.8	871 ± 335
St. Maarten												
SXM01	23.0	4237	7.0	3255	1.5	224	1.0	279	0.5	180	1.0	278
SXM02	20.5	2021	8.5	886	4.5	401	3.5	464	0.5	23	0	0
All St. Maarten (mean ± standard error)	21.8 ± 1.8	3129 ± 1567	7.8 ± 1.2	2071 ± 1675	3.0 ± 2.4	313 ± 126	2.3 ± 1.5	371 ± 131	0.5 ± 0.2	101 ± 111	0.5 ± 0.7	139 ± 197
N.A. Region (mean ± standard error)	19.3 ± 7.4	3150 ± 2033	9.3 ± 2.9	2206 ± 332	2.2 ± 0.9	455 ± 143	1.6 ± 0.5	322 ± 33	0.5 ± 0.3	140 ± 101	2.4 ± 1.4	538 ± 302

¹See Table 1 for site names corresponding to site codes.²*Epinephelus* spp. and *Mycteroperca* spp.