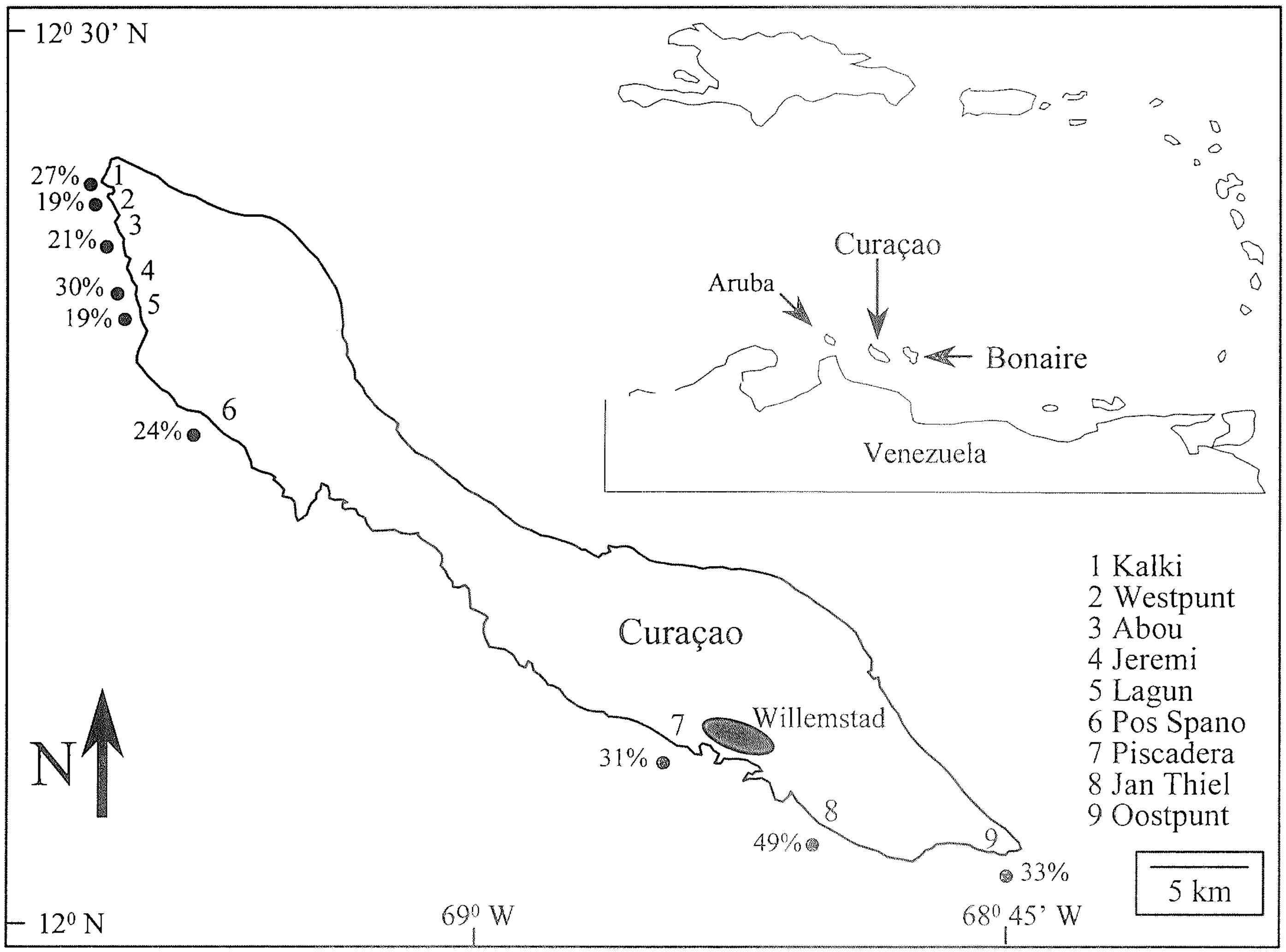

Figure 1. AGRRA survey sites (Kalki, Westpunt, Jeremi, Lagun, Oostpunt) on the leeward coast of Curaçao. Percentages = mean percentage of diseased stony corals (all species and all sizes) in belt transects at 10 m, 15m and 20 m that had been found in 1997 at these sites, and at four other reefs.

CONDITION OF CORAL REEFS OFF LESS DEVELOPED COASTLINES OF CURAÇAO (PART 1: STONY CORALS AND ALGAE)

BY

ANDREW W. BRUCKNER[1] AND ROBIN J. BRUCKNER[2]

ABSTRACT

Coral reefs at 10-20 m depth off eastern and western Curaçao, Netherlands Antilles had high abundance and high cover (25-50%) of stony corals, although the latter declined between 1998 and 2000, primarily from impacts associated with Hurricane Lenny in November 1999 and coral disease. Most corals had lost 15-40% of their live tissues and the amount of partial mortality declined with depth. Little recent mortality was observed (0.6% in 2000). Reefs were dominated by the *Montastraea annularis* species complex (46% of all corals ≥20 cm in diameter), which were 40% larger than other species. Overall, colonies of the *M. annularis* species complex sustained somewhat greater total (recent + old) partial-colony mortality (24%) than other stony corals (19%), and had a higher prevalence of disease. Yellow-blotch disease affected 14.5% of all colonies of the *M. annularis* species complex in January 2000; infected corals had twice as much total partial-colony mortality (44%) as uninfected conspecifics. Shallow reef communities at 8-12 m appear resilient to disturbance, as evidenced by low macroalgal cover, a high abundance of stony coral recruits and juveniles, and declining disease incidence and prevalence overall. However, the high incidence of yellow-blotch disease in the *M. annularis* species complex and the absence of recruits of these species suggests their condition may continue to decline and a shift in species dominance may be underway.

INTRODUCTION

Curaçao, located 60 km north of Venezuela, forms part of the leeward Netherlands Antilles. The small oceanic island (61 km long; 443 km^2 total) is surrounded by fringing coral reefs, which are better developed along the leeward coast. The shallow reef community, which begins 20 m to 250 m from the shoreline, consists of a terrace that slopes gradually seaward to 7-13 m depth and

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then slopes steeply to a sand terrace at 50-60 m (Pors and Nagelkerken, 1998). Twenty-five years ago, the vertical reef profile was characterized as having a shallow *Acropora palmata* zone dominated by elkhorn coral and gorgonians, fields of *Acropora cervicornis* from 4-5 m depth, and a reef slope dominated by the *Montastraea annularis* species complex, *Agaricia* spp. and *Madracis mirabilis* (Bak, 1975). Coral cover and diversity were high on the reef slope, but decreased rapidly below 35-40 m. Fifty-seven species of scleractinian corals were identified by Bak (1975).

The coral reefs surrounding Curaçao are affected by a number of natural and anthropogenic stressors. The island is located south of the hurricane belt and rough seas are rare on the leeward coast. However, tropical storms pass within 200 km of the island about every four to five years, and associated wave surge has caused considerable damage to the shallow reefs (Van Duyl, 1985; Van Veghel and Hoetjes, 1995). Development and industry are concentrated in Willemstad and along the adjacent southeastern, leeward coast where the majority of Curaçao's population (155,000) resides. In these developed areas coral abundance, cover, and species diversity declined precipitously at 10-20 m on fore reefs between 1973 and 1992 (Bak and Nieuwland, 1995). Much of this change was attributed to sewage discharge and to sedimentation associated with beach construction (Bak and Nieuwland, 1995). The island-wide mass mortality of the herbivorous sea urchin *Diadema antillarum* in 1983 also contributed to a general decrease in the cover of live corals and coralline algae, while turf algae and macroalgae increased in abundance (Bak et al., 1984; De Ruyter van Steveninck and Bak, 1986). Branching acroporids (*A. palmata*, *A. cervicornis*) suffered high mortality in 1980 and 1981 from white-band disease (WBD) (Bak and Criens, 1981; Van Duyl, 1985), but other stony coral diseases were only minor sources of mortality (Bak and Nieuwland, 1995). Bleaching events occurred in 1987 (Williams and Bunkley-Williams, 1990), 1990 (Meesters and Bak, 1993), 1995 (CARICOMP, 1997) and 1998 (A. Bruckner, unpublished data). Yellow-blotch disease (YBD) was first noticed in late 1995 as colonies of the *M. annularis* species complex began to recover from the mass bleaching event. It is not known whether colonies with YBD had bleached during this event (P. Hoetjes, pers. comm.).

While Curaçao's reefs clearly have degraded near its population center, its eastern and western coasts are relatively unaffected by pollution or sedimentation and their reefs are thought to be in better condition (Van Veghel, 1997). Subsistence fishers occur throughout the island, and although spearfishing and coral collection were prohibited in 1976 regulations were not enforced until 1998. The Curaçao Underwater Park, established in 1983 and extending 21 km from the outskirts of Willemstad to the eastern tip of the island, includes a 12 km stretch of coastline that is undeveloped and uninhabited. In total, the park encompasses 600 hectares of coral reef habitat and 436 hectares of inner bays. Hook-and-line fishing is allowed within the park, but spearfishing and anchoring are prohibited. All dive sites have mooring buoys. A Caribbean Coastal Marine Productivity CARICOMP) coral reef site has been monitored here at Spaanse Water since 1994. Lagun and Westpunt are two small communities at the western end of Curaçao where there is no industry and very limited coastal development. A second underwater park has been proposed for these reefs (Banda Abao reef complex).

The purpose of this study was to utilize the Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol to characterize the reefs off the eastern and western ends of Curaçao, in particular to determine whether diseases are an important factor contributing to coral mortality in the absence of significant human activities. Our data suggest that coral diseases have become more prevalent on Curaçao's reefs during the late 1990s and that one disease in particular is causing significant partial mortality to the most abundant and most important of its reef-building corals. Another unexpected source of mortality was attributed to wave energy associated with Hurricane Lenny in October, 1999. Fish assessments made in June 2000 are reported separately in Bruckner and Bruckner (this volume).

METHODS

Baseline data were initially obtained in June 1997 by tallying the total number of healthy and diseased colonies of each species of stony coral (scleractinian corals and hydrozoan fire corals) observed within belt transects (2 m wide x 30 m long; 1-4 transects/site) along depth gradients (at 10, 15, 20 m) for nine leeward reefs (Fig. 1). In August 1998 and January 2000, detailed reexaminations were conducted at strategically chosen sites on the less populated eastern and western coasts using the AGGRA Version 2 benthos protocol (Appendix One, this volume), with the following modifications. The minimum diameter of assessed corals was 20 cm and size measurements were recorded to the nearest 5 cm. Smaller colonies of reef-building corals (5-20 cm) were tallied and recorded to species. Scleractinian recruits, defined as <2.5 cm diameter, were recorded to genus only (except for *Montastraea cavernosa)*, omitting taxa that do not obtain a large size (e.g., *Scolymia* spp., *Favia fragum*). Colonies of the *Montastraea annularis* species complex were separated according to Weil and Knowlton (1994) as *M. annularis*, *M. faveolata* or *M. franksi*. Forms or morphotypes of *Agaricia agaricites*, *Colpophyllia natans, Meandrina meandrites* and *Porites porites* were combined under the respective species. Encrusting forms of *Madracis* were recorded as *M. decactis.*

Recent mortality was defined in this study as any tissue loss occurring within approximately the last 60 days, and signs included: (1) white coral skeleton that lacked algae (surfaces denuded of tissue within the last five-seven days); (2) skeletal areas with readily recognizable corallites that had not been substantially eroded but were colonized by green filamentous algae; or (3) white, exposed skeletal surfaces, or eroded skeletal surfaces with fine filamentous algae that had been physically abraded by fish or other agents but had not yet been colonized by macroalgae or coralline algae. Causes of recent mortality were identified as disease [separated into WBD, YBD, black-band disease (BBD), white plague (WP), dark-spots disease (DSD) or other diseases], corallivory [fish bites, damselfish (*Stegastes planifrons*) algal lawns, or snail predation], overgrowth by algae or an invertebrate (cnidarian, sponge or tunicate), or were recorded as unknown. In January 2000, when toppled corals were observed throughout the reefs, especially at 8-12 m, colonies that had become stabilized were measured and described as above, but were tallied as overturned. The long-dead portions that had been recently exposed through toppling were recorded as old mortality; only skeletal areas that met the criteria described above as recent mortality were tallied as such. Dislodged or overturned corals that had not become stabilized were not included in this survey. To standardize observations, all measurements of mortality were performed by the first author and algal quadrats were completed by the second author. Both authors collected information on colony size. All corals along two pilot transects (Lagun and Jeremi, 10 m length) were measured by both authors and measurements were discussed and compared to ensure consistency prior to the actual surveys.

All statistical analyses were performed with the Systat (version 9.0) program. Comparisons among species, locations, and depths were made using a student's *t*-test (for examination of the *M. annularis* species complex versus all other species pooled) or ANOVA (single-factor or two-factor) and correlations were examined with a Pearson product-moment test. A one- or two-factor ANOVA was also used to examine for differences in coral composition, size frequency distribution and percent partial mortality, surveys from different years on western reefs or between eastern and western reefs. When relevant, post-hoc analyses were performed using a Tukey HSD multiple comparison test. For these tests, coral species were lumped into the following six groups based on colony abundance, mean colony size, susceptibility to disease or predation, colony morphology or sexual reproductive character: (1) *C. natans*; (2) the *M. annularis* species complex; (3) other broadcast spawners with massive morphologies (*Diploria* spp., *M. cavernosa*, *Siderastrea siderea*, *Stephanocoenia intersepta*); (4) small branching corals (*P. porites* species complex, *Eusmilia fastigiata* and *Madracis* spp.); (5) *Agaricia* spp.; and 6) other species (*Porites astreoides*, *M. meandrites*, *Mycetophyllia* spp., *Mussa angulosa)*. Data were checked graphically to assure that all assumptions of ANOVA were met; log-transformation for length measurements and arc-sine transformation for percentages were used as appropriate prior to analyses.

RESULTS

Stony Corals

AGRRA surveys were performed at 9-13 m on the reef terrace at one eastern (Oostpunt) and three western (Kalki, Jeremi, Lagun) sites during August 1998 (Table 1). Further surveys were made at four western sites (Kalki, Westpunt, Jeremi, Lagun) two months after Hurricane Lenny in January 2000, at ~10 m on the reef terrace and to a maximum depth of ~20 m on the reef slope.

Reefs at 10-20 m were characterized by 18-24 species of scleractinian corals (at least 20 cm in diameter) and the hydrozoan *Millepora complenata*, but were dominated by the *Montastraea annularis* species complex, *Agaricia agaricites*, *Montastraea cavernosa*, *Colpophyllia natans* (Fig. 2) and, at 15-20 m, by *A. lamarki* and *Stephanocoenia intersepta*. In 1998, species composition at 10 m in the six pooled coral groups (see Methods) did not differ among locations (ANOVA, p=0.09). Numerically the most abundant corals at all sites and depths (46% of total) belonged to the *M. annularis* species complex which collectively are the primary live cover and structural element of Curaçao's fringing reefs. At the western sites 70% of all corals at 10 m depth consisted of the *M. annularis* species complex, with *M. faveolata* >*M. annularis*>*M. franksi*; 35-42% of all corals at 15 and 20 m (respectively) consisted of these species, with *M. faveolata*>*M. franksi* > *M. annularis*. Similarly, 40% of the corals examined at 10 m in Oostpunt were *M. annularis* and *M. faveolata*.

Small, isolated colonies of *Acropora cervicornis* (staghorn coral) and numerous patches of dead staghorn rubble were identified between colonies of the *M. annularis* species complex within transect areas at Oostpunt. On western reefs, the substratum at 7-10 m depth often consisted of dead, consolidated staghorn rubble, but live colonies of *A. cervicornis* were not observed within transect areas nor in the surrounding reefs. Shallow areas (2-4 m) outside of transect areas at Oostpunt had a low abundance of live *A. palmata*. This species was rare or absent in other locations, and the shallows (0-5 m) were nearly devoid of living coral. Large patches of *Madracis mirabilis*, a number of which were several meters in diameter, occurred in 10-15 m on the Kalki reef, and less frequently at other locations.

Colony density (for stony corals of ≥20 cm diameter) generally ranged from 1.3-2.1 corals per meter (Table 1); data from 2000 indicates that colony density increased with depth (r^2=0.61; p=0.0016). Coral cover varied among locations, depths and years. In 1998, coral cover ranged from about 20-40% along transects at 10 m depth and was greatest off Kalki. Coral cover at the same depth was substantially lower on the western reefs in January 2000, except for Jeremi, where high variation among the transects, and the presence of several large colonies of *M. faveolata*, may have skewed its mean value (Table 1). The greatest decline in live cover was observed at Kalki where most corals had been removed at 2-12 m from the reef terrace by wave surge. Overall, coral coverage was greater at 15-20 m on reef slopes (Table 1) with the highest percentage occurring at 20 m on Jeremi Reef (49%). Live coral cover was lowest off Westpunt even though this site was minimally impacted by Lenny. Westpunt Reef terminates in sand at 15 m and living corals are absent below this depth.

Transects performed on western reefs in 1998 and 2000 were similar in composition (two-factor ANOVA; p=0.59) and diameter of corals (p=0.54), with no interaction between years and species (p=0.79) with respect to coral size. Colony size recorded during 1998 in the six pooled coral groups did not differ among locations (ANOVA, p=0.91). Coral diameter did, however, differ among

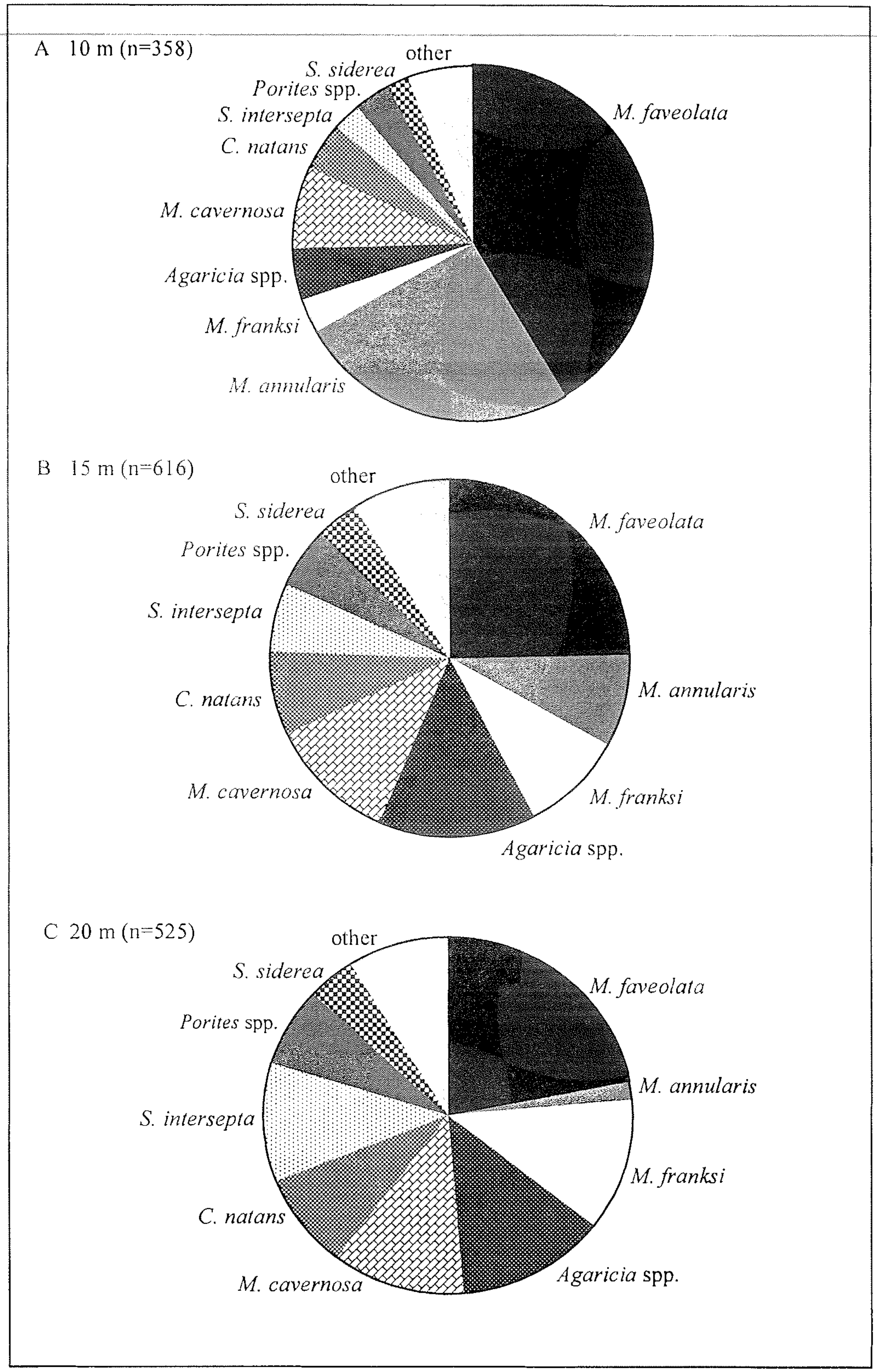

Figure 2. Species composition and mean relative abundance of all stony corals (>20 cm diameter) in January 2000 at (**A**) 10 m, (**B**) 15 m, (**C**) 20 m, in western Curaçao.

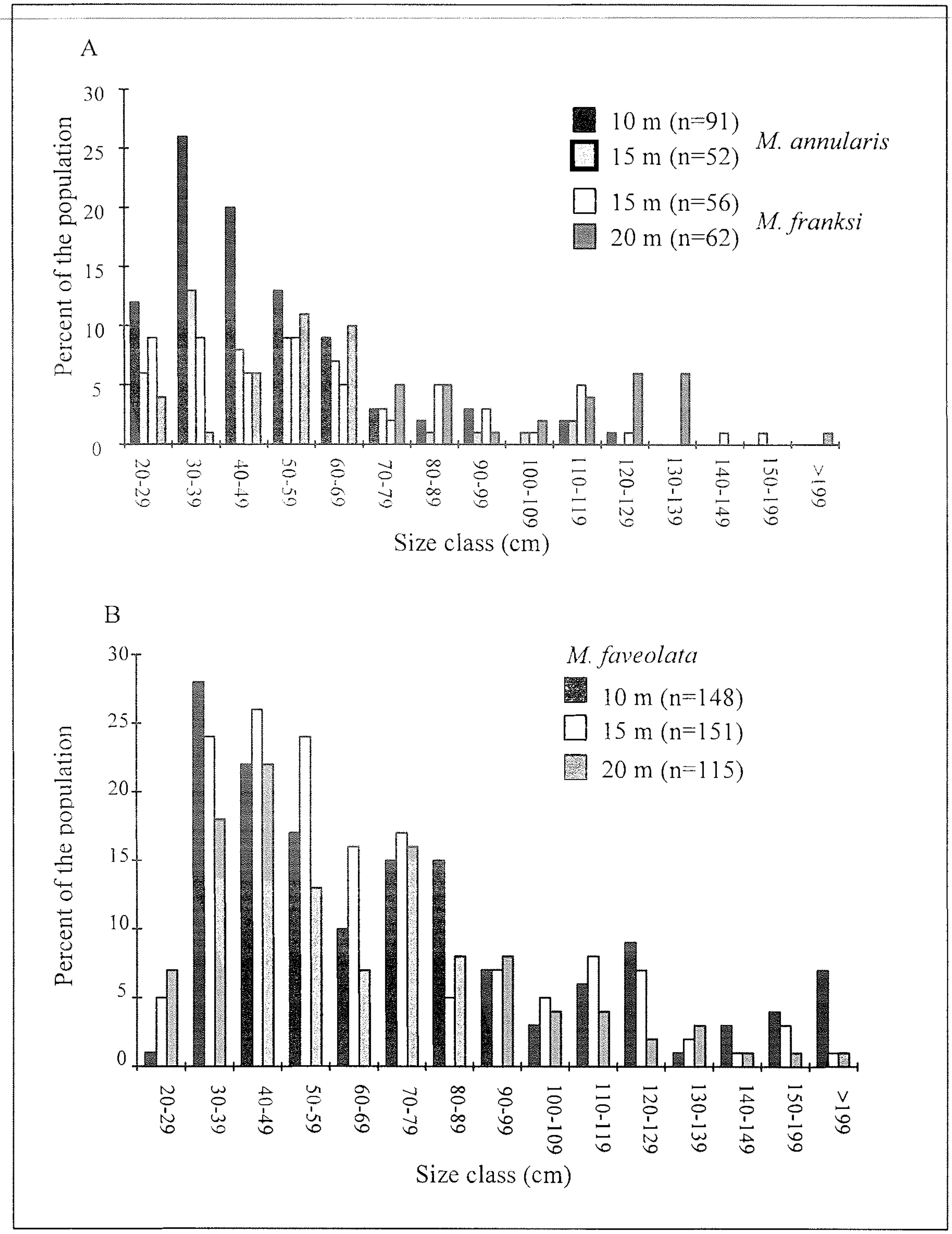

Figure 3. Size-frequency distribution of colonies ($\geq$20 cm diameter) in Janaury 2000 of (**A**) *Montastraea annularis* (10 m, 15 m) and *M. franksi* (at 15 m, 20 m), (**B**) *M. faveolata* (at 10 m, 15 m, 20 m) in western Curaçao.

the species groups (two-factor ANOVA; $P<0.001$) and an interaction between diameter and location was observed ($P=0.009$). The largest colonies observed within transect areas were *M. faveolata* and *C. natans,* while most of the brooding species (e.g., *Agaricia* spp. and *Porites* spp.) showed a predominance of the smaller size classes. In January 2000, a large number of the smaller colonies, especially *M. annularis,* were overturned or displaced. The effects of the storm were highly localized, however, as deeper areas and larger corals were minimally impacted. Most corals examined in January 2000 were intermediate in size (30-80 cm diameter, mean=53 cm, n=1501; Fig. 3). Colonies of the *M. annularis* species complex were significantly larger in diameter (mean=63 cm) than all other species combined (mean=45 cm) (all depths pooled; t-test, $t=12.5$, $df=1497$, $p<0.001$). In addition, colonies of *M. faveolata* and *M. franksi* (mean=67 cm) were larger than *M. annularis* (mean=46 cm; ANOVA, MS=1.13, $F=24.7$, $p<0.001$), but no differences were noted among *M. faveolata* and *M. franksi*. Colony size did not differ among depths for the *M. annularis* species complex (ANOVA, MS=0.11, $F=2.35$, $p=0.095$) or other species (ANOVA, MS=0.03, $F=1.01$, $p=0.36$).

Small corals (5-20 cm diameter) recorded in 1998 along transects (mean abundance=0.5/meter, range=3-9/10 m) consisted predominantly of *A. agaricites* (1.3/10 m), *P. porites* (0.6/10 m), *M. annularis* (0.5/10 m), *M. meandrites* (0.5/10 m), *M. mirabilis* (0.5/10 m) and 16 other species (Fig. 4A). A low abundance of recruits (<2.5 cm diameter) was identified within quadrats at 10 m depth (0.5 - 0.7 recruits/0.0625 m^2) in 1998 (Table 3), most individuals of which were brooders including *Agaricia* and *Porites*. However, broadcasters like *M. cavernosa*, *Dichocoenia, Colpophyllia*, *Stephanocoenia* and *Meandrina* were also observed (Fig. 4B). An absence of recruits of the *M. annularis* species complex was noted, even though these were the dominant corals on all reefs. Recruits were also recorded in 2000 but lower numbers were seen (mean=0.12 recruits/0.0625m^2 at 10 m depth). In shallow transects (9-12 m), recruits were not observed on reef substrata with a high cover of macroalgae (Jeremi and Lagun) or on substrates that had been exposed relatively recently (e.g., at Kalki). Recruits were observed on long-dead coral skeletons and reef substrata not directly affected by the hurricane with a higher number at 15 m on reef substrata (up to five recruits/0.0625m^2 mean=0.61) than on denuded coral (especially *M. faveolata*, *M. annularis*, *M. franksi*) skeletons (mean=0.13) (t test, $t=3.5$; $df=108$; $p<0.001$).

Coral Condition

In this study we examined the condition of 1,939 scleractinian and hydrozoan reef-building corals (1998 and 2000, all sites and depths pooled). Overall, in 32% of all corals total (recent + old) partial-colony mortality (hereafter total partial mortality) affected less than 10% of their planar surface area. Mean values of total partial mortality at each site (all corals pooled, 1998 and 2000) ranged from 15-32% with less than 20% of all corals missing more than half their tissues (Fig. 5). Distinct differences in percent total partial mortality were also noted among the six species groups (all years and depths are pooled, $p<0.001$).

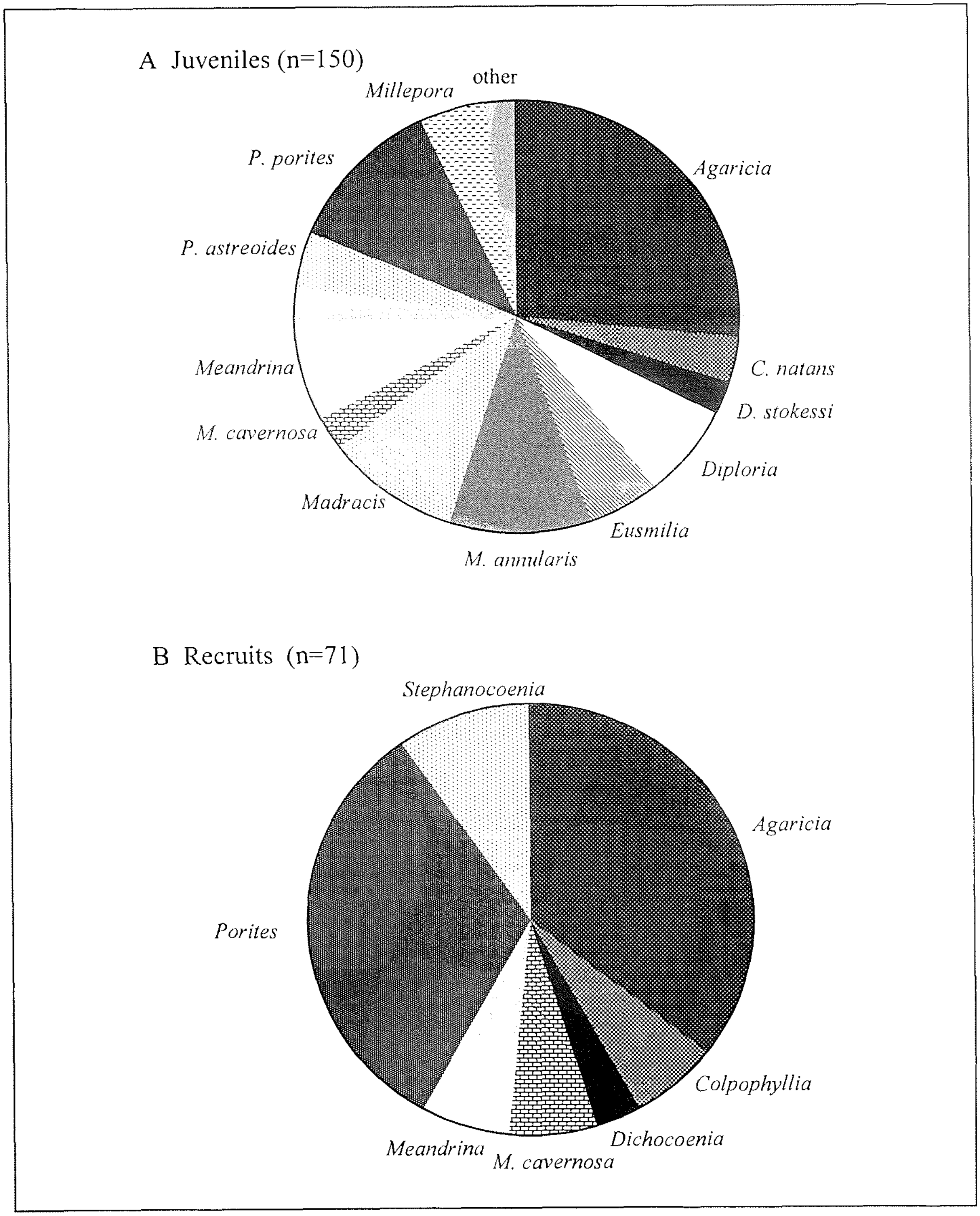

Figure 4. Species composition and mean relative abundance in August 1998 of (**A**) all "juvenile" (5-20 cm diameter) stony corals and (**B**) all recruits (<2.5 cm diameter, excluding species that are small as adults) at 10 m, 15 m and 20 m in western (four sites) and eastern (one site) Curaçao.

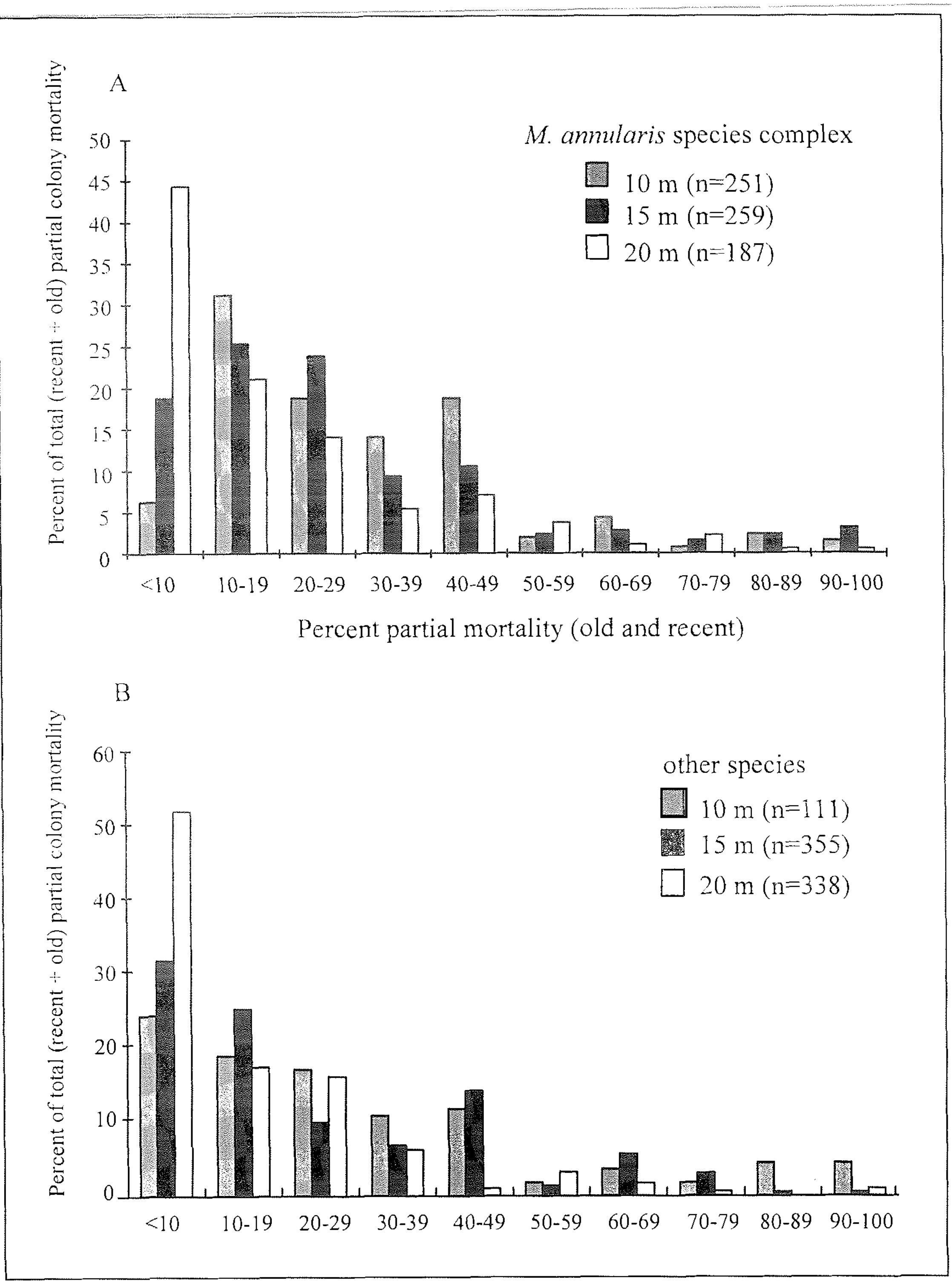

Figure 5. Frequency distribution in January 2000 of total (recent + old) partial colony mortality of all colonies (≥20 cm diameter) of (**A**) the *Montastraea annularis* species complex, (**B**) other species, in western Curaçao.

From 20-40% of each small clump of *A. cervicornis* consisted of dead branches. Colonies of the widely distributed *M. annularis* species complex overall exhibited a significantly greater amount of total partial mortality than all other species (pooled) except *A. cervicornis* (all sites, depths and years are pooled, mean partial mortality=24%; t-test, t=6.2, df=1497, p<0.0001). No relationship was observed between percent tissue loss and colony diameter for the *M. annularis* species complex (r^2= 0.002; p=0.28) or other pooled species (r^2=0.04), possibly due to the high amount of variation observed within each size class.

In 1998, the amount of total partial mortality in the six pooled species groups was found to vary among species (two-factor ANOVA; P<0.001), with minor differences among locations (p=0.066) and a significant species-location interaction with respect to total partial mortality (p<0.001). Total partial mortality was greatest among the *M. annularis* species complex and branching corals (*Porites porites, Eusmilia fastigiata, Madracis* spp.) while the group of brooding species had the lowest percentage (Tukey test). Post-hoc analysis indicates that total partial mortality in 1998 was slightly higher on western reefs (21% versus 19% at Oostpunt), yet the greatest amount overall (35%) was recorded for the *M. annularis* species complex at Oostpunt.

In 2000, a large number of small-to-intermediate-sized corals were dislodged or overturned in shallow water (7-13 m depth), and numerous unattached colonies had been transported down the reef slope to 15-20 m or deeper. Overturned colonies identified along transects that were 20 cm or larger had a mean size of 49.5 cm (maximum=160 cm). Overturned colonies were substantially larger on Jeremi (mean=60.5 cm) than on Lagun (mean=39.5 cm), but the total proportion of overturned colonies versus those that were unaffected was higher at Lagun (26%) than on Jeremi (20%). A small number (<3% of all corals examined) experienced total partial mortality; most of the corals that survived had sustained a low amount of recent partial-colony mortality (hereafter recent mortality) with the exception of areas on the colony now in contact with the substrata. The amount of total partial mortality in 2000 varied significantly among depths for the *M. annularis* species complex (ANOVA, MS=5628, F=24.8, p<0.001) and other species (ANOVA, MS=4103, F=13.2, p<0.001) with the greatest loss at 10 m depth and the least at 20 m (Table 2). Whereas the amount of recent mortality at 10 m on western reefs was greater in 1998 than 2000 (3.7% versus 0.6% of colony surfaces, respectively), the amount of total partial mortality at 10 m was significantly greater in 2000 (mean=29%) than in 1998 (mean=21%; two-factor ANOVA, p=0.003). Minor differences in percent total partial mortality were noted among the six species groups (p=0.06) but there was no interaction between the survey period and species (p=0.175). Overall, *S. intersepta*, the *M. annularis* species complex, *S. siderea* and *E. fastigiata* respectively exhibited the greatest amount of total partial mortality (22-31%), while the lowest values were observed in *M. meandrites*, *D. strigosa*, *D. stokesii*, *P. astreoides* and *P. porites* (10-13%). The other dominant species (*C. natans*, *M. cavernosa*, and *Agaricia* spp.) exhibited 17-19% total partial mortality.

The most common sources of recent mortality were coral diseases, in particular YBD, DSD, WP, WBD and red-band disease (Table 4). On all reefs, a high percentage of the *M. annularis* species complex exhibited signs of YBD; this condition was not recorded in other taxa. WBD was only observed at the Oostpunt, susceptible aeroporid corals being absent at the western sites. A high prevalence of DSD was noted in 2000. It is not known whether DSD was common in 1998 because the affected species (*S. intersepta*, *S. siderea*) were predominantly recorded at 15 and 20 m, at depths which had not been surveyed in 1998.

Coral diseases appeared to be most common in 1997 (Bruckner and Bruckner, 1999; unpublished data), and have since declined. The highest prevalence of YBD was observed along the east coast, near Willemstad (30.6% of the 264 colonies of the *M. annularis* species complex examined at Piscadera; 49%, N=165 at Jan Thiel) and at Oostpunt (37.5%, N=474), with fewer infections seen off the western coast (24%, N=607). In 1998 fewer infections were observed in western sites at 10 m depth (15.6-19.2% of the *M. annularis* species complex) while Oostpunt had a higher prevalence of YBD (68% of all colonies of the *M. annularis* species complex). Although the occurrence of new YBD infections was lower in January 2000 on western reefs, many older infections still plagued colonies (total=14.5% of 698 of the *M. annularis* species complex) as indicated by the large amount of partial mortality immediately adjacent to the YBD-affected tissues. Moreover, colonies of the *M. annularis* species complex with YBD had lost a significantly greater percentage of their tissues than had unaffected conspecifics (mean loss=44% versus 20%, respectively; t-test, t=10.6, df=127, p<0.0001; Fig. 6A) and were larger in size (mean diameter=72 cm) than uninfected corals (61 cm). Diameter was correlated to incidence of YBD (r^2=0.45, p=0.0001): 25% of all colonies greater than 0.5 m diameter were infected, versus only 7% of the smaller colonies (Fig. 6B). BBD and WP were also more prevalent during the summer of 1998 (3.6%) than in January 2000 (0.1%); however, these differences may relate to seasonal variations associated with water temperature rather than an overall decline in disease.

An additional source of coral mortality was attributed to predation. Stoplight parrotfish (*Sparisoma viride*) bites were observed on all reefs. Focused biting was primarily observed among *M. annularis* and *C. natans* and spot-biting affected these and 12 other species. Overall, the most extensive skeletal and tissue destruction from *S. viride* occurred on *M. annularis* (9.8% of all colonies) at 10 m in Oostpunt in 1998. Lesions from fish bites were very common in 1997 and 1998 (4.4% of all colonies of *M. annularis*), and affected 2.2% of all colonies examined at 10 m depth in 1998. Although fewer colonies appeared to be affected by fish predation on western reefs in 2000, affected colonies were highly aggregated and areas exhibiting focused biting in 1998 also had affected colonies in 2000. Predation by the snail *Coralliophila abbreviata* (in 5/14 surveys) and overgrowth by sponges and the tunicate *Trididemnum solidum* (4/14 surveys) were also noted (Table 4).

Bleaching was not recorded during the August 1998 and January 2000 surveys. However, bleached colonies were observed in November 1998, primarily among *Agaricia* spp. and the *M. annularis* species complex (personal observations). During this bleaching event about 30% of the *M. annularis* species complex became pale, especially on their upper surfaces, but did not turn

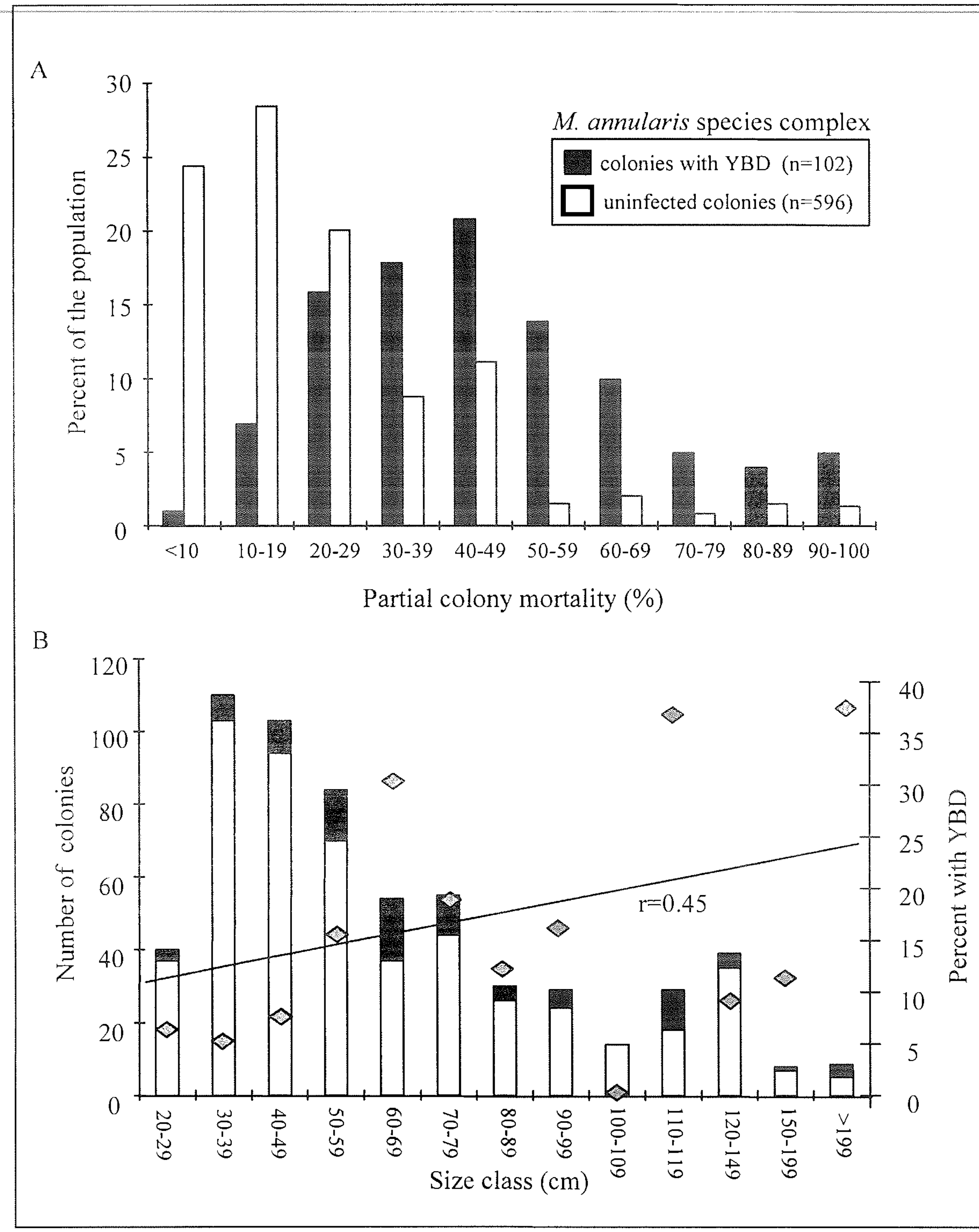

Figure 6. Relationship between the presence (or absence) in January 2000 of YBD and (**A**) percent of total (recent + old) partial colony mortality, (**B**) size frequency distribution, for the *M. annularis* species complex (≥20 cm diameter) in western Curaçao. Data are pooled from 10 m, 15 m and 20 m. Grey diamonds in (**B**) indicate the percent of each size class affected by YBD; a best fit line and r-value are presented.

completely white. Approximately 80% of all colonies of *A. lamarki* in deeper water (18-25 m depth) were completely bleached (white). Bleaching affected other species but was less prevalent. We tagged and photographed 30 of these corals (*A. lamarki* and the *M. annularis* species complex) in November 1999 and reexamined them in January 2000. Over 75% (n=26) of these regained full pigmentation and did not experience any mortality. In the other four colonies, tissue mortality affecting 5-30% of the surface of each plate was noted but the remaining live tissues had regained most pigmentation.

Algae

Algal communities at 10 m in 1998 were dominated by crustose coralline algae (50 %) and sparse turf algae (38 %) that did not trap considerable amounts of sediment. Macroalgae were codominant on exposed coral skeletons and at the bases of coral heads (Table 3). Where present, macroalgae consisted primarily of *Dictyota* spp., *Halimeda* spp. and *Lobophora variegata*, and were usually less than 1.5 cm in height. The algal community was very different in January 2000, possibly due to the effects of Hurricane Lenny two months previously. At Kalki, the newly exposed reef substrata consisted primarily of cemented *A. cervicornis* skeletons that were being colonized by fine filamentous turf algae; macroalgae and crustose corallines were rare. Mats of cyanobacteria, which had been observed here and at Jeremi in August 1998, were uncommon at both sites. At Lagun, Jeremi and Westpunt, a dense growth of red algae (*Liagora* spp., *Trichogloea* spp., *Trichogloeopsis pedicellata* and other similar fleshy algae; mean height 5 ± 21.5 cm) occupied much of the exposed substrata in January 2000. On Jeremi, these algae occupied 43% of open substrata at 10 m depth but were not growing on living corals. Dead coral surfaces (i.e., areas on colonies denuded of tissue) had similar algal communities in 1998 and 2000 composed predominantly of fine filamentous turfs and crustose corallines with sparse macroalgae. In most cases, patches of macroalgae (*Dictyota* spp, *Lobophora* spp. and *Halimeda)* occurred at the base of coral heads, between lobes of living coral, and in crevices, while up to 80% of the exposed surfaces were colonized by turfs and crustose coralline algae. *Diadema antillarum* was not observed along transects, although signs of grazing were apparent on exposed coral surfaces and herbivorous fish (mean densities in 1998: surgeonfish, 5/100 m^2 and parrotfish, 4/100 m^2) were recorded in belt transects (30 m long x 2 m wide) (Bruckner and Bruckner, this volume).

DISCUSSION

Coral reefs examined off Curaçao in 1998 and 2000 were dominated by intermediate to large-sized massive scleractinian taxa, including *M. faveolata*, *M. annularis*, *M. franksi*, *S. intersepta*, *S. siderea and C. natans,* and smaller colonies of *P. astreoides* and *A. agaricites*. *Acropora palmata* and *A. cervicornis* were prevalent in the 1970s, declined in the early 1980s as a result of a regional disease epizootic (Van Duyl, 1985), and were uncommon (Oostpunt, Jan Thiel, Piscadera) or were not observed (western reefs) during these surveys. Living coral cover ranged from 17-49% with the exception of one shallow site on the western coast that lost >95% of its live stony corals as a result of a hurricane in 1999. Most colonies over 20 cm (69%) had experienced total partial mortality that affected at least 10% of their planar surface area, with a mean tissue loss in all colonies of 22%. The major sources of mortality noted in this study were coral diseases (prevalent in all sites and years) and hurricane damage (affecting western reefs in 2000). *Diadema antillarum* was rare or absent in all sites but a low abundance of macroalgae and turf algae suggests that herbivorous fish are effectively controlling algal populations.

In general, the eastern reefs were in poorer condition than the western reefs. A precipitous decline in coral abundance, cover, and species diversity had been reported on reefs near Willemsted in previous studies (e.g., Bak and Nieuwland, 1995). In 1997, these areas had the highest prevalence of disease with up to 49% of the $\geq$20 cm diameter colonies affected in one location. Oostpunt, a protected area located off the uninhabited eastern end of Curaçao, was reported to be in good shape as recently as 1995 (Van Veghl, 1997). This site experienced a mass bleaching event in the fall of 1995 and present surveys revealed a high incidence of disease in 1997 (38%) and 1998 (21%) and other biotic disturbances (especially focused biting by *S. viride*). Colonies at this site had also sustained a higher percentage of total partial mortality, and there were more entirely dead colonies, than observed at the same depth on western reefs.

The amount of total partial mortality differed among species, and was highest in the slowly reproducing, large, massive broadcasters *(M. annularis* species complex, *S. siderea, S. intersepta, C. natans)* that dominated eastern and western reefs. In particular, colonies of the *M. annularis* species complex, which were the most abundant and largest corals at all sites and depths, had experienced a high degree of total partial mortality. They were also affected most severely by disease: between 7-49% of all colonies were observed with signs of disease in surveys conducted in 1997, 1998 and 2000. The main disease affecting the *M. annularis* species complex was YBD, a condition that causes relatively slow rates of mortality (1-2 cm spread per month), but may affect individual colonies for several years (Bruckner and Bruckner, 2000).

The prevalence of large colonies of the *M. annularis* species complex that are hundreds of year old and few colonies less than 30 cm in diameter suggests that recruitment events of significance have not occurred among these species in several decades. These large, ecologically-dominant colonies have exhibited high rates of survivorship, and are presumably well adapted to deal with chronic disturbances such as predation, bioerosion and disease (Bythell et al., 1993). However, this may no longer be the case for these reefs as recent disease epizootics have primarily plagued these species. Overall, larger colonies of the *M. annularis* species complex were infected with YBD more frequently than small colonies. In addition, colonies with active signs of YBD have lost a mean of 44% of their tissue area in January 2000 or roughly twice that of uninfected colonies of the same species. Chronic YBD infections on these reefs may have serious ramifications for the persistence of the *M. annularis* species complex, as continued tissue loss and fission may significantly reduce the reproductive potential of these colonies and the proportion of small, non-breeding colonies in the population may increase. Furthermore, several decades or more may be required for their replacement because of their slow rate of growth, delayed reproduction, and infrequent, episodic recruitment (Szmant, 1991).

Although coral reefs surveyed in this study have a high prevalence of coral disease and have been impacted by a recent hurricane, Curacao's reefs appear to be relatively resilient to recent disturbances and have a high potential for continued growth and sexual recruitment. Crustose coralline algae are prevalent on exposed reef substrata; macroalgae and turf algae have remained sparse with the exception of a benthic algal bloom in shallow water that lasted for three months after Hurricane Lenny and has since disappeared. Most locations have relatively high cover of live coral (over 25%), a high abundance of small corals less than 20 cm (3-9/10 m) and new recruits are present (0.5-0.7 recruits/.0625 m^2). Longer-term effects associated with the hurricane appear to be minimal. Most colonies overturned during Lenny have become stabilized; fragmented and overturned corals contained substantial amounts of surviving tissue which were not diseased, bleached or injured. In addition, surveys from January 2000 indicate that the number of active and new YBD infections have declined and other diseases were less abundant.

Reefs at the western end of the island have experienced coral mortality as a result of disease and hurricane damage but ensuing mortality appears to be declining, coral cover remains high and remaining corals are in relatively good condition. In light of an ongoing accelerated decline of reefs located near human population centers, including those off populated coastlines of southeastern Curaçao (Bak and Nieuwland, 1995), conservation efforts should be directed towards the island's more remote western end. The western reefs may serve as a refuge for important reef-building species and a source of larvae for these and other reefs down current. Recent prohibitions on spearfishing, along with the proposed establishment of a marine park for western Curaçao, are two steps forward that may help ensure the long-term persistence of its reef ecosystems.

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Table 1. Site information for AGRRA stony coral and algal surveys off Curaçao, Netherlands Antilles. *1998 sites are italicized.*

Site name	Reef type	Latitude (N° ' ")	Longitude (W° ' ")	Survey date	Depth (m)	Benthic transects (#)	>20 cm stony corals (# /10 m)	% live stony coral cover (mean ± se)
Eastern								
Oostpunt	*Fringing*	*12 01*	*68 44 59.8*	*Aug 15 98*	*10*	*7*	*15*	*27 ± 2.9*
Western								
Lagun	Fringing	12 19 6.9	69 09 54.0	*Aug 13 98*	*10*	*9*	*13*	*25 ± 3.0*
				Jan 13 00	10	9	14	17 ± 1.5
				Jan 12 00	15	9	16	38 ± 4.5
				Jan 10 00	20	9	18	35 ± 1.2
Jeremi	Fringing	12 19 44.3	69 09 1.2	*Aug 14 98*	*10*	*7*	*16*	*31 ± 3.9*
				Jan 10 00	10	9	17	29 ± 1.5
				Jan 14 00	15	9	19	36 ± 3.7
				Jan 12 00	20	9	21	49 ± 1.9
Westpunt	Fringing	12 21 37.2	69 09 42.1	Jan 14 00	10	6	13	21 ± 1.6
				Jan 14 00	15	9	16	25 ± 1.4
Kalki	Fringing	12 22 31.3	69 09 29.8	*Aug 14 98*	*10*	*7*	*15*	*40 ± 4.1*
				Jan 13 00	10	6	0.8	1.6 ± 0.9
				Jan 13 00	15	9	17	37 ± 1.8
				Jan 11 00	20	9	18	38 ± 2.1

Table 2. Size and condition (mean ± standard error) of all stony corals (≥20 cm diameter), by site off Curaçao.

Site name	Year	Depth (m)	Stony corals (#)	Stony corals Diameter (cm)	Partial-colony surface mortality (%) Recent	Old	Total	Stony corals (%) Standing dead	Diseased	with Damsefish
Eastern										
Oostpunt	*1998*	*10*	*110*	*56 ± 3.8*	*3.5 ± 0.6*	*16 ± 2.3*	*19 ± 2.5*	*7*	*21.5*	*3*
Western										
Lagun	*1998*	*10*	*118*	*51 ± 2.0*	*2.0 ± 0.4*	*17 ± 2.0*	*19 ± 2.3*	*2*	*10*	*1*
	2000	10	131	49 ± 2.2	0.5 ± 0.2	27 ± 1.9	28 ± 1.9	0	15	1
	2000	15	145	57 ± 2.6	0.5 ± 0.2	23 ± 2.0	24 ± 2.0	2	7	0.5
	2000	20	165	52 ± 1.7	0.5 ± 0.2	16 ± 1.4	17 ± 1.4	2	8	2.5
Jeremi	*1998*	*10*	*110*	*53 ± 2.7*	*3.0 ± 0.8*	*22 ± 2.1*	*25 ± 2.3*	*2*	*12*	*0*
	2000	10	152	64 ± 3.7	0.5 ± 0.1	28 ± 1.7	29 ± 1.7	0	9.5	3.5
	2000	15	171	47 ± 2.1	0.5 ± 0.2	21 ± 1.3	22 ± 1.4	0	8	0.5
	2000	20	191	51 ± 2.1	0.5 ± 0.1	16 ± 1.4	17 ± 1.4	1	8	4.5
Westpunt	2000	10	79	60 ± 4.3	0.5 ± 0.2	29 ± 2.5	30 ± 2.5	0	10.5	0.5
	2000	15	142	53 ± 2.2	1.0 ± 0.3	25 ± 1.9	26 ± 1.9	0	8	12
Kalki	*1998*	*10*	*107*	*54 ± 3.3*	*3.0 ± 0.5*	*16 ± 2.0*	*19 ± 2.2*	*0*	*16*	*17*
	2000	15	156	53 ± 2.3	1.0 ± 0.2	18 ± 1.6	19 ± 1.6	0	10.5	3.5
	2000	20	169	54 ± 2.6	0.5 ± 0.9	16 ± 1.5	17 ± 1.5	0	11.5	0.5
All sites	*1998*	*10*	*445*	*53 ± 1.8*	*3.0 ± 0.5*	*18 ± 1.1*	*21 ± 1.2*	*3*	*14.6*	*5*
Western sites	*1998*	*10*	*335*	*52 ± 1.6*	*2.7 ± 0.3*	*19 ± 1.2*	*21 ± 1.3*	*1*	*12.5*	*6.3*
	2000	10	362	57 ± 2.0	0.6 ± 0.3	28 ± 1.1	28 ± 1.1	0	11.4	2
	2000	10-20	1501	53 ± 0.8	0.6 ± 0.1	21 ± 0.5	22 ± 0.6	0.3	9.4	3

Table 3. Algal characteristics and stony coral recruit abundance (mean ± standard error), by site off Curaçao.

Site name	Year	Depth	Quadrats (#)	Relative abundance (%) Macroalgae	Relative abundance (%) Turf algae	Relative abundance (%) Crustose coralline alage	Macroalgal Height	Macroalgal Index[2]	Recruits (#/.0625 m²)
Eastern									
Oostpunt	*1998*	*10*	*30*	*15 ± 4.1*	*38 ± 6.0*	*47 ± 5.9*	*1.3 ± 0.1*	*15*	*0.50 ± 0.15*
Western									
Lagun	*1998*	*10*	*35*	*14 ± 2.6*	*35 ± 4.5*	*52 ± 4.1*	*1.2 ± 0.1*	*16*	*0.74 ± 0.17*
	2000	10	16	23 ± 5.1	53 ± 6.8	24 ± 6.6	1.0 ± 0.1	24	0.14 ± 0.08
	2000	15	50	26 ± 2.6	49 ± 2.4	25 ± 1.8	1.5 ± 0.1	39	0.28 ± 0.11
Jeremi	*1998*	*10*	*44*	*7 ± 1.3*	*38 ± 3.4*	*55 ± 3.3*	*0.7 ± 0.1*	*3*	*0.59 ± 0.14*
	2000	10	24	43 ± 4.3	42 ± 4.2	15 ± 1.6	8.5 ± 1.2	366	0.44 ± 0.18
	2000	15	32	17 ± 2.7	57 ± 3.3	26 ± 2.4	1.3 ± 0.1	17	0.16 ± 0.08
Kalki	*1998*	*10*	*30*	*21 ± 3.0*[1]	*35 ± 5.5*	*44 ± 5.2*	1.3 ± 0.12	*14*	*0.67 ± 0.15*
	2000	10	20	7 ± 2.2	83 ± 4.3	10 ± 2.3	0.5 ± 0.14	4	0.24 ± 0.09
	2000	15	34	15 ± 3.0	55 ± 3.3	30 ± 2.9	1.3 ± 0.14	19	0.33 ± 0.14
All sites	*1998*	*10*	*139*	*12 ± 1.5*	*37 ± 2.4*	*50 ± 2.3*	1.1 ± 0.05	*11.2*	*0.58 ± 0.08*
Western sites	2000	10	57	27 ± 4.8	56 ± 3.8	17 ± 2.6	4.9 ± 0.90	152	0.20 ± 0.09
	2000	15	116	20 ± 1.8	57 ± 1.7	23 ± 1.4	1.4 ± 0.07	28	0.26 ± 0.14

[1]Includes 9% cyanobacteria.
[2]Macroalgal index = relative macroalgal abundance x macroalgal height

Table 4. Causes of recent mortality for all scleractinians (≥20 cm diameter), as numbers and percentages of all colonies, by site off Curaçao.

Site name	Year	Depth (m)	Corals (#)	YBD[1] # (%)	DSD[2] # (%)	WP[3] # (%)	BBD[4] # (%)	PFB[5] # (%)	Snail[6] # (%)	Overrowth[7] # (%)
Eastern										
Oostpunt	*1998*	*10*	*110*	*17 (16.5)*	*0*	*5 (5)*	*0*	*4 (4)*	*3 (3)*	*0*
Western										
Lagun	*1998*	*10*	*118*	*12 (10)*	*0*	*0*	*0*	*3 (2.5)*	*0*	*5 (4.0)*
	2000	10	131	15 (11.5)	2 (1.5)	1 (1)	1 (1)	3 (2.5)	3 (2.5)	2 (1.5)
	2000	15	145	10 (7)	0	0	0	0	0	0
	2000	20	165	8 (5)	5 (3)	0	0	6 (3.5)	0	0
Jeremi	*1998*	*10*	*110*	*10 (9)*	*0*	*3 (2.5)*	*0*	*3 (2.5)*	*4 (3.5)*	*3 (2.5)*
	2000	10	152	14 (9)	0	0	0	0	0	0
	2000	15	171	10 (5.5)	0	0	0	0	0	0
	2000	20	191	8 (4)	6 (3)	1 (0.5)	0	1 (0.5)	1 (0.5)	0
Westpunt	2000	10	79	11 (14)	0	0	0	6 (7.5)	0	0
	2000	15	142	7 (9)	1 (0.5)	0	0	0	0	0
Kalki	*1998*	*10*	*107*	*7 (6.5)*	*2 (2)*	*6 (5.5)*	*2 (2)*	*0*	*4 (3.5)*	*0*
	2000	15	156	11 (7)	5 (3)	0	0	1 (0.5)	0	0
	2000	20	169	7 (4)	12 (7)	0	0	1 (0.5)	0	1 (0.5)
All sites	*1998*	*10*	*445*	*13.0*	*0.4*	*3.2*	*0.5*	*2.2*	*2.5*	*1.8*
Western sites	**2000**	**10**	**1501**	**6.7**	**2.1**	**0.1**	**0.07**	**1.2**	**0.3**	**0.2**

[1]YBD = yellow-band disease; [2]DSD = dark-spot disease; [3]WP = white-plague disease; [4]BBD = black-band disease; [5]PFB = parrotfish bites;
[6]Snails = *Coralliophila abbreviata* predation; [7]Overgrowth = overgrowth by a sponge or tunicate.
Note that some conditions, such as YBD and DSD, affect a relatively small number of species; infection rates are substantially higher among individual species than at the community level.

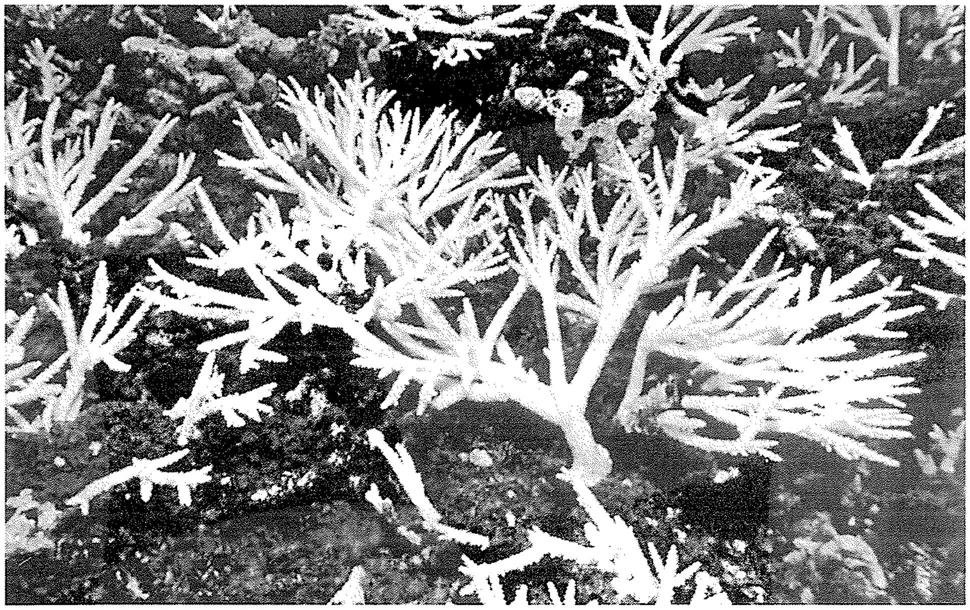

Plate 9A. Each stony coral, as in these colonies of *Acropora cervicornis*, is assessed for the presence and intensity of any bleaching that is related to mass bleaching events. (Photo Kenneth W. Marks)

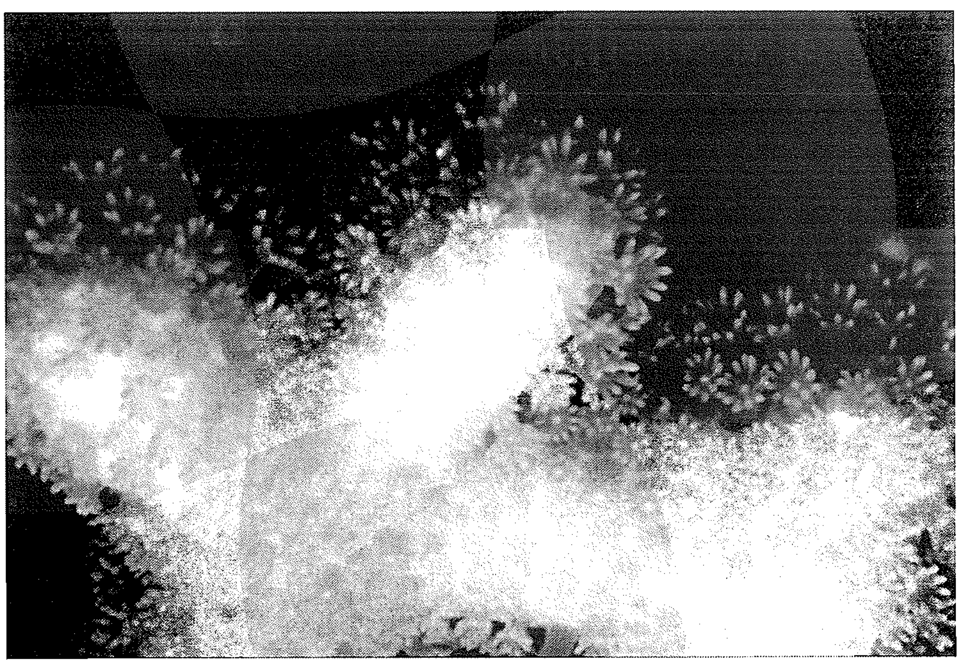

Plate 9B. Bleaching is characterized according to the approximate severity of tissue discoloration as *pale* (discoloration of coral tissues); *partly bleached* (patches of fully bleached or white tissue); and *bleached* (tissues are totally translucent, and the white skeleton is visible), as shown for this *Porites*. (Photo Larry Benvenuti)