

Figure 1. AGRRA survey sites (Akumal, Xcalak) in Quintana Roo, México. Modified from Núñez-Lara et al. (this volume).

RAPID ASSESSMENT OF MÉXICO'S YUCATÁN REEF IN 1997 AND 1999: PRE- AND POST-1998 MASS BLEACHING AND HURRICANE MITCH (STONY CORALS, ALGAE AND FISHES)

BY

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ABSTRACT

Rapid assessments were made along México's Yucatán coast in six fore reefs each off Akumal (northern area) and Xcalak (southern area) and in two Xcalak patch reefs. Live stony coral cover averaged <20% overall in March 1999. At this time, both recent and old partial-colony mortality of the ≥ 25 cm stony corals were significantly higher in the Xcalak patch reefs than in the fore reefs, and more corals were moderately bleached at all depths off Xcalak than off Akumal. Anomalously high sea surface temperatures, having caused widespread bleaching in September 1998, possibly persisted longer at Xcalak because different exposure to hurricanes caused the southern Yucatán to cool later than the northern area. Bleaching may have rendered the *Montastraea annularis* species complex more susceptible to white-band disease, particularly in the Xcalak patch reefs. Partial mortality of stony corals and macroalgal abundance increased significantly in the Akumal fore reefs between 1997 and 1999, when macroalgal abundance and biomass were significantly higher than in Xcalak. Macroalgal increases off Akumal could have resulted from anthropogenic nutrient enrichment from groundwater and/or reduced grazing by *Diadema antillarum* and herbivorous fishes.

INTRODUCTION

Are coral reefs "dying" throughout the wider Caribbean? If they are, at what scale and at what rate? The Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocols are tools for rapidly quantifying spatial and temporal patterns in the condition of coral reefs. Their value is in providing species-explicit and commensurable ways of comparing reefs within regions, larger scale bioregions, or the entire, tropical western Atlantic (Ginsburg et al., 2000; Steneck et al., 2000; Kramer, this volume).

The AGRRA protocols were also designed to record indicators of stress and potential agents of disturbance. We use stress to mean any loss of *productivity* and disturbance to mean any loss of *biomass* in the organism or assemblage in question (after

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Grime, 1977, 1989; Steneck, 1988; Steneck and Dethier, 1994). Specifically for stony corals, transient, nonlethal bleaching indicates stress whereas disturbances are indicated by signs of disease and patterns of mortality.

Early versions of the AGRRA protocols were prototyped off two villages of the Mexican Caribbean (Fig. 1). Narrow fringing and fringing-barrier reefs skirt the eastern flank of the Yucatán Peninsula- where many coastal ecosystems are under assault from the rapid growth of the tourist industry (Jordán Dahlgren, 1993; Lang et al., 1998). Akumal, a resort community with a resident population of >600 near the southern end of the northerly Cancún-Tulum corridor, is surrounded by numerous large-scale developments. Xcalak, near the southern border with Belize, has a population of about 300 and is being transformed from a reliance on offshore fishing to ecotourism.

Our initial assessments of these reefs were made in March and August 1997. Resurveys in March 1999 were conducted six-seven months after the first reports of thermally induced (Fig. 2) bleaching in the Yucatán (Kramer et al., 2000), five months after Hurricane Georges passed near the northern Yucatán, and four months after Hurricane Mitch affected the southern area. We sought to determine patterns in coral mortality, whether particular species were suffering higher than average mortality, and whether mortality patterns corresponded with known stressors and disturbance agents (bleaching, hurricanes, macroalgae) or with inferred changes in the reefs' trophic structure (i.e., reductions in herbivory).

METHODS

Chosen for assessment were six, moderate-relief "middle-lobe" fore reefs at depths of 11-18 m near Akumal (Fig. 1; Table 1). Comparable habitats were selected at 8.5-16.5 m in six fore reefs off Xcalak along with two shallow (1-3 m) patch reefs in its wider lagoon. All sites were considered to be representative of local reefs based on the knowledge and advice of residents who had dived there for years.

The draft AGRRA benthos protocol was utilized by six divers in early March 1997. The following August two divers applied the revised AGRRA Version 1 procedures at two reefs off Akumal (Dick's, Las Redes). In early March 1999, when three-six divers used the AGRRA Version 2.0 protocols (see Appendix One, this volume) at all 14 reef sites, live coral cover was measured to the nearest 5 cm. The maximum diameter of stony corals (i.e., scleractinians and *Millepora complanata*) was approximated to the closest 5 cm with one side of the algal quadrat for scale. Bleaching was scored as "light" or "moderate," completely bleached stony corals being absent at this time. Two species of *Colpophyllia* (*C. breviserialis*, *C. natans*) were recognized. Humann (1993) served as the primary field guide for other scleractinians. Stony coral recruits were not quantified. Surficial sediment was removed from the algal quadrats by gentle hand sweeping before estimating crustose coralline algal abundance.

A limited number of fish surveys were made by one diver (Steneck) in 1999. The AGRRA version 2.0 fish belt-transect protocol (see Appendix One) was modified by swimming three transects, each 30 long x 2 m wide, in six of the fore reefs (Akumal-Média Luna, Dick's, Xcalak-Coral Gardens, Chimney, El Quebrado, Dos Cocos). Scarids (parrotfish) and haemulids (grunts) <5 cm in length were not counted. Although

Maximum Monthly Temperature Anomalies

NOAA/NESDIS 50 km SST

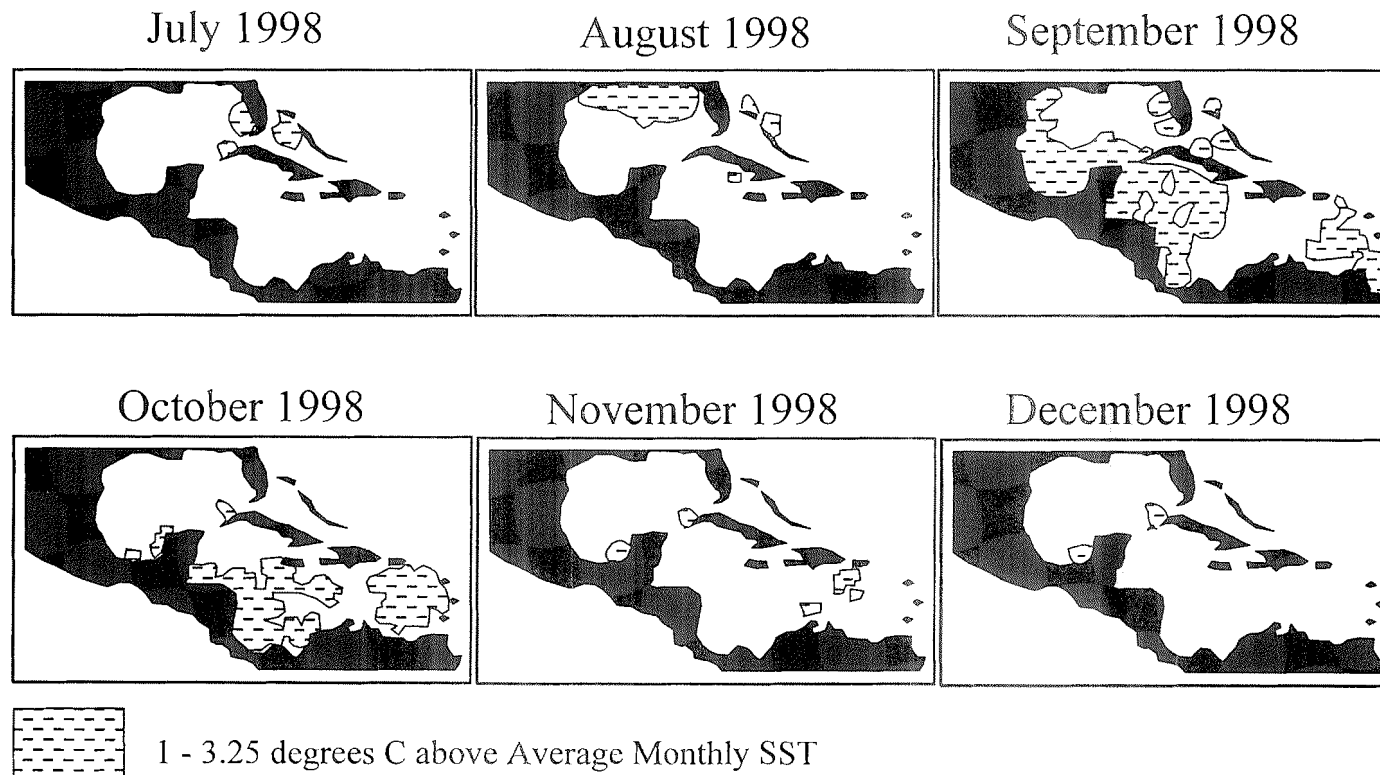


Figure 2. Sea surface thermal anomalies in 1998 (for July 4, Aug. 1, Sept. 1, Oct. 6, Nov. 1 and Dec. 1) show the development of a thermal anomaly around the entire Yucatán by early September, its contraction to the south by early October and disappearance by early November. (Images from NOAA/NESDIS).

dives were made from 9 a.m. to 5:30 p.m., most of the fish surveys were conducted during mid-day hours (10 a.m.-2 p.m.). The Fish Bite Method (see Appendix One) was used to assess herbivory in Dick's and Las Redes reefs by one diver (J. Reichman) in August 1997.

Data for all species were pooled for certain sites in some analyses; in other analyses the data for certain species were pooled across sites. Variance is given either as standard deviation (sd) or as standard error (se). Changes in the AGRRA benthos protocol between March 1997 and 1999 render some comparisons (e.g., of mortality patterns and macroalgal biomass) between those two dates impossible.

RESULTS

Stony Corals

Live stony coral cover, first measured in March 1999, averaged less than 20% for most (10/14) of the surveyed reefs (Fig. 3A; Table 1). Variance among the fore reefs was lower off Akumal than Xcalak, where the live cover in one reef was about four times higher than at three others (37% versus ~9%, respectively).

Nineteen species of "large" (≥ 25 cm maximum diameter) stony corals were quantified in our surveys. Eighteen were found in the fore reefs where the *Montastraea annularis* species complex predominated, numerically comprising $>50\%$ of the surveyed colonies in 1999 (with *M. annularis* $>$ *M. faveolata* \gg *M. franksi*) and each remaining species constituting $<7\%$ (Fig. 4; Table 2).

The maximum diameter of the ≥ 25 cm fore-reef corals averaged 76 cm (se=24, n=12 reefs). Colonies were somewhat smaller off Xcalak (mean=62, se=22, n=6 reefs) than in Akumal (mean=89, se=20, n=6 reefs) and there was considerable variation within some reefs, especially Akumal's Média Luna (Fig. 3B; Table 3). *A. palmata* was clearly the largest of the fore-reef corals, averaging 205 cm in maximum diameter (Fig. 5; Table 2), and three (*A. palmata*, *M. franksi*, *M. faveolata*) of the four largest species were among the six most abundant of the fore-reef corals. Nevertheless, when abundance is expressed as percent relative coverage (mean number of colonies/m \times mean maximum diameter in cm), co-dominants were *M. annularis* and *M. faveolata*, each with 10.5% of the total.

Only nine species of ≥ 25 cm stony corals were recorded in the Xcalak patch reefs. *M. annularis* was the numerical dominant with 75% of all colonies. *Acropora cervicornis* and *Agaricia tenuifolia* each had 8.5%, *Porites porites* comprised 6.5%, while all the remainder (*A. palmata*, *Agaricia agaricites*, *Porites astreoides*, *Colpophyllia natans*, *Millepora complanata*) were each $<3\%$. Stony corals were substantially larger in the two patch reefs than in the fore reefs (Table 3), with an overall mean of 150 cm (se=14), primarily due to the higher abundance of *M. annularis* which here averaged ~165 cm in maximum diameter.

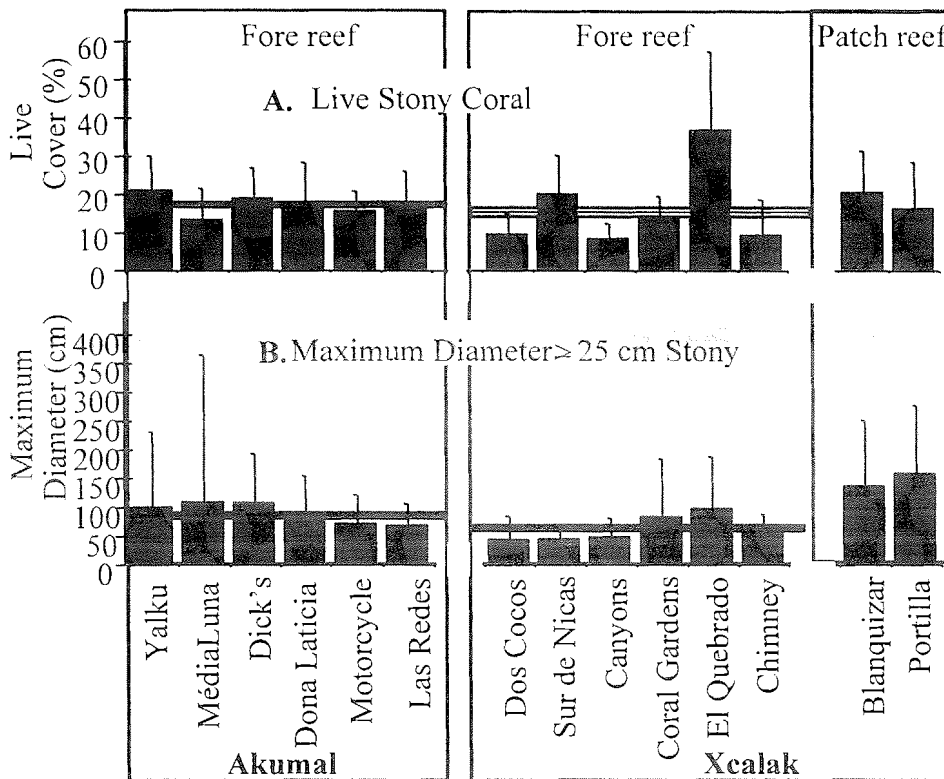


Figure 3. Mean (\pm standard deviation) for (A) percent live stony coral cover and (B) maximum (max.) diameter of all stony corals (≥ 25 cm max. diameter) in March 1999 by site for Akumal ($n=336$) and Xcalak ($n=333$ in fore reefs and 196 in patch reefs). Horizontal lines = pooled mean \pm standard error for each habitat.

Stony Coral Condition

We saw no evidence of bleaching during the 1997 surveys. In March 1999, moderate bleaching affected $<3\%$ of the ≥ 25 cm stony corals in the Akumal fore reefs and about 10% in each habitat off Xcalak (Fig. 6A; Table 3). A further 4-18% of the colonies in each reef were considered to be lightly bleached at this time.

None of the ≥ 25 cm stony corals that were censused at Dick's and Las Redes reefs in August 1997 appeared diseased, although signs of white-band disease (WBD) and yellow-blotch disease were noticed in a few colonies of *A. palmata* and *M. faveolata*, respectively (Lang, personal observations). White plague was widespread in March 1999, however, with surveyed corals in 5/6 of the Akumal fore reefs, 3/6 of the Xcalak fore reefs and both patch reefs showing signs of infection (Fig. 6B; Table 3). The percentage of diseased colonies varied between areas and habitats, being $\sim 1\%$ in the Xcalak fore reefs, $\sim 5\%$ in Akumal and $\sim 10\%$ in the Xcalak patches. Most affected were colonies of *Montastraea annularis* (fore reefs—60% at Akumal and 57% at Xcalak; patch reefs—95%),

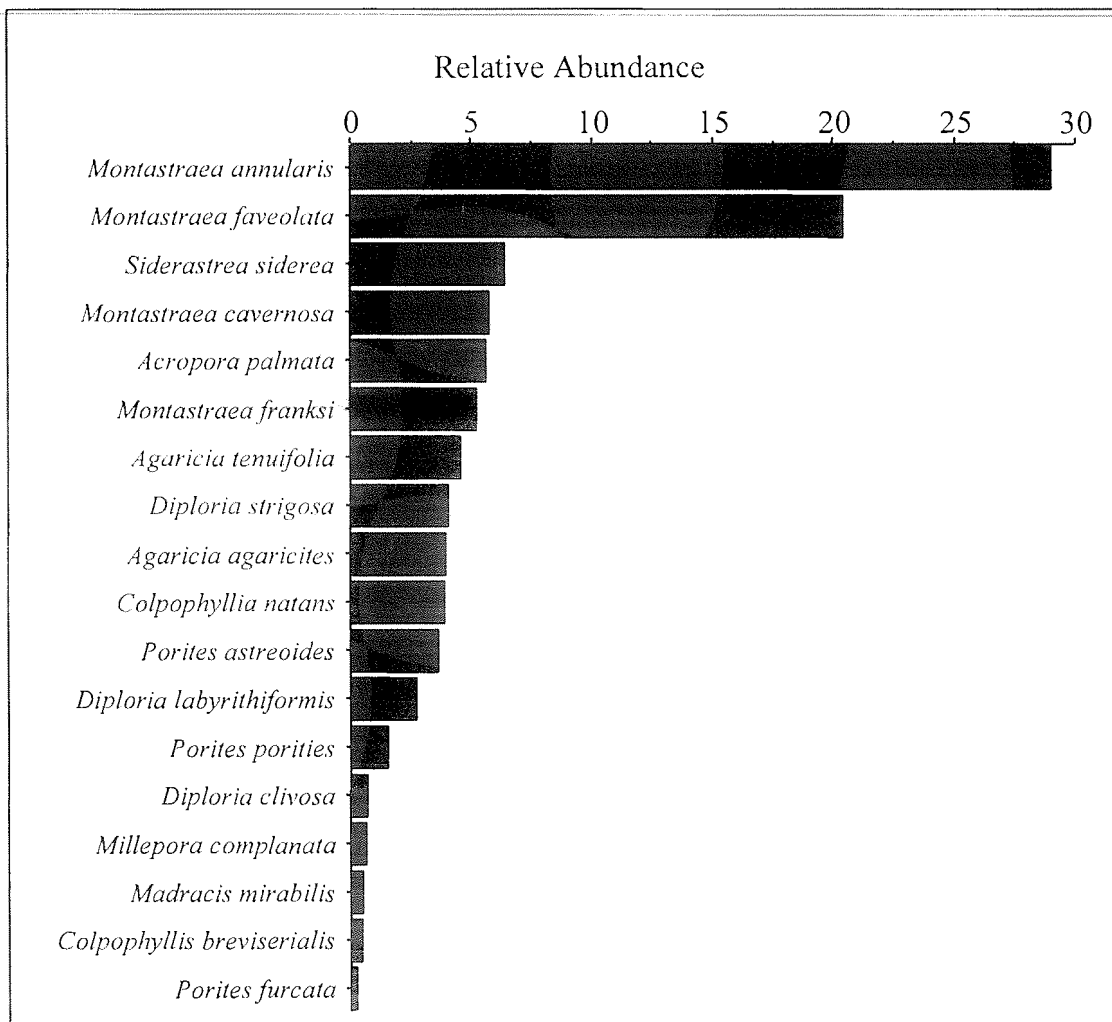


Figure 4. Relative abundance as % of the Akumal and Xcalak fore-reef stony corals (all ≥ 25 cm max. diameter; $\Sigma=669$) in March 1999, ordered from most abundant to least abundant species.

followed by *M. faveolata* and *M. franksi*. Black-band disease was seen in one colony of *Agaricia tenuifolia* off Akumal (Table 3, footnote).

Recent partial-colony mortality (hereafter recent mortality) of large stony corals averaged 1.5% (sd = 2.5) in the two Akumal fore reefs that were surveyed in August 1997. Overall estimates of recent mortality in the fore-reef were higher (Akumal–4.5%, Xcalak–5.0%) in March 1999, but revealed no large-scale differences between the two areas (Fig. 7, Table 3). Old partial-colony mortality (hereafter old mortality) in the two Akumal fore reefs averaged 31.5% (se=2) in August 1997. Old mortality was somewhat elevated in fore reefs with above-average values for recent mortality, but overall estimates in 1999 were virtually identical in the two areas, averaging 27.5% (se=7.0, n=12 reefs).

Recent partial mortality averaged 28% in the two Xcalak patch reefs in 1999, when mean values of old partial mortality were ~40%. Hence total (recent + old) partial mortality in the patch reefs was approximately twice as high as in the fore reefs (Fig. 7; Table 3). Regardless of location, recent mortality declined steadily between 7 and 15 m in

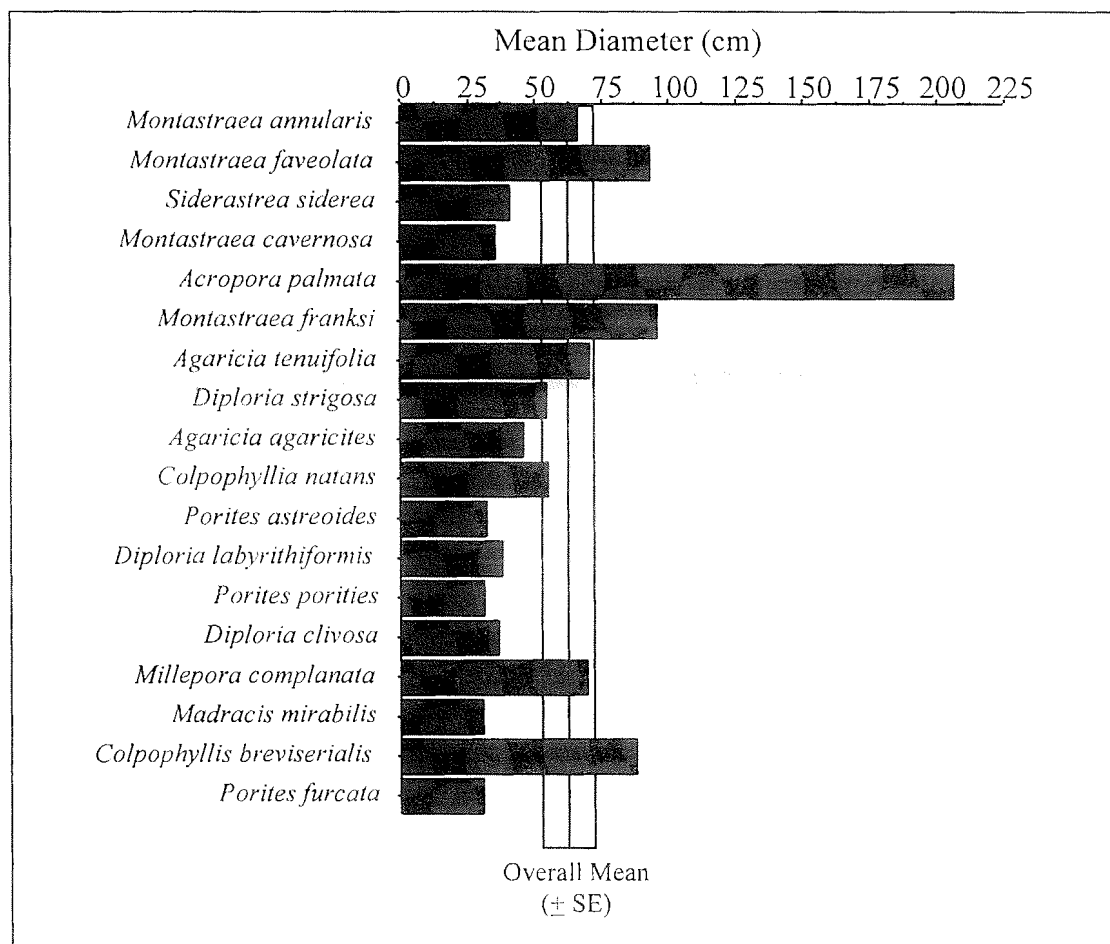


Figure 5. Mean maximum diameter of the Akumal and Xcalak fore-reef stony corals (all ≥ 25 cm max. diameter, $n=669$) in March 1999, ordered from most abundant to least abundant species (as in Figure 4). Vertical lines = mean \pm standard error for all species pooled.

the fore reefs (Fig. 8) and a similar, but less, dramatic depth-related decline was evident in old mortality as well.

The percentage of large stony corals that were “standing dead” (entire upper surfaces dead, colony still in growth position) in March 1999 was very variable among sites (Table 3), averaging 4-5% overall in the fore reefs and about 9% in the patch reefs. However, a much higher proportion of the *A. palmata* were standing dead ($n=16/41$ colonies in the fore reefs, $n=2/6$ colonies in the patch reefs). Detached or fallen stony corals were rare in all the surveyed reefs.

Recent mortality in *Millepora* and *Agaricia* is likely to be underreported. Their corallite structures are relatively indistinct, and soon after death the skeletons are probably scored as “old dead” by the AGRRA protocol. Bearing this caveat in mind, recent and old mortality patterns varied by species in 1999, with mean values of 3% and 22%, respectively, for the 18 fore-reef species (Fig. 9; Table 2). Values for recent mortality that were well above the average were found in *M. annularis* and *M. faveolata*, whereas lower than average values were recorded for *Montastraea cavernosa*, *M. complanata* and *Colpophyllia breviserialis* (Fig. 9, Table 2). Percent recent mortality of

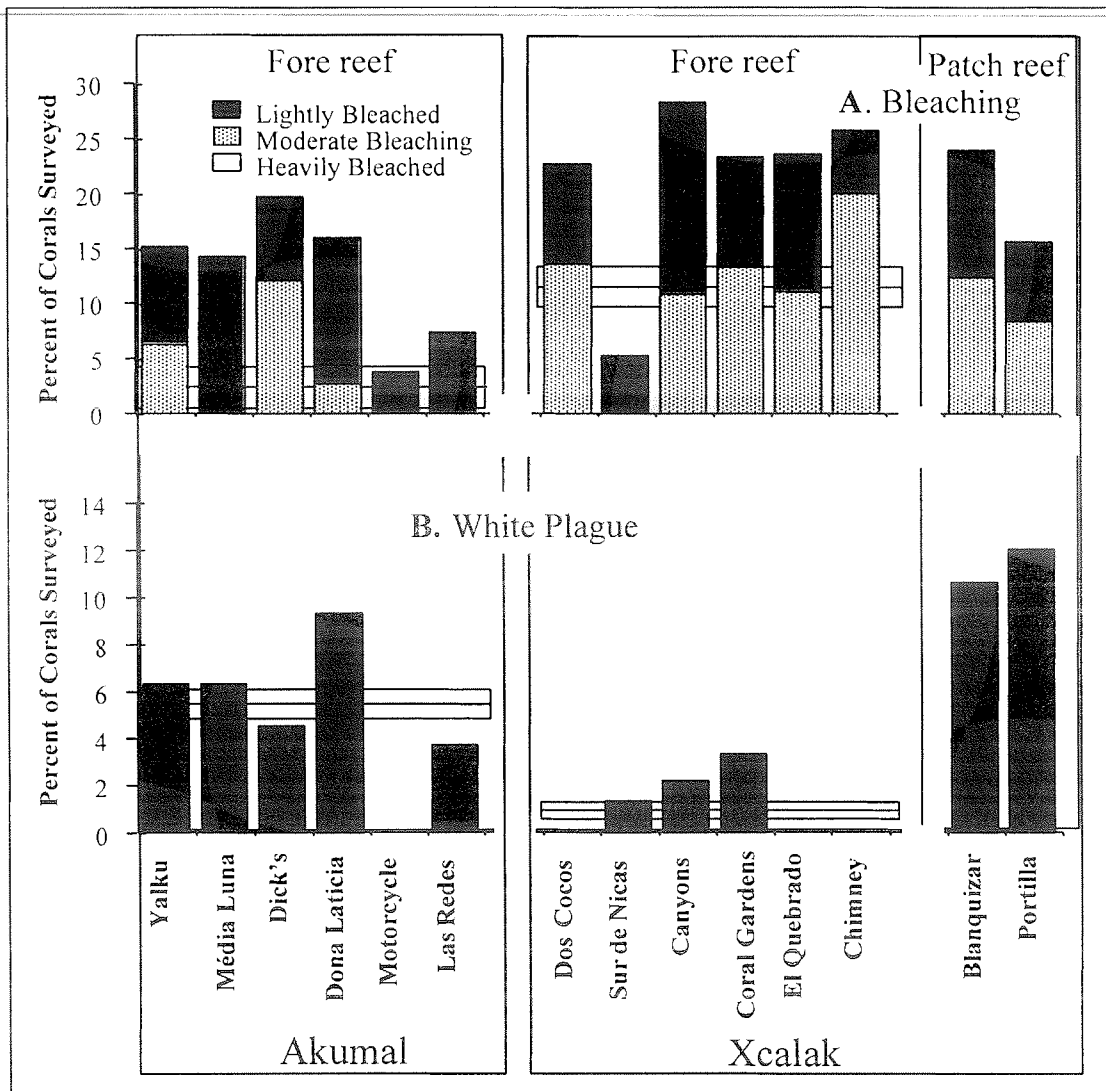


Figure 6. Percent of (A) bleaching with averages among reefs only determined for moderate bleaching and (B) white plague in stony corals (all ≥ 25 cm max. diameter) in March 1999 by site for Akumal ($n=336$) and Xcalak ($n=333$ in fore reefs and 196 in patch reefs). Mean and standard error notation as in Figure 3.

colony surfaces of *A. palmata* was somewhat greater in Akumal (mean=6.5, se=3, $n=31$ colonies) than off Xcalak (mean=2, se=2, $n=10$ colonies). Fore-reef species with higher than average values for old (and total) partial-colony mortality were *A. palmata* >> *Agaricia tenuifolia* > *M. mirabilis* ~ *M. annularis*.

Mean values of recent mortality in the patch reefs were especially high for *M. annularis* (31.5%), *A. agaricites* (24%), *Acropora cervicornis* and *A. tenuifolia* (each 15%), while old mortality was greatest in *A. palmata* (87%), *P. porites* (64%), *A. agaricites* (55%) and *M. annularis* (37%). The only colony of *Millepora complanata* censused here was scored as having 100% old mortality.

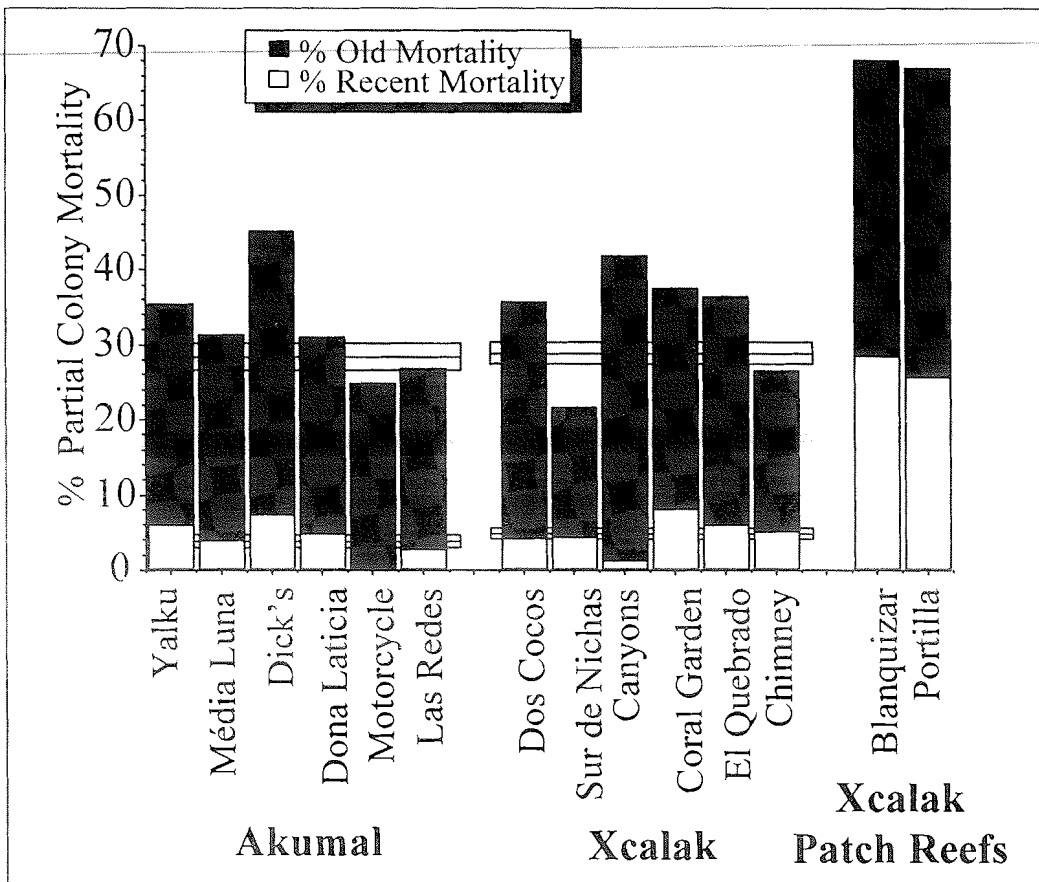


Figure 7. Total (recent and old) partial colony mortality of all stony corals (≥ 25 cm max. diameter) in March 1999 by site for Akumal ($n=336$) and Xcalak ($n=333$ in fore reefs and 196 in patch reefs). Mean and standard error notation as in Figure 3.

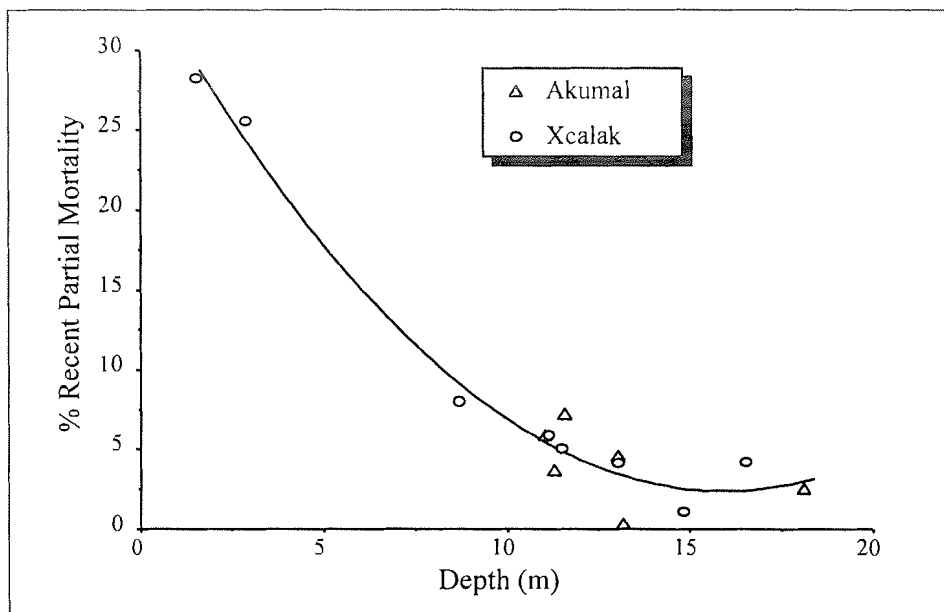


Figure 8. Plot of mean recent partial mortality of all stony corals (≥ 25 cm max. diameter) versus water depth in March 1999 at each site off Akumal and Xcalak. Curve fit is 3rd order polynomial.

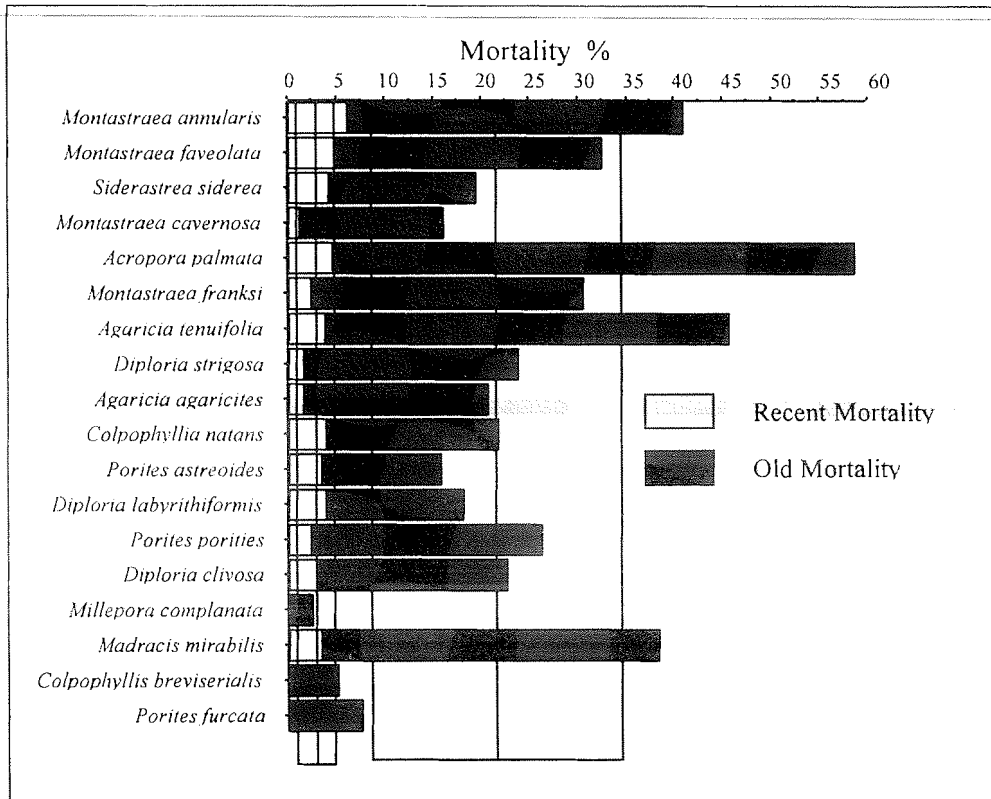


Figure 9. Total (recent and old) partial colony mortality as % of the Akumal and Xcalak fore-reef stony corals (≥ 25 cm max. diameter, $n=669$) in March 1999 ordered from most abundant to least abundant species (as in Figure 4). Mean and standard error notation as in Figure 5.

Algae

In March 1997, the relative abundance of macroalgae averaged $\sim 25\%$ in the fore reefs of both regions and $\sim 12\%$ in the Xcalak patch reefs. Two years later, their relative abundance had significantly increased in the Akumal fore reefs (averaging 44%), whereas the reefs at Xcalak were essentially unchanged (Figs. 10, 11; Table 4). Macroalgal heights in 1999 were also slightly higher in Akumal, thus macroalgal indices (an approximation of their biomass, see Table 4) were three to four times greater here than in Xcalak. Turf algae off Akumal showed a pattern opposite that of the macroalgae, having declined from 62% in 1997 to nearly 35% in 1999. However, turfs were still the predominant algal group in both habitats off Xcalak. The relative abundance of crustose coralline algae in 1999 varied from $>15\%$ in the patches to nearly 30% in the Xcalak fore reefs.

Fish and *Diadema antillarum*

The total abundance of fore-reef fishes surveyed in the belt transects in numbers/100 m^2 was slightly higher off Xcalak (mean=34.6, se=3.1) than Akumal (mean=26.1, se=0.8). Most common on the fore reefs in 1999 were herbivores; acanthurids (mean=7.7, se=0.8) were the most abundant in Xcalak whereas scarids

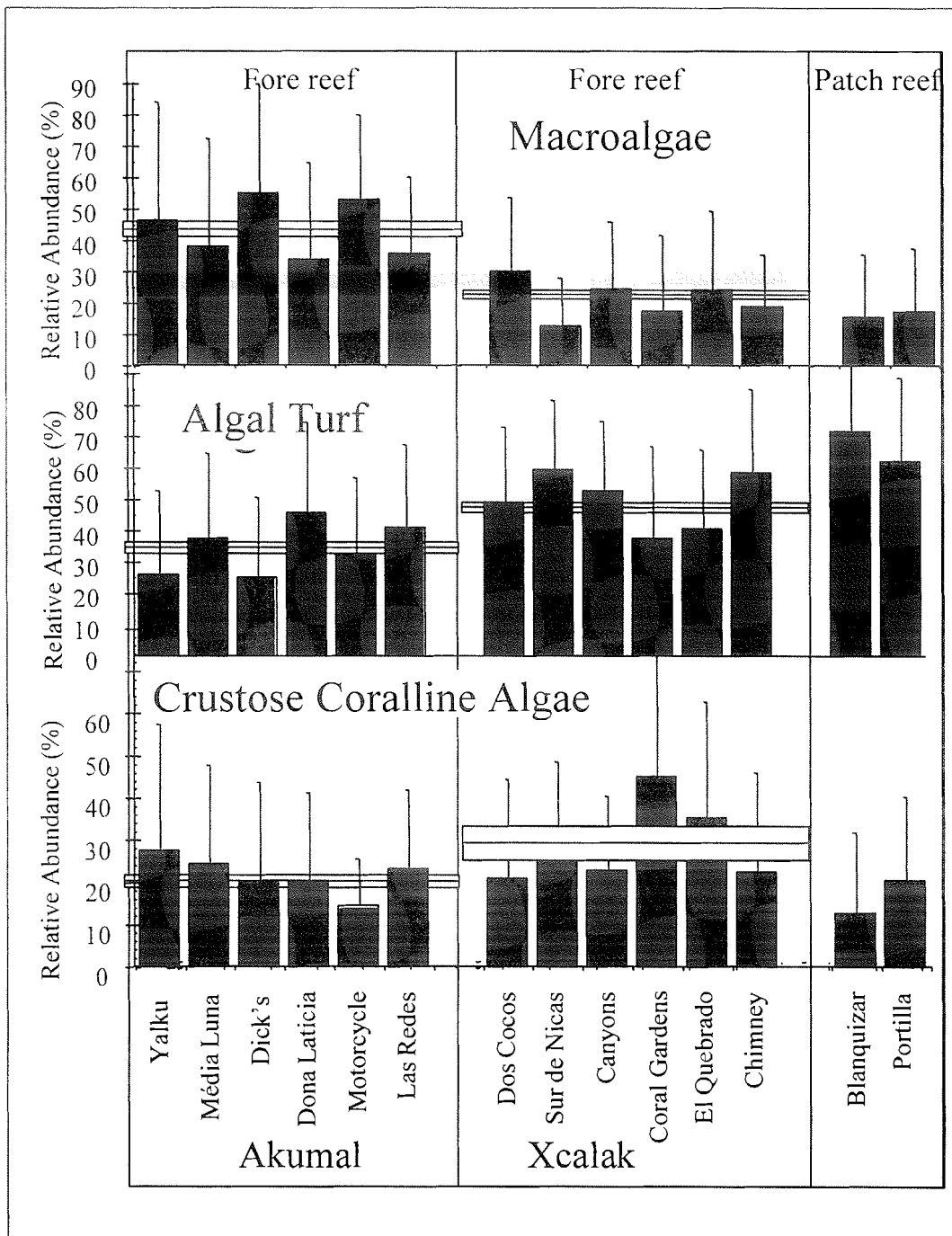


Figure 10. Relative abundance (mean \pm standard deviation) of (A) macroalgae, (B) turf algae, and (C) crustose coralline algae in March 1999 by site for Akumal ($n=301$ quadrats) and Xcalak ($n=361$ quadrats in fore reefs and 136 in patch reefs). Mean and standard error notation as in Figure 3.

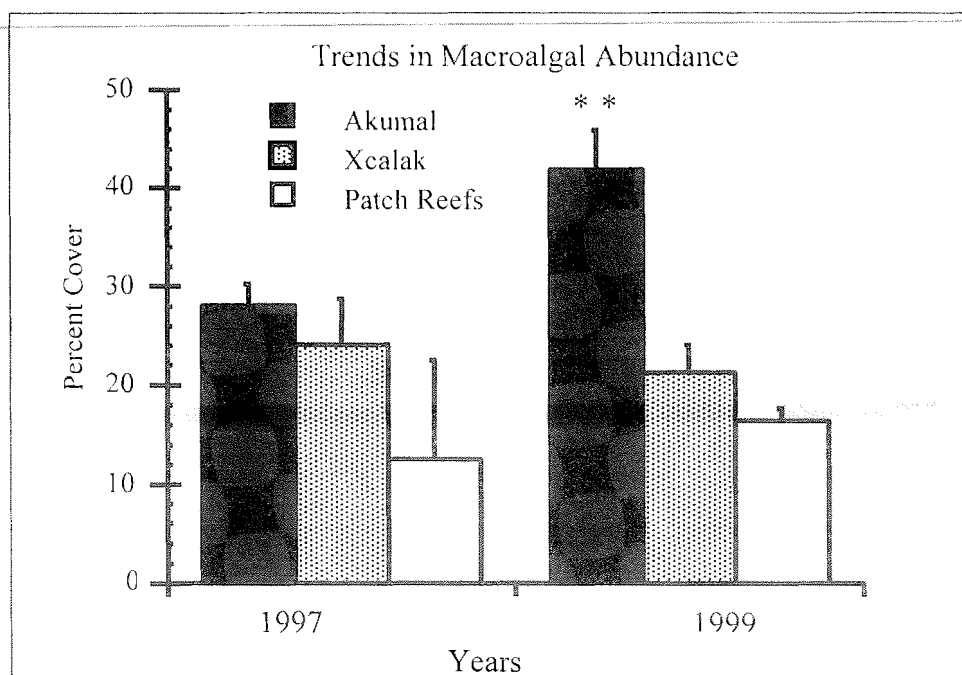


Figure 11. Temporal trends (mean \pm standard error) in relative abundance of macroalgae in the Akumal and Xcalak fore reefs and the Xcalak patch reefs for March 1997 and March 1999. The increase in abundance in the Akumal fore reefs was the only significant difference (ANOVA, $p < .0001$) between the surveys.

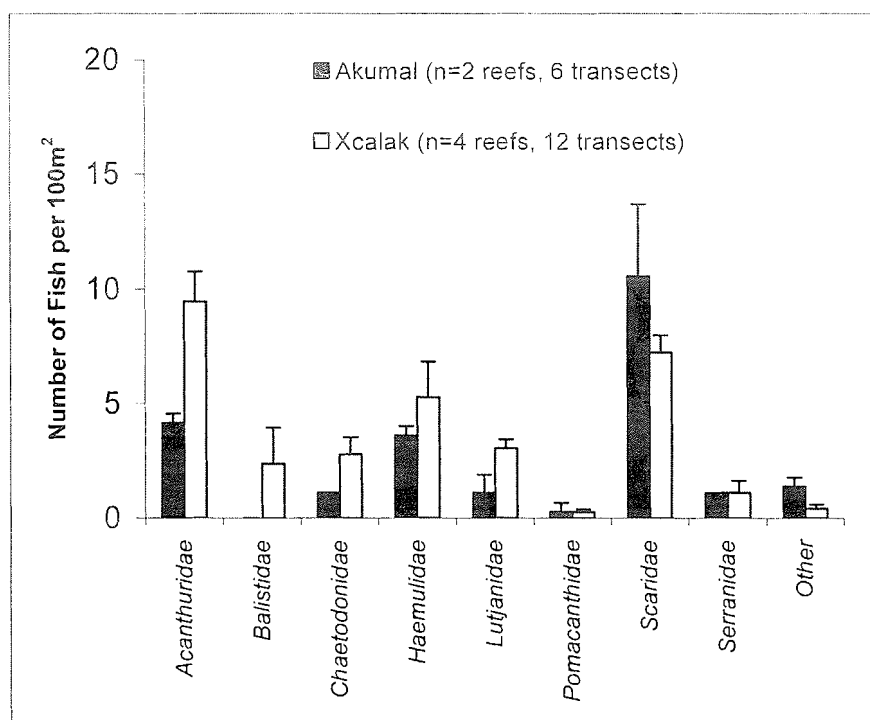


Figure 12. Density (mean no. fish/100m² \pm standard error) of AGRRA fishes in the Akumal and Xcalak fore reefs in March 1999. Other = *Bodianus rufus*, *Caranx ruber*, *Microspathodon chrysurus*.

(mean=8.3, se=0.6) were predominant off Akumal (Fig. 12). Parrotfish (scarids) were slightly larger in the southern fore reefs: average lengths of the five species present in belt transects were 16.33 cm (se=1.15) off Xcalak versus 14.64 cm (se=0.99) off Akumal. Large-sized groupers (serranids) were absent, but smaller species such as coneys (*Epinephelus fulvus*), red hinds (*E. guttatus*) and graysbys (*E. cruentatus*) collectively averaged between 1.4 and 3.3/100 m² off Akumal and Xcalak, respectively. Bite rates for grazing fishes (acanthurids, scarids, *Microspathodon chrysurus*) averaged 175/m²/hour (se=160) at Dick's and Las Redes reefs in Akumal in August 1997; similar results were obtained at two other fore-reef sites in this area.

The long-spined sea urchin, *Diadema antillarum*, was rarely seen in fore-reef habitats and none were counted in any of the transects in March or August 1997. However, a few (3.5/100m²) were found in one of the Xcalak patch reefs in March 1999 (Table 4).

DISCUSSION

Are coral reefs "dying" throughout the Caribbean? To address this question, we need baseline information against which comparisons can be made. Our data for reefs in two areas of the Yucatán can contribute to a baseline, but no single study can address this question because each is too limited in its spatial and temporal coverage. Comparisons require combining our results with other AGRRA studies throughout the Caribbean as discussed by Kramer (this volume).

It must also be noted that rapid assessments are little more than "snapshots" of reef condition. We have no way of determining variability in time outside of our survey periods. Although assessments were conducted in the same reefs and during the same weeks of March 1997 and 1999, we cannot say if a month earlier or later the patterns would have remained the same. However, populations of key fish groups at least are unlikely to exhibit short-term increases, particularly given ongoing spearfishing around Akumal (personal observations) and the as-yet unregulated poaching that occurs in Xcalak (S. Redman, personal communication).

Nevertheless, many of the AGRRA indices for 1999 are suggestive that the Yucatán reefs we studied may be in decline. For example, average live stony coral cover overall was <20% (Fig. 3A; Table 1) and, for the Akumal-area fore reefs, was somewhat lower than Munoz-Chagin and de la Cruz-Aguera's (1993) previous *area*-based estimate (18% versus 23%, respectively). Population densities of the AGRRA fishes were low in the seven examined fore reefs (Fig. 12), and the abundance of macroalgae had increased significantly over a period of two years off Akumal (Fig. 11). Mean values of recent and old partial mortality for surveyed corals were extremely high in the two Xcalak patch reefs (Fig. 7).

Partial (recent and old) mortality values for the ≥25 cm stony corals were similar in the fore reefs off Akumal and Xcalak (Fig. 7) in March 1999. Nonetheless, the underlying causes for their mortality may differ since numerous potential stressors and disturbance agents, such as hurricanes, fishing, groundwater input and outbreaks of disease, complicate simple explanations. Below, we discuss how the sudden "pulse"

events of 1998 may have interacted with “chronic” stresses and disturbances in the region from 1997 to 1999 to produce the patterns of mortality we recorded.

Recent Pulse Events: Mass Bleaching and Hurricanes of 1998

High temperatures can induce stony corals to bleach, and they will die if the thermal condition persists (e.g., Fitt et al., 2001). Over the past century tropical oceans have been warming which, together with El Niño-related periods of elevated temperatures, have contributed to an increased frequency of coral bleaching (Glynn, 1993; Brown, 1997). The strong El Niño of 1997-1998 resulted in unusually warm sea surface temperatures and widespread lethal bleaching of stony corals worldwide (Wilkinson, 2000). By September 1, an enormous area that was nearly $+1.5^{\circ}\text{C}$ above the average monthly high temperature had developed throughout the western Caribbean (Fig. 2; see also Kramer et al., 2000; Kramer and Kramer, in press). As September is the warmest month in the Caribbean, a warm anomaly at this time is most likely to exceed the thermal thresholds (sensu Fitt et al., 2001) of many stony corals. Indeed local divers observed widespread bleaching at Akumal (D. Brewer and S. Slingsby, personal communication) and Xcalak (T. Biller, personal communication).

Subsequent spatial and temporal patterns of sea-surface cooling are consistent with hurricane activity in the area. Hurricanes propagate large-amplitude, low-frequency storm swells that can mix warm surface water layers with deep cooler water. Two hurricanes traversed the western Caribbean in 1998. On September 25, Georges passed over the northwest coast of Cuba, adjacent to the northeast Yucatán coast, as a Category 2 hurricane with sustained winds of 169 km/hour and continued northwest toward the Mississippi delta. The satellite image for October 6 shows an entirely different thermal anomaly pattern from that of the previous month, with most of the western Caribbean north of 19°N latitude, including Akumal, being only about $+0.5^{\circ}\text{C}$ above the monthly average (Fig. 2). This rapid cooling resulted in only transient rather than lethal bleaching over much of the Mexican Caribbean.

Nevertheless, a warm region of nearly $+1.5^{\circ}\text{C}$ persisted throughout the southwestern Caribbean from southern Mexico (including Xcalak) through Belize and Honduras to Colombia. Then Hurricane Mitch developed off the Colombian coast on October 24. Over the next four days it slowly built to a Category 5 hurricane with sustained winds of 290 km/hour as it stalled in the Gulf of Honduras adjacent to Belize. Mitch generated 10 m-high storm swells that crested and broke on the Xcalak reefs (T. Biller, personal communication). Three days later, the November 1 satellite image recorded no thermal anomalies anywhere in the western Caribbean. In fact, the only remaining warm spots were localized off northwestern Cuba, in the southwestern Gulf of Mexico and areas in the ordinarily hurricane-free region from south of Puerto Rico to Venezuela.

That moderately-bleached ≥ 25 cm stony corals were more common in March 1999 off Xcalak (both habitats) than in the Akumal fore reefs (Fig. 6) is consistent with the pattern of a longer-duration thermal event in the south having created greater stress and allowed less time for recovery. Reef organisms would have experienced higher temperatures (and presumably higher solar irradiance) in the shallow (1-2 m), calm waters of the Xcalak lagoon than in its offshore fore reefs. Lethal bleaching probably

contributed to the extremely high values of recent partial mortality (~27% of colony surfaces) found in the patch reefs, and thereby reduced the percentage of colonies still showing residual levels of light or moderate bleaching in March 1999 to approximate those in the fore reefs nearby (Table 3).

Bleaching-induced mortality of *A. tenuifolia* was first reported in the Yucatán in October 1998 (Kramer et al., 2000). As the transition from what appears to be “recent” to what is scored as “old” probably occurs relatively quickly in species of *Agaricia*, we also suspect that at least some of the comparatively high values for old mortality in the ≥ 25 cm fore-reef colonies of this species (Table 2; Fig. 9) had occurred as a result of the 1998 bleaching event.

Mexican reefs sustained relatively little physical damage from hurricanes in 1998, as evidenced by the scarcity of detached and fallen colonies in the March 1999 transects (see also Kramer et al., 2000). That macroalgal blooms were conspicuous off Akumal immediately following Hurricane Mitch (S. Slingsby, personal communication) is consistent with the significant increase in their abundance recorded in the Akumal fore reefs (but not at Xcalak) between 1997 and 1999 (Fig. 11).

Chronic Events: Trends and Agents of Mortality

Recent and old partial-colony mortality of the ≥ 25 cm stony corals increased significantly between 1997 and 1999 in the two Akumal fore reefs for which commensurable protocols were applied (Fig. 13; T-test, $p < 0.05$). We do not know how long “recently dead” coral skeletons generally remain in that category before being recorded as “old dead” according to criteria in the AGRRA protocol (Appendix One). However, colonies of the abundant *Montastraea annularis* species complex and of *Acropora palmata* frequently retain surficial corallite structures for months after death, particularly when grazing pressures are low (personal observations). Thus we suspect that a majority of the increase in recent mortality recorded in March 1999 was the result of events occurring since the previous summer whereas, apart from *A. tenuifolia*, the higher values of old mortality reflected cumulative impacts of disturbances which had occurred since the 1997 surveys.

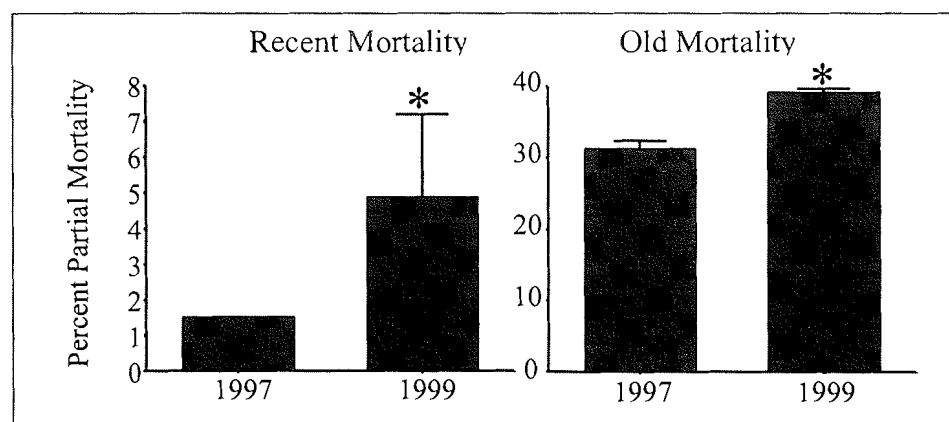


Figure 13. Temporal trends (mean \pm standard error) in recent and old partial colony mortality of stony corals (all ≥ 25 cm max. diameter; $n=52$ in August 1997 and 93 in March 1999) in Las Redes and Dick's reefs off Akumal. Comparable data do not exist for March 1997 because of changes in the AGRRA protocol.

Outbreaks of disease (and potential disease states, sensu Richardson, 1998) appear to have increased in diversity and severity throughout the Caribbean in recent decades, and had probably contributed to the above-average levels of partial mortality observed in some species in March 1999 (Fig. 9; Table 2). In particular, the stress of the 1998 bleaching event might have increased the susceptibility of *Montastraea annularis* and related species to white plague. A high percentage of diseased colonies were also reported throughout the Mesoamerican reef system after the 1998 bleaching event, although the incidences (at least in Belize) had decreased by 2000 (Kramer et al., 2000; Kramer and Kramer, in press).

WBD is apparently specific to species of *Acropora* and it spreads relatively slowly (Gladfelter, 1982). A few live *A. palmata* can still be found in fore-reef habitats to depths of about 15 m and we have seen signs of WPD in some of the colonies off Akumal. Thus disease might have caused the above-average levels of both old and recent partial mortality observed in this species in 1999 (Table 2; Fig. 9).

High macroalgal biomass often correlates with mortality of stony corals (Lewis, 1986; Hughes, 1994; Steneck, 1994), and may result in reduced growth (Lewis, 1986; Lirman, 2001) as well as decreased recruitment of juvenile scleractinians (Birkeland, 1977). By having provided substrata for algal colonization and growth, the skeletons of *A. palmata* (Aronson and Precht, 2000) and other corals killed by disease or lethal bleaching (such as the *M. annularis* species complex and *A. tenuifolia*, respectively) may have facilitated the expansion of macroalgae in the Yucatán's fore reefs. In turn, overgrowth of live coral polyps by macroalgae may have contributed to the relatively high values of recent mortality found in the Akumal population of *A. palmata*.

Proliferations of macroalgae can also occur as a result of increases in nutrients (e.g., Lapointe, 1997) and/or declines in herbivory (e.g., Hughes, 1994; Steneck 1994). Hasty development of coastal infrastructures, locally high human populations, inadequate sewage treatment (especially in the pueblos), and the hydrography of the Caribbean coast of México make it particularly vulnerable to nutrient enrichment. Groundwater discharged from a ramified underground river complex of cenotes permeates much of the northern Yucatán coast. At Akumal, where discharges are commonly observed in the deep, shelf-edge reefs (D. Brewer, personal communication), nutrients in groundwater potentially pose an elevated risk because of the close proximity of the reefs to the shore.

Although herbivorous acanthurids and scarids were among the more common fishes quantified in the fore-reefs off Akumal and Xcalak (Fig. 12), their population densities were low (combined means of 16/100m²) compared to many other areas in the wider Caribbean (Kramer, this volume). The 1997 fish herbivory rates off Akumal resembled those found at 10 m depths in 1988 on the severely overfished reefs of Jamaica, but were less than 10% the rates which had been obtained that year in St. Croix (Steneck, 1994).

The key herbivore, *Diadema antillarum*, was very rare, particularly in the fore reefs (Table 4), and other grazing echinoids, such as *Echinometra viridis* and *Triptneustes ventricosus* (e.g., Aronson and Precht, 2001; Edmunds and Carpenter, 2001), were notably scarce (personal observations). Hence, low levels of herbivory may well have contributed to the high relative abundance and biomass of macroalgae, particularly off Akumal.

As populations of *Diadema* have begun to recover in some Caribbean reefs, macroalgae are becoming less abundant (personal observations). Edmunds and Carpenter (2001) have recently reported an upsurge in coral recruitment at shallow (<9m) fore reefs near Discovery Bay, Jamaica in which densities of *Diadema* had increased. Since 1999, populations of *Diadema* have similarly rebounded in lagoonal patch reefs off both Akumal (R. Roy, personal communication) and Xcalak (S. Redman, personal communication). Should similar increases occur in the Akumal fore reefs, the build-up seen in its macroalgal populations might be reversed at least partially.

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REFERENCES

- Aronson, R.B. and W.F. Precht
2001. White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25-38.
- Birkeland, C.
1977. The importance of rates of biomass accumulation in early successional stages of benthic communities. *Proceedings of the Third International Coral Reef Symposium*, Miami 1:15-21.
- Brown, B.E.
1997. Coral bleaching: causes and consequences. *Coral Reefs* 16, Suppl.:S129-S138.
- Cho, L. and J. Woodley
2000. *Diadema antillarum*: a facilitator of recovery on the reefs of Discovery Bay, Jamaica. *Proceedings of the Ninth International Coral Reef Symposium Abstract*, p. 79.
- Edmunds, P.J., and R.C. Carpenter
2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings of the National Academy of Sciences* 98:5067-5071.

- Fitt, W.K., B.E. Brown, M.E. Warner, and R.P. Dunne
2001. Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* 20:51-65.
- Ginsburg, R., P. Alcolado, E. Arias, A. Bruckner, R. Claro, A. Curran, A. Deschamps, A. Fonseca, J. Feingold, C. Garcia-Saez, D. Gilliam, S.D. Gittings, A. Glasspool, G. Horta-Puga, K. Klomp, P.A. Kramer, P.R. Kramer, Z. Leao, J. Lang, C. Manfrino, R. Nemeth, C. Pattengill-Semmens, P. Peckol, J. Posada, B. Riegl, J. Robinson, P. Sale, R. Steneck, J. Vargas, and E. Villamizar
2000. Status of Caribbean Reefs: Initial results from the Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program. *Proceedings of the Ninth International Coral Reef Symposium Abstract*, p. 211.
- Gladfelter, W.B.
1982. White-band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. *Bulletin of Marine Science* 32:639-643.
- Glynn, P.W.
1993. Coral reef bleaching: ecological perspectives. *Coral Reefs* 12:1-17.
- Grime, J.P.
1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169-1194.
- Grime, J.P.
1989. The stress debate: symptom of impending synthesis? *Biological Journal of the Linnean Society* 37:3-17.
- Hughes, T.P.
1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547-1551.
- Humann, P.
1993. *Reef Coral Identification*. New World Publications, Inc., Jacksonville, FL, 252 pp.
- Jordán Dahlgren, E.
1993. *Atlas de Los Arrecifes Coralinos del Caribe Mexicano. I. El Sistema Continental*. Centro de Investigaciones de Quintana Roo Instituto de Ciencias del Mar y Limnología México, D. F. 110 pp.
- Kramer, P.A., and P. Richards Kramer
In press. Transient and lethal effects of the 1998 coral bleaching event on the Mesoamerican Reef System. *Proceedings of the Ninth International Coral Reef Symposium*.
- Kramer, P.A., P.R. Kramer, A. Arias-González, and M. McField
2000. Status of coral reefs of northern Central America: México, Belize, Guatemala, Honduras, Nicaragua and El Salvador. Pp: 287-313. In: C. Wilkinson (ed.), *Status of Coral Reefs of the World: 2000*. Australian Institute of Marine Science. Cape Ferguson, Queensland and Dampier, Western Australia.
- Lang, J., P. Alcolado, J.P. Carriart-Ganivet, M. Chiappone, A. Curran, P. Dustan, G. Gaudian, F. Geraldès, S. Gittings, R. Smith, W. Tunnell, and J. Wiener
1998. Status of coral reefs in the northern areas of the Wider Caribbean, Pp. 123-134. In: C. Wilkinson (ed.), *Status of Coral Reefs of the World: 1998*, Australian Institute of Marine Science.

Lapointe, B.E.

1997. Nutrient thresholds for eutrophication and macroalgal overgrowth of coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography* 42:1119-1131.

Lewis, S.M.

1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* 56:183-200.

Lirman, D.

2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19:392-399.

Muñoz-Chagin, R.F., and G. de la Cruz-Aguera

1993. Corales del arrecife de Akumal, Quintana Roo. Pp. 761-771. In: S.I. Salazar-Vallejo and N.E. González (eds.), *Biodiversidad Marina y Costera de México*. Com. Na. Biodiversidad CONABIO y CIQRO, México, D.F.

Richardson, L.L.

1998. Coral diseases: what is really known? *Trends in Ecology and Evolution* 13:438-442.

Smith, J.E., C.M. Smith, C.L. Hunter

2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19:332-342.

Steneck, R.S.

1988. Herbivory on coral reefs: a synthesis. *Proceedings of the Sixth International Coral Reef Symposium*, Australia 1:7-49.

Steneck, R.S.

1994. Is herbivore loss more damaging to reefs than hurricanes? Case studies from two Caribbean reef systems (1978-1988). Pp. 220-226. In: Ginsburg, R.N. (compiler). *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History*. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami.

Steneck, R.S. and M.N. Dethier

1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 69:476-498.

Steneck, R.S., R.N. Ginsburg, P. Kramer, J. Lang, and P. Sale

2000. Atlantic and Gulf Rapid Reef Assessment (AGRRA): a species and spatially explicit reef assessment protocol. *Proceedings of the Ninth International Coral Reef Symposium Abstract*, p. 220

Wilkinson, C.

2000. Executive summary. Pp. 7-17. In: C. Wilkinson (ed.), *Status of Coral Reefs of the World: 2000*. Australian Institute of Marine Science, Cape Ferguson, Queensland and Dampier, Western Australia

Table 1. Site and transect information for AGRRA surveys in March 1999 off Akumal and Xcalak, México.

Site name	Reef type	Latitude (° ' N) ¹	Longitude (° ' W) ¹	Survey date	Depth (m)	Benthic transects (#)	≥25 cm stony corals (#/10m)	% live stony coral cover (mean ± sd)
Akumal								
Yalkul	Fringing-barrier fore reef	20 24.5	87 18.0	Mar 12 99	11	12	6.5	21.0 ± 9.0
Média Luna	Fringing-barrier fore reef	20 21.1	87 18.2	Mar 12 99	11.5	14	4.5	13.5 ± 8.0
Dick's	Fringing-barrier fore reef	20 24.0	87 18.4	Mar 12 99	11.5	10	6.5	19.0 ± 8.0
Doña Laticia	Fringing-barrier fore reef	20 23.8	87 18.4	Mar 12 99	13	12	6.5	18.0 ± 10.5
Motorcyle	Fringing-barrier fore reef	20 23.5	87 18.5	Mar 8 99	13	7	3.5	15.5 ± 5.5
Las Redes	Fringing-barrier fore reef	20 23.5	87 18.6	Mar 8 99	18	7	4	17.0 ± 9.0
Xcalak								
Dos Cocos	Fringing-barrier fore reef	18 19.7		Mar 10 99	13	10	4.5	9.5 ± 5.5
Sur de Nicas	Fringing-barrier fore reef	18 16.9	87 49.0	Mar 9 99	16.5	12	6.5	20.0 ± 10.0
Canyons	Fringing-barrier fore reef	18 15.5	87 49.1	Mar 9 99	15	17	2.5	8.5 ± 4.0
Coral Gardens	Fringing-barrier fore reef	18 14.4	87 49.6	Mar 10 99	8.5	10	6	14.0 ± 6.0
El Quebrado	Fringing-barrier fore reef			Mar 10 99	11	12	6	37.0 ± 20.5
Chimney	Fringing-barrier fore reef	18 13.3	87 52.3	Mar 10 99	11.5	16	2	9.5 ± 9.5
Blanquezar	Lagoonal patch reef	18 19.5	87 48.9	Mar 11 99	1.5	15	7.5	20.5 ± 11.0
Portillas	Lagoonal patch reef	18 14.1	87 49.9	Mar 9 99	3	16	5	16.0 ± 12.5

¹Missing locations resulted from GPS failures.

Table 2. Abundance, size and mortality of large (≥ 25 cm diameter) reef-building corals in March 1999, by species in fore reefs off Akumal and Xcalak.

Species	Colonies			Maximum diameter (cm)	% Live cover	Partial-colony mortality (%)		
	(#)	%	Density (#/m)			Recent	Old	Total
<i>Acropora palmata</i>	43	5.55	0.031	205	6.36	4.5	54.0	58.5
<i>Agaricia agaricites</i>	28	3.90	0.019	45	0.86	1.5	19.0	20.5
<i>Agaricia tenuifolia</i>	35	4.53	0.025	70	1.75	3.5	42.0	45.5
<i>Colpophyllia natans</i>	27	3.82	0.019	55	1.03	4.0	18.0	22.0
<i>Colpophyllia breviserialis</i>	2	0.36	0.001	85	0.09	0	5.0	5.0
<i>Diploria clivosa</i>	4	0.65	0.003	35	0.11	3.0	19.5	22.5
<i>Diploria labyrinthiformis</i>	16	2.63	0.013	35	0.48	4.0	14.0	18.0
<i>Diploria strigosa</i>	26	4.04	0.020	55	1.08	1.5	22.0	23.5
<i>Madracis mirabilis</i>	3	0.44	0.003	30	0.09	3.5	35.0	38.5
<i>Millepora complanata</i>	4	0.59	0.003	70	0.21	0	2.5	2.5
<i>Montastraea annularis</i>	188	28.94	0.139	65	9.04	6.0	34.5	40.5
<i>Montastraea cavernosa</i>	36	5.68	0.026	35	0.91	1.0	15.0	16.0
<i>Montastraea faveolata</i>	136	20.34	0.104	95	9.67	5.0	27.5	32.5
<i>Montastraea franksi</i>	33	5.17	0.026	95	2.47	2.5	28.0	30.5
<i>Porites astreoides</i>	25	3.58	0.019	30	0.61	3.5	12.5	16.0
<i>Porites furcata</i>	2	0.22	0.001	30	0.03	0	7.5	7.5
<i>Porites porities</i>	11	1.48	0.009	30	0.28	2.5	24.0	26.5
<i>Siderastrea siderea</i>	32	6.36	0.026	40	1.04	4.0	15.0	19.0
Mean \pm standard error	36.0 \pm 48.5	5.5 \pm 7.5	0.025 \pm 0.035	60 \pm 40	2.0 \pm 3.0	3.0 \pm 2.0	22.0 \pm 13.0	24.5 \pm 14.5

Table 3. Size and condition (mean \pm standard deviation) of all stony corals (≥ 25 cm diameter) in March 1999, by site off Akumal and Xcalak.

Site name	Stony corals		Partial-colony mortality (%)			Standing dead	Stony corals (%)		Diseased ¹
	(#)	Diameter (cm)	Recent	Old	Total		Bleached		
							Light	Moderate	
Akumal									
Fore reefs									
Yalku	79	100 \pm 130	6.5 \pm 14.5	29.5 \pm 30.5	35.0 \pm 33.0	6	9	6	6
Média Luna	63	110 \pm 255	4.0 \pm 7.5	27.5 \pm 30.5	31.0 \pm 32.0	8	14	0	6
Dick's	66	110 \pm 85	8.5 \pm 21.5	37.5 \pm 33.5	43.5 \pm 35.5	15	8	12	4
Doña Laticia	75	75 \pm 80	4.5 \pm 10.5	26.0 \pm 26.0	31.0 \pm 31.0	2	14	2	11
Motorcyle	26	70 \pm 50	0.5 \pm 1.0	24.5 \pm 19.0	24.5 \pm 19.0	0	4	0	0
Los Redes	27	70 \pm 40	2.5 \pm 5.0	23.5 \pm 19.0	25.5 \pm 20.0	0	8	0	4
Xcalak									
Fore reefs									
Sur de Nichas	76	45 \pm 25	4.0 \pm 8.5	17.5 \pm 17.0	21.5 \pm 20.0	0	6	0	2
Canyons	46	50 \pm 35	1.0 \pm 3.0	40.5 \pm 37.5	41.5 \pm 37.5	6	18	11	2
Coral Gardens	60	85 \pm 100	8.5 \pm 15.5	29.0 \pm 33.5	37.5 \pm 37.0	8	10	14	4
Chimney	35	55 \pm 30	5.5 \pm 11.5	21.5 \pm 26.0	26.5 \pm 27.5	6	6	20	0
El Quebrado	72	95 \pm 90	6.0 \pm 10.5	30.5 \pm 27.5	36.5 \pm 29.5	4	12	11	0
Dos Cocos	44	45 \pm 40	4.0 \pm 7.5	31.5 \pm 28.0	35.5 \pm 29.0	0	9.0	14	0
Patch Reefs									
Blanquezar	113	140 \pm 115	29.0 \pm 22.0	39.5 \pm 27.0	67.5 \pm 25.5	12	12	12	10
Portillas	83	160 \pm 120	26.5 \pm 25.0	41.5 \pm 26.5	67.0 \pm 25.0	6	7	8	12

¹All diseased corals had white plague, except for one colony at Doña Laticia which had black-band disease.

Table 4. Algal characteristics, and density of *Diadema antillarum* (mean \pm standard deviation) in March 1999, by site off Akumal and Xcalak.

Site name	Quadrats (#)	Relative abundance (%)			Macroalgal		<i>Diadema</i> (#/100m ²)
		Macroalgae	Turf algae	Crustose coralline algae	Height	Index ¹	
<i>Akumal</i>							
<i>Fore reefs</i>							
Yalku	63	46.5 ± 38.0	26.0 ± 27.0	27.5 ± 30.0	2.0 ± 1.5	93	0
Média Luna	68	38.0 ± 34.5	37.5 ± 27.0	24.5 ± 23.5	2.0 ± 2.0	76	0
Dick's	45	55.0 ± 35.0	25.0 ± 25.5	20.0 ± 24.0	3.0 ± 1.5	165	0
Doña Laticia	59	34.0 ± 31.0	45.5 ± 29.0	20.5 ± 21.0	2.0 ± 1.5	68	0
Motorcyle	33	53.0 ± 27.0	32.5 ± 24.5	14.5 ± 11.5	2.5 ± 1.5	132.5	0
Los Redes	33	36.0 ± 24.5	41.0 ± 26.5	23.0 ± 18.5	2.5 ± 1.5	90	0
<i>Xcalak</i>							
<i>Fore reefs</i>							
Sur de Nichas	55	13.0 ± 15.0	59.5 ± 22.0	28.0 ± 21.0	1.5 ± 1.5	19.5	0
Canyons	85	24.5 ± 21.5	52.5 ± 22.5	23.0 ± 17.5	2.0 ± 1.5	49	0
Coral Gardens	40	17.5 ± 24.5	37.5 ± 29.5	45.0 ± 33.0	0.5 ± 1.0	9.0	0
Chimney	79	19.0 ± 16.5	58.5 ± 26.5	22.5 ± 23.5	1.5 ± 1.5	28.5	0
El Quebrado	57	24.0 ± 25.5	40.5 ± 25.5	35.5 ± 27.5	2.0 ± 2.0	48	0
Dos Cocos	45	30.0 ± 24.0	49.0 ± 24.0	21.0 ± 23.5	1.5 ± 1.0	45	0
<i>Patch reefs</i>							
Blanquezar	62	15.5 ± 20.0	71.5 ± 26.0	12.5 ± 19.0	1.0 ± 1.5	15.5	3.5
Portillas	74	17.5 ± 20.5	62.0 ± 26.5	20.5 ± 20.0	2.0 ± 2.0	35	0

¹Macroalgal index = % relative macroalgal abundance x macroalgal height