

Figure 1. AGRRA survey reefs in central-southern Quintana Roo, México.

* = Location of the Campechen, Boca Paila and San Miguel Lagoons. Modified from Núñez-Lara and Arias-González (1998).

CONDITION OF CORAL REEF ECOSYSTEMS IN CENTRAL-SOUTHERN QUINTANA ROO, MEXICO (PART 1: STONY CORALS AND ALGAE)

BY

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ABSTRACT

In 1999 *Montastraea faveolata* and *M. annularis* were the most numerous “large” (≥ 25 cm diameter) stony corals at ~ 10 m on fore reefs in the central and southern areas, respectively, of Quintana Roo, México. Reductions in live stony coral cover (from $\sim 25\%$ to $\sim 12\%$ in < 10 years) and high recent partial-colony mortality (7-27.5%) are indications of declining reef conditions. Diseases in the five more northerly reefs, as well as tissue loss from the 1998 El Niño Southern Oscillation (ENSO) bleaching event and/or from on-going bleaching during June-July 1999 in the three southernmost reefs, appeared responsible for much of the recent mortality. Although turf algae predominated everywhere, macroalgae were relatively more abundant in the five more northerly reefs (four of which are in a reserve where herbivorous fishes currently are less numerous than further south). Additional perturbations associated with tourism development in the southern area could result in a loss of resilience of these coastal reefs.

INTRODUCTION

The greatest reef development in México is found in its Caribbean reefs which are principally of the fringing type. Extending for over 350 km along the coast of the state of Quintana Roo (Gutiérrez et al., 1995), they comprise the northernmost part of the Mesoamerican Reef System which continues through the neighboring countries of Belize, Guatemala and Honduras.

Tourism has become the principal economic activity along the Quintana Roo coast representing $\sim 75\%$ of the state's 1999 Gross Internal Product (INEGI, 2000). At

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present this activity is concentrated throughout the northern coastal area, such as at Isla Mujeres, Cozumel, and along the Cancún-Tulum Corridor. However, tourism infrastructure is either planned or developing in some southern areas of the state, particularly between Pulticub and Xcalak (Daltabuit Godás, 1999). Specific threats associated with this development include ecologically inappropriate forms of coastal development, diving, pollution from solid and liquid wastes, vessel traffic, and fishing (Daltabuit Godás, 1999).

Another important aspect of the Mexican Caribbean is that a number of protected areas have been created with a view towards direct or indirect protection of its coral-reef ecosystems. The largest among these is the Sian Ka'an Biosphere Reserve established in 1986 between 19°05' N and 20°06' N in the central area of the coast. This reserve is protected by regulations restricting commercial fishing activities, aquatic sports, and development.

Hence coral reefs are severely threatened by intense tourism activity in the northern area, protected in the central area, and potentially at risk in the south. Consequently, reef "health" within each area of the Mexican Caribbean may vary as a function of these differing levels of anthropogenic input. The aim of this study was to evaluate benthic reef condition in the spur-and-groove habitat of the fore-reef slope zone in the central and southern areas using the Atlantic and Gulf Rapid Reef Assessment (AGRRA) methodology.

METHODS

The study area extends along approximately 230 km of the Quintana Roo coast (Fig. 1) and includes eight fringing reefs, four of which are located in the central area within the Sian Ka'an Biosphere Reserve. On the basis of morphology and degree of development, the Quintana Roo reef system has been divided into 16 subregions (ICRI, 1998). Three reefs (Boca Paila, Punta Yuyum, Punta Allen) are in the Sian Ka'an North subregion which is characterized as having a narrow continental shelf with steep slopes, "intermediate amounts" of freshwater input, narrow to "moderately wide" lagoons and, generally, highly developed fore-reef spurs and grooves. Coral cover averaged nearly 25% in the early 1990's when 42 species of scleractinian corals were found in this subregion (Gutierrez et al., 1993; ICRI 1998). These three reefs are distinguished from the remainder in having submerged crests and lagoons that are open to the ocean, and by their close proximity to coastal bays (Ascensión and Espíritu Santo) and lagoons (Campechen, Boca Paila and San Miguel).

Reef structures are more highly developed and complex overall on the five southernmost reefs (one of which, Tampalam, is located within the Biosphere Reserve in the central geographic area). The extreme northern portion of their reef crests runs into the shore, thereby enclosing and protecting large seagrass meadows landward of the reef flats. Tampalam and El Placer in the Sian Ka'an South subregion have narrow reef crests and slightly lower values for coral cover and scleractinian species number (22% and 41, respectively). Two reefs (Mahahual and Xahuayxol) in the Mahahual subregion, which are in the "shadow" of an offshore bank (Banco Chinchorro), have particularly well-developed fore-reef terraces with high-relief spurs and grooves, and back reefs that

extend almost to the beach. The highest values for coral cover (nearly 28%) and species richness (46) occurred in this subregion. Xcalak, in the Xcalak Trench subregion, has a well-developed lagoon and breaker zone and well-developed spurs and grooves on the fore reef and is somewhat under the shadow of Banco Chinchorro. Coral cover here was nearly 25% but there were only 33 species of corals in the early 1990s.

A characteristic of all the studied reefs is that the fore reef develops as a series of “strips” (spurs and grooves) that run parallel to the coast and are usually separated from each other by intervening sand channels. Hence it is possible to differentiate between an inner fore reef (at depths ranging from 6 m to as much as 25 m), an outer fore reef (from ~15 m to as deep as 40 m), and a deep fore reef (from ~35 to ~50 m) terminating in a shelf-edge reef at the continental margin (ICRI, 1998).

It has been suggested that the Mexican Caribbean reef system has been molded by the high frequency of tropical storms and hurricanes crossing this area, particularly near the Belizean border in the southern geographic area and between Cozumel and the Yucatán Channel in the northern area (ICRI, 1998). The last significant storm that passed near our study areas was Hurricane Mitch in October 1998; nevertheless, there are just three descriptions of its effects at Mahahual (Garza-Pérez, 1999; Garza-Pérez et al., 2000; Bastida-Zavala, 2000). Similarly, there is only one formal report of the 1998 mass bleaching event, which is an important recent disturbance. Its effects were documented at Xcalak, Mahahual, Tampalam, and further north at Akumal by Garza-Pérez (1999), who continued to assess the condition of the Mahahual reef through 2000 (Garza-Pérez, in preparation).

This study was conducted in the fore-reef spur-and-groove habitat at an average depth of 10 m where stony coral cover in central-southern Quintana Roo is highest (Gutiérrez et al., 1993; Gutiérrez et al., 1995). We did not survey the outer-reef crest, another important habitat, for logistical reasons and because it is not well-developed on all the study reefs.

We established a hierarchical survey design based on three spatial scales: geographic area (central and southern), reefs (four in each area), and subreefs (three per reef). Reefs that were known to exhibit maximum spur-and-groove development were chosen on the basis of previous field work and from published descriptions (Gutiérrez et al., 1993; Jordán, 1993) and were thus selected on the basis of both strategic and representative criteria (see Appendix One). The distance between reefs, which were named after the nearest town or coastal feature (Fig. 1), was approximately 20-30 km, except for Tampalam which is ~75 km south of Punta Allen. To avoid pseudoreplication (i.e., Oxley 1997), the north (N), center (C) and south (S) subreef for each reef were positioned 0.9-1 km apart. This separation distance was chosen to prevent large geomorphological changes between the subreefs of any given reef. Their geographical coordinates were established by GPS (Table 1). Borders delimiting each subreef were temporarily established within which surveys were performed on haphazardly positioned transects over the spur structures in the inner spur-and-groove zones.

Fieldwork was carried out by two observers (Ruiz-Zárate on the transects and Hernández-Landa on the quadrats) between June and October 1999 (Table 1), using the AGRRA Version 2.2 benthos protocols (see Appendix One, this volume). The sizes of the individually surveyed stony corals (scleractinians and *Millepora* spp.) were measured to the nearest cm. Crustose coralline algae were exposed by vigorous removal of

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sediment and pushing apart any macroalgae and species of scleractinians that are small as adults were omitted from the counts of tiny (<2 cm diameter) corals. Training exercises were conducted in the field prior to performing the surveys. Humman's (1993a, 1998b) field guides aided in the identification of organisms.

Averages were computed for each spatial scale (subreef, reef, and area). Correlation and regression analyses were then applied to find statistical tendencies.

RESULTS

Stony Corals

Four morphological forms of *Agaricia agaricites* (*A. agaricites agaricites*, *A. agaricites carinata*, *A. agaricites danai*, *A. agaricites purpurea*) that were recognized in this study have not previously been discriminated in the Mexican Caribbean and, for matters of comparison, they were considered as a single species (*Agaricia agaricites*). A total of 24 species of "large" stony corals (colonies ≥ 25 cm maximum diameter) were recorded in our transects, representing nearly 60% of the 47 species listed in central-southern Quintana Roo by Beltrán-Torres and Carricart-Ganivet (1999). Of these 47 species, 37 can be expected to occur in depths of about 10 m (Cuadro 2; Beltrán-Torres and Carricart-Ganivet, 1999; personal observations). Twenty-six are reported to grow larger than 25 cm in diameter (after Humann, 1993), seven to be smaller than 25 cm, and three of the four species for which no sizes were given (*Porites furcata*, *Montastraea faveolata*, *M. franksi*) are well known to exceed 25 cm in diameter while the fourth, *Porites divaricata*, is usually small. Included in our surveys were 23 (79 %) of the 29 large species known to occur in this habitat and one species (*Madracis decactis*) that Humann (1993) had characterized as being less than 25 cm in diameter.

Four species numerically constituted 50% of the total: *Montastraea annularis* > *M. faveolata* > *M. cavernosa* > *Diploria strigosa* (Fig. 2). Species with relative frequencies of 70-100% (i.e., recorded at 17-24 of the subreefs), in order of decreasing frequency, were *D. strigosa*, *M. faveolata*, *M. cavernosa*, *M. annularis*, *Siderastrea siderea*, *Colpophyllia natans*, *D. labyrinthiformis*, *Porites astreoides* and *M. franksi*.

The two reefs (Xcalak, El Placer) with the lowest mean live stony coral cover (~9%), and Mahahual, with the highest mean cover (~17%), were all in the southern area (Table 1). Mean live stony coral cover for the four reefs in the central area was virtually identical to that of the four southern reefs and averaged 12.0% overall (sd = 6.2, n = 311 transects). The mean density of large (≥ 25 cm diameter) stony corals varied from 1.5-6.0/10 m transect.

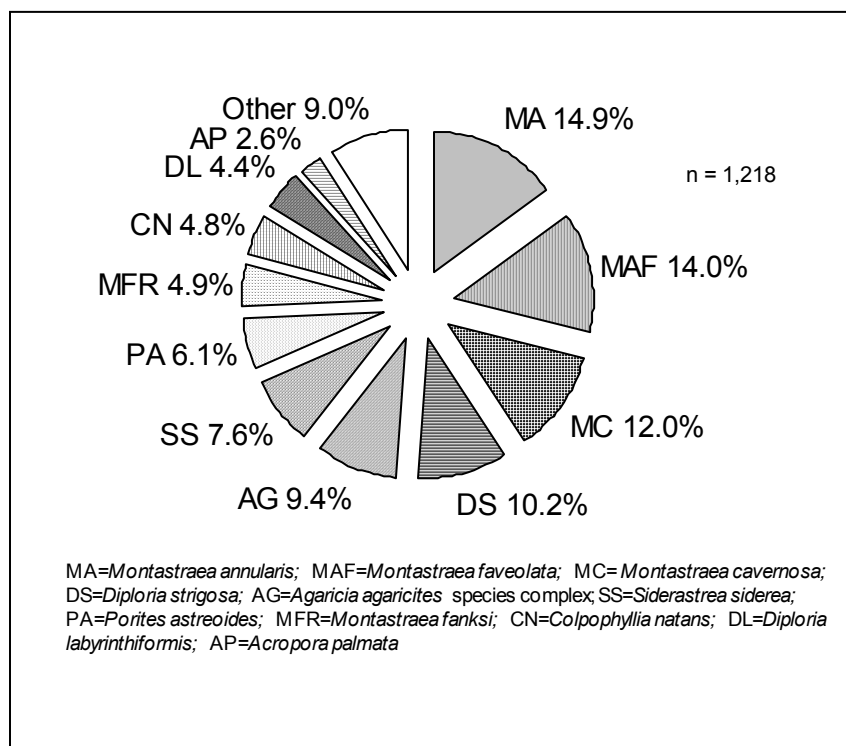


Figure 2. Species composition and mean relative abundance of the most abundant stony corals (≥ 25 cm diameter) at 8-12 m on fore reefs in central-southern Quintana Roo, México. Other = *Agaricia tenuifolia*, *Meandrina meandrites*, *Porites furcata*, *P. porites*, *Acropora cervicornis*, *Madracis mirabilis*, *M. decactis*, *Millepora complanata*, *M. alcicornis*, *Mycetophyllia ferox*, *M. danaana*, *Dendrogyra cylindrus*, *Eusmilia fastigiata*, and standing dead colonies of *Diploria*, *Montastraea* and *Agaricia*.

The diameters of large stony corals were smallest in El Placer (~ 48 cm) and largest in Boca Paila (~ 65 cm) (Table 2). Stony corals were slightly larger overall in the central area than in the southern area; the mean diameter for both areas combined was 56.3 cm (sd = 40.6, n = 1,218 corals). The size-frequency distributions, both as maximum diameter and as maximum height, of the five most abundant large species in each geographic area are summarized in Figures 3A, B. Colonies of *M. faveolata*, which were more abundant in reefs of the central area, constituted the largest corals in both areas. Apart from *M. faveolata*, most of the surveyed colonies were in small to intermediate size classes (30-50 cm for maximum diameter, 10-60 cm for maximum height).

The mean density of stony coral recruits in the different reefs varied from 0.1-0.4/0.0625 m², averaging 0.2 /0.0625 m² in both geographic areas (Table 3). In many cases, it was not possible to identify the coral recruits to the species level. The three most important genera, in order of relative abundance, were *Agaricia*, *Siderastrea* and *Porites* (Fig. 4). Only one individual of the herbivorous echinoid *Diadema antillarum* was found in a belt transect in one subreef (Tampalam N).

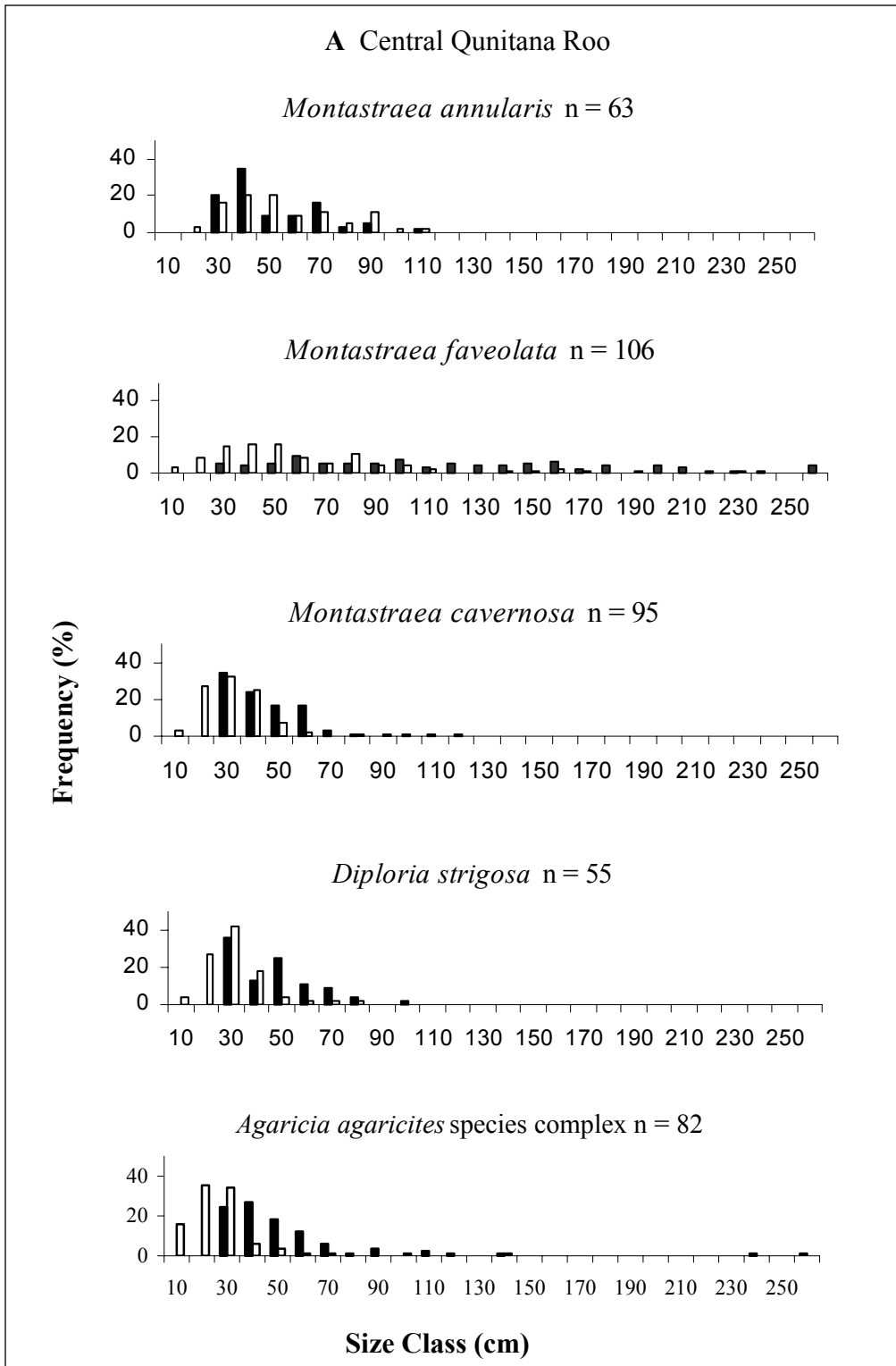


Figure 3A. Size-frequency distribution as diameter (dark bars) and height (white bars) of colonies (≥ 25 cm diameter) at 8-12 m on fore reefs in central Quintana Roo, México.

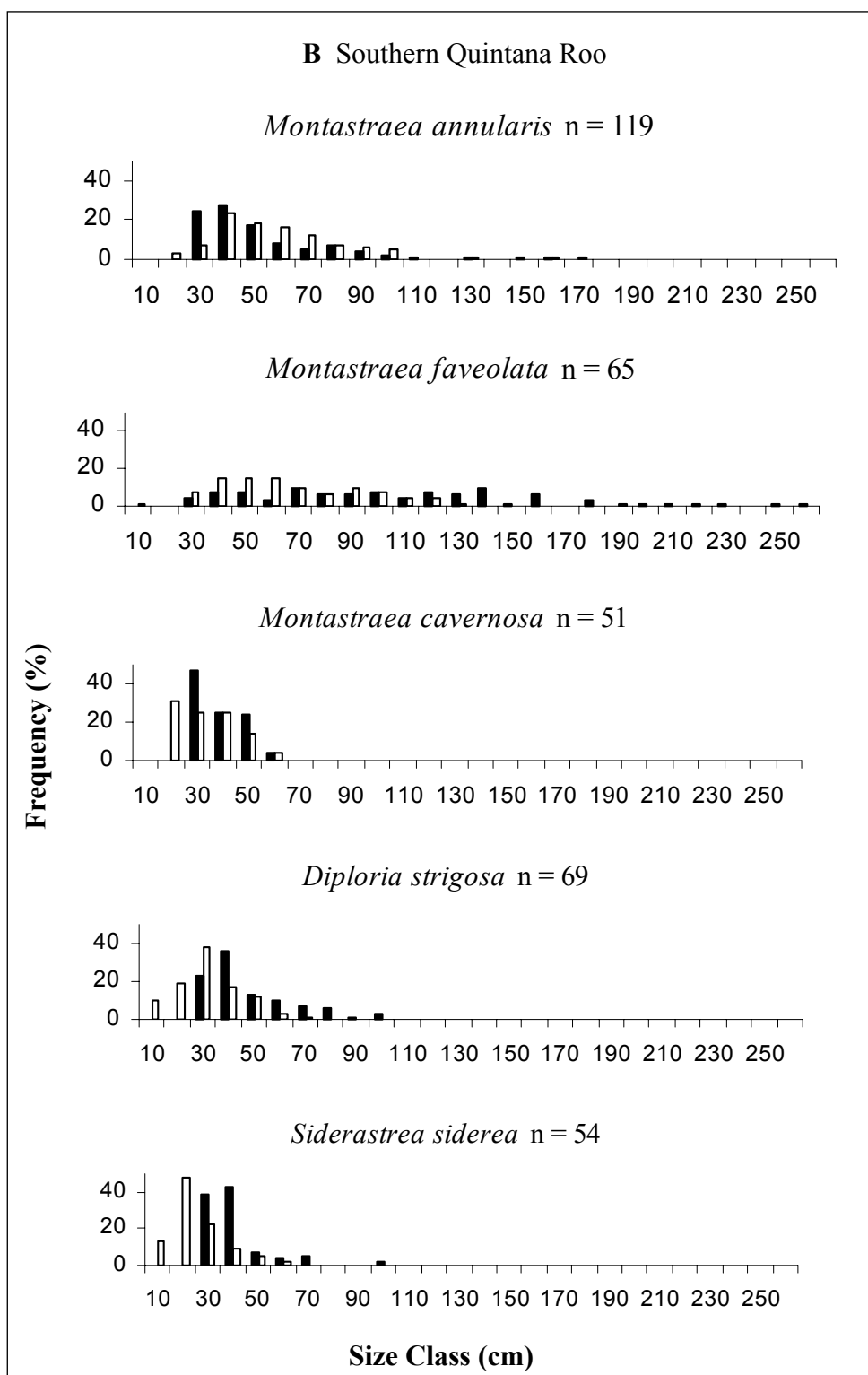


Figure 3B. Size-frequency distribution as diameter (dark bars) and height (white bars) of colonies (≥ 25 cm diameter) at 8-12 m on fore reefs in southern Quintana Roo, México.

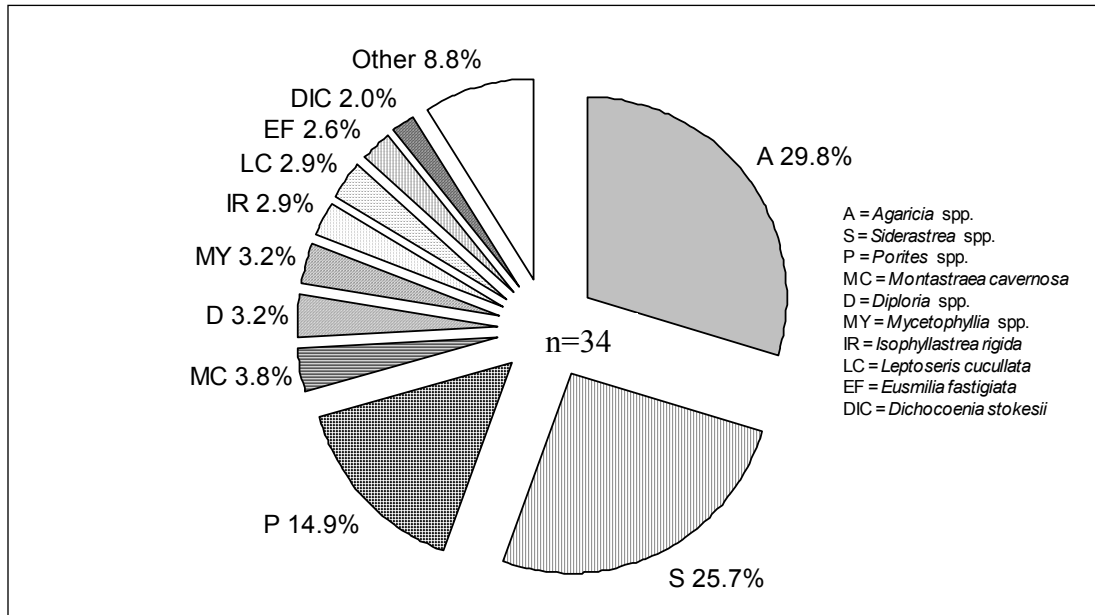


Figure 4. Species composition and mean relative abundance of all stony coral recruits (≥ 2 cm diameter, excluding species that are small as adults) at 8-12 m on fore reefs in the central and southern Mexican Caribbean. Other = *Stephanocoenia intersepta*, *Montastraea* spp., *Madracis* spp., *Meandrina meandrites*, *Manicina areolata*, *Acropora cervicornis*, *Isophyllia sinuosa*, *Colpophyllia natans*, *Millepora alcicornis* and a tiny unknown scleractinian.

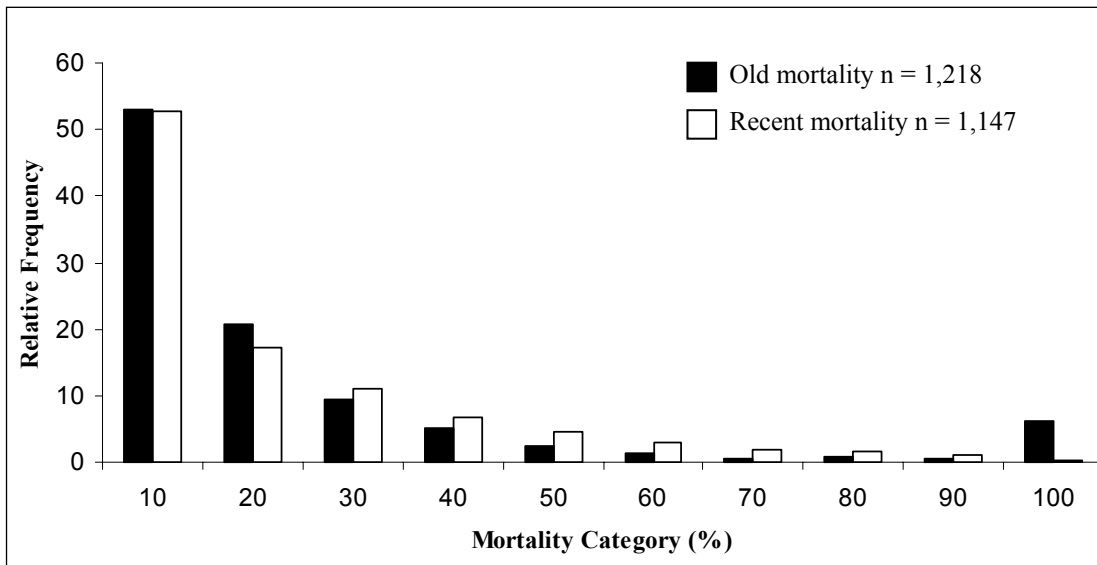


Figure 5. Frequency distribution as % of old partial colony mortality (black bars) and recent partial colony mortality (white bars) of all stony corals (≥ 25 cm diameter) at 8-12 m on fore reefs in central-southern Quintana Roo, México.

Coral Condition

Recent partial-colony mortality (hereafter recent mortality) was relatively high, exceeding 15% in 70 % (17/24) of the subreefs, with only one reef each in the central (Tampalam) and southern (Xcalak) areas having mean values of <15%. Levels of recent mortality in the two areas were very similar, and the overall mean was 18.0% (sd = 20.0, n = 1146 stony corals).

The two reefs (Mahahual, Xahuayxol) with the lowest mean levels of old partial-colony mortality (hereafter old mortality), as well as the reef with the highest mean old mortality (Xcalak) were all in the southern area. Mean values of old mortality overlapped at the area scale and the overall mean of 19.3% (sd. = 25.4, n = 1218 stony corals) was close to that for recent mortality. Nonetheless, the most frequent percentage class category for both recent and old coral mortality was 0-10% (Fig. 5).

Total (recent + old) partial-colony mortality in the reefs ranged between about 30% at Xahuayxol in the southern area to 43% at Punta Yuyum in the central area. The percentage of “standing dead” stony corals (i.e., 100% mortality of upward facing surfaces of colonies still in the original position of growth) exhibited two pronounced peaks: between Punta Yuyum and Punta Allen in the central area (6-16% of all colonies, n=6 subreefs), and at Xcalak in the southern area (12-24% of colonies, n = 3 subreefs). *Acropora palmata* accounted for about half to two-thirds of the standing dead corals in Punta Allen (10/18) and Xcalak (13/19) but *Diploria* represented half (10/19) of the standing dead colonies in Punta Yuyum. Corresponding values for standing dead on the remaining subreefs ranged from 0-6% (Table 2).

Except for two subreefs in the central area (Punta Allen N, Tampalam N), bleaching was restricted to the southern geographic area, principally between Mahahual N and Xahuayxol C (Fig. 6). “Partly bleached” was the most common condition in these five subreefs affecting 18–35% of the large stony corals. Only in Mahahual, where the highest percentages of stony corals with bleached tissues were found, were all three bleaching categories (pale, partly bleached, bleached) recorded (Fig. 6).

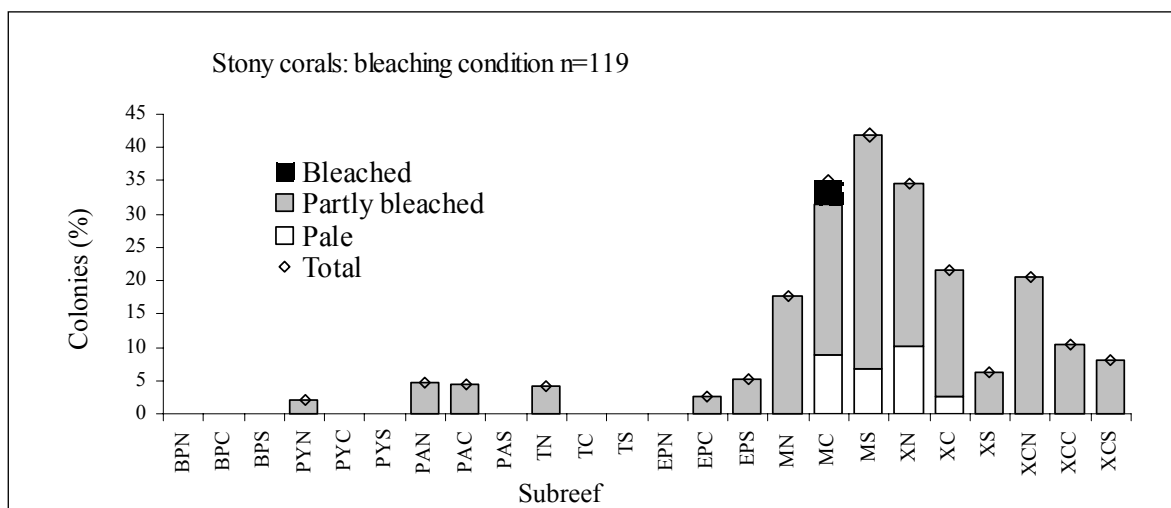


Figure 6. Percentages of all stony corals (≥ 25 cm diameter) affected by bleaching (as pale, partly bleached, bleached) at 8-12 m on fore reefs in central-southern Quintana Roo, México.

Diseased stony corals were relatively rare in the three most southerly of the reefs (being 0% at Xahuayxol) (Table 2). Percentages of diseased corals were highest in Boca Paila (~30%) and Tampalam (25%) in the central geographic area and in El Placer (21%), the most northerly of the southern reefs. After pooling the data for each subreef, the southern area was considerably less affected overall than the central area (mean = 7.1 %, sd = 9 versus mean = 19.4%, sd = 11.7, respectively; for each n = 12 subreefs).

White plague (WPD) was the only disease recorded in Boca Paila, where *M. faveolata* constituted 50-75% of all diseased colonies. WPD was responsible for 66-88% of all diseased colonies in Tampalam (*M. annularis* species complex >> *A. agaricites* and *P. astreoides*) and 62-80 % in El Placer (*M. annularis* species complex >> *S. siderea*, *A. agaricites*, *D. strigosa*, *A. tenuifolia* and *Meandrina meandrites*). Some colonies of *M. meandrites* at Tampalam and El Placer were affected by black-band disease and by what appeared to be a form of red-band disease. Dark-spots disease (in *S. siderea*) and unknown diseases were also seen at Tampalam and a colony of *Diploria strigosa* with signs of a disease resembling yellow-blotch disease was seen at El Placer.

Algae

Turf algae were the predominant algal group at all but one of the most northerly subreefs (Table 3). The mean relative abundance of macroalgae was higher in the central area and in El Placer (20-41%, n = 15 subreefs) than further south (13-19%, n = 9 subreefs). Crustose coralline algae were more abundant than macroalgae in most (8/9) subreefs in the three most southerly reefs and they were comparable to macroalgae in relative abundance in El Placer and in the central area.

Mean macroalgal canopy heights showed comparatively little variation among reefs, ranging between 3 cm in Xcalak and ~5.5 cm in Tampalam. Mean macroalgal indices (macroalgal relative abundance x canopy height, a proxy for macroalgal biomass) were lowest (<80) in most (seven/nine) of the subreefs at Xcalak, Xahuayxol and Mahahual; the highest values (>110) were found in all subreefs in Punta Allen and Tampalam, in two subreefs at Boca Paila and in El Placer N. Overall, the average macroalgal index was somewhat greater in the central area (mean = 114.8, sd = 61, n = 838 quadrats) than in the southern area (mean = 82.0, sd = 60 cm, n = 875 quadrats).

Relationships

Significant relationships detected via correlation and regression analyses include: (1) positive relationships between mean coral maximum diameter and live coral cover ($r = 0.60$, $r^2 = 0.36$, $p < 0.01$); (2) positive relationships between mean density of stony coral recruits and (a) mean live coral cover ($r = 0.50$, $r^2 = 25.4$, $p = 0.01$) and (b) mean macroalgal relative abundance ($r = 0.45$, $r^2 = 20.8$, $p = 0.025$); (3) positive relationships between standing dead colonies and nearest human population size ($r = 0.58$, $r^2 = 33.4$, $p < 0.01$); and (4) inverse relationships between mean macroalgal abundance or macroalgal index and mean herbivorous fish density by subreef ($r = -0.44$, $r^2 = 19.5$, $p = 0.03$; $r = -0.55$, $r^2 = 30.3$, $p < 0.01$, respectively; fish data from Núñez-Lara et al, this volume). No significant ($p > 0.05$) relationships were found among the other tested variables.

DISCUSSION

The species composition of the predominant large (≥ 25 cm in diameter) stony corals was relatively homogeneous among the subreefs of any given reef. *Montastraea faveolata* was the most frequently encountered species at 9/12 subreefs in the central area, whereas in the southern area *M. annularis* was the most abundant species at over half (7/12) of the subreefs. As *M. faveolata* grows larger than *M. annularis* (Weil and Knowlton, 1994), it is not surprising that maximum diameters were slightly larger in the central area reefs even though total cover overall was the same in both areas.

The high rates of recent partial-colony mortality in the central area and at El Placer (the most northerly reef in the southern area and, like Tampalam, in the Sian Ka'an subregion) are perhaps explained by the high percentage of diseased corals that were present at the time of our surveys (~9.5-30. %, n = 5 reefs). Delayed effects of the 1998 mass bleaching event may have been partially responsible for the high rates of recent mortality in the three most southerly reefs (Mahahual, Xahuayxol, Xcalak) where relatively few corals showed signs of disease.

Coral bleaching can be manifested in different intensities, can occur locally or over large geographic areas, and can have diverse causes. Mass bleaching events are generally associated with periods in which sea surface temperature (SST) is above average (at least 1°C higher than the summer maximum, Hoegh-Guldberg, 1999). The scleractinians that were bleached during this study were localized in two of the three reefs in the southern area that were surveyed in June-July, 1999 (Mahahual and Xahuayxol; Table 2). During April-July of 1999, SST averaged ~29.3°C in the southern area of Quintana Roo (SST/AVHRR images courtesy of Ocean Remote Sensing Group, Johns Hopkins Applied Physics Laboratory, Garza-Pérez et al., in preparation). We suspect that a minor warming which continued over several months may have triggered the bleaching observed in these two reefs and/or perhaps the stony corals had not yet fully recovered from the effects of the mass bleaching event in 1998.

Damage from the passage of Hurricane Mitch in October 1998 is also possible, although unlikely to have contributed very much to total mortality given the relatively high values for large standing dead colonies of *Acropora palmata* in Xcalak, which is probably more exposed to storm waves than Mahahual and Xahuayxol located in the lee of Banco Chinchorro (Fig. 1). Acroporids had earlier experienced massive mortality around the Caribbean (Goreau et al., 1998), primarily from white-band disease which presumably had also killed the standing dead colonies of *A. palmata* in Xcalak, Punta Allen and, to a lesser extent, in Punta Yuyum. The demise of *Diploria* at Punta Yuyum may either have resulted from some combination of bleaching-related mortality (*Diploria labyrinthiformis* was one of the most affected species during the 1998 mass bleaching event, Garza-Pérez, 1999) or from mortality produced by disease.

It was anticipated that the reefs in Mahahual and Xcalak (southern area) and in Punta Allen (central area) might have the lowest live stony coral cover and/or the highest rates of disease or mortality, given their proximity to long-established villages (~ 50 years; Bastida-Zavala et al., 2000). In fact, standing dead colonies presented the only significant positive relationship with human population size. Even this relationship could be compromised if colonies that we were unable to identify as standing dead were actually present in higher abundances in the other reefs and/or if *Acropora palmata*

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happened to have been relatively more abundant historically at 10 m in the Xcalak and Punta Allen fore reefs than elsewhere.

Nevertheless, in terms of live coral cover, old mortality, and standing dead corals, Xcalak, which is one of the oldest settlements in the Mexican Caribbean, was the most impacted of the eight study reefs. Our results are in agreement with Garza-Pérez's (1999) comparative analysis of the same spur-and-groove habitat in Xcalak, Mahahual, Tampalam, and Akumal. Xcalak was so important in fishing and coconut cultivation at the beginning of the 20th Century that an artificial canal was constructed to connect the fisherman of the coast with the city of Chetumal (the present capital of Quintana Roo). Long-term anthropogenic impacts, such as wastewater discharge and fishing, could have contributed to its current condition. However, Xcalak was also the closest study reef to the prolonged high SST anomaly that resulted in high rates of bleaching-related mortality in Belize during the 1998 ENSO event (see Peckol et al., this volume).

Herbivorous fishes and echinoids are important determinants of the distribution and abundance of benthic algae and stony coral communities in the wider Caribbean (Wood, 1999). Increases in the abundance of macroalgae are correlated with the mass mortality of *Diadema antillarum* throughout the region in 1983-84 and with declines in the abundance of herbivorous fishes (Porter and Meier, 1992; Steneck, 1994). The converse has also been found when macroalgae decline after *D. antillarum* reappears (Aronson and Precht, 2000). Given the almost total absence of *D. antillarum* in our surveys, and the inverse relationships between mean herbivorous fish density (Núñez-Lara et al., this volume) and both the mean relative abundance of macroalgae and macroalgal index, differential fishing inside and outside of Sian Ka'an Biosphere Reserve may have exerted a primary control on the abundance and biomass of macroalgae in the central-southern Quintana Roo reefs. In other words, the somewhat higher relative abundance of macroalgae in the central area compared to the southern area may be a consequence of reductions in the local herbivorous fish community as populations of piscivorous fishes have rebounded within the reserve. Effects of protection on the abundance of benthic organisms and fishes have been demonstrated previously in the Mexican Caribbean (Arias-González, 1998; Arias-González et al., 1999) and other parts of the world (e.g., Edgar and Barrett, 1999).

If the presence of coral recruits is a sign that a reef is maintaining itself, and has the potential to continue to do so in the future, then all the reefs in the study area are in good condition. However, the complete lack of correspondence between genera that are most abundant as large colonies and those present as recruits (Fig. 2 versus Fig. 4) may suggest a dominance of asexual reproduction in the maintenance of the primary reef-building corals, as has been reported elsewhere in the Caribbean (Jackson, 1985). Hence, the 50% decrease in live stony coral cover that had occurred throughout the region between the early 1990's and 1999 (from ~25% to ~12%) and the high rates of recent partial-colony mortality (7-27.5%) seen in our 1999 surveys are cause for concern regarding the future status of these reef ecosystems. Further indications of widespread disturbance are provided by the size-frequency distributions of most species of large corals being skewed towards small-intermediate sizes (Fig. 3A, B).

In general, it can be said that the condition of the stony corals at 10 m depth in the fore-reef spur-and-groove habitat in the central and southern areas of the Mexican Caribbean already has deteriorated from natural and possibly anthropogenic

perturbations, particularly the effects of diseases (in stony corals and *Diadema*) and bleaching. Its fish communities are also being affected by extractive activities, particularly in the southern area (see Núñez-Lara et al., this volume), possibly leading to further deterioration in total reef condition. Thus the introduction of new disturbances related to urbanization and tourist development in the southern area (Daltabuit Godás, 1999) could potentially overwhelm the natural resilience of these coastal coral reefs (i.e., Nyström et al., 2000).

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Table 1. Site information for AGRRA stony coral and algae surveys in central-southern Quintana Roo, México.

Site name	Site code	Nearest human population (#) ¹	Reef type	Latitude (°' " N)	Longitude (°' " W)	Survey date(s)	Depth (m)	Benthic transects (#)	≥25 cm stony corals (#/10 m)	% live stony coral cover (mean ± sd)
Boca Paila North	BPN		Fringing S&G ²	20 06 51	87 27 23	Aug. 30 99	11.5	10	6	15.5 ± 4.5
Boca Paila Center	BPC	<20	Fringing S&G	20 06 21	87 27 34	Aug. 31 99	9.5	7	6	19.0 ± 9.5
Boca Paila South	BPS		Fringing S&G	20 05 51	87 27 47	Sept. 01 99	9	10	2	8.5 ± 2.5
Punta Yuyum North	PYN		Fringing S&G	19 58 30	87 27 10	Aug. 27 99	10	11	4.5	10.5 ± 5.5
Punta Yuyum Center	PYC	0	Fringing S&G	19 58 00	87 27 06	Aug. 26,28 99	10	14	4	12.5 ± 6.0
Punta Yuyum South	PYS		Fringing S&G	19 57 30	87 26 52	Aug. 25,28 99	10.5	14	4.5	10.5 ± 6.0
Punta Allen North	PAN		Fringing S&G	19 50 30	87 26 15	Aug. 20,23 99	10.5	14	4.5	11.5 ± 3.5
Punta Allen Center	PAC	<300	Fringing S&G	19 50 00	87 26 36	Aug. 21,23 99	12	15	4.5	14.5 ± 7.5
Punta Allen South	PAS		Fringing S&G	19 49 30	87 26 52	Aug. 22,23 99	11	15	3.5	10.5 ± 4.5
Tampalam North	TN		Fringing S&G	19 09 15	87 32 00	Oct. 2 99	10.5	15	1.5	8.5 ± 5.5
Tampalam Center	TC	<20	Fringing S&G	19 08 45	87 32 10	Sept. 30, Oct. 1,3 99	8	14	5	15.0 ± 9.0
Tampalam South	TS		Fringing S&G	19 08 15	87 32 13	Sept. 30, Oct. 1,3 99	8	12	6	18.0 ± 6.5
El Placer North	EPN		Fringing S&G	18 54 48	87 37 03	Sept. 24-25 99	12	14	2	6.0 ± 2.5
El Placer Center	EPC	<20	Fringing S&G	18 54 08	87 37 24	Sept. 23-24,26 99	12	15	2.5	9.0 ± 3.5
El Placer South	EPS		Fringing S&G	18 53 35	87 37 36	Sept. 22-23,25 99	13	15	4	12.0 ± 4.0
Mahahual North	MN		Fringing S&G	18 43 24	87 41 56	June 25-27, July 22 99	9.5	13	5	17.0 ± 7.0
Mahahual Center	MC	<150	Fringing S&G	18 43 01	87 42 09	June 26,28 99	10.5	13	4.5	17.0 ± 6.0
Mahahual South	MS		Fringing S&G	18 42 30	87 42 20	June 29, July 22 99	10	12	6	16.5 ± 5.5
Xahuayxol North	XN		Fringing S&G	18 30 55	87 45 02	July 9-10,20 99	9.5	14	3.5	11.5 ± 3.0
Xahuayxol Center	XC		Fringing S&G	18 30 25	87 45 13	July 10,20-21 99	11	14	2.5	12.0 ± 5.5
Xahuayxol South	XS	< 5	Fringing S&G	18 29 55	87 45 22	July 18,21 99	10.5	14	3.5	11.5 ± 5.5
Xcalak North	XCN		Fringing S&G	18 13 43	87 49 51	July 13-15 99	11	12	3.5	9.0 ± 4.5
Xcalak Center	XCC	<300	Fringing S&G	18 13 09	87 49 54	July 14-15,17 99	9	11	3.5	9.5 ± 3.0
Xcalak South	XCS		Fringing S&G	18 12 39	87 49 47	July 16-17 99	10	13	3	7.5 ± 4.5

¹from INEGI (1996)²S&G = spur and groove

Table 2. Size and condition (mean \pm standard deviation) of all stony corals (≥ 25 cm diameter) by subreefs in central-southern Quintana Roo, México.

Site name	Stony corals		Partial-colony mortality (%)			Live tissues bleached (%)	Stony corals (%)		
	#	Diameter	Recent	Old	Total		Standing dead	Bleached	Diseased
Boca Paila North	59	66.5 \pm 44.0	17.5 \pm 18.0	18.0 \pm 23.5	35.0 \pm 26.5	0	5	0	44
Boca Paila Center	42	73.0 \pm 55.5	14.5 \pm 13.0	16.0 \pm 22.0	30.0 \pm 23.0	0	5	0	28.5
Boca Paila South	22	46.5 \pm 30.5	25.5 \pm 17.0	19.5 \pm 17.0	45.0 \pm 19.5	0	0	0	18
Punta Yuyum North	51	59.5 \pm 40.0	20.5 \pm 23.0	25.5 \pm 31.5	44.0 \pm 32.5	5.0 (n=1)	10	2	8
Punta Yuyum Center	55	53.5 \pm 36.0	23.0 \pm 21.5	17.5 \pm 28.0	39.0 \pm 29.0	0	7.5	0	12.5
Punta Yuyum South	63	66.0 \pm 61.5	18.5 \pm 21.0	28.5 \pm 35.0	44.0 \pm 35.5	0	16	0	8
Punta Allen North	64	51.0 \pm 34.5	19.0 \pm 24.0	23.0 \pm 32.5	39.5 \pm 33.5	25.0 \pm 8.5 (n=3)	12.5	4.5	17
Punta Allen Center	66	65.5 \pm 52.5	16.0 \pm 23.0	14.5 \pm 25.5	29.5 \pm 31.0	0	6	4.5	12
Punta Allen South	55	64.5 \pm 42.5	20.5 \pm 24.0	19.0 \pm 31.0	37.5 \pm 32.5	0	11	0	9
Tampalam North	24	47.0 \pm 24.5	13.0 \pm 13.0	18.5 \pm 13.0	31.0 \pm 19.5	8.0 (n=1)	0	4	37.5
Tampalam Center	68	45.0 \pm 26.0	13.5 \pm 13.5	17.0 \pm 16.5	30.5 \pm 22.0	0	0	0	16
Tampalam South	70	62.0 \pm 51.0	16.0 \pm 17.0	19.5 \pm 17.5	35.0 \pm 24.0	0	1.5	0	21.5
El Placer North	30	38.5 \pm 11.5	15.0 \pm 18.0	20.5 \pm 19.0	35.5 \pm 24.5	0	0	0	16.5
El Placer Center	40	45.0 \pm 25.5	16.0 \pm 16.5	18.5 \pm 22.5	34.0 \pm 27.0	3.0 (n=1)	5	2.5	20
El Placer South	57	56.5 \pm 37.5	22.5 \pm 20.0	18.5 \pm 18.0	40.5 \pm 27.0	4.5 \pm 1.0 (n=3)	2	5.5	26.5
Mahahual North	68	46.5 \pm 31.0	12.0 \pm 19.0	18.0 \pm 21.0	30.0 \pm 25.5	18 (n=12) ¹	1.5	17.5	6
Mahahual Center	57	60.5 \pm 45.0	18.5 \pm 17.5	16.5 \pm 14.0	35.0 \pm 21.0	100 (n=20) ¹	2	35	5.5
Mahahual South	74	67.5 \pm 43.5	27.5 \pm 22.5	17.0 \pm 22.5	43.5 \pm 28.5	45 \pm 39.5 (n=31) ¹	4	42	4
Xahuayxol North	49	48.0 \pm 31.0	18.5 \pm 23.5	10.5 \pm 12.5	29.0 \pm 26.5	39.5 \pm 42.0 (n=17)	0	34.5	0
Xahuayxol Center	37	51.5 \pm 38.0	13.5 \pm 16.5	13.5 \pm 24.0	26.0 \pm 29.0	21.5 \pm 33.0 (n=8)	5.5	21.5	0
Xahuayxol South	48	54.5 \pm 33.0	20.5 \pm 23.5	14.0 \pm 17.0	34.0 \pm 27.0	7.5 \pm 2.5 (n=3)	2	6.5	0
Xcalak North	44	49.0 \pm 29.0	16.0 \pm 16.5	22.0 \pm 34.0	36.5 \pm 34.5	11.5 \pm 6.5 (n=9)	11.5	20.5	4.5
Xcalak Center	38	53.0 \pm 30.5	7.0 \pm 8.5	38.5 \pm 41.0	43.5 \pm 38.5	6.0 \pm 5.5 (n=4)	23.5	10.5	2.5
Xcalak South	37	51.0 \pm 30.5	20.0 \pm 22.0	24.0 \pm 35.5	41.0 \pm 35.5	14.5 \pm 5.5 (n=3)	13.5	8	0

¹ Overestimate, due to some missing data

Table 3. Algal characteristics, density of stony coral recruits and *Diadema antillarum* (mean \pm standard deviation) by subreefs in central-southern Quintana Roo, México.

Site name	Quadrats (#)	Relative abundance (%)			Macroalgae		Recruits	<i>Diadema</i>
		Macroalgae	Turf algae	Crustose coralline algae	Height (cm)	Index ¹	(#/0.0625 m ²)	(#/100 m ²)
Boca Paila North	66	23.0 \pm 7.0	51.5 \pm 10.5	25.0 \pm 9.5	4.0 \pm 1.5	90	0.1 \pm 0.4	0
Boca Paila Center	30	41.0 \pm 15.5	32.0 \pm 15.5	27.0 \pm 14.5	3.0 \pm 1.0	130	0.8 \pm 1.0	0
Boca Paila South	50	24.5 \pm 9.0	55.5 \pm 12.5	20.0 \pm 10.0	4.5 \pm 1.5	113	0.4 \pm 0.8	0
Punta Yuyum North	58	23.5 \pm 7.0	53.5 \pm 8.5	23.0 \pm 7.5	4.0 \pm 2.0	96	0.1 \pm 0.3	0
Punta Yuyum Center	74	22.0 \pm 7.5	56.0 \pm 10.5	22.0 \pm 8.5	3.5 \pm 2.0	81	0.2 \pm 0.5	0
Punta Yuyum South	76	20.0 \pm 8.5	56.5 \pm 15.0	23.5 \pm 13.0	3.5 \pm 2.0	81	0.1 \pm 0.4	0
Punta Allen North	78	25.5 \pm 7.0	49.0 \pm 12.0	25.5 \pm 12.5	5.5 \pm 2.0	142	0.1 \pm 0.4	0
Punta Allen Center	81	22.5 \pm 6.5	52.0 \pm 10.5	25.5 \pm 10.5	5.0 \pm 2.0	116	0.1 \pm 0.2	0
Punta Allen South	76	24.5 \pm 9.0	44.0 \pm 13.5	31.5 \pm 12.0	5.0 \pm 2.0	126	0.1 \pm 0.2	0
Tampalam North	78	23.5 \pm 5.0	57.5 \pm 11.5	19.0 \pm 9.5	6.5 \pm 2.0	149	0.1 \pm 0.3	0.7
Tampalam Center	87	23.5 \pm 9.0	49.0 \pm 15.5	27.5 \pm 11.0	5.5 \pm 2.0	126	0.3 \pm 0.7	0
Tampalam South	84	24.5 \pm 9.5	46.0 \pm 17.0	29.5 \pm 13.0	5.0 \pm 2.0	124	0.3 \pm 0.6	0
El Placer North	73	22.0 \pm 5.5	56.5 \pm 10.5	21.5 \pm 10.0	6.5 \pm 2.5	135	0.1 \pm 0.4	0
El Placer Center	81	21.5 \pm 6.5	48.5 \pm 14.5	30.0 \pm 11.5	4.5 \pm 2.0	104	0.3 \pm 0.5	0
El Placer South	88	26.0 \pm 9.0	46.0 \pm 15.0	28.0 \pm 11.0	4.0 \pm 1.5	107	0.2 \pm 0.4	0
Mahahual North	73	13.0 \pm 11.5	63.0 \pm 16.5	24.0 \pm 16.0	4.0 \pm 2.5	64	0.4 \pm 0.6	0
Mahahual Center	88	16.0 \pm 12.5	69.5 \pm 15.0	15.0 \pm 13.0	6.5 \pm 4.0	108	0.4 \pm 0.6	0
Mahahual South	72	18.0 \pm 10.0	56.0 \pm 18.0	26.0 \pm 12.5	4.0 \pm 2.5	74	0.2 \pm 0.4	0
Xahuayxol North	77	18.0 \pm 6.0	53.5 \pm 10.5	28.5 \pm 10.5	4.0 \pm 1.5	75	0.2 \pm 0.4	0
Xahuayxol Center	73	18.0 \pm 7.5	57.5 \pm 10.5	24.5 \pm 9.5	4.5 \pm 1.5	83	0.3 \pm 0.7	0
Xahuayxol South	86	19.0 \pm 6.5	47.0 \pm 14.0	34.0 \pm 13.0	3.5 \pm 1.5	71	0.1 \pm 0.3	0
Xcalak North	74	14.5 \pm 8.5	55.5 \pm 12.5	30.0 \pm 11.0	3.0 \pm 1.5	52	0.1 \pm 0.4	0
Xcalak Center	55	16.5 \pm 8.5	48.0 \pm 17.0	35.5 \pm 17.5	3.0 \pm 1.0	49	0.1 \pm 0.4	0
Xcalak South	69	18.0 \pm 8.5	50.5 \pm 17.0	31.5 \pm 16.0	3.0 \pm 1.5	53	0.1 \pm 0.3	0

¹ Macroalgal index = relative macroalgal abundance x macroalgal height