

Figure 1. AGRRA survey sites along the Belize barrier reef system.

ASSESSMENT OF SELECTED REEF SITES IN NORTHERN AND SOUTH-CENTRAL BELIZE, INCLUDING RECOVERY FROM BLEACHING AND HURRICANE DISTURBANCES (STONY CORALS, ALGAE AND FISH)

BY

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ABSTRACT

The condition of coral, algal, and fish populations in fore reefs, patch reefs, and coral reef ridges was investigated at 13 sites along the northern and south-central Belize barrier reef during May 1999, documenting effects of the 1998 warming episode and Hurricane Mitch. We found high percentages of partial, or even complete, colony mortality of major reef-builders (*Acropora palmata*, the *Montastraea annularis* species complex and *Agaricia tenuifolia*) that were rarely censused as recruits. *A. tenuifolia*, formerly a space-dominant coral in reef ridges, had incurred nearly 100% mortality after bleaching. Nearly 45% of the *M. annularis* complex was still discolored (50% had been bleached in January 1999) on some south-central patch reefs where the total (recent + old) partial mortality exceeded 60% of colony surfaces. Although turf algae dominated patch reefs and coral reef ridges, macroalgae were quite prevalent representing >30% cover at six sites. Parrotfish densities exceeded surgeonfishes at most sites (11/13). Consistent patterns of lower partial-colony mortality of stony corals and greater fish densities and sizes near and within the Hol Chan Marine Reserve highlight the ecological benefits of protected areas for the maintenance of reef corals and attendant fish populations.

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INTRODUCTION

Over the past two decades, there has been widespread deterioration of coral reefs worldwide (Wilkinson, 2000). Following the mass mortality in 1983 of a “keystone” herbivore, the sea urchin *Diadema antillarum*, Caribbean reefs emerged as an area of particular concern (see Ginsburg, 1994) when macroalgal abundances increased at many reefs (Lessios, 1988; Hughes et al., 1999; but see Lapointe, 1997, 1999). The Belize barrier reef system largely was spared from the negative effects of the disappearance of *D. antillarum* because, prior to the mass mortality event, its densities were extremely low compared with those on reefs experiencing concurrent pressures of overfishing (Hay, 1984). Until 1995, the Belize reefs had also escaped the mass coral bleaching events reported in many other areas of the Caribbean (Macintyre and Aronson, 1997; McField, 1999). In addition, Belize has a very low human population density (about 230,000 or about nine people/km²). The central and southern regions of the Belize barrier reef are distant from the effects of terrestrial development and, at least until recently, fishing has been primarily at the subsistence level. The Belize barrier reef ecosystem thus must have served as a large and important regional source of larvae and juvenile corals, other invertebrates, and fishes (Cortés, 1997). The coupling of low incidence of large-scale natural disturbances and minimal anthropogenic effects conserved this reef system in a nearly pristine state with a unique array of reef types and luxuriant coral communities (Perkins and Carr, 1985). However, the hurricanes in the ‘60s and 70’s that Stoddart (e.g., 1974) made famous and the effects of white-band disease, all occurring before the 1995 bleaching, demonstrate that natural perturbations pre-1995 are not without their effects in Belize.

The Belize barrier reef complex is the largest continuous reef system in the western North Atlantic-Caribbean Province extending a distance of 250 km south from the northern end of Ambergris Caye. It is one of the best-studied coral-reef areas in the western hemisphere (Cortés, 1997), particularly since the establishment of the Smithsonian Institution’s field station on Carrie Bow Caye in 1972 (Rützler and Macintyre, 1982; Macintyre and Aronson, 1997). A major NNE-trending fault system is clearly reflected in the alignment of the coastline, barrier reef, and three oceanic atolls. The reef is fringing at its northernmost end, but as it extends southward the system becomes a nearly continuous barrier with well-developed fore reefs, reef crests, and extensive back-reef (lagoonal) areas. In the shallower portions of the fore-reef zone, interdigitating coral buttresses and sandy troughs form a sometimes massive spur-and-groove system. The reef crest is a high-energy zone consisting of a shallow rampart built of coral rubble and dominated by the coral *Acropora palmata* (James and Ginsburg, 1979). The back-reef area has a large number of cayes (cays, or small islands), many with associated patch reefs. There is a complex network of steep-sided, rhomboidal-shaped shoals and reefs (herein referred to as coral reef ridges) in the south-central lagoon, which originated in fault patterns enhanced by subsequent Pleistocene karst solution and differential carbonate deposition (Macintyre and Aronson, 1997; Macintyre et al., 2000). Coral reef ridges previously supported spectacular coral development dominated by the staghorn *Acropora cervicornis* at depths of 3-8 m. Following mass mortality in the 1980s of *A. cervicornis* from white-band disease, the ridges were rapidly colonized by *Agaricia* spp., primarily *A. tenuifolia* (Aronson and Precht, 1997).

The biologically rich Belize barrier reef ecosystem contributes to a multimillion-dollar fishing industry and serves as a prime attraction for sport fishermen and scuba/snorkel divers. Tourism in Belize (see <http://www.belize tourism.org/arrival.html>) has been expanding rapidly from less than 100,000 visitors in 1985 to over 326,000 in 2000 and growing. Tourism generates over 26% of the Belizean gross national product (Higinio and Munt, 1993). Ambergris Caye has borne the brunt of the effects of coastal tourism including degradation of the reef, dwindling fish stocks, and surface runoff. In 1987, the Government of Belize established the Hol Chan Marine Reserve off Ambergris Caye in an effort to conserve a small but complete portion of this reef ecosystem including the coral reef, lagoon, and mangrove habitats (Carter et al., 1994). Modeled in large part after the Australian Great Barrier Reef management plan, this reserve is zoned with a multi-use management scheme that has achieved some success. Although the Hol Chan Marine Reserve does not encompass an expansive reef tract, it was designed to serve as an impetus for the creation of additional reserves in the future (Carter et al., 1994).

Within the past decade the Belize barrier reef has undergone a noticeable decline (Kramer et al., 2000), particularly as fishing pressures have reduced stocks (Carter et al. 1994). Several major disturbances, including warming events during 1995/96 (Burke et al., 1996; McField, 1999) and 1998 (Mumby, 1999; Aronson et al., 2000), and a near direct hit by Hurricane Mitch in autumn 1998, have accelerated its degradation. The 1998 bleaching event began in September following a month of calm weather and increasing water temperatures. The eye of Hurricane Mitch, a category 5 storm, passed ~200 km SE of Glovers Reef in late October 1998 (Mumby, 1999). The subsequent demise of *Agaricia tenuifolia* on the coral reef ridges in the south-central region, a phenomenon unprecedented in recent geologic history, has been particularly well described by Aronson et al. (2000).

Given the large size and the diversity of reef types present on the Belize barrier, there is a great need for larger-scale monitoring to document the short- and long-term effects of these widespread disturbances on this very important reef system. In addition, understanding the effects of marine reserves on the health and conservation of coral and fish populations is critical for long-term management decisions. Hence, we investigated the condition of stony coral, algae and fish populations at 13 sites along the northern and south-central regions of the Belize barrier reef, including fore reefs, patch reefs and coral reef ridges. The timing (May 1999) of our survey enabled us to document the effects of the major 1998 warming event and Hurricane Mitch. The Hol Chan Marine Reserve was included in our surveys to provide information useful for management decisions regarding this and other reserves planned for the Belize barrier reef.

METHODS

The 13 sites that we surveyed during May 1999 were selected as being representative of the reef types and conditions in the northern and south-central regions of the Belize Barrier Reef (Fig. 1). The four northern sites near Ambergris Caye were also strategically chosen to compare areas within and outside the Hol Chan Marine Reserve.

Five fore-reefs were censused. San Pedro Canyon, located south of Mexico Rocks off Ambergris Caye at 12-15 m depth, is characterized by a low-relief (~2 m) spur-and-groove topography with small colonies of the *Montastraea annularis* species complex and numerous gorgonian corals. Eagle Ray Canyon (depth 12-18 m), which lies north of the Hol Chan Channel but is still within the reserve, has a well-developed spur-and-groove system. It supports a high diversity of corals in good condition dominated by large colonies of the *M. annularis* complex and *Agaricia tenuifolia*. Tobacco Reef, in south-central Belize, has a low-relief spur-and-groove formation at depths of about 12-13 m with large, healthy colonies of the *M. annularis* complex. *A. tenuifolia* was overgrowing dead skeletons of *Millepora complanata* on the fore-reef spurs. (In May 1999, the large coral-rubble ridge that runs a considerable distance from north of Tobacco Caye southward to near South Water Caye was covered with large fragments of what appeared to be recently dead coral colonies that were reported by locals to have been deposited by Hurricane Mitch.) The fore reef off South Water Caye (up to 14 m depth) has a high-relief (3-5 m) spur-and-groove development with much *Siderastrea siderea* and some large colonies of the *M. annularis* complex, *Millepora complanata* and *Agaricia* spp. were abundant on the spurs. Curlew Bank fore reef, located just south of Carrie Bow Caye, is characterized by a low-relief spur-and-groove formation with colonies of the *M. annularis* complex, *S. siderea*, *Diploria* spp., and *A. palmata* (both living and dead colonies).

Five surveys were in patch reefs. Mexico Rocks, seaward of Ambergris Caye, is an irregularly shaped complex of approximately 100 patch reefs at about 4 m depth. These patch reefs are dominated by large stands of the *M. annularis* complex (Burke et al., 1998), separated by sand and seagrass. Although this reef exhibited low coral diversity, live coral cover values were average for this reef type. Near the patch reef in the Hol Chan Marine Reserve, which is dominated by *Acropora palmata* (both living and dead colonies) and the *M. annularis* complex, a 10-m deep channel (Hol Chan Channel) runs through the reef crest and into the back-reef region. The three patch reefs in the south-central region were at depths of about 2-5 m on the windward sides of Wee-Wee, Bread and Butter, and Norvall Cayes, where the *M. annularis* complex is the dominant coral species. Most colonies of *A. palmata* were "long dead" and were covered with turf algae.

The three surveys in coral reef ridges were conducted at depths of 2-15 m off Wee-Wee Caye, Peter Douglas Caye, and an area locally known as "Tunicate Cove" within the Pelican Cayes. At these reefs most colonies of the dominant coral, *A. tenuifolia*, had died since the beginning of the 1998 warming event.

Coral and algal populations were assayed by six-seven divers on each dive. Atlantic and Gulf Rapid Reef Assessment (AGRRA) Version 1 benthos protocols (see Appendix One, this volume) were used with the following modifications: stony corals ≥ 10 cm in diameter were included in the surveys; coral diameter and height were measured to the nearest cm for smaller corals (10-25 cm in diameter) and to the nearest 5 cm for larger (>25 cm) colonies. The *Montastraea annularis* complex was treated as a single species. Sediment deposits in the algal quadrats were removed by hand before estimating the abundance of crustose coralline algae. As space occupied by turf algae growing on live crustose corallines was allocated to both functional groups, total values for absolute abundance at some sites are in excess of 100%. *Diadema antillarum*, being

rare, was not counted. Training sessions were conducted with all divers [most of whom were already well-trained from the 1998 San Salvador Island, Bahamas AGRRA assessment (Peckol et al. this volume)] censusing “practice” transects on patch reefs. Species identifications, percent cover estimates, and coral disease and bleaching assessments were compared to ensure sampling consistency. We used Humann’s (1993) reef coral guide for coral species identifications; Littler and Littler (2000) was later consulted for macroalgae.

A stationary visual census technique (Bohnsack and Bannerot 1986) was employed by two divers to survey the fish populations. All sampling occurred between 10:00 a.m. and 3:00 p.m. At each sampling point, all species belonging to eight families (Acanthuridae, Chaetodontidae, Haemulidae, Labridae, Lutjanidae, Pomacentridae, Scaridae, Serranidae) observed in five minutes within a 7.5 m radius cylinder were recorded. Each census was begun three minutes after laying a measuring tape on the substratum by counting all individuals of all species observed in the pre-set radius within the initial field of view. New sectors of fields of view were then scanned by rotating in one direction. Abundances of species moving in schools were taken when first observed in the sampling cylinder (it was important to count fishes moving in schools immediately because they were unlikely to remain in the sampling area). When very large schools were present it was sometimes necessary to estimate numbers in 10s or 50s. Fish lengths in cm were estimated using a T-shaped tool marked every 5 cm to help avoid underwater magnification problems (Bohnsack and Bannerot, 1986). We recorded the number of individuals, plus the minimum, maximum, and mean estimated lengths for each of the eight fish families. We used Humann’s (1994) reef fish guide for species identifications.

Herbivorous fish grazing rates were measured by two divers at 12 sites (all but the Eagle Ray fore reef), following the AGRRA methodology given in Appendix One. Grazing rate measurements were all made between 10:00 a.m. and 2:00 p.m. during the peak time for grazing activity (Lewis, 1986).

RESULTS

Stony Corals

Species composition. At each site we censused between 12-18 10-m transects, each of which generally had about 15 stony corals that were at least 10 cm in diameter (Table 1). At most sites we measured >250 coral colonies. Coral species abundance patterns varied greatly among the three reef types (Fig. 2A-C). Numerically, the most abundant coral species censused in the fore-reef spurs were *Porites astreoides* (22% of total) and the *Montastraea annularis* species complex (14% of total). *Acropora palmata* occurred here in relatively low abundance (<5% of total) but showed high total (recent and old) partial mortality of colony surfaces ranging from 25% (South Water Caye) to 100% (Tobacco Caye) and averaging >55%. Due to high wave-energy conditions, we were unable to sample the reef crest where *A. palmata* dominated (some colonies were alive). The *M. annularis* complex was clearly dominant in patch reefs (45% of total). Collectively, the mound corals, *Siderastrea siderea*, *Diploria strigosa*, and the *M. annularis* complex represented ~60% of the corals sampled in patch reefs. Because their

colony sizes are generally larger, the numerically less abundant *D. strigosa* contributed more than *S. siderea* to reef habitat. Mostly dead *Agaricia tenuifolia* (30%) and *P. astreoides* (23%) dominated the south-central coral reef ridges. The *M. annularis* complex was a minor component, and species richness was highest in this unique reef type (30 scleractinian species sampled along transects compared with ~24 species on patch reefs and fore reefs).

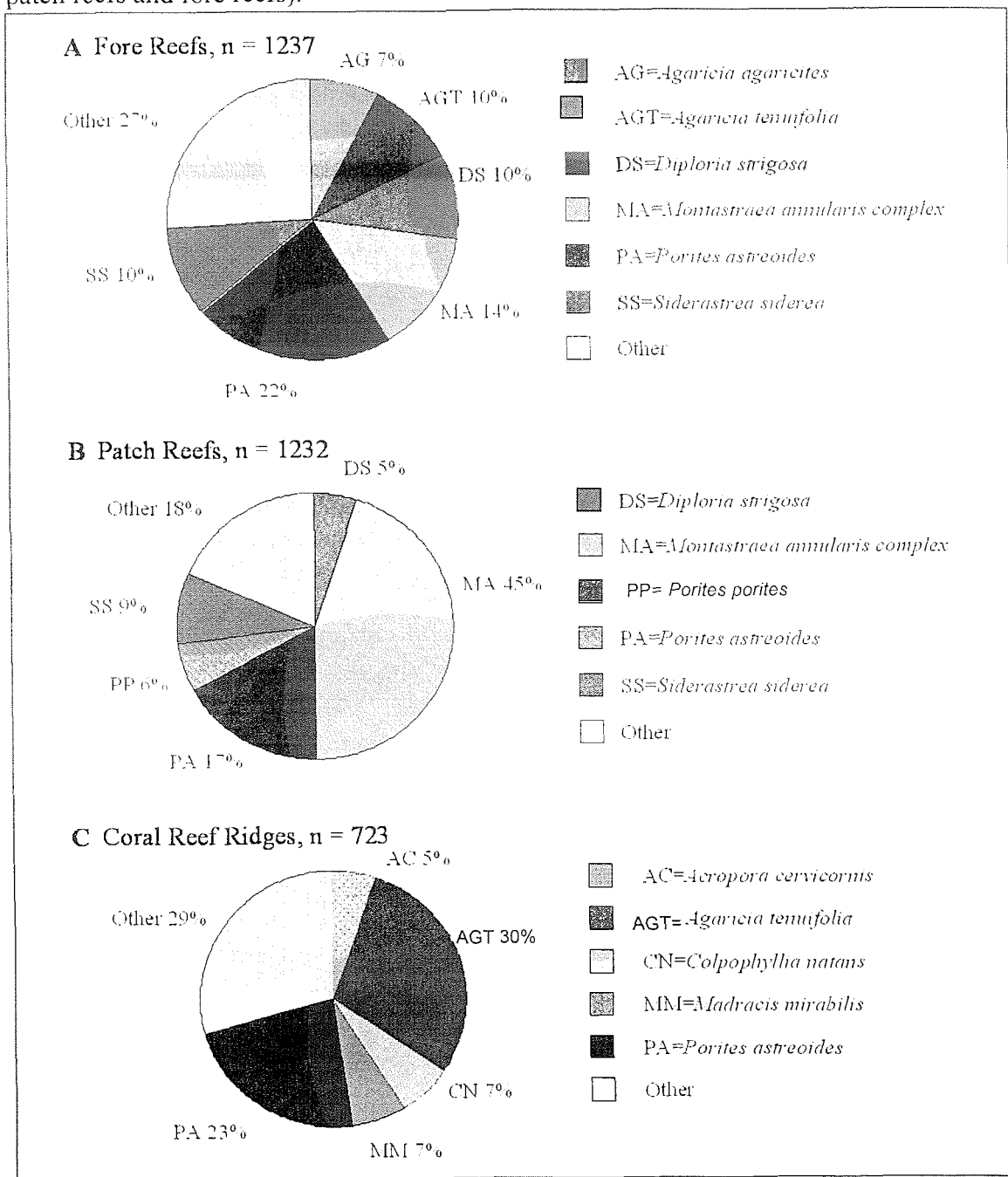


Figure 2. Species composition and mean relative abundance of the most abundant stony corals (≥ 10 cm diameter) at (A) fore reefs; (B) patch reefs; (C) coral ridge reefs along the Belize barrier reef system. Other category = combined coral species, each with $< 5\%$ abundance of occurrence.

Recruits. The most abundant of the coral recruits was *Porites astreoides*, which ranged from 31% of the total in the fore reefs to 50% in the patch reefs (Fig. 3A-C). Recruits of the *M. annularis* complex were rare (<2%) in the fore reefs and only represented 9% of the total in the patch reefs. Recruits of *A. palmata* were only found in

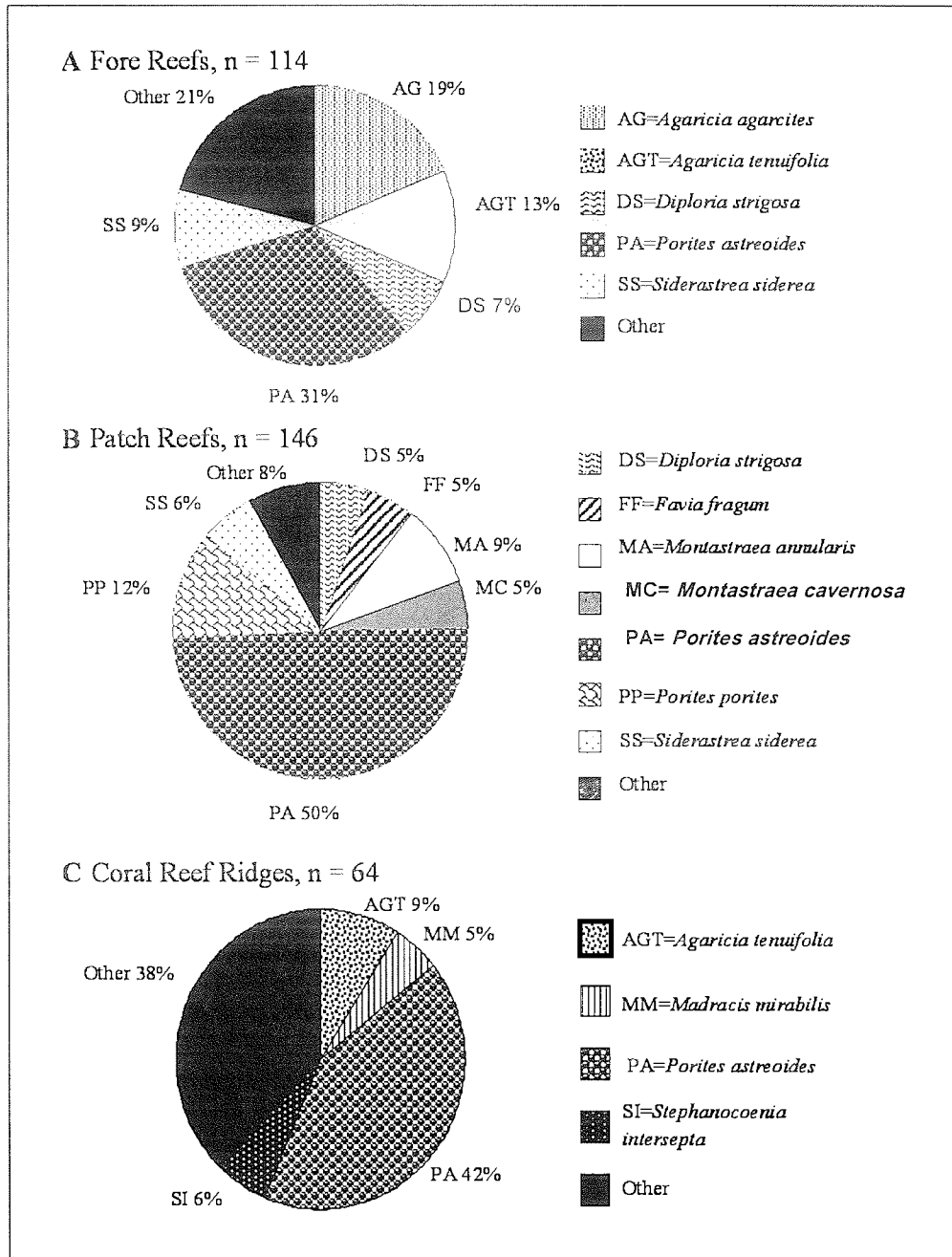


Figure 3. Species composition and mean relative abundance of all stony coral recruits (≤ 2 cm diameter) at (A) fore reefs; (B) patch reefs; (C) coral ridge reefs along the Belize barrier reef. Other category = combined coral species, each with <5% abundance of occurrence.

the patch reefs but in extremely low abundance (<1% of total). *A. tenuifolia* was represented by 9% of the recruits in the ridges, but was more abundant (13% of total) in the fore reefs.

Coral size. The mean sizes of individually surveyed corals (≥ 10 cm in diameter) varied nearly threefold (22-60 cm) and were more variable among reefs in the fore reefs and reef ridges than in the patch reefs (Table 2). While most colonies of the *M. annularis* complex in the fore reefs and patch reefs (and *Siderastrea siderea* in patch reefs) were <100 cm in diameter, we also measured a number of large, massive colonies (especially on the fore reefs), some being greater than 200 cm in diameter (Figs. 4A-B). *A. palmata*, although not abundant in the fore reefs, showed a large range in colony size from <20 cm to > 200 cm. *A. tenuifolia* in the reef ridges also showed a great range in size, but most colonies were <50 cm in diameter (Fig. 5A).

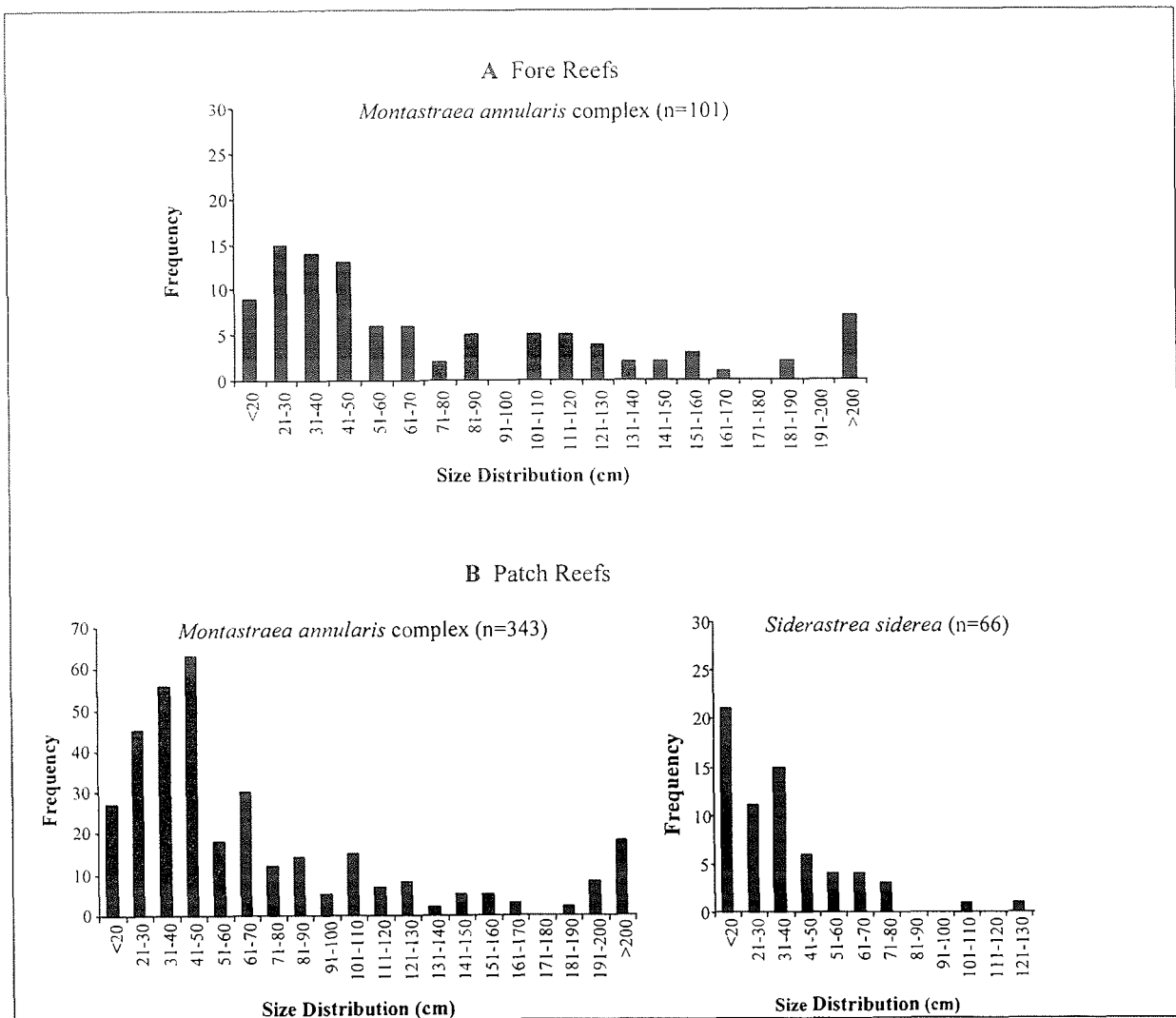


Figure 4. Size-frequency distribution as % of dominant stony corals (≥ 10 cm diameter) at (A) fore reefs and (B) patch reefs along the Belize barrier reef.

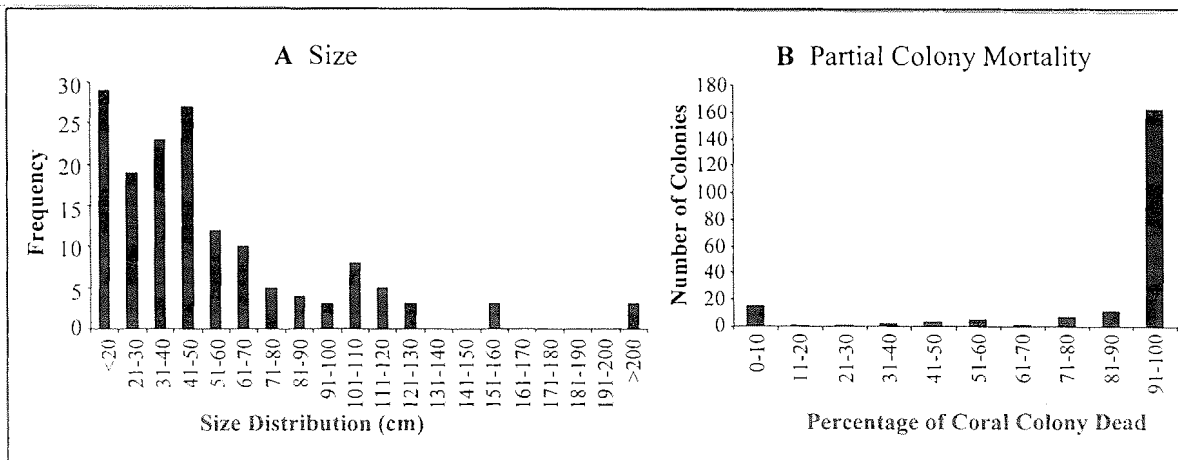


Figure 5. (A) Size-frequency distribution as % and (B) frequency distribution of total (recent + old) partial-colony mortality of *Agaricia tenuifolia* (≥ 10 cm diameter) at coral reef ridges in south-central Belize.

Coral condition. No diseased corals were found in the coral reef ridges and in the Hol Chan patch reef. Elsewhere, signs of disease were relatively low ($\sim 2\%$) except in the South Water Caye fore reef where 5% of the censused corals were diseased (primarily black-band disease; Table 2). There was no clear difference in incidence of disease in fore reefs versus patch reefs but, considered together, the incidence of coral disease was twice as high in the south-central sites as in the northern region.

Long-term effects from the 1998 warming event were still evident in May 1999. Bleaching affected $>44\%$ of the *M. annularis* complex in the south-central patch reefs, and 42% in both the northern and south-central fore reefs, while 26% of the colonies in the northern patch reefs were bleached. Fewer colonies ($\sim 15\%$) of each of the other common mound corals, *Diploria* spp. and *Siderastrea siderea*, were affected by bleaching. The relatively high percentages of bleached corals in most (4/5) of the fore reefs and all five patch reefs, particularly Norvall Caye, were obviously significant (Table 2). The percentages of bleached corals were higher on the south-central patch reefs (17-40%) than in the corresponding northern reefs (15-16%). The fore reefs showed an opposite pattern with the northern reefs having proportionately more bleached corals than those in the south-central region ($\sim 22\%$ versus $\sim 13\%$, respectively). Overall we found no clear spatial differences in extent of bleaching either between the fore reefs and patch reefs or between the northern and south-central regions (Table 2).

Mortality characteristics of the corals censused at the 13 sites are summarized in Table 2. Recent partial-colony mortality ranged from $\sim 2\%$ of upper surfaces in the fore reefs to sometimes $>13\%$ in the reef ridges. Comparable levels of old partial-colony mortality in the patch reefs and reef ridges were each about twice those in the fore reefs ($\sim 35\%$ versus $\sim 20\%$). Most colonies of *Agaricia tenuifolia* in the reef ridges were dead (Fig. 5B, with most of the *A. tenuifolia* in the 91-100% interval) and were covered by macroalgae and encrusting sponges (*Chondrilla* cf. *nucula* Schmidt; K. Rützler, pers. comm.). While the percent of colonies scored as "standing dead" (100% mortality of upper colony surfaces and still in growth position) was 4% and 8% in the fore reefs and patch reefs, respectively, standing dead ranged from 18-50% in the coral reef ridges.

Total (recent + old) partial-colony mortality (hereafter total mortality) was considerably higher in the south-central ridges and patch reefs (both ~45%) than in the northern patch reefs and south-central fore reefs (both ~25%) and relatively low in the northern fore reefs (~15%; Table 2). At the regional scale, the north Belizean fore reefs and patch reefs had lower total mortality than similar reefs in the south-central region (~20% versus ~35%, respectively). Total mortality for stony corals off Bread and Butter, Wee-Wee, and Norvall Cayes (mean = 45.5%, n = 3 reefs) was nearly two times greater than in the northern patch reefs. The greatest percentage was contributed by the *M. annularis* complex, for which total mortality values ranged between 34% (Bread and Butter) and >60% (Norvall, Wee-Wee) in the south-central patch reefs and from 35% (Hol Chan) to 50% (Mexico Rocks) in the northern region.

We plotted the frequency distributions of total mortality for sites located in northern (Fig. 6A,B) and south-central Belize (Fig. 7A-C) to illustrate these large-scale spatial differences. A majority of censused corals (>55-75% in patch reefs and fore reefs, respectively) in the northern region showed $\leq 10\%$ total mortality of the colony surface. Although a substantial number of corals from the south-central region also had $\leq 10\%$ total mortality, there was a greater proportion of colonies with higher percentages. For example, more than one-third of the censused corals at the coral reef ridges (n = 723) showed total mortality values of >90% of their surfaces (~75% of the colonies in this interval were *A. tenuifolia*). We also found a substantial number (>10%) of colonies with over 90% total mortality in the patch reefs (~28% of these colonies were the *M. annularis* complex).

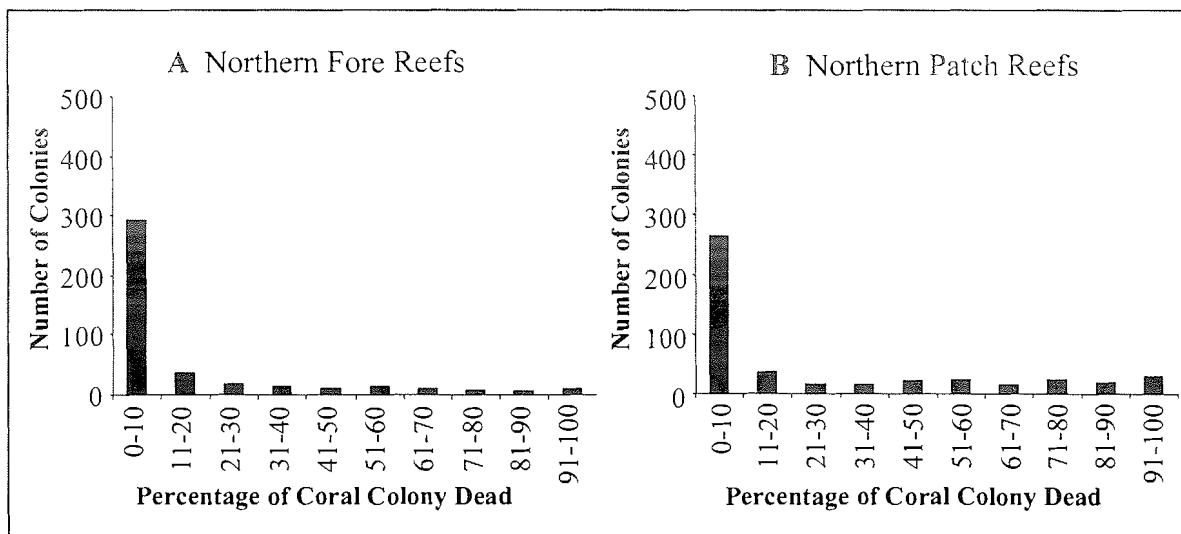


Figure 6. Frequency distribution of total (recent + old) partial colony mortality of all stony corals (≥ 10 cm diameter) at (A) fore reefs, (B) patch reefs in northern Belize.

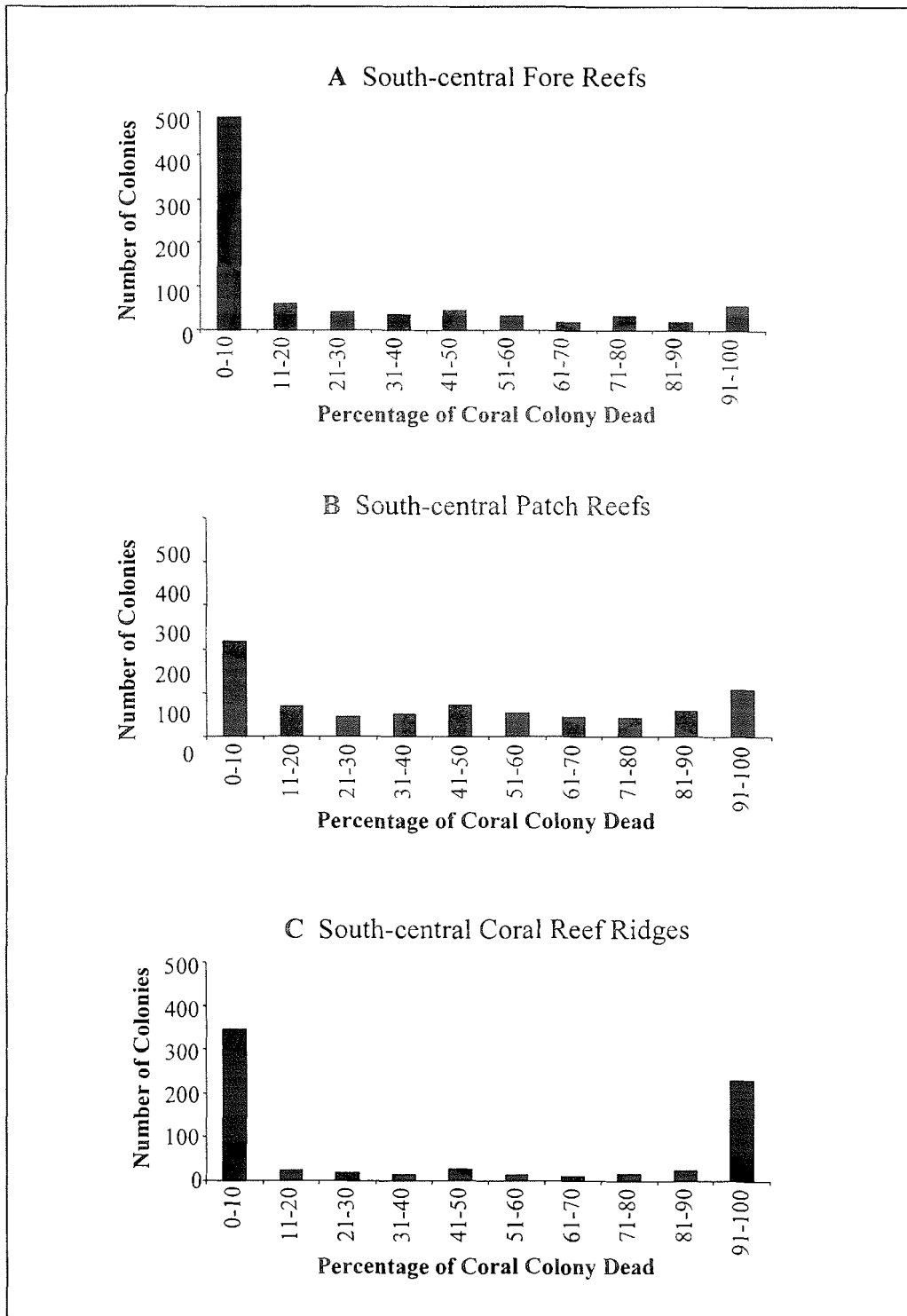


Figure 7. Frequency distribution of total (recent + old) partial colony mortality of all stony corals (≥ 10 cm diameter) at (A) fore reefs, (B) patch reefs, C) coral reef ridges in south-central Belize.

The dominant component of the algal assemblage was turf algae in all patch reefs, all coral reef ridges, and one of the fore reefs. Macroalgae predominated in one fore reef, crustose corallines in a second, and the all three functional groups were approximately equally abundant in a third (Table 3). No difference was noted in macroalgal abundance between the northern and south-central fore reefs or patch reefs. Macroalgae in the fore reefs included the brown seaweeds, *Dictyota humifusa*, *Lobophora variegata*, and *Styopodium zonale*, and the calcified green, *Halimeda*. Dominant macroalgae in the patch reefs were *D. pulchella*, *Turbinaria turbinata*, and the red alga, *Galaxaura oblongata*. Overall, mean macroalgal height was low (< 2 cm). Macroalgae indices (mean absolute macroalgal abundance x mean macroalgal height) were: <25 in two of the reef ridges, the two most southerly patch reefs and the most southerly fore reef; <100 at six sites; and >100 in one each of the south-central fore reefs and patch reefs.

Fishes

For the eight censused families, the highest fish abundances were in the Tunicate Cove ridge reef (mean = 105.1 individuals/200 m³, se = 26). Mean fish densities in the five fore reefs ranged from 38.2 (se = 8.7) at San Pedro Canyon to 86 (se = 20.7) individuals/200m³ at Curlew but showed no regional trend (Table 1). The patch reefs showed relatively little spatial variation with fish densities ranging from 41.6 (se = 6.1) in Norvall to 60.3 (se = 12.2) individuals/200m³ in Bread and Butter. The two other reef ridges had low fish abundances (overall averaging about 30 individuals/200 m³).

While damselfishes (Pomacentridae) were most abundant in the fore reefs (Fig. 8A), dominance was shared by four fish families in the patch reefs (Fig. 8B): surgeonfish (Acanthuridae), damselfish, parrotfish (Scaridae) and grunt (Haemulidae). Large (sometimes >100) schools of white grunt (*Haemulon plumieri*) associated with nearby seagrass habitat at Tunicate Cove ridge (Table 4) largely accounted for the high grunt densities in the reef ridges (Fig. 8C). Damselfish represented nearly a half (45%) of the total abundances in the other reef ridges. Parrotfish were more abundant than acanthurids in most (11/13) sites, and the latter were rare in the ridges. Only Mexico Rocks in northern Belize showed dominance by surgeonfishes over other herbivorous fishes.

Densities of seabasses (Serranidae), snappers (Lutjanidae) and grunts varied greatly among sites (Table 4), ranging from combined totals of ~2 individuals/200 m³ (Wee-Wee reef ridge) to 86 individuals/200 m³ (Tunicate ridge). The latter also had the highest abundances of serranids and grunts, whereas snappers were most common in the Tobacco Caye fore reef. Excluding Tunicate Cove, the Hol Chan Marine Reserve patch reef showed highest combined densities (~30 individuals/200 m³) of these three families with snappers and grunts contributing the greatest proportion to that total.

The size-frequency distributions for two major guilds of fishes, the herbivores (parrotfishes, surgeonfishes, the yellowtail damselfish *Microspathodon chrysurus*) and carnivores (groupers and snappers) in each of the three reef types are shown in Figure 9. While the 6-10 cm length category clearly predominated in patch reefs and reef ridges for the herbivores, the 11-20 cm category was slightly more common in the fore reefs. Few herbivorous fishes were greater than 20 cm in length in any site. Although the majority

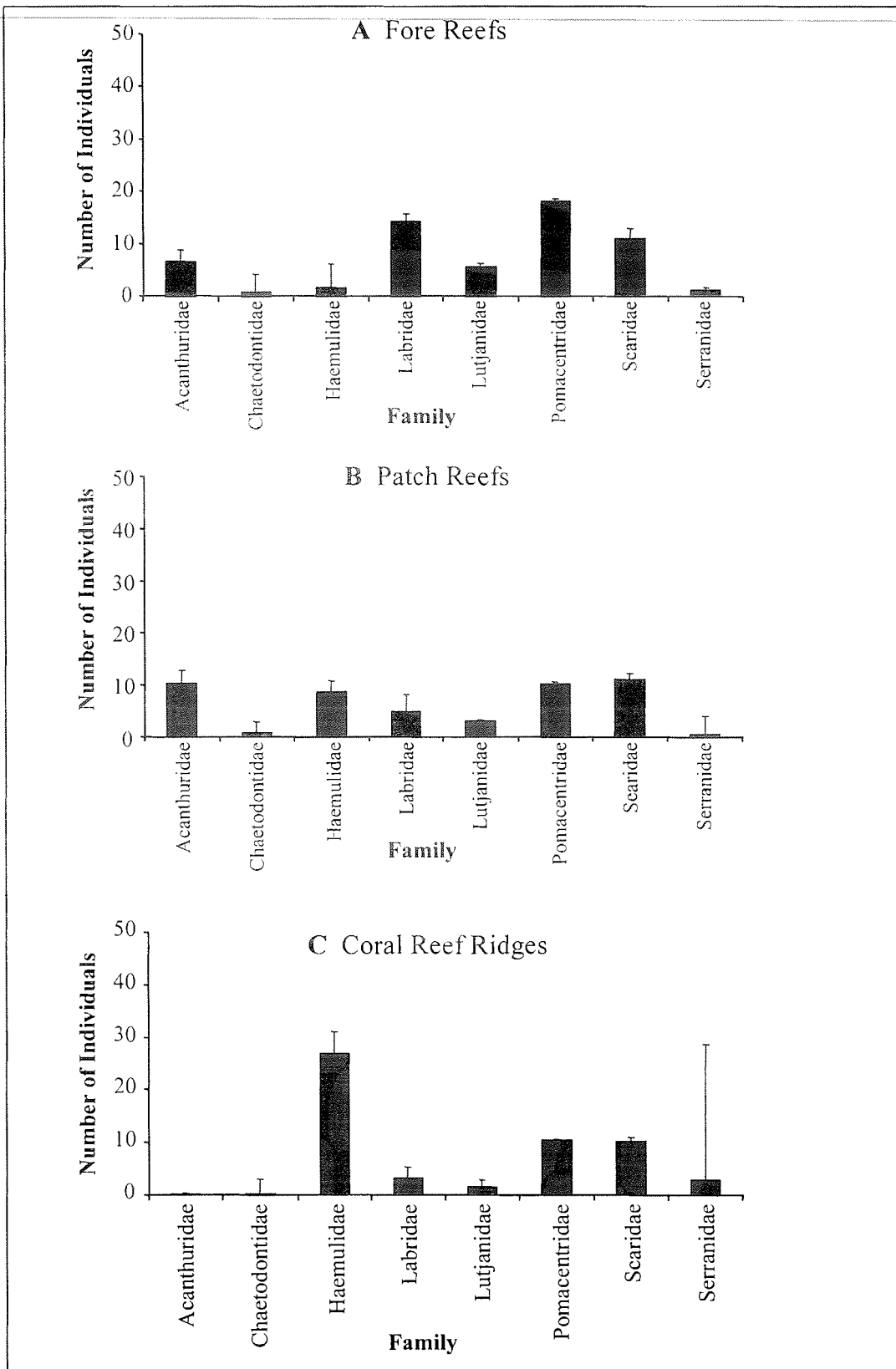


Figure 8. Mean fish density (no. individuals/200 m³ ± se) for eight fish families at (A) fore reefs; (B) patch reefs; (C) coral ridge reefs along the Belize barrier reef.

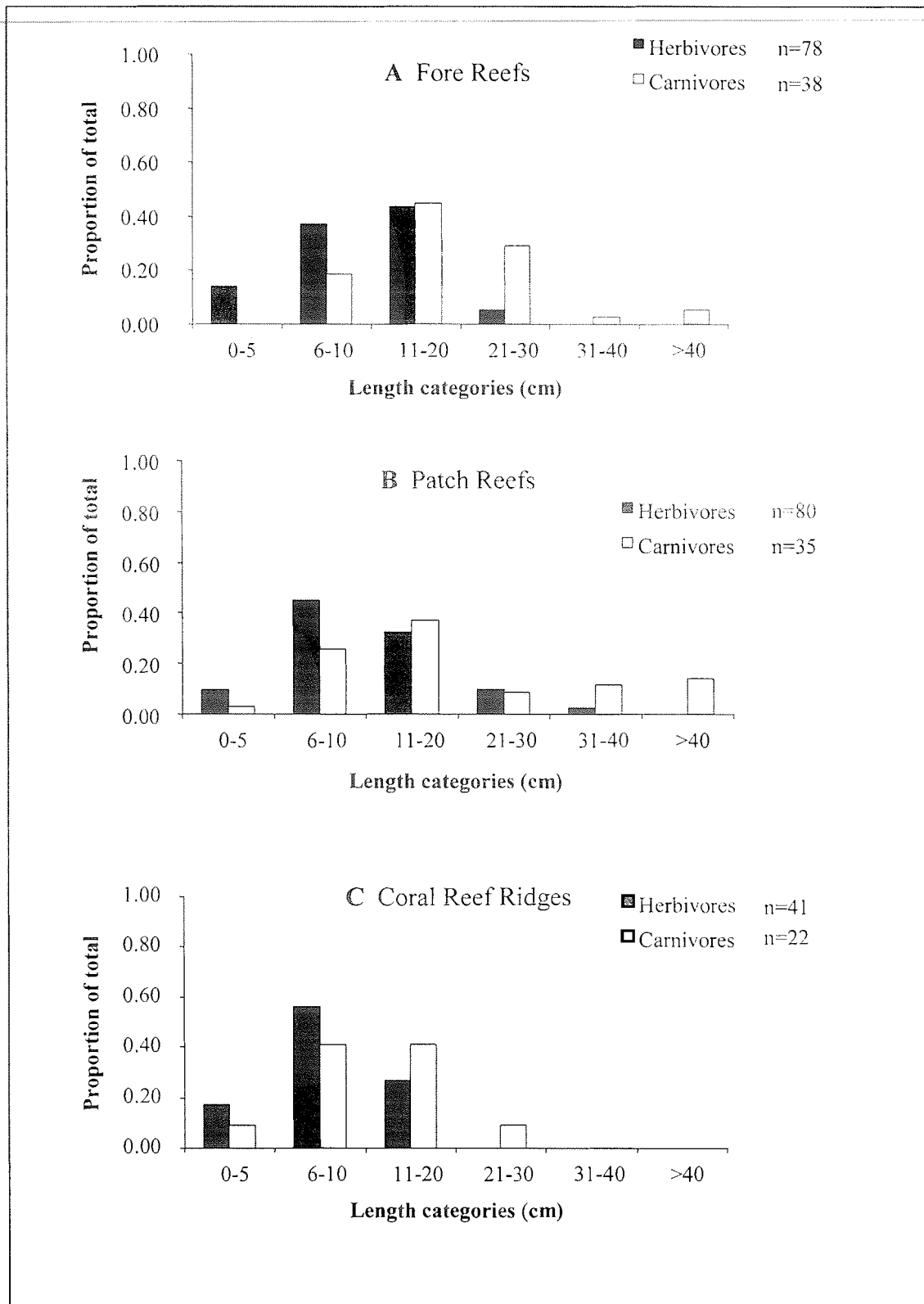


Figure 9. Size-frequency distribution of herbivores (all acanthurids and scarids, *Microspathodon chrysurus*) and carnivores (all lutjanids and serranids) at (A) fore reefs; (B) patch reefs; (C) coral ridge reefs along the Belize barrier reef.

(80%) of the carnivores fell within the 6-10 cm or 11-20 cm length range, a greater range of sizes was present in the fore reefs and patch reefs than in the reef ridges. In particular, the patch reefs supported a substantial number (15% of the sample) of carnivores of the largest (>40 cm) size category, all of which were found within the Hol Chan Marine Reserve.

At the 12 sites for which we have measurements, herbivorous fish grazing rates ranged from 1.4 bites/min. (Peter Douglas reef ridge) to 13.4 bites/min. (Norvall Caye patch reef; Table 5). Overall, grazing rates were slightly higher in the patch reefs (mean = 6.4 bites/min., $n = 5$ reefs) than in the fore reefs (mean = 3.2 bites/min., $n = 5$ reefs). Generally, parrotfishes and surgeonfishes were the predominant grazers in patch reefs and fore-reefs, respectively. No relationship was found between herbivorous fish density and macroalgal index (Fig. 10) nor between grazing rate and macroalgal index (regression analysis, $F < 1$).

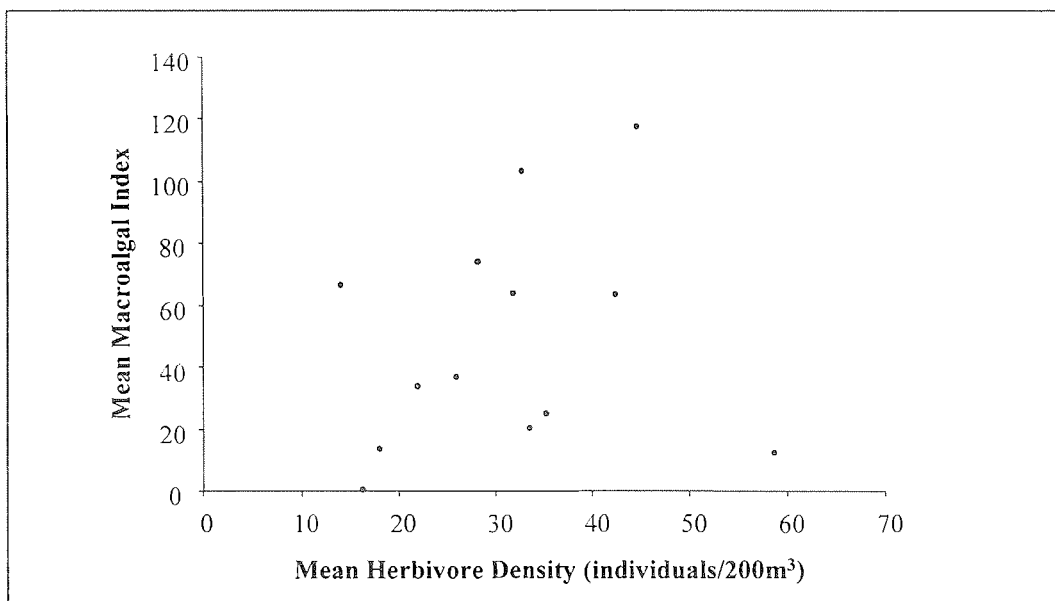


Figure 10. Regression plot between mean herbivore density (no. individuals/200 m³) and mean macroalgal index, by site along the Belize barrier reef.

DISCUSSION

Our May, 1999 AGRRA surveys along the northern and south-central regions of the Belize barrier reef were conducted approximately seven-eight months after the occurrence of two large-scale disturbances, a major thermal anomaly and the passage of Hurricane Mitch. Many corals had not yet recovered from the September 1998 warming event. Although the fore reefs and patch reefs appeared to have lower recovery rates than the coral reef ridges, this is only because *Agaricia tenuifolia*, the species most affected by the thermal anomaly, had sustained high rates of total colony mortality (see also Aronson et al., 2000). In the south-central patch reefs, 50% of the colonies of another major reef

builder, the *Montastraea annularis* complex had been bleached the previous January (Peckol et al., 2001). Over 44% of this population was still affected in May, 1999 when comparable percentages in the northern patch reef averaged 26%. However, earlier bleaching data are lacking from these northern sites, and we do not know if this regional difference represents more rapid recovery or is related to a lower initial stress during the thermal anomaly. Other common mound corals (*Diploria* spp. and *Siderastrea siderea*) showed higher incidences of recovery; whereas ~34% had been bleached in January, only 15% of all species remained discolored in May in south-central sites.

In May 1999, 42% of the *M. annularis* complex in our fore reefs had discolored tissues. The following month Kramer and Kramer (2000) found significant remnant bleaching (to >40% of the colonies) at depths of 8-20m in 36 fore reefs off Belize. In contrast, Mumby (1999) reported that though 70-90% of coral colonies in the fore reef (at 8-10 m) of Glovers Atoll (Belize) appeared to be either fully or partially bleached in response to the 1998 warming event, these colonies rapidly (by late December 1998) regained their usual coloration.

A number of studies have reported that recovery from bleaching proceeds more slowly in corals occurring at greater depths (see Kramer and Kramer, 2000). The long-term impacts and potential for recovery of the Belize barrier reef from such a large-scale thermal anomaly are uncertain. Generally, our survey of the Belize barrier reef suggests a degradation of this once largely pristine reef environment (Perkins and Carr, 1985; Cortés, 1997). Such deterioration may stem from a combination of direct and indirect effects from global climate change (Aronson et al., 2000) and regional human activities (Higinio and Munt, 1993; Carter et al., 1994).

Within-region partial mortality rates of stony corals were higher in lagoonal reefs than in corresponding fore reefs, suggestive of greater effects overall from the 1998 coral bleaching event than from Hurricane Mitch. The greatest impacts from this major storm were found in fore reefs and outer atoll reefs off Belize (Mumby, 1999). Kramer and Kramer (2000) reported major damage at several sites off Belize where damage from Hurricane Mitch resulted in a notable loss of reef structure; they noted storm damage down to their deepest survey site at 20 m in the fore reef. During a previous AGRRA survey in January 1999 in a fore reef near South Water Caye (Peckol et al., unpublished data), we documented breakage of branching corals, including *Millepora alcicornis* (33%), *M. complanata* (10%), and *Porites porites* (30%). We also recorded toppling of about 3% of the colonies of the *M. annularis* complex. Substantial amounts of rubble and entire mound corals had been transported onto and behind the reef crest. By May 1999, however, our AGRRA survey found limited evidence of the hurricane effects on the attached corals occurring in fore reefs.

Because major frame-builders, such as the *Montastraea annularis* complex and *Acropora palmata*, were rare as recruits in our sites, reef recovery may be slow following major disturbances like hurricanes and widespread bleaching. For example, although the *M. annularis* complex represented nearly 50% of the colonies ≥ 10 cm diameter in the patch reefs, it showed relatively low (9%) recruit abundance. Moreover, increasing macroalgal and sponge cover on the dead colonies of *Agaricia tenuifolia* in the coral reef ridges following the thermal anomaly (Peckol et al., unpublished data) may limit coral recruitment onto this substrate. Aronson and Precht (2001) reported that *Echinometra viridis* had suppressed macroalgal growth after the mass mortality of *A. cervicornis* from

white-band disease in the 1980s, allowing recruitment of *A. tenuifolia*. Although *Porites astreoides* was the dominant recruit (nearly 50% numerically) in this habitat, we did find some recruits (9% of total) of the formerly dominant *A. tenuifolia*.

Turf algae dominated in patch and coral reef ridges, yet macroalgae were quite prevalent representing >30% absolute abundance in the quadrats at 6/13 sites and exceeding 40% in two of the fore reefs (Table 3). Many Caribbean reefs have experienced exponential increases in macroalgal cover (Hughes, 1994; Shulman and Robertson, 1996; Peckol et al., this volume) often attributed to reductions in the sea urchin, *Diadema antillarum*, and herbivorous fishes (Hughes, 1994; Hughes et al., 1999). However, densities of *D. antillarum* were relatively low in the Belize barrier reef before the mass mortality event (Hay, 1984) and, until recently, much of this reef system has experienced low fishing pressures. Rapidly increasing abundances of brown macroalgae have been reported in a number of fore reefs in several studies of the Belize barrier reef (Littler et al., 1987; Aronson et al., 1994), including areas considered relatively remote from human activities (McClanahan et al., 1999). The local cause(s) of such change for the Belize barrier reef remains unclear although high rates of coral mortality, the two warming events of the 1990s, nutrient loading, and reduced herbivory from fishes have been suggested (Aronson and Precht 1997; McClanahan et al., 1999; Aronson et al., 2000). Because many areas experiencing increased macroalgal cover are remote from human activities, nutrient loading is unlikely to be the direct cause of such changes (McClanahan et al., 1999).

The grazing rates measured in the present study were approximately twice as high in patch reefs as in fore reefs. In addition, mean parrotfish densities were somewhat greater in south-central patch reefs compared with other sites in Belize and grazing by parrotfish represented >50% of the observed activities in these patch reefs where turf algae still dominate. Parrotfish densities overall ($\sim 5.2/200 \text{ m}^3$ and in leeward patch reefs ($\sim 6.5/200 \text{ m}^3$) documented in a 1998 AGRRA survey off San Salvador Island, Bahamas (Peckol et al., this volume) were about half those measured in the Belize barrier reef (overall $1\sim 10.9/200 \text{ m}^3$; patch reefs $\sim 11.2/200 \text{ m}^3$). Absolute macroalgal abundances were approximately two (44% overall) to three (59% on patch reefs) times greater off San Salvador Island than in Belize ($\sim 25\%$). Similar to Belize, the San Salvador reefs are also experiencing increases in cover by brown seaweeds. Lewis (1985) reported that parrotfishes actively grazed on several brown algal genera not consumed by surgeonfishes. Perhaps changing abundance patterns of parrotfishes, particularly in fore reefs, in part has contributed to increases in brown macroalgae in the Belize barrier reef. Further study should allow us to document such a relationship.

The Hol Chan patch reef had the highest combined densities of carnivorous fishes (seabasses, snappers, grunts) of all the surveyed patch reefs and the largest carnivores were found within the reserve. Partial-coral mortality was lower in the northern region than at the south-central sites. These spatial differences in reef condition (coral colony mortality, fish population abundance, and size) in part may be related to the establishment of the Hol Chan Marine Reserve in 1987. Prior to its establishment, the area was subject to uncontrolled fishing pressures that had removed most of the large and mobile fish from the reef and to burgeoning numbers of tourists who often damaged its corals. With the establishment of the reserve, these issues were largely addressed (e.g., installation of mooring buoys, education of tourists by local guides about behavior while

diving on reefs), and the community gained a critical conservation ethic and pride in their unique marine resource (Carter et al., 1994). Recent studies, which included the Hol Chan Marine Reserve (Sedberry et al., 1992; Roberts, 1995), have demonstrated that snapper and grouper populations are more abundant and fishes are larger within reserves than outside their boundaries. The added benefit of marine reserves is that they can result in increased fish abundances in adjacent reefs as a "spill-over effect" (Russ and Alcala, 1996). Clearly, this small but successful reserve admirably serves as a model for future reef conservation for the Belize barrier reef system as well as elsewhere.

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Table 1. Site information for AGRRA stony coral, algal and fish surveys off Belize, May 1999.

Site name	Reef type	Latitude (°N)	Longitude (°W)	Survey date	Depth (m)	Benthic transects (#)	≥10 cm stony corals (#/10 m)	Fish cylinders (#)	Fish species ¹ (#)	Fish density (#/200 m ³)
Eagle Ray Canyon	forereef	17.92	87.95	May 21 99	12-17	13	15	6	23	46.0
San Pedro Canyon	forereef	17.92	87.94	May 21 99	12-15	13	14.5	8	16	38.3
Tobacco	forereef	16.87	88.07	May 21 99	11-14	14	16.5	8	31	82.3
South Water	forereef	16.81	88.06	May 25 99	10-14	17	16.5	8	31	50.1
Curlew	forereef	16.78	88.08	May 24 99	10-13	16	15	7	29	86.0
Hol Chan	patch reef	17.89	87.96	May 20 99	2-5	18	13.5	10	32	55.1
Mexico Rocks	patch reef	17.94	87.94	May 20 99	2-4	12	13	7	16	52.0
Wee Wee Patch	patch reef	16.76	88.14	May 25 99	2-5	15	17.5	8	26	42.3
Bread & Butter	patch reef	16.77	88.16	May 28 99	1-5	13	20.5	8	22	60.3
Norvall	patch reef	16.71	88.17	May 27 99	1-4	12	18	8	25	41.6
Wee Wee Ridge	coral reef ridge	16.76	88.14	May 26 99	5-13	13	12	8	17	39.9
Peter Douglas	coral reef ridge	16.71	88.17	May 27 99	7-13	12	17.5	6	14	21.7
Tunicate	coral reef ridge	16.66	88.19	May 27 99	5-14	12	16	7	21	105.1

¹Fish species = all species of acanthurids, chaetodontids, haemulids, labrids, lutjanids, pomacentrids, scarids and serranids.

Table 2. Size and condition (mean \pm standard error) of all stony corals (≥ 10 cm diameter) by site off Belize.

Site name	Stony corals		Partial-colony surface mortality (%)			Stony corals (%)		
	(#)	Diameter (cm)	Recent	Old	Total	Standing dead	Bleached	Diseased
Fore reefs								
Eagle Ray	205	29.0 \pm 2.2	1.5 \pm 0.6	16.0 \pm 1.8	17.0 \pm 2.0	1.5 \pm 1.0	26	2
San Pedro	209	22.0 \pm 1.5	2.5 \pm 0.7	10.5 \pm 1.5	13.0 \pm 1.5	1.5 \pm 1.5	18	1
Tobacco	256	50.5 \pm 5.3	1.5 \pm 0.5	22.5 \pm 2.0	24.0 \pm 2.0	8.5 \pm 2.5	13	1
South Water	297	49.5 \pm 2.6	3.0 \pm 0.7	21.0 \pm 1.7	24.0 \pm 2.0	3.5 \pm 1.5	18	5
Curlew	270	51.0 \pm 6.4	2.0 \pm 0.5	21.5 \pm 1.9	23.5 \pm 2.0	3.0 \pm 1.0	7	2
Patch Reefs								
Mexico Rocks	178	46.0 \pm 6.3	2.0 \pm 0.6	20.5 \pm 2.4	22.5 \pm 2.5	3.0 \pm 1.5	16	2
Hol Chan	287	46.0 \pm 3.7	2.1 \pm 0.6	26.5 \pm 1.9	28.5 \pm 2.0	5.0 \pm 2.0	15	0
Bread & Butter	278	52.0 \pm 3.1	5.5 \pm 0.3	34.0 \pm 2.0	39.0 \pm 2.3	10.5 \pm 3.0	17	2
Wee-Wee	278	48.5 \pm 3.3	4.5 \pm 1.0	46.5 \pm 2.7	50.5 \pm 2.8	14.5 \pm 4.5	23	2
Norvall	211	60.0 \pm 4.8	5.5 \pm 1.0	41.5 \pm 2.3	47.0 \pm 2.2	6.5 \pm 2.0	40	2
Coral Reef Ridges								
Wee-Wee	222	29.0 \pm 4.9	3.5 \pm 0.9	32.0 \pm 2.7	35.5 \pm 2.8	18.0 \pm 4.0	2	0
Peter Douglas	266	29.0 \pm 1.7	7.0 \pm 1.3	28.5 \pm 2.4	35.5 \pm 2.6	26.5 \pm 4.5	7	0
Tunicate	235	56.5 \pm 7.4	13.5 \pm 1.9	45.5 \pm 3.0	58.5 \pm 3.0	50.0 \pm 6.5	6	0

Table 3. Algal characteristics and stony coral recruit abundance (mean \pm standard error) by site off Belize.

Site name	Quadrats (#)	Absolute abundance (%)			Macroalgal		Recruits (#/.0625m ²)
		Macroalgae	Turf algae	Crustose coralline algae	Height (cm)	Index ¹	
Fore reefs							
Eagle Ray	35	40.0 \pm 5.5	19.0 \pm 4.0	35.5 \pm 4.5	0.7 \pm 0.1	37 \pm 7	0.4 \pm 0.1
San Pedro	37	33.0 \pm 4.0	51.0 \pm 4.0	15.5 \pm 3.5	1.0 \pm 0.1	34 \pm 5	0.4 \pm 0.1
Tobacco	60	33.5 \pm 4.5	33.5 \pm 4.0	35.3 \pm 4.5	1.4 \pm 0.1	63 \pm 12	0.5 \pm 0.1
South Water	62	43.5 \pm 1.5	49.0 \pm 2.0	40.5 \pm 2.0	1.6 \pm 0.1	103 \pm 7	0.4 \pm 0.1
Curlew	39	18.5 \pm 4.5	27.5 \pm 5.0	43.0 \pm 5.5	0.2 \pm 0.1	12 \pm 6	0.5 \pm 0.1
Patch Reefs							
Mexico Rocks	38	26.5 \pm 5.0	60.0 \pm 5.5	10.0 \pm 4.0	1.4 \pm 0.2	64 \pm 17	0.5 \pm 0.1
Hol Chan	61	26.5 \pm 4.0	54.0 \pm 4.5	17.5 \pm 3.5	1.5 \pm 0.2	66 \pm 13	0.6 \pm 0.1
Bread & Butter	63	37.5 \pm 5.0	48.5 \pm 4.5	9.0 \pm 3.0	1.7 \pm 0.2	117 \pm 23	0.3 \pm 0.1
Wee-Wee	72	21.0 \pm 3.5	61.0 \pm 4.5	5.0 \pm 2.0	0.7 \pm 0.1	25 \pm 6	0.4 \pm 0.1
Norvall	40	12.0 \pm 3.0	68.5 \pm 4.5	2.5 \pm 2.0	0.9 \pm 0.1	20 \pm 6	0.3 \pm 0.1
Coral Reef Ridges							
Wee-Wee	40	30.5 \pm 4.5	35.5 \pm 6.5	5.0 \pm 2.5	1.5 \pm 0.3	74 \pm 14	0.7 \pm 0.1
Peter Douglas	11	2.0 \pm 2.5	54.5 \pm 11.0	4.5 \pm 3.0	0.1 \pm 0.0	<1 \pm <1	0.7 \pm 0.1
Tunicate	31	10.5 \pm 2.5	32.5 \pm 5.5	9.5 \pm 3.0	0.7 \pm 0.2	13 \pm 4	0.6 \pm 0.1

¹Macroalgal index = absolute macroalgal abundance x macroalgal height.

Table 4. Density (mean \pm standard error) of selected fish families by site off Belize.

Site name	Herbivores (#/200 m ³)		Carniivores (#/200 m ³)		
	Acanthuridae	Scaridae	Haemulidae	Lutjanidae	Serranidae
Fore reefs					
Eagle Ray	4.2 \pm 0.8	11.2 \pm 2.1	0.6 \bullet 0.3	1.4 \bullet 0.4	3.2 \pm 0.8
San Pedro	2.7 \bullet 1.2	7.0 \bullet 2.8	1.6 \bullet 0.7	6.9 \bullet 3.9	1.3 \pm 0.5
Tobacco	7.4 \bullet 0.8	14.1 \pm 2.4	3.5 \pm 1.9	12.3 \pm 4.1	1.3 \bullet 0.6
South Water	6.9 \pm 0.9	12.1 \bullet 1.8	1.9 \pm 0.4	4.3 \pm 1.4	0.3 \pm 0.3
Curlew	13.4 \pm 7.2	11.3 \pm 2.8	1.4 \pm 0.4	4.1 \pm 1.9	0.4 \pm 0.3
Patch Reefs					
Mexico Rocks	18.3 \pm 12.0	5.1 \pm 1.3	6.4 \pm 1.9	3.3 \pm 0.9	0.1 \pm 0.1
Hol Chan	3.6 \pm 2.2	4.9 \pm 1.1	20.6 \pm 11.1	7.5 \pm 1.9	0.7 \pm 0.3
Bread & Butter	12.5 \pm 9.8	22.5 \pm 5.9	11.4 \pm 8.8	1.6 \bullet 0.6	0.8 \pm 0.4
Wee-Wee	8.4 \pm 5.3	9.1 \pm 2.4	3.5 \pm 1.8	1.8 \pm 0.7	0.0 \pm 0.0
Norvall	9.0 \pm 6.2	14.3 \pm 1.8	1.9 \pm 0.3	1.4 \pm 0.3	1.3 \pm 0.1
Coral Reef Ridges					
Wee-Wee	0.1 \pm 0.1	10.4 \pm 2.6	0.2 \pm 0.2	0.6 \pm 0.3	1.6 \pm 0.4
Peter Douglas	0.0 \pm 0.0	6.7 \pm 0.8	2.8 \bullet 1.2	0.8 \pm 0.3	1.3 \pm 0.2
Tunicate	0.4 \pm 0.4	13.6 \pm 2.5	77.6 \pm 24.5	3.0 \bullet 1.5	5.4 \pm 2.7

Table 5. Herbivorous fish grazing rates (mean \pm standard error) for sites in Belize.

Site name	Observations (#)	Grazing rate (#bites/min.)
Fore reefs		
Eagle Ray		not done
San Pedro	5	2.6 \pm 1.2
Tobacco	4	5.4 \pm 1.9
South Water	4	4.7 \pm 2.2
Curlew	2	2.1 \pm 0.5
Patch Reefs		
Mexico Rocks	5	10.1 \pm 3.8
Hol Chan	10	3.5 \pm 1.1
Bread & Butter	4	3.2 \pm 1.2
Wee-Wee	4	2.8 \pm 0.8
Norvall	4	13.4 \pm 6.2
Coral Reef Ridges		
Wee-Wee	4	2.8 \pm 0.9
Peter Douglas	4	1.4 \bullet 0.8
Tunicate	4	7.8 \pm 1.9