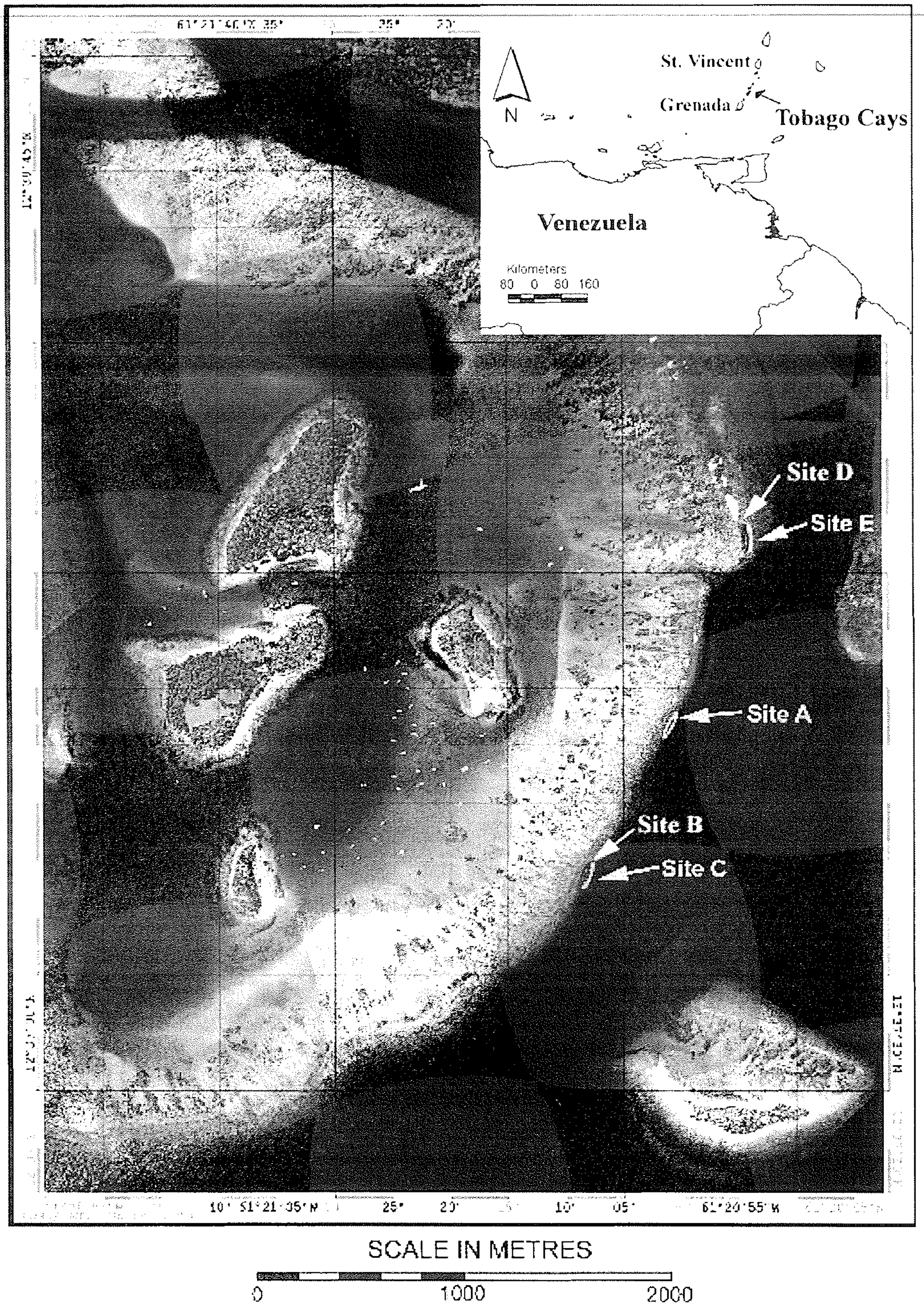

Figure 1. Photo mosaic of the AGRRA survey sites on Horseshoe Reef, Tobago Cays, in St.Vincent and the Grenadines. See Table 1 for site codes.

A RAPID ASSESSMENT OF THE HORSESHOE REEF, TOBAGO CAYS MARINE PARK, ST. VINCENT, WEST INDIES (STONY CORALS, ALGAE AND FISHES)

BY

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ABSTRACT

Fore reefs at Horseshoe Reef, Tobago Cays, had an average live stony-coral cover of 30% at 3-4 m and nearly 40% at 9-11 m in June 1999. "Large corals" (≥25 cm maximum diameter) were dominated by *Montastraea annularis*, *Porites astreoides* and *P. porites*. However, live colonies of *Acropora palmata,* which once flourished in the high-energy shallow-reef zones, had virtually disappeared. The maximum diameter of large reef corals averaged 58 cm which may be indicative of steady juvenile replenishment. The low values of recent partial-colony mortality (≤3%) and minor disease occurrences (≤6% of colonies) at all sites indicated that the large corals on Horseshoe Reef had experienced no major recent disturbance events. Pale, or partially bleached, colonies on the deeper reefs (about 10% of large corals) were probably still recovering from the 1998 mass bleaching event. Algal communities in the shallower reefs were dominated by crustose coralline algae (>50% relative abundance) whereas macroalgae (mainly *Halimeda* and *Dictyota*) were slightly more abundant than crustose corallines at 9-11 m. *Diadema antillarum* was uncommon in the deeper reefs but moderately abundant at 3-4 m. Eighty-one species of fish were recorded at Horseshoe Reef. The assemblage of censused fishes was dominated by herbivorous scarids (parrotfishes) and acanthurids (surgeonfishes). Herbivores, scarids in particular, also accounted for most of the censused fish biomass on the reef. Commercially valuable serranids, lutjanids and haemulids (groupers, snappers, grunts) were present in low densities (<1 individual/100m^2), indicative of overfishing.

INTRODUCTION

This study was located in the Tobago Cays, four small, uninhabited islands in St. Vincent-Grenadines (Fig.1) that are partially surrounded by fringing reefs. The Tobago

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Cays are protected on their windward sides by Horseshoe Reef, a semicircular, well-developed Holocene bank-barrier reef that is one of the longest (≈ 4km) in the southern Grenadine Islands (Dey and Smith, 1989). Seaward of its reef flat, the Horseshoe fore reef slopes steeply eastward to depths of about 20 meters.

The Grenadines are eroded remnant peaks and ridges of older volcanic islands that were partially or completely drowned during the post-Pleistocene rise in sea level. They arise from the submarine Grenadine Bank which runs NE-SW for about 180 km between St.Vincent and Grenada. The Bank is 15- to 20- km wide and 20-30 meters deep with local shallows at 3-6 m (Dey, 1985). The absence of rivers on these small islands prevents terrigenous sediments from being carried offshore and permits reef growth (Dey, 1985).

The Grenadines Bank lies within the Trade Wind belt where strong northeast winds develop during late autumn and winter and easterly winds during spring, summer and early autumn (Clack, 1977). The Equatorial Current moves over the Grenadine Bank, passes through the channels and reefs, and is diverted around the islands giving considerable local variation in current direction and strength (0.3-1.5 knots) (Dey and Smith, 1989). Tides in the Grenadines have a small range (0.6 m) and are mixed with a semidiurnal component dominating in the Tobago Cays area (Clack, 1977). Their strength, duration and general direction are influenced by local topographic variations present on the sea bottom of the shallow Bank. Temperature and salinity are both relatively constant over Grenadine Bank (Dey, 1985). The Bank is south of the region usually affected by hurricanes. The most violent recent storms to strike the Grenadine islands were Hurricanes Janet in 1955 and Allen in 1980 (Dey and Smith, 1989). No other hurricanes during the past 50 years have seriously affected the Tobago Cays' reefs (Kurt Cordice, personal communication).

The Tobago Cays are 3 km from Mayreau, the closest inhabited Grenadine Island with a population of approximately 250. Union Island, the closest major population center, with approximately 3500, is about 5 km away. The Cays are frequently visited by fishermen harvesting conch and lobster and are now increasingly used by tourists for sailing, snorkeling and diving.

Over the past 15 years a number of informal reports have indicated that reefs in the Tobago Cays have deteriorated as a result of physical damage from storms, anchors, and fishing gear, as well as from white-band disease, other diseases, and localized nutrient pollution from yachts (Wells, 1988; Smith et al., 1997). The Tobago Cays Marine Park (TCMP) protected area was established in 1998 and is gradually developing its management plans. Horseshoe Reef lies within the TCMP and some fishing regulations have been established. Conversations with local residents revealed, however, that illegal fishing with spearguns is a common practice in the local artisanal fishing community and that any sizable fish, including parrotfish, are targeted. Indeed, we witnessed fishing activity within the marine park on a daily basis during the course of our survey.

Except for preliminary descriptions by Lewis (1975), the Tobago Cay reefs have received little scientific attention (Wells, 1988; Smith et al., 1997). Hence, we aimed to characterize the present condition of Horseshoe Reef using the Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol.

METHODS

Field data were collected from June 7-16, 1999. Dive sites (Fig.1) that were representative of areas of maximum reef development were selected with the help of true color aerial photographs (scale 1:10 000, March 1991), nautical charts (Hydrographic Office of the United Kingdom, 1999), reconnaissance dives, and the local knowledge of experienced divers and dive-shop operators. Site selection was limited, however, by accessibility to boats and by strong tidal currents. Two shallow reefs (B, D), located between 1 and 5 m in the shallow fore reef, consisted of dead *A. palmata* pavement, largely encrusted by crustose coralline algae and colonized by *Millepora* and scattered *Porites*. Three deeper reefs (A, C, E), located between 8 and 15 m on the fore-reef slope, consisted of dead coral pavement, largely colonized various coral species dominated by *Montastraea* and *Porites* with scattered patches of Halimeda.

Stony corals, algal groups, and *Diadema antillarum* were censused by one or two divers/survey. The following modifications were made to the AGRRA Version 2.2 protocols (see Appendix One, this volume). The size of individual corals was recorded to the closest 5 cm. Damselfish that were defending territories on censused corals were counted. Sediment in the algal quadrats was lightly brushed away before scoring the abundance of crustose coralline algae. Macroalgal heights were measured to the nearest 0.5 cm. Small (<2 cm diameter) corals of species that are tiny as adults (e.g., *Favia fragum*) were not counted as "recruits." Before starting the surveys, pilot transects were conducted in the back reef and results compared to ensure consistency between divers.

All fish surveys were made by one diver between 9:00 a.m. and 4:00 p.m. Counts of serranids (groupers) were restricted to species of *Epinephelus* and *Mycteroperca*; scarids (parrotfishes) and haemulids (grunts) less than 5 cm in length were not tallied. Roving Diver Transect (RDT) surveys averaged 30 minutes each. Fish biomass was estimated using the length-weight relationships given in Appendix Two (this volume). Field guides included Humann (1994, 1996).

RESULTS

A total of 60 benthic line transects with 531 corals, 268 algal quadrats, 10 roving diver fish counts and 50 fish-belt transects were conducted on the Horseshoe Reef (Fig. 1, Table 1). Weather conditions were good during most dives with horizontal visibility estimated at approximately 20-25 meters.

Stony Corals

The assemblage of "large" stony corals (≥25 cm maximum diameter) was represented by 16 species and dominated overall by *Montastraea annularis* (31%), *Porites astreoides* (23%), *P. porites* (23%), *Montastraea faveolata* (5%), *Millepora complanata* (4%), *Colpolphyllia natans* (2%) *and Siderastrea siderastrea* (2%). Nine large coral species predominated at the two shallow reefs (Fig. 2A) with *P. astreoides* > *M. annularis*

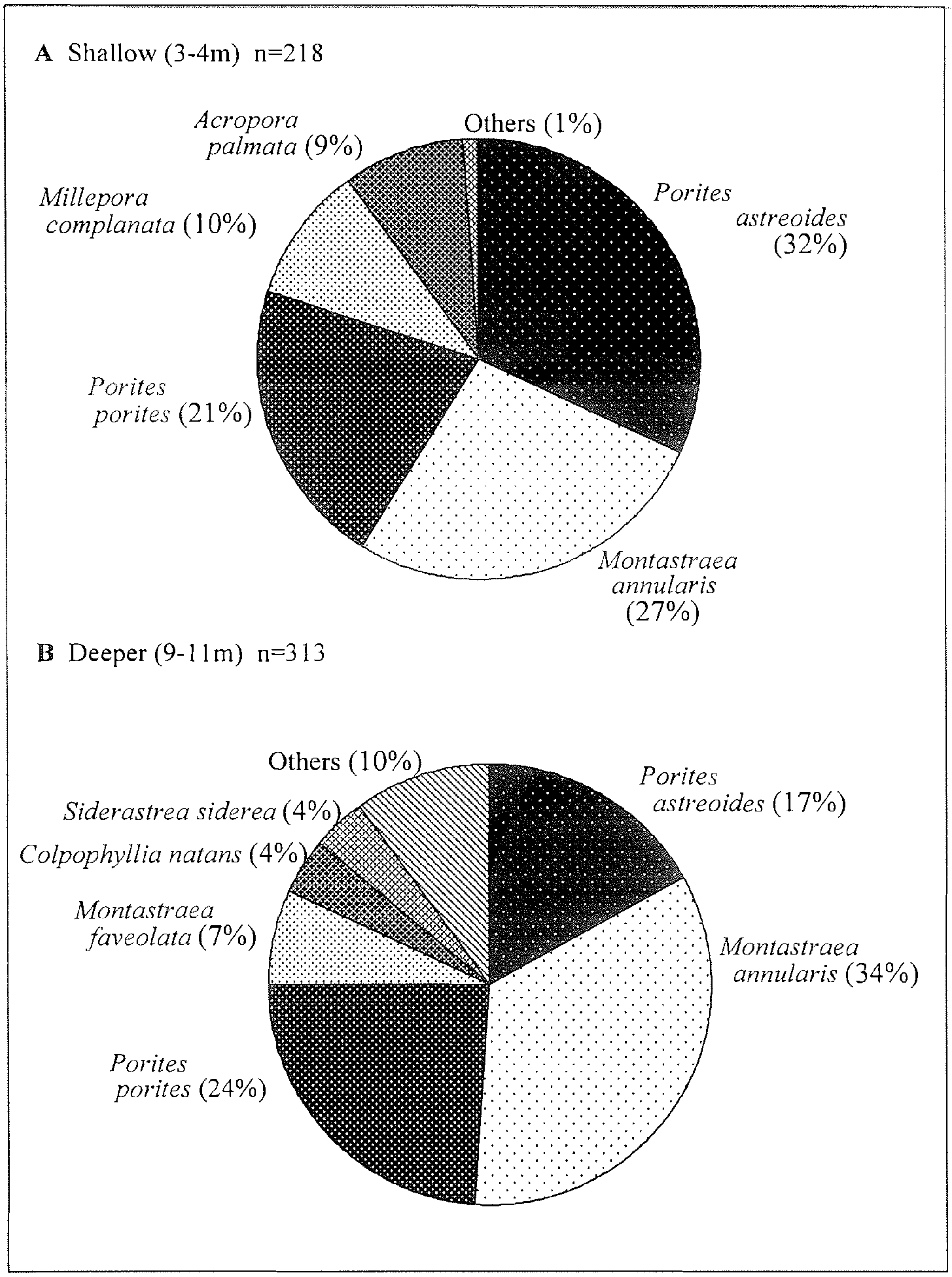

Figure 2. Species composition and mean relative abundance of all stony corals (≥25 cm diameter) on (**A**) shallow, (**B**) deeper fore reefs at Horseshoe Reef.

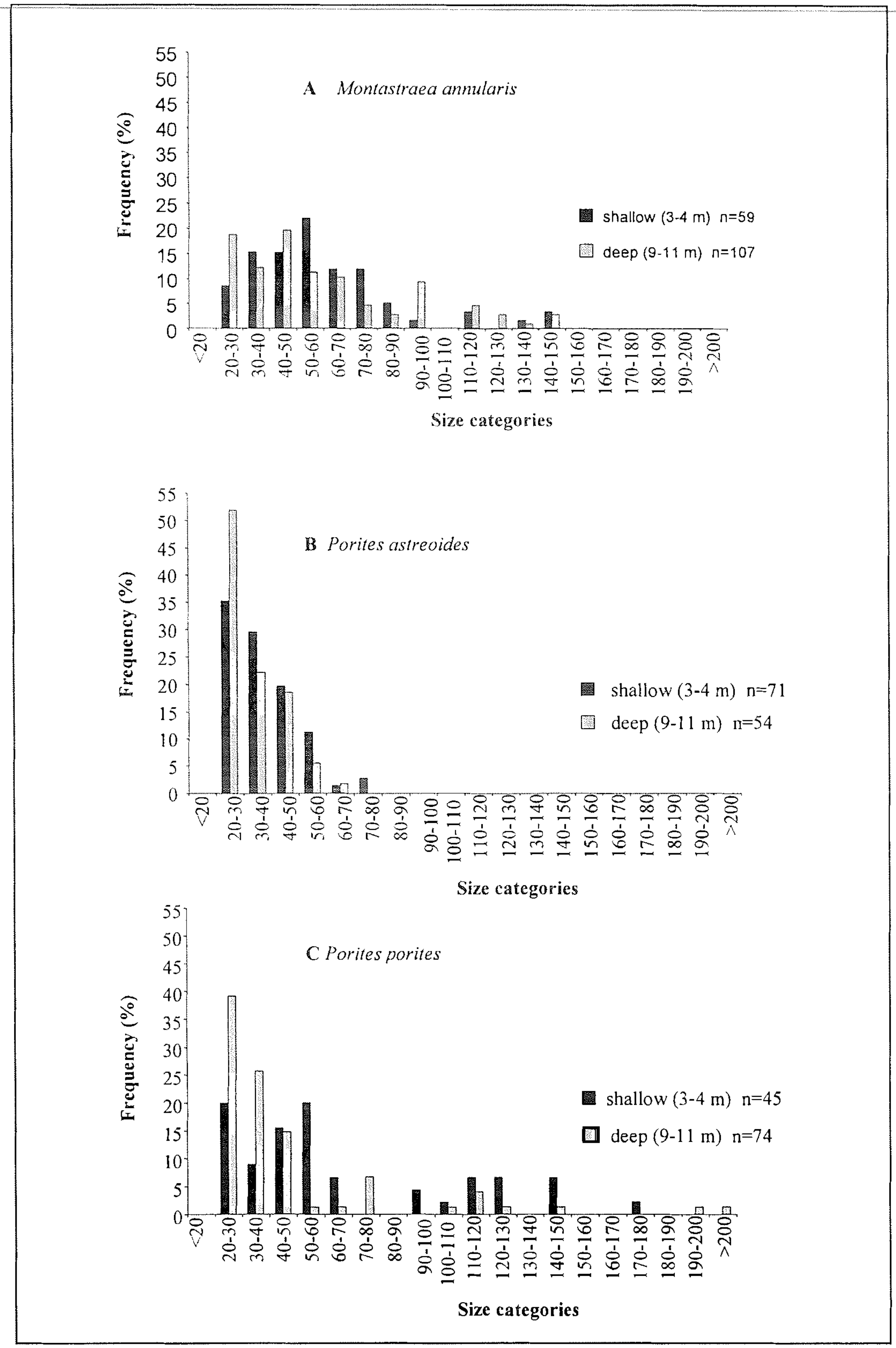

Figure 3. Size-frequency distribution in cm of colonies (≥25 cm diameter) of (**A**) *Montastraea annularis*, (**B**) *Porites astreoides*, (**C**) *Porites porites* at Horseshoe Reef.

> *P. porites* > *M. complanata* ~ standing dead colonies of *Acropora palmata* (recognizable by their characteristic colony shape, and only present at site B). The deeper reefs, which had a total of 15 large coral species, were dominated by *M. annularis* > *P. porites* > *P. astreoides* > *M. faveolata* > *C. natans* ~ *S. siderea* (Fig. 2B).

Live stony coral cover averaged about 30% at the shallow reefs and 38% at the deeper reefs (Table 1). The mean diameter of the large colonies among sites ranged from 50 to 65 cm (Table 2). Size-frequency distributions for the three major reef builders (*M. annularis, P. astreoides, P. porites*) were skewed towards smaller colonies (Fig. 3). Larger clumps of *P. porites* (to 300 cm) and mounds of *Montastraea annularis* (to 150 cm) were also present but relatively uncommon. Coral recruitment averaged 0.25/0.625 m^2 (~4/m^2) the shallow reefs and 0.16/0.625 m^2 (~2.5/m^2) in the deeper reefs (Table 3). *Agaricia* and *Porites* were the most commonly seen recruits.

Fewer than 4% of the large corals at the shallow and deep sites of Horseshoe Reef showed signs of disease (Table 2). Four percent of the colonies of *Montastraea* were affected by yellow-blotch disease (YBD) while 2% of all massive corals had black-band disease (BBD). Whereas BBD was only present at one deeper reef (E), YBD occurred at all sites but C. No large corals were completely bleached and the percentage that were either pale or partially bleached varied from about 2.5% to 10.5% in the shallow and deeper reefs, respectively (Table 2). *Montastraea* accounted for 45% of the bleached corals in shallow reefs and 84% of bleached corals in deeper reefs. However, the overgrowing mat tunicate, *Trididemnun solidum*, which was present at all five sites, had partially encrusted about 10% (54/531) of the surveyed corals, primarily *Porites, Montastraea* and, occasionally, *Millepora.*

Partial-colony mortality on the upward-facing surfaces of surveyed corals averaged 2% for recent mortality (hereafter recent mortality) and 25% for old mortality (hereafter old mortality) (Table 2). Frequency distributions (Fig. 4 A, B) reveal that recent mortality for over 95% of these corals was less than 10% at both shallow and deeper sites, whereas fewer than 50% had old mortality values within this range. The most commonly observed sources of recent mortality were predation by *Coralliophila abbreviata*, parrotfish bites, and incorporation in damselfish algal gardens. Over 60% of the 143 damselfish counted were associated with the *M. annularis* species complex, with about a quarter of the colonies having at least one resident algal gardener. At the deeper reefs, localized bleaching was associated with dense stands of the calcareous macroalga *Halimeda* that were observed overgrowing the margins of some stony corals.

Algae and *Diadema antillarum*

Algal communities at the two shallow and one of the deeper sites were dominated by crustose coralline algae, whereas macroalgae (particularly the calcareous *Halimeda* spp., and, to a lesser degree, the fleshy *Dictyota* spp.) were the predominant algal functional group at the remaining two deeper reefs (Table 3). Average macroalgal canopy height was 1.5 cm (Table 3). Macroalgal indices (macroalgal relative abundance x macroalgal height) were considerably higher in the deeper reefs (~26 at 3-4 m versus ~64 at 9-12 m respectively). *Diadema antillarum* was present with mean densities of about five individuals/100 m^2 in the shallower reefs and about 0.5/100 m^2 in the deeper reefs.

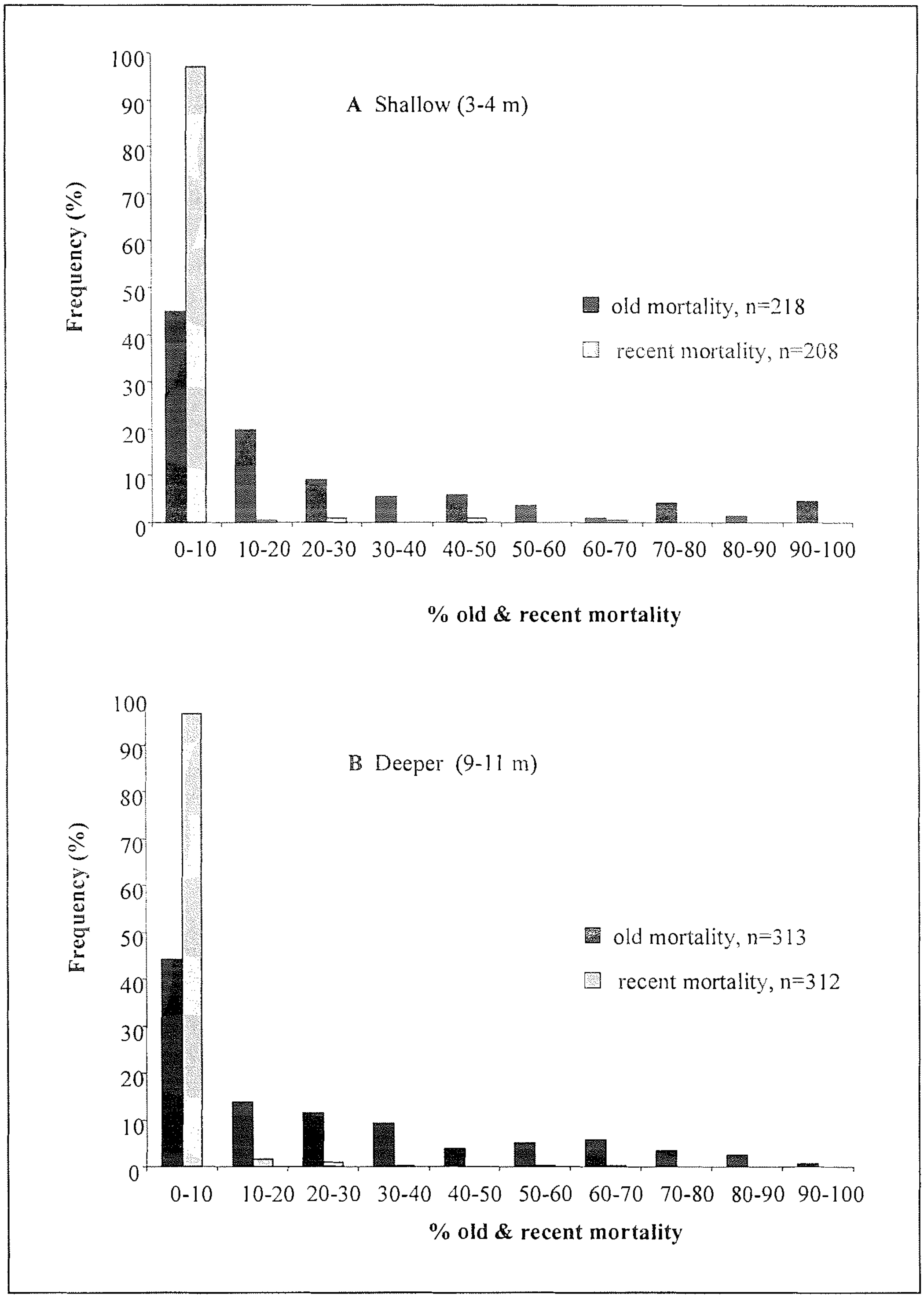

Figure 4. Frequency distribution for all stony corals (≥25 cm diameter) of old partial colony mortality and of recent partial colony mortality at (**A**) shallow and (**B**) deeper fore reefs at Horseshoe Reef.

Fishes

A total of 81 species of fish were recorded during the 10 roving diver surveys (≈7 hours). The most commonly sighted were planktivorous pomacentrids and herbivorous scarids, pomacentrids and acanthurids, followed by planktivorous labrids (Table 4). *Aulostomus maculatus* (trumpetfish), present in all surveys, was the most common predator. The fish assemblage quantified in the belt transects was dominated by scarids with 28 and 36 individuals/100 m^2 having body lengths of at least 5 cm in shallow and deeper sites, respectively (Fig. 5). Acanthurids were present with higher average densities at 3-4 m than at 9-12 m (12 versus 2 individuals/100 m^2, respectively). Similarly, *Microspathodon chrysurus* (yellowtail damselfish) were more abundant in shallow reefs (9 individuals/100 m^2) than in the deeper reefs (3 individuals/100 m^2). Commercially valuable species of select serranids, lutjanids (snappers), and haemulids (≥5 cm only) were collectively present at densities of less than 1 individual/100 m^2 ($\sum n$ = <20 individuals). It is notable, however, that although lutjanids were less commonly encountered in the belt transects than serranids or haemulids, *Lutjanus mahogoni* (mahogany snapper) were sighted more frequently (90 percent of dives) than serranids or haemulids during the roving diver surveys (Table 4).

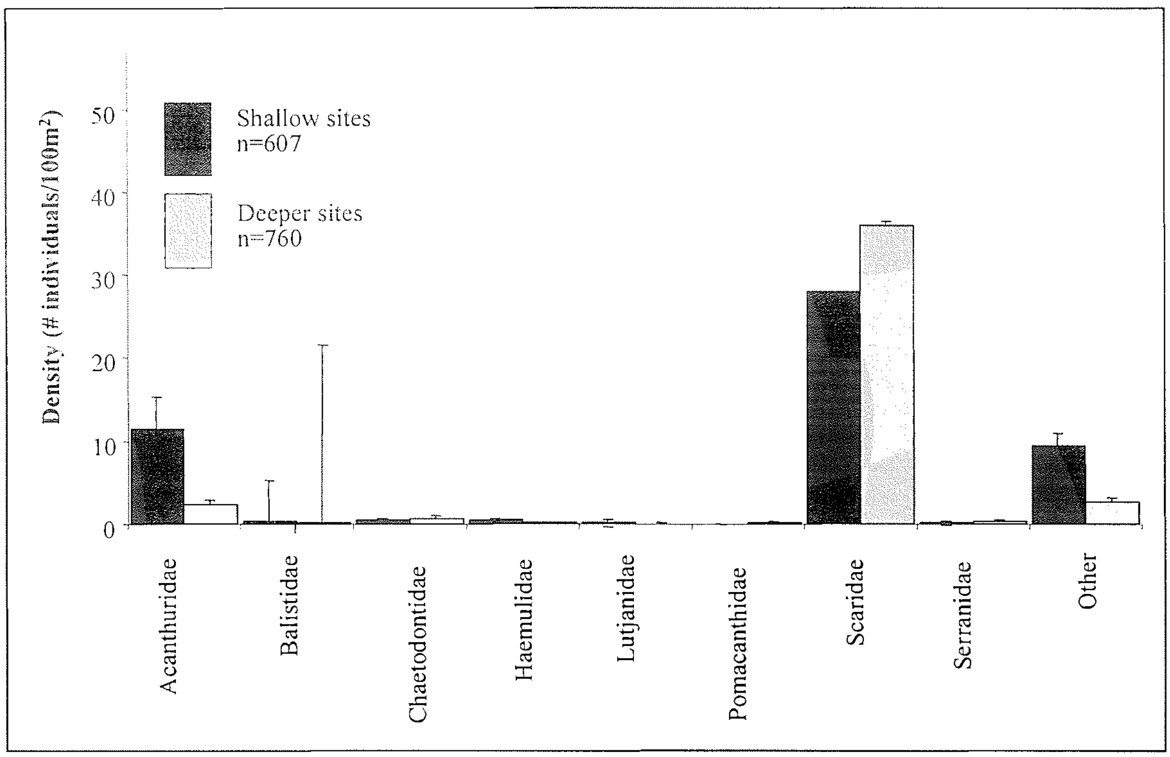

Figure 5. Mean fish abundance (no. individuals/100 m^2 ± se) for AGRRA fishes at Horseshoe Reef. Other = *Microspathodon chrysurus* > *Bodianthus rufus.*

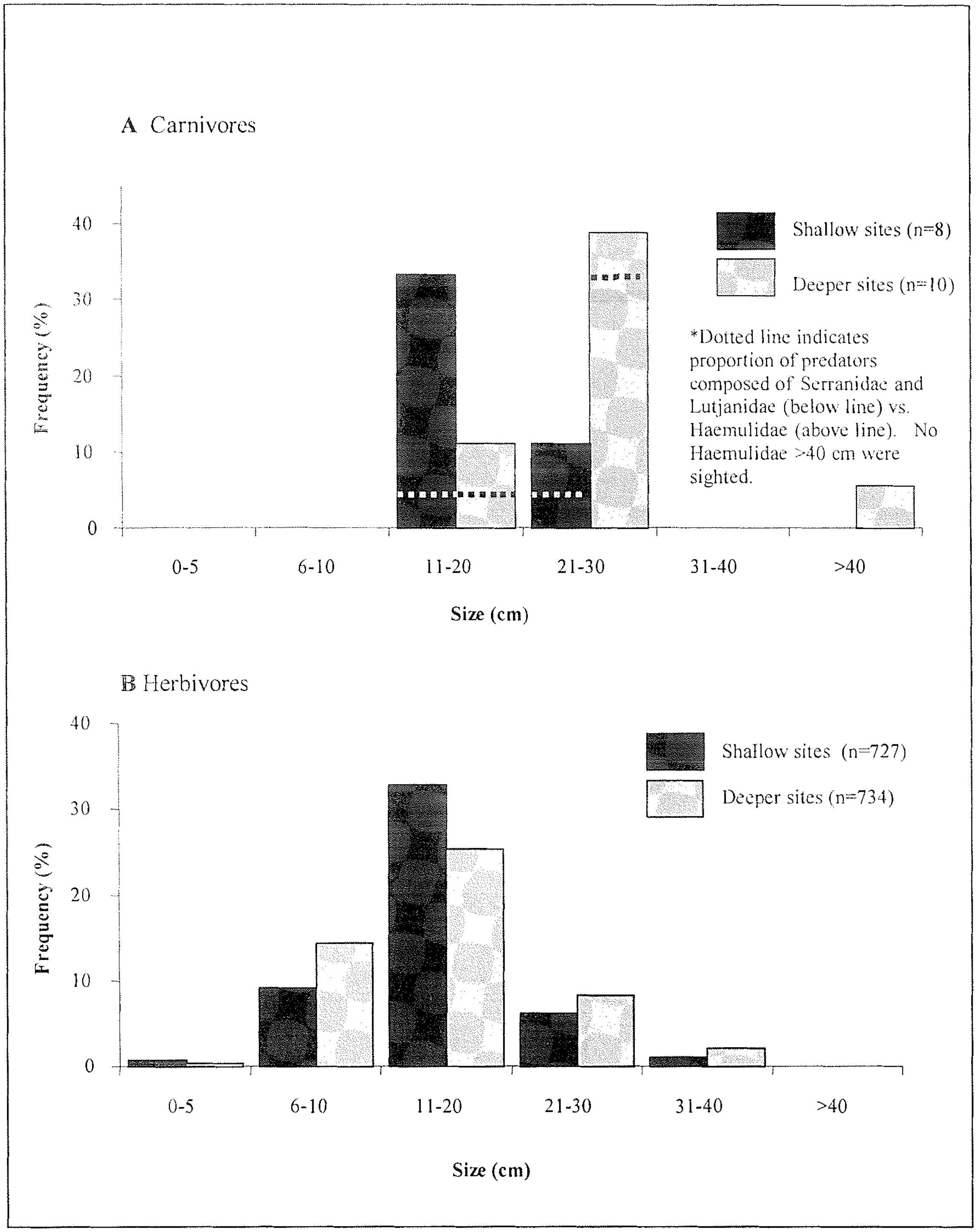

Figure 6. Size frequency distribution of (**A**) carnivores (lutjanids, select serranids, haemulids $\geq$5 cm), (**B**) herbivores (all acanthurids, scarids $\geq$5 cm, *Microspathodon chrysurus*) at Horseshoe Reef

Although commercially significant predators were rare in our belt transects, half (shallow) to most (deeper) of the groupers and snappers encountered ranged in size from 21-30 cm (Fig. 6A). Serranids (mean = 29 cm) were about twice as long as lutjanids (mean = 16 cm), which overlapped in size with the haemulids (all of which were ≥5 cm) (Fig. 7A). The lengths of half or more of each of the herbivorous groups (scarids ≥5 cm, acanthurids and *Microspathodon chrysurus)* were in the 11-20 cm length class and averaged about 15 cm (Figs. 6B, Fig. 7B).

Of the AGRRA fishes surveyed in the belt transects, the biomass of the herbivorous guild was 90 percent greater than that of the commercially valuable carnivores (Fig. 8). The scarid biomass was evenly distributed between shallow and deeper sites. Biomass estimates of acanthurids and *M. chrysurus* were considerably greater in the shallow reefs than in the deeper fore reefs (Table 5).

DISCUSSION

The coral assemblage and coral cover on Horseshoe Reef are typical of high-energy, windward Caribbean reefs and, except for the near disappearance of live *A. palmata* from the reef flat and shallow fore reef, very similar to the descriptions of Lewis (1975) (some juvenile *A. palmata* are present in the back-reef area immediately behind the reef crest). The presence of standing dead colonies of *A. palmata* in the shallow fore reefs is a good indication that they were not killed by hurricanes. Hence, we concur that their demise at Horseshoe Reef, as elsewhere in St. Vincent-Grenadines, was probably due to white-band disease (Antonius, 1981; Aronson and Precht, 1997).

The positively skewed size distribution of the three major reef-building corals may be an indication of a reef system with adequate juvenile input (Bak and Meesters, 1998) since large-scale fragmentation by hurricanes seems unlikely on Horseshoe Reef (see Introduction). The slightly lower density of coral recruits on the deeper reefs is probably related to the generally higher abundance of macroalgae as well as the relatively lower abundance of crustose coralline algae and the near absence of *Diadema antillarum* (Birkeland 1977; Pearson, 1981; Hughes et al., 1987).

None of the factors contributing to recent mortality are responsible for major damage to the corals at Horseshoe Reef. The pale or partially bleached corals seen during our survey, particularly on the deeper reefs, were possibly still recovering from the 1998 Caribbean-wide bleaching event (Strong et al., 1998) that affected reefs in the Tobago Cays (Kurt Cordice, personal communication). *Halimeda,* engaged in marginal overgrowth of some stony corals, may also have contributed to the higher occurrence of bleaching on these deeper reefs.

Competitive overgrowth by organisms such as *Trididemnun solidum,* which was not noted in the Tobago Cays by Lewis (1975), may be influenced by environmental perturbations that reduce the efficiency of affected organisms to defend themselves. Thus, its relatively high abundance (on 10% of the large colonies) at Horseshoe Reef is cause for concern. Although the effects of *T. solidum* were scored as "old mortality" in accordance with the AGRRA protocol, there were many cases for which we suspected that loss of coral tissues had occurred within recent months. Had *T. solidum* been recorded under "recent" mortality, our estimates of the latter would have been substantially larger.

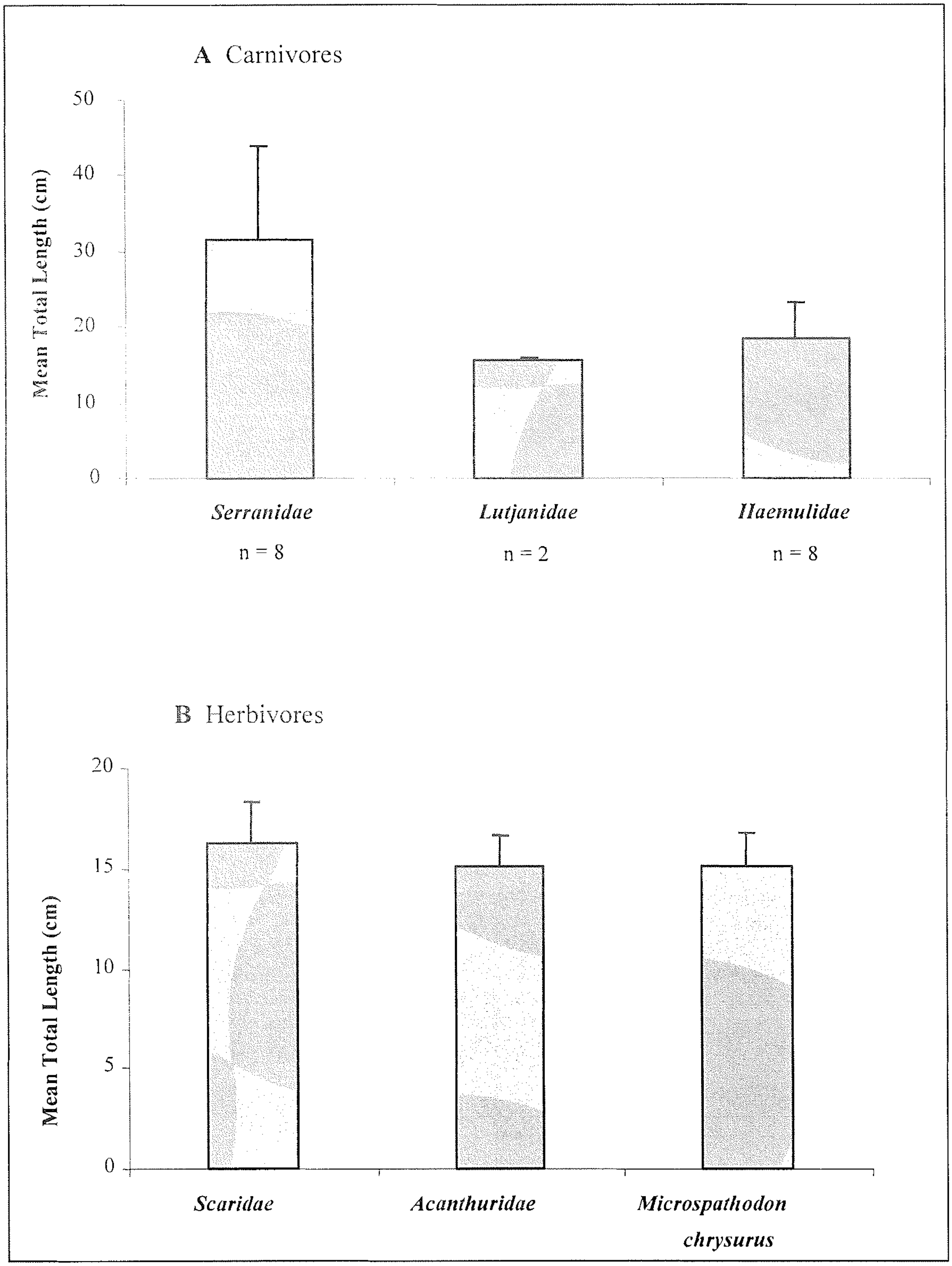

Figure 7. Mean total length (± se) of key (**A**) carnivores, (**B**) herbivores at Horseshoe Reef.

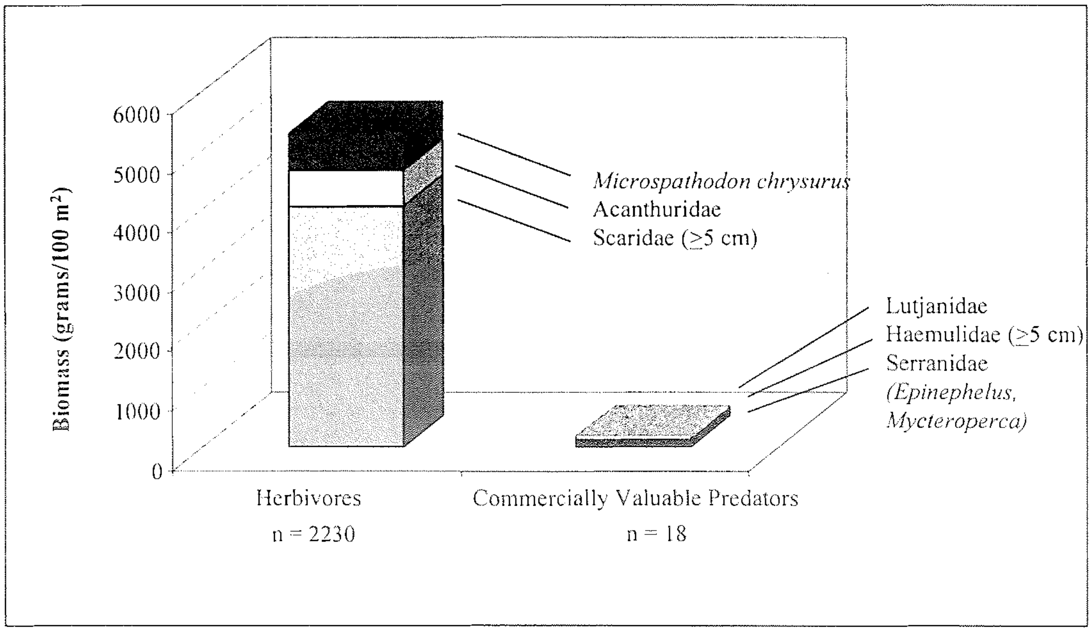

Figure 8. Mean biomass of key herbivores and carnivores at Horseshoe Reef.

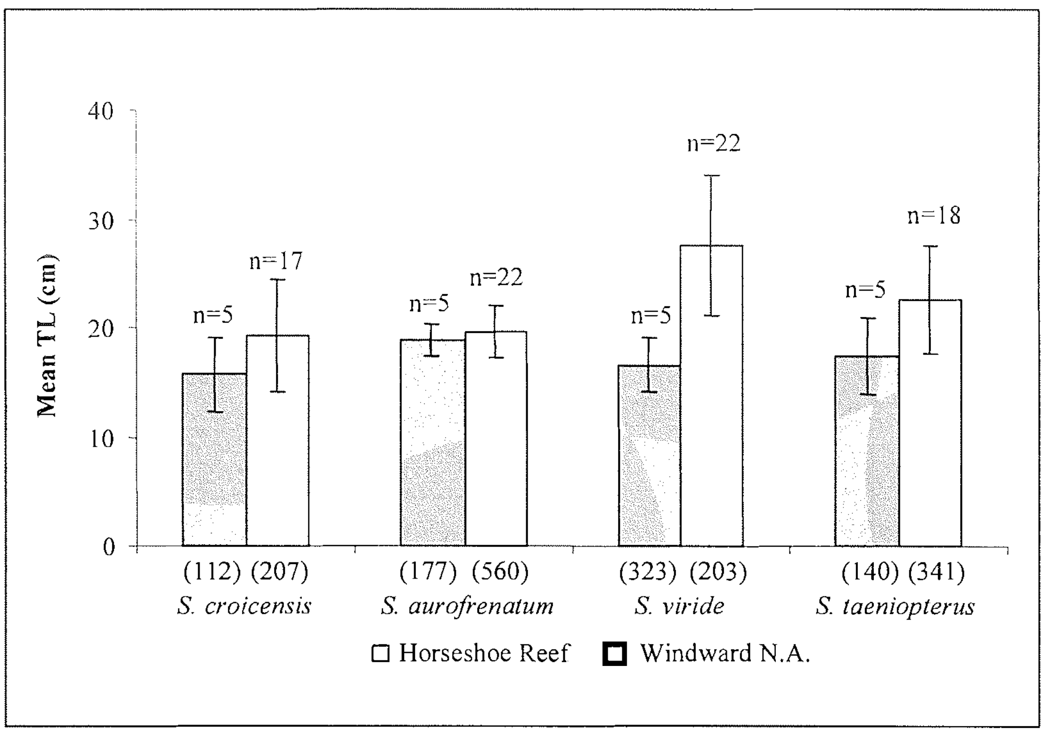

Figure 9. Mean total length (± se) of common scarids at Horseshoe Reef and from the windward Netherland Antilles (Kloomp and Kooistra, this volume). n = number of sites; number of individual fishes is in parentheses.

Algal community structure is greatly affected by the spectrum of grazers present on an individual reef and by fishing pressures that significantly alter these natural grazing patterns (McClanahan and Muthiga, 1998). Macroalgae can easily overgrow smaller algal turfs and crustose coralline algae (Lewis, 1986). We suspect that the herbivores (e.g., scarids, *D. antillarum;* to a lesser degree, acanthurids and *M. chrysurus*) on the shallow fore reefs at Horseshoe Reef are maintaining a benthic algal assemblage in which crustose corallines are spatial dominants. The somewhat greater proportion of turf algae at 3-4 m relative to 9-12 m may be a result of higher productivity rates which have been attributed to greater photosynthic activity in shallower habitats, to the forces of herbivory that enhance growth by maintaining algal assemblages in an early successional stage, and to recycling of nutrients by herbivores back into the benthic community (Hatcher, 1997). Grazing intensity generally decreases with depth on fore reefs (Morrison, 1988) which may explain the relatively higher densities and biomass (Table 5) of herbivorous acanthurids and *M. chrysurus* at 3-4 m than at 9-11 m.

The macroalgae that predominated at two-thirds of the deeper reefs (*Halimeda, Dictyota*), where macroalgal grazers (particularly *Diadema*) are relatively less abundant, are of genera known to be avoided by herbivorous fishes (Schmitt, 1998). A reduction in herbivorous grazing pressure allows macroalgae to outcompete sessile reef invertebrates for space and can ultimately result in the degradation of coral communities (Hughes, 1989; Hughes et al., 1987). However, live stony coral cover was higher on the deeper fore reefs than in the shallow at the time of our survey.

As reported in Table 4, *L. mahogoni* was one of the 25 most frequently sighted species in the roving diver surveys, appearing in 9/10 surveys, yet was not seen in any of the belt transects. Its presence in the roving diver surveys was recorded as "few" (i.e., 2-10 individuals) in seven of these dives and as "many" (i.e., 11-100 individuals) in two dives. This may be an indication that the belt transect method is not adequately quantifying fish such as *L. mahogoni*, which are inherently wary of divers, or that a larger sample size is needed to adequately quantify species that are present but not necessarily abundant. Of additional interest from the roving diver surveys, *Chromis multilineata* (brown chromis) and *C. cyanea* (blue chromis) were recorded as being the most frequently sighted and "abundant" (>100 individuals) fishes on Horseshoe Reef. The prevalence of these planktivores may be an indication of reduced predation in the presence of an adequate food source. However, they are commonly found throughout the greater Caribbean strategically feeding above reefs where plankton is plentiful (Bohlke and Chaplin, 1993).

The Scaridae was the dominant fish family present in our belt transects on Horseshoe Reef (Fig. 5, Table 5). Scarids were represented primarily by *Sparisoma viride* (stoplight parrotfish) with lesser densities of *S. aurofrenatum* (redband parrotfish), *Scarus taeniopterus* (princess parrotfish), *S. vetula* (queen parrotfish) and *S. croicensis* (striped parrotfish) (Table 6). Average total lengths for *S. croicensis* and *S. aurofrenatum* were similar at Horsehoe Reef and in the windward Netherlands Antilles (N.A.) which have received a lesser degree of fishing pressure (Klomp and Kooistra, this volume). *S. viride* and *S. taeniopterus*, however, were both significantly smaller on average (F-test; $p=0.001$ and $p=0.044$, respectively) than their conspecifics in the windward NA (Fig. 9). Although we cannot conclusively determine from this assessment the cause for the relatively small size of these parrotfishes in Horseshoe Reef, it may be further evidence of high harvesting levels.

Reduced abundance or biomass and a decreased size structure in targeted fishes as a result of intense fishing has been well-documented (Bohnsack, 1982; Munro, 1983). It was not common to see fish larger than 30 cm total length on Horseshoe Reef (Fig. 6) and we suspect that this is an effect of larger fish being targeted for harvest. Additionally, overfishing likely explains the low densities of grouper, snapper and grunts on Horseshoe Reef since these are favored food fishes. It is possible that these common carnivores have been replaced by other species, such as the "voracious predator" *Aulostomus maculatus* (trumpetfish), which is known to feed on young acanthurids and haemulids (Randall, 1967). *A. maculatus* are common residents of Caribbean-area reefs but ordinarily are not abundant (Bohlke and Chaplin, 1993). Randall (1967) found trumpetfish in the stomachs of snappers and groupers. Given the paucity of serranids and lutjanids, we suspect that the Horseshoe Reef population of *A. maculatus* is thriving due to reduced predation pressure and adequate prey supplies. This phenomenon may warrant further investigation if marine park managers seek to restore populations of snappers, groupers or grunts. The Vincentians rely on their artisanal fishery as a source of dietary protein. A restored population of commercially valuable carnivores within the marine park could serve as a source stock of fish and possibly create a spillover effect into legal fishing areas, providing harvestable resources for the fishing community.

In sum, strengthening and enforcing fishing regulations in the Tobago Cays Marine Park are critical steps to avoid further degradation of its fish assemblages. The AGRRA survey, being the first quantitative, assessment of Horseshoe Reef, provides baseline information against which to measure future changes in its condition.

ACKNOWLEDGMENTS

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Table 1. Site information for AGRRA stony coral, algal and fish surveys on Horseshoe Reef, Tobago Cays, St. Vincent.

Site name	Latitude (° ' " N)	Longitude (° ' " W)	Survey date	Depth (m)	Benthic transects (#)	≥25 cm stony corals (#/10 m)	Live stony coral cover (mean ± se)	30 m fish transects (#)	RDT fish species (#)[1]
B	12 38 00.48	61 20 56.88	June 8-9 1999	3.5	14	8	29.0 ± 1.5	10	45
D	12 38 08.58	61 20 55.38	June 14, 1999	3	13	8	31.5 ± 1.5	10	44
Shallow				**3.5**	**27**	**8**	**30.5 ± 1.0**	**20**	**56**
A	12 38 00.48	61 20 56.88	June 7-8 1999	11.5	11	10	42.5 ± 2.5	10	49
C	12 37 48.06	61 21 04.02	June 10-11 1999	9	11	9	44.0 ± 2.5	10	41
E	12 38 08.58	61 20 54.46	June 10-11 1999	11	11	9	28.5 ± 2.5	10	50
Deep				**10.5**	**33**	**9**	**38.0 ± 1.0**	**30**	**77**

[1]RDT = Roving Diver Technique

Table 2. Size and condition (mean ± standard error) of all stony corals (≥25 cm diameter) by site on Horseshoe Reef.

Site name	Stony corals		Partial-colony surface mortality (%)			Stony corals (%)		
	(#)	Diameter (cm)	Recent	Old	Total	Standing dead	Bleached	Diseased
B	109	53.5 ± 3.0	1.0 ± 0.5	26.5 ± 3.0	27.5 ± 3.0	9	3	1
D	109	65.0 ± 3.5	3.0 ± 1.0	24.0 ± 2.0	27.0 ± 2.0	0	2	2
Shallow	**218**	**59.0 ± 2.5**	**2.0 ± 0.5**	**25.0 ± 2.0**	**27.5 ± 2.0**	**4.5**	**2.5**	**1.5**
A	108	55.0 ± 3.0	1.0 ± 0.5	22.5 ± 2.5	24.0 ± 2.5	0	15	4.5
C	104	64.0 ± 4.0	2.5 ± 0.5	25.5 ± 2.5	28.0 ± 2.5	1	6.5	1
E	101	50.0 ± 3.0	2.0 ± 0.5	28.0 ± 2.5	30.0 ± 2.7	0	10	6
Deep	**313**	**56.5 ± 2.0**	**2.0 ± 0.5**	**25.5 ± 1.5**	**27.0 ± 1.5**	**0.5**	**10.5**	**4**

Table 3. Algal characteristics (mean ± standard error), abundance of stony coral recruits and *Diadema antillarum*, by site on Horseshoe Reef.

Site name	Quadrats	Relative abundance (%)			Macroalgal Height (cm)	Macroalgal Index[1]	Recruits (#/ 0625 m^2)	Diadema (#/100 m^2)
		Macroalgae	Turf algae	Crustose coralline algae				
B	58	21.5 ± 3.5	23.0 ± 3.5	56.5 ± 4.0	1.5 ± 0.5	32	0.41± 0.14	**7**
D	51	12.0 ± 3.0	35.0 ± 3.5	35.0 ± 3.5	1.5 ± 0.5	18	0.09 ± 0.04	**3**
Shallow	**109**	**17.0 ± 2.0**	**28.5 ± 2.5**	**54.5 ± 3.0**	**1.5 ± 0.5**	**26**	**0.25 ± 0.07**	**5**
A	53	55.0 ± 3.0	17.0 ± 2.0	28.0 ± 3.0	1.5 ± 0.5	82	0.03 ± 0.01	**0**
C	54	48.0 ± 4.0	14.0 ± 1.5	38.0 ± 3.5	1.5 ± 0.5	72	0.28 ± 0.08	**2**
E	52	23.5 ± 4.0	27.5 ± 4.0	48.5 ± 4.0	2.0 ± 0.5	47	0.20 ± 0.07	**0**
Deep	**159**	**42.5 ± 2.0**	**19.5 ± 1.5**	**38.0 ± 2.0**	**1.5 ± 0.5**	**64**	**0.16 ± 0.03**	**0.5**

[1]Macroalgal index = macroalgal relative abundance x macroalgal height

Table 4. Twenty-five most frequently sighted fish species during rover diver surveys on Horseshoe Reef, with densities (mean ± standard error) for species recorded in belt transects

Fish Species	Fish Species	Sighting frequency[1]	Density (#/100 m^2)
Chromis multilineata	Brown Chromis	100	-
Chromis cyanea	Blue Chromis	100	-
Sparisoma viride	Stoplight Parrotfish	100	10.8 ± 3.2
Sparisoma aurofrenatum	Redband Parrotfish	100	5.9 ± 1.8
Microspathodon chrysurus	Yellowtail Damselfish	100	5.0 ± 3.2
Halichoeres garnoti	Yellowhead Wrasse	100	-
Acanthurus coeruleus	Blue Tang	100	3.6 ± 4.6
Mulloidichthys martinicus	Yellow Goatfish	100	-
Aulostomus maculatus	Trumpetfish	100	-
Halichoeres maculipinna	Clown Wrasse	100	-
Thalassoma bifasciatum	Bluehead Wrasse	90	-
Clepticus parrai	Creole Wrasse	90	-
Stegastes partitus	Bicolor Damselfish	90	-
Stegastes planifrons	Threespot Damselfish	90	-
Lutjanus mahogoni	Mahogany Snapper	90	0
Holocentrus rufus	Longspine Squirrelfish	90	-
Canthigaster rostrata	Sharpnose Puffer	90	-
Scarus taeniopterus	Princess Parrotfish	80	4.7 ± 3.3
Scarus vetula	Queen Parrotfish	80	5.2 ± 6.8
Ophioblennius atlanticus	Redlip Blennie	80	-
Acanthurus bahianus	Ocean Surgeonfish	80	2.1 ± 1.1
Hypoplectrus chlorurus	Yellowtail Hamlet	80	-
Abudefduf saxatilis	Sergeant Major	70	-
Scarus croicensis	Striped Parrotfish	70	3.7 ± 1.5
Paranthias furcifer	Creole-fish	70	-

[1]Percent sighting frequency = percent of dives in which the species was recorded.

Table 5. Biomass of major fish families (as mean ± standard error), by depth on Horseshoe Reef.

Sites	Herbivores (grams/100 m^2)			Carnivores (grams/100 m^2)		
	Acanthuridae	Scaridae (≥5 cm)	*Microspathodon chrysurus*	Haemulidae (≥5 cm)	Lutjanidae	Serranidae
All Shallow	1081 ± 364	3827 ± 487	1145 ± 354	84 ± 228	6 ± 7	22 ± 12
All Deep	269 ± 67	4217 ± 605	330 ± 231	28 ± 128	4 ± 6	198 ± 25

Table 6. Mean density of the ≥5 cm scarids, by site on Horseshoe Reef.

Site	Density (# individuals/100 m^2)				
	S. aurofrenatum (redband) (n = 177)	*S. taeniopterus* (princess) (n = 140)	*S. viride* (stoplight) (n = 323)	*S. croicensis* (striped) (n = 112)	*S. vetula* (queen) (n = 156)
Shallow B	4.3	1.3	11.5	5.3	1.8
D	6.7	2.7	14.0	2.7	5.0
Deep A	5.3	3.0	5.3	2.3	1.2
C	8.7	8.0	12.0	5.5	17.0
E	4.5	8.3	11.0	2.8	1.0
All sites mean ± se	**6.2 ± 2.2**	**6.4 ± 3.0**	**9.4 ± 3.6**	**3.6 ± 1.7**	**6.4 ± 9.2**

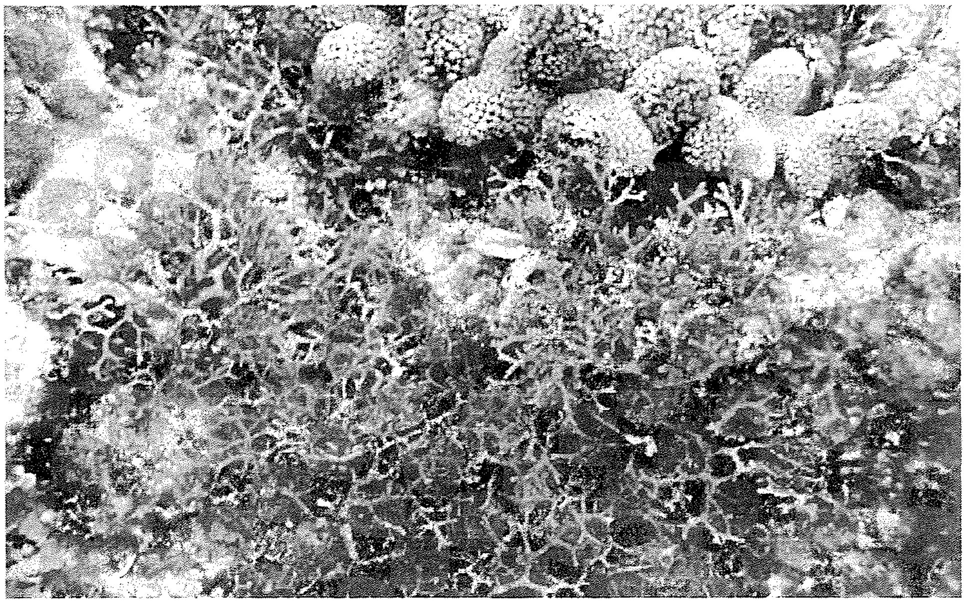

Plate 11A. Reef condition is strongly dependent on the interplay of complex relationships involving stony corals, herbivores and benthic algae. Algae are assessed in the AGRRA benthos protocol as the relative abundance of several key functional algal groups, including macroalgae like the *Dictyota* shown here, in relation to coral condition and herbivorous fishes. (Photo Robert W. Steneck)

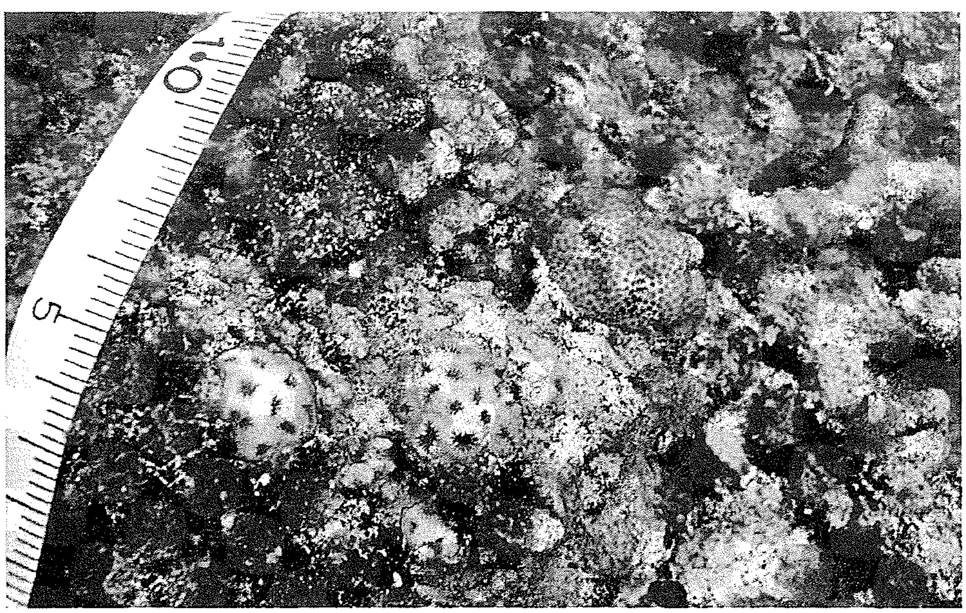

Plate 11B. Crustose coralline algae that grow around and between coral fragments may eventually immobilize loose pieces of coral rubble and may serve as recruitment sites for coral larvae. Recruitment is estimated as the number of small (<2 cm diameter) stony corals visible in the algal quadrats, like those shown here. (Photo Robert W. Steneck)