

## Complex interactions in the control of coral zonation on a Caribbean reef flat

M.M. Littler<sup>1</sup>, P.R. Taylor<sup>2</sup>, and D.S. Littler<sup>1</sup>

<sup>1</sup> Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA

<sup>2</sup> Biological Oceanography Program, Division of Ocean Sciences, National Science Foundation, Washington, DC 20550, USA

**Summary.** This study uses short-term assays and long-term transplant experiments to document the potential importance of fish predation and herbivory to the distribution and abundance of reef-building corals in a Caribbean back-reef system. Experimental manipulations of fish access reveal that the zonal patterns of the two reef-building corals *Porites astreoides* and *P. porites* f. *furcata*, dominant on shallow back-reef habitats, are strongly associated with the feeding intensity of parrotfishes. Differential palatability of the two corals to parrotfishes, the proximity of protective cover for large grazers and the availability of small refugia to harbor a cryptic grazer fauna are suggested as major features contributing to the observed patterns. A model predicting the interactions of various algivore/corallivore guilds on the relative dominance of *Porites* and algal populations is presented.

**Key words:** Algivore/corallivore guilds – Caribbean – Fish-coral interactions – *Porites* – Reef zonation

The feeding activities of herbivorous fishes play a profound role in controlling the distributions and abundances of marine macrophytes on tropical reefs (e.g. reviewed by Littler and Littler 1988). Grazing fishes, such as parrotfishes of the genera *Scarus* and *Sparisoma*, forage on virtually all types of hard substrata, except where eliminated by fishing pressure (Hay 1984). This activity restricts the potential macroalgal prey of fishes to refugia, unless structural or chemical defenses allow them to coexist with consumers. The result is that grazing by fishes often maintains certain areas barren of fleshy algae and, as predicted by the relative dominance paradigm of Littler and Littler (1984), coralline algae and corals dominate the benthos.

Recent works (Glynn 1976; Kaufman 1977; Neudecker 1979; Wellington 1982) have shown significant effects of corallivorous fishes on the local distributional patterns of corals. Such predation by fishes may restrict the wider occurrences of some coral species (Neudecker 1979; Wellington 1982); it may also exert a positive influence on recruitment by providing a source of settlement sites for other corals (Vine 1974). Given that benthic macrophytes show differential susceptibilities to reef herbivores (e.g. Littler et al. 1983a), it is reasonable to hypothesize that fish predation

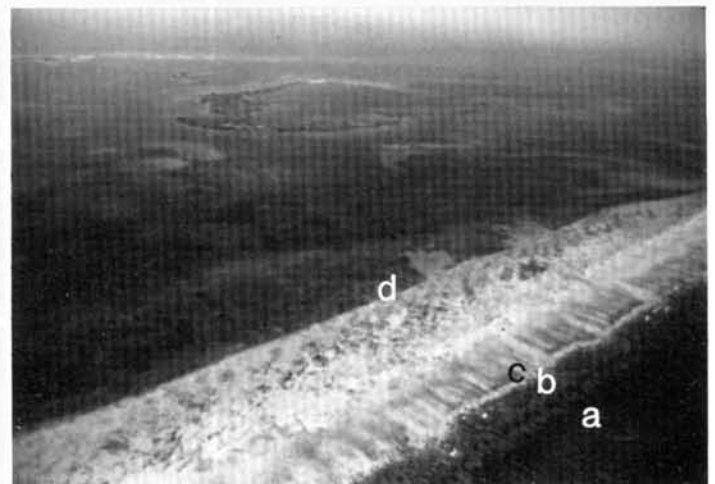
on corals has selected for comparable adaptations to minimize mortality.

In this paper, we report on new experimental observations, our previous studies and findings of other investigators to develop and partially test a model proposed to explain the distributional patterns observed for *Porites* on Caribbean back-reef flats. The model is based on predictions concerning the complex interactions of algal/coral competitive encounters under predation pressure from various algivore/corallivore guilds.

### *Belizean reef communities*

The Belizean barrier-reef complex is the largest reef tract in the Atlantic Ocean (over 250 km in length and from 10 to 32 km wide), consisting of an almost unbroken barrier reef containing hundreds of patch reefs and mangrove islands along its shoreward boundary. On the back-reef flats (Fig. 1), assemblages of framework-building corals and calcareous algae have the same general taxonomic composition along the entire barrier reef (Burke 1982), but the relative abundances of species vary greatly.

Reefs of the central area, such as those characterized



**Fig. 1.** Oblique view of Tobacco Reef toward the northwest showing emergent reef-crest and back-reef habitats characteristic of reef trends within the Central Province. *a* Fore reef, *b* Reef crest, *c* Rubble-pavement zone and *d* *Thalassia*-sediment apron. The Tobacoo Range mangrove system is visible in the upper portion of the photograph (cf. Fig. 2)

by Carrie Bow Cay and Tobacco Reef (Fig. 1), are the most extensive with abundant communities of living corals (Burke 1982). These reefal habitats and surrounding environs comprise a well-developed barrier-reef system removed from major anthropogenic influences. The topography, geology and general biology are well known due to more than a decade of study (see Rützler and Macintyre 1982).

The primary study site (Fig. 2), located directly shoreward of the intertidal and spatially complex reef crest on the east side of Carrie Bow Cay ( $16^{\circ}48'N$ ,  $88^{\circ}05'W$ ), and the site on Tobacco Reef ( $16^{\circ}49'N$ ,  $88^{\circ}04'W$ , Fig. 1), are typical of the back-reef sections of the reef system as it extends throughout much of the entire Belizean barrier tract

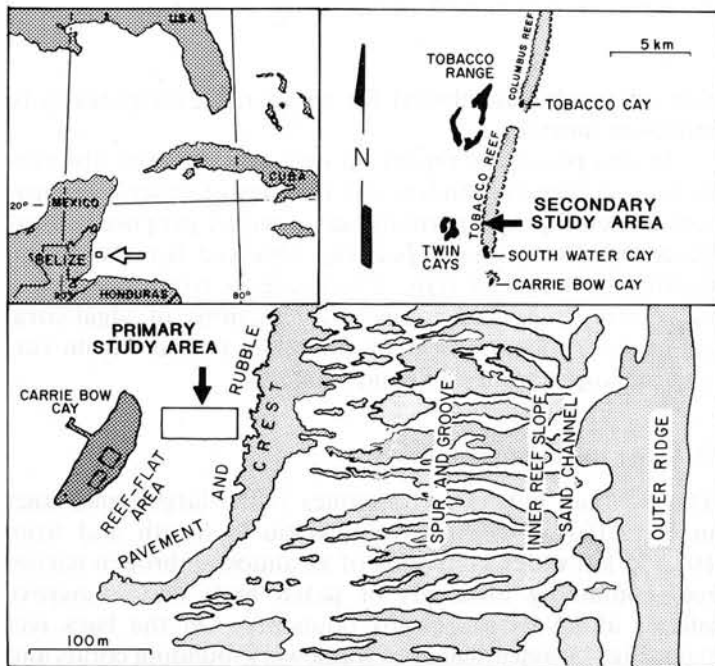


Fig. 2. Region of primary reef-flat study sites and other zonal habitats seaward of Carrie Bow Cay and the location of the back-reef study area on Tobacco Reef

(James et al. 1976; Burke 1982). The bottom characteristics exhibit a shoreward (i.e. westward) transition from smooth, flat pavement near the crest, to rubble followed by gravel-sized fragments and sand (with associated changes in the coral and algal assemblages), finally grading to a *Thalassia*-covered sand and rubble apron.

*Porites*, represented by *P. astreoides* Lamarck (Fig. 3a) and *P. porites* (Pallas) (Fig. 3b), is the most common coral genus in the shallow back-reef habitat. We have observed a characteristically high abundance of *P. astreoides* in the rubble-pavement zone just behind the reef crest, followed by a belt of *P. porites* lagoonward on many back-reef flats; this same pattern has been seen along the extensive outer reef margins of Glovers Reef and Lighthouse Reef (Belizean atolls). Both species of *Porites* also are reported (Burke 1982; Cairns 1982) in most Belizean fore-reef habitats, but the latter occurs cryptically and in a more compact form (forma *porites*) that may be less accessible to fishes. *Porites porites* does appear capable of dominating some Caribbean fore-reef areas where fish trapping has been intensive (Figs. 3c and 3d, personal observations).

Water movement and depth have been suggested (Rützler and Macintyre 1982) to be the main factors controlling the biological/geological patterns of zonation at Carrie Bow Cay. The back-reef flat gradually slopes from 1.0-m deep just behind the crest to 0.1-m deep in the *Thalassia* bed and is subjected to strong currents that transport sediments away from the reef crest and toward the lagoon behind (Fig. 1). The water over the intertidal reef crest is in an almost constant state of high turbulence. The back reef is strongly affected by waves related to both normal trade wind conditions and storms (Macintyre et al. 1987).

The important role of herbivory in structuring macrophyte communities has been extensively investigated for the Carrie Bow Cay reef and surrounding environs (Hay 1981; Littler et al. 1983b, 1986, 1987; Lewis and Wainwright 1985; Lewis 1986; Taylor et al. 1986; Lewis et al. 1987; Macintyre et al. 1987; Coen 1988). The back-reef rubble-pavement habitat (Figs. 2 and 3) is characterized by high densities of herbivorous fishes (Table 1), primarily sur-

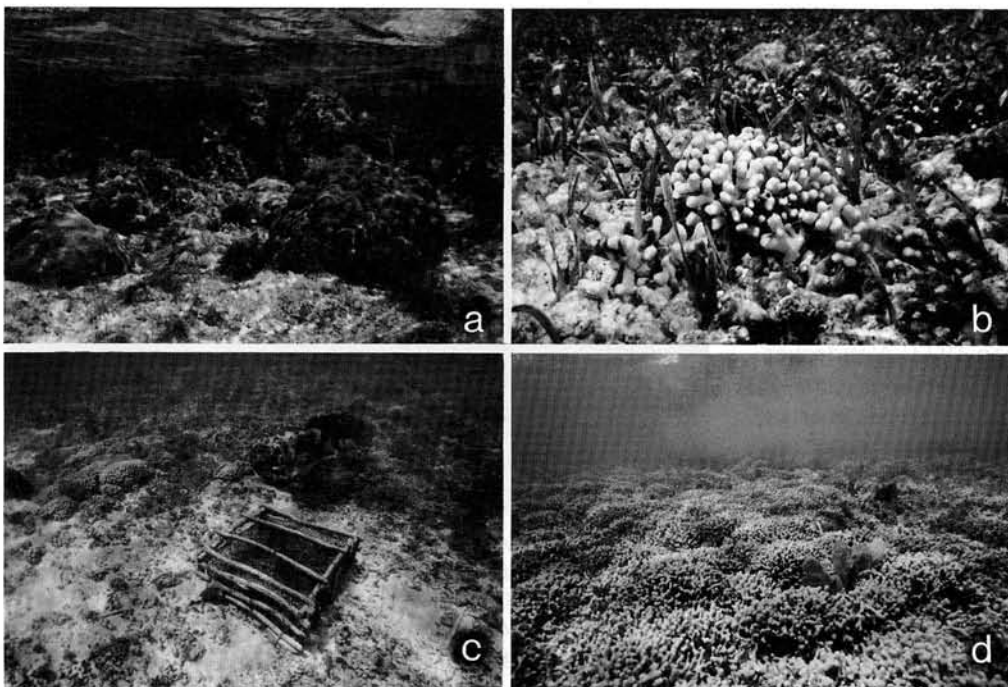


Fig. 3. a Underwater view of the region of *Porites astreoides* dominance in the rubble-pavement zone at Carrie Bow Cay. b View of *P. porites* f. *furcata* in its zone of dominance farther shoreward of a. c Semi-permanent fish trap typically found in use or abandoned on the shallow reefs of Little Saint Vincent, Lesser Antilles showing abundant *P. porites* in the background. d Closer view of *P. porites* which dominates back-reef areas of overfished habitats throughout the Lesser Antilles



geonfishes (*Acanthurus*) and parrotfishes (*Sparisoma*, *Scarus*). The parrotfishes are also predators on corals. These fishes are highly mobile, visually orienting consumers. The most common herbivorous fish species in the rubble-pavement zone are: *Acanthurus bahianus* Castelnau, *A. coeruleus* (Bloch), *Scarus iserti* Bloch (= *S. croicensis* Bloch), *Sparisoma chrysopterum* (Bloch & Schneider), *Sparisoma viride* (Bonnaterre) and *Sparisoma rubripinne* (Cuvier & Valenciennes). Repeated censuses from April 1982 to March 1983 (see Table 2 of Lewis 1986), as well as during April 1984 and April 1985 (see Table 1 of Littler et al. 1987), indicate that the species composition and relative abundances of herbivorous fishes are reasonably stable. These fishes move into the rubble-pavement zone shortly before sunrise, forage singly or in small schools throughout the day and leave at sunset for shelter in deeper fore-reef areas.

#### Experimental organisms

*Porites astreoides* (Fig. 3a) is a massive coral that forms encrusting flat or hemispherical colonies up to half a meter in diameter and, in the study area, is usually bright yellow-green in color. It is present in nearly all Belizean reef environments (see Burke 1982) and occurs down to at least 28 m around Carrie Bow Cay (Cairns 1982), reaching its maximum abundance in the reef-flat area behind the crest. In contrast, *P. porites* f. *furcata* (Figs. 3b and 3d) is a delicate branching coral that forms colonies consisting of grey-yellow, mostly dichotomous, cylindrical branches; in the study areas, it can reach heights of up to 40 cm. Several forms of this species are present in most Belizean reef communities. At Carrie Bow Cay, it occurs to a depth of at least 27 m (Cairns 1982), but forms cryptic, tightly-bunched patches (forma *porites*) on fore-reef habitats (personal observations). *Porites porites* can be conspicuous in patch-reef areas of the back reef where it receives protection near predator or damselfish territories (e.g. *Stegastes planifrons*, personal observations). We hypothesized that forms of *P. porites* are softer, easier to bite and much more easily broken by physical forces than the massive unbranched *P. astreoides*. Because we expected that these sessile, hermatypic corals might be affected by the feeding activities of grazing fishes (primarily parrotfishes in the Belizean system), we initiated the present manipulative study within the *Porites porites* f. *furcata* and *P. astreoides* zones on several representative areas of the back-reef flat portion of the reef system seaward of Carrie Bow Cay.

#### Methods

The primary study site on Carrie Bow Cay (Fig. 2) was transected on compass heading 270° magnetic. Sampling was begun on the shoreward portion of the reef crest in 0.4 m of water and extended 100 m westward across the shallow reef flat to a 0.2 m deep sand channel next to the island's beach. Quantitative samples of *Porites* cover were obtained by photographing 0.15 m<sup>2</sup> (30 × 50 cm) quadrats (delineated by a stainless steel frame) at every third meter through a clear plexiglas viewing box. Photographs were taken with the focal plane parallel to the substratum using a 35-mm Nikonos camera equipped with a 35-mm lens, an electronic flash unit and Kodachrome-64 transparency film. A second site, selected as representative of the extensive reef tract that extends north of Southwater Cay

(Fig. 1), was transected on compass heading 270° magnetic, with samples taken at 2.0 m intervals from the crest to m 20, and at 5.0 m intervals between m 20 and m 150.

The developed transparencies were projected onto a sheet (40 × 40 cm) of white paper containing a uniform grid pattern of dots at 2.0 cm intervals on the side of the reflected light (see Littler and Littler 1985 for details). The number of dots superimposed on each species of *Porites* was then scored twice (i.e. replicated after blind movement of the grid), with the percentage cover values estimated as the number of "hits" for each species divided by the total number of dots (about 700) contained in the quadrats. The replicate scorings were then averaged to yield the estimate of substratum covered.

To assess the relative resistances to predation of *Porites porites* f. *furcata* and *P. astreoides*, two replicate assays were run on 7 and 8 March 1987. Prior to both days, 140 specimens of each coral were collected and cut into approximately 3 × 7 cm portions and held in an open flow seawater system for 24 h, which allowed healing to occur, as evidenced by cessation of excess mucous production. The holding time was kept to 24 h to minimize trauma from unnatural conditions. While each of the species grow to substantially larger colony size, the specimens used in the experiment are of a size similar to small natural colonies. The living coral specimens were then carefully attached in a realistic position by small grey rubber bands to 10 cm long fragments of naturally occurring coral rubble. The specimens of each species resembled small natural colonies (i.e. terete for *P. porites* and encrusting or mound-like for *P. astreoides*), because the form of colonies within each species does not differ with growth to larger sizes (i.e., colonies grow isomorphically) after a very small juvenile size. Ten linear series, each consisting of 10 individual pairs of *P. porites* and *P. astreoides*, arranged ca. 0.5 m apart and parallel to the shoreline and reef crest, were placed at 5 m intervals from 0 to 70 m behind the reef crest. This produced a density of presentation similar to that found naturally in many portions of the back-reef area. The palatability assay on 7 March 1987 was conducted along the southern margin of the Carrie Bow Cay study site, while that on 8 March 1987 took place at a comparable site 100 m to the north. Throughout the comparative experiments, both species and all areas studied received identical treatments. No unusual repulsion or attraction of fishes was observed during several hours of distant observation, so we assume that the fishes' behavior toward the samples was not artifactual.

Note that herbivory by fishes has been shown (Table 1, Hay 1981; Lewis and Wainwright 1985) to decrease from a maximum in the rubble-pavement zone behind the reef crest to negligible levels farther lagoonward. The data on herbivory levels for seven relatively palatable algae reported by Macintyre et al. (1987) also revealed a transition of decreasing fish herbivory as a function of distance shoreward (i.e. westward) on the back reef. Data on grazing intensity from these previous studies, along with the coral distributions at the Tobacco Reef study area are summarized in the results (Table 1, Fig. 4). *Diadema antillarum* (Phillipi), a grazer that was present on the Carrie Bow Cay reef flat before its widespread die-off (Lessios et al. 1983), was not encountered in this study.

Feeding activity on the *Porites* fragments was verified visually at haphazard intervals. After 24 h, the number of

**Table 1.** Herbivorous fish densities and grazing intensity for the Carrie Bow Cay rubble-pavement zone and the *Thalassia* zone near the primary study site (see Fig. 2). Data abstracted from Lewis and Wainwright (1985), except *Thalassia* (from Hay 1981). NA = not available

Taxa	<i>Thalassia</i> zone	Rubble-pavement zone
Acanthuridae (No·100 m <sup>-2</sup> )	0.1	12.6*
Scaridae (No·100 m <sup>-2</sup> )	0.1	11.5*
<i>Acanthophora spicifera</i> (Vahl)	5.3	81.7*
Boergesen (% loss·8 h <sup>-1</sup> )		
<i>Thalassia testudinum</i> Banks ex Koenig (% loss·3 h <sup>-1</sup> )	NA	92.8 (95% C.I. = 4.6)

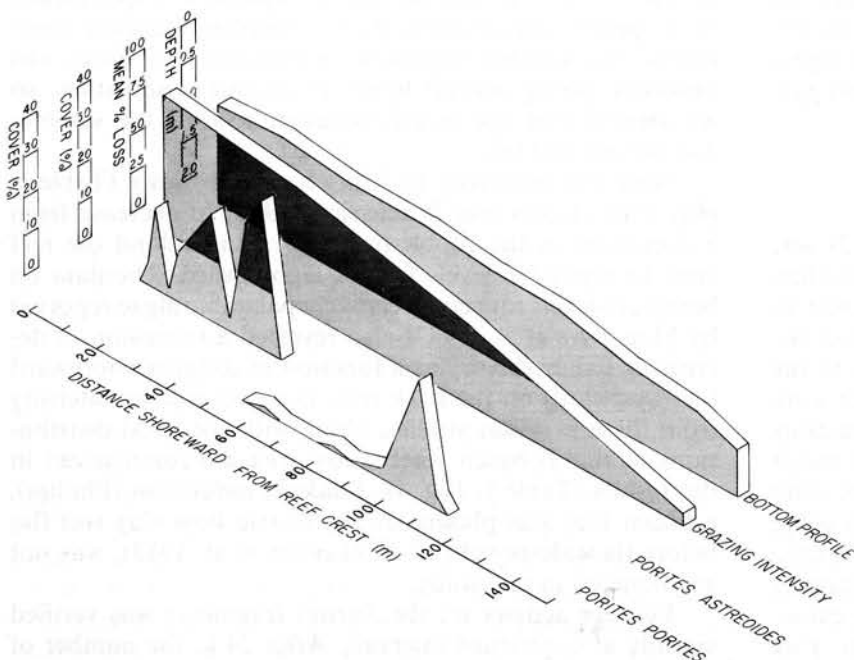
\* All values between zones significantly different ( $P < 0.01$ , Kruskal-Wallis)

grazing scars was determined by direct counts, and percent loss of living tissue area was estimated by measurements of the remaining, tissue-covered corallum. Counts of feeding scars underestimate feeding because (1) new bites can overlap with previous scars, and (2) portions of the species that are removed are not available for analysis. This underestimation should be disproportionate; the more preferred a species is, the greater the underestimation. This should represent a conservative estimation of differences between species. All losses of the securely held coral samples were attributable to fish bites, and the unbitten tissues were alive and healthy. A three-way ANOVA (Sokal and Rohlf 1969) of amount eaten and number of bites contrasting species, distance from the reef crest and the two sites was performed using SAS (1985). The Bonferroni, *a posteriori*, multiple-classification analysis (SAS 1985) was used to identify significant groupings.

We estimated the resistance of the corallum of *P. porites* f. *furcata* and *P. astreoides* to a simulated fish bite by measuring resistance to penetration. A stainless-steel, cylindrical, sewing-machine needle (Organ #20) was fastened to

a cylindrical steel piston weighing 387 g. This was then dropped 1.0 cm through a precisely fitted cylinder (guide) and onto a coral sample. The sample was oriented so that the needle dropped perpendicular onto the surface. Two types of samples of each species were used: one in which the tested surface was covered with intact calices, the other in which the surficial calices had been removed (ca. 2 mm) exposing the denser subsurface of the corallum. Penetration of the needle was measured in 0.5 mm increments. Differences between species were analyzed with a t-test.

Because *Porites porites* f. *furcata* is abundant only in the shoreward regions of the study areas, we conducted long-term (23-mo duration) transplant studies to assess its survivorship in the seaward rubble-pavement zone of Carrie Bow Cay. Specimens were collected on 18 April 1985 and cut into approximately 2 cm<sup>2</sup> (projected area) fragments. Ten samples were attached haphazardly to the natural substratum several meters apart in the rubble-pavement zone using marine epoxy cement and another five transplant controls were glued to the natural pavement substratum 50 m shoreward; all transplants were then photographed using a 1:3 extension tube with framer on a Nikonos camera. Five of the 10 replicate specimens were selected at random and immediately enclosed within individual 15 × 20 × 30 cm stainless steel cages (16-gauge, 1.3 × 1.6 cm mesh size) in the pavement-rubble zone to eliminate fish grazing. Cages were attached to the substratum with masonry nails embedded in marine epoxy. Transplantations of five 2 cm<sup>2</sup> colonies of *P. astreoides* set several meters apart (haphazard placement) were also made into the rubble-pavement zone of high grazing, accompanied by five transplants into the zone of low herbivory 50 m shoreward on 18 April 1985 and photographed. After 23 mo, the transplanted colonies were rephotographed from the same orientation so that two-dimensional areal growth could be determined by the dot method. Survivorship and growth were compared [one-way ANOVA or t-test (see Table 2)]. The five cages containing *P. porites* f. *furcata* were then removed and subsequent losses to grazing again assayed photographically after 19 h (i.e. the following morning) and analyzed by t-test.

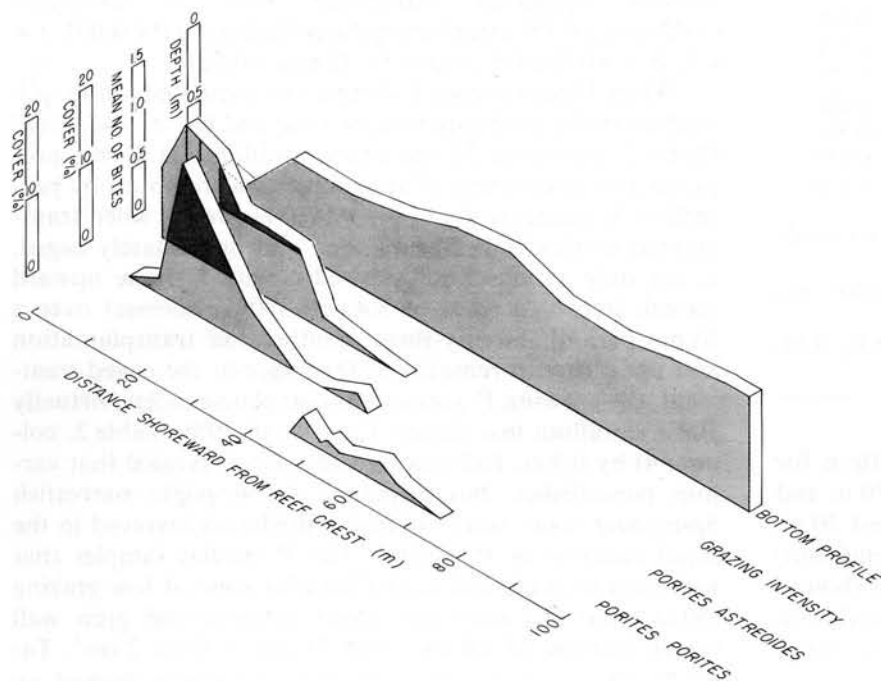


**Fig. 4.** Abundance patterns of *Porites*, depth profile and levels of fish herbivory (in percent palatable algae eaten per hour, from Macintyre et al. 1987) for the Tobacco Reef study area

**Table 2.** Changes in living surface area (cm<sup>2</sup>) of *Porites* under various levels of fish predation. The initial sizes of each sample were approximately 2 cm<sup>2</sup> in living surface area. The changes listed in columns 1 through 3 are after 23 mo; in column 4 they are after 19 h

	1. Low grazing		2. High grazing		3. High grazing (caged) <i>P. porites</i>	4. Changes (cm <sup>2</sup> ) in <i>P. porites</i> (from column 3) after cage removal
	a. <i>P. porites</i>	b. <i>P. astreoides</i>	a. <i>P. porites</i>	b. <i>P. astreoides</i>		
	3.0	-0.3	-1.4	3.1	1.3	-2.1
	7.4	0.2	-1.6	3.3	0.3	-1.9
	9.8	7.4	-1.4	2.9	11.9	-13.5
	2.2	7.7	-1.9	0.6	2.6	-4.2
	1.9	2.8	-1.6	0.7	1.1	-2.7
Mean	4.9	3.6	-1.6	2.1	3.4	-4.9
S.E. ±	1.5	1.7	0.1	0.6	2.1	2.1

\* Contrasts 1a, 2a, 3, one-way ANOVA,  $F=4.82$ ,  $P=0.029$ ; 1b, 2b, t-test,  $t=0.79$ ,  $P=0.451$ ; 3, 4, t-test,  $t=2.71$ ,  $P=0.027$ . The *a posteriori* multiple range test (Bonferroni) indicated that 1a and 3 are significantly ( $P<0.05$ ) different from 2a



**Fig. 5.** Abundance patterns of *Porites*, depth profile and levels of fish herbivory (in bites to *Porites* samples per 24 h, summed from Fig. 7) shoreward of the Carrie Bow Cay reef crest.

## Results

*Porites astreoides* reaches its maximum within a discrete zone near the shoreward margin of the reef crest at both study areas (Figs. 4 and 5). At Carrie Bow Cay, this species covered 1.6% of the rubble-pavement zone and attained its maximum cover (17.6%) as individual mounds approximately 13 m toward the island from the reef crest (Figs. 3a and 5). From this point, *P. astreoides* declined to trace amounts at 44 m and was absent from samples beyond 46 m. On the reef flat, the branched form, *P. porites* f. *furcata*, attained its maximum cover in a well-defined band between meters 46 and 67 from the crest and shoreward of the *P. astreoides* zone (Figs. 3b and 5). *Porites porites*, although present as occasional small colonies, did not occur in samples taken within 44 m of the crest and reached a peak coverage of 2.8% at about 46 m. A similar zonal relationship (Fig. 4) was documented at the Tobacco Reef site, with *P. astreoides* occurring in samples between 12 to 45 m

from the crest (peak of 38.2% cover at about 45 m) and *P. porites* from 60 to 110 m (peak of 30.4% cover at approximately 105 m).

Marked differences in resistance to predation were observed between the two species of *Porites* when assayed throughout the zones in which either occurred (Figs. 6 and 7, Table 3). Based on a *a posteriori* analysis of differences between days, data from the two replicated feeding trials were pooled for presentation in Figures 6 and 7. The numbers of bite scars per segment of transplanted *P. porites* f. *furcata* and *P. astreoides* (Fig. 6) showed significantly ( $P<0.05$ , Bonferroni analysis) greater damage by fishes in the zone from 5 to 35 m from the inner margin of the reef crest than in the 40 to 70 m zone; however, the numbers for *P. astreoides* were significantly lower ( $P<0.001$ ) than for *P. porites*. This analysis (Table 3B), however, identified significant interactions between species, sites and zones, necessitating a *a posteriori* single species and site analyses. *Porites porites* exhibited significant differences ( $P<0.05$ , Bon-



**Table 3A, B.** Three-way ANOVA results (crossed factors, fixed treatments) for the contrasts of the grazing experiments depicted in Figs. 6 and 7

Source	df	ss	F-value	Probability
<b>A Grazing scars (see Fig. 6)</b>				
Species	1	84.09	175.05	<0.001
Sites	1	2.44	5.09	0.024
Species × Sites	1	0.64	1.34	0.257
Zones	13	126.02	20.18	<0.001
Species × Zones	13	102.14	16.36	<0.001
Sites × Zones	13	22.78	3.65	<0.001
Species × Sites × Zones	13	14.78	2.37	0.004
<i>A posteriori</i> Bonferroni multiple classification analysis for single species (site by zone).				
<i>Porites porites</i> : Zones 5–40 m > 45–70 m; $P < 0.05$ .				
<i>Porites astreoides</i> : Zero losses in all zones				
<b>B Percent losses (see Fig. 7)</b>				
Species	1	3064.46	67.19	<0.001
Sites	1	68.40	1.50	0.221
Species × Sites	1	68.40	1.50	0.221
Zones	13	4910.07	8.28	<0.001
Species × Zones	13	4910.07	8.28	<0.001
Sites × Zones	13	969.41	1.64	0.072
Species × Sites × Zones	13	969.41	1.64	0.072
<i>A posteriori</i> Bonferroni multiple classification analysis for single species (site by zone).				
<i>Porites porites</i> , site 1: 10–30 m > 5 m and 35–70 m; $P < 0.05$ ; site 2: 5–15 m and 25 m > 20 m and 35–70 m; $P < 0.05$ .				
<i>Porites astreoides</i> , site 1: no significant zone differences; $P > 0.05$ ; site 2: no significant zone differences; $P > 0.05$ .				

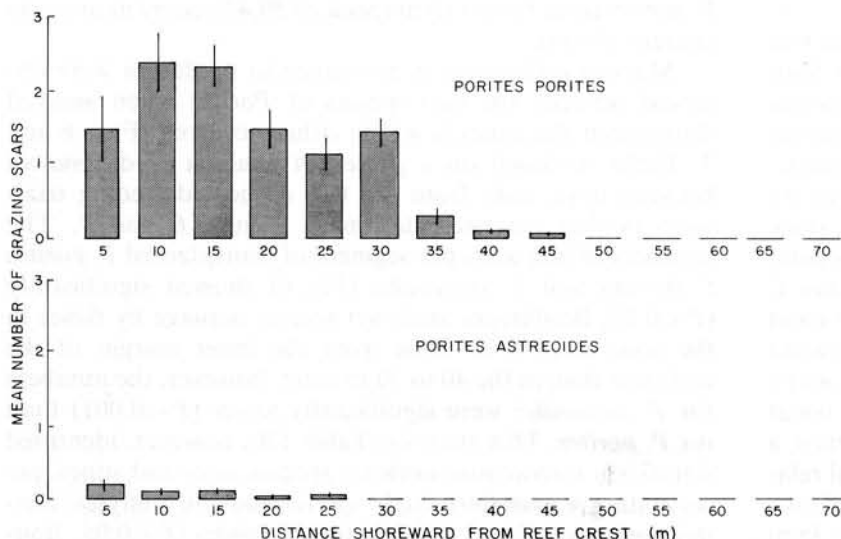
ferroni) between zones with the same general pattern for both sites as follows: site 1, zones 10–30 m > 35–70 m and 5 m; site 2, zones 5–15 m and 25 m > 35–70 m and 20 m. Intermediate zones showed overlapping (non-significant) grouping with the above groups. *Porites astreoides* showed no differences between zones ( $P > 0.05$ , Bonferroni) with uniformly low numbers of grazing scars across the range of habitats investigated.

When calculated as the percent of living tissue removed by predation on an areal basis (Fig. 7), *P. astreoides*, al-

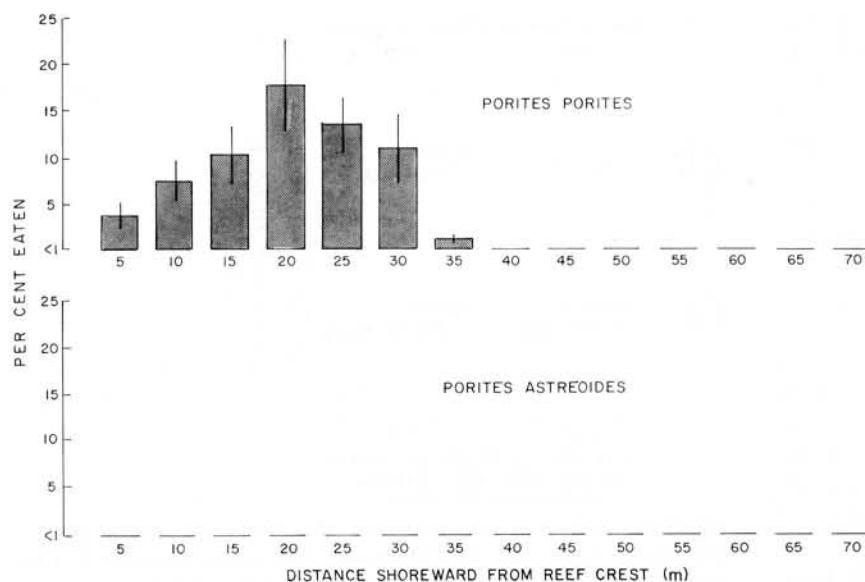
though containing traces of grazing scars, showed no measurable losses in either zone. This contrasts markedly with *P. porites*, which averaged 9.4% tissue area loss per 24 h to predation in the region between meters 5 and 35, versus zero loss in the 40 to 70 m zone (significant at  $P < 0.05$ , Fig. 7). *Porites porites* lost significantly ( $P < 0.001$ ) more total living tissue than *P. astreoides* throughout the region nearest to the rubble-pavement habitat (Fig. 7). The significant interactions between species and zones was due to the different patterns of loss for each species. *Porites porites* exhibited decreased losses away from the reef crest (Fig. 7), while *P. astreoides* showed a uniform zero loss across the range of habitats in the experiment. The Bonferroni *a posteriori* analysis (Table 3B) showed significant zone-related differences for *P. porites* and no interactions ( $P < 0.05$ ).

The upper surfaces of *Porites porites* f. *furcata* and *Porites astreoides* exhibited similar resistances to the penetration rod ( $1.52 \text{ mm} \pm 0.50$  and  $1.77 \text{ mm} \pm 0.53$ , respectively;  $P > 0.05$ ,  $t = 1.9$ ,  $N = 30$ ). The subsurface portions, however, showed significant differences with *P. astreoides* ( $1.02 \text{ mm} \pm 0.19$ ) exhibiting greater hardness ( $P < 0.001$ ,  $t = 8.8$ ,  $N = 30$ ) than *P. porites* ( $1.92 \text{ mm} \pm 0.52$ ).

When *Porites porites* f. *furcata* was cemented to the substratum in the rubble-pavement zone and left unobstructed (Table 2, treatment 2), the entire corallum (ca.  $2 \text{ cm}^2$  projected-area fragments) of all colonies was removed by parrotfish (Scaridae) in fewer than 24 h. However, when transplanted to this high-grazing zone and immediately caged, it not only survived but showed significant new upward growth [mean increase of  $3.4 \text{ cm}^2$  (70% increase) over a 23 mo period]. Twenty-three months after transplantation and upon careful removal of the cages in the caged treatment, the growing *P. porites* was completely eaten (virtually 100% corallum loss within a matter of 19 h; Table 2, column 4) by fishes. Extensive observations revealed that various parrotfishes, but primarily the stoplight parrotfish *Sparisoma viride*, were the major predators involved in the rapid removal of *P. porites*. The *P. porites* samples that had been transplanted to the reef-flat zone of low grazing (50 m from the inner reef crest) survived and grew well (mean increase of  $4.9 \text{ cm}^2$  over  $23 \text{ mo}^{-1}$ , from  $2 \text{ cm}^2$ , Table 2). The ca.  $2 \text{ cm}^2$  *P. astreoides* transplants showed no marked difference in growth after 23 mo ( $P = 0.45$ , Table 2) between the low-grazing and high-grazing habitats.



**Fig. 6.** Mean number of grazing scars per 24 h penetrating the corallum on  $3 \times 7 \text{ cm}$  coral samples ( $N = 20$ ) placed at various distances westward from the Carrie Bow Cay reef crest. Bars represent  $\pm$  S.E., statistical analysis are given in Table 3



**Fig. 7.** Per cent losses of living tissue area per 24 h for  $3 \times 7$  cm coral samples ( $N=20$ ) placed at various distances westward from the Carrie Bow Cay reef crest. Bars represent  $\pm$  S.E., statistical analysis are given in Table 3

## Discussion

Although *Porites astreoides* and *P. porites* are present in most fore-reef habitats to below 25 m, the belt-like zonal patterns of peak abundance shown by these two species on the reef flats of Carrie Bow Cay and Tobacco Reef (Figs. 3a, b, 4, 5) appear to be characteristic of much of the barrier-reef platform (see Burke 1982). The same zonal relationship prevails on both study areas (see also Macintyre et al. 1987), even though at Carrie Bow Cay depth decreases with an increase in distance from the crest up to the Cay itself, whereas on Tobacco Reef depth increases westward from the crest into the lagoon. We have observed similar zonal patterns on seaward reefs in the San Blas Islands (Panama), in the Bahamas and on the extensive outer reef margins at both Glovers Reef and Lighthouse Reef (Belizean atolls) suggesting that the distributional phenomena under study are widespread throughout the Caribbean.

This study represents an experimental analysis of direct responses of Caribbean reef-building corals to fish predation. The results coincide with other investigations of the effects of predators on both coral- and algal-dominated reef communities. The distribution and abundance patterns of the two *Porites* species in separate back-reef zones are related to their differential palatability, probably due to the marked differences in shape and subsurface corallum hardness. The softer-textured branched form, *Porites porites* f. *furcata*, can survive and grow at a rapid rate in the pavement-rubble habitat of high herbivory when grazing fishes are excluded (Table 2). One caged specimen showed a six-fold increase in area over the 23 mo period. When protection was removed, the *P. porites* transplants were consumed in fewer than 19 h. Conversely, *P. astreoides*, a harder, unbranched, mound-shaped coral, showed little colony mortality under high grazing pressure, even though often bitten by parrotfishes (Figs. 6 and 7, personal observations).

The segregated abundance patterns of these two reef-building corals hypothetically relate to the proximity of complex reef structures (see Table 1 of Lewis and Wainwright 1985) that provide shelter to grazing fishes (herbivorous and corallivorous) and the resultant gradient of preda-

tion by parrotfishes. Comparable spatial variations in herbivore consumption intensity (Vine 1974; Hay 1981, 1984; Hatcher 1982; Hay et al. 1983; Macintyre et al. 1987) and herbivorous fish abundances (Miller 1982; Russ 1984; Lewis and Wainwright 1985; Lewis 1986) have been noted across various reef systems. The limitation of grazer abundances in spatially simple habitats may involve some critical distance factor away from nearby topographically complex areas that provide shelter from higher-level carnivores. Proximity to shelter in adjacent patch reefs from potential predators has been noted (Randall 1965) to be an important determinant of the foraging ranges of herbivorous fishes in *Thalassia* beds. The influence of herbivorous fishes along barrier and fringing reefs may be similarly dependent on distance from shelter in adjacent topographically complex habitats. For example, parrotfish densities (fish sighted per transect) along  $2 \times 50$  m transects at various distances westward away from the topographically complex reef crest on nearby Tobacco Reef are as follows (Macintyre et al. 1987): 0 m = 16.2, 40 m = 5.8, 90 m = 3.2 and 150 m = 0.2. Grazing by parrotfish and surgeonfish is heaviest from 0 to 40 m behind the reef crest (Macintyre et al. 1987, see Fig. 4); however, it is much reduced beyond this distance from shelter. High densities of herbivorous fishes also were recorded (Lewis and Wainwright 1985, see Table 1) in the rubble-pavement back-reef zone of Carrie Bow Cay, situated adjacent to the spatially complex reef crest, compared with other nearby regions.

Although damage to mature coral colonies (Glynn 1973; Frydl 1977) and impacts on juvenile coral densities and recruitment (Sammarco 1980, 1982) by animals classified as herbivores has been known for some time, it has not always been clear whether the disturbances are produced while the grazers are haphazardly foraging, or if they result from intentional predation on corals. Randall (1967) in his synoptic analysis of the food habits of reef fishes in the West Indies, failed to observe any scraping of live coral by parrotfishes, nor were significant amounts of coral found in any of the stomachs. However, other evidence indicates considerable scraping of coral polyps from living coral heads by parrotfishes in the Marshall Islands (Hiatt and Strasburg 1960) with bites often extending deeply into the calcareous corallum. Parrotfish appear to scrape corals

preferentially, particularly massive forms of *Porites* off Palao (Motoda 1940), Enewetak Atoll and Fanning Island (Bakus 1967), in the Eastern Pacific near Panama (Glynn et al. 1972), Bermuda (Gygi 1975) and Belize (Macintyre 1984). We recorded heavy predation on *Porites porites*, (Figs. 7 and 8) with relatively minor feeding on *P. astreoides*, although sometimes the latter can show varying degrees of surficial grazing scars. The differences in palatability between the species are hypothetically related to differences in growth form and subsurface corallum hardness. The reasons for variation in the degree of grazing scars observed at the individual colony level in *P. astreoides* are unknown, but this scraping occurred on colonies that were not overgrown by macroalgae or other potential prey organisms. Speculatively, there may be an energetic or nutrient yield per unit-of-effort to parrotfishes that is great enough to be of occasional benefit when more attractive prey items are not abundant.

Rützler and Macintyre (1982) and Burke (1982) have suggested that the direction and force of water motion controls the zonation of the Belizean barrier-reef biota; this hypothesis has been supported for the distributional patterns of some fore-reef corals by the work of Geister (1977). However, predation, due primarily to fishes, is a major factor regulating the seaward abundance of *Porites porites* f. *furcata* on the back-reef flat. Correlative evidence for this interpretation comes from our observations of high abundances of *P. porites* in overfished areas of the Lesser Antilles, where larger parrotfishes should normally occur but have been removed by semi-permanent fish traps (Figs. 3c and 3d). These areas appear to contain the complex, three-dimensional reef structure of the type that we hypothesize is needed to harbor a grazer population capable of limiting the abundance of *P. porites*.

The role of fishes and sea urchins in the reef systems around Carrie Bow Cay have been sufficiently studied to enable inferences to be made concerning the causes of the relative abundances of the predominant macrophytes (Hay 1981; Littler et al. 1983a, 1983b, 1986, 1987; Lewis and Wainwright 1985; Lewis 1986; Taylor et al. 1986; Lewis et al. 1987; Macintyre et al. 1987). Assays of grazing intensity and fish abundances consistently have shown herbivory on the rubble-pavement portion of the back reef to exceed that in spatially simple habitats farther behind the crest. Because adult grazing fishes (e.g. parrotfish and surgeonfish) have limited access to the reef-flat zone from 45–70 m, a region which is homogeneously simple and shallow, the relatively palatable *Porites porites* f. *furcata* (Fig. 3b) becomes abundant in this environment. Even during exceptionally high tides, the lack of protective cover would make those fish that are capable of feeding on *P. porites* vulnerable to predatory fishes (such as Sphyraenidae) and ospreys [*Pandion balaetus* (Linnaeus)], which often forage on the shallow reef flat (personal observations).

We have used the findings presented above and the research of colleagues working in the Belizean reef system to develop and partially test a model (Fig. 8) explaining the mechanisms responsible for the distributional patterns of *Porites* on Caribbean back-reef flats. Lewis (1986) conducted experimental exclusions of herbivorous fish in the rubble-pavement region of the back reef at Carrie Bow Cay; while her study did not directly address the zonation of corals, the results imply a mechanism explaining the shoreward decrease in *Porites astreoides* (Fig. 5). Her experi-

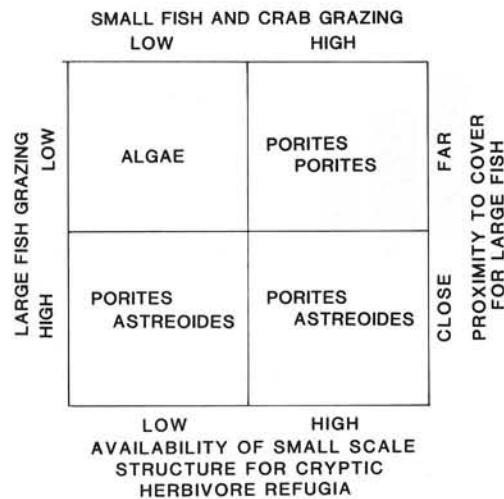


Fig. 8. Interactive model predicting the influence of various grazer/corallivore guilds on the differential dominance between *Porites* and algal populations on Caribbean back-reef systems

mental exclusion of large herbivorous fishes by coarse chicken-wire fences (2.5 cm mesh) led to overgrowth of portions of *P. astreoides* colonies within 10 wk by frondose and filamentous turf-forming algae. Coral polyps were killed and the surrounding skeletons were bleached as a direct result. Where grazing is low, it is well documented (e.g. Banner 1974, Potts 1977, Antonius 1982) that frondose macroalgae are capable of overgrowing and killing corals, unless the latter can attain a refuge in size (Birkeland 1977). We predict that *P. astreoides* cannot survive competitive overgrowth by fleshy algae on portions of the back reef that are effectively inaccessible to grazing fishes. Experiments by Coen (1988) are similarly relevant to explaining the shoreward abundance peak of *P. porites* (Fig. 8). He noted that when herbivorous crabs (*Mithrax*) were excluded from *P. porites* in its zone of peak abundance, again in the same area we studied around Carrie Bow Cay, colonies were also overgrown by newly recruited frondose and filamentous algae, and necrotic zones on the corals were formed. A similar role may be played by other small herbivores that can also take refuge in the highly branched colonies of *P. porites* (e.g. juvenile surgeonfish, personal observations) or the rubble matrix forming much of the bottom in this zone.

The subsequent reintroduction of large herbivorous fishes [in the case of *P. astreoides* (Lewis 1986)], and parallel treatments for herbivorous crabs [in the case of *P. porites* (Coen 1988)], resulted in rapid removal of the overgrowing macroalgae that had become established in the respective exclusion treatments, suggesting that herbivory can indirectly mediate competitive interactions among corals and frondose algae. Both species of *Porites* ultimately become limited at great distances behind the reef crest, where sediment aprons develop on Carrie Bow Cay and Tobacco Reef (Fig. 1, also see Macintyre et al. 1987), presumably by the lack of large hard substrata suitable for attachment.

We conclude that a complexity of direct and indirect interactions are instrumental in structuring the back-reef communities as modeled in Fig. 8. It is important to note that fish feeding preferences and predation (on both algae and corals), coral morphology (at the level of entire colonies) and refugia (at two very different spatial scales) interplay to dictate the pattern of zonation in the back-reef envi-



ronment. Our studies combined with those of Lewis (1986) and Coen (1988), suggest and support the following hypotheses:

(1) The success of *Porites astreoides* in the relatively deep back-reef region near the highly structured reef crest is determined by its low preference to coral-eating parrotfish predators (due to hardness and morphology) and the selective elimination of effective competitors (frondose and turf-forming filamentous algae) by herbivorous fishes (parrotfishes and surgeonfishes). The corallivorous and herbivorous fishes are abundant in this region in part because the three-dimensional structure of the habitat (large coral heads and complex channels of the reef crest) relative to the size of the adult fish (10–75 cm) and depth (>1 m) allows ample refuge from marine and avian predators.

(2) Conversely, we suggest that *P. porites* f. *furcata* is easily eliminated from this region by predation because it is quite palatable to the abundant coral-eating parrotfishes.

(3) *Porites porites* is restricted in the back reef to the reef-flat region, where adult herbivorous fishes are uncommon because the dimensionality of this environment is on a size scale that does not offer refuge from carnivorous predators. Spatial heterogeneity is primarily due to the *P. porites* colonies themselves with crevices on a scale of several centimeters. Because large refugia near the reef crest are too distant, ambush from above by ospreys or by carnivorous fishes from the surrounding waters is too likely to permit corallivore foraging. Depth differences over the relatively shallow ranges encountered (0.2–0.4 m vs 0.7–1.4 m at Carrie Bow Cay and Tobacco Reef, respectively) do not appear to be as critical as the proximity to shelter, because the same pattern occurs at both study sites.

(4) The dimensionality of the reef flat is conducive to the occurrence of abundant smaller herbivores that can use the highly branched *P. porites* colonies and surrounding rubble for refuge from predators. This particularly includes *Mithrax* crabs (Coen 1988) and juvenile surgeonfishes (personal observations). The small herbivore guilds preclude competitive overgrowth of *P. porites* by frondose and filamentous algae without substantial damage to the coral, thereby assuming the same hypothetical role as the larger fish play toward *P. astreoides* in the area nearer the reef crest.

(5) Finally, it is the lack of sufficient dimensionality at this smaller scale that precludes the success of *P. astreoides* in the reef-flat region. There is ample light (undoubtedly not excessive) and adequate depth in most reef-flat areas to foster growth of many algal species. However, the morphology of *P. astreoides* (best approximated by a hemisphere without substantial indentations or convolutions) lacks the spatial complexity on a size scale appropriate to harbor abundant small herbivores such as *Mithrax* or juvenile surgeonfishes that could serve to eliminate overgrowing algal competitors.

Although we find support for this model of reef-flat interactions (Fig. 1), both from our own experiments and those of others (Lewis 1986; Coen 1988), the tests must still be regarded as partial. Other untested explanations for the zonal patterns observed could include the effects of wave action. *Porites porites* is a more delicate species that conceivably could be excluded from the rubble-pavement zone even without predation by periodic battering and dislodgment. The extension of *P. porites* into this back-reef zone and onto the fore reef in island systems where overfish-

ing occurs (Figs. 4c and 4d) argues against this possibility. Sediment scour might also affect the relative survivorship of these two species; however, this was not the case (Table 2) when small (~2 cm<sup>2</sup>) colonies were cemented down and protected by cages in the back reef where, of the areas studied, turbulence and sediment scour should be highest. Also, slightly raised areas are present throughout the rubble-pavement zone on which cryptic juvenile colonies of both *Porites* can be found. Other physiological explanations, variations in dispersal, differential settlement and survivorship or chemical defense also might play a role in the observed abundance patterns. However, Cairns (1982) indicated that *P. astreoides* and cryptic or compact forms of *P. porites* survive and reach maturity in many back-reef and fore-reef habitats from shallow waters to at least 27 m in depth.

Irrespective of alternative explanations, this study does document a direct potential role of fish in controlling coral zonation on a Caribbean reef flat and synthesizes a hypothetical model for the mechanisms regulating coral community structure that may have applicability throughout Caribbean back-reef systems. The generality and predictiveness of the model can only be tested as more reef-flat systems are studied.

*Acknowledgements.* We thank Barrett L. Brooks who provided valuable assistance in the field and laboratory. We are grateful to Loren D. Coen, Stephen C. Jamison, Stephen D. Cairns and C.H. Peterson for helpful comments on an earlier version of this manuscript. The field work was supported by grants from the Smithsonian Institution's Caribbean Coral Reef Ecosystems Program and Exxon Corporation. (CCRE Contribution No. 269).

## References

- Antonius A (1982) Coral reef pathology: a review. Proc 4th Int Coral Reef Symp 2:3–6
- Bakus GJ (1967) The feeding habits of fishes and primary production at Eniwetok, Marshall Islands. Micronesica 3:135–149
- Banner AH (1974) Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. Proc 2nd Int Coral Reef Symp 2:685–702
- Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc 3rd Int Coral Reef Symp 1:15–21
- Burke RB (1982) Reconnaissance study of the geomorphology and benthic communities of the outer barrier reef platform, Belize. In: Rützler K, Macintyre IG (eds) The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities. Smithsonian Institution Press, Washington, DC, Smithsonian Contrib Mar Sci 12:509–526
- Cairns SD (1982) Stony corals (Cnidaria: Hydrozoa, Scleractinia) of Carrie Bow Cay, Belize. In: Rützler K, Macintyre IG (eds) The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities. Smithsonian Institution Press, Washington, DC, Smithsonian Contrib Mar Sci 12:271–302
- Coen LD (1988) Herbivory by crabs and the control of algal epibionts on Caribbean host corals. Oecologia 75:198–203
- Frydl P (1977) The geological effect of grazing by parrotfish (Scaridae) on a Barbados coral reef. M.Sc. thesis. McGill University, Montreal, Canada
- Geister J (1977) The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Proc 3rd Inter Coral Reef Symp 1:23–29
- Glynn PW (1973) Aspects of the ecology of coral reefs in the western Atlantic region. In: Jones OA, Endean R (eds) Biology and geology of coral reefs. Academic Press, New York, pp 271–324

- Glynn PW (1976) Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecol Monogr* 46:431–456
- Glynn PW, Stewart RH, McCosker JE (1972) Pacific coral reefs of Panama: structure, distribution and predators. *Geol Rundsch* 61:483–519
- Gygi RA (1975) *Sparisoma viride* (Bonnaterre), the stoplight parrotfish, a major sediment producer on coral reefs of Bermuda. *Ecolgae Geol Helv* 68:327–359
- Hatcher BG (1982) The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. *Proc 4th Int Coral Reef Symp* 2:515–524
- Hay ME (1981) Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquat Bot* 11:97–109
- Hay ME (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 65:446–454
- Hay ME, Colburn T, Downing D (1983) Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. *Oecologia* 58:299–308
- Hiatt RW, Strasburg DW (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol Monogr* 30:65–127
- James NP, Ginsburg RN, Marszalek DS, Choquette PW (1976) Facies and fabric specificity of early subsea cements in shallow Belize (British Honduras) reefs. *J Sediment Petrol* 46:523–544
- Kaufman L (1977) The three spot damselfish: effects on benthic biota of Caribbean coral reefs. *Proc 3rd Int Coral Reef Symp* 1:559–564
- Lessios HA, Glynn PW, Robertson DR (1983) Mass mortalities of coral reef organisms. *Science* 222:715
- Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol Monogr* 56:183–200
- Lewis SM, Wainwright PC (1985) Herbivore abundance and grazing intensity on a Caribbean coral reef. *J Exp Mar Biol Ecol* 87:215–228
- Lewis SM, Norris JN, Searles RB (1987) The regulation of morphological plasticity in tropical reef algae by herbivory. *Ecology* 68:636–641
- Littler MM, Littler DS (1984) A relative-dominance model for biotic reefs. In: *Advances in reef sciences. Proceedings of the Joint Meeting of the Atlantic Reef Committee and the International Society of Reef Studies*, Miami, Florida
- Littler MM, Littler DS (1985) Non-destructive sampling. In: Littler MM, Littler DS (eds) *Handbook of phycological methods. Ecological field methods: macroalgae*. Cambridge University Press, Cambridge, pp 161–175
- Littler MM, Littler DS (1988) Structure and role of algae in tropical reef communities. In: Lembi CA, Waaland JR (eds) *Algae and human affairs*. Cambridge University Press, Cambridge, pp 29–55
- Littler MM, Littler DS, Taylor PR (1983a) Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *J Phycol* 19:229–237
- Littler MM, Taylor PR, Littler DS (1983b) Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* 2:111–118
- Littler MM, Taylor PR, Littler DS (1986) Plant defense associations in the marine environment. *Coral Reefs* 5:63–71
- Littler MM, Littler DS, Taylor PR (1987) Animal-plant defense associations: effects on the distribution and abundance of tropical reef macrophytes. *J Exp Mar Biol Ecol* 105:107–121
- Macintyre IG (1984) Preburial and shallow-subsurface alteration of modern scleractinian corals. *Ealaeonpographica Americana* 54:229–244
- Macintyre IG, Graus RR, Reinthal PN, Littler MM, Littler DS (1987) The barrier reef sediment apron: Tobacco Reef, Belize. *Coral Reefs* 6:1–12
- Miller AC (1982) Effects of differential fish grazing on the community structure of an intertidal reef flat at Enewetak Atoll, Marshall Islands. *Pac Sci* 36:467–482
- Motoda S (1940) The environment and the life of massive reef coral, *Goniastrea aspera* Verrill, inhabiting the reef flat in Palao. *Palao Tropical Biol Sta Studies* 2:61–104
- Neudecker S (1979) Effects of grazing and browsing fishes on the zonation of corals in Guam. *Ecology* 60:666–672
- Potts DC (1977) Suppression of coral populations by filamentous algae within damselfish territories. *J Exp Mar Biol Ecol* 28:207–216
- Randall JE (1965) Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* 46:255–260
- Randall JE (1967) Food habits of reef fishes of the West Indies. *Stud Trop Oceanogr* 5:665–847
- Russ G (1984) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. *Mar Ecol Prog Ser* 20:35–44
- Rützler K, Macintyre IG (1982) The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. In: Rützler K, Macintyre IG (eds) *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities*. Smithsonian Institution Press, Washington, DC, *Smithsonian Contrib Mar Sci* 12:9–45
- Sammarco PW (1980) *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *J Exp Mar Biol Ecol* 45:245–272
- Sammarco PW (1982) Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. *J Exp Mar Biol Ecol* 65:83–105
- SAS (1985) *SAS user's guide: basics*. SAS Institute Inc., Cary, North Carolina
- Sokal RR, Rohlf FJ (1969) *Biometry*. Freeman, San Francisco
- Taylor PR, Littler MM, Littler DS (1986) Escapes from herbivory in relation to the structure of mangrove island macroalgal communities. *Oecologia* 69:481–490
- Vine PJ (1974) Effects of algal grazing and aggressive behaviour of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral-reef ecology. *Mar Biol* 24:131–136
- Wellington GM (1982) Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. *Ecol Monogr* 52:223–241