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**SPATIAL AND TEMPORAL VARIATIONS IN GRAZING PRESSURE BY  
HERBIVOROUS FISHES: TOBACCO REEF, BELIZE**

**BY**

**PETER N. REINTHAL AND IAN G. MACINTYRE**

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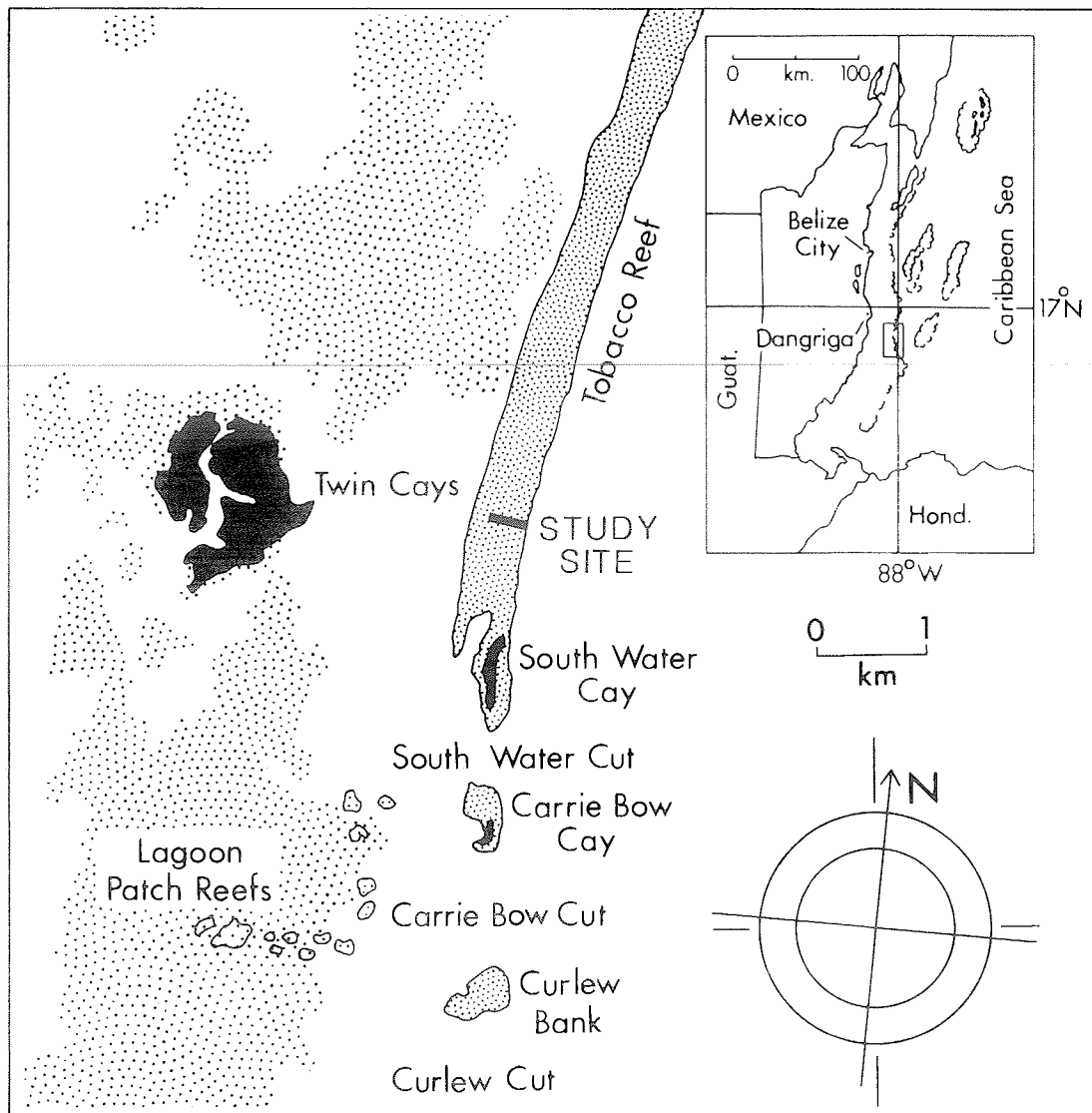


FIGURE 1 - Index map showing location of study transect on Tobacco Reef.

SPATIAL AND TEMPORAL VARIATIONS IN GRAZING  
PRESSURE BY HERBIVOROUS FISHES:  
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BY

PETER N. REINTHAL<sup>1</sup>

and

IAN G. MACINTYRE<sup>2</sup>

ABSTRACT

Fish herbivory appears to play an important role in the pattern of macrophyte zones running parallel to the crest of the Belizean barrier reef. The experimental relocations of reef macrophytes seaward of the reef in 1984 and 1989 revealed that algal species with herbivore-resistant strategies are predominant in the zones of strongest herbivory near the reef crest, whereas those highly susceptible to fish grazing occur well lagoonward of the reef crest. The foraging ranges of herbivorous fish are thought to depend in large part on their proximity to suitable shelter. These trends in herbivore activity were observed in both 1984 and 1989, although the grazing pressure was uniformly less for all algal species studied in 1989. These findings may be related to seasonal (May 1984 versus March 1989) or annual variations in grazing pressure, or to a general decrease in grazing pressure over the five-year study period.

INTRODUCTION

The patterns of abundance and distribution of coral reef macrophytes are well known to be influenced by grazing activities of herbivorous fishes (Stephenson and Searles 1960, Randall 1961, 1965, John and Pope 1973, Wanders 1977, Hay 1981a, b, Hay *et al.* 1983, Hay 1984, Lewis 1986, Horn 1989, Choat 1991, Hay 1991) and urchins (Ogden *et al.* 1973, Sammarco *et al.* 1974, Sammarco 1980, Lawrence and Sammarco 1982, Hay 1981a, b, 1984). However, only recently have studies been conducted on spatial variation in herbivore activity patterns and the effects of spatial patterns of herbivory on macrophyte distributions (Hay *et al.* 1983, Lewis 1986, Macintyre *et al.* 1987, Morrison 1988; Hay 1991). Spatial heterogeneity in grazing intensity has been found to contribute to regional diversity among and within tropical reef habitats (e.g. Lewis 1986) and fishes appear to play a major role in structuring shallow water macrophyte communities (e.g. Morrison 1988).

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<sup>1</sup>Department of Biology, Eastern Michigan University, Ypsilanti, Michigan 48197, and

<sup>2</sup>Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington D.C. 20560



FIGURE 2 - Aerial view of Tobacco Reef looking south towards South Water and Carrie Bow Cays. Note location of study transect and biogeological zones on sediment apron. (1. Coralline-Coral-Dictyota pavement; 2. Turbinaria-Sargassum rubble; 3. Laurencia-Acanthophora sand and gravel; 4. Bare sand; 5. Thalassia sand.) Emergent reef crest and deep fore-reef on left.

In this study we used transplanted samples of various reef macrophytes as a bioassay for an assessment of fish grazing in the backreef habitat. The grazing activity was then compared to observed patterns of macrophyte zonation and evaluated to determine relative grazing pressures on various macrophytes as a function of distance from the reef crest. Varying selective pressures from fish herbivory and substrate requirements appear to be important factors in determining the distribution and zonation patterns of reef macrophytes (Macintyre *et al.* 1987).

Preliminary results found in 1984 (Macintyre *et al.* 1987) prompted us to repeat similar experiments in 1989 when we were able to replicate the treatments at three separate locations (versus one location in 1984) and provide a caged control treatment at one of the locations. This approach allowed us to look at spatial variation in grazing as both a function of distance from the reef crest and variation along the reef crest. The results raise a number of interesting questions concerning spatial and temporal variation in fish grazing activity in the back reef habitat.

## MATERIALS AND METHODS

This study was conducted during May 1984 and March 1989 in the backreef habitat at Tobacco Reef, north of the Smithsonian Institution's field station at Carrie Bow Cay, Belize, Central America (16°48' N, 88°05' W; Fig. 1). The topography, geology and zonation of the region and the floristic and fish distribution patterns are described in detail elsewhere (Rutzler and Macintyre 1982, Norris and Bucher 1982, Lewis and Wainwright 1985, Macintyre *et al.* 1987). A primary study site representative of the reef was identified on the sediment apron of Tobacco Reef approximately 1 km north of South Water Cay (Fig. 1). Three sites that were separated approximately 100 m (north, middle and south) were used as replicate localities.

We transplanted samples of eight reef macrophytes to 0 m., 40 m., 90 m. and 150 m. from the reef crest to determine fish grazing activity as a function of distance from the reef crest. The distances were related to the observed patterns of macrophyte zonation and five distinct biogeological zones (Fig. 2): (1) 0 m: coralline-coral-*Dictyota* pavement, (2) 40 m: *Turbinaria-Sargassum* rubble, (3) 90 m: *Laurencia-Acanthophora* sand and gravel, (4) 150 m: bare sand and (5) *Thalassia* sand. These zonation patterns and various abiotic factors affecting macrophyte distribution are discussed elsewhere (Macintyre *et al.* 1987).

The eight macrophytes used in the grazing assay were *Turbinaria turbinata*, *Sargassum polyceratum*, *Thalassia testudinum*, *Padina jamaicensis*, *Acanthophora spicifera*, *Laurencia papillosa*, *Laurencia intricata* and *Dictyota* sp. The *T. testudinum* blades and other species were free of epiphytes as were all macrophytes. These macrophytes were chosen because they are common and abundant members of the backreef community and show variation in distribution patterns. A mixed assay allowed us to determine grazing intensity with respect to the variety of herbivore groups observed to be active in this area. For example, previous studies (Lewis 1985) have shown that *T. turbinata*, *S. polyceratum*, *T. testudinum* and *P. jamaicensis* are preferred and primarily consumed by parrotfish (*Sparisoma* and *Scarus* spp.). In contrast the red algal species, *A. spicifera*, *L. papillosa* and *L. intricata*, are preferred and primarily consumed by acanthurid species (*Acanthurus bahianus*, *A. coeruleus* and *A. chirugus*) (Lewis 1985). Another herbivore, *Diadema antillarum*, was not considered in this study because it had undergone a massive die-off throughout the Caribbean (Lessios *et al.* 1983) and was never common on this back-reef sediment apron of Tobacco Reef. Moreover, fish are considered to be the grazers of prominent

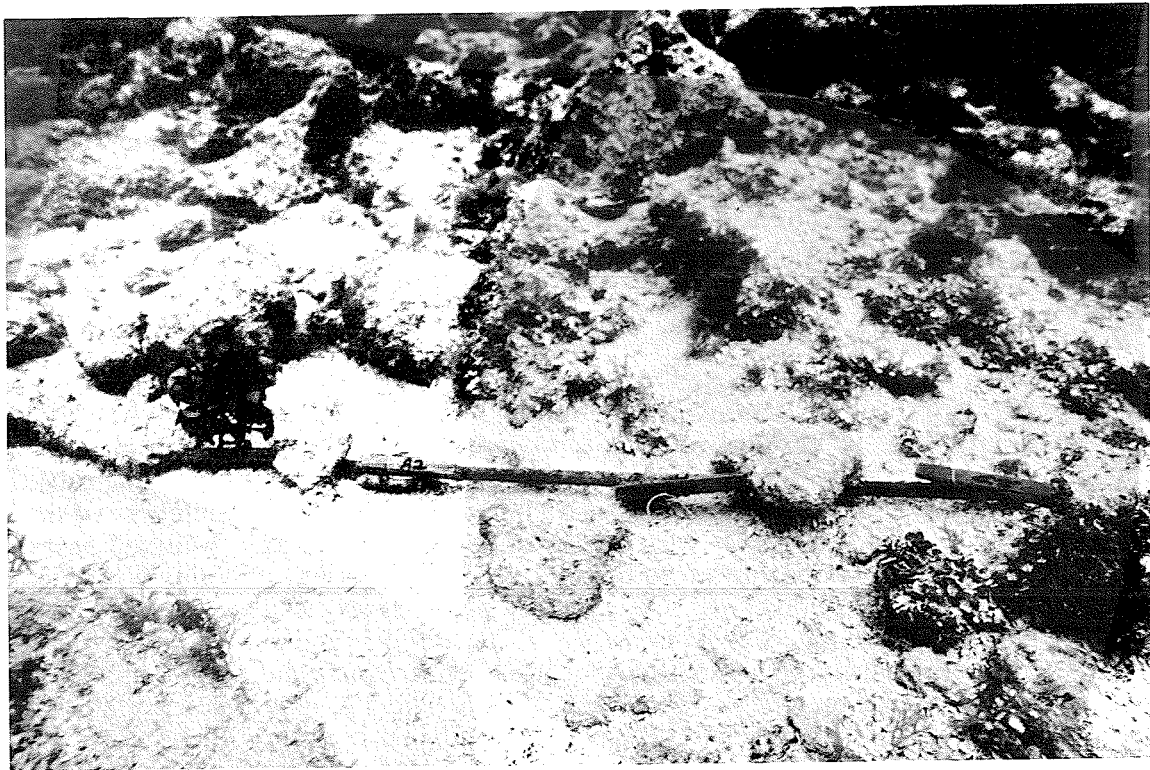
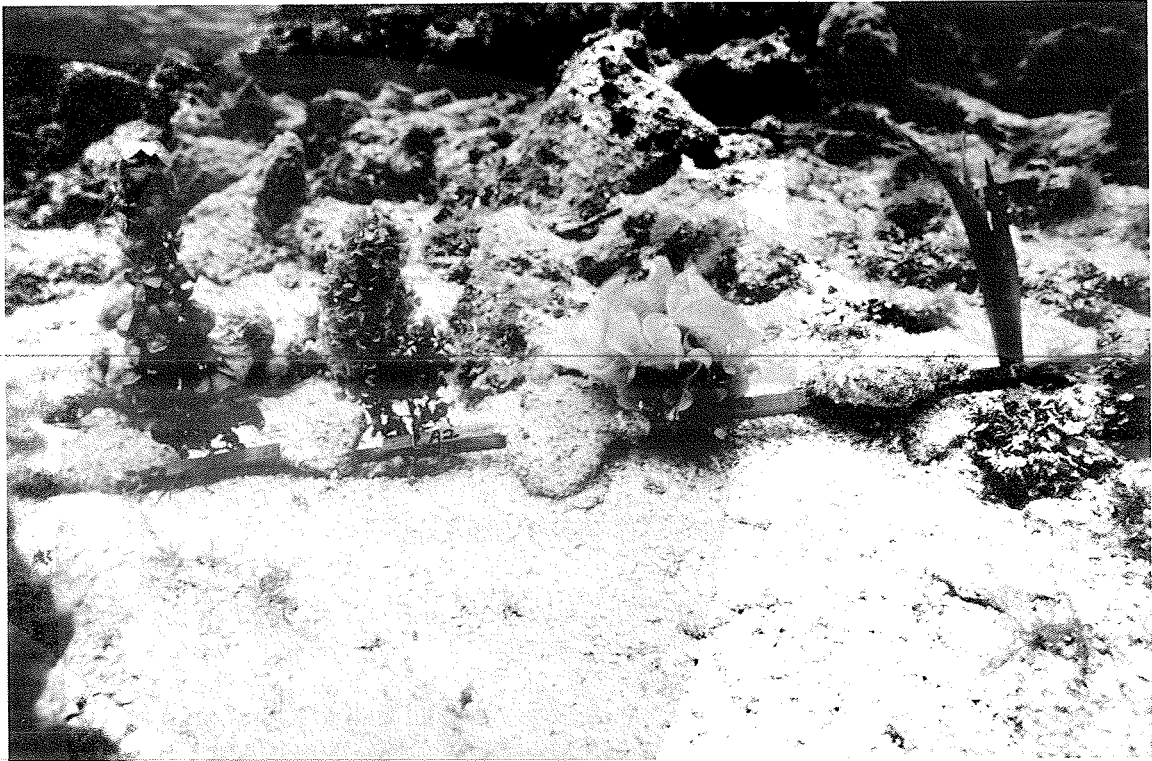


FIGURE 3 - Before and after photographs of test set of four macrophytes (left to right: Turbinaria turbinata, Sargassum polyceratium, Padina jamaicensis, and Thalassia testudinum) at reef crest site.

importance on many tropical reefs (Hay 1984, Lewis 1986, Morrison 1988). No other organisms were found grazing on any of the assays.

The pattern of herbivore pressure as a function of distance from the reef crest was measured by placing complete spin dried and weighed sets of the assay in the back reef at distances of 0, 40, 90 and 150 m behind the reef crest. Samples of each of the macrophyte species were held in wooden clothespins attached to metal rods (Fig. 3). All trials were run for 8 h from 0830 to 1630 h at each experimental grazing site. The samples were then spin dried and reweighed. In 1984, four trials were conducted at each distance at one location each on different days. The amount of macrophyte used in the assays was consistent with the size of macrophytes observed in the study area. In all trials a small piece of the macrophyte remained in the clothespins where it was inaccessible to herbivores. The remaining macrophytes, grazing scars and field observations indicated that macrophytes were not lost by wave action.

In 1989 the trials were replicated on different days three times at each of three locations approximately 100 m apart for all four distances from the reef crest. The middle site was approximately at the same location as that used in 1984. At the northern most locality, 1 m<sup>3</sup> cages constructed from 1/4" wire mesh were placed at each distance from the reef crest. Grazing assays with the eight macrophytes were placed in the cages as controls for the amount of macrophyte lost due to wave action when fish grazers are excluded. Special care was taken to avoid placing macrophyte assays near the guarded territories of damselfish.

Fish counts were made in 1984 along a series of four replicated visual line transect censuses (50 m x 2 m) between 0800 and 1600 h at each experimental grazing site. All parrotfish (*Scarus* and *Sparisoma* spp.) and surgeonfish (*Acanthuridae*) were counted to determine distribution patterns and densities. The methodology applied here is similar to that used by Lewis and Wainwright (1985) in their study of distributions of herbivores among reef habitats.

## RESULTS

### 1984 Experiments

In 1984, a distinct fish-grazing pattern emerges from the data on percent weight loss for the macrophyte species used in this study. Average percent weight loss generally decreases with distance from the reef crest for seven of the macrophytes studied (the exception being *Dictyota* sp.) and shows highly significant weight-loss differences with respect to distance from the reef crest (ANOVA,  $P < 0.005$  in all cases) (Table 1).

For all macrophytes except *Dictyota divaricata*, grazing pressure was homogeneously heavy in 1984 at 0 and 40 m from the reef crest as indicated by Duncan multiple range tests (Table 1): the average percent weight loss at 0 and 40 m are included in the same homogeneous subset whose highest and lowest means do not differ by more than the shortest significant (.05 level) range for a subset of that size. For two macrophyte species, *Padina jamaicensis* and *Thalassia testudinum*, the homogeneity of heavy grazing pressure extends to 90 m. These two macrophyte species are highly preferred by parrotfish in field feeding trials (Lewis 1985, Lewis and Reinthal in prep.). *Turbinaria turbinata* and *Sargassum polyceratum*, also preferred by parrotfish, appear to be subject to the same heavy grazing pressure at 0 and 40 m, but little or moderate grazing pressure at 90 and 150 m.

The situation was similar for the macrophytes preferred by surgeonfish (*Acanthuridae*) (Lewis 1985, Lewis and Reinthal, in prep.). The grazing pressure on *Acanthophora spicifera* and *Laurencia papillosa* is homogeneously heavy at 0 and 40 m,

moderate at 90 m, and light at 150 m as indicated by the homogeneous subsets in the Duncan's Multiple range test (Table 1). Heavy grazing pressure is also observed at 0 and 40 m for *L. intricata* but grazing is homogeneously moderate to weak at 90-150 m.

In the case of *Dictyota divaricata* sp., grazing pressure was homogeneously light and no significant differences were found between average weight loss at various distances (ANOVA,  $P = 0.68$ ) (Table 1). The Duncan's Multiple range test included all distances in the same homogeneous subset. The weight loss in this case is thought to be due primarily to experimental error caused by the removal of small fragments through wave action and this was the only macrophyte that proved difficult to retain as one piece in a clothespin.

Distribution patterns identified for herbivorous fish (Table 2) coincide with grazing patterns identified here. Fish densities were highest at 0 and 40 m, the areas with the greatest grazing pressure. Even though most of the fish observed at 90 m were juvenile *Acanthurus bahianus*, the sighting of a large heterospecific school of adult herbivorous fish outside the transect area (approximately 60 *A. bahianus*, 10 *A. chirugus*, 4 *A. coeruleus* and 13 *Sparisoma chrysopterum*) indicates these fish do extend their foraging to 90 m. Many heterospecific schools were also observed at 0 and 40 m. No schools were sighted at 150 m and only 1 individual was counted in the transects.

### 1989 Experiments

There were no significant differences between the three replicate locations for all eight macrophytes nor were there any significant distance\*location interaction effects (ANOVA  $p > .05$  in all cases). Thus, the three locations were grouped together for purposes of analyses.

The caged treatment showed no significant distance effects for macrophyte loss due to wave action (ANOVA  $p > .05$  in all cases) and all distances were included in the same homogeneous subset (Table 1).

For the experimental assays, a similar pattern of spatial variation in grazing intensity emerges with respect to distance from the reef crest as that found in 1984 (Table 1) but grazing pressure was uniformly weaker. At all distances, for all macrophyte species, the percent weight loss was less in 1989 than that found in 1984 (ANOVA;  $p < .01$ ). For six of the eight macrophytes there was a significant difference between the distances (ANOVA;  $p < .0005$ ; Table 1). Only *Turbinaria turbinata* and *Dictyota* sp. showed no significant differences between distances.

The grazing intensity observed in 1989 appears to be uniformly less than that found for all macrophytes in 1984. The Duncan's multiple range tests for 1989 show the same grazing pattern but a fairly consistent shift in the grazing pressure toward the reef crest and in no cases was grazing pressure heavier nor further extended than that found in 1984 (Table 1).

## DISCUSSION

### Spatial Patterns of Herbivory

The data presented here show distinct spatial grazing patterns on the macrophyte species under study. For all macrophyte species, except *Dictyota divaricata*, the grazing pressure in 1984 is heavy at 0 and 40 m from the reef crest, moderate to light at 90 m and absent at 150 m. The same general results were found in 1989 but the grazing pressure was uniformly less. These results are associated with zonation patterns and biogeologic zones observed for this backreef habitat and the distribution of biological assemblages appears to be controlled mainly by a combination of grazing



pressure of herbivorous fish, which is a function of distance from the reef crest, and both physical factors and hydrodynamic conditions which are discussed elsewhere (Macintyre *et al.* 1987). Thus, while spatial heterogeneity in herbivore grazing represents a biotically generated mechanism contributing to high regional diversity among reef habitats (Lewis 1986, Hay 1981a, 1985; Morrison 1988), the patterns of zonation and habitat diversity within the Tobacco Reef backreef appear to be under a similar mechanistic control.

*Dictyota* spp. in general, probably because they contain noxious chemical compounds (Gerwick 1981, Norris and Fenical 1982), are notably avoided by herbivorous fish (Montgomery 1980, Hay 1981a, Littler *et al.* 1983). Surgeonfish were occasionally observed taking single bites of *D. divaricata* but would not continue to feed or graze with the same intensity as they did on *Laurencia papillosa* or *Acanthophora spicifera*.

The grazing pressure may be determining the zonation pattern through either direct effects or an indirect effect by inhibiting an efficient competitor. Lewis (1986) directly compared grazed backreef versus ungrazed backreef and found that *Sargassium*, *Padina* and *Turbinaria* did increase significantly in the absence of fish herbivory and outcompeted corals and other slow-growing benthic species. Hay (1981a, b) and Hay *et al.* (1983) showed that algal species characteristic of the deep sand plains and intertidal reef flats may be restricted from the reef slope by herbivory, and suggested that these species would represent potentially dominant competitors on the reef slope in the absence of herbivory. The same may be true for the Tobacco Reef backreef habitat.

Macroalgae species found at the greatest distances from the reef crest and found in low-herbivory habitats were found to be the macrophytes most highly susceptible to grazing by herbivorous fishes. Other studies have indicated that many algal species characteristic of habitats with high grazing intensities are resistant to herbivorous fish grazing and, conversely, algae in habitats with low grazing intensity are susceptible to herbivory (Hay 1981b, 1984, Littler *et al.* 1983, Lewis 1985, 1986). For example, the coralline-coral-*Dictyota* zone (Macintyre *et al.* 1987) is the zone in which we measured the highest levels of herbivory. The dominant biota have well-documented herbivore defense strategies (Norris and Fenical 1982, Paul and Hay 1986).

Fish grazing intensity has been found to decrease with depth on forereefs and exhibits an inverse relationship to algal abundance (Morrison 1988). The decreasing herbivory is thought to be the result of diminishing trophic carrying capacity and increased risk of predation (Hay and Goertemiller 1983, Steneck 1983, Lewis 1986). The latter may well apply to the habitat studied here but the argument concerning trophic carrying capacity is not applicable in the shallow back-reef.

Proximity to suitable shelter has long been recognized as a critical factor in determining herbivore foraging ranges on patch reefs in tropical seagrass beds (Randall 1965), on deep sand plains adjoining reef slopes (Earle 1972, Hay 1981a, b) and in the backreef areas remote from the reef crest (Lewis 1986, Lewis and Wainwright 1985). Although we have no experimental evidence to explain why herbivorous fish do not graze further from the reef crest, they may be constrained by predatory piscivorous fishes (Ogden *et al.* 1973) and birds. Barracuda (Sphyraenidae), jacks (Carangidae) and snapper (Lutjanidae) were often seen swimming in the study area. This might also explain why only heterospecific schools of fishes, not solitary adult individuals, were seen at the 90 m site. Heterospecific schooling is considered to provide predator avoidance advantages to participants (see Morse 1977 for review).

All three study areas for 1989 showed the same pattern of herbivory and no significant differences were found between the different locations for all macrophytes. Thus, while the data clearly indicates that herbivore pressure varies perpendicular to the reef crest, it is also consistent along the reef at any one distance from the crest.

### Temporal Patterns of Herbivory

In 1989, the grazing pressure for all macrophytes was homogeneously less than the grazing pressure found in 1984. These differences could represent seasonal fluctuations in herbivory pressure or resource availability (May versus March) or longer term patterns of variation (1984 versus 1989). The seasonal patterns could be the result of differences in productivity or resource availability to the herbivorous fish. Unfortunately, seasonal variation in grazing pressure or herbivore diets has been largely ignored and warrants further research. There may also be seasonal differences in fish movement patterns or community composition that may influence herbivory patterns.

Alternatively the long term effects could be the result of the *Diadema* die-off (Lessios *et al.* 1983) such that there is less competition for resources among herbivores. Morrison (1988) demonstrated that fish grazing intensity tripled after the *Diadema* die-off. Thus the increased herbivore pressure in 1984 could be the fish responding to the lack of a competition and a new equilibrium is established by 1989. An alternative explanation could be that in 1984, the macrophytes had not yet responded to the overall decrease in grazing and the fish were showing the same grazing pattern had *Diadema* been present. By 1989 the fish were no longer required to venture as far into the backreef to graze on macrophytes since they were no longer competing with *Diadema*.

Fish grazing intensity has also been found to vary between reefs because of heavy fishing pressure (Hay 1984). Thus the decrease in grazing pressure from 1984 to 1989 could also be the result of a decrease in the fish populations through an increase in fishing pressure.

## CONCLUSION

From these data we may conclude that herbivorous fish have a strong impact on the distribution patterns of various reef macrophytes and this impact is a function of the distance from the reef crest. The data also indicate that there is temporal variation in herbivory patterns. While grazing pressure did not vary at three locations along the reef crest, it appears effective in preventing the establishment of many macrophytes within 90 m of the reef crest in the backreef habitat. The herbivory patterns found here are consistent with the macrophyte distribution patterns and suggests that fish grazers are of primary importance in controlling these distributional patterns. These patterns are, in turn, directly correlated with the distance from the reef crest.

## ACKNOWLEDGEMENTS

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**Table 1.** Results of macroalgal transplant experiments: mean percentage macrophyte weight loss ( $\pm$  standard deviation) after exposure to or caging from herbivores at varying distances from the reef crest in the Tobacco Reef backreef habitat for 8-h trials. Four replicate trials were conducted at one location at each distance in 1984 (N=4) and three replicate trials were conducted at each of three locations in 1989 with no differences found between locations (N=9). 1989 Cage are the results from three replicate trials placed in fish exclusion cages at one location (N=3). Groupings between distances are based on Duncan's multiple range test.

SPECIES	MEAN PERCENT WEIGHT LOSS ( $\pm$ S.D.)				ANOVA	
	0 m	40 m	90 m	150 m	F	P
<i>Thalassia testudinum</i>						
1984	83.4 (6.2)	76.4 (10.7)	78.7 (6.5)	11.7 (23.3)	24.98	<.0001
1989	77.3 (6.7)	36.9 (40.0)	0.0 (0.0)	0.0 (0.0)	30.39	<.0001
1989 Cage	0.0 (0.0)	2.3 (3.3)	0.0 (0.0)	0.0 (0.0)	1.00	<.4411
<i>Padina jamaicensis</i>						
1984	93.8 (3.0)	91.5 (5.1)	87.8 (9.8)	11.8 (6.8)	142.2	<.0001
1989	81.3 (29.3)	42.4 (33.4)	6.4 (6.4)	11.0 (6.8)	21.17	<.0001
1989 Cage	10.3 (5.6)	15.0 (6.4)	14.0 (4.5)	11.3 (8.4)	0.23	<.8707
<i>Turbinaria turbinata</i>						
1984	86.4 (25.3)	61.1 (44.3)	8.9 (3.5)	7.1 (5.5)	9.37	<.0018
1989	21.8 (28.5)	6.9 (4.5)	5.4 (5.0)	3.8 (2.0)	2.26	<.1031
1989 Cage	4.3 (0.9)	5.7 (1.7)	4.7 (2.9)	4.0 (0.0)	0.35	<.7934
<i>Sargassum polyceratum</i>						
1984	97.3 (2.0)	61.2 (42.2)	31.2 (36.1)	10.0 (4.3)	7.40	<.0046
1989	48.7 (36.0)	9.4 (5.4)	5.8 (3.6)	7.4 (4.2)	9.32	<.0002
1989 Cage	4.7 (3.3)	10.7 (4.6)	8.0 (6.2)	6.3 (3.1)	0.65	<.6023

**Table 1 (cont.).**

SPECIES	MEAN PERCENT WEIGHT LOSS ( $\pm$ S.D.)				ANOVA	
	0 m	40 m	90 m	150 m	F	P
<i>Acanthophora spicifera</i>						
1984	93.3 (2.8)	89.1 (11.7)	71.2 (11.6)	4.0 (6.1)	87.14	<.0001
	-----	-----	-----	-----		
1989	74.8 (26.7)	73.1 (19.8)	18.6 (16.5)	5.3 (6.4)	31.22	<.0001
	-----	-----	-----	-----		
1989 Cage	3.3 (1.2)	19.3 (12.5)	2.7 (2.0)	5.3 (3.9)	2.79	<.1090
	-----	-----	-----	-----		
<i>Laurencia intricata</i>						
1984	73.6 (19.7)	77.9 (18.5)	39.8 (19.4)	13.7 (8.7)	12.35	<.0006
	-----	-----	-----	-----		
1989	42.1 (16.5)	28.0 (17.7)	15.1 (13.3)	10.1 (4.6)	8.13	<.0005
	-----	-----	-----	-----		
1989 Cage	19.7 (7.0)	16.3 (5.3)	18.0 (5.0)	21.3 (6.9)	0.25	<.8621
	-----	-----	-----	-----		
<i>Laurencia papillosa</i>						
1984	93.4 (3.1)	95.1 (3.7)	51.4 (27.9)	10.9 (6.9)	30.20	<.0001
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1989	82.7 (15.9)	77.8 (17.4)	8.6 (7.9)	4.3 (5.6)	85.65	<.0001
	-----	-----	-----	-----		
1989 Cage	13.0 (8.5)	20.0 (10.2)	8.3 (4.1)	8.0 (7.8)	0.98	<.4477
	-----	-----	-----	-----		
<i>Dictyota sp.</i>						
1984	28.5 (11.7)	27.3 (6.5)	21.0 (11.3)	27.4 (7.5)	0.52	<.6778
	-----	-----	-----	-----		
1989	17.4 (7.3)	17.4 (9.1)	15.1 (6.8)	14.6 (9.4)	0.28	<.8371
	-----	-----	-----	-----		
1989 Cage	29.0 (10.7)	29.7 (9.3)	29.0 (9.4)	29.7 (10.9)	0.00	<.9998
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**Table 2.** Mean fish counts (densities per 100 m<sup>2</sup>, N=4) along line transects (50 x 2 m) at the four distances (m) from the reef crest (herbivory test sites) (from Macintyre *et al.* 1987). The Acanthuridae juveniles (Juv) and adults (Ad) were both counted and the species represented are Bah. = *A. bahianus*, Coe. = *A. coeruleus* and Chi. = *A. chirugus*. All Scaridae individuals were included in counts and species represented are Ise. = *S. iserti*, Chr. = *S. chrysopterus*, Rub. = *S. rubripinne*, Vir. = *S. viride* and Rad. = *S. radians*

Dist. (m)	ACANTHURIDAE						SCARIDAE				
	Bah.		Coe.		Chi.		Ise.	Chr.	Rub.	Vir.	Rad.
	Juv	Ad	Juv	Ad	Juv	Ad					
150	0	0	0	0	0	0	0.25	0	0	0	0
90	16	0	0	0	0	0	0.50	0	0	0	2.75
40	23	4.5	0	2.5	1.3	1.3	5.00	0.50	0	0	0.25
0	14	1.5	0.5	2.5	0	0.8	10.5	1.25	1.0	3.5	0