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PATTERNS OF FISH AND URCHIN GRAZING ON CARIBBEAN CORAL REEFS: ARE PREVIOUS RESULTS TYPICAL?¹

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Abstract. Strips of the seagrass *Thalassia testudinum* were used in a field bioassay to assess herbivory on 11 coral reefs scattered throughout the Caribbean. Patterns of herbivory on overfished reefs in Haiti and the United States Virgin Islands were compared to patterns on seven less fished reefs (United States Virgin Islands, Panama, Honduras, Belize, and the Bahamas). On the overfished reefs, the rate of *Thalassia* removal increased significantly with depth, urchin densities were high, and urchin grazing was equal to, or greater than, fish grazing in shallow (<10 m deep) habitats. On reefs subject to little fishing pressure, the rate of *Thalassia* removal decreased with depth, urchin densities were low, and herbivorous fishes were responsible for almost all *Thalassia* removal. Previous studies assessing the importance of urchin grazing in the Caribbean have been conducted on overfished reefs where urchin densities were unusually high and the density of grazing fish unusually low. It is doubtful that the intensity of urchin-algal and urchin-coral interactions observed on these heavily fished reefs occurs on reefs unaffected by humans.

Key words: Caribbean Sea; coral reef; *Diadema*; fish; herbivory; *Thalassia*; urchins.

INTRODUCTION

The grazing activity of herbivorous fishes and urchins may affect the distribution and abundance of marine invertebrates (Newman 1960, Bakus 1964, 1966, Glynn et al. 1979, Sammarco 1980) as well as plants (Stephenson and Searles 1960, Randall 1961, 1965, Ogden et al. 1973b, Sammarco et al. 1974, Wanders 1977, Hay 1981a, b, c, Hay et al. 1983). Since urchins and herbivorous fishes differ in feeding mechanism and behavior (Ogden 1976, Ogden and Lobel 1978), selective regimes in habitats affected primarily by urchins may differ significantly from those in habitats affected primarily by herbivorous fishes. Man's active removal of herbivores such as fishes, manatees, and sea turtles, could affect the distribution, abundance, and, thus, impact of unharvested herbivores such as urchins. If changes of Caribbean reef communities have occurred due to intensive fishing, these changes might be both recent and localized. Therefore, an evaluation of the magnitude, location, and history of human-induced changes in reef communities would be necessary before the evolutionary implications of available data on reef herbivory could be assessed. This study provides an initial assessment of patterns of fish and urchin grazing on reefs scattered throughout the Caribbean and suggests that intense fishing may have resulted in unusually high urchin numbers on reefs where most previous studies on herbivory have been conducted.

Early studies of herbivory on Caribbean reefs (Randall 1961, 1965) showed that reef-associated grazers were responsible for the paucity of seaweed biomass observed on most reefs and for the halo of bare sand that characteristically separated reefs from seagrass

beds. Field observations suggested that the herbivores of primary importance were parrotfishes (Scaridae) and surgeonfishes (Acanthuridae), but this was not rigorously tested.

In Knight Bay, St. Croix, United States Virgin Islands, Ogden et al. (1973b) removed over 7000 urchins (*Diadema antillarum*) from a shallow patch reef of ≈ 1000 m² that was surrounded by a halo. Within 8 mo, seagrasses had regrown near the patch reef, and the halo had disappeared. This study clearly demonstrated the potential impact of urchins on marine plants and stimulated further work on the effects of urchins on reef communities in St. Croix (Ogden et al. 1973a, 1976, Abbott et al. 1974, Sammarco et al. 1974, Ogden 1976, Carpenter 1981) and in Discovery Bay, Jamaica (Sammarco 1980, Carpenter 1981, Williams 1981). The results of these studies have often been reported as typical for Caribbean reefs, despite the clear warnings by Ogden et al. (1973b) that St. Croix had been severely overfished, and a prominent statement by Sammarco (1980) that he was working in areas where urchins were "extraordinarily abundant." It has become commonly accepted that urchins play a primary role as herbivores on Caribbean reefs and that they have a large impact on the organization of these communities. As an example, a recently published text on marine ecology states that "urchins are probably the most important grazing animals in reef environments" (Levinton 1982:433). Although this statement seems well founded given the large number of papers documenting the importance of grazing urchins, almost all of these studies were conducted on either two small patch reefs in Knight Bay, St. Croix (part of the Tague Bay lagoon), or a few small patch reefs in Discovery Bay, Jamaica. Thus, most of our information on reef herbivory (1) comes from patch reefs, not fore

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reefs, (2) involves only two study sites, whose combined areas equal roughly half of a football field, and (3) comes from reefs where the abundance and mean size of many fish species have been reduced by overfishing (Ogden et al. 1973*b*, Woodle 1979). (Carpenter's [1981] work is a notable exception to this in that it covers several sites, but all of these are either on St. Croix or in Discovery Bay.) This does not decrease the value of these studies for explaining interactions occurring on patch reefs in these areas, but the generality of these data for other Caribbean reefs should be questioned.

In this study, I attempt to test the generality of past results by comparing the pattern of fish and urchin grazing on overfished reefs in Haiti and the United States Virgin Islands to the pattern on seven less fished reefs scattered throughout the Caribbean. The overfished reefs were shown to be different from other reefs in (1) the density of urchins, (2) the relative magnitudes of fish and urchin grazing, and (3) the spatial distribution of grazing intensity along a gradient of depth.

STUDY SITES

Descriptions of the Galeta, Panama (Meyer et al. 1975, MacIntyre and Glynn 1976, Hay 1981*a, c*), Carrie Bow Cay, Belize (Rutzler and MacIntyre 1982), and Knight Bay, St. Croix (Ogden et al. 1973*a*), sites are available; detailed descriptions of most other sites will be published elsewhere (W. H. Adey, *personal communication*). A brief description of each study site is given in the Appendix.

METHODS

Spatial and daytime vs. nighttime patterns in herbivory were assessed using the seagrass *Thalassia testudinum*. *Thalassia* was chosen as the bioassay organism because: (1) it is readily eaten in the field by both herbivorous fishes and urchins (Randall 1965, Ogden et al. 1973*a, b*, Ogden 1976), (2) it is a plant of intermediate preference for reef herbivores (i.e., it is eaten fast enough to give quick results, but not so fast that it is completely consumed during an experimental period), (3) its broad, flat blade allows the ragged scars of urchin grazing to be differentiated from the crescent-shaped scars of herbivorous fishes, and (4) it is abundant near all Caribbean reefs, thus assuring the availability of fresh material at each study site.

Clean, freshly collected sections of *Thalassia* were fastened in wooden clothespins, which were cable tied to small coral fragments and distributed haphazardly within the habitats where grazing rate was to be measured. All *Thalassia* sections were 5 cm long and separated by distances of 1–3 m when placed in the field. During all grazing tests, care was taken to work the clothespin and coral apparatus down into the substrate or to wedge it into cracks or fissures so that it would be both stable and even with the surrounding sub-

strate. This assured that the *Thalassia* blades would be equally available to both urchins and fishes. At the end of each experiment, *Thalassia* removal was quantified by measuring the remaining length of each blade to the nearest 0.5 cm. Identity of the grazer was determined by the presence of either crescent-shaped fish scars or ragged urchin scars (Hay et al. 1983). On very rare occasions when both types of scars appeared on the same *Thalassia* section, the amount eaten was divided equally between fishes and urchins.

Grazing rate as a function of depth was measured at 9 of the 11 reefs studied. With two exceptions, trials were run for 3–5 h during the day. Longer (18–22 h), replicate tests were run at Haiti and Tague Bay, St. Croix, to be sure that the unique pattern seen on these reefs could be repeated. To assess nocturnal grazing, *Thalassia* replicates were put into the habitat after dark and collected before dawn. Most nocturnal assessments were made only on the shallower (2–10 m) portions of reefs where urchins were most abundant.

At Lighthouse, Belize, a patch reef surrounded by an especially distinct halo of bare sand (12–15 m wide) was studied to determine the pattern of fish and urchin grazing on both the reef and the halo. During daytime and nighttime grazing tests, *Thalassia* blades were placed on the reef (1–3 m from the junction of the reef and the halo) and in the halo at 1, 5, and 10 m from the reef edge. In the halo area, the clothespins holding the *Thalassia* sections were buried beneath the sand surface, so that only the *Thalassia* blade was exposed. A circle was drawn in the sand around each replicate to facilitate retrieval at the end of the test.

At most study sites, total urchin densities were measured by counting individuals in 880-cm² quadrats placed haphazardly within the study area ($N = 20$ –50 quadrats for each area). Counts from these quadrats were converted to number of urchins per square metre to facilitate comparisons with other studies. Urchin counts on St. Thomas and St. Croix were made using 1-m² quadrats. In structurally simple areas where urchins could not hide, counts were made during either day or night; in structurally complex areas, counts were made only at night. At a few sites where urchin densities were very low (visually estimated to be <1 per 10 m²), densities were listed at <1 urchin/m², and quadrat counts were not made. All data from the reef at Salt River, St. Croix, were provided by R. Steneck; his group used methods similar to those outlined here.

Limitations of the Thalassia assay

The *Thalassia* bioassay is best at measuring herbivory on macrophytes that is attributable to urchins and larger, herbivorous fishes. Grazing by crustaceans and smaller fishes such as damsels (Pomacentridae) and juvenile surgeonfishes (Acanthuridae) is underestimated since it is difficult or impossible for most of these animals to bite through the *Thalassia* blade. These small herbivores are undoubtedly important in affect-

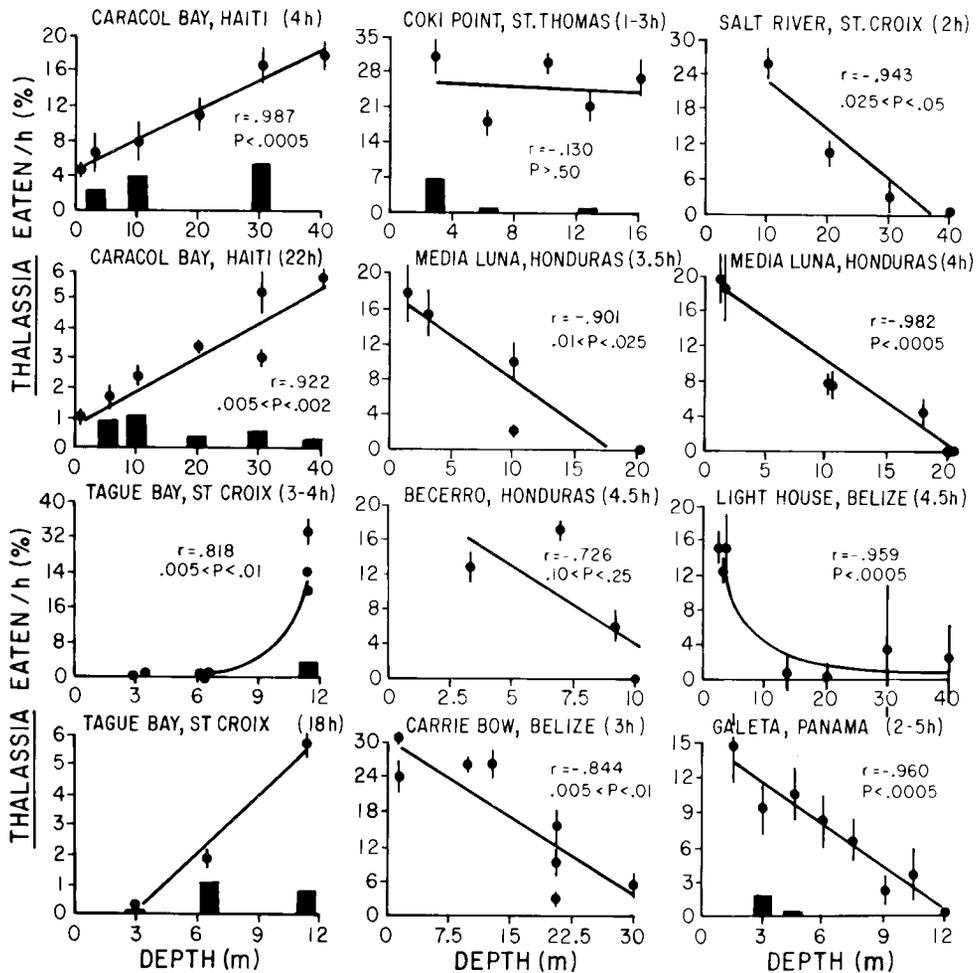


FIG. 1. Mean percentage of *Thalassia* eaten per hour as a function of depth. Vertical lines are ± 1 standard error. Shaded bars show the mean percent eaten per hour by urchins. P and r values are from the regression analysis. The number in parentheses gives the duration of each experiment. Carrie Bow data are from Hay (1981b). Galeta data are from Hay et al. (1983). Salt River data were provided by R. Steneck. The overnight measurement of grazing at Tague Bay has only three data points, and thus a regression analysis cannot be run for that graph. This line therefore was drawn by eye. Measurements at Becerro, Honduras, were made on 30–31 May 1981. Measurements at Tague Bay and Salt River, St. Croix, were made on 17 April–5 May 1982. Dates for measurements at other sites are given in Table 1.

ing the distribution and abundance of small filamentous algae and of larger macrophytes during their spore and sporeling stages. The method underestimates the impact of these herbivores. Also, since fish are visual searchers, they may be better than urchins at rapidly locating and consuming patches of palatable macrophytes such as *Thalassia*. In areas of high urchin density, urchins appear to feed by randomly rasping the substrate and consuming small filaments that may be too inconspicuous for fish to recognize. Therefore, the rates at which *Thalassia* is consumed by fishes and urchins may not adequately assess, under all conditions, the proportion of community productivity that flows through each herbivore guild. The assay best answers the questions: if a palatable macrophyte appears on the reef, is a fish or an urchin more apt to eat

it, and how does this vary with depth and location? Addressing these questions should allow (1) an assessment of the relative impact of herbivorous fishes vs. urchins on reef macrophytes and (2) a comparison of the magnitude and spatial distribution of this impact on different reefs.

RESULTS

On the reefs at Caracol Bay, Haiti, and Tague Bay, St. Croix, rate of *Thalassia* removal increased with depth (Fig. 1). On the Haitian reef, the relationship was linear and highly significant during both test periods ($P < .001$ and $< .01$, regression analysis), with depth and rate of grazing closely correlated ($r = 0.987$ and 0.922). The pattern was similar on the reef at Tague Bay, but the relationship was best explained by

TABLE 1. Grazing on *Thalassia* attributable to urchins or fishes during daytime and nighttime trials in shallow habitats on eight different Caribbean reefs. Nighttime trial data are italicized. At Becerro, Honduras, and Tague Bay and Salt River, St. Croix, United States Virgin Islands (USVI), no exclusively nocturnal feeding trials were conducted; therefore, data from these reefs are not included in the table. Caracol Bay and Knight Bay are heavily fished. Coki Point has recently been made a preserve and is thus fished less intensely. All other reefs appear to be subject to little fishing pressure.

Location	Date	Depth (m)	Time	N	<i>Thalassia</i> consumed by		Fish grazing ÷ urchin grazing	
					Fishes	Urchins		
(I) Caracol Bay, Haiti (fore reef)	12-14 May 1981	3-10	0900-1300	38	% eaten per hour ($\bar{x} \pm SE$)		1.3	
		3-10	1100-0900	39	4.0 ± 1.2	3.1 ± 1.2	1.0	
		3-10	1930-0530	69	1.0 ± 0.3	1.0 ± 0.3	0	
(II) Knight Bay, St. Croix, USVI (patch reef)*	17 April-5 May 1982	2-3	1215-1430	41	0 ± 0	0.4 ± 0.2	0	
		2-3	1430-1730	40	1.7 ± 0.8	6.2 ± 2.5	0.3	
		2-3	1345-1645	39	3.7 ± 1.4	5.6 ± 1.9	0.7	
		2-3	1700-1900	39	4.1 ± 1.3	7.9 ± 2.0	0.5	
		2-3	1700-1900	39	4.6 ± 1.6	5.6 ± 2.4	0.8	
		2-3	0600-1030	38	7.9 ± 1.4	2.1 ± 1.0	3.8	
(III) Coki Point, St. Thomas, USVI (fore reef)	27 March-9 April 1982	2-3	1200-1600	30	2.8 ± 0.7	4.6 ± 1.7	0.6	
		2-3	2200-0600	51	0 ± 0	2.1 ± 0.6	0	
		3	1500-1730	20	9.6 ± 3.2	5.6 ± 3.1	1.7	
		3	0930-1200	20	20.8 ± 3.5	4.6 ± 2.7	4.5	
		3	1515-1615	25	53.8 ± 9.4	10.8 ± 5.6	5.0	
(IV) Media Luna, Honduras (fore reef)	25-28 May 1981	3	1510-1640	22	4.2 ± 8.2	0 ± 0	∞	
		3	1930-0630	111	0 ± 0	1.0 ± 0.2	0	
		2-3	1000-1300	37	16.4 ± 0.2	0 ± 0	∞	
		2	1500-1800	36	18.2 ± 2.3	1.0 ± 0.8	18.2	
(V) Eleuthera, Bahamas (patch reef)	6-9 May & 13-14 June 1981	2	2200-0630	40	0 ± 0	0.2 ± 0.2	0	
		3	1100-1500	86	1.7 ± 0.5	0 ± 0	∞	
		3	2000-0600	84	0 ± 0	0.1 ± 0.1	0	
(VI) Carrie Bow Cay, Belize (back reef)†	17 March-1 April 1980	1	1000-1300	42	27.6 ± 1.5	0 ± 0	∞	
		1	1900-0600	40	0 ± 0	0 ± 0	∞	
(VII) Galeta, Panama (fore reef)‡	27 June-21 July 1979	2-3	day‡	1550	25.9 ± 0.9	0.7 ± 0.2	37.0	
		2-3	night	218	0.5 ± 0.2	0.2 ± 0.3	2.5	
(VIII) Lighthouse, Belize (fore reef)	4-6 June 1981	3	1300-1730	25	14.9 ± 1.9	0 ± 0	∞	
		(patch reef)	1-2	0700-1300	49	12.2 ± 1.0	0 ± 0	∞
		(halo at 1 m)	2-3	0700-1300	20	16.7 ± 0.0	0 ± 0	∞
		(halo at 5 m)	2-3	0700-1300	20	16.4 ± 0.2	0 ± 0	∞
		(halo at 10 m)	2-3	0700-1300	20	5.8 ± 1.6	0 ± 0	∞
		(patch reef)	1-2	1330-1415	38	14.9 ± 4.9	0 ± 0	∞
		(halo at 1 m)	2-3	1230-1350	20	34.5 ± 5.6	0 ± 0	∞
		(halo at 5 m)	2-3	1230-1350	20	0 ± 0	0 ± 0	∞
		(halo at 10 m)	2-3	1230-1350	20	0 ± 0	0 ± 0	∞
		(patch reef)	1-2	2330-0630	57	0 ± 0	0.2 ± 0.2	0
		(halo at 1 m)	2-3	2330-0630	20	0 ± 0	0 ± 0	∞
		(halo at 5 m)	2-3	2330-0630	20	0 ± 0	0 ± 0	∞
		(halo at 10 m)	2-3	2330-0630	20	0 ± 0	0 ± 0	∞

* The same patch reef was used by Ogden et al. (1973a, b), and by Sammarco et al. (1974).

† Data are from Hay (1981b).

‡ Data are from Hay et al. (1983). Trials were run at different times throughout the day and night; thus, specific times cannot be given for trials. Most daytime trials were ≈ 1 h in duration.

an exponential model ($r = 0.818$, $P < .01$). The moderately fished reef at Coki Point, St. Thomas, showed no significant relationship between depth and intensity of grazing ($r = -0.130$, $P > .50$). On all the other reefs studied (including a little-fished reef on St. Croix), grazing rate decreased with depth (Fig. 1). The regressions were significant ($P < .05$) on all reefs but Becerro Cay. The nonsignificant results from Becerro Cay may be due to the low sample size and shallowness of the reef: the basic pattern is similar to that found on

the other undisturbed reefs. On Lighthouse reef (Fig. 1) the relationship between depth and grazing rate was hyperbolic as opposed to linear; this may be a result of the unusual morphology of the reef at this study site. At a depth of ≈ 12 m the reef formed a ledge that dropped straight down to well beyond 60 m. This ledge habitat was characterized by low structural heterogeneity and herbivorous fishes, and urchins were rare.

The proportion of *Thalassia* removal attributable to urchins was higher at Caracol Bay, Haiti; Tague Bay,

TABLE 2. Urchin densities reported for previous studies from (A) St. Croix, United States Virgin Islands and Discovery Bay, Jamaica, and urchin densities recorded during this study for (B) little-fished and (C) heavily fished reefs. For this study, urchin densities represent means from 20 to 50 quadrats.

Study site	Urchin density (no./m ²)	Depth (m)	Species	Reference
A. Previously reported studies				
(I) Discovery Bay (patch reef)	71 100	2-5 2-5	<i>Diadema</i> all species	Sammarco 1980 Sammarco 1980
(II) Discovery Bay (patch reef)	as high as 73	2-5	<i>Diadema</i>	Lawrence and Sammarco 1982 (citing Sammarco 1977)
(III) Discovery Bay (patch reef)	6-13* 10-16*	3-5 3-5	<i>Diadema</i> <i>Echinometra</i>	Williams 1981 Williams 1981
(IV) St. Croix (patch reef)	5-10	1-6	<i>Diadema</i>	Ogden et al. 1973b
(V) St. Croix (patch reef)	≈ 10	1-6	<i>Diadema</i>	Sammarco et al. 1974
B. Unfished or lightly fished reefs				
(I) Media Luna, Honduras (fore reef)	0.6	2	<i>Diadema</i>	This study
(II) Becerro, Honduras (fore reef)	<1	2-3	<i>Diadema</i>	This study
(III) Lighthouse, Belize (fore reef)	<1	2-3	<i>Diadema</i>	This study
(patch reef)	8	1	<i>Diadema</i>	This study
(halo)	0	2-3	<i>Diadema</i>	This study
(IV) Salt River, St. Croix (fore reef)	0.2	10	<i>Diadema</i>	This study
(V) Eleuthera, Bahamas (patch reef)	<1	2-3	<i>Diadema</i>	This study
(VI) Carrie Bow, Belize (back reef)	<1	1		S. M. Lewis and
(fore reef)	4	4		P. C. Wainwright
(fore reef)	<1	9	<i>Diadema</i>	(personal communication)
C. Heavily fished reefs				
(I) Coki Point, St. Thomas (fore reef)	5	3	<i>Diadema</i>	This study
(II) Caracol Bay, Haiti (fore reef)	20	3-10	<i>Diadema</i>	This study
(III) Tague Bay, St. Croix (fore reef)	16	2-5	<i>Diadema</i>	This study
(IV) Knight Bay, St. Croix (patch reef)	9	2-4	<i>Diadema</i>	This study

* Data reported as no./m².

St. Croix; Knight Bay, St. Croix; and Coki Point, St. Thomas, than on any of the less disturbed reefs, and urchins were also more abundant (Fig. 1, Tables 1 and 2). Urchin densities reported by other investigators for study areas in Jamaica and in the United States Virgin Islands (Table 2) were similar to, or greater than, urchin densities found on the heavily fished reefs studied here (Table 2). The disparity between urchin densities on overfished reefs and undisturbed reefs suggests that higher urchin numbers may be correlated with increased fishing pressure.

Daytime and nighttime grazing assessments (Table 1) show that herbivorous fishes generally feed only during the day (at Galeta there was some nocturnal feeding during one trial [Table 1]), while urchins may

feed during either day or night. Although urchins may continue to feed at night, when herbivorous fishes are inactive, their grazing rate averaged over 24 h is usually one to several orders of magnitude less than that of fishes (Table 1). On reefs unaffected by humans the overall impact of urchins on macrophytes is minor relative to the impact of grazing fishes. In shallow areas (where urchins are most abundant), the ratio of fish grazing/24 h to urchin grazing/24 h was very high (ratio = 17-68 and above) on all reefs except Knight Bay, St. Croix (0.6), Caracol Bay, Haiti (1.0), and Coki Point, St. Thomas (3.5). (This ratio could not be computed for Tague Bay, St. Croix, since no exclusively nighttime measurements were made.)

At Lighthouse, Belize, there were several patch reefs

where urchins were abundant (8 urchins/m²) compared to other undisturbed reefs (Table 2) and where halos were especially prominent. Of the little-fished reef systems reported on here, these patch reefs appeared to offer the greatest likelihood of showing significant urchin impact on the maintenance of the halo. During daytime assessments, *Thalassia* placed in the halo area was rapidly eaten by fishes, with grazing intensity decreasing in areas further removed from the reef edge (Table 1). During nighttime trials, there was no loss of *Thalassia*, and urchins did not move into the halo area. Although several hundred metres along the reef margin were searched at 2300–2400 and again at 0530–0630, not one urchin was found in the halo. The patch reef used in this study was in a protected lagoon, the seas were not rough, and the *Thalassia* transplants were placed on the more protected, leeward edge of the reef; turbulence and currents were not restricting urchins from moving into the halo.

DISCUSSION

Most of the data presented here were collected during a period of only a few days on each reef. The potential limitations of such data sets are obvious, but the extreme consistency of grazing patterns on undisturbed reefs (Fig. 1), and on individual reefs where experiments were replicated, suggests that these patterns are predictable and highly characteristic attributes of reefs in the Caribbean. On the overfished reefs in Haiti and St. Croix, the relationship between grazing and depth (Fig. 1) was opposite that found on all of the relatively unfished reefs, and urchins were much more abundant and removed more plant biomass (Fig. 1, Tables 1 and 2). The Coki Point, St. Thomas, reef, which is partially protected from fishing, showed patterns that were intermediate between those on overfished reefs and those found on reefs subject to little fishing (Fig. 1). Comparisons between the heavily fished reef system at Tague Bay, St. Croix, and the little-fished (J. Ogden, *personal communication*, R. Steeneck, *personal communication*) reef at Salt River, St. Croix, suggest that differences in these patterns are due to differences in fishing pressure and not differences between eastern and western Caribbean reefs.

The Knight Bay patch reef, which has been the location of several pivotal studies on grazing by Caribbean urchins (Ogden et al. 1973a, b, Sammarco et al. 1974), had the lowest ratio of fish grazing to urchin grazing of any of the reefs studied here (Table 1). This difference is especially evident when Knight Bay is compared with any of the less fished reefs.

On the Haitian reef and the reefs at Tague Bay and Knight Bay, St. Croix, the density of fishes that feed on (Balistidae, Diodontidae, Pomadasyidae, and Scaridae) and compete with urchins (Scaridae and Acanthuridae) was very low. The difference in the density of urchin predators, particularly in the family Balistidae, was especially striking when the heavily

fished reefs were compared with the reefs most remote from human settlements. At Media Luna, I could often see 10–40 queen triggerfish at one time and at Carrie Bow Cay, I often saw schools of 5–15 ocean triggerfish. These fishes are easily harvested and highly prized by Caribbean fishermen. In the Virgin Islands, triggerfish are among the most preferred food fishes: they make up a significant portion of the fishes taken on St. Thomas, but have been severely depleted on St. Croix, and thus make up a very small portion of the catch on that island (D. Olsen, *personal communication*). Low rates of grazing on shallow portions of heavily fished reefs are not surprising since fishes in these habitats are easily removed. The large increases in herbivory by fishes at greater depths are more difficult to explain. It is possible that fish grazing normally decreases with depth because deeper areas are less structurally complex and leave herbivorous fishes more exposed to attack by predatory fishes. If fishermen (especially spear fishermen) working in deeper areas concentrate their efforts on the more highly prized carnivores and decrease the number of predators, this may allow herbivorous fishes to increase their use of deeper areas without a concomitant increase in their probability of being preyed upon.

Most of the available information on plant-herbivore interactions in the Caribbean, and on coral reefs in general, comes from studies conducted in the United States Virgin Islands (Randall 1961, 1965, Ogden et al. 1973a, b, 1976, Sammarco et al. 1974, Abbott et al. 1974, Ogden 1976, Carpenter 1981), or in Discovery Bay, Jamaica (Sammarco 1980, Carpenter 1981, Williams 1981, Lawrence and Sammarco 1982). Both of these areas are subject to high fishing pressure (Ogden et al. 1973b, Randall cited in Ogden 1976, Woodley 1979, J. B. C. Jackson, *personal communication*), and urchin numbers reported in the above-mentioned studies are similar to, or higher than, those found in this study on reefs in Haiti, St. Croix, and St. Thomas (Table 2). Numerous studies from St. Croix and Discovery Bay show that urchin grazing has a large impact on these reef communities (Ogden et al. 1973a, b, Sammarco et al. 1974, Sammarco 1980, Carpenter 1981, Williams 1981, Lawrence and Sammarco 1982). In contrast to this, a greater importance of fish grazing as opposed to urchin grazing has been reported for Curaçao, Netherlands Antilles (Wanders 1977); San Blas, Panama (Tribble 1981); Galeta, Panama (Hay 1981a, Hay et al. 1983); Carrie Bow, Belize (Hay 1981b); Heron Island, Australia (Stephenson and Searles 1960); the Red Sea (Vine 1974); and Tema Harbor, Ghana (John and Pople 1973). It appears that fishes may be the grazers of primary importance on most tropical reefs and not merely in the Caribbean.

Selection for specific defense mechanisms in the face of intense fish grazing vs. intense urchin grazing may be different since fishes and urchins feed in different ways and have different effects. Caribbean urchins

sometimes feed on live coral (Bak and van Eys 1975, Carpenter 1981) and may severely erode carbonate substrate (Sammarco et al. 1974, Sammarco 1980). Herbivorous fishes in the Caribbean generally do not feed on live coral (Randall 1974) and on the Caribbean coast of Panama, avoid scraping even very small (3-mm) coral colonies (Birkeland 1977). In areas of the Pacific where fishes are not effective urchin predators, urchin grazing can limit the establishment and growth of coral reefs; reefs in these areas may have a maximum thickness that is only 12–25% of the thickness of similar reefs in areas where fishes prey heavily upon urchins (Glynn et al. 1979). The selective value of various herbivore deterrents used by marine plants, and the defensive behavior adopted by territorial pomacentrids, could also change, depending upon the relative importance of fish or urchin grazing.

The fact that much of our information on reef ecology comes from a very few, heavily fished sites is not comforting. Long-term, in-depth studies that focus on one locality have many obvious benefits; their limitations may be less apparent. As shown in Fig. 1, spatial patterns of herbivory determined at Caracol Bay, Haiti, or Tague Bay, St. Croix, would certainly not be predictive of spatial patterns found on any of the less fished reefs. Whenever possible, in-depth studies conducted at one site should be preceded by less extensive investigations of several similar sites that are widely separated. This would provide a data-based rationale for study site location.

This study has focused on grazing by fishes and urchins, but similar problems might be raised concerning manatees, sea turtles, sea otters, and other organisms whose removal could have a large impact on the surrounding community (Estes and Palmisano 1974, Dayton 1975, Estes et al. 1978). The potential importance of such "missing organisms" should not be overlooked when extracting evolutionary implications from ecological data (Janzen and Martin 1982).

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APPENDIX

Caracol Bay, Haiti (19°45'N, 72°00'W)

From an *Acropora*-dominated area near the surface, the reef sloped gently to a depth of ≈ 10 m; below this, it dropped steeply to a depth of 40 m. Between 40 and 50 m the slope was more gentle, but at 50–60 m a sheer ledge formed and dropped straight down out of sight. Urchins were abundant above 10 m (20 urchins/m²), and both predatory and herbivorous fishes were very rare over the entire reef. In 9 h of SCUBA diving and several more of snorkeling, I saw fewer than 200 herbivorous fishes (excluding territorial pomacentrids) and no large predatory fish.

Each day, numerous fishing boats worked the reef, using nets, fish traps, and spears. Once caught, no fish were released. Fish as small as 10–12 cm in length were commonly harvested, even by the spear fishermen.

Media Luna, Honduras (15°13'N, 82°35'W)

The shallowest portion of the forereef (<3 m deep) was dominated by *Acropora palmata* and thus had a high degree of structural heterogeneity. Between 3 and 20 m deep, the reef sloped gently and exhibited little structural heterogeneity: hard corals were rare, but gorgonians were abundant. At 20 m, the reef adjoined a flat, sand plain. Herbivorous fishes were most abundant on shallow, structurally complex portions of the reef, and urchins were extremely rare in almost all areas (<1 urchin/m²). Predatory fish were common in all habitats. Queen triggerfish (*Balistes vetula*), which are voracious urchin predators (Randall 1968), were abundant in grassbeds near the reef; triggerfish were seen over most holes or coral outcrops that provided potential hiding places.

Becerro Cay, Honduras (15°55'N, 83°15'W)

The reef extended to a depth of only 10 m. *Acropora palmata* and *Acropora cervicornis* were very abundant on the upper half of the reef slope. The lower slope was dominated by gorgonians. Urchin numbers were very low on the reef slope (<1 urchin/m²) but high at the junction of the reef flat and reef slope where the water was only a few centimetres deep. When seas were calm, ocean triggerfish (*Canthidermis sufflamen*) lay on their sides, swam into the shallow water (8–10 cm deep), and ate urchins. These shallow areas appeared to provide the urchins with a refuge from predation when seas were rougher.

Lighthouse, Belize (17°11'N, 87°32'W)

Patches of *Acropora* and *Montastrea* species separated by areas of coral rubble characterized the shallow reef slope to a depth of 7 m. Between 7 and 12 m there was a sandy slope with no coral cover. At ≈ 12 m deep, a narrow coral ridge formed the top of a ledge that dropped straight down to well beyond 60 m. Herbivorous fishes were common on the shallow reef slope but rare on the sandy slope and ledge. Urchins were rare in all areas (<1 urchin/m²).

In the protected lagoon, there were several large patch reefs at ≈ 3 m deep that were bordered by clearly defined halos of bare sand. Urchin densities on these patch reefs were high (8 urchins/m²) compared to those on the forereef.

Carrie Bow Cay, Belize (16°48'N, 80°05'W)

Acropora palmata was abundant above 3 m deep and *A. cervicornis* above ≈ 15 m deep. The shallow reef was struc-

turally heterogeneous, and complexity decreased with depth. From the island, the reef sloped gradually to a sand plain at a depth of 27 m. Beyond the sand plain, an outer ridge rose to 13 m before dropping steeply to well beyond 60 m on its seaward side. Both herbivorous and predatory fishes were abundant. Urchin numbers were low.

Eleuthera, Bahamas (25°31'N, 76°54'W)

The study site was in a large complex of patch reefs ≈3 km northwest of the western corner of Royal Island. Reef bases were at ≈8 m deep, with most reefs extending to within 1–3 m of the surface. On the reef used for grazing tests, *Acropora palmata* and gorgonians were abundant. The reef had more structural heterogeneity, fewer upright plants, and more urchins (although still <1 urchin/m²) than other patch reefs in the area.

Galeta, Panama (9°24'N, 79°52'W)

Gorgonians were abundant on the shallow reef slope (<4 m), with the deeper reef slope (4–12 m) being composed primarily of coral rubble. Compared to other reefs, structural heterogeneity was low over the entire area. Urchins, primarily *Echinometra*, were abundant in the shallows (<1–2 m) but rare on deeper areas of the reef. Herbivorous fishes were most common on shallow areas of the reef.

Coki Point, St. Thomas, United States Virgin Islands (18°21'N, 64°52'W)

Hard substrate in shallow (≈3 m) areas was covered primarily by encrusting coralline algae; colonies of *Acropora palmata* were common but not abundant. *Diadema* were numerous (5 urchins/m²) in shallow waters and decreased with depth. Between 6 and 16 m deep, the reef was composed of a sandy slope populated primarily by gorgonians and massive corals. The base of the reef merged with a very gently sloping sand plain. Coki Point has recently been designated as a marine preserve, but there are usually 1–3 fish traps present on the small reef.

Tague Bay, St. Croix, United States Virgin Islands (17°46'N, 64°36'W)

Between the surface and 12 m deep, the reef was gently sloping and composed almost entirely of *Acropora palmata*.

At 12 m, the reef joined a flat, sandy plain populated by a sparse cover of *A. cervicornis* and scattered heads of more massive corals. *Diadema* were common on shallow (3-m) portions of the reef (16 urchins/m²), and their density decreased with depth (R. Steneck, *personal communication*). Larger grazing fishes (Scaridae and Acanthuridae) appeared to be most common at the border of the reef slope and the sand plain. Small grazing fishes (Pomacentridae and immature Acanthuridae) were often common in shallow areas. The Tague Bay area has been heavily fished, and the abundance and mean size of many fish species appear to be decreasing (Ogden et al. 1973b, J. Ogden, *personal communication*).

Knight Bay, St. Croix, United States Virgin Islands (17°46'N, 64°36'W)

Knight Bay is a small bay within the lagoon of the Tague Bay reef system. The small patch reef investigated here is patch reef number 3, which was used as the control reef for earlier experiments on urchin grazing conducted by Ogden and Sammarco (Ogden et al. 1973a, b, Sammarco et al. 1974). There are a few colonies of *Acropora palmata* around the edge of the reef, but a large portion of the reef is covered by a coralline algal pavement that has little spatial complexity. Urchin density is high (9 urchins/m²), and herbivorous fishes are rare. An excellent description of the reef is provided in Ogden et al. 1973a.

Salt River, St. Croix, United States Virgin Islands (17°47'N, 64°45'W)

A pavement supporting gorgonians, massive corals, and some *Acropora palmata* makes up a broad reef flat at a depth of 10 m. Below this the reef slopes rapidly to beyond 50 m. *A. palmata* is common between 10 and 20 m. Below 30 m, massive corals growing in plating morphologies are most common. Urchin density was low at 10 m deep (0.2 urchins/m²) and highest at 20 m deep (1.4 urchins/m²). No urchins were found below 30 m (R. Steneck, *personal communication*). Because of the steep slope of the reef, fish traps are easily lost or tangled; thus, the reef is seldom fished (R. Steneck and J. Ogden, *personal communication*).