

Predation and the Control of the Sea Urchin *Echinometra viridis* and Fleshy Algae in the Patch Reefs of Glovers Reef, Belize

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ABSTRACT

The massive reduction in sea urchin *Diadema antillarum* populations since the mid-1980s has been associated with large increases in the abundance of fleshy algae on many Caribbean reefs despite the availability of other sea urchin and finfish grazers. This study examined the ecology of a grazer living sympatrically with *D. antillarum*, the common and abundant sea urchin *Echinometra viridis*. I examined the role that finfish and invertebrate predators play in controlling the distribution of *E. viridis* as well as the ability of this sea urchin to control exposed fleshy algae on the patch reefs of the Glovers Reef Atoll lagoon. I found that the major predators of this sea urchin were *Calamus bajonado* (jolthead porgy), *Balistes vetula* and *Canthidermis sufflamen* (queen and ocean triggerfish), *Lachnolaimus maximus* (hogfish), and a gastropod, probably *Cassis madagascariensis*. The abundance of *E. viridis* is constrained by predation, which restricts *E. viridis* to cryptic locations,

such as crevices. Sea urchins bit a smaller percentage of experimental algal assays than finfish. Finfish herbivory was associated positively with patch reef topographic complexity. Unexpectedly, *E. viridis* abundance was positively correlated with fleshy algal abundance, but negatively correlated with the frequency of finfish bites. Predators restrict *E. viridis* to crevices and therefore reduce their influence on exposed fleshy algae, even at moderately high population densities (up to 10 per square meter). Since net benthic primary production of coral reefs is most strongly associated with herbivory on exposed surfaces, it would appear that *E. viridis* is unable to maintain the same production as reefs dominated by *D. antillarum*.

Key words: carnivory; *Echinometra viridis*; ecological redundancy; fleshy algae; herbivory; sea urchin predators.

INTRODUCTION

Feeding interactions between sea urchins, their algal prey, and their predators are an important structuring force in the ecology of shallow-water coral reefs (Knowlton 1992; Hughes 1994; McClanahan 1995a). Sea urchins, when abundant, are known to control algal abundance, production, and nutrient dynamics on coral reefs (Hay and Taylor 1985; Foster 1987; Carpenter 1981, 1988, 1990a; Hughes

and others 1987; Levitan 1988; Williams and Carpenter 1988; McClanahan 1997). Sea urchin populations and behavior are often controlled by predators (Carpenter 1984; Hay 1984; McClanahan and Muthiga 1989; McClanahan 1998). The simple three-level trophic food chain of algae–sea urchins–sea urchin predators appears to be an important simplified series of links in a more complex coral reef food web that may be important in determining the overall ecological state of coral reefs (Knowlton 1992; McClanahan 1995a).

This trophic model is oversimplified as each trophic group includes numerous species that differ

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sufficiently in their ecologies; hence, species replacement is not always possible. For example, Lessios (1988a) showed that the pan-Caribbean mass mortality of the sea urchin *Diadema antillarum* did not result in significant changes in the populations of other sympatric sea urchin species in his study sites, despite increases in fleshy macroalgae, the preferred food of sea urchins. In contrast, Aronson and Precht (1997) suggested that ecological redundancy between *D. antillarum* and *Echinometra viridis* prevented algal recruitment in their Belizean study sites that allowed one species of coral, *Agaricia tenuifolia*, to replace another, *Acropora cervicornis*, after the disease induced die-off of both *D. antillarum* and *A. cervicornis*. Other studies have shown increases in fish abundance after the *D. antillarum* die-off or the experimental removal of sea urchins (Carpenter 1990b; Robertson 1991; McClanahan and others 1994). Consequently, species' responses to the loss of an important sympatric species may depend on the levels of ecological redundancy and limiting resources, sea urchins being less food limited than herbivorous fishes (McClanahan 1992). Consequently, there may be species-specific ways that herbivores respond to shelter, food, and predators such that a simple aggregated trophic or guild model, as proposed above, may, at times, require significant modification or qualification.

This study focuses on the ecology of one of the most common Caribbean sea urchins *E. viridis* and the potential influence of this species on the ecology of patch reefs in Glovers Reef Atoll, Belize. I compare the role of this sea urchin with herbivorous fishes in controlling exposed erect benthic algae and the role of reef complexity in modifying the algal-herbivore interactions (Andrew 1993). *Echinometra* is one of the most widely distributed and abundant sea urchin genera in the tropics (Ebert 1982; Palumbi and Metz 1991) and frequently is found in shallow wave-washed locations, usually in crevices or burrows (Grunbaum and others 1978; Tsuchiya and Nishihira 1984; Neill 1988; McClanahan and Kurtis 1991), but also is exposed and in deeper reef locations, when predators are not abundant (McClanahan and Muthiga 1989; McClanahan and Kurtis 1991). Investigators, however, have noted diverse morphologies and behaviors often associated with different habitats (Lewis and Storey 1984; Tsuchiya and Nishihira 1984; Neill 1988; McClanahan and Kurtis 1991) among this genus. Consequently, genetic morphological and behavioral plasticity are common to this sea urchin genus and may influence its response to predator and competitor loss.

Fleshy algae have dominated the benthos of many Caribbean reefs since the die-off of *D. antillarum* in 1983 (Carpenter 1990a; Hughes 1994, 1996; Shulman and Robertson 1997; McClanahan and Muthiga 1998; McClanahan and others 1999). Factors that control these fleshy algae are of considerable management interest and debate (Lapointe and others 1997). Specifically, this study identifies the dominant predators of *E. viridis*, their effectiveness in controlling *E. viridis* behavior and mortality, and estimates *E. viridis* feeding rates and ability to control exposed erect fleshy algae. My hypothesis for this study was that *E. viridis* is susceptible to and controlled by predation and therefore is restricted to inhabiting burrows and crevices and largely unable to replace the role of *D. antillarum* in controlling fleshy algae and benthic production in exposed reef environments.

METHODS

Species and Study Sites

E. viridis is widespread throughout the Caribbean and generally inhabits reef areas with significant three-dimensional structure (H. Lessios, personal communication). It is a common inhabitant of patch reefs where it typically is found by day in crevices and burrows. It is the dominant sea urchin inhabiting the patch reefs of Glovers Reef Atoll.

Glovers Reef Atoll is a 260-km² atoll containing approximately 850 patch reefs within its central lagoon. This atoll is located approximately 30 km offshore from the Belizean (Central America) coastline. Patch reefs are contained within the atoll's lagoon and are shallow (less than 2 m) isolated outcrops of coral and algae of various sizes (25–10,000 m²) separated by sand and seagrass. The atoll's lagoon is surrounded on all sides by exposed reef flat such that the physical energies of waves and currents are low on the patch reefs. Patch reefs are formed by massive coral species in the genera *Diploria*, *Montastrea*, *Porites*, and *Siderastrea* containing thickets of *Agaricia* and *Acropora cervicornis* and a variety of algae and sea whips growing on the dead coral surfaces. Brown algae in the genera *Lobophora*, *Dictyota*, *Turbinaria*, and *Sargassum* were notably abundant on these patch reefs. Fleshy algae abundance on these patch reefs has increased during the past 25 years (McClanahan and Muthiga 1998) as reported in many Caribbean sites in recent years (Carpenter 1990a; Hughes 1994, 1996; Shulman and Robertson 1997; McClanahan and others 1999).

I studied sea urchins, their predators, and algal prey on 14 patch reefs during June and July 1996

and 1997. I examined variance in benthic cover, sea urchin abundance, and predation rates on tethered sea urchins and algae within and between patch reefs. Patch reefs grow towards the dominant trade winds, from the northeast, and have similar reef morphologies along this axis. Three different locations along this axis were compared: the windward patch reef edge, shoulder, and leeward center. Consequently, each transect or assay described below was repeated at each of these three locations on each patch reef. In some cases, when comparing between-reef differences, I pooled data from these three locations. Statistical comparisons between sites were undertaken by ANOVA and the Tukey-Kramer honestly significant difference (HSD) for a posteriori tests of means (Sall and Lehman 1996).

Benthic Cover and Sea Urchin Populations

Benthic cover was described using the line-intercept transect method by using a loosely draped 10 m x 0.5-cm nylon line (McClanahan and Shafir 1990). In each of the three patch reef locations, one loosely draped line was placed along the reef bottom, and the length of algae and hard coral greater than 3 cm under the line was measured and categorized into the following groups: hard coral, soft coral (that is, *Gorgonia*, *Eunicea*, and *Plexaurella*), seagrass (that is, *Thalassia*), turf algae, coralline algae (that is, *Porolithon* and others), calcareous algae (that is, *Halimeda*), fleshy algae (that is, *Lobophora*, *Sargassum*, and *Turbinaria* and others), sponge, and sand (McClanahan and Shafir 1990). Fleshy algae also were further identified to genera by using the descriptions of Littler and others (1989). From these measurements the relative abundance of the dominant cover forms was calculated for each location and patch reef. I also estimated the complexity of the reef substrate along each transect by pressing the 10-m line along the bottom's contour, measuring the straight-line length that this 10-m line traveled, and dividing this value into 10 m to estimate the bottom's rugosity (McClanahan and Shafir 1990). The depth of each line also was estimated by making three random depth measurements along the line (the tidal range is approximately 20 cm). Sea urchins were identified to species and counted in three 10-m² circular plots randomly located along each line transect (total $n = 126 \times 10 \text{ m}^2$ plots).

Predation Experiments

To determine the relative rates of predation on *E. viridis* in each location, I undertook a series of tethering experiments described and tested by McClanahan and Muthiga (1989). In this experiment, 360 *E. viridis* were pierced through their test with a

hypodermic needle and threaded with an approximately 25-cm monofilament line. Ten threaded urchins were tied to loops on a second nylon line of 25 m x 4 mm, which had loops at approximately 2-m intervals, laid close and parallel to the above line transect. The tether allowed urchins to move and chose a resting site in an area of approximately 0.20 m². Sea urchins were visited daily for 3 days to determine the number of individuals that died over each daily interval and to classify the condition of the carcass (McClanahan and Muthiga 1989). Tethering introduces artifacts (Peterson and Black 1994; Aronson and Heck 1995), such as a pierced body wall and restricted movement that allows for calculation of relative rates of predation only. Therefore, the relative index of predation (PI) for each individual urchin was calculated as $PI = (3 - S)/3$, where S is the last day the urchin was seen alive, and 3 is the maximum possible survival in days. If the urchin was killed or disappeared before the first 24-h interval, it was given an $S = 0$; if it disappeared on the second day, it was given $S = 1$ and so on until the experiment ended on the fourth day and $S = 3$. This index produces a value between zero and one, where zero corresponds to no sea urchin eaten over 3 days, and one to all individuals eaten during the first day. Predation on the individual urchin was the measure used in the calculations of averages and the statistical analyses.

The condition of the carcass is a crude estimate of the type of predator that fed on the sea urchin (McClanahan and Muthiga 1989). Carcasses were classified as (a) gone—if the urchin's body could not be found, but the monofilament tether was still present, which is attributable to fish predators, such as sparids and labrids that often consume urchins whole (McClanahan 1995b); (b) broken—if the urchin's body was present but broken, which is often attributable to fish predators, such as balistids, that methodically break open carcasses and leave part of the test (McClanahan 1995b); and (c) a single hole, which is an indication of a gastropod predator, such as *Cassis madagascariensis* (Lamarck) (McClanahan and Muthiga 1989). Ten tethered individuals were placed in wire mesh cages (approximately 25 cm x 50 cm with 1-cm mesh) at 13 of the patch reefs for 3 days (control $n = 130$) to act as controls and for determination of possible artifact effects (Peterson and Black 1994) associated with the handling and piercing procedure. The control individuals were visited daily, and carcass condition was noted as above.

To determine whether the urchin's body size and location in the reef were important factors in determining predation rates, I measured the body size of

a subsample of the tethered individuals with calipers to the nearest millimeter and performed correlations between body size and the predation index. During a second subsample, the position of 274 tethered *E. viridis* was classified as being (a) exposed or out in the open; (b) hidden under seagrass, algae, or soft coral; or (c) within a crevice or burrow. The predation index, for each position that the individual urchin was last recorded in, was calculated and compared by a single classification ANOVA to test the hypothesis that survival decreased with the urchin's exposure. I also examined whether the frequency of the three possible positions changed over time for individuals that were not preyed upon. During this experiment, the individuals were pierced, tethered, and tied to the nylon line and given between 2 and 24 hs to adjust to the tethering. Afterwards, their position was classified, revisited for two additional days, and reclassified if the animal had changed position.

Sea Urchin Predators

The identity of the important daylight predators and scavengers of *E. viridis* was determined by direct daytime (0800 to 1700 h) observations at sites baited with whole and live *E. viridis* (McClanahan 1995b). Adult *E. viridis* were collected from the patch reefs and placed in a floating bucket. I placed 5 to 10 *E. viridis* at the base of the reef (water depth approximately 2 m) and hid behind a coral head or floated on the water surface 5 to 10 m from the baited site. The site was observed for approximately 15 min. If no predators were attracted to the baited site after approximately 3 min, a few urchins were tossed towards the site, to attract fish and predators. This was repeated at approximately 3-min intervals until the end of the 15-min interval. This process and 15-min observation period were repeated at two to six different sites at each patch reef, and results are based on 50 x 15-min observations (12.5 h of observation). During the observation interval, I recorded predator species, the time they first arrived at the baited site, and the number of individuals of each species and estimated the body size of fishes feeding on *E. viridis*. Additionally, I recorded species that attempted to prey but failed and those that scavenged on opened carcasses. Fish active around the baited area therefore were classified into three categories: (a) predator guild: species that break open the sea urchin's body wall; (b) attempted predator guild: species that bit but did not open the body; and (c) scavenger guild: species that bite an already opened sea urchin (McClanahan 1995b). The diversity D of each guild was calculated using a modification of the Simpson's Index where $D = 1 - \sum p_i^2$ and $p_i = n_i/N$, where n_i is the number of

individuals for each species, and N is the total number of individuals across all species.

Herbivory Experiments

Herbivory by sea urchins and fishes were examined in each reef location by using the fleshy algae *Lobophora variegata* ["fluffy ruffles" variety (Littler and others 1989) and *Padina sanctae-crucis* as assays (Hay 1981; McClanahan and others 1994)]. These two species are common to these patch reefs, have different susceptibilities to predators (Hay and others 1983; Lewis 1985), and have completely smooth margins that make it easy to recognize fresh bite marks. Thalli of *L. variegata* were placed on 10 of the patch reefs; *P. sanctae-crucis* was placed on seven reefs. I selected epiphyte-free thalli of approximately 15 to 25 cm² with completely unbitten margins from these two species, attached them to weighted clothespins, left them for approximately 24 h, and examined the margins for bites. Nine assays of each algal species were placed along each of the above line transects. Bites were classified as either sea urchin, fish, or amphipod bites based on the shape of the bites (McClanahan and others 1994). Sea urchins typically leave ragged edges, fish leave elliptical bites with smooth edges, and amphipods leave irregular scars with smooth edges (Hay 1984; McClanahan and others 1994). It is possible that one type of bite was removed or hidden by another type of bite, and therefore this study only considered bites at the final collection period of 24 h. Missing thalli were eliminated from the data analysis. The frequency of bites in each reef location was calculated as a percentage of fish or urchin bites for each of the nine thalli per transect. These frequencies were arcsin transformed before comparing differences among the different reef locations by ANOVA and by the Tukey-Kramer HSD for a posteriori tests (Sokal and Rohlf 1981; Sall and Lehman 1996). The ability of *E. viridis* and herbivorous fishes to control algal abundance on patch reefs was examined by correlating their abundance and herbivory rates on *L. variegata* with the abundance of fleshy algae on each of the 10 patch reefs where the *L. variegata* assay was completed ($n = 10$ reefs).

RESULTS

Benthic Cover

The dominant cover on these patch reefs was fleshy macroalgae (Table 1), which covered approximately 45% of the benthos. *Lobophora* was the dominant genus (Table 2). Fleshy macroalgae were least abundant on the edge of the patch reefs ($P < 0.02$, Tables 1 and 2, Tukey-Kramer HSD), but no statistically significant differences were found for

Table 1. Benthic Cover^a on the 14 Studied Patch Reefs in the Three Reef Locations Where Transects Were Placed

Cover (%)	Patch Reef Position						ANOVA		Tukey-Kramer HSD (P < 0.05)
	Center (n = 14)		Shoulder (n = 14)		Edge (n = 14)		Statistical Test		
	Mean	SD	Mean	SD	Mean	SD	F-value	P-value	
Fleshy macroalgae	51.4	19.8	49.9	11.2	34.7	15.4	4.8	0.01	C < E, S < E
Hard coral	15.5	11.5	28.3	7.3	21.2	8.8	6.6	0.00	C < S
Sand	13.2	18.0	2.8	4.5	19.1	19.6	3.9	0.03	S < E
Calcareous algae	5.5	4.0	4.5	2.9	6.0	3.9	0.7	0.51	NS
Coralline algae	5.8	4.1	5.6	4.1	4.0	4.9	0.7	0.50	NS
Turf algae	4.7	5.2	3.7	3.1	6.4	5.4	1.2	0.31	NS
Sponge	1.4	2.0	0.9	1.3	5.1	4.3	9.0	0.00	C < E, S < E
Gorgonia	1.5	1.6	3.9	2.9	1.8	1.8	5.2	0.01	C < S, S < E
Seagrass	1.1	1.7	0.4	1.2	1.8	3.0	1.5	0.23	NS
Rugosity, m/m	1.22	0.15	1.35	0.14	1.34	0.17	3.2	0.05	NS, t-test = C < S, C < E

C, center; S, shoulder; E, edge. Overall ANOVA and results of the a posteriori Tukey-Kramer HSD statistic (P < 0.05) are given.
^a% $\bar{x} \pm SD$.

Table 2. Cover Percentage of the Major Algal Genera in the 14 Studied Patch Reefs in the Three Locations in the Three Reef Positions

Algae Genera	Patch Reef Position						ANOVA		Tukey-Kramer HSD (P < 0.05)
	Center (n = 14)		Shoulder (n = 14)		Edge (n = 14)		Statistical Test		
	Mean	SD	Mean	SD	Mean	SD	F-value	P-value	
<i>Lobophora</i>	31.9	17.9	14.6	7.6	11.8	11.5	9.7	0.00	C > S, C < E
<i>Dictyota</i>	8.7	5.9	8.8	4.7	8.6	5.2	0.0	1.00	NS
<i>Turbinaria</i>	4.9	4.0	9.4	4.6	3.9	2.7	8.0	0.00	C < S, S > E
<i>Halimeda</i>	3.7	2.5	2.1	1.9	3.5	2.1	2.2	0.13	NS
<i>Dictyosphaeria</i>	2.1	1.9	3.4	2.1	2.4	2.3	1.5	0.24	NS
<i>Sargassum</i>	2.0	2.1	7.9	7.9	4.4	5.5	3.8	0.03	C < S
<i>Padina</i>	0.9	1.3	2.4	2.5	2.0	2.9	1.6	0.22	NS
<i>Amphiroa</i>	0.9	1.3	3.3	2.7	2.1	2.7	3.9	0.03	C < S
<i>Hypnea</i>	0.0	0.2	2.0	3.6	0.9	3.0	1.9	0.16	NS

C, center; S, shoulder; E, edge. Overall ANOVA and results of the a posteriori Tukey-Kramer HSD statistic (P < 0.05) are given.

comparisons of the center and shoulder positions (Table 1). Stony coral was the second most abundant group at approximately 20% cover of the benthos and most abundant on the patch reef shoulder and edges (P < 0.001, Table 1). Other algal groups covered approximately 5% of the bottom (Table 2). The rugosity of these reefs was highest on the reef shoulder and edge and lowest in the center location (t-test, P < 0.05, Table 1).

Sea Urchin Abundance, Distribution, and Patterns of Predation

From control carcass observation, it was possible to distinguish between death caused by tethering and deaths from predation. Control carcasses often were

bleached only around the hypodermic needle hole with the remaining body and coloration intact. Approximately 15% of the tethered urchins in both the control and experimental groups died from the handling and tethering procedure. The high similarity between the patterns of tether-associated mortality between control and experimental animals suggests that there are unlikely to be strong interactive effects between the artifact of intervention (handling and tethering) and the experimental treatment (Peterson and Black 1994). Because it was easy to distinguish tethering and handling from predation mortality, I removed individuals dying from the tethering procedure from the analysis and calculation of the predation index. It is possible that

Table 3. Population Density^a of the Two Most Common Sea Urchins in the Studied Patch Reefs Where Quadrats Were Placed at Center, Shoulder, and Edge Positions

Sea Urchin Species	Center		Shoulder		Edge		Total		Statistical test		Tukey-Kramer HSD ($P < 0.05$)
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	F-value	P-value	
<i>Echinometra viridis</i>	17.5	14.6	48.6	28.6	12.4	9.6	26.2	25.0	43.1	0.00	S > C, S > E
<i>Echinometra lucunter</i>	0.4	1.0	0.5	1.0	0.0	0.0	0.3	1.0	4.4	0.01	S > E

C, center; S, shoulder; E, edge. Overall ANOVA and results of the a posteriori Tukey-Kramer HSD statistic ($P < 0.05$) are given. Three other species were found but only one or two individuals for the 1260-m² area sampled.

^a#/10 m², n = 42 replicates per location.

Table 4. Predation Index and *Echinometra viridis* Position after an Initial Resting Period^a and Carcass Condition in Each of the Three Locations

Patch Reef Position	Predation Index		Position (%)			Carcass Condition (%)			
	Mean	SD	Crevice	Hiding	Open	Gone	Broken	Hole	Total
Center (n = 120)	0.36	0.45	57.4	27.8	14.8	90.2	2.4	7.3	82.5
Shoulder (n = 116)	0.19	0.36	74.1	16.0	9.9	70.0	15.0	15.0	11.1
Edge (n = 124)	0.51	0.46	42.9	39.3	17.9	81.5	15.4	3.1	6.3
F-value	17.18								
P-value	0.00								
Tukey-Kramer HSD, $P < 0.05$; C > S, C < E, S < E									

^a2–24 h.

some urchins died of tethering and then were eaten by a predator, but this error is likely to be much less than the 15% mortality of the tethered urchins and therefore a minimal influence on the total sample.

E. viridis was, by far, the dominant sea urchin on these patch reefs followed by *E. lucunter* Linnaeus. Only one or two individuals of *Diadema antillarum*, *Eucidaris tribuloides*, and *Lytechinus variegatus* were found in the 1260 m² covered by the census plots (Table 3). Nearly 100% of *E. viridis* were found in crevices or hidden under coral rubble or boulders. *E. viridis* was approximately three times more abundant on the patch reef shoulder than on the patch reef edge and center plots ($P < 0.001$, Table 3). The predation index was also lowest on the patch reef shoulders being approximately one-half of the index of the patch reef edge and center plots ($P < 0.001$, Table 4). Correlation between the overall abundance of *E. viridis* and the predation index was not statistically significant, but the scatterplots indicate that predation constrains *E. viridis* populations when intense, but less so at intermediate to low levels of predation (Figure 1a). Of the dead urchins 83% were gone, 11% were broken, and 6% had a single hole in the test. The frequency of broken tests was higher on the reef edge and shoulder sites (15%) than the reef center (2.4%). The frequency

of carcasses with single holes was higher in the center (15%) and shoulder (7.3%) than reef edge locations (3.1%, Table 4).

Correlation of the effect of body size and urchin position suggest that body size ($r^2 = 0.04$, NS) and water depth ($r^2 = 0.03$, NS) were not important factors in determining predation rates for the ranges I measured (an approximately 15-mm range for body sizes and an approximately 1.5-m range for water depth). In contrast, the urchin's position was a strong factor in determining rates of predation ($F = 46.4$, $P < 0.001$, Figure 1b) with the lowest predation on those individuals in crevices and hidden under benthic-attached organisms (mostly algae) compared with those exposed in the open. Most tethered individuals that survived the initial adjustment period moved into crevices (Figure 2a), and those individuals that changed their positions over time moved from positions exposed and hidden under algae to crevices (Figure 2b).

Daytime Sea Urchin Predators

Four species of fish predator were recorded from the 60 observations on individual predators during the 12.5-h observation period (Figure 3). Approximately half of the predator observations were attributable to the jolthead porgy (*Calamus bajonado*

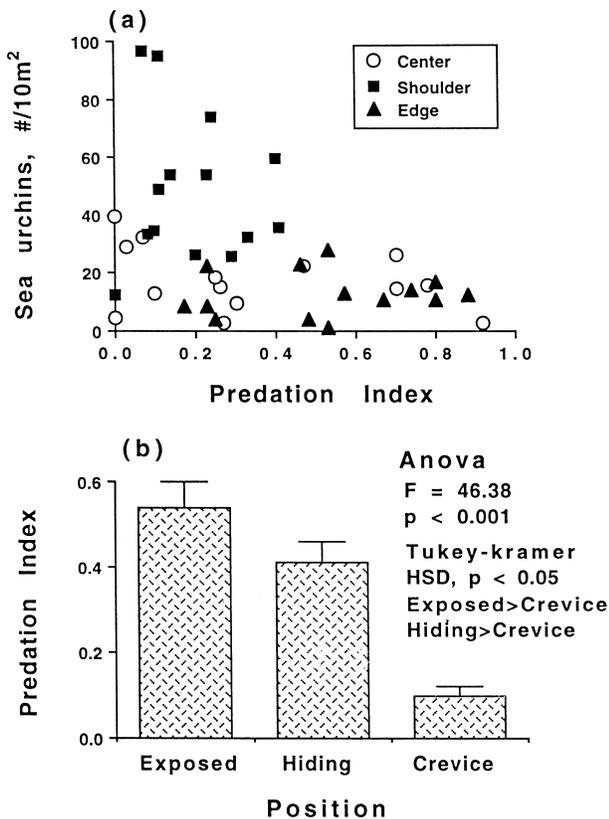


Figure 1. (a) The relationship between the predation index and the abundance of sea urchins in each reef location on the 14 studied patch reefs. (b) Predation index on *Echinometra viridis* in the three possible positions, exposed or out in the open, hidden under a plant or algae, and inside a crevice or burrow (bars are standard error of mean).

Bloch and Schneider) followed by two triggerfish species (*Balistes vetula* Linnaeus = queen triggerfish and *Canthidermis sufflamen* Mitchell = ocean triggerfish) and lastly the hogfish wrasse (*Lachnolaimus maximus* Walbaum). Individuals of each of these species were large, with my estimates of average body lengths ranging from approximately 50 to 65 cm (Table 5). There was no statistically significant difference in the time to arrive of the four species (Table 5). The time taken to finish eating *E. viridis* varied among the species with jolthead porgy having the shortest eating times, followed by the ocean and queen triggerfish, and lastly the hogfish. The jolthead porgy was also the most common of the seven recorded species in the attempted predator guild followed by the white grunt (*Haemulon plumieri*) and the saucereye porgy (*Calamus calamus*) (Figure 3b). A number of species of grunts were often the first species to arrive at the baited site, but none was ever observed eating *E. viridis*, and only *H. plumieri* was seen to occasionally bite them. The scavenger guild contained 10 species of which *Hali-*

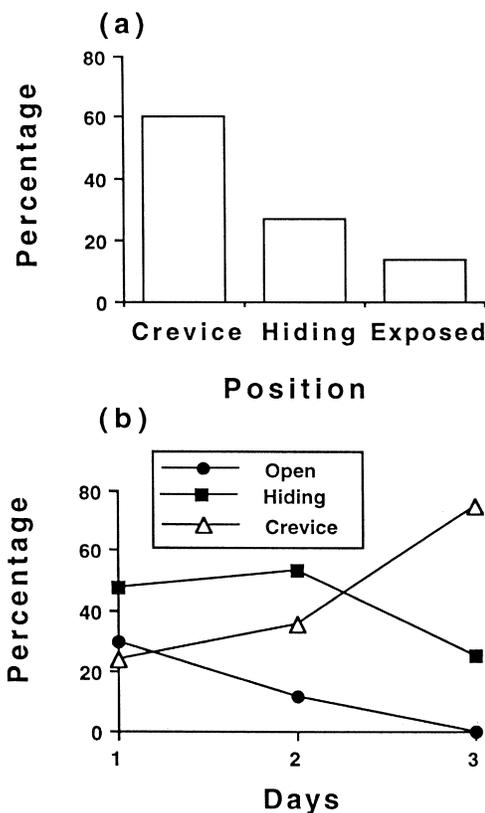


Figure 2. (a) The percentage of tethered individuals in the three possible positions after an initial adjustment period; (b) over a 3-day period for those individuals that were not eaten and changed their position.

choeres spp. and *Thalassoma* spp. wrasses were the dominant species (Figure 3c).

Patterns of Herbivory

Bite frequencies on *Lobophora* and *Padina* thalli differed with the less abundant *Padina* experiencing a greater bite frequency (91.5% ± 14.5 SD) than the dominant fleshy macroalgae *Lobophora* (57.2% ± 28.7 SD). Bite frequencies on *Padina* were not different among reef locations, but for *Lobophora* total bites were highest in the reef edge and lowest on the shoulder and center locations (Table 6, Tukey-Kramer HSD). Sea urchin bites on *Lobophora* were highest on the reef shoulder whereas finfish bites were highest on the reef edge and center positions (Table 6, Tukey-Kramer HSD). Fish were the dominant herbivore type biting the assays, biting 86.6% ± 17.1 of the *Padina* and 53.4% ± 29.9 of the *Lobophora* assays. Sea urchins only bit 8.1% ± 13.7 of the *Padina* and 4.2% ± 7.6 of the *Lobophora* assays, and amphipods had a negligible bite frequency on the assays.

There was a positive relationship between sea urchin population density and fleshy algae abun-

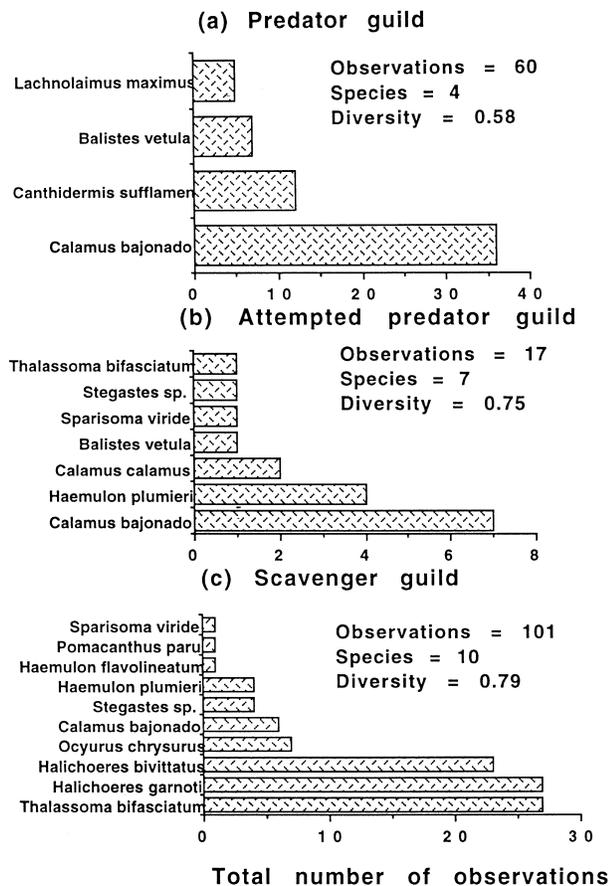


Figure 3. Species of fish that (a) killed and ate, (b) bit but did not open, and (c) bit already opened carcasses of the sea urchin *Echinometra viridis* in baited sites around the patch reefs of Glovers Reef Atoll. Data based on 50 x 15-min interval observations.

dance based on the sea urchin densities studied (1–96 per 10 m²), and the data from the 30 sites (Figure 4a, three locations on 10 reefs). The relationship was strong when pooling site location data into patch reefs ($y = 11.56 + 43.68 \log x$, $r^2 = 0.70$, $n = 10$). The relationship between the frequency of bites by finfish on the *Lobophora* assay and fleshy algae abundance was negative at the highest levels of finfish herbivory, with no clear relationship at low levels of finfish herbivory (Figure 4b). At the whole patch reef scale, the frequency of finfish bites was positively correlated with the rugosity of the reef (Figure 5).

DISCUSSION

Sea Urchin Predators

Randall (1967) reported sea urchin body parts in the gut of 34 species of Caribbean fish, and sea urchins were the principal food of six of these species. Gut

Table 5. Mean Body Sizes of the Observed Predators and Time for Species to Arrive at the Baited Area and to Fully Consume *Echinometra viridis*

Predator Species	Body Size (cm)		Time to Arrival (min)		Time to Eat (min)	
	Mean	SD	Mean	SD	Mean	SD
<i>Balistes vetula</i>	52.9	2.7	5.8	5.3	2.4	1.6
<i>Calamus bajonado</i>	50.3	9.2	4.6	3.9	0.5	0.0
<i>Canthidermis sufflamen</i>	62.1	9.2	1.5	0.7	1.2	0.8
<i>Lachnolaimus maximus</i>	53.0	12.5	8.0	5.2	2.9	1.5
F-value	5.0		1.1		22.0	
P-value	0.0		NS		0.0	

content analysis cannot, however, distinguish predators from scavengers. The results of this study suggest that the scavenger guild is more than twice as species rich as the predator guild. Randall (1967) did note that species with sea urchins as a small part of their gut content were more likely to be scavengers than predators. His reported top six predators included *Haemulon macrostomum* (Gunther, Spanish grunt), *Balistes vetula* (queen triggerfish), *Anisotremus surinamensis* (Bloch, black margate), *Calamus bajonado* (jolthead porgy), *Diodon hystrix* (Linnaeus, porcupinefish), and *Canthidermis sufflamen* (ocean triggerfish). My observations differ in that I observed no Spanish grunt, black margate, or porcupine fish. The lack of observations on these three species may be attributable to either their nocturnal foraging or their rarity in this region of the Caribbean (J. Carter, personal communication). A similar study on sea urchin predators in East Africa found eight species of predator and 18 species of scavenger (McClanahan 1995b) whereas a comparable study from the northwest Mediterranean found six predators and 17 species of scavengers (Sala 1997). All studies suggest that the number of species able to kill urchins is smaller than those that feed on carcasses.

My method for studying sea urchin predators also suffers from possible biases associated with daytime sampling of exposed sea urchins in the presence of a human observer. The method is likely to bias results towards daytime predators that are vagile, opportunistic, and brave. This may explain the dominance of *C. bajonado* as a predator compared with the two species of triggerfish, as *C. bajonado* is a vagile predator often foraging in sand-dominated ecosystems (H. Lessios, personal communication). Further-

Table 6. Herbivory^a on Two Genera of Fleshy Macroalgae Three Locations for 24 Hours

Assay Genus/ Bites (%)	Patch Reef Position						ANOVA		Tukey-Kramer HSD <i>P</i> < 0.05
	Center		Shoulder		Edge		Statistical Test		
	Mean	SD	Mean	SD	Mean	SD	<i>F</i> -value	<i>P</i> -value	
<i>Padina</i> patch reef ^b									
Total bites	95.2	12.6	82.7	22.6	96.6	5.8	1.7	0.20	NS
Urchins	11.9	20.9	8.1	12.4	4.8	12.6	0.4	0.70	NS
Finfish	83.3	21.5	79.4	23.5	96.6	5.8	1.6	0.22	NS
<i>Lobophora</i> patch reef ^c									
Total bites	56.1	30.8	31.3	25.2	84.2	15.5	11.5	0.00	C < E, S < E
Urchins	1.1	3.5	11.4	11.8	0.0	0.0	7.9	0.00	C < S, S > E
Finfish	55.0	31.0	21.0	15.9	84.2	15.5	20.6	0.00	C < E, C > S, S < E

^aPercentage bitten per day.

^bn = 7.

^cn = 10.

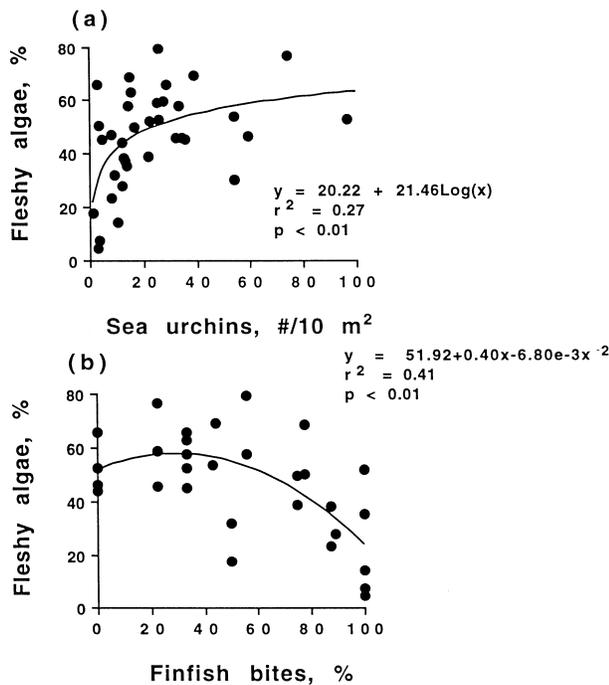


Figure 4. The relationship between a sea urchin abundance and fleshy algal abundance and b the finfish bite rate on *Lobophora* and the abundance of fleshy algae based on three locations in the 10 patch reefs where the *Lobophora* assay experiment was completed.

more, I found that *L. maximus* (hogfish) was present and fed at my baited sites whereas Randall (1967) reported that this species' main diet is molluscs with echinoids being approximately 5% of their diet. Perhaps this species is able to feed on *E. viridis* when exposed but less so when they are hidden in crevices. The method used in this study is good at determining potential predators but perhaps less effective in distinguishing the relative frequency of

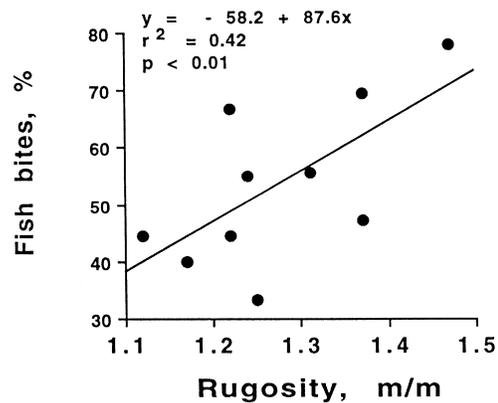


Figure 5. The relationship between rugosity of the patch reef and the bite frequency on *Lobophora* by finfish pooling data from the three locations on the 10 patch reefs where the *Lobophora* assay experiment was completed.

actual predators under the more likely conditions of *E. viridis* living in burrows. There also may be seasonal patterns in the abundance of predators that were not addressed by this study.

Predators observed in this study were all generally large individuals (greater than 35 cm in length) but differed in their feeding behavior as suggested by the time required to eat *E. viridis*. The two species of triggerfish ate slowly and carefully. I found a similar eating pattern for the dominant triggerfish predator in East Africa, *Balistapus undulatus* (Park), and suggest that this is an attribute of site-attached, territorial, and experienced predators (McClanahan 1995b). It would appear that triggerfish that feed on sea urchins exhibit similar behaviors in different ocean basins and are, arguably, well-adapted to feeding on sea urchins. They therefore may be more

important predators than *C. bajonado* when urchins are living in burrows.

Sparids, some labrids, and haemulids, however, may be more vagile and social and perhaps less-experienced sea urchin predators. This behavior may explain their rapid consumption of the experimental urchins (McClanahan 1995b; Sala 1997). The most social species, the jolthead porgy, often arrived in groups and ate the fastest. This may be their response to intraspecific competition found within social groups (McClanahan 1988; Sala 1997). Similarly the sparids *Diplodus sargus* (Linnaeus) and *D. vulgaris* (Geoffrey Saint-Hilaire) in the Mediterranean arrive in groups and quickly consume sea urchins (less than 90 s; Sala 1997). *C. bajonado* and *L. maximus* frequently bite and consume *E. viridis* whole and leave little trace of the test. The more solitary *L. maximus* and *B. vetula* (sometimes seen in pairs) were, however, the shyest of the species and had the longest arrival times. This behavior may have been due to the presence of the observer or low population density rather than an inability to find and handle their prey. These two species are also among the target species of spearfishermen on these patch reefs (C. Acosta, personal communication). *L. maximus* had slow consumption times largely because of this shy behavior. They often consumed *E. viridis* in a single bite, but before this they often would nip at the urchin and observe me for some time before quickly consuming the sea urchin.

Carcass condition of tethered *E. viridis* and direct observations suggest that the main predators of adult *E. viridis* were *C. bajonado*, the two species of triggerfish, *L. maximus*, and predatory gastropods, probably *Cassidulus madagascariensis* (T. McClanahan, personal observation). Other species, such as wrasses, may be important predators of juvenile and smaller sea urchins (Sala 1997). Predatory gastropods were more important in the shallower reef center and shoulder than reef edge location. This contrasts with Levitan and Genovese's (1989) findings that the gastropod *Cassidulus tuberosus* (Linnaeus) fed mostly on *D. antillarum* in exposed sandy bottoms. Although *E. viridis* seldom moves outside of its burrows, it still is preyed on by gastropods. This suggests that *C. madagascariensis* is not restricted to sandy bottoms and does forage on hard-bottom patch reefs. Sea urchin tethering experiments in East Africa (McClanahan and Muthiga 1989) and northwest Mediterranean (Sala and Zabala 1996) also found that predatory gastropods ate less than 10% of the experimental urchins. In both cases, greater gastropod predation was found in the fished areas. These studies suggest that finfish are the dominant predators of shallow-water sea urchins, and in their

absence or low abundance, there is a minor compensation by predatory gastropods. In undisturbed tropical reefs, triggerfish (mostly species in the genera of *Balistapus*, *Balistes*, *Balistoidea*, *Pseudobalistes*, and *Canthidermis*) are probably the dominant predators, but their populations appear to be affected by even light to moderate fishing. In their absence a variety of labrids, sparids, lethinids, or haemulids may become more dominant predators (McClanahan 1995b, unpublished data).

Predator Avoidance of *E. viridis*

E. viridis were nearly always observed in crevices in the day and night, and when physically moved out of crevices they usually moved under algae or back into a crevice. Tethering experiments suggest that this is a predator-avoidance response as the predation rates on *E. viridis* in crevices was considerably lower than for those hidden under benthic-attached organisms or exposed. Parker and Shulman (1986) found that even the presence of body fluids of a damaged neighbor could cause *Echinometra* to retreat into burrows. Increased body size and decreased water depth appeared to be much weaker factors in deterring predators within the relatively small range of variation I measured. A previous study of *E. mathaei* showed that increased body size was weakly correlated with predation whereas water depth was a strong factor in an old marine protected area but not in heavily fished reefs (McClanahan and Muthiga 1989). Body size and water depth therefore are weaker predator-avoidance factors than crevice or burrow habitation, particularly in these shallow patch reefs.

E. viridis appeared to exhibit lower levels of agonistic behavior than described for *E. mathaei* and *E. lucunter* (Grunbaum and others 1978; McClanahan and Kurtis 1991). *E. viridis* often were found living close together within large crevices or under corals and less frequently found in the single-occupant burrows, as commonly described for other species of *Echinometra*. Nonetheless, crevice occupation appears to be a dominant adaptation of species in this relatively small-bodied and short-spined genus compared with the larger-bodied and spined species of *Diadema*. *Diadema* also occupy crevices, albeit larger, but adults move out or live entirely outside of crevices (Williams 1981; Carpenter 1984; McClanahan 1988). *E. mathaei* has been described as living outside of crevices but only on reefs with very low levels of predation (greater than 100 individuals per 10 m²; McClanahan and Kurtis 1991). *E. viridis*, however, are largely restricted to crevices at the moderate levels of predation and population density found in the Glovers reef patch reefs.

I suggest that this difference in crevice fidelity, size, and duration of occupation, associated with different levels of tolerance to predation, produces relatively little ecological overlap between species in the two genera of *Diadema* and *Echinometra*. *Echinometra* largely feed in crevices and cryptic locations whereas *Diadema* feed in more exposed areas (McClanahan 1988). *Echinometra* is able to occupy the more exposed *Diadema* niche only at the very lowest levels of predation (McClanahan and Kurtis 1991; McClanahan 1998), and consequently the loss of *Diadema* seldom may be compensated by the presence of *Echinometra*. Aronson and Precht's (1997) studies on a cay of the Belizean barrier reef found that the disease-induced loss of the sea urchin *D. antillarum* and coral *Acropora cervicornis* resulted in a switch in coral dominance to *Agaricia tenuifolia*, with *E. viridis* population densities between 4 and 10 individuals/m², and moderate increases in erect algae (McClanahan and others 1999). This contrasts markedly with the findings presented here where nearly the same *E. viridis* population densities were associated with much larger increases in erect algae (this study; McClanahan and Muthiga 1998). Algal overgrowth on Glovers Reef Atoll was restricted to lagoonal patch reefs, whereas fore reef environments, which lack *E. viridis* populations below 1 m, were unchanged by recent diseases (McClanahan and Muthiga 1998; McClanahan and others 1999). Consequently, differences in the abundance of erect algae may be more attributable to habitat features than *E. viridis* populations. Deeper fore reefs may have lower algal production and greater losses due to disturbance caused by lower light levels, greater herbivory by fishes, currents and waves, and saltating sediments.

E. viridis distributions may not entirely reflect predation pressure, however, because reef complexity and perhaps water flow also may influence distributions. *E. viridis* populations were most abundant in the shallow patch reef shoulder position where water flow and algal drift are likely to be most abundant. Casual examination of damaged *E. viridis* indicated guts that were not at full capacity and low fractions of calcium carbonate. This suggests some reliance on drift algae. The reliance of *E. viridis* on drift versus attached algae may illuminate the surprising positive relationship between *E. viridis* and erect algae.

Control of Fleshy Algal Abundance

Fleshy brown algae were the dominant cover on these patch reefs despite their remote location (McClanahan and Muthiga 1998). McClanahan and Muthiga (1998) found that patch reef alga increased by approximately 350% over the past 25 years,

associated with the above-mentioned diseases (Lesios 1988b; Aronson and Precht 1997). In addition, increases in fishing pressure or nutrients may have contributed to this change but are at moderate levels. McClanahan and Muthiga (1998) crudely estimated fishermen densities to be low, between 0.1 and 1.0 people per km². Measured nitrate–nitrogen concentrations are variable between 0.1 and 3.1 M whereas phosphorus is less variable, approximately 0.35–0.40 M (P. Mumby, unpublished data). These nutrient concentrations are above the coral reef eutrophication threshold suggested by some authors (P, 0.1 M; N, 1.0 M; Bell 1992; Lapointe and others 1997), but this threshold is of limited value because many of the earth's most remote reefs have concentrations exceeding the thresholds (Smith and Jokiel 1978; Johannes and others 1983; Raynor and Drew 1984; Chavez and others 1985; Wafar and others 1985), and few of these reefs historically have been macroalgal dominated. The population density of the grazer *D. antillarum* on Glovers Reef, before the disease, is not known, and so it is difficult to determine their previous role in controlling fleshy brown algae. Nonetheless, the present level of herbivory on open surfaces by sea urchins is low, and fleshy algae actually appear to increase with increased abundance of sea urchins up to the maximum recorded sea urchin density (96 individuals per 10 m² per patch reef location). Consequently, there is no indication that *E. viridis* populations are able to control fleshy algae and net primary productivity as has been documented for *D. antillarum* (Carpenter 1981, 1988, 1990a; Sammarco 1982; Foster 1987; Hughes and others 1987; Levitan 1988; Morrison 1988). *E. viridis*' cryptic behavior and possible reliance on drift algae may contribute to the poor relationship between them and exposed erect algae abundance. *Echinometra*, however, may be better able to control algae and associated production in cryptic or crevice locations. It is notable that Jackson and Kaufmann (1987) found no change in the cryptofauna associated with the demise of *D. antillarum*, and, perhaps, cryptic grazers like *E. viridis* played a role in maintaining this ecological structure.

The cause for this unexpected positive relationship between fleshy algae and sea urchin abundance is unknown but provocative. Perhaps both fleshy algae and *E. viridis* abundance are measures of reef degradation due to overfishing and the loss of fish consumers on these reefs. Szmant (1997) suggested that the maintenance of feeding groups and reef complexity are more important than nutrient availability in maintaining coral rather than algal-dominated reefs. My data supports this hypothesis

in that herbivorous fish constituted the greatest fraction of herbivory, and that reef complexity was closely associated with finfish herbivory. Herbivorous fishes are caught (J. Asueno, M. Paz, and A. Avilez personal communications) but are not the focus of efforts in this region (J. Carter and C Acosta, personal communications). Consequently fishing is culpable only if its effects are manifested at low levels (Jackson 1997). Alternatively, the loss of reef complexity, through the *A. cervicornis* white-band disease, may have caused the demise of herbivorous fishes and their contribution to herbivory. Some of the studied patch reefs were recently gazetted within the Belizean marine protected area network, and future studies of their ecological response to reduced fishing should help distinguish the roles of fishing, fish consumers, algal drift, and reef complexity in controlling sea urchins and algae abundance.

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