

Jocelyn Brown-Saracino · Paulette Peckol
H. Allen Curran · Martha L. Robbart

Spatial variation in sea urchins, fish predators, and bioerosion rates on coral reefs of Belize

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Abstract Although sea urchins are critical for controlling macroalgae on heavily fished coral reefs, high densities threaten reefs, as urchins are also prodigious bioeroders. This study examined urchin population characteristics, bioerosion rates, their fish predators (Labridae), and potential competitors (Scaridae) on unprotected reefs and a reef within a marine protected area (MPA) in the lagoonal regions off Belize. Urchin density ($<1\text{ m}^{-2}$) and bioerosion rates ($\sim 0.2\text{ kg CaCO}_3\text{ m}^{-2}\text{ year}^{-1}$) were lowest and members of the Labridae were the highest ($\sim 20\text{ fish }200\text{ m}^{-3}$) within the MPA, while several unprotected reefs had higher ($\sim 18\text{--}40\text{ m}^{-2}$) urchin densities, lower Labridae abundances ($1\text{--}3\text{ fish }200\text{ m}^{-3}$), and bioerosion rates ranging from $\sim 0.3\text{--}2.6\text{ kg CaCO}_3\text{ m}^{-2}\text{ year}^{-1}$. Urchin abundances were inversely related to Labridae (wrasses and hogfish) densities; however, on reef ridges, low algal cover ($\sim 15\%$), small urchin size ($\sim 14\text{ mm}$), and low proportion of organic material in urchin guts suggested food limitation. Both top-down (predation) and bottom-up factors (food limitation) likely contribute to the control of urchins, predominantly *Echinometra viridis*, off Belize, thereby potentially diminishing the negative impacts of bioerosion activities by urchins.

Keywords Belize · Bioerosion · Coral reefs · Mesoamerican Barrier Reef · Overfishing · Sea urchins

Introduction

Over the past several decades coral reefs worldwide have been in a state of decline. Natural (e.g., hurricanes, El Niño episodes) and anthropogenic (e.g., pollution, overfishing) disturbances have disrupted the complex balance of these ecosystems and led to large-scale reductions in fish populations, massive declines in live coral cover, and increases in macroalgal cover on reefs (Wilkinson 2000, 2002; Aronson et al. 2002b).

Declines in reef fish populations due to heavy fishing pressure have resulted in increases in sea urchin populations in many regions of the world (McClanahan 1987, 1997; Hughes 1994; McClanahan et al. 1999). McClanahan (1997) found that urchin abundances were two orders of magnitude greater on unprotected reefs than on reefs protected from fishing, and predation by fish on urchins was three times more intense at protected sites. On reefs off Kenya, lower urchin abundances were correlated with the length of time a reef had been protected (Carreiro-Silva and McClanahan 2001). These studies suggested that fish predators exert a strong top-down control on urchins.

On reefs with reduced herbivorous fish populations owing to overfishing, grazing by urchins becomes critical to maintaining low macroalgal cover (Sammarco et al. 1974; Carpenter 1981; Sammarco 1982). However, these areas are then subject to higher rates of bioerosion by urchins (Reaka-Kudla et al. 1996; Carreiro-Silva and McClanahan 2001). Consequently, the shift from fish to sea urchins as the dominant herbivore has such a large impact on the health of coral reef ecosystems that variation in urchin abundance is the major difference between pristine and degraded reefs in many regions of the world (McClanahan 1987).

In recent decades, the Mesoamerican Barrier Reef System (MBRS) off Belize has experienced several large-

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J. Brown-Saracino · P. Peckol (✉)
Department of Biological Sciences, Smith College,
Northampton, MA 01063, USA
E-mail: ppeckol@email.smith.edu
Tel.: +1-413-5853844
Fax: +1-413-5853786

H. Allen Curran
Department of Geology, Smith College,
Northampton, MA 01063, USA

M. L. Robbart
PBS&J Environmental Services,
2001 Northwest 107th Avenue,
Miami, FL 33172, USA

scale disturbances (e.g., hurricanes, thermal anomalies), increased fishing pressures (Carter et al. 1994), and burgeoning urchin densities. Two severe coral bleaching events in the 1990s due to elevated sea-surface temperatures resulting from ENSO (El Niño-Southern Oscillation) episodes (McField 1999; Mumby 1999; Aronson et al. 2000) have contributed to a general degradation of the MBRS (McClanahan and Muthiga 1989; McClanahan et al. 2001; Aronson et al. 2002a, b; Peckol et al. 2003). The urchin *Diadema antillarum* occurred in very low abundances on patch reef and shallow fore reef areas off Belize even prior to its mass-mortality event of the early 1980s, and other urchin species were notably absent from earlier surveys (Hay 1984; Lewis and Wainwright 1985). More recently, *Echinometra viridis* has been the most abundant urchin species of the shallow lagoonal regions off southern Belize (Aronson et al. 2002a) and most likely for the northern reefs as well. High population abundances ($\sim 20\text{--}100$ urchins m^{-2}) of *Echinometra* spp. have been connected to bioerosion and consequent reef damage at a number of locations beyond Belize (e.g., Ogden 1977; Glynn 1988; McClanahan and Muthiga 1988). Further, at elevated densities, sea urchins may negatively affect herbivorous fishes, i.e., parrotfishes, because scarids feed directly on coral substrata (Carpenter 1990; McClanahan 1992).

Changes in reef conditions on the MBRS and in the importance of *E. viridis* as a major herbivore allowed a unique opportunity to examine population characteristics of this grazer and bioeroder on several lagoonal reefs in northern and south-central Belize. This study compared density and size of urchins, and estimated rates of bioerosion on unprotected reefs and a reef within a marine protected area (MPA). Abundance patterns of fish predators (wrasses), and potential competitors (parrotfishes) of urchins were studied; an inverse relationship between fish predators and urchin densities was predicted.

Materials and methods

Study sites

Off Belize, the MBRS consists of a forereef area and an extensive lagoonal area (Macintyre and Aronson 1997). In the south-central region of the reef system, there is a complex network of steep-sided, rhomboidal-shaped shoals and reefs (Macintyre and Aronson 1997; Macintyre et al. 2000) herein referred to as coral reef ridges. The most recent space-dominant coral species at these sites included *Agaricia tenuifolia* (Aronson et al. 2000, 2002a, b). Wee Wee, Peter Douglas, and Tunicate Cove ridges (no sites protected from fishing; Fig. 1) were surveyed at depths from 2 to 10 m. The patch reefs surveyed included northern sites off Ambergris Caye (Mexico Rocks, San Pedro, and Hol Chan, located within the Hol Chan Marine Reserve established in 1987), Caye Caulker (Mitchell Rocks and Coral Gardens), and sites in the

south-central region off Belize (Bread and Butter, Wee Wee patch, and Norvall; Fig. 1). Only Hol Chan was protected from fishing. All patch reefs surveyed were dominated by the coral *Montastraea annularis* (Peckol et al. 2003), and sampling occurred at depths of 2–6 m. More detailed study site locations and descriptions are given in Peckol et al. (2003).

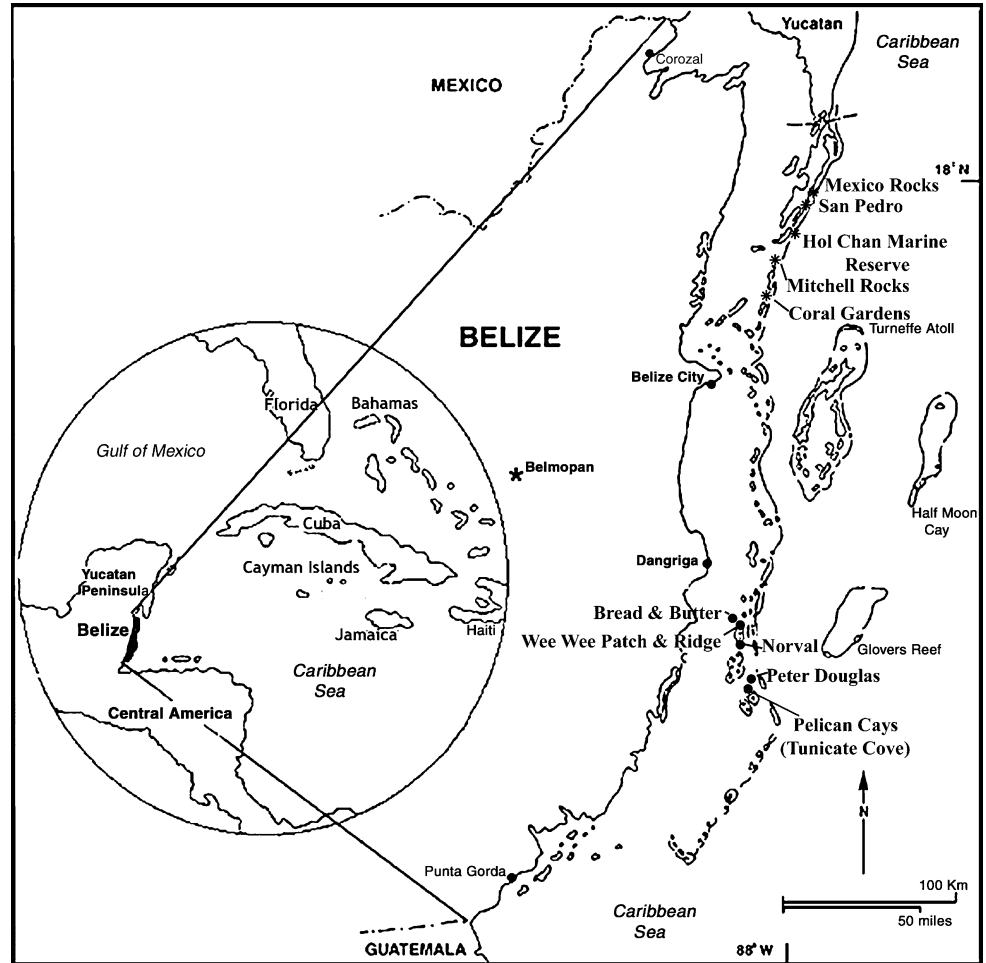
Population characteristics

Population data on corals and algae were collected during June 2002 and 2003 using the Atlantic Gulf rapid reef assessment (AGRRA) protocol with some modifications (Kramer and Lang 2003; Peckol et al. 2003). Ten-meter transect lines (7–15 transects per site) were positioned haphazardly on the reef surface parallel to direction of reef growth (8–10 m apart) along the reef ridges and patch reefs. The following information was collected for all corals under the transect lines: genus and species of coral (identifications from Humann and DeLoach 2002a), water depth, maximum colony diameter, and percent of colony dead. To express percent live coral cover each transect was considered a replicate. Because an estimate of 10% live cover of small versus large coral colonies can represent quite different amounts of live coral cover, percent live cover estimates were adjusted for colony diameter (percent of colony alive \times colony diameter). The sum of the adjusted percent live cover estimates was expressed as a percentage of the 10 m transect. Reported percentages thus reflect the overall (total) live coral cover along replicate 10 m transects. Algal cover (percent macroalgae, crustose coralline, and turf functional groupings) was recorded in quadrats ($=0.063 \text{ m}^2$) placed approximately every meter near the transects on areas with $>80\%$ coverage by algae of any functional group ($n = 60\text{--}90$ per site).

Population data on urchins were determined within quadrats (0.25 m^2 , $n = 20\text{--}35$ per site), 3 m apart along haphazardly placed 10 m transects. Urchin species, density, and test diameter (to the nearest millimeter using Vernier calipers) were recorded.

Fish populations were surveyed using a stationary visual technique (Bohnsack and Bannerot 1986). Data were collected between the hours of 1000 to 1500 for each site. Divers surveyed a 7.5 m radius cylinder, rotating to observe all individuals within the region ($n = 8\text{--}10$ cylinders per site). Censuses began 3 min after a transect line was placed to demarcate the radius. All fishes observed within a 15-min interval were counted and all species belonging to nine families [Acanthuridae (surgefishes), Balistidae (triggerfishes), Chaetodontidae (butterflyfishes), Haemulidae (grunts), Labridae (wrasses and hogfish), Lutjanidae (snappers), Pomacentridae (angelfishes), Scaridae (parrotfishes), Serranidae (groupers)] were identified using the Humann and DeLoach guide (2002b) for total fish abundances. When schools of fish entered the radius they were counted immediately. Large schools were counted by the 10 s and 50 s when necessary. This report presents results of densities of members of the Balistidae and Labridae (predators of

Fig. 1 Belize barrier reef and lagoon system of the Mesoamerican Barrier Reef showing locations of survey areas. Asterisks and bullets indicate northern and southern sites, respectively



urchins, McClanahan 1995, 2000), as well as Scaridae (potential competitors of urchins, McClanahan 1992, 1994).

Urchin gut analysis

Specimens of *E. viridis*, the most abundant urchin species at all but one site, were collected haphazardly ($n = 6-12$) from each site by the hour of 1000 and immediately preserved in 8% formalin-seawater solution. Prior to dissection, wet weight and test diameter of each urchin were recorded. Urchin gut contents were analyzed using the methods of Carreiro-Silva and McClanahan (2001). Gut contents were separated from the intestine wall with repeated rinses with water, and each sample was examined under a dissecting microscope to ensure that all urchin tissue was removed. Gut contents were dried at 70°C for 24 h and weighed, then transferred to a 500°C oven for 5 h to combust the organic material. The samples were weighed again and the difference in weight prior to and after combustion was used as a measure of the organic material in each sample. Hydrochloric acid (5%) was then used to dissolve the calcium carbonate from the samples. The samples were allowed to dissolve until all visible reaction had stopped (~1 h), and then were filtered and dried for 24 h at 70°C. The difference in

the weight prior to and after dissolution was used as a measure of the amount of calcium carbonate in the guts of the urchins. The remaining gut contents were considered as non-calcium carbonate inorganic portion (e.g., siliceous sponge spicules, quartz grains, and silt).

Bioerosion estimates

Yearly urchin bioerosion rates per square meter of reef were estimated using the data obtained in the gut content analyses along with urchin test diameters and density measurements for each site following methods of Carreiro-Silva and McClanahan (2001). Individual urchin test diameters taken from surveys were converted into biomass estimates using the equation ($y = 0.0009x^{2.746}$) obtained from the relationship ($n = 56$, $R^2 = 0.97$, ANOVA, $F = 495.1$, $P < 0.0001$) between test diameter and weight of the sampled urchins. Urchin biomass was then summed for each quadrat and adjusted to gram per square meter. The relationship ($y = 0.017 + 0.014x$) between individual urchin biomass and calcium carbonate in the urchin guts ($n = 52$, $R^2 = 0.67$, ANOVA, $F = 101.9$, $P = 1.2E-13$) was used to calculate bioerosion rates on the reefs. Because of the difference in size between *D. antillarum* (large) and other urchin species (smaller) surveyed in this study, bioerosion

rates for *D. antillarum* were determined following equations of Scoffin et al. (1980), and these values were added to those of other urchin species for site estimates ($\text{kg CaCO}_3 \text{m}^{-2} \text{year}^{-1}$).

Previous efforts to quantify the amount of algae and calcium carbonate consumed daily by urchins have used rates of gut evacuation as a measure of consumption. Carreiro-Silva and McClanahan (2001) found that the gut evacuation rate for *Echinometra* spp. ranged from ~14 h (for urchins ~37 mm in diameter) to 21 h (for urchins ~104 mm in diameter), and for *Diadema* spp. ~24 h (urchins ~69 mm in diameter). Thus, calculated bioerosion rates in the present study represented a range (12 and 24 h rates of gut evacuation) for all urchin species except *D. antillarum*; bioerosion rates for this species were based on an assumption of a single daily gut turnover.

Statistical analysis

One-way analysis of variance (ANOVA) was used to compare means of urchin densities, size, and bioerosion rates, and for fish (Labridae and Scaridae) abundances; a two-tailed *t* test was used to compare means of percent organic content found in urchin guts collected from patch reefs and reef ridge sites. The Tukey–Kramer test was used to make multiple comparisons among means from significant ANOVA tests. When data were not normally distributed as detailed in Quinn and Keough (2002), transformed values were used for the ANOVAs. Square-root or log transformations were applied as recommended by Sokal and Rohlf (1981). Regression analysis was used to explore the relationship between fish abundance (Labridae and Scaridae) and urchin density. To highlight the link between urchins and Labridae densities, the potentially interactive effect of percent coral cover was removed by stratification of sites into high and low (<40%) live coral cover (Rothman and Greenland 1998; N. Horton, personal communication).

Results

Coral and algal abundance

Although Hol Chan Marine Reserve had amongst the highest percentages of live coral cover (>43%), several other northern (unprotected) patch reefs, including San Pedro and Coral Gardens, showed similar values (Table 1). Percent live coral cover at patch reef sites ranged from ~20% (Mexico Rocks) to over 50% (Bread and Butter). Coral reef ridges (Wee Wee, Peter Douglas and Tunicate Cove, all sites not protected from fishing) were characterized by less than half (~11–25%) of the live coral cover of most patch reefs. Low coral cover at Tunicate Cove ridge reflected the lack of coral recovery at this site following the 1998 mass mortality of *A. tenuifolia* (Aronson et al. 2000). Encrusting sponge cover, primarily *Chondrilla* cf. *nucula* Schmidt, exceeded 50% on dead coral substrata at this site.

The percent cover of algae (macroalgal and turf functional groups combined) ranged from ~60% (Bread and Butter) to nearly 100% on northern and south-central patch reefs (Table 1). Little variation in algal abundance at the ridge sites was found, but cover was much lower on reef ridges (~15%) than on patch reefs.

Urchin population characteristics

Six species of urchins were found at the study sites, including *D. antillarum*, *Echinometra lucunter*, *E. viridis*, *Eucidaris tribuloides*, *Lytechinus variegatus*, and *L. williamsi* (Table 2). The rock urchin *E. viridis* was the dominant species at all patch reef (except San Pedro) and reef ridge sites surveyed. *Diadema antillarum* was found in low abundances, and only at northern sites. *Echinometra viridis* was the single urchin species observed on the reef ridges. Total urchin densities varied significantly among sites (ANOVA, $F = 29.7$, $P < 0.001$) ranging from ~1 m^{-2} (Hol Chan Marine Reserve) to 40 m^{-2} at Tunicate

Table 1 Sample sizes and percent live coral and algal cover (mean \pm SE) on patch reef and reef ridge sites off Belize

Sites	Coral		Algae (% cover)		
	No. of transects	Cover (%)	No. of quadrats	Macroalgae	Turf
Northern					
Mexico Rocks	15	22.3 \pm 1.8	90	28.8 \pm 2.3	68.5 \pm 2.3
San Pedro	7	46.9 \pm 6.4	80	8.9 \pm 1.8	62.4 \pm 4.4
Hol Chan (MPA)	15	43.6 \pm 3.5	90	12.1 \pm 2.3	78.6 \pm 2.1
Mitchell Rocks	9	33.9 \pm 6.7	80	30.7 \pm 2.9	67.8 \pm 2.9
Coral Gardens	10	41.1 \pm 6.3	80	8.3 \pm 1.7	83.7 \pm 2.8
Southern					
Bread and Butter	10	52.3 \pm 4.6	60	15.0 \pm 3.1	46.5 \pm 6.0
Wee Wee Patch	10	30.3 \pm 4.4	60	21.6 \pm 4.5	65.1 \pm 5.6
Norvall	10	42.5 \pm 6.7	60	11.6 \pm 2.9	52.9 \pm 4.8
Wee Wee Ridge	10	21.5 \pm 1.9	60	13.1 \pm 3.4	3.3 \pm 2.0
Peter Douglas Ridge	10	24.5 \pm 4.7	60	14.4 \pm 2.8	1.6 \pm 1.1
Tunicate Cove Ridge	11	11.5 \pm 2.2	78	12.9 \pm 2.4	0.4 \pm 0.3

Table 2 Mean (\pm SE) urchin densities (number m^{-2}) at patch reef and reef ridge sites off Belize

Sites	<i>Diadema antillarum</i>	<i>Echinometra lucunter</i>	<i>Echinometra viridis</i>	<i>Eucidaris tribuloides</i>	<i>Lytechinus variegatus</i>	<i>Lytechinus williamsi</i>	Total
Northern							
Mexico Rocks	0.5 \pm 0.2	0.3 \pm 0.2	16.8 \pm 2.4	0 \pm 0	0.1 \pm 0.1	0.1 \pm 0.1	17.6 \pm 2.6b
San Pedro	1.1 \pm 0.4	1.9 \pm 0.5	0.8 \pm 0.3	2.7 \pm 0.6	0 \pm 0	0 \pm 0	6.5 \pm 1.5c
Hol Chan (MPA)	0.2 \pm 0.1	0.1 \pm 0.0	0.5 \pm 0.2	0.1 \pm 0.1	0 \pm 0	0 \pm 0	0.8 \pm 0.2c
Mitchell Rocks	0.3 \pm 0.2	0.5 \pm 0.2	11.1 \pm 1.6	0.6 \pm 0.2	0 \pm 0	0 \pm 0	12.5 \pm 1.8b
Coral Gardens	0.1 \pm 0.1	0.2 \pm 0.1	16.8 \pm 1.6	0.3 \pm 0.2	0 \pm 0	0 \pm 0	17.3 \pm 1.4b
Southern							
Bread and Butter	0 \pm 0	0 \pm 0	32.8 \pm 6.6	0 \pm 0	0 \pm 0	0 \pm 0	32.8 \pm 6.6ab
Wee Wee Patch	0 \pm 0	0 \pm 0	30.0 \pm 6.2	0 \pm 0	0 \pm 0	0 \pm 0	30.0 \pm 6.2ab
Norvall	0 \pm 0	0 \pm 0	24.8 \pm 3.5	0.3 \pm 0.3	0 \pm 0	0 \pm 0	25.0 \pm 3.6ab
Wee Wee Ridge	0 \pm 0	0 \pm 0	17.8 \pm 3.6	0 \pm 0	0 \pm 0	0 \pm 0	17.8 \pm 3.6b
Peter Douglas Ridge	0 \pm 0	0 \pm 0	31.6 \pm 5.4	0 \pm 0	0 \pm 0	0 \pm 0	31.6 \pm 5.4ab
Tunicate Cove Ridge	0 \pm 0	0 \pm 0	40.0 \pm 7.2	0 \pm 0	0 \pm 0	0 \pm 0	40.0 \pm 7.2a

Total means not designated by the same letter are significantly different ($P < 0.05$, Tukey–Kramer)

Cove. Southern patch reefs showed no significant site variation in urchin densities ($\sim 30 m^{-2}$).

Urchins ranged in average diameter from ~ 13 to 34 mm in test size at patch reef and ridge sites (Table 3). Several of the northern sites, including Hol Chan Marine Reserve, had the largest urchins (ANOVA, $F = 45.3$, $P < 0.0001$, Tukey–Kramer < 0.05) due to a relatively high proportion of *D. antillarum* ($\sim 25\%$ of urchins surveyed at Hol Chan, Table 2). Average test diameters for urchins on the reef ridges (Wee Wee ridge, Peter Douglas, and Tunicate Cove) were significantly smaller (Tukey–Kramer, $P < 0.05$) than urchins on patch reefs.

Fish abundance

Total fish abundance varied greatly among sites, ranging from ~ 25 to 145 individuals $200 m^{-3}$ (Table 4). Several of the patch reef sites, including Hol Chan Marine Reserve, had fish densities that were 2–6 times the abun-

dances measured at reef ridge sites. However, fish abundance was noticeably low at Bread and Butter.

Fish of the Family Labridae (includes wrasses and hogfish) were relatively abundant (~ 14 – 20 fish $200 m^{-3}$) at all but two (Mexico Rocks and Coral Gardens) northern patch reef sites (ANOVA, $F = 12.6$, $P < 0.0001$), including Hol Chan Marine Reserve (Table 4). The three south-central patch reefs and two reef ridges had low abundances of Labridae, ~ 2 – 3 fish $200 m^{-3}$ (Tukey–Kramer, $P < 0.05$). Notably, only one hogfish (*Lachnolaimus maximus*) was surveyed in the south-central region of Belize, at Peter Douglas ridge. In contrast, both hogfish and/or Spanish hogfish (*Bodianus rufus*) were censused at all northern sites except San Pedro patch reef. Fishes in the Family Balistidae (includes triggerfish and filefish), also predators of urchins, were rare at all sites and did not occur within the survey areas.

There was a significant inverse relationship between the abundances of Labridae (wrasses and hogfish) and

Table 3 Mean (\pm SE) test diameter (mm), biomass ($g m^{-2}$) and calculated bioerosion rates ($kg CaCO_3 m^{-2} year^{-1}$) of urchins at patch reef and reef ridge sites off Belize

Sites	Test diameter	Biomass	Bioerosion rates	
			One turnover per day	Two turnovers per day
Northern				
Mexico Rocks	27.5 \pm 0.7a	222.3 \pm 34.3	1.2 \pm 0.2ab	2.1 \pm 0.3
San Pedro	28.7 \pm 1.7a	160.1 \pm 98.1	0.6 \pm 0.3abc	0.7 \pm 0.3
Hol Chan (MPA)	34.1 \pm 2.5a	36.4 \pm 13.5	0.2 \pm 0.1c	0.2 \pm 0.1
Mitchell Rocks	24.4 \pm 0.9bc	154.9 \pm 17.2	0.8 \pm 0.1abc	1.6 \pm 0.2
Coral Gardens	28.6 \pm 1.0ab	245.7 \pm 39.6	1.4 \pm 0.2a	2.6 \pm 0.4
Southern				
Bread and Butter	23.7 \pm 0.8c	232.7 \pm 55.3	1.2 \pm 0.3ab	2.4 \pm 0.5
Wee Wee Patch	21.1 \pm 1.1c	207.0 \pm 106.3	1.1 \pm 0.5ab	2.1 \pm 1.1
Norvall	25.6 \pm 0.9abc	258.1 \pm 51.6	1.3 \pm 0.3ab	2.7 \pm 0.5
Wee Wee Ridge	16.4 \pm 0.9d	51.9 \pm 11.0	0.3 \pm 0.1c	0.5 \pm 0.1
Peter Douglas Ridge	14.0 \pm 1.1d	53.9 \pm 7.1	0.3 \pm 0.03bc	0.6 \pm 0.1
Tunicate Cove Ridge	13.3 \pm 0.6d	60.5 \pm 13.0	0.3 \pm 0.1bc	0.6 \pm 0.1

The range in bioerosion values reflects rates of one (for all urchin species) and two (for all urchin species except *D. antillarum*) gut turnovers per day. Means of test diameters and bioerosion rates (one gut turnover per day) not designated by the same letter are significantly different ($P < 0.05$, Tukey–Kramer)

Table 4 Mean (\pm SE) fish abundances (number 200 m⁻³) for totals, Labridae (wrasses and hogfish), and Scaridae (parrotfishes) at patch reef and reef ridges sites off Belize

Sites	Total	Labridae	Scaridae
Northern			
Mexico Rocks	61.5 \pm 9.6	8.3 \pm 1.3b	6.1 \pm 3.8b
San Pedro	89.3 \pm 17.6	14.4 \pm 2.8ab	8.3 \pm 7.0b
Hol Chan (MPA)	144.8 \pm 12.8	19.1 \pm 2.0a	6.3 \pm 5.1b
Mitchell Rocks	63.0 \pm 17.5	20.8 \pm 2.8a	7.5 \pm 7.0b
Coral Gardens	42.1 \pm 12.4	4.9 \pm 2.8bc	13.3 \pm 5.0b
Southern			
Bread and Butter	25.6 \pm 14.9	1.6 \pm 1.8c	11.8 \pm 6.0b
Wee Wee Patch	88.1 \pm 14.9	2.2 \pm 1.8c	55.7 \pm 6.0a
Norvall	47.1 \pm 14.4	3.0 \pm 1.7c	12.6 \pm 5.7b
Wee Wee Ridge	24.6 \pm 15.0	2.8 \pm 1.8c	7.3 \pm 6.0b
Peter Douglas Ridge	31.5 \pm 20.3	7.5 \pm 2.1bc	9.8 \pm 8.1b
Tunicate Cove Ridge	32.0 \pm 20.1	2.9 \pm 2.2c	10.3 \pm 8.1b

Means for Labridae and Scaridae not designated by the same letter are significantly different ($P < 0.05$, Tukey–Kramer)

urchin densities at patch reefs and ridge sites [$y = -11.2 \ln(x) + 40.1$, $R^2 = 0.68$, ANOVA, $F = 18.9$, $P < 0.001$].

Densities of parrotfishes (Scaridae) were not significantly different among patch reef and ridge sites (Table 4). Parrotfish varied significantly (ANOVA, $F = 5.9$, $P < 0.001$) only at Wee Wee patch reef, where abundances of Scaridae were 4–9 times higher than at other sites (Tukey–Kramer, $P < 0.05$). Parrotfish and urchin densities were not related.

Urchin gut analysis and estimates of bioerosion rates

Calcium carbonate comprised $\sim 90\%$ of urchin gut contents (Fig. 2). The second largest component of gut contents was organic material. Organic material comprised a significantly greater proportion of the gut contents of urchins collected at patch reefs ($\sim 10\%$) than reef ridges ($\sim 4\%$) ($t = 4.8$, $P = 0.001$). The total amount of gut contents was also over three times greater in urchins taken from patch reefs than from reef ridges due to the small urchin size at the latter sites (Table 3).

Calculated bioerosion rates were used to estimate the impact of urchins on patch reefs and reef ridge sites (Table 3). On patch reefs, bioerosion rates (based on one gut turnover per day) ranged (ANOVA, $F = 7.8$, $P < 0.0001$) from lowest at Hol Chan Marine Reserve (~ 0.2 kg CaCO₃ m⁻² year⁻¹) to highest at Coral Gardens (~ 1.4 kg CaCO₃ m⁻² year⁻¹; Table 3). There was no significant difference in bioerosion rates between northern and southern sites. Bioerosion rates were relatively low for reef ridges. When rates were calculated based on two gut turnovers per day (for all urchin species except *D. antillarum*), bioerosion estimates remained relatively low, ~ 0.2 – 0.7 kg CaCO₃ m⁻² year⁻¹, at Hol Chan Marine Reserve and San Pedro, respectively, due to the large contribution by *D. antillarum* to calculated rates at those sites. Notably, bioerosion rates at several sites, including Coral Gardens and Norvall, were a magnitude

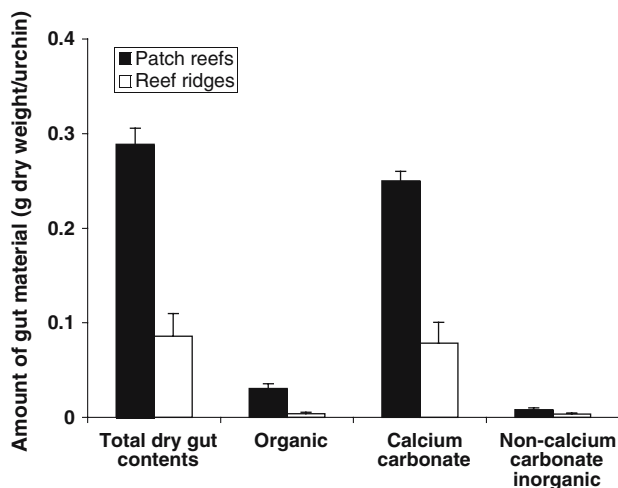


Fig. 2 Mean (\pm SE) urchin gut constituents (g urchin⁻¹) from patch reef and reef ridge sites off Belize

higher (> 2 kg CaCO₃ m⁻² year⁻¹) than rates calculated for Hol Chan Marine Reserve.

Discussion

This study documented large spatial variations in urchin abundance, predominantly *E. viridis*, and size at patch reefs and coral reef ridges in the lagoonal region off Belize (Mesoamerican Barrier Reef System), that translate into varying rates of bioerosion and potentially critical impacts on reef health and biogeochemical balances. Urchin abundances were inversely related to densities of fish of the Family Labridae (wrasses and hogfish), which includes some of their main predators. On reef ridges, low algal cover ($\sim 15\%$), small urchin size (~ 14 mm), and low proportion of organic material in urchin guts suggest that this herbivore assemblage is food limited. Taken together, these results indicate that both top-down (predation) and bottom-up factors (food limitation) contribute to the control of urchin populations in the lagoonal region off Belize.

Several studies have demonstrated that carnivorous fish densities were strongly coupled with urchin abundances in shallow coral reef sites (Hughes 1994; McClanahan et al. 1994; Carreiro-Silva and McClanahan 2001). For example, McClanahan and Muthiga (1989) suggested that wrasses even fed on urchin recruits, while Tuya et al. (2004) found that labrids acted as a controlling force on populations of *D. antillarum*. Off the eastern coast of Kenya, urchin populations increased dramatically with the reduction of their predators such as the red-lined triggerfish, *Balistapus undulatus* (Carreiro-Silva and McClanahan 2001); other species of triggerfish (Balistidae), the jolthead porgy (Sparidae), and hogfish (Labridae), also prey directly on urchins (McClanahan et al. 1994; McClanahan 1998, 1999). Although no members of the Balistidae were recorded in our surveys,

another reef survey team using a roving diver technique reported that members of the Family Balistidae occurred in frequencies of rare- to single-sightings at monitored fore reef and atoll sites (>100 h surveys per site) off northern Belize (The Reef Environmental Education Foundation, unpublished data; <http://www.reef.org>). Earlier fish surveys (Peckol et al. 2003) off Belize documented highest abundances of Labridae at fore reef sites and lowest densities at coral reef ridges. In the present study, between-site variation in urchin densities on lagoonal reefs was strongly (inversely) related to abundances of members of the Family Labridae, and, with one exception (Peter Douglas ridge), hogfish (*L. maximus*) and Spanish hogfish (*B. rufus*) were only encountered in surveys at northern sites. Such top-down controls on urchin abundances likely predominate in reef systems experiencing no to low fishing pressures.

The range in urchin densities at the reef ridge sites was not well correlated with Labridae abundances. Instead, low algal cover (~15%), small but numerous urchins, and low proportion of organic content in urchin guts together suggest bottom-up controls on urchin populations at ridge sites. In fact, declines in percent cover of turf algae (from ~40 to ~2%) were concomitant with three to four-fold increases in herbivorous fish (parrotfish and surgeonfish) abundances from June 1999 to 2002 at reef ridge sites (Brown-Saracino 2003; Peckol et al. 2003), further suggestive of food limitation in urchins. Similarly, McClanahan and Kurtis (1991) argued that small body sizes of *Echinometra mathaei* indicated food limitation.

The high abundance of *E. viridis* on several lagoonal reefs off Belize underscores the importance of understanding the impacts of this species on coral framework through its bioerosion activities. The present study found that bioerosion rates ranged from ~0.2 kg CaCO₃ m⁻² year⁻¹ (Hol Chan Marine Reserve) to greater than 2 kg CaCO₃ m⁻² year⁻¹ at several patch reef sites. Similarly, Carreiro-Silva and McClanahan (2001) reported bioerosion rates ranging from 0.5 kg CaCO₃ m⁻² year⁻¹ at protected areas to 1.2 kg CaCO₃ m⁻² year⁻¹ on unprotected reefs. Although bioerosion rates at ridge sites (~0.3–0.6 kg CaCO₃ m⁻² year⁻¹) were lower than values calculated for most patch reefs in the present study, Griffin et al. (2003) suggested that higher densities of small urchins can have a larger bioerosion impact than low densities of larger individuals. A comparable range (0.1–4 kg CaCO₃ m⁻² year⁻¹) of bioerosion rates of *E. viridis* (size = 20 mm; densities 1–62 m⁻²) was estimated by Griffin et al. (2003) for reefs off Puerto Rico, while Conand et al. (1997) reported rates ranging from 2.8 to 7.7 kg CaCO₃ m⁻² year⁻¹ for another rock urchin species, *E. mathaei*, that occurred in densities of 19–45 m⁻². Although bioerosion rates (5 kg CaCO₃ m⁻² year⁻¹) of larger-bodied *D. antillarum* at relatively low (9 m⁻²) densities (Ogden 1977) were much higher than rates for rock urchins found at comparable densities, *D. antillarum* occurred in very low abundances in the present study. On reefs off the Galápagos Islands, urchin bioerosion rates were estimated at 8 kg CaCO₃ m⁻² year⁻¹; at these rates,

urchins may be literally endangering the very existence of the reefs (Reaka-Kudla et al. 1996). Similarly, Bak (1990) suggested that bioerosion rates of 4.5–7.5 kg CaCO₃ m⁻² year⁻¹ could devastate coral reef areas. Clearly, many urchin species are major bioeroders and their activities may significantly alter the calcium carbonate balance on reefs.

Without accurate estimates of calcium carbonate accretion rates, it is difficult to determine the degree to which bioerosion is affecting reef growth on the MBRs; however, a rough approximation can be attempted. *Agaricia agaricites* has been reported to grow at rates of 2 g CaCO₃ m⁻² year⁻¹ on reefs off Barbados at depths of 5 m (Stearn and Scoffin 1977). If *A. tenuifolia*, the former space-dominant coral species on the reef ridges (Aronson et al. 2000; Peckol et al. 2003), grew at comparable rates, bioerosion on ridges by sea urchins alone would be over two orders of magnitude greater than the coral growth rates. Under normal conditions, growth rates of *M. annularis* on reefs at less than 12 m depth off St. Croix, USVI were 0.7–0.9 cm year⁻¹ (Hubbard and Scaturro 1985). On patch reefs off south-central Belize, this coral species suffered high partial and complete colony mortality in 1998 due to severe ENSO-induced bleaching (Peckol et al. 2003). These reefs may thus be more vulnerable to damage from bioerosion following a major environmental stress like an ENSO episode.

Studies of the impact of rock urchins within and outside of marine protected areas off Kenya (Carreiro-Silva and McClanahan 2001) indicated that MPAs play a vital role in reef recovery and balance as well as conserving fish populations. Of the sites surveyed in the present study, Hol Chan Marine Reserve had among the highest wrasse/hogfish abundances and percent live coral cover, coupled with the lowest urchin densities and rates of bioerosion. The importance of fish in controlling urchin densities suggests that MPAs may provide the means for effectively limiting the number of urchins on coral reefs and subsequently returning the calcium carbonate cycle to a more balanced state.

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