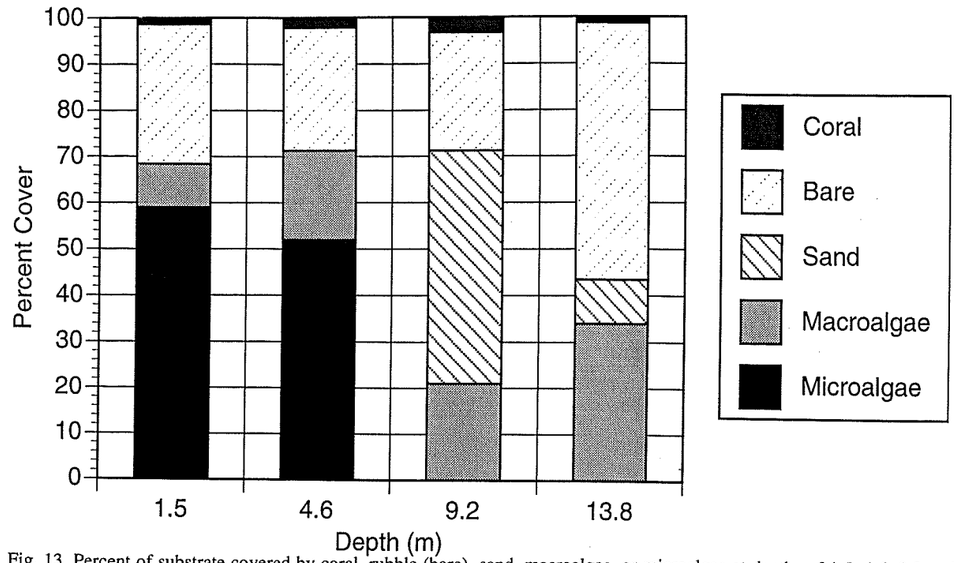

Fig. 13. Percent of substrate covered by coral, rubble (bare), sand, macroalgae, or microalgae at depths of 1.5, 4.6, 9.2 and 13.8 m on the west fore reef at Discovery Bay, Jamaica.

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Appendix. Common and Scientific names of species we observed 1 March - 8 March 1996 on the west fore reef, Discovery Bay, Jamaica.

Common Name	Scientific Name
Blue Tang	*Acanthurus coeruleas*
Ocean surgeonfish	*Acnthurus bahianus*
Coney	*Cephalopholis cruentata*
Bluehead Wrasse	*Thalassoma bifasciatum*
Creole Wrasse	*Clepticus parrai*
Yellowhead Wrasse	*Halichoeres garnoti*
Clown Wrasse	*Halichoeres maculipinna*
Shy Hamlet	*Hypoplectrus guttavarius*
Barred Hamlet	*Hypoplectrus puella*
Damselfish	*Stegastes* spp.
Yellowtail Damselfish	*Microspathodon chrysurus*
Yellow Goatfish	*Mulloidichthys martinicus*
Striped Parrotfish	*Scarus iserti*
Princess Parrotfish	*Scarus taeniopterus*
Harlequin Bass	*Serranus tigrinus*
Redband Parrotfish	*Sparisoma aurofrenatum*
Yellowtail Parrotfish	*Sparisoma rubripinne*
Stoplight Parrotfish	*Sparisoma viride*

FACTORS DETERMINING THE ABUNDANCE AND DISTRIBUTION OF *ECHINOMETRA LUCUNTER* AND *E. VIRIDIS*

P. PARKER C. SHELBY

Abstract. Coexisting species may alleviate interspecific competition by partitioning habitat resources. On the west back reef of Discovery Bay, Jamaica, *E. viridis* and *E. lucunter* seek shelter in similar rock and coral crevices or under rubble. Experimental manipulations demonstrated that *E. lucunter* is competitively dominant in aggressive fights for shelter. I hypothesized that the aggressively dominant *E. lucunter* excludes *E. viridis* from shelters and this competitive exclusion is responsible for the decline of *E. viridis*.

Key Words: burrow defense, competitive exclusion, Echinometra lucunter, Echinometra viridis, *niche partitioning*

INTRODUCTION

A diverse assemblage of sea urchins coexist in tropical coral reef communities. Past studies have shown that different urchin species spatially segregate in reefs to reduce competition for food and burrow shelters (McClanahan 1988). High diversity is also supported by local partitioning of resources. Two species of *Echinometra*, *E. lucunter* and *E. viridis* occupy similar food and shelter niches and have the potential to be in direct competition (Hendler et al. 1995). *E. lucunter* and *E. viridis* share similar geographic ranges, extending from the southern United States to northern South America, and similar depth ranges from 0 to 40 m. Although traditionally considered omnivores, *E. lucunter* subsists primarily on drift algae. *E. viridis* also consumes drift algae, but may leave its burrow at night to feed on macroalgae. Both species face similar predation risks from ruddy turnstones, grunts, jacks, wrasses, conchs and a parasitic gastropod. *Echinometra* seek shelter in coral burrows, crevices, or underneath broken rubble in shallow reef environments for protection from surge dislodgement and predation (Grunbaum 1978). *E. lucunter* is a rock-boring species and may create its own burrows by spine abrasion and ingestion of the coral or rock substrate. In contrast, *E. viridis* shelters within established crevices or under rubble. *Echinometra* actively defend their burrow against intruders (Shulman 1990), and burrow space has been shown to be limiting in some habitats (McClanahan 1991). I hypothesized that competition for space limits the abundance of the inferior competitor, *E. viridis*. Although I was not able to show that space was limiting, I predicted that *E. lucunter* and *E. viridis* share the same microhabitats across the reef. Because *E. lucunter* is the more abundant species at shallow depths, I also predicted that *E. lucunter* is a better defender of and competitor for burrows.

METHODS

All urchins were censused in six 1 m^2 plots inshore (10 m from the shoreline) and eight 1 m^2 plots offshore (20 m inside the reef crest) in the west back reef of Discovery Bay, Jamaica on 28 February - 7 March , 1996. For each urchin located, total diameter, including extended spines, was measured. Shelters used by urchins were classified into four categories: crevice or hole within coral, beneath rubble, beneath protective ledges, and within turtle grass. Depth of the shelter below the water surface and total water column depth were measured. Distance to the three nearest urchin neighbors was measured and averaged. Interspecific differences in shelter type were compared using a G-test. Interspecific differences in depth to shelter, total water column depth and average distance to the nearest 3 urchin neighbors were compared using ANOVAs. Interspecific differences in species densities among inshore and offshore habitats were analyzed using a students t-test.

Competition trials between *E. lucunter* and *E. viridis* were run in a 4 m^2 outside tank filled with running sea water. Each defending urchin was placed inside a plastic cylinder weighted down with iron bolts. The defending urchin was given > 15 minutes to acclimatize to the artificial shelter. A second urchin of the other species was placed at the entrance and allowed to enter the "burrow". At the end of each trial, only one species remained in the burrow and the other species was expelled; the remaining species was termed

the winner. The species that won the burrow was recorded along with whether any biting was observed. Sixty trials were run. In 40 trials with competing urchins of equal size, the defender was predicted to win. In 10 trials where the defender was > 1.5 x larger and 10 trials where the defender was < 0.67 x smaller, the larger urchin was predicted to win (see Grunbaum 1978). In 30 trials, *E. lucunter* defended against E. viridis, and 30 trials were the reverse. Differences in competitive outcomes among species and size classes were analyzed using a G-test.

Results

Of the 115 urchins censused, 113 were hidden in shelters, but different species were found in different shelters (Table 1; G = 26.70, df = 12, P < 0.001). All 95 Echinometra were found in rockholes or beneath rubble. Both *E. lucunter* and *E. viridis* occurred more frequently in rockholes than in rubble ($X^2 = 0.329$, df = 1, P = 0.56). The five common urchins were found at different shelter depths (F = 14.992, df = 6, 108, P < 0.001) and different total water column depths (Table 2; F = 9.638, df = 6, 108, P < 0.001). *E. lucunter* was generally found at shallower depths and in shallower water than *E. viridis* (F = 26.117, df = 1, 93, P < 0.001 and F = 23.235, df = 1, 93, P < 0.001, respectively).

E. lucunter occurred at significantly higher densities than *E. viridis* in both inshore and offshore habitats (Table 3). *E. lucunter* also had closer average nearest neighbor distances than *E. viridis* (mean ± SE = 0.262 ± 0.028 vs. 0.523 ± 0.079; F = 9.63, df = 93, P = 0.0025).

In the competition trials *E. lucunter* was more successful at defending its shelter against both smaller and same-size intruders than *E. viridis* (Table 4). *E. lucunter* displayed biting behavior three times against an *E. viridis* of the same size, and once against a smaller *E. viridis*; *E. viridis* was never observed biting *E. lucunter.*

Discussion

E. lucunter and *E. viridis* share similar ecological niches in the west back reef at Discovery Bay, Jamaica. Both *E. lucunter* and *E. viridis* occur with greater frequency in coral and rock holes then beneath rubble. Given that the two species have the same mean diameter (*E. lucunter* = 43 cm ± 2 vs. *E. viridis* = 42 cm ± 5) and urchin size is related to shelter size, the two urchins probably utilize shelters of similar sizes. Both species occurred in shelters at the similar depths and total water column depths. The major difference between the two species is abundance: *E. lucunter* is found at higher densities in both inshore and offshore transects. *E. lucunter* also tolerated closer cohabitation of other urchin species. In the competition trial, *E. lucunter* better defended its burrow than *E. viridis*. Consequently, I conclude that *E. lucunter* excludes *E. viridis* from shelter spaces.

If space is limited on the reef, this competitive exclusion could limit the abundance and distribution of *E. viridis*. Although never directly tested, shelter space does appear to be limited in the west back reef. Field observations suggest that all potential shelters are occupied. In 1973, *Echinometra* density was higher throughout the back reef. Although this implies that currently there are empty shelters, shelter density on coral reefs is not constant. The reef has since undergone many changes: in 1980 Hurricane Allen struck and greatly reduced coral cover across the northern coast of Jamaica (Woodley *et al* 1981). Also, the burrowing behavior of *E. lucunter* bioerodes coral and reduces potential shelter spaces (Bak 1994).

Data from the aggression trials contradicts past studies that found that *E. lucunter* and *E. viridis* are equal competitors for shelters (Shulman 1990). But these studies also demonstrated that there is high variation among populations in competitive abilities.

Table 1. Number of urchins of each species found in four shelter types on the west back reef of Discovery Bay, Jamaica.

Species	Rockhole	Rubble	Turtle grass	Under Ledge	Total
Diadema antillarum	5	0	0	4	9
Lytechinus variegatus	0	1	2	0	3
Eucidaris tribuloides	6	0	0	1	7
Echinometra lucunter	70	14	0	0	84
Echinometra viridis	10	1	0	0	11

Table 2. Maximum, minimum, and average depth of urchin shelter, and average total depth of the water column for five common urchin species in the west back reef of Discover Bay, Jamaica.

Species	n	Min. Depth (m)	Max. Depth (m)	Avg. Depth (m) (x ± SE)	Avg. Water Column Depth (m) (x ± SE)
D. antillarum	9	0.5	1.5	1.13 ±0.12	1.27 ±0.16
L. variegatus	3	0.1	1.6	0.90 ±0.25	1.23 ±0.29
E. tribuloides	7	0.7	1.5	1.04 ±0.14	1.36 ±0.19
E. lucunter	8	0.8	1.3	0.35 ±0.04	0.55 ±0.05
E. viridis	1	0.1	1.5	0.97 ±0.11	1.34 ±0.15

Table 3. Density of *E. lucunter* and *E. viridis* in the west back reef of Discovery Bay, Jamaica.

		Density (# / m^2) (x ± SE)				
Habitat	n	E. lucunter	E. viridis	t	df	P
Inshore	6	11.72 ± 3.16	0.33 ± 0.21	2.28	10	0.005
Offshore	8	1.71 ± 0.37	0.25 ± 0.16	2.14	14	0.002
Total	14	6.00 ± 1.89	0.28 ± 0.12	2.05	26	0.005

Table 4. Number of defender wins and losses in *E. lucunter* and *E. viridis* interspecific competition trials at Discovery Bay, Jamaica.

		E. lucunter defending against *E. viridis* intruder		*E. viridis* defending against *E. lucunter* intruder				
Intruder Size	n	Win	Loss	Win	Loss	G	df	P
Small	5	5	0	4	1	1.50	1	> 0.05
Equal	20	20	0	13	7	11.20	1	< 0.05
Large	5	3	2	4	1	0.48	1	> 0.05

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