foraging, while at night they may seek refuge in macroalgae. This may be especially true for the polychaetes, which were driving a large portion of our day versus night differences in abundance and richness and overall accounted for 54% of the variation in total abundance. Alternatively, zooplankton may migrate upward into the water column to forage at night (Porter and Porter 1977). Some of these zooplankton, such as amphipods, isopods and larval polychaetes, may settle into macroalgae during the night, which could explain our observations of higher abundance and richness.

According to island biogeography theory, we would expect higher abundance and species richness on larger islands, as was found for the macroalga *Penicillus capitatus* (Stoner 1985). In clumps of *H. opuntia,* we found no relationship between size of the clump and either abundance or richness of macro-invertebrates. This suggests that island biogeography theory does not apply to these *H. opuntia* patches. Instead, it appears that *H. opuntia* is one alga among a matrix of many algal species and organisms are free to move among them. Future studies should examine a broader range of clump sizes in a variety of microhabitats to further validate the patterns we found.

Although *H. opuntia* exists in a matrix of other algae, studies have shown that invertebrates are more abundant in it (Glastris et al 2001; pers. obs.). In our experimental arenas, organisms (adults and juveniles) did not actively prefer *H. opuntia.* Perhaps larval stages show an active preference through some cue in *H. opuntia;* further studies could test this hypothesis. It is also possible that larvae disperse randomly among algal species. The growth morphology of *H. opuntia* is dense and low to the substrate, creating a refuge from predation and turbulence for these larvae. The larvae that settle in other algae, for example in the stalk-like structure of *T. turbinata*, could be exposed to higher predation and increased turbulence from wave action. Thus macro-invertebrates may not actively choose *H. opuntia*, but instead may experience higher survival in the refuge of its dense structure, resulting in the distribution pattern observed by Glastris et al. (2001).

Predation, together with the three-dimensional habitat structure provided by macroalgal species, could be responsible for the patterns in macro-invertebrate distribution and abundance that we found. Further studies could explore the interaction of these two factors by adding predators in controlled experiments and by manipulating other algae species in the field to resemble the growth form of *H. opuntia.*

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Differential diel movement of *Diadema antillarum* size classes

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Abstract: The long-spined urchin, *Diadema antillarum*, is an important grazer of macro-algae in Caribbean reef systems. *D. antillarum* seek refuge on patch reefs during the day and forage off reefs at night, often returning to the same position on their home reef each day. This behavior has been shown to be positively correlated with predator abundance and therefore predation risk. Because smaller urchins are likely out-competed by large urchins for optimal foraging sites around home reefs, we hypothesized that small and large urchins would differ in site fidelity and time spent away from reefs. We examined urchin abundance and site fidelity on patch reefs in Discovery Bay, Jamaica, a reef system characterized by depressed populations of *D. antillarum* predators and high macro-algal cover. We predicted that the low predation pressure in Discovery Bay, Jamaica would lead to relatively low site fidelity. Contrary to our predictions, we found that site fidelity was high among patch reefs, with tagged urchins often returning to the same crevice occupied on the first day of the study. Both large and small individuals tended to leave the patch reef at night, but this trend was stronger for small individuals. Contrary to previous evidence, the high site fidelity of *D. antillarum* in Discovery Bay cannot be explained by high predator abundance. Small urchins may be driven off of patch reefs during the night; however, further research is needed to determine the mechanism of this pattern.

Key Words: competitive exclusion, intraspecific interaction

Introduction

The long-spined sea urchin, *Diadema antillarum*, is an important grazer on shallow Caribbean reefs, particularly in areas where herbivorous fish populations are depressed. These urchins graze micro- and macro-algae on reef substrates as well as sea grasses. *D. antillarum* generally forages at night and seeks refuge on patch reefs during the day. The diel pattern in *D. antillarum* activity may be an adaptation to reduce predation risk as many predators of the urchin are diurnal such as the Jolthead Porgy and the Queen Triggerfish (Kaplan 1982).

Carpenter (1984) has suggested that in the absence of predators *D. antillarum* is less likely to seek cover during the day and is less likely to "home" or return to the same position on reefs in consecutive days. We hypothesized that this behavioral plasticity may also extend to variation in site fidelity between size classes. For example, large urchins might show greater site fidelity than small urchins, because they are better competitors for optimal foraging habitat on patch reefs. Alternatively, large urchins may forage on preferred sites away from home reefs in the absence of predation and, therefore, show lower site fidelity than small urchins. We examined urchin populations in Discovery Bay, Jamaica, an atypical reef system due to reduced fish populations and high macro-algal cover. Because macro-algal cover is abundant at Discovery Bay, optimal foraging sites are more likely to be located on patch reefs. Thus, we expected site fidelity to be greater in large urchins, and also expected large urchin abundance to have less variation than small urchin abundance.

Methods

This study was conducted on the western reef of Discovery Bay, Jamaica on 23 - 25 February 2002. We haphazardly chose three different patch reefs occupied by *D. antillarum*. Reef 1 was located northwest of the Discov-

ery Bay Marine Lab (DBML) ~400 m and was ~19 m long and 1 m wide, at depth ~1 m. Reef 2 was located ~350 m due north of DBML and was 4 m long and 3.5 m wide. Reef 3 was located ~320 m due north of DBML and was 10.5 m long and 1.2 m wide. Both Reefs 2 and 3 were at depths of ~2 m.

We recorded abundance of large and small *D. antillarum* between 10:00 – 11:30 on three successive days (Feb. 23 - 25) at each reef and abundance between 21:30 - 23:00 on two successive nights (Feb. 23 - 24) for reefs 2 and 3. We were unable to survey reef 1 on the night of Feb. 23 and therefore night abundance at reef 1 was surveyed on Feb. 24 only. *D. anitllarum* was classified as large if its diameter (test and spine) was >10 cm and small if its diameter was <10 cm.

To determine the homing frequency of *D. antillarum*, we marked 2 - 3 large and 2 - 3 small individuals at each reef with colored bands made by hole-punching surgical tubing. The resulting bands were colored with permanent markers and placed on the urchins using two hollow plastic tubes, one on top of the other. We marked the crevices where tagged individuals were found during the initial survey on Feb. 23. We defined each marked urchin's "home" as the position on the reef where that urchin was originally marked. We then defined the return ratio as the number of marked urchins (small or large) found at home during a survey divided by the total number of marked urchins of that size class at that reef. Return ratios were calculated for each reef and each successive survey.

We compared differences between small and large *D. Antillarum* populations for both day and night across all reefs (Appendix I). Variation from the mean was standardized using the expression below:

$$\frac{\text{urchins surveyed} - \text{mean number of urchins at reef}}{\text{mean number of urchins at reef}}$$

Thus, a large negative value at night means that urchins were rare on the reef at that particular time. Differences and return ratios for large and small urchins were compared across time (day or night) and across days (Feb. 23 - 25) using Kruskal-Wallace non-parametric tests.

Results

Urchin abundance was consistent from day to day. For large and small urchins respectively, day did not affect abundance among sites ($\chi^2 = 1.79$, df = 2, P = 0.409; $\chi^2 = 0.112$, df = 2, P = 0.976 respectively), or return ratio among sites ($\chi^2 = 0.05$, df = 2, P = 0.976; $\chi^2 = 3.28$, df = 2, P = 0.194 respectively).

Numbers of urchins varied across reefs (Fig. 1). Reef 1 had more small urchins than either reef 2 or 3 (mean ± SE, reef 1 = 101.25 ± 14.6, reef 2 = 6.6 ± 2.1 and reef 3 = 5.6 ± 1.9). Large urchin abundance was greatest on reef 3, intermediate at reef 1 and lowest at reef 2 (reef 1 = 17.25 ± 0.6, reef 2 = 6 ± 0.3, reef 3 = 26 ± 1.3).

The abundance of both small and large urchins on reefs tended to be higher during the day then at night though this trend was stronger for small urchins (Fig. 2). Variation in small urchin abundance between day and night was greater at reefs 1 and 2 than at reef

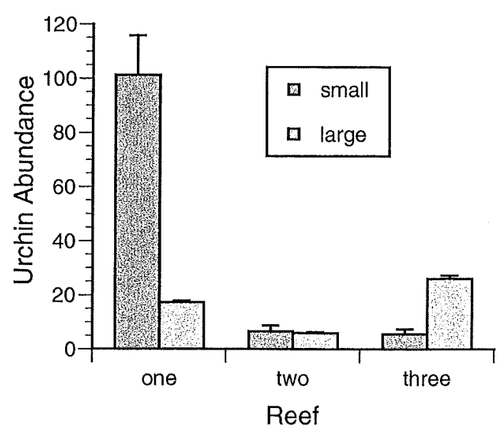

FIG. 1. Mean abundance of small and large urchins at three patch reefs near Discovery Bay Marine Laboratory, Jamaica.

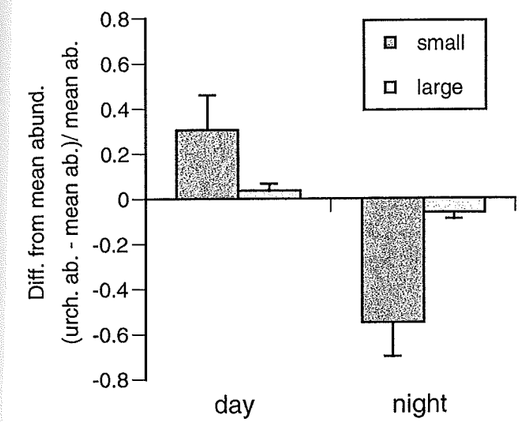

FIG. 2. Differences in small and large *D. antillarum* abundance between night and day surveys across all sites .

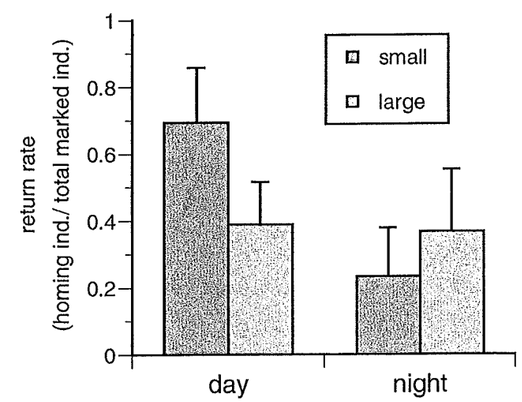

FIG. 3. Return rates (± SE) of large and small marked *D. antillarum* at 3 patch reefs at Discovery Bay, Jamaica.

3 ($\chi^2 = 5.76$, df = 2, P = 0.056), but there was no statistical difference in the variation of large urchin abundance between reefs ($\chi^2 = 0.088$, df = 2, P = 0.957).

We tagged fifteen urchins on the three reefs, eight large and seven small. Eleven of fifteen exhibited site fidelity by returning to their home during at least one of the successive surveys. The return ratio of small urchins tended to be smaller at night than during the day ($\chi^2 = 3.24$, df = 1, P = 0.07), but the return ratio of large urchins did not vary significantly between night and day ($\chi^2 = 0.14$, df = 1, P = 0.71; Fig. 3).

Discussion

We found that a higher proportion of small urchins than large urchins left the reef at night to forage (Fig. 1). We also found that small, tagged individuals were more likely to be present during the day than at night, while larger individuals showed no such trend. Both these results support our hypothesis that large and small urchins differ with respect to their site fidelity and diel movement patterns.

Because of low predation pressure in Discovery Bay, we had expected to see a relaxation in site fidelity. However, comparing our results with those reported by Carpenter (1984), we found higher than expected site fidelity for all urchins (58.3%). Our results suggest that other factors, in addition to predation risk, influence the site fidelity of *D. antillarum* across all size classes.

Further research could investigate the potential mechanisms for the observed differences in site fidelity and diel movement patterns. We have suggested that the observed differences are caused by the competitive exclusion of small urchins by large urchins for optimal foraging sites. Alternatively, this phenomenon might be caused by intraspecific niche partitioning or perhaps as some adaptive behavior to facilitate colonization of new habitats. A future study could observe the activity of the urchins during the hours immediately following sunset to determine the movement patterns of small individuals.

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APPENDIX I. Urchin abundance (and normalized variation) from mean abundance (small, large) at three reefs for each day and night sampled during our study and the mean abundance across all surveys by reef.

Reef	Day 1	Night 1	Day 2	Night 2	Day 3	Reef Mean
1	62, 17 (-0.39, -0.02)		118, 17 (0.16, -0.02)	97, 16 (-0.04, -0.08)	128, 19 (0.26, 0.10)	101.3, 17.3
2	5, 6 (-0.24, 0)	1, 5 (-0.85, -0.17)	12, 7 (0.82, 0.17)	4, 6 (-0.39, 0.00)	11, 6 (0.67, 0.00)	6.6, 6.0
3	11, 25 (0.96, -0.04)	2, 25 (-0.64, -0.04)	6, 31 (0.07, 0.19)	1, 25 (-0.82, -0.04)	8, 24 (0.43, -0.08)	5.6, 26.0

APPENDIX II. Urchins tagged during initial survey and presence at home crevice during subsequent surveys (night one (N1), day two (D2), night two (N2) and day three (D3)).

Reef	Size	Tag	Observed at home crevice
One*	large	clear	D2, N2, D3
		green/red	
		blue	D2, N2, D3
	small	clear	D2
		clear/green	D2, D3
		red	D2, D3
Two	large	blue	N1, D2, N2, D3
		red/blue	N1
	small	red	N2
		clear	
Three	large	clear	
		blue	
		red	N1
	small	green	D2, D3
		red	D2, D3

*Reef one was not surveyed on night one.