for future study.

It did not appear that the presence of multiple species of damselfish contributed to algal diversity in high herbivory locations on the reef. Inside territory species composition was similar between three spot and dusky damselfish, and all of the species that occurred in yellowtail territories also occurred in three spot and dusky territories. There was considerable overlap in the algal species consumed by all three damselfish three species, and this suggests that the extent of territoriality is the most important difference between species.

The considerable differences in algal richness and composition between mangrove, back reef, and fore reef locations many biotic and abiotic factors affect algal distribution. The low algal diversity in the mangrove site could be due to high nutrient levels or low salinity favoring a few competitively dominant algal species. Alternatively, algal composition in the mangrove reef may have been most affected by intense parrotfish grazing around territories.

Our study did not measure algal abundance inside and outside territories and was consequently limited to assessments of species richness and similarity. Future studies might better understand the effects of territoriality by looking at diversity. Studies could also expand upon our feeding observations by placing different algae species inside territories and watching for feeding preference and by looking at damselfish gut contents.

Literature Cited

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science **199**: 1302-1310.

Hay, M.E. 1981. Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. Aquat. Bot. **11**: 97-109.

Hay, M.E. 1991. Fish-Seaweed Interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. The Ecology of Fishes on Coral Reefs. Academic Press, Inc.

Hixon, M.A. and W.N. Brostoff. 1996. Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. Ecological Monographs: **66**: 67-90.

Lewis, S.M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecological Monographs **56**: 183-200.

HOMING BEHAVIOR AND REFUGE SELECTION IN *DIADEMA ANTILLARUM*

Suzanne P. Bird and Angela C. Rutherford

Abstract: Homing behavior in *Diadema antillarum* has been shown to be important in maintaining an effective refuge against predators. However, homing behavior has not been studied in areas with low predation pressure. Homing behavior, refuge quality, and habitat complexity were measured on west back reef at Discovery Bay, Jamaica. We found that urchins homed 73% of the time, suggesting that homing may be driven by mechanisms other than predation, or may be an adaptive fixed behavior of *D. antillarum*. Urchins also tended to inhabit, and home to higher quality refuges and areas of the reef that were topographically more complex, suggesting active habitat selection on their part. Further study could elucidate the the affects of abiotic factors such as topographical complexity and surge on *D. antillarum* homing behavior and abundandces.

Key words: D. antillarum, *homing, predation, refuge quality, wave action*

Introduction

Sea urchins are among the most important groups of benthic grazers in marine ecosystems, (Sammarco 1982), and *Diadema antillarum* are is of the most common grazing echinoids of tropical reef areas. Carpenter (1984) showed *D. antillarum* to greatly impact algal abundance and diversity as well as coral reef community structure. There are both abiotic and biotic factors limiting *D. antillarum* abundance and distribution; the most important are wave action or surge, and predation pressure. Adverse wave action inhibits *D. antillarum* grazing activity, as well as possibly washing the urchins from their substrate, thereby increasing mortality (Foster 1987). Predation is a major component of many tropical reef systems and affects urchin densities and behavior patterns (Carpenter, 1984).

D. antillarum hides in crevices during the day when predation is highest and emerges at night to feed. Carpenter has shown that 33-84% of *D. antillarum* return to the same crevice on subsequent mornings. Carpenter proposed that this homing behavior, or the maintenance of a single, suitable refuge is adaptive in areas of high predation where daytime hiding is essential. Carpenter suggested that in a low predation system, it may be less adaptive to home, because hiding is not necessary and would limit urchin feeding hours.

High fishing pressure at Discovery Bay, Jamaica has led to a decrease in predatory reef fish and consequently reduced predation pressure on *D. antillarum*. The lack of knowledge of urchin homing behavior in a system with low predation raised the question of whether D. antillarum demonstrates homing at Discovery Bay. Two alternative hypotheses may explain the possible homing behavior of *D. antillarum*. If *D. antillarum* exhibits low homing behavior, we would conclude that predation is the driving force behind hiding and therefore homing behavior as predicted by Carpenter. Alternatively, if Discovery Bay *D. antillarum* homes at levels comparable to those shown in previous studies, we may conclude that predation is not the only factor influencing urchin behavior. Homing may be a fixed behavior that has not had time to, or cannot, change. Alternatively, in the absence of predation, adverse wave action may be sufficient to lead to homing because it elicits a similar hiding behavior

Because homing involves the maintenance and defense of a single refuge, it is also appropriate to ask the question of whether refuge quality affects homing behavior in addition to other biotic and abiotic factors. We predict that an urchin would be more likely to home to, and expend energy defending a higher quality, more protective, refuge in the case that homing behavior is observed in Discovery Bay. Because of the availability of substrate in Discovery Bay, we would also expect this refuge preference by *D. antillarum* to be reflected in the overall habitat selection, irregardless of homing behavior. Urchins should ideally still be living in the most protected areas of reef. Topographical complexity of substrate has been used as an overall measure of refuge quality (Kaveeshwar *et al*, 1995). We therefore predicted that areas of high topographical complexity would support greater

urchin abundance than areas of low topographical complexity.

METHODS

We studied *D. antillarum* from 29 February to 6 March 1996 at Discovery Bay Marine Laboratory, Jamaica. Four 2 x 30 m transects were laid in the west back reef parallel to and 5 - 10 m inside the reef crest. All urchins were counted on the transects and the number of individuals in each urchin clump (coexisting on the same coral patch or butress) were recorded.

To monitor homing behavior, we tagged 18 urchins. Two individuals were tagged in each of 7 urchin clumps, as well as 4 solitary individuals. Our tagging method approximately followed the technique described by Carpenter (1984). Tags were square- and triangle-shaped sections (1 cm diameter) of rubber with a centered hole made with a dissecting probe. The tag was stretched over the end of a 5 mm plastic pipette and pushed to the proxial end. Two 6 mm metal hole borers were slid over the pipette, and the pipette was placed over an urchin spine as near as possible to the base. The hole borers were used to push the tag off the pipette onto the spine.

Because indelible ink comes off of rubber, we initially attached knotted string to each tag in order to identify individual urchins. This method was abandoned because the string seemed to facilitate tag removal by the urchins. Instead, we tagged one or two individuals in a given clump of urchins, at least 5 m from any other clump. One individual was tagged with a square; the other with a triangle. Because *D. antillarum* travels only 100 - 300 cm a night (Carpenter, 1984), we assumed no mixing of tagged individuals between clumps. The location of each tagged urchin was precisely marked with a numbered buoy. On three consecutive mornings, tagged urchins were located and recorded as having homed or not homed, which we defined as returning to the exact crevice that had been occupied the day before. When an urchin moved to a new crevice, the buoy was moved to the new location.

Each marked refuge was assessed for three parameters important in providing protection to an urchin: diameter of crevice opening, depth of crevice, and number of sides protected by solid substrate. Topographical complexity was measured for all inhabited coral mounds, as well as for each 30 m transect. Complexity was calculated by the following equation: $c = 1 - (d / l)$, where c = complexity, d = length of chain when it is held taught above the coral head, measured from one side to the other, and l = length of a chain when it is laid directly on the mound and made to conform to all of the curves and crevices in the coral (measured between the same two points as for d). Complexity was adjusted for size of each mound by multiplying c * l to calculate complexity independently from size of mound.

Homing behavior was determined by finding the percentage of *D. antillarum* that homed on all subsequent mornings of our study. Because Carpenter evaluated homing behavior in the same way (if not more loosely) in a high predation system, we compared our percentages directly. We analyzed the effect of depth, diameter of crevice and the number of sides protected on homing behavior with non-paramentric Wilcoxon/ Kruskal Wallis tests. We looked at overall quality by using the equation: quality = (depth * sides protected) / diameter. This equation assumes that increased crevice depth, more sides protected and a smaller crevice opening increase refuge quality. We used Spearman's rank sum tests to analyze the effect of topographical complexity on urchin abundance. We compared complexity of inhabited coral mounds with overall transect complexity with a Student's t-test assuming unequal variance.

RESULTS

We found 48 urchins on four transects. All but six urchins were found in clumps, ranging from 6 - 15 individuals per clump. Urchins remained hidden in individual crevices throughout the day. Between morning and afternoon observations, urchins showed no movement from their refuges. Urchins began leaving crevices at 1630 - 1700 to begin night feeding. Observations at night showed that all tagged urchins had moved from their refuges, and most were positioned on tops of mounds, presumably feeding on the preferred algal turf and crustose algae. Urchins were found primarily on dead and live coral mounds covered with algal turf.

Of the 18 tagged urchins in four transects, 73% returned to their refuge: 12 exhibited homing behavior, 5 did not, and one lost its tag. Individuals exhibited either 100% homing or non-homing behavior, with the exception of one urchin that left its refuge the first night for a higher quality neighboring crevice and remained there for two consecutive days. The abandoned refuge was immediately occupied by another urchin.

In evaluating refuge quality, we found that the diameter of the crevice opening was most important in influencing homing behavior (Table 1). The number of sides protected and the depth of crevice did not play as important roles in determining refuge quality. When we combined all three parameters of quality, we found increased refuge quality tended to lead to increased homing behavior (Table 1)

Table 1. Results of Wilcoxon / Kruskal-Wallis test comparing *D. antillarum* homing behavior with depth of crevice (d), diameter of crevice opening (D), number of sides protected (s), and refuge quality [(d * s) / D].

	s value	z value	P value
Depth	24969	0.14	0.89
Diameter	37276	11.03	< 0.001
Sides	24598	-0.27	0.79
Quality	27000	-1.92	0.054

The average topographical complexity of coral heads colonized by urchins was greater than the average complexity for all transects ($t = -4.02$, $df = 21$, $P < 0.001$). Of the substrate colonized by urchins, however, increased complexity did not result in greater urchin abundance (Figure 1; $Rho = 0.371$, $df = 16$, $P = 0.12$).

DISCUSSION

We found that *D. antillarum* in Discovery Bay exhibits a high degree of homing behavior and hides during the day, despite low predation pressure. In our study, rates of homing were as high or higher than those found by Carpenter (1984) in a system with high predation pressure. This similarity in homing behavior between the two systems suggests that predation is not the only factor driving homing behavior. Because wave action has been shown to negatively impact *Diadema*, (Foster, 1987), and hiding in crevices is an advantageous strategy to minimize adverse surge effects, wave action may have an important influence on homing behavior in Discovery Bay. If crevices are needed to protect against wave action it would be equally advantageous for urchins to home in Discovery Bay as in a system driven by predation. An alternative explanation for the observed homing behavior is that homing is an innate or genetically-based behavior. Homing behavior may have originally evolved as a defense against predation, but continues to be exhibited in this area because low predation is a relatively recent result of high fishing pressure (J. Gilbert, pers. comm.).

In addition to predation pressure and possibly other abiotic factors and stresses, refuge quality seems to influence urchin homing behavior. Urchins homed with greater frequency to higher-quality refuges; this suggests that they prefer certain crevices and are more likely to defend a better refuge. The coral mounds where urchins were found were significantly more complex than those of the surrounding substrate, suggesting active habitat selection on their part. Results showing that increased complexity of suitable habitat did not lead to increased urchin abundance may be explained by low urchin abundance and high availability of refuges in Discovery Bay (pers. obs.). There is a surplus of high-quality substrate available to urchins so within the inhabited areas, a further increase in complexity does not lead to increased urchin abundance.

High topographical complexity and refuge quality may increase protection of urchins against adverse wave action. Changes in the effects of surge as a result of varying wave action or refuge quality has been shown to greatly alter urchin abundance (Foster, 1987), and may therefore influence homing behavior in *D. antillarum*. Future studies could compare the fore and back reefs to look at the effects of variation in topographical complexity and wave action on urchin abundance and homing behavior.

LITERATURE CITED

Carpenter, R.C. 1984. Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. Journal of Experimental Marine Biology and Ecology. **82**: 101-108.

Foster, S.A. 1987. The relative impacts of grazing by Caribbean coral reef fishes and *Diadema*: effects of habitat and surge. Journal of Experimental Marine Biology and Ecology. **105**: 1-20.

Kaveeshwar, J.A. 1995. Aggregated distribution of Diadema antillarum in a shallow forereef habitat. Pages 177-181 *in* C. D. Wray, editor. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH, USA.

Sammarco, P.W. 1982. Effects of grazing by *Diadema antillarum* philippi (Echinodermata: Echinoidea) on algal diversuty and community structure. Ecology. **65**: 83-105.