Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum* *

R. C. Carpenter

Institute of Ecology, University of Georgia; Athens, Georgia 30602, USA

Abstract

The frequency of homing behavior (percent returns to the same crevice) of *Diadema antillarum* Philippi varied from 30 to 84% among areas. Frequency of homing was positively correlated with predator abundance and negatively correlated with sea urchin density. *D. antillarum* evaluates the protective quality of crevices and more readily vacates low quality crevices than more protective ones when a simulated predation attempt occurs. Previously grazed portions of the foraging range of homing individuals do not appear to be regrazed on successive nights and an avoidance of such areas is suggested. This predator-mediated behavior pattern and its effects on coral reef communities may be a tropical analog to predator–sea urchin–algal relationships in temperate marine communities.

Introduction

Diadema is a common circumtropical echinoid genus (Mortensen, 1940). *Diadema antillarum* is the Western Atlantic species ranging from Florida, throughout the Caribbean and south to Surinam. *Diadema* spp. are light sensitive (Millot, 1953, 1954) and exhibit a diel activity pattern (Thorton, 1956; Randall *et al.*, 1964; Ogden *et al.*, 1973). Individuals are most often in crevices during the day, emerge at dusk (usually before sunset) and forage until dawn. A similar diel pattern occurs in *Centrostephanus coronatus*, a diadematid in which some individuals return to the same crevices for up to 240 d (Nelson and Vance, 1979). Such homing behavior has been demonstrated over short time-periods for *D. mexicanum* on the Pacific side of

Panama (Birkeland and Gregory, 1971), but has not been shown to occur in *D. antillarum*.

It is most commonly hypothesized that a homing strategy is advantageous when predation makes the occupation of a shelter site mandatory and the availability of such sites is limited (Cook, 1979; Nelson and Vance, 1979), or as a resource partitioning mechanism to ensure adequate food resources in the face of competition (Stimson, 1973; Grünbaum *et al.*, 1978). If homing behavior occurs, the repeated use of a foraging range can lead to changes in the diet breadth of the homing animal (Vance and Schmitt, 1979) and a shift in community composition (Vance, 1979).

The objectives of this study were: (1) to determine the degree to which crevice fidelity (homing) was exhibited by *Diadema antillarum;* (2) to elucidate the factors important in controlling this behavior; and (3) to investigate the utilization of a constant foraging range by these individual sea urchins.

Material and methods

The populations of *Diadema antillarum* Philippi studied were located at St. Croix, US Virgin Islands (Lat. 17°45′N, Long. 64°42′W). Study sites included shallow backreef (< 1-m depth) and forereef (< 2-m depth) habitats on Tague Bay reef and the eastern reef of Buck Island, lagoonal patch reefs (2-m depth) at Buck Island and deeper forereef sites ranging in depth from 5 to 10 m on Tague Bay reef. Buck Island Reef National Monument is a park area that has had minimal fishing pressure since the early 1960's and has larger fish populations than many reef areas around St. Croix (Gladfelter *et al.*, 1979). The study sites spanned the range of reef habitats available at St. Croix. All field work, with the exception of the foraging range studies, was conducted from June, 1981 to May, 1982.

A technique of tagging *Diadema antillarum* allowed identification of individuals for up to 12 months. The tags were circular sections (6-mm diameter) of surgical tubing made with a hole punch. Identifying numbers were written with indelible ink on the tags and a small hole was made in the center using a hypodermic needle. The tag was stretched over the end of a plastic 1-ml pipette (Falcon Plastics, Oxnard, Calif.) with the number side up. A section of glass tubing (5-mm i.d.) was then placed over the pipette from the distal end. A spine, preferably near the aboral pole for maximum visibility, was selected for tagging and the pipette was placed over this spine until near the base. While holding the distal end of the pipette, the tag was pushed off the end using the glass tubing. The rubber tag constricted around the base of the spine and the tagging apparatus was withdrawn. This procedure usually took less than 30 s, but occasionally took longer due to excessive spine movement in response to tactile stimulation. The immediate response of the tagged individual was to use the pedicellariae and secondary spines to push the tag up the spine. Because *D. antillarum* has primary spines that exceed the reach of the pedicellariae, this behavior usually resulted in a tag being positioned one-half to two-thirds of the way up a spine. Another individual response to spine tagging was to drop the spine entirely. This occurred in less than 10% of the individuals tagged. To insure against the loss of tagged individuals due to tag loss, they were retagged at 4- to 5-d intervals if observations revealed the impending loss of an existing tag. Using this procedure, some individuals were identifiable for more than six months.

After tagging, the maximum test diameter (MTD) of each individual was measured to the nearest millimeter using long-jawed calipers. The crevice occupied was also tagged. The positions of tagged individuals at each site were determined on several consecutive nights and randomly chosen nights thereafter. The following morning the positions were again noted. If an individual did not return to the same crevice, the crevice tag was moved to the new location. Data were obtained over four to ten consecutive nights. Weekly measurements were also made on some individuals for up to six months and casual observations continued in some cases for more than a year. The percent crevice fidelity of an individual was computed as the total number of times which that individual returned to its tagged crevice, divided by the total number of outings, times 100. These data were arcsine-transformed before statistical analyses.

The density of *Diadema antillarum* was determined at each tagging location in ten randomly thrown 1-m² quadrats. All density estimates were made at night when individuals were more evenly distributed.

Estimates of fish predator abundance at each site were made using a modification of the random swim technique in which absolute numbers of all potential fish predators of *Diadema antillarum* were counted over a 10-min period (Jones and Thompson, 1978; Helfman, 1983). Predator sizes were not recorded. Each census was repeated on six

consecutive days between 10.00 and 14.00 hrs. With the exception of *Diodon hystrix*, all known fish predators of *D. antillarum* are diurnal and include species in the families Balistidae, Labridae, Haemulidae and Sparidae (Randall, 1967). No *D. hystrix* were present at any site and few juveniles were encountered of any of the species censused. In order to weight each species by its importance as a predator of *D. antillarum*, the mean species abundances at each site were multiplied by the proportion of the gut contents that was represented by echinoids [mainly *D. antillarum*, as reported by Randall (1967)] for each fish species. These weighted species abundances were then summed over species for each site, yielding estimates of the degree of predation pressure. The mollusc *Cassis tuberosa*, another echinoid predator, was not present at any site.

To investigate how homing individuals utilize their foraging ranges, the positions of tagged individuals were determined at hourly intervals throughout the night for three consecutive nights. Although it is probable that individuals did not follow a straight-line path between hourly positions, such an estimate of nightly foraging paths allows inspection of the direction and area of the foraging range grazed each night. A mean direction of foraging (mean angle: Zar, 1974) for each night was calculated from the compass bearings of these hourly positions. The frequencies with which individuals foraged in the same or different quadrants (1–90, 91–180, 181–270, and 271–360 degrees, 0° = north) on consecutive nights were compared to the frequency distribution expected if the foraging directions were random. The expected probabilities were determined from the binomial distribution with $P = 0.25$ (the probability that any quadrant will be grazed on a given night). It follows that the probability of grazing the same quadrant the next night is $(0.25)^2$. Such comparisons were made for all individuals over the three successive nights. This field work was done in April, 1981 on a patch reef in Tague Bay (depth, 2 m).

To investigate whether *Diadema antillarum* can evaluate the quality of a crevice in terms of how much protection is provided, a relative measure of the readiness with which an individual would abandon a crevice was devised. I assumed that a sea urchin should be less likely to abandon a high-quality crevice than one of low-quality when a predation attempt occurred. Predation attempts were simulated by repeated probing of spines and test at five-second intervals. The number of probes required to initiate displacement of the individual was recorded. If 20 probes did not result in movement, I assumed that the individual would not abandon the crevice. The percent of the sea urchin test that was protected by the crevice was also estimated and provided a measure of crevice quality. An individual not inhabiting any crevice was given a value of zero percent test cover. An individual in a crevice allowing only the spines to protrude in one direction was assigned a maximum value of 80% cover. Test coverage of other individuals was estimated between these two extremes. This experiment was conducted at a Tague Bay backreef study site at mid-day and was repeated on 20
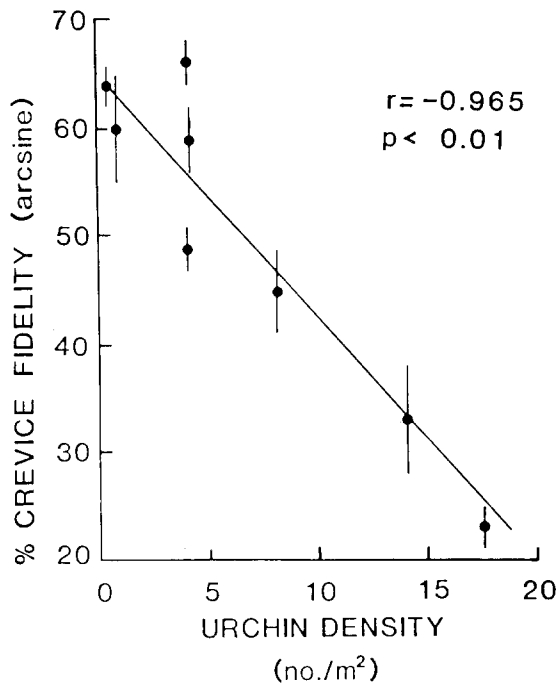
Fig. 1. *Diadema antillarum*. Relationship between % crevice fidelity (mean ±95% confidence limits, arcsine-transformed) and mean density (*n* = 10)

individuals in each of three size classes; small (30 to 50 mm, MTD), medium (51 to 70 mm) and large (>70 mm).

Results

Mean percent crevice fidelity varied among areas from 30 to 84% (Table 1). The majority of returns to a crevice by a homing individual were to the crevice originally tagged (81% for returns pooled over all sites). Returns to alternate crevices were more prevalent in areas where mean crevice fidelity was low. Crevice fidelity was negatively correlated with the density of *Diadema antillarum* (Fig. 1, $r = -0.965$, $P < 0.01$, partial correlation coefficient with predator abundance held constant: Sokal and Rohlf, 1981), indicating that individuals are more likely to home at low sea urchin densities.

The densities of *Diadema antillarum* were negatively correlated with the sums of the weighted predator abundances (Table 2) at each site (Table 3). Although the correlation between crevice fidelity and sea urchin density was the strongest, mean crevice fidelity across sites was positively correlated with the sums of the weighted predator abundances, even when sea urchin density was held
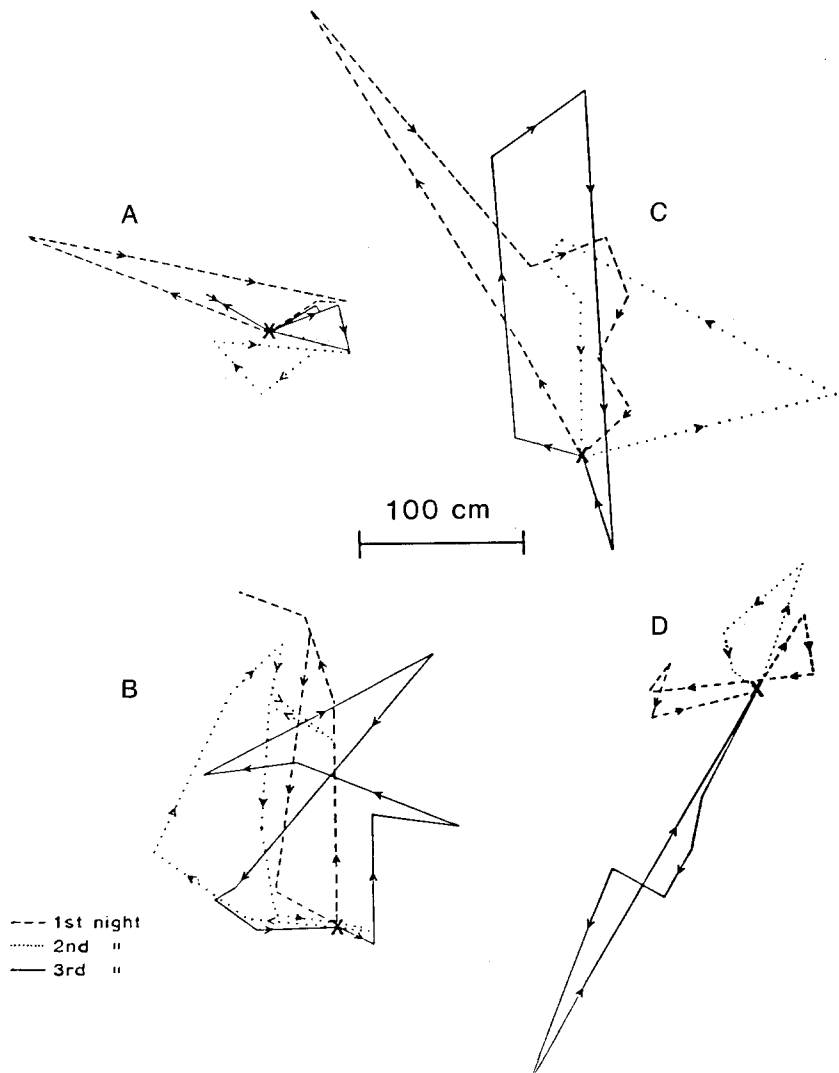
Fig. 2. *Diadema antillarum*. Estimated foraging paths from hourly positions of four homing individuals. Note the tendency for consecutive nightly paths not to overlap, especially for Individuals A, C and D (Table 4). Individual sizes: A – 47 mm, MTD; B – 87 mm; C – 79 mm; D – 59 mm. MTD: maximum test diameter

Table 1. *Diadema antillarum.* Depth, mean no. per m², mean individual sea urchin size, mean percent crevice fidelity ±SE, ranks of percent crevice fidelity and N's at each site. N(1)= no. of *D. antillarum* tagged. N(2)=N(1) times the number of nights followed

Site	Depth (m)	Mean no. m⁻²	Mean MTD (mm)	N(1)	N(2)	Mean % crevice fidelity ± SE
BI-L (Buck Island lagoon)	2	8.2	66.3	25	275	50.1 ± 3.3
BI-TR (Buck Island trail)	2	0.9	59.4	20	220	83.6 ± 2.8
TB-BR (Tague Bay backreef)	2.5	3.9	81.7	18	270	73.9 ± 2.5
TB-FR2 (Tague Bay forereef)	2	17.5	37.9	15	165	15.7 ± 1.4
TB-FR5 (Tague Bay forereef)	5	14.3	33.5	21	231	30.1 ± 3.5
TB-FR10 (Tague Bay forereef)	10	3.8	43.5	17	187	56.8 ± 2.3
BB (Boiler Bay)	1.5	1.5	75.2	6	42	75.5 ± 4.3

Table 2. Mean number (± SD) of fish predators of *Diadema antillarum* at each study site, and the proportion of the gut contents that is composed of echinoids, [the weighted species abundances at each site] and the sum of these abundances across species. The number of censuses for each site is six

Predator species (% of gut contents comprised of echinoids)	Buck Island lagoon	Buck Island trail	Tague Bay backreef	Tague Bay forereef (2 m)	Tague Bay forereef (5 m)	Tague Bay forereef (10 m)	Boiler Bay
Balistes vetula (queen trigger) (0.73)	0.2 (0.8) [0.15]	(2.1) (2.8) [1.53]	0	0	0	0.3 (0.5) [0.21]	0
Bodianus rufus (Spanish hogfish) (0.14)	0.7 (0.8) [0.10]	2.5 (1.6) [0.35]	1.3 (1.2) [0.18]	1.3 (1.0) [0.18]	2.1 (1.8) [0.29]	1.7 (1.6) [0.24]	0
Canthidermis sufflamen (ocean trigger) (0.25)	0	0.8 (0.8) [0.20]	0	0	0	0	0
Calamus bajonado (jolthead porgy) (0.45)	0.2 (0.4) [0.09]	1.3 (1.0) [0.59]	0.7 (0.8) [0.32]	0	0	0	0
Haemulon sciurus (blue-striped grunt) (0.09)	12.7 (5.3) [1.14]	20.2 (9.2) [1.82]	17.5 (7.1) [1.58]	4.3 (2.9) [0.39]	6.5 (3.3) [0.59]	12.0 (5.4) [1.08]	9.8 (4.0) [0.88]
Haemulon album (margate) (0.20)	0	0.5 (0.5) [0.10]	0	0.2 (0.4) [0.04]	0	0.2 (0.4) [0.04]	0
Halichoeres radiatus (puddingwife) (0.20)	1.0 (0.9) [0.20]	4.0 (1.4) [0.80]	2.7 (1.4) [0.54]	2.6 (2.3) [0.52]	1.8 (1.5) [0.36]	0.5 (0.8) [0.10]	4.7 (1.8) [0.94]
Lachnolaimus maximus (hogfish) (0.05)	0	1.7 (1.6) [0.09]	1.3 (1.5) [0.07]	0	0	0	0
Total weighted abundance	1.68	5.48	2.69	1.13	1.24	1.66	1.82

Table 3. *Diadema antillarum.* Correlation coefficients and levels of significance between % crevice fidelity, density and size of *D. antillarum,* and weighted predators-abundance. Percent crevice-fidelity values were arcsine-transformed and weighted predator abundances log-transformed, before analysis

Variables	Variable held constant	Partial corr. coefficient	Correlation coefficient	Level of significance
% crevice fidelity and density of *D. antillarum*	Predator abundance	−0.965	–	$P < 0.01$
% crevice fidelity and mean individual size of *D. antillarum*	–	–	0.755	$P < 0.05$
% crevice fidelity and mean individual size of *D. antillarum*	*D. antillarum* density	0.473	–	ns
% crevice fidelity and mean individual size of *D. antillarum*	Predator abundance	0.702	–	ns
% crevice fidelity and weighted predator abundance	*D. antillarum* density	0.725	–	$P < 0.067$
Density of *D. antillarum* and weighted predator abundance	–	–	−0.748	$P < 0.054$

Table 4. *Diadema antillarum.* Expected frequencies (based on binomial distribution) and observed frequencies of *D. antillarum* foraging in the same or different quadrants on successive nights. Frequency distributions are compared by the chi-square test for goodness of fit, $n = 8$

	Expected frequency	Observed frequency
Same quadrant grazed on consecutive nights $(P^2 = 0.0625)$	0.50	0
Different quadrants grazed on consecutive nights $[(1-P)^2 = 0.5625]$	4.50	8
Same quadrant grazed one night, different quadrant grazed other night $[2p(1-P) = 0.3750]$	3.00	0

$\chi^2 = 6.22$
$P < 0.014$
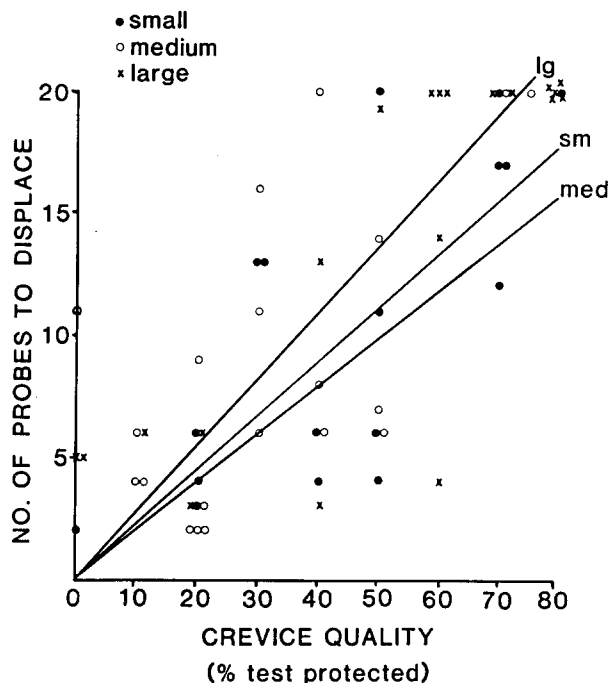
Fig. 3. *Diadema antillarum.* Relationship between the ease of displacement of *D. antillarum* (no. of probes) and crevice quality (percent of test protected) for three size classes: small, $r = 0.68$, $P < 0.01$; medium, $r = 0.63$, $P < 0.01$; large, $r = 0.83$, $P < 0.01$ ($n = 20$ for all size classes)

constant (Table 3). Homing behavior was much more prevalent at sites with higher estimated predation pressure.

The correlation of crevice fidelity and mean individual size was significant ($r = 0.755$, $P < 0.05$), but when sea urchin density was held constant, the partial correlation coefficient was not significant ($r = 0.473$). There was also no correlation between crevice fidelity and size when predator abundance was held constant (Table 3). This suggests that factors other than size are responsible for this

behavior and that size is weakly correlated with these factors.

The estimated foraging paths of four homing individuals (Fig. 2) show a tendency for different areas of the foraging range to be grazed on successive nights. The highly significant departure of the observed frequencies from those predicted by a random null hypothesis (Table 4) suggest that these sea urchins may be avoiding previously grazed areas.

In the simulated predation experiment, all size classes showed a significant correlation ($P < 0.01$) between the ease of displacement and the quality of the crevice (Fig. 3). A flight response was exhibited from low-quality crevices, whereas abandonment of high-quality crevices seldom occurred.

Discussion

Homing behavior

Homing specifically refers to the repeated occupation of the same location (Emlen, 1973). Although all "homing" individuals of *Diadema antillarum* in this study did not return to one crevice, the majority (> 80%) of the returns were to a specific crevice. All uses of the term homing or crevice fidelity in the remainder of this paper refer to this qualified definition.

Diel activity patterns in diadematids are generally considered a response to predation pressure (Ogden *et al.*, 1973; Fricke, 1974; other references in Lawrence, 1975). Such a relationship occurs with *Centrostephanus coronatus* and its major predator *Pimelometopon pulchrum* in California (Nelson and Vance, 1979). The results reported in the present study suggest that predator abundance also has a controlling effect on homing behavior.

Where potential predation pressure was greater, individuals were much more faithful to a given crevice. The relationship between predator abundance and crevice-fidelity behavior may be partially direct, but largely indirect. Predation reduces the population density of *Diadema antillarum*, which has been shown to partially control algal abundance in reef environments (Sammarco *et al.*, 1974; Carpenter, 1981). As a result, food resources become more abundant as sea urchin density decreases, possibly favoring the exclusive use of a single foraging range. Such a reduction in foraging range has been demonstrated for *Strongylocentrotus purpuratus* (Lowry and Pearse, 1973), *S. franciscanus* (Mattison *et al.*, 1977) and the limpet *Lottia gigantea* (Stimson, 1973). In addition, increased predation pressure will place a premium on the occupation of crevices that provide adequate diurnal protection. Crevices of this quality are probably limiting and the likelihood of finding another high-quality crevice on any given morning may be low, considering the mobility of an urchin. Therefore the repeated occupation of a crevice would be adaptive. The results of the simulated predation experiment suggest that *D. antillarum* can

evaluate crevice quality. *Diadema* spp. react to different light levels (Millot, 1953, 1954) and dark shapes (Woodley, 1982); crevice evaluation may therefore be a photo-sensitive response to how much of the test is shaded. This is supported by observations that sea urchins in areas with higher potential predation pressure more often inhabit crevices that cover more of the test (Carpenter, personal observation).

Individual size was not correlated with crevice fidelity when density or predator abundance were held constant. Although homing individuals are usually larger than non-homing individuals, this appears to be more a density-related result, controlled by predation pressure, rather than a purely size-dependent behavior. Although the trend for data pooled across sites would suggest that large individuals home more frequently than small ones, similar to Nelson and Vance's (1979) findings for *Centrostephanus coronatus*, the within-site determinant appears to be predation pressure which may alleviate resource competition between *D. antillarum* individuals, thereby directly controlling sea urchin density and indirectly controlling individual size and behavior (Table 5).

Although little is known about the larval dispersal of *Diadema antillarum*, it is probable that settling larvae are transported by currents and settle outside the area where the gametes were spawned. Since predator abundance is naturally variable and regional fishing pressure adds to this variability, the predation pressures encountered by settling larvae may well be different than those encountered by the parents. As a result, the degree of homing behavior exhibited by sea urchins may vary in response to local predation intensity. Unsuccessful predation attempts could provide a stimulus for exhibiting this behavior, as Lawrence (1975) suggested for diadematid diel activity patterns. When predation pressure is reduced or eliminated, individuals may be released from this behavior (Fricke, 1974). This is evident in some reef areas of St. Croix and Jamaica, where *D. antillarum* individuals often feed in the open during the day (Carpenter, personal observation). Under such conditions, homing could be disadvantageous due to a reduction in the time available for feeding. Such a behavioral shift could lead to intense overgrazing of the algal community.

Table 5. Summary of the relationships between sea urchin predator abundance, population density of *Diadema antillarum*, algal food abundance, individual *D. antillarum* size and the degree to which crevice-fidelity behavior is exhibited by this sea urchin

abundant	Sea urchin predators	rare
low	*D. antillarum* population density	high
high	Algal food abundance	low
large	*D. antillarum* size	small
frequent	Crevice-fidelity behavior	rare

Foraging range use

As a result of being limited to a restricted range, homing sea urchins are also limited with respect to food resources. Individuals do not graze the same areas on successive nights and the lack of randomness in the distribution of their foraging directions indicates an avoidance of previously grazed areas. *Diadema antillarum* grazes the substratum, removing attached algal filaments (Carpenter, 1981) and algal crusts (Hawkins, 1981). Many of the filaments have upright portions that arise from a creeping basal filament attached to the substratum by rhizoids. Observations of areas grazed by *D. antillarum* reveal that these basal filaments often remain and quickly regenerate upright branches. Although foraging data were only obtained over three consecutive nights, this interval is sufficient for the regeneration of the algal community in the grazed areas (Carpenter, unpublished data). Sea urchins are known to have the chemosensory ability to detect and move toward food items (see references in Lawrence, 1975; Sloan and Campbell, 1982). This ability may allow *D. antillarum* to recognize areas that have not been recently grazed, similar to what Scheibling (1981) suggested for a deposit-feeding asteroid. Since fecal pellet production is more or less continuous in *D. antillarum*, another possible hypothesis is that areas with fecal pellets are avoided as an indication of areas recently grazed. Fecal pellets remain on the substratum for at least 2 to 3 d, depending on turbulence (based on repeated close-up photographs of marked areas containing fecal pellets: Carpenter, unpublished data). Nelson and Vance (1979) also found that *Centrostephanus coronatus* did not forage along the same path every night.

Areas close to the home crevice should be grazed more often than those further away, assuming that a sea urchin feeds as it moves (an energetically feasible assumption as long as food is encountered along the way). Although other grazers (herbivorous fishes) utilize the same areas, a pattern of increasing algal biomass outward from crevices harboring *Diadema antillarum* is evident (Carpenter, unpublished data) and supports this hypothesis. This may provide a natural test of the intermediate disturbance hypothesis (Paine, 1966; Connell, 1978; Lubchenco, 1978; Hixon and Brostoff, 1983) and the effects of grazing intensity on algal species diversity. Such effects have been demonstrated experimentally using cages with sea urchins at different densities (Carpenter, 1981; Sammarco, 1982) and with algal substrata placed inside and outside damselfish territories (Hixon and Brostoff, 1983).

The abundances of *Diadema antillarum* in several areas of the Caribbean may be elevated in areas with high fishing pressure (Hay, 1984). Presumably this is the result of the removal of sea urchin predators. This present study suggests that release from predation pressure may lead to behavioral modifications that result in more time available for feeding (abandonment of homing). Combined with increased sea urchin density, this may lead to an overgrazed algal community and a reduction in the survival of settling

corals (Sammarco, 1980). Sea urchins can also excavate the carbonate substratum (Ogden, 1977; Stearn and Scoffin, 1977) and further modify the habitat. Under such conditions *D. antillarum* may have a profound effect on both the biological and physical structure of a coral reef. The relationship between predator abundance, sea urchin behavior and the effects of overgrazing on coral reef structure may be analogous to the sea otter–sea urchin–kelp (Estes and Palmisano, 1974; Duggins, 1980) and lobster–sea urchin–kelp (Mann and Breen, 1972; Wharton and Mann, 1981) relationships that have been documented in temperate rocky habitats on the west and east coasts of North America.

Literature cited

Birkeland, C. and B. D. Gregory: Feeding behavior of a tropical predator *Cyphoma gibbosum* Linnaeus. *In:* Tektite 2. Scientists in the sea, pp VI-58–VI-69. Ed. by J. W. Miller and J. G. Vanderwalker. Washington: U.S. Department of the Interior 1971

Carpenter, R. C.: Grazing by *Diadema antillarum* Philippi and its effects on the benthic algal community. J. mar. Res. *39*, 749–765 (1981)

Connell, J. H.: Diversity in tropical rain forests and coral reefs. Science, N.Y. *199*, 1302–1310 (1978)

Cook, A.: Homing in the Gastropoda. Malacologia *18*, 315–318 (1979)

Duggins, D. O.: Kelp beds and sea otters: an experimental approach. Ecology *61*, 447–453 (1980)

Emlen, J. M.: Ecology: an evolutionary approach. Reading, Massachusetts: Addison-Wesley 1973

Estes, J. A. and J. F. Palmisano: Sea otters: their role in structuring nearshore communities. Science, N.Y. *185*, 1058–1060 (1974)

Fricke, H. W.: Möglicher Einfluß von Feinden auf das Verhalten von *Diadema*-Seeigeln. Mar. Biol. *27*, 59–64 (1974)

Gladfelter, W. B., E. H. Gladfelter, D. K. Hubbard, R. C. Carpenter and G. J. Simpson: Environmental studies of Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. Report to the Department of Interior, National Park Service 1979

Grünbaum, H. G., D. P. Abbott and J. C. Ogden: Intraspecific agonistic behavior in the rock-boring sea urchin *Echinometra lucunter* (L.) (Echinodermata: Echinoidea). Bull. mar. Sci. *28*, 181–188 (1978)

Hawkins, C. M.: Efficiency of organic matter absorption by the tropical echinoid *Diadema antillarum* Philippi fed non-macrophytic algae. J. exp. mar. Biol. Ecol. *49*, 245–253 (1981)

Hay, M. E.: Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology *65*, 446–454 (1984)

Helfman, G. S.: Underwater methods. *In:* Fisheries techniques manual, Chapter 19, pp 349–369. Ed. by L. A. Nielsen and D.

L. Johnson. Bethesda, Maryland: American Fisheries Society 1983

Hixon, M. A. and W. N. Brostoff: Damselfish as keystone species in reverse: intermediate disturbance and diversity of reef algae. Science, N.Y. *220*, 511–513 (1983)

Jones, R. S. and M. J. Thompson: Comparison of Florida reef fish communities by the employment of a rapid visual technique. Bull. mar. Sci. *28*, 159–172 (1978)

Lawrence, J. M.: On the relationship between marine plants and sea urchins. Oceanogr. mar. Biol. A. Rev. *13*, 213–286 (1975)

Lowry, L. F. and J. S. Pearse: Abalones and sea urchins in an area inhabited by sea otters. Mar. Biol. *23*, 213–219 (1973)

Lubchenco, J.: Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. *112*, 23–39 (1978)

Mann, K. H. and P. A. Breen: The relationship between lobster abundance, sea urchins and kelp beds. J. Fish. Res. Bd Can. *29*, 603–605 (1972)

Mattison, J. E., J. D. Trent, A. L. Shanks, T. B. Akin and J. S. Pearse: Movement and feeding activity of red sea urchins (*Strongylocentrotus franciscanus*) adjacent to a kelp forest. Mar. Biol. *39*, 25–30 (1977)

Millot, N.: Light emission and light perception in species of *Diadema*. Nature, Lond. *171*, 973–974 (1953)

Millot, N.: Sensitivity to light and the reactions to changes in light intensity of the echinoid *Diadema antillarum* Philippi. Phil. Trans. R. Soc. *238*, 187–220 (1954)

Mortensen, T.: A monograph of the Echinoidea. III, I. *Aulodonta*. Copenhagen: C. A. Reitzel 1940

Nelson, B. V. and R. R. Vance: Diel foraging patterns of the sea urchin *Centrostephanus coronatus* as a predator avoidance strategy. Mar. Biol. *51*, 251–258 (1979)

Ogden, J. C.: Carbonate-sediment production by parrotfish and sea urchins on Caribbean reefs. Bull. Am. Assoc. Pet. Geol. *4*, 281–288 (1977)

Ogden, J. C., R. A. Brown and N. Salesky: Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. Science, N.Y. *182*, 715–716 (1973)

Paine, R. T.: Food web complexity and species diversity. Am. Nat. *100*, 56–75 (1966)

Randall, J. E.: Food habits of reef fishes of the West Indies. Stud. trop. Oceanogr. *5*, 665–847 (1967)

Randall, J. E., R. E. Schroeder and W. A. Starck: Notes on the biology of the echinoid *Diadema antillarum* Caribb. J. Sci. *4*, 421–433 (1964)

Sammarco, P. W.: *Diadema* and its relationship to coral spat mortality: grazing, competition and biological disturbances. J. exp. mar. Biol. Ecol. *45*, 245–272 (1980)

Sammarco, P. W.: Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. J. exp. mar. Biol. Ecol. *65*, 83–105 (1982)

Sammarco, P. W., J. S. Levinton and J. C. Ogden: Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. J. mar. Res. *32*, 47–53 (1974)

Scheibling, R. E.: Optimal foraging movements of *Oreaster reticulatus* (L.) (Echinodermata: Asteroidea). J. exp. mar. Biol. Ecol. *51*, 173–185 (1981)

Sloan, N. and A. Campbell: Perception of food. *In:* Echinoderm nutrition. Ed. by M. Jangoux and J. M. Lawrence. Rotterdam: A. A. Balkema 1982

Sokal, R. R. and F. J. Rohlf: Biometry, the principles and practice of statistics in biological research, 2nd ed., 859 pp. San Francisco, Calif.: W. H. Freeman 1981

Stearn, C. W. and T. P. Scoffin: Carbonate budget of a fringing reef, Barbados. Proc. Third Int. Coral Reef Symp. *2*, 471–476 (1977)

Stimson, J.: The role of the territory in the ecology of the intertidal limpet *Lottia gigantea* (Gray). Ecology *54*, 1020–1030 (1973)

Thorton, I. W. B.: Diurnal migrations of the echinoid *Diadema setosum* (Leske). Br. J. Anim. Behav. *4*, 143–146 (1956)

Vance, R. R.: Effects of grazing by the sea urchin, *Centrostephanus coronatus*, on prey community composition. Ecology *59*, 679–685 (1979)

Vance, R. R. and R. J. Schmitt: The effect of predator-avoidance behavior of the sea urchin, *Centrostephanus coronatus*, on the breadth of its diet. Oecologia *44*, 21–25 (1979)

Wharton, W. G. and K. H. Mann: Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus ameri-canus*, on the Atlantic coast of Nova Scotia. Can. J. Fish. aquat. Sci. *38*, 1339–1349 (1981)

Woodley, J. D.: Photosensitivity of *Diadema antillarum:* does it show scototaxis? Abstract. *In:* Echinoderms: Proc. Int. Conf., Tampa Bay. Ed. by J. M. Lawrence. Rotterdam: A. A. Balkema 1982

Zar, J. H.: Biostatistical analysis. Englewood Cliffs, New Jersey: Prentice-Hall 1974