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Substratum-dependent predator–prey dynamics: patch reefs as refuges from gastropod predation

Don R. Levitan¹ and Salvatore J. Genovese²

¹Ecology Program, School of Life and Health Sciences, University of Delaware, Newark, Delaware, U.S.A.

²Department of Biology, Swarthmore College, Swarthmore, Pennsylvania, U.S.A.

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Abstract: The impact of the gastropod predator *Cassia tuberosa* (Linnaeus) on the local distribution of the sea urchin *Diadema antillarum* Philippi was investigated. Artificial reefs stocked with *Diadema* were established 5 m off the fringing reef of St John, US Virgin Islands. *Cassia* preyed upon 17% of the urchins after 30 days. All predation by *Cassia* occurred on sand rather than on artificial reefs or a nearby fringing reef. Arenas containing a single *Diadema* and *Cassia* were set up with sand, flat rock and piled rock habitats. This resulted in urchin mortality of 70, 40 and 10% for the three treatment groups, respectively. The results suggest that *Diadema* distribution and foraging may be restricted to reef habitats by predation pressure. The risks of mortality from predation may outweigh the costs of remaining in high-density food-limited conditions.

Key words: *Cassia tuberosa*; Coral Reef; *Diadema antillarum*; Predator–prey; Refugium

INTRODUCTION

Predation pressure can exert a dominant influence on the distribution and abundance of prey organisms (Paine, 1966, 1976; Zaret & Paine, 1973; Lubchenco & Menge, 1978). In many cases, predators can limit the distribution of prey organisms to discrete refugia (Jackson, 1961; Stein, 1977; Nelson & Vance, 1979; Bertness et al., 1981; Mittelbach, 1984; Witman, 1985). When predator-free space is suboptimal for the prey, there exists a possible trade-off between living in a poor habitat vs. facing the risks of predation (Stein & Magnuson, 1976; Sih, 1982; Werner et al., 1983). Living in refugia may result in increased competition and food limitation and, therefore, result in depressed growth rates, reduced fecundity and, possibly, starvation (Werner et al., 1983; Buss, 1986; Kareiva, 1986; Werner, 1986). For selection to favor these costs, the risk of predation must be sufficiently high to limit migration.

The tropical sea urchin *Diadema antillarum* Philippi may periodically face a trade-off between food limitation and the risk of mortality due to migration. Prior to the Caribbean-wide mass mortality, occurring between 1983 and 1984 (Lessios et al., 1984),

Correspondence address: D. R. Levitan, Ecology Program (SLHS), University of Delaware, Newark, DE 19716, U.S.A.

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Diadema was often found in high abundance (e.g., $72 \cdot \text{m}^{-2}$; Sammarco, 1980) and exhibited an inverse relationship between body size and population density (Carpenter, 1981; Hunte et al., 1986; Levitan, 1988a). This relationship was due to individual urchins regulating body size in response to food limitation (Levitan 1988a, in press). Further evidence of food limitation comes from the effects of the mass mortality. Following the mortality event, median urchin body size increased from 20 to 200 g, suggesting a release of body size from food limitation (Levitan, 1988b).

Despite the evidence that *Diadema* was food-limited, resources were available only meters away from these urchins. The fringing reefs of St John, US Virgin Islands, are separated from seagrass beds by a sand halo only 5–10 m wide. The formation of this sand halo is due to herbivory. Ogden et al. (1973) removed *Diadema* from a patch reef, on St Croix, and noted that seagrass quickly filled in the halo. They also examined migration of *Diadema* over a diel cycle and noted that a small percentage (7–9%) of the urchins migrated into the halo to graze at night. However, they also reported that *Diadema* never entered the grass beds to feed; foraging was restricted to the reef and several meters into the halo. Observations of *Diadema* foraging on St John indicated no significant movement of *Diadema* towards the halo or grass beds (D. R. Levitan, unpubl. data). In fact, during the 5 yr following the *Diadema* mass mortality, the halos surrounding the fringing reefs of St John remained sandy and free of seagrass (pers. obs.). This study was conducted within the boundaries of the US Virgin Islands National Park and fish abundance was high (pers. obs.). Apparently, on St John, fish herbivory is important in maintaining reef halos.

It is possible that predators present in the halo and grass beds limit the foraging range of *Diadema*, thus restricting this urchin to food-limited conditions on the reef. Previous researchers (Ogden et al., 1973; Fricke, 1974; Nelson & Vance, 1979; Carpenter, 1984) have suggested that diademid urchins graze nocturnally to avoid diurnal predators. We investigated predation pressure on *Diadema* in the halo to estimate the risks associated with migrating out of food-limited conditions on the reef.

METHODS

ARTIFICIAL REEF EXPERIMENT

To determine predation rates on *Diadema* in halos, five artificial reefs were constructed in Lameshur Bay, St John. The reefs were 1 m^2 in area, ≈ 30 cm high, 30 m apart and 5 m off the fringing reef. The artificial reefs were built with rocks from the nearby reef and had crevices large enough to provide refuges for *D. antillarum*.

On 2 March 1986, the artificial reefs were each stocked with 20 urchins. Each urchin was measured (vernier calipers) and tagged (Carpenter, 1984) with two 5-mm pieces of surgical tubing placed around a spine. The tags were cut in different patterns to allow individual identification. Two tags were used so if one was lost the urchin could still be identified. Daily, between 0900 and 1200, for 30 days, the artificial reefs were

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monitored and the position (on the artificial reef, distance from the artificial reef, on the fringing reef, or missing) and status (alive or dead, if preyed upon, by what) of the urchins were recorded. Predation by the gastropod *Cassia tuberosa* (Linnaeus) leaves a dead urchin pressed into the sand with a 5-mm hole rasped into the test. When an urchin was eaten, or had moved > 5 m away from the reef, it was replaced with another urchin that was not tagged but had one-fourth of the spines shaved off for identification. These urchins maintained experimental densities but were not used as data.

On 26 April 1986, the experiment was repeated with new urchins. This time urchins were not tagged (since tag loss was frequent in the previous experiment) and experimental densities were not maintained with additional urchins.

ARENA EXPERIMENT

To determine if *Cassia* predation rates varied on different substrata, 1-m² arenas were placed in Lameshur Bay. Three round arenas with tops were constructed from hardware cloth and placed on a sand bottom at a depth of 3 m. One arena was left with a sand bottom, the second arena was covered with a flat rock bottom and the third arena had rock piled on the bottom, providing cryptic refuges. All cages were high enough to allow *Cassia* to lift its shell to attack prey but not high enough to allow urchins to climb away from *Cassia*.

The *Cassia* used in the experiments ($n = 6$, size range 15–21 cm in length) were collected from Lameshur Bay and stored in underwater cages near the arenas. All *Cassia* were starved for 2 days before being used in an experiment. Three *Cassia* were chosen randomly and one was placed in each arena, with a *Diadema*, for 48 h. The urchin was measured and only used once. A total of 20 trials was run for each treatment; the success of predation was recorded after 24 and 48 h.

SPEED OF MOVEMENT

It may be that *Diadema* does not enter the grass to feed because of the time required to travel across the halo. If this time is great compared to the time available to graze at night, then grazing in the grass beds may not be cost-effective. To measure the speed of *Diadema* movement across sand substratum, urchins were placed on a sand bottom and stimulated to move by tapping the spines with a metal probe. Markers set behind the urchin were later used to measure the distance moved in 3 min (20 trials).

RESULTS

ARTIFICIAL REEF EXPERIMENT

For both trials, 17% of the *Diadema* were preyed upon by *Cassia*. Successful *Cassia* predation occurred only while the urchins were off the artificial reef in the sand halo. On the one occasion, when *Cassia* was seen attacking *Diadema* on the artificial reef, the

TABLE I

Artificial reef experiment. In both trials, there were five replicate islands and 20 urchins · island

Fate	Trial 1			Trial 2			\bar{x}
	\bar{x}	SD	%	\bar{x}	SD	%	%
Remained on artificial reef	6.8	2.8	34	2.0	1.7	10	22
Migrated to fringing reef	7.0	3.1	35	6.6	4.8	33	34
Migrated and preyed upon by							
<i>Cassisi</i>	3.4	1.9	17	3.4	2.3	17	17
other	0.4	0.5	2	0.2	0.4	1	1.5
Unknown	2.2	2.3	11	8.0	3.4	40	25.5

attempt was unsuccessful and the urchins on the reef scattered. Of those urchins that left the reef, 22% were preyed upon by *Cassisi* (Table I). We directly observed *Cassisi* predation several times. *Cassisi* would locate the urchin, apparently by olfaction, using its siphon. When the urchin was several centimeters away, the helmet would reach out with one eye-stalk and stimulate the test of the urchin. The urchin would direct half of its spines to the side of the stimulus. The helmet shell would then stimulate the other side of the urchin with the other eye-stalk and the urchin would direct the rest of the spines towards that side. At this point, the urchin would have its spines parted in the middle, exposing the top portion of the test. The helmet shell would then rear up and crash down on the urchin, digging its radula into the urchin.

A large number (40%) of urchins had an unknown fate in the second trial as compared to the first trial (10%). Most of this difference was due to a decrease in the number of *Diadema* remaining on the artificial reefs (10% as compared to 34%). During the second trial, a large storm passed over St John creating a strong wave surge over the artificial reefs. The disruptive nature of the storm and the deletion of tagging in the second trial are possible explanations for the increase in missing urchins.

ARENA EXPERIMENT

Predation by *Cassisi* was most successful on sand bottom (70%), followed by flat rock bottom (40%) and finally the spatially heterogenous rock bottom (10%) (Table II). Sandy substratum was associated with significantly higher predation than rocky (flat or heterogenous) substrata and flat substrata (sand and flat rock) had significantly higher predation than heterogenous substrata (*G* tests of independence, Table II). Successful predation events generally occurred during the first 24 h of the trial (83%). Nonlethal injuries due to unsuccessful attacks were only seen in rock treatments (three times on flat and two times on piled rock treatments).

Although *Cassisi* was ineffective at preying on *Diadema* on rocky substrata, it is often found on the reef; 75% of the helmets collected for this experiment were found on reef

habitats. In addition, > 50% of the tests of the sea urchin *Echinometra viridis* collected from St John reefs had a gastropod drill hole (D. R. Levitan, unpubl. data). Although this is a biased estimate (since this sample only contains intact tests), it appears that gastropod predation on the reef may be an important source of mortality for some less mobile echinoid species.

TABLE II
C. tuberosa predation experiment. Fate of urchins in three treatment groups and *G* tests of independence.

Treatment	Eaten	Survived	Total
Flat sand	14	6	20
Flat rock	8	12	20
Piled rock	2	18	20
Total	24	36	60

R × C <i>G</i> tests		
Test	<i>G</i>	<i>P</i>
All treatments	8.22	<0.025
Sand vs. rock	5.68	<0.025
Flat vs. piled	6.36	<0.010

SPEED OF MOVEMENT

We determined that *Diadema* can move 292.3 cm in 3 min (SD = 44.2). Since the grass beds are 5–10 m away from the reef, it would take a minimum of 5–10 min to cross the sand halo. The time required to cross the halo is slight compared to the nocturnal time available to graze.

DISCUSSION

The artificial reef study indicates that *Diadema* faces a high mortality risk while in the sand halo. There was no evidence of *Cassiss* predation on the reef, however, 22% of the urchins which left the reef were preyed upon by *Cassiss*. If some of the missing urchins were also preyed upon by *Cassiss*, the estimate could be as high as 56%. The arena experiment indicates that the risk of predation is associated with substratum type; *Cassiss* is much more efficient a predator on sand than on rocky substrata. The type of substratum and topographic relief can deter *Cassiss* predation on *Diadema*.

The majority of urchins (78%) were off the artificial reefs after 30 days. This emigration could be due to the small refuge size and flight response of *Diadema*. *D. antillarum* exhibits a flight response to both *Cassiss* (Snyder & Snyder, 1970) and crushed conspecifics (Snyder & Snyder, 1970; Parker & Shulman, 1986). We observed

Diadema scattering when *Cassia* moved on the artificial reefs. Since the artificial reefs were small, a flight response of 10–20 cm could place urchins off the reef [Parker & Shulman (1986) noted flight responses of this magnitude]. Once off the reef, the urchins may have continued to migrate in search of suitable refugia.

The majority of the dead urchins found were killed by the gastropod *Cassia* but predation by fish may be important and could partially explain the fate of the missing urchins (25.5%). Randall (1967) documented 15 species of fish predators on *Diadema*. Since fish are more mobile than *Cassia* as predators, they may be more efficient at preying on *Diadema* in reef habitats. *Diadema* is scototaxic, remaining in crevices during daylight hours, possibly to protect themselves from fish predators. This response also may be responsible for the aggregative behavior seen in this black urchin (Woodley, 1982); aggregative behavior does not appear to be linked to the reproductive cycle (Levitan, 1988c). When a *Diadema* is in a crevice or next to a conspecific, this protection may deter fish predators that try to circumvent its poisonous spines. Carpenter (1984) observed that high predation pressure by fish is correlated with low *Diadema* density and high crevice fidelity.

The predation pressure that influences *Diadema* activity is likely to be due to both fish and invertebrates. Visual predators, such as fish, induce aggregative behavior and crevice fidelity during the day. Olfactory predators, such as gastropods, limit foraging to spatially heterogeneous refuges at night. The ubiquity of *Cassia* predation limiting *Diadema* foraging in other locations will be difficult to assess without experimentation. It is an onerous task estimating the abundance of this burrowing gastropod. We did not realize the abundance or impact of this predator until we witnessed them erupting out of the sand during our artificial reef experiment.

Organisms at high density may be food-limited. This can result in reduced fecundity and increased mortality (Frank et al., 1957; Spight & Emlen, 1976; Keller, 1983). Another response to food-limited conditions is dispersal (Vadas et al., 1986). When emigration requires leaving a suitable habitat, in a patchy environment, the risks of migration increase. There is a risk of mortality while crossing unsuitable habitat. There is also a chance of not finding another suitable location. Finally, there is the risk that if suitable habitat is found, it may not be better than the habitat the organism left.

The fitness costs associated with high-density food-limited conditions are reduced for *Diadema*. This urchin has the capacity to reduce body size so that energy requirements can be lowered when resources are scarce (Levitan, 1988a, in press). The reduction in gamete number associated with reduced size can be compensated for by increased fertilization success, due to high population density (Pennington, 1985; Levitan 1988c, 1989). The risks of mortality on a sandy substratum or in the grass beds may outweigh the costs of remaining on the reef under high-density food-limited conditions since (1) crevices and aggregative behavior may provide a refuge from predators, (2) high local density may be important for fertilization success and (3) *Diadema* does not suffer increased mortality when food-limited.

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REFERENCES

- Bertness, M.D., S.D. Garrity & S.C. Levings, 1981. Predation pressure and gastropod foraging: a tropical-temperate comparison. *Evolution*, Vol. 35, pp. 995-1007.
- Buss, L.W., 1986. Competition and community organization on hard surfaces in the sea. In, *Community ecology*, edited by J. Diamond & T.J. Case, Harper & Row, New York, pp. 517-536.
- Carpenter, R.C., 1981. Grazing by *Diadema antillarum* (Philippi) and its effect on the benthic algal community. *J. Mar. Res.*, Vol. 39, pp. 749-765.
- Carpenter, R.C., 1984. Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. *Mar. Biol.*, Vol. 82, pp. 101-108.
- Frank, P.W., S.D. Boll & R.W. Kelly, 1957. Vital statistics of laboratory cultures of *Daphnia pulex* De Geer as related to density. *Physiol. Zool.*, Vol. 30, pp. 287-305.
- Fricke, H.W., 1974. Möglicher Einfluß von Feinden auf das Verhalten von *Diadema*-Seeigeln. *Mar. Biol.*, Vol. 27, pp. 59-64.
- Hunte, W., I. Cote & T. Tomascik, 1986. On the dynamics of the mass mortality of *Diadema antillarum* in Barbados. *Coral Reefs*, Vol. 4, pp. 135-139.
- Jackson, P.B.N., 1961. The impact of predation, especially by the tiger-fish (*Hydrocyon vitatus* Cast.) on African freshwater fishes. *Proc. Zool. Soc. London*, Vol. 136, pp. 603-622.
- Kareiva, P., 1986. Patchiness, dispersal, and species interaction: consequences for communities of herbivorous insects. In, *Community ecology*, edited by J. Diamond & T.J. Case, Harper & Row, New York, pp. 192-206.
- Keller, B.D., 1983. Coexistence of sea urchins in seagrass meadows, an experimental analysis of competition and predation. *Ecology*, Vol. 64, pp. 1581-1598.
- Lessios, H.A., D.R. Robertson & J.D. Cubit, 1984. Spread of *Diadema* mass mortalities through the Caribbean. *Science*, Vol. 226, pp. 335-337.
- Levitan, D.R., 1988a. Density-dependent size regulation and negative growth in the sea urchin *Diadema antillarum* Philippi. *Oecologia (Berlin)*, Vol. 76, pp. 627-629.
- Levitan, D.R., 1988b. Algal-urchin biomass responses following the mass mortality of *Diadema antillarum* Philippi at St John. *J. Exp. Mar. Biol. Ecol.*, Vol. 119, pp. 167-178.
- Levitan, D.R., 1988c. Asynchronous spawning and aggregative behavior in the sea urchin *Diadema antillarum* Philippi. In, *Echinoderm biology*, edited by R. Burke et al., A.A. Balkema, Rotterdam, The Netherlands, pp. 181-186.
- Levitan, D.R., 1989. Life history and population consequences of body size regulation on the sea urchin *Diadema antillarum* Philippi. Ph.D. diss., University of Delaware, Newark, Delaware, 209 pp.
- Levitan, D.R., in press. Density-dependent size regulation in *Diadema antillarum*: effects on fecundity and survivorship. *Ecology*.
- Lubchenco, J. & B.A. Menge, 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.*, Vol. 48, pp. 67-94.
- Mittelbach, G.G., 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology*, Vol. 65, pp. 499-513.
- Nelson, B.V. & R.R. Vance, 1979. Diel foraging patterns of the sea urchin *Centrostephanus coronatus* as a predator avoidance strategy. *Mar. Biol.*, Vol. 51, pp. 251-258.
- Ogden, J.C., R.A. Brown & N. Salesky, 1973. Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science*, Vol. 182, pp. 715-717.
- Paine, R.T., 1966. Food web complexity and species diversity. *Am. Nat.*, Vol. 100, pp. 65-75.
- Paine, R.T., 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology*, Vol. 57, pp. 858-873.

- Parker, D. A. & M. J. Shulman, 1986. Avoiding predation: alarm responses of Caribbean sea urchins to simulated predation on conspecific and heterospecific sea urchins. *Mar. Biol.*, Vol. 93, pp. 201-208.
- Pennington, J. T., 1985. The ecology of fertilization of echinoid eggs: the consequence of sperm dilution, adult aggregation, and synchronous spawning. *Biol. Bull. (Woods Hole, Mass.)*, Vol. 169, pp. 417-430.
- Randall, J. E., 1967. Food habits of reef fish of the West Indies. *Stud. Trop. Oceanogr.*, Vol. 5, pp. 665-847.
- Sammarco, P. W., 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *J. Exp. Mar. Biol. Ecol.*, Vol. 45, pp. 245-272.
- Sih, A., 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notoneta hoffmanni*. *Ecology*, Vol. 63, pp. 786-796.
- Snyder, N.F.R. & H. A. Snyder, 1970. Alarm responses of *Diadema antillarum*. *Science*, Vol. 168, pp. 276-278.
- Spight, T. M. & J. Emlen, 1976. Clutch sizes of two marine snails with a changing food supply. *Ecology*, Vol. 57, pp. 1162-1178.
- Stein, R. A., 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology*, Vol. 58, pp. 1237-1253.
- Stein, R. A. & J. J. Magnuson, 1976. Behavioral response of crayfish to a fish predator. *Ecology*, Vol. 57, pp. 751-761.
- Vadas, R. L., R. W. Elnor, P. E. Garwood & I. G. Babb, 1986. Experimental evaluation of aggregative behavior in the sea urchin *Strongylocentrotus droebachiensis*: a reinterpretation. *Mar. Biol.*, Vol. 90, pp. 433-448.
- Werner, E. E., 1986. Species interactions in freshwater fish communities. In, *Community ecology*, edited by J. Diamond & T. J. Case, Harper & Row, New York, pp. 344-358.
- Werner, E. E., J. F. Gilliam, D. J. Hall & G. G. Mittelbach, 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, Vol. 64, pp. 1540-1548.
- Witman, J. D., 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. *Ecol. Monogr.*, Vol. 55, pp. 421-445.
- Woodley, J. D., 1982. Photosensitivity of *Diadema antillarum*: does it show scototaxis? In, *Int. Echinoderm Conf. Tampa Bay*, edited by J. M. Lawrence, A. A. Balkema, Rotterdam, The Netherlands, p. 61.
- Zaret, T. M. & R. T. Paine, 1973. Species introduction in a tropical lake. *Science*, Vol. 182, pp. 449-453.