

Niche Partitioning among three
species of Caribbean sea urchins:
Diadema antillarum, Echinometra
viridis and Tripleneustes ventricosus

Liz and Kim:

A nice study with a very
good discussion of your
results.

John

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Abstract:

Each of the three most abundant species of sea urchin around coral reefs at Discovery Bay, Jamaica (Diadema antillarum, Tripneustes ventricosus and Echinometra viridis) seems to dominate a geographically defined core area and occur only infrequently outside this core area. This study investigates the possible causes of spatial separation of species as well as the mechanisms that might maintain habitat differentiation such as partitioning of resources. A series of transects characterized the differential dispersions of the three sea urchin species studied. Feeding tests run under lab conditions attempted to ascertain the food preferences of the urchin species. Urchin encounter tests, also run under lab conditions, assessed the extent of both intra- and interspecific urchin interactions, including aggression. Finally, field tests in which ten urchins were introduced into an area already occupied by urchins provided a measure of an area's ability to support more than its natural concentration of urchins.

Introduction:

Tripneustes ventricosus, Diadema antillarum and Echinometra viridis are three species of urchins occurring sympatrically among the coral reefs of Discovery Bay, Jamaica. Tripneustes is largest of the three species with a test diameter ranging approximately from 8 cm to 13 cm. Many dense white 1-1.5 cm spines cover the pinkish test and black pedicellaria darken the 5 ambulacral plates. Tripneustes occurs

almost exclusively in the Thalassia beds of the back reef. Here, Thalassia dominates the flora, interspersed with occasional green calcareous algae such as Penicillus and Udotea. The Thalassia beds constantly sway with wave motion. The substrate of the entire bed is coral sand and organic sediments. Infrequently, an old head of coral rises above the Thalassia and breaks the otherwise uniform field.

The Diadema antillarum dealt with in this study ranged from approximately 5-7.5 cm test diameter. Smaller Diadema do occur in deeper areas of the reef. Diadema is a purplish black with iridescent blue markings close to the test. Spine length is usually 2-3 times the test diameter. When undisturbed, a black sac with a single opening extends from the dorsal anal surface of the test. Diadema antillarum is the predominant urchin along the reef flat and those areas immediately parallel to it. These nocturnal urchins nestle in reef crevices during the day, sometimes occurring in tightly packed intra-specific aggregations. Diadema can be found in Thalassia beds when a pile of rocks or coral offers some protection. Rarely, a group of Diadema may be found in a short seagrass bed removed from any sort of rock protection. Many different types of algae grow within the Diadema core areas. Among these are Halimeda, Dictyota, Thalassia, Penicillus, Coelothrix and Padina.

Echinometra viridis, smallest of the urchins in this study, has an oval test ranging from approximately 2-5 cm along the longest ^{diameter} radius. Olive conical spines of 2-3 cm fade to a light red or orange

base and join the dark red test along a faint white line. The only Echinometra unable to scrape burrows in rock, E. viridis most commonly clings with surprising tenacity to old overgrown reef flats exposed to strong wave turbulence. Urchins used in these studies inhabited an Acropora cervicornis reef off Columbus Park overgrown primarily by Zoanthus sociatus, a red encrusting algae, Caulerpa racemosa and the Dictyota-covered territories of Damselfish. Another old A. cervicornis reef overgrown by Halimeda and Dictyota also housed a sizable population of Echinometra; however, this study did not specifically examine that urchin population. Both these A. cervicornis reefs provided Echinometra with a complex three dimensional substrate.

Although each of the three species enumerated occupies a core area, marginal areas of urchin overlap do occur. Diadema can occur in limited numbers in both the Tripneustes and Echinometra core areas. Very much less frequently, Tripneustes and Echinometra can occur in a Diadema core area. Echinometra never seem to occur in a Tripneustes core area.

Given the habitat diversification of the three urchin species described, one might next speculate about the ecological strategies of each respective species. An urchin specialist should tend to penetrate the core areas of its fellow urchins less than would an urchin generalist. Urchins may maintain habitat differentiation and resource partitioning in several ways. As Vadas (1978) has demonstrated, urchin food selection follows the traditional

predator strategy of maximizing energy intake per unit time. If urchins have different food preferences, their nutritional requirements need not overlap despite a spatial overlap of species.

Spatial separation of urchins might also result from different substrate requirements of different species. Diadema with its long spines cannot withstand wave action unless it can find a protected place large enough to accommodate it. Echinometra also seems to require a substrate replete with nooks and crannies. Since a crevice too small for a Diadema may nicely house an Echinometra, the two species could feasibly overlap spatially without having overlapping substrate requirements.

Temporal separation of resource requirements might possibly prevent urchin niche overlap. This, however, does not seem likely to be the case, because the three species of urchin studied are all basically nocturnal, spending the day in hiding or at rest.

A specialist urchin, sufficiently expert in obtaining resource requirements shared with another urchin might be able to outcompete the other species. Such a competitive ability could result in the spatial distribution patterns observed in the field. Direct aggression of one species towards another - a form of interference competition - could also be causing the urchin distributions. These various strategies of resource partitioning seem to occur in other echinoids such as the starfish, Pisaster ochraceus and Lepasterias hexactis (Menge, J.L. + B.A., 1974).

Methods

In order to attempt to answer the questions of resource partitioning mechanisms between the three sea urchin species, this study involved three approaches: 1) field interactions and density experiments 2) laboratory food preferences experiments and 3) laboratory interactive-aggressive behavior experiments. In addition, six belt transects were made in the study areas to characterize the type environments these urchins inhabit.

The field interaction and density experiments involved the addition of ten urchins to a site previously censused. In the Diadema and the Tripneustes sites, a 1m radius circle was used to define the area, while in the Echinometra sites a .5m radius was used, owing to the much greater natural density of Echinometra. This resulted in the total area of each site being 3.14m^2 and $.785\text{m}^2$ for the Diadema-Tripneustes, and the Echinometra, respectively. Both intra and interspecific additions were performed so that seven different combinations resulted. These were 1) Diadema + 10 Diadema, 2) Tripneustes + 10 Tripneustes, 3) Echinometra + 10 Echinometra, 4) Diadema + 10 Tripneustes, 5) Diadema + 10 Echinometra, 6) Tripneustes + 10 Diadema, and 7) Echinometra + 10 Diadema. In several instances in the interspecific combinations, a number of individuals of the species being added were already present. In such cases their number was also recorded in the original census. These sites were then re-censused for possible migrations after 6 and 24 hours. The results would either indicate the saturation status of the microhabitat or the effects of interactions between the original urchins and those added. Since only one type combination was set up per day, i.e. only interspecific or only intraspecific (due to length of time the experimenters were able to tolerate the water temperature), only four trials of each combination were carried out in the time allotted.

The food preference experiments were done over a six day period — three trials of 48 hours each. Four types of algae (Dictyota, Padina, Coelothrix and Halimeda) plus Thalassia blades were collected fresh on the afternoons prior to the beginning of each trial. These were air dried approximately 30 min., then blotted dry with paper napkins, then weighed out to $\pm .1g$ into four sets on a three beam balance. One set was placed into a clean sea water from the tap and served as the control. Each of the other three sets was placed in one of three $.75 \times .5m$ tanks containing aerated seawater and six individuals of one of the urchin species. These tanks were observed at 10:00pm, 8:00am, and 4:00pm for the following 48 hours and feeding, if any, on each food type for each urchin species was recorded. At the end of the 48 hour period each food set was removed from its tank, air and blot dried, and reweighed to determine quantitatively how much, if any, feeding had taken place. The changes in weight of control foods were used to distinguish the amount weight loss (or gain) due to deterioration from that due to feeding done by the urchins. Differences in feeding patterns between the three urchin species were compared and interpreted as food preferences.

Experiments to characterize type and length of interaction between individual urchins both intra and inter-specifically were carried out in the following manner. Five pair-combinations of urchins were studied (Diadema-Diadema, Tripneustes-Tripneustes, Echinometra-Echinometra, Diadema-Tripneustes, and Diadema-Echinometra). Each pair was placed together in the center of a $36 \times 90cm$ tank filled to 14cm depth with seawater. Each interaction was observed for 15 min. or until both urchins attained a stationary positions in the tank. Descriptions of the type of interaction resulting, whether spine waving, physical

contact, pushing, chasing or avoidance, was recorded as well as length of contact time and distance apart at their final positions. Each combination pair was repeated ten times. Differences in types of interaction between species both inter and intraspecifically were noted.

Results:

Transects and Densities

Transects #1 and #2 (see Table 1) cut across the Thalassia beds of the West Back Reef through Tripneustes core area. Transects #3 and #4 contain a mixture of Diadema and Tripneustes. These transects were also made through the Thalassia beds of WBR but lay closer to the actual reef flat. Diadema became more numerous and Tripneustes less numerous as the transect passed closer to the reef flat. Transect #5, taken at the Acropora palmata reef flat zone of WBR passed through Diadema core area shared neither with Tripneustes nor Echinometra. Not only do these 2 species disappear from the transect data, but also the number of Diadema per meter increases over values taken outside the Diadema core area. Transect #4 passed directly through two large aggregations of Diadema and as a result, yielded an unusually high number of urchins per meter.

Transect #6 characterized the urchin population of Columbus Park. Echinometra occur roughly four times as frequently as do Diadema. On certain patches of exposed, encrusted coral, Echinometra occur monospecifically in even higher densities. (See Table 1).

Natural sea urchin densities in core area patches are highest for Echinometra ($29.78/m^2$), medial for Diadema ($4.37/m^2$) and lowest for Tripneustes ($2.27/m^2$). (See Table 2)

Field Interactions:

When ten urchins were introduced to a site containing a natural urchin density of either the same species or a different species, in 6 of 7 test types, the experimental density at the end of 24 hrs. had begun to return to the original natural density. (See Figure 1). Interspecific experimental interaction sites involved the addition of ten urchins to a natural density core area of another urchin species. In all four interspecific trial types, the added species fell from being a higher percentage of the total urchin population at the time of introduction, to being a lower percentage by the end of 24 hrs. Perhaps some sort of core area dominance is causing this trend. When *Diadema* were added to an *Echinometra* area, the percent abundance fell 28% from 32.2% to 6.25%. *Diadema* added to a *Triplonustes* area fell from 51.3% of the urchin population at the time of introduction to 23.7% after 24 hours. *Triplonustes* shows a less dramatic exodus when added to a *Diadema* area, falling from an initial 45.6% to a 24 hr value of 27%. *Echinometra* when added to a *Diadema* area prove least likely of all to move away. In 24 hrs, the *Echinometra* fell from 47.5% of the total urchin population to 42.5% of the population.

Intraspecific additions of urchins to a site of natural density produce smaller changes in overall urchin density / m² than do the interspecific additions. Urchins steadily leave the newly crowded area at a rate of 2-3 over a 24 hr. period.

Food Preferences

The observed feeding data, that is the number of urchins that were observed feeding at the check times, indicates first that Tripneustes feeds the most regularly in 33.3% of its opportunities, followed by Diadema - 5.6% of its opportunities, and finally Echinometra which was never observed feeding. (See Table 3B) Secondly it shows that Tripneustes feeds most often on Padina, then Thalassia, followed by Dictyota and Halimeda, and never on Coelothrix. Diadema feeds most often on the Coelothrix, then Padina and Halimeda, but never on Dictyota or Thalassia. One of the problems with this data, however, is that the urchins were not able to be observed 24 hours a day, making it very likely that some feeding went on that was not observed - especially at night.

For this reason the change in weight of each food type after each 48 hour trial may be more accurate for determining the actual amount of feeding taking place. The mean percent weight change for each of the five food types for each of the urchin species and the control is compared in Table 4A. Perhaps more germane to this study are the figures in 4B which give the mean absolute weight changes for all the algae in all the trials. Since there was so much variability (both positive and negative) in the controls as well as the experimental sets, a test for significance between the control means and each of the experimental means was not performed. Instead, the extremes of the control data were used as limits, and points falling ~~between~~ outside these (with a few exceptions) were considered to indicate some feeding. The exceptions were for cases where the observed data contradicts the weight data.

Diadema showed evidence of feeding on both Halimeda and Thalassia using the weight criteria, but

not Coelothrix which it had been observed eating. In addition, the weight criteria indicated it had eaten Dictyota. However, the variability in Dictyota weight was such that this value may actually be within the limits. Ranking the various foods according to preference by Diadema results in 1) Thalassia 2) Halimeda and 3) Coelothrix, which is somewhat different from the observed results but probably more accurate. The data for the Tripneustes trials gives striking evidence for their eating and preference for Padina, and somewhat less so for Thalassia. Although Tripneustes was observed eating Dictyota on the first trial, this proved not to be significant by the weight criteria when averaged with the other two trials. Finally, by the weight criteria, the Echinometra were shown to have eaten all food types except Padina. Their feeding on Thalassia and Coelothrix is most doubtful numerically considering the control limits. It might be possible that they were eating some Halimeda or Dictyota at night unobserved, but it is more likely that these numbers could just as easily be included as part of the control variability.

Aggressive-Interactive Behavior

The five possible pair-wise combinations tested produced a variety of types of responses. (See Table 5) The most obvious possibility would be that the two urchins would simply move away from one another, avoiding contact. This was the case in 54.5% of the Tripneustes-Tripneustes pairs, 35.7% of the Diadema-Tripneustes pairs, 66.7% of the Diadema-Echinometra pairs, and 52.9% of the Diadema-Diadema pairs. Although these percentages could not be tested for significance, it seems clear that an Echinometra-Echinometra pair is less likely to move immediately away from each other than any of the other pairs, and that a

Diadema is more likely to move away immediately from Echinometra than from another Diadema or a Tripneustes.

In cases where the members of the pair did not immediately move away, some kind of interaction occurred. For Tripneustes-Tripneustes pairs this took the form of spine to spine contact where one urchin would rotate around the other in what has been termed non-aggressive cog action. The sole purpose of such action appears to be for one to feel its way around the other, as the pair would separate afterwards. The mean time in contact with one another for this type of interaction was 3.60 min. In one case this cog action did take on an aggressive air, and was followed by one urchin climbing on top of the other, possibly to orient its mouth for spine biting.

When Diadema were paired with Tripneustes, the 9 cases in which the Diadema did not immediately move away resulted in the Diadema waving its spines at, poking and pushing the Tripneustes, a response termed sparring, until the Tripneustes moved out of reach or the Diadema lost interest and moved away. This type interaction produced a mean contact time of 3.04 min. In only four cases where a Diadema was paired with another Diadema did this aggressive type sparring occur, and in all cases the pair later came together and settled peacefully within spine contact distance. Mean contact time increased to 4.90 min. Although initially all the Diadema moved away when paired with an Echinometra, the Echinometra attempted a chase in a number of cases, and actually succeeded in re-encountering the Diadema in four instances. In such instances the Echinometra was clearly the aggressor, pushing the Diadema around, in spite of its small size. Because of the greater mobility of the Diadema, the Diadema was able to hold mean contact time to 4.09 min. When two Echinometra

were placed together, they also displayed clear aggressive behavior (pushing, sparring, and once an oral-biting orientation) toward each other. Six times the encounter was either still going on after 15 min, or the urchins had established themselves one on top of the other within a spines distance. The mean contact time for this combination was 10.38 min, which although failing to be significant when compared with the others using the Kruskal-Wallis test, still seems to demonstrate a difference in this type of interaction, (namely that Echinometra are ready and willing to fight).

Table 1 Transect Data

meter	WBR						WBR reef flat		CP shallow surge zone	
	inner Thalassia			outer Thalassia						
1	Trip. 1	Trip. 0	Diad.	Trip.	Diad.	Trip.	Diad.	3	Diad.	0.5 Echin
2	only 0	only 0	1	0	0	2	only 4	0	0	0
3	1	0	0	0	0	3	0	0	0	2
4	0	0	0	0	0	1	1	0	0	0
5	0	3	0	2	0	0	1	0	0	2
6	0	2	0	0	14	0	2	2	2	3
7	1	2	0	2	18	0	3	2	2	7
8	2	1	1	0	0	0	4	3	3	8
9	4	1	2	1	0	0	2	0	0	11
10	3	0	0	0	0	0	3	1	1	8
11	0	1	0	0	0	0	2			
12	1	0	0	2	12	1	8			
13	1	0	0	3	13	0	0			
14	3	1	0	1	0	0	0			
15	0	2	0	1	0	1	0			
#/m	1.3	.87	.27	0.8	3.8	.53	2.2	1.1	4.6	
tot #/m	1.3	.87	1.07	4.33	2.2	5.7				
	# 1	# 2	# 3	# 4	# 5	# 6				

Table 2 Original sea urchin densities at urchin addition sites

Triplonites			Diadema			Echinometra		
#/m ²	mean #/m ²	S.D.	#/m ²	mean #/m ²	S.D.	#/m ²	mean #/m ²	S.D.
2.23	2.27	1.96	5.09	4.37	1.67	29.30	29.78	10.30
1.59			3.82			48.40		
1.27			4.14			29.30		
7.00			2.55			21.67		
.96			3.18			19.11		
1.91			2.86			42.04		
1.91			4.77			22.93		
1.27			2.86			25.48		
			5.41					
			3.81					
			8.59					
			5.41					

Table 3

Observed Feeding Data
combined result of 6 days of trials

	Padina			Halimeda			Coelothrix			Dictyota			Thalassia			
	10 pm	8 am	4 pm	10 pm	8 am	4 pm	10 pm	8 am	4 pm	10 pm	8 am	4 pm	10 pm	8 am	4 pm	
Tripneustes																70 35
Diadema	1			1			1	2	11							
Echinometra	1															

Table 3B Observed
Percent of Total Feeding Opportunities Taken on Each Food Type

	Padina	Halimeda	Coelothrix	Dictyota	Thalassia	Total 108*
Tripneustes	21.3%	3.0%	—	3.0%	12.0%	33.3%
Diadema	.95%	.95%	3.6%	—	—	5.5%
Echinometra	—	—	—	—	—	0%

* Arrived at by multiplying 6 urchins by 6 time periods x 3 trials

Table 4A Feeding Preference Data

	Podina	Halimeda	Coelothrix	Dictyota	Thalassia
control	+4.77%	+1.80%	-3.80%	-32.13%	+9.27%
Diadema	-1.27%	-1.20%	-8.3%	-33.73%	-25.57%
Tripneustes	-56.33%	-1.03%	-13.13%	-28.07%	-10.17%
Echino-metra	-4.5%	-1.93%	-18.17%	-34.17%	-6.6%

Mean % wt. change of 5 food types

	Podina	Halimeda	Coelothrix	Dictyota	Thalassia
control	+ .3g	+ .83g	+ 1.1g	- 6.23g	+ 1.07g
extremes	-2.4 / +2.7	+ .5 / +1.6	-4.1 / +4.5	-7.8 / -4.9	0 / +2.5
Diadema	- .27g	* -2.53g	-2.07g	*? -8.70g	* -3.07g
Tripneu-stes	** -12.83g	- .53g	-3.00g	-6.53g	* -6.60g
Echino-metra	- .7g	*? -1.27g	*? -4.63g	*? -8.53g	*?? - .4g

Mean Absolute Weight Changes of 5 Food Types

- * - significantly different using control limits only
- ** highly sig. different → preferred
- *? - of questionable significance

TRIPNEUSTES		DIADEMA		ECHINOMETRA		DIADEMA		DIADEMA	
TRIPNEUSTES		TRIPNEUSTES		ECHINOMETRA		ECHINOMETRA		ECHINOMETRA	
immediately move away		Diadema moves away immediately		immediately move away		Diadema moves away immediately		Diadema moves away immediately	
# Cases	S.D.	# Cases	S.D.	# Cases	S.D.	# Cases	S.D.	# Cases	S.D.
6 = 54.5%	7.34	5 = 35.7%	21.9	3 = 25%	10.01	10 = 66.7%	25.21	9 = 52.9%	25.86
mean distance away all n=8		mean distance away all n=8		mean distance away all n=4		mean distance away all n=8		mean distance away all n=6	
35.12 cm		49.88 cm		23.75 cm		47.62 cm		53.33 cm	
agg action - non aggressive		Diadema spars, chases, pushes Tripneustes		pushing - sparring		Echinometra pushes on Peacock		Spine waving, sparring	
# Cases	S.D.	# Cases	S.D.	# Cases	S.D.	# Cases	S.D.	# Cases	S.D.
4	3.60 min.	9	3.04 min	9	10.38 min.	4	4.09 min	4	4.90 min
mean contact time n=4		mean contact time		mean contact time		mean contact time		mean contact time	
3.09		2.24		5.43		2.25		2.30	
agg action + other aggressive		still contact at termination		still in contact at termination		still in contact at termination		non-aggressive encounters	
# Cases	Time S.D.	# Cases	S.D.	# Cases	S.D.	# Cases	S.D.	# Cases	S.D.
1	15.0 min	2	2	6	6	2	2	4	4.82 min

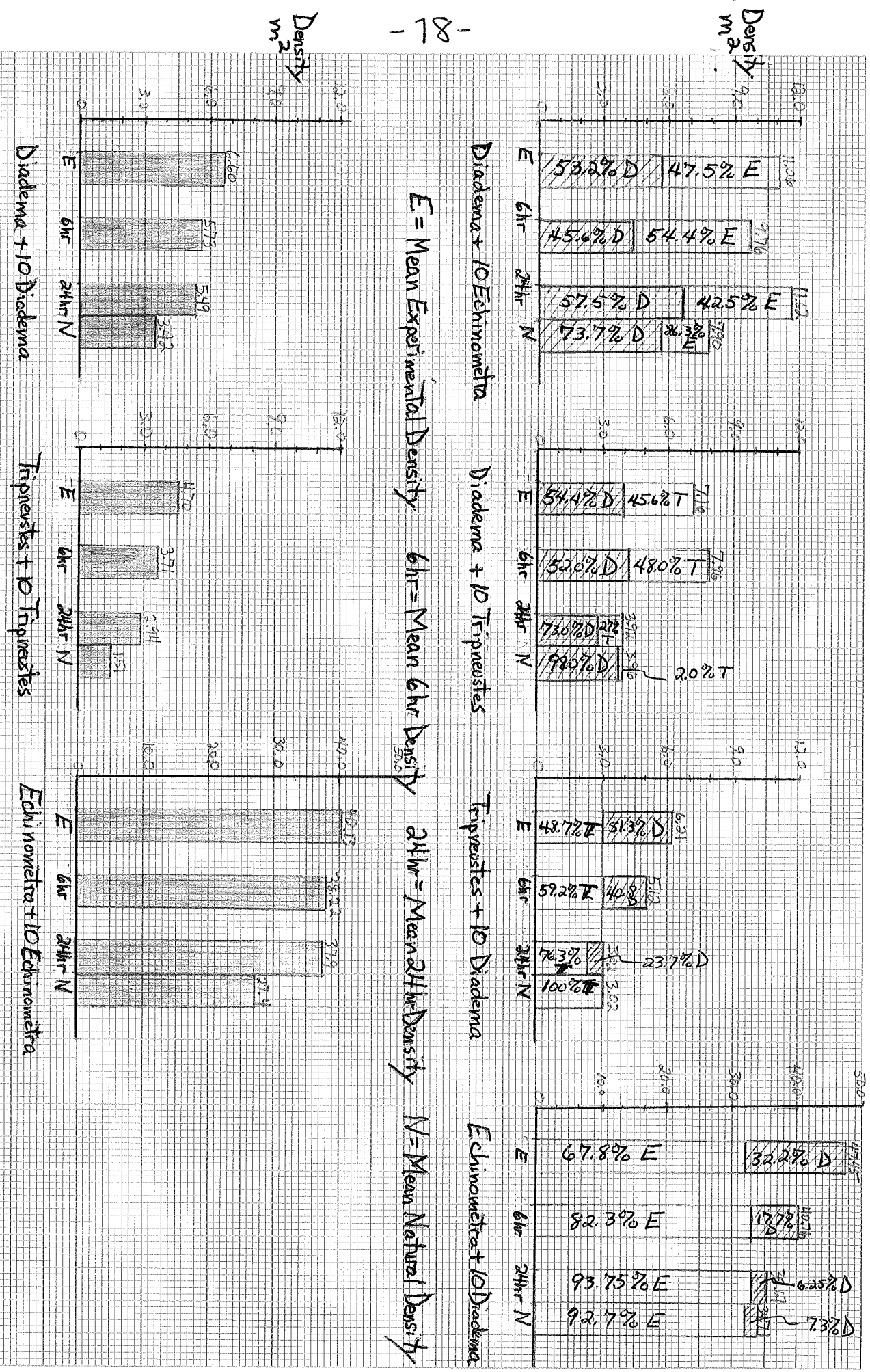
I

II

III

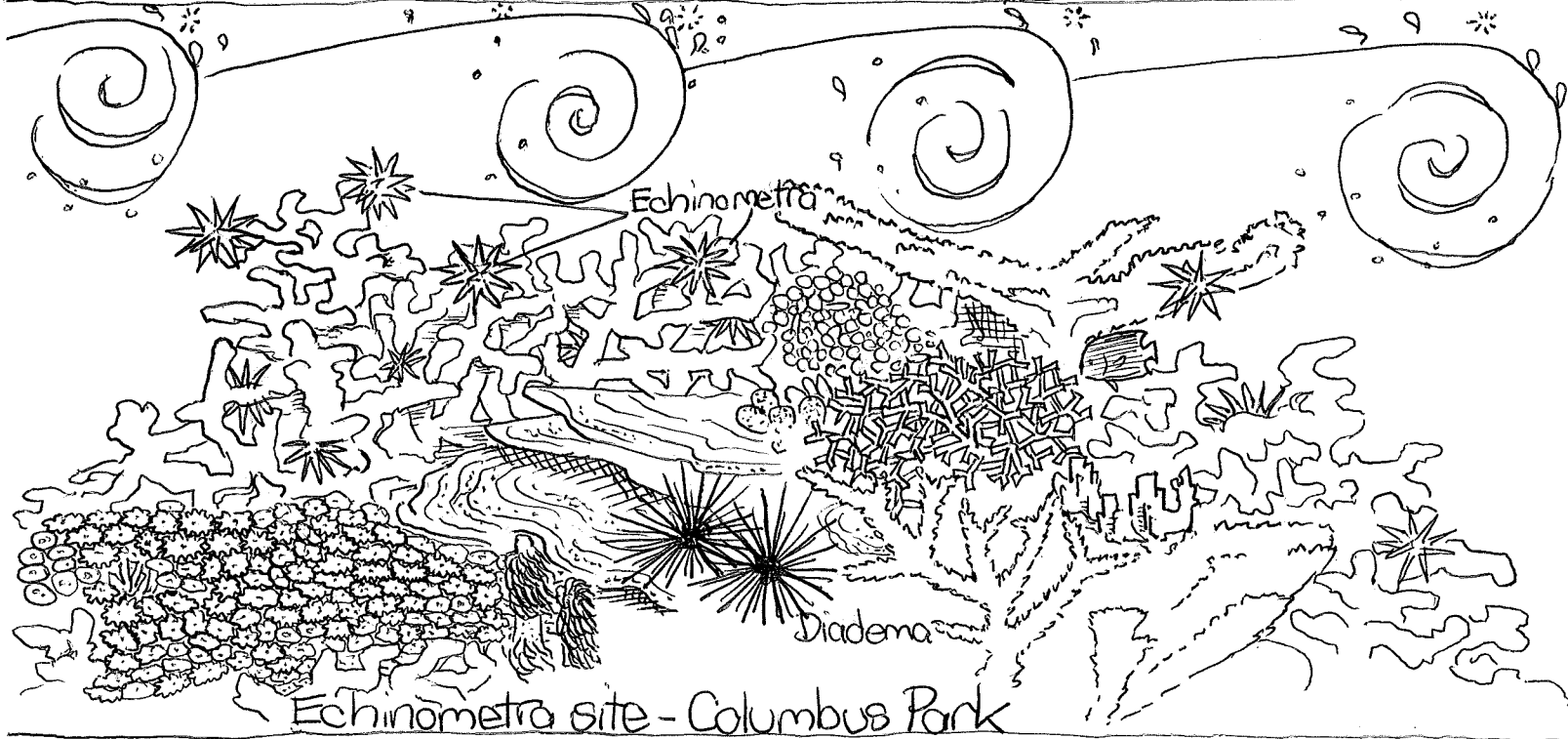
Table 5 Categorization of Types of Interactions Observed in Lab Experiments. Total number of Trials for Each Type = 10*
 * (some pairs had multiple encounters.)

Fig. 1 Graph of Sea Urchin Density Changes Over Time at Experimental Interaction Sites

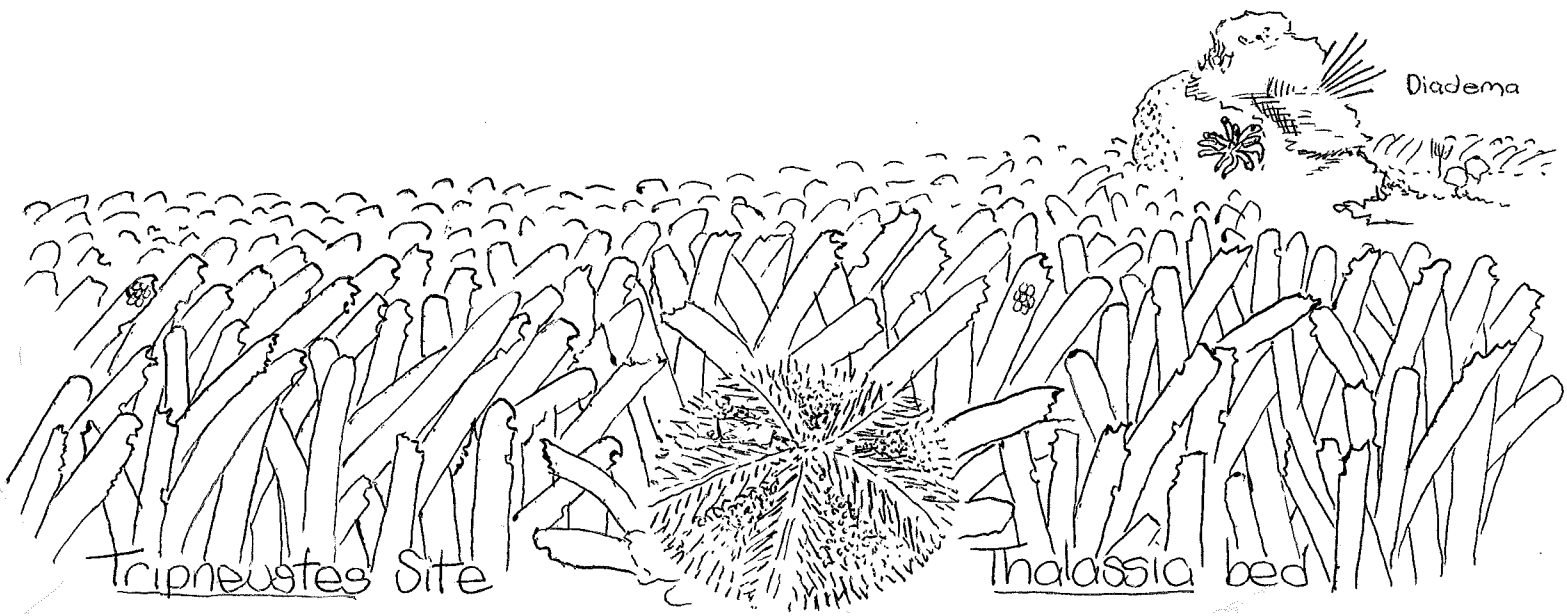




Diadema site - WBR



Echinometra site - Columbus Park



Tripneustes Site

Thalassia bed

Discussion

As our transect results show, Tripneustes, Diadema and Echinometra occur monospecifically in certain core areas and intergrade with each other at core area margins. This study attempted to identify and evaluate the various mechanisms that might effect the observed habitat separations of these three urchin species. This assumes that these differential urchin distributions represent situations of ecological equilibrium and are not purely the result of chance.

When urchins are introduced into an area of natural urchin density, two possible situations might arise. Urchins might remain in the area, or migrate from the area of high urchin density to an area of lower urchin density. In the latter case, such a migration might be due to aggressive interactions between individuals, a lack of food, or a lack of protective cover. Furthermore, interspecific interactions might differ from intraspecific interactions. ~~Urchins of all~~

Urchins of all introduced species began to leave the area of introduction by the 6th hour, and in all cases but one, continued leaving the area through the 24th hour. Those emigrations occurring before the 6th hour might possibly be due to a lack of hiding spaces or individual interactions, but are less likely to be due to a lack of food since the urchins studied are primarily nocturnal feeders. Diadema showed this trend most strongly when added to Tripneustes or Echinometra core areas. This could in part be due to their greater mobility. Those emigrations occurring between the 6th and 24th hours are possibly attributable to feeding activities as well as the above reasons. The net effect of these emigrations ~~activities~~ tended to reduce the higher experimental urchin densities to levels approaching the original natural density of the area and to return the relative species composition to its original values. Additions of Echinometra to an Echinometra environment showed little change over a 24 hour period relative to other species

additions, perhaps due to Echinometra's lesser mobility and the greater availability of short term resting places. Random movement of urchins might ^{also} feasibly have accounted for the observed decline in urchin numbers through time much the way any chance congregation of randomly moving objects might redistribute themselves from areas of high density to areas of lower density.

Lab experiments demonstrate that aggressive interactions may occur both intra and interspecifically among these three sea urchin species. Tripneustes and Diadema tend to show less aggression toward conspecifics than Echinometra. This trend might be due to lessened intra-specific competition for resting spaces. Echinometra tend to rely more upon a single resting space from which to center their feeding activities thus giving an advantage to individuals that are able to defend such a space against invasion by conspecifics. Echinometra also tended to show interspecific aggression toward Diadema, although Diadema was generally able to avoid such contact by moving out of reach. In their natural environment Echinometra are only rarely found to be in contact with one another, a fact that supports the theory of aggression used as a spacing mechanism (Grünbaum, et al 1978).

When Diadema and Tripneustes were placed and aggressive behavior as shown by pushing and sparring ensued, Diadema was always the aggressor. However, Diadema also avoided contact with the Tripneustes in a considerable number of trials. Because of the ambivalence of these results, and the inefficiency of extreme levels of aggression is probably not the major factor contributing to habitat separation between these two species although it

2 Lab Diadema to
top of Tripneustes
aggregation.

may exert a minor influence.

Alternatively, in areas where urchin density is relatively low and fertilization is external, aggression toward conspecifics may hinder reproductive success. Such a hypothesis was proposed by Menge and Menge (1974) to explain the lack of intraspecific aggression in starfish. The naturally high density of Echinometra, however, might still allow for intraspecific aggression without inhibiting reproduction.

Those experiments done to determine the food preferences of the three urchins studied failed to yield conclusive results. Echinometra and to a lesser extent Diadema, perhaps disturbed by the unnatural lab conditions and handling appeared to rely upon their ability to go without food for long periods of time. (Vadas, 1977) As far as this data goes, it does support the food preferences found by others for each of the three urchin species

(Lawrence, 1975). Because Echinometra feeding strategy is to ensnare drifting plant material brought in by wave action, it is not surprising that they were not observed feeding under laboratory conditions in which they would have to actively search out food items. According to Vadas (1977), food preferences among sea urchins are strongly correlated with absorption efficiencies. If urchin food preferences do not overlap, two different urchin species could then exist without competition in the same geographical area. Since the diets of Tripleneustes, Echinometra and Diadema do

overlap, any habitat separation observed is probably not due to any differential dietary requirements. However, differential foraging strategies may separate Diadema and Echinometra and differential foraging times may separate Diadema from Tripneustes.

Certain physical factors present in the different zones of coral reefs might limit the core areas of each of the urchin species. For example, the clinging ability and small size of the Echinometra best suit it for areas of high wave turbulence and complex physical structure. Diadema, with its ability to withstand turbulence when provided with a sufficiently protected crevice, can partially exploit both the Echinometra core area and the Thalassia bed which is the Tripneustes core area.

Tripneustes is more or less limited to the Thalassia beds because of its large size and inability to cling tightly to a substrate.

It is possible that even in areas of urchin species habitat overlap, some microhabitat partitioning occurs. Diadema in the Tripneustes core area tend to seek out protection beside and within scattered coral rock and outcroppings while Tripneustes do not. Diadema in the Echinometra core area tend to occupy larger cracks and crevices than are used by the smaller Echinometra. Evidence for such microhabitat partitioning repeatedly occurred even in this study. The social aggregation behavior of Diadema (Pearse, 1969)

provided them an alternative means of exploiting a habitat in the absence of crevices.

Having analyzed many possible factors that might contribute to the observed habitat separation of the three urchin species under study, we feel that physical environmental factors such as turbulence and bathymetric features probably contribute most to the differential urchin distributions. Of the urchins studied, *Diadema* appears to be the greatest generalist. Its ability to aggregate in the absence of crevices has allowed it to penetrate core areas not its own. The potential breadth of its diet allows it to survive in the reef flat, *Thalassia* beds and encrusted coral zones of the *Echinometra* core area, although these environments have few algal species in common. *Triplonustes*, limited as it is to the *Thalassia* beds, appears to be more of a specialist. Although *Triplonustes* outnumber *Diadema* in the *Thalassia*, it lacks the ability to weather the wave turbulence in the *Diadema* core area.

Both the *Echinometra*'s ability to cling tightly to a substrate subjected to heavy surf and its behavioral habit of feeding opportunistically on drifting algae or plant material enable it to specialize in areas unsuitable for other urchins.

Only when sufficiently large crevices are lacking in areas of high wave turbulence or when dense *Thalassia* beds grow on

areas of flat, undifferentiated sandy substrate are the Diadema at a disadvantage. It is in these environments that the greater specialists, Echinometra and Tripneustes are capable of outnumbering and, indeed, displacing the Diadema.

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