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PATTERNS OF DIEL MIGRATION IN

Tripneustes ventricosus

Rebecca Elizabeth Todd
Peter Harris Kilmarx

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PATTERNS OF DIEL MIGRATION IN TRIPNEUSTES VENTRICOSUS

Abstract Nocturnal activity of the sea urchin Tripneustes ventricosus was quantified by means of a diel census. In the daytime Tripneustes is typically found on sand / Thalassia beds, moderately exposed and covering itself with organic matter. In the night-time it is typically on coral rock promontories with high exposure and no covering. Gut analyses show that Tripneustes is scraping algae off the coral rock at night and is eating algae encrusted Thalassia during the day. At least some of the Thalassia is egested undigested. The diel migration and covering response are probably predator avoidance strategies.

Introduction Nocturnal patterns of activity have been reported for many different classes within the Echinodermata, including the sea urchins, Echinoidea (Ogden et. al., 1973; Houlihan and Duthie, 1981; Hammond 1982). These patterns have been investigated in Paracentrotus lividus and Arbacia lixula, which were found to be more active and consume more O_2 at night (Houlihan and Duthie, 1981). Diadema antillarum was found to migrate from the reef at night to feed on Thalassia testudinum beds (Ogden et. al., 1973). However, activity patterns for the Toxopneustid Tripneustes ventricosus have never been investigated.

Tripneustes is a black urchin with short white spines, and its diameter is less than 15 cm. It is a predominant member of the shallow back reefs and Thalassia testudinum beds in Caribbean coral reef ecosystems.

Preliminary observations of Tripneustes suggested that they migrate from Thalassia beds during the day to coral rock promontories at night. We hypothesized that a census would show Tripneustes to be positioned higher, to be more exposed, and to prefer coral rock to sandy Thalassia beds at night.

Tripneustes also shows a covering response whereby it holds bits of Thalassia, algae, and molluscs to the aboral surface with its podia. We investigated day-night differences in this behaviour.

We hypothesized that Tripneustes is feeding ^{while} on the rock promontories. We expected to find different gut contents in urchins collected from Thalassia beds during the day, and the promontories at night. Other studies have found Tripneustes to feed on Thalassia, algae, and bottom materials (Mortenson, 1943; Lewis, 1958; Moore, et al., 1958; Stevenson et al., 1966; all via Lawrence, 1975).

Other investigations include differences between day and night light intensity as possible cues for diel migrations. We also examined the possibility that Tripneustes is capable of zooplankton feeding or suspension feeding.

Materials and Methods Censusing was done in three plots on the West Bank Reef, Discovery Bay, Jamaica. The plots had dimensions of approximately $3 \times 4 \text{ m}$, $10 \times 12 \text{ m}$, and $12 \times 12 \text{ m}$, and were established so as to contain a diversity of habitats: coral rock promontories, live coral heads, bare sand, and beds of Thalassia. One plot was censused each day on March 2, 3, and 5, 1983. Each plot was censused twice: at 1330 or 1430 and again at 2030 or 2230.

For each urchin, the height of its position above the sand lagoon floor, the diameter including spines, the substrate upon which it was found, the relative exposure, and the presence or absence of material on the aboral surface were recorded.

Three aquaria were set up in the laboratory to investigate the effects of light on diel migration. One tank with two urchins had natural illumination. Another, with three urchins, was kept dark for two days, being enclosed in black plastic. A third tank with 3 urchins was illuminated with a fluorescent light for two days. Light and dark periods were reversed for 24 hours in one tank. The tanks contained 5 cm. of sand, a coral rock promontory, Thalassia testudinum, and Dictyota sp. Day and night positions of the urchins were recorded.

Gut analyses were conducted on urchins collected from Thalassia at 1430 hours and from coral rock at 2230 hours. Both dissecting and compound microscopes were used to identify matter found in the gut, and also of feces egested by laboratory animals.

Feeding of particulate matter was attempted in the lab and *in situ*. Small pieces of *Thalassia*, *Dictyota* sp., and limpets, were placed on the aboral surfaces of laboratory urchins and response observed. Zooplankton were attracted to urchins *in situ* at night by means of a flashlight, and urchin behaviour was recorded.

An attempt was also made to feed podia to fish in the laboratory, to test the palatability of the urchin.

Study site The study site was located in West Discovery Bay, on the north coast of Jamaica, in the shallow rear zone of the reef crest. The three plots were approximately 50 m south of, and parallel to, the reef crest. The depth of each ranged from 1 to 1.5 m. The floor was composed of sand. *Thalassia* beds, live brain coral heads, coral rock formations, and bare sand areas were found throughout the zone, and in each of the plots. High variability within this area is credited to the high disturbance level (Woodley and Robinson, 1977).

Results Results of the census are given in Table 1 and Figure 1.

Tripneustes ventricosus showed a diel migration pattern. The daytime census found *Tripneustes* typically on a sand / *Thalassia* substrate, with medium exposure, and covering itself with *Thalassia*, Mollusca, *Dictyota*, or other organic matter. The nighttime census found the urchin typically on a coral rock substrate with high exposure, and little or no covering.

The Mann-Whitney U Test showed the height versus time of day correlation to be significantly different to less than the .001 level. The G test for goodness of fit

vertical

showed the substrate, exposure, and cover versus time of day correlation to be significant to less than the .001 level.

The spatial orientation of the urchins in constant dark, constant light and natural light aquaria revealed no great differences between tanks in the behavior of urchins. During the first day, they were found on the promontories, the aquaria walls, and the sand, moving slowly. During the night, about half were on the promontories while the rest were on the wall at the top of the tank. None were observed in the lower half of the tank.

In the light reversal experiment, the urchins were found on the walls both during the day and during the night. They did not seem to respond to illumination in any way.

But material from urchins collected at 1430 hours was composed mainly of pieces of Thalassia and its encrusting algae. Some of the pieces appeared old and brown. Four taxa of Protozoa were found alive and feeding within the stomachs of the urchins. Urchins collected at 2230 hours from coral rock promontories were found to have little Thalassia in their digestive tracts. The majority of material was encrusting algae, both red and green, and was either loose, or in small bolus-like spheres. Sand, small pieces of coral rock, and three Protozoan taxa were also found.

The feces egested by laboratory animals was composed mainly of undigested pieces of Thalassia. Also found were tiny bits of encrusting algae.

When particulate Thalassia, Dictyota, and limpet were placed on the aboral surfaces of Tripneustes, no positive response was observed. Similarly, in situ

attempts at feeding them zooplankton elicited no response. The zooplankton were seen to dart to the surface of the urchin, remain among the podia, pedicellariae, and spines for a while, and then dart away.

When the podia were cut from urchins and placed in a tank with fishes, the pieces were ignored.

In field observations included sighting two juvenile Striped parrotfish which quickly pecked at Tripneustes. This may have been directed toward the urchin, or at its Thalassia cover. In the midst of schooling parrotfishes, several urchins were flipped over, revealing the fleshier oral surface. The fishes noticed the upside down urchins, but otherwise ignored them. Also, the organic cover was removed from several urchins found in Thalassia beds at 1430 hours. Over a 10-15 minute period, most were seen to affix other Thalassia blades which wave action swept near them.

Discussion There is a marked diel migration in Tripneustes ventricosus. It may appear that their higher exposure at night is only a function of being on coral rock, but in fact those on the rock and even those in the Thalassia are more exposed than they are during the day.

The first question proposed by this is why do the urchins go up onto the promontories? We have rejected the possibility that they are zooplankton feeding, based on field observations and gut content analyses. Similarly, we rejected the possibility that they are feeding on suspended particles based on our laboratory feeding attempts.

They may have been
collecting very small
particles

Gut content analyses show that they have different day and night diets. *Tripneustes* feeds predominately on *Thalassia* during the day. The *Thalassia* may not be digested but may be ingested along with the encrusting red algae on which the urchin is primarily feeding. *Thalassia* is often egested undigested. At night, *Tripneustes* seems to be scraping encrusting algae off the coral rock. Red and green encrusting algae and bits of coral rock were found in the gut, with a marked decrease in *Thalassia* pieces.

It has been observed that sea urchins can take up dissolved amino acids across their body wall (Pearse and Pearse, 1973). It may be that *Tripneustes* is doing this at a greater rate at night when it is exposed to a greater volume of the water column. This may also help explain why the urchin sheds the organic cover, which could slow absorption if present.

The second question is why does *Tripneustes* go up onto the promontories at night? We hypothesize that this is a predator avoidance behavior. Hobson (1975) observed that there are diel predation differences such that echinoids are more susceptible to predation by fish during the day. It is also known that triggerfish are capable of turning over and eating sea urchins. Triggerfish populations have been seriously depleted by overfishing, but their presence has certainly been important over evolutionary time.

If *Tripneustes* behavior is governed by their avoidance of diurnal predation, we can make two predictions:

1. The urchins will be less exposed during the day.
2. The covering response will be observed more often during the day.

Our data agree with both of these predictions and support the daytime predation pressure theory. Note, however, that throughout the field work only two fish-urchin interactions were observed.

One would predict that the diel migrations and covering response will be more important where triggerfish are present, and daytime predation pressure is stronger.

The covering response may be a form of camouflage against any predation. It may also be a shield against selective ripping of podia and pedicellariae. However, it may also attract predators to the Thalassia or algae covering. The covering response may also serve to protect Tripneustes from ultraviolet radiation. Jokiel (1980) has observed that UV radiation is harmful to coral reef invertebrates and noted UV avoidance strategies. This possibility would also give the observed diel differences in the covering response.

The behavior of the urchins in the laboratory differed greatly from those in the field. However, we can conclude that the diel migration is not due to a negative phototropic response (i.e., when there is no light, the urchins climb to the promontories). We predict, then, that diel migration is internally controlled, in a circadian rhythmic manner. The light/dark reversal experiment gave no enlightening data, aside from the observation that the urchin's behavior is altered in the lab.

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A very good study and contribution to our knowledge of Tripneustes biology. Good, critical evaluation and discussion of results.

The attempt at feeding fishes podia was unsuccessful for several reasons. The fish density was low, so that the chance of a fish encountering podia was low, and the podia are so small as to be almost inconspicuous in the water. It was impossible, therefore, for us to discern the palatability of the urchin.

The observational studies reveal several things. There is some type of predator interacting with Tripneustes (Striped Parrotfish), whether it be for the urchin, or for its organic covering. Fishes do not seem to be more attracted to the more exposed oral surface of the urchin. Also, the covering response is one that is actively maintained. This would seem indicative of its importance to the urchin.

Although this study had very few problems, a few points should be mentioned. The altered behavior in the lab inhibited experimental possibilities. Good observational skills were needed at night because of the unintentional bias toward urchins on promontories, caused by poor visibility with a flashlight.

Despite its relative conspicuousness in shallow water back reef zones in the Caribbean Sea, Tripneustes ventricosus has been only cursorily studied. This investigation sheds new light on the diel migration pattern, and provides some observational data. Further studies could explore the possibility of endosymbionts within the digestive tract, gut passage times, and more detailed gut and fecal analyses. Diel sampling would show when and how quickly the urchin is moving. And tagging experiments could be used to follow the movement of individual urchins over time.

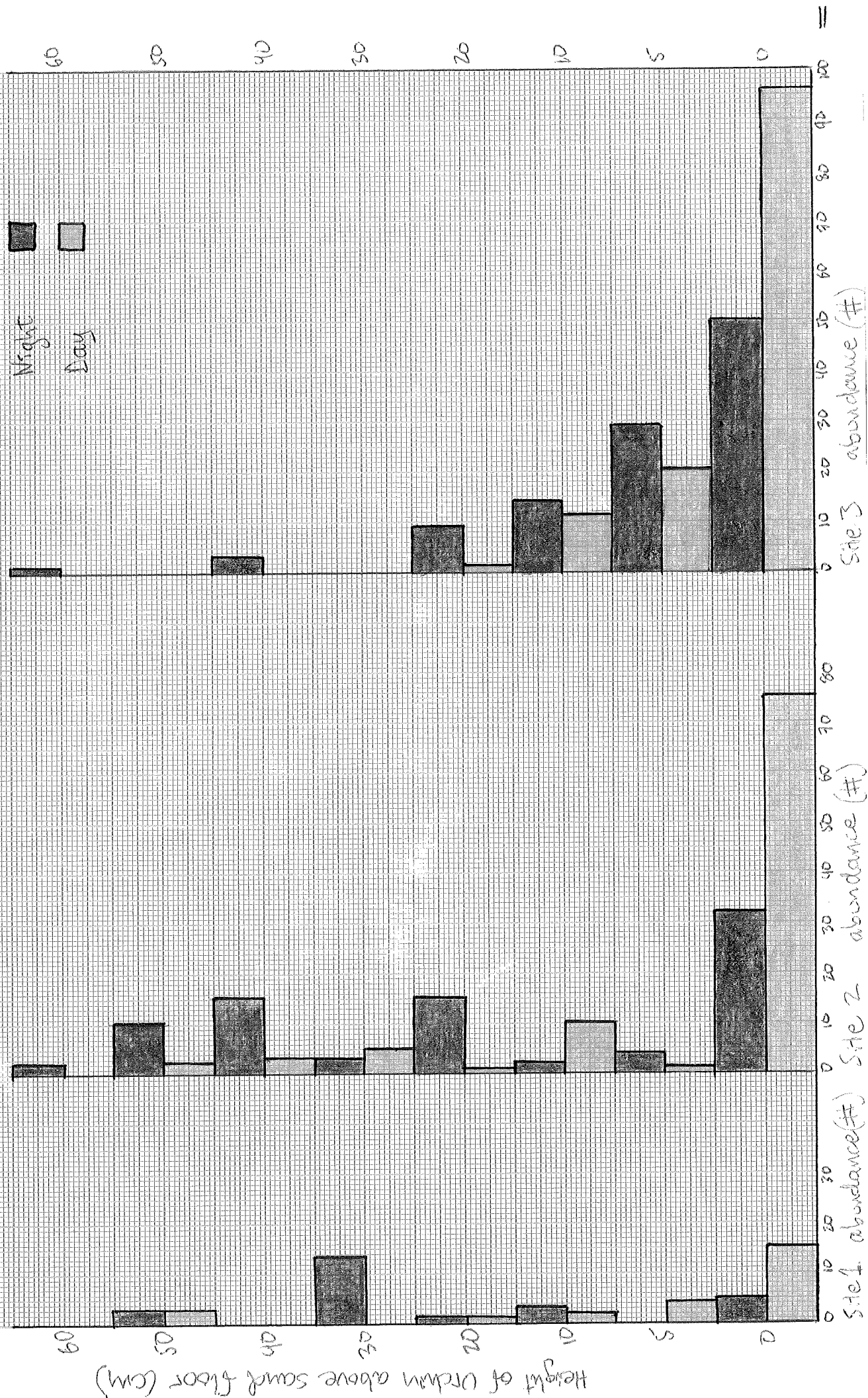
Table 1 Results of Census

Substrate	Day	Night	Statistics
Coral Rock	48	121	G-test 3 degrees of freedom $G = 72.74$ $p < 0.001$
Sand	33	2	
Sand/Thalassia	136	77	
Thalassia	16	12	
Exposure			G-test 2 degrees of freedom $G = 246.226$ $p < 0.001$
High	30	176	
Moderate	185	37	
Low	18	0	
Cover			G-test 1 degree of freedom $G = 248.10$ $p < 0.001$ <i>correct?</i>
Present	157	183	
Absent	57	5	

Time of census

Height (cm)	Site 1		Site 2		Site 3		Mann Whitney U-Test day $n_1 = 235$ night $n_2 = 214$ $U_s = 49357$ $t_s = 17.03$ $p < 0.001$
	1330	2030	1430	2230	1430	2230	
0	15	5	75	32	96	50	
5	4		1	4	10	29	
10	2	3	10	2	6	14	
20	1	1	1	15	1	9	
30		13	5	3			
40			3	15		3	
50	3	3	2	10			
60				2		1	

Figure 1: Height or Uremus vs. Time of day.



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