NICHE SEPARATION IN TWO CLOSELY RELATED SEA URCHINS, LYTECHNIUS VARIEGATUS AND TRIPNEUSTES VENTRICOSUS, IN A SHALLOW BACK REEF ENVIRONMENT

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ABSTRACT (BEM, PLK, and MEB)

We studied coexistence and niche separation between the closely related sea urchins Lytechnius variegatus and Tripneustes ventricosus, both of which are abundant in the shallow back reef of Discovery Bay, Jamaica, by comparing differences in urchin size, distribution, substrate use, and diet. T. ventricosus was twice as large as L. variegatus, and was more abundant in the habitats closest to the reef crest, while L. variegatus was more abundant further from the crest. Near to the reef crest, neither species was selecting substrate, while far from the reef crest T. ventricosus selected for algal covered substrata, and L. variegatus selected for Thalassia grass. Gut content analysis revealed little diet differentiation. We concluded that niche separationof these two urchin species was due primarily to distributional differences in relation to distance from the reef crest and less a factor of dietary or substrate differences as has been previously suggested.

Key Words: Lytechnius variegatus , Tripneustes ventricosus, spatial distribution

INTRODUCTION (MEB)

Coral reefs support extremely diverse communities. It is likely that several factors are involved in maintaining this diversity: high productivity, competition and resource partitioning, predation, topographic complexity, nonequilibrium dynamics, recruitment limitations, and environmental fluctuations (McClanahan, 1988a). Resource partitioning may explain the coexistence of ecologically similar species.

The closely related sea urchins Lytechinus variegatus and Tripneustes ventricosus (Taxopneustidae) are abundant in the shallow back reef of Discovery Bay, Jamaica. Keller (1983) found no evidence of significant effects of interspecific competition on mortality, growth, or fecundity, and suggested that coexistence may be a result of differences in diet, although both species are generalized grazers. We examined the hypothesis that L. variegatus and T. ventricosus show niche separation by examining their distributions, substrate use, and stomach contents.

METHODS (MEB)

We conducted this study on the back reef north of the Discovery Bay Marine Lab in Discovery Bay, Jamaica. To examine urchin distribution and substrate use, in the shallow back reef habitat we established three 97m transects perpendicular to the reef crest, at a distance of ≈50-147m shoreward from the crest, on 2-4 March, 1994. Transects were composed of 17 $1m^2$ quadrats separated by 5m, and transects were 10m apart. We measured depth, rugosity (bottom contour distance/straight line distance), and substrate cover (sand, Thalassia, algae,

coral, rock) in each plot.

We examined distributions on each transect during the day (10:30-12:30) and night (21:00-23:00). For each L. variegatus and T. ventricosus in each plot, we recorded diameter, substrate type, height above bottom, and distance to the nearest urchin neighbor.

We used a correlation matrix to examine the relationships between: distance from the reef crest, depth, rugosity, substrate availability, and day and night L. variegatus and T. ventricosus abundances. We used Chi-square tests to compare substrate use in the day and night within each species, and to compare substrate use between the two species in both day and night. We compared mean urchin height above bottom between day and night within each species, and between species, using Mann-Whitney U-tests.

In order to examine distributions, we divided our transects into three zones, one proximal, one intermediate, and one distal to the reef crest. We compared species abundances between these zones using a Chi-square test, and compared substrate use with substrate availability for each species in each zone using G-tests. In addition, we compared species abundance in proximal and distal plots characterized by high Thalassia cover using a Chi-square test. We predicted an average distance between urchins in each of these zones using observed urchin densities (predicted distance between evenly distributed urchins =

$$2\left[\frac{m^2}{\text{urchin}}\cdot\frac{1}{\pi}\right]^{1/2} - \text{mean urchin diameter})$$

and tested for clumping by using t-tests to compare these predicted distances to observed distances.

We qualitatively examined gut contents of both species to further examine food resource use. We collected 3 urchins of each species from Thalassia beds distal to the reef crest at 14:00 on 5 March, and 4 of each species, half from Thalassia beds distal to the reef crest, and half from algae and rock substrate proximal to the reef crest, at 06:30 on 6 March. Gut contents were examined under a binocular microscope.

We qualitatively examined habitat preferences by testing the tendency of urchins to remain in or leave different substrate types. We established six $1m^2$ monitoring plots at 11:00 on 6 March. We placed three plots in Thalassia beds distal to the reef crest, and three on algae and rock substrate proximal to the reef crest. After clearing all plots and immediate surroundings of urchins, we randomly selected one plot in each location to receive each of three treatments: 15 L. variegatus, 7 L. variegatus and 2 T. ventricosus, or 4 T. ventricosus. We used urchin densities which we observed naturally, and used more L. variegatus than T. ventricosus because of their smaller size and higher natural density. Plots were check after 24 hours, and remaining urchins were recorded.

RESULTS (BME)

Increased distance from the reef crest was strongly correlated with increased water depth and sand cover and with decreased algae and rock cover ($r = 0.821$, $p < 0.05$; $r = 0.404$, $p <$

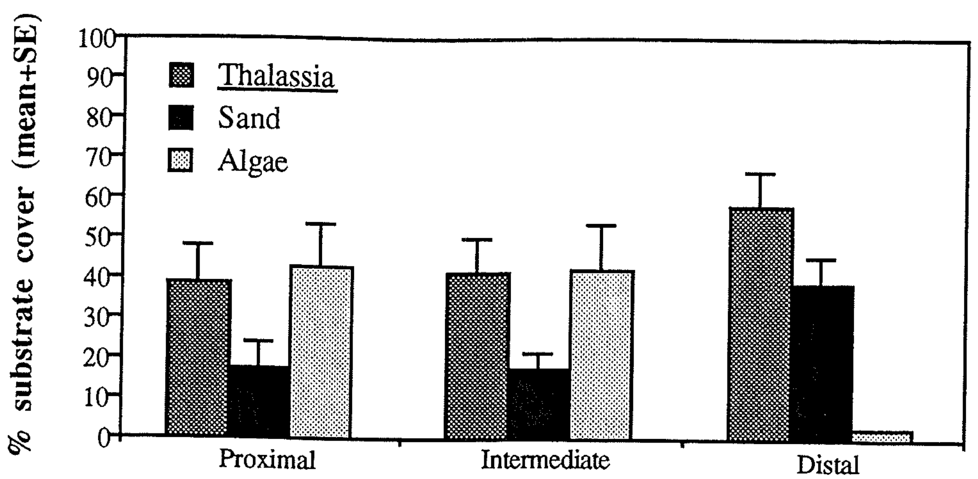

Figure 1. Substrate cover

0.05; $r = 0.414$, $p < 0.05$, $r = -0.485$, $p < 0.05$, respectively). Thalassia cover remained relatively constant (Figure 1). Increased rugosity was associated with increased coral, increased rock, and decreased Thalassia cover ($r = 0.369$, $p < 0.05$; $r = 0.432$, $p < 0.05$; $r = -0.298$, $p < 0.05$, respectively).

We examined 149 L. variegatus and 55 T. ventricosus during the day. One hundred fifty

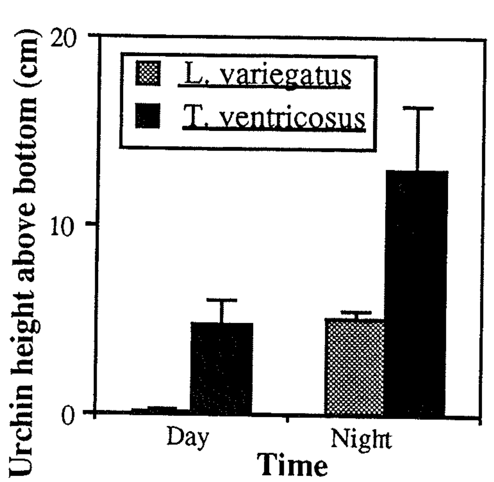

Figure 2. Diel patterns of urchin vertical migration.

one L. variegatus and 41 T. ventricosus were found at night. The mean diameter of the Tripneustes was almost twice that of Lytechinus (mean ± SE: 10.84 ± 0.22cm vs. 5.72 ± 0.11cm, respectively; $t = 20.89$, $df = 203$, $p < 0.001$). Thirty L. variegatus urchins considered recruits (diameter ≤ 3cm) were found, while the sampled T. ventricosus population showed a noticable lack of recruits (the smallest measured was 7cm in diameter).

L. variegatus tended to spend the day close to the bottom of the reef, off any promontories on Thalassia blades (Figure 2). During the day T. ventricosus was found significantly higher than L. variegatus ($U = 35.759$, $n_1 = 149$, $n_2 = 55$, $p = 0.002$; Figure 2). At night, both T. ventricosus and L. variegatus migrated higher onto promontories or Thalassia blades ($U = 739$, $n = 55$, $n_2 = 41$ $p = 0.005$; and $U = 4045$, $n_1 = 150$, $n_2 = 149$, $p = 0.001$, respectively; Figure 2) until they were at statistically indistinguishable heights ($U = 2950$, $n_1 = 150$, $n_2 = 41$, $p = 0.6824$; Figure 2).

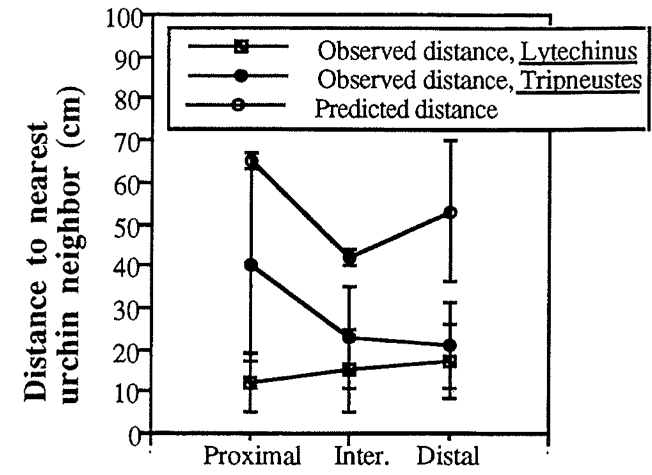

Figure 3. Distances to nearest urchin neighbors, a measure of clumping.

All of the plots, whether proximal, intermediate or distal, showed a very strong trend of urchin clumping. Both L. variegatus and T. ventricosus were closer to their nearest neighbor than would be predicted based on their densities (Figure 3).

Lytechinus was far more common in the area most distal to the reef crest, while Tripneustes showed the opposite trend, with the highest abundance on proximal plots (Figure 4). The two species showed no substrate selectivity in the proximal plots, although some selectivity was apparent in other two areas. In the intermediate plots, Lytechinus selected for Thalassia and against algae and sand ($G = 25.34$, $df = 2$, $p < 0.001$). Tripneustes showed no selection in the intermediate plots, but both species showed strong selection in the distal plot: T. ventricosus selected for algae and against sand ($G = 13.7$, $df = 2$, $p < 0.005$), and L. variegatus selected for Thalassia and against sand ($G = 10.5$, $df = 2$, $p < 0.025$). Both appeared at the expected fre-

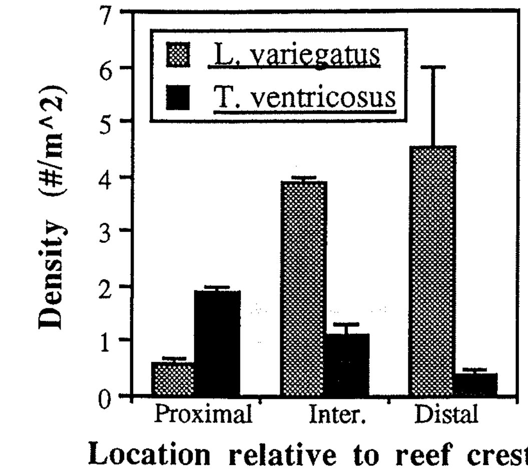

Figure 4. Urchin distributions (day data)

quency on the third substrate type.

Tripneustes distributions in plots with high percent Thalassia cover near and far from the reef crest (82 ± 4% vs. 78 ± 6%, respectively; $t = 0.59$, $df = 14$, $p > 0.5$) were almost 4 times as high proximal than distal the reef crest ($X^2 = 8.2$, $df = 1$, $p < 0.005$). Lytechinus showed the opposite trend, with 4.5 times as many individuals distal to the reef crest ($X^2 = 23.1$, $df = 1$, $p < 0.001$).

The guts of T. ventricosus contained far more material during both day and night than the guts of L. variegatus, which appeared to be empty. The T. ventricosus guts were equally full day and night, and contained a large proportion of green Thalassia leaves with intact epibouts. Lytechinus' largely empty guts contained Thalassia leaves, the majority of which appeared to have been detritus material. More algae was present in both of the species' guts then from the area closer to the reef crest.

Of the 15 Lytechinus placed in each of the manipulated plots with only Lytechinus, 8 had left the distal plot and 11 had left the proximal plots. The manipulated plots with both species had 2 Lytechinus and 2 Tripneustes leave the distal plot and 6 Lytechinus and 1 Tripneustes leave the proximal plot. No Tripneustes were left in either of the exclusively Tripneustes plots, although 2 Lytechinus had entered the distal plot.

DISCUSSION (PLK)

Previous studies by Keller (1983) and McClanahan (1988a) examined the roles of predation and competition on the distribution patterns and coexistance of sea urchins. In the overfished Discovery Bay reef zones, predation on adult sea urchins presumably has little or no effect on their distribution. Our investigations, therefore, focused on the effects of food resources and substrate availability on the natural distributions of L. variegatus and T. ventricosus. The results led us to conclude that niche separation of these species was due primarily to microspatial habitat preferences. These findings were contradictory to our predictions and those of Keller (1983) which stated that the coexistance of L. variegatus and T. ventricosus was a function of dietary differences.

The spatially distinct distribution patterns of L. variegatus and T. ventricosus seems to be more a function of their distance from the reef crest than substrate preference. The day and night gut content analyses of both species indicated few differences in feeding habits, also suggesting that substrate may not be crucial in determining urchin distributions. T. ventricosus appears to use habitats proximal to the reef crest, whereas L. variegatus uses habitats distal to the reef crest, selections made independently of Thalassia cover, which is relatively constant. We speculate that the larger size and possibly greater specific gravity of T. ventricosus may convey a selective advantage in the shallower waters proximal to the reef crest where surge is presumably greater, whereas the deeper waters distal to the reef crest may provide a refuge for the smaller L. variegatus. T. ventricosus is able to make use of a habitat and resources which are not accessible to L. variegatus. While we maintain that distance from the reef crest is the controlling factor influencing these urchin distributions. Substrate use is still important in determining small scale microspatial preferences within the larger habitats. This includes the selection of L. variegatus and T. ventricosus for specific substrates within the three zones such as the significant selection by L. variegatus for Thalassia and against algae and sand in the intermediate plots.

The significantly different mean diameters of T. ventricosus and L. variegatus may be a function of the greater relative abundance of L. variegatus recruits in addition to the fact that adult L. variegatus are smaller McClanahan (1988a) reported that settlement of urchins is periodic, which may explain why we found more L. variegatus than T. ventricosus recruits. An alternate explanation may simply be because of divergent life history strategies. Which involve different abundances of recruits or recruit mortality rates. Future studies could also investigate the effects of predation on urchin re-

cruits.

The differences in mean diameter may also explain the discrepancies in urchin abundances. L. variegatus was found three times as often as T. ventricosus over the total study area during both day and night censuses. At these densities, the total biomass of each species may be nearly equal because of their differences in size.

Two interesting behavioral patterns also emerged in the two urchin species. The tendency of both T. ventricosus and L. variegatus to move to higher positions on the substrate and onto promontories at night may be for feeding or spawning purposes. The nearest neighbor analysis indicated clumping in both species, which may be due to patchy resource distribution or may serve as another mechanism to protect against surge.

Our investigation of habitat preferences in the field revealed that L. variegatus was more likely to remain in the habitat in which it naturally occurred. This confirms our previous conclusion that L. variegatus preferentially selects habitats distal to the reef crest. This particular portion of our study was meant solely as a preliminary investigation, and requires further study to confirm the accuracy and relevance of the trends.

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