# THE DISTRIBUTION OF *TRIPNEUSTES VENTRICOSUS* AND *DIADEMA ANTILLARUM* IN THE BACK REEF AND FORE REEF OF DISCOVERY BAY, JAMAICA

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*Abstract. Diadema antillarum* dominated the echinoid community in the fore reef of Jamaican coral reefs until a species specific waterborne pathogen caused mass mortality of this urchin. The die-off of *D. antillarum* opened up a niche for *Tripneustes ventricosus,* which was previously confined to the back reef. This study examines the recent densities and distribution of both *D. antillarum* and *T. ventricosus* and how *T. ventricosus* is faring in its new fore reef habitat. We hypothesized that *T. ventricosus* would have different population dynamics in back reef and fore reef habitats, as indicated by the lantern : test ratio, test diameter, and abundance. We also hypothesized that both *D. antillarum* and *T. ventricosus* densities are continuing to increase over time in the fore reef. Thirdly, we hypothesized that urchin densities would vary with vertical complexity of the substrate, and water depth, and that fleshy macroalgal cover would decrease as urchin abundance increased. We found that *T. ventricosus* and *D. antillarum* densities have not increased since 1991 at the Discovery Bay fore reef, suggesting that population growth at this site has leveled off. We observed *D. antillarum* almost exclusively in areas of high topographic complexity, while *T. ventricosus* was generally found on flatter substrate. Overall there was no difference in macroalgal cover between 1991 and the present; however, there was significantly less cover at 9.1 m in 1998. *T. ventricosus* at Pear Tree Bottom appears to be more food-limited in the fore reef than in the back reef. Given that *T. ventricosus* appears to be stressed in the fore reef, and that *D. antillarum* density may increase, we predict that *D. antillarum* will once again dominate the fore reef, and that *T. ventricosus* will eventually be restricted again to the back reef.

*Key Words: Aristotle's lantern: test ratio, 1983* Diadema antillarum *die-off, echinoids, fleshy macroalgae, food limitation, topographic complexity*

## INTRODUCTION

The spiny sea urchin *Diadema antillarum* Philippi was once one of the most abundant and ubiquitous marine animals of the West Indian faunal region (Randall et al. 1964). However, following a massive die-off in 1983, presumably caused by a species specific waterborne pathogen, more than 93% of existing *D. antillarum* perished. In Jamaica, the mortality was approximately 95 to 98%, representing a major shift in reef dynamics (Lessios 1988). *D. antillarum* profoundly affects reef communities, by limiting macroalgae and, at high densities, by grazing corals and other benthic invertebrates on the substrate (Carpenter 1986, Sammarco 1980). Macroalgal cover in shallow water increased from as low as 1% before the *D. antillarum* die-off to as high as 95% in the first two years after the die-off (Lessios 1988). This increase in macroalgal cover was partially responsible for the reduction in total coral cover, because it reduced available settlement sites for coral larvae, and damaged existing coral colonies through overgrowth (Hughes et al. 1987).

*D. antillarum* also competes with herbivorous fish (Sammarco and Williams 1982) and other species of urchins (Williams 1981). Prior to the 1983 die-off, *Tripneustes ventricosus* was found almost exclusively in *Thalassia testudinum* beds in the back reef of Discovery Bay, and in 1989 only one was documented in 300m$^2$ in the fore reef (Dols and Walters 1989). In 1991, Gilmartin and Young documented a much more extensive invasion of *T. ventricosus* in the fore reef, indicating that the *D. antillarum* die-off represented a competitive release and allowed *T. ventricosus* to move into the fore reef habitat from which it had been excluded. Our initial observations indicated that the density of *T. ventricosus* has further increased in the fore reef since 1991, and that the two urchin species may use different substrates in the fore reef.

This study examines the distribution of

*D. antillarum* and *T. ventricosus*, in the fore reef and compares the abundance, size, and food limitation of *T. ventricosus* in fore reef and back reef regions. We hypothesized that *D. antillarum* and *T. ventricosus* densities have continued to increase in the fore reef since 1991 and that these two urchins occur on different types of substrate in the fore reef. We also hypothesized that *T. ventricosus* differs in its ability to exploit food resource in the back reef and fore reef. To test this we compared lantern : test ratio, test diameter, and abundance. Thirdly, we hypothesized that the densities of the two urchins in the fore reef would vary with vertical complexity of the substrate, and with water depth. Finally, we hypothesized that macroalgal cover in the fore reef would decrease as urchin abundance increased.

## METHODS

We surveyed the abundance of *D. antillarum* and T. *ventricosus* in the fore reef and back reef at Discovery Bay, Jamaica, from 3 to 10 March 1998. At two sites in the fore reef (directly south of the M1 and LTS moorings), we conducted three 10 x 2m transects at four depths (4.6, 6.1, 7.6, and 9.1m). In the back reef, we ran five 10 x 2m transects in the *Thalassia testudinum* beds and five transects along the back of the reef crest. All transects were east-west, parallel to the reef crest.

In each transect, we counted the number of *D. antillarum* and *T. ventricosus* within 1m on either side of the 10m transect, estimated the percent fleshy macroalgae cover with a grid, and assessed the topographic complexity of the substrate. We estimated macroalgal cover in the same five 9 x 9 cm squares of a 25-square grid two times per transect. The grid was haphazardly dropped in each transect from ≈ 3m above the substrate. We assessed topographic complexity twice per transect by laying a 5.35m chain along substrate contours and then measuring the horizontal distance covered by the chain. Complexity was calculated as $C = 1 - d/l$, where $d$ is the horizontal distance covered by the chain when conformed to the substratum and $l$ is the length of the chain when fully extended (Aronson and Precht 1995).

To assess food limitation in *T. ventricosus*, we collected eight urchins in the back reef and in shallow (3 - 4 m) and deeper (7 - 8 m) fore reef sites at Pear Tree Bottom (due to sampling restrictions at Discovery Bay) and then measured the test diameter and the length of the Aristotle's lantern (Black 1982). These ratios were not adjusted for allometric growth because lantern : test ratio was constant across all test diameters. In addition, to compare between Pear Tree Bottom and Discovery Bay we haphazardly surveyed the urchin test diameter in shallow and deep fore reef sites and in the back reef at Discovery Bay (n = 148 urchins).

We performed Wilcoxon and Kruskal-Wallis nonparametric ANOVAs to test the effects of site, depth, and time (1991 vs. 1998) on densities of *T. ventricosus* and *D. antillarum*. When comparing 1991 and 1998 urchin densities and macroalgal cover we used data from M1. However, for current comparisons of back reef and fore reef we pooled M1 and LTS data. We excluded the back reef crest for these analyses because it does not seem to represent urchin habitat, as seen in the extremely low densities of both urchins, possibly due to extreme wave surge. We used one-way ANOVAs to test the effects of habitat on the lantern : test ratio, and on the mean lantern diameter of *T. ventricosus*. arcsin-transformed macroalgal cover measurements were analyzed with one way ANOVAs for the effects of site, depth and the interaction between these two factors. We tested the effects of vertical complexity on relative and absolute densities of both urchins, and total urchin density with Spearman rank correlations. The effects of *D. antillarum* and *T. ventricosus* on macroalgal cover were tested with Spearman-rank correlations.

## RESULTS

We counted a total of 807 urchins in 680 $m^2$. The two fore reef sites at Discovery Bay (LTS and M1) were not significantly different in terms of macroalgal cover or urchin densities (Tukey Test: $P > 0.05$) and were pooled for fore reef vs. back reef comparisons. *T. ventricosus* and *D. antillarum* densities were not significantly different in the back reef and fore reef at Discovery Bay (Wilcoxon and Kruskal-Wallis ANOVA: $X^2 = 0.12$, $P = 0.73$, $X^2 = 2.70$, $P = 0.10$).

Densities of *D. antillarum* in the fore reef of Discovery Bay were significantly higher at 4.6 m than at other depths (Tukey Test, $P < 0.05$; Fig. 1). *T. ventricosus* density decreased with depth although this trend was not statistically significant (Wilcoxon and Kruskal-Wallis ANOVA: $X^2 = 7.02$, $P = 0.07$; Fig. 1). Total urchin density was greater in the shallow fore reef than in the deep fore reef (Wilcoxon and Kruskal-Wallis: $X^2 = 9.07$, $P = 0.01$; Fig. 2). There were no relationships between *T. ventricosus* or *D. antillarum* densities and percent macroalgal





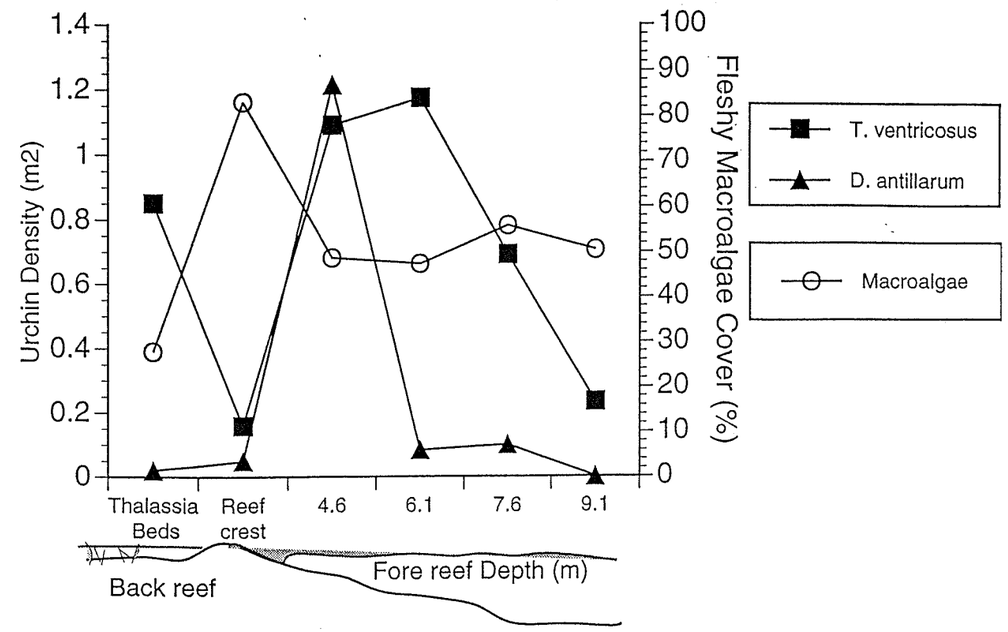


FIG. 1. Densities of *Diadema antillarum* and *Tripneustes ventricosus* and fleshy macroalgae cover in the Western coral reef of Discovery Bay in 1998.

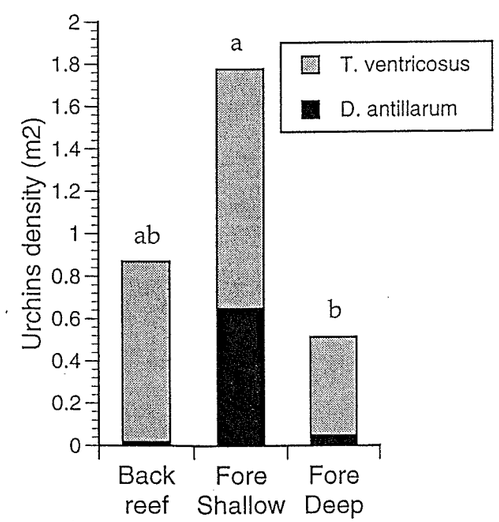


FIG. 2. Current densities of *T. ventricosus* and *D. antillarum* urchins in back reef turtle grass beds, shallow (4.6-6.1m) and deep fore reef (7.6-9.1m) of Discovery Bay, Jamaica.

cover or vertical complexity (Spearman Rank correlations : all $P > 0.05$). There was no difference in macroalgal cover across the four depths in the fore reef (ANOVA: $F_{3,15} = 0.34$, $P = 0.80$).

Mean test diameter of *T. ventricosus* was significantly greater in the back reef than in the fore reef at Discovery Bay ($F_{2,145} = 31.73$, $P < 0.0001$; Fig. 3), showing the same pattern as Pear Tree Bottom ($F_{2,21} = 8.29$, $P = 0.002$). The lantern : test ratio was higher in the fore reef than in the back reef at Pear Tree Bottom, indicating that *T. ventricosus* is relatively more food-limited in the fore reef than the back reef ($F_{2,21} = 25.18$, $P < 0.0001$; Fig. 4).

In 1991, Gilmartin and Young conducted their study at M1. Thus, for comparisons of 1991 vs. 1998 we used M1 data only. We compared urchin density and percent macroalgal cover across all depths and at each depth. *D. antillarum* and *T. ventricosus* densities and percent macroalgal cover did not change in the fore reef (M1) of Discovery Bay from 1991 to 1998 (Table 1, Table 2). However, macroalgal cover showed a significant decrease at 9.1 m from 1991 to 1998 (Table 2).

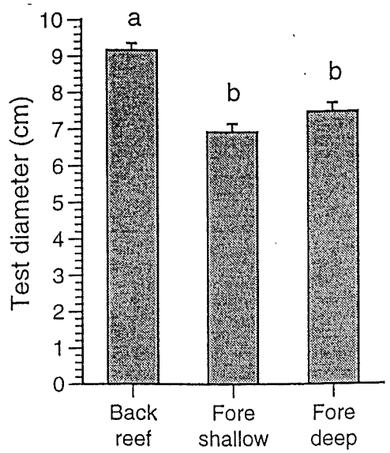


FIG. 3. Mean test diameter for *T. ventricosus* in three sites at Discovery Bay.. Fore reef shallow = 3-4m, Fore reef deep = 7-8m. Bars with different letters were significantly different.

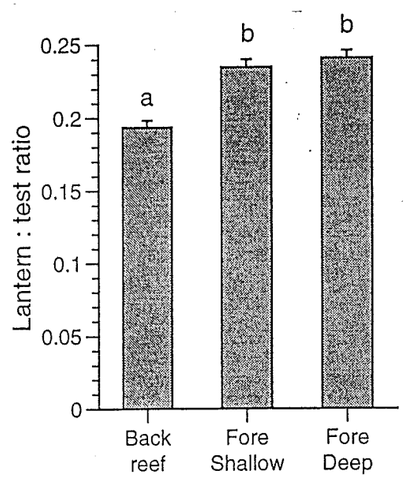


FIG. 4. Lantern : test ratio (mean ± 1SE) for *T. ventricosus* in three sites at Pear Tree Bottom.. Fore reef shallow = 3-4m, Fore reef deep = 7-8m. Bars with different letters were significantly different.

TABLE 1. Summary of urchin density (number/m$^2$ ± 1SE) as a function of depth for the fore reef (M1) of Discovery Bay in 1991 and 1998 (Gilmartin and Young 1991, and Eaken et al 1998). P values are the results from Wilcoxon and Kruskal-Wallis ANOVAs comparing 1991 and 1998 values.

| | *T. ventricosus* | | | *D. antillarum* | | |
|---|---|---|---|---|---|---|
| Depth (m) | 1991 | 1998 | P value | 1991 | 1998 | P value |
| 4.6 | 0.52 ± 0.41 | 1.07 ± 0.35 | 0.13 | 1.32 ± 0.81 | 1.60 ± 0.78 | 0.65 |
| 6.1 | 0.82 ± 0.82 | 0.42 ± 0.16 | 0.65 | 0.03 ± 0.07 | 0.05 ± 0.00 | 0.14 |
| 7.6 | 0.19 ± 0.13 | 0 | 0.06 | 0 | 0.15 ± 0.08 | 0.05 |
| 9.1 | 0.16 ± 0.10 | 0.47 ± 0.47 | 0.45 | 0 | 0 | 1.00 |
| Overall | 0.42 ± 0.11 | 0.49 ± 0.17 | 0.65 | 0.34 ± 0.15 | 0.45 ± 0.26 | 0.16 |

TABLE 2. Summary of percent fleshy macroalgal cover in the fore reef (M1) of Discovery Bay. 1991 data taken from Gilmartin and Young (1991). P values are the results of t-tests comparing 1991 and 1998 values.

| Depth (m) | 1991 | 1998 | P value |
|---|---|---|---|
| 4.6 | 38.3 ± 20.5 | 45.3 ± 5.7 | 0.60 |
| 6.1 | 62.0 ± 8.6 | 67.0 ± 5.8 | 0.60 |
| 7.6 | 77.7 ± 14.0 | 69.2 ± 6.16 | 0.67 |
| 9.1 | 76.9 ± 13.0 | 44.8 ± 5.05 | 0.004 |





## DISCUSSION

The density of *D. antillarum* relative to total urchin density was higher in the shallow fore reef than in the deep fore reef or the back reef, suggesting that this is a more suitable habitat for them. Although the density of *T. ventricosus* did not differ between the fore reef and back reef, the mean test diameter was higher in the back reef, likely due to the high abundance of *Thalassia testudinum*, their preferred food (J. Gilbert, pers. comm.). Though we did not measure this directly, we found *T. ventricosus* at Pear Tree Bottom to be more food limited in its new fore reef habitat than in the back reef as measured by the lantern:test ratio. This result may be attributable to higher urchin densities at Pear Tree Bottom, but the similar relationship of test diameters between Discovery Bay and Pear Tree suggest that there may be food limitation in the fore reef at both sites. Thus, it appears that the fore reef may be a less suitable habitat than the back reef for *T. ventricosus*.

Within the fore reef, urchin densities showed a decreasing trend with depth. Although we had initially postulated that vertical complexity and macroalgal abundance would be correlated with urchin density, we found no such relationships. Based on our observations, *D. antillarum* was found almost entirely in rock and coral outcroppings while *T. ventricosus* was observed most often on flatter substrate. However, due to the patchiness of urchin distribution and the possibility that areas of high vertical complexity in the fore reef may not be saturated, our results do not reflect these habitat preferences. Our finding that macroalgae did not change with depth or urchin density in Discovery Bay is puzzling, as a previous study has shown this relationship (Gilmarten and Young 1991). At Pear Tree Bottom, however, we observed trends similar to those reported at Discovery Bay in 1991. It is possible that other factors such as damselfish territories or changes in herbivorous fish populations in Discovery Bay have affected current macroalgae patterns.

Following the massive die-off of *D. antillarum* in 1983, it was eight years before *T. ventricosus* began to colonize the fore reef of Discovery Bay in 1991 (Gilmartin and Young 1991). We found no increase in urchin density from 1991 to 1998, suggesting that population growth of both urchins may have leveled off. Given that *T. ventricosus* appears to be relatively stressed in the fore reef, we expect that *T. ventricosus* density may eventually decrease. Perhaps *D. antillarum* will again dominate the fore reef, with *T. ventricosus* being confined to the back reef.

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APPENDIX A. Summary of data for urchin densities, algal cover, and vertical complexity in the back reef (BR) and at different depths at LTS and M1, Discovery Bay, Jamaica.

| Site | Depth (m) | Transect # | Relief | % Algal Cover | # Diad | # Trip |
|---|---|---|---|---|---|---|
| LTS | 15 | 1 | 0.19 | 49.5 | 24 | 26 |
| | | 2 | 0.20 | 54.5 | 9 | 8 |
| | | 3 | 0.15 | 52 | 17 | 33 |
| | 20 | 1 | 0.11 | 35 | 1 | 51 |
| | | 2 | 0.16 | 18.5 | 1 | 26 |
| | | 3 | 0.15 | 29.5 | 5 | 39 |
| | 25 | 1 | 0.25 | 40.5 | 3 | 28 |
| | | 2 | 0.25 | 17.5 | 0 | 39 |
| | | 3 | 0.16 | 82.5 | 0 | 16 |
| | 30 | 1 | 0.23 | 46 | 0 | 0 |
| | | 2 | 0.20 | 52.5 | 0 | 0 |
| | | 3 | 0.19 | 70 | 0 | 0 |
| M1 | 15 | 1 | 0.29 | 53 | 45 | 32 |
| | | 2 | 0.18 | 28 | 50 | 8 |
| | | 3 | 0.21 | 55 | 1 | 24 |
| | 20 | 1 | 0.18 | 92 | 1 | 2 |
| | | 2 | 0.14 | 52.5 | 1 | 10 |
| | | 3 | 0.25 | 56.5 | 1 | 13 |
| | 25 | 1 | 0.26 | 70 | 0 | 0 |
| | | 2 | 0.24 | 68.3 | 4 | 0 |
| | | 3 | 0.23 | - | 5 | 0 |
| | 30 | 1 | 0.34 | 39.5 | 0 | 28 |
| | | 2 | 0.17 | 48 | 0 | 0 |
| | | 3 | 0.21 | 47 | 0 | 0 |
| BR | 1-2 | 1 | 0.07 | 94.5 | 0 | 14 |
| | | 2 | 0.03 | 56.5 | 0 | 21 |
| | | 3 | 0.02 | 68.5 | 0 | 21 |
| | | 4 | 0.07 | 96.5 | 2 | 9 |
| | | 5 | 0.06 | 100 | 0 | 20 |
| | 1-2 | 1 | 0.25 | 3 | 1 | 0 |
| | | 2 | 0.26 | 47 | 4 | 3 |
| | | 3 | 0.21 | 25 | 0 | 2 |
| | | 4 | 0.28 | 37 | 0 | 6 |
| | | 5 | 0.17 | 27.5 | 0 | 5 |





APPENDIX B. Summary of data for test diameter in the back reef (BR), fore reef shallow (FR shallow), and fore reef deep (FR deep) at Discovery Bay, Jamaica.

| Site | Depth (m) | Test Diameter | | | |
|---|---|---|---|---|---|
| BR | 1-2 | 7.5 | 8.3 | 10 | 10.5 |
| | | 8.4 | 11.1 | 10.5 | 6.5 |
| | | 9.6 | 9 | 8.5 | 9.5 |
| | | 8.3 | 9 | 8.5 | 10.5 |
| | | 7 | 9.5 | 8 | 10 |
| | | 11 | 8 | 9.5 | 7.5 |
| | | 10 | 10 | 10 | 11.5 |
| | | 8 | 8.5 | 7.5 | 8 |
| | | 7.5 | 8 | 11 | 9.5 |
| | | 8.5 | 10 | 11 | 7.5 |
| | | 10 | 9 | 8 | 10 |
| | | 9.5 | 8.5 | 9 | 14 |
| | | 6.5 | 8.5 | 6.5 | 8 |
| | | 10 | 9.5 | 11 | 11 |
| | | 9 | 11 | 11 | 11 |
| | | 6 | 9 | 8.5 | |
| FR Shallow | 15 | 7 | 6 | 3 | 9 |
| | | 8 | 6 | 6 | 8.5 |
| | | 9 | 6 | 8 | 8 |
| | | 8.5 | 7.5 | 5 | 7.5 |
| | | 6.5 | 6 | 4.5 | 10 |
| | | 5 | 6 | 4.5 | 7 |
| | | 6.5 | 8 | 6.5 | 8.5 |
| | | 7.5 | 7 | 4 | 7.5 |
| | | 7.5 | 7 | 5.5 | 6 |
| | | 9 | 8 | 5 | 8 |
| | | 9 | 5.5 | 7.5 | |
| FR Deep | 20 | 8 | 6 | 8.5 | 7 |
| | | 8.5 | 6 | 8.5 | 5.5 |
| | | 8.5 | 5 | 9 | 6.5 |
| | | 8.5 | 8 | 8.5 | 7 |
| | | 10 | 6.5 | 8 | 5 |
| | | 9 | 8 | 8.5 | 7.5 |
| | | 6.5 | 8.5 | 9.5 | 9.5 |
| | | 11 | 6 | 7 | 7.5 |
| | | 9.5 | 6.5 | 7 | 6 |
| | | 8.5 | 5 | 6.5 | 5 |
| | | 5.5 | | | |

APPENDIX C: Lantern: Test Ratios of *Tripneustes ventricosus* taken from the fore reef and back reef at Pear Tree Bottom, Discovery Bay, Jamaica.

| Site | Demipyramid length | Test diameter | Lantern:Test Ratio |
|---|---|---|---|
| BR | 72 | 14 | 0.194444 |
| | 88 | 17 | 0.193182 |
| | 96 | 21 | 0.21875 |
| | 87 | 16.5 | 0.189655 |
| | 90 | 16 | 0.177778 |
| | 80.5 | 16.5 | 0.204969 |
| | 111 | 21 | 0.189189 |
| | 95 | 17 | 0.178947 |
| FR shallow | 68 | 15 | 0.220588 |
| | 85 | 18 | 0.211765 |
| | 64 | 15.5 | 0.242188 |
| | 77 | 18.5 | 0.240260 |
| | 70 | 15.5 | 0.221429 |
| | 70 | 17 | 0.242857 |
| | 72 | 18.5 | 0.256944 |
| | 79.5 | 19 | 0.238994 |
| FR deep | 71 | 18 | 0.253521 |
| | 70 | 16 | 0.228571 |
| | 85 | 21 | 0.247059 |
| | 86.5 | 19 | 0.219653 |
| | 64 | 17 | 0.265625 |
| | 76.5 | 18 | 0.235294 |
| | 74 | 18 | 0.243243 |
| | 78 | 18 | 0.230769 |