

INTERTIDAL ZONATION OF TWO GASTROPODS, *NERITA PLICATA* AND *MORULA GRANULATA*, IN MOOREA, FRENCH POLYNESIA

VANESSA R. WORMSER

Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. Intertidal zonation of organisms is a key factor in ecological community structure and the existence of fundamental and realized niches. The zonation of two species of gastropods, *Nerita plicata* and *Morula granulata* were investigated using field observations and lab experimentation. The *Nerita plicata* were found on the upper limits of the intertidal zone while the *Morula granulata* were found on the lower limits. The distribution of each species was observed and the possible causes of this zonation were examined. Three main factors, desiccation, flow resistance and shell size were tested for their zonation. In the field, shell measurements of each species were made to see if a vertical shell size gradient existed; the results showed an upshore shell size gradient for each species. In the lab, experiments were run to see if the zonation preference found in the field existed in the lab as well. This experiment confirmed that a zonation between these species does in fact exist. Additional experiments were run to test desiccation and flow resistance between each species. A difference in desiccation rates and flow resistance were found with the *Nerita plicata* being more resistant to both flow and desiccation. The findings of this study provide an understanding on why zonation between these two species could exist as well as why zonation is important within an intertidal community and ecosystems as a whole.

Key words: *community structure; gastropod; zonation; intertidal; morphometrics; Morula granulata; Nerita plicata; Mo'orea, French Polynesia;*

INTRODUCTION

The main goal of an ecological survey is to explore and understand the key dynamic relationships among organisms living in a community (Elton 1966). With the recent developments on climate change, it is predicted that severe weather conditions such as tropical cyclones have and will continue to increase (Emmanuel 2008). These weather conditions make it difficult for organisms to live in their biological communities. Due to various physical changes on habitats, it is important to study ecological communities within these habitats and how they adapt in response to changing environmental factors (Augustin 1999). However, interpreting the significance and intensity of the interactions among species is difficult (Paine 1974); most studies do not get past the preliminary stage of identifying and describing the community because of the difficulties of sampling and identification (Fager 1963). Additionally, most community studies have been done on terrestrial rather than marine environments because they are easier to access (Olsgard, *et al.* 2003). In spite of this, for many years, rocky intertidal shores have attracted attention

because of the high species diversity, the convenience of the habitat as well as the easy collection of the sessile organisms that inhabit these shores (Connell 1972). Unfortunately, species richness and diversity are most threatened in these rocky coastal areas (Gray 1997). Thus, the rocky intertidal zone is an important place to study community ecology.

Communities in the rocky intertidal are predominantly zoned (Lubchenco 1980). According to Connell 1972, zonation is the distribution of habitats along a gradient based on both biotic and abiotic factors. Biotic factors include interactions with other organisms such as competition and predation, while abiotic factors include desiccation, light intensity, wave and flow resistance, as well as many others (Quinn and Dunham 1983, Karlson and Herd 1983). As Gause said in 1934, often the limiting factor is space and a fight for the resources within that space. But this does not exclude the fact that environmental factors, such as physiological traits also affect vertical zonation (Broekhuysen 1940). These different factors create fundamental and realized niches which explain the zonation of organisms.

The studies on the factors affecting

zonation show that the majority of vertical zonation is amongst sessile organisms, including gastropods (Lalli and Parsons 1993). The zonation of gastropods is of particular interest because these organisms fulfill important ecological roles from grazers and scavengers to carnivores, and they also inhabit a large range of habitats. (Sturm *et al* and Suominen 2006). They can be found anywhere from outside in the grass of ones garden to deep down on the ocean floor (Sturm *et al* and Suominen 2006). Gastropods are also abundant and easy to collect, making them good organisms to observe and manipulate in lab.

In Moorea, French Polynesia, two species of gastropods are prevalent along the rocky intertidal shores (Salvat and Rives 1984). *Morula granulata* (Muricidae) and *Nerita plicata* (Neritidae) are both widely found on Moorea. Previously in gastropod distribution studies on French Polynesia, there were few *N.plicata* and *M.granulata* species (Augustin 1999 and Wilson 2009). However, upon personal observation, both species were found to be abundant. *Nerita plicata*, is an herbivorous snail found along the rocks of the upper limits of the intertidal zone (Frey 2008), while *Morula granulata* is a slow carnivorous snail found in rock crevices submerged in water in the lower parts of the intertidal region (Devi *et al* 1987). There is an apparent vertical zonation between these two species of gastropods found along the same rocky intertidal shore.

The purpose of this study was to explore in detail the spatial variation of *Nerita plicata* and *Morula granulata*. Easy to manipulate and abundant, these two species were ideal to study and understand zonation patterns along the intertidal shore. However, no studies have been done on why these two specific species are found in different zones of the intertidal coast. The following explanation were tested: (1) there is a shore level shell size gradient for each species (2) each species desiccates at different rates, with *Morula granulata* desiccating at a faster rate than *Nerita plicata*, (3) each species has different resistance to flow, the *Nerita plicata* is more resistant to stronger currents and higher flow rates than the *Morula granulata*.

METHODS

Study site

Nerita plicata and *Morula granulata* individuals were observed and collected at three different sites in Moorea French Polynesia (149°50'W and 17°30'S). The three sites were chosen because they each had conglomerate platforms. The first site was located at the public beach of Temae (17°29'53.58"S, 149°45'40.46"W), the second at the motu Tiahura (149°54'43"W 17° 29'15 S), and the third at pineapple beach (17°33'50.16"S 149°51'58.05"W) (Fig. 1). Each site was chosen because of the presence and abundance of each species, additionally making the collection of these gastropods for experiments possible. The sites each had an intertidal zone composed of rock, coral and coral rubble.

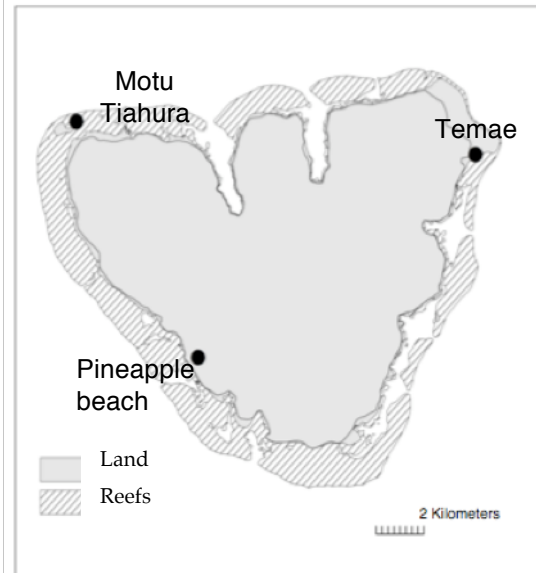


FIG. 1. Map of Moorea, French Polynesia with study sites shown. Map from the support and services of UC Berkeley's Geospatial Innovation Facility (GIF). Gif.berkeley.edu

Study Organisms

Nerita plicata is a species of intertidal gastropod in the Neritidae family. It is an herbivorous snail found in the western Pacific and the Indian oceans (Frey 2008). As an algae grazer it is found on rocks and inside crevices on the upper limits of the intertidal shore (Taylor 1971). Its shell color ranges from cream to rose with black markings on it and

its shell is of a globose shape with a water reservoir to retain water (Frey 2008). It is also nocturnal and migrates as the tide changes (Ruwa 1988). This species has been previously studied in Moorea through a Berkeley student in a *Nerita* of Moorea study (Boyer 1998). However, no studies have been done on its zonation in relation to other genera and species in the intertidal zone of Moorea.

Morula granulata is a species of intertidal gastropod in the Muricidae family. It is a slow moving carnivorous snail found in the Pacific and off of African coasts (Devi 1986). It lives in a variety of habitats, which differ depending on the amount of wave action, tidal fluctuation, exposure periods, rock morphology and environmental conditions (Sarma 1972). In a previous study on intertidal zonation in Aldabra, the *M. granulata* was found at the lower end of the cliff at the sublittoral fringe (Taylor 1971). *M. granulata* has previously been studied in French Polynesia in a gastropod distribution survey study, but no studies have been done on the habitats it lives in relation to other species in Moorea.

Preliminary observations and collections

At each of the six sites, five 10m transects were performed between October 1st 2012 and November 10th 2012. The width of each transect was 40cm, measured by a 40cm*40cm quadrat continuously shifted for 10m. The number of snails of all species were counted and identified. Shell heights, widths as well as aperture heights and widths of the *Nerita plicata* and the *Morula granulata* were recorded. A diagram of the measurements is shown in Appendix A (Fig A). The initial water level as well as the instantaneous current was recorded and each snail that was measured was also given a horizontal distance from the water as well as a vertical distance. The transects at all three sites were run perpendicular to shore to study the vertical zonation.

For statistical analysis, linear regression tests with the shell size and the distance from the water were conducted for all three sites and for both species with JMP. Additionally, discriminant analyses were conducted using JMP. The discriminant analysis was performed on the three sites for the shell measurements of each species and the parametric multivariate Wilks' Lambda test was used to determine if there was statistical significance between the measurements at each site.

A total of 40 snails, twenty *Nerita plicata* and twenty *Morula granulata* were collected at a time to be brought back into the lab. These collections were done 6 times. The snails were collected and put into a tupperware containing seawater as well as rock from the site and then brought back into the lab within two hours of collection. *Nerita plicata* and *Morula granulata* individuals were acclimated in a flow tank with circulating seawater at the University of California Berkeley research station for 12 hours.

After the acclimation period was over, the individuals were put into a tank with rocks and coral rubble mimicking an intertidal zone. In the tank, the water level was recorded and the location of each individual was noted. After these observations were noted, manipulations could begin. No more than forty specimens were ever in the tank.

Zonation Preference

The first experiment was an observational study on the zonation of the *Nerita plicata* and the *Morula granulata*. The two species were put in a tank together and then separated and their location as well as their distance from the water was noted every three hours for a total of 24 hours. The experiment was run with both species of snails together in the tank for 12 hours and then both species separated for 12 hours. Afterwards with a different collection of snails, it was run with first the snails separated for 12 hours and then put together in the tank for 12 hours. Additionally the tidal charts for the days the experiments were run were checked to know when low and high tide occurred. When it was low tide, the water level in the tank was brought down to 8cm. Alternatively, when it was high tide, the water level was at 25cm. The 17cm difference was made in order to mimic the tide differences that occur in Moorea and to see if the snails migrated as the tides fluctuated. In each three-hour increment, the numbers of snails above the water and below were noted for each species.

To evaluate if there was a significant preference for zonation, a T-test with the number of snails above the water for each species was conducted using JMP.

Effects of Desiccation

The second experiment was performed to test the desiccation rates of the *Nerita plicata* and the *Morula granulata*. In each experiment, a total of five individuals of one species were

put into a tray with desiccant and mesh; they were then covered up and left for six hours. The individuals were weighed before being put onto the desiccant. Every hour each snail was weighed and the color changes were noted. This experiment was run five times for each species. Once the snails were on the tray for six hours, they were then placed into water and their recovery time was noted. Recovery was defined as any movement observed in the snail. At the end of each experiment the percent water loss of each individual snail was calculated. Additionally, each experiment was run with no more than 10 snails collected from the same location.

To test for a relationship between the percent water loss and the snail species a T-test was conducted using JMP.

Flow Resistance

The third experiment tested the resistance to flow between each species. A flow tank was used with three different levels of current, low, medium and high. The snails were placed in a line in the flow tank and the amount of snails that fell off their substrates was noted. Every minute the flow rates were increased as the snails' locations were marked. A total of ten snails of each species were used in each experiment and the experiment was run 10 times. The snails were originally collected with the substrate they were found on and then brought back into the lab to be placed in the flow tank.

To analyze the difference in flow resistance between each species, a T-test, with the number of snails that stayed on their substrates amongst each species, was conducted using JMP. The test was only used with the high flow results because there was no difference in resistance between low and medium flow.

RESULTS

All data were analyzed with statistical software JMP. 10 SAS institute Inc. 2012

Field observations

Shell heights and widths as well as aperture heights and widths of the *Nerita plicata* and the *Morula granulata* were correlated with the distance from the tide line. An initial linear regression test was run with the different measurements to see if they were correlated with each other. Shell height, shell width and aperture height and width were all

significantly related with $p < 0.001$. After this test, it was assumed that shell height was a good representative of shell size.

In the linear regression test with the shell heights of each species in the y-axis and the distance from the water in meters in the x-axis, a significant positive relationship was found between the shell heights and the distance for the *N. plicata* ($R^2 = 0.3$ and $p < 0.0001^*$) (Fig. 2a). However, a relatively constant shell size was found for the *M. granulata*; this continuous trend was significant ($R^2 = 0.16$ and $p = 0.04$) (Fig. 2b).

In the discriminant analysis of all the shell measurements categorized by sites (Temae, Motu Tiahura and Pineapple beach) each species was different. The discriminant analysis for the *Morula granulata* produced significant separation between sites (Wilks' Lambda, $F = 4.67$, $DF = 8$, $p < 0.0001^*$) (Fig. 3a). Alternatively, the discriminant analysis for the *Nerita plicata* distinguished one of the sites, Temae, from the other two sites (Wilks' Lambda, $F = 8.10$, $DF = 8$, $p < 0.0001^*$) (Fig. 3b).

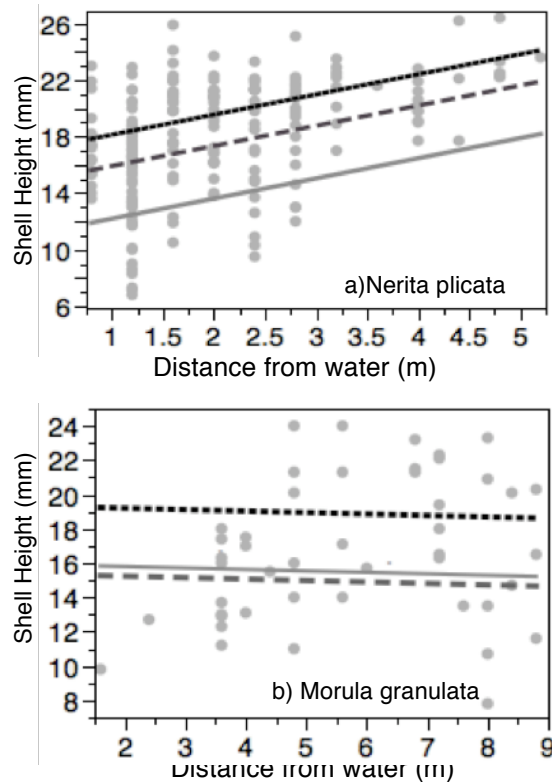


FIG. 2a-b. Linear regression test showed a positive correlation for *Nerita* ($R^2 = 0.3$ and $p < 0.0001^*$) and no correlation for *Morula* ($R^2 = 0.16$ and $p = 0.04$) between shell height and distance from water at each site. Black line=Temae, Grey dashed line= Motu Tiahura, Grey line=Pineapple beach

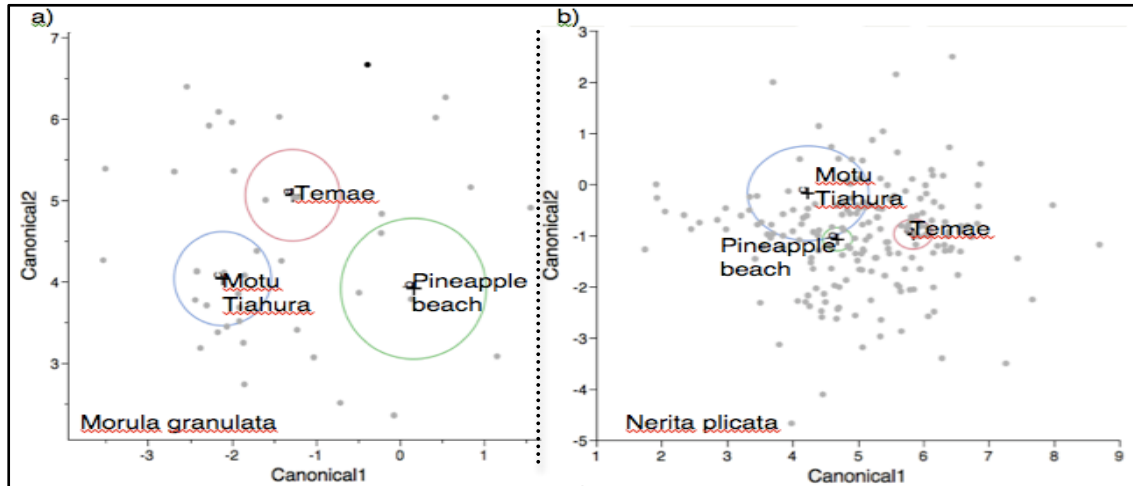


FIG. 3a-b. Discriminant analysis of shell measurements categorized by sites. The confidence interval circles show the distinction between sites. Fig. 3a shows three distinct sites (Wilks' Lambda $F=4.67$, $DF=8$, $p<0.0001^*$). Fig. 3b shows overlap between Motu Tiahura and Pineapple beach circles making them more similar but Temae is different (Wilks' Lambda, $F=8.10$, $DF=8$, $p<0.0001^*$).

Zonation preference

Each species of gastropod were found in different zones throughout the experiment. The *Nerita plicata* snails were more often found above the water level while the *Morula granulata* snails were found more frequently below the water level. (Fig.4). The T-test showed a highly significant zonation preference between each species ($p<0.0001^*$).

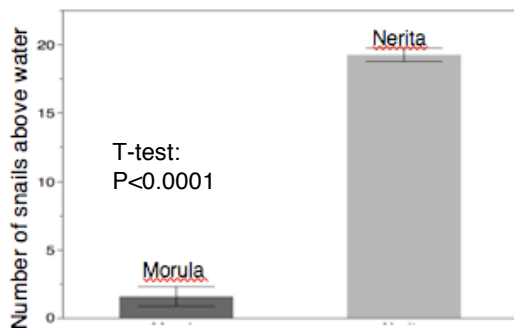


FIG. 4. Average number of snails above the water for each species. Significantly more *Nerita* found above. T-test ($p<0.0001^*$) shows significant preference for zonation. Error bars are the 95 % confidence interval.

Effects of Desiccation

The percentage of water loss between each species differed throughout the experiment. The *Nerita plicata* lost on average less water during the 6 hours than did the *Morula granulata* (Fig.5). However, the T-test between each species was not significant and the 95% confidence intervals on the bar graph overlap ($p=0.07$).

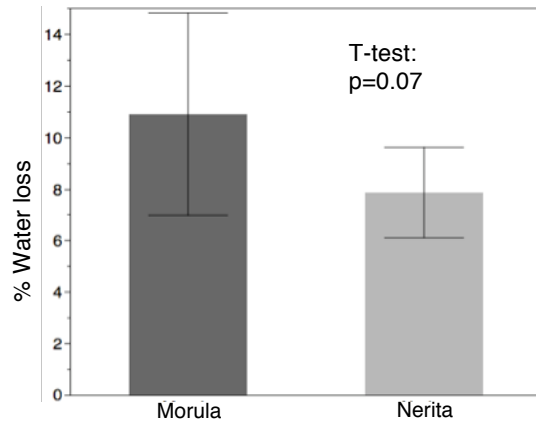


FIG. 5. Average % water loss over 6 hours of desiccation for each species. Error bars represent the 95% confidence interval. They overlap so there is no significance. T-test was insignificant ($p=0.07$).

Flow Resistance

Each species of gastropod exhibited different resistance to flow rates. The *Nerita plicata* snails on average were more resistant to higher flow rates than the *Morula granulata* (Fig. 6). At lower flow rates, there was no difference in resistance between the two species. The T-test for the higher flow rates was highly significant showing a difference in flow resistance ($p < 0.0001^*$).

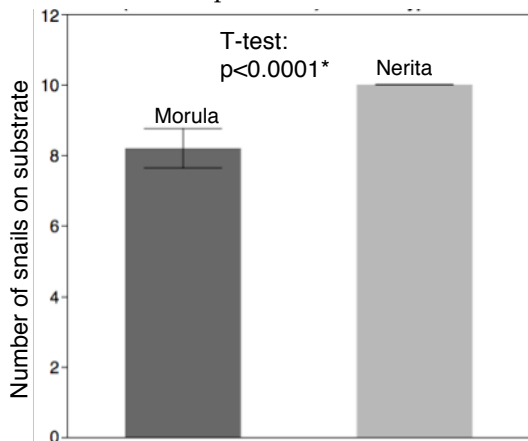


FIG. 6. Average number of snails that stayed on their substrate at high flow for each species. Error bars represent the 95% confidence intervals. A T-test showed significance ($p < 0.0001^*$). *Nerita* is more resistant to higher flow rates.

DISCUSSION

The results of my study lead to four main points: (a) differences in the shell and aperture size along the intertidal shore throughout Moorea; (b) the zonation of these two species of snails; (c) the difference in desiccation rates between the *Nerita plicata* and the *Morula granulata*; and (d) the effects of flow rates on each species.

Field observations

Between each species: *Nerita plicata* and *Morula granulata* there were different relationships found between the shell and aperture sizes and the distance from the shore. In general, shell sizes of molluscs have been reported to increase in an upshore direction in species of the higher intertidal zone, with larger and older species found in the upper limit of the intertidal shore (Vermeij 1971). As the distance from the water increases, the shell

sizes increase; which was found to be true with the *Nerita plicata*.

However with the *Morula granulata*, as the distance from the water increased the shell and aperture sizes did not increase. The shell sizes stayed relatively constant throughout the intertidal zone. The literature states that the shell sizes of species from the lower intertidal levels tend to decrease in an upshore direction (Vermeij 1971). In a previous study on the *Morula granulata*, on the beaches of the Waltair coast, the location of the snail and its shell morphology were significantly related. A wide shell with a wide aperture was found in stronger wave action areas because a wider aperture has a firmer hold on rocky substrates (Devi 1986). This was not found to be the case in Moorea.

Most studies done on shore level size gradients in intertidal gastropods have been done in wave swept rocky coastal areas such as the California or Washington coast. However in Moorea, there is very little difference between low and high tide therefore very little wave action in the intertidal zone (Boyer 1998). Additionally, the intertidal zone is shorter than a rocky coast. The size level gradient in the intertidal shore is generally the result of the resistance to wave action (Koehl 1985). It is therefore interesting that we would find this same gradient in a non-wave swept area for the *Nerita plicata*. The change in flow can be attributed to the currents, there is no reason we should see a significant increase or decrease in shell or aperture sizes.

Not only was there a size gradient, but for the *N.plicata* there was also a significant difference in shell size between the east and west side of the island. The shells were on average much larger on the east side of the island at Temae. This difference may be due to the winds or the currents from the ocean on that side of the island. Shell morphology is highly influenced by environmental factors therefore a slight change in current or temperate can vastly change the size the shells will ultimately grow to (Taylor 1971).

Zonation preference

The two species of gastropods seem to prefer distinct zones in the intertidal shores; the *Nerita plicata* prefers to be out of the water above the tide and the *Morula granulata* prefers to be in the water right below the tide. In the laboratory, as the water level was lowered to mimic low tide the *Nerita plicata* snails stayed above the water and the *Morula granulata*

snails migrated to a lower part of the tank to be below the water level. When the water level was higher, similar to high tide, the *Nerita plicata* snails migrated above the water and the *Morula granulata* snails stayed below. Each species seemed to follow the movement of the tide when put into a tank mimicking the intertidal zone.

However when the two species were put into a flat tank, they also zoned and were not disturbed by presence of each other species. This indicates that the zonation observed between both species is most likely not due to direct competition for space between them.

Effects of Desiccation

Over a six-hour period, each of the two species of gastropod examined desiccated at different rates. The *Nerita plicata* on average lost a lower percentage of water than the *Morula granulata*. Because the *Nerita plicata* is found on the upper limits of the intertidal shores, it would suggest that *N. plicata* would desiccate at a slower rate than the *Morula granulata*, which prefers to stay in the water.

However the insignificance of the statistical test may be due to sample size or the fact that the *M. granulata* has a bigger range of desiccation rate, as seen by the confidence intervals (Fig.4). As far as recovery time, both species recovered almost completely within an hour of being in the water.

Smaller shelled snails did not necessarily desiccate much faster than the bigger shelled snails. This was found true for both species. This observation helps support the findings that there is no significant correlation between shell sizes and the distance from the shore for the *Morula granulata*. In general, the bigger shelled snails tend to desiccate at a slower rate, which is another reason why they can survive further from the water (Broekhuysen 2010).

Resistance to Flow

Each species of gastropod exhibited different behaviors in response to flow rates. At higher flow rates, the *Nerita plicata* snails would try to cluster together and hold on to each other for protection against the stronger current. This is similar to how they are found in the field in the intertidal zones where they are often in large numbers clustered together in small crevices to insure more protection and water retention (Frey 2008). In contrast, the *Morula granulata* snails tend to exhibit a

more independent behavior, found more often alone or with one other snail and hiding in rocks in the water.

This difference in resistance between the two species could be attributed to several factors. The shells of the *Nerita plicata* snails could be more hydrodynamic than the shells of the *Morula granulata* snails. However the resistance could also be the result of adhesion. The *Nerita plicata* snails may have more adhesive force than the *Morula granulata* snails. Unfortunately, the tests run to evaluate whether the resistance was the result of more adhesion or shell morphology proved to be inconclusive or too difficult to determine.

Conclusion

Intertidal zonation was examined between two species of gastropods. After testing possible reasons for this zonation, no clear cause and effects could be concluded. There is a correlation between the distance from the shore and the shell sizes of the *Nerita plicata*, but there is no such correlation for the *Morula granulata*. Although there was a difference in the resistance to flow between each species, there was no significant difference in desiccation rates. Furthermore, these findings provide insight on some of the possible reasons for this zonation. However, many more abiotic and biotic factors could be tested for, which could also be responsible for this zonation.

This study shows the zonation of relatively sessile organisms in the intertidal zone and how ecological communities with distinct areas are present. An ecosystem full of different organisms has separate requirements to survive together, which are shown through their apparent zonation and niches. This zonation may be due to abiotic or biotic factors. Studies on zonation and distribution help scientists understand how the dynamic relationships between organisms in ecological communities work. In essence it helps better understand how an ecosystem functions. Additionally, studies on intertidal zonation of species can help us predict and see the rise in sea level. As the ice melts and the sea rises, the zonation of these species adapts and changes. Something as seemingly minute as the zonation of two species of gastropods can actually serve as a good indicator to this rise in sea level.

ACKNOWLEDGMENTS

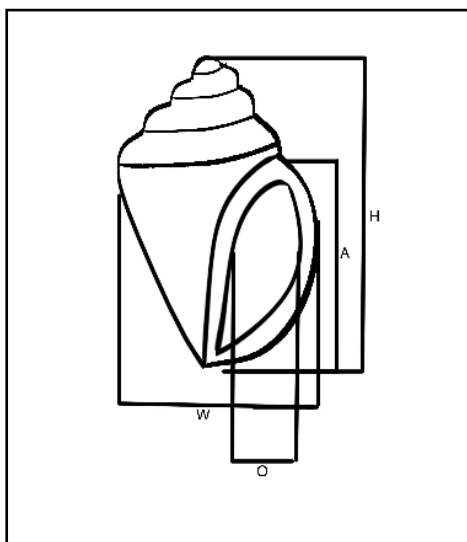
I would like to thank my Professors George Roderick, Vincent Resh, Brent Mishler and Jonathon Stillman for all the invaluable knowledge and help they have provided me with for my research. I am also grateful for my GSIs Matthew Luskin, Rosemary Romero and Darcy Kato Ernst for all of their support and guidance. Lastly I would like to thank all of my classmates from the Moorea class of 2012, all of which made my experience unforgettable.

LITERATURE CITED

- Augustin, D., G. Richard, and B. Salvat (1999). Long-term variation in mollusk assemblages on a coral reef, Moorea, French Polynesia Coral Reefs. *Science*: 1532-1535
- Boyer, S. L. (1998). The Neritidae (Gastropoda, Prosobranchia) of Moorea, French Polynesia. *Integrative Biology*. M.A., 57. Berkeley: University of California Berkeley.
- Broekhuysen, J. G Ph.D.(1940). A preliminary investigation of the importance of desiccation, temperature, and salinity as Factors controlling the vertical distribution of certain intertidal marine gastropods in False Bay, South Africa. *Transactions of the Royal Society of South Africa*, 28:3, 255-292
- Connell, J. H. (1972). Community Interactions on Marine Rocky Intertidal Shores. *Annual Review of Ecology and Systematics*, 3, 169-192.
- Devi, V. U., Rao, Y. P., & Rao, D. G. (1987). Habitat relationships of shell morphology in an intertidal gastropod, *Morula granulata* (Duclose). *Folia Morphologica*, 35, 1, 24-35
- Elton, C. S. (1966). *The pattern of animal communities*. New York: Wiley. 432pp
- Emanuel, Kerry, Ragoth Sundararajan, John Williams, 2008: Hurricanes and Global Warming: Results from Downscaling IPCC AR4 Simulations. *Bull. Amer. Meteor. Soc.*, 89, 347-367.
- Fager, E. W. (1963). *Communities of organisms*. The Sea, ed. M. N. Hill. New York: Wiley 2:415-37 Hayes, F. R. 1929. *Contributions*
- Frey, M. A. (2008). A revised classification of the gastropod genus *Nerita*. *The Veliger*. 51, 1-7.
- Frey, M. A., & Vermeij G. J. (2008). Molecular phylogenies and historical biogeography of a circumtropical group of gastropods (Genus: *Nerita*): implications for regional diversity patterns in the marine tropics. *Molecular Phylogenetics and Evolution*. 48(3), 1067-1086. Abstract
- Gause, G.F. 1934. *The Struggle for Existence*. Hafner Publ. Co., New York 163pp
- Gray, J.S. 1997. Marine biodiversity: patterns, threats and conservation needs *Biodiversity and Conservation* : 153-175
- Karlson RH. Herd LE (1993). Disturbance, coral reef communities and changing ecological paradigms. *Coral reefs* 12: 117-125
- Lalli, C. M., & Parsons, T. R. (1993). *Biological oceanography: An introduction*. Oxford: New York.
- Lubchenco, J. (1980). Algal Zonation in the New England Rocky Intertidal Community: An Experimental Analysis. *Ecology*, 61, 2, 333-344.
- Olsgard, F., T. Brattegard, and T. Holthe. 2003. Polychaetes as surrogates for marine biodiversity: lower taxonomic resolution and indicator groups *Biodiversity and Conservation* : 1033-1049
- Paine, R. T. (1974). Intertidal Community Structure. *Experimental Studies on the Relationship between a Dominant Competitor and Its Principal Predator*. *Oecologia*, 15, 2, 93-120.
- Quinn JF, Dunham AE (1983) On hypothesis testing in ecology and evolution. *Am Nat* 122:602-617
- Ruwa, R. K., & Jaccarini, V. (1988). Nocturnal feeding migrations of *Nerita plicata*, *N. undata* and *N. textilis* (Prosobranchia: Neritacea) on the rocky shores at Mkomani, Mombasa, Kenya. *Marine Biology*, 99, 2, 229-234.
- Salvat, B. C. Rives, G. Richard 1984. *Shells of Tahiti*. Les Editions du Pacifique Papeete, French Polynesia
- Sturm, F.C, T.A. Pearce A. Valdés. 2006. *The Mollusks: A guide to their study, collection and preservation*. Universal Publishers, Boca Raton, Florida, USA.
- Suominen, O, L. Edenius, G. Ericsson, and V.R. de Dios. (2003). Gastropod diversity in aspen stands in coastal northern Sweden. *Forest Ecology and Management* 175: 403-412
- Taylor, J. D. (March 04, 1971). Intertidal Zonation at Aldabra Atoll. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 260, 836, 173-213.

- Vermeij, G. J. (1973). Morphological patterns in high-intertidal gastropods; Adaptive strategies and the limitation. *Marine Biology*. 20, 319-346
- Vermeij, G. J. (1971). Temperature relationships of some tropical Pacific intertidal gastropods. *Marine Biology*. 10, 308-314.

APPENDIX A



H= Shell Height
W=Shell Width
A=Aperture Height
O=Aperture Width

FIG. A. Shell measurements performed

Species used in study



FIG. B. *Morula granulata* (Muricidae)



FIG. C. *Nerita plicata* (Neritidae)

