RESOURCE PATCHINESS AS A DETERMINANT FOR NERITA PLICATA ZONATION

CHRISTOPHER HERNANDEZ

Environmental Science Policy and Management, University of California Berkeley, Berkeley, California 94720 USA

Abstract. Zonation in rocky littoral shores is a common ecological occurrence, especially among sessile organisms. Abiotic and biotic factors have been extensively studied as reasons for the observed zonation patterns. The gastropod *Nerita Plicata* is an herbivorous snail that inhabits the upper limits of intertidal zone on the rocky shores. The zonation of *N.plicata* was investigated in relation to its ability to track resources. Different factors were taken into account, including tide, time of day, and periphyton quality. Vertical transects of both N. *plicata* activity and periphyton reveal that the snails can find their preferred grazing grounds throughout the day, migrating down to the middle and lower limits of the intertidal zone. Additionally, dispersion analysis revealed that *N. plicata* can clump in resource rich patches in the lower intertidal zone. Exclosures in the field prevented *N. plicata* from grazing on patches of algae, but algae did not respond to the absence of grazing. These findings reveal that *N.plicata* zonation is not confined to the upper limits of the intertidal zone and are temporally dynamic. The patterns are influenced by the availability of resources that are differentially distributed throughout the habitat.

Key words: gastropod; zonation; littoral zone, Nerita plicata*; Mo'orea, French Polynesia; periphyton*

INTRODUCTION

Gradients in biotic and abiotic factors affect organism distributions, including gradients in resource availability. A predictable distribution of species along an environmental gradient is known as zonation. Species zonation is common in nature and understanding it is essential to understanding community assembelages. Zonation patterns have been studied in relation to various biotic and abiotic factors and have been found to be influenced by a combination of both (Chappuis et. Al 2014). The Ideal Free Distribution Hypothesis has gained attention in the field of ecology, which predicts that organisms are capable of choosing certain patches to maximize their fitness (Stewart and Komers 2012). If an organism has perfect knowledge of its habitat, is free to move between resource patches, and does so to maximize fitness, its distribution will be determined by resource availability. For example, armored catfish in Panamanian streams distributed themselves along patches such that all of the catfish received similar amounts of resources regardless of the patch quality they inhabited (Power 1984). When a high-quality patch became too dense with catfish, fish chose the next best patch to minimize competition. Additionally, it was observed that the dispersal of *Helicopsyche borealis*, a caddisfly, can change from random to clumped when a resource patch is experimentally enhanced (Lamberti and Resh 1983). Once the improved algae patches returned to background levels, the dispersal of the larvae became random again.

Zonation in littoral rocky shores has long been studied. They often have clear zones delimiting organism's realized niches (Bennett and Pope 1953). Zone demarcation in the littoral zone is caused by strong environmental stresses related to desiccation, temperature, and irradiance; all of which have more extreme values toward the upper limits (Underwood and Jernakoff 1981). Resource availability has also been shown to play an important role in littoral shore zonation, as suggested by studies on habitat selection by periwinkle snails (Apolinário et. Al 1999). Furthermore, littoral zonation has been most often observed in sessile animals, including gastropod grazers along rocky shores (Lalli and Parson 1993). Gastropods are of particular importance because of their ubiquity and their important ecological functions (Bloch 2012). Studies on the surfaces of rocks from littoral shores concluded that diatoms are the dominant primary producers and have high turnover rates because of the intense grazing activity by snails (Vadeboncoeur and Power 2017). Other types of algae may have been absent or imperceptible in that study because they were grazed upon the moment they arrived at a patch inhabited by snails, suggesting that snails can keep track of the resource changes on their patches.

Zonation patterns have been observed for *Nerita plicata* and *Morula granulata* snails in Moorea, French Polynesia. The effects of desiccation, flow resistance, and shell size were studied as the possible causes of their zonation in rocky shores (Wormser 2012). Although differences in desiccation and flow resistance between the two snails were observed, the causes of the preferential zonation between the snails is still unclear. The feeding habits and resource tracking abilities of these snails have not yet been explored. From personal observations, there is an interesting distribution pattern of the grazer *Nerita plicata* and its periphyton food. Periphyton is mostly visible at the lower to middle limits of the intertidal zone, where it is submerged by the high tide but is exposed during the low tide. Snails, however, occupy the upper limits of the intertidal zone where periphyton is mostly absent. Characterizing temporal and spatial patterns of *N. plicata* activities and determining whether the snails are capable of tracking their resources may offer insights to the zoning patterns observed.

The goal of this study was to determine the resource tracking abilities of the snail *Nerita plicata* and how it plays a role in their zonation along littoral rocky shores. The following questions were addressed: 1) Are *N. plicata* free to move around their habitat? 2) Do N. plicata follow their resources within the habitat? 3) Do *N. plicata* snails control the quality of the periphyton through grazing activity?

METHODS

Study site

Data collection of vertical transects and exclosures began October 19 and ended November 14, 2017 at one site in Moorea, French Polynesia (Fig. 1). *N. plicata* and habitat surveys were conducted from Cook's Bay, at the Gump Station (17.490° S, 149.826° W). The study site was chosen because of the abundance of the N. plicata found on the rocky littoral shores. Additionally, there were several unique sites within the Gump property that allowed the replication of methods.

Study organism

Nerita plicata is a species of intertidal gastropod in the Neritidae family. It is an herbivorous snail and is found on rocks and inside crevices near the upper limits of the intertidal shore (Taylor 1971). The shell coloration ranges from cream to rose with black markings on it and contains a water reservoir within its shell (Frey 2008).

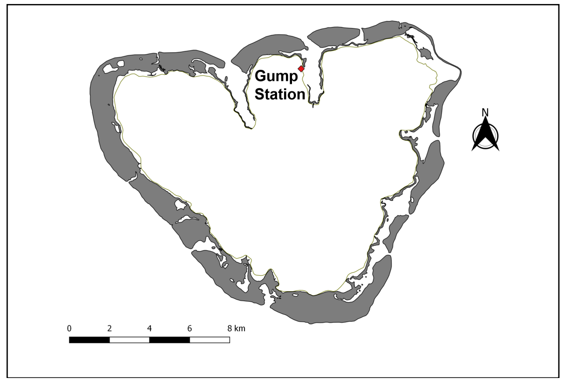

FIG. 1. Map of Moorea, French Polynesia with study site shown. Map from the support and services of UC Berkeley's Geospatial Innovation Facility (GIF). Gif.berkeley.edu

Vertical transects in the field

In order to determine if *N. plicata* are free to move around their habitat, vertical transects on each snail were done, as well as an examination of their movement abilities within their habitats. This study was conducted on study site 1 and study site 2 (Fig. 2). Study site 1 consisted of 11 boulders each in contact with one another. Each boulder averaged 1.5 meters high and had a population of 10 *N. plicata* individuals per boulder. This site was chosen because *N. plicata* were not as free to migrate to adjacent habitats as study site 2, but were able to move among the boulders within the study site. Additionally, this study site showed a strong vertical gradient of resource availability, allowing *N. plicata* to choose resource patches within the boulders themselves. Study site 2 consisted of 11 boulders that were not in contact with each other. Each boulder averaged .5 meters in height. This study site was chosen because *N. plicata* were able to move freely among the boulders as well as leave the habitat to other sites that may offer better resources, given that this habitat showed a weak vertical gradient of resources within boulders.

FIG. 2. Study site 1 shown above, study site 2 is below.

To determine whether *N. plicata* were free to move around their habitat in study site 1, vertical transects of each snail were conducted. This was done on three full sunny days, at times 6:00 am, 9:00 am, 12:00 pm, 3:00 pm, and 6:00 pm, to coincide with the low, high, and low tides. A transect tape was used to measure the vertical height of every snail that was visible on the face of the boulders. The vertical distance was defined as the distance between the position of the snail on the rock to the sand bar below. A score of 1 or 0 was given to snails that were active or inactive, respectively. An active snail was defined as a snail that was out of its shell, regardless if it was grazing. Additionally, periphyton quality and wetness were determined. Periphyton quality was determined based on a color scheme numbered 1-5, where a score of 1 indicated bare rock with no visible periphyton, 2 indicated some visible periphyton and perceptible green hues, 3 indicated clearly visible periphyton with green hues, 4 indicated a slippery dark green biofilm but boulder was still visible, and 5 indicated the algal mat where the boulder surface was no longer visible due to a thick algal mat. Wetness was also quantified on a scheme of 1-5 where a score of 1 indicated complete dryness, a score of 2 indicated that the boulder was visibly wet, score 3 indicted that the boulder was within the splash zone of the tides, a score of 4 indicated that the boulder was partially under water when the tides hit, and score of 5 indicated that the boulder was under water. To determine the correlation between time and activity, a correlation analysis in R was performed, and set alpha equal to 0.05.

Given that there was a visible gradient in periphyton quality within study site 1, a quantitative assessment of the gradient was done to correlate snail activity and periphyton quality. To do this, data from part one, snail height and periphyton quality was correlated. Additionally, height to snail activity and periphyton quality to snail activity were correlated. Since periphyton was most abundant at lower heights, it was predicted that the *N. plicata* would be most active at these heights. *N. plicata* were predicted to be most active at locations of high periphyton abundance. To determine the correlation

between periphyton quality to activity, periphyton quality to height, and height to activity, a correlation analysis in R was performed, and set alpha equal to 0.05. These three parameters tested whether *N. plicata* can preferentially choose patches within their habitat.

Mark-recapture studies

To determine the distance *N. plicata* were capable of moving in their habitat, 55 *N. plicata* individuals were collected from study site 2, marked with a number using non-toxic paint, and relocated at study site 2. To relocate them, 5 *N. plicata* were placed on each of the 11 boulders in numerical order so that boulder 1 had snails 1-5, boulder 2 had snails 6-10, and so on until all 55 snails were repatriated. After 24 hours, 48 hours, and 72 hours, the numbered *N. plicata* were searched for and the distance they traveled from their original boulder was estimated using a transect tape. It was noted if the *N. plicata* traveled from boulder to boulder or from boulder to a different substrate. An analysis of the averages was conducted to determine the distances *N. plicata* individuals moved.

Dispersion studies

Since dispersion of organisms can be influenced by the gradients in resource availability, the dispersion of the *N. plicata* was determined in 7 boulders with periphyton quality score of 4. The 7 boulders were absent of *N. plicata* at 12:00 pm, but populated with several *N. plicata* at 5 pm (Fig. 3), suggesting that the snail can temporally and spatially track resource patches. To do this, photographs were taken from the seven rocks at 5 pm, the distance between each snail and its nearest neighbor measured, and the "picante" package (Kembel et al. 2009) was used to generate a null hypothesis using the R programming language (R Development Core Team 2009). The observed value was then compared to the expected dispersion under completely random distribution given the observed range of values and total snail population across the seven boulders.

Exclosure studies

To determine whether algae abundance is controlled by *N. plicata* and not by other factors, 9 exclosures were set up on rocks from site 1 and site 2 that were populated by *N. plicata*. Of the 9 exclosures, 8 were placed at .5 meters in height in locations where snail density was highest at 12:00 pm. These heights mark the upper limits of the intertidal zone, the location which *N. plicata* most commonly inhabit. The 9th exlcosure was set on a patch with periphyton quality of 5. These exclosures prevented *Neritina plicata* from grazing on the periphyton inside. Any subsequent growth of periphyton was measured using the number scheme 1-5. Since the periphyton mats were not found in sufficient quantities for standing crop analysis, the changes over time were characterized based on the numerical score color scheme. After 21 days, the average change for periphyton quality was determined among the 8 replicates.

TABLE. 1. Average height occupied by snails at times 6:00 am, 9:00 am, 12:00 pm, 3:00 pm, 6:00 pm. Proportion of snails active at times surveyed is also reported.

Time	Mean height	Standard deviation	Proportion of active snails
6:00 AM	0.477	0.12151	0.075472
9:00 AM	0.5786	0.169802	0.102041
12:00 PM	0.4971	0.099055	0.285714
3:00 PM	0.4357	0.163916	0.313433
6:00 PM	0.3082	0.127158	0.733333

FIG. 3. Boulders at lower limits of intertidal zone. Boulder at top at 12:00 pm is absent of snails. Boulder at bottom at 5:00 pm has clumped snails.

Additionally, net photosynthetic activity of two exclosed areas, two areas adjacent to the exclosed areas, and two areas that had periphyton quality 4 were determined at 21 days by measuring the difference between oxygen concentrations in the light and dark chambers. The periphyton within a 5X5 cm perimeter was gently scrubbed for 60 seconds, added to 15 milliliters of seawater in a sealed container, and placed in the light or dark chambers. After 6 hours of incubation, the change in oxygen concentration change was determined. The averages of oxygen concentration change among the three sites were compared.

RESULTS

Vertical transects in the field

Snails exhibited a temporal variation in activity. Most snail individuals start the day in an inactive state, and the proportion of active snails increases significantly as the day progresses, with the highest proportion seen at 6:00 pm (Table 1).

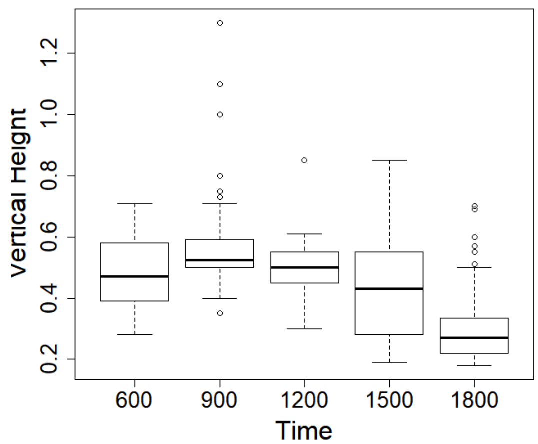

FIG. 4. Bar plot showing the average vertical height occupied by snails at times 6 am, 9 am, 12 pm, 3 pm, 6 pm.

Snails showed preference to higher elevations earlier day. Snails were most commonly found at heights 0.47 meters above the sand bar at 6:00 am and moved slightly upwards to 0.49 meters by 12:00 pm (Table 1). By 6:00 pm, snails were most likely to be found at 0.31 meters above the sand bar.

There is a significant negative correlation coefficient -0.09 ($p < .05$) between algae quality and vertical height (Table 2). At very low heights (0.01-0.20 meters) the algae mats cover the rocks completely. From there, algae quality lowers along a steady gradient as height increases. Additionally, it was found that most snail activity occurs at lower heights where periphyton quality is highest (Table 2), although it should be noted snails were mostly absent from patches of quality 5 periphyton.

TABLE. 2. Correlation between algae and vertical height, algae and snail activity, and vertical height and snail activity.

Parameters	Correlation Coefficient	P-Value
Algae~ vertical height	-0.09	2.00E-16
Algae~ activity	-7.22	1.50E-15
Vertical height~ activity	1.36	2.00E-16

Mark-recapture studies

Thirty-five snails were recovered in the field after 24 hours and moved from their original position an average of .39 meters ± .47 standard deviation (Table 3). After 48 hours, most snails were hidden within coral rubble or underneath large boulders, making it difficult to locate more than 8 snails. The average movement of the 8 snails was 0.86 meters ± 0.74 meters. After 72 hours, 14 snails were located, and their average movement was 0.30 meters ± 0.52 meters.

TABLE. 3. Average distance of snails after 24, 48, and 72 hours.

Time Elapsed	Average Distance	Standard Deviation
24 hours	0.392857	0.470004
48 hours	0.8625	0.738604
72 hours	0.300714	0.523898

Dispersion studies

The observed distribution of distances between snails and their nearest neighbor was 0.17, which was significantly lower than the null (Fig. 5). This makes the observed snail distances under-dispersed compared to what would be predicted under completely random circumstances.

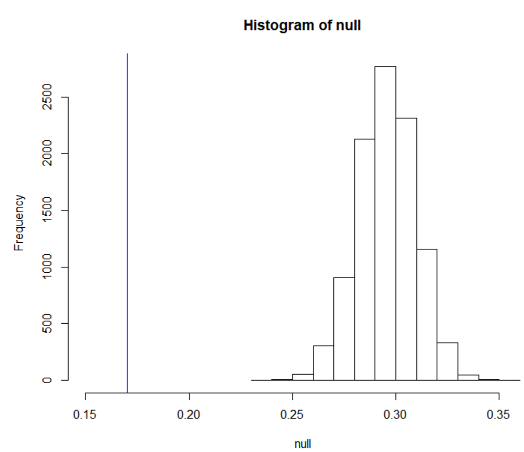

FIG. 5. Distribution of the distances between a snail and its nearest-neighbor predicted under completely random

circumstances given the observed range and total population shown as series of bars. Observed distribution given by vertical line.

Exclosure studies

The quality of algae was assigned a value of one before exclosures were placed over. After 7, 14, and 21 days, the quality of periphyton remained one, with no visible growth of periphyton or change in color against the surroundings. The quality of the periphyton in the control exclosure remained at a quality of 5 for the entire time (Fig. 6).

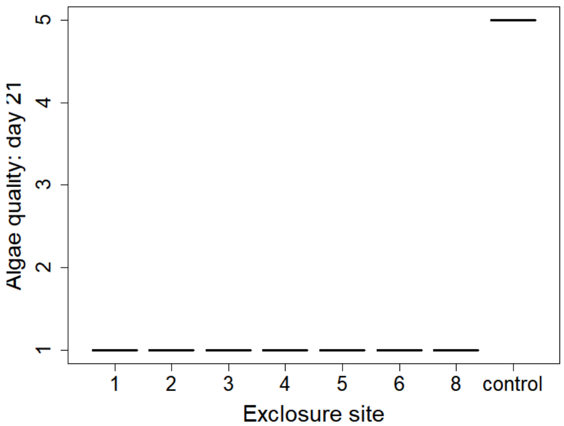

FIG. 6. Algae quality after 21 days of exclosing area of snail grazing.

Oxygen evolution studies

Oxygen-evolution measure indicated that there was no oxygen production in any of the zones inhabited by snails (Fig. 7). The highest oxygen consumption was at the rocks scraped at the lowest elevations with an average of -1.32 mg/L ± 0.18 standard deviation. The lowest oxygen consumption occurred at areas adjacent to exclosures with an average of -.93 mg/L ± 0.35. Exclosed areas had an average of -1.18 mg/L ± 0.19 of oxygen consumed.

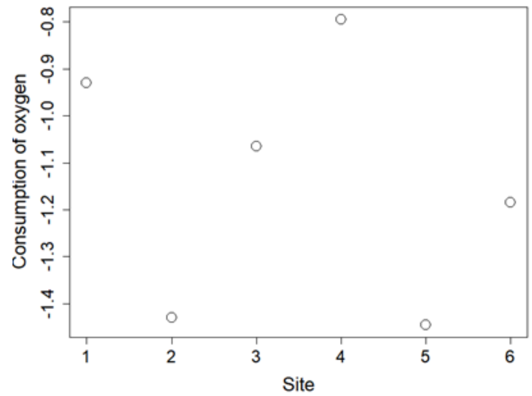

FIG. 7. Consumption of oxygen in mg/L at the 6 sites. Sites 1 and 2 were in exclosed areas after 21 days. Sites 3 and 4 were in area adjacent to exlcosures. Sites 5 and 6 were at low vertical heights where algae quality was 4.

DISCUSSION

N. Plicata individuals demonstrated an ability to migrate vertically on their boulders (Fig. 4) as well as among boulders. This shows that the snails are capable of moving within their habitat to find grazing areas when its feeding time or hiding spots during the hotter parts of the day. On average, *N. plicata* are capable of moving around .39 meters per day away from their original boulders. This probably means that they can emigrate to habitats that hold better quality resources, although it was not determined that they move to better habitats.

The observed dispersion was lower than the expected dispersion under completely random circumstances. This means that the snails are clumped within the resource-rich patches at lower elevations. Since the resource patches only occur at low elevation, snails must have learned to find them during their grazing times. This suggests that they may be able to track resource-rich patches within their habitats. These resource rich areas have a much lower surface area than the resource-poor areas, and therefore snails funnel down from large overhead boulders to the smaller boulders.

If *N. plicata* snails could track the growth of periphyton within the habitat, then they would be expected to be an important factor in keeping the boulders free of visible periphyton. If this were true, freeing the periphyton from the grazing pressure of snails would encourage the growth of periphyton to visible quantities. The absence of algae growth in the exclosures suggests that the snails are not responsible for keeping the mid to upper heights of the boulders free of periphyton growth. Given that all grazers were excluded, the algae might be controlled by other factors such as nutrient or resource limitation, or the long exposure to dry and high temperature conditions. Additionally, it is possible that the exclosure times were not adequately long enough to see changes in periphyton quality.

The light and dark chambers revealed that exclosures, exclosure-adjacent areas, and lower heights contain a microbial community of organisms that consume oxygen (Fig. 7). Although periphyton contains autotrophic organisms, such as algae and cyanobacteria, the net consumption of oxygen could be attributed to a heterotrophic community of bacteria and fungi. This is interesting to note since it reveals the possibility of an invisible community of bacteria and fungi that occupy the higher vertical elevations of the boulders. This community may also serve as a food source for *N. plicata* and help explain why they spend time at higher vertical elevations.

These results suggest that snails know their habitat and preferentially choose locations based on time of day and quality of resources within the zones. *Nerita. plicata* have been shown to be nocturnal in some studies (Ruwa 1988), but they do show some activity throughout day. They may not be actively grazing, but it is clear that they are migrating vertically as the day progresses. Doing transect analysis at night may help determine if their active times are influenced more by time of day than tides. It might also be useful to explore *N.plicata* feeding habits in more detail. They are known to be herbivorous but can be potentially grazing on biofilms of non-photosynthetic periphyton whose zonation might differ from photosynthetic biofilms. Additionally, snails move to adjacent habitats. Determining if there is a pattern to their movement, such as moving to areas with better qualities of periphyton might also provide a better insight to the causes of their zonation.

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