A STUDY OF THE EFFECTS OF INDIVIDUAL AGGREGATION POSITION, MOVEMENT PATTERN, SEX, AND INITIAL SIZE ON SHELL GROWTH OF THE HIGH INTERTIDAL LIMPET, *LOTTIA DIGITALIS*

by

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Organisms in the rocky intertidal zone have diverse adaptations for survival in this harsh environment. The effect of specific traits and behaviors on the fitness of an organism may be manifest in an external variable such as growth. This study looks at the effects of aggregation position, movement patterns, sex, and initial size on shell growth of the limpet, *Lottia digitalis* (Rathke). Individual limpets were tagged and observed at two study sites in Coos Bay, Oregon, USA. A large variation in position and movement patterns existed between sites. No significant effects on shell growth were associated with position, movement patterns or sex. Data analysis revealed a significant negative correlation between initial size and total growth. Additionally, there was a significant difference between initial size and sex. Female limpets had a higher average initial size than male limpets.

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CHAPTER I

INTRODUCTION

Life in the intertidal zone is continuously affected by the daily rise and fall of tides. On the West Coast, intertidal organisms are submerged about two times per day by high tides, and based on their vertical position in the zone, they experience differing periods of submergence and exposure. Intertidal organisms must be able to tolerate fluctuations in physical factors such as temperature, salinity, and oxygen concentrations. Additionally, organisms in this zone must be able to endure heavy wave action from harsh seasonal storms. Due to the continuous shifting of this harsh environment animals living in this zone have developed many adaptations for survival.

My study organism is the high intertidal marine invertebrate *Lottia digitalis* (Rathke), commonly called the finger limpet (Mohler et al., 1997) (Figure 1). These limpets range from the Aleutians to Baja California, and are quite common in Oregon. They prefer to live on vertical (or nearly vertical) rock walls (Frank, 1965). So long as they are wetted by the ocean spray these limpets are found as high as 2-3 meters above median high tide. They have separate sexes, releasing their gametes into the water column for fertilization. *Lottia digitalis* uses a toothed radula to scrape and consume the microscopic algae, diatoms, and blue-green algae that coat rock surfaces. Limpets forage only during high tides. During low tides the limpets adhere tightly to the rock surface (Hobday, 1995).

Many species of limpets display homing behavior, returning consistently to a home scar (a carved divot in the rock) (Reviewed in Branch, 1981). In *L. digitalis*,

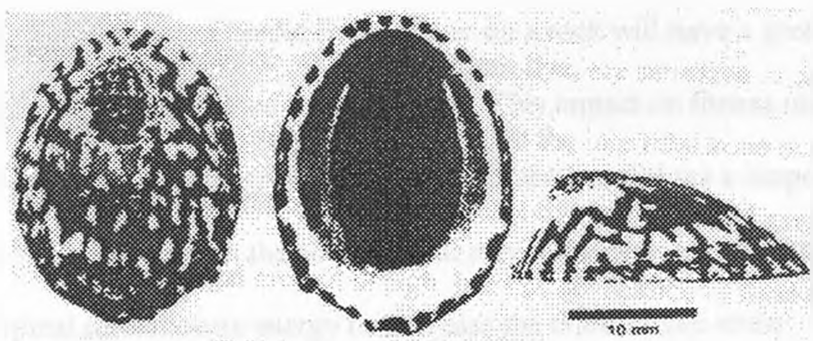

FIGURE 1: *Lottia digitalis* shell (top view, bottom view, and side view). The shell color is brown to black with white chevron markings or blotches. *From*: Lindberg, 1981.

however, homing is less strict. Individuals return to a broader home range, or aggregate, rather than a home scar. *Lottia digitalis* has been observed to form distinct aggregations on rocks in the intertidal zone (Willoughby, 1973; reviewed in Branch, 1981; Santina et al., 1995). Studies have demonstrated that each limpet aggregation is persistent, but that not all of the individuals within the aggregation return after each tidal cycle (Branch, 1981).

As a member of the high intertidal fauna, *L. digitalis* has developed a number of morphological and behavioral adaptations to help it survive. Specific traits and behaviors may affect limpet fitness, making certain limpets better able to survive and grow than other limpets. For instance, a limpet living lower on a rock will have a greater period of submergence, leading to increased foraging time. This impact on fitness may be manifest in an external variable, such as growth. Under favorable conditions a limpet may be able to increase in size. Stressors in the environment may negatively affect limpet fitness, causing the animal to reallocate energy to decrease the effect of the stress. This could result in less energy available for growth. Limpets with very successful adaptations to dealing with stress would likely demonstrate higher growth than less adapted animals.

This study investigated variations in the shell growth of individual limpets based on four variables: aggregation position, movement patterns, sex, and initial size. The hypotheses which this study addressed follow:

H_1: *There are variations in growth of individual limpets based on the organism's average position in the aggregation over time.*

H_2: *There are variations in growth of individual limpets based on individual movement patterns.*

H_3: *There are variations in growth of individual limpets based on sex.*

H_4: *There are variations in growth of individual limpets based on initial size.*

Additionally, I examined at the effect of sex in determining limpet aggregation positions and movement patterns. These auxiliary hypotheses follow:

H_5: *There are variations in aggregation position based on sex.*

H_6: *There are variations in limpet movement patterns based on sex.*

H_7: *There are variations in limpet sizes based on sex.*

Background to Hypotheses

Researchers have suggested that the formation of limpet aggregates relates to desiccation stress (Branch, 1981). If aggregating does help limpets to reduce the stress of desiccation, one might expect limpets in an aggregation to have higher growth than loners under the same desiccation stress. Limpets located in the middle of an aggregation might receive the most protection from desiccation, and consequently have the highest growth rates of all. Alternatively, aggregating could diminish growth due to reduced foraging time. Limpets in the aggregate middle could not begin foraging until their neighbors had moved away. Not only would these limpets be the last to begin foraging, they would also travel a greater distance to find food, since they are in the middle of an area already scavenged by their neighbors. A study by Frank (1965) emphasizes the importance of available foraging time, as affected by vertical position, on growth rates.

If limpets were affected by some combination of desiccation stress and available foraging time, I hypothesized that movement patterns would affect shell growth. Limpets that spent part of their time in an aggregation and part as a loner might benefit from both reduced desiccation stress and adequate foraging time, resulting in increased shell growth. Other patterns of limpet movement could result in intermediate growth.

I predicted differences in growth as a result of sex. The energy cost of producing gametes is higher for females of many species (Nicol et al, 1995; Rose and Bradley, 1998). Since eggs are more costly to produce than sperm, I expected female limpets to exhibit lower growth than males.

Studies by Frank (1965) and Hobday (1995) found that larger limpets were found higher in the intertidal zone. In accordance with the results in the literature (Frank, 1965) I expected larger limpets to grow slower than smaller limpets. Limpet growth was measured as shell diameter, however shell growth is actually cubic, increasing as a function of the elliptical shell shape.

CHAPTER II

MATERIALS AND METHODS

Study Sites and Field Conditions

Two study sites were located on the southern Oregon coast near Cape Arago, Oregon (43° 20' 0 N; 124° 22' 30 W) (Figure 2). Both sites were characterized by immense rocky outcrops and heavy wave action. Site 1 is within a cove located between Sunset Bay and Norton Gulch, Cape Arago. At this site I monitored 3 rocks, each with distinct limpet aggregations made up from 4 to 40 limpets. One of these populations inhabited the north face of the rock; the other two populations inhabited the east faces of the rocks. All of the rocks at this site were wetted by incoming high tides of approximately 1 meter and above. Site 1 was shielded from direct onslaught by large waves by a large rock wall.

Site 2 was located in a cove further south along the coast, just north of Shore Acres, Cape Arago. At this location I monitored 2 rocks with aggregations of about 40 limpets each. Aggregations were found on the north and east sides of the rocks. Both of these rocks were wetted by incoming high tides of approximately 1 meter and above. Limpets in this study area were sheltered by a nearshore reef, but received more intense wave action than site 1.

Several months were spent constructing, testing, and improving equipment and techniques. All final data measurements (with the exception of sex data) were made during low tides in the winter months of December, January, and February (Table 1). These months were characterized by severe storms, which increased tidal height, wave

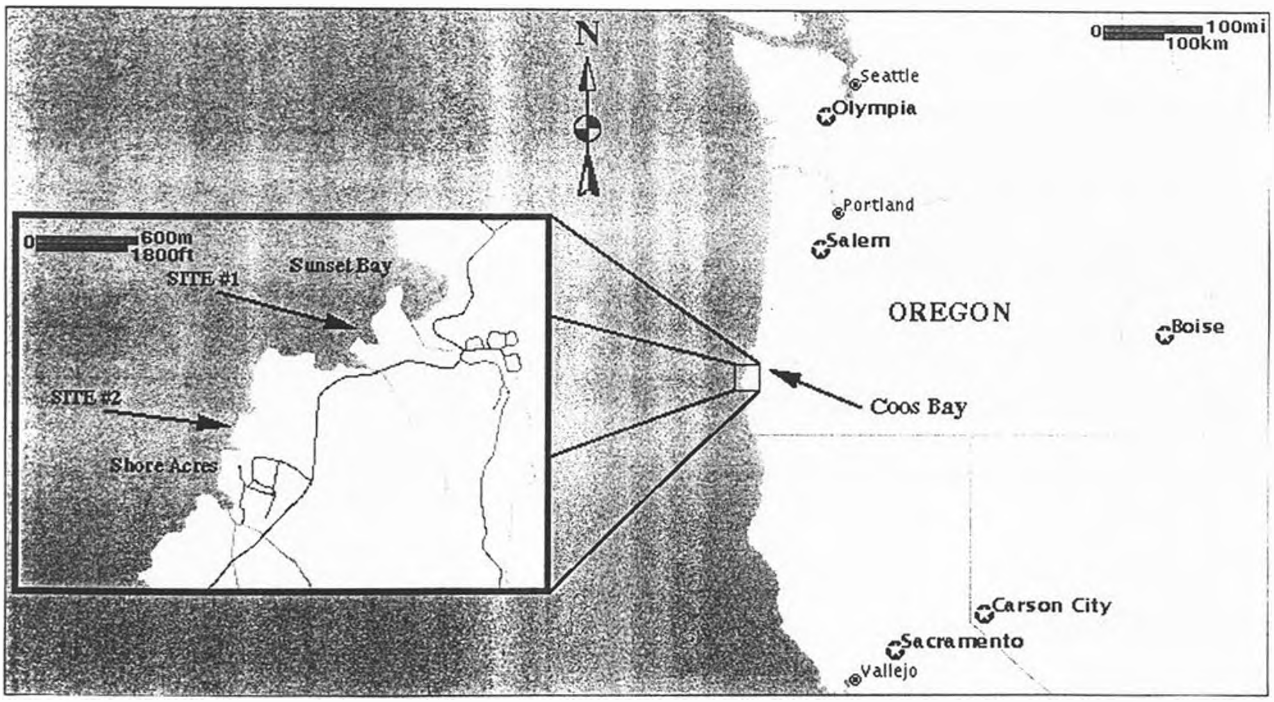

FIGURE 2: Location of study sites 1 and 2 in Coos Bay, Oregon.

TABLE 1. Dates of field observations for each site.

Site #	Observations					
1	12/26/98	12/28/98	12/29/98	1/1/99	1/16/99	2/20/99
2	12/27/98	12/31/98	1/2/99	2/20/99		

action, winds, and precipitation (including snow and ice). Due to diminished daylight hours much sampling was conducted using headlamps and flashlights, but low visibility made navigating boulder fields a time-consuming process. These factors restricted the window of time available to complete data collection during low tides, making rapid and accurate methods essential. Due to these challenging field conditions and the access distance between sites it was rarely possible to take all measurements for all five rocks during one low tide period.

Individual Limpet Identification

Since individual identification of limpets was basic to each of my observations it was necessary to tag each animal. Limpets were marked in the field using numbered plastic tags manufactured by Floy Co. Tags were carefully affixed to the postero-dorsal shell surface using a quick drying glue adhesive ('Quick Gel' by Duro available from Loctite Corporation) (Figure 3). Similar tagging methods have been employed by other researchers studying limpets (Choat & Black, 1979; Frank, 1965).

Monitoring Position

For convenience in locating the animals a removable mesh grid was superimposed on each rock. The grid was hooked onto lag bolts that had been positioned to correspond to the four corners of the grid. The holes for the bolts were drilled in each rock using a masonry bit and cordless drill. Wooden pegs were wedged into the holes with the lag bolts to keep the bolts firmly positioned.

The grid was divided into squares measuring 4.3 cm by 4.3 cm. The columns of squares were marked at 5 square intervals using colored yarn in the sequence red, orange, yellow, green, blue, indigo, and violet (ROYGBIV). Rows were also marked at 5 square

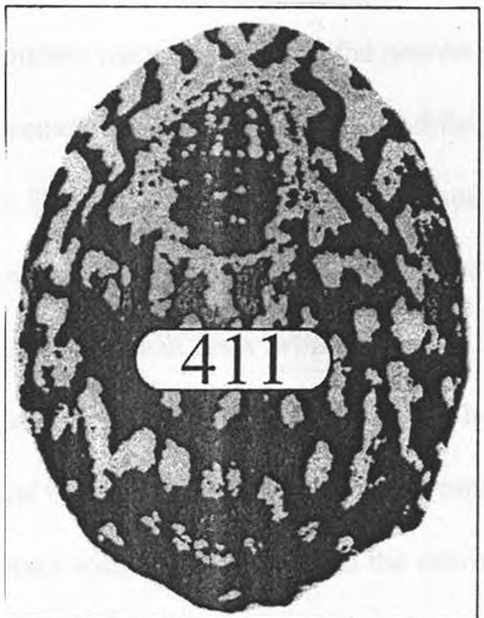

FIGURE 3: Limpet shell depicted with attached numeric tag placed postero-dorsally.

intervals using the corresponding column yarn color (Figure 4). Limpet positions were recorded according to column and row numbers. Since limpets were smaller than grid squares an additional approximation was made to further specify limpet position (Figure 5). The detachable grid was preferable to a fixed structure because it had minimal impact on the study animals and reduced equipment loss resulting from harsh environmental conditions.

Measuring Growth

Limpet shell diameters were measured to the nearest millimeter from anterior to posterior edges. Measurements were made using a modified micrometer (Craftsman 0-1" available from Sears). The micrometer was specially modified to allow me to measure individual limpets without removing the animal from the rock. To do this the micrometer was fitted with tapered, stainless steel lever arms (Figure 6). One of the lever arms was fixed tangential to the stationary face of the micrometer. The other lever arm pivoted about a fulcrum tangential to the moving face of the micrometer. A return spring maintained constant contact with the lever arm and the moving face to ensure that the ratio of movement of the lever tips was linear to the movement of the micrometer faces. Plastic zip ties were used to secure the lever arms and the return spring to the micrometer. The micrometer was equipped with a ratchet stop to ensure similar amounts of pressure were delivered to all subjects being measured. Measurements were read by hand from the micrometer scale and these data were later converted from inches to millimeters ($SE=0.0015$, $n=10$).

Sex Observations

Determining the sex of a limpet requires the removal of the muscular foot to examine the underlying gonads (Choat & Black, 1979; Frank, 1965). As a consequence

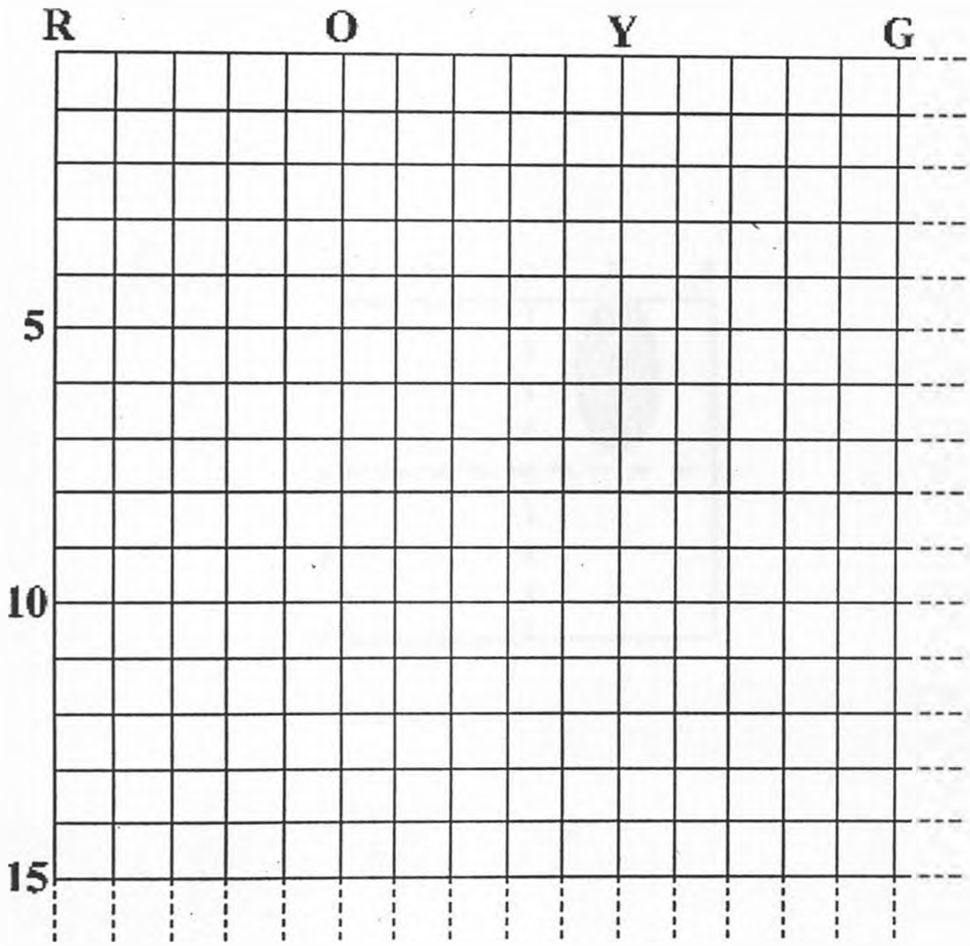

FIGURE 4: Diagram of grid used to monitor limpet positions. Colored yarn is used to mark 5 square intervals using to color scheme ROYGBIV (red, orange, yellow, green, blue, indigo, and violet).

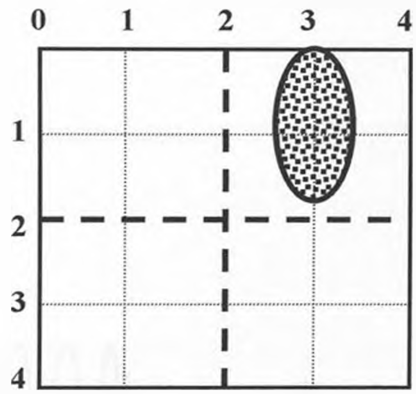

FIGURE 5: Diagram of a single grid square with estimated divisions. The limpet pictured would be recorded as position 1(vertical), 3 (horizontal).

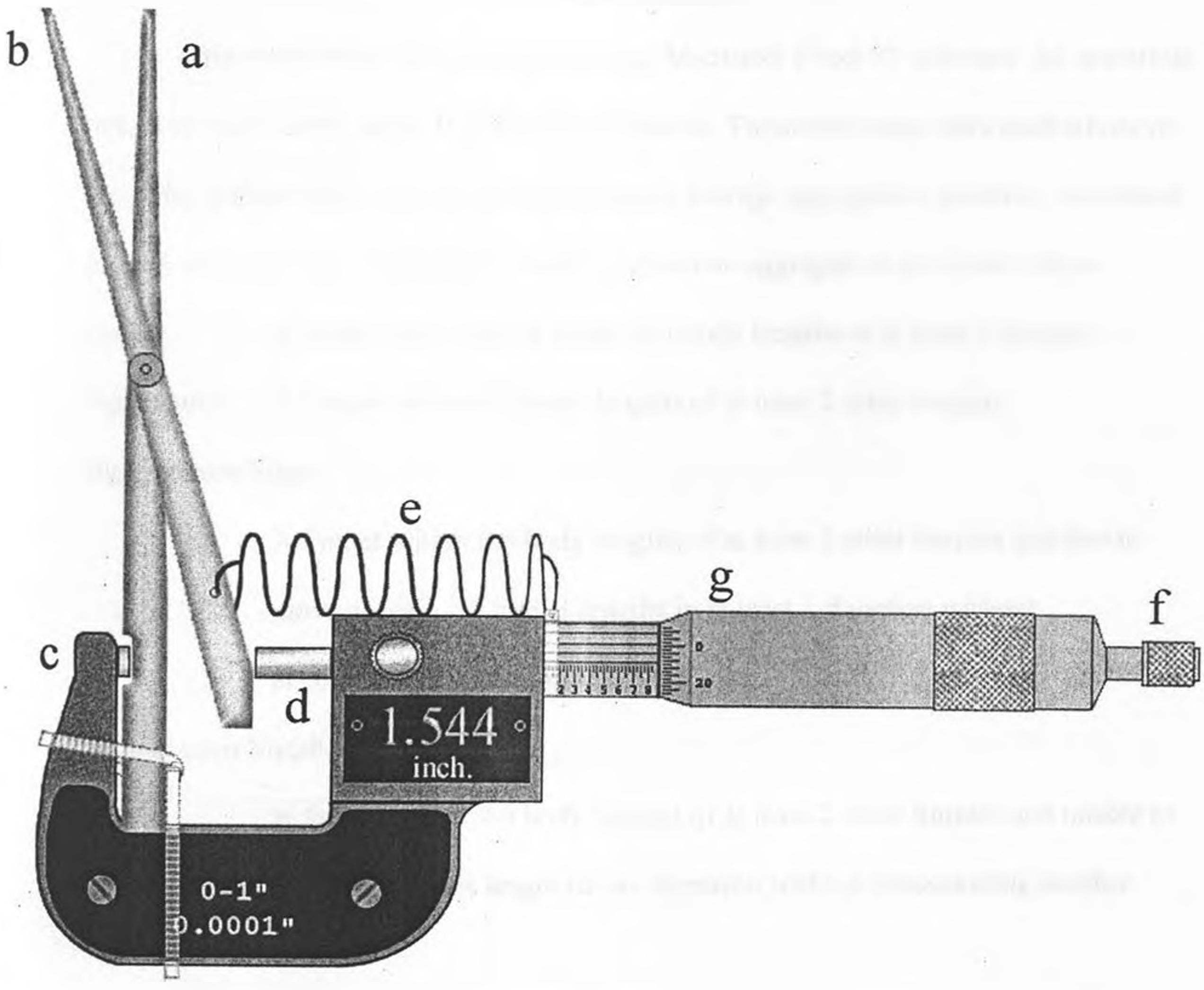

FIGURE 6: Diagram of micrometer with special modifications. (a) stationary lever arm, (b) pivoting lever arm, (c) stationary micrometer face, (d) moving micrometer face, (e) return spring, (f) ratchet stop, (g) measurement scale.

these data were gathered at the conclusion of the experiment during a time of year when gonads were ripe (Choat and Black, 1979). On 4/4/99 all remaining labeled limpets were removed from their rocks and killed by submersion in freshwater. Dissection revealed either beige colored male gonads or ruddy colored female gonads.

Data Analysis

Data were assembled and sorted using Microsoft Excel 97 software. All statistical tests were performed using Statistica 4.1 software. Parametric tests were used whenever possible. Limpet data were sorted according to average aggregation position, movement pattern, sex, and size. Definitions used to determine aggregation positions follow:

Loner — A limpet that was not within 0.5 body lengths of at least 2 limpets

Aggregator — A limpet within 0.5 body lengths of at least 2 other limpets

Aggregation Edge

A limpet within 0.5 body lengths of at least 2 other limpets and free to move at least 0.5 limpet lengths in at least 1 direction without encountering another limpet.

Aggregation Middle

A limpet within 0.5 body lengths of at least 2 other limpets and unable to move 0.5 limpet length in any direction without encountering another limpet.

Limpets were separated into five categories of movement pattern based on trends in their positions relative to an aggregation over time. Movement patterns were determined mathematically using Excel formulae. Measurements based on average limpet size use the mathematical average of all limpet shell diameters for each rock. Movement pattern definitions follow:

A "Strict Homer"

Limpet resided at same place (within 0.5 average limpet size) on same rock for all measurements. This limpet could exist in an aggregation or as a loner.

B "Strict Aggregator"

Limpet resided in same aggregation throughout observations and is not in category A. This limpet was not a loner.

C "Traveling Aggregator"

Limpet changed aggregations throughout observations and was not in category B. This limpet was not a loner.

D "Strict Loner"

Limpet was a loner for at least 2/3 of all observations. This limpet was not in category A.

E "Switcher"

Limpet spent $\geq$ 1/3 of the observations as a loner $\geq$1/3 of observations in an aggregation.

CHAPTER III

RESULTS

In the course of this study 104 limpets were individually tagged and monitored. Limpet loss was kept to about 10% of those marked, resulting in a final sample size of 90 limpets. Site 1 contained 46 limpets and Site 2 had 44 limpets. Data were grouped together for analysis, which revealed wide variation in aggregation position and movement pattern between sites (Figure 7). The large differences between sites illustrate a lack of homogeneity among the sampled areas. There were also large differences between rocks. Average growth rates per rock varied widely (Figure 8), with 2 of the 5 study rocks exhibiting negative average growth rates. Negative growth rates occur when new shell addition does not equal shell erosion.

Aggregation Position

H1: Does aggregation position affect individual growth?

There was a significant correlation between limpet position and site (Spearman Rank=-0.207, p=0.0503, n=90). At both sites the majority of limpets in the study were aggregators, yet site 1 was comprised almost completely of aggregators while limpets at site 2 were more regularly distributed between aggregators and loners. Total growth (final – initial) and growth rate (final-initial/time) were not significantly associated with position (Table 2).

a

b

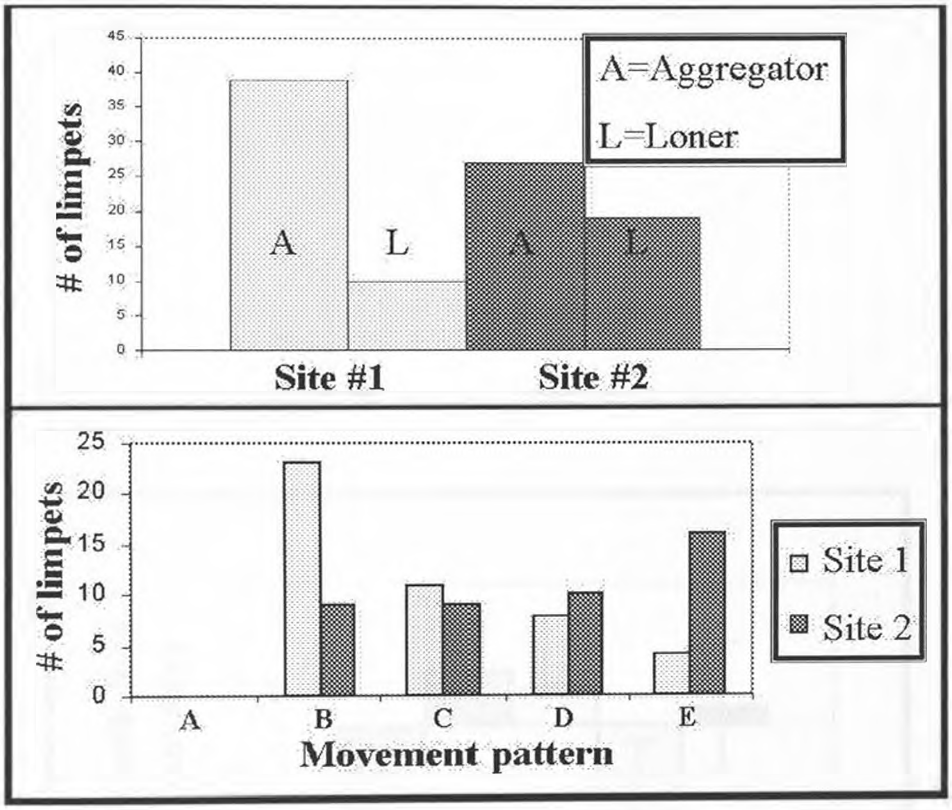

FIGURE 7. Variations in aggregate position (a) and movement pattern (b) between sites. For both graphs n=90.

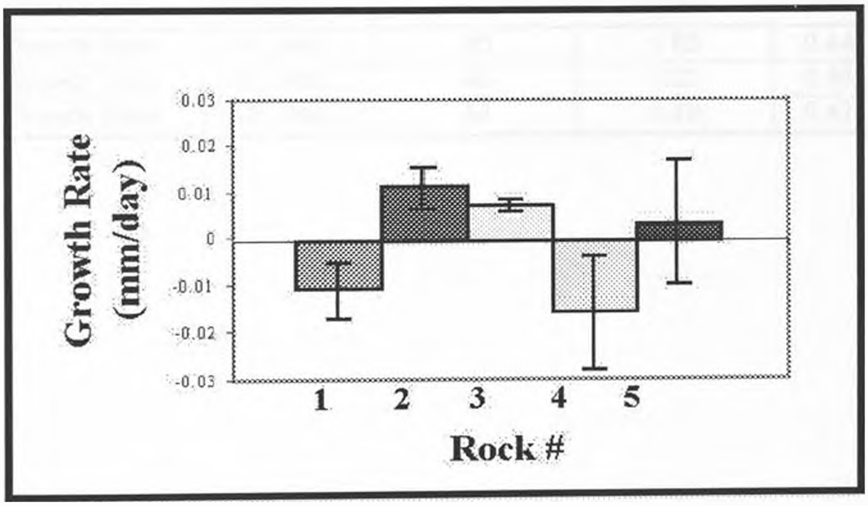

FIGURE 8. Variation in growth rates of limpets per rock.

TABLE 2. Results of Kruskal-Wallis ANOVA by Ranks comparing the distribution of total growth based on position, and growth rate based on position. Limpets were divided into position categories A or L (aggregators or loners) and AE, AM, L (aggregation edge, aggregation middle, or loner).

Site #	Dependent variable	Independent variable	Sample Size, n	Kruskal-Wallis Test	p-level
1 & 2	Total Growth	A or L	90	0.575	0.448
1	Total Growth	A or L	46	0.026	0.873
2	Total Growth	A or L	44	0.659	0.412
1 & 2	Total Growth	AE, AM, L	90	2.31	0.314
1	Total Growth	AE, AM, L	46	0.186	0.911
2	Total Growth	AE, AM, L	44	3.23	0.199
1&2	Growth Rate	A or L	90	0.00	1.00
1	Growth Rate	A or L	46	0.576	0.448
2	Growth Rate	A or L	44	0.036	0.849
1&2	Growth Rate	AE, AM, L	90	1.63	0.442
1	Growth Rate	AE, AM, L	46	1.20	0.550
2	Growth Rate	AE, AM, L	44	1.49	0.474

Movement Pattern

H2: Does movement pattern affect individual growth?

While none of the limpets were described by movement pattern A, there was a significant correlation between patterns B, C, D, and E and sites 1 and 2 (Spearman Rank=0.3843 p=0.00002 n=90). Movement pattern B ("strict aggregator") was most frequently observed at Site 1, while movement pattern E ("switcher") was most prevalent at Site 2 (Figure 9). Observations of total growth and growth rate were not significantly associated with movement patterns for all data combined (Table 3). However, limpets at Site 2 demonstrated a significant difference in total growth versus movement pattern (Table 3). Pattern E ("switcher") had the highest growth and pattern B ("strict aggregator") had the lowest total growth.

Sex

H3: Does sex affect individual growth?

Sex ratios of male limpets to female limpets were nearly 1 to 1 at both sites, with no significant difference in sex between sites (Spearman Rank=-0.015 p=0.89). Analysis of differences in total growth and growth rate based on sex were not significant (Table 4).

Size

H4: Does initial size affect individual growth?

There was no significant difference in average limpet size between sites (Kruskal Wallis ANOVA=1.72 p=0.19). A significant correlation between total growth and size was demonstrated (r=-0.21, p=0.04) with smaller limpets experiencing greater total growth than larger limpets (Figure 10). No significant correlation between growth rate and size was found (Table 5).

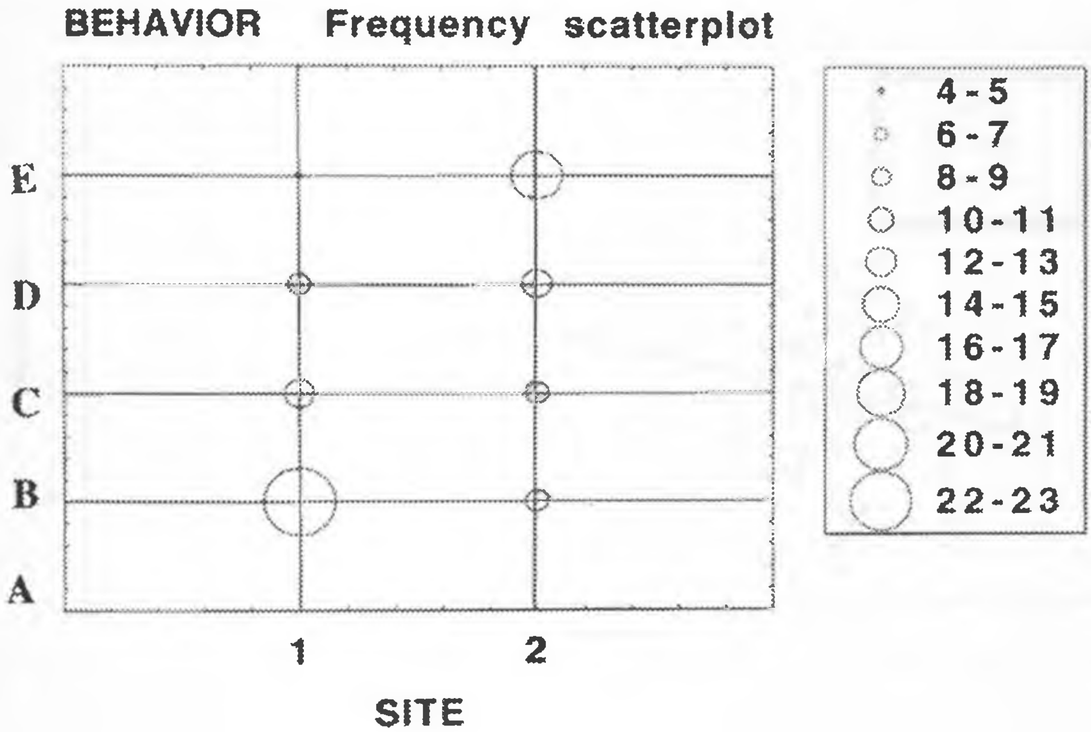

FIGURE 9. Frequency of movement patterns B, C, D, and E for sites 1 and 2.

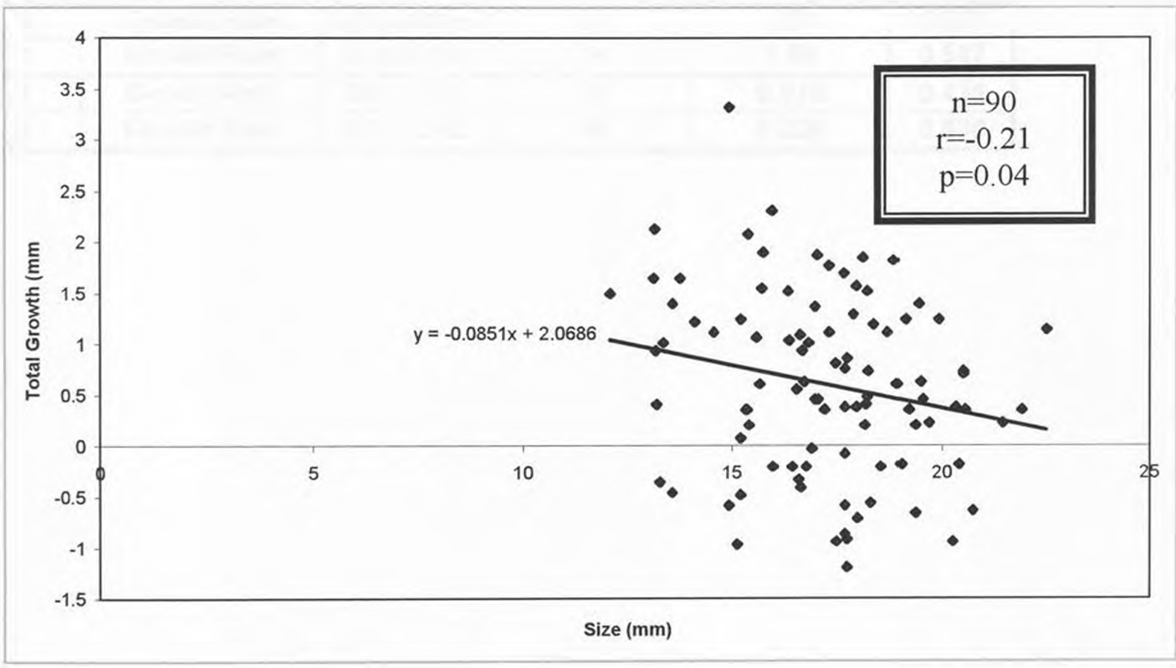

FIGURE 10: Correlation between total growth (mm) and initial size (mm) for all limpets.

TABLE 3. Results of Kruskal-Wallis ANOVA by Ranks comparing the distribution of total growth based on movement patterns, and growth rate based on movement patterns. Limpet movement patterns were combined into 2 groups, B&C (mostly aggregators) D&E (sometimes loners).

Site #	Dependent variable	Independent variable	Sample Size, n	Kruskal-Wallis Test	p-level
1	Total Growth	All patterns	46	0.336	0.953
2	Total Growth	All patterns	44	6.25	0.100 *Sig*
1	Total Growth	B&C, D&E	46	0.013	0.910
2	Total Growth	B&C, D&E	44	2.37	0.124
1	Growth Rate	All patterns	46	1.61	0.658
2	Growth Rate	All patterns	44	1.88	0.597
1	Growth Rate	B&C, D&E	46	0.510	0.476
2	Growth Rate	B&C, D&E	44	0.228	0.630

TABLE 4. Results of Kruskal-Wallis ANOVA by Ranks comparing the distribution of total growth based on sex, and growth rate based on sex.

Site #	Dependent variable	Independent variable	Sample Size, n	Kruskal-Wallis Test	p-level
1 & 2	Total Growth	Sex	90	3.47	0.062
1 & 2	Growth Rate	Sex	90	1.56	0.211

TABLE 5. Results of cross-correlation between total growth and initial size, and growth rate and initial size.

Site #	Sample Size, n	Correlation coefficient, r	p-level
1 & 2	90	-0.214	0.04 *Sig*
1 & 2	90	-0.003	>0.05

Interactions Between Positon, Movement Pattern, Size, and Sex

H5: *Is there a difference in position based on sex?

H6: *Is there a difference in movement pattern based on sex?

H7: *Is there a difference in size based on sex?

There was no significant difference between sex and position or sex and movement pattern (Table 6). Analysis of sex versus size demonstrated a significant difference (Student's t-test $t=1.96$, $df=59$, $p=0.05$), with males having a lower average size than females (Figure 11).

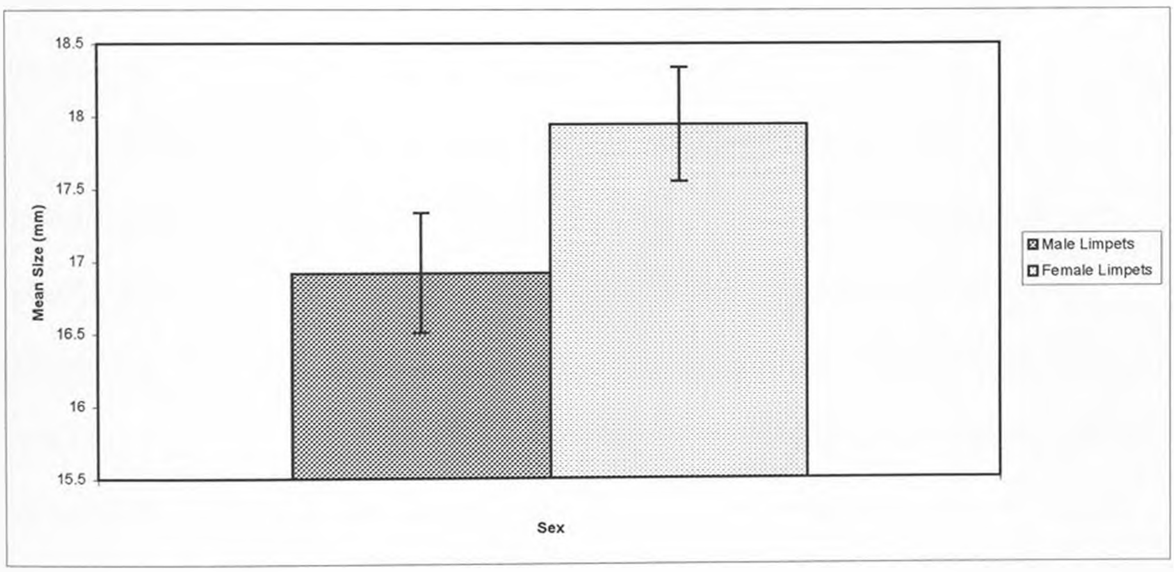

FIGURE 11: Mean size (mm) for all male and female limpets.

TABLE 6. Results of Spearman Rank Order correlations for position and sex, and movement pattern and sex. Position is divided into the categories A or L (aggregators or loner) and AE, AM, L (aggregation edge, aggregation middle, loner). Movement pattern is analyzed as all categories or B&C (mostly aggregators) and D&E (sometimes loners).

Site #	Variable 1	Variable 2	Sample Size, n	Spearman R	p-level
1 & 2	A or L	Sex	90	-0.001	0.99
1 & 2	AE, AM, L	Sex	90	-0.410	0.68
1 & 2	All patterns	Sex	90	0.066	0.61
1 & 2	B&C, D&E	Sex	90	0.08	0.54

CHAPTER IV

DISCUSSION

The data set from this study helps to illustrate the complex nature of the rocky intertidal zone. The study attempted to illuminate effects from four possible factors affecting limpet shell growth. Results from this study do not support significant effects of aggregation position, movement pattern, or sex on shell growth for total limpets. Indeed, a significant negative correlation between size and total growth was found. Again, this result may reflect the non-linear pattern of shell growth in limpets. Shell volume may be a more accurate description of growth.

No difference was observed in growth between males and females. It is interesting to note that contrary to my expectations, average female limpet size was slightly larger (17.9 mm, SE=0.41, n=34) than average male limpet size (16.3 mm, SE=0.39, n=31). This trend was also observed in a study of the limpet *Patella vulgata* (Orton et al, 1956); researchers found that smaller sized limpets were composed almost entirely of males, and larger limpets were predominately female.

Notably, there were several significant differences in limpet traits (position and movement pattern) between Site 1 and Site 2, and even some significant differences in limpet traits between rocks. More limpets at Site 1 were aggregators, but Site 2 had a more even distribution of aggregators and loners. Also, movement pattern B ("strict aggregator") was the most prevalent at Site 1, while pattern E ("switcher") was more common at Site 2. This lack of homogeneity suggests that local environments play a large role in shaping limpet biology. A study of another limpet, *Patella vulgata* (Linnaeus), by Thompson (1980) also concluded that each population has a distinct biological history which is likely to have a profound effect on the population structure observed at any one time.

The large variations between sites may be due to unique local topography of each rock, disproportionate amounts of stressors at each site, variations in hydrodynamics (such as degree of wave exposure, quantity of spray), and other unknown variables. Probably the most significant factor affecting limpet biology is individual rock topography. The numerous cracks and divots eroded into the sandstone may provide additional shade or hold small pools of water to minimize desiccation stress (Frank, 1965; Thompson, 1980). Furthermore, variation may be amplified by the small sample size and patchiness of the data set. If all limpets were observed on every low tide, or throughout the entire tidal cycle, average positions and movement patterns would be more accurate.

There are also factors that may have caused effects on shell growth to be masked or diminished. Particularly relevant are seasonal factors such as precipitation, temperature, and food availability. Since this study was conducted in the winter when temperatures were low, precipitation was high, and food was abundant, stress due to desiccation may have been minimal. A correlation between growth rates and season has been demonstrated by researchers, however the period of peak growth differs among studies. While Frank (1965) reported *L. digitalis* growth rates to be fastest in the fall and winter months, a study by Choat & Black (1979) lists *L. digitalis* growth rates as highest in spring, and lower in the winter. Additionally, limpet gonad production peaks in the winter (Shanks, 1998). A study of *Patella vulgata* indicates that a high index of gonad ripeness may inhibit movement, which in turn limits foraging ability (Santina et al, 1995).

As noted by Frank (1965) it is important to address the generality of these results: how can this study, limited in time and geography, contribute to a broader understanding of similar species over the entire range of distribution? The striking differences between sites suggest that the results may not be applicable beyond the study area. For instance, monitoring the fitness of limpets at Site 1 would not likely be a good measure of Site 2 limpet fitness. This has important implications in applied ecology, demonstrating the difficulties in applying site specific results to larger areas.

CHAPTER V

FURTHER STUDIES

This study provides basic data about some of the factors affecting limpet shell growth. Further studies with more refined procedures and longer sampling times may reveal significant effects. One of the biggest challenges in this study was the presence of numerous site-specific variables. Any further limpet study would benefit from a large sample size, and continuous data sets. Following are experiments that would control for some of the site-specific variation:

1. Introduce permanent, uniform structures in the field which are suitable for limpet habitat. Transplant limpet populations to the structures and conduct growth measurements for various subgroups (sex, size, position, et cetera). The introduced structures would help to minimize variation due to unique rock topography.
2. Develop a procedure for monitoring total limpet movement during high tide activities (underwater camera, LED trailmarking (as used by Chelazzi et al, 1983)). This would provide an accurate measure of limpet behavior. Perhaps observations of total movement would elucidate patterns of movement contributing to growth rate.
3. Increase an environmental stressor (e.g. desiccation, food availability, available foraging time). This could be done by the experimenter (manually drying limpets with a light or heat gun, scraping off diatom layers, creating barriers to limit foraging, et cetera), or could consist of observing limpets throughout the year when certain stressors are naturally augmented.

Additionally, bringing the organisms into the lab for observation could allow even tighter control of external variables.

4. Rear limpets in the lab on identical surfaces which experience equal exposure to all possible factors. Each structure could serve as a replicate to eliminate differences between rock and between site.

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