PREDATOR-PREY INTERACTIONS IN THE NEW ENGLAND INTERTIDAL ZONE: POSSIBLE INDUCED SHELL THICKENING IN THE COMMON PERIWINKLE LITTORINA LITTOREA IN RESPONSE TO THE ASIAN SHORE CRAB, HEMIGRAPSUS SANGUINEUS.

An Undergraduate Research Scholars Thesis

by

JACQUELINE KELEHER

Submitted to the Undergraduate Research Scholars program at
Texas A&M University
in partial fulfillment of the requirements for the designation as an

UNDERGRADUATE RESEARCH SCHOLAR

Approved by Research Advisor: Dr. Anja Schulze

May 2018

Major: Marine Biology
Marine Fisheries

TABLE OF CONTENTS

ABSTRACT

Predator-prey Interactions in the New England Intertidal Zone: Possible Induced Shell Thickening in the Common Periwinkle, *Littorina littorea*, in Response to the Asian Shore Crab, *Hemigrapsus sanguineus*.

Jacqueline Keleher
Department of Marine Biology
Texas A&M University

Research Advisor: Dr. Anja Schulze
Department of Marine Biology
Texas A&M University

Hemigrapsus sanguineus, also known as the Asian shore crab, began to invade the Northwestern Atlantic in the 1980's and interferes with the existing food web of the rocky intertidal zone. The crabs prey upon primary consumers such as *Littorina littorea*, the Common periwinkle. The objective of this study is to determine whether *H. sanguineus* induces changes in shell morphology in *L. littorea*. Two hypotheses were tested: 1) shell thickness increases and 2) more force will be required to crush the shells in response to the presence of the crab. During the first stage the 43 *L. littorea* from two locations were separated in three 10-gallon tanks for 187 days. The control had solely *L. littorea* (n=16), the second tank had *L. littorea (n=12)* and free-roaming *H. sanguineus* (n=6), and third tank had *L. littorea* (n=15) and *H. sanguineus* in enclosed containers (n=6). For the second stage, the thicknesses of the shells were measured at predetermined points and the shells were crushed using a loading frame. The data show that there are significant differences in the change in shell thickness, peak load of crushing force and modulus between the New Hampshire and Maine snail populations. The average thickness of

the shells at one point differed by treatment although most of the observed variation was between locations.

DEDICATION

This project is dedicated to my inspiration and the first Marine Biologist I knew Kathy Watson and my kindred spirit great-uncle Richard. Kathy, without your love, support and encouragement from a young age my love of the ocean, my love for Jesus and research would not have flourished. Watching you love science and Jesus has showed me how to live a life that shines bright while using knowledge and wisdom to speak truth into situations. Uncle Richard, even though you won't get see to see this project to completion, your love and spirit have given me the drive to finish what I started 5 years ago.

ACKNOWLEDGEMENTS

I would like to thank my advisor Dr. Schulze for allowing me to pursue the dream of finishing this project 2,000 miles away from where it started, for her guidance and support throughout the past year and a half and for her encouragement and insight into new ways to expand the scope of the project.

I would like to extend my gratitude to Dr. Marshall, for taking me under his wing and teaching me that you can't undo a crush, to take more data than you think you will need, and how to use the loading frame, as well as his encouragement and direction when the loading frame stopped working.

To Candace I would like to extend my gratefulness for helping me figure out the statistics that I needed to run and for her help with R.

To all friends and family in New Hampshire, Maine, Texas, and Papua New Guinea, thank you for the late nights, long talks and constant encouragement. Without you this project would not have survived past 2014. To Ethan, thank you for being my sounding board, for learning more about my project than you ever would have wanted to, and for being my supply of caffeine and chocolate on all of the late nights.

To my father thank you for shaping me and instilling a love of the natural world and inquiry in me. To my mother, thank you for learning what Asian Shore Crabs and Common Periwinkles are, for being my companion on my collecting trips, and for the hours spent in suboptimal conditions picking up snails and crabs. Thank you both for your patience and willingness to listen to me talk about my snails and crabs for hours, I love you.

CHAPTER I

INTRODUCTION

Over the past 242 years at least 50,000 alien-invasive, non-native, species have been introduced and become fully established in the United States of America. Some introductions of invasives have been purposeful such as the watermelons, apples, and pigs that the settlers brought to the Americas in the seventeenth and eighteenth centuries (Taylor 2002), while others have been unfortunate accidents like the Burmese Python, Indo-Pacific lionfish, and the Eurasian zebra mussel (Dorcas et al. 2012; Muñoz, Currin, and Whitfield 2011; Ricciardi 1998). Invasions often cause significant damage to the ecosystems in which they establish themselves as well as economies that rely on natural resources. It is estimated that 42% of threatened or endangered species are at risk due to invasive species; invasive species are also estimated to cost the United States 120.105 billion dollars annually (Pimentel *et. al.* 2005).

Coastal estuarine and marine systems are some of the most heavily invaded ecosystems. Invasions have become so severe in San Francisco Bay that as of 1995 100% of shallow water habitats in the bay were categorized as invaded by exotic species (Cohen and Carlton 1995). Studies of invasive species in coastal areas rarely appeared in literature before the late twentieth century. Many of these studies focused on analyzing invasion pathways, and specific categories of ecological impacts such as how a specific invasive species impacts native species. Many recent studies have analyzed the impact of invasive species on the functioning of entire ecosystems, aiming to understand how invasive species interact with each other and what determines their success (Grosholz 2002; Steinberg and Epifanio 2011; Davidson, Jennions, and Nicotra 2011; Pyšek and Richardson 2010).

Invasive species display a wide range of phenotypic plasticity, but co-occurring non-invasive species responded similarly, or better than invasive species, and maintained fitness homeostasis better than invasive species when tested in stressful conditions or limited resources (Davidson et. al, 2011). Phenotypic plasticity is the ability of a singular genotype to express more than one phenotypic morphology, physical state, and/or behavior as a response to a change in environmental conditions (West-Eberhard 1989)

This study examined the ecological interactions between two alien-invasive, intertidal invertebrates in New England: the Asian Shore Crab, *Hemigrapsus sanguineus*, and the Common Periwinkle, *Littorina littorea*. While *Littorina littorea* has been present in Maine and New Hampshire since the mid-to-late 1800s, *H. sanguineus* is a relatively new invader to the New England coast and has been spotted in New Hampshire since the late 1990's (Tyrell and Harris, 2000). There have been reported sightings as far North as Owls Head Light in Owls Head, Manie (Blakeslee, 2017; Lord & Williams, 2017). Owls Head Lighthouse is 86 miles directly south of point B, however, there are more than 160 miles of coast between the two locations. (Google Maps, 2018). This study will specifically examine the variation in shell thickness, elasticity and strength of *Littorina* from two locations in two conditions: contact solely with effluent from the *H. sanguineus* and direct contact with the *H. sanguineus*.

A number of studies have shown that shell thickness of intertidal mollusks can vary due to the presence and predation of crabs, although additional factors may contribute to the observed variation (Kitching and Lockwood 1974; Kitching, Muntz, and Ebling 1966; Vermeij 1976, 1978; Seeley 1986; Trussell 1996). When crabs prey on thinner shelled mollusks, the response is usually that the shell thickens (Seeley 1986), which has also been shown to be caused by a phenotypic plasticity (Appleton and Palmer 1988; Palmer 1985; Palmer 1990;

Freeman and Byers 2006). In 2006 Blue Mussels, *Mytilus edulis*, from Southern New England, where the invasive Asian Shore Crab, *Hemigrapsus sanguineus*, had been established for 15 years, showed an inducible thickening of their shells when exposed to waterborne cues from *H. sanguineus*. When *M. edulis* from Northern New England, where *H. sanguineus* was not present, were exposed to waterborne cues from *H. sanguineus* they showed no increase in shell thickness (Freeman and Byers 2006). This type of phenotypic plasticity is a defense response to crabs that can affect community and environmental structures. Other mollusks, such as the gastropod *Littorina obtusata*, have displayed shifts in shell thicknesses when introduced to another invasive, intertidal crab species, *Carcinus meanas*, in as little as 45 days (Trussell and Smith 2000). Invasions such as the Asian Shore Crab's, *Hemigrapsus sanguineus*, on both shores of the United States and Common Periwinkle Snails, *Littorina littorea*, along the Eastern shores of the U.S. have incited much research into the plasticity of these organisms and their impacts on ecosystems they have invaded (Trussell 1996; Trussell and Smith 2000; Freeman and Byers 2006; Lord 2017). So far, however, there has been little to no research on how *H. sanguineus* could affect *L. littorea*.

Hemigrapsus sanguineus was introduced to New York on the east coast of the United States in the 1990s. The crabs settled quickly and have become successful invaders of coastal New England. Currently, the northmost point that *H. sanguineus* has been found is more than 400 miles away in Owls Head, Manie (Lord and Williams, 2017). The ecological effects of their invasion and spread on both sides of the country have been well documented (Blakeslee et al. 2017; Epifanio 2013; Steinberg and Epifanio 2011; Lord and Williams, 2017). Concerns for the Northwest Atlantic include competition with native crabs, predation on native species, and the introduction of parasites due to their documented status as a host to many Asian parasites

(Epifanio 2013). There is some debate about the origin of *Littorina littorea*, however, most researchers agree that they have spread to New England from the Southeastern Canadian coast in the late nineteenth century (Brenchley and Carlton 1983). These snails are commonly found at densities of 400-800 snails/m^2 from high tide lines to subtidal environments (Bertness 1984). *Hemigrapsus sanguineus* is a predator to *L. Littorina* and inhabits similar ranges in the intertidal zones as the *L. littorea*, in a lower density (Gerard, Cerrato, and Larson 1999).

This study will examine the predator-prey interactions between the two non-native, invasive species *Hemigrapsus sanguineus* and *Littorina littorea* from the New Hampshire and Maine coasts. The goals of this study are (1) to determine the amount of force, relative to the thickness of the shells, it takes to crush the shells of the *Littorina littorea* (2) to determine if *L. littorea* from Northern Maine present shell thickening to similar those from New Hampshire when put in indirect and direct contact with *H. sanguineus* and (3) to determine if phenotypic plasticity is presented by the *L. littorea* when in contact with *H. sanguineus.*

CHAPTER II

METHODS

Collection

This study focused on two study sites, Machiasport, Maine and Rye, New Hampshire, sites A and B respectively, see figure 1. The *Littorina littorea* at site B were collected in a rocky area with *Fucus spp.* and *Ascophyllum nodosum* for cover. Only one out of every three individuals (N=33) was collected in a particular area as to not decimate the local population. The *L. littorea* at site 2 were collected in a rocky area with *Fucus spp., Ascophyllum nodosum, Chondrus crispus*, and *Laminaria spp.* Similar collection methods were used, taking 1 in every 3 *L. littorea* in the area as they are more readily available in the second area (N=61). The *Hemigrapsus sanguineus* collection occurred at site B, and the individuals were found in the same tidal pools as the *L. littorea*. All observed individuals of *H. sanguineus* were collected (N=12). The *H. sanguineus* were stored in bags with seaweed with a maximum of two individuals per bag and stored in a cooler with ice for vehicular transportation. Additional algae were collected at both sites and frozen for feeding purposes during the trials. Upon arrival at the first location the specimens were stored in a refrigeration unit. For aerial transport the specimens were all contained in the same bags they were collected in, with the addition of seawater dampened paper towels and several layers of plastic bags with algae to prevent desiccation and provide additional insulation. They were transported in an insulated cooler bag with layers of gel ice packs and were carried on to the plane as personal items.

Figure 1: Locations of collections; location A is Machiasport, Maine, location B is Rye, NH

Experimental Setup

Three tanks were set up upon arrival at the Sea Life Facility at Texas A&M Galveston, control, contained, and exposed. Each of the tanks were equipped with a Tetra Whisper Internal Power Filter i10 systems with Bioscrubber pads, Biobags for filtration, Marina Floating thermometers, rocks and *Placopecten magellanicus* shells for substrate. The control tank had 8 *Littorina littorea* from site A and 8 *Littorina littorea* from site B. The exposed tank had 9 *Littorina littorea* from site A and 6 *Littorina littorea* from site B as well as 3 male *H. sanguineus* and 3 female *Hemigrapsus sanguineus.* The contained tank had 8 *Littorina littorea* from site A and 4 *Littorina littorea* from site B as well as 3 male and 3 female *Hemigrapsus sanguineus.* The *H. sanguineus* were contained in plastic containers with holes to allow the flow of water to keep them from floating. The tanks had 2-4 ice packs to maintain a relatively constant temperature that were changed twice daily. The *H. sanguineus* were fed Mysis shrimp three times a week to

discourage them feeding on the *Littorina littorea.* *Ascophyllum nodosum* and *Ulva lactuca* were kept in the tanks for the *Littorina littorea.*

Pre-Experimental Measurements

Before the experiment began the *L. littorea* were sorted and separated by tank, then placed in tubs to ensure correct placement at the end of the measurements. Each *L. littorea* was marked on the top, middle, and bottom of the aperture with a waterproof marker (See Appendix 1). Before the measurements were taken and recorded each *L. littorea* was given a number and marked with the waterproof marker and nail polish with a color coordinate system. The shells of the *L. littorea* were measured from the apex to outer spot on the aperture and at each of the three points using Oemtools 25363 Six Inch Electronic Digital Caliper. Each snail was photographed at the time of measurement. The *H. sanguineus* were measured in three places: between the eyes, from the outer edges of the spines, and from the base of the eyes to the posterior end of the carapace using the same Oemtools caliper. The experiment ran for a total of 187 days, from June 11 through December 15, 2017. After the experiment concluded the *L. littorea* were collected by tank, identified, and measured as described below.

Post-Experimental Measurements

Each snail shell was marked at a total of 14 points to maintain consistent measurements (see Appendix 1, 2 and 3). Shell mass, length, width, thickness, and center and whorl diameter were recorded prior to measuring the shell breaking force. Shell mass was taken using an Ohurus Navigator TX scale to the nearest 0.1gram. Shell length, width, thickness, and whorl diameter measurements were executed to the nearest 0.01mm using Oemtools 25363 Six Inch Electronic Digital Calipers. Shells were then photographed using a Cannon EOS-1D stabilized on a RPS Lighting RS-CS1070 Copy Stand from 35 cm (see Appendix 4). After the full shells

were crushed the pertinent data were recorded. When present, a small piece of shell was selected. The mass, length, width, and thickness were recorded, and the shape was traced. The broken pieces were then photographed again with the selected piece made obvious for reference.

Shell Breaking Force

The force required to break each shell was measured using a MTS Insight Electromechanical Testing system with a Kistler FSH 9312A piezoelectric force transducer (see appendix 5). Signals from the transducer were amplified by a handheld charge amplifier (Kistler FSH 5995) and displayed through MTS TestWorks4. Compression plates were inserted into the crosshead and onto the loading platform. The plate on the loading platform was marked to identify the center point where the shell was placed to ensure consistency. Each shell was placed on the bottom plate with the apex pointing to the left of the transducer and checked to ensure that the center of the compression plate in the crosshead would hit the marked center diameter (see Appendix 6). Constant pressure was applied to the shell using the transducer. The maximum force required to break the shell was recorded as the measurement of prey hardness.

The following data were recorded for each full snail shell: number of pieces that each shell broke into, mean force in Newtons (N) required to crush the shells, modulus in Newtons per millimeter squared (N/mm^2) of each shell, and the total stress measured (N/mm^2) required to crush each individual snail shell. The mean force was produced by the transducer and measures the mean force applied over the course of the test, the modulus measures the elasticity of the shell, and the total stress measures the amount of force being applied to the shell at the point of failure. A mean for all individuals per treatment measured was calculated.

The selected piece of each shell was placed on the plate on the loading platform at the marked spot ensuring that the shell was under the center of the compression plate in the

crosshead. Constant pressure was applied to the shell at the prescribed speed and pressure from the protocol. The number of pieces that each shell broke into, mean force (N), modulus (N/mm^2), and the total stress (N/mm^2) were measured. The mean for all individuals per treatment was calculated. The shell breaking force and modulus were compared between treatments and origin of location for the full shell and the selected piece.

Student T tests were run comparing exposed and contained for the modulus and peak load of the full shells, comparing predator and no predator for the modulus and peak load of the full shells and availability of predator vs. no predator. Welch's t-tests were run for location of origin for the full shell for modulus and peak load. Student T tests were also run comparing exposed and contained for the modulus and peak load of a portion of the shells, comparing predator and no predator for the modulus and peak load of the full shells and availability of predator vs. no predator. In addition, an ANOVA test was run to compare the variability in the three treatments in the two sites of origin for modulus and peak load.

CHAPTER III

RESULTS

Means and standard deviations for all measurements of the snails from New Hampshire and Maine are summarized in Tables 1 and 2, respectively. Tables 3 and 4 summarize the data on the crushing force on shell pieces.

Table 1: Means and standard deviation for each all recorded data from New Hampshire snails for all three treatments for the full shell.

Location	Treatment	Mass	Length	Width	Diameter	Thickness	Pieces	Modulus	Peak Stress	Peak Load
NH	Control	1.1	15.79	10.93	7.71	0.92	4.00	1173.562	8.496	380.139
	STDEV	0.3	1.94	1.60	1.16	0.23	2.07	386.028	2.218	66.460
NH	Contained	0.9	14.86	10.81	9.66	1.10	6.75	888.943	10.098	427.889
	STDEV	0.2	0.53	0.67	4.21	0.26	3.59	861.918	5.266	151.374
NH	Exposed	0.8	14.61	10.67	7.21	0.99	5.83	1310.139	9.457	371.924
	STDEV	0.0	0.27	1.89	1.08	0.23	3.49	440.619	3.189	99.307

Table 2: Means and standard deviation for each all recorded data from New Hampshire snails for all three treatments for the full shell.

Location	Treatment	Mass	Length	Width	Diameter	Thickness	Pieces	Modulus	Peak Stress	Peak Load
ME	Control	3.5	24.1	16.44	11.13	1.67	8.88	750.148	5.784	517.719
	STDEV	0.9	2.47	1.4	1.49	0.67	3.64	528.533	3.542	286.976
ME	Contained	3.2	24.07	16.7	11.4	1.71	6.38	576.986	5.603	553.36
	STDEV	0.7	2.8	1.58	1.66	0.71	2	155.812	1.772	98.86
ME	Exposed	3.1	24.04	16.56	11.78	1.68	8.63	585.411	32.418	649.013
	STDEV	0.8	1.97	1.35	1.2	0.61	2.67	253.185	78.47	350.072

Table 3: Means and standard deviation for each treatment for the selected portion of the shell from New Hampshire Samples

Location	Treatment	PIECES	MODULUS	PEAK STRESS	PEAK LOAD
NH	Control	1.857	258.232	1.449	37.758
	STDEV	0.900	165.383	0.582	22.733
NH	Contained	2.500	128.960	0.660	33.091
	STDEV	1.000	52.590	0.221	12.209
NH	Exposed	2.800	164.615	2.617	79.578
	STDEV	0.837	190.038	2.034	81.320

Table 4: Means and standard deviation for each treatment for the selected portion of the shell from Maine Samples.

Location	Treatment	PIECES	MODULUS	PEAK STRESS	PEAK LOAD
ME	Control	2.25	250.803	2.034	53.223
	STDEV	0.707	308.11	2.329	66.77
ME	Contained	2.429	129.425	0.767	40.451
	STDEV	0.535	160.944	0.847	30.242
ME	Exposed	2.571	137.036	0.6	21.662
	STDEV	0.976	121.155	0.464	15.554

The average thickness of *L. littorea* shells was significantly higher in the Maine population than in the New Hampshire population (Figures 6 and 7, F=9.973, P=0.0003, df=2). Welch's T-Test showed that modulus and peak load were significantly different between the two sample locations (Figure 8, P=0.002876, T=-3.2941, df=25.735; Figure 9 P=0.002876, T=31.996, df=3.2521 respectively).

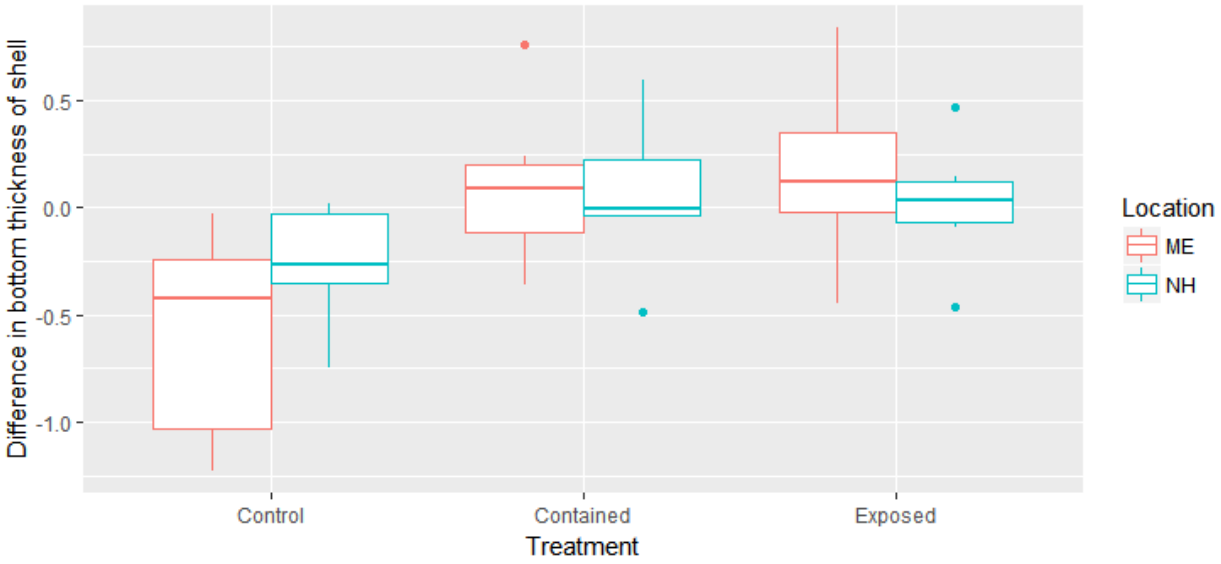


Figure 6: Average change in shell thickness of point B by treatment and location over the course of the experiment.

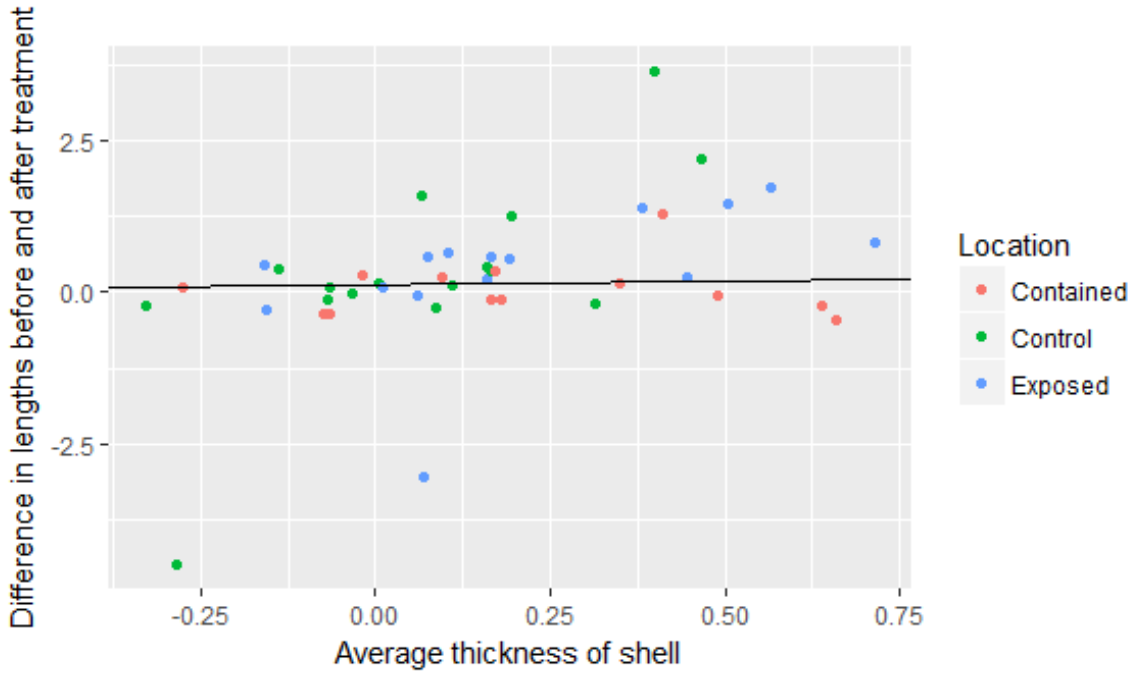


Figure 7: Difference in average thickness of shell at points T and B in relationship to the average change in the length of the shell by treatment.

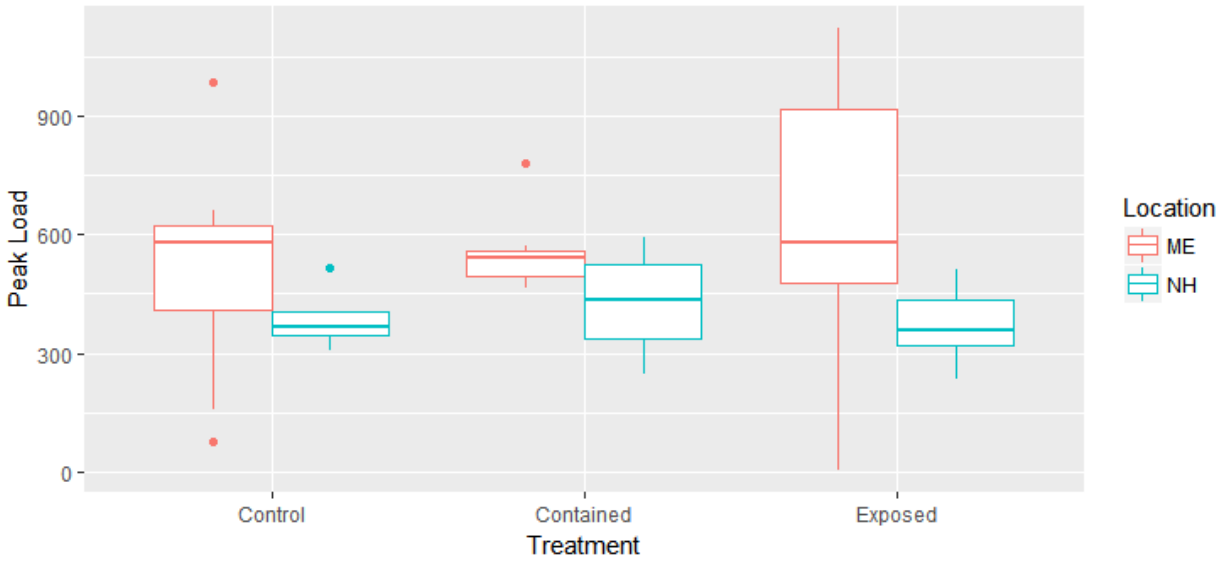


Figure 8: Peak load in Newtons for each treatment and location (p=0.002876)

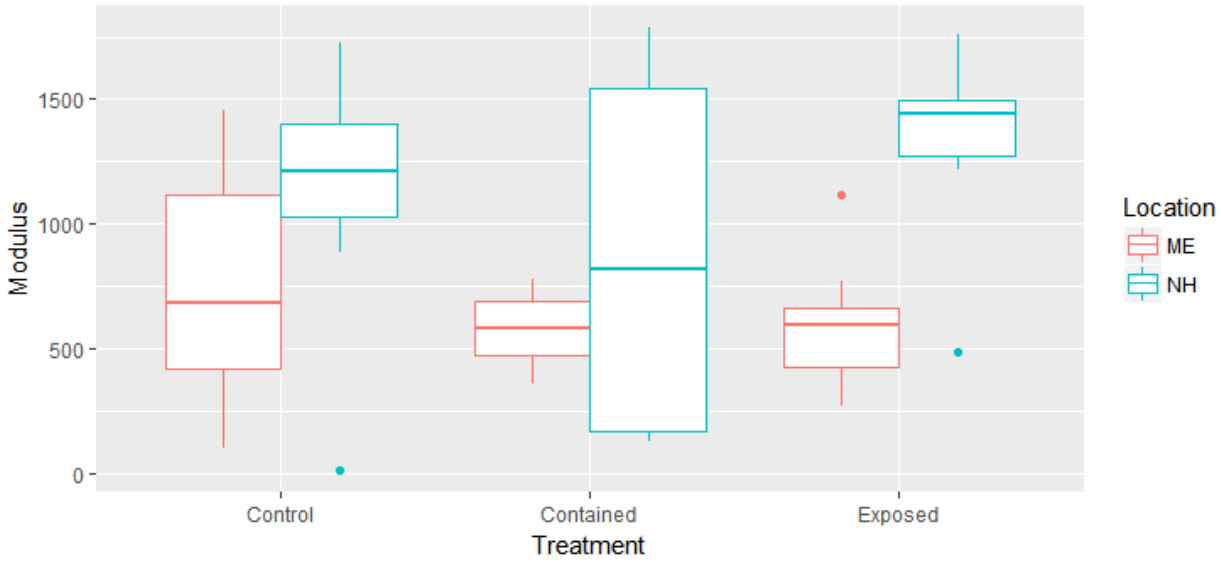


Figure 9: Modulus in Newtons for shell by treatment and location.

There was a significant difference of the thicknesses of the shells between the treatments for the bottom measurement (see figure 10 and table 5; p=0.0003, f=9.973, df=2). A Tukey hsd multiple comparison test revealed that control was significantly different than both the contained and the exposed (p-value= 0.002; p-value 0.00079 respectively). The Tukey hsd multiple comparison test revealed also revealed that the exposed-contained was not significantly different (p-value=0.9817).

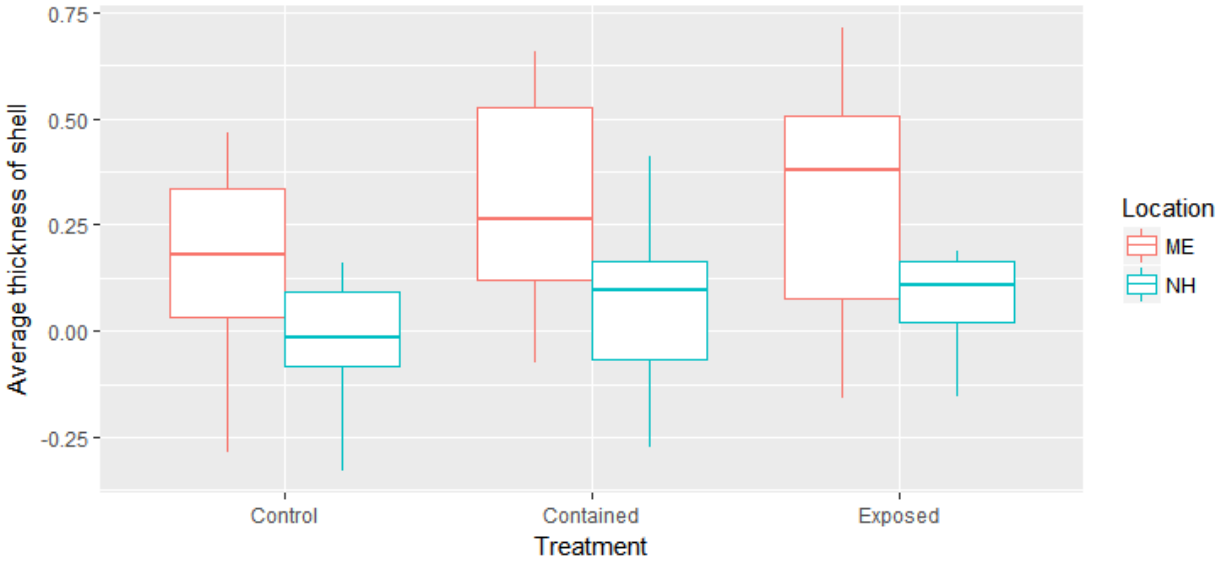


Figure 10: Boxplots of the change in bottom thickness (point B) of *Littorina littorea* shells for each treatment and location.

Table 5: Slope and Y-Intercept for the linear regression of average thickness by change in length for sites independently and combined

	slope	y-intercept
NH	0.30	-0.016
ME	0.076	0.229
Combined	0.092	0.134

CHAPTER IV

CONCLUSION

The data show that there are significant differences in the change in shell thickness, peak load of crushing force and modulus between the New Hampshire and Maine snail populations. However, the differences in the measured parameters were generally not statistically significant among the treatments (control, exposed, contained). Though the change in thickness was not significant by treatment when averaged between points T and B, when data from only point B was tested, the average thickness of the shells varied by treatment with a trend of variability between locations (Trussell 1996). The control group showed significantly less change in shell thickness at point B than the contained and exposed group, but there were no significant differences between the exposed and the contained group. Taken all together, the data show that the presence of crabs in the tank with the *Littorina* has an effect on the snails.

The change in shell thickness of point B but not point A may be due to the way in which snail shells grow with age. Since snail shells grow in an outward spiral fashion point T would not increase in thickness as fast as point B. This is because the shells at point T are constantly increasing in length whereas point B is amassing density and does not grow as quickly outward (Vermeji,1995).

The development of inducible defenses suggests that the expense of shell production to the organisms is great, which would explain why organisms such as *Littorina littorea* do not present thicker shells until in contact with predators (Lively et. al.). The trend in the thickness between the contained and exposed shows that thickness of mollusk shells may not be due to one factor (Seeley 1986; Appleton and Palmer 1988; A. Palmer 1985; 1990; Freeman and Byers

2006). As seen in this experiment snails that were exposed to predation efforts had a thicker shell than those that had predators in contained in vessels in the enclosure and had a significantly stronger response than the snails that had no predator in their enclosure. This promotes the idea that the snails in direct contact with the crabs responded to two factors, a biological and a physical, whereas the snails that were not in direct contact with the crabs only responded to a biological factor and therefore did not have as strong of a response.

The modulus and peak load of the shells varied by location of origin. The mean modulus for New Hampshire tended to be higher than the modulus of the snails from meaning that the shells have less elasticity and can withstand a lower amount of force being applied before failing. This is reflected in the peak load data, which is the maximum amount of pressure a structure is able to support before failing (Biewenere, 1992).

Variation in salinity has been shown to impact shell formation of strombid gastropods which may explain the variation of the shell elasticity between the locations (Geary et. al. 1992). Salinity causes calcareous organisms to have a reduction uptake of calcium carbonate, this could cause a reduced modulus, as seen in this experiment (Chan et al 2013). The northeastern channel of the Gulf of Maine, near Sample Location B, has a salinity that tends to be between 31.5 and 32.5 (NERACOOS 2018). South Newington, New Hampshire, near Sample location B, has a salinity that can get as low as 4 but does not reach above 28 (Brown et al 2015).

The aim of this study is to increase awareness of the effects that invasive species can have. It has brought to light the variation in *Littorina littorea* between the upper and lower ranges of their inhabitance in the Gulf of Maine. This study has also shown that the invasive predator *Hemigrapsus sanguineus* may induce changes in the morphology of the *Littorina littorea* shells. Further research should be done to determine whether the observed variation

between the two sites has a genetic basis. To improve upon the accuracy and precision of this study more samples and replicates, the project could be run over a longer period of time, and an index could be calculated to correct for the disparity of sizes between the sizes of the two locations.

REFERENCES

Appleton, Robert D., and A. Richard Palmer. 1988. "Water-Borne Stimuli Released by Predatory Crabs and Damaged Prey Induce More Predator-Resistant Shells in a Marine Gastropod." *Proceedings of the National Academy of Sciences* 85 (12): 4387–91. http://www.pnas.org/content/85/12/4387.

Bertness, Mark D. 1984. "Habitat and Community Modification by An Introduced Herbivorous Snail." *Ecology* 65 (2): 370–81. https://doi.org/10.2307/1941400.

Blakeslee, April M. H., Yumi Kamakura, Jaclyn Onufrey, Wataru Makino, Urabe Jotaro, Susan Park, Carolyn L. Keogh, et al. 2017. "Reconstructing the Invasion History of the Asian Shorecrab, Hemigrapsus Sanguineus (De Haan 1835) in the Western Atlantic." *Marine Biology* 164 (47): 47. https://doi.org/10.1007/s00227-017-3069-1.

Brenchley, G. A., and J. T. Carlton. 1983. "Competitive Displacement of Native Mud Snails by Introduced Periwinkles in the New England Intertidal Zone." *The Biological Bulletin* 165 (3): 543–58. https://doi.org/10.2307/1541464.

Brown, L. E., Chen, C. Y., Voytek, M. A., & Amirbahman, A. (2015). The effect of sediment mixing on mercury dynamics in two intertidal mudflats at Great Bay Estuary, New Hampshire, USA. *Marine chemistry*, *177*, 731-741.

Cohen, Andrew N., and James T. Carlton. 1995. "Nonindigenous Aquatic Species in a United States Estuary: A Case Study of the Biological Invasions of The." http://bioinvasions.org/wp-content/uploads/1995-SFBay-Invasion-Report.pdf.

Chan, V. B., Thiyagarajan, V., Lu, X. W., Zhang, T., & Shih, K. (2013). Temperature dependent effects of elevated CO2 on shell composition and mechanical properties of Hydroides elegans: insights from a multiple stressor experiment. *PLoS one*, *8*(11), e78945.

Davidson, Amy Michelle, Michael Jennions, and Adrienne B. Nicotra. 2011. "Do Invasive Species Show Higher Phenotypic Plasticity than Native Species and, If so, Is It Adaptive? A Meta-Analysis." *Ecology Letters* 14 (4): 419–31. https://doi.org/10.1111/j.1461-0248.2011.01596.x.

Dorcas, Michael E., John D. Willson, Robert N. Reed, Ray W. Snow, Michael R. Rochford, Melissa A. Miller, Walter E. Meshaka, et al. 2012. "Severe Mammal Declines Coincide with Proliferation of Invasive Burmese Pythons in Everglades National Park." *Proceedings of the National Academy of Sciences of the United States of America* 109 (7): 2418–22. http://www.jstor.org/stable/41477487.

Epifanio, Charles E. 2013. "Invasion Biology of the Asian Shore Crab Hemigrapsus Sanguineus: A Review." *Journal of Experimental Marine Biology and Ecology* 441 (March): 33–49. https://doi.org/10.1016/j.jembe.2013.01.010.

Freeman, Aaren S., and James E. Byers. 2006. “Divergent Induced Responses to an Invasive Predator in Marine Mussel Populations.” *Science* 313 (5788): 831–33. https://doi.org/10.1126/science.1125485.

Geary, D. H., Brieske, T. A., & Bemis, B. E. (1992). The influence and interaction of temperature, salinity, and upwelling on the stable isotopic profiles of strombid gastropod shells. *Palaios*, 77-85.

Gerard, V. A., R. M. Cerrato, and A. A. Larson. 1999. “Potential Impacts of a Western Pacific Grapsid Crab on Intertidal Communities of the Northwestern Atlantic Ocean.” *Biological Invasions* 1 (4): 353–61. https://doi.org/10.1023/A:1010093329077.

Google Maps. (2018). *Owls Head Lighthouse to Miachiasport ME*. Retrieved from https://www.google.com/maps/d/viewer?mid=ziZA4YH0pTUs.ktJc02G0F-O4&ie=UTF8&oe=UTF8&msa=0

Grosholz, Edwin. 2002. “Ecological and Evolutionary Consequences of Coastal Invasions.” *Trends in Ecology & Evolution* 17 (1): 22–27. https://doi.org/10.1016/S0169-5347(01)02358-8.

Ricciardi, A., Neves, R. J., & Rasmussen, J. B. (1998). Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (Dreissena polymorpha) invasion. *Journal of animal ecology*, *67*(4), 613-619.

Lord, J. P. 2017. “Potential Impact of the Asian Shore Crab Hemigrapsus Sanguineus on Native Northeast Pacific Crabs.” *Biological Invasions* 19 (6): 1879–87. https://www.cabdirect.org/cabdirect/abstract/20183002423.

Lord, P. Joshua., and Larissa Williams. 2017. “Increase in Density of Genetically Diverse Invasive Asian Shore Crab (Hemigrapsus Sanguineus) Populations in the Gulf of Maine” n.d. Accessed February 22, 2018. https://link.springer.com/article/10.1007/s10530-016-1304-1.

Kitching, J. A., and J. Lockwood. 1974. “Observations on Shell Form and Its Ecological Significance in Thaisid Gastropods of the Genus <Emphasis Type="Italic">Lepsiella</Emphasis> in New Zealand.” *Marine Biology* 28 (2): 131–44. https://doi.org/10.1007/BF00396304.

Kitching, J. A., Louise Muntz, and F. J. Ebling. 1966. “The Ecology of Lough Ine. XV. The Ecological Significance of Shell and Body Forms in Nucella.” *Journal of Animal Ecology* 35 (1): 113–26. https://doi.org/10.2307/2693.

Muñoz, Roldan C., Carolyn A. Currin, and Paula E. Whitfield. 2011. “Diet of Invasive Lionfish on Hard Bottom Reefs of the Southeast USA:: Insights from Stomach Contents and Stable Isotopes.” *Marine Ecology Progress Series* 432: 181–93. http://www.jstor.org/stable/24874561.

Northeastern Regional Association of Coastal and Ocean Observing Systems. 2018. Ocean Climate Display. http://neracoos.org/datatools/climatologies_display

Nourinezhad, J., Mazaheri, Y., & Ahi, M. R. (2015). Metrical analysis of dromedary digital bones. *Anatomical science international*, *90*(2), 113-122.

Palmer, A. Richard. 1990. “Effect of Crab Effluent and Scent of Damaged Conspecifics on Feeding, Growth, and Shell Morphology of the Atlantic Dogwhelk <Emphasis Type="Italic">Nucella Lapillus</Emphasis> (L.).” In , 155–82. Developments in Hydrobiology. Springer, Dordrecht. https://doi.org/10.1007/978-94-009-0563-4_13.

Palmer, A. Richard 1985. “ADAPTIVE VALUE OF SHELL VARIATION IN THAIS-LAMELLOSA - EFFECT OF THICK SHELLS ON VULNERABILITY TO AND PREFERENCE BY CRABS.” *Veliger* 27: 349–56. http://www.biodiversitylibrary.org/page/42481405.

Pimentel, David, Rodolfo Zuniga, and Doug Morrison. 2005. “Update on the Environmental and Economic Costs Associated with Alien-Invasive Species in the United States.” *Ecological Economics*, Integrating Ecology and Economics in Control Bioinvasions, 52 (3): 273–88. https://doi.org/10.1016/j.ecolecon.2004.10.002.

Pyšek, Petr, and David M. Richardson. 2010. “Invasive Species, Environmental Change and Management, and Health.” *Annual Review of Environment and Resources* 35 (1): 25–55. https://doi.org/10.1146/annurev-environ-033009-095548.

Seeley, Robin Hadlock. 1986. “Intense Natural Selection Caused a Rapid Morphological Transition in a Living Marine Snail.” *Proceedings of the National Academy of Sciences* 83 (18): 6897–6901. http://www.pnas.org/content/83/18/6897.

Steinberg, Mia K., and Charles E. Epifanio. 2011. “Three’s a Crowd: Space Competition among Three Species of Intertidal Shore Crabs in the Genus Hemigrapsus.” *Journal of Experimental Marine Biology and Ecology* 404 (1): 57–62. https://doi.org/10.1016/j.jembe.2011.04.014.

Taylor, Alan. 2002. *American Colonies: The Settling of North America (The Penguin History of the United States, Volume 1)*. Penguin.

Trussell, Geoffrey C. 1996. “Phenotypic Plasticity in an Intertidal Snail: The Role of a Common Crab Predator.” *Evolution* 50 (1): 448–54. https://doi.org/10.2307/2410815.

Trussell, Geoffrey C., and L. David Smith. 2000. “Induced Defenses in Response to an Invading Crab Predator: An Explanation of Historical and Geographic Phenotypic Change.” *Proceedings of the National Academy of Sciences* 97 (5): 2123–27. https://doi.org/10.1073/pnas.040423397.

Tyrrell, M. C., & Harris, L. G. (2000). Potential impact of the introduced Asian shore crab, Hemigrapsus sanguineus, in northern New England: Diet, feeding preferences, and overlap with the green crab, Carcinus maenas. In *Marine Bioinvasions: Proceedings of*

the First National Conference, Cambridge, MA, 24-27 January 1999 (pp. 208-220). MIT Sea Grant College Program.

Vermeij, Geerat J. 1976. “Interoceanic Differences in Vulnerability of Shelled Prey to Crab Predation.” *Nature* 260 (5547): 135–36. https://doi.org/10.1038/260135a0.

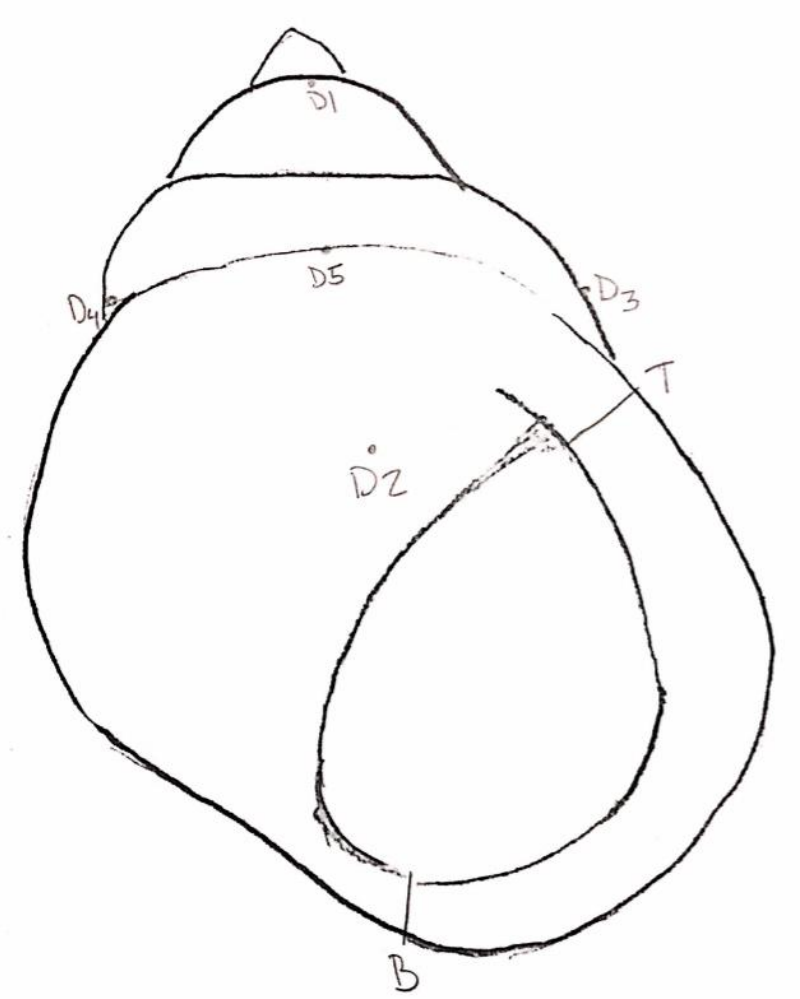
Vermeij, Geerat J.. 1978. *Biogeography and Adaptation: Patterns of Marine Life*. Harvard University Press.

Vermeij, Geerat J. "Environmental change and the evolutionary history of the periwinkle (Littorina littorea) in North America." *Evolution* 36, no. 3 (1982): 561-580.

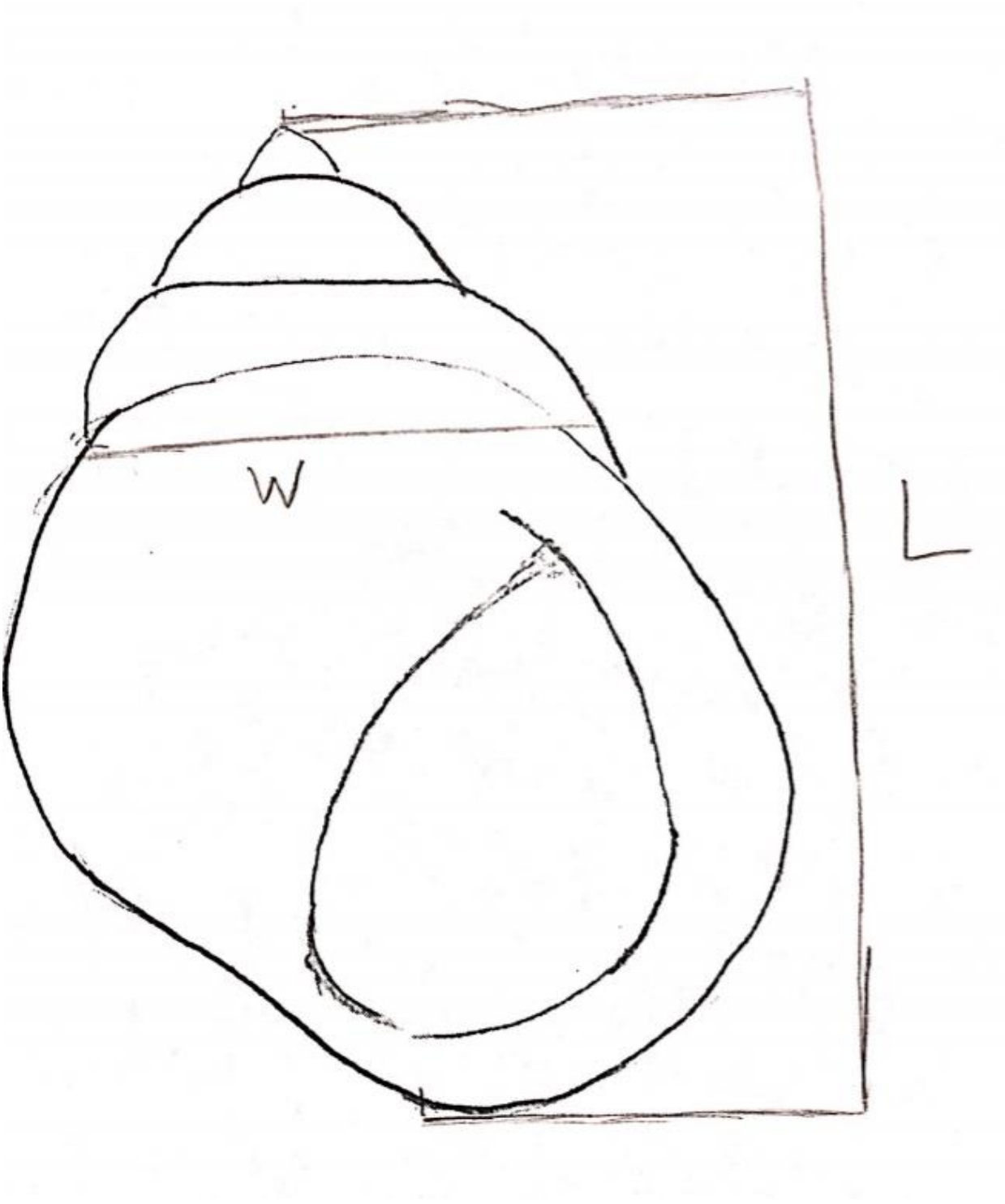
Vermeij, G. J. (1995). *A natural history of shells*. Princeton University Press.

West-Eberhard, M. J. 1989. “Phenotypic Plasticity and the Origins of Diversity.” *Annual Review of Ecology and Systematics* 20 (1): 249–78. https://doi.org/10.1146/annurev.es.20.110189.001341.*of Ecology and Systematics* 20 (1): 249–78. https://doi.org/10.1146/annurev.es.20.110189.001341.

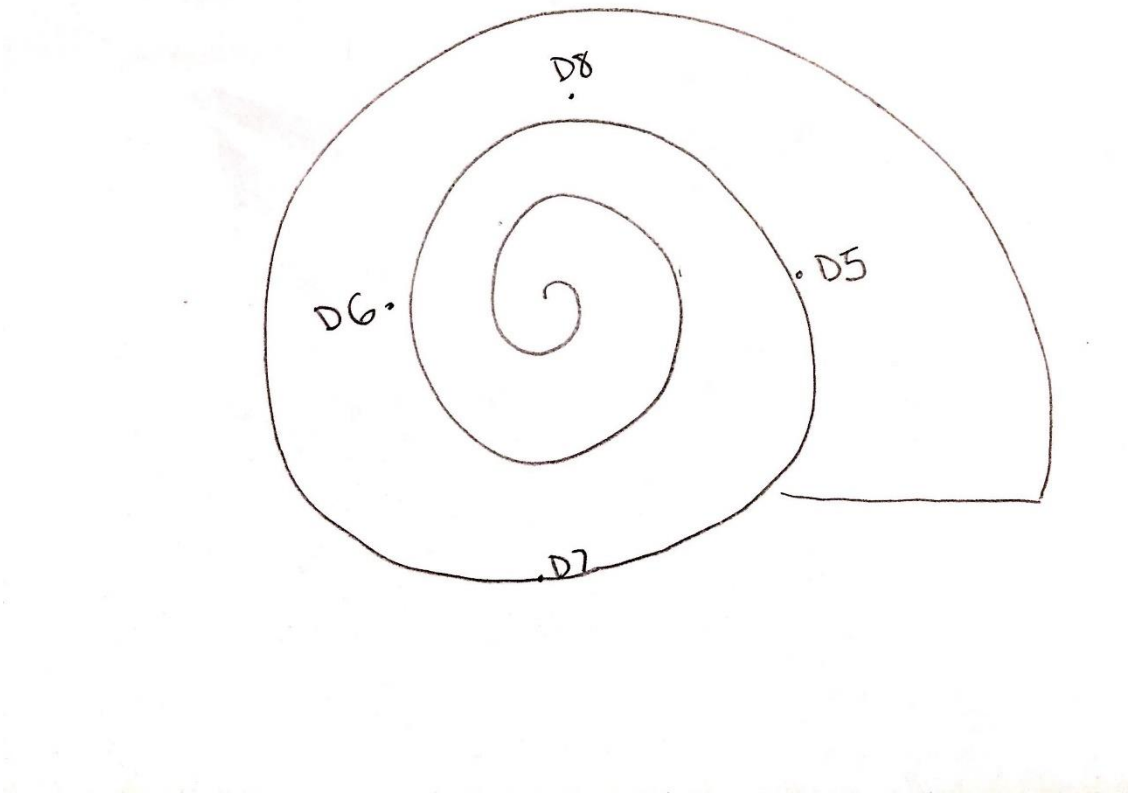
APPENDIX



Appendix 1: Aperture thickness measurement points bottom (B) and top (T). Points for measurements of diameter of the area where the load cell would touch, D1-D2 were used to calculate the diameter across the length of the shell that the cell would touch and D3-D4 were used to calculate the diameter across the width of the shell that the cell would touch. D5 is a reference for placement of the four points used to calculate the diameter of the spiral of the shell seen in Appendix 3

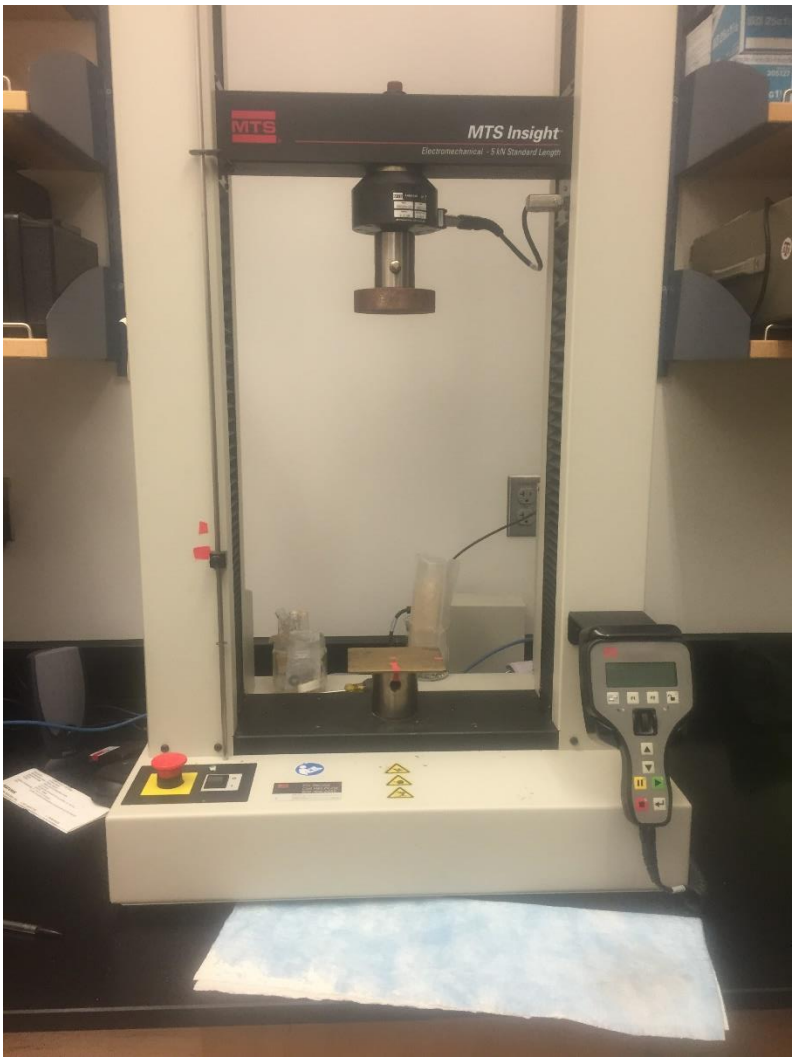


Appendix 2: Length and width measurement points.

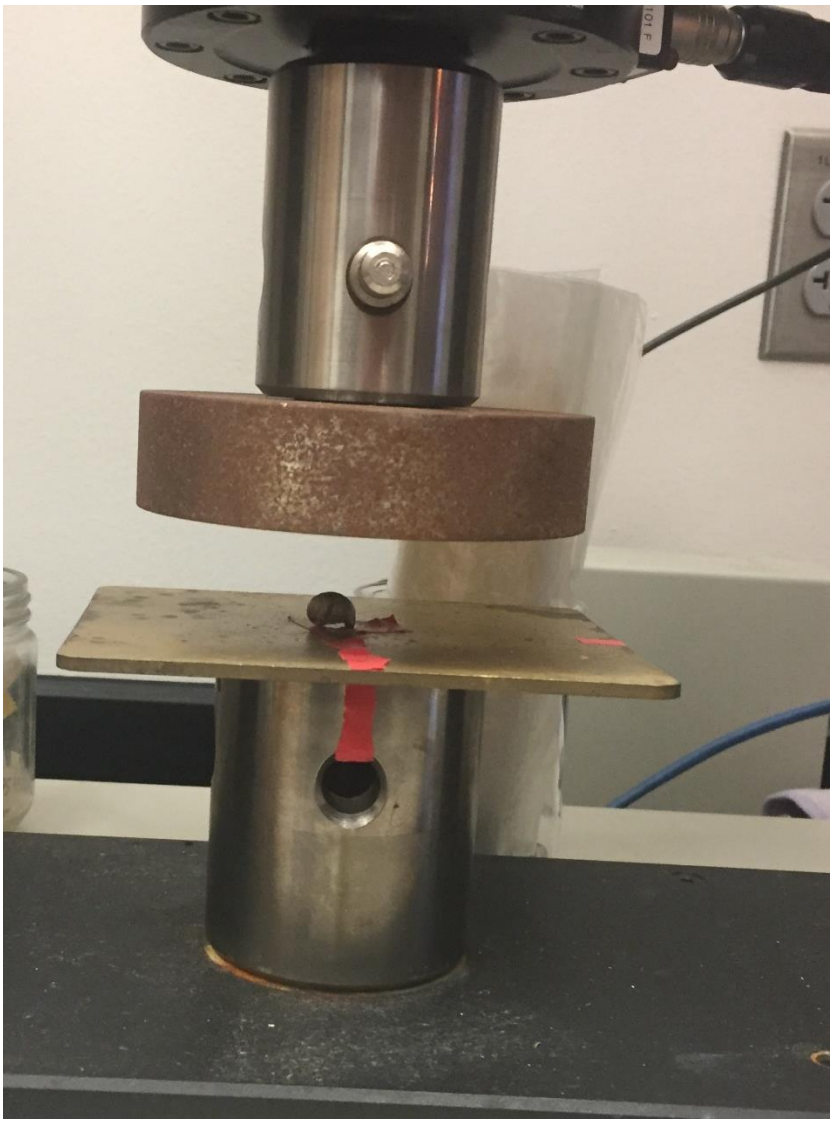


Appendix3: Measurement of the diameter of the spiral, D5-D6 were used to calculate the diameter of the width of the spiral and D7-D8 were used to calculate the diameter of the length of the spiral.

Appendix 4: Copy stand apparatus for photographing the snails



Appendix 5: MTS Insight Electromechanical Testing system with a Kistler FSH 9312A piezoelectric force transducer loading cell and full view.



Appendix 6: snail configuration on MTS Insight Electromechanical Testing system with a Kistler FSH 9312A piezoelectric force transducer for first crush test of each shell.