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Zonation pattern and spatial arrangement of a *Geukensia granosissima* population in a mixed mangrove forest of Tampa Bay

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Zonation pattern and spatial arrangement of a *Geukensia granosissima* population in a mixed
mangrove forest of Tampa Bay

by

Derrick Shane Hudson

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Integrative Biology
with a concentration in Ecology and Evolution
College of Arts and Sciences
University of South Florida

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DEDICATION

I dedicate this thesis to Heather Broome. If not for her support and encouragement to pursue my dreams this thesis would not have been possible.

ACKNOWLEDGMENTS

I would first like to thank my thesis advisor Dr. Susan Bell of the Department of Integrative Biology at University of South Florida, for her patience, motivation, and immense knowledge. I would also like to thank the committee members who were involved in the development of this research project: Dr. Bradford J. Gemmell and Dr. Christopher D. Stallings. Without their invaluable participation and input, the study could not have been successfully conducted. Furthermore, I would also thank Erin P. Kiskaddon, Elizabeth A. Salewski, and Stephen G. Hesterberg for their comments on this thesis. Finally, I express my gratitude to the Astronaut Trail Shell Club who partially supported this research.

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ABSTRACT

Here I provide the first report on *Geukensia granosissima* patterns of abundance along a tidal gradient within a mixed mangrove stand located in Tampa Bay, Florida, USA. Specifically, I examined 1) the relationship between *G. granosissima* size and density with mangrove root type (e.g. prop root, pneumatophore), and of density within the intertidal zones; and 2) the possible role of predation in shaping the lower zonation patterns displayed. Transect surveys located along the lower and upper population limit boundaries were conducted every two months over a ten-month period. Variables measured include size distribution, density of mussels, above ground mangrove prop and pneumatophore roots. To evaluate potential predator influence on mussel distribution, predator exclusion experiments were conducted in March and June 2016, using mock pneumatophore platforms at both high and low tidal elevations. Surveys indicated that over all dates mean mussel densities and percent cover were higher along the lower limit tidal elevation [mean (\pm SD) = $1280.3 \pm 665.9 \text{ m}^{-2}$ and $20.6 \pm 3.78\%$ respectively], versus that in the higher limit tidal elevation [$102.4 \pm 50.7 \text{ m}^{-2}$ and $0.52 \pm 0.17\%$]. Survivorship of mussels in the predator exclusion platforms placed at higher position within lower edge of the mussel tidal distribution was approximately 100% on both experimental dates. During March 2016, mussel survivorship was lower when predators had access to mussels with the greatest loss of mussels in the lower (26% survivorship) vs. higher (66.5%) tidal elevations after 48h. Similarly, when predators had access to mussels in June experiments, after just 24 h mussel loss was greater at lower (1% survivorship) vs. higher (80% survivorship) tidal elevations, possibly reflecting differences in predator densities, identities, and/or functional responses. Overall trends

in the patterns of distribution of this population of *G. granosissima* suggest that the lower tidal boundary of the mussel is shaped by predation but that predation plays a lesser role in the high tidal areas.

INTRODUCTION

Understanding how natural communities are structured is a central goal of ecological inquiry and community structure can be shaped by both biotic factors (e.g., predation, facilitation) and abiotic factors (e.g., temperature, salinity). Examination of the structure of communities began in the early 1900's with an emphasis on describing plant communities (Clements, 1916), but evolved to using field experiments in the 1970s. Many of these early experiments were conducted on sessile organisms in rocky intertidal habitats and involved physical manipulation/alteration of competition and/or predation (e.g., Menge, 1976; Paine, 1974). Subsequently, field manipulations became paramount in efforts to understand the mechanisms influencing community structure (Underwood, 2000). A combination of descriptive and experimental approaches has also provided valuable insight into factors controlling abundance of intertidal organisms (Connell, 1972; Dayton, 1971; Menge, 1976; Paine, 1976).

The tidal zone is an area of transition between marine and terrestrial ecosystems. Tidal settings have been popular locations for exploring questions about the relative importance of biological interactions or physical factors for impacting distributional patterns of organismal abundance. This often relatively narrow boundary spans the region between low and high tides. Organisms established in the intertidal zone can be subject to desiccation, salinity and temperature extremes, submersion/emersion, and oxygen reduction (Connell, 1972). The high variability of abiotic factors and periodic tidal cover provide an ideal location to assess the impacts of both biotic and abiotic factors on community structure.

Mussels of many taxa are found in intertidal habitats including the rocky intertidal (Connell, 1972; Dayton, 1971; Hunt and Scheibling, 2001; Menge, 1976; Paine, 1976), soft sandy sediments (Commito *et al.*, 2014; Jager *et al.*, 2011; Koppel *et al.*, 2008), saltmarshes (Alan and Sue, 1992; Bertness, 1984; Bertness and Grosholz, 1985; Honig *et al.*, 2015), and mangroves (Bacon, 1975). Unlike other benthic sessile fauna that exhibit no secondary movement after attachment to substrates, mussels may move by detaching and reattaching new byssus threads (Jager *et al.*, 2011; Koppel *et al.*, 2008). Movement (secondary settlement) by mussels, along with larval settlement onto other mussels, can lead to the formation of aggregations ranging in size from tens of centimeters to kilometers and composed of densities ranging from 200 to 3000 mussels per square meter (Bacon, 1975; Commito *et al.*, 2014; Franz, 2001). The aggregations formed by mussels occupying soft-sediment intertidal habitats can exhibit wave-like bands or power-law spatial distribution (Commito *et al.*, 2014). Within rocky intertidal and saltmarsh habitats, mussel aggregations can display clear zonation across the mid-high intertidal zones (e.g. Connell, 1972; Menge, 1976; Paine, 1974). Within the intertidal zone, it is generally accepted that the upper limit tidal distribution of mussel is shaped by a gradient of longer emersion times resulting in stress and eventually mortality, as opposed to the lower limit tidal distribution that is often shaped by competition and predation (Connell, 1972; Harley and Helmuth, 2003; Menge, 1976; Paine, 1974). Whether the same zonation pattern and controlling factors exist for mussels inhabiting the mangrove dominated intertidal are presently unknown.

The Ribbed mussels (*Geukensia spp.*) are particularly well adapted to live in the high intertidal zone. Both *Geukensia granosissima* and its congener, *Geukensia demissa* (formerly *Modiolus demissus*), have previously been reported from salinity ranges of 3-48psu (Lent, 1969; Neufeld and Wright, 1998) and temperature ranges of -22°C to 45°C (Hilbish, 1987; Jost and

Helmuth, 2007; Lent, 1969; Montagna, *et al.*, 2008). *Geukensia* spp. have a broad latitudinal distribution from Canada to South America with *G. demissa* along the Pacific and Atlantic coasts of the United States down to Venezuela and *G. granosissima* found through the Gulf of Mexico (Romero *et al.*, 2002; Sarver *et al.*, 1992). Most literature has focused primarily on *G. demissa* within intertidal saltmarsh habitat (e.g., Bertness and Grosholz, 1985; Franz, 2001; Stiven and Gardner, 1992) and limited documentation exists for *G. demissa* in the mangroves of Venezuela (Romero *et al.*, 2002). To date, one study exists that describes recruitment, growth, and density of *G. granosissima* in a saltmarsh habitat (Honig *et al.*, 2015). Here I provide the first report on *G. granosissima* patterns of abundance along a tidal gradient within a mixed mangrove stand located in Tampa Bay, Florida, USA.

Unlike the habitat provided by salt marsh vegetation, *Rhizophora mangle* (red mangrove) and *Avicennia germinans* (black mangrove) provide a unique suite of both above-ground root structures as well as fine root structures within the sediments. The above-ground structures of *R. mangle* is represented by prop roots typically with a circumference at the sediment surface between 6.0-12.5cm (Thayer *et al.*, 1987). In contrast, the circumference of *A. germinans* pneumatophores at the sediment surface is 3.0-4.7cm. Prop roots are characterized by arching above ground aerial roots starting at the trunk, branches, and other roots (Figure 1a) (Gill and Tomlinson, 1977); conversely, black mangrove pneumatophores are characterized by comparatively smaller and thinner roots projecting upward from the sediment surface (Figure 1b)(Mckee *et al.*, 1988). Preliminary surveys revealed that *Geukensia granosissima* can be partially immersed within the sediment and attached to the absorptive roots of both red and black mangroves and display a clear, banded distribution with lower and upper limit boundaries at +0.5m to +0.8m MLW, respectively (Hudson, pers. observ.).

The goal of this research was to describe patterns of mussel distribution associated with features of mangrove vegetation across a tidal gradient and evaluate whether predator pressure controls the lower limit tidal distribution. I used both descriptive and experimental methods to examine factors shaping patterns of mussel distribution in the mangrove intertidal. Specifically, I examined; 1) the relationship between *Geukensia granosissima* size and density with mangrove root type (prop root, pneumatophore) and root density, at low versus high tidal zones; and 2) the possible role of predation influencing the lower zonation patterns displayed by this *Geukensia granosissima* population.



Figure 1 A: Image of *R. mangle* prop roots Tampa Bay, FL February 2015. B: Image of *A. germinans* pneumatophores Tampa Bay, FL February 2015. Scale bars in both images are 15cm and arrow indicates location of mussels.

MATERIALS AND METHODS

Descriptive Surveys

A field study was conducted to assess the arrangement and distribution of *G. granosissima* at a site located in Tampa Bay (27°53'N, 82°38'W) within a mixed (black and red) mangrove-rimmed tidal zone. Of interest were the density of mussels at high and low tidal zones as well as mussel density and amount/type of mangrove root. A survey of mussel density around red and black mangrove was conducted using quadrats placed around the red or black roots. A study area 500m in length was demarcated parallel to shore and subdivided into 10 plots (50m x 20m) within which mussel abundance, percent cover, and root density were quantified.

To compare *Geukensia granosissima* size distribution and density with root density of red and black mangroves, mussel and mangrove root densities were collected from a series of 0.25m² quadrats within each of the 10 plots at two different tidal heights (low = +0.5m above MLW and high = +0.8m above MLW) that coincided with the lower and upper edges of the mussel distribution (Fig. 2). A single quadrat was placed haphazardly into mussel aggregations associated with either black or red mangroves at the low and high tidal heights. Within each 0.25m² quadrat all mangrove roots (red, black) were identified and counted and five subsamples of 5cm x 5cm (total 125cm² per quadrat) were randomly chosen and marked. Then all mussels within the area were excavated to 3cm depth, every two months over ten-months from September 2015 to July 2016. All excavated mussels were transported to the laboratory, enumerated and shell length was measured to 0.1mm with digital calipers. From these collections

conducted within mussel aggregations, density (no. mussel x 125cm⁻²) and mussel size (shell length) of all collected mussels were determined.

To complement the sampling of mussel aggregations, a survey of mussel percent cover was conducted in May 2016 to estimate overall abundance of mussels along both tidal height transects. Mussel coverage was collected using transects of 500m long parallel to shore at the same tidal heights used for sampling of mussel aggregations, +0.5m above MLW and +0.8m above MLW. Each transect was subdivided into ten plots of 50m in length. Within each plot, randomly placed 0.25m² quadrats (n = 20) subdivided into 5cm x 5cm (n = 100) squares were placed and percent cover of mussels was estimated by presence/absence of mussels within each square.

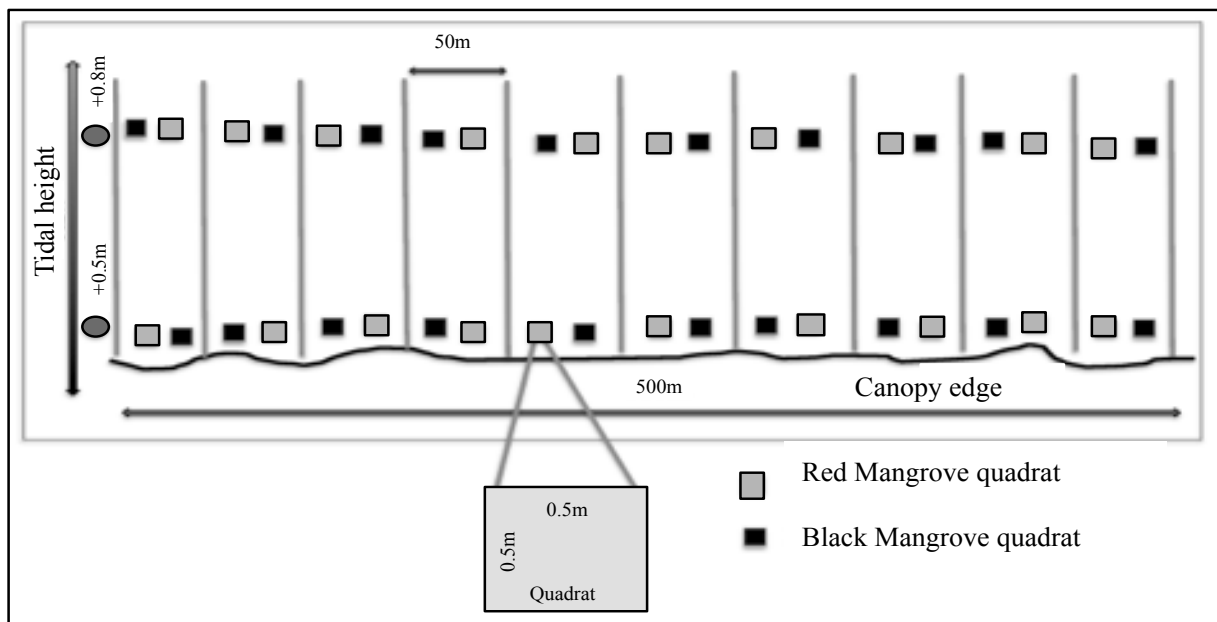


Figure 2 Layout of quadrats with transects along +0.5m and +0.8m MLW used in mussel survey. Tidal height was determined with Old Port Tampa data station as the reference station (NOAA, 2016).

Predator Exclusion Experiment

Two field experiments were conducted in March and June 2016 to evaluate if predation shaped the lower tidal distribution of mussels among the mangrove taxa at the study site in Tampa Bay. To accomplish this, a combination of artificial pneumatophores and predator exclusion cages was utilized to manipulate predator access to a fixed density of mussel prey at tidal heights within the lower boundary of mussel distribution.

Wooden platforms 15 x 15 x 3 cm (L x W x D) were constructed to which mussel prey and cage treatments were added. Each platform also contained six pneumatophore mimics constructed from wooden dowels (Diameter = 5 mm, L = 4 cm), which were attached vertically to the center of the platform in a consistent configuration (Fig. 4). The number of pneumatophores added represented the mean pneumatophore density observed at the study site (1224 roots x m⁻²). Coconut mat was utilized to mimic below ground absorptive root structure of black mangroves to and represent the primary point of mussel attachment. This mat was covered with 0.5 cm of field-collected sediment passed through a 2 mm sieve. Full and partial exclusion cages were constructed using vinyl mesh (1 x 1 cm opening) that either completely or partially-surrounded the mock pneumatophore platforms. The design of the partial cage was identical to that of the cage platform, except vinyl mesh covered only two sides (Fig. 4).

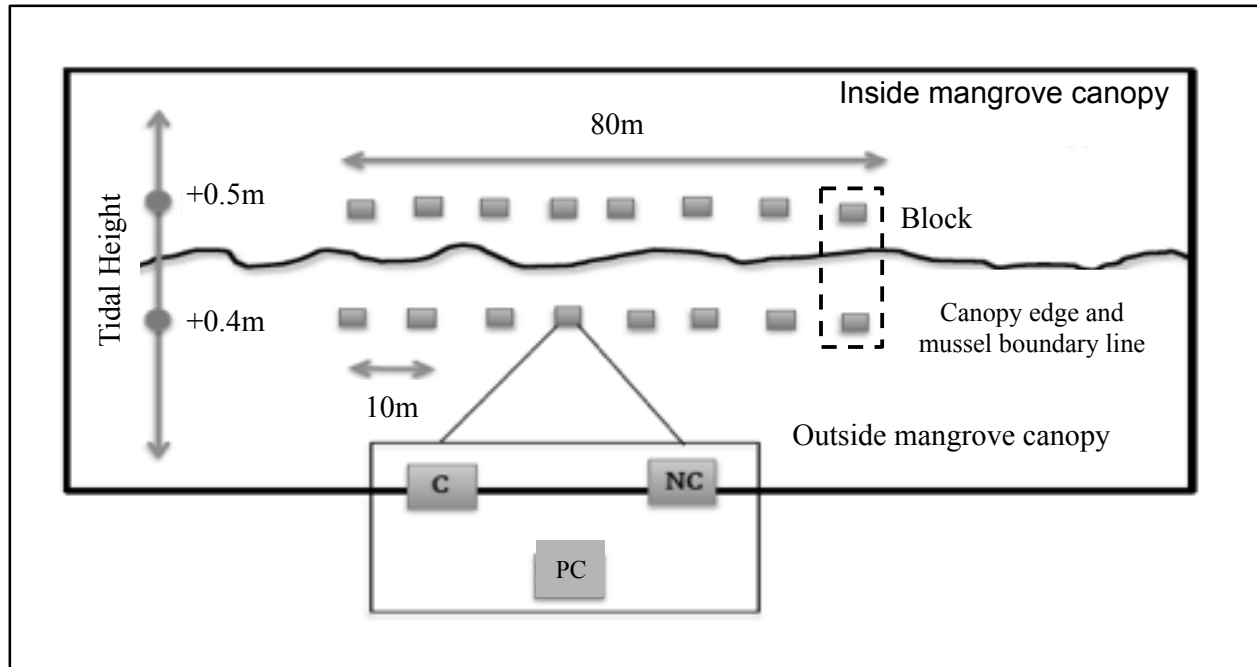


Figure 3 Diagram illustrating experimental layout relative to tidal height and mangrove canopy. Small squares are replicates and within each, three treatments were randomly placed. Treatments are: C = caged, NC = no cage, PC = Partial cage. Eight replicated blocks (---) of treatments at two tidal heights were established for each experiment.

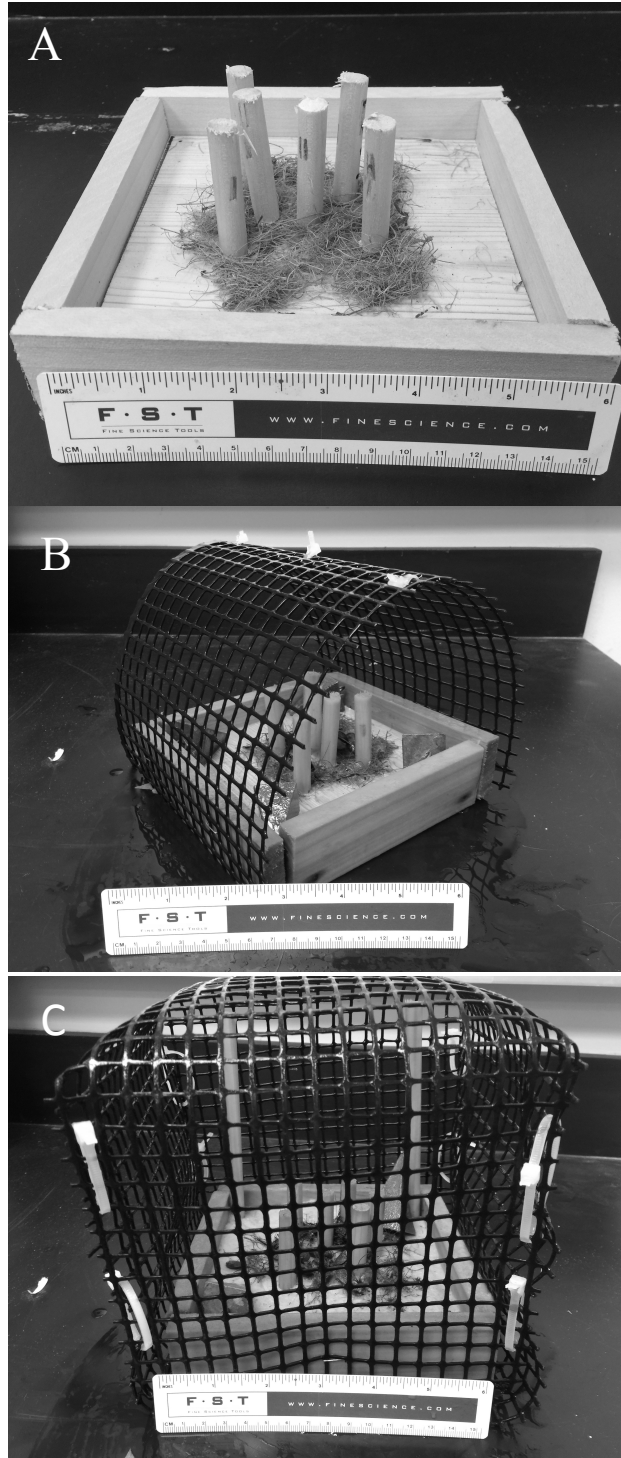


Figure 4 Mock pneumatophore platforms, 15cm x 15cm, containing six 5mm diameter dowels, and coconut mat. Cage types A: No cage, B: Partial cage, C: Full cage with mesh (1cm x 1cm) openings. Scale bar in all images is 15cm.

In the laboratory, before the deployment of the structures, 20 paint pen-marked mussels of 20mm (± 1 mm) shell length were placed on the platforms. Ten mussels were placed within the pneumatophores centered on each platform and ten placed around the margin of the pneumatophores left for 24 hours to allow mussels to produce byssal thread attachments. Mussels of 20mm shell length were chosen for the experiment as they have limited movement but are of sufficient size that they are consumed by relatively small (*Panopeus herbstii*) and large (*Callinectes sapidus*) predators (Lin, 1990; Seed, 1980).

In the field, based upon a power analysis, eight replicate experimental platforms were randomly set out at low tide and arranged by cage type at both low tidal positions (Fig. 3). Specifically, experimental platforms ($n = 48$) were assigned to one of three types of predator exclusion cage [i.e., cage (C), no cage (NC), partial cage (PC)] and placed at each of two different tidal heights at the lower edge of the mussel tidal distribution (i.e., + 0.4 or + 0.5 m MLW). The tidal positions utilized here are noteworthy because they represent elevations that not only vary in their emersion times but also are either inside or outside of the mangrove fringe. Experimental platforms were arranged into blocks spaced 10 m apart to control for environmental heterogeneity between specific deployment locations (Fig. 3).

After a 48- and 24-h deployment periods in March and June, respectively, all platforms were removed and mussels were counted *in situ*. Survivorship was recorded as a proportion, or the number of individuals out of the 20-initial prey present on each platform.

Statistical Analysis

One-way ANOVA, Mann-Whitney U, and Kruskal-Wallis tests were used to compare mussel shell length and densities associated with the two different tidal elevations and root

densities of red and black mangroves that were assessed along with a single percent cover survey. In predator exclusion experiment mussel survivorship was compared across cage treatments using a logistic regression generalized linear model with binomial distribution along with logistic link and an analysis of deviance with cage treatment, position treatment, and block as factors. Post-hoc Tukey tests were conducted on all pairwise contrasts. March and June experiments were analyzed separately. Data were Log_{10} transformed, if necessary, to meet assumption of normality or heterogeneity.

RESULTS

Descriptive Surveys

Surface water temperature at the site ranged from 16.6-28.9°C and surface salinity ranged from 14-26 ppt. Mangrove root densities varied by species and between tidal positions. Mean (\pm SE) black mangrove root densities were significantly higher in low relative to high tidal position, $1411 \pm 63.8 \text{ m}^{-2}$ and $588 \pm 43.5 \text{ m}^{-2}$, respectively (Fig. 5a, One-way ANOVA $F_{1,10} = 113.59$, $P < .0001$). However, no significant difference in red mangrove root densities was observed between low and high tidal positions, $35 \pm 4.8 \text{ m}^{-2}$ and $39 \pm 4.2 \text{ m}^{-2}$ (Fig. 5b, One-way ANOVA $F_{1,10} = 0.606$, $P = 0.479$).

Density of *G. granosissima* varied by tidal position (low, high) and with root type (red vs. black roots). Comparison of mussel densities by tidal elevation across all survey dates indicated that mean (\pm SE) mussel density at the + 0.5 m elevation ($1280.3 \pm 221.9 \text{ m}^{-2}$) was higher than at the + 0.8 m position ($102.4 \pm 16.8 \text{ m}^{-2}$), (Fig. 6, ANOVA $F_{1,21} = 129.25$, $P < 0.001$). Quadrats with black mangrove pneumatophores also contained higher densities of *G. granosissima* than quadrats with red mangrove prop roots, but only at the lower tidal position (Fig. 6, ANOVA $F_{1,21} = 47.341$, $P < 0.001$). All Tukey HSD combinations were found to be significantly different at ($p < 0.05$) with the exception of mussel densities within black and red mangroves at the higher tidal position (Fig. 6). Conversely, at the higher tidal position, densities of mussels co-occurring with

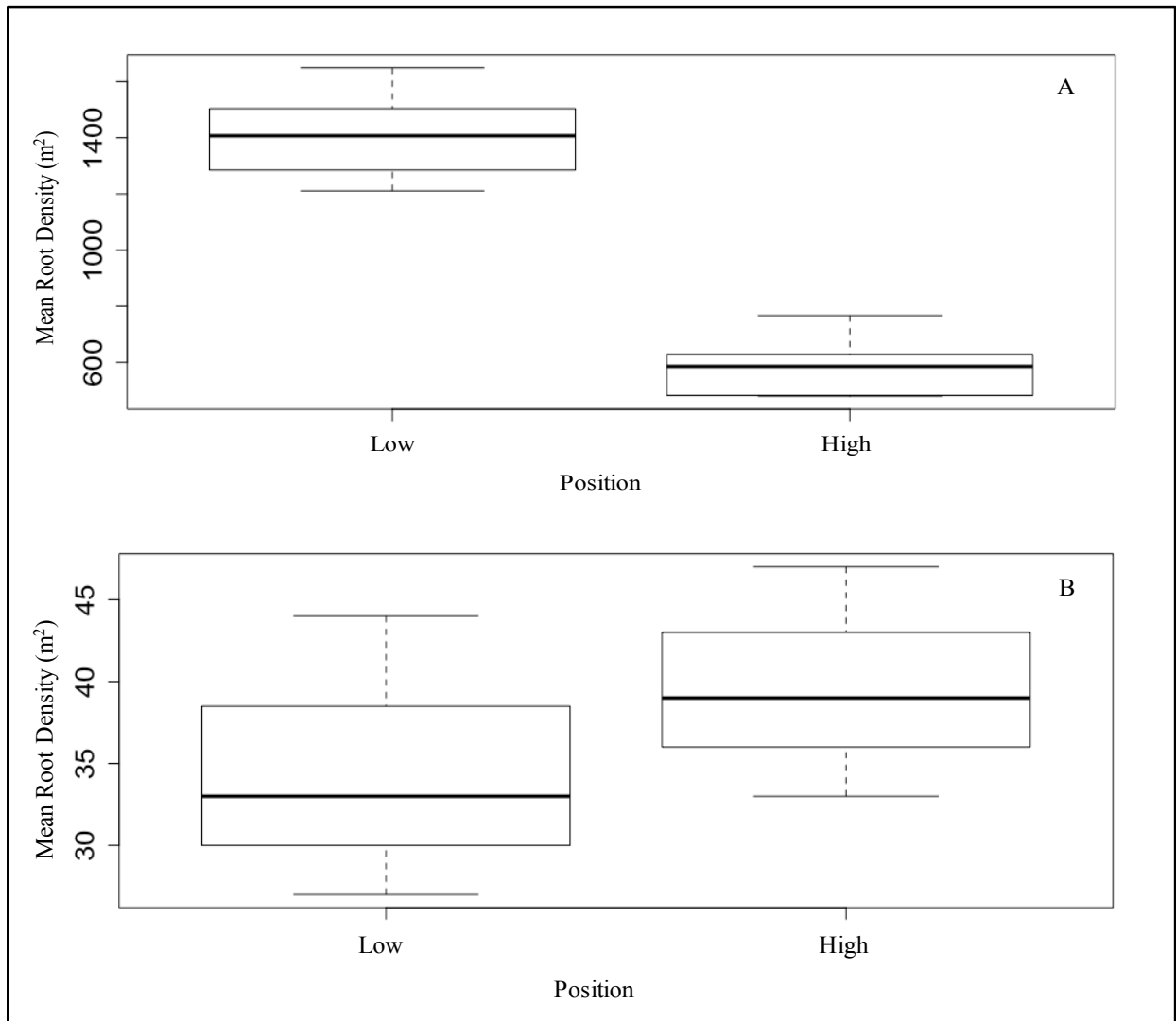


Figure 5 Mean root number m⁻² by tidal elevation Low = +0.5m MLW and High = +0.8m MLW, plot (A) *A. germinans* root density was higher in low position than high position ($F_{1,10} = 113.59$, $P < 0.001$) and (B) no difference in red mangrove root density was indicated between low and high tidal positions ($F_{1,10} = 606$, $P = 0.479$).

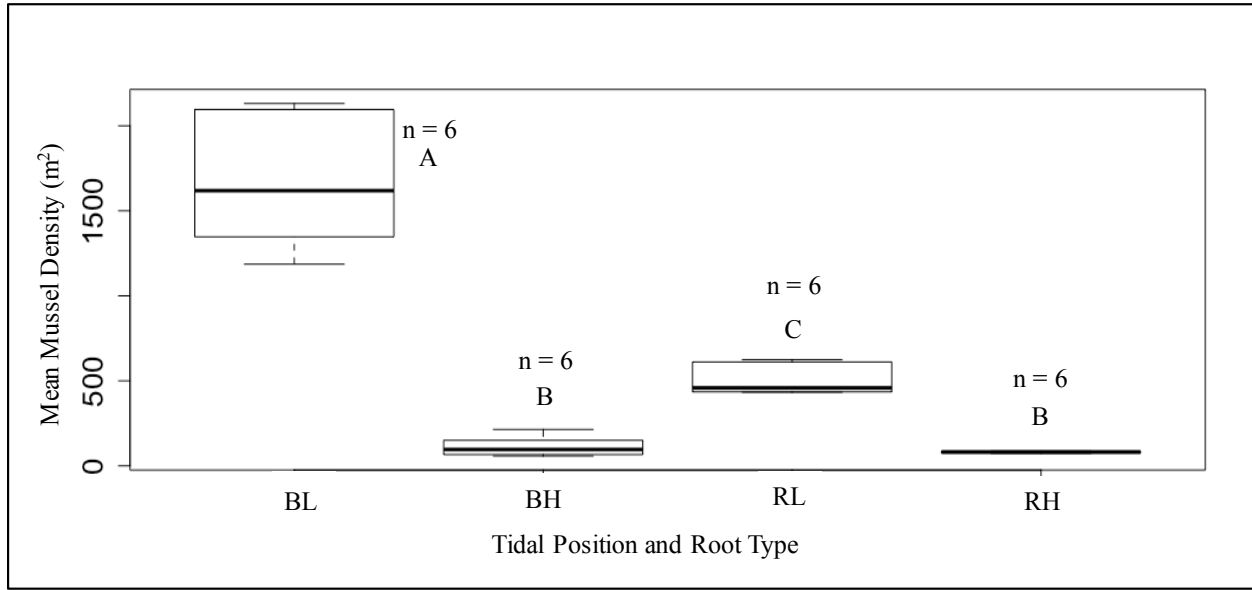


Figure 6 Mean \pm SE of mussel densities ($\#/m^2$) by root type and tidal height ($n = 6$). (BL) black mangrove low tidal position (+0.5m MLW), (BH) black mangrove high tidal position (+0.8m MLW), (RL) red mangrove low position, RH red mangrove high position. Letters denotes Tukey HSD comparison results found to be significantly different ($P < 0.05$).

black mangrove pneumatophores were similar to that found within red mangrove prop roots (Fig. 6, Tukey HSD, $P = 0.993$). Mussel percent cover was significantly higher at high tidal height compared to low (Mann-Whitney $U = 91.5$, $P < 0.001$) with a mean (\pm SE) of percent cover of 20.6 ± 3.78 in lower and 0.52 ± 0.17 in lower and higher tidal positions. Size-structure of the *G. granosissima* population varied with respect to tidal height and mangrove root type. Median mussel shell length for the *G. granosissima* population at the field site was 16.3 mm ($n = 8524$), with a size range of 1.0-63.2 mm. Fifty percent of the mussels were between 10.6 mm and 25.2 mm SL. Median shell length was highest for individuals associated with black mangrove pneumatophores at the +0.8 m tidal position relative to all other root type and position combinations (Fig. 7, Kruskal-Wallis $\chi^2 = 32.78$, $P < 0.001$). Pairwise comparisons using Dunn's-test with Bonferroni corrections for multiple comparisons of independent samples confirmed all other combinations of tidal position (high/low) and mangrove root type (red/black) were not significantly different from one another (Fig. 7).

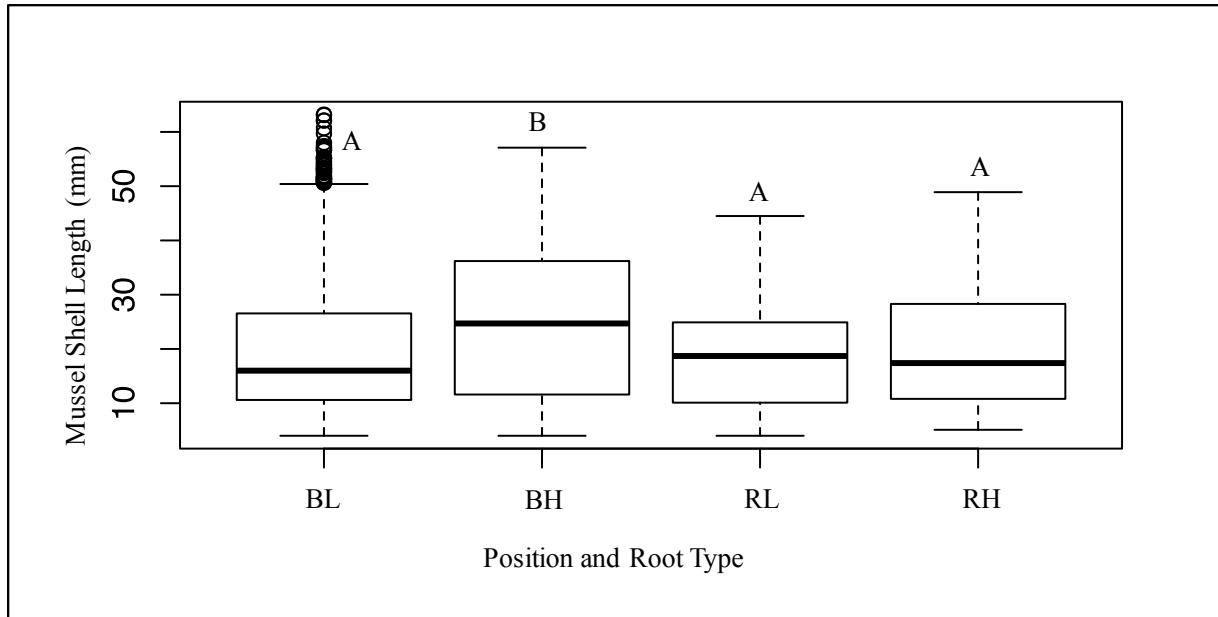


Figure 7. Boxplot of shell length (mm) of *G. granosissima* by mangrove root type and tidal position. (BL) black mangrove low tidal position (+0.5m MLW), (BH) black mangrove high tidal position (+0.8m MLW), (RL) red mangrove low position, RH red mangrove high position. The black line of the boxplot marks the median, with the upper and lower margin of the box indicating the 75th and 25th percentiles respectively; the upper and lower whiskers indicate the 90th and 10th percentiles and black circles indicate outliers. Letters identify those treatments that had similar shell lengths as determined with a multiple comparisons test (Dunn's-test with Bonferroni corrections).

Predator Exclusion Experiments

In both March and June experiments, mussels placed onto mock pneumatophore platforms with predator access (partial and no cages) and in low tidal position were consumed while those inside cages with predators exclude displayed almost complete survivorship. Specifically, mussel survivorship (mean $\# \pm$ SE surviving) was higher inside cages in March (19.9 ± 0.34 , $n = 16$) and June (20 ± 0.00 , $n = 16$) than when predators were allowed access to mussel prey in either month (March: 9.3 ± 6.46 mussels, $n = 16$; June: 8.2 ± 8.37 mussels, $n = 16$). Survivorship of mussels on platforms without cages was lowest at low tidal height (+ 0.4m MLW) in March after 48 h (5.3 ± 6.01 , $n = 8$) and most dramatic at low tidal height during June after 24 h (0.25 ± 0.46 , $n = 8$) (Fig. 8A and 8B). Mussels exhibited intermediate survivorship within partial cage platforms compared to cage and no cage platforms along both tidal positions and deployment dates (Fig. 8A and 8B). In March, a significant effect of cage presence and tidal position on survivorship was detected using logistic regression GLM (Position: $df = 1$, $X^2 = 5.082$, $p = 0.024$), (Cage type: $df = 2$, $X^2 = 16.273$, $p = 2.92e^{-4}$) (Table 1). In June similar outcomes were recorded, with mussel survivorship being affected by tidal position and cage type [(Position: $df = 1$, $X^2 = 14.339$, $p = 1.53e^{-04}$), (Cage type: $df = 2$, $X^2 = 22.42$, $p = 1.354e^{-05}$)] (Table 1). No interaction effect between position and cage type was detected during either of the experimental deployments (Table 1) and no variation between blocks was detected during either March or June deployments.

Table 1 Summary of Logistic GLM Analysis for mussel survivorship March and June predator exclusion experiments for cage (Full cage/Partial cage/No cage), block, and tidal position (n = 8).

	March			June		
	<u>LR Chi-square</u>	<u>Df</u>	<u>Pr (>Chi-square)</u>	<u>LR Chi-square</u>	<u>Df</u>	<u>Pr (>Chi-square)</u>
Position	5.082	1	0.024 *	115.47	1	1.527e ⁻⁰⁴ ***
Cage	16.27	2	2.92e ⁻⁴ ***	180.54	2	1.354e ⁻⁰⁵ ***
Block	0.173	1	0.677	0.061	1	0.9281
Position:Cage	0.067	2	0.966	1.253	2	0.534
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1						

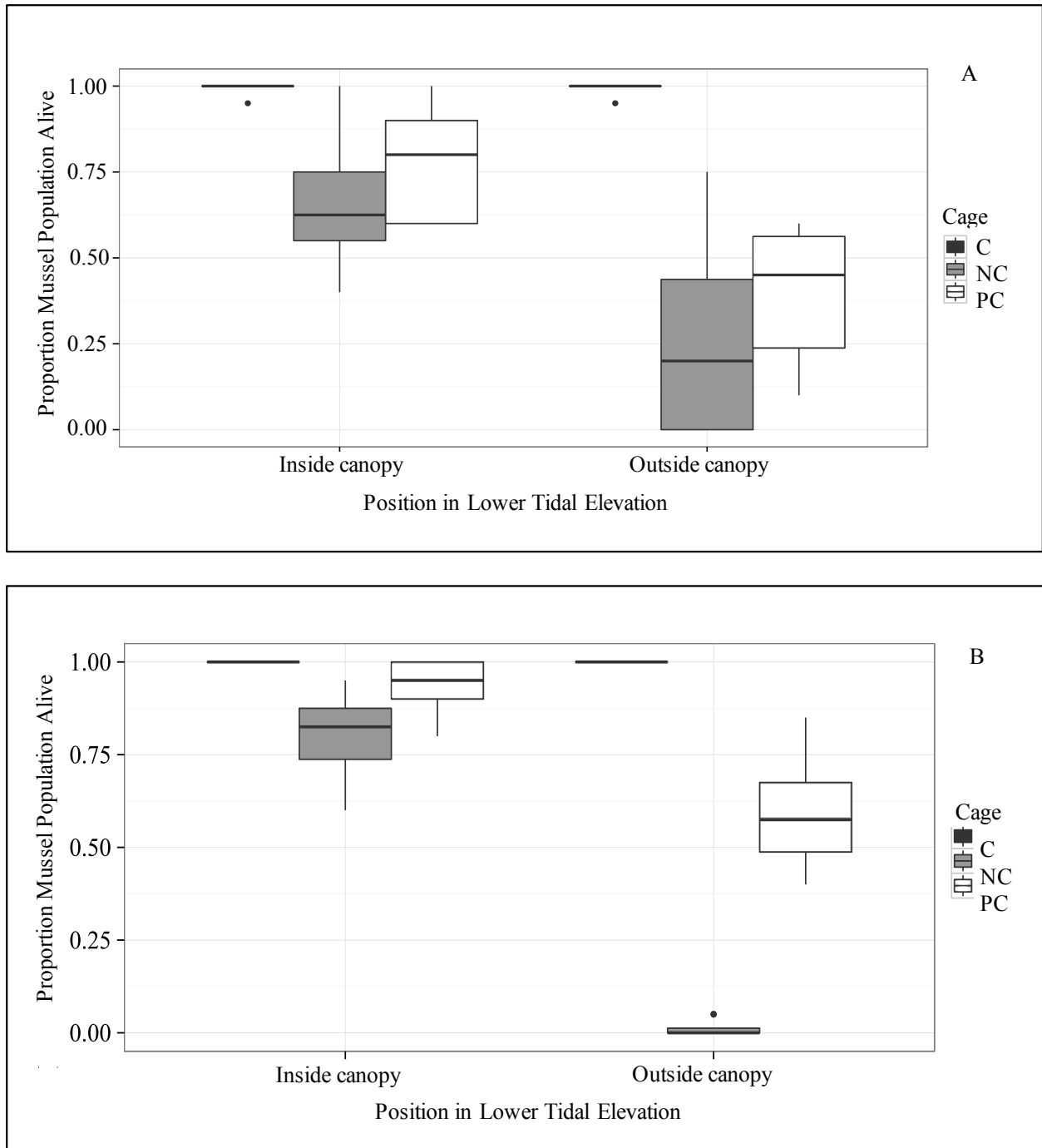


Figure 8. Box plot of proportional survivorship of *G. granosissima* placed on three caging treatments with mock pneumatophore platforms (C = cage, NC = no cage, PC = partial cage) in (A) March 2016 for 48 h and (B) June 2016 for 24 h. Platforms were located in two tidal positions, Inside canopy = +0.5m (n = 8) Outside canopy = +0.4m (n = 8) above MLW.

DISCUSSION

Tidal distributions of *G. granosissima*, the southern ribbed mussel, extended from +0.5m MLW to +0.8m MLW in a mixed mangrove stand in Tampa Bay, FL. The upper boundary limit of this population coincides with the mean high tide at this location suggesting tidal limitation (i.e., desiccation) helps shape the upper limit distribution of this population as has been commonly reported for other intertidal organisms (e.g. Connell, 1972; Davenport and Davenport, 2005; Somero, 2002). Intertidal organisms are specially adapted to exploit the relatively extreme and constantly shifting conditions of the marine/terrestrial interface and mussels possess biochemical, physiological, and behavioral adaptations to cope with such environmental gradients (Buckley *et al.*, 2001; Evans and Somero, 2010; Jokumsen and Fyhn, 1982). Mussels may also exhibit behavioral responses to physical stressors during times of emersion by closing their valves to reduce desiccation or by opening (air-gaping) to reduce internal temperature (Shick *et al.*, 1986). Air-gaping behavior may also enhance respiratory function through increasing gas exchange (Lent, 1969). The relative role of these biological and behavioral adaptations in mussels inhabiting the mangrove setting has yet to be explored.

Mussel size distribution was similar between red and black mangroves at the lower tidal height, but mean size distribution was skewed to larger values within black mangroves located in the higher tidal position. The variation in mean mussel size distribution may be due to the limited number of 5.1-20.0 mm mussels surveyed within those quadrats. The absence of 5.1-20.0 mm

mussels located within the black mangroves in the high tidal position may be related to the difference in amount of accumulated fine grain sediments between low and high tidal heights in this location. At the field site, the depth of fine-grained sediments increased with increasing tidal height and accumulation of silt-clay within pneumatophores was readily noticeable. As tides rise through the mangroves, substrate and root friction allows flocs to be deposited and fine-grain sedimentation to occur (Adame *et al.*, 2010). With increased depth of fine sediments, the distance that mussels must burrow to find attachment sites increases. Therefore, small sized mussels maybe completely buried upon attaching to mangrove roots with a few individuals finding refuge from burial. Such accumulation of fine-grain sediment is not frequently recorded at either tidal height with red mangrove prop roots possibly because prop roots are an order of magnitude lower in density than that of black mangrove roots.

Although mussel size distribution was similar between red and black mangroves at the lower tidal level, the density of mussels along the lower tidal height was remarkably higher within areas containing black mangrove pneumatophores compared to areas with red mangrove prop roots located at the same tidal elevation. Mussel densities may be influenced by differences between subsurface attachment substrates provided by black and red mangrove taxa. Red mangrove prop roots produce a pattern of subterranean lateral roots branching at 45° angles and small absorptive roots branching off of lateral roots (Gill and Tomlinson, 1977). The sub-sediment branching is similar in shape to a tapered cone with the point facing downward. In contrast, black mangroves produce horizontal cable roots that stem outward from the trunk with negatively geotropic pneumatophores and absorptive roots growing out from both cable roots and pneumatophores (Mckee *et al.*, 1988). These differences in root growth forms become important when attachment behaviors of *G. granosissima* are considered, specifically, the

behavior of adult mussels' partially submerging themselves into the sediment (Lin, 1991) and attaching their byssal threads to the sub-sediment absorptive roots of the mangroves. Given the typical size range of mussels found at the field site, their attachment is loosely restricted to roots found in the top <1-3cm of sediments. The shallow growth pattern of black mangrove roots combined with the high densities of pneumatophores of black mangrove likely offer more attachment sites for mussels than red mangrove prop roots. If so, then these features of below ground structure may play a previously unreported role in controlling mussel abundances in mangrove habitats.

Mussel density and percent cover were higher along the lower tidal limit compared to that of the higher tidal limit. This disparity is not likely due to lack of suitable substrate for mussel attachment, which was observed to be abundant during the percent cover survey. Specifically, mussel coverage was 40x higher in lower than higher tidal elevations but red mangrove root densities did not vary between tidal heights (Figure 5). Black mangrove root densities were in fact 3x greater in low tidal position versus high. However, mussel density reflects mussels attached to roots as well as mussels attached to other individuals. Thus, the pattern of decreasing mussel density with increasing tidal height may also reflect preferential larval recruitment onto conspecifics (Neilson and Franz, 1995) at lower tidal elevations rather than lack of usable substrate at high tidal elevations. However, Porri *et al.* (2008) suggests that fine-scale spatial and hydrodynamics factors influence larval settlement of the mussel, *Perna perna* more than larva conspecific preference, which could also be true for *G. granosissima* at this site. Therefore, further analysis of site-specific hydrodynamic regimes may be essential for accurately determining the underlying mechanisms influencing population size and distribution of mussels at lower tidal elevations.

In addition to belowground root morphology and mussel behavior, larval supply and settlement may also influence mussel density differences in the red and black mangroves. Added complexity provided by *A. germinans* pneumatophores could create additional turbulent flow and reduce tidal velocities compared to that associated with *R. mangle*. A reduction of the boundary layer due to an increase in turbulence could result in increased settlement (Butman *et al.*, 1994; Harvey *et al.* 1995; Nowell and Jumars, 1984). Due to the high density of above sediment structure black mangrove pneumatophores may provide hydrodynamic conditions conducive to starting and maintaining mussel aggregations, which ranged from 3-4 cm² to 1-3 m² across the site. The dense patches of mussels found among the black mangrove roots may offer interesting opportunities to explore the benefits of aggregation in an entirely new setting.

The variation of mussel densities between red and black mangrove root types could also be a function of patch/aggregation size and positive feedback mechanisms (Hunt & Scheibling, 2001; Koppel *et al.*, 2005). Mussel aggregations with a patch size exceeding 30cm x 30cm were only associated with black mangroves at the lower tidal position at the study site (Hudson, pers. observ.). This is important given that size of aggregations is thought to play an important, but complex, role in individual mussel survivorship (Okamura, 1986). More specifically, many of the positive and negative effects associated with group living for mussels are based on two factors: 1) the size of the aggregation; and 2) the location of a mussel within a patch (interior vs. edge). Mussels within aggregations are suggested to be provided protection from predators, wave dislodgement, ice scour, and desiccation (Bertness and Grosholz, 1985; Koppel *et al.*, 2005; Nicastro *et al.*, 2012; Okamura, 1986). Secondarily, mussels within interior locations may gain increased reproductive success and larval settlement (Koppel *et al.*, 2005; Okamura, 1986).

The benefits of group living as aggregation come at the cost of resource competition (e.g., food, space), which leads to reduced growth and reduced reproductive output (Hunt & Scheibling, 2001; Okamura, 1986). Thus, the cost/benefit of aggregation maybe spatially dependent, as well. Specifically, mussels at the edge of an aggregation do not receive the same protection from predators or susceptibility to dislodgment as mussels located in the interior of aggregations; however, they do not show signs of reduced growth experienced by interior mussels (Hunt & Scheibling, 2001; Okamura, 1986). Interestingly, an increase of surface heterogeneity of mussel aggregations may positively influence feeding rates (Butman *et al.*, 1994; Nowell and Jumans, 1984) and larval settlement (Harvey *et al.*, 1995) by altering small-scale hydrodynamics, which results in increased access to plankton and larvae.

In both March and June experiments, mean (\pm SE) of percent cover of 46.5 ± 0.11 proportion survive in March and 40.9 ± 0.10 in June of mussels outside of cages were consumed while those inside cages had almost complete survivorship. During both experiments, more mussels were consumed outside of cages at the outside canopy (March = 73.75%, June = 98.75%) compared to the inside canopy at higher position platforms (March = 33.12%, June = 19.37%). These trends were more pronounced in June compared to March (Fig. 8). Not only was mussel survivorship reduced outside of cages in June compared to March but mussel loss occurred more rapidly as well (24 versus 48 h). Clearly the presence of a cage increased mussel survivorship, likely due to predator exclusion. Also, the overall pattern of the no cage platforms having lowest survivorship, partial cage platforms having intermediate survivorship, and full cage platforms having highest survivorship was consistent across all tidal positions and dates. Combined these results suggest that predation may strongly influence the lower limit tidal

distribution of this *G. granosissima* population and may explain why comparatively higher numbers of mussels are formed at the edge of the mangrove canopy.

Although the identity of predators which consumed mussels was not directly evaluated in the study, numerous crushed and broken mussel valves were observed on the platforms, suggesting probable predation by the fish, *Archosargus probatocephalus* (Sheepshead) which has been demonstrated to consume *G. granosissima* in Tampa Bay (Fernandez and Motta, 1997) and *Callinectes sapidus* (Blue crab), which is common in Tampa Bay and a major predator of *G. demissa* (Bertness and Grosholz, 1985; Stiven and Gardner, 1992). Although effects of predator exclusion were detected on both experimental dates, a greater than 50% difference in mean mussel survivorship between the partial cage and the no cage platforms in the lower tidal position treatment was recorded in the June experiment. Such variation in survivorship between partial cage and no cage platforms may have been the result of different predator activity and/or larger-sizes of similar predators being present during June compared to March. In a laboratory feeding experiment, Seed (1982) demonstrated that larger Blue Crabs ate more of the mussel, *G. demissa*, per unit time than small crabs. Likewise, different predators (e.g., Sheepshead), which could exhibit different feeding strategies, may also have been active at the study site during either of the experiments. Overall while predation on mussels was consistently detected, differently- sized predators or variation in the composition of predators utilizing the mangrove setting may have exerted differential predator pressures on the mussel population on the two experimental dates.

During this study, I did not survey *G. granosissima* in mangrove stands outside of the study location nor exhaustively search for them. However, isolated mussel patches and singletons were sighted throughout Tampa Bay but the patches observed elsewhere were smaller

than those found at the study site where black mangroves are located at the lower fringe of the forest distribution and oyster (*Crassostrea virginica*) are rarely found on prop roots. In the Caribbean and Florida, mangrove communities generally follow a tidal gradient pattern of red mangroves (*R. mangle*) at the fringe, then black mangroves (*A. germinans*) at the mid to upper intertidal, and finally white mangroves (*Laguncularia racemosa*) occupying the upper intertidal (Lugo and Snedaker, 1974). Within this study site, the forest edge is located at mid intertidal height with red and black mangroves intermixed. The intermixing of red and black mangrove with the mangrove fringe being located at mid intertidal height may have reduced oyster attachment to the prop roots within the study site. Importantly, the absence *C. virginica* may remove an important barrier to larvae access by *G. granosissima* to the mid to upper intertidal zone. It has been well documented that filter-feeding invertebrates heavily prey upon pelagic larvae (Lehane and Davenport, 2004; Tamburri and Zimmer-Faust, 1996; Troost *et al.*, 2008). While these site characteristics are not unique, they do suggest features of the mangrove forest and vegetation where other associated *G. granosissima* populations may occur in high densities.

This study adds to the body of literature determining factors that shape intertidal mussel communities by extending investigations to a previously unknown setting. This study also expands documentation of *G. granosissima* in the Gulf of Mexico, representing the first documentation of the mussel within the mangrove habitat. Through utilization of both descriptive and experimental study designs, I determined factors which may possibly shape the lower tidal distribution of this population of *G. granosissima* as similarly reported for other intertidal sessile marine organisms (Connell, 1972; Davenport and Davenport, 2005; Somero, 2002). Likewise, I demonstrated the strong association between mangrove roots and mussels especially *G. granosissima* and *A. germinans* pneumatophores.

REFERENCES

- Adame, M. F., D. Neil, S. F. Wright, and C. E. Lovelock. 2010. Sedimentation within and among mangrove forests along a gradient of geomorphological settings. *Estuarine, Coastal and Shelf Science* **86**:21-30.
- Alan, E. S. and A. G. Sue. 1992. Population processes in the ribbed mussel *Geukensia demissa* (Dillwyn) in a North Carolina salt marsh tidal gradient: spatial pattern, predation, growth and mortality. *Journal of Experimental Marine Biology and Ecology* **160**:81-102.
- Bacon, P. R. 1975. Shell form, byssal development and habitat of *Mytella guyanensis* (Lamarck) and *M. falcata* (Orbigny) (Pelecypoda: Mytilidae) in Trinidad, West Indies. *Journal of Molluscan Studies* **41**:511-520.
- Bertness, M. D. 1984. Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. *Ecology* **65**:1794-1807.
- Bertness, M. D. and E. Grosholz. 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: The costs and benefits of an aggregated distribution. *Oecologia* **67**:192-204.
- Bertness, M. D. and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* **9**:191-193.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* **18**:119-125.
- Buckley, B. A., M. E. Owen, and G. E. Hofmann. 2001. Adjusting the thermostat: the threshold induction temperature for the heat-shock response in intertidal mussels (genus *Mytilus*) changes as a function of thermal history. *Journal of Experimental Biology* **204**:3571-3579.
- Butman, C. A., M. Frechette, W. R. Geyer, and V. R. Starczak. 1994. Flume experiments on food supply to the blue mussel *Mytilus edulis* L. as a function of boundary-layer flow. *Limnology and Oceanography* **39**:1755-1768.
- Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington.

- Commito, J. A., A. E. Commito, R. V. Platt, B. M. Grupe, W. E. D. Piniak, N. J. Gownaris, K. A. Reeves, and A. M. Vissichelli. 2014. Recruitment facilitation and spatial pattern formation in soft-bottom mussel beds. *Ecosphere* **5**:1-26
- Commito, J. A., N. J. Gownaris, D. E. Haulsee, S. E. Coleman, and B. F. Beal. 2016. Separation anxiety: mussels self-organize into similar power-law clusters regardless of predation threat cues. *Marine Ecology Progress Series* **547**:107-119.
- Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. *Annual review of ecology and systematics* **1**:169-192
- Davenport, J. and J. L. Davenport. 2005. Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna. *Marine Ecology Progress Series* **292**:41-50.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*:351-389.
- Evans, T. G. and G. N. Somero. 2010. Phosphorylation events catalyzed by major cell signaling proteins differ in response to thermal and osmotic stress among native (*Mytilus californianus* and *Mytilus trossulus*) and invasive (*Mytilus galloprovincialis*) species of mussels. *Physiological and Biochemical Zoology* **83**:984-996.
- Fernandez, L. and P. Motta. 1997. Trophic consequences of differential performance: Ontogeny of oral jaw-crushing performance in the sheepshead, *Archosargus probatocephalus* (Teleostei, Sparidae). *Journal of Zoology* **243**:737-756
- Franz, D. R. 2001. Recruitment, survivorship, and age structure of a New York ribbed mussel population (*Geukensia demissa*) in relation to shore level a nine year study. *Estuaries* **24**:319-327.
- Gill, A. and P. B. Tomlinson. 1977. Studies on the growth of red mangrove (*Rhizophora mangle* L.) 4. The adult root system. *Biotropica* **9**:145-155.
- Harley, C. D. and B. S. Helmuth. 2003. Local-and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnology and Oceanography* **48**:1498-1508.
- Harvey, M., E. Bourget, and R. G. Ingram. 1995. Experimental evidence of passive accumulation of marine bivalve larvae on filamentous epibenthic structures. *Limnology and Oceanography* **40**:94-104.
- Hilbish, T. J. 1987. Response of aquatic and aerial metabolic rates in the ribbed mussel *Geukensia demissa* (Dillwyn) to acute and prolonged changes in temperature. *Journal of Experimental Marine Biology and Ecology* **105**:207-218.

- Honig, A., J. Supan, and M. L. Peyre. 2015. Population ecology of the gulf ribbed mussel across a salinity gradient: recruitment, growth and density. *Ecosphere* **6**:1-13.
- Hunt, H. L. and R. E. Scheibling. 2001. Patch dynamics of mussels on rocky shores: integrating process to understand pattern. *Ecology* **82**:3213-3231.
- Jager, M., F. J. Weissing, P. M. Herman, B. A. Nolet, and J. van de Koppel. 2011. Lévy walks evolve through interaction between movement and environmental complexity. *Science* **332**:1551-1553.
- Jokumsen, A. and H. J. Fyhn. 1982. The influence of aerial exposure upon respiratory and osmotic properties of haemolymph from two intertidal mussels, *Mytilus edulis* L. and *Modiolus modiolus* L. *Journal of Experimental Marine Biology and Ecology* **61**:189-203.
- Jost, J. and B. Helmuth. 2007. Morphological and ecological determinants of body temperature of *Geukensia demissa*, the Atlantic ribbed mussel, and their effects on mussel mortality. *The Biological Bulletin* **213**:141-151.
- Koppel, J., M. Rietkerk, N. Dankers, and P. M. Herman. 2005. Scale-dependent feedback and regular spatial patterns in young mussel beds. *The American Naturalist* **165**:E66-E77.
- Koppel, J., J. C. Gascoigne, G. Theraulaz, M. Rietkerk, W. M. Mooij, and P. M. Herman. 2008. Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems. *Science* **322**:739-742.
- Lehane, C. and J. Davenport. 2004. Ingestion of bivalve larvae by *Mytilus edulis*: experimental and field demonstrations of larviphagy in farmed blue mussels. *Marine Biology* **145**:101-107.
- Lent, C. M. 1969. Adaptations of the ribbed mussel, *Modiolus demissus* (Dillwyn), to the intertidal habitat. *American Zoologist* **9**:283-292.
- Lin, J. 1991. Predator-prey interactions between blue crabs and ribbed mussels living in clumps. *Estuarine, Coastal and Shelf Science* **32**:61-69.
- Liu, Q.-X., E. J. Weerman, P. M. Herman, H. Olf, and J. van de Koppel. 2012. Alternative mechanisms alter the emergent properties of self-organization in mussel beds. *Proceedings of The Royal Society B*. **279**:2744-2753.
- Lugo, A. E. and S. C. Snedaker. 1974. The ecology of mangroves. *Annual review of ecology and systematics* **5**:39-64.
- McKee, K. L., I. A. Mendelssohn, and M. W. Hester. 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *American Journal of Botany* **75**:1352-1359.

- Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* **46**:355-393.
- Montagna, P. A., E. D. Estevez, T. A. Palmer, and M. S. Flannery. 2008. Meta-analysis of the relationship between salinity and molluscs in tidal river estuaries of southwest Florida, USA. *American Malacological Bulletin* **24**:101-115.
- Neufeld, D. and S. Wright. 1998. Effect of cyclical salinity changes on cell volume and function in *Geukensia demissa* gills. *Journal of Experimental Biology* **201**:1421-1431.
- Nicastro, K. R., G. I. Zardi, C. D. McQuaid, G. A. Pearson, and E. A. Serrão. 2012. Love thy neighbour: group properties of gaping behavior in mussel aggregations. *PloS one* **7**:e47382.
- Nielsen, K. J. and D. R. Franz. 1995. The influence of adult conspecifics and shore level on recruitment of the ribbed mussel *Geukensia demissa* (Dillwyn). *Journal of Experimental Marine Biology and Ecology* **188**:89-98.
- NOAA. 2016. Tides and currents, Old Port Tampa station, Tampa, Florida (station 8726607). <https://co-ops.nos.noaa.gov/stationhome.html?id=8726607> . Accessed July 2016
- Nowell, A. and P. Jumars. 1984. Flow environments of aquatic benthos. *Annual review of ecology and systematics* **15**:303-328.
- Okamura, B. 1986. Group living and the effects of spatial position in aggregations of *Mytilus edulis*. *Oecologia* **69**:341-347.
- Paine, R. 1974. Intertidal community structure. *Oecologia* **15**:93-120.
- Paine, R. 1976. Size-limited predation: an observation and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* **57**:858-873
- Pennington, J. T. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. *The Biological Bulletin* **169**:417-430.
- Porri, F., C. McQuaid, S. Lawrie, and S. Antrobus. 2008. Fine-scale spatial and temporal variation in settlement of the intertidal mussel *Perna perna* indicates differential hydrodynamic delivery of larvae to the shore. *Journal of Experimental Marine Biology and Ecology* **367**:213-218.
- Rilov, G. and D. R. Schiel. 2006. Seascape-dependent subtidal-intertidal trophic linkages. *Ecology* **87**:731-744.

- Romero, J., Severeyn, H., Ramírez, Y., Chavez, R. y López, M. 2002. *Geukensia demissa* (Dillwyn, 1817) (Bivalvia: Mytilidae), nuevo género y especie de mejillón para Venezuela y el Caribe. Bol. Cent. Invest. Biol. **36**: 231–243.
- Sarver, S., M. Landrum, and D. Foltz. 1992. Genetics and taxonomy of ribbed mussels (*Geukensia* spp.). Marine Biology **113**:385-390.
- Seed, R. 1980. Predator-prey relationships between the mud crab *Panopeus herbstii*, the blue crab, *Callinectes sapidus* and the Atlantic ribbed mussel *Geukensia* (= *Modiolus*) *demissa*. Estuarine and Coastal Marine Science **11**:445-458.
- Shick, J., E. Gnaiger, J. Widdows, B. Bayne, and A. De Zwaan. 1986. Activity and metabolism in the mussel *Mytilus edulis* L. during intertidal hypoxia and aerobic recovery. Physiological zoology **1**:627-642.