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Incorporating Life Into Living Shorelines: Can Gulf Ribbed Mussels Reduce Shoreline Erosion and Enhance Restoration Practices?

Jordan Logarbo
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INCORPORATING LIFE INTO LIVING SHORELINES: CAN GULF RIBBED MUSSELS REDUCE SHORELINE EROSION AND ENHANCE RESTORATION PRACTICES?

A Thesis

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Master of Science

in

The School of Renewable Natural Resources

by

Jordan Rita Logarbo
B.S., Nicholls State University, 2017
August 2021
No matter the successes of those around you. You will still bloom in the way you were meant to.
– Morgan Harper Nichols, quote from “Blooming”

If you want to get warm you must stand near the fire-- if you want to be wet you must get into the water. If you want joy, power, peace, eternal life, you must get close to or even into, the thing that has them.
– C. S. Lewis, “Nearer”

Just like moons and like suns,
With the certainty of tides,
Just like hopes springing high,
Still I'll rise.
– Maya Angelou, excerpt from “Still I Rise”

It is possible to commit no mistakes and still lose. That is not a weakness; that is life.
– Cpt Jean-Luc Picard

"We must remember three things," he said to them. "I will tell them to you in the order of their importance. Number one and first in importance, we must have as much fun as we can with what we have. Number two, we must eat as well as we can, because if we don't we won't have the health and strength to have as much fun as we might. And number three and third and last in importance, we must keep the house reasonably in order, wash the dishes, and such things. But we will not let the last interfere with the other two."
- John Steinbeck, quote from The Log from the Sea of Cortez

“We can be truly successful only at something we’re willing to fail at. If we’re unwilling to fail, then we’re unwilling to succeed.” - Mark Manson, quote from The Subtle Art of Not Giving a F*ck: A Counterintuitive Approach to Living a Good Life
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ABSTRACT

The gulf ribbed mussel (Geukensia granosissima) exists throughout the Gulf of Mexico and influences biotic and abiotic environmental attributes as an ecosystem engineer. Ribbed mussels are an important component of marsh ecosystems providing services including filtering particulate matter, depositing and transforming nutrients in the system, increasing soil strength via byssal threads and providing structure via their shells.

The spatial distribution of mussels along the marsh edge of Sister Lake, LA was investigated via a broad survey of 150 sites, in relation to elevation, exposure and vegetation percent cover. This survey was followed by a second survey at a subset of 21 focal sites exploring mussel density, vegetation and soil characteristics associations. Of the 150 sites surveyed, gulf ribbed mussels were present at 46% of the sites, and where present, surface density ranged up to 350 mussels m$^{-2}$ with the highest density (mean ± standard error, 34.9 ± 62.9 m$^{-2}$) and presence (64%) on the north shore, and lower densities and presence along the south (1.8 ± 4.8 m$^{-2}$ and 38%) and west (3.7 ± 7.6 m$^{-2}$ and 36%) shorelines. For both likelihood of mussel presence and density across all sites, total percent vegetation cover was the only significant predictive variable retained in models. Total percent vegetation cover was lower at south and west shorelines (south: 42.8 ± 2.0 %; west: 30.7 ± 2.3%), compared to north (47.8 ± 2.6%), with Juncus roemerianus percent cover following this pattern (south: 2.2 ± 0.9 %; west:10.9 ± 2.2%; north: 16.1 ± 3.0%). Exposure and elevation parameters showed no statistical significance but trended towards the north shoreline having the lowest relative elevation and the highest relative shoreline exposure, consistent with higher inundation, compared to the south and west shorelines. At the 21 focal sites, mussel density ranged from 0 to 400 mussels m$^{-2}$. Overall, mussel density decreased with increased soil water content, and increased with total live belowground biomass. These surveys characterize G. granosissima distribution and habitat associations, providing insight to inform future studies, including examining more specifically, the potential role of G. granosissima in marsh production, and shoreline stabilization.

In a separate study, survivorship and movement of G. granosissima was explored in a marsh located near Cocodrie, Louisiana. 1,375 mussels were transplanted into five replicate blocks of 4 density treatments (0, 50, 100, or 400 mussels m$^{-2}$) along a 75 m Spartina alterniflora marsh shoreline. Treatments were applied to the front half of each 1 m$^{2}$ plot with all mussels cleared in the back half. The plots were monitored for one year, and final mussel density and location (front, back) were examined. Total mussel density decreased on average by 50.1 ± 16.1% regardless of initial density, with greater survival in, and redistribution to, more protected inland locations with higher stem densities (i.e., back plots, protected shoreline areas).

These studies demonstrate that gulf ribbed mussels are ubiquitous in coastal Louisiana marshes, can be found in high densities, and are able to be successfully transplanted. Important environmental variables characterizing mussel habitat was explored to determine where transplantations could best occur in the marsh. Together, these studies suggest gulf ribbed mussels may play a vital role in the marsh ecosystem, and this better understanding of their preferred environment means they may be viable for potential use in future coastal restoration efforts.
CHAPTER 1. INTRODUCTION

Coastal wetlands provide many services including storm protection, nutrient cycling, fisheries production, and long-term carbon storage. Forty percent of the United States coastal and estuarine wetlands are in Louisiana (Williams, 1997). Louisiana’s coast is rapidly disappearing as are many coastal ecosystems worldwide (Lotze et al., 2006). Between 1932 and 2010 over 4,875 km$^2$ (~14%) of these wetlands were lost, likely from multiple natural and anthropogenic stressors (Boesch et al., 1994; Williams et al., 1997; Couvillion et al., 2011). Anthropogenic as well as natural stressors, including sea level rise, severe storms, and eutrophication are increasing this loss of coastal and estuarine habitat (Boesch et al., 1994; Williams et al., 1997; Couvillion et al., 2011). Louisiana coastal wetlands face high subsidence rates (Blum & Roberts, 2009), altered salinity attributed to sea level rise and freshwater discharge from the Mississippi River (Roy et al., 2013; Day & Templet, 1989), and land loss due to shoreline erosion (Boesch et al., 1994; List et al., 1997) among a multitude of changes.

Ecosystem engineers modify, maintain, and create habitats by modulating the availability of resources to other species, thereby exerting a large influence over local abiotic conditions (Jones et al., 1994). Autogenic engineers are able to change their environments through use of their own physical structures and allogenic engineers are able to transform biotic or abiotic materials in their environments (Jones et al., 1994). Because of these potentially large impacts, ecosystem engineers have been used in ecological restoration efforts (Byers et al., 2006). For example, along the Atlantic and Gulf coasts, the native ecosystem engineer, Spartina alterniflora, is often used in marsh restoration and creation plantings since it is the dominant vegetation type in coastal marshes. While S. alterniflora has been used extensively in coastal restoration, few other species identified as potential ecosystem engineers have yet to be explored for use in coastal restoration such as in living shoreline projects. Further, interactions between ecosystem engineers have rarely been explored, yet positive interactions between ecosystem engineers offer the potential to increase coastal resilience.

One example involving interactions of two ecosystem engineers include S. alterniflora and the Atlantic ribbed mussel, Geukensia demissa. Their combined interactions have been shown to increase and enhance marsh productivity and stabilization from drought and salinity stress (Bertness, 1984; Angelini et al., 2016). Because S. alterniflora modifies its environment through its above- and belowground structures there is a reduction in water velocity caused by the shoots (Knuston et al., 1982) and increases in sediment accretion rates caused by its roots (Gleason et al., 1979; Leonard & Luther, 1995; Christiansen et al., 2000). S. alterniflora also provides increased aeration into the sediment through its extensive root system (Arenovski & Howes, 1992) as well as providing areas for attachment for sessile organisms, including G. demissa (Altieri et al., 2007). G. demissa change their environments through use of their byssal threads that attach to nearby shells and belowground plant biomass contributing to soil strength and erosion mitigation (Bertness, 1984; Franz, 1997). Additionally, G. demissa modify nutrients in their environment through filtering in the water column and transforming nutrients into more bioavailable forms easier for plant uptake, which increases plant productivity (Jordan & Valiela, 1982; Bertness, 1984; Huang & Newell, 2002). G. demissa filter feeding affects the flow of materials through accumulation and biodeposition of nutrient rich feces and pseudofeces (Jordan & Valiela, 1982). G. demissa shell structure also provides additional habitat structure along with S. alterniflora belowground biomass (Gutiérrez & Iribarne, 1999; Lenihan, 1999).
In Louisiana saltmarshes, *S. alterniflora* and the gulf ribbed mussel *Geukensia granosissima* are coexisting ecosystem engineers that may form a mutualistic relationship that could enhance marsh stability and living shoreline restoration efforts. Although *G. granosissima* may play a similar role along the Gulf coast as *G. demissa* does on the Atlantic coast, studies similar to those conducted along the Atlantic coast for *G. demissa* are lacking for *G. granosissima* along the Gulf coast. Current shoreline protection efforts in the Gulf of Mexico have mostly relied on non-living materials such as stone revetments, bulkheads and seawalls. While these protect the shoreline adjacent to them, they often promote loss of sediment, increase vertical erosion and erosion of flanking shores (Douglass & Pickel, 1999; Campbell et al., 2005). Given the dynamic nature of estuarine ecosystems, long-term shoreline stabilization and sustainability efforts need to be prioritized. Future restoration efforts using a multifaceted approach of targeting the restoration and recovery of native plant communities while maximizing sediment retention and accretion, stabilizing the shorelines, and enhancing ecosystem services that coastal wetlands contribute could provide benefits to coastal Louisiana. *S. alterniflora* and *G. granosissima* provide a potential natural partnership for use in mitigating shoreline loss and enhancing marsh resiliency and productivity in the face of increasing natural and anthropogenic stressors. This work seeks to better understand the distribution, and habitat associations of *G. granosissima* in coastal Louisiana through a set of two studies.

Chapter 2 investigates the spatial distribution of gulf ribbed mussels along the marsh edge of Sister Lake, Louisiana via a broad survey of 150 sites, in relation to elevation, exposure and vegetation cover. A second survey at a subset of 21 focal sites explores mussel density, vegetation and soil characteristics associations with gulf ribbed mussel density. This two-phase approach gives quantitative insight into the distribution of gulf ribbed mussels around the fringing marsh edge of Sister Lake by examining vegetation characteristics, extractable nutrients, and sediment shear strength associated with gulf ribbed mussel presence and density.

Chapter 3 examines the survivorship and displacement of transplanted *G. granosissima* along a *S. alterniflora* dominated shoreline in Cocodrie, Louisiana. In this study, 1,375 mussels were transplanted into five replicate blocks of 4 density treatments (0, 50, 100, or 400 mussels m$^{-2}$) along a 75 m *Spartina alterniflora* marsh shoreline. This study evaluates the gulf ribbed mussel’s potential for use in living shoreline projects through a quantitative before and after transplant analysis along with one year of monitoring.

Combined, this work examines whether the mutualism between the *G. granosissima* and *S. alterniflora* has potential to aid in coastal restoration efforts in coastal Louisiana. The use of gulf ribbed mussels and *S. alterniflora* could provide an additional restoration tool in living shoreline projects in coastal Louisiana and contribute to coastal protection. By taking an ecosystems ecology approach to understanding the relationship between *G. granosissima* and *S. alterniflora*, I address the important questions where and at what densities are mussels found and are they able to survive large-scale transplantations? These answers can be readily applied to active and future living shoreline projects in coastal Louisiana.
CHAPTER 2. DEMOGRAPHIC SURVEY OF THE SPATIAL DISTRIBUTION AND HABITAT ASSOCIATION OF GULF RIBBED MUSSELS IN SOUTHEAST LOUISIANA SALT MARSHES

2.1. Introduction

Ribbed mussels (Geukensia spp.) exist in marshes along the Atlantic and Gulf of Mexico coasts from eastern Canada to the Yucatán and have been introduced in California and South America (Abbot, 1974; Carlton, 1992; Torchin et al., 2005). Ribbed mussels settle on hard substrate such as oyster reefs, man-made structures or marsh cordgrass (Spartina alterniflora), as well as Juncus roemerianus and other similar vegetation roots or shoots (Bertness & Grosholz, 1985; Waite et al., 1989; Coen & Walters, 2005; Torchin et al., 2005). Once settled, ribbed mussels remain mostly sedentary, although they can move laterally, or horizontally in response to environmental changes (Lent, 1969; Bertness, 1984; Lin, 1989; Franz, 1993). When ribbed mussels are inundated, they filter feed on microscopic plankton and detritus particles (Riisgård, 1988; Alber and Valiela, 1994; Kreeger and Newell, 1996; Galimany et al., 2013).

Ribbed mussels are ecosystem engineers that alter their environment via biotic and abiotic processes. They contribute to soil strength and erosion mitigation by anchoring to nearby substrates via their byssal threads (Bertness, 1984; Franz, 1997; Angelini, 2015; Derkens-Hooijberg et al., 2018; Gutiérrez, 2020). The hard shell of the ribbed mussel provides solid surface area for vegetation and other sessile bivalves to attach which may increase shoreline and soil stability (Gutiérrez & Iribarne, 1999; Lenihan, 1999). Additionally, ribbed mussels modify nutrients in their environment via filter feeding and pseudofeces deposition which transforms nutrients into more bioavailable forms leading to increased plant productivity (Kuenzler, 1961; Jordan & Valiela, 1982; Bertness, 1984; Huang and Newell, 2002). Ribbed mussels are also a key prey item for commercially important shellfish (e.g., blue crabs) and ecologically important marsh birds (e.g., rails), and are important components of the overall marsh food web (Laughlin, 1982; Lin, 1990; McCann et al., 2017).

Along the United States Atlantic coast, the native ribbed mussel, Geukensia demissa, is found along marsh edges (and to a lesser extent in the interior) with densities frequently in the hundreds of mussels m$^{-2}$ and as high as 9000 mussels m$^{-2}$ in S. alterniflora dominated marshes (Bertness, 1984; Bertness and Grosholz, 1985; Lin, 1990). Increased mussel densities at the edge of the marsh are also related to increased S. alterniflora percent cover (Kennedy, 1976; Griffiths, 1981; Bertness & Grosholz, 1985; Franz, 1993) and increased tidal inundation (Franz, 1993). G. demissa presence has been further shown to lead to increased vegetation productivity, drought mitigation, shoreline stability, soil nutrients, and a decrease in sulfide stress in the marsh (Jordan and Valiela, 1982; Bertness, 1984; Culbertson et al., 2008; Angelini et al., 2015; Angelini et al., 2016).

Fewer studies have explored distribution or habitat associations of the gulf ribbed mussel (Geukensia granosissima) in Louisiana, but recent observations indicate densities of 82 ± 18 ind. m$^{-2}$ in Barataria Bay, Louisiana and 12 ± 1.5 ind. m$^{-2}$ in Cocodrie, Louisiana and even higher densities at some marshes (Spicer, 2007; Rietl et al., 2017). G. granosissima has been found to associate with both Spartina alterniflora and J. roemerianus across a broad, but lower salinity range than G. demissa. Gulf ribbed mussels along a salinity gradient (~4 - ~15) in Barataria Bay, Louisiana were associated more strongly with J. roemerianus than S. alterniflora with greatest mussel density, growth, recruitment, and survival occurring along the marsh edge and in higher
salinities (Honig et al., 2015). Gulf ribbed mussels were also reported to occur in higher densities (highest mean density = 98 ind. m$^{-2}$) along marshes adjacent to open water bodies and natural creek sites in Barataria Bay compared to dredged sites (Spicer, 2007). While these studies provide some insight into the distribution of the gulf ribbed mussel, there has not been a systematic assessment of how frequently mussels occur and there is currently a limited understanding of the factors that drive mussel presence and density and the broader role gulf ribbed mussels play in marsh ecosystems of this region.

It remains unclear whether the gulf ribbed mussel plays a similar role and exists within a similar environment, spatially and temporally, as the Atlantic ribbed mussel. Coastal Louisiana marshes include saline marshes dominated by several vegetation species including S. alterniflora, J. roemerianus, S. patens and Distichlis spicata. Along coastal Louisiana, extensive marsh provides habitat across a range of salinity and vegetation types. Louisiana marshes experience microtidal (mean amplitude typically less than 30 cm), diurnal tides with inundation often driven more by winds than tides (Valentine & Mariotti, 2019). To document gulf ribbed mussel distribution, and to identify potential habitat characteristics associated with gulf ribbed mussel presence and density, I used two surveys to investigate the broad distribution of gulf ribbed mussels in the fringing marsh surrounding an estuarine lake. I hypothesized that gulf ribbed mussel distribution is positively associated with increased vegetation percent cover, elevation, and relative shoreline exposure along the marsh edge. I also hypothesized that increased mussel density may be associated with an increase of vegetation density, soil organic matter and nutrient availability, and shoreline strength. Determining gulf ribbed mussel distribution, environmental drivers, and habitat associations is the first step in determining whether these mussels can support Louisiana coastal marsh production and shoreline stabilization. This information will aid in determining whether gulf ribbed mussels may be a critical ecosystem engineer in supporting future coastal marsh restoration efforts.

2.2 Methods

Study site

The study was conducted in Sister Lake (Calliou Lake), Terrebonne Parish, Louisiana (29.2347° N, -90.9200° W; Figure 1). Sister Lake represents a typical estuarine system in this region, surrounded by euryhaline marsh dominated by S. alterniflora or co-dominated by S. alterniflora and J. roemerianus (La Peyre et al., 2014). The marshes surrounding Sister Lake have Bellpass muck, tidal soil with bulk densities between 0.29 and 0.43 g cm$^{-3}$ (Coastal Reference Monitoring System sites CRMS 0383 and 4455; https://lacoast.gov/crms/). Sister Lake sits within the rapidly subsiding Terrebonne delta with all shorelines experiencing erosion (La Peyre et al., 2014). The eastern shoreline is so severely eroded it provides limited marsh and was therefore excluded from sampling. The 10-year (2009 to 2019) mean ± standard error temperature and salinity of Sister Lake were 23.0 ± 6.7°C (range 0.5 to 32.9°C) and 10.5 ± 5.3 (range 0.4 to 30) (LDWF/USGS site 07381349). Winds are predominantly from the southeast during most of the year, and from the north in the winter, with the 2015 - 2018 mean wind speed ~15 km h$^{-1}$ (Coastal Reference Monitoring System sites CRMS 0383 and 4455; https://lacoast.gov/crms/; Iowa State University Agronomics 2020).
Figure 1. Study plots sampled for ribbed mussels and environmental characteristics along the marsh edge (1 m) of Sister Lake (located in Terrebonne Parish, Louisiana, USA). All circles were sampled for the broad survey (n = 150) and closed circles indicate sites also sampled during the focal survey (n = 21). Stars indicate long term monitoring sites: LDWF / USGS site 07381349, denoted by the blue star; https://waterdata.usgs.gov/usa/nwis/uv?site_no=07381349 and Coastal Reference Monitoring System sites CRMS 0383, denoted by the yellow star, and CRMS 4455, denoted by the red star; https://lacoast.gov/crms/.

Study Design

The distribution of gulf ribbed mussels along the marsh edge of Sister Lake was assessed during two surveys in summer 2019: (1) a broad survey of 150 plots exploring gulf ribbed mussel presence and surface density in relation to percent vegetation cover, elevation, and shoreline exposure on all shorelines, and (2) a focal survey at a sub-set of 21 of the initial 150 plots supporting varying ribbed mussel densities across all shorelines to determine potential drivers of gulf ribbed mussel distribution across the lake.
Broad survey of mussel distribution and environmental characteristics

I sampled the north, west, and south shorelines of Sister Lake. To ensure geographic representation, I stratified the samples by shoreline, and randomly selected 50 plots across each shoreline (150 plots total) using ArcMap 10.7, ensuring a minimum of 50 m between sampling plots (Figure 1). These sample plots were accessed by boat and assessed onshore. Each plot was visited once, between June 8, 2019 and June 31, 2019 and sampled for surface ribbed mussel density, vegetation percent cover, and marsh elevation.

Sample Collection

At each sample plot, I placed a 1 m² quadrat within 0 - 1 m of the marsh edge. All mussels visible in the 1 m² quadrat were counted and recorded. Species-specific vegetation percent cover was estimated using the Braun-Blanquet (1932) technique in each quadrant of the 1 m² plot. Marsh elevation (cm), standardized to NAVD88, was measured using a Trimble Geo 7 X in the middle of each plot. Relative shoreline exposure to wind and wave energy, was calculated using fetch measurements from coastal Landsat imagery (2018) with data for 36 compass bearings, or at 10-degree intervals, using the WAVES tool (USGS, 2012) in ArcMap 10.7 (ESRI, 2018). Wind speed and frequency were calculated using 2015 - 2018 mean windrose data from Iowa State University Agronomics (2020). As relative exposure is a unitless measure, the final calculation multiplied wind speed, wind frequency, and fetch measurements for each 10-degree interval, and summed the 36 values according to the equation:

Relative exposure = \sum_{R=0}^{360} speed \times frequency \times fetch  

Eqn. 1

Focal survey of environmental characteristics driving mussel distribution

Mussel distribution in Sister Lake was further explored to examine their distribution relative to potential drivers including vegetation characteristics, soil strength, soil water content, soil organic matter content, and soil nutrient pools by revisiting 21 of the 150 previously sampled plots. These 21 sample plots were selected based on S. alterniflora dominance in the sampled plots and stratified based on surface mussel densities observed during the broad survey to ensure a range of densities representing absence (0 ind. m⁻²), moderate (1 - 90 ind. m⁻²) and high mussel density (91 - 350 ind. m⁻²). Using these groupings, samples were stratified by shoreline (north, west, south), and 3 plots of each group per shoreline were selected, with the exception of the high mussel density group which only occurred on the north shoreline as it was the only shoreline where densities high enough were encountered. Plots were sampled once, on August 15, 2019.

Sample Collection and Processing

Vegetation - At each sample location, a 0.25 m x 0.25 m (0.0625 m²) quadrat was randomly placed within the original, broad survey 1 m² sample plot. Within each plot, we estimated aboveground vegetation percent cover for each species present, assessed mean S. alterniflora stem height (measured 5 stem heights (cm) by selecting the closest stem to each corner and one in the middle of the quadrat), and determined density of live and dead S. alterniflora stems by counting the total number of live and dead stems. Soil shear strength (kN/m²) was measured at a depth of 15 cm within the root zone at 5 locations within the 0.25 m
x 0.25 m plot using a hand-held shear vane (Humboldt, New Zealand Geotechnical Society Inc.) (Lin et al., 2016).

One auger core (6.35 cm diameter x 30 cm depth) was collected within each plot for belowground biomass, placed in a labelled plastic bag, stored on ice and returned to LUMCON for processing. Within five days of collection, each core was gently rinsed with tap water over a 0.5 mm sieve to remove all sediment. Belowground material was sorted into live and dead roots and rhizomes by floating rinsed material in a white plastic pan with clean deionized water for 40 minutes (Hill & Roberts, 2017). Sorted material was dried at 80°C for 5 days and then live and dead biomass of roots and rhizomes (g) was recorded and standardized to g m⁻².

**Soils** - A second core was collected in each plot using a clear acrylic tube with beveled edges (6.7 cm diameter x 5 cm depth) for determination of soil water content, soil organic matter and available nutrient pools. Cores were taken, avoiding mussels within the plot. All samples were placed in labeled Whirl-Paks®, stored on ice, and returned to LUMCON for processing. Mussels were harvested from within the 0.25 m x 0.25 m plot down to 10 cm (Spicer, 2007). Mussels were kept on ice and brought to LUMCON where they were kept at 4°C until processed.

Upon returning to the lab, approximately 10 g of field-moist homogenized soil from the 5 cm soil core was placed in a pre-weighed aluminum tin, dried to a constant weight at 80°C and re-weighed to calculate soil water content. In a separate pre-weighed aluminum tin, approximately 10 g of field-moist homogenized soil from the 5 cm soil core was dried to a constant mass at 80°C and re-weighed, then aluminum tins were combusted at 550°C for 4 hours and re-weighed in order to calculate soil organic matter content based on the organic matter loss on ignition (LOI) method (Marton & Roberts, 2014).

The 5 cm soil cores were processed for extractable dissolved inorganic nutrient concentrations (NO₃ (nitrate + nitrite), NH₄⁺ (ammonium), and PO₄³⁻ (orthophosphate)) following the protocols detailed in Schutte et al. (2020). NO₃ and NH₄⁺ samples were measured by weighing 2-3 g of homogenized field-moist soil in a 50 mL centrifuge tube inoculated with 30 mL of a potassium chloride (KCl) solution, then gently shaken at 250 rpm for 2 hours. PO₄³⁻ samples were measured by weighing 2-3 g of homogenized field-moist soil in a 50 mL centrifuge tube inoculated with 30 mL of a 0.5 M sodium bicarbonate (0.5 M NaCHO₃) solution and gently shaken at 250 rpm for 16 hours. After shaking, samples were centrifuged at 3000 rpm for 10 minutes and the supernatant was filtered through a 0.2 µm syringe filter. Samples were analyzed for dissolved NO₃ using Cu-Cd reduction followed by azo colorimetry using a Lachat Instruments QuickChem® FIA+ 8000 Series Automated Ion Analyzer with an ASX-400 Series XYZ Autosampler (APHA, 1992). Samples were analyzed for dissolved NH₄⁺ (using phenate colorimetry) and dissolved PO₄³⁻ (using the ascorbic acid reduction method) on a Shimadzu UV-1800 Spectrophotometer (APHA, 1992). Standard curves were prepared by diluting NO₃⁻, NH₄⁺ and PO₄³⁻ stock solutions (Hach, Loveland CO) and yielded r² values of > 0.99 for each analyte (Roberts & Doty, 2015).

**Mussels** - Mussels were excavated down to 10 cm within each plot. Removed mussels were cleaned with tap water and a wire brush. Each whole mussel was placed in a pre-weighed and labeled aluminum tin, dried at 80°C for 72 hours, weighed to ± 0.01 g and then combusted at 550°C for 4 hours and re-weighed to ± 0.01 g in order to calculate ash-free dry mass (g m⁻²) using protocols similar to those in Spicer (2007) and Rietl et al. (2018). Ribbed mussel ash-free dry mass (g m⁻²) was scaled to biomass per meter-squared.
Statistical Analysis

For both surveys, correlation analyses were run on measured variables to determine which variables to use for further analysis. Logistic regression was conducted to examine the probability of mussel presence based on measured environmental characteristics (S. alterniflora cover (%), J. roemerianus cover (%), total vegetation cover (%), S. alterniflora mean height (cm), elevation (cm), and relative shoreline exposure (unitless) for all 150 broad survey sample plots. To examine the relationship between surface mussel density (ind. m$^{-2}$) and measured environmental characteristics at the 150 broad survey sample plots, a backward selection multiple regression was run for all 150 sample plots together, and then by shoreline (north, west, south).

Simple linear regression was used to explore how well individual environmental characteristics predicted mussel density across the 21 plots sampled in the focal survey. Backward selection multiple regression was used to further explore the relationship between environmental characteristics and excavated mussel density, where only the most significant environmental characteristics were retained. Regression of excavated mussel density on surface mussel density was explored for 14 of the 21 plots containing mussels. Retained environmental characteristics had values of $p$ less than 0.1 and $r^2$ greater than 0.7. All analyses were conducted in R studio using packages tidyverse, psych, ggplot2, MASS, and leaps (Venables & Ripley, 2002; Wickham, 2016; R Core Team, 2019; Wickham et al., 2019; Revelle, 2019; Lumley, 2020). Unless otherwise specified, mean and standard error are reported together.

2.3. Results

Broad Survey

Mussels were present at 46% (69) of the 150 sites sampled along the shoreline of Sister Lake (Figure 2). This distribution varied by shoreline with the north shoreline having mussels present at almost twice as many sites than the south and west shorelines (64% versus 38% and 36%, respectively). S. alterniflora percent cover and J. roemerianus percent cover were highly correlated with total vegetation percent cover ($r = 0.27, p < 0.0001$), so only total vegetation percent cover was used in the logistic regression. Total vegetation percent cover (range 2.5 - 90.5%; mean 40.5% with S. alterniflora contributing 30.7%, and J. roemerianus contributing 9.7%) suggested a minimal increased likelihood of mussels occurring as total vegetation percent cover increases (Table 1) (Coxe and Snell $r^2 = 0.087$; predicted logit of mussel presence = -1.6583 + 1.037 * total vegetation percent cover).
Figure 2. Distribution of sites sampled with mussel absence (density = 0 ind. m\(^2\), yellow circles), and presence, indicating moderate (1 - 90 ind. m\(^2\), green circles) and high (91 - 350 ind. m\(^2\), blue circles) density on the north (orange box), west (blue box), and south (green box) shorelines in Sister Lake, Terrebonne Parish, Louisiana, USA.

Table 1. Logistic regression analysis of 150 sites examined for presence of mussels by elevation (cm), relative shoreline exposure (unitless), and total vegetation percent cover (%). Model: mussel density = -1.6583 + (1.037) total vegetation percent cover.

| Coefficients: | Estimate | Std. Error | t value | Pr(>|t|) | Significance |
|---------------|----------|------------|---------|----------|--------------|
| (Intercept)   | 6.822E+00 | 1.33E+01  | 0.514   | 0.608    |              |
| vegetation percent cover | 4.22E-01  | 1.86E-01  | 2.264   | 0.025    | *            |
| elevation     | 4.58E-01  | 2.92E-01  | 1.569   | 0.119    |              |
| exposure      | 2.22E-05  | 1.35E-05  | 1.644   | 0.102    |              |

---

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Residual standard error: 38.84 on 146 degrees of freedom
Multiple R-squared: 0.05295,
F-statistic: 2.721 on 3 and 146 DF, p-value: 0.04663
Adjusted R-squared: 0.03349
R code: lm(formula = mussel.m2 ~ pcover.veg + elevation + exposure, data = tier1)

Surface mussel densities around the lake ranged from 0 to 350 mussels m\(^2\) with a mean of 13.5 ± 3.2 mussels m\(^2\) (Table 2). The north shore had the highest observed mussel density of
350 mussels m$^{-2}$ with a mean of 34.9 ± 8.9 mussels m$^{-2}$, while the maximum surface mussel density for the west and south shores were 33 and 25 mussels m$^{-2}$, respectively, with means of 3.8 ± 1.1 and 1.8 ± 0.7 mussels m$^{-2}$, respectively (Table 2). Mean density when mussels were present across the entire lake was 29.3 ± 6.5 mussels m$^{-2}$. Elevation tended to be lower on the north shore (16.1 ± 1.8 NAVD88, cm) compared to the south and west shores (21.4 ± 1.3 and 24.2 ± 1.3 NAVD88, cm, respectively), while relative shoreline exposure and percent cover of *J. roemerianus* tended to be higher on the north shore compared to the south and west shores (Table 2). A stepwise backward regression of elevation, exposure and total vegetation percent cover against mussel density retained only total vegetation percent cover at the 0.1 significance level ($F_{3,146} = 2.721; p = 0.047$; mussel density $= -6.82 + 0.42 \times$ total vegetation percent cover $- 0.46 \times$ elevation $+ 0.22 \times 10^{-4} \times$ exposure). When explored by shoreline, no variables were significant enough to be retained in regression models for the north and south shorelines. For the west shoreline, exposure was retained in the final significant model ($F_{1,48} = 10.58, p = 0.0021$) and was found to be negatively associated with mussel density (mussel density $= 11.09697 - 0.00001297 \times$ exposure, Adj $r^2 = 0.16$).

Table 2. Summary of mean ± standard error and (range) for measured variables at 150 sites on the south, west, and north shorelines (< 1 m from water’s edge). Shoreline exposure values are divided by 10,000.

<table>
<thead>
<tr>
<th>Shoreline</th>
<th>South</th>
<th>West</th>
<th>North</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mussel presence (%)</td>
<td>38</td>
<td>36</td>
<td>64</td>
<td>46</td>
</tr>
<tr>
<td>Mussel density (ind. m$^{-2}$)</td>
<td>1.8 ± 0.7 (0 - 25)</td>
<td>3.8 ± 1.1 (0 - 33)</td>
<td>34.9 ± 8.9 (0 - 350)</td>
<td>13.5 ± 3.2 (0 - 350)</td>
</tr>
<tr>
<td>Elevation (NAVD88, cm)</td>
<td>21.4 ± 1.3 (-5.7 - 37.8)</td>
<td>24.2 ± 1.3 (-3.2 - 49.2)</td>
<td>16.1 ± 1.8 (-31.1 - 41.3)</td>
<td>20.6 ± 0.9 (-31.1 - 49.2)</td>
</tr>
<tr>
<td>Shoreline exposure (unitless)</td>
<td>44.2 ± 2.5 (5.5 - 83.6)</td>
<td>56.6 ± 3.5 (7.1 - 102.2)</td>
<td>70.2 ± 3.3 (22.3 - 110.3)</td>
<td>57.0 ± 2.0 (5.5 - 110.3)</td>
</tr>
<tr>
<td>Vegetation cover (%)</td>
<td>42.8 ± 2.0 (12.5 - 73.8)</td>
<td>30.7 ± 2.3 (2.5 - 59)</td>
<td>47.8 ± 2.6 (8.8 - 90.5)</td>
<td>40.5 ± 1.4 (2.5 - 90.5)</td>
</tr>
<tr>
<td><em>S. alterniflora</em> cover (%)</td>
<td>40.6 ± 2.3 (5 - 73.8)</td>
<td>19.8 ± 2.7 (0 - 57.5)</td>
<td>31.7 ± 2.3 (0.3 - 88.8)</td>
<td>30.7 ± 1.6 (0 - 88.8)</td>
</tr>
<tr>
<td><em>J. roemerianus</em> cover (%)</td>
<td>2.2 ± 0.9 (0 - 28.8)</td>
<td>10.9 ± 2.2 (0 - 58.8)</td>
<td>16.1 ± 3.0 (0 - 86.3)</td>
<td>9.7 ± 1.3 (0 - 86.3)</td>
</tr>
<tr>
<td><em>S. alterniflora</em> stem height (cm)</td>
<td>77.0 ± 1.8 (49.2 - 102.3)</td>
<td>88.2 ± 2.1 (30 - 116.8)</td>
<td>90.5 ± 2.7 (46.8 - 134.6)</td>
<td>84.0 ± 1.3 (30 - 134.6)</td>
</tr>
</tbody>
</table>

**Focal Survey**

In the 21 sites sampled, excavated mussel density (mussels excavated from surface down to 10 cm) ranged from 0 – 400 mussels m$^{-2}$ with a mean of 42.7 ± 19.2 mussels m$^{-2}$ on the north
shore, a mean of 56.0 ± 38.9 mussels m⁻² on the west shore, and a mean of 18.7 ± 12.7 mussels m⁻² on the south shore for the moderate mussel density class across all three shorelines, and a mean of 293.3 ± 122.2 mussels m⁻² on the north shore for the high mussel class (Table 3). Mean biomass for individual mussels collected was 7.7 ± 0.7 gdw⁻¹. Surface mussel density was 7.4 ± 2.4% (mean ± SE) of the excavated mussel density (Figure 3). Excavated mussel density was highly correlated with mussel biomass (r = 0.95; p < 0.0001), so subsequent analysis were conducted using only mussel density. Soil water content was positively correlated with soil organic matter (r = 0.88; p < 0.0001) and negatively correlated with soil shear strength (r = -0.70; p < 0.0001), so subsequent analysis were conducted using only soil water content and soil shear strength. Total live belowground biomass was positively correlated with roots and rhizomes biomass (r = 0.83, p < 0.0001; r = 0.94, p < 0.0001, respectively), so subsequent analyses were conducted using only total live belowground biomass.

Table 3. Summary of mean, standard error and range for environmental characteristics assessed across Sister Lake, Louisiana during the focal survey (n = 21). Shoreline exposure values are divided by 10,000.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Mean ± Standard error</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Excavated mussel density (ind. m⁻²)</td>
<td>69.3 ± 25.2</td>
<td>0.0</td>
<td>400.0</td>
</tr>
<tr>
<td>Excavated mussel biomass (gdw⁻¹ m⁻²)</td>
<td>33.2 ± 11.1</td>
<td>0.0</td>
<td>175.8</td>
</tr>
<tr>
<td>S. alterniflora density (ind. m⁻²)</td>
<td>315.4 ± 38.2</td>
<td>48.0</td>
<td>688.0</td>
</tr>
<tr>
<td>S. alterniflora mean height (cm)</td>
<td>61.2 ± 3.8</td>
<td>23.7</td>
<td>84.9</td>
</tr>
<tr>
<td>Total live belowground biomass (g m⁻²)</td>
<td>908.6 ± 136.1</td>
<td>66.2</td>
<td>2,357.2</td>
</tr>
<tr>
<td>Elevation (NAVD 88, cm)</td>
<td>22.7 ± 1.8</td>
<td>-3.2</td>
<td>34.1</td>
</tr>
<tr>
<td>Shoreline exposure (unitless)</td>
<td>65.2 ± 4.2</td>
<td>30.2</td>
<td>96.3</td>
</tr>
<tr>
<td>Soil water content (%)</td>
<td>68.5 ± 2.4</td>
<td>42.3</td>
<td>80.8</td>
</tr>
<tr>
<td>Soil organic matter (%)</td>
<td>17.5 ± 1.5</td>
<td>5.2</td>
<td>32.5</td>
</tr>
<tr>
<td>Soil extractable DIN (nmol N gdw⁻¹)</td>
<td>664.0 ± 46.4</td>
<td>304.5</td>
<td>1,048.6</td>
</tr>
<tr>
<td>Soil extractable DIP (nmol P gdw⁻¹)</td>
<td>607.8 ± 103.3</td>
<td>153.2</td>
<td>2,213.0</td>
</tr>
<tr>
<td>Soil shear strength (kN/m²)</td>
<td>14.0 ± 2.1</td>
<td>0.0</td>
<td>43.5</td>
</tr>
</tbody>
</table>
Figure 3. Relationship between excavated and surface gulf ribbed mussel density in Sister Lake, Louisiana with focal survey plots ($y = 7.3092x + 37.312; r^2 = 0.39; n = 12$)

Mussel density decreased with increased soil water content ($r^2 = 0.62, p < 0.0001, y = 646.4 - 8.4 * $ \text{soil water content};$ Figure 4b) and increased with increased total live belowground biomass ($r^2 = 0.18, p = 0.058, y = -1.3 + 0.08 * $ \text{total live below ground biomass};$ Figure 4e). Backward selection of multiple linear regression model retained the same variables of soil water content and live belowground biomass (adjusted $r^2 = 0.75; y = 561.53 - 7.94 * $ \text{soil water content} + 0.057 * $ \text{total live belowground biomass}). No significant relationship was found between mussel density and $S. \ alterniflora$ stem density, soil extractable dissolved inorganic nitrogen ($\text{DIN} = \text{NO}_x + \text{NH}_4$), soil extractable phosphorus, soil shear strength, elevation, or relative shoreline exposure (Figure 4a, c, d, f, and h).
2.4. Discussion

Gulf ribbed mussels were found to be relatively ubiquitous and located more frequently with increased percent cover of *Juncus roemerianus* within the estuarine lake investigated. While these mussels were present at almost half of the sites sampled, their distribution was not random. There was a significantly higher occurrence of mussels at the north shoreline which was characterized by lower elevation (approximately 16 cm NADV88), higher soil moisture content, and shoreline exposure compared to the south and west shorelines. Higher mussel densities were also significantly associated with greater vegetation percent cover and belowground vegetation biomass in general. These findings suggest gulf ribbed mussels are common and often found embedded within areas of higher marsh vegetation percent cover and biomass, while also inhabiting areas that likely have great inundation, and could be a valuable tool to consider in marsh restoration projects in coastal Louisiana.

Mean mussel surface density reported in the broad survey (13.5 ± 3.2 ind. m\(^{-2}\)) was similar to surface densities previously reported in Cocodrie, Louisiana (12 ± 1.5 ind. m\(^{-2}\); Rietl et
Differences in recruitment salinity, ribbed mussels, with fewer adults Honig et al. (2014) found that salinity affected the extent and timing of sexual maturity in reflect north shoreline of Sister 2010; influence, and currents et al., 2015; Honig et al., 2015; Moody et al., 2020). broadcast spawners therefore may not be feasible at 150 sites as in the broad survey) will 
understanding vegetation how mussels are impacting vegetation, soils, and nutrients, within the root zone of accurate representation of mussel densities percent cover (range: 2.5 – 31.1; Moody et al., 2020). Although not captured in this random survey, higher excavated mussel densities have been reported in the study site, ranging from 752 to 8704 ind. m$^{-2}$ (McDonald et al., personal observation, 2017) suggesting a need to identify and characterize these high density locations more fully. If these higher densities exist, this could indicate similar densities of mussels in Louisiana as reported for the Atlantic ribbed mussel throughout the Atlantic coast (e.g., Barrington, RI: 100 – 400 ind. m$^{-2}$ in tall form S. alterniflora and 900 – 2000 ind. m$^{-2}$ on seaward edge of the marsh; Bertness, 1984), Narragansett Bay, RI: 25 – 1164 ind. m$^{-2}$; Chintala et al., 2006, and Jamaica Bay, NY: 5754 ± 632 m$^{-2}$; Franz, 1993). Differences in densities may reflect not just the methods used, but the range of habitat conditions sampled, including vegetation cover, density, or site elevation. None of the Atlantic studies provided a broad survey across an extended area of marsh, within brackish waters, and all of these studies report densities from productive S. alterniflora marshes. In contrast, this study captured a much broader range of conditions. This study documented densities across a range of habitats, as defined by vegetation percent cover (range: 2.5 - 90.5%), and elevation (range: -31.1 - 49.2 NADV88, cm). Having an accurate representation of mussel densities through excavation gives a better understanding of how mussels are impacting vegetation, soils, and nutrients, within the root zone of marsh vegetation, and would also enable documentation of mussel size and potentially aid in a better understanding of population dynamics. However, large scale mussel excavations (e.g., 1 m$^2$ plots at 150 sites as in the broad survey) will result in significant marsh shoreline destruction and therefore may not be feasible.

Mussel recruitment drives local population dynamics (i.e., density) as ribbed mussels are broadcast spawners and are sessile for most of their lives (Franz, 2001; Altieri et al., 2007; Casas et al., 2015; Honig et al., 2015; Moody et al., 2020). As a result, salinity, temperature, tidal influence, and currents (important drivers of marsh bivalve distributions; (Domínguez et al. 2010; Wilberg et al., 2013; Byers et al., 2015; La Peyre et al., 2016) may influence where and when gulf ribbed mussels establish, grow and reproduce in coastal Louisiana. There were higher excavated mussel densities, but similar surface mussel densities, of gulf ribbed mussels on the north shoreline of Sister Lake in 2017 (McDonald et al., personal observation, 2017). This may reflect lower mean salinities during 2019 (6.9 ± 0.03) than 2017 (11.4 ± 0.05) (USGS, 2018). Honig et al. (2014) found that salinity affected the extent and timing of sexual maturity in gulf ribbed mussels, with fewer adults reaching maturity with lower salinity. It is possible that, due to salinity, reduced mussel recruitment over two years resulted in lower ribbed mussel densities. Differences in recruitment may also be impacted by dominant winds and transportation of larvae which could also explain differences in shoreline mussel densities. With dominant winds from

al., 2017), but lower than excavated mussel densities reported for Barataria Bay (82 ± 18 ind. m$^{-2}$; Spicer, 2007), and Hackberry Bay (66.6 ± 16.3 ind. m$^{-2}$; Honig et al., 2015) collected across similar salinity regimes. Differences in reported densities likely reflect differences in sample methodology as reported surface densities potentially under report mussel densities. Excavated mussel densities (to 10 cm depth) were approximately 10 times greater than surface mussel densities in this study. Surface mussel densities as a percentage of total excavated densities was only 7.4%, which would indicate that the mean density across the broad survey may actually be on the order of greater than 130 ind. m$^{-2}$. This under reporting of surface mussel densities may be particularly evident when estimating mussel density in dense vegetation, or in lower elevation (higher flooding) locations. As mussels live within the plant root zone, and move with water height for feeding, surface densities may provide only a rough estimate of actual density (Bertness, 1984; Coen, 2005; Angelini et al., 2015).
the south / southeast in Sister Lake, entrainment (or retention) of mussel larvae on the north shore may contribute to the observed higher presence and densities.

Mussel density, in relation to vegetation characteristics, may provide an indicator of ribbed mussel impacts on soil characteristics including soil nutrient pools and sediment strength. Higher *G. granosissima* densities in Sister Lake were found in shoreline areas with higher percent vegetation cover and belowground biomass; consistent with observations for *G. demissa* on the Atlantic coast (Bertness, 1984; Angelini et al., 2015; Angelini et al., 2016; Derkson-Hooijberg et al., 2018). Both *G. granosissima* on the Gulf coast and *G. demissa* on the Atlantic coast have been shown to strongly associate with *S. alterniflora* but have also been shown to associate with *S. patens* and *J. roemarianus* (Bertness, 1984; Honig et al., 2015; Angelini, 2016). The range of mussel densities surveyed may not have been enough to detect any significant differences in soil nutrient properties given low means surveyed in this study.

Ribbed mussels provide nutrients to their habitat via their pseudofeces deposition into the soil which is taken up by vegetation leading to an increase in vegetation production and belowground biomass (Jordan & Valiela, 1982; Bertness, 1984). Ribbed mussel association with *S. alterniflora* also aids in salt marsh nitrogen removal (Bilkovic et al., 2017). Another environmental factor that showed positive trends in relation to gulf ribbed mussel density is soil shear strength, with the plot containing the highest mussel density (400 ind. m^-2^) also having the greatest soil shear strength (43.5 ± 17.1 kN/m^-2^). Mussel density was also negatively associated with percent soil water content. Contrary to what I found, Angelini et al. (2016) reported that mussel mounds of 320 ind. m^-2^ in close proximity to *S. alterniflora* in marshes experiencing drought enhanced soil water storage in the marsh, allowing *S. alterniflora* to withstand periods of drought. This could be due to where the samples were taken in either study, and / or the fact that water stress was not an issue at any of the sites sampled in this study.

**2.5. Implications**

This study is the first large-scale systematic survey of gulf ribbed mussel demography on the Gulf coast, and provides critical data defining gulf ribbed mussel distribution and habitat associations. Gulf ribbed mussels commonly occurred and often in high densities across a typical Louisiana brackish marsh. Ribbed mussel density was positively associated with increased percent vegetation cover and belowground vegetation biomass indicating a potential positive interaction between ribbed mussels and dominant marsh vegetation (i.e., *S. alterniflora, J. roemarianus*). Elevation and relative shoreline exposure which are related to inundation and recruitment may be drivers of mussel demography, as shown along the north shoreline of Sister Lake. These positive relationships may mean that gulf ribbed mussels can be used as a tool for enhancement of coastal resilience in Louisiana. Understanding where and in what densities gulf ribbed mussels are found in the marsh, and their impact on marsh production may play an important role in considering their contribution to coastal resilience.
CHAPTER 3. SURVIVORSHIP OF GULF RIBBED MUSSELS FOLLOWING TRANSPLANTATION IN A LOUISIANA SALT MARSH

3.1. Introduction

Wetlands are rapidly being lost due to natural and anthropogenic stressors, with Louisiana experiencing among the highest rates of loss in the world (Williams et al., 1997; Blum and Roberts, 2009; Couvillion et al., 2011). In response, significant restoration and protection efforts have been implemented (Hijuelos & Reed, 2017). Marsh cordgrass (*Spartina alterniflora*) and the gulf ribbed mussel (*Geukensia granosissima*) coexist as ecosystem engineers that may form a mutualistic relationship enhancing salt marsh stability. The closely related Atlantic ribbed mussel, *Geukensia demissa*, modifies nutrients in its environment via filter feeding and depositing pseudofeces which transforms available nutrients into more bioavailable forms leading to increased plant productivity (Bertness, 1984; Jordan & Valiela, 1982; Huang &Newell, 2002). Ribbed mussels also provide habitat structure via their shells, allowing vegetation and other sessile bivalves to attach, potentially increasing shoreline and soil stability (Gutiérrez & Iribarne, 1999; Lenihan, 1999).

Existing living shorelines, where native vegetation or shellfish species are used to provide shoreline protection services, are largely comprised of salt marsh vegetation, and sessile bivalve species, with a focus on the eastern oyster (*Crassostrea virginica*) along the U.S. Gulf coast (La Peyre et al., 2015; La Peyre et al., 2016; Smith et al., 2020). Recent studies have increased our understanding of the distribution and ecology of ribbed mussels (Spicer, 2007; Fields et al., 2012; Honig et al., 2015); however, little is known about survival of transplanted mussels or their potential redistribution (i.e., movement) within the salt marsh as mussel movement has been reported elsewhere (Franz, 2001). I evaluated their potential for use in living shoreline projects by examining the survival and potential movement of transplanted mussels along a *S. alterniflora* shoreline in a Louisiana brackish marsh.

3.2. Methods

**Study site**

This study was conducted from October 2019 to October 2020 in a well-studied *S. alterniflora* dominated marsh near the Louisiana Universities Marine Consortium (LUMCON) in Cocodrie, Louisiana (Figure 5a, b). Salinity ranged from 0.8 – 20.2 and water temperature from 8.1 – 34.5°C throughout the study (DeFelice Marine Center Environmental Monitoring Station Data, 2019 & 2020). Study site soil and vegetation characteristics were typical of this region (Hill & Roberts, 2017), and similar across the experimental site.
Figure 5. Map of A) Site location in Cocodrie, Louisiana, U.S.A denoted by a red circle, B) the marsh located near the Louisiana Universities Marine Consortium (LUMCON) with the study site denoted by a red square, C) a close-up of the study site with the 5 blocks denoted with their respective block number in red and D) example of a randomized distribution of mussel density treatments in the front half of plots within each block. LiDAR data (panels B and C) is from 2015 LiDAR Project Report: G15PD00057, South Terrebonne and Gulf Islands using QL2 LiDAR for USGS; Contract: #G10PC00093, Contractor: Digital Aerial Solutions, Task Order: #G15PD0057.

Study design & data collection

A total of five, 10 m sections (hereafter “block”), each separated by 5 m along a 75 m S. alterniflora shoreline were selected to examine survival and movement of transplanted gulf ribbed mussels (Figure 5c). Within each block, 4 treatment plots (1 m², and 20 cm from the water edge) were established, with 2 m between each plot. Mussel density treatments (0, 50, 100 and 400 individuals m⁻²) spanning the range of densities reported in coastal Louisiana (Honig et al., 2015; Chapter 2) were randomized across each block (5 blocks x 4 treatments = 20 plots total; Figure 5d). Mussels were planted at target densities in the front half (water edge) of each plot in
order to examine changes in mussel density along the shoreline edge, with the back half of the plot cleared of all mussels to examine potential mussel redistribution (Figure 5d).

**Mussels** - Hand trowels were used to collect 1,375 gulf ribbed mussels (55 – 100 mm in shell height so that only adult mussels were included) from *S. alterniflora* marsh adjacent to LUMCON. Harvested mussels were placed in cages located at the edge of the *S. alterniflora* marsh at LUMCON to ensure survival after harvest. After two weeks, surviving mussels (> 95%) were randomly placed in buckets and transplanted in experimental plots to achieve target treatment densities. Mussels were planted at target densities across the front half of each m² plot using a 10 cm grid to ensure even distribution. Mussel surface densities for the whole 1 m² plot were counted 7 times (January, February, March, June, July, September, October 2020; Figure 6). In October 2020, mussels were harvested to a depth of 10 cm with total mussel density recorded for front and back sections of plots separately.

**Vegetation** - Vegetation stem height (cm), number of live and dead stems, flowers (ind. m⁻²), and percent cover (%) were quantified for each experimental treatment plot following methods detailed in Hill and Roberts (2017). Briefly, a subsample was taken by haphazardly placing a 0.25 x 0.25 m quadrat within the front and back half of each plot (n = 20). *S. alterniflora* stem height, live and dead stem density, flowering density, and percent cover were quantified in each subsample. *S. alterniflora* stem height was assessed by measuring 5 stem heights (cm) (selecting the closest stem to each corner and one in the middle of the quadrat). I determined density of live and dead *S. alterniflora* stems and flowers by counting the total number of live and dead stems within the 0.25 m x 0.25 m quadrat. *S. alterniflora* percent cover was estimated using the Braun-Blanquet (1932) technique within the 0.25 m x 0.25 m quadrat.

One auger core (6.35 cm diameter x 30 cm depth) was collected in the 2 m between each plot for belowground biomass, placed in a labelled plastic bag, stored on ice and returned to LUMCON for processing by block only, with samples collected between each plot within a block (n = 15, 3 per block). Within five days of collection, each core collected for belowground vegetation was gently rinsed with tap water over a 0.5 mm sieve to remove all sediment. Belowground material was sorted into live and dead roots and rhizomes by floating rinsed material in a white plastic pan with clean deionized water for 40 minutes (Hill & Roberts, 2017). Sorted material was dried at 80°C for 5 days and then live and dead biomass of roots and rhizomes (g) was recorded and standardized to g m⁻².

**Soils** - A second core was collected from the 2 m between plots (n = 15, 3 per block) using a clear acrylic tube with beveled edges (6.7 cm diameter x 5 cm depth) for determination of soil water content, soil organic matter and available nutrient pools as described in Marton and Roberts (2014) and Schutte et al. (2020). All samples were placed in labeled Whirl-Paks®, stored on ice, and returned to LUMCON for processing. Upon returning to the lab, approximately 10 g of field-moist homogenized soil from the 5 cm soil core was placed in a pre-weighed aluminum tin, dried to a constant weight at 80°C and re-weighed to calculate soil water content. In a separate pre-weighed aluminum tin, approximately 10 g of field-moist homogenized soil from the 5 cm soil core was dried to a constant mass at 80°C and re-weighed, then aluminum tins were combusted at 550°C for 4 hours and re-weighed in order to calculate soil organic matter content based on the organic matter loss on ignition (LOI) method. The soil cores were immediately processed for extractable dissolved inorganic nutrient concentrations (NO₃ (nitrate + nitrite), NH₄⁺ (ammonium), and PO₄³⁻ (orthophosphate)) following the protocols detailed in Schutte et al. (2020). NO₃ and NH₄⁺ samples were measured by weighing 2-3 g of homogenized field-moist soil in a 50 mL centrifuge tube inoculated with 30 mL of a potassium chloride (KCl)
solution, then gently shaken at 250 rpm for 2 hours. PO₄³⁻ samples were measured by weighing 2-3 g of homogenized field-moist soil in a 50 mL centrifuge tube inoculated with 30 mL of a 0.5 M sodium bicarbonate (0.5 M NaCHO₃) solution and gently shaken at 250 rpm for 16 hours. Samples were centrifuged at 3000 rpm for 10 minutes and the supernatant was filtered through a 0.2 µm syringe filter. After shaking, samples were analyzed for dissolved NO₃⁻ using Cu-Cd reduction followed by azo colorimetry using a Lachat Instruments QuickChem® FIA+ 8000 Series Automated Ion Analyzer with an ASX-400 Series XYZ Autosampler (APHA, 1992). Samples were analyzed for dissolved NH₄⁺ (using phenate colorimetry) and dissolved PO₄³⁻ (using the ascorbic acid reduction method) on a Shimadzu UV-1800 Spectrophotometer (APHA, 1992). Standard curves were prepared by diluting NO₃⁻, NH₄⁺ and PO₄³⁻ stock solutions (Hach, Loveland CO) and yielded r² values of > 0.99 for each analyte (Roberts & Doty, 2015).

**Soil shear strength** - Soil shear strength (kN/m²) was measured using a (3.3 cm diameter x 15 cm long) shear vane (Humboldt, New Zealand Geotechnical Society Inc.) attached directly to a reading torque gauge (Geotechnics Ltd., Auckland, NZ) within the *S. alterniflora* rootzone at a depth of 15 cm at 5 haphazard locations between each plot and averaged by block (n = 15, 3 per block). Measurements were made by inserting shear vane into the soil, twisting the vane clockwise until failure, and recording the raw measurement then repeating as described in Lin et al. (2016).

**Statistical Analysis**

Initial soil (soil shear strength, percent water content, percent soil organic matter, extractable nitrate) and vegetation conditions (below ground vegetation biomass, stem density (live, dead), stem height, flowers and percent cover) were examined by block using a one way ANOVA. Initial vegetation stem density (live, dead), stem height, flowers and percent cover were further examined and compared using a one-way ANOVA to compare front and back of the plots. All statistical analysis was determined with R studio (package: ggplot2; Wickham, 2016; R Core Team, 2019). Mussel movement was explored using calculations based on final mussel densities against original transplanted mussel densities in the front and back for each 1 m² plot in every block (front loss – back gain = mussel movement).

**3.3. Results**

Mussel density declined over 1 year for all mussel density treatments with a rapid initial decline and then somewhat of a plateau towards completion of sampling in October 2020 (Figure 6). All plots with transplanted mussels decreased in mussel density with final reported densities for each treatment of 0.4 ± 0.4 ind. m⁻² (treatment: 0), 14.4 ± 6.0 ind. m⁻² (treatment: 50), 37.2 ± 15.2 ind. m⁻² (treatment: 100), and 136.8 ± 50.8 ind. m⁻² (treatment: 400) (Table 4). Percent loss by treatment ranged from 62.8 ± 15.2 to 71.2 ± 12.0 % (Table 4). There was a consistent trend of decreasing loss for all treatments moving into more protected areas of the shoreline (Figure 5c). The highest mussel losses were observed in Block 1 where an average of 97.8% of transplanted mussels were lost across all treatment levels (Table 4). In contrast, Blocks 4 and 5 saw the lowest mussel losses with averages of 40.5% and 47.7%, respectively, of transplanted mussels being lost across all treatment levels (Table 4).
Figure 6. Surface mussel density counts (mean ± SE) by treatment for the entire 1 m² plot (combined front and back plot totals). From October 2019 (when mussels were initially transplanted) through January 2020, mussel densities were monitored and maintained in front and back plots. Treatment legend references initial mussel transplant density in the front plots so that the whole m² plot mussel density was 200 mussels m⁻² for treatment 400, 50 mussels m⁻² for treatment 100, 25 mussels m⁻² for treatment 50, and 0 mussels m⁻² for treatment 0.

All back plots, with the exception of those located in Block 1, gained mussels throughout the year, with final reported densities for back plots of 2.8 ± 1.9 ind. m⁻² (treatment: 0), 10.4 ± 3.4 ind. m⁻² (treatment: 50), 14.0 ± 7.0 ind. m⁻² (treatment 100), and 62.8 ± 19.2 ind. m⁻² (treatment: 400) (Table 4). Back plots gained mussels as a percentage of the initial transplanted front plot density across all treatments (14 - 21%) (Table 4). Overall, the gain of mussels in the back plots, offset the loss of mussels in the front plots by approximately 17%, resulting in an average loss of approximately 50% of mussels from the entire square meter experimental plot across all treatments (front loss – back gain = 66.6 – 16.8 = 49.6%). Re-distribution of mussels across the whole m² experimental plot resulted in approximately 30% (final mean ind. m² from back plot / original front plot density) of the mussel density being accounted for in the back plots at the end of the experiment.

Vegetation stem height had a trend of increasing heights from Block 1 through Blocks 4 and 5 (Table 5). No significant differences in initial belowground vegetation, soil organic matter, live and dead stems or percent cover were found by block (Table 5). Initial soil shear strength and soil water content differed significantly by block and followed similar trends with significantly higher values in Block 1 as compared to Block 3 and 4 and Blocks 2 and 5 being similar to all other blocks (Table 5). Extractable NO₃⁻ was significantly greater in Block 2 as compared to Block 4, with no differences between all other blocks (Table 5). Analyses of front
and back plot vegetation characteristics indicated differences in stem height and live stems (ind. m\(^2\)) with both greater at the back half of the plot compared to the front; no differences in dead stems, flowers or percent cover were found (Table 6).
Table 4. Final harvested mussel density (ind. m\(^{-2}\)) in planted front ½ m\(^2\) plot, and percent loss (% loss = 100 – final front density / initial front treatment density * 100) by treatment and block (top), and final harvested mussel density in cleared back ½ m\(^2\) plot, and % mussels gained (% gain = final back density / initial front treatment density * 100) from front plot migrating into back plots (bottom). Treatments are planted densities; n/a indicates not applicable.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Block 1</th>
<th>Block 2</th>
<th>Block 3</th>
<th>Block 4</th>
<th>Block 5</th>
<th>Mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ind. m(^{-2})</td>
<td>% loss</td>
<td>Ind. m(^{-2})</td>
<td>% loss</td>
<td>Ind. m(^{-2})</td>
<td>% loss</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>50</td>
<td>0</td>
<td>100.0</td>
<td>4</td>
<td>92.0</td>
<td>32</td>
<td>36.0</td>
</tr>
<tr>
<td>100</td>
<td>6</td>
<td>94.0</td>
<td>6</td>
<td>94.0</td>
<td>38</td>
<td>62.0</td>
</tr>
<tr>
<td>400</td>
<td>2</td>
<td>99.5</td>
<td>80</td>
<td>80.0</td>
<td>92</td>
<td>77.0</td>
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<tr>
<td>Mean ± SE</td>
<td>n/a</td>
<td>97.8 ± 1.1</td>
<td>n/a</td>
<td>88.7 ± 2.5</td>
<td>n/a</td>
<td>58.3 ± 6.9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Block 1</th>
<th>Block 2</th>
<th>Block 3</th>
<th>Block 4</th>
<th>Block 5</th>
<th>Mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ind. m(^{-2})</td>
<td>% gain</td>
<td>Ind. m(^{-2})</td>
<td>% gain</td>
<td>Ind. m(^{-2})</td>
<td>% gain</td>
</tr>
<tr>
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<td>0</td>
<td>-</td>
<td>2</td>
<td>-</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>50</td>
<td>0</td>
<td>0.0</td>
<td>18</td>
<td>36.0</td>
<td>18</td>
<td>36.0</td>
</tr>
<tr>
<td>100</td>
<td>0</td>
<td>0.0</td>
<td>4</td>
<td>4.0</td>
<td>10</td>
<td>10.0</td>
</tr>
<tr>
<td>400</td>
<td>0</td>
<td>0.0</td>
<td>5</td>
<td>12.5</td>
<td>58</td>
<td>14.5</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>n/a</td>
<td>0.0</td>
<td>n/a</td>
<td>17.5 ± 9.6</td>
<td>n/a</td>
<td>20.2 ± 8.0</td>
</tr>
</tbody>
</table>
Table 5. Mean ± standard error of initial environmental (soil, nutrients, vegetation) parameters by replicate block (n = 3 / block). Soil, nutrient and belowground vegetation parameters were measured between blocks in October 2019. Above ground vegetation measures were taken within replicate plots within each block (n = 4). Significant differences (ANOVA) for each parameter, by block, are indicated by different superscript letters. No letters indicate no significant differences.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>BLOCK 1</th>
<th>BLOCK 2</th>
<th>BLOCK 3</th>
<th>BLOCK 4</th>
<th>BLOCK 5</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil shear strength (kN/m²)</td>
<td>11.4 ± 1.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4.4 ± 1.4&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>3.7 ± 0.8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.7 ± 1.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.2 ± 1.4&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>5.4 ± 0.7</td>
</tr>
<tr>
<td>Soil water content (%)</td>
<td>35.6 ± 0.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>27.0 ± 3.9&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>20.4 ± 1.7&lt;sup&gt;b&lt;/sup&gt;</td>
<td>21.3 ± 3.0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>24.6 ± 1.0&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>25.8 ± 2.0</td>
</tr>
<tr>
<td>Soil organic matter (%)</td>
<td>16.0 ± 0.5</td>
<td>17.2 ± 2.4</td>
<td>16.0 ± 1.0</td>
<td>17.7 ± 0.2</td>
<td>17.9 ± 1.3</td>
<td>17.0 ± 0.5</td>
</tr>
<tr>
<td>Extractable NO₃&lt;sup&gt;-&lt;/sup&gt; (nmol NO₃·gdw&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>12.1 ± 1.3&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>13.9 ± 0.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10.4 ± 0.2&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>6.0 ± 2.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10.6 ± 0.9&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>10.6 ± 1.0</td>
</tr>
<tr>
<td>Belowground vegetation (g m⁻²)</td>
<td>413.4 ± 91.4</td>
<td>932.2 ± 124.0</td>
<td>648.2 ± 125.6</td>
<td>542.3 ± 137.4</td>
<td>521.0 ± 137.1</td>
<td>611.4 ± 61.2</td>
</tr>
<tr>
<td>Vegetation stem height (cm)</td>
<td>99.4 ± 3.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>120.9 ± 4.2&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>128.0 ± 8.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>143.1 ± 5.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>133.6 ± 6.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>125.0 ± 3.4</td>
</tr>
<tr>
<td>Live stems (ind. m⁻²)</td>
<td>230.0 ± 33.5</td>
<td>194.0 ± 22.5</td>
<td>284.0 ± 27.0</td>
<td>290.0 ± 18.5</td>
<td>284.0 ± 21.3</td>
<td>256.4 ± 12.3</td>
</tr>
<tr>
<td>Dead stems (ind. m⁻²)</td>
<td>6.0 ± 4.2</td>
<td>34.0 ± 9.8</td>
<td>28.0 ± 6.6</td>
<td>52.0 ± 14.7</td>
<td>24.0 ± 8.6</td>
<td>28.8 ± 4.7</td>
</tr>
<tr>
<td>Flowers (ind. m⁻²)</td>
<td>64.0 ± 12.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>30.0 ± 8.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>60.0 ± 14.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>118.0 ± 10&lt;sup&gt;c&lt;/sup&gt;</td>
<td>90.9 ± 19.1&lt;sup&gt;d&lt;/sup&gt;</td>
<td>72.4 ± 7.4</td>
</tr>
<tr>
<td>Percent cover (%)</td>
<td>28.8 ± 7.2</td>
<td>38.8 ± 6.3</td>
<td>49.4 ± 4.4</td>
<td>38.1 ± 5.7</td>
<td>39.4 ± 1.8</td>
<td>38.9 ± 2.5</td>
</tr>
</tbody>
</table>
Table 6. Mean ± standard error of initial environmental vegetation parameters comparing front and back half of experimental plots (n = 20) in October 2019. Significant differences (ANOVA, p < 0.05) between front and back parameters are indicated by italics.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Front</th>
<th>Back</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation stem height (cm)</td>
<td>116.7 ± 3.5</td>
<td>133.4 ± 5.2</td>
</tr>
<tr>
<td>Live stems (ind. m⁻²)</td>
<td>249.6 ± 19.3</td>
<td>263.2 ± 15.5</td>
</tr>
<tr>
<td>Dead stems (ind. m⁻²)</td>
<td>32.8 ± 7.8</td>
<td>24.8 ± 5.1</td>
</tr>
<tr>
<td>Flowers (ind. m⁻²)</td>
<td>81.6 ± 10.3</td>
<td>63.2 ± 10.5</td>
</tr>
<tr>
<td>Percent Cover (%)</td>
<td>43.0 ± 3.3</td>
<td>34.8 ± 3.6</td>
</tr>
</tbody>
</table>

3.4. Discussion

Loss of transplanted mussels after 1 year was greater than 50% across most treatment plots, regardless of initial treatment density. These findings are similar to past studies using both natural populations (Franz, 2001) or transplanted populations (Honig et al., 2015) which all reported similar loss rates of 45% and 56%, respectively. Franz (2001) documented a survivorship curve for *G. demissa* with estimated 50% mortality every year across two marsh elevations in Jamaica Bay, NY, USA. In other studies, it was found that differences in survivorship reflected horizontal distance from the edge versus interior marsh and higher vegetation stem densities positively associated with lower mortality (i.e., Lin, 1990; Franz, 2001; Honig et al., 2015; Derksen-Hooijberg, 2018). Mortality could be due to temperature stress, predation, salinity stress, and local competition (Lin, 1990; Franz, 2001; Honig et al., 2015). The rate of loss found in this study for transplanted mussels is not very different from those reported in natural populations. This suggests an important consideration when designing a restoration project (i.e., if the goal is to have 400 ind. m⁻² at the end of the study, consider planting 800 ind. m⁻²).

Immigration and emigration of mussels occurred as evidenced by the originally cleared back half of the plots containing over 30% of the final mussel density, although, individual mussels were not tracked. These redistribution estimates may not be accurate since I am not 100% confident that mussels found in back plots came from the front plots as there were no barriers installed to prevent movement from outside of the plot, nor were the individual mussels transplanted in the front of plots tagged. However, all mussels from the front and back of each plot were removed before initiation of the experiment so that the only mussels present were the mussels manually transplanted.

Mussel movement in response to environmental stressors has been documented along the Atlantic coast (Bertness, 1984; Bertness & Grosholz, 1985; Isdell et al., 2018). For example, Franz (2001) found that *G. demissa* in marsh interiors were likely populated, not by larval settlement directly, but by immigration over the first two years of the mussel’s life. Ribbed mussels are able to move by splicing their byssal thread proteins from their bodies and then regrowing and attaching them on substrate somewhere else if they become dislodged (Bell & Gosline, 1996). After transplantation, it is possible that mussels placed at the front half of the plot immigrated towards the marsh interior where *S. alterniflora* stem densities were higher, and lower wave and tide exposure were observed, providing more protected habitat. This may also
explain greater final densities at less exposed blocks (4, 5) which experienced less than 48% mussel loss, as opposed to more exposed blocks (1, 2) which experienced more than 93% mussel loss (Table 4). Maintenance of higher densities at less exposed blocks may suggest that there are some environmental conditions and locations more favorable for successful living shoreline restoration projects using gulf ribbed mussels.

Incorporating mussels into living shorelines may be difficult due to mortality and movement, but overall survivorship matched documented survival curves of natural and transplanted populations along the Atlantic coast and its ability to migrate to favorable conditions may be its strength as a potential tool for coastal restoration (Derksen-Hooijberg, 2018). Shoreline consideration is important when determining a mussel transplantation site. In this study the highest mussel loss occurred in Block 1, which was the most exposed block to the open channel and had the lowest amount of vegetation percent cover. The lowest mussel loss occurred in the more protected blocks, Blocks 4 and 5. These blocks were the farthest away from the open channel and were characterized by having higher amounts of vegetation percent cover. It also may be worthwhile to have a target final mussel density and initially transplant at least two times the target density to account for loss rates reported in this study as well in transplanted and natural ribbed mussel populations on the Atlantic coast when designing a living shoreline project incorporating gulf ribbed mussels. Living shorelines can be used to adapt to the dynamic and changing coastal environment in Louisiana marshes and may be particularly valuable. Combined, ribbed mussels and marsh vegetation provide valuable benefits to salt marsh production (Franz, 1997; Angelini et al., 2015; Derksen-Hooijberg, 2018); consequently, ribbed mussels could prove to be an integral part of healthy marshes. Better understanding of the gulf ribbed mussel habitat needs, and population dynamics would help inform design of future living shoreline restoration projects.

3.5. Implications
This study provides valuable insight and critical data for mussel transplantation success and movement in a large-scale field manipulation experiment for southeast Louisiana. Shoreline characteristics (e.g., relative shoreline exposure and vegetation cover) appear to be important considerations for establishing successful living shoreline restoration projects using transplanted ribbed mussels. This study suggests that similar living shoreline projects should transplant at least double the final target mussel density to account for the anticipated loss in density that was observed here and in studies on the Atlantic coast. Understanding the dynamic relationship between the gulf ribbed mussel and the environmental characteristics in which it lives is necessary to augment implementing native ecosystem engineers into coastal restoration efforts. The results of this study can be used to inform future studies of a similar nature and living shoreline restoration efforts throughout coastal Louisiana should be continued.
CHAPTER 4. SUMMARY AND CONCLUSIONS

Gulf ribbed mussels are important in estuarine systems on local and large scales. Studies along the Atlantic coast have shown how important ribbed mussels are in marine and estuarine ecology; similar evidence along the Gulf coast would improve our understanding of coastal marsh dynamics and ecology. As I have shown in these studies, there is a facultative mutualism between the gulf ribbed mussel and *S. alterniflora*. This work provides the first systematic surveys and assessments of gulf ribbed mussel presence over a large area of fringing marsh, and the first look at using this species as a potential living shoreline restoration tool in coastal Louisiana. Gulf ribbed mussels are relatively ubiquitous in southeast Louisiana marshes and are found in a range of densities. The knowledge gained here on gulf ribbed mussel distribution, density, and habitat associations, provides insight into its potential use as a tool in future restoration efforts.

As ecosystem engineers, ribbed mussels could help improve marsh resilience. Gulf ribbed mussels were found to be common and often in high densities along the marsh edges sampled in a large-scale survey. The distribution of mussels was not consistent along the lake edge, with mussels more commonly found and in significantly higher densities on the north shoreline relative to the south and west shorelines of Sister Lake. Mussel presence and density was found to be more likely and higher where there was greater vegetation percent cover. The north shoreline had some of the highest vegetation percent cover along with being characterized, in general, by having the lowest relative elevation and highest relative shoreline exposure with a dominant wind from the southeast. Elevation and relative shoreline exposure on the north shoreline allow for more inundation and mussel recruitment. Inundation is important for gulf ribbed mussels as they are filter feeders and rely on high tides in order to feed. Dominant winds from the southeast may carry mussel larvae to the north shoreline where they are able settle and grow well. Having new knowledge of these potential drivers of gulf ribbed mussel habitat association and distribution gives insight as to which type of shoreline may be ideal for gulf ribbed mussel transplantations in future living shoreline restoration projects.

Densities reported here are similar to what is seen for the more well studied *G. demissa* on the Atlantic coast where their role in ecosystem function and nutrient cycling is well documented and established. This suggests the need to further explore the role that gulf ribbed mussels play in Gulf of Mexico marshes. These findings show promise that *G. granosissima* may be critical in supporting marsh productivity and stability through increased nutrient deposition and sediment strength, which has the potential to reduce environmental stressors increasing with climate change.

In order to incorporate native ecosystem engineers into living shorelines in southeast Louisiana, understanding mussel transplantation success and movement in a large-scale field manipulation is necessary. Mussel survivorship was not uniform along a gradient of environmental conditions in this study. Block 1 had the highest mussel loss out of all the blocks and was characterized by high exposure to the open channel and lowest vegetation percent cover. Blocks 4 and 5 saw the highest mussel survivorship and were characterized by being the most sheltered blocks from the channel and having higher vegetation percent cover. This increase of shelter and vegetation percent cover may have provided extra substrate for the mussels to latch onto with their byssal threads and survive. During monitoring of the gulf ribbed mussels’ transplantation, there was a ~50% loss in overall mussel density (based on the assumption that mussels found in the back half of plots migrated from the front half) compared to initial transplantation density after a year. This rate of loss is comparable to what is seen in natural
populations of *G. demissa* and should be taken into consideration when planning a mussel transplantation event for restoration efforts. In order to account for this anticipated rate of mussel loss, when designing a transplantation event or restoration project the end goal mussel density should be doubled in the initial mussel planting to cover the loss that will occur. Ribbed mussels are also known to move (albeit, slowly) from adverse environmental conditions, such as changes in salinity, inundation, or shoreline movement over time. This may limit their immediate use as land loss remediation tools in living shoreline projects along the coast of Louisiana as there is high marsh loss and increased inundation in many areas along the coast. Further work is needed to better quantify gulf ribbed mussel impacts on soil nutrients and plant productivity in coastal Louisiana along with a better understanding of gulf ribbed mussel recruitment, survivorship, and growth across a range of environmental conditions. Living shorelines can be used to adapt to dynamic and changing coastal Louisiana marshes and the continued exploration of gulf ribbed mussels as a tool should continue to be considered. Understanding gulf ribbed mussel habitat characteristics, ecology, and environmental drivers in southeast Louisiana and along the entire Gulf coast is important to better inform future restoration projects in this region.

These studies reveal that mussels could be a viable restoration tool in coastal Louisiana. Gulf ribbed mussels are commonly present in Louisiana marshes, and can be found in high densities required for transplantations in living shoreline projects. These mussels are also able to be successfully transplanted and monitored for a year and proved to be adaptive and resilient over time. This work is important for the future resilience of coastal Louisiana and may potentially aid in land loss mitigation efforts in the future. Further work exploring the gulf ribbed mussel as a restoration tool in coastal Louisiana should be prioritized and continued.
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VITA

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