POPULATION ECOLOGY OF THE RIBBED MUSSEL IN SOUTHEASTERN LOUISIANA

A Thesis

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I have argued in this book that we are human in good part because of the particular way we affiliate with other organisms. They are the matrix in which the human mind originated and is permanently rooted, and they offer the challenge and freedom innately sought. To the extent that each person can feel like a naturalist, the old excitement of the untrammeled world will be regained. I offer this as a formula of reenchantment to invigorate poetry and myth: mysterious and little known organisms live within walking distance of where you sit. Splendor awaits in minute proportions.

E. O. Wilson, Biophilia

So speak out loud of
the things you are proud
And if you love this coast
Then keep it clean as it hopes
'Cause the way that it shines
May just dwindle with time
With the changes it will confront
And with each gift that you share
You may heal and repair
With each choice you make
You may help someone's day
Well I know you are strong
May your journey be long
And now I wish you the best of love

Xavier Rudd

A human being is a part of the whole called by us universe, a part limited in time and space. He experiences himself, his thoughts and feeling as something separated from the rest, a kind of optical delusion of his consciousness. This delusion is a kind of prison for us, restricting us to our personal desires and to affection for a few persons nearest to us. Our task must be to free ourselves from this prison by widening our circle of compassion to embrace all living creatures and the whole of nature in its beauty.

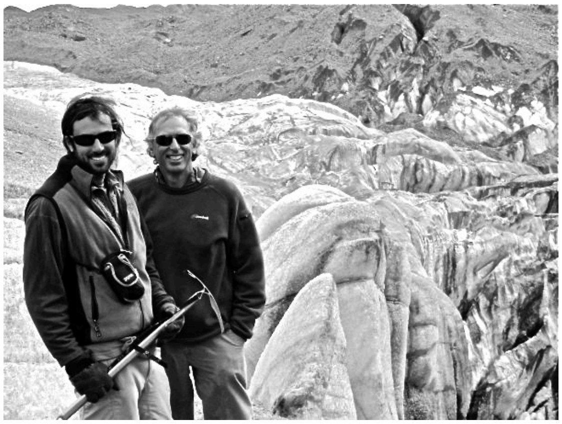
Albert Einstein

The Road goes ever on and on
Down from the door where it began.
Now far ahead the Road has gone,
And I must follow, if I can,

Pursuing it with eager feet,
Until it joins some larger way
Where many paths and errands meet.
And whither then? I cannot say.

Yet feet that wandering have gone
Turn at last to home afar.
Eyes that fire and sword have seen,
And horror in the halls of stone
Look at last on meadows green
And trees and hills they long have known.

The mountains are calling. And I must go.
~ John Muir



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ABSTRACT

Benthic intertidal bivalves play an essential role in estuarine ecosystems by contributing to habitat provision, water filtration, and promoting productivity. As such, ecosystem level changes that impact population distributions and persistence of local bivalve populations may have large ecosystem level consequences, making it important to better understand the population distribution and ecology of native bivalve populations. Gametogenesis, recruitment, growth, mortality, size structure and density of the ribbed mussel, *Geukensia demissa*, were examined across a salinity gradient in southeastern Louisiana. In summer 2012, 100-m transects were placed at interior and edge marsh plots to collect data on mussel density, and vegetation data at duplicate sites in upper (salinity ~4), central (salinity ~8) and lower (salinity ~15) Barataria Bay, LA. Caged growth and recruitment plots were established adjacent to each transect, in April, and growth, mortality and recruitment of individually marked mussels within plots were recorded in November 2012. Mussels were randomly sampled monthly from low (~ 5) and high (~25) salinity marsh sites, and histologically processed to determine the seasonal progression of gametogenesis. Mussel densities were greatest within mesohaline marsh (66.6 $\pm$ 18 m^{-2}), *J. roemerianus* vegetation (191.2 $\pm$ 42.7 m^{-2}) and plots experiencing 20-60% annual flooding rates (46.7 $\pm$ 13.8 m^{-2}). Mussel recruitment, growth, size and survival were significantly higher at mid and high salinity marsh edge sites as compared to all interior and low salinity sites. Peak gametogenic ripeness occurred between April and September, positively correlated with temperature, and coincidental with seasonal shifts in salinity. The observed patterns of density, growth and mortality in Barataria Bay may reflect detrital food resource availability due to local site flooding rates, vegetation community distribution along the salinity gradient, and reduced predation at higher salinity edge sites.

CHAPTER 1. INTRODUCTION

Salt marshes are incredibly important habitats that provide a myriad of environmental services for both human and wildlife communities. Such services include mitigation of storm surge-induced coastal erosion (Redfield,1972; Leonard and Reed 2002), detoxification of industrial and agricultural run-off (Seitzinger, 1988), habitat for juvenile nekton (McIvor and Odum 1988) as well as habitat for resident nekton species (Minello et al., 1994; Peterson and Turner, 1994). However, salt marsh habitats throughout the United States have suffered incredible losses, particularly in Louisiana, where habitat loss through subsidence and erosion has been estimated at over 50 km^2 yr^{-1} (Barras et al., 2003).

Salt marshes in southeastern Louisiana are increasingly vulnerable to wave-driven erosion that is projected to increase with rising sea level (Barras et al., 2003). Horizontal marsh retreat can result in the continued erosion of sunken marsh platforms, allowing wave-driven erosion to play a greater role in converting marsh areas to open water (Wilson and Allison, 2008). In particular, Barataria and Terrebonne Bays have experienced significant marsh retreat, which is attributed to decreased sediment accretion rates resulting from the damming of nearby Bayou Lafourche in 1904, and the construction of an artificial levee along the Mississippi River in 1927 (FitzGerald, 2003). Combined with wave-driven erosion from tropical storm exposure and expected sea-level rise in the Gulf of Mexico, the salt marshes of Barataria and Terrebonne Bays are particularly threatened (Baumann, 1984).

Greater understanding of the complex ecological processes occurring within coastal marshes, including the assessment of faunal communities involved in nutrient cycling, soil stabilization and trophic energy transference, is needed to evaluate the present state and future threats to vulnerable marsh communities (CPRA, 2012). While recent focus has centered on the economically valuable eastern oyster (*Crassostrea virginica*; Coen and Luckenbach, 2000), the ecology of other estuarine bivalves, such as the ribbed mussel (*Geukensia demissa*) is largely unknown in southeastern Louisiana.

The ribbed mussel, *Geukensia demissa*, is an euryhaline benthic bivalve, native to the western Atlantic coast from the Gulf of St. Lawrence to the northern Gulf of Mexico (Watt et al., 2011; Bertness, 1984; Spicer, 2007). Recent studies have revealed an expansion of ribbed mussel distribution, primarily as a result of ballast dumping and shellfish shipping leading to successful invasions of northern Venezuela (Baez and Severeyn, 2005), San Francisco Bay, Anaheim Bay and Baja California (Torchin et al., 2005). A large majority of studies have focused on Atlantic populations, particularly within temperate marshes (Evgenidou and Valiela, 2002; Franz, 1993; Borrero, 1988). Several studies have documented population structure and distribution as far south as Georgia (Kuenzler, 1961), while relatively little is known about Gulf populations (Spicer, 2007).

Ribbed mussels typically inhabit coastal marshes, in large aggregations upon hard rocky shore and within marsh sediments (Stiven and Gardner, 1992). Individuals anchor to nearby shells, nearby hard substrate or marsh vegetation with strong byssal thread attachments (Franz, 1997). Mature adults average 8 cm in length and have been recorded in population densities of greater than 2000 m^{-2} in southern New England salt marshes (Chintala et al., 2006). Ribbed mussels are r-selected cast spawners, producing large numbers of small planktonic eggs (Brousseau, 1982). Development and subsequent settlement typically lasts 3-4 weeks, after which juveniles migrate short distances to final attachment sites using a muscular foot and by byssal-drifting within local currents (Widdows, 1991). Through final settlement within large aggregations, ribbed mussels are capable of filtering large volumes of flooded marshes each tidal cycle, ingesting a wide selection of phytoplankton, detrital cellulose, bacteria and protists (Jordan and Valiela, 1982). Ribbed mussels thus play an important role in marsh nutrient cycling, incorporating nitrogen into growth and metabolism, excreting ammonia or dissolved organic nitrogen and depositing feces and pseudofeces into host sediments (Jordan and Valiela, 1982). Such nutrient deposition may contribute to a mutualistic relationship where mussels promote vegetative growth and strengthen rootmass through byssal attachment while host cordgrass provides mussels with stable anchoring substrates, detrital food resources, shade protection, defense from predation and flow reduction, ultimately strengthening host soils (Bertness, 1984; Lin, 1991; Watt et al., 2011).

The high tolerance of ribbed mussels to environmental stressors including extreme temperature (Hilbish, 1987), salinity (Neufeld and Wright, 1998) and relative flooding rates (Franz, 1997) is well-documented and may contribute to their successful invasion within introduced habitats (Torchin et al., 2005, Baez and Severeyn, 2005). Interestingly, while ribbed mussels in both tropical and temperature marshes were found in greater densities and smaller size classes at the marsh edge, gametogenic timing in Venezuela was found to coincide with seasonal fluctuations in salinity in contrast to seasonal temperature-driven gametogenesis observed along the Atlantic coast (Brousseau, 1982). Therefore, while some aspects of mussel population ecology may be similar across disparate climatic regimes, specific population processes may differ including patterns of reproduction, juvenile recruitment, growth and mortality.

Such population processes of ribbed mussels are well documented within temperate Atlantic populations (Kuenzler, 1961; Bertness, 1984; Franz, 1993; Culbertson at al. 2008; Watt et al., 2011). Seasonal spawning of mussels in Atlantic populations typically occurs mid-summer, as temperatures rise and is often greater at the marsh edge where increased flooding and detrital food availability fuel greater metabolic and reproductive investment (Brousseau, 1982; Franz, 1996). Juvenile recruitment consequently peaks mid-summer, as larval mussels require 2-3 weeks to fully develop, and is often greater at the marsh edge where increased flooding rates carry suspended larval mussels towards host vegetation and conspecific settlement substrates (Nielsen and Franz, 2005). As well, increased temperatures during peak seasonal vegetation productivity promotes relative faster growth rates during summer months, particularly at the marsh edge (Evgenidou and Valiela, 2002). Within marsh interiors, reduced flooding rates limit growth and can result in high rates of starvation mortality (Franz, 1997). Conversely, greater flooding rates at marsh edge expose mussel populations to invertebrate predators including the mud crab, *Panopeus herbstii* and the blue crab, *Callinectes sapidus*, resulting in greater predation mortality (Lin, 1991).

Variations in ambient salinity may also significantly affect population processes in ribbed mussels. Mussels exhibit a euryhaline distribution, inhabiting oligohaline marsh to salinities up to 70, although peak population densities are typically found between 15-34 (Bertness, 1984). Sophisticated metabolic osmoregulation and a range of adaptive behaviors allow ribbed mussels to survive within such a wide range of salinities (Strange and Crowe, 1979). Recent studies suggest that such osmoregulation is mediated through a rapid decrease in tissue volume, followed by active transport of solutes through the hemolymph (Biship et al., 1994; Deaton, 2001). Long-term acclimation to salinity stress involves the extended facilitation of amino acid transport within ventricular tissues, while gill and mantle tissues are less regulated due to their repeated exposure to salinity change during tidal fluxes (Neufeld and Wright, 1996). Behavioral responses included metabolic depression and shell-closure, with eventual death under long-term chronic conditions (Wang et al. 2011).

Although ribbed mussels are capable of surviving within a broad range of salinities, osmotic stress can significantly affect patterns of mussel gametogenesis. In Venezuelan marshes experiencing large seasonal shifts in salinity, reproductive timing was found to coincide with the transitions between dry to wet seasons (Baez and Severeyn, 2005). As well, relative flooding rates may be greater in polysaline marsh environments along coastal margins subject to tidal fluctuations, marine weather fronts and relative sea level rise (Feagin et al., 2010). Similarly, vegetation diversity and density may vary greatly among salinity and flooding regimes (DeLaune et al., 2003, Davis et al., 2011). Host vegetation density, *S. alterniflora* in particular, has been shown to be an important determinant of ribbed mussel population density and structure by ameliorating environmental stress, serving as attachment substrates for larval mussels, providing necessary detrital resources, and providing physical protection from crab predation (Bertness, 1984; Franz, 2001; Lin, 1991).

While the effects of vegetation density and flooding rates on mussel ecology within Atlantic polysaline marsh have been extensively studied (Jordan and Valiela, 1982; Bertness, 1984; Chinatala et al., 2006), relatively few studies have examined estuarine ribbed mussel populations along a strong salinity gradient, particularly within Mississippi deltaic marshes along the northern Gulf of Mexico (see Spicer, 2007). Understanding these basic distribution and population processes is critical to predicting effects of environmental change on local ecosystems.

The Terrebonne Bay and Barataria Bay estuarine systems in southeastern Louisiana both experience large salinity gradients from their headwaters near Mississippi River distributaries through coastal barrier islands along the northern Gulf of Mexico (Inoue and Wiseman Jr., 2000; Inoue, 2008). Temperatures vary little between each bay, but seasonally range from 5 °C in January to over 33 °C in August (Feng and Li, 2010). In contrast, seasonal patterns of salinity vary greatly within the mesohaline marshes of Cocodrie, Terrebonne Bay (0-10) and among three salinity regimes present in Barataria Bay (Turtle Bay: 0-5, Hackberry Bay: 10-15, Raccoon Lake: 15-25; Wiseman Jr. et al., 1990; Louisiana Office of Coastal Protection and Restoration, 2012). Seasonal flooding of both bays occurs during the spring as fresh runoff flows through extensive marsh Mississippi River distributaries. Barataria and Terrebonne bays are also subject to significant marine influx from both summer southerly warm fronts and thermal expansion within the Gulf of Mexico (Barbe, 2000). Conversely, strong northerly cold fronts result in annual low water between November and January (Feng and Li, 2010).

Long-term salinity data from southeastern Louisiana suggests recent increases in salinity which may result in decreased productivity and death of marsh vegetation, accelerating land loss, and increasing environmental stress on native fauna, with potentially long-term cascading trophic consequences (Byrne, et al., 1976; Wiseman et al., 1990). Proposed coastal restoration plans involving Mississippi riverine diversions may also significantly affect long-term salinity, marsh elevation and subsequently floral and faunal intertidal community structure.

The first chapter of this thesis focused on examining the distribution, and processes governing ribbed mussel populations within Barataria Bay, Louisiana. Specifically, this chapter quantifies ribbed mussel distribution and population structure in low, mid and high salinity (~3, 8, 15 salinity mean) zones at interior and marsh edge sites in Barataria Bay. To help explain the observed patterns, the work also quantifies mussel recruitment, growth and mortality in relation to salinity, marsh zone, flooding and vegetation community parameters.

Within the three salinity regimes present in Barataria Bay, it is hypothesized that ribbed mussel density will be greatest in mesohaline marsh edges where the greatest densities and coincide with peak *S. alterniflora* density as has been found along the northeast coast of the U.S. (Bertness, 1984, Franz, 1997). In the upper regions of the estuary, reduced densities are expected due to non-optimal vegetative species and hypo-osmotic stress, potentially resulting in reduced growth rates, increased environmental stress and greater mortality. In polyhaline marshes exhibiting greater densities of the two most well-known marine consumers of ribbed mussels, the mud crab and the blue crab, predation may limit population densities at the marsh edge where greater submergence increases vulnerability and mortality despite high *S. alterniflora* density and adequate salinity. Mussel recruitment and growth rates are expected to be relatively greater and mortality rates lower in mesohaline marsh hosting high mussel and *S. alterniflora* densities due to increased attachment substrates and detrital resources, respectively.

The second chapter of this thesis compares the seasonal timing of gametogenesis at a high salinity site (Raccoon Lake, Barataria Bay, ~15 salinity), and a low salinity site (Cocodrie, Terrebonne Bay ~5 salinity). This work examines the relationship between peak ripeness and temperature and salinity interactions on ribbed mussels. Understanding reproduction triggers of ribbed mussels is important in explaining both natural distribution patterns, as well as provides critical information for the development of hatchery spawning techniques that could be used to enhance natural populations after extreme events and in the event of large environmental changes triggered by coastal restoration activities.

1.1 References

Baez, M. and Y. Severeyn. 2005. “Ciclo reproductivo de *Geukensia demissa* (Bivalvia:Mytilidae) en la playa de Nazaret, El Mojan, Estado Zulia, Venezuela.” *Ciencias Marinas* 31(001A): 111-118.

Barbe, D., Cruise, J. and K Crowder. 2000. “Sediment transport in a shallow coastal estuary during the winter season.” *Jour. Amer. Water Res. Ass.* 36(4):1-10.

Barras, J., S. Beville, D. Britsch, S. Hartley, S. Hawes, J. Johnston, P. Kemp, Q. Kinler, A. Martucci, J. Porthouse, D. Reed, K. Roy, S. Sapkota and J. Suhayda. 2003. “Historical and projected coastal Louisiana land changes: 1978–2050.” *Historical and Projected Coastal Louisiana LandChanges: 1978–2050*, *U.S. Geological Survey Open-File Report* 03-334.

Baumann, R. H., J. W. Day, et al. 1984. "Mississippi deltaic wetland survival - sedimentation versus coastal submergence.” *Science* 224(4653):1093-1095.

Bertness, M. 1984. “Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh.” *Ecology* 65(6): 1794-1807.

Bishop, S.H., Greenwalt, D.E., Kapper, M.A., Paynter, K.T. and L.H. Ellis. 1994. “Metabolic regulation of proline, glycine and alanine accumulation as intracellular osmolytes in ribbed mussel gill tissue”. *J. Exp. Zoo*l. 268:151–161.

Borrero, F.J. and T.J. Hilbish. 1988. “Temporal variation in shell and soft tissue growth of the mussel *Geukensia demissa*.” *Mar. Ecol. Prog. Ser.* 42:9-15.

Brousseau, D. 1982. “Gametogenesis and spawning in a population of *Geukensia demissa* (Pelecypoda: Mytilidae) from Westport, Connecticut.” *Veliger* 24(3):247-251.

Byrne, P., Borengasser, M., Drew, G., Muller, R.A., Smith Jr., B.L. and C. Wax, 1976. “Barataria Basin: Hydrologic and Climatologic Processes.” *Louisiana State University Center for Wetland Resources Sea Grant Publ.* No. LSU-T-76-010.

Chintala, M.,Wigand, C and G. Thursdby. 2006. “Comparison of *Geukensia demissa* populations in Rhode Island frings salt marshes with varying nitrogen loads.” *Mar. Ecol. Prog. Ser.* 320:101-108.

Coastal Protection and Restoration Authority (CPRA). 2012. “Louisiana’s Comprehensive Master Plan for a Sustainable Coast.” *Coastal Protection and Restoration Authority*. 1-172.

Coen, L.D. and M.W. Luckenbach. 2000. "Developing success criteria and goals for evaluating oyster reef restoration: Ecological function or resource exploitation?" *Ecological Engineering* 15(3-4): 323-343.

Culbertson, J.B., Valiela, I., Olsen, Y.S., and C.M Reddy. 2008. “Effect of field exposure to 38-year-old residual petroleum hydrocarbons on growth, condition index, and filtration rate of the ribbed mussel, *Geukensia demissa*.” *Environmental Pollution* 154: 312-319.

Deaton, L.E. 2001. "Hyperosmotic volume regulation in the gills of the ribbed mussel, *Geukensia demissa*: rapid accumulation of betaine and alanine." *Jour. of Exp. Mar. Biol. and Ecol.* 260 (2): 185-197.

Delaune, R.D., Reddy, C.N. and W.H. Patrick. 1981. "Accumulation of plant nutrients and heavy-metals through sedimentation processes and accretion in a Louisiana salt-marsh.” *Estuaries* 4(4): 328-334.

Feagin, R. A., Martinez., M.L., Mendoza-Gonzalez, G. and R. Costanza. 2010. “Salt marsh zonal migration and ecosystem service change in response to global sea level rise: a case study from an urban region.” *Ecology and Society* 15(4): 14.

Feng, Z. and C. Li. 2010. “Cold-front-induced flushing of the Louisiana Bays.” *Jour. Mar. Sys.* 82: 252-264.

Evgenidou, A. and I. Valiela. 2002. “Response of growth and density of a population of *Geukensia demissa* to land-derived nitrogen loading, in Waquioit Bay, Massachusetts.” *Estuarine, Coastal and Shelf Science* 55:125-138.

FitzGerald, D. et al., 2003. "Tidal prism changes within Barataria Bay and its effects on sedimentation patterns and barrier shoreline stability." *Trans. - Gulf Coast Assoc. of Geol. Soc*. 53: 243-251.

Franz, D. 1993. “Allometry of shell and body weight in relation to shore level in the intertidal bivalve *Geukensia demissa* (Bivalvia: Mytilidae).” *Jour. Exp. Mar. Biol. Ecol.* 174.:193-207.

Franz, D. 1996. “Size and age at first reproduction of the ribbed mussel *Geukensia demissa* (Dillwyn) in relation to shore level in a New York salt marsh.” *Jour. Exp. Mar. Biol. Ecol.* 205:1-13.

Franz, D. 1997. “Resource allocation in the intertidal salt-marsh mussel *Geukensia demissa* in relation to shore level.” *Estuaries* 20(1):134-148.

Franz, D.R. 2001. "Recruitment, survivorship, and age structure of a New York ribbed mussel population (*Geukensia demiss*a) in relation to shore level - A nine year study." *Estuaries* 24(3): 319-327.

Hilbish, T.J. 1987. “Response of aquatic and aerial metabolic rates of the ribbed mussel *Geukensia demissa* (Dillwyn) to acute and prolonged changes in temperature.” *J. Exp. Mar. Biol. Ecol.* 105:207-218.

Inoue, M., Park, D., Justic, D., and W. Wiseman, Jr.. 2008. “A high-resolution integrated hydrology- hydrodynamic model of the Barataria Basin system.” *Env. Model. Softw.* 23:1122-1132.

Jordan, T.E. and Valiela, I. 1982. “A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its signifiance in nitrogen flow in a New England salt marsh.” *Limnology and Oceanogr.* 27(1): 75-90.

Kuenzler, E. J. 1961. “Structure and energy flow of a mussel population in a Georgia salt marsh. *Limnol. Oce*anogr. 6:191-204.

Leonard, L.A., and D.J. Reed. 2002. “Hydrodynamics and sediment transport through tidal marsh canopies.” *Jour. of Coastal Reseach Special Issue* 36: 459-469.

Lin, J. 1991. “Predator-prey interactions between blue crabs and ribbed mussels living in clumps.” *Estuarine, Coastal and Shelf Science* 32: 61-69.

Louisiana Office of Coastal Protection and Restoration. 2012. Coastwide Reference Monitoring System-Wetlands Monitoring Data. Retrieved from Strategic Online Natural Resource Information System (SONRIS) database. http://coastal.louisiana.gov/index.cfm?md=pagebuilder&tmp=home&pid=92. Accessed 12/10/2012.

McIvor C.C. and W.E. Odum. 1988. “Food, predation risk, and microhabitat selection in a marsh fish assemblage.” *Ecology* 69:1341–1351.

Minello, T.J., Zimmerman, R.J., and R. Medina. 1994. “The importance of edge for natant macrofauna in a created salt marsh.” *Wetlands* 14: 184-198.

Neufeld, D.S. and S.H. Wright. 1996. "Salinity change and cell volume: the response of tissues from the estuarine mussel Geukensia demissa." *The Jour. of Exp. Biol.* 199 (Pt 7): 1619-1630.

Neufeld, D.S. and S.H. Wright. 1998. “Effect of cyclical salinity changes on cell volume and function in *Geukensia demissa* gills.” *Jour. Exp. Biol.* 201: 1421-1431.

Peterson, G.W. and R.E. Turner. 1994. “The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh.” *Estuaries.* 17: 235–262.

Pierce, S.K. and M.J Greenberg. 1972. “The nature of cellular volume regulation in marine bivalves.” *J. Exp. Biol.* 57: 681–692.

Redfield, A.C. 1972. “Development of a New England salt marsh.” *Ecological Monographs* 42: 201-237.

Seitzinger, S.P. 1988. “Denitrification in freshwater and coastal marine ecosystems: ecological and geochemical significance.” *Limnol. Oceanogr.* 33: 702-724.

Spicer, J. 2007. “A comparison of channel morphology, marsh elevation and biological processes in natural and dredged tidal salt marshes in Louisiana.” *Louisiana State University. School of Oceanography and Coastal Sciences*. *Doctoral Dissertation*. 1-104.

Stiven, A.A. and S.A Gardner. 1992. “Population processes in the ribbed mussel *Geukensia demissa* (Dillwyn) in a North Carolina salt marsh tidal gradient: spatial pattern, predation, growth and mortality.” *Jour. Exp. Mar. Biol. Ecol.* 160:81-102.

Strange, K.B. and J.H. Crowe. 1979. Acclimation to successive short term salinity changes by the bivalve *Modiolus demissus*. I. Changes in hemolymph osmotic concentration, hemolymph ion concentration and tissue water content. *J. Exp. Zool.* **210**, 221–226.

Torchin, M.E., Hechinger, R.F., Huspeni, T.C., Whitney and K.D Lafferty. 2005. “The introduced ribbed mussel (*Geukensia demissa*) in Estero de Punta Banda, Mexico: interactions with the native cord grass, *Spartina foliosa*.” *Biological Invasions*. 7:607-614.

Wilson, C.A., and M.A. Allison. 2008. “An equilibrium profile model for retreating marsh shorelines in southeast Louisiana.” *Estuarine, Coastal and Shelf Science*. 80:483-494.

Wang, Y., Hu, M., Wong, W.H., Shin, P., and S. Cheung. 2011. “The combined effects of oxygen availability and salinity on physiological responses and scope for growth in the green-lipped mussel *Perna viridis*.” *Mar. Poll. Bull.* 63:255-261.

Watt, C., Garbary, D.J. and C. Longtin. 2011. “Population structure of the ribbed mussel *Geukensia demissa* in salt marshes in the southern Gulf of St. Lawrence, Canada.” *Helgol. Mar. Res.* 65: 275-283.

Widdows, J. 1991. “Physiological ecology of mussel larvae.” *Aquaculture* 94:147-163.

Wiseman Jr., W. J., Swenson, E.M. and J. Power. 1990. “Salinity trends in Louisiana Estuaries.” *Estuaries* 13(3) 265-271.

CHAPTER 2. MUSSEL DENSITY, GROWTH, MORTALITY AND RECRUITMENT

2.1 Introduction

Benthic intertidal bivalves play an essential role in several marsh processes, contributing to physical habitat construction for resident invertebrate and vertebrate species while promoting vegetative productivity through suspended nitrogen filtration and biodeposition, ultimately strengthening host soils (Bertness, 1984). As such, ecosystem level changes that impact population distributions and persistence of local bivalve populations may have larger ecosystem consequences on vegetative communities, and soil properties (Jordan and Valiela, 1982). Given recent significant natural and man-made habitat alterations (i.e., Deepwater Horizon oil spill), combined with significant coastal land loss across Louisiana (DeLaune et al., 2003), it is important to better understand the population distribution and ecology of native bivalve populations and the potential impacts of coastal changes on the provision of these critical services.

The ribbed mussel, *Geukensia demissa*, is a euryhaline benthic bivalve, native to the western Atlantic coastal marsh from the Gulf of St. Lawrence to the northern Gulf of Mexico (Watt, 2011; Kuenzler, 1961; Spicer, 2007). Ribbed mussels generally form large aggregations within marsh sediments, byssally attached to conspecifics and salt-tolerant vegetation such as the cordgrass *Spartina alterniflora* (Chintata et al., 2006). Furthermore, ribbed mussels have been shown to filter large volumes of suspended detritus and microalgae each tidal cycle (Espinosa et al., 2008). This filtration may contribute to a mutualistic relationship with host vegetation where mussels promote shoot growth and strengthen root mass through nitrogenous biodeposition while the host cordgrass provides mussels with stable anchoring substrates, detrital food resources, defense from predation, ultimately strengthening host soils (Watt, 2011; Lin, 1991; Bertness and Leonard, 1997). While such ecosystem services have been well-documented within temperate and sub-tropical Atlantic coastal marshes (Stiven and Gardner, 1992), there is little data quantifying the contribution or role of non-commercial bivalve populations along the northern coastal areas of the Gulf of Mexico (but see Spicer 2007).

Ribbed mussel populations have been relatively well documented and studied along the Atlantic coast (Watt, 2011; Nielsen and Franz, 1995; Culberton at al., 2008; Bertness, 1984; Fell, 1982; Kuenzler, 1961). Along the Atlantic coast and in recent invasions to Venezuela (Baez et al., 2005) and Pacific Mexico (Torchin et al., 2005) studies have shown that salinity, marsh elevation and vegetation type and density affect the timing of gametogenesis, spatial and temporal patterns of juvenile recruitment and adult growth and mortality by varying seasonal cues triggering spawning, suitable substrate for new recruits, access to detrital resources, and vulnerability to predation (Brousseau, 1982; Nielsen and Franz, 1995; Lin, 1991). Within Louisiana, only one study has attempted to document ribbed mussel distribution, and this study was limited to mesohaline marsh in eastern Barataria Bay (Spicer, 2007), making it difficult to extrapolate out to a larger gradient of environmental conditions that exist across the coast, and to predict how shifting salinity, land loss and flooding from restoration, river management and climate may impact ribbed mussel populations.

Mussels exhibit a euryhaline distribution, and are typically found in marsh exposed to salinities of 15-34, although they are reportedly capable of surviving salinities of 3-48 (Pierce, 1970). Recent studies on the population distribution of ribbed mussels have been conducted in brackish and polyhaline marshes (>15), with little known about mussel densities within oligohaline marsh (Strange and Crowe,1979*;* Shumway and Youngson, 1979), although mussels

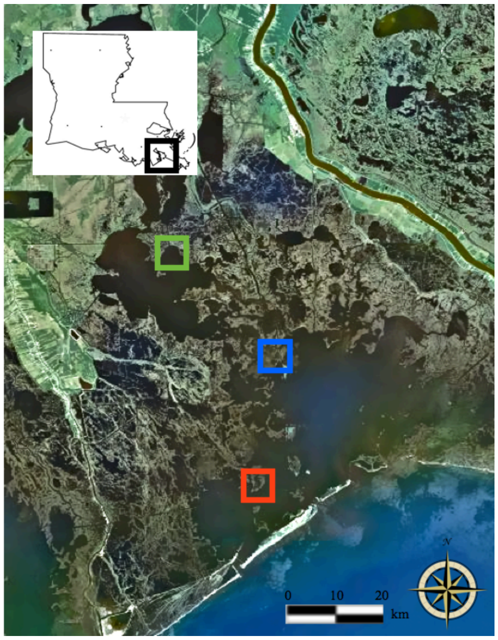


Figure 1.1. Field survey plots (Density), experimental cages (Growth and Mortality) and experimental pots (Recruitment) were placed in two sites in each of three salinity regimes. Oligohaline marsh was sampled in Turtle Bay (green), mesohaline marsh in Hackberry Bay (blue) and polyhaline marsh in Raccoon Lake (red) from 2011 - 2012.

are known to close their shells in response to hypo-osmotic stress (60% of seawater), possibly resulting in reduced filtration rates and eventual death of stressed mussels (Wang et al. 2011). Future restoration plans to divert Mississippi River water to threatened mesohaline coastal marsh in Louisiana (CPRA, 2012) may result in reduced salinities in areas of native mussel populations.

Host vegetation has been shown to be highly correlated with ribbed mussel population density and structure (Bertness, 1984). Well-documented associations with *S. alterniflora* have been shown to significantly affect mussel growth rates, reproductive output and mortality, as well as vegetative growth and productivity (Franz, 1997; Bertness and Leonard, 1997). In Rhode Island marsh, natural mussel density was found to be strongly correlated with above and below-ground *S. alterniflora* (cordgrass) density (Bertness, 1984). Cordgrass density and height could increase mussel density and survivorship through greater attachment substrate for juvenile recruits (Nielson and Franz, 1995), increasing suspended detrital food resources (Bertness and Grosholz, 1985) and spatial refuge from crab predation (Lin, 1991).

Marsh elevation and relative flooding rates affect site soil and vegetation characteristics, food and oxygen delivery and accessibility to both larval recruits and potential predators (Franz, 1993; Nielsen and Franz, 1995; Seed, 1980). Along the Atlantic coast, juvenile recruitment of several mussel species was largely determined by marsh elevation and relative flooding rates (Porri et al., 2007), and aggregations found to be exposed more than 50% of the time were found to have limited food resources and decreased metabolic respiration (Stiven and Gardner, 1992). Mussels experienced faster growth but higher mortality rates at the marsh edge due to greater access to suspended detritus and increased vulnerability to predators (Jordan and Valiela, 1982;

Lin, 1991), with higher densities in New England marsh recorded at edge versus interior marsh zones (Bertness, 1984). In similar studies, growth rate, reproductive output, juvenile recruitment and predation all decreased towards high interior marsh plots (Franz, 1997; Bertness, 1984), suggesting that flooding rates significantly affect mussel densities through several mechanisms.

While ribbed mussels have been extensively studied along the east coast, and shown to provide valuable ecosystem services (Watt 2011, Lin , Bertness and Leonard 1989), little is known about their role in providing critical ecosystem services within estuaries of the northern coast of the Gulf of Mexico, or about their population distribution. In areas with significant coastal change from both human and natural events occurring, understanding how these events may impact current populations, and potentially alter future populations of important bivalve populations is critical.

This study examined the effects of salinity, and marsh zone on ribbed mussel distribution across Barataria Bay. Across the salinity gradient typically present in Barataria Bay, (0-25),I hypothesized that ribbed mussel density will be greatest in mid-salinity marsh edges and coincide with peak *S. alterniflora* density (Bertness, 1984). In the upper regions of the estuary, mussel densities may be limited by reduced *S. alterniflora* densities and salinity. In the lower estuary, increased vulnerability to crab predation may limit mussel densities within marshes hosting intermediate *S. alterniflora* densities.

This study also sought to determine the effects of salinity and marsh zone (edge and interior) on mussel growth, mortality and juvenile recruitment in Barataria Bay. I expected that low salinity stress within interior low-salinity marsh will result in reduced growth rates and greater non-predation mortality, while crab populations along the edges of high-salinity marsh will result in faster growth rates but greater rates of predation mortality. Greater rates of recruitment may occur within mid-estuary and lower estuary marshes where the greatest adult mussel densities are thought to exist. Increased recruitment is expected at the marsh edge, which typically experience greater flooding rates and subsequent exposure to suspended larval mussels.

2.2 Methods

Study Site

Barataria Bay is a well-mixed, microtidal coastal plain estuary in southeastern Louisiana. Barataria Bay is located between the Mississippi River and Bayou Lafourche atop remnants of an abandoned deltaic lobe culminating in a chain of barrier islands separating Barataria Bay from the Gulf of Mexico (Figure 1.1, Delaune, 2003). Water temperature ranges from 6 to 33 ºC over the year. Mean salinity increases from fresh (0) near northern Mississippi River distributaries to polyhaline (25) near the Gulf of Mexico. Seasonally, riverine discharge, runoff and northerly cold fronts promote reduced salinities in the winter and early spring while southern warm fronts, Mississippi countercurrents and Gulf thermal expansion increase marine influx and salinities during the summer and fall (Walker et al., 2005). Water levels increase in the spring from riverine discharge and runoff, and remain high as marine influx and salinity increase through the late summer before falling to a winter low as northerly cold fronts rapidly flush Bay waters (Feng and Li, 2010). Vegetation in oligohaline marsh in upper Barataria Bay is dominated by *Spartina patens, Schoenoplectus americanus* and *Distichlis spicata* while transitional and polyhaline marshes are dominated by *S. alterniflora* and *Juncus roemerianus* (Louisiana Office of Coastal Protection and Recreation, 2012).

Sampling Design

Six sites were selected, with two sites located in oligohaline marsh (Turtle Bay; TB), two sites in low mesohaline marsh (Hackberry Bay; HB) and two sites in high mesohaline marsh (Raccoon Lake; RL). TB sites (29°32' 42 N 89°59'32 W) are located in upper Barataria Bay near Little Lake with 5-year salinity (2008-2012) averaging 3.5 (range 0.2-16.9; CRMS 6303, Figure 1.1). The surrounding marsh is dominated by *Spartina patens, Schoenoplectus americanus* and *Distichilis spicata*, with some *Paspalum vaginatum, Batis maritima and Avicennia germinans*. HB sites (29°24' 33 N 89°59'32 W) are located in mid-Barataria Bay, with five-year salinity (2008-2012) averaging 7.4 (range: 0.6-25.3; CRMS 0237). The surrounding marshes are dominated by *Spartina alterniflora, Juncus roemerianus* and *D. spicata*. RL sites (29°17' 46 N 90°01'15 W) are located in lower Barataria Bay, with 5-year salinity (2008-2012) averaging 15.5 (range 1.2-31.2; CRMS 0178). The surrounding marshes are dominated by *S. alterniflora* and *J. roemerianus.*

Field Survey

Sampling design

Transects were established at each site along the salinity gradient at edge and interior marsh to examine mussel distribution in relation to salinity and marsh zone (1, 5 m from water edge, Figure 1.2). Transects were 100 m in length, with 0.25 m^2 quadrats placed every 10 m for a total of 120 plots (3 salinity zones x 2 sites x 2 transect types x 10 sample plots = 120; hereinafter called "zone plots"). Five interior *S. alterniflora*, and five interior *J. roemerianus* plots were established where these species were present to examine relationships between dominant vegetation and mussel density (3 salinity zones x 2 sites x 2 vegetation types x 5 replicates = 60 plots; hereinafter called "vegetation plots").

Environmental variables

Salinity, temperature and water level data were downloaded from Coastwide Reference Monitoring System (CRMS) stations (RL: 0178, HB: 0237, RB: 6303) located near each study site. Within each quadrat, the depth of water and or distance to water level and current time were recorded. Flooding rates for each quadrat were calculated by relating water depth or soil elevation recorded in each plot to water levels recorded at CRMS station for the same time and day. Vegetation species presence, and stem density were quantified within each sample quadrat by counting and recording the number of stems for each species.

Mussel distribution

Within each quadrat, quadrats were excavated to 30 cm depth and all mussels removed and mussel densities (indiv. m^{-2}) calculated from abundance counts. Mussels were sized (mm) along the greatest distance between the shell's umbo and anterior edge with hand calipers. Surveys were conducted from May through July 2012.

Growth and mortality

Five caged quadrats were placed at both edge and interior marsh (1, 5 m from edge) at each of the six sites to determine the effects of salinity and marsh zone on mussel growth and mortality. Quadrats consisted of plastic mesh stretched over 0.25 m^2 PVC bases and raised 20 cm (Figure 1.3). Five randomly collected mussels from mid-salinity marsh (HB) were placed within each quadrat across all sites in accordance with previously observed mussel densities in

Figure 1.2. Mussel density was sampled within quadrats (0.25 m^2) placed along transects constructed in Barataria Bay, Louisiana from May to July, 2012.

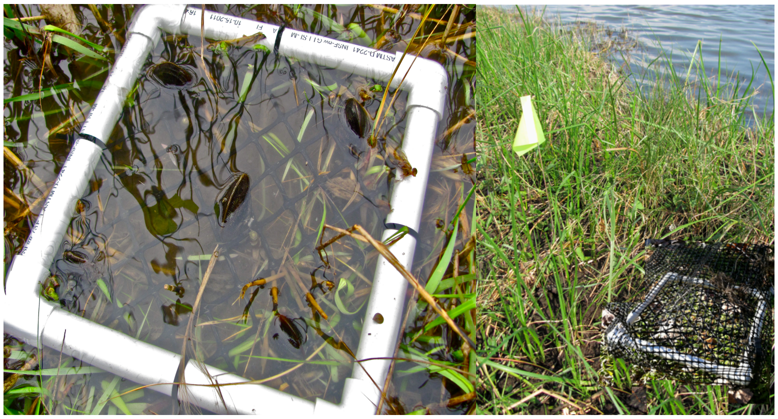


Figure 1.3. Caged quadrats (A) used in growth and mortality treatments consisted of plastic mesh stretched over 0.25 m^2 PVC with mesh sides raised 20 cm to create cubed enclosures. Mussels were placed within mesh grids, while quadrats were anchored at field sites from March-October, 2012.

Barataria Bay (Spicer, 2007). The mussels were evenly spaced between mesh spaces, with both shells and quadrats embedded in the marsh. Once placed, mussels were checked after 1 week to confirm byssal attachment within PVC quadrats. Mean size (± SE) of deployed mussels was 81.5 ± 5.1 mm.

All experimental quadrats were deployed in March and sampled in October 2012. The initial and final size of all live mussels was recorded by measuring the greatest distance between the shell's umbo and anterior edge (mm). Mussels were classified as "predated" if shells were broken or exhibited clear signs of forced entry, while intact shells were classified as "dead", implying mortality related to non-predation events.

Figure 1.4. Recruitment study. Flower pots (15 cm diam.) containing local filtered organic sediment were embedded at the marsh edge and interior (1, 5 m from channel). Five intact mussel shells (dead) were randomly collected from polyhaline marsh in Barataria Bay, cleaned of all fouling organisms and secured within plastic mesh anchored within each pot.

Recruitment

Three clay flower pots (15 cm diam.) were embedded at both marsh edge and interior (1, 5 m from channel, Figure 1.4) at the six sites to determine the effects of salinity and marsh zone on juvenile mussel recruitment. The pots were filled with local organic sediment, filtered over 13 mm mesh to remove vegetation and infauna. Five intact mussel shells were randomly collected in Barataria Bay, cleaned of all fouling organisms and secured within plastic mesh anchored within each pot. The pots were placed in the marsh in June, and sampled monthly with replacement through September 2012. Juvenile recruitment was determined by recording the number of recruits attached to sampled pots (shells, pots, mesh) each month using a dissecting microscope in the laboratory, and recorded as # recruits per pot.

Statistical Analysis

Environmental factors

Multivariate analysis of variance (MANOVA) was used to examine differences in flooding rates and dominant vegetation density between salinity and marsh zone. A significant MANOVA model resulted in examination of individual two-factor ANOVA for flooding rate, *J. roemerianus* stem density and *S. alterniflora* stem density. Significant results were examined with a Tukey's post-hoc comparison test.

Mussel density

Extremely high mussel densities were observed in several experimental plots, while no mussels were found in the majority of plots (64%). Due to resulting data overdispersion, the effects of salinity, marsh zone and their interaction on ribbed mussel density were assessed using a GLMM, with a negative binomial distribution function (Proc Glimmix, SAS). For transect plots, vegetation density and flooding rate were tested as covariates, only vegetation density was significant and retained in the model.

Mussel size

The effects of salinity were examined on all zone and vegetation plots combined using an ANOVA with a Tukey's post-hoc comparison test. For zone plots, the effects of salinity and zone were examined. However, very few mussels were found in *S. alterniflora* vegetation plots (5), precluding statistical comparison with *J. roemerianus* vegetation plots, where the most mussels were found (956).

Growth and mortality

The effects of salinity and marsh zone on mussel growth were examined using a 2-way ANOVA (factors: salinity [TB, RL, HB], marsh zone [edge, interior]. Tukey's post-hoc pairwise tests were used when significant single interactions were found. The effects of salinity and marsh zone on mussel mortality were examined using a chi-square test. At the highest salinity site only, the effects of marsh zone on predation-related mortality were examined using a chi-square test.

Juvenile recruitment

The effects of salinity, marsh zone on mussel recruitment was determined using a two-way ANOVA (factors: salinity [TB, RL, HB] and marsh zone [edge, interior]. Tukey's post-hoc tests were used for single significant effects.

2.3 Results

Environmental site characteristics

During 2012, water temperature in Barataria Bay averaged 23.6 ºC, ranged 10.2 ºC (February) - 32.1 ºC (August) and was similar at all field sites (Figure 1.5). Salinity gradients in Barataria Bay followed long-term averages (2008-2012). In the upper bay near TB, mean salinity averaged 3.16 ± 0.2, ranging from 0.44 - 15.9. HB, located mid-estuary, averaged 8.1 ± 0.2, ranging from 0.1 - 31.3 while at RL, in lower Barataria Bay, mean salinity averaged 16.4 ± 0.1, and ranged from 1.5 - 31.1.

Flooding rate was significantly greater within RL and HB than TB sites (RL: 31.6 ± 0.7, HB: 33.5 ± 0.5, TB: 16.2 ± 0.2 % annually, $F = 9.18$, $p < 0.01$, Table 1). Flooding rate also varied significantly by marsh zone with greater flooding at edge sites as compared to interior sites (edge: 31.0 ± 0.1, interior: 17.1 ± 0.3% annually, $F = 4.6$; $p < 0.01$, Figure 1.6A). Within vegetation plots, *S. alterniflora* plots flooded more often than *J. roemerianus* plots (*S. alterniflora:* 48.6 ± 0.2, *J. roemerianus*: 31.2 ± 0.6 % annually; $F = 6.04$, $p = 0.02$, Figure 1.6A).

Specifically, mean vegetation stem density was greater at the mid-salinity site (HB) as compared to the low (TB) salinity site, which was greater than at the high (RL) salinity site (HB: 1,146.2 ± 60.9, RL: 629.3 ± 12.4, TB: 464.1 ± 13.6 stems m^{-2}; $F = 5.7$, $p < 0.01$; Table 1). Species composition also varied by site. While *S. alterniflora* was found in similar densities at all sites, just over 50% of sites at TB hosted such vegetation while *S. alterniflora* was far more widespread at HB and RL (82, 98% of sites, Table 1). HB sites hosted the greatest densities of *S. alterniflora* and *J. roemerianus* (1, 468.7 ± 112.3, 322.2 ± 19.9 stems m^{-2}; $F = 3.69$; $p < 0.01$; Table 1). While *J. roemerianus* was also observed in high densities at TB, such vegetation was only found in less than 5% of plots while being far more common at HB (42%). Conversely, while the greatest densities of "Other" vegetation were found at HB sites (665.1 ± 112.3 stems m^{-2}), such vegetation was more widespread at TB, found in over 80% of plots (Table 1).

Within zone plots, vegetation density was similar at marsh edge and interior (637.4 ± 69.3, 693.6 ± 70.9, stems m^{-2}; Figure 1,6B). However, within targeted vegetation plots, *J. roemerianus* plots hosted greater vegetation densities than *S. alterniflora* plots (1,667.3 ± 220.7 stems m^{-2}, 462.3 ± 96.1 stems m^{-2}, $F = 25.0$, $p < 0.01$).

Mussel Density and Size

Within zone plots hosting mussels, salinity significantly affected mussel density ($n = 120$, $F = 10.01$, $p < 0.01$). Specifically, mussel densities were significantly higher at the mid-salinity site (HB), as compared to the high-salinity marsh (RL), which was significantly higher than at the low-salinity (TB) marsh sites (HB: 20.9 ± 5.8, RL: 11.1 ± 3.6, TB: 0.8 ± 0.2 m^{-2}; Figure 1.7A). Marsh zone was not a significant factor as edge and interior plots hosted similar mussel densities (edge: 10.0 ± 3.1, interior: 11.9 ± 4.5 m^{-2}). However, vegetation density was a significant covariate within the model with greater mussel densities associated with higher vegetation density ($n = 120$, $F = 4.27$, $p = 0.04$).

Within zone plots ($n=120$), mussel density increased with total vegetation density ($R^2 = 0.3$, $p < 0.01$, Figure 1,8A). Within the vegetation plots ($n=40$), mussel density increased with *J. roemerianus* density at HB ($R^2 = 0.9$, $p < 0.01$, Figure 1.8B) and was not significantly affected by *S. alterniflora* or other vegetation species. Overall, the majority of mussels were found within *J. roemerianus* plots in low-salinity TB (81.4%), mid-salinity HB (78.6 %) and RL (54.6%).

Flooding rate was not a statistically significant factor affecting mussel densities, although within zone plots, peak mussel densities were found in sites experiencing 40-60% annual flooding, with the greatest densities observed within interior plots at RL and edge and interior plots at HB (Figure 1.9A). In vegetation plots, peak densities were found in sites experiencing 20-40% flooding, within *J. roemerianus* plots at HB (Figure 1.9B).

At all sites (zone and vegetation plots), mean mussel size was found to be significantly greater at the two higher salinity sites (RL, HB) as compared to the low salinity site (TB) (RL: 53.6 ± 3.1, HB: 42.5 ± 3.6, TB: 11.7± 2.9 mm, ANOVA $t = -3.88, -51.6$, $p < 0.001$). Size class distributions at all plots within each site reflect similar relationships, as mussel size ranged from 29.5 - 76.6 mm ($n = 247$) at RL, 9.5-87.1 mm ($n = 999$) at HL, and from 2.8-27.7 mm ($n = 43$) at TB (Figure 1.10).

Within zone plots, mussels found within interior marsh plots were slightly larger than those at the marsh edge, but not significantly larger (interior: 47.8 ± 7.6 mm, edge: 32.1 ± 3.1 mm; ANOVA, $t = -2.37$, $p = 0.09$, Figure 1.10). However, size class distributions within edge plots were much more limited, ranging from 9.5- 55.9 mm ($n=150$), while mussels within interior plots represented a larger range of size classes ranging from 2.8 - 110.6 mm ($n = 178$). Within vegetation plots, mean mussel size within *J. roemeranius* plots averaged 49.3 ± 7.5 mm ($n = 956$) while the few mussels within *S. alterniflora* plots averaged 76.5 ± 15.3 mm ($n = 5$). Mean mussel size was similar among all observed flooding rates ($n = 1289$, $F = 0.86$, $p = 0.55$).

Growth and Mortality

Across salinity zones there was a significant salinity by marsh zone interaction for mussel growth ($F = 8.02$, $p < 0.01$). Differences were due to faster growth rates of mussels in edge plots at the two higher salinity sites (HB: 1.3 ± 0.1 mm mo^{-1}; RL: 1.1 ± 0.1 mm mo^{-1}) as compared to the lower salinity edge plot (TB: 0.3 ± 0.1 mm mo^{-1}) and all interior plots (RL: 0.5 ± 0.1 mm mo^{-1}, HB: 0.5 ± 0.2 mm mo^{-1} , TB: 0.25 ± 0.07 mm mo^{-1} ; Figure 1.11).

There was a significant effect of salinity on cumulative mussel mortality with the lowest

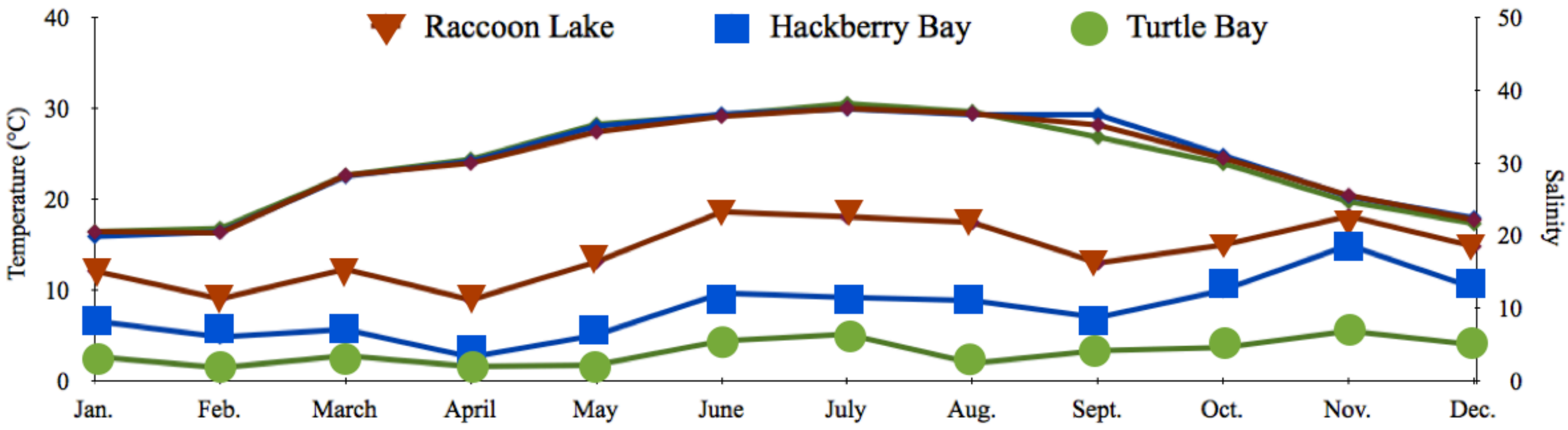


Figure 1.5. Mean monthly temperature and salinity were calculated from hourly data recorded at Coastwide Reference Monitoring System (CRMS) stations 0178, 0237 and 6303, located near experimental sites in Barataria Bay, during 2012. Small notched lines represent seasonal temperature. Salinity is represented by triangles at Raccoon Lake, squares at Hackberry Bay and circles at Turtle Bay.

Table 1. Mean (± SE) salinity, flooding rates and vegetation densities were recorded within zone and vegetation plots at three sites in Barataria Bay. Salinity was calculated from hourly data recorded at Coastwide Reference Monitoring System (CRMS) stations 0178, 0237 and 6303 located near field sites. Annual flooding rates were calculated from site elevation measurements correlated with annual flooding rates observed at nearby CRMS stations. Mean vegetation densities were calculated only for sites hosting such vegetation, with sample sizes noted within parentheses.

Site	Salinity	Flooding Rate (% annually)	*S. alterniflora* density (stems m^{-2})	*J. roemerianus* density (stems m^{-2})	"Other" density (stems m^{-2})	Total Vegetation Density (stems m^{-2})
Turtle Bay (44)	3.2 ± 0.2	16.2 ± 0.2	241.6 ± 23.1 (24)	1,030.0 ± 367.2 (2)	550.9 ± 71.3 (36)	464.1 ± 13.6 (44)
Hackberry Bay (60)	8.1 ± 0.2	33.5 ± 0.5	322.2 ± 19.9 (52)	1,468.7 ± 196.5 (25)	665.1 ± 112.3 (23)	1,146.2 ± 60.9 (56)
Raccoon Lake (56)	16.4 ± 0.1	31.6 ± 0.7	251.5 ± 13.3 (55)	621.4 ± 47.3 (14)	182.8 ± 19.8 (13)	629.3 ± 12.4 (60)

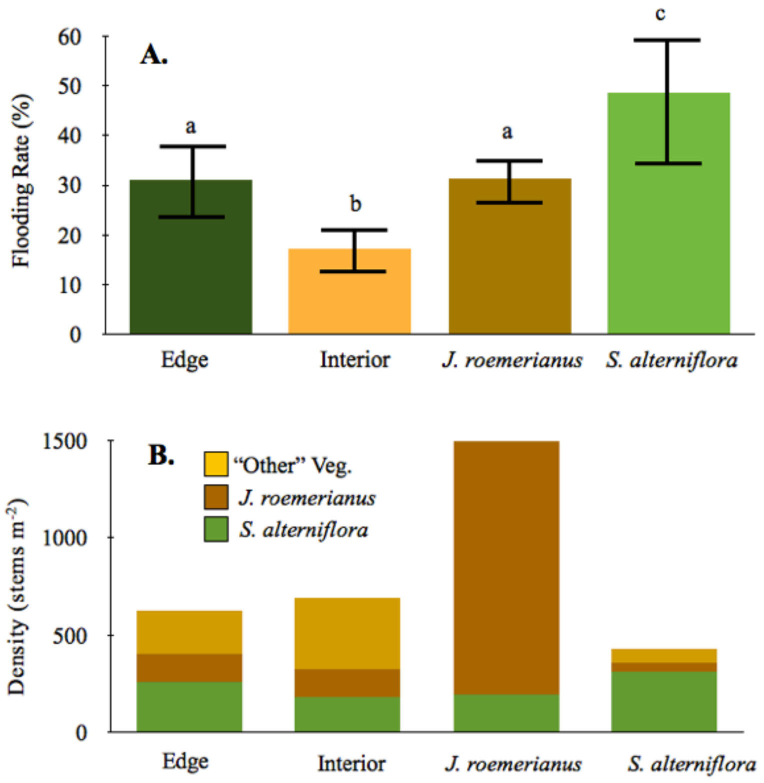


Figure 1.6. Mean annual flooding rates in marsh zone and vegetation plots (A) were calculated by comparing local site elevation to seasonal fluctuations in water depths recorded hourly at CRMS sites 0178, 0237 and 6303 in 2012. All vegetation within marsh zone and vegetation plots were counted and converted to density (B). "Other" vegetation included all species present excluding *S. alterniflora* and *J. roemerianus.* See text for inclusive list. Standard error indicated by bars, while statistically similar data share letters (α= 0.05).

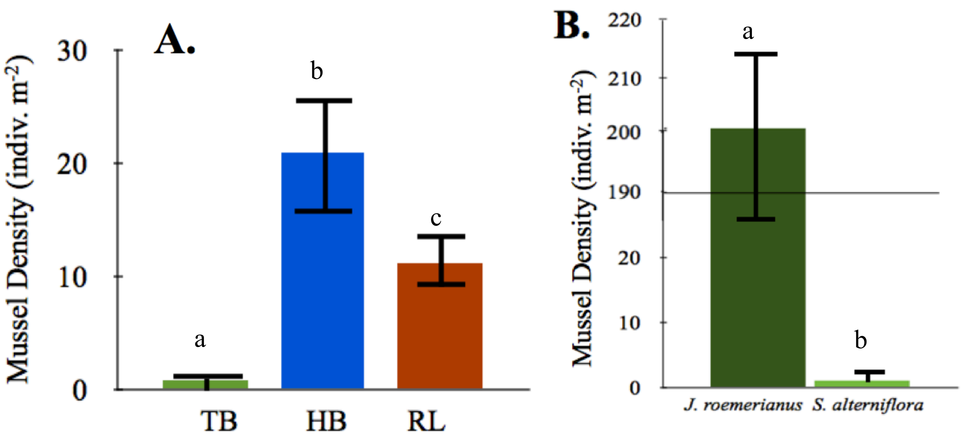


Figure 1.7. Mussel density at all plots (A) and vegetation plots (B) was determined by excavating all mussels to 30 cm depth, counted and converted to density (indiv m^{-2}) at three sites of increasing salinity in Barataria Bay, LA in 2012 (TB = Turtle Bay, HB = Hackberry Bay, RL = Raccoon Lake). Standard error indicated by bars, while statistically similar data share letters (α= 0.05).

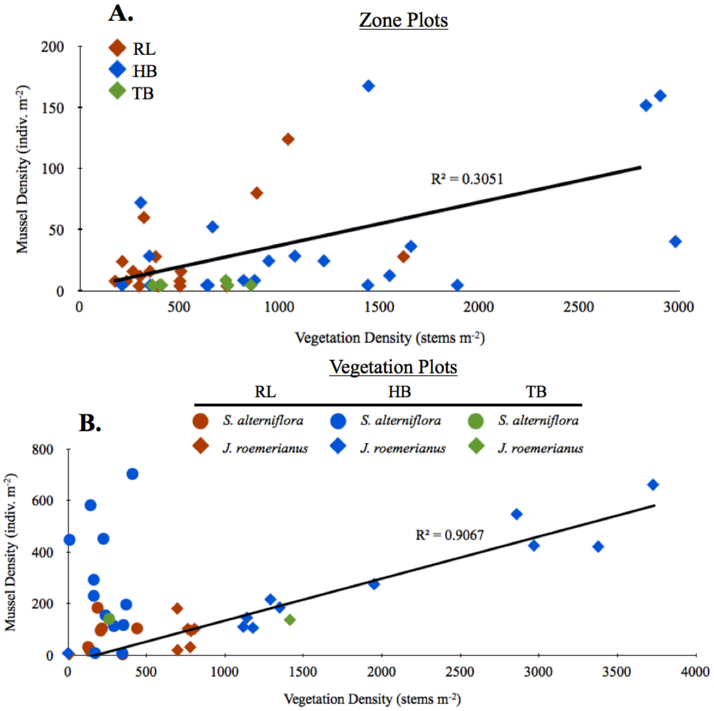


Figure 1.8. Vegetation and mussel density at zone plots (A) and vegetation plots (B) were determined by counting all stems and excavating all mussels to 30 cm depth, and converting to density (indiv m^{-2}) at three sites of increasing salinity in Barataria Bay, LA in 2012. Only sites hosting mussels are displayed. Regression lines represent correlations of total vegetation density and mussel density at zone plots (A) and of *J. roemerianus* density and mussel density at vegetation plots (B). TB = Turtle Bay, HB = Hackberry Bay, RL = Raccoon Lake.

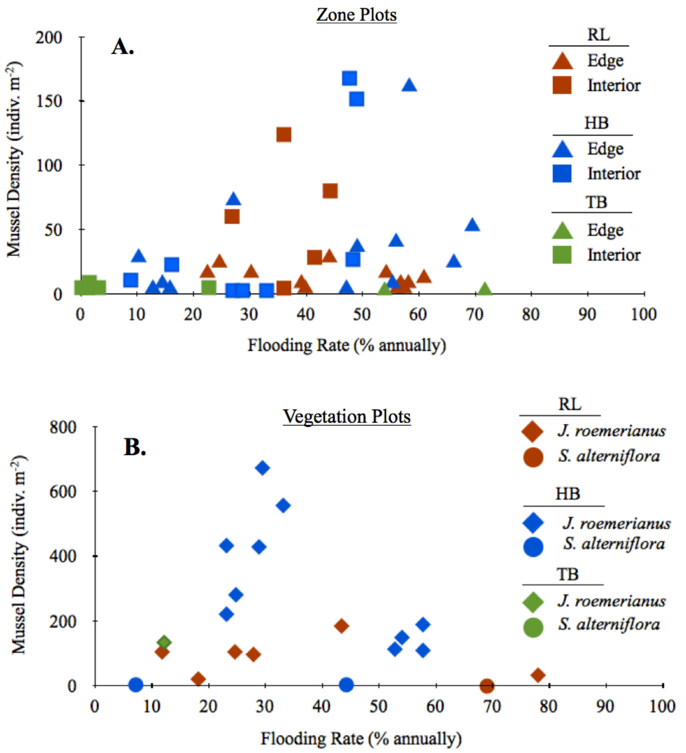


Figure 1.9. Annual flooding rates were calculated within zone plots (A) and vegetation plots (B) by correlating site elevation with annual flooding rates at CRMS stations 0178, 0237 and 6303 at three sites of increasing salinity in Barataria Bay, LA. Mussel densities were determined by excavating all mussels to 30 cm depth, and converting to density (indiv m^{-2}). Only sites hosting mussels are displayed. TB = Turtle Bay, HB = Hackberry Bay, RL = Raccoon Lake.

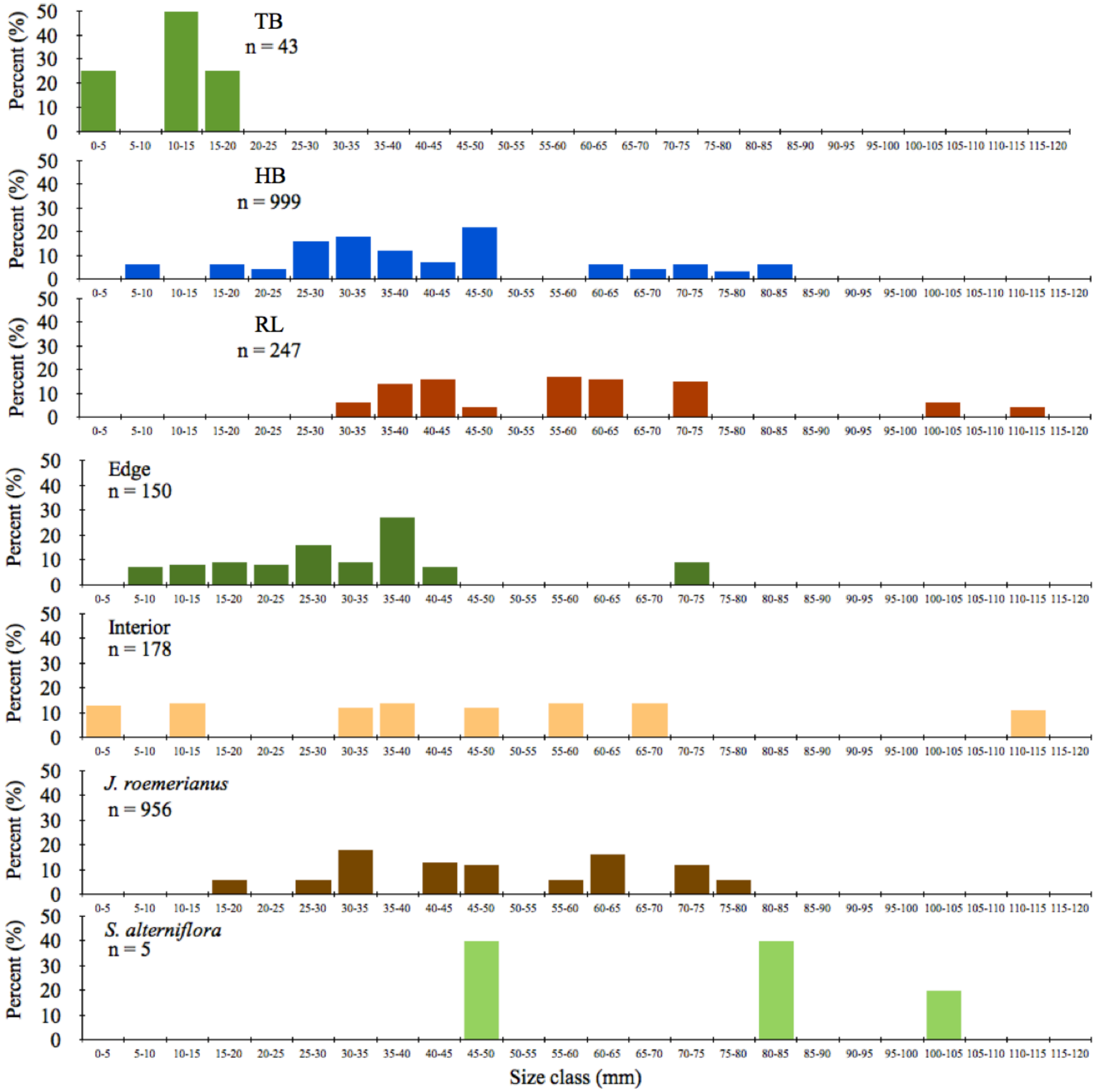


Figure 1.10. Percentage of sampled mussels within size classes among treatments. Mussel size was determined within all plots at each site, and zone plots and vegetation plots at all sites, by measuring the greatest distance between umbo and anterior shell edge. TB = Turtle Bay, HB = Hackberry Bay, RL = Raccoon Lake.

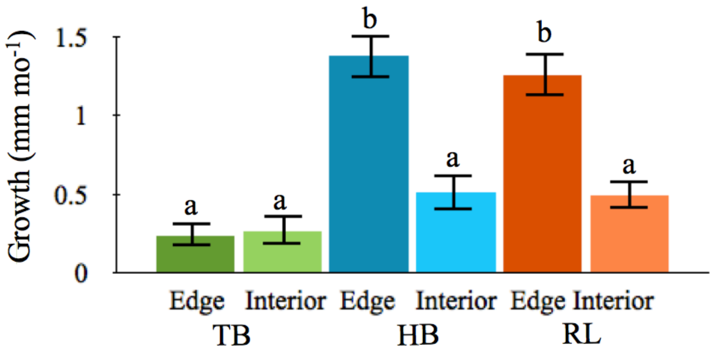


Figure 1.11. Mean shell growth rates in Barataria Bay, LA. Initial and final shell length was measured from the greatest length between umbo and anterior shell margins from March to October, 2012. TB = Turtle Bay, HB = Hackberry Bay, RL = Raccoon Lake. Standard error indicated by bars, while statistically similar data share letters (α= 0.05).

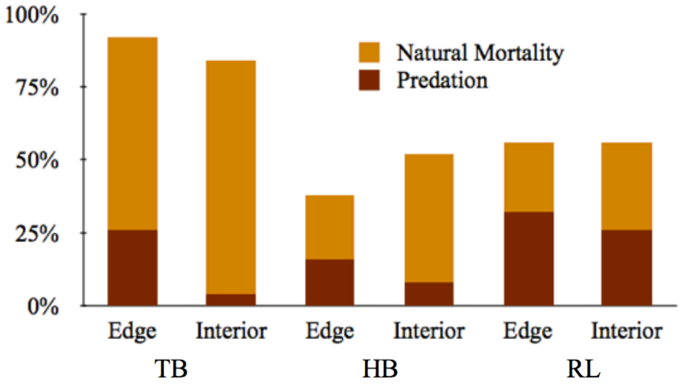


Figure 1.12. Mortality rates of mussels in Barataria Bay, LA. Intact mussel shells with no signs of damage were classified as "Dead", signifying natural mortality, while broken shells exhibiting extensive damage were classified as "Predated".

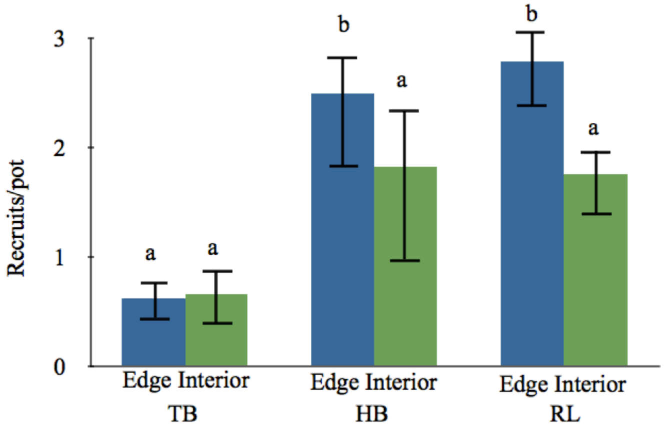


Figure 1.13. Juvenile mussel recruitment in Barataria Bay, LA. All recruits attached to experimental pot assemblages were counted. Standard error indicated by bars, while statistically similar data share letters (α= 0.05).

salinity site, TB, experiencing significantly higher mortality (88.4 ± 5.6%) than the two higher salinity sites (HB, RL), which had similar cumulative mortalities (RL: 56.5 ± 4.3%, HB: 44.3 ± 6.7%; p=0.02; Figure 1.12). There was no significant difference by marsh zone. Overall, the frequencies of mortality type (predation versus natural) differed significantly by salinity. Greater predation rates were recorded at the highest salinity site (RL) as compared to the low salinity site (TB) which experienced significantly greater natural mortality (Predation: RL: 18.3 ± 2.3%, HB: 7.5 ± 1.2%, TB: 2.4 ± 0.4%, $\chi^2 = 61.7$, $p < 0.01$; Natural Mortality: RL: 16.5 ± 4.5%, HB: 28.3 ± 5.5%, TB: 72.5 ± 8.4%; $\chi^2 = 56.2$, $p < 0.01$).

Recruitment

The majority of mussel recruits were found attached to mussel shell surfaces within pot assemblages (76%). There was a significant effect of salinity ($p < 0.01$) and marsh zone ($p = 0.03$) on recruitment of mussels. There were no significant interactions between salinity and marsh zone. Specifically, there were significantly fewer recruits quantified at the lowest salinity site (TB) as compared to the two higher salinity sites (RL, HB) which did not differ from one another (TB: 0.5 ± 0.1, HB: 2.1 ± 0.2, RL: 2.3 ± 0.3 recruits pot^{-1}; $t = 4.8, 5.1$, $p < 0.01$; Figure 1.13). Furthermore, at all sites recruitment was significantly higher at the marsh edge as compared to interior sites (edge: 1.9 ± 0.2, interior: 1.3 ± 0.1 recruits pot^{-1}; $t = 2.1$, $p = 0.03$; Figure 1.13).

2.4 Discussion

Ribbed mussels were found to extend from the low salinity areas of Barataria Bay, to high salinity areas, with larger mussels, and higher densities of mussels closely associated with mid salinity areas and with dense stands of *Juncus roemerianus*. Differences in densities and size distributions are likely explained by reduced growth and recruitment observed at the lowest salinity sites, and high predation observed at the highest salinity sites. No difference in marsh zone is likely due to a balance between higher higher growth and recruitment at marsh edge sites, likely resulting from increased exposure and flooding effects providing more resources, balanced by increased exposure to predation, offsetting some of the advantages of the marsh edge. Changes in salinity regimes, and extent of interior marsh areas may significantly affect the distribution and density of ribbed mussels in this region, and ultimately, their contribution to overall estuarine and marsh communities.

Ribbed mussels were found to be fairly ubiquitous across Barataria Bay, with densities across the salinity gradient similar to other mean densities reported for southeast ribbed mussel populations. Specifically, in this study, mean mussel densities at the three salinity areas ranged from 3.9 ± 0.4 to 66.6 ± 16.3 ind m^2. These densities cover the range reported in past studies from Barataria Bay, LA, along the gulf coast up to North Carolina which report means ranging from 82 ± 18 ind m^2 in Louisiana (Spicer, 2007), 5 indiv. m^{-2} in Alabama (West and Williams, 1986) 52 indiv. m^{-2} in Georgia (Kuenzler, 1961) and 38 indiv. m^{-2} in North Carolina (Lin, 1991). These densities however are surprisingly low in comparison to densities reported from northern temperate marshes. In Massachusetts, mussel densities ranged from 200 ± 1 indiv. m^{-2} (Culberton at al., 2008) to 2859 ± 257 indiv. m^{-2} (Evginidou et al., 2002), while in Rhode Island, mussel densities ranged from 470 - 1412 indiv. m^{-2}, and were often found in beds 2-3 mussels deep, covering 90% of exposed surfaces (Bertness, 1984). In Connecticut, mean density in a single plot were as high as 4,048 indiv. m^{-2} (Fell et al., 1982) and 9,227 ± 731 indiv. m^{-2} in New York marsh (Nielsen and Franz, 1995).

Ribbed mussel densities within estuarine subtropical marshes such as in Louisiana may be reduced due to osmotic stress experienced within the large salinity variation, and in particular to the relatively typical periods of extended low salinity events. While ribbed mussels are reported to withstand large variations in salinity (3-48; Bertness, 1984), they are typically reported to occur in salinity ranging from 15-34 (Pierce 1970), and it is not clear if populations can continue to survive (recruit, grow) if constantly exposed to salinity. In the Pacific mussel, *Perna viridis*, low salinity stress (< 10) resulted in low mortalities rates after four weeks, primarily due to metabolic depression and shell-closure, leading to eventual death under long-term chronic conditions (Wang et al., 2011). As a result, low salinity stress was found to result in reduced filtration rates and eventual death of stressed mussels. In this study, mussel growth rate was lower and non-predation mortality greater at the lowest salinity sites, possibly due to the adaptive physiological responses of mussels to osmotic stress. Extended and regular low salinity may greatly limit mussel growth, and be a critical factor limiting mussel distributions.

While salinity may impose physiological limits on mussel populations, vegetation density may provide valuable attachment substrate, and possible protection from predation. During the study, growth rates and juvenile recruitment were significantly and positively correlated with densities of *J. roemerianus*. Interestingly, in previous studies along the Atlantic coast, high *S. alterniflora* density has clearly been associated with increased mussel growth rates, reduced mortality and increased ribbed mussel population densities (Chintala et al., 2006; Lin, 1991). And a number of studies have suggested a strong mutualistic relationship between ribbed mussels and host vegetation (*S. alterniflora*) where mussels promote shoot growth and strengthen rootmass through nitrogenous biodeposition while *S. alterniflora* provides mussels with stable anchoring substrates, detrital food resources, defense from predation, ultimately strengthening host soils (Watt, 2011; Lin, 1989; Bertness and Leonard, 1989). *S. alterniflora* is a dominant species in these northeast marshes, and is also thought to be the key source of food for ribbed mussels with detritus from *S. alterniflora* estimated to supply over 50% of ribbed mussel diets in New England marshes (Langdon and Newell, 1990; Jordan and Valiela, 1982).

In this study, highest densities of ribbed mussels were significantly and positively related to *J. roemerianus* density. Interestingly, the region has dense and extensive *S. alterniflora* stands which were sampled, but were not highly present along the transects sampled as it tends to be outcompeted at lower salinities by other species. Determining if other vegetative species, including *J. roemerianus*, may provide similar benefits, and have similar mutualistic relationships would be valuable. In subtropical estuarine salt marshes, detritus derived from the C_4 plant *S. alterniflora*-derived often dominates primary productivity, and has been shown to be a major food source for benthic invertebrates through ^{13}C isotope analysis (Teal, 1962). Vegetation contributing to estuarine food webs also include *Juncus roemerianus* which instead exhibit C_3 carbon-fixation. However, in a comparison of relative decomposition, *J. roemerianus* exhibited slower rates of decomposition than *S. alterniflora* (Haines and Hansen, 1979), and the greatest increase in microbial biomass and nitrogen content was found in *S. alterniflora* decomposition, within both aerobic and anaerobic cultures, suggesting that *S. alterniflora* detritus may yield a more available and nutritious food source for benthic invertebrates than detritus from *J. roemerianus*.

Mussels within sites hosting *S. alterniflor*a or *J. roemerianus* (higher salinity sites) had higher growth rates at the marsh edge, likely due to increased detrital resources (Bertness, 1984, Franz, 1997). In this study, mussel growth rates were highest at the mesohaline marsh edge sites dominated by *S. alterniflora* and *J. roemerianus* (RL, HB: 31% annual flooding, 15 mm yr^{-1}

growth, 47.4 ± 12.3 mm) than interior oligohaline marsh dominated by *S. patens*, *S. robustus* and *D. spicata* (TL: 17.1 % annual flooding, 2.4 mm yr^{-1} growth; 11.7 ± 2.3 mm). These growth rates were similar to those found along the Atlantic coast during their growing season. Specifically, in Massachusetts, ribbed mussel growth rates ranged from 2-10 mm yr^{-1} and were inversely proportional to shore level (Culbertson et al., 2008; Evgenidou and Valiela, 2002). In Rhode Island, shell growth ranged from 1 - 4.5 mm yr^{-1}, decreasing with increasing tidal height (Bertness and Grosholz, 1985). In North Carolina, mussel growth ranged from 1.5-18 mm yr^{-1}, (Stiven and Gardner, 1992) while in South Carolina, mean shell growth ranged from 13-20 mm, peaking in low-elevation marsh edge (Hillard and Walters, 2009).

Differences in mortality patterns across salinity and marsh zones further help explain overall mussel populations and their distributions. Higher mortality at low salinity sites may be due to a combination of lower flooding time (about half that of higher salinity sites), low salinity stress, and decreased access to detrital food resources resulting from the lower flooding (Jordan and Valiela, 1982; Stiven and Gardner, 1992). Low predation related mortality at the low salinity site likely results from this decreased exposure time, possible refuge benefits from high vegetation density, and potentially lower marine predatory crab populations in upper Barataria Bay (Jones et al., 2002).

In contrast, mortality rates at higher salinity sites, may be controlled partly by a mix of predation from higher exposure along the marsh edge (higher flooding rates), and refuge from high densities of salt marsh predation. Predation risk may be offset by dense *S. alterniflora* and *J. roemerianus* vegetation which may restrict access to mussels, reducing predation mortality in vulnerable edge marsh. When host *S. alterniflora* density was experimentally increased, access to mussels by blue crabs was found to be reduced, resulting in decreased rates of mussel predation mortality (West, 1986; Lin, 1991). Past studies have clearly shown increased predation due to prolonged submergence at the marsh edge, individuals are often exposed to higher rates of predation, primarily by the mud crab, *Panopeus herbstii*, and blue crab, *Callinectes sapidus* (Lin, 1991; Seed and Hughes, 1995, Stiven and Gardner 1992). Both crabs were found to be important predators of ribbed mussels, potentially consuming up to 20 30-mm mussels $crab^{-1}$ day^{-1}, respectively (Seed, 1980). In this study, predation mortality, (evidenced by chipped and broken shells) was found to be greater at Raccoon Lake than Hackberry Bay, where vegetation densities were significantly reduced (RL: 464 ± 36 stems m^{-2}, HB: 1,146 ± 65.3 stems m^{-2}). During plot excavation, dense shoots and root masses of *J. roemerianus* were difficult to break apart, often requiring trowels to break open clumps and extract mussels while most *S. alterniflora* vegetation could be examined by hand.

Relative flooding rates, availability of substrate, and proximity to spawning populations are thought to control recruitment in many bivalve species. This study found highest recruitment at edge marsh, and in areas with higher mussel densities (higher salinity sites). Similar patterns of recruitment have been observed in a New York marsh, where recruitment was greatest at marsh edge as compared to interior marsh plots (Nielsen and Franz, 1995). Greater flooding at the marsh edge may increase access to recruitment substrates such as conspecifics and vegetation shoots by suspended mussel larvae (Nielsen and Franz, 1995). Substrate is also critical for recruitment and in New England it was found that juvenile settlement decreased by over 60% when *S. alterniflora* shoots were removed from experimental plots (Bertness and Grosholz, 1985). This affect may be due to the provision of appropriate substrate, protection from mortality, and may also due to the reduction of tidal flow velocities (Watt, 2011), which may increase larval settlement during slack high-water. The observed patterns of mussel recruitment in this study may be due to relative proximity to adult spawning populations. Ribbed mussels typically reach sexual maturity at 20 mm in length, after two growing seasons (Brousseau, 1982), although is highly dependent on relative temperature, salinity, flooding rates and food quality (Franz, 1996). At Hackberry Bay and Raccoon Lake sites, the majority of mussels were greater than 20 mm in length (HB: 91% (913/999); RL: 96% (10/247)) while in Turtle Bay only 19% had reached that size (8/43).

Mussels, like most benthic bivalves, are r-selected broadcast spawners that depend on producing large numbers of eggs (8×10^6 eggs female $^{-1}$) to sustain adult populations (Brousseau, 1982). At average larval growth rates, (12 µm day^{-1}; Pechenik et al., 1990) the primary settlement of larval mussels usually occurs 20-30 days post-spawn, although this depends heavily on several factors including temperature, food availability and substrate suitability (Widdows, 1991). Raccoon Lake and Hackberry Bay, where the greatest mussel densities were observed, are located 13 km apart, while Turtle Bay is located nearly 25 km further north in upper Barataria Bay. Therefore, spatial proximity between sampled marsh sites and adult spawning populations may have contributed to the greater recruitment rates observed at Hackberry Bay and Raccoon Lake.

Overall, the observed trends in mussel recruitment, growth, mortality and population density may be the result of interacting effects of salinity tolerances, vegetation density and relative marsh flooding in Barataria Bay. Patterns of mussel density in Barataria Bay may be the result of bottom-up control in oligohaline Turtle Bay driven by detrital resource limitation, and top-down control at mesohaline Raccoon Lake driven by greater crab predation. Ribbed mussels were distributed throughout the salinity range, and likely provide important ecosystem services as an important component of the estuarine system. Changes in salinity, marsh vegetation and marsh extent may impact the ribbed mussel population, and affect the provision of these services. With relatively high recruitment and growth rates, and reduced mortality rates within mesohaline areas, it is possible that ribbed mussels play an important role in marsh nutrient cycling, and soil structure, but these services have yet to be quantified.

2.5 References

Barbe, D., Cruise, J. and K. Crowder. 2000. "Sediment transport in a shallow coastal estuary during the winter season." *Jour. Amer. Water Res. Ass.* 36(4):1-10.

Bertness, M. 1984. "Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh." *Ecology* 65(6): 1794-1807.

Bertness, M and E. Grosholz. 1985. "Population dynamics of the ribbed mussel, *Geukensia demissa:* the costs and benefits of an aggregated population." *Oecologia* 67:192-204.

Bertness, M. and G.H. Leonard. 1997. "The role of positive interactions in communities: lessons from intertidal habitats." *Ecology* 78(7): 1976-1989.

Booth, J., Miller, R., McKee, B., and R.A. Leathers. 2000. "Wind-induced bottom sediment resuspension in a microtidal coastal environment." *Cont. Shelf Res.*20:785-806.

Brousseau, D. 1984. "Age and growth rate determinations for the Atlantic ribbed mussel, *Geukensia demissa*." *Estuaries* 7: 233-241.

Chintala, M.,Wigand, C and G. Thursby. 2006. "Comparison of *Geukensia demissa* populations in Rhode Island frings salt marshes with varying nitrogen loads." *Mar. Ecol. Prog. Ser.* 320:101-108.

Culbertson, J.B., Valiela, I., Olsen, Y.S., and C.M Reddy. 2008. "Effect of field exposure to 38-year-old residual petroleum hydrocarbons on growth, condition index, and filtration rate of the ribbed mussel, *Geukensia demissa*." *Environmental Pollution* 154: 312-319.

DeLaune, R.D., Jugsujinda, A., Peterson, G.W. and W.H. Patrick Jr.. 2003."Impact of Mississippi River freshwater reintroduction on enhancing marsh accretionary processes in a Louisiana estuary." *Estuarine, Coastal and Shelf Science* 58: 653-662.

Espinosa, E.P., Allam, B. and S. E. Ford. 2008. "Particle selection in the ribbed mussel *Geukensia demissa* and the Eastern oyster *Crassostrea virginica*: Effect of microalgae growth stage." *Estuarine and Coastal Science* 79:1-6.

Evgenidou, A. and I.Valiela. 2002. "Response of growth and density of a population of *Geukensia demissa* to land-derived nitrogen loading, in Waquioit Bay, Massachusetts." *Estuarine, Coastal and Shelf Science* 55:125-138.

Fell, P., Olmstead, N., Calson, E., Jacob, W., Hitchcock, D. and G. Silber. 1982. "Distribution and abundance of macroinvertebrates on certain Connecticut tidal marshes, with emphasis on dominant molluscs." *Estuaries* 5(3): 234-239.

Franz, D. 1997. "Resource allocation in the intertidal salt-marsh mussel *Geukensia demissa* in relation to shore level." *Estuaries* 20(1):134-148.

GIllmor, R.B. 1982. "Assessment of intertidal growth and capacity adaptations in suspension feeding bivalves." 68:277-286.

Haines, E.B. and R.B. Hanson. 1979. "Experimental degradation of detritus made from salt marsh plants *Spartina alterniflora* Loisel., *Salicornia virginica* L., and *Juncus roemerianus* Scheele." *Jour. Exp. Mar. Biol. Ecol.* 40:27-40.

Hillard, R. and K. Walters. 2009. "Prevalence, patterns, and effects of shell damage on *Geukensia demissa* in South Carolina estuarine habitats." *Mar. Biol.* 156:2149-2160.

Huang, S.C., Kreeger, D.A. and R.I.E. Newell. 2003. "Seston available as a food resource for the ribbed mussel (*Geukensia demissa*) in a North American, mid-Atlantic saltmarsh." *Estuarine, Coastal and Shelf Science* 56:561-571.

Inoue, M., Park, D., Justic, D., Wiseman, Jr., W. 2008. "A high-resolution integrated hydrology-hydrodynamic model of the Barataria Basin system." *Env. Model. Softw.* 23:1122-1132.

Coastal Protection and Restoration Authority (CPRA). 2012. "Louisiana's Comprehensive Master Plan for a Sustainable Coast." *Coastal Protection and Restoration Authority*. 1-172.

Jordan, T.E. and I. Valiela. 1982. "A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance in nitrogen flows in a New England salt marsh." *Limnology and Oceanography.* 27(1): 75-90.

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." *Biol. Bull.* 213:141-151.

Kreeger, D.A, and R.I. Newell. 2000. "Trophic complexity between producers and invertebrate consumers in salt marshes". In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. *Kluwer Academic Publishers, Dordrecht*. 187–220.

Kuenzler, E.J. 1961. "Structure and energy flow of a mussel population in a Georgia salt marsh. *Limnol. Oce*anogr. 6:191-204.

Langdon, C.J. and R.I.E. Newell. 1990. "Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa*." *Mar. Ecol. Prog. Ser.* 58: 299-310.

Lin, J. 1991. "Predator-prey interactions between blue crabs and ribbed mussels living in clumps." *Estuarine, Coastal and Shelf Science* 32: 61-69.

Louisiana Office of Coastal Protection and Restoration. 2012. Coastwide Reference Monitoring System-Wetlands Monitoring Data. Retrieved from Strategic Online Natural Resource Information System (SONRIS) database. http://coastal.louisiana.gov/index.cfm?md=pagebuilder&tmp=home&pid=92. Accessed 12/10/2012.

Nielsen, K.J. and D.R. Franz. 1995. "The influence of adult conspecifics and shore level on recruitment of the ribbed mussel *Geukensia demissa* (Dillywn)." *Jour. Exp. Mar. Biol. Ecol.* 188:89-98.

Pierce, S. K. 1970. "The water balance of *Modiolus* (Mollusca: Bivalvia: Mytilidae): osmotic concentrations in changing salinities". *Comp. Biochem. Physiol*. 36: 521–533.

Porri. F., Zardi, G.I., McQuaid, C.D. and S. Radloff. 2007. "Tidal height, rather than habitat selection for conspecifics, control settlement in mussels." *Mar. Biol.* 152:631-637.

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.

Seed, R. and R. N. Hughes. 1995. "Criteria for prey size selection in mollus- civorous crabs with contrasting claw morphologies." *J Exp Mar Biol Ecol.* 193:177–195.

Shumway, S. E. and A. Youngson. 1979. "The effects of fluctuating salinity on the physiology of *Modiolus demissus*." *Jour. Exp. Mar. Biol. Ecol.* **40**, 167–181.

Smith, L.D. and J.A. Jennings. 2000. “Induced defensive responses by the bivalve *Mytilus edulis* to predators with divergent attack modes.” *Mar Biol.* 136:461–469.

Spicer, J. 2007. “A comparison of channel morphology, marsh elevation and biological processes in natural and dredged tidal salt marshes in Louisiana.” *Louisiana State University. School of Oceanography and Coastal Sciences. Doctoral Dissertation*. 1-104.

Stiven, A.A. and S.A. Gardner. 1992. “Population processes in the ribbed mussel *Geukensia demissa* (Dillwyn) in a North Carolina salt marsh tidal gradient: spatial pattern, predation, growth and mortality.” *Jour. Exp. Mar. Biol. Ecol.* 160:81-102.

Strange, K. B. and J.H. Crowe. 1979. Acclimation to successive short term salinity changes by the bivalve *Modiolus demissus*. I. Changes in hemolymph osmotic concentration, hemolymph ion concentration and tissue water content. *J. exp. Zool.* 210: 221–226.

Torchin, M. E., Hechinger, R.F., Huspeni, T.C., Whitney and K.D. Lafferty. 2005. “The introduced ribbed mussel (*Geukensia demissa*) in Estero de Punta Banda, Mexico: interactions with the native cord grass, *Spartina foliosa*.” *Biological Invasions*. 7:607-614.

Walker, N.D., Wiseman, W.J., Rouse, A. Babin. 2005. “Effects of river discharge, wind stress, and slope eddies on circulation of the Mississippi River plume.” *J. Coast. Res*. 21: 1228–1244.

Wang, Y., Hu, M., Wong, W.H., Shin, P. and S. Cheung. 2011. “The combined effects of oxygen availability and salinity on physiological responses and scope for growth in the green-lipped mussel *Perna viridis*.” *Mar. Poll. Bull.* 63:255-261.

Watt, C., Garbary, D.J. and C. Longtin. 2011. “Population structure of the ribbed mussel *Geukensia demissa* in salt marshes in the southern Gulf of St. Lawrence, Canada.” *Helgol. Mar. Res.* 65: 275-283.

West, D.L. and A.H. Williams. 1986. “Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes.” *Jour. Exp. Mar. Biol. Ecol.* 100: 75-95.

3.1 Introduction

The distribution of estuarine populations of benthic, sessile invertebrates is inherently dependent on the spatial and temporal frequencies of larval recruitment (Beukema and Dekker, 2007; Knights and Walters, 2010). The seasonal timing of gametogenesis and spawning are often extremely important considerations in determining larval output, juvenile settlement and subsequent adult density and distribution (Franz, 1996). Larval spawning must coincide with limited food resources, and preferential currents which may be responsible for transporting pelagic larvae to more desirable recruitment zones while limiting larval exposure to the often extremely high rates of daily predation mortality experienced by defenseless planktonic larvae (Whitton et al., 2012).

The ribbed mussel (*Geukensia demissa*) is a benthic intertidal bivalve often forming large aggregations within dense coastal salt marsh vegetation (Bertness, 1984). Populations along the western Atlantic coastline have been well-documented from Maine to Georgia (Chintala, 2006; Levinton and Suchanek, 1978; Stiven and Kuenzler 1979), while a recent study observed a successful invasion of *G. demissa* within the Lago de Maracaibo in northwestern Venezuela (Baez and Severeyn, 2005). However, because ribbed mussels are not a species of economic interest, little is known about their reproductive biology within coastal Louisiana. Gametogenic assays in temperate Atlantic populations suggest that the seasonal growth and development of reproductive tissues within adult mussels are significantly affected by the abundance and quality of available microalgae and vegetative detritus during throughout the early fall to late winter (Brousseau, 1982). This seems likely as ribbed mussels are often associated with the salt marsh grass, *Spartina alterniflora* (Brousseau, 1984; Franz, 1993). A recent study on ribbed mussel ecology in Louisiana examined mussel distribution in the northeastern marshes of Barataria Bay and found *G. demissa* populations to be positively correlated with density of *S. alterniflora* and *Juncus roemerianus,* specifically within the raised mounds found at the base of stem clusters (Spicer, 2007, personal obs.).

Gametogenesis and peak spawning of ribbed mussels in temperate salt marshes along the Atlantic coast generally occurs during a single reproductive season lasting from late spring through midsummer (Brousseau, 1982; Borrero, 1987). Increased summer temperatures have been strongly correlated with the onset of gametogenesis in ribbed mussels (Franz, 1997) in addition to many other invertebrate taxa (Hackney, 1983; Palmer, 1980; Mladineo et al., 2007). Increased temperatures may promote greater metabolic growth and development of reproductive tissues (Kuenzler, 1961), accelerating gametogenesis and eventual spawning in mussel populations.

However, recently introduced ribbed mussel populations within tropical marshes experiencing slight seasonal temperature variation undergo an extended reproductive season, highlighted by two distinct peaks of spawning activity (Baez, 2005). While such marsh habitats are uniformly warm throughout the year, large fluctuations in ambient salinity occur during the onset of the tropical rainy season in midsummer, and again during the extended dry season from midwinter through spring. Ambient salinity has been shown to have far-reaching effects on mussel physiology (Mladineo, 2007) including changes in filtration, excretion and biodeposition rates, suggesting that salinity may significantly affect growth of reproductive tissues (Resgalla Jr. at al., 2007; Wang et al., 2011). Gametogenesis in tropical ribbed mussel populations was found to be strongly correlated with large biannual decreases in salinity (Baez and Severeyn, 2005).

Similar reproductive timing has been observed across several tropical molluscan taxa (Ruiz et al., 1998; Puyana, 1995) suggesting that seasonal shifts in salinity may be an important determinant of gametogenesis in ribbed mussels.

The Terrebonne Bay and Barataria Bay estuarine systems in southeastern Louisiana both experience large salinity gradients from their headwaters near Mississippi River distributaries through coastal barrier islands along the northern Gulf of Mexico (Inoue et al., 2008). Temperatures vary little between each bay, but seasonally range from 15 °C in January to 30 °C midsummer (Feng and Li, 2010). In contrast, seasonal patterns of salinity vary greatly within the mesohaline marshes of northern Terrebonne Bay (5-10) and the polyhaline wetlands of lower Barataria Bay (15-25; Wiseman Jr. et al., 1990). Finally, seasonal flooding of both bays occurs during the spring as fresh runoff flows through extensive marsh Mississippi River distributaries. Barataria and Terrebonne Bays are also subject to significant marine influx from both summer southerly warm fronts and thermal expansion within the Gulf of Mexico (Barbe, 2000). Conversely, strong northerly cold fronts result in annual low water between November and January (Feng and Li, 2010). As a result, in contrast to both temperate Atlantic marshes where temperatures seasonally vary and tropical marshes experiencing large shifts in salinity, ribbed mussels in southeastern Louisiana are subject to large seasonal fluctuations in temperature, salinity and marsh flooding. Gametogenesis of local ribbed mussel populations may be subsequently determined by seasonal variations in temperature and salinity.

While the reproductive physiology of ribbed mussels in Atlantic marshes is well known (Brousseau, 1982; Franz, 1996), seasonal gametogenesis in subtropical populations is largely unexplored. This study examined the seasonal gametogenesis of ribbed mussels in Terrebonne Bay and Barataria Bay, Louisiana. Specifically, this study explored the effects of temperature and salinity on observed patterns of reproductive maturation of ribbed mussels in the northern Gulf of Mexico. It is hypothesized that mussel ripeness will be positively correlated with seasonal temperature and negatively correlated with salinity due to increased metabolic feeding and reproductive investment in warm marshes, coinciding with hyper-osmotic stress release from spawned mussel larvae during low-salinity events. Results from this study may help explain patterns of spawning, juvenile recruitment and subsequent population densities of ribbed mussels within coastal Louisiana. Such information would be useful in forecasting potential ecosystem impacts of expanded ribbed mussel populations within southern coastal marshes, particularly with respect to predicted change in temperature and salinity in the northern Gulf of Mexico.

3.2 Methods

To determine the effects of salinity and temperature on the timing of gametogenesis in ribbed mussels, ten individuals were collected monthly from two locations within coastal Louisiana, and hourly salinity, temperature and water level data collected from nearby continuous data recorders. The two locations represented different salinity regimes (mesohaline versus polyhaline) and included a site adjacent to Louisiana Universities Marine Consortium center in Cocodrie, Terrebonne Bay (29°15’ 26.52 N 90°39’44.09 W) and a site in Barataria Bay (29°17’46.11 N 90°01’15.54 W) in southeastern Louisiana (Figure 2.1). Mean monthly salinity, temperature were calculated from hourly data recorded by the U.S. Geological Survey Coastwide Reference Monitoring System (CRMS) at Station 0178 (Barataria Bay) and Station 0369 (Terrebonne Bay). Mussels were collected monthly from July 2011 to October 2012 where they were placed on ice, transported back to the laboratory at Louisiana State University Agricultural Center and processed within 48 hours.

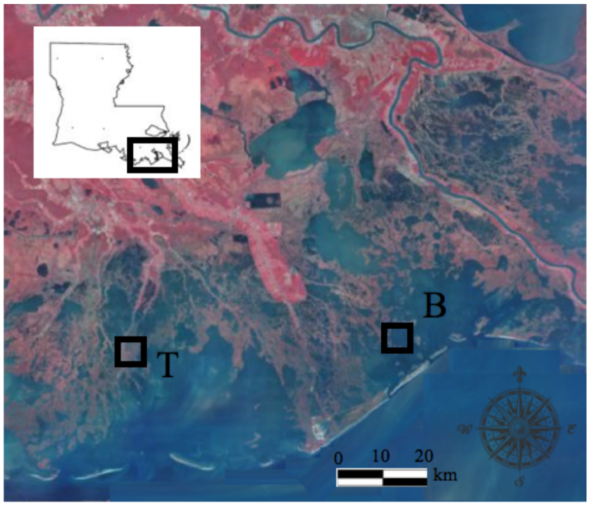


Figure 2.1. Location of field sites. Mussels were collected near the Louisiana Universities Marine Consortium located in Cocodrie, Terrebonne Bay (T) and from Raccoon Lake in lower Barataria Bay (B). Both bays are located between abandoned distributaries within the Mississippi deltaic plain in Louisiana.

Visual observations of mantle and visceral mass tissues were used to qualitatively determine sex and relative ripeness in sampled mussels following the methods of Cerwonka (1968) and Brousseau (1982). The stages of gametogenic development were determined through the histological preparation of excised visceral mass and mantle tissues. Reproductive tissues were removed, fixed in 10% formalin for 24 hrs and stored in 70% ethyl alcohol solution. Tissues were then prepared for histological analysis as in Cowan et al. (2012). Stages were defined as indifferent, developing, ripe, partially spawned and spent, as in Brousseau (1982). Within indifferent mussel tissues (Stage 1), sex was indeterminate and follicles or spermatozoan aggregates were not observed. In mussels exhibiting early gametogenic development (Stage 2), small follicles were apparent in females, while sparse clusters of sperm cells were scattered across sampled tissues. In fully ripe mussels (Stage 3), female vesicles contained densely packed and nucleated eggs separated from the follicular wall. Ripe male mussel tissues exhibited widespread dense spermatozoan aggregates, in slight bands oriented towards the center of the lumen. In post-spawned mussels (Stage 4), female vesicles were sparsely packed, and eggs were visible along genital canals, presumably being exported through sampled visceral mass tissues. In spawned males, significant thinning of vesicles left empty bands within aggregations, and sperm cells were found along dense conduits through visceral mass tissues. Spent mussels (Stage 5) exhibited very few sparsely packed female vesicles and spermatozoan clusters. Follicular walls began to collapse and cellular waste was observed in many areas of sampled visceral mass. Peak gametogenesis was determined by calculating the percentage of ripe (Stage 3) mussels sampled monthly from each site.

Gametogenic stage were determined for all mussels to examine the timing of ripeness across months, and sites, to relate the patterns to temperature and salinity.

3.3 Results

Environmental characteristics

The mean monthly temperature ranged from 16 °C in December to 31 °C in August, and did not differ among study sites (Figure 2.2). The mean salinity in Barataria Bay ranged from a peak of 25 °C in November to 12 °C in February and April (Figure 2.2). In contrast, the salinity in Terrebonne Bay was observed to be 5 throughout the spring and summer, with a high monthly mean of 17 °C in November, 2011.

Gametogenic state determination

In total, 317 mussels were analyzed, of which 162 were males, and 155 were females. Analysis of histologically prepared tissues consistently confirmed visual observations of seasonal sexual maturation. Specifically, sexual maturation of ribbed mussels was visually detected as mantle tissues thickened and underwent distinct changes in surface pigmentation (Figure 2.3). Ripe males exhibited orange and cream-colored mantle tissues (Figure 2.3A-C), while mature female tissues ranged in color from dark brown to purple (Figure 2,3D-F). In contrast, indifferent mussel tissues remained thinly translucent and yellow.

Morphologically, female gametogenesis was initially observed through increased budding from the follicular walls of vesicles (Figure 2.4-I). Oocytes slowly grew larger before separating from vesicle walls, and were clearly nucleated at larger stage of development (Figure 2.4-I-D). Fully ripe, female mussel tissues contained many densely packed vesicles filled with nucleated eggs (Figure 2.4-I-C, G). Spawning states of female mussels were observed as eggs were found within transitory tubules outside of dense egg clusters, presumably as they were being transported externally during the multiple physiological stages of spawning (Figure 2.4-I-H).

Post-spawned mussel tissues exhibited increasingly sparse vesicles containing few nucleated eggs, leading to completely indifference in mid-winter (Figure 2.4-I-F, I). However, some regeneration of the follicular membranes was observed in female mussels. Such morphological redevelopment often took the form of limited budding from vesicle walls, leading to some egg development during the late fall, particularly in mussels collected from Barataria Bay (Figure 2.4-I-A, B).

In contrast, gametogenesis in males was marked by the gradual formation of spermatozoa clusters within sampled mantle and visceral mass tissues (Figure 2,4-II). Ripe males contained widespread aggregations of densely packed sperm cells (Figure 2.4-II-C, G). As males spawned, spermatozoa was transported through tubules, leaving linear tracks within previously dense aggregations (Figure 2.4-II-D, E). Male gamete aggregations thinned in the late fall, leading to a uniform undeveloped state throughout the winter, particularly in Barataria Bay (Figure 2.4-II-F, I). In Terrebonne Bay, several male individuals exhibited dense sperm aggregates late in November, but all mussels collected between December and February exhibited no signs of gametogenic development. Undeveloped mussels exhibited no aggregations and sexes were difficult to determine from midwinter through the early spring. As development initiated with the budding of female vesicle walls and the appearance of growing spermatozoan aggregates, sex again became distinct.

Patterns of seasonal gametogenesis

Patterns of gametogenesis varied slightly between study sites. The higher salinity site, Barataria Bay, showed a longer period of ripeness with ripe mussels observed from March through October while in Terrebonne Bay, ripe mussels were observed for a lesser time from

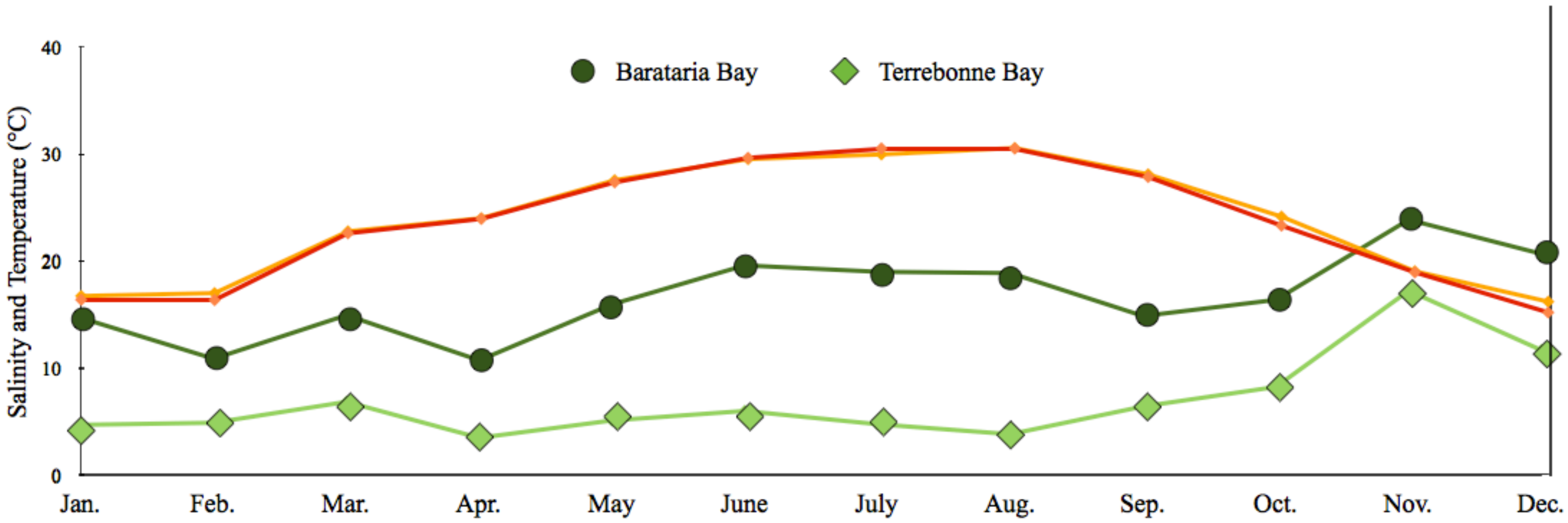


Figure 2.2. Seasonal salinity, temperature and water elevation in Barataria and Terrebonne Bays, LA. Blue shades represent mean monthly water elevation, red shares represent mean temperature and green shades represent mean salinity. Barataria Bay is represented by darker shades and Terrebonne Bay by lighter shades of each color. Mean monthly temperature and salinity were calculated from hourly measurements recorded at USGS Coastwide Reference Monitoring System stations CRMS0178 and CRMS0369 in 2011 and 2012. Mean monthly water elevation was calculated from hourly measurements at the same stations. Local water depths at CRMS sites were recorded and adjusted to local mean sea level by USGS and used here to illustrate meaningful comparisons between Barataria and Terrebonne Bays.

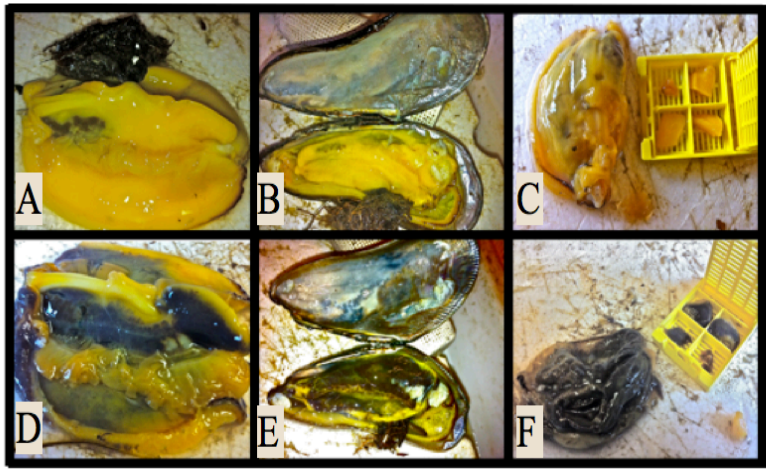


Figure 2.3. Ripeness in male and female ribbed mussels. Ripe male mussels (A-C) exhibited thickened orange and cream-colored mantle tissues while ripe female mantle tissues ranged from dark brown to purple. Note dark posterior tissue (A) represents vegetative gut contents. Reproductive stages were determined through histological preparation of visceral mass and mantle tissues (C, F) sampled monthly from ribbed mussels collected from LUMCON, Cocodrie, Terrebonne Bay and Raccoon Lake, Barataria Bay, LA in 2011 and 2012.

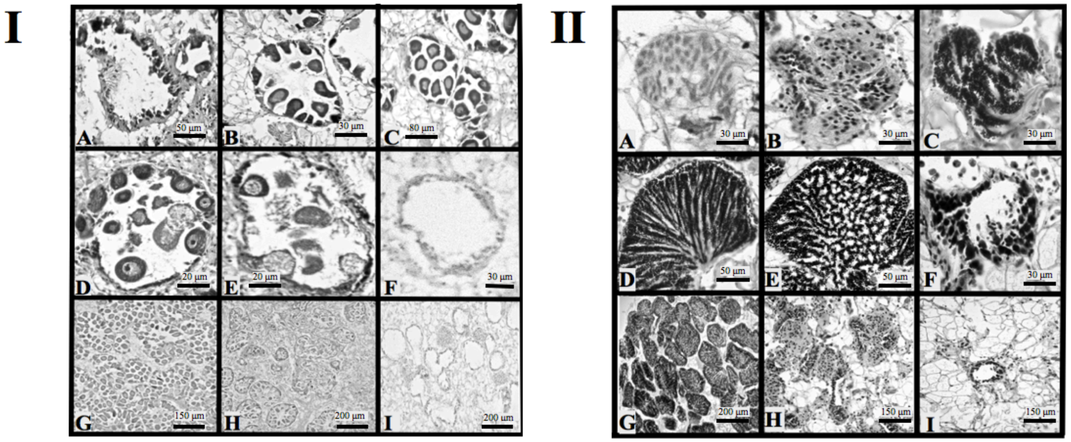


Figure 2.4. Seasonal gametogenesis of female (I) and male (II) ribbed mussels. Reproductive stages were classified as in Brousseau (1982): Stage 1 = Indifferent (not shown), Stage 2 = Developing (A, B), Stage 3 = Ripe/Spawning (C, D), Stage 4 = Post-spawned (E), Stage 5 = Spent (F). The morphology and density of gametes was considered, ranging from ripe (G) to spawning (H) and spent (I). Note linear removal of spermatocytes from aggregates and egg wasting (D, E) and aggregate disintegration and transport of gametes during spawning (H). Reproductive stages were determined through histological preparation of visceral mass and mantle tissues sampled from ribbed mussels collected from LUMCON, Cocodrie, Terrebonne Bay and Raccoon Lake, Barataria Bay, LA in 2011 and 2012.

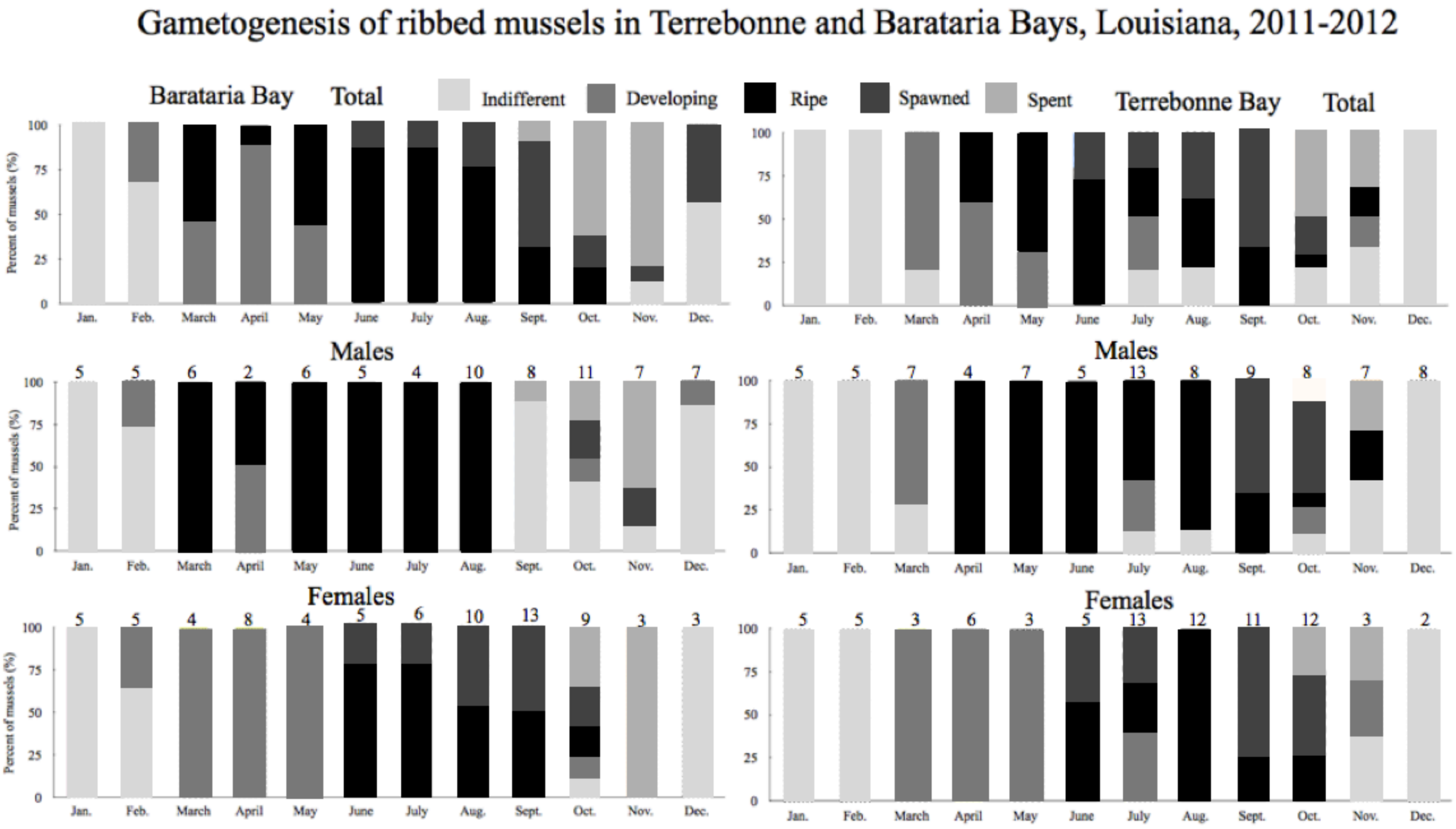


Figure 2.5. Seasonal gametogenesis of female and male ribbed mussels in Terrebonne and Barataria Bay. Gametogenic stage was classified as Stage 1 (indifferent), Stage 2 (Developing), Stage 3 (Ripe), Stage 4 (Post-spawned) and Stage 5 (Spent) through histological preparation of visceral mass and mantle tissues sampled monthly from ribbed mussels collected randomly near LUMCON Cocodrie, Terrebonne Bay, and Raccoon Lake, Barataria Bay, LA from July, 2011 - Oct. 2012. Therefore, data from July - Oct represents 2 years of data. Numbers above bars indicate sample sizes.

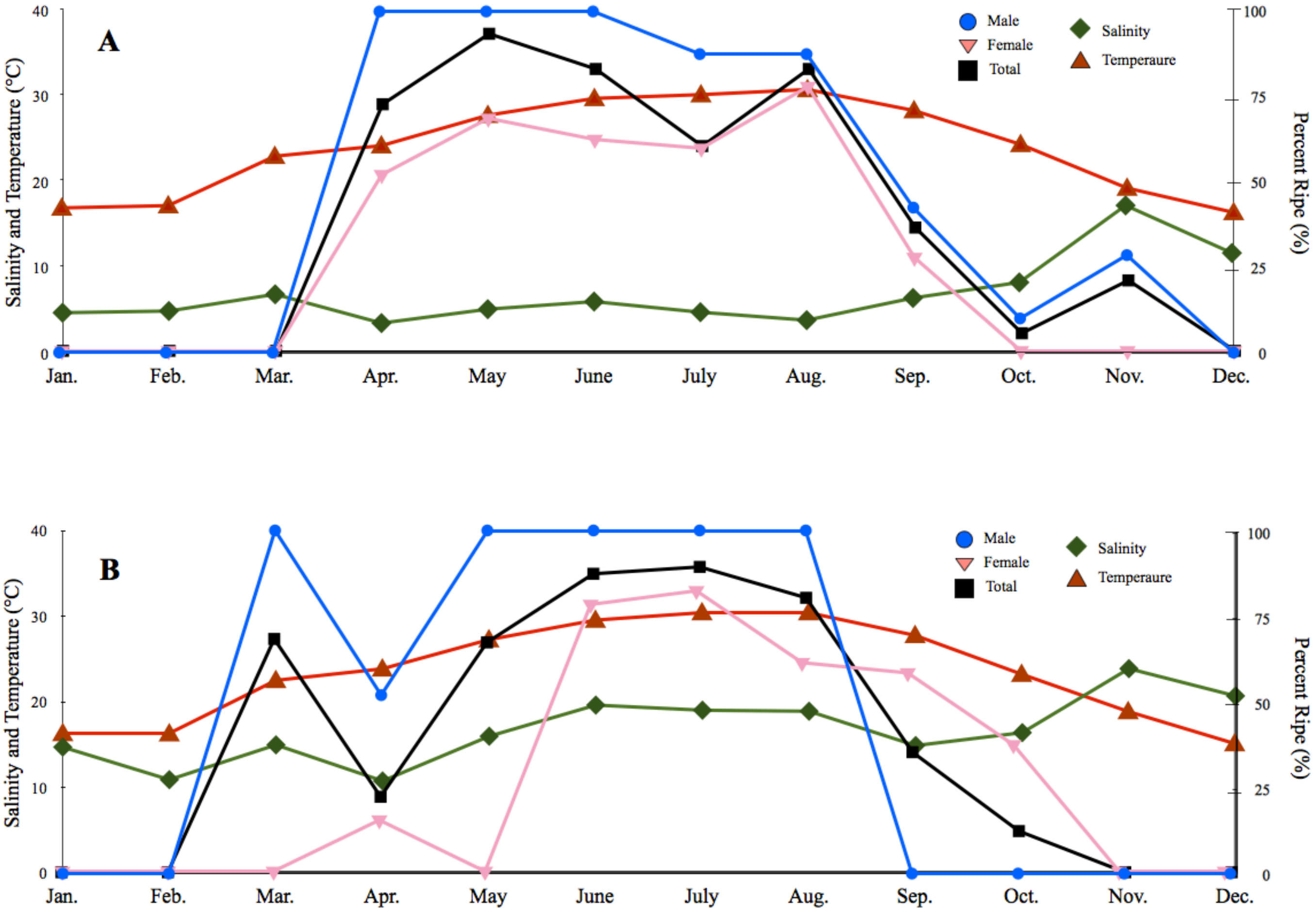


Figure 2.6. Seasonal temperature, salinity and ripeness of ribbed mussels in Terrebonne (A) and Barataria Bay (B). Gametogenesis is represented by circles in males, downward triangles in females and squares for all mussels. Diamonds represent salinity while upward triangles represent temperature. Data from July-Oct. represent the monthly mean of two years.

April through September with a few sexually mature individuals observed in November (Figure 2.5). Furthermore, during the period of gamete maturation, mussels in Barataria exhibited high rates of ripeness (> 90%) than in Terrebonne Bay (75%). In Barataria, males were found to develop earlier in the season, reaching peak ripeness from March through August while female gamete maturation peaked in June, lasting through October. In Terrebonne Bay, gametogenesis occurred simultaenously in both sexes. Nearly 100% of males were ripe from May through August in both bays, while peak ripeness occurred in only 80% and 70% of females in Barataria and Terrebonne Bays, respectively (Figure 2.5).

Effects of temperature and salinity on gametogenesis

Ripe mussels in Barataria Bay were observed at a mean temperature of 28.4 °C, and salinity of 18.5, for both males and females, while ripe mussels in Terrebonne Bay were found at a mean temperature of 28.6 °C and a salinity of 5.7. Ripeness in males in Barataria Bay peaked in March as ambient temperature rose above 20°C and salinity rose to 15 (Figure 2.6). Female ripeness in Barataria Bay rose briefly in April, and peaked in June and July during periods of elevated salinity and temperature. In Terrebonne Bay, ripeness in female and male mussels peaked in April, as salinity decreased from 6 to 3.5 and temperature rose to 24 °C.

3.4 Discussion

During this study, peak ripeness in ribbed mussels was recorded from late spring through summer in both mesohaline Terrebonne Bay and polyhaline Barataria Bay. The low salinity site differed only by having a slightly shorter period of reproductive activity, and lower percent ripeness during peak times as compared to the high salinity sites. However, differences were fairly minimal suggesting that the ribbed mussel is not limited reproductively by salinity within the range tested (5-25).

Sexual maturation and spawning along the Atlantic coast generally takes place from mid-spring through late summer, with little latitudinal variation (Franz, 1996). In Massachusetts, mussels were found to ripen in June, with spawning observed as late as September (Jordan and Valiela, 1982). In Connecticut, ripe mussels were observed in March and spawned during July and August (Brousseau, 1982). Similar gametogenic timing was observed in ribbed mussels of North Carolina (McDougall, 1943) and Georgia (Kuenzler, 1961). Consequently, differences in the reproductive timing of ribbed mussels have been largely attributed to within-site variation in several environmental stimuli (Franz, 1996). Temperature, salinity and marsh flooding have all been suggested as important determinants of mussel gametogenesis by regulating seasonal metabolic activity (Dominguez et al., 2010).

The acceleratory effects of increased temperature on reproductive development are well documented in both wild and hatchery-raised populations of several mussel species (Brousseau, 1982; Hilbish, 1987). Particularly within temperate marshes experiencing large fluctuations in seasonal temperature, early gonadal development has been documented in spring, as waters warm above 15 °C (Brousseau, 1982). Across similar climates, spawning in mussels typically occurs once over an extended period during the warmest months of the year, followed by large reductions in the growth of reproductive tissues during colder winter months (Franz, 1996). Such patterns of gametogenesis may be a result of increased metabolic activity and increased carbon investment within reproductive tissues as temperatures increase (Barber and Blake, 1991).

Seasonal temperature fluctuations are often accompanied by other environmental stimuli which collectively promote reproductive maturation in mussels (Franz, 1996). In a study of the effects of artificial conditioning on gametogenesis in the Mediterranean mussel, *Mytilus galloprovincialis*, attempts to spawn hatchery-raised mussels suggested that individuals require exposure to increased ambient temperatures and food concentrations for at least two months prior to ripeness (Dominguez et al., 2010). However, while reproductive tissues reach morphological ripeness under such conditions, attempts to artificially spawn individuals in warm water during winter months were unsuccessful despite histological analysis demonstrating that all mussels were morphologically ripe (Dominguez et al., 2010). Therefore, other environmental stimuli may be important to mussel gametogenic development.

Seasonal fluctuations in salinity may partially determine gametogenic timing in ribbed mussels. Ripeness of ribbed mussels in tropical marshes experiencing minimal seasonal temperature variation have been shown to coincide with biannual shifts in ambient salinity between wet and dry seasons (Baez and Severeyn, 2005). Introduced ribbed mussels recently documented in northern Venezuala were found to spawn both in midsummer and late fall, when mean salinity fell from 25 to 10, and then again to 1 in December. Similar coincidence of spawning and salinity fluctuations have been found in several other tropical molluscan species, including the Colombian freshwater mussel, *Mytilus sallei*, the Venezuelan mangrove oyster, *Crassostrea rhizophorae* and several species of the marine ark clam genus, *Anadara* (Puyana, 1995; Velez, 1976). In nearly all cases, peak reproduction of bivalves in tropical systems occurs during the onset of the rainy season (summer through late fall), when sharp decreases in salinity may relieve inhibitory environmental stress experienced during drier months (Baez and Severeyn, 2005). In this study, temperature seems to be the dominant control on gametogenesis as both sites experienced similar temperature, but very different salinity regimes; it is possible that low salinity delays gametogenesis due to physiological stress.

Gametogenesis of ribbed mussels may also be determined by relative marsh flooding, increasing access to detrital resources, promoting greater reproductive metabolic investment. In previous studies, ribbed mussels at the marsh edge were found reached sexually maturity earlier than those at marsh interiors, primarily due to increased submergence and food abundances (Borrero, 1987; Franz, 1996). Mussels within high interior marsh experienced a two-month delay in sexual maturation when compared to mussels found at the marsh edge (Borrero, 1987). Spawning then took place only during September, in contrast to the continuously observed spawning activity in edge mussels from March through August. As well, mussels experienced reduced growth of somatic and reproductive tissues during winter months when flooding was minimal and limited detrital resources were available. Greater investment in reproductive tissue growth during warmer months resulted in increased ripeness due to greater submergence and subsequent food availability (Brousseau, 1982).

Within the microtidal marshes of lower Barataria Bay, seasonal flooding is partially driven by seasonal weather fronts and marine influx (Barbe, 2000). During the winter, northerly cold fronts pass along the Gulf Coast, typically lasting 3-7 days, effectively flushing Barataria Bay. During this study, annual low water elevation was recorded in January, nearly 30 cm less than during summer months. In contrast, southerly warm fronts contribute to up-estuary particle transport within Barataria Bay (Li et al., 2011; Booth, et al., 2000). As well, discharge from the Mississippi River's Southwest Pass creates an anticyclonic eddy towards the mouth of Barararia Bay, driving marine inflow between the Bay's barrier islands resulting in seasonal floodingii (Walker et al., 2005). Seasonal flooding is also driven by the thermal expansion of Gulf waters, particularly during the summer nadir of freshwater input to the estuarine system (Das, 2010). Early gametogenesis of ribbed mussels in Barataria and Terrebonne Bays was observed between February and May, possibly coinciding with increased flooding, although specific flooding rates at experimental sites were not determined in this study.

Male mussels during this study reached sexual maturity earlier and in greater percentages than female mussels in Barataria Bay. Early male reproductive development has been observed in several ribbed mussel populations along the temperate and subtropical Atlantic coast (Brousseau, 1982; Jordan and Valiela, 1982; Kuenzler, 1961), and within the introduced population in northern Venezuela (Baez et al., 2005). Such gametogenic dimorphism has also been recorded in several other bivalve species, including the horse-bearded mussel, *Modiolus -barbatus* (Mladineo, 2007), the blue mussel, *Mytlius edulis*, and the bay mussel, *Mytilus trossulus* (Toro et al., 2002). As spermatogenesis is typically a less energy-intensive process than oogenesis (Ropes et al., 1984), male gametogenesis can proceed rapidly in the spring as environmental stimuli including temperature, water elevation, salinity and food availability reach sufficient levels.

Sexual variation in gametogenic timing may help ensure that maximal successful spawning occurs when slow maturing female mussels finally reach peak ripeness. Particularly for sexually reproducing r-selected broadcast spawners such as the ribbed mussel, simultaneous spawning of both males and females is necessary for significant fertilization to occur (Brousseau, 1982). While mussels are known to spawn large numbers of eggs and sperm ($8x10^6$, $4x10^{11}$; Bayne et al., 1978), unfertilized gametes can only survive for less than one week (Widdow, 1991). Although unexplored in the current study, a slight female-bias has been documented in several ribbed mussel populations (Mladineo et al., 2007; Toro et al., 2002). Greater rates of spermatogenesis in female-biased ribbed mussel populations may ensure that a sufficient percentage of eggs are successfully fertilized at minimal metabolic cost. Males that spawn as the first females ripen may have sufficient time and resources to regenerate sufficient gametes for multiple spawning events before the senescence of ripe females.

Gametogenic timing observed in this study may also ensure optimal environmental conditions for vulnerable mussel larvae. Unlike several other molluscan taxa, mussel larvae are not lecithotrophic (Widdows, 1991), and require regular ingestion of bacterioplankton and microdetritus to prevent significant delays in growth and development (Sprung, 1984). Maximal growth rates of mussel larvae typically occur at algal concentrations more than twice those found in coastal marshes (Sprung, 1984). Larval growth is greatly reduced at temperatures below 20 °C, particularly within warm-water populations (Bayne, 1965). Further, mussel larvae exposed to acute salinity stress have resulted in nearly 50% reduction in developmental growth rate (Hrs-Brenko and Calabrese, 1969). The planktonic developmental stages of mussel larvae, typically lasting 12-30 days, may be significantly delayed in adverse conditions resulting in greater depredation (Widdows, 1991). The seasonal timing of mussel spawning with seasonal fluctuations in temperature, salinity, flooding rates and subsequent food availability may accelerate larval growth and ensure sufficient juvenile recruitment to southeastern Louisiana marshes.

The anticipated increases in ambient temperature, salinity and relative sea level in Barataria and Terrebonne Bays (Wiseman Jr., et al., 1990; Wilson and Allison, 2008) may significantly alter the timing, duration and reproductive output of gametogenesis in ribbed mussels. The results from this study suggest that both increases in temperature and relative marsh flooding rate may lengthen the reproductive season, approximating the year-round reproductive activity observed in tropical marshes (Baez et al., 2005). Consequently, as temperatures become consistently warm, seasonal changes in salinity may play a larger role in promoting early gonadal development.

The seasonal variability in salinity within southeastern Louisiana marshes may increase greatly with planned spring freshwater diversions from the Mississippi River as a coastal restoration strategy in the Louisiana Comprehensive Master Plan for a Sustainable Coast (CPRA, 2012). Greatly reduced salinities during spring diversion events (DeLaune et al., 2003), and increased salinities in the late summer and fall due to land loss and Gulf thermal expansion (Walker et al., 2005) may significantly affect gametogenic timing and reproductive output of ribbed mussels in southeastern Louisiana. Consequently, the anticipated effects of land loss and riverine diversions on ribbed mussels gametogenesis should be explored through expanded histological examination of sampled mussels within the Gulf coast, as well as laboratory culturing and artificial spawning under anticipated environmental conditions.

3.5 References

Baez, M. and Y. Severeyn. 2005. "Ciclo reproductivo de *Geukensia demissa* (Bivalvia:Mytilidae) en la playa de Nazaret, El Mojan, Estado Zulia, Venezuela." *Ciencias Marinas* 31(001A): 111-118.

Barbe, D., Cruise, J. and K. Crowder. 2000. "Sediment transport in a shallow coastal estuary during the winter season." *Jour. Amer. Water Res. Ass.* 36(4):1-10.

Barber, B.J. and J. Blake. 1983. "Growth and reproduction of the bay scallop, *Argopecten irradians* (Lamarck) at its southern distributional limit." *Exp. Mar. BioL EcoL* 66: 247-256.

Bayne, B.L., Holland, D.L., Moore, M.N., Lowe, D.L. and J. Widdows. 1978. "Further studies on the effects of stress in the adult on the eggs of *Mytilus edulis*." *J. Mar. Biol. Assoc. U.K.*, 58: 825-841.

Bertness, M. 1984. "Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh." *Ecology* 65(6): 1794-1807.

Beukema, J.J. and R. Dekker. 2007. "Variability in annual recruitment success as a determinant of long-term and large-scale variation in annual production of inertidal Wadden Sea mussels (*Mytilus edulis*)." *Helgol. Mar. Res.* 61:71-86.

Borrero, F. 1987. "Tidal height and gametogenesis: reproductive variation among populations of *Geukensia demissa*." *Biol. Bull.*173:160-168.

Brousseau, D. 1982. "Gametogenesis and spawning in a population of *Geukensia demissa* (Pelecypoda: Mytilidae) from Westport, Connecticut." *Veliger* 24(3):247-251.

Brousseau, D. 1984. "Age and growth rate determinations for the Atlantic ribbed mussel, *Geukensia demissa*." *Estuaries* 7: 233-241.

Chintala, M., Wigand, C. and G. Thursby. 2006. "Comparison of *Geukensia demissa* populations in Rhode Island frings salt marshes with varying nitrogen loads." *Mar. Ecol. Prog. Ser.* 320:101-108.

Coastal Protection and Restoration Authority (CPRA). 2012. "Louisiana's Comprehensive Master Plan for a Sustainable Coast." *Coastal Protection and Restoration Authority*. 1-172.

Das, A., Justic, D. and E. Swenson. 2010. "Modeling estuarine-shelf exchanges in a deltaic estuary: Implications for coastal carbon budgets and hypoxia."*Ecol. Modelling* 221:978-985.

DeLaune, R.D., Jugsujinda, A., Peterson, G.W. and W.H. Patrick Jr. 2003."Impact of Mississippi River freshwater reintroduction on enhancing marsh accretionary processes in a Louisiana estuary." *Estuarine, Coastal and Shelf Science* 58: 653-662.

Dominguez, L., Villalba, A., and J. Fuentes. 2010. "Effects of photoperiod and the duration of conditioning on gametogenesis and spawning of the mussel *Mytlius galloprovincialis* (Lamarck). *Aquaculture Research* 41:807-818.

Feng, Z. and C. Li. 2010. "Cold-front-induced flushing of the Louisiana bays." *Jour. Mar. Sys.* 82:252-264.

Franz, D. 1993. "Allometry of shell and body weight in relation to shore level in the intertidal bivalve *Geukensia demissa* (Bivalvia: Mytilidae)." *Jour. Exp. Mar. Biol. Ecol.* 174.:193-207.

Franz, D. 1996. "Size and age at first reproduction of the ribbed mussel *Geukensia demissa* (Dillwyn) in relation to shore level in a New York salt marsh." *Jour. Exp. Mar. Biol. Ecol.* 205:1-13.

Franz, D. 1997. "Resource allocation in the intertidal salt-marsh mussel *Geukensia demissa* in relation to shore level." *Estuaries* 20(1):134-148.

Hackney, J.T. 1983. "A note on the reproductive season of the Carolina marsh clam *Polymesoda caroliniana* (Bosc) in an irregularly flooded Mississippi marsh." *Gulf Res. Rep.* 7(3): 281 -284.

Hilbish, T.J. 1987. "Response of aquatic and aerial metabolic rates of the ribbed mussel *Geukensia demissa* (Dillwyn) to acute and prolonged changes in temperature." *J. Exp. Mar. Biol. Ecol.*105:207-218.

Hrs-Brenko, M. and A. Calabrese. 1969. "The combined effects of salinity and temperature on larvae of the mussel *Mytilus edulis." Mar. Biol*., 4: 224-226.

Inoue, M., Park, D., Justic, D. and W. Wiseman, Jr. 2008. "A high-resolution integrated hydrology- hydrodynamic model of the Barataria Basin system." *Env. Model. Softw.* 23:1122-1132.

Jordan, T.E. and I. Valiela. 1982. "A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its signifiance in nitrogen flow in a New England salt marsh." *Limnology and Oceanogr.* 27(1): 75-90.

Knights, A and K. Walters. 2010. "Recruit-recruit interactions, density-dependent processes and population persistence in the eastern oyster *Crassostrea virginica*." *Mar. Ecol. Prog. Ser.* 404: 79-90.

Kuenzler, E. J. 1961. "Structure and energy flow ofa mussel population in a Georgia salt marsh. *Limnol*. *Oce*anogr. 6:191-204.

Levinton, J. and T.H. Suchanek. 1978. "Geographic variation, niche breadth and genetic differentiation at different geographic scales in the mussels *Mytilus californianus* and *M. edulis*." *Mar. Biol.* 49: 363-375.

Li, C., White, J., Chen, C., Lin, H., Weeks, E., Galvan, K and S. Bargu. 2011. "Summertime tidal flushing of Barataria Bay: transports of water and suspended sediments." *Jour. of Geophys. Res.*116: C04009.

McDougall, ,K. D. 1943. "Sessile marine invertebrates of Beaufort, North Carolina." *EcoL Monogr.* 13: 321-374.

Mladineo, I., Peharda, M., Orhanovic, S., Bolotin, J., Vrancic, M.P. and B. Treursic. 2007. "The reproductive cycle, condition index and biochemical composition of the horse-bearded mussel *Modiolus barbatus*." *Helgol Mar Res.* 61:183-192.

Palmer, M. A. 1980. "Variation in life-history patterns between intertidal and subtidal populations of the meiobenthic copepod *Microarthridion littoraie*." *Mar. Biol.* 60: 159-165.

Puyana, M. 1995. "Aspectos biologicos y ecologicos de *Mytilopsis sallei* (Recluz, 1849) (Bivalvia: Dreissenidae) en bancos de ostras de la Cienaga Grande de Santa Marta, Caribe Colombiano. *Biol. Inst. Inves. Mar. Punta Betin.* 24: 39-53.

Resgalla, Jr., C., Brasil, E. S., Salomao, L.C. 2007. "The effect of temperature and salinity on the physiological rates of the mussel *Perna perna* (Linnaeus 1758)." *Braz. Arch. Biol. Tech.* 50(3):543-556.

Ruiz, E., Cabrera, J., Cruz, R., Palacios, J. 1998. "Crecimiento y ciclo reproductivo de *Polymesoda radiata* (Bivalvia: Corbiculidae) en Costa Rica. *Rev. Biol. Trop.* 46: 643-648.

Ropes, J.W., Murawski, S.A., Serchuk, F.M. 1984. "Size, age, sexual maturity and sex ratio in ocean quahogs, *Arctica islandica* Linne, off Long Island, New York." *Fish. Bull.* 82:253–267.

Spicer, J. 2007. "A comparison of channel morphology, marsh elevation and biological processes in natural and dredged tidal salt marshes in Louisiana." *Louisiana State University. School of Oceanography and Coastal Sciences.Doctoral Dissertation*. 1-104.

Sprung, M., 1984. "Physiological energetics of mussel larvae (*Mytlus edulis*). II. Food uptake." *Mar. Ecol. Prog. Ser.,* 17: 295-303.

Stiven, A.E. and E.J. Kuenzler. 1979. "The response of two salt marsh mollusks, *Littorina irrorata* and *Geukensia demissa*, to field manipulations of density and *Spartina* litter." *Ecological Mongraphs* 49 (2): 151-171.

Toro, J.E., Thompson, R.J. and D.J. Innez. 2002. "Reproductive isolation and reproductive output in two sympatric mussel species (*Mytilus edulis, M. trossulus*) and their hybrids from Newfoundland." *Mar. Biol.*141: 897-909.

Velez, A. 1976. "Credimiento, edad y madurez sexual del ostion *Crassostrea rhizophorae* de Bahia de Mochima. *Bol. Inst. Oceanogr. Univ. Oriente*. 15: 65-72.

Walker, N.D., Wiseman, W.J., Rouse and A. Babin. 2005. "Effects of river discharge, wind stress, and slope eddies on circulation of the Mississippi River plume." *J. Coast. Res*. 21: 1228–1244.

Wang, Y., Hu, M., Wong, W.H., Shin, P. and S. Cheung. 2011. "The combined effects of oxygen availability and salinity on physiological responses and scope for growth in the green-lipped mussel *Perna viridis*." *Mar. Poll. Bull.* 63:255-261.

Whitton, T., Jenkins, S., Richardson, C. and J. Hiddink. 2012. "Aggregated prey and predation rates: juvenile shore crabs (*Carcinus maenas*) foraging on post-larval cockles (*Cerastoderma edule*)." *Jour. Exp. Mar. Biol. Ecol.* 432: 29-36.

Widdows, J. 1991. "Physiological ecology of mussel larvae." *Aquaculture* 94: 147-163.

Wilson, C.A., and M.A. Allison. 2008. "An equilibrium profile model for retreating marsh shorelines in southeast Louisiana." *Estuarine, Coastal and Shelf Science*. 80: 483-494.

Wiseman, W. J., Jr., E. M. Swenson, and J. Power. 1990. "Salinity trends in Louisiana estuaries." *Estuaries* 13(3): 265-271.

CHAPTER 4. SUMMARY AND CONCLUSIONS

Benthic intertidal bivalves play an essential role in several marsh processes, contributing to physical habitat construction for resident invertebrate and vertebrate species while promoting vegetative productivity through suspended nitrogen filtration and biodeposition, ultimately strengthening host soils. In response to land loss in coastal Louisiana, the ecological significance of native intertidal bivalve populations has received recent attention. Greater understanding of the complex ecological processes occurring within coastal marshes, including the assessment of faunal communities involved in nutrient cycling, soil stabilization and trophic energy transference, is needed to evaluate the present state and future threats to vulnerable marsh communities. While recent focus has centered on the economically valuable eastern oyster (*Crassostrea virginica*), the ecology of other estuarine bivalves, such as the ribbed mussel (*Geukensia demissa*) is largely unknown in southeastern Louisiana. While such ecosystem services provided by ribbed mussel populations have been well-documented within temperate and sub-tropical Atlantic coastal marshes, relatively little is known about subtropical mussel populations in the Gulf of Mexico, which this study addressed.

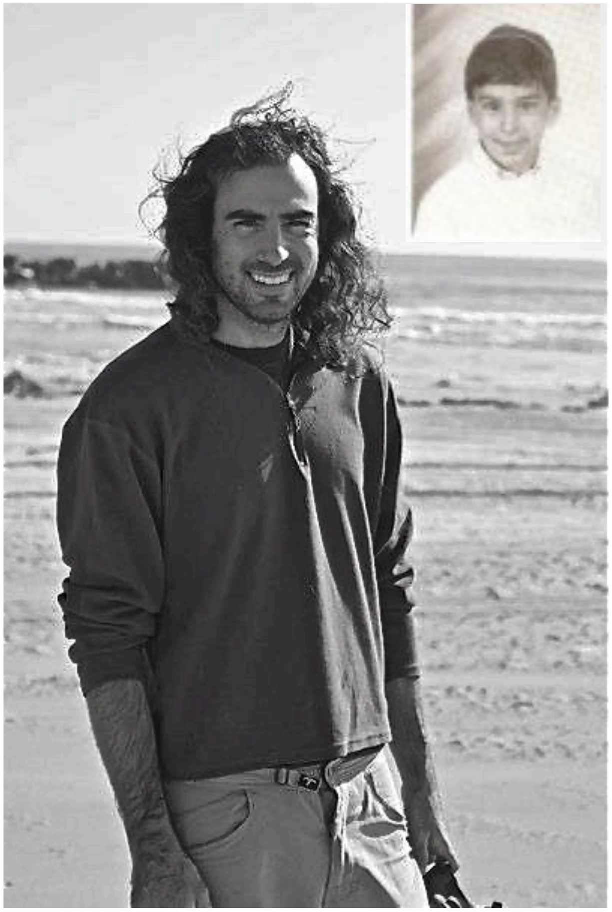
The observed patterns of recruitment, growth, mortality and density in Barataria Bay found in this study may be explained by low salinity stress, abundant detrital food resources and reduced predation in high-vegetation density mesohaline marsh. Relatively low *S. alterniflora* densities may limit suitable recruitment substrates for larval mussels, reduce available detrital resources for adult mussels, ultimately leading to the relatively low recruitment rates, growth rates, high natural mortality rates and low population densities observed in oligohaline marsh. Conversely, dense *J. roemerianus* densities within mesohaline marsh, accompanied by *S. alterniflora* vegetation, may limit crab predation while providing adequate detrital resources. Understanding the dominant factors that determine mussel distributions and densities is critical to better understand the potential impacts of changing local conditions on this native bivalve, and is important in assessing changes to the estuarine ecosystem. As critical components of estuarine systems, native bivalves contribute to physical habitat construction for resident invertebrate and vertebrate species while promoting vegetative productivity through suspended nitrogen filtration and biodeposition, ultimately strengthening host soils, and thus changes in their distribution and population densities can have significantly impact the overall system.

Critical to any population, is their reproduction, and understanding what conditions are required for gametogenesis is necessary for ensuring their survival in the wild, and/or for developing hatchery techniques which could be used to enhance or restore native bivalve populations. Sexually ripe mussels were observed from March through October in Barataria Bay while in Terrebonne Bay, ripe mussels were observed from April through September with few sexually mature individuals observed in November. In Terrebonne Bay, ripe individuals were observed in both sexes in April, with males exhibiting greater rates of ripeness than females throughout the summer. In contrast with Barataria Bay where ripe females were observed in late fall, no ripe females were observed after September in Terrebonne Bay while mature males were observed as late as November. Ripeness in both bays was found to be strongly correlated with increases in seasonal temperature and not ambient salinity. In Barataria Bay, temperatures above 20 °C and salinities above 15 coincided with large increases in ripeness, while in Terrebonne Bay, ripeness coinciding with nearly 50% decreases and increases, respectively. Such patterns of gametogenesis suggest that reproductive maturation in mussels at Terrebonne Bay may be triggered by seasonal shifts in ambient salinity.

In contrast to temperate Atlantic marshes experiencing strong seasonal temperature variation between winter and summer, and tropical marshes experiencing strong salinity variation between wet and dry seasons, ribbed mussels in Barataria and Terrebonne bays experience both large-scale seasonal temperature and salinity shifts. Mussel gametogenesis in southeastern Louisiana appears to be triggered by seasonal salinity shifts, occurring during the warmest months, during periods of increased water levels. Such reproductive timing may ensure optimal culturing environments for spawned larvae, potentially maximizing juvenile recruitment and subsequent population growth. Consequently, anticipated effects of climate change, coastal land loss and riverine diversions on ribbed mussels gametogenesis should be explored through expanded histological examination of sampled mussels within the Gulf coast, as well as laboratory culturing and artificial spawning under anticipated environmental conditions.

Relatively high recruitment and growth rates, and reduced mortality rates within Hackberry Bay suggest that ribbed mussels may play vital ecological roles in coastal marsh habitats in southeastern Louisiana, particularly in mesohaline sites hosting dense *J. roemerianus* vegetation. As well, the majority of studies have focused on ribbed mussel ecology within *S. alterniflora*-dominated marsh. Results from this study suggest that the importance of *J. roemerianus* vegetation on mussel population ecology may be underestimated within subtropical marshes of the Gulf of Mexico, and should be explored further. As well, future research examining mussel physiology including rates of filtration, excretion and biodeposition may be important to determine the potential ecological significance of ribbed mussels, and should be undertaken. Such studies may determine the potential for ribbed mussel population management to contribute to marsh restoration efforts in threatened southeastern Louisiana coastal marshes.

VITA



Aaron Honig was born in Worcester, Massachusetts. After attending Solomon Schecter Day School and Worcester Academy, he received his B.S. in Biology at Tufts University. After graduation, he studied leaf-cutter ant ecology in cloud forests at Bilsa National Park, Ecuador, worked as an aquarist at the New England Aquarium, a science teacher at the W. Alton Jones Earth Camp at the University of Rhode Island and Massachusetts Audubon Society before finding himself a marine ecology instructor called HoneyBear at the Catalina Island Marine Institute on Santa Catalina Island, located second star to the right and straight on ‘til morning. He then spent a year studying sea turtle ecology while thwarting poachers in Tortuguero, along the northeastern beaches of Costa Rica. He is currently a graduate student in the School of Renewable Natural Resources at the Louisiana State University AgCenter, and will earn his Master’s Degree in Renewable Natural Resources with a Fisheries Concentration in 2013. He is researching ribbed mussel population ecology in southeastern Louisiana coastal marshes. He loves his parents, Robert and Sandra, and his sister, Rachel, very much. And his cat, Simcha, too.