

Population ecology of the gulf ribbed mussel across a salinity gradient: recruitment, growth and density

AARON HONIG,¹ JOHN SUPAN,² AND MEGAN LA PEYRE^{3,†}

¹*School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, Louisiana 70803 USA*

²*Louisiana Sea Grant, Louisiana State University Agricultural Center, Baton Rouge, Louisiana 70803 USA*

³*U.S. Geological Survey, Louisiana Cooperative Fish and Wildlife Research Unit, School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, Louisiana 70803 USA*

Citation: Honig, A., J. Supan, and M. La Peyre. 2015. Population ecology of the gulf ribbed mussel across a salinity gradient: recruitment, growth and density. *Ecosphere* 6(11):226. <http://dx.doi.org/10.1890/ES14-00499.1>

Abstract. Benthic intertidal bivalves play an essential role in estuarine ecosystems by contributing to habitat provision, water filtration, and promoting productivity. As such, changes that impact population distributions and persistence of local bivalve populations may have large ecosystem level consequences. Recruitment, growth, mortality, population size structure and density of the gulf coast ribbed mussel, *Geukensia granosissima*, were examined across a salinity gradient in southeastern Louisiana. Data were collected along 100-m transects at interior and edge marsh plots located at duplicate sites in upper (salinity ~4 psu), central (salinity ~8 psu) and lower (salinity ~15 psu) Barataria Bay, Louisiana, U.S.A. Growth, mortality and recruitment were measured in established plots from April through November 2012. Mussel densities were greatest within the middle bay (salinity ~8) regardless of flooding regime, but strongly associated with highest stem densities of *Juncus roemerianus* vegetation. Mussel recruitment, growth, size and survival were significantly higher at mid and high salinity marsh edge sites as compared to all interior marsh and low salinity sites. The observed patterns of density, growth and mortality in Barataria Bay may reflect detrital food resource availability, host vegetation community distribution along the salinity gradient, salinity tolerance of the mussel, and reduced predation at higher salinity edge sites.

Key words: density; *Geukensia*; *Juncus*; flooding; growth; Louisiana; mortality; recruitment; salinity; salt marsh; *Spartina*.

Received 9 December 2014; revised 4 May 2015; accepted 6 May 2015; **published** 16 November 2015. Corresponding Editor: D. P. C. Peters.

Copyright: © 2015 Honig et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

† **E-mail:** mlapey@lsu.edu

INTRODUCTION

Benthic intertidal bivalves play an essential role in several marsh processes, contributing to physical habitat for species while promoting vegetative productivity through suspended nitrogen filtration and biodeposition (Jordan and Valiela 1982). As a foundation species of ecosystem engineering, ecosystem level changes that impact local bivalve population dynamics and distribution may lead to trophic cascades with

large ecosystem consequences (Jordan and Valiela 1982, Bertness 1984). Given recent and ongoing anthropogenic (i.e., river control, coastal restoration) and natural events (i.e., sea level rise) affecting coastal habitats along the northern Gulf of Mexico, it is important to develop a better understanding of the distribution and ecology of native bivalve populations. Only by understanding the factors controlling their population dynamics can we effectively assess how coastal changes might impact the services they provide.

Ribbed mussels are euryhaline benthic bivalves, native to the western Atlantic coast from the Gulf of St. Lawrence to the northern Gulf of Mexico (Bertness 1984, Watt et al. 2011), although they have also been found in northern Venezuela (Baez et al. 2005) and California (Torchin et al. 2005). 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 ind m⁻² in 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).

The high tolerance of ribbed mussels to environmental stressors including extreme temperature (0–45°C; Hilbish 1987, Jost and Helmuth 2007) and salinity (3–48; Pierce 1970, Neufeld and Wright 1998) is well-documented, and allow these mussels to exist across large environmental gradients (Baez et al. 2005, Torchin et al. 2005). Although the mussels have a wide tolerance to environmental gradients, changes or extremes in environmental variables (i.e., salinity, temperature) affect basic demographic processes, such as the timing of gametogenesis, spatial and temporal patterns of juvenile recruitment, adult growth and mortality (Bayne et al. 1983, Widdows 1991, Baez et al. 2005, Thompson et al. 2012, Le Corre et al. 2013). For example, physiological responses to osmotic stress at the extremes of their salinity tolerance result in lower growth and increased mortality (Strange and Crowe 1979, Wang et al. 2011).

Ribbed mussels along the U.S. Atlantic coast provide important ecosystem services as critical facilitators of nutrient cycling in coastal ecosystems, contributing to estuarine filtration, fertilization of host vegetation and soil strengthening (Jordan and Valiela 1982, Culbertson et al. 2008). These populations have been extensively studied in *Spartina alterniflora* saltmarshes, quantifying population responses to host-vegetation density, substrate characteristics, and nutrient and flooding regimes (Jordan and Valiela 1982, Bertness

1984, Klaus and Crow 1985, Franz 1996, Chintala et al. 2006). However, latitudinal differences in population dynamics and distribution suggest potential regional population differences related to environmental variation, and differences in predation dynamics (Lin 1991).

Research on ribbed mussel dynamics along the Atlantic coast of North America have focused exclusively on *Spartina alterniflora* salt marshes, providing little insight on U.S. Gulf coast communities, where other vegetation species are equally dominant to *S. alterniflora*, where salinity regimes differ dramatically, and where a putative different species of ribbed mussel exists (Sowerby 1914). The Gulf ribbed mussel (*Geukensia granossissima*), like its Atlantic cousin, *Geukensia demissa*, is a benthic intertidal bivalve forming large aggregations within dense salt marsh vegetation, and exists along the U.S. gulf coast. Few studies in this region have examined ribbed mussel populations, particularly within Mississippi River deltaic marshes. Understanding these basic distribution and population dynamics is critical to predicting effects of environmental change on local ecosystems and their survival.

We examined the recruitment, growth, mortality and distribution of the ribbed mussel (*G. granossissima*) within Barataria Bay, Louisiana. We quantified ribbed mussel distribution and population structure in low, mid and high salinity (~4, 8, 15 salinity mean) zones at interior and marsh edge sites in Barataria Bay. Among the salinity regimes and marsh zones present in Barataria Bay, it was hypothesized that mid-salinity marsh edges would host the greatest ribbed mussel densities, coinciding with peak *S. alterniflora* density. Such a hypothesis is supported by similar patterns documented in temperate Atlantic populations (Bertness 1984, Franz 1997). In the low-salinity upper regions of the estuary, reduced mussel densities were expected due to hypo-osmotic stress and reduced resource availability (bottom-up control) potentially resulting in reduced growth rates and greater mortality. In the high salinity zone, it was hypothesized that predation (top-down control) would limit mussel densities due to greater densities of known bivalve predators associated with the higher salinity and halophytic vegetation density (i.e., *Callinectes sapidus*; Williams et al. 1990).

METHODS

Study site

Barataria Bay is a well-mixed, microtidal coastal plain estuary in southeastern Louisiana. Located between the Mississippi River and Bayou Lafourche, the bay lies atop remnants of an abandoned deltaic lobe culminating in a chain of barrier islands separating Barataria Bay from the Gulf of Mexico. Water temperature ranges from 5°C in January to 33°C in August (Feng and Li 2010) and there is a distinct salinity gradient ranging from freshwater to a high salinity of 25 psu near the Gulf of Mexico. 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).

Sampling design

We selected three sampling areas along the salinity gradient in Barataria Bay (Fig. 1), located near Coastwide Reference Monitoring Stations (CRMS 2014). Within each sample area, duplicate sites were selected for establishment of transects along which were located sample plots. Low salinity sites were located in upper Barataria Bay in Turtle Bay (TB) with 3-year salinity (2010–2012) averaging 3.5 psu (TB sites: 29°32'42 N 89°59'32 W; CRMS 6303). TB sites are dominated by *Spartina patens*, *Schoenoplectus americanus* and *Distichlis spicata*. Mid-salinity sites were located mid-Barataria Bay in Hackberry Bay with a 3-year salinity averaging 7.4 psu (HB sites: 29°24'33 N 89°59'32 W; CRMS 0237). HB sites are dominated by *Spartina alterniflora*, *Juncus roemerianus* and *D. spicata*. The highest salinity area was established at Raccoon Lake (RL). RL sites (29°17'46 N 90°01'15 W; CRMS 0178) are located in lower Barataria Bay, with 3-year salinity (2010–2012) averaging 15.5 psu (range 1.2–31.2 psu; Fig. 2). RL sites are dominated by *S. alterniflora* and *J. roemerianus*.

Field survey

Sampling design.—Two transects were established at each of the six sites (3 sampling areas × 2 sites), with transects located parallel to the water's edge in two marsh zones; one along the marsh edge (<1 m from the water edge), and one

in interior marsh (>5 m from the water edge). Sample areas represented differences in salinity while zones represented potential differences in site exposure and flooding rates. Each transect was 100 m in length, with 0.25 m² quadrats placed every 10 m for a total of 120 plots (3 areas (salinity) × 2 sites × 2 zones (edge, interior) × 10 sample plots = 120; hereinafter called “zone plots”).

Environmental variables.—Salinity, temperature and water level data were downloaded from Coastwide Reference Monitoring System (CRMS) stations located near each study site. Stem density of each vegetation species was quantified within each quadrat.

Mussel distribution.—Within each quadrat, all mussels were excavated to 30 cm depth and mussel densities (ind 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 framed grids for mussel attachment 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 (3 areas × 2 sites × 2 zones × 5 grids). Grids consisted of plastic mesh stretched over 0.25 m² PVC bases placed in the marsh. 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 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, and immediate survival. Individual mussels were identified by their unique, anchored placement within quadrat mesh, and were not observed to move during the experiment.

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). Mean size (± SE) of deployed mussels was 81.5 ± 5.1 mm. Dead mussels were classified as either predation

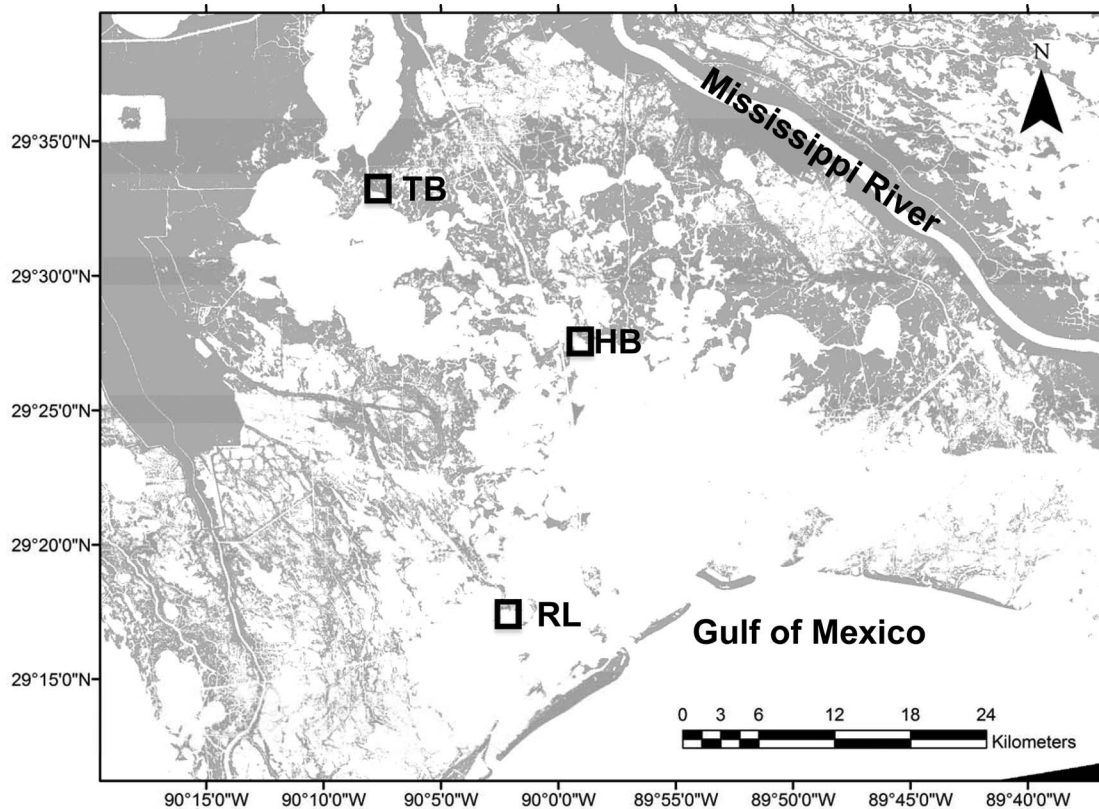


Fig. 1. Location of study sites in Barataria Bay, Louisiana, USA. Study sites were located along a salinity gradient from low salinity (annual salinity mean ~ 3 psu) at Turtle Bay (TB), to mid-salinity (annual salinity mean ~ 8 psu) at Hackberry Bay (HB) to high salinity (annual salinity mean ~ 16 psu) at Raccoon Lake (RL).

mortality 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. While it is possible that shells were broken by crabs after non-predation mortality, valves weaken considerably post-mortem, allowing for thorough scavenging without shell destruction (Lin 1991).

Recruitment.—Three clay flower pots (15 cm diam.) were embedded at both the marsh edge and interior (1, 5 m from channel) at each of the six sites. The pots were filled with local sediment that was filtered through 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 deter-

mined 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 number of recruits per pot per month.

Statistical analyses

For all tests, a significance value of $p < 0.05$ was used. Temperature, salinity, total and dominant vegetation density and flooding rates were examined by sample area (TB, HB, RL) and marsh zone (edge, interior) using a general linearized mixed model. Interactive and single effects were examined. Significant results were examined using LSMeans post hoc test.

A general linearized mixed model was used to examine differences in mussel density, size, growth, mortality and recruitment between sample areas (TB, HB, RL) and marsh zone (edge, interior). Vegetation density and flooding

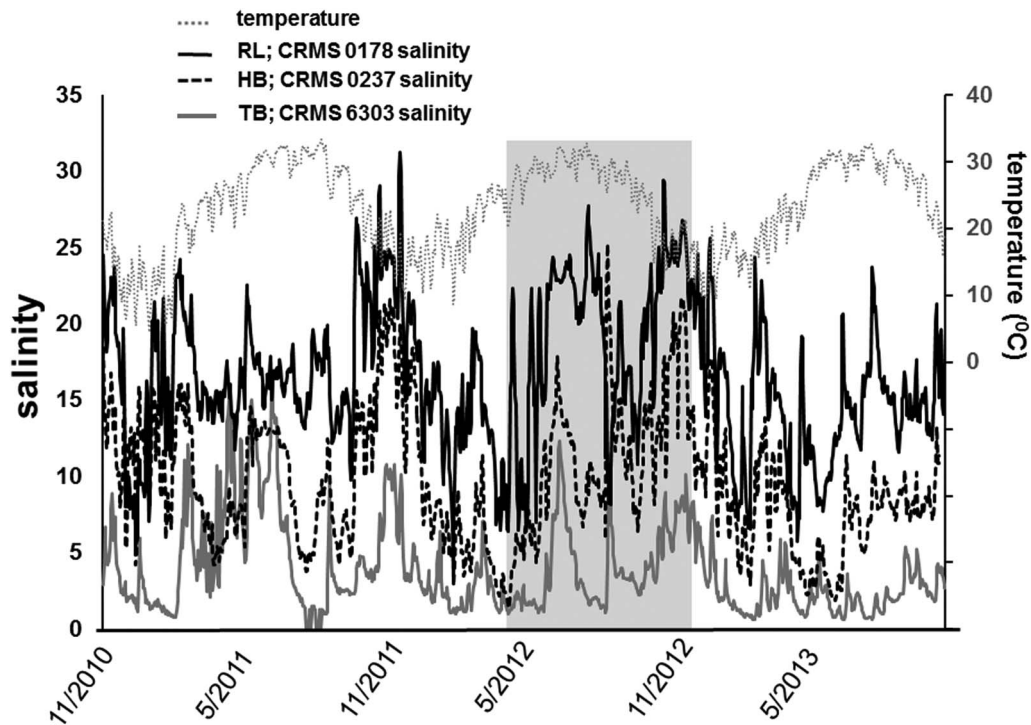


Fig. 2. Daily salinity and temperature ($^{\circ}\text{C}$) taken from Coastwide Reference Monitoring System (CRMS) stations (CRMS 0178, Raccoon Lake; CRMS 0237, Hackberry Bay; CRMS 6303, Turtle Bay) located near field sites. Highlighted grey box represents time period of study survey, growth, recruitment and mortality plots.

rates were tested as co-variables in all models. Significant results were examined with LSMeans post-hoc test. Extremely high mussel densities were observed in several experimental plots, while no mussels were found in the majority of plots (64%). Due to overdispersion, ribbed mussel density was assessed using a GLM negative binomial distribution function. Mortality data were examined using a binomial distribution function. All results are presented as mean \pm standard error unless otherwise indicated.

RESULTS

Environmental site characteristics

Water temperature did not differ by area or zone (Fig. 2). During 2012, water temperature in Barataria Bay averaged 23.7°C , and ranged from 10.2°C (February) to 32.1°C (August). Salinity differed significantly by area, with salinity (mean \pm SE) increasing from TB ($3.2 \text{ psu} \pm 0.2$) to HB ($8.1 \text{ psu} \pm 0.2$) and RL ($16.4 \text{ psu} \pm 0.1$).

Flooding rate (% time flooded) differed significantly by area and zone. Flooding rate was greater within RL and HB sites compared to TB sites ($F = 10.68$, $p < 0.001$; RL: $31.6\% \pm 0.7$, HB: $33.5\% \pm 0.5$, TB: $16.2\% \pm 0.2$) and at edge sites compared to interior sites ($F = 16.72$; $p < 0.01$; $31.0\% \pm 0.1$, $17.1\% \pm 0.3$).

Vegetation stem density differed significantly by area only. Specifically, mid-salinity sites (HB) had the highest density of vegetation which was greater than both the high salinity site and the low salinity site ($F = 13.03$, $p < 0.01$; RL: 629.3 ± 12.4 , HB: 1146.2 ± 60.9 , 464.1 ± 13.6). Species composition also varied by site. *S. alterniflora* was found at only 50% of TB sites, while occurring at 82% and 98% of the HB and RL sites. *J. roemerianus* occurred more frequently at HB and RL sites (TB: 5% of sites; RL: 25% of sites, HB: 42% of sites). TB sites were dominated by fresher mixes of species including *Spartina patens*, *Schoenoplectus americanus* and *Distichlis spicata*, with some *Paspalum vaginatum*, *Batis maritima* and *Avicennia germinans*.

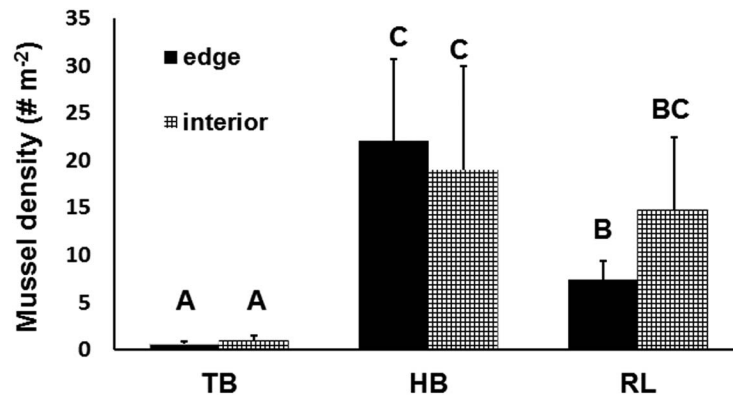


Fig. 3. Mean mussel density (ind m⁻²) ± standard error at edge and interior sites at low salinity (TB), mid-salinity (HB) and high salinity (RL). Different letters above the bars indicate significant differences in mussel density.

Mussel density and size

Mussel density differed by salinity ($F = 10.1, p < 0.01$; Fig. 3). Mussel densities were greatest at mid-salinity sites while densities at high-salinity sites were greater than those at low salinity sites (RL: 17.6 ± 5.0 , HB: 66.6 ± 18.1 , TB: 3.9 ± 3.17). Vegetation density was a significant covariate, with greater mussel densities associated with higher total vegetation density ($n = 120, F = 4.27, p < 0.04$; Fig. 4). Mussel density was most

significantly related to density of *J. roemerianus* ($R^2 = 0.74, p < 0.01$).

Mean mussel size differed significantly by salinity with significantly greater sizes 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; Fig. 5). Mean size varied by salinity and marsh zone with significant interaction ($F = 4.9, p = 0.02$). Covariates of dominant vegetation and flooding rates were not

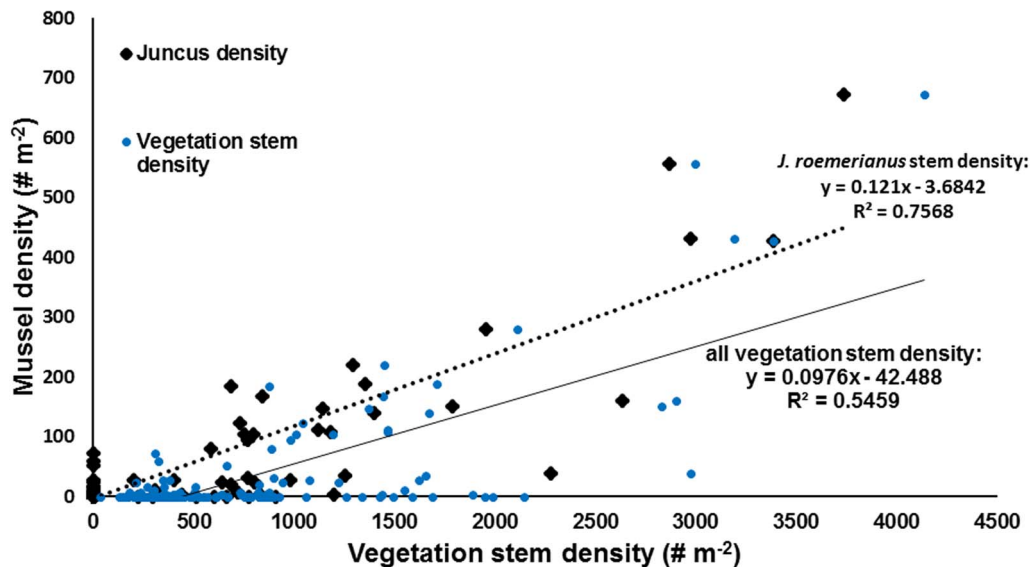


Fig. 4. Relationship between mussel density and the significant covariate, vegetation stem density. Regression equation represents relationship between mussel density and total vegetation stem density ($r^2 = 0.54$), and for mussel density and *J. roemerianus* stem density ($r^2 = 0.76$).

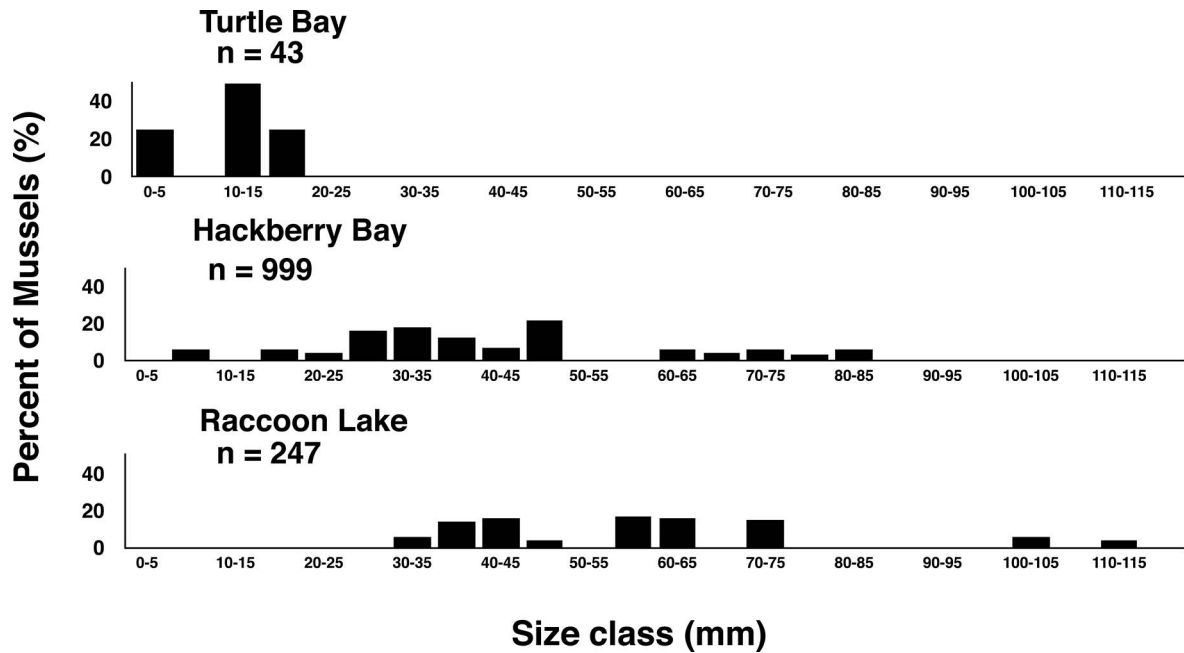


Fig. 5. Size class distribution (mm) as percentage of the mussel populations located along the salinity gradient (low salinity, TB; mid-salinity, HB; high salinity, RL).

significant.

Growth and mortality

There was a significant salinity by marsh zone interaction for mussel growth ($F = 13.7, p <$

0.001 ; Fig. 6). Growth rates of mussels in edge plots at the two higher salinity sites were greater than in lower salinity edge plots (RL: 1.3 ± 0.3 mm mo^{-1} ; HB: 1.4 ± 0.3 mm mo^{-1} ; TB: 0.3 ± 0.1 mm mo^{-1}) and all interior plots (RL: 0.5 ± 0.1

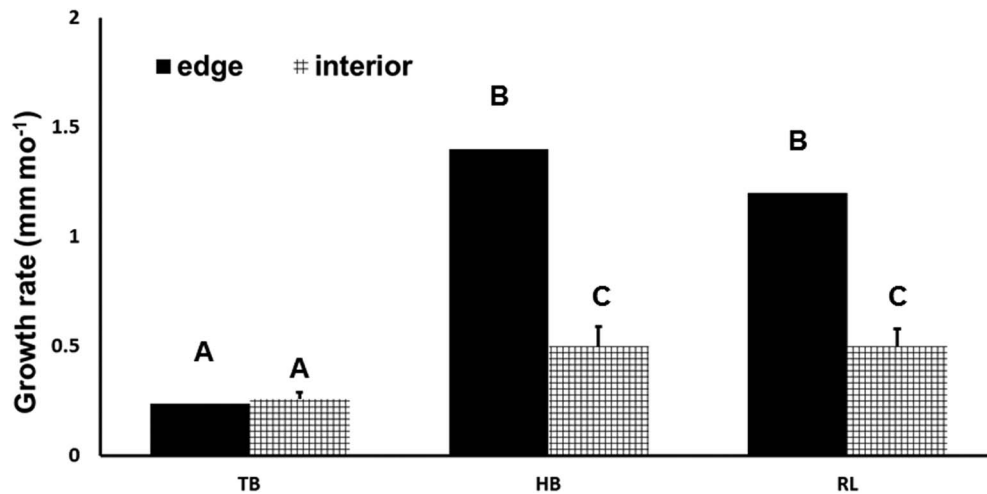


Fig. 6. Growth rate (mm mo^{-1}) \pm standard error at edge and interior marsh sites located across the salinity gradient at low salinity (TB), mid-salinity (HB) and high salinity (RL). Different letters above the bars indicate significant differences in growth rates.

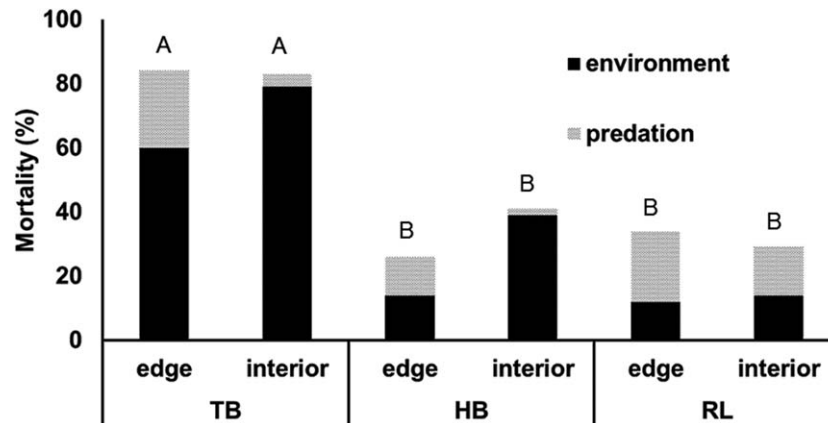


Fig. 7. Mortality (%) of mussels at edge and interior marsh sites located across the salinity gradient at low salinity (TB), mid-salinity (HB) and high salinity (RL). Mortality estimates from predation (crushed shells) versus environmental factors (no evidence of predation) are split out. Different letters above the bars indicate significant differences in mortality.

mm mo⁻¹, HB: 0.5 ± 0.1 mm mo⁻¹, TB: 0.25 ± 0.07 mm mo⁻¹; Fig. 6).

There was a significant effect of salinity on cumulative mussel mortality with the lowest salinity site, TB, experiencing higher mortality (88.4 ± 8.6%) than the two higher salinity sites (HB, RL), which had similar cumulative mortalities (RL: 56.5 ± 4.3%, HB: 45.3 ± 6.7%; $F = 7.9$, $p < 0.001$; Fig. 7). Cumulative mortality was similar across marsh zone (Edge: 56.3 ± 6.2; Interior: 61.2 ± 6.3%). Greater predation mortality was observed in edge plots than interior plots at lower salinity (TB, HB) sites, while predation mortality was similar across both zone plots at higher salinity (RL) sites.

Recruitment

Mussel recruitment was greater at high and mid-salinity sites than at low-salinity sites ($F = 16.0$, $p < 0.001$; RL: 2.3 ± 0.2, HB: 2.1 ± 0.2, TB: 0.6 ± 0.2; Fig. 8) and was similar across marsh zones (Edge: 1.9 ± 0.2, Interior: 1.4 ± 0.2).

DISCUSSION

Ribbed mussel distribution in Barataria Bay extended from low (~salinity 4 psu) to high salinity (~salinity 15 psu) marsh with larger mussels and higher densities of mussels closely associated with mid-salinity marsh and dense vegetation stands dominated by *J. roemerianus*.

The peak in mussel densities and size at the mid-salinity sites is likely explained by reduced recruitment and growth observed at low salinity sites, and greater predation mortality observed at the high salinity sites. These results support our original hypotheses, with the exception that higher densities of mussels were associated with *J. roemerianus* as opposed to *S. alterniflora*. Overall, the observed patterns of mussel population dynamics likely reflect detrital food resource availability and predation related mortality due to local site flooding rates and host vegetation community along the salinity gradient, as well as salinity tolerance of the ribbed mussel. Changes in salinity regimes and concomitant marsh vegetation communities may significantly affect the distribution and density of ribbed mussels in this region, and ultimately, their contribution to overall estuarine and marsh ecosystem services.

Ribbed mussels were found to be fairly ubiquitous across Barataria Bay, with densities across the salinity gradient similar to other mean densities reported for Gulf ribbed mussel populations. In this study, mean mussel densities among the three salinity regimes ranged from 3.9 ± 0.4 (low salinity) to 66.6 ± 16.3 ind m⁻² (mid-salinity). These densities are within the range reported in past studies of ribbed mussels in Barataria Bay (82 ± 18 ind m⁻²; Spicer 2007) and Alabama (5 ind m⁻²; West and Williams 1986),

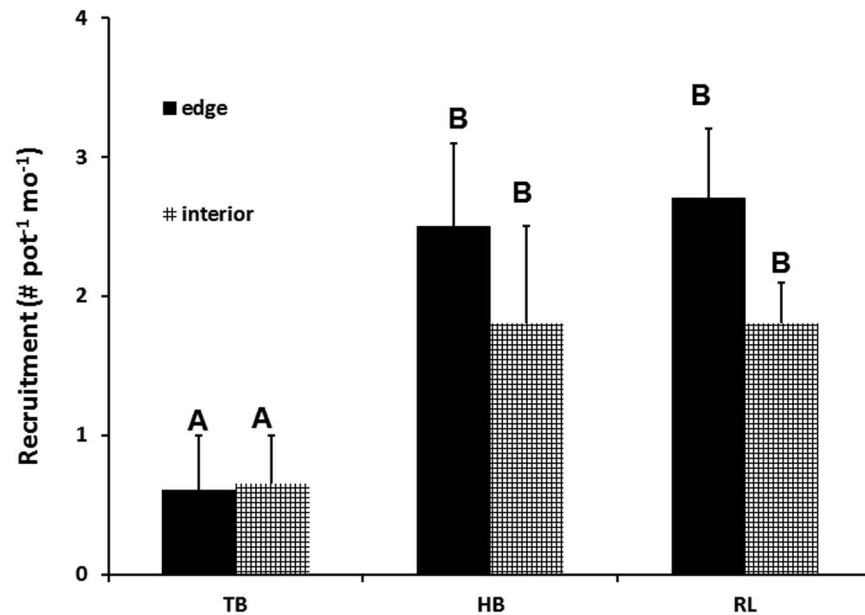


Fig. 8. Monthly recruitment estimates (no. individuals $\text{pot}^{-1} \text{mo}^{-1}$) \pm standard error at edge and interior marsh sites located across the salinity gradient at low salinity (TB), mid-salinity (HB) and high salinity (RL).

and are similar to densities of the Atlantic ribbed mussel (*G. demissa*) in Georgia (52 ind m^{-2} ; Kuenzler 1961) and North Carolina (38 ind m^{-2} ; Lin 1991). These densities however are surprisingly low in comparison to densities of *G. demissa* reported from northern temperate marshes that ranged from a mean of 200 ± 1 ind m^{-2} to a high of $9,227 \pm 731$ ind m^{-2} (Fell et al. 1982, Nielsen and Franz 1995, Evgenidou and Valiela 2002, Culbertson et al. 2008). In Rhode Island, mussel densities ranged from 470–1412 ind m^{-2} , and were often found in beds 2–3 mussels deep, covering 90% of exposed surfaces in *S. alterniflora* salt marshes (Bertness 1984).

Ribbed mussel densities within estuarine subtropical marshes such as in Louisiana may be lower compared to the Atlantic east coast populations due to osmotic stress resulting from the large range in salinity and high variation in salinity. While ribbed mussels can withstand large variations in salinity (3–48; Bertness 1984), they occur in high salinity or “salt marsh” (18–30 psu) areas (Bertness and Grosholz 1985, Chintala et al. 2006). Only one study that we could determine based on site description data documented high densities (470–1412 ind m^{-2}) in an area with salinity ranging from 10 to 15 psu (Bertness 1984). This salinity range covers the

range between our mid and high salinity sites, but densities were considerably lower than the minimum of this range. Examining annual salinity variation and ranges may provide insight in comparing these two locations; Louisiana estuaries are marked by enormous variation and ranges in salinity. Other factors, such as flooding rates, or vegetation composition and density may explain some differences. In this study, flooding rates ranged from 15% to 45%, similar to the 20–49% range reported in Rhode Island with high densities of mussels (Chintala et al. 2006).

While salinity may impose physiological limits on mussel populations, vegetation stem density may provide valuable attachment substrate, and possible protection from predation. In previous studies along the Atlantic coast, vegetation stem density has been associated with increased mussel growth rates, reduced mortality and increased ribbed mussel population densities (Lin 1991, Chintala et al. 2006). Results from several studies suggest a strong mutualistic relationship between ribbed mussels and the dominant host vegetation (*S. alterniflora*) where mussels promote shoot growth and strengthen root mass through nitrogenous biodeposition while *S. alterniflora* provides mussels with stable

anchoring substrates, detrital food resources, defense from predation, ultimately strengthening host soils (Lin 1989, Bertness and Leonard 1997, Watt et al. 2011). In this study, there was a clear positive relationship between mussel density and vegetation density; more specifically, mussel density was most strongly correlated with *J. roemerianus*, a co-dominant in this region with *S. alterniflora*.

As most studies have examined ribbed mussels where *S. alterniflora* is the dominant vegetation species, it is unclear if it is simply the structure provided by the stems, or the species that is important. Atlantic coast *S. alterniflora* stem densities in past studies ranged from 100 to over 2000 stems m^{-2} (Morris and Haskins 1990, Havens et al. 1995, Dai and Wiegert 1996, Altieri et al. 2007). Similar overall stem densities were quantified at the coastal Louisiana plots; however while *S. alterniflora* was present in the majority of plots (>90%), the highest stem densities and mussel densities were associated with a different species, *J. roemerianus*. In this region, stem densities are similar to those reported in the mid-Atlantic, but *J. roemerianus* stem densities are on average 4 times greater than those recorded for *S. alterniflora* (i.e., this study, Nyman et al. 1995, Lin and Mendelssohn 2012). In Mexico, invasive ribbed mussels were found to be positively and significantly associated with their native cordgrass, *Spartina foliosa* (Torchin et al. 2005). Determining if other vegetative species, including *J. roemerianus*, may provide similar benefits and have similar mutualistic relationships would yield important insights into mussel ecology across vegetatively diverse marshes, and within different salinity zones, and is important as salinity and vegetation zones are altered in the Mississippi delta region.

Mussel growth rates were greater at the mid and high salinity marsh edge sites (RL, HB) than all interior and low salinity sites. The growth rates at the two higher salinity edge sites (1.3–1.5 $mm\ mo^{-1}$; April–November) are similar to those found in the Atlantic ribbed mussel during their shorter growing seasons (1.5–20 $mm\ yr^{-1}$, Bertness and Grosholz 1985, Stiven and Gardner 1992, Culbertson et al. 2008, Hillard and Walters 2009). The growth rates in this study reflect areas with, on average, lower salinity but greater salinity variation, higher temperatures, different

dominant host-vegetation, and a longer growing season than most reported in the literature for ribbed mussel species. These environmental differences may contribute to other population dynamic differences which explain differences in mussel populations between past studies and this gulf coast study.

Understanding both rates and causes of mortality of a species are critical in determining environmental limits and thresholds, and understanding overall population dynamics. In this study, the low salinity sites experienced over 75% mortality, most from environmental stress (salinity), and likely a combination of low flooding rates resulting in decreased access to detrital food resources (Jordan and Valiela 1982, Stiven and Gardner 1992). At the high salinity sites, predation mortality was highest, although still lower than that found by Lin (1990) who estimated over 50% predation mortality. This lower predation mortality overall may be due to dense host vegetation which was equally dense on the edge as the interior. In particular, root masses of *J. roemerianus* were difficult to break apart, and extract mussels while most *S. alterniflora* vegetation could be examined by hand suggesting *J. roemerianus* may be preferred as it offers better refuge overall. It seems likely that such dense vegetation may serve as spatial refuge from crab predation and may explain the high mussel *J. roemerianus* association found in this region.

Along with mortality, differences in recruitment are critical in controlling population densities; 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. Similar patterns of recruitment have been observed in salt marsh in the northeast U.S., 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 larval access to recruitment substrates such as conspecifics and vegetation shoots by suspended mussel larvae (Bertness and Grosholz 1985, Nielsen and Franz 1995), while greater vegetation densities reduce tidal velocity and limit access to invertebrate predators, increasing larval settlement during slack high-water (Watt et al. 2011).

Equally important in recruitment is the presence of reproductively mature mussels. Ribbed mussels typically reach sexual maturity at 20 mm in length, after two growing seasons (Brousseau 1982), although this is highly dependent on relative temperature, salinity, flooding rates and food quality (Franz 1996, Honig et al. 2014). The low salinity site had less than 20% of the mussel population over 20 mm, and was located nearly 25 km up estuary from the mid and high salinity areas with higher mussel density, and populations with greater than 90% larger than 20 mm. Consequently, mussel populations contributing to larval supply may be concentrated towards higher salinity sites in Barataria Bay. As a result, recruitment was likely affected by larval transport within Barataria Bay. The most significant physical forces affecting fluid transport in the central areas of the bay, where ribbed mussel population densities were the greatest, were southerly winds occurring midsummer, when spawning likely takes place (Baumann 1987).

With relatively high recruitment and growth rates, and reduced mortality rates within mesohaline areas, it is likely that the gulf ribbed mussel contributes to marsh nutrient cycling and soil structure, but these services have yet to be quantified in this region. Mussel biodeposition may contribute to a mutualistic relationship with local vegetation 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. Ongoing restoration projects exploiting such environmental services conferred by ribbed mussel populations include the Delaware Living Shoreline Initiative, where stabilized fibrous bio-logs increase mussel recruitment within planted *S. alterniflora* clusters (Kreeger et al. 2011). Given the results of this study, restoration techniques exploiting ecosystem services of ribbed mussels may be most effective within mid-salinity sites, particularly in association with *J. roemerianus*.

CONCLUSIONS

The relative size distribution, growth rates and mortality rates of mussels across salinity, vegeta-

tion and flooding regimes in Barataria Bay suggest that population densities may be primarily limited by bottom-up control in low-salinity, high elevation, *S. patens*-dominated marsh sites with lower flooding rates and by top-down control in high-salinity, low elevation, *J. roemerianus*/*S. alterniflora*-dominated marsh sites with high predation mortality. Greater recruitment at high-salinity sites driven by relative proximity to dense adult spawning populations in lower Barataria Bay may reinforce existing differences in mussel densities in southeastern Louisiana salt marshes. Changes in salinity, marsh vegetation and marsh extent may impact the ribbed mussel population, and affect their contributions to ecosystem services. With many areas of deltaic Louisiana facing reduced salinity regimes due to proposed freshwater and sediment diversions, the density and distribution of these mussels may be significantly affected. However, with relatively high recruitment and growth rates, and reduced mortality rates within mesohaline areas, it is likely that the gulf ribbed mussel contributes to marsh nutrient cycling and soil structure, and could be important in helping maintain marsh integrity within these mesohaline areas; however these services have yet to be quantified in this region. Understanding population ecology of a native bivalve is critical to informing management on the effects of their activities on native populations, and ecosystem functioning.

ACKNOWLEDGMENTS

These data were collected with the help of numerous individuals including Bran Wagner, Nathan Yeldell, Molly Rybovich, Shea Miller, Lindsay Schwarting, Erin Leonhardt, Justin Leonhardt, Lisa Borrassa, James Ialeggio and Clayton Kern for their assistance in the field, and in the laboratory. R. Eugene Turner and Robert Romaine provided comments on early versions of this work. We thank Ron Etter for insightful comments on an earlier draft. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Altieri, A., B. Silliman, and M. Bertness. 2007. Hierarchical organization via facilitation cascade in intertidal cordgrass bed communities. *American Naturalist* 169(2):195–206.

- Baez, M., Y. G. de Severeyn, and H. Severeyn. 2005. Reproductive cycle of *Geukensia demissa* (Bivalvia: Mytilidae) on a beach at Nazaret, El Mojan, Zulia State, Venezuela. *Ciencias Marinas* 31:111–118.
- Baumann, R. H. 1987. Physical variables. Pages 8–18 in W. H. Conner J. W. Day, editors. *Ecology of the Barataria Basin, Louisiana: an estuarine profile*. Biological Report 85. U.S. Fish and Wildlife Service.
- Bayne, B. L., P. N. Salkeld, and C. M. Worrall. 1983. Reproductive effort and value in different populations of the marine mussel, *Mytilus edulis* L. *Oecologia* 59:18–26.
- Bertness, M. 1984. Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. *Ecology* 65:1794–1807.
- 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. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78:1976–1989.
- Brousseau, D. 1982. Gametogenesis and spawning in a population of *Geukensia demissa* (Pelecypoda: Mytilidae) from Westport, Connecticut. *Veliger* 24(3):247–251.
- Chintala, M., C. Wigand, and G. Thursdby. 2006. Comparison of *Geukensia demissa* populations in Rhode Island fringe salt marshes with varying nitrogen loads. *Marine Ecology Progress Series* 320:101–108.
- CRMS [Coastwide Reference Monitoring System]. 2014. Wetlands monitoring data. Strategic Online Natural Resource Information System (SONRIS) database. <http://coastal.louisiana.gov/index.cfm?md=pagebuilder&tmp=home&pid=92>
- Culbertson, J. B., I. Valiela, Y. S. Olsen, 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.
- Dai, T., and R. Wiegert. 1996. Ramet population dynamics and net aerial primary productivity of *Spartina alterniflora*. *Ecology* 77(1):276–288.
- Evgenidou, A., and I. Valiela. 2002. Response of growth and density of a population of *Geukensia demissa* to land-derived nitrogen loading, in Waquoit Bay, Massachusetts. *Estuarine, Coastal and Shelf Science* 55:125–138.
- Fell, P., N. Olmstead, E. Calson, W. Jacob, D. Hitchcock, and G. Silber. 1982. Distribution and abundance of macroinvertebrates on certain Connecticut tidal marshes, with emphasis on dominant molluscs. *Estuaries* 5(3):234–239.
- Feng, Z., and C. Li. 2010. Cold-front-induced flushing of the Louisiana Bays. *Journal of Marine Systems* 82:252–264.
- 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. *Journal of Experimental Marine Biology and Ecology* 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.
- Havens, K., L. Varnell, and J. Bradshaw. 1995. An assessment of ecological conditions in a constructed tidal marsh and two natural reference tidal marshes in coastal Virginia. *Ecological Engineering* 4:117–141.
- 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. *Journal of Experimental Marine Biology and Ecology* 105:207–218.
- Hillard, R., and K. Walters. 2009. Prevalence, patterns, and effects of shell damage on *Geukensia demissa* in South Carolina estuarine habitats. *Marine Biology* 156:2149–2160.
- Honig, A., M. K. La Peyre, and J. Supan. 2014. Effects of low and high salinity regimes on seasonal gametogenesis of the ribbed mussel *Geukensia granosissima* in coastal Louisiana, USA. *Sexuality and Early Development in Aquatic Organisms* 1:75–82.
- 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. *Biological Bulletin* 213:141–151.
- Klaus, M. L., and J. H. Crow. 1985. Distribution of the ribbed mussel, *Geukensia demissa* (*Modiolus demissus*), on a tidal creek bank in southern New Jersey. *Estuaries* 8(2B):237–243.
- Kreeger, D., P. Cole, D. Bushek, J. Kraueter, and J. Adkins. 2011. Partnership for the Delaware Estuary: 2011. Marine Bivalve Shellfish Conservation Priorities for the Delaware Estuary. PDE Report 11-03.
- Kuenzler, E. J. 1961. Structure and energy flow of a mussel population in a Georgia salt marsh. *Limnology and Oceanography* 6:191–204.
- Le Corre, N., A. Martel, F. Guichard, and L. E. Johnson. 2013. Variation in recruitment: differentiating the roles of primary and secondary settlement of blue mussels *Mytilus* spp. *Marine Ecology Progress Series* 481:133–146.
- Lin, J. 1989. Importance of location in the salt marsh

- and clump size on growth of ribbed mussels. *Journal of Experimental Marine Biology and Ecology* 128:75–86.
- Lin, J. 1990. Mud crab predation on ribbed mussels in salt marshes. *Marine Biology* 107(1) 103–109.
- Lin, J. 1991. Predator-prey interactions between blue crabs and ribbed mussels living in clumps. *Estuarine, Coastal and Shelf Science* 32:61–69.
- Lin, Q., and I. Mendelssohn. 2012. Impacts and recovery of the *Deepwater Horizon* oil spill on vegetation structure and function of coastal salt marshes in the northern Gulf of Mexico. *Environmental Science Technology* 46:3737–3743.
- Morris, J., and B. Haskins. 1990. A 5-yr record of aerial primary production and stand characteristics of *Spartina alterniflora*. *Ecology* 71:2209–2017.
- Neufeld, D. S., and S. H. Wright. 1998. Effect of cyclical salinity changes on cell volume and function in *Geukensia demissa* gills. *Journal of Experimental Biology* 201:1421–1431.
- Nielsen, K. J., and D. R. Franz. 1995. The influence of adult conspecifics and shore level on recruitment of the ribbed mussel *Geukensia demissa* (Dillwyn). *Journal of Experimental Marine Biology and Ecology* 188:89–98.
- Nyman, J., C. Crozier, and R. DeLaune. 1995. Roles and patterns of hurricane sedimentation in an estuarine marsh landscape. *Estuarine, Coastal and Shelf Science* 40:665–679.
- Pierce, S. K. 1970. The water balance of *Modiolus* (Mollusca: Bivalvia: Mytilidae): osmotic concentrations in changing salinities. *Comparative Biochemistry and Physiology* 36:521–533.
- Sowerby, G. 1914. Description of new species of Mollusca from New Caladonia, Japan and other localities. *Proceedings of the Malacology Society of London* 11:5–10.
- Spicer, J. 2007. A comparison of channel morphology, marsh elevation and biological processes in natural and dredged tidal salt marshes in Louisiana. Dissertation. Louisiana State University, Baton Rouge, Louisiana, USA.
- 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. *Journal of Experimental Marine Biology and Ecology* 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. *Journal of Experimental Zoology* 210:221–226.
- Thompson, C. M., R. H. York, and S. M. Gallagher. 2012. Species-specific abundance of bivalve larvae in relation to biological and physical conditions in a Cape Cod estuary. *Marine Ecology Progress Series* 469:53–69.
- Torchin, M. E., R. F. Hechinger, T. C. Huspeni, K. L. 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.
- Wang, Y., M. Hu, W. H. Wong, P. Shin, 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*. *Marine Pollution Bulletin* 63:255–261.
- Watt, C., D. J. Garbary, and C. Longtin. 2011. Population structure of the ribbed mussel *Geukensia demissa* in salt marshes in the southern Gulf of St. Lawrence, Canada. *Helgolander Marine Research* 65:275–283.
- West, D. L., and A. H. Williams. 1986. Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. *Journal of Experimental Marine Biology and Ecology* 100:75–95.
- Widdows, J. 1991. Physiological ecology of mussel larvae. *Aquaculture* 94:147–163.
- Williams, A., L. Coen, and M. Stoelting. 1990. Seasonal abundance, distribution, and habitat selection of juvenile *Callinectes sapidus* (Rathbun) in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology* 137(3):165–183.