Tracking Biological Invasions: An Assessment of Mussel Species in the St. Johns River, Jacksonville, FL

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Abstract - *Perna viridis* (Asian Green Mussel) and *Mytella charruana* (Charru Mussel) have been found within the estuaries of Florida, including the St. Johns River, for the past 30 y. This study verified the continuing presence of these 2 invasive mussels as well as the native *Ischadium recurvum* (Hooked Mussel) within the St. Johns River estuary. We found Hooked Mussels and Charru Mussels at all sampling locations, whereas we documented the Green Mussel at 2 sites. The overall densities and sizes of the Hooked Mussels and Charru Mussels varied by location. We observed higher densities of Charru Mussels at sites with lower salinities; none were observed at sites with salinity greater than 30‰. We noted the greatest Hooked Mussel density at moderate salinities, and those mussels had greater mean shell length compared to other mussel species at sites upriver. Our study highlighted the co-existence of native and non-native mussels within the estuary, and stressed the importance of continued monitoring of introduced mussel species in the southeastern US.

Introduction

Many invasive species (hereafter, invasives) reach new environments through anthropogenic means, and usually begin to thrive in their newly established habitat if conditions support the species (Sodhi and Ehrlich 2010). Invasives compete with native inhabitants for resources such as food, water, and living space, thus disrupting natural ecosystem dynamics (Sodhi and Ehrlich 2010). Not only can invasives disturb the balance of entire ecosystems, they can also impose high economic and ecological costs (Pimentel et al. 2001, Ruiz et al. 1997). The introduction of the non-native *Dreissena polymorpha* (Pallas) (Eurasian Zebra Mussel) to the North American Great Lakes provides an example of the economic and ecological damage a single species can cause to the environment that it has invaded. The species' invasion has resulted in the decline of native bivalve unionids and is estimated to cost $1 billion/year in damages and control efforts (Hebert et al.1991, Nalepa and Schloesser 1992, O'Neill 1997, Ricciardi et al. 1998, Pimental et al. 2005). *Pterois volitans* (L.) (Red Lionfish) and *P. miles* (J. W. Bennett) (Common Lionfish) are also responsible for deleterious environmental effects that have led to the decline of native coral-reef fishes in the Bahamas (Green et al. 2012).

One of the ways that invasives are introduced into marine ecosystems is via release of ballast water in a port from large commercial oceangoing vessels such as cargo and cruise ships (Carlton 1989). When taking on ballast water, ships can inadvertently draw up marine organisms including mussel larvae. These ships often travel to other ports around the globe, where they are required to comply

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Manuscript Editor: Paul M. Stewart

with separate international and local laws related to the release of ballast water offshore (USEPA 2001).

An additional vector for the introduction of marine invasives is through hull fouling—the accumulation of marine animals attached to the hull of a ship (Carlton 1987). These fouling organisms are transported from one port to another and could spawn if and when conditions are suitable. The larvae can then settle in their new location and they often survive if environmental conditions are favorable. To limit the transfer of fouling organisms from one site to another, the US Department of Homeland Security (2015) requires vessel-hull cleaning on a regular basis, as per their classification maintenance plan.

Complete monitoring of seagoing traffic is not feasible. The National Invasive Species Act of 1996 was implemented to reduce marine invasives; however, this legislation was likely enacted too late, after many invasions had already occurred.

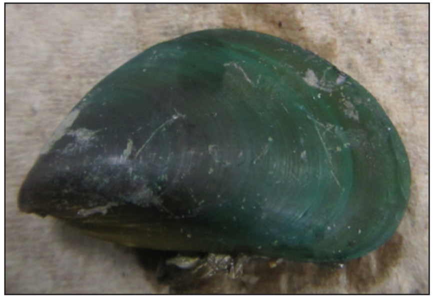
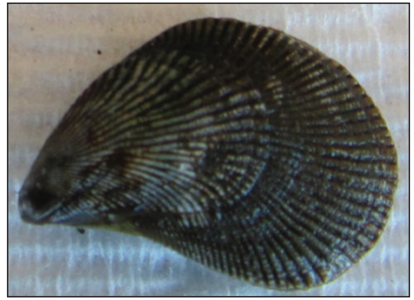
Jacksonville Harbor, a domestic and international trade port located on the St. Johns River, has a rich history of growth and development dating back to its foundation in 1822. Jacksonville Harbor, operated by the Jacksonville Port Authority (JAXPORT), currently ranks 3rd in the state of Florida for tonnage of foreign and domestic cargo imports and exports, and ranks 35th of the 150 ports nationwide (US Army Corps of Engineers 2016). Catering to the growing demands of cargo traffic, plans to deepen the river channel to accommodate larger oceangoing vessels to allow them to enter and exit the river during any tidal cycle have been formulated and could result in an increased volume of cargo and cruise ships within the harbor (Jacksonville Port Authority 2016). The growth in maritime shipping traffic within the St. Johns River could further increase the probability of more invasives entering the port.

Over the past 3 decades, at least 2 marine mussel species have been introduced to the southeastern US: *Mytella charruana* (d'Orbigny) (Charru Mussel), and *Perna viridis* (L.) (Asian Green Mussel). These mussels possess several characteristics that make them successful invaders, including the ability to develop dense aggregations on human-made and natural substrates, and wide temperature and salinity tolerances (Table 1). The potential impact of these non-native mussels on the native *Ischadium recurvum* (Rafinesque) (Hooked Mussel) and ecosystem of the St. Johns River, and their potential to cause substantial economic impacts is important to understand, yet the St. Johns is an understudied system. Therefore, the objectives of this study were to determine distributions and quantify the densities and shell morphometries for the native Hooked Mussel and the introduced Charru Mussel and Asian Green Mussel present in the St. Johns River estuary.

Field-Site Description

The St. Johns River (SJR) estuary is located in Duval County on the northeast Atlantic coast of Florida. The Trout, Arlington and Broward rivers are the main sources of freshwater and nutrient inputs in this portion of the SJR estuary (Bellino and Spechler 2013). Additional tributaries include Dunn and Clapboard creeks as well as the Intracoastal Waterway (Bellino and Spechler 2013). The SJR estuary is

Table 1. Summary of the introduction history (if applicable) and mussel preferences in the St. Johns River.

Characteristic	Charru Mussel (*Mytella charruana*)	Asian Green Mussel (*Perna viridis*)	Hooked Mussel (*Ischadium recurvum*)
			
Native range	Eastern Pacific Central/South America; Western Atlantic South America (Carlton 1992, Keen 1971)	Indo-Pacific (Siddall 1980, Vakily 1989)	Cape Cod, MA to West Indies (Abbott 1974)
First US introduction	Jacksonville, FL, 1986 (Lee 1987)	Tampa Bay, FL, 1999 (Benson et al. 2001, Ingrao et al. 2001)	Native
Subsequent introductions	Disappearance from Jacksonville, FL following initial sighting. Re-documentation in Jacksonville, FL, 2006 (jaxshells.org). Present from New Smyrna Beach, FL to Savannah, GA (Spinuzzi et al. 2013)	Separate introduction possible before 2002 on the Atlantic coast of FL between Ponce de Leon Inlet and Jacksonville (Baker et al. 2007). Later detected in subtidal and lower intertidal zones in Georgia in 2003 (Power et al. 2004) and Charleston Harbor, SC (South Carolina Department of Natural Resources 2006)	Native
Salinity tolerance	2–40‰ (Yuan et al. 2010)	15–64‰ (de Bravo et al. 1998, McFarland et al. 2013, Sivalingam 1977)	4.6–30‰ (Allen 1960)
Thermal tolerance	6–40 °C (Brodsky et al. 2009)	6–37.5 °C (de Bravo et al. 1998)	Unknown

also flanked by saltwater marshes mostly to the north and partially to the south close to the mouth of the river (Bellino and Spechler 2013).

Methods

Sampling procedures

We selected 8 public floating docks within the SJR in relation to the salinity gradient within the estuary and for their ease of public access (Table 2; Fig. 1). Four field sites were located on the north side and 4 were located along the south side of the river. We conducted field studies at each site on 2 separate occasions (8–10 December 2015 and 9–11 May 2016). During each field study, we laid out transect tapes along the seaward edges of the floating docks and we used a random number generator to select 5 sampling points along each transect. We collected samples by scraping all fouling organisms within a 40 cm x 40 cm (0.16 m^2) quadrat (placed vertically on the dock float beneath the water line) into a net. We used a YSI 556 datasonde (Yellow Springs Instrument Company, Yellow Springs, OH) to record water-quality data (temperature and salinity) at each site when sampling was conducted.

Table 2. Sampling-site names and geographic coordinates.

Site	Site name	Latitude, longitude
1	Alimacani Park	30°25'16.05"N, 81°25'15.49"W
2	Jim King Park at Sisters Creek	30°23'43.68"N, 81°27'31.91"W
3	Palms Fish Camp	30°24'17.25"N, 81°30'25.25"W
4	Brown’s Fish Camp	30°25'02.88"N, 81°31'57.47"W
5	Reddie Point Preserve	30°23'24.96"N, 81°37'09.16"W
6	Lonnie Wurn Boat Ramp	30°22'34.79"N, 81°35'05.35"W
7	Fort Caroline National Memorial	30°23'12.00"N, 81°29'56.62"W
8	Mayport Marina and Boat Ramp	30°23'50.76"N, 81°25'43.48"W

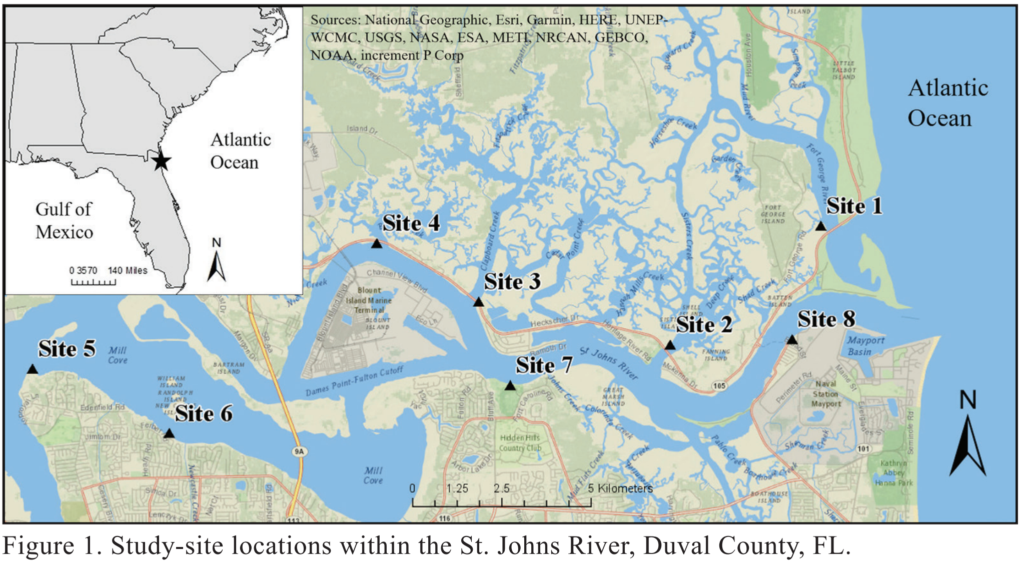


Figure 1. Study-site locations within the St. Johns River, Duval County, FL.

We placed each net sample into an individual Ziploc bag that was then labeled and promptly transported to the laboratory for processing. We identified mussel specimens to species, which were then sorted, counted, and weighed. Using digital calipers, we also took morphometric shell measurements (length, width, and height; to nearest 0.01 mm) of each specimen (after Bell and Gosline 1997).

Data analysis

We standardized the total number of mussels collected per site to the number of individuals per m^2 (individuals/m^2) to compare mussel densities among locations (Fig. 2). We employed a 2-way factorial ANOVA to test the effects of species (fixed; Charru Mussel versus Hooked Mussel) and field site (fixed; sites 1–8) on shell length. We evaluated significant differences among treatments with a Bonferroni post-hoc test of an ANOVA. We performed correlation analyses to assess the relationship between mussel density and salinity using Pearson's test and used a 1-way ANOVA to compare salinities of field sites. We employed a Holm–Sidak post-hoc test of an ANOVA to evaluate significant differences among treatment means. We omitted Asian Green Mussels from these tests due to their low abundance. Also, we did not evaluate temperature because there was little difference among sites. We conducted all statistical analyses in SPSS (IBM SPSS Software, Armonk, NY).

Results

Field surveys in 2015 and 2016 yielded 4979 mussels from 8 sampling locations (Table 3). We found mussels fouling the vertical surface of all 8 floating docks sampled (concrete: sites 1–3 and 5–8; plastic: site 4), which included attachment to oysters and conspecific and heterospecific mussel shells. The native Hooked

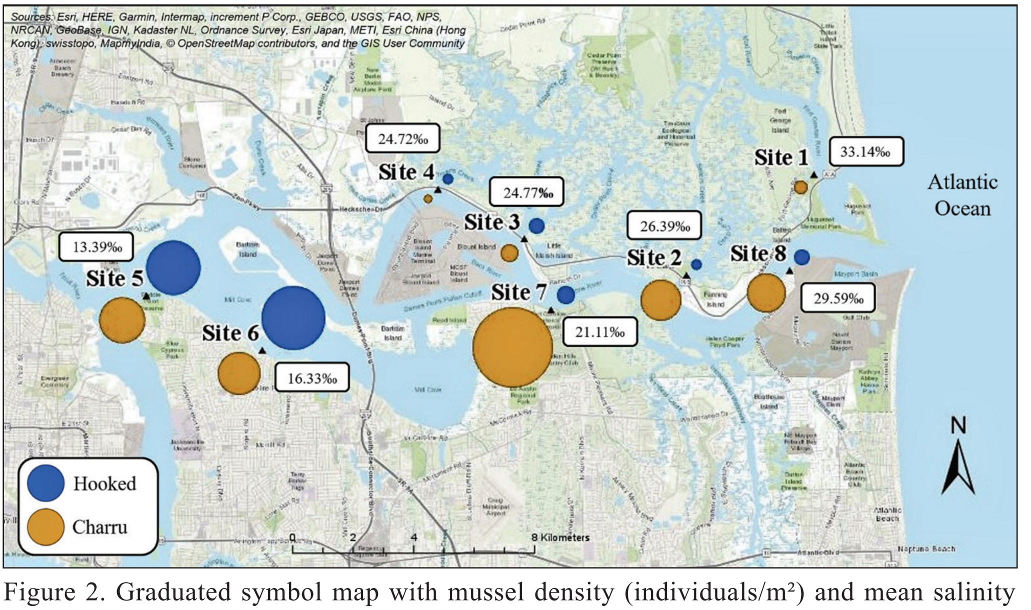


Figure 2. Graduated symbol map with mussel density (individuals/m²) and mean salinity (‰) for each survey site. Larger symbols represent higher densities per site.

Mussel accounted for 62% of mussels sampled and was present at each site, although densities among sites varied (Fig. 2). The Charru Mussel comprised nearly 38% of the total mussels collected but was absent from site 1 (Fig. 2). The Charru Mussel was particularly abundant at sites 5 and 6, which are located at the points farthest upriver within the study area (in an area with lower salinity; Fig. 3) and are situated between 2 major Jaxport facilities (Fig. 2). The Asian Green Mussel was only present at sites 7 and 8, and represented 0.2% of the total mussels surveyed (Fig. 2). There were little differences in mussel densities between the 2 sampling events.

We detected significant differences in salinity among sites ($P < 0.001$; Fig. 3). There was a negative correlation between overall mussel density and salinity (r = -0.789, $n = 8$, $P = 0.02$; Fig. 4), with total mussel density increasing with decreasing salinity. This negative correlation was very strong at the species level for the Charru

Table 3. Total mussel counts and densities (individuals/m²) for all species at each field site. We calculated densities ([total mussel counts] / 1.6). We sampled a combined total of 1.6 m^2 at each site.

	Total mussel count			Total mussel density (individuals/m²)		
Site	Hooked Mussel	Charru Mussel	Asian Green Mussel	Hooked Mussel	Charru Mussel	Asian Green Mussel
1	79	-	-	49.38	-	-
2	471	31	-	294.38	19.38	-
3	132	118	-	82.50	73.75	-
4	4	33	-	2.50	20.63	-
5	516	647	-	322.50	404.38	-
6	492	798	-	307.50	498.75	-
7	972	137	27	607.50	85.63	16.88
8	422	117	5	263.75	73.13	3.13

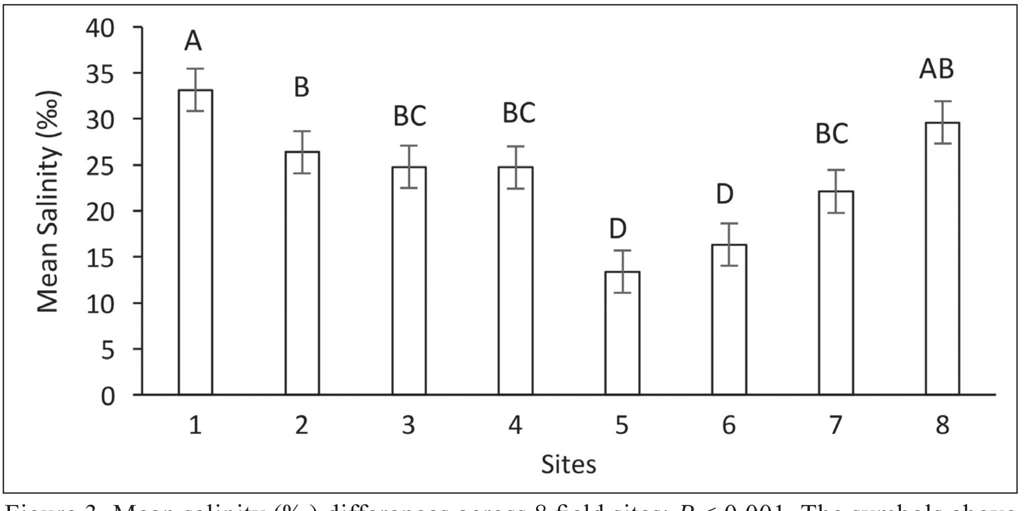


Figure 3. Mean salinity (‰) differences across 8 field sites; $P < 0.001$. The symbols above the error bars denote significant differences between the treatment means based on a Holm–Sidak post-hoc test of an ANOVA.

Mussel (r = -0.860, n = 8, P = 0.006; Fig. 5). These findings offer additional evidence that Hooked Mussels are found at various salinity levels and Asian Green Mussels are very scarce in the river (Fig. 2).

The Hooked Mussel had a greater mean shell length (± SE) (site 5: 21.84 ± 0.57 mm; site 6: 27.62 ± 0.59 mm) compared to the Charru Mussel (site 5: 13.66 ± 0.52 mm; site 6: 20.7 ± 0.47 mm) (P < 0.001; Table 4, Fig. 6) at sites 5 and 6 where Charru Mussel densities were higher (Table 3; Fig. 2). Conversely, the Charru Mussel had a greater mean shell length (± SE) (site 3: 16.54 ± 1.19 mm; site 8: 18.13 ± 1.24 mm,) than the Hooked Mussel at sites 3 and 8 (site 3: 12.45 ± 1.12 mm; site 8: 15.01 ± 0.61 mm,) (P < 0.001; Table 4, Fig. 6), where Hooked Mussel densities were higher (Table 3; Fig. 2).

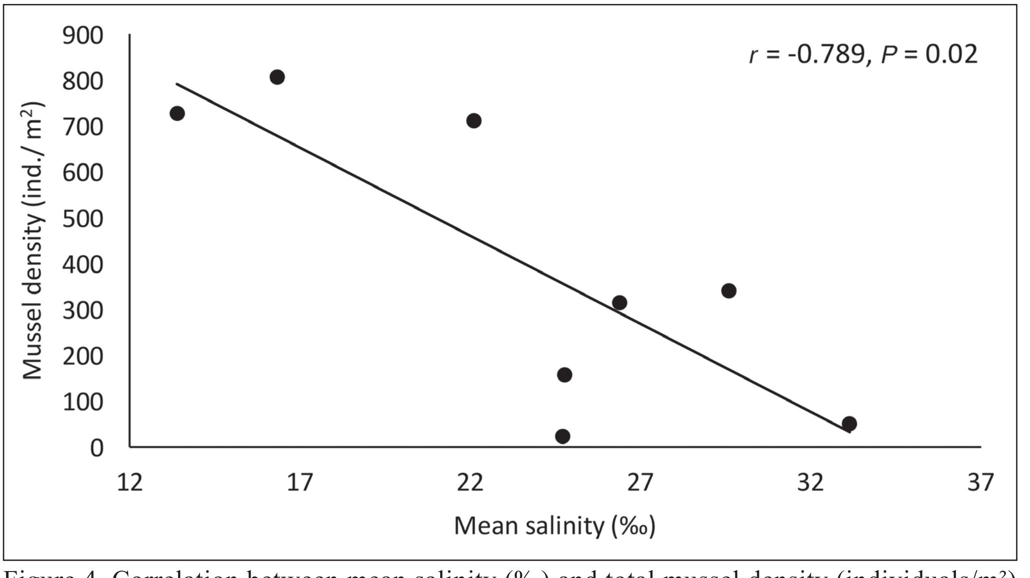


Figure 4. Correlation between mean salinity (‰) and total mussel density (individuals/m²) across field sites; P = 0.02.

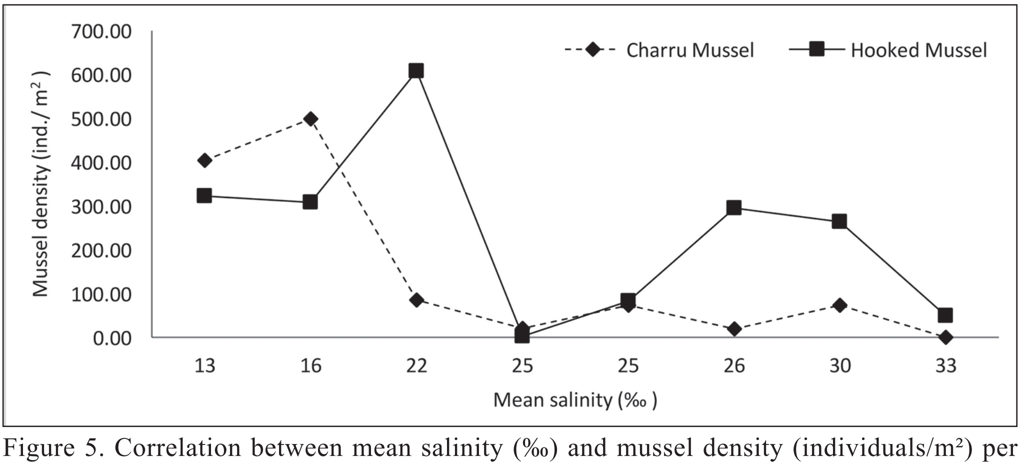


Figure 5. Correlation between mean salinity (‰) and mussel density (individuals/m²) per species across study sites; Charru Mussel, P = 0.006; Hooked Mussel, n.s., P = 0.284.

Discussion

Salinity and spatial distribution

Salinity gradients found within an estuary are influenced by tidal mixing, freshwater discharge from rivers/streams, and daily/annual rainfall (Wong 1995). Such gradients are found in the St. Johns River estuary and are supported by the current study (Fig. 2) and work by Spinuzzi et al. (2013). Salinity varies among seasons and years; thus, the study by Spinuzzi et al. (2013) recorded lower salinity levels and wider salinity ranges within the St. Johns River estuary than the current data show. Such fluctuations in salinities influence where mussel species survive within an estuary (Bayne 1976), which could play a role in the dispersal and abundance of the mussel species in this study.

In a survey to assess the abundance and distribution of non-native invertebrates in the southeastern US, Spinuzzi et al. (2013) sampled for invasive mollusks at several sites in the St. Johns River including sites 2, 3, 6, and 8 in the current study. Those authors found Charru Mussels and Asian Green Mussels

Table 4. Results of 2-way ANOVA for mean shell length (mm) with species and site as fixed factors (df = degrees of freedom, MS = mean square, *F* = value of the *F*-statistics, *P* = *P*-value).

Source of variation	df	MS	*F*	*P*
Species	1	4.365	0.026	0.871
Site	7	10,004.562	60.570	<0.001
Species x site	6	3362.713	20.359	<0.001
Error	4954	165.174		

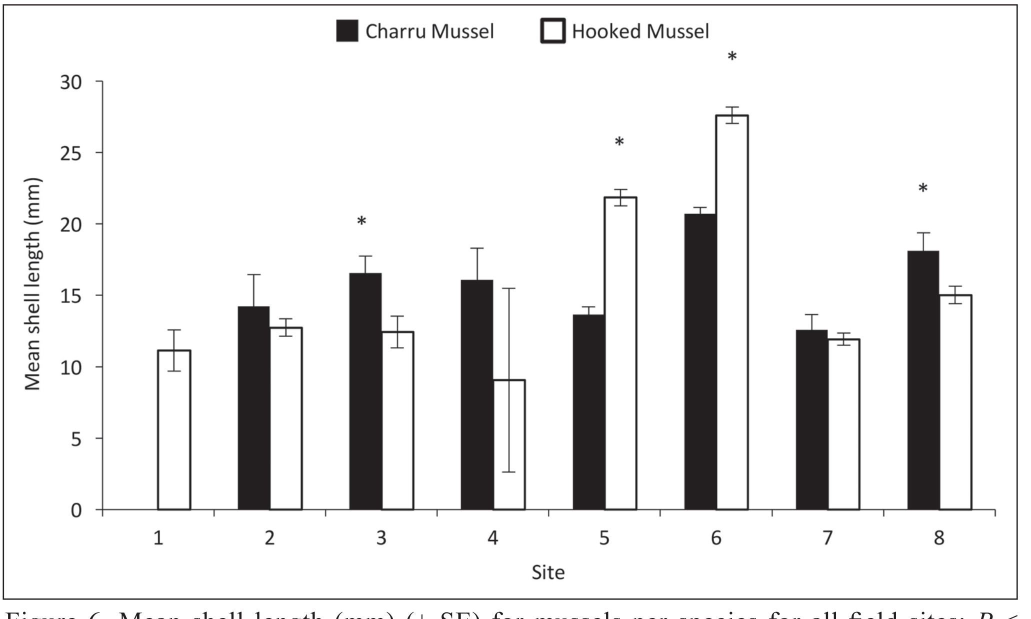


Figure 6. Mean shell length (mm) (± SE) for mussels per species for all field sites; $P < 0.001$. The symbols above the error bars denote significant differences between the treatment means based on a Bonferroni post-hoc test of an ANOVA.

at sites 2, 3, 6, and 8, while in the current study Charru Mussels were present at all of these sites, but Asian Green Mussels were only present at site 8. These differences in distribution and abundance of the Asian Green Mussel between the biannual (June 2006–June 2011) sampling by Spinuzzi et al. (2013) and the surveys we conducted in December 2015 and May 2016 could be due to lower water temperatures, especially in the colder winter months. Spinuzzi et al. (2013) did not mention if they conducted their surveys in the intertidal or subtidal zones (as in the current study); thus, it is difficult to draw conclusions regarding any changes in the mussel distribution and abundance over time because tropical mussels show high mortality when exposed to colder air temperatures during low tide (Firth et al. 2011). If Spinuzzi et al. (2013) found Asian Green Mussels in the intertidal zone, there is reason to believe that exposure to cold air-temperatures from tidal fluctuations, especially in the winter of 2014 when temperatures dropped below freezing for 10 h on 7 January (NOAA 2014), could have reduced the number of Asian Green Mussels at these sites prior to the start of our study. Studies to quantify temperature tolerances of the Asian Green Mussel in its introduced range are needed to better understand these trends. Spinuzzi et al. (2013) did not include the native Hooked Mussel, and the present study appears to be the first to report survey data for that species in the St. Johns River.

The greater number of individual Charru Mussels that we detected at sites 5 and 6 suggests that they prefer lower-salinity habitats than either Hooked Mussels and Asian Green Mussels. A study by Yuan et al. (2010) suggested that the Charru Mussel survives best at salinity levels from 2–23‰ and follows trends in the current data that demonstrate an inverse relationship between Charru Mussel density and mean salinity. It should be noted that sites 5 and 6 are located between 2 Jaxport cargo facilities that could be sites of introduction. Furthermore, freshwater inputs from the Trout and Broward rivers, which are sources of nutrient input into the St. Johns River estuary, could explain the greater number of native and non-native mussels at these locations because marine mussels are filter feeders that rely on tidal currents and other inputs (e.g., rivers, streams, and run-off) for sources of plankton and detritus (Wright et al. 1982).

Hooked Mussels were present at greater densities than Charru Mussels closer to the mouth of the river, which suggests their ability to better survive in areas of higher salinity than the Charru Mussel. These trends are consistent with previous findings in which the Hooked Mussel exhibited wide salinity tolerances from 4.6‰ to 30‰ (Allen 1960).

The Asian Green Mussel was present in low densities at only 2 sites located close to the mouth of the river. This finding is consistent with those of previous studies in the species' native range, where Asian Green Mussels thrive in seawater with a mean salinity of 32‰ but can tolerate higher salinities (Sivalingam 1977). In laboratory studies, McFarland et al. (2013) demonstrated that Asian Green Mussels are intolerant of salinities at or below 15‰, which parallels findings from the current study, where we found that Asian Green Mussels were absent from all upriver (i.e., lower salinity) sites.

Charru Mussels and Asian Green Mussels prefer settling on disarticulated oyster shells compared to man-made substrates, even though larval mussels will settle on most hard surfaces regardless of substrate type (Gilg et al. 2010). In the present study, differences in mussel density among sites could be due to floating-dock substrate types, especially the observed low mussel densities at site 4, which had a plastic substrate, compared to all other sites that had concrete substrates. Mussel settlement preferences are complex; thus, it is possible that additional factors such as length of time the docks have been in the field, competition, and presence of conspecifics and predators could have also affected mussel densities observed in this study.

Shell length

Although the overall size of a mussel can be related to growth, mussel shell length is most often used as a reference for growth because it is easily measurable (Bayne 1976, Sprung 1984). Mussel shell size is, therefore, a promising indicator of habitat conditions (Bayne 1976) as areas of higher nutrient availability result in the formation of larger mussels within species (Newell 1990, Phillips 2002, Sprung 1984). We recorded greater mean shell length for the Hooked Mussel at sites 5 and 6 and for the Charru Mussel at site 6 compared to other sites, which supports our suggestion that nutrient availability is higher upriver.

Interestingly, sites with greater mussel density for 1 species had relatively lower mean shell length compared to other species present. For example, we found the Hooked Mussel at greater densities at sites 2, 3, 7, and 8; however mean shell length at these sites was lower than for the the Charru Mussel. Conversely, we found Charru Mussels in greater densities at sites 5 and 6, but mean shell length for the Hooked Mussel was significantly greater at these sites.

Results from a study by Bertness and Grosholz (1985) revealed a decrease in growth rate due to intraspecific competition in high-density mussel aggregations, which could suggest why the Charru Mussel did not show the same increase in mean shell length as the Hooked Mussel at sites 5 and 6 due to its high density. Arribas et al. (2016) proposed that the presence of the mussel *Brachidontes rodriguezii* (d'Orbigny) led to increased growth in the mussel *Perumytilus purpuratus* (Lamarck) when found co-occurring in dense assemblages with an equal number of individuals. It is possible that, in a similar manner, the presence of increased numbers of Charru Mussels led to the significant increase in mean shell length for Hooked Mussels at sites 5 and 6 in the current study. Additional studies are needed to determine if direct competition between Hooked Mussels and Charru Mussels increases or reduces growth in either species.

The tropical Charru Mussel could experience winter die-offs particularly in the shallow subtidal environments established by the construction of the floating docks that we sampled in this study. Experiments by Yuan et al. (2016) suggested that adult Charru Mussels experienced higher rates of mortality than juvenile mussels when exposed to combined low salinities and temperatures. Therefore, adult Charru Mussels may have experienced higher winter mortality resulting in a higher proportion of juvenile mussels during sampling. Further study is required to determine the possible influence of larval supply and water-flow patterns in the estuary on the distribution and density of mussels in the St. Johns River.

Due to the introduction of 2 tropical mussels, the Charru Mussel and the Asian Green Mussel (Baker et al. 2007, Lee 1987), to the Atlantic coast of the southeastern US, monitoring the distribution, density, and range of these invaders is increasingly important. Rising seawater-temperatures associated with climate change (Domingues et al. 2008), may cause northward shifts in the ranges of warm-water non-native mussels, such as the Charru Mussel and Asian Green Mussel, which may threaten native fauna. Therefore, continued monitoring of non-native mussel species and their ranges is important, especially near major commercial ports such as Brunswick and Savannah, GA, and Charleston, SC, which could serve as potential introduction sites.

Acknowledgments

This research was supported by the Department of Biology and the College of Science and Mathematics at the University of West Georgia. We thank Melchisedec Adobah, Jeff Carson, Gretchen Harrison, Davin Holt, Melissa Holt, Eric Mashburn, Marty Sims, J.T. Sparks, Jasmine Starnes, Brian Stogner, and Megan Whitaker for field and lab assistance, and Helen Cheng, Frank Fontanella, Janet Genz, and Megan McCuller for experimental-design guidance. We extend our thanks to Harry Lee and Quinton White for counsel on the local fauna and field sites, and to the Marine Science Research Institute at Jacksonville University for the generous use of laboratory space and equipment.

Literature Cited

Abbott, R.T. 1974. American Seashells. Von Nostrand Reinhold Company, New York, NY. 663 pp.

Allen, J.F. 1960. Effect of low salinity on survival of the curved mussel, *Brachidontes recurvus*. Nautilus 74:1–8.

Arribas, L.P., M. Bagur, S.A. Soria, J.L. Gutiérrez, and M.G. Palomo. 2016. Competition between mussels at the rocky intertidal zone of La Lobería, Río Negro, Argentina. Revista del Museo Argentino de Ciencias Naturales 18(1):1–7.

Baker, P., J.S. Fajans, W.S. Arnold, D.A. Ingrao, D.C. Marelli, and S.M. Baker. 2007. Range and dispersal of a tropical marine invader, the Asian Green Mussel, *Perna viridis*, in subtropical waters of the southeastern United States. Journal of Shellfish Research 26(2):345–355.

Bayne, B.L. (Ed.). 1976. Marine Mussels: Their Ecology and Physiology. Cambridge University Press, New York, NY. 506 pp.

Bell, E., and J. Gosline. 1997. Strategies for life in flow: Tenacity, morphometry, and probability of dislodgment of two *Mytilus* species. Marine Ecology Progress Series 159:197–208.

Bellino, J.C., and R.M. Spechler. 2013. Potential effects of deepening the St. Johns River navigation channel on saltwater intrusion in the surficial aquifer system, Jacksonville, Florida. US Geological Survey Scientific Investigations Report 2013-5146. Jacksonville, FL. 34 pp.

Benson, A.J., D.C. Marelli, M.E. Frischer, J.M. Danforth, and J.D. Williams. 2001. Establishment of the Green Mussel, *Perna viridis* (L., 1758) (Mollusca: Mytilidae) on the west coast of Florida. Journal of Shellfish Research 20(1):21–29.

Bertness, M.D., and E. Grosholz. 1985. Population dynamics of the Ribbed Mussel, *Geukensia demissa*: The costs and benefits of an aggregated distribution. Oecologia 67(2):192–204.

Brodsky, S., L.J. Walters, E. Hoffman, and K. Schneider. 2009. Thermal tolerances of the invasive mussel *Mytella charruana*. P. e205, *In* Proceedings of the Society for Integrative and Comparative Biology Annual Meeting; Boston, MA. 141 pp.

Carlton, J.T. 1987. Patterns of transoceanic marine biological invasions in the Pacific Ocean. Bulletin of Marine Science 41(2):452–465.

Carlton, J.T. 1989. Man's role in changing the face of the ocean: Biological invasions and implications for conservation of near-shore environments. Conservation Biology 3(3):265–273.

Carlton, J.T. 1992. Introduced marine and estuarine mollusks of North America: An end-of-the-20th-century perspective. Journal of Shellfish Research 11:489–505.

de Bravo, M.S., K.S. Chung, and J.E. Perez. 1998. Salinity and temperature tolerances of the Green and Brown Mussels, *Perna viridis* and *Perna perna* (Bivalvia: Mytilidae). Revista De Biologia Tropical 46(5):121–125.

Domingues, C.M., J.A. Church, N.J. White, P.J. Gleckler, S.E. Wijffels, P.M. Barker, and J.R. Dunn. 2008. Improved estimates of upper-ocean warming and multi-decadal sea-level rise. Nature 453(7198):1090–1093.

Firth, L.B., A.M. Knights, and S.S. Bell. 2011. Air temperature and winter mortality: Implications for the persistence of the invasive mussel *Perna viridis* in the intertidal zone of the southeastern United States. Journal of Experimental Marine Biology and Ecology 400(1):250–256.

Gilg, M.R., E.A. Hoffman, K.R. Schneider, J. Ryabinov, C. El-Khoury, and L.J. Walters. 2010. Recruitment preferences of non-native mussels: Interaction between marine invasions and land-use changes. Journal of Molluscan Studies 76:333–339.

Green, S.J., J.L. Akins, A. Maljković, and I.M. Côté. 2012. Invasive lionfish drive Atlantic coral-reef fish declines. PloS one 7(3):e32596.

Hebert, P.D., C.C. Wilson, M.H. Murdoch, and R. Lazar. 1991. Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. Canadian Journal of Zoology 69(2):405–409.

Ingrao, D.A., P.M. Mikkelsen, and D.W. Hicks. 2001. Another introduced marine mollusk in the Gulf of Mexico: The Indo-Pacific Green Mussel, *Perna viridis*, in Tampa Bay, Florida. Journal of Shellfish Research 20(1):13–19.

Jacksonville Port Authority. 2016. Jaxport. Available online at http://www.jaxport.com. Accessed 25 June 2016.

Keen, A.M. 1971. Sea Shells of Tropical West America: Marine Mollusks from Baja California to Peru, 2nd Edition. Stanford University Press, Palo Alto, CA. 1064 pp.

Lee, H.G. 1987. Immigrant mussel settles in Northside generator. The Shell-O-Gram 28:7–9.

McFarland, K., L. Donaghy, and A.K. Volety. 2013. Effect of acute salinity changes on hemolymph osmolality and clearance rate of the non-native mussel, *Perna viridis*, and the native oyster, *Crassostrea virginica*, in Southwest Florida. Aquatic Invasions 8(3):299–310.

Nalepa, T.F., and D.W. Schloesser. Eds. 1992. Zebra Mussels: Biology, Impacts, and Control. Lewis Publishers, Boca Raton, FL. 832 pp.

National Oceanic and Atmospheric Administration (NOAA). 2014. Tides and Currents. Available online at https://www.tidesandcurrents.noaa.gov. Accessed 2 February 2016.

Newell, C.R. 1990. The effects of mussel (*Mytilus edulis*, L., 1758) position in seeded bottom-patches on growth at subtidal lease sites in Maine. Journal of Shellfish Research 9(1):113–118.

O'Neill, C.R., Jr. 1997. Economic impact of Zebra Mussels: Results of the 1995 National Zebra Mussel information clearinghouse study. Great Lakes Research Review 3(1):35–44.

Phillips, N.E. 2002. Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. Ecology 83(9):2562–2574.

Pimentel, D., S. McNair, J. Janecka, J. Wightman, C. Simmonds, C. O'Connell, E. Wong, L. Russel, J. Zern, T. Aquino, and T. Tsomondo. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agriculture, Ecosystems, and Environment 84(1):1–20.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273–288.

Power, A.J., R.L. Walker, K. Payne, and D. Hurley. 2004. First occurrence of the nonindigenous Green Mussel, *Perna viridis* (L., 1758) in coastal Georgia, United States. Journal of Shellfish Research 23(3):741–744.

Ricciardi, A., R.J. Neves, and J.B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the Zebra Mussel (*Dreissena polymorpha*) invasion. Journal of Animal Ecology 67(4):613–619.

Ruiz, G.M., J.T. Carlton, E.D. Grosholz, and A.H. Hines. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent, and consequences. American Zoologist 37(6):621–632.

Siddall, S.E. 1980. A clarification of the genus *Perna* (Mytilidae). Bulletin of Marine Science 30(4):858–870.

Sivalingam, P.M. 1977. Aquaculture of the Green Mussel, *Mytilus viridis* L., in Malaysia. Aquaculture 11(4):297–312.

Sodhi, N.S., and P.R. Ehrlich. 2010. Conservation Biology for All. Available online at http://conbio.org/publications/free-textbook/. Accessed 20 July 2016.

South Carolina Department of Natural Resources. 2006. Asian Green Mussels Found in Lowcountry Waters. #06-282. Available online at http://www.dnr.sc.gov/marine/sertc/DNR%20News%20release%20Perna%20viridis.pdf Accessed 12 March 2016.

Spinuzzi, S., K.R. Schneider, L.J. Walters, W.S. Yuan, and E.A. Hoffman. 2013. Tracking the distribution of non-native marine invertebrates (*Mytella charruana*, *Perna viridis* and *Megabalanus coccopoma*) along the southeastern USA. Marine Biodiversity Records 6:e55.

Sprung, M. 1984. Physiological energetics of mussel larvae (*Mytilus edulis*). IV. Efficiencies. Marine Ecology Progress Series 18:179–186.

US Army Corps of Engineers. 2016. US Waterway Data: Principal ports of the United States. Available online at http://www.navigationdatacenter.us/db/pport/xls/. Accessed 25 June 2016.

US Department of Homeland Security. 2015. The Vessel Environmental Manual. COMDTINST M16455.1A. Washington, DC. Available online at http://govdocs.rutgers.edu/mil/cg/CIM_16455_1A.pdf. Accessed 25 June 2016.

US Environmental Protection Agency Office of Water (USEPA). 2001. Aquatic nuisance species in ballast water discharges: Issues and options. Washington, DC. Available at https://www.epa.gov/sites/production/files/2015-09/documents/ballast14h.pdf. Accessed 25 June 2016.

Vakily, J.M. 1989. The Biology and Culture of Mussels of the genus *Perna*. International Center for Living Aquatic Resources Management, Manila, Philippines. 63 pp.

Wong, K.C. 1995. On the relationship between long-term salinity variations and river discharge in the middle reach of the Delaware Estuary. Journal of Geophysical Research: Oceans 100(C10):20705–20713.

Wright, R.T., R.B. Coffin, C.P. Ersing, and D. Pearson. 1982. Field and laboratory measurements of bivalve filtration of natural marine bacterioplankton. Limnology and Oceanography 27(1):91–98.

Yuan, W., L.J. Walters, K.R. Schneider, and E.A. Hoffman. 2010. Exploring the survival threshold: A study of salinity tolerance of the non-native mussel *Mytella charruana*. Journal of Shellfish Research 29(2):415–422.

Yuan, W.S., L.J. Walters, S.A. Brodsky, K.R. Schneider, and E.A. Hoffman. 2016. Synergistic effects of salinity and temperature on the survival of two non-native bivalve molluscs, *Perna viridis* (L., 1758) and *Mytella charruana* (d'Orbigny, 1846). Journal of Marine Biology 2016:9261309, 14 pp. Available online at https://doi.org/10.1155/2016/9261309. Accessed 22 February 2017.