Fall 2011

Density, Shell Use and Species Composition of Juvenile Fiddler Crabs (Uca Spp.) at Low and High Impact Salt Marshes on Georgia Barrier Islands

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ABSTRACT

DENSITY, SHELL USE AND SPECIES COMPOSITION OF JUVENILE FIDDLER CRABS (*UCA* SPP.) AT LOW AND HIGH IMPACT SALT MARSHES ON GEORGIA BARRIER ISLANDS

by

MICHELLE D. CARLSON

(Under the Direction of Sophie B. George and Laura B. Regassa)

Coastal wetlands offer refuge for juveniles of many species, with protection often coming in the form of dense vegetation. Human impacts have led to a 67% loss of coastal wetlands worldwide in the past 300 years, thus decreasing available refuges. There are no studies that show what affect this has on fiddler crabs (*Uca* spp.), a key species in salt marsh habitats. The present study looks at how human impacts are affecting juvenile fiddler crab densities, shell use, and species compositions. This study was conducted at 3 low and 3 high impact sites on Tybee and Skidaway Island, Georgia. Six collection trips were completed from June to August 2010 to each of the 6 sites. During each trip ten quadrats ($1m^2$) were placed at each site, and juvenile fiddler crab densities, *Littoraria irrorata* shell availability, and percent shell use were recorded. In the lab, juvenile fiddler crab carapace width and sex were determined and multiplex PCR was used to identify juvenile fiddler crab species. Juvenile fiddler crab densities were lower at high impact sites, while shell availability and shell use were similar at both low and high impact sites. Juvenile fiddler crab sizes and sex ratios did not differ between low and high impact sites on the substrate, nor did the sex ratios in shells. However low impact sites had significantly larger juvenile fiddler crabs found in shells as compared to high impact sites. Species compositions differed between low and high impact sites on the substrate and in shells, with an increase in *Uca pugilator* and *U. minax* at high impact sites. Impacts to salt marshes can cause a decrease in available refuge for juvenile fiddler crabs which could lead to higher mortality rates and an overall decrease in juvenile fiddler crab densities. Fiddler crabs are important in aerating the soil, soil drainage, and decomposition rates. A change in fiddler crab densities and behavior can have an adverse affect to the salt marsh and could lead to the loss of an important ecosystem.

INDEX WORDS: *Uca pugnax, Uca pugilator, Uca minax*, Salt marsh, Impact, Juveniles

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BS Biology, Georgia Southern University, 2009

MS Biology, Georgia Southern University, 2011

A Thesis Submitted to the Graduate Faculty of Georgia Southern University in Partial

Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

DEPARTMENT OF BIOLOGY

STATESBORO, GEORGIA

December 2011

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Electronic Version Approved:
December 2011

ACKNOWLEDGMENTS

I would like to thank Drs. Daniel F. Gleason, C. Ray Chandler, and Jill Stackhouse (Georgia Southern University) for help with project design, statistics, and GIS maps, respectively. I would also like to thank Georgia Southern University undergraduates Nick Sasser and Charlotte Radford for their assistance in data collection; James Welch (Wittenberg University) for the multiplex PCR protocol; and Skidaway Institute of Oceanography for access to study sites and for housing. This work was supported by the National Science Foundation Grant No. 0841146 (PI: Regassa) and the M.K. Pentecost Ecology fund (PI: George).

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CHAPTER 1

LITERATURE REVIEW

Salt marshes

The salt marsh plays a role in wildlife conservation and coastal defense against storms and erosion. Salt marshes occur on the east coast of the United States from Maine to Florida (Ferguson et al. 2009). Georgia has more than 378,000 acres of salt marsh, more than any other east coast state (Georgia Department of Natural Resources 2011). In general, salt marshes develop on shorelines where salt tolerant plants bind the sediment and water movement is limited (Ewanchuk and Bertness 2004), thus forming transitional areas between aquatic and terrestrial ecosystems. Salt marshes filter contaminants from water and are an important source of nutrients and organic materials (Boorman 1999, Gedan et al. 2009). The salt marsh habitat is highly variable due to flood and ebb tides (Ewanchuk and Bertness 2004); salinities can range from 0‰ to 70‰ depending on tidal fluctuations and the amount of evaporation (Teal 1958). Animals that reside in the salt marsh have to be able to survive or escape these abiotic fluctuations.

The limited numbers of organisms that have been able to adapt to this fluctuating ecosystem have few competing species and enemies (Teal 1962). Some are resident in the salt marsh (e.g. marsh crabs, snails, mussels, Teal 1962), while others visit the marsh for use as a hatchery, nursery, or for feeding (e.g. deer, rabbits, geese, raccoons; Ford and Grace 1998). The shallow waters of the salt marsh are a sanctuary providing refuges and nursery areas for the juveniles of many economically important species (Boesch and Turner 1984, Boorman 1999).

The salt marsh as a refuge

Marine invertebrate mortality is known to be caused by factors such as ultraviolet light, physiological stress, competition for food and space, predation, and delay of metamorphosis (Thorson 1964, Thorson 1966, O'Connor 1993, Hunt and Scheibling 1997, Gosselin and Qian 1997). The salt marsh provides needed refuge from many of these factors. A variety of animals hide in the muddy areas of the marsh; mussels and clams can be found in the mud while fiddler crabs dig burrows (Aspey 1978). In addition, small fish may take refuge in wet mud during low tide to keep from desiccation (Kneib 1984). Another abundant and well studied form of protection comes from the use of shells. Many gastropods create outer shells to protect their soft bodies from predators. When they die the shells are left behind and become protection for other animals (Wilson et al. 2005). Unlike the well known hermit crab that travels with a shell, these animals inhabit a shell for a short time. Shells may be chosen based on a host of features such as size, weight, and level of damage (Reese 1968); and most likely serve as a shelter from the environment. This has been observed in other ecosystems for organisms such as fishes, octopi, and crustaceans (Reese 1968, Barnes and DeGrave 2002, Wilson et al. 2005).

Salt marsh inhabitants

Primary producers of the salt marsh include marsh grasses and algae. Salt marsh plants must be able to grow in soils with a high salt content and low oxygen levels. Many of the plants that thrive in the salt marsh have salt secreting cells on their leaves (Phleger 1971) and surface roots in the top layer of the soil used to compensate for the low oxygen levels (Anderson and Treshow 1980). The dominant plants of salt marshes worldwide include *Spartina, Salicornia*, *Distichlis* and *Juncus* (Aspey 1978). *Salicornia, Distichlis* and *Juncus* are predominantly found in sandy soils (Teal 1958). *Spartina*, found throughout marsh habitat, reaches heights of over 2 m in the low marsh, but is often less than 30 cm tall in the high marsh (Anderson and Treshow 1980). Georgia salt marshes are often dominated by *Spartina alterniflora* and *Salicornia virginica*, with shrubs and trees found on higher land and along the marsh perimeter (Ewanchuk and Bertness 2004).

Insects and snails feed directly on primary producers, but bacteria must break down the marsh grasses to make nutrients accessible to the other primary consumers. These detritus-algae feeders include fiddler crabs, annelids, nematodes and mussels. The marsh snail, *Littoraria irrorata*, is abundant in the salt marsh (Ewanchuk and Bertness 2004). The snails traverse the mud to feed on organic matter during the low tide and climb cordgrass during the high tide to feed on microbes found on dead *S. alterniflora* and to avoid predation (Ewanchuk and Bertness 2004). Fishes, turtles, and mud crabs feed on the snails, keeping them from over populating the marsh (Wolff 2000). Other secondary consumers include blue crabs, raccoons, and many species of residential and migratory birds (Ribeiro et al. 2003).

Fiddler crab species in Georgia salt marshes

One of the most noticeable organisms in the salt marsh is the fiddler crab. Fiddler crabs are in the family Ocypodidae and are easily identified by eye stalks that are set close together (Teal 1958). They are found in intertidal zones, but their distribution depends both on biotic factors, such as predation levels and competition for living space, and abiotic factors including salinity, temperature, sediment grain size and organic content (Koch et al. 2005). Fiddler crab densities can be as high as 260 individuals per m^2

(Aspey 1978), with juvenile densities reaching 140 juvenile crabs per m^2 (Hubbard 2008). High fiddler crab densities correspond with a healthy salt marsh ecosystem and areas with fiddler crabs have been shown to have higher productivity levels (Smith et al. 1991, Holdredge et al. 2010). Fiddler crabs are an important food source, and their burrows affect sediment dynamics (Escapa et al. 2008), aerate the soil, and increase soil drainage and decomposition rates (Bertness 1985). Fiddler crabs are among the most important prey in salt marsh habitats (Wolff 2000). Adult blue crabs, mud crabs, shrimp, raccoons, and fish all feed on fiddler crabs. In addition, they are often taken from the salt marsh by predatory birds, but studies have shown that bird predation does not significantly impact the fiddler crab population (Ribeiro et al. 2003).

The sex ratio of fiddler crab populations was highly debated for many years. Some early sex ratio studies found fiddler crab populations to be female dominated in all size ranges (Zucker 1978, Colby and Fonesca 1984), while others found populations to be male dominant (Ahmed 1976). A more recent study by Johnson (2003) reported that adult populations were male dominated, with the percentage of males increasing with size; while juvenile stages tended to be female dominated. This was later confirmed by Bergey and Weis (2008).

In the presence of danger, fiddler crabs first look for refuges; if no refuge is available then they tend to act in selfish herds (McLain et al 2005). Large males are less likely to herd than small males and females (McLain et al. 2005), which may be due to fiddler crab sexual dimorphism. Male fiddler crabs have one feeding claw and one enlarged claw that can be up to half the mass of the crab (Crane 1943). This enlarged claw is used in territorial disputes (Allen and Levington 2007), species-specific displays, and threats (Sturmbauer et al. 1996). Ribeiro et al. (2003) found the reproductive benefits of the displays were much higher than the cost of predation. Female fiddler crabs have two same size feeding claws which are used to strain organic matter out of the mud (Teal 1962), but give them no form of protection.

There are three fiddler crab species found in the Georgia salt marsh. These include *Uca minax, U. pugilator* and *U. pugnax.* All three species can osmoregulate, but they have different preferred environmental osmostic concentrations and tolerance ranges (Thurman 2003). *Uca minax* is isosmotic around 650 mOsm, but can survive ranges from 550 to 2100 mOsm. *Uca pugilator* and *U. pugnax* are isosmotic around 880 mOsm and can tolerate ranges from 600 to 3400 mOsm (Thurman 2003). This has a large impact on their distributions in the salt marsh. *Uca minax* tend to be found in muddy and sandy areas of low salinity (O'Connor 1990) and can often be found inland around rivers and streams (Teal, 1958, Brodie et al. 2005). *Uca pugilator* is generally found in sandy parts of the salt marsh that are less likely to be flooded by tides. *Uca pugnax* is the most abundant of fiddler crabs on the east coast (Bergey and Weis 2008) and is found predominantly in muddy habitats. Adult populations of *U. pugnax* (mud fiddler crab) and *U. pugilator* (sand fiddler crab) sometimes overlap in sandier habitats characteristic of *U. pugilator*. In these mixed populations, *U. pugnax* is more aggressive and has higher recruitment than *U. pugilator* (Behum et al. 2005). In addition, the presence of *U. pugnax* causes a decline in *U. pugilator* and *U. minax* burrow densities (Aspey 1978, Teal 1958).

All adult species of *Uca* can be identified morphologically. They differ in many ways including color (Crane 1943). Color is controlled by the blood-gland of Hanstrom that is located in the middle part of the eye-stalk (Carlson 1935). *Uca pugilator* are characterized by a unique pattern found on the carapace which is accompanied by a dark purple spot near the eye stalks (Crane 1943). They also have an abundance of spoon-tipped setae present on the second maxilliped used in feeding on sand (O'Connor 1990). *Uca pugnax* are known to have a spot found between the eye-stalks on the carapace that can range from turquoise to dark blue (Crane 1943) and they have very few specialized setae on the second maxilliped (O'Connor 1990). *Uca minax* is known as the red jointed fiddler crab and, as its name suggests, is easily identified by the reddish coloring found on its back and legs.

Fiddler crab reproductive cycle

The life cycle and habitat of fiddler crabs have been well documented. Male fiddler crabs are territorial and often protect the area surrounding their burrows. The highest quality burrows are located in the high marsh and are protected by large males (Christy 1983). Males attempt to attract mates to their burrows using complex waving displays. Each species of male fiddler crab has its own distinct display for mating. *Uca pugilator* has the most energetic display with claw waves exceeding one per second (Crane 1943). *Uca pugnax* has a slightly slower display and often begins and ends its display with a bobbing curtsy (Crane 1943). *Uca minax* has the slowest display with claw waving as slow as once every 3 seconds. Displays are also very smooth with slight jerking of the claw (Crane 1943).

Large males have higher reproductive success and may have up to 3 females in their burrow at the same time (Christy 1983). Females are most likely to mate with males who defend quality resources (Christy 1983), and receptive females will follow the male into his burrow (Bergey and Weis 2008). Once a female enters a burrow the male will mate with her for up to 3 days (Christy 1983). After the eggs have been laid, the male leaves the burrow and guards it during the 12 to 15 day egg incubation period (Christy 1982, Sturmbauer et al. 1996).

Females release larvae during nocturnal high tides (Houser and Allen 1996). The larvae use selective tidal stream transport to help in dispersal to primary estuaries and coastal habitats (Tankersley and Forward 1994, Godley and Brodie 2007). This can increase the chance of transport to different areas and increase gene flow across subpopulations (Bilton et al. 2002). During development, fiddler crabs pass through a number of planktonic larval stages with the megalopal stage being the last larval stage (Hyman 1920). The megalopae settle in salt marsh habitats in response to chemicals released by adult fiddler crabs and environmental cues (Teal 1958, O'Connor 1993, Godley and Brodie 2007). A laboratory study by Christy (1989) showed that fiddler crab settlement is also dependent on temperature and substrate. The megalopae settle twice as fast when presented with substrate from the adult habitats (Christy 1989, O'Connor 1991, O'Connor and Greg 1998). In addition, juvenile fiddler crabs are sensitive to salinity ranges and are distributed across salinity gradients (Godley and Brodie 2007). The complete cycle to a juvenile stage takes from 4 to 6 weeks (Bergey and Weis 2008).

Juvenile fiddler crab identification

Juvenile fiddler crabs lack the defining morphological features of adult fiddler crabs, making differentiation between juvenile species very difficult. Traditionally, researchers reared juvenile crabs to the carapace width of 3mm to identify the species morphologically by counting the number of spoon-tipped setae found on their claws. *Uca pugnax* have 10 to 20 setae, *U. pugilator* has up to 200 and *U. minax* has less than 10

(Crane 1943, O’Connor 1990). This method of identification is labor intensive (O’Connor 1990), so early juvenile population study sizes were historically limited. However, the recent development of PCR (polymerase chain reaction)-based restriction fragment length polymorphism analysis (Brodie et al. 2005) and multiplex PCR (McGuire and Welch 2010) methods have made large scale megalopae and juvenile fiddler crab studies examining habitat use feasible (Behum et al. 2005, Brodie et al. 2005, Lopez-Duarte and Tankersley 2009, George et al. 2010).

Juvenile fiddler crab habitat use and refuges in the salt marsh

Juvenile stages of fiddler crabs have a higher mortality rate than the adults of the species (Thorson 1966, Gosselin and Qian 1997, Hunt and Scheibling 1997). Juvenile survival rates are type 3, meaning that the survival rate of the population decreases rapidly over time then levels off (Hunt and Scheibling 1997). To enhance survival of early juveniles, many species are found primarily in protected habitats (Knieb and Stiven 1978, Boesch and Turner 1984, Kneib 1984, Hettler 1989, O’Connor 1993, Boorman 1999, Behum et al. 2005, Brodie et al. 2005, George et al. 2010).

Until juvenile fiddler crabs reach a carapace width of over 3mm, they are too small to dig burrows (Herrnkind 1968, Behum et al. 2005) and must find an alternative form of refuge. Vegetation (Teal 1958, O’Connor 1990, Behum et al. 2005, Brodie et al 2005) or empty snail shells (George et al. 2010) can protect small juveniles from the incoming tides, desiccation, high temperatures, competition for space, predation, and storms (Kneib 1984, Hunt and Scheibling 1997). Juvenile *U. pugnax* and *U. minax* find refuge in covered areas consistent with those of the adult conspecifics (Teal 1958, O’Connor 1990, Behum et al. 2005, Brodie et al 2005), but habitat choice by juvenile *U.*

pugilator differs from that of the adults. Juvenile *U. pugilator* are found in covered habitats that are muddy, while adults are found in sandy habitats (O'Connor 1993). The *U. pugilator* juveniles might prefer the muddy areas rather than sandy areas because they do not have the specialized mouthparts needed to sift through sandy substrate (Crane 1975, O'Connor 1993, Brodie et al. 2005). Once *U. pugilator* fiddler crabs have carapace widths larger then 3mm, they move into habitats of the adult conspecifics (O'Connor 1993, Behum et al. 2005, Brodie et al. 2005).

Impacts to salt marshes

The salt marsh ecosystem is a habitat that is quickly being depleted, so the need for conservation is crucial. Salt marshes can be accessed from land and sea which makes them vulnerable to human impacts (Gedan et al. 2009). Some examples of direct human impacts in the salt marsh include dredging, reclamation, waste disposal, and live stock pastures (Kennish 2001, Gedan atal. 2009). Draining also occurs in salt marshes, turning habitat into residential areas, highways, farmland, and areas for tourism including beaches and boat ramps. In addition, the creation of harbors, canals, and artificial waterways can alter the sediment flow and plant distribution within the salt marsh (Gedan et al. 2009). Indirect human impacts to the salt marsh include the introduction of invasive species (Geller et al. 1997, Crooks 1998, Byers 1999, Talley et al. 2001), an increase in grazing pressure (Smith and Odum 1981, Silliman and Zieman 2001), the rise in sea level (Warren and Niering 1980, Carton et al. 2005), and the elevation of atmospheric carbon dioxide (Drake et al.1989). Direct and indirect human impacts have caused > 67% decrease in salt marsh habitat worldwide in the past 300 years (Kennish 2001, Lotze et al. 2006, Gedan et al. 2009).

Marshes without human development on the shoreline are under bottom-up control, while highly impacted areas may be changing to top-down control (Ewanchuk and Bertness 2004). Human impacts often have negative effects on the salt marsh habitat including the introduction of invasive species, the over-harvesting of top predators and primary producers, and an increase in nitrogen levels from fertilizers (Gedan et al. 2009). *Spartina alterniflora*, which is native to the southeastern United States, has been introduced to France, England and the west coast of the United States for fodder, fiber and coastal defense (Silliman et al. 2009). *Spartina alterniflora* out competes native species and causes a change in sediment composition and water flow (Ayers et al. 1999). Over harvesting of fish and crabs has resulted in an increase in *Littoraria irrorata*, the periwinkle snail, in Eastern salt marshes. These snails feed extensively on the cordgrass and at high densities can cause complete destruction, leaving nothing but mud flats (Silliman et al. 2005). Salt marsh grasses are also overharvested for use in animal food, bedding, and commercial products (Gedan et al. 2009); and recent increases in geese densities have had negative effects on *Spartina* spp. densities (Silliman et al. 2009).

A recent study conducted at high impact sites by George et al. (2010) found that juvenile fiddler crabs were residing in snail shells. Juvenile fiddler crabs may be using these shells as a refuge in response to a decrease in vegetation at high impact sites. Shell use by juvenile fiddler crabs fluctuated temporally and with environmental conditions and was greatest in the summer months and during high tide. Juvenile fiddler crabs were found in up to 79% of snail shells, with the majority of the crabs being female and of the species *U. pugnax* (George et al. 2010). Since the study was done only at heavily impacted site, it is unknown if shell use is a learned behavior in response to a decrease in other forms of refuges. The purpose of the current study is to see how human impact is affecting the distribution and behavior of juvenile fiddler crabs including densities, species composition and shell use.

CHAPTER 2
DENSITY, SHELL USE AND SPECIES COMPOSITION OF JUVENILE FIDDLER CRABS AT LOW AND HIGH IMPACT SITES

Introduction

Post-larval and juvenile stages of marine invertebrate species often experience high mortality rates during dispersal and after settlement (Thorson 1966, Hughes 1990, Gosselin and Qian 1997, Hunt and Scheibling 1997). Sources of mortality include predation, competition, cannibalism, desiccation, and heat stress (O'Connor 1993, Hunt and Scheibling 1997). Near-shore ecosystems such as seagrass meadows, mangrove forests and salt marshes (Beck et al. 2003) provide needed protection for juveniles of many species to reach the adult stage. Near-shore ecosystems can provide needed refuge, often in the form of dense vegetation (Beck et al. 2003), and increase the chance of juveniles surviving to adult stages; but a variety of human activities threaten the quality and quantity of refuges in these near-shore ecosystems. A recent review by Gedan et al. (2009) identified 7 types of human impacts that threaten plant and animal communities in salt marshes: resource exploitation and extraction, land conversion, species introductions, hydrological alteration, pollution, changes in consumer control, and climate change. Human activity in the high marsh zone is prevalent in the southeastern United States in the form of urbanization and road construction. Encroaching on salt marsh habitat has negative effects on salt marsh vegetation (Gedan et al. 2009), decreasing the availability of refuges and possibly affecting the distribution and density of juvenile species.

For example, juvenile fiddler crabs, one of the most abundant invertebrates in the salt marsh, make use of *Spartina alterniflora*-covered habitats. The *S. alterniflora* grass helps juvenile fiddler crabs escape predators such as fish and shrimp that come in with the tides; as well as birds, mud crabs, and other crab species that forage at low tide (Wolff 2000). It is possible that disrupted habitats may alter behavior in the salt marsh with juvenile fiddler crabs transitioning from vegetation as a refuge to other forms of refuge. A recent study on Tybee Island, Georgia by George et al. (2010) examined shell use by juvenile *U. pugnax* and *U. pugilator* at high impact sites. While shell use has been documented for a variety of vertebrates (Wilson et al. 2005) and invertebrates (Barnes and De Grave 2002), this was the first report of shell use by juvenile fiddler crabs. The loss of suitable covered habitats at high impact sites might cause juvenile fiddler crabs to resort to other forms of refuge, such as shell use.

The three fiddler crab species commonly found in the southeastern United States salt marshes are*, Uca minax, U. pugnax* and *U. pugilator.* Juvenile *U. minax* are known to occur in both muddy and sandy areas of low salinity (O'Connor 1990, Godley and Brodie 2007), including inland areas around tidally influenced rivers and streams (Teal 1958, Brodie et al. 2005). Juvenile *U. pugnax* and *U. pugilator* are found in grass-covered, muddy habitats at high salinity (Behum et al. 2005, Godley and Brodie 2007). *Uca pugilator* juveniles move into open, sandy habitats when they get to sizes >3mm carapace width, and can dig burrows (O'Connor 1993, Behum et al. 2005, Brodie et al. 2005), a source of refuge from predation and desiccation.

The current study was implemented to examine the effect of human impact in the salt marsh ecosystem on juvenile fiddler crab distribution and behavior. The overall objective was to investigate juvenile fiddler crab densities and distribution including, the number of individuals, sex ratios, sizes, shell use, and species composition between low and high impact sites along the Georgia coast.

I expected to find lower densities of juvenile fiddler crabs at high impact sites due to the disruption of the habitat by human activity. I also expected significantly higher shell availability and shell use at high impact sites due to an increase in disturbances. In addition, I expected human disturbances to affect both sexes and all sizes, keeping the sex ratios and size distribution of juveniles similar between low and high impact sites. Finally, I expected to find *U. pugnax* and *U. pugilator* juveniles in the high marsh at low and high impact sites because of the presence of adult conspecifics and the preference for muddy substrate and high salinities characteristic of the study sites.

Methods

Study sites. The study was conducted at low tide in the high intertidal zone on 2 barrier islands off the southeastern coast of the United States (Savannah, Georgia; Figure 1). A total of six sites were surveyed (Table 1): three high impact areas (Old Tybee Road [site 1], Catalina Drive [site 2], and Rodney J. Hall Boat Ramp [site 3] and three low impact areas (Skidaway Institute of Oceanography, sites 4-6).

High impact sites. All three high impact sites (1-3) had paved roads that ran through the salt marsh and disrupted tidal flow, as well as large areas of the salt marsh transformed for commercial use. Old Tybee Road and Highway 80 cut through the high zone of the salt marsh at site 1; Catalina Drive bissects the high zone of the salt marsh at site 2; and Highway 204 cuts through the high marsh at site 3. All three sites were easily accessible to humans for recreation or commercial purposes, with a large parking lot at site 3. The sites were littered with trash and plants were often trampled. The boat ramp at site 3 was re-paved in 2006 and was under renovation at the time of the study. Catalina drive at site 2 was also re-paved during the study period. The high impact sites were characterized by sparse vegetation (Table 2). Pore water salinity at these sites ranged from 33-55‰ and water temperature on sample dates was 27-37°C.

Low impact sites. The low impact sites were characterized by large expanses of salt marsh far from any residential, commercial or industrial development (Table 1). The 3 low impact salt marshes (sites 4-6) near Skidaway Institute of Oceanography were off limits to human activity, with no paved roads going through the marsh (Figure 1). These sites were characterized by tall and dense vegetation (Table 2). Pore water salinity ranged from 24-36‰ and water temperature on sample dates was 27-34°C.

Juvenile fiddler crab density, shell use, and shell availability. Ten quadrats ($1m^2$) were haphazardly placed at each study site. The number of juvenile fiddler crabs (< 9mm in carapace width) and the number of shells within each quadrat was immediately recorded after quadrat placement (O'Connor 1993, Johnson 2003). This was repeated 6 times at each site from June to August 2010, which covered the annual peak density for fiddler crabs (Hyman 1920, O'Connor 1993, Koch et al. 2005). During each of these six trips to the study sites (June to August 2010), one hundred snail shells were randomly collected per site and examined in the lab for the presence of crabs.

Juvenile fiddler crab size, sex, and species. To examine juvenile fiddler crab size, sex, and species distribution on the salt marsh substrate and in *Littoraria irrorata* shells, two trips were made to each study site once in July and once in August 2010. Twenty juvenile fiddler crabs were randomly collected from the substrate and 20 from shells in the high zone at each of the six study sites during each visit, except when insufficient crabs were present. Collections with fewer than 20 samples occurred twice at site 1 (18 crabs in July and 13 in August) and once at site 2 (18 crabs in August). A total of 240 juvenile fiddler crabs were collected from the substrate and 229 from shells. Juvenile crabs were taken back to the lab; the sex determined based on abdominal shape and presence of a large claw; the carapace width measured using a dissecting scope; and the species determined based on molecular characteristics (see below). Juvenile fiddler crabs less than 3mm in size were not identified to sex due to the lack of asymmetrical differentiation (Hyman 1920, Ahmed 1976, Johnson 2003).

Species identification of juvenile crabs. Species-specific PCR amplification of the internal transcribed spacer region (ITS-1) was used to identify the juvenile fiddler crabs. DNA extraction was attempted from a total of 469 juvenile fiddler crabs using a DNeasy Tissue Kit (Qiagen, Valencia CA); genomic DNA was successfully isolated from 417 crabs. Multiplex PCR was then used to amplify DNA between the 18S and 5.8S rRNA genes (McGuire and Welch 2010). Specifically, segments of the ITS-1 were PCR amplified using a mixture of species-specific primers (ITS 1-F, UPGR-2R, UMX-1R, UPX-2R). PCR conditions included an initial denaturation for 3 minutes at 96°C followed by 35 cycles of 94°C for 15 seconds, 57°C for 45 seconds, and 72°C for 60 seconds. Products were visualized on a 3% agarose gel with a 100-base pair ladder (Promega, Madison, WI). Amplification of DNA from morphologically identified adult fiddler crabs served as internal controls and resulted in major products of the following sizes: 300 ± 20bp for *U. pugnax*, 400 ± 20bp for *U. minax*, and 500 ± 20bp for *U. pugilator*. Product sizes for the 367 successful amplifications were determined using

Kodak 1D imaging software (version 3.6), with the calculated size of the predominant product being used for species determination.

Statistical analyses. Juvenile fiddler crab densities, sizes, shell use, and shell availability were tested for normality (Shapiro-Wilk test) and equal variance (Levene test). Data was not normal and had unequal variances, multiple transformations were attempted, but did not fix the assumptions. One way repeated measures with replication ANOVA's were used due to the fact that ANOVA analysis is robust from departure of normality. To determine whether the ratio of juvenile fiddler crab sexes and species differed between low and high impact sites on substrate and in shells, model 2 contingency tables with likelihood ratios were used and then a goodness of fit test was used to compare each individual species between impact designations. All data analysis was done according to guidelines in Sokal and Rohlf (1995) using JMP software (JMP, version 8. SAS Institute Inc., Cary N.C, 2009).

Results

Juvenile fiddler crab density, shell availability and shell use. Low impact sites had significantly higher densities of juvenile fiddler crabs as compared to high impact sites (Figure 2a, Table 3). This was consistent over time, with five out of the six trips (June-August 2010) having significantly greater densities of juvenile fiddler crabs at the low impact sites (Figure 2a; Table 3). Maximum densities at low impact sites reached 54.8 juvenile crabs/m^2, but only 18.6 juvenile crabs/m^2 at high impact sites. There was, however, an impact by trip interaction due to higher densities at high impact sites on the first sampling trip (Figure 2a, Table 3). Shell availability was not significantly different between low and high impact sites (Figure 3) and shell use by juvenile fiddler crabs occurred at both low and high impact sites (Figure 2b; Table 3). There was a significant difference in shell use between trips and a significant interaction between impact and trip. The interaction is due to the fluctuation in shell use between impact and sampling trips (Figure 2b; Table 3). Maximum shell use at low impact sites reached 35% of shells with juvenile fiddler crabs; the maximum shell use at high impact sites was 30%. Juvenile densities were compared to shell availability and shell use to see if the number of juvenile fiddler crabs present to the number affected shell use. There was no significant difference in shell use between low and high impact sites (Table 3).

Juvenile fiddler crab size, sex, and species on the substrate. Juvenile fiddler crab sizes were similar between impact (Tables 3 & 4). Similarly, the sex ratio did not differ significantly between low (1.35 female: 1 male) and high (1.75 female: 1 male) impact sites (Tables 4 & 5). Species composition differed significantly between low and high impact salt marsh sites (Figure 4; Table 5). Significantly more *Uca minax* and *U. pugilator* were observed on the substrate at high impact sites than at low impact sites (Table 5; low impact 3% and high impact 10%; low impact 12% and high impact 26%, respectively). The percentage of *U. pugnax* did not differ significantly between high and low impact salt marshes (Table 5; low impact 84 % and high impact 74%).

Juvenile fiddler crab size, sex, and species in shells. Juvenile fiddler crabs found in shells significantly differed in size between low and high impact sites (Table 3), with larger juvenile fiddler crabs found in shells at low impact sites (Table 4). However, the sex ratio of juvenile fiddler crabs found in shells was not significantly different between low (1 female: 1 male) and high (1.45 female: 1 male) impact sites (Table 4 & 5).

The species composition in shells differed between low and high impact sites (Figure 4). High impact sites had significantly more *Uca pugilator* and *U. minax* in shells (Table 4; low impact 0% and high impact 25%; low impact 5% and high impact 15%, respectively), and significantly less *U. pugnax* (Table 5; low impact 95% and high impact 60%).

Discussion

The present study was designed to address the effect of human activity on the distribution and behavior of juvenile fiddler crabs near the high intertidal zone of salt marshes, looking specifically at densities, shell use, and species composition. As predicted, low impact salt marsh sites maintained higher densities of juvenile fiddler crabs than high impact salt marshes, with densities in the low impact sites increasing over time during the summer recruitment period. All 3 high impact sites were characterized by sparse and short vegetation. Juvenile fiddler crabs might be actively avoiding these open areas of the high marsh or recruiting into these areas but suffering high mortality rates due to lack of adequate refuges. Larval recruitment may affect juvenile fiddler crab populations. Larvae can either be transported offshore or remain inshore, depending on their location in the water column, current speed and direction, and wind speed (Morgan and Fisher 2010). If larvae from low and high impact sites are dispersed offshore where they can mix and reenter the salt marshes, then one subpopulation may be influenced by juveniles from another subpopulation. However, if larvae remain inshore, then differential density is more likely due to local factors such as human impact. More studies are needed to determine the role of larval retention and export in postlarval distribution within the rivers and creeks surrounding our sites. Another factor important for juvenile populations are the effects of sediment composition on larval recruitment. Trampling in the high salt marsh disrupts the sediment and affects grain-size composition (Fossi et al. 2007, Gedan et al. 2009). Sediment changes may alter juvenile fiddler crab densities, feeding, species compositions, burrowing and behavior.

Contrary to predictions, shell availability and the frequency of shell use did not significantly differ between low and high impact sites. While shell availability remained similar between low and high impact sites and over time, shell use fluctuated from June through August with no clear pattern differentiating low and high impact sites. This suggests that under some conditions shell use is favorable. A few environmental factors have been shown to affect shell use including tidal range and weather conditions (George et al. 2010), but shell use does not seem to be affected by the number of available shells or the level of human impact. Even, when taking in consideration the higher density of juvenile fiddler crabs at low impact sites, there was no clear pattern with shell use over time. Empty snail shells can be a form of refuge for small juvenile fiddler crabs (<3mm) that are unable to dig burrows. Once the juveniles are large enough to dig burrows it may also be more energy efficient to use the empty snail shells rather than burrowing. Energy saved from digging burrows may be allocated towards growth to reach a larger size that makes the crabs less vulnerable to predation (Gosselin and Qian 1997, Hunt and Scheibling 1997).

As expected, juvenile fiddler crab size and sex on the substrate did not significantly differ between low and high impact sites. This suggests that human impacts are decreasing the densities of juvenile fiddler crabs in all size classes and both sexes. The sex ratio found in shells was also similar between low and high impact sites, but juvenile fiddler crabs found in shells at low impact sites were significantly larger than at high impact sites. This may mean that shell use at low impact sites is a behavioral trait and if they use shells they are more likely to use them for an extended period of time. Shell use by juvenile fiddler crabs is a recent discovery (George et al. 2010), and more research is needed to better understand the fluctuations in shell use along with shell preference and size limitations.

Contrary to predictions, the species composition on the substrate and in shells significantly differed between low and high impact sites. Differences in juvenile species composition could not be due to variation in reproductive seasons as all three species spawn between May and September (Brodie et al. 2005). Species composition at low and high impact sites appeared to mirror historical (see Teal 1958, Aspey 1978) and present-day distributions (O'Connor 1993, Behum et al. 2005, Brodie et al. 2005, Godley and Brodie 2007) in the Southeastern United States. *Uca pugnax* was the predominant species followed by *U. pugilator* and *U. minax* on the substrate and in shells. However, some interesting trends were observed. A significantly higher proportion of juvenile *U. minax* and *U. pugilator* were characteristic of high impact salt marsh sites where salinities were between 33-55‰ throughout the summer months in 2010. Our results were contrary to those of Brodie et al. (2005) and Godley and Brodie (2007), who observed a decreasing proportion of juvenile *U. minax* in areas of high salinity. It was equally surprising to find a high percentage of *U. pugilator* in shells at high impact sites but none in shells at low impact sites. This might be an example of behavioral plasticity in *U. pugilator. Uca pugilator* might prefer the dense *Spartina alterniflora* covered habitats provided at the low impact sites and might simply be making do with a bad situation by using shells at the high impact sites.

It should be noted that not all specimens collected were identified to species. PCR amplification resulted in low-yield or no product for 50 (12%) of the juvenile samples in duplicate trials. While poor amplification could be due to technical problems (e.g. template purity), these isolates could be alternate species with divergent sequences at the PCR primer sites. The number of unsuccessful PCR reactions approximated the 9% seen by George et al. (2010) using a different PCR-based method (Brodie et al. 2005) for *Uca* species determination.

Previous studies on fiddler crab distributions showed that adult and juvenile *U. pugnax* are found in grass-covered, muddy habitats at high salinity (Behum et al. 2005, Godley and Brodie 2007). Adult and juvenile *U. minax* occur in both muddy and sandy areas of low salinity (O'Connor 1990, Godley and Brodie 2007), including inland areas around tidally influenced rivers and streams (Teal 1958, Brodie et al. 2005). Juvenile and adult *U. pugilator* have slightly different preferences, with juveniles being found in covered, muddy habitats of high salinity and adults in sandy open habitats of high salinity (O'Connor 1993). When comparing the juvenile species compositions found in the present study to observed adult species, this pattern held true for *U. pugnax* and *U. pugilator*. For *U. minax,* adult and juvenile fiddler crab distributions did not always match those previously reported. Juvenile *U. minax* were found at all sites except for one low impact site (Site 6), while adult *U. minax* were only found at 1 low (site 4) and 1 high (site 3) impact site. This suggests that *U. minax* may recruit into areas of higher salinity, but not survive to adult stages or the adult stages move to preferred habitat.

The present study demonstrated that the high impact areas surveyed had significantly less vegetation cover and lower juvenile fiddler crab densities than low impact sites. Human impacts have led to a 67% loss of coastal wetlands worldwide in the past 300 years. Human impacts in salt marshes may cause lower vegetation cover, which decreases the available habitat for survival of juvenile species. While vegetation is important for fiddler crab survival, fiddler crabs are important to the vegetation as well. Salt marshes are harsh environments made up of plant and animals that have mutualistic interactions. Areas with high fiddler crab densities are known to have higher levels of primary productivity (Smith et al. 1991, Holdredge et al. 2010); fiddler crab burrows aerate the soil, increase soil drainage, and increase decomposition rates (Bertness 1985). If human impacts are decreasing the densities of juvenile fiddler crabs and fiddler crabs are important to the health of the salt marsh, there may be compounding effects that could ultimately lead to the loss of a very important ecosystem. Further studies are needed to see if fiddler crab densities are correlated to the percent cover and height of salt marsh vegetation. Studies should also include sites within all three marsh zones (high, mid, and low) and an examination of how human impacts may be affecting other macroinvertebrate species.

CHAPTER 3

CONCLUSION

The present study demonstrated that the high impact areas had significantly less vegetation cover and lower juvenile fiddler crab densities than low impact sites. The effects of human impacts on plant species has been well studied. For example, the creation of canals and waterways are known to change plant distribution (reviewed in Gedan et al. 2009). However, animal communities have had mixed responses to human impact and the effects of disturbances on the individual species of the salt marsh have not been extensively studied. Low percent cover decreases the available habitat needed for the survival of juvenile fiddler crabs. Maintaining high fiddler crab densities is important to the health of the salt marsh ecosystem. Areas with fiddler crabs have been shown to have higher productivity levels (Smith et al. 1991, Holdredge et al. 2010). Their burrows aerate the soil, increase soil drainage, and increase decomposition rates (Bertness 1985).

The species composition also differed between low and high impact sites. An increase of juvenile *Uca pugilator* and *U. minax* were seen in areas corresponding to habitats historically known for *U. pugnax*. The loss of salt marsh habitat, the creation of roads and highways through the high marsh, along with the altering of sediment composition may be forcing the fiddler crab species from their preferred niches. Adult populations of *U. pugnax* and *U. pugilator* are known to overlap in sandier habitats characteristic of *U. pugilator*. In these mixed populations, *U. pugnax* was found to be more aggressive and have higher recruitment (Aspey 1978, Behum et al. 2005). Studies have also shown that in the presence of *U. pugnax* there is a decline in *U. pugilator* and

U. minax burrow densities (Teal 1958, Aspey 1978). If the three *Uca* species found in Georgia are forced into similar habitats, there may be increased competition that could lead to a decrease in species diversity.

Salt marsh ecosystems worldwide are being negatively affected by forms of human impact including dredging, reclamation, urban development, waste disposal, pasture lands, drainage, water diversion, and the introduction of invasive species (Kennish 2001, Gedan et al. 2009, Silliman et al. 2009). In addition to direct human impact, temperature change and sea level rises due to global climate change will present additional factors for species to overcome (Gedan et al. 2009). Impacts to sites that were seen in this study included resource exploitation, land conversion, and hydrological alterations. Further study is needed to see how fiddler crabs and other salt marsh species will be affected across all types of impacted marshes (agricultural, pasture lands, salt extraction, etc.).

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Table 1. Study site locale and characteristics during a May 2010 survey.

Site	Location	Rivers and creeks	Vegetation present	*Uca* spp. (ratio)[1]	Distance from roads (meters)	Distance from buildings (meters)
1	Old Tybee Road, Tybee Island (32° 00'50" N, 80° 52'50" W)	Bull River Savannah River Lazaretto creek	*Spartina alterniflora* *Salicornia virginica* *Distychilis spicata*	*U. pugnax* *U. pugilator* (3:1)	9.5 m	74.4 m
2	Catalina Drive, Tybee Island (32° 00'5771" N, 80° 52'152" W)	Bull River Tybee creek	*Spartina alterniflora* *Salicornia virginica*	*U. pugnax*[3]	22.9 m	213.4 m
3	Rodney J. Hall Boat Ramp, Skidaway Island (31° 56'883" N, 81° 0'4101" W)	Skidaway River tidal creeks[2]	*Spartina alterniflora*	*U. pugilator* *U. pugnax* *U. minax* (6.5:2:1)	40.2 m	158.2 m
4	Skidaway Island (31° 58'379" N, 81° 01'824" W)	Skidaway River tidal creeks[2]	*Spartina alterniflora* *Limonium carolinianum*	*U. pugnax* *U. minax* (5.7:1)	134.1 m	537.7 m
5	Skidaway Island (31° 58'533" N, 81° 01'833" W)	Skidaway River tidal creeks[2]	*Spartina alterniflora*	*U. pugnax*[3]	209.4 m	761.7 m
6	Skidaway Island (31° 58'567" N, 81° 1'826" W)	Skidaway River tidal creeks[2]	*Spartina alterniflora*	*U. pugnax*[3]	222.5 m	816.6 m

[1] Ratio of adult *Uca* species visually identified at study sites.
[2] Small permanent creeks (< 2 meters in width).
[3] *Uca pugilator* was found at the study site but was not present within the study area.

Table 2. Mean percent plant cover at low and high impact sites in May 2010.

	Percent Plant Cover[1]	***Spartina alterniflora* Height**[2]
Low Impact	83.2 ± 1.52 %	42.0 ± 2.9 cm
High Impact	61.8 ± 3.64 %	30.8 ± 4.09 cm

[1] Between impact nested ANOVA F=7.1, df=1, 4, p=0.05; the mean cover ± standard error was calculated from ten $1m^2$ quadrats at each site.
[2] Between impact nested ANOVA F=4.886, df=1,4, p=0.09; the mean height ± standard error was calculated from ten random individual *S. alterniflora* plants within ten $1m^2$ quadrats at each site.

Table 3. Repeated Measures ANOVA for juvenile fiddler crab densities, shell use, shell availability, and sizes between low and high impact sites[1].

Variable	Factor	df	F	P
Juvenile fiddler crab densities	Impact	1, 4	14.70	0.020*
	Trip	5, 20	5.40	0.003*
	Impact x Trip	1, 5	4.90	0.004*
Shell availability	Impact	1, 4	0.18	0.690
	Trip	5, 20	2.30	0.080
	Impact x Trip	1, 5	1.10	0.400
Shell use	Impact	1, 4	0.01	0.940
	Trip	5, 20	5.90	0.002*
	Impact x Trip	1, 5	3.80	0.010*
Juvenile crabs substrate/ shells[2]	Impact	1, 4	0.47	0.530
	Trip	5, 20	2.70	0.050*
	Impact x Trip	1, 5	3.90	0.010*
Size: Substrate	Impact	1, 233	3.37	0.140
	Trip	1, 4	0.07	0.790
	Impact x Trip	1, 1	2.45	0.120
Size: Shell	Impact	1, 221	16.30	0.010*
	Trip	1, 4	0.55	0.460
	Impact x Trip	1, 1	0.58	0.450

[1]Six trips from June-August were made to each of 6 study sites. Trip (6 trips) and Impact (low or high) were fixed factors.

[2] Extrapolated from densities and shell availability per m^2

*Significance at $\alpha = 0.05$

Table 4. Juvenile fiddler crab size and sex ratios.[1]

	Size (mm)[2]		Sex Ratio (%)[2,3]	
	Substrate (n)	Shell (n)	Substrate (n)	Shell (n)
Low Impact	4.3 ± 0.1 (120)	4.8 ± 0.1 (120)	F 59.0 ± 0.3 M 41.0 ± 0.3	F 48.6 ± 0.5 M 51.4 ± 0.5
High Impact	4.7 ± 0.1 (120)	4.4 ± 0.1 (108)	F 63.7 ± 0.4 M 36.3 ± 0.5	F 59.3 ± 2.4 M 40.7 ± 2.8

[1] Survey completed in the high tidal zone during June-August 2010.
[2] Mean values reported ± standard error.
[3] The number of study subjects for the female (F) and male (M) sex ratios were as follows: low impact substrate n=107, high impact substrate n=113, low impact shell n=110, high impact shell n= 93.

Table 5. Likelihood ratios of juvenile fiddler crab sexes and species between low and high impact sites[1].

Variable	**df**	**G**	**P**
Sexes: Substrate	1	0.91	0.34
Sexes: Shell	1	2.24	0.13
Species: Substrate	2	12.5	<0.001*
Uca minax	1	12.28	0.002*
Uca pugnax	1	2.97	0.08
Uca pugilator	1	5.28	.02*
Species: Shell	2	47.9	<0.001*
Uca minax	1	5.23	0.02*
Uca pugnax	1	7.97	0.005*
Uca pugilator	1	34.7	<0.001*

[1] When likelihood ratios were significant, a goodness of fit test was used to compare each individual species between impact designations.
* Significance at $\alpha = 0.05$

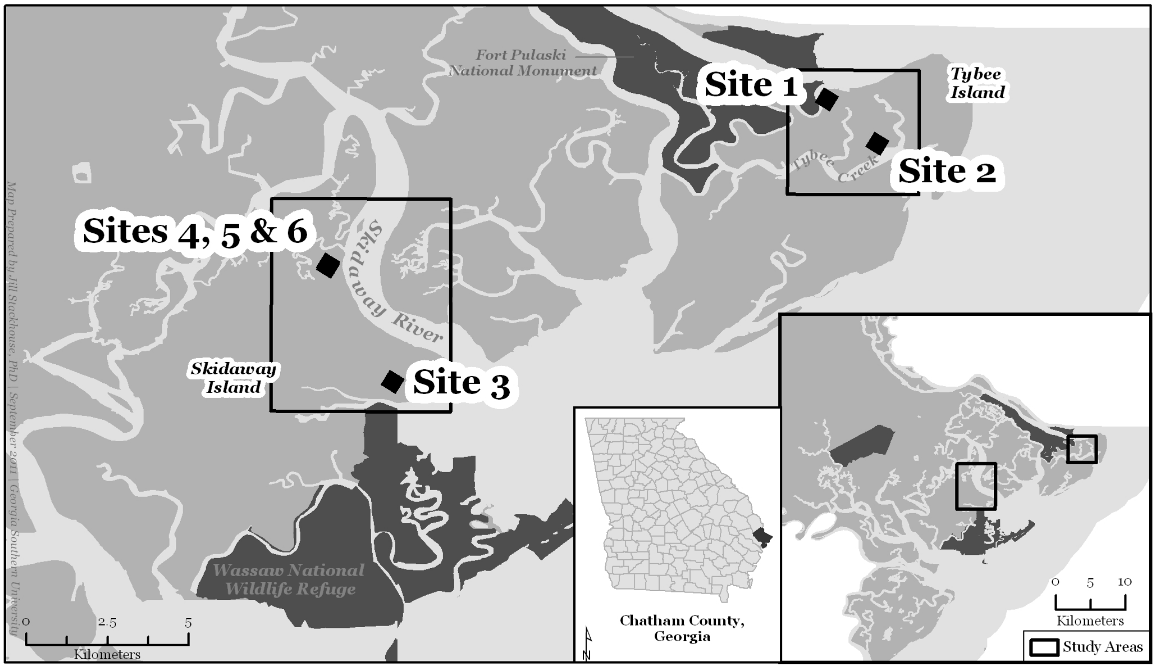


Figure 1. Study site map. Study sites were located on Tybee Island and Skidaway Island off the coast of Savannah, Georgia (Chatham County, Table 2). Sites 1-3 were designated high impact sites for this study and sites 4-6 were low impact.

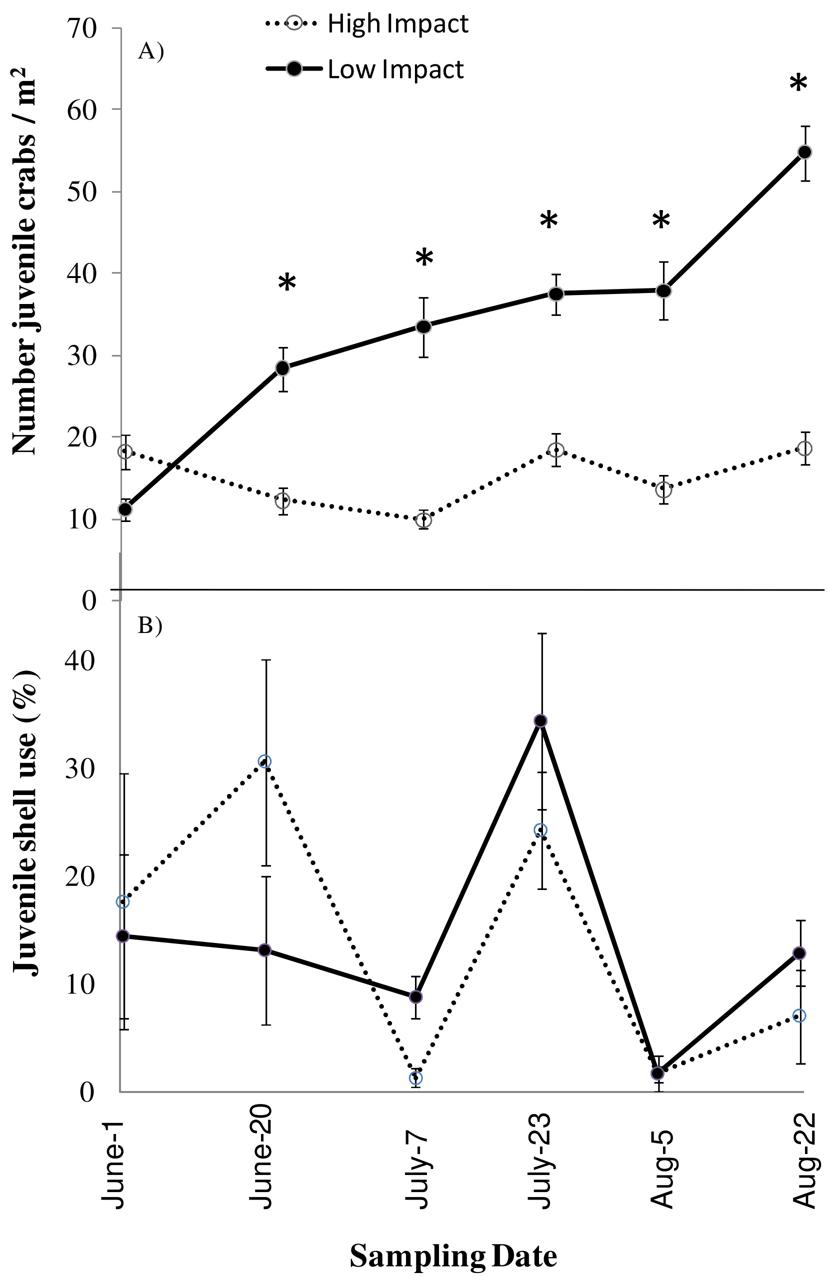


Figure 2. Juvenile fiddler crab densities on the substrate and prevelance in shells. Data collected from the high tidal zone of low and high impact sites from 10 quadrats/site/month from June-August 2010. (A) The mean (±1 standard error) density of juvenile fiddler crab. An asterisk indicates statistical significance between samples. (B) The mean (±1 standard error) percent of shells that contained juvenile fiddler crabs.

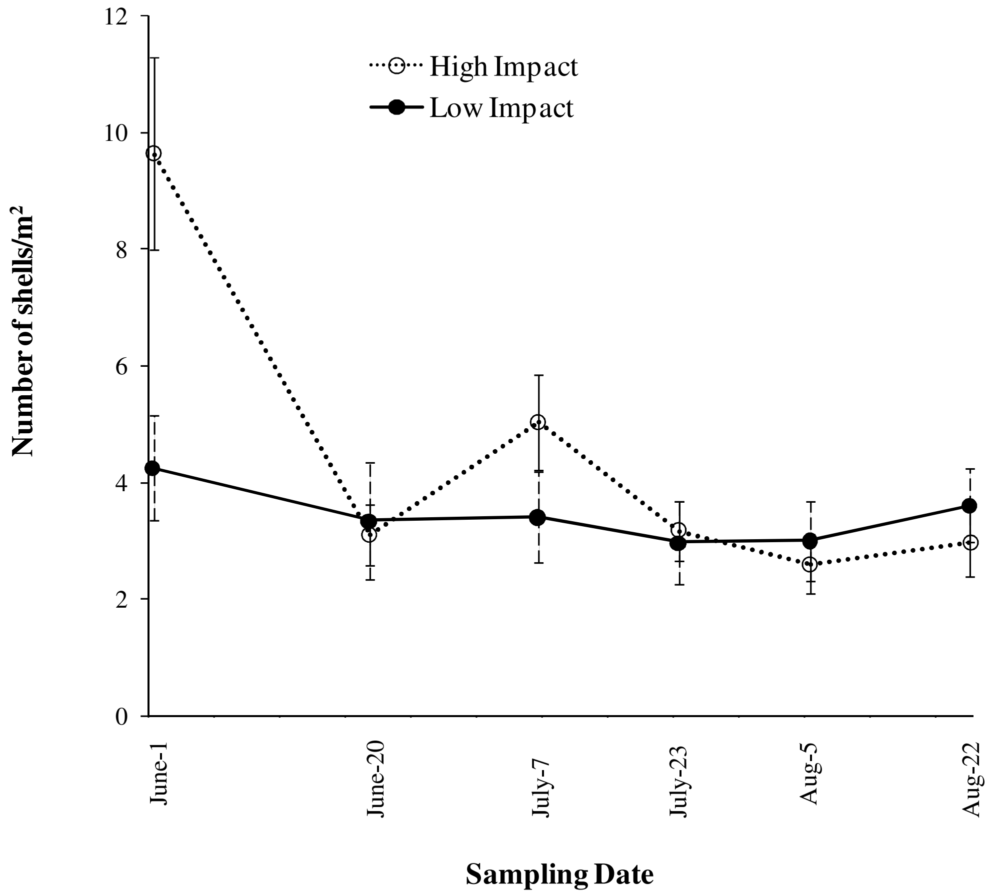


Figure 3. Snail shell availability. Data collected from the high tidal zone of low and high impact sites from 10 quadrats/site/month from June-August 2010. The mean (± 1 standard error) of *Littoraria irrorata* snail shells per m^2.

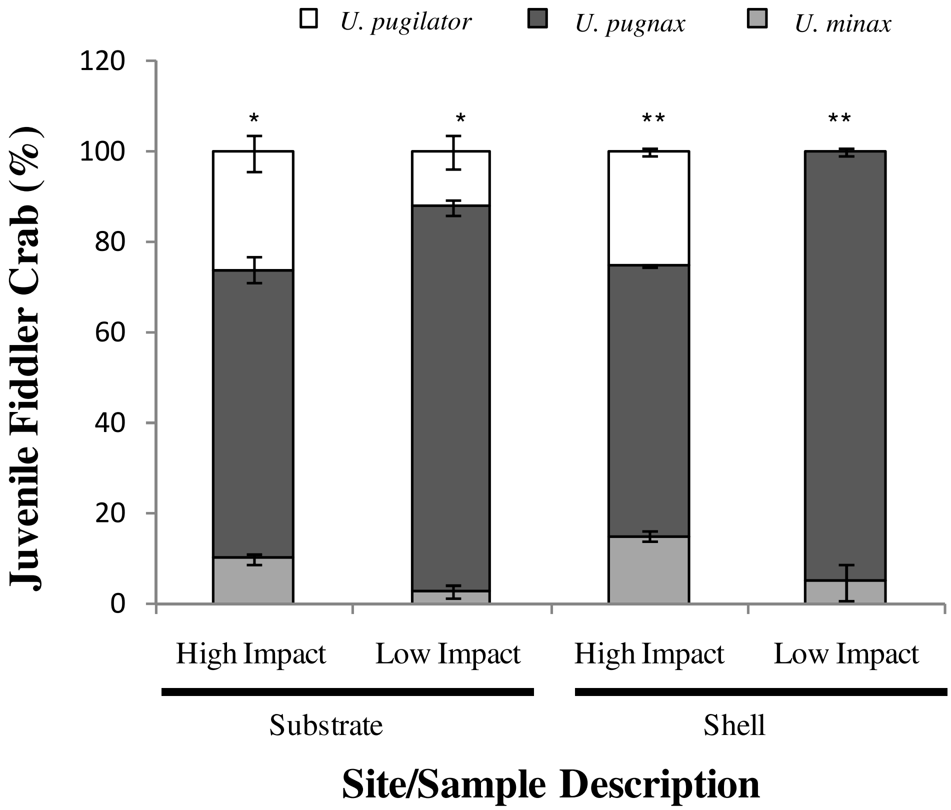


Figure 4. Juvenile fiddler crab species composition. The species composition (%) of juvenile fiddler crabs found in the high intertidal zone during 6 trips from June-August 2010 on the substrate (low impact n=99, high impact n=89) or in shells (low impact n= 95, high impact n=84) at high impact and low impact sites. Error bars indicate standard error and an asterisk indicates a statistically significant difference in species composition between the impact designation either on substrate (*) or in shells (**).

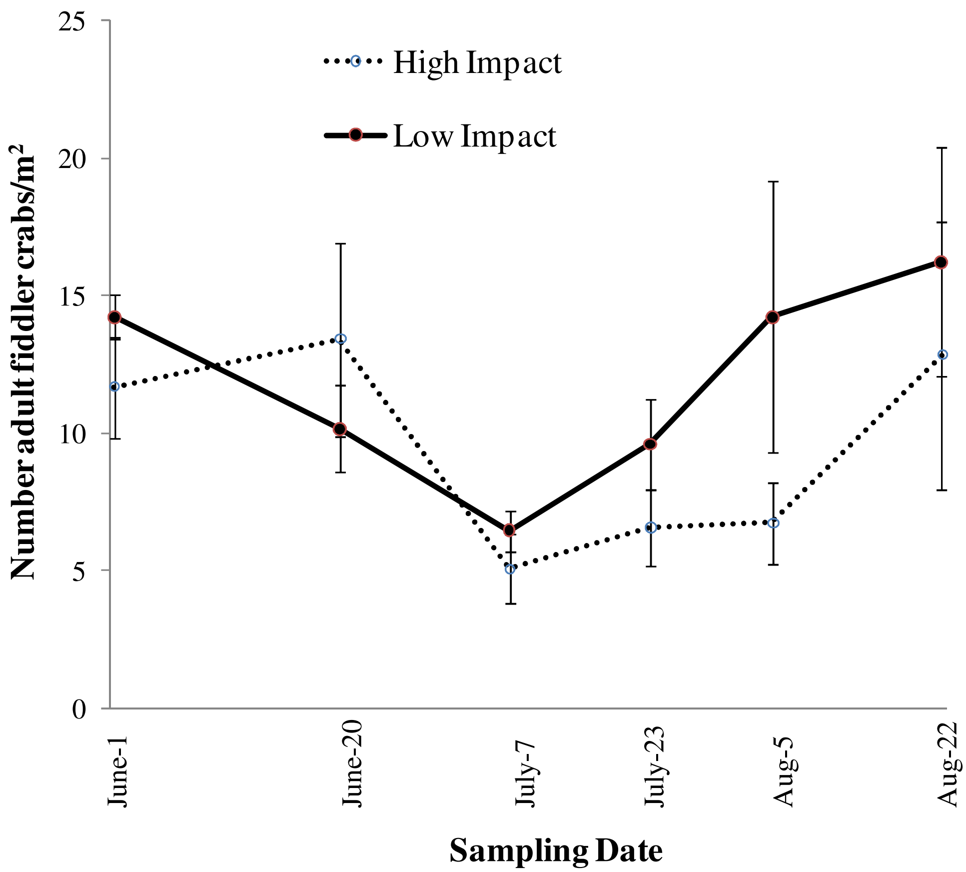
APPENDICES

APPENDIX A. Mean (± 1 standard error) pore water conditions at low and high impact sites. A refractometer was used to measure salinity, a pH meter to measure pH, and a mercury thermometer to measure temperature. Values represent means of 3 sampling trips from June-August 2010[1].

		Sample Date					
Variable	**Impact**	**1-Jun**	**18-Jun**	**6-Jul**	**21-Jul**	**4-Aug**	**21-Aug**
pH	**Low**	5.5 ± 0.2	5.9 ± 0.3	6.3 ± 0.4	6.9 ± 0.3	6.3 ± 0.1	6.1 ± 0.1
	High	7.4 ± 0.8[2]	5.4 ± 0.1	6.2[3]	6.3 ± 0.1[2]	6.2 ± 0.8[2]	6.5 ± 0.3
Salinity (‰)	**Low**	25.0 ± 0.6	31.0 ± 2.1	29.0 ± 1.0	31.3 ± 0.7	34.3 ± 1.2	29.7 ± 0.9
	High	37.5 ±2.5[2]	34.3 ± 0.7	50.0[3]	55.5 ± 0.5	38.5 ± 10.5[2]	43.7 ± 1.3
Temperature (°C)	**Low**	31.0 ± 0.6	27.3 ± 0.3	28.7 ± 0.7	32.0 ± 1.2	29.3 ± 0.9	31.7 ± 0.3
	High	31.7 ± 0.7	28.7 ± 1.2	30.7 ± 1.5	33.0 ± 2.1	29.3 ± 0.7	32.3 ± 1.9

[1]Data from 3 sites per impact (n=3) used to calculate mean ± standard error unless otherwise indicated
[2] n=2
[3] n=1

Appendix B. The mean (± 1 standard error) number of adult fiddler crabs per m^2 on the substrate in the high intertidal zone. A total of 6 samplings were completed from June-August 2010 at low and high impact sites. Densities were recorded by counting the number of adult (>9mm) fiddler crabs within 10 randomly placed 1 m^2 quadrats per site per trip. Adult fiddler crab densities at low and high impact sites did not differ significantly (Repeated measures: Impact $F_{(1,4)}$ =0.09, p=0.78, Trip $F_{(5,20)}$=5.75, p=0.002, Impact x Trip $F_{(1,5)}$ = 2.15, p=0.10).



Appendix C. The mean (± 1 standard error) number of *Littoraria irrorata* snails per m^2 found on *Spartina alterniflora* or on the substrate in the high tidal zone. A total of 5 samplings were completed from June-August 2010 at low and high impact sites. Densities were recorded by counting the number of snails within 10 randomly placed 1 m^2 quadrats per site per trip. Snail densities did not significantly differ between low and high impact sites (Repeated measures: Impact $F_{(1,4)}$ =1.49, p=0.29, Trip $F_{(4,16)}$=1.82, p=0.17, Impact x Trip $F_{(1,4)}$ = 0.49, p=0.75).