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LINKAGES BETWEEN MARSH FRAGMENTATION, PREY AVAILABILITY, AND

BLUE CRAB (*CALLINECTES SAPIDUS*) ABUNDANCE AND MORTALITY

by

Lennah Maheen Shakeri

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LINKAGES BETWEEN MARSH FRAGMENTATION, PREY AVAILABILITY, AND

BLUE CRAB (*CALLINECTES SAPIDUS*) ABUNDANCE AND MORTALITY

by Lennah Maheen Shakeri

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ABSTRACT

Coastal marshes are important nursery habitats for many commercially important invertebrate species, yet these marshes are being lost worldwide at an unprecedented rate due to subsidence, erosion, climate change, and human activity. As marsh is lost, it creates the opportunity for submerged aquatic vegetation (SAV) colonization and establishment in newly created open water areas. Blue crabs, *Callinectes sapidus*, use both marsh edge and SAV habitat during the juvenile stages and support one of the largest fisheries in the Gulf of Mexico, worth over $70 million in 2015. This thesis studied the linkages between habitat type, SAV cover, benthic prey availability, and blue crab abundance and mortality due to predation. In different habitat types and across a gradient of marsh fragmentation, crab pots and throw traps were used to conduct monthly crab abundance surveys and benthic cores sampled benthic invertebrate communities. This study found that blue crab abundances, benthic invertebrate biomass, and benthic invertebrate community composition were insensitive to marsh fragmentation but did vary significantly with habitat type. These results have implications for future blue crab populations in coastal Louisiana where if marsh loss occurs as projected, poor recruitment by juvenile blue crabs into the adult population due to less available nursery habitat and food availability may lead to time-lagged decreases in the commercial blue crab fishery, unless SAV colonizes areas of high marsh fragmentation to serve as an alternative nursery habitat for juvenile blue crabs.

ACKNOWLEDGMENTS

DEDICATION

I would like to thank my friends and family for their unending support and encouragement in this endeavor. In no particular order, I would like to especially thank: the Golden Mean Girls Club; Keith Hughes Boxing; the graduate student body at GCRL; the graduate student body at Nicholls State University; Anne Catherine Darnell; Andrea Jerabek; Angie Munguia; my family, Hameed, Susan, Haleh, Shirin, and Beau Shakeri; Craboratory members; my West Coast friends; the Read; Beyonce; and Luke Mohar.

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CHAPTER I - INTRODUCTION

Habitat fragmentation and subsequent habitat loss occur both naturally and anthropogenically and are of great concern in areas where the fragmenting habitat cannot be restored. Habitat fragmentation breaks an intact habitat into patches interspersed with a new habitat type (Ewers and Didham 2006). The concern over habitat fragmentation centers around consequent losses in habitat connectivity and interior area and how decreases in these factors can affect species dependent on them. Often, a habitat edge will act as a barrier to emigration, disrupting habitat connectivity that can ultimately result in decreased species richness for habitat specialists (Ries and Debinski 2001; Brückmann et al. 2010). Some species can be endemic to a habitat type and require relatively large home ranges wherein food, shelter, and mating opportunities can be found. Examples include the Northern spotted owl and Belding's Savannah sparrow, where these species' populations and genetic variability can and do suffer with habitat fragmentation and net habitat loss (Lamberson et al. 1992; Powell 2006). Sometimes these edges can be successfully crossed if the distance between patches is small enough or there is a structure in place to rectify loss of connectivity (Glista et al. 2009).

In some cases, fragmentation is not necessarily a detriment to all local organisms. Some species thrive in edge habitat, which increases in the initial stages of habitat fragmentation. Fonderflick et al. (2013) found that birds classified as habitat generalists, in that they use both open and forested habitat, were more abundant near forest edges than in the forest interior. Menke et al. (2012) also found higher species richness and frugivore abundance at forest-farmland edges than in forest interior, where habitat generalists were more abundant than habitat specialists at edge habitat. In fact, plant-

frugivore networks were more robust and more connected at forest-farmland edge than in forest interior (Menke et al. 2012). These positive edge effects can be explained by resource distribution, where edge habitat can support greater abundances than interior habitat because some resource, like food, is more abundant near the edge habitat (Macreadie et al. 2010; Fonderflick et al. 2013). Other studies posit that habitat fragmentation independent of habitat loss could actually prevent invasive species establishment (Alofs and Fowler 2010; Brown et al. 2012; Rahel 2013).

One particular habitat that is experiencing substantial fragmentation in many areas is coastal salt marsh. A total of 15,845 km^2 of coastal marsh was lost over the course of 14 years in 14 river deltas worldwide (Coleman et al. 2008). Satellite imagery analysis found that from 1998 to 2004 approximately 181.3 km^2 (17,900 ha) of saltwater wetlands were lost in the Gulf of Mexico (Stedman and Dahl 2008). The rate of decrease accelerated in the Gulf between 2004 and 2009, with an average annual loss of 55.8 km^2 (5,520 ha) leading to an estimated 384.5 km^2 (38,000 ha) lost over five years (Dahl 2011; Dahl and Stedman 2013). Salt marshes serve as important nursery areas for many fish and invertebrate species, including those that support commercial and recreational fisheries (Thomas and Zimmerman 1990; Minello and Rozas 2002; Lipcius et al. 2005; Strange et al. 2008). Fragmentation of these habitats is thus concerning not only in the context of biodiversity and species abundances, but also for the economic livelihood of coastal communities. While some species do occupy the salt marsh interior, many of these commercially and recreationally harvested species occupy the marsh edge habitat (Thomas and Zimmerman 1990; Rozas et al. 2012). Responses to fragmentation are thus likely to be complex, depending on the stage of progression and the species in question.

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This thesis focuses on the responses of blue crab (*Callinectes sapidus* Rathbun) populations to fragmentation of their salt marsh habitat. Blue crabs support valuable commercial fisheries throughout their range, worth up to $216 million (NMFS 2017). Juvenile blue crabs settle into estuarine vegetated nursery habitats during the megalopae stage and remain in these structured habitats where prey availability is high and predation pressure is low (Heck and Thoman 1984; Orth and van Montfrans 1987; Minello et al. 2003; van Montfrans et al. 2003). Marsh fragmentation could impact crab populations directly, through effects on recruitment, growth, or mortality, or indirectly through impacts on prey availability. Understanding how blue crab populations will respond as marsh landscapes fragment will inform future management plans for this commercially important species.

Each chapter of this thesis is written in the form of an independent manuscript. As a result, some introductory material is repeated in multiple chapters. Chapter topics are as follows:

Chapter II. Linkages between marsh fragmentation, SAV cover, and blue crab abundance and mortality due to predation.

Chapter III. Assessment of benthic invertebrate communities in a fragmenting marsh landscape.

CHAPTER II – LINKAGES BETWEEN MARSH FRAGMENTATION, SAV COVER,

AND BLUE CRAB ABUNDANCE AND MORTALITY DUE TO PREDATION

Introduction

Habitat fragmentation occurs in landscapes worldwide and is often blamed for

decreases of biodiversity, although that is perhaps an incorrect conclusion as positive

biodiversity responses to habitat fragmentation, independent of habitat loss, have been

found (Fahrig 2003). The process of fragmentation occurs both naturally and

anthropogenically and can eventually lead to habitat loss. Some species that utilize a

habitat are documented to react negatively to habitat fragmentation and subsequent

habitat loss (Lamberson et al. 1992; Powell 2006) while other species exhibit increased

abundances near habitat edges provided by increased habitat complexity (Menke et al.

2012; Fonderflick et al. 2013).

One type of habitat experiencing extensive fragmentation and loss are coastal

wetlands. Coleman et al. (2008) examined aerial photographs of 14 river deltas

worldwide and found that 15,845 km^2 of coastal wetland was lost over 14 years due to

conversion into agricultural or industrial land and open water expansion. More than

300,000 km^2 are predicted to also be lost over the next 20 years (Coleman et al. 2008).

Images of the Mississippi River delta reveal that coastal wetlands were lost at an average

rate of 30 km^2 per year from 1985 to 1997 (Coleman et al. 2008). Further satellite

imagery analysis found that from 1998 to 2004 approximately 44,800 acres (17,900 ha)

of saltwater wetlands were lost in the Gulf of Mexico (Stedman and Dahl 2008). This

decrease continued in the Gulf between 2004 and 2009 with an average annual average of

13,800 acres (5,520 ha) saltwater wetlands lost leading to an estimated 95,000 acres

(38,000 ha) lost over five years (Dahl 2011; Dahl and Stedman 2013). This loss is caused by a high subsidence rate, exacerbated by sea level rise and anthropogenic landscape changes such as canal dredging and land use conversion (Coleman et al. 2008; Stedman and Dahl 2008; Dahl 2011; Dahl and Stedman 2013). Saltwater intrusion also has an effect on loss, as increasing salinities will change soil chemistry, vegetation communities, and sediment accretion rates (Day et al. 2000; Strange et al. 2008; Day et al. 2011). Decreasing marsh elevation due to subsidence leads to longer tidal inundation periods, which lower sediment retention rates so that the marsh vegetation cannot uptake required minerals (Day et al. 2000; Day et al. 2011). Vegetation stress levels then increase to the point where marsh vegetation will die and further intensify elevation loss through loss of root turgor, oxidation of soil organic matter, and elevation collapse (Day et al. 2000; Day et al. 2011).

As these coastal wetlands sink and disappear they often fragment by breaking into smaller patches surrounded by open water. Marsh fragmentation reduces marsh interior area and increases edge habitat. Edge is beneficial for some species including many fish and macroinvertebrates because individuals can utilize the marsh platform as a nursery habitat during tidal inundation periods and still rely on open water habitat for survival when the marsh is not inundated (Thomas and Zimmerman 1990; Minello and Rozas 2002; Lipcius et al. 2005; Strange et al. 2008).

There is also the potential for submerged aquatic vegetation (SAV) to colonize the newly bare substrate between marsh patches potentially providing an alternate habitat for species dependent on marsh edge (Strange et al. 2008; Saunders et al. 2013). SAV have high light requirements and are therefore limited to shallow water habitats with low

turbidity (Strange et al. 2008). Rising sea levels may promote landward migration of SAV as coastal marshes subside and SAV colonizes areas that were formerly marsh (Strange et al. 2008). Juvenile crustacean and fish densities are higher and predation rates lower in SAV relative to bare sediment (Heck and Thoman 1981; Wolcott and Hines 1990; Lipcius et al. 2005; Canion and Heck 2009). Yet SAV species generally prefer low nutrient sandy substrates over substrates with high organic content, such as a newly submerged marsh (Strange et al. 2008; see citations within). Therefore, the extent to which SAV will colonize the newly bare substrate created by fragmenting marsh is unknown (Strange et al. 2008).

One species of nekton that may benefit from marsh fragmentation is the blue crab, *Callinectes sapidus* Rathbun. This euryhaline crab is common along the Atlantic and Gulf Coasts of the United States and supports a large commercial fishery (NMFS 2016). Blue crabs first enter estuaries as megalopae and generally settle into vegetated nursery habitats before metamorphosing into the first juvenile stage (Orth and van Montfrans 1987; Boylan and Wenner 1993; van Montfrans et al. 2003), although they have also been found to settle initially onto bare sediment prior to dispersal to vegetated habitats (Rakocinski and McCall 2005). These early juvenile blue crabs remain in structured habitats, where predation pressure is lower and prey availability is presumably higher, until they reach a size that offers a refuge from predation (Heck and Thoman 1984; Minello et al. 2003). Because juvenile blue crabs rely on marsh edge and SAV as nursery habitat, it is important to understand how these habitats interact reciprocally in terms of their use by crabs and how different stages of habitat fragmentation can affect blue crabs. Identifying the complex relationships between juvenile blue crab populations, marsh

fragmentation, and SAV cover is vital to understanding how blue crab populations will respond to future scenarios.

This study investigated the impacts of marsh fragmentation and submerged aquatic vegetation (SAV) cover on blue crab abundance and mortality due to predation in Terrebonne Basin, Louisiana. The Terrebonne Basin supports a large blue crab fishery, with annual landings averaging 12.2 million pounds between 2000 and 2013 (Bourgeois et al. 2014), and is currently facing substantial land loss at a rate of 11.9 km^2 yr^{-1} (Barras et al. 2003). Specific objectives of this study were (1) to quantify juvenile and adult blue crab abundances in different habitats (marsh edge, SAV, bare substrate open water) along a marsh fragmentation gradient, and (2) to determine if there are differences in predation rates on juvenile blue crabs in different habitats.

<center>Methods</center>

Study design

This research was conducted at three study sites in Terrebonne Basin, Louisiana. Each site (2×2 km) was centered on a Coastwide Reference Monitoring System station (CRMS 0369, 0345, and 0311, Figure 1) and contained three 500×500 m subsites selected to cover a range of marsh fragmentation. Site selection was based on local occurrence of a range in the degree of marsh fragmentation, accessibility, and land-owner permission. Collaborators at The Water Institute of the Gulf quantified the distribution of habitats at each subsite using satellite imagery, by delineating marsh and water boundaries on a 1-m scale (Figure 2).

<center>7</center>
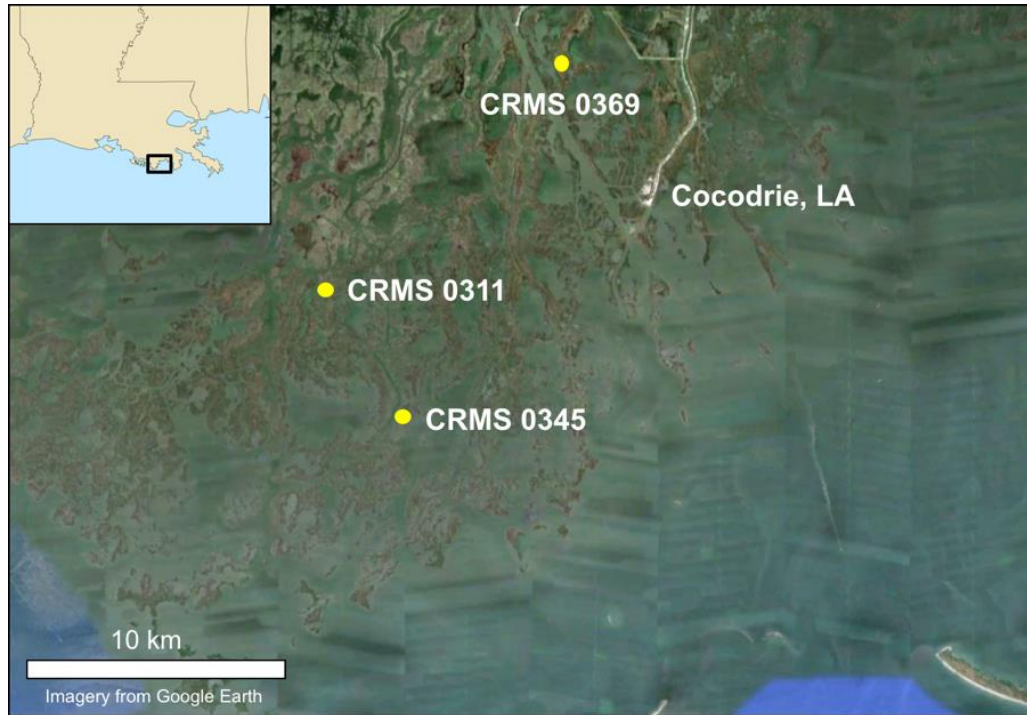
Figure 1 Locations of study sites in Terrebonne Basin, Louisiana, USA.

The yellow dots represent the locations of the three sites centered around CRMS 0369, 0311, and 0345.

Figure 2 Subsite land-water delineations.

Delineations are at the 1-m scale for a) CRMS 0369, b) CRMS 0311, and c) CRMS 0345 in Terrebonne Basin, Louisiana. The bring green color indicated land and the other colors indicate water. Super-imposed are the unified, continuous fragmentation values of the individual subsite, where higher values represent areas of low marsh fragmentation and lower values represent areas of high marsh fragmentation.

These delineations were used to calculate a unified, continuous fragmentation metric that included normalized measures of marsh perimeter, marsh area, and marsh patch number, following Bogaert et al. (2000). Each component is normalized relative to the maximum and minimum value possible for the geographic space analyzed and are independent of the used units of measurement (Bogaert et al. 2000). Although Bogaert et al. (2000) also included patch isolation in their fragmentation metric, we did not include patch isolation due to computational difficulties driven by the large number of marsh

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patches in some areas (up to 680 patches in a single 500×500 m subsite). This

fragmentation metric was calculated at spatial scales relevant to the life history stage

being examined due to differences between mobility: at the 500 m $\times 500$ m subsite level

for adult blue crabs (≥ 40 mm carapace width, collected using crab pots), and at the 50 m

$\times 50$ m level for juvenile blue crabs (< 40 mm carapace width, collected using a throw

trap). The resulting fragmentation metric is a continuous variable with higher values

representative of lower marsh fragmentation and lower values representative of higher

marsh fragmentation (Figure 2).

Adult and juvenile blue crab abundance

Adult and sub-adult blue crab abundances were assessed monthly from April–

September 2016 using modified commercial crab pots (24" × 24" × 13.5" high, 1.5"

mesh, 3 entry funnels, no escape rings) with terrapin-excluding devices installed in the

entry funnels. Nine pots were deployed throughout each subsite each month for a total of

27 pots per study site. Pot deployment locations were randomly selected from a set of

locations that had previously been surveyed for depth and SAV presence by Water

Institute personnel. Pots were baited with three previously-frozen menhaden (3 menhaden

per pot) and collected 24 ± 2 hours after deployment. All caught crabs were sexed,

measured for carapace width (CW), and weighed to determine total crab biomass per pot.

Missing limbs were noted. Date and time of deployment and collection, site,

fragmentation level, water depth, and presence of SAV were also recorded.

Juvenile crab abundances were surveyed monthly by throw trapping (Rozas and

Minello 1997; Hitch et al. 2011; La Peyre and Gordon 2012) from May through

September 2016 at two randomly selected stations within each subsite in each habitat

(marsh edge, bare sediment, and SAV [if present]). SAV was only present at the northernmost site (CRMS 0369). Throw sampling in the marsh habitat occurred at the marsh edge, as juvenile blue crab density is greatest within 1 m from the marsh edge (Minello and Rozas 2002). The throw trap is a 1-m × 1-m aluminum frame with 1.6-mm nylon mesh covered sides. The trap was tossed from a boat into the sampling habitat to land squarely and the sides checked to ensure there were no gaps between the trap bottom and the substrate. Date, time, site, habitat, water depth, and salinity were recorded. For marsh and SAV habitat throw traps, percent cover by plant species was estimated visually and recorded. Height of four plants of the dominant species were also measured and recorded. Above-water vegetation was cut and discarded outside the throw trap. Below-water vegetation was removed and bagged. A 1-m bar seine, constructed of 1" PVC and 1.6-mm nylon mesh fabric, was swept through the trap 3 times from each side, for a minimum of 12 total sweeps. During sweeps, the net disturbed the sediment to capture any buried crabs. After each sweep net contents were examined, and any observed blue crabs were separated and bagged. Remaining detritus was bagged after each sweep. Sweeping continued until 5 consecutive sweeps yielded no blue crabs. Bagged crabs, detritus, and vegetation were frozen upon return from the field. In the lab, blue crabs were sorted from thawed samples and measured for carapace width (CW).

Data were analyzed using linear mixed-effects models or generalized linear mixed-effects models, depending on the response variable in question (Table 1). Analyses were broken down to address specific questions. Adult blue crab catch-per-unit-effort (CPUE) and biomass were first analyzed for all samples where SAV was absent, testing for effects of subsite-level fragmentation and month. Adult CPUE and biomass

were then analyzed for the only site where SAV was present (North site, CRMS 0369), testing for effects of SAV presence/absence and month. Juvenile density and individual CW were first analyzed for all samples where SAV was absent, testing for effects of habitat type (marsh edge vs. bare sediment), fragmentation (calculated as described above in a 50 m $\times$ 50 m area surrounding the throw trap), and month. To examine differences in marsh vs. SAV usage by juvenile blue crabs, juvenile density and individual CW were then analyzed for SAV and marsh samples at the northernmost site only (CRMS 0369, the only site where SAV was present), testing for effects of habitat type (marsh edge vs. SAV), percent cover of vegetation within the throw trap, and month. Marsh fragmentation and percent cover of vegetation values were scaled prior to analyses, which standardized the values to a mean of 0 and standard deviation of 1 for ease of analysis and interpretation. For full model details, see Table 1.

Table 1

Details of models used in adult and juvenile blue crab data analyses

Life history stage	Response variable	Subset of data used	Model type	Family (link)	Fixed factors	Random factors
Adult	CPUE (crabs pot^{-1})	Samples with SAV absent	GLMM	Neg. binomial (log)	Fragmentation[a], Month, Fragmentation[a] × Month	Site
Adult	CPUE (crabs pot^{-1})	Samples from CRMS 0369	GLMM	Neg. binomial (log)	SAV presence, Month, SAV presence × Month	Subsite
Adult	Biomass + 0.0001	Samples with SAV absent	GLMM	Gamma (log)	Fragmentation[a], Month	Site
Adult	Biomass + 0.0001	Samples from the CRMS 0369	GLMM	Gamma (log)	SAV presence, Month	Subsite
Juvenile	Density (crabs m^{-2})	Marsh edge and bare samples from all sites	GLMM	Neg. binomial (log)	Fragmentation[b], Habitat, Month, Fragmentation[b] × Month	Site, Subsite (nested within site)
Juvenile	Density (crabs m^{-2})	Marsh and SAV samples from CRMS 0369	GLMM	Neg. binomial (log)	Habitat, Percent plant cover, Month	Subsite
Juvenile	Log$_{10}$(CW)	Marsh edge and bare samples from all sites	LMM	N/A	Fragmentation[b], Habitat, Month, Fragmentation[b] × Month, Habitat × Month	Site, Subsite (nested within site)
Juvenile	Log$_{10}$(CW)	Marsh and SAV samples from CRMS 0369	LMM	N/A	Habitat, Percent plant cover, Month, Habitat × Month, Percent plant cover × Month, Habitat × Percent plant cover × Month	Subsite

Note: Details are after model selection using AIC scores. GLMM indicates generalized linear mixed-effects models, while LMM indicates linear mixed-effects models.

[a]For analyses of adult CPUE and biomass, fragmentation was calculated at the 500 m × 500 m subsite-scale.

[b]For analyses of juvenile density and CW, fragmentation was calculated at the 50 m × 50 m scale, centered on the throw trap.

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For all adult and juvenile analyses, AIC-based model selection was used to determine the most parsimonious model. Certain interactions involving predictor variables of great interest (i.e., the interactions between fragmentation and habitat type) were always retained in the final models, but other interactions were dropped if they were not included in the most parsimonious model as determined by comparing AIC scores. Thus, higher-order interaction terms are included in some models but not others. *P*-values for fixed effects were obtained using Type III Likelihood Ratio tests. Insignificant interactions with continuous variables (i.e., fragmentation and percent plant cover) were removed and the analysis re-run to obtain *p*-values for fixed effects. All analyses were conducted in R, v. 3.4.3, using the lme4, afex, multcomp, and AICcmodavg packages.

Juvenile blue crab mortality due to predation

Mortality risk of juvenile blue crabs was assessed using tethering experiments (Heck and Wilson 1987; Aronson et al. 2001; Hovel and Lipcius 2002) conducted during the summers (June and July) of 2016 and 2017. Three to four crabs were tethered simultaneously in each habitat (marsh edge, bare sediment, and SAV) in each subsite at the North site. Each simultaneous round of tethering was considered a block for statistical analyses, and a total of 8 blocks were conducted. Juvenile blue crabs ranging from 10–30 mm carapace width (CW) were collected with a throw trap and bar seine the mornings of the experiments. Tethers (100–110 cm long), constructed of 10 and 20 lb.-test monofilament fishing line, were attached to the carapaces of the crabs using cyanoacrylate glue. The other end of the tethers was tied through holes drilled near the top of 2-foot-long 0.5" PVC tethering poles, with one tether/crab attached to each pole. Deployed tethering poles were pushed their entire length into the bottom substrate

leaving the tethered crabs on the substrate surface. Crabs were left for 24 ± 2 hours before collection. The absence of a crab after 24 hours was assumed to be mortality due to predation, based on tethering trials conducted in the lab and the field prior to the experiments that indicated minimal tether failure. Date, time, marsh fragmentation level, habitat, vegetation data, individual crab CW, and crab presence/absence after deployment were measured as necessary and recorded.

Mortality rates were analyzed using a generalized linear mixed-effects model with a binomial distribution and a logit link function. Habitat type was a fixed factor and block was a random factor. Model selection occurred to determine the best way to include individual crab CW: as a fixed effect with interactions or as a fixed effect without interactions. Models were compared by AIC score, and the most parsimonious model was determined to include the fixed effects of habitat and CW and the random effects of block and subsite. Fixed effect P-values were obtained with Type III Likelihood Ratio tests. Analyses were conducted in R, v. 3.4.3, using the lme4, afex, and multcomp packages.

Results

Effects of marsh fragmentation on adult blue crab CPUE and biomass

Adult blue crab CPUE varied significantly across the months of this study (Figure 2) but was not related to subsite-level fragmentation (Table 2). There was a significant month $\times$ fragmentation interaction, which was investigated by fitting separate GLMMs for each month, with all other model specifications identical to those described in Table 1. Adult blue crab CPUE increased with increasing marsh fragmentation in July but was unrelated to marsh fragmentation during the other months of the study (Figure 3). Adult biomass showed similar temporal patterns as with adult CPUE, varying significantly

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across the months of the study with the lowest biomass in April and the highest biomass

in June, and was not related to subsite-level fragmentation (Table 2).
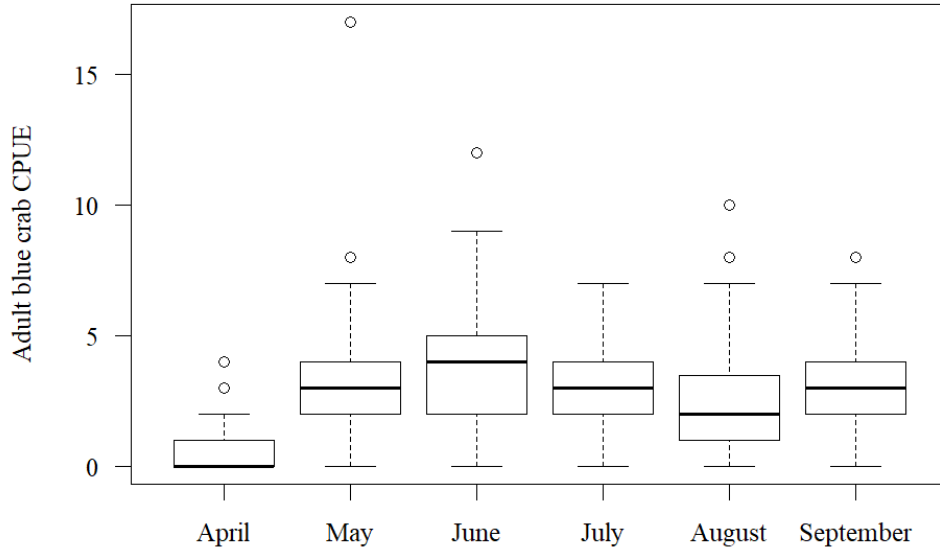
Figure 3 Median adult blue crab CPUE over the months of this study.

The lower bound of the box signify the first quartile of CPUE, the dark bar within the box marks the media CPUE, and the upper

bound of the box is the third quartile. Whiskers indicate 95% confidence intervals, while open circles represent CPUE outliers for that

month.

Table 1

Results of marsh fragmentation analyses on adult blue crab CPUE and biomass

Effect	DF	χ^2	P
CPUE			
Fragmentation	1	2.99	0.08
Month	5	148.42	< 0.0001
Fragmentation $\times$ Month	5	13.21	0.02
Biomass			
Fragmentation	1	0.67	0.41
Month	5	23.67	0.0003

Note: *P*-values are from Type III Likelihood Ratio tests.

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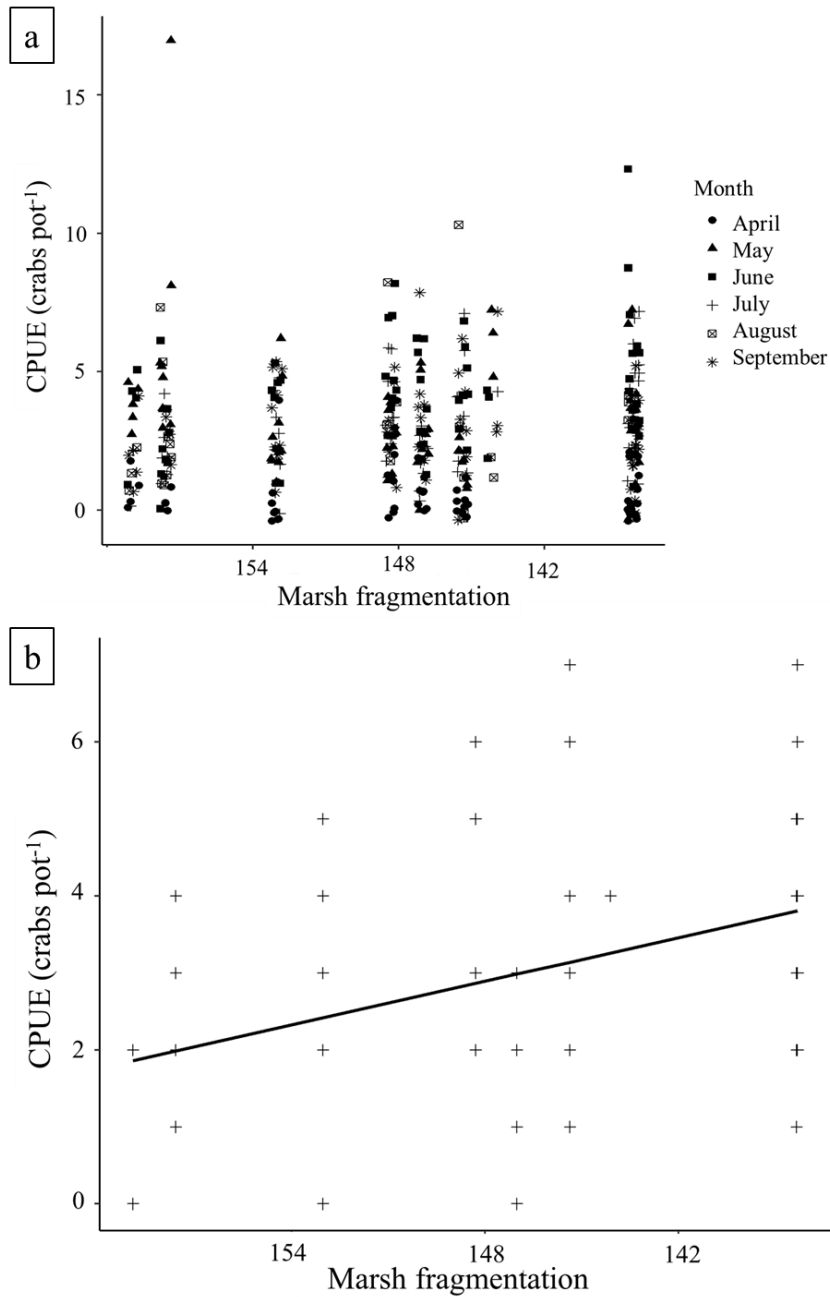
Figure 4 Adult blue crab CPUE across marsh fragmentation.

Adult blue crab CPUE across marsh fragmentation during the months of the study across all three sites (a) and during the month of July (b). Marsh fragmentation, on the x-axis, increases from left to right. Points in panel A have been jittered slightly to reduce overlap and aid visualization.

Effects of SAV presence on adult blue crab CPUE and biomass

Both adult crab CPUE and biomass were significantly influenced by the presence of SAV, with greater abundance and biomass when SAV was present (Table 3). On average, 4.22 ± 2.25 (mean $\pm$ SE) blue crabs were caught per pot with a biomass of 476.1 ± 39.62 g when SAV was present, compared to 2.95 ± 2.46 crabs with a biomass of 302.3 ± 33.62 g when SAV was absent. Month again had a significant effect on abundance but did not have a significant effect on biomass (Table 3). There was a significant effect of the interaction between SAV presence and month, where in the months of June, August, and September adult CPUE was significantly higher in areas with SAV present. The months of April, May, and July saw no significant trend in CPUE and SAV presence.

Table 2

Results of SAV presence analyses on adult blue crab CPUE and biomass

Effect	DF	χ^2	*P*
CPUE			
SAV presence	1	21.89	< 0.0001
Month	5	50.04	< 0.0001
SAV presence $\times$ Month	5	18.68	0.002
Biomass			
SAV presence	1	6.57	0.01
Month	5	5.19	0.39

Note: *P*-values are from Type III Likelihood Ratio tests.

Effects of marsh fragmentation on juvenile blue crab density

Juvenile density was significantly greater in marsh edge habitat (9.17 ± 1.75 crabs m^2) than in bare, unvegetated sediment (1.42 ± 0.37 crabs m^2), and varied across the months of the study. While there was no significant main effect of marsh fragmentation

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on juvenile blue crab density there was a significant marsh fragmentation × habitat interaction, where density increased in bare sediment habitat as marsh fragmentation increased but was unrelated to marsh fragmentation in marsh edge habitat (Table 4, Figure 4).

Table 3

Results of marsh fragmentation analysis on juvenile blue crab density

Effect	DF	χ^2	P
Fragmentation	1	1.77	0.18
Habitat	1	50.66	< 0.0001
Month	4	69.21	< 0.0001
Fragmentation × Habitat	1	4.32	0.04

Note: *P*-values are from Type III Likelihood Ratio tests.
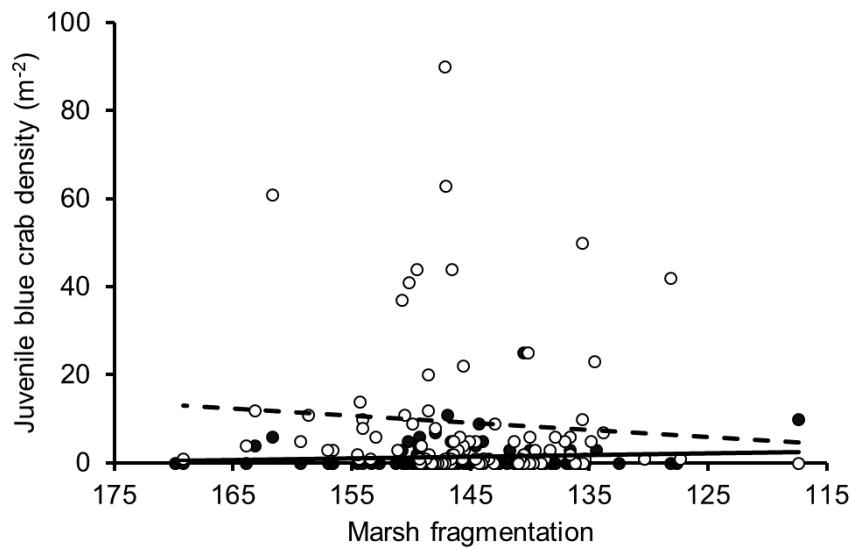
Figure 5 Juvenile blue crab density across marsh fragmentation.

Closed circles indicate densities from bare sediment and open circles indicate densities in marsh edge habitats. The dashed line indicates the trend in marsh edge and the solid line indicates the trend in bare sediment. Marsh fragmentation, on the x-axis, increases from left to right.

Effects of marsh fragmentation on juvenile blue crab carapace width

Individual juvenile blue crab CW was significantly affected by habitat, month, the fragmentation × month interaction, and the habitat × month interaction (Table 5). Although raw mean and SE individual juvenile CW in marsh edge habitats was higher (8.87 ± 0.20 mm) than in bare sediment (9.01 ± 0.28 mm), LMM analysis indicated the opposite pattern, with greater CW in marsh edge than bare ($P = 0.001$). This is likely due to the significant habitat × month interaction (see below), and to the unbalanced nature of the CW analysis. Juvenile CW varied significantly with marsh fragmentation in the month of September, but not during the other months. In the months of June and July juvenile CW was higher in marsh edge habitat than bare sediment (n = 110 and 88, respectively), while in the month of September CW was higher in bare sediment than marsh edge (n = 605). May and August did not have significant differences in juvenile CW between habitat type (n = 42 and 88, respectively). In marsh habitat, month had a significant effect on juvenile CW where juvenile CW was lower in September than all other months. Neither month nor fragmentation exhibited significant effects on juvenile CW in bare sediment habitats.

Table 4

Results of marsh fragmentation analysis on juvenile blue crab CW (mm)

Effect	DF	χ^2	P
Fragmentation	1	0.51	0.48
Habitat	1	10.48	0.001
Month	4	35.58	< 0.0001
Fragmentation × Month	4	36.78	< 0.0001
Habitat × Month	4	27.97	< 0.0001

Note: *P*-values are from Type III Likelihood Ratio tests.

Effects of habitat and percent plant cover on juvenile blue crab density and CW

Juvenile density and CW both varied significantly with habitat type and month (Table 6). On average, marsh edge habitat had 8.80 ± 2.70 (mean $\pm$ SE) juvenile crabs m^{-2} measuring 9.76 ± 0.36 mm CW, while SAV habitat had 19.14 ± 4.99 juvenile m^{-2} measuring 8.18 ± 0.18 mm CW. Percent plant cover had a significant effect on individual juvenile crab CW, where CW increased as percent cover increased. Juvenile crab CW also varied with the percent plant cover $\times$ month and habitat $\times$ percent plant cover $\times$ month interactions (Table 6). In marsh edge habitat, juvenile CW did not vary with percent plant cover but did across months, where CW in the month of September was lower than in the other months of the study. In SAV juvenile CW was not significantly influenced by percent plant cover but did vary significantly across month, where CW was higher in August than the other months. There was a significant habitat $\times$ percent plant cover interaction influencing juvenile CW where during the months of May, July, and September juvenile CW decreased in SAV as percent plant cover increased, but in August juvenile CW increased in SAV as percent plant cover increased. Juvenile CW in June was not influenced by the habitat $\times$ interaction.

Table 5

Results of habitat and percent plant cover analyses on juvenile blue crab density and CW

Effect	DF	χ^2	P
Density			
Habitat	1	12.66	0.0004
Percent plant cover	1	0.03	0.87
Month	4	25.20	< 0.0001
CW			
Habitat	1	28.88	< 0.0001
Percent plant cover	1	9.05	0.003
Month	4	121.36	< 0.0001
Habitat × Month	4	8.36	0.08
Percent plant cover × Month	4	19.16	0.0007
Habitat × Percent plant cover × Month	4	18.34	0.003

Note: *P*-values are from Type III Likelihood Ratio tests.

Effects of habitat type on juvenile blue crab mortality due to predation

Juvenile mortality due to predation was reduced in SAV (31.3% of crabs consumed in 24 h) compared to marsh edge (48.3% of crabs consumed) and bare habitat (46.7% of crabs consumed, Table 7), but this reduction in mortality was not statistically significant when considered in the context of an α-level of 0.05 (Table 8). Carapace width did not have an effect on mortality due to predation (Table 9).

Table 6

Summary of results from tethering experiments examining mortality due to predation

Habitat type	No. of crabs consumed	No. of crabs unconsumed	Proportion of crabs consumed
SAV	26	57	0.313
Marsh edge	43	46	0.483
Bare sediment	42	48	0.467

Table 7

Results of habitat type analyses on juvenile blue crab mortality due to predation

Comparison	z	*P*
Marsh edge vs. bare sediment	0.136	0.9898
SAV vs. bare sediment	-2.119	0.0858
SAV vs. marsh edge	-2.262	0.0611

Note: Values are from Tukey contrasts/ multiple comparison of the mean.

Table 8

Results of habitat type and CW analysis on juvenile blue crab mortality due to predation

Effect	DF	χ^2	*P*
Habitat	2	6.42	0.04
CW	1	0.74	0.39

Note: *P*-values are from Type III Likelihood Ratio tests.

Discussion

This study examined blue crab abundance, size, and distribution in a fragmenting salt marsh landscape, at both the juvenile and adult stages. Crab pots were used to sample adults, while a throw trap was used to sample juveniles.

Adult blue crab abundance and biomass did not vary across levels of marsh fragmentation, at least across the range of fragmentation levels sampled in this study. Adult abundance and biomass did differ among the habitats examined, however, and were higher in areas with SAV present than in areas without SAV. SAV likely offers additional protection from predators due to the increased structure present in the SAV (Heck and Thoman 1981; Canion and Heck 2009). Alternatively, greater adult abundance and biomass in SAV relative to bare sediment could also be related to food availability, as densities of many organisms are higher in SAV than adjacent bare sediment (Harrod

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1964; Thayer et al. 1975; Heck and Wetstone 1977). It should be noted that although CPUE was higher in SAV than bare sediment, the nature of the sampling method does lend some uncertainty to these conclusions. Crab pots are baited and attract crabs from variable distances depending on water flow, bait freshness, water temperature, and a number of other variables. Because SAV can be quite patchy, and although we sampled for SAV immediately adjacent to the pot, it is possible that crabs were attracted from outside the SAV. Given the water depth and bottom type, however, we feel that crab pots represented the most efficient and effective method for sampling adult blue crabs for this study.

Relationships between juvenile blue crab density and marsh fragmentation were dependent on habitat type. Juvenile density increased in bare sediment habitat as marsh fragmentation increased but was unrelated to marsh fragmentation in marsh edge habitat. When considering the lack of an overall effect of marsh fragmentation, results are similar to previous studies. Hovel and Lipcius (2002) also did not see juvenile blue crab density change with fragmentation, nor did Hitch et al. (2011) find a significant effect of fragmentation within a marsh type on nekton densities. Higher juvenile blue crab density in bare sediment habitats at higher marsh fragmentation levels could be due to increased habitat complexity: at higher marsh fragmentation levels, there would be greater amounts of edge habitat in the vicinity, allowing the juveniles to venture into the unvegetated bare sediment. Alternatively, there could be increased densities in bare sediment at higher fragmentation levels due to a decrease in available marsh habitat with crabs avoiding conspecifics to avoid cannibalism or other density-dependent factors at higher densities within edge habitat (Perkins-Visser et al. 1996).

Juvenile crab density varied significantly across the three habitats assessed in this study. Although we were unable to compare densities across all three habitats due to computational difficulty, overall juvenile densities were greatest in SAV followed by marsh and lowest in bare, unvegetated habitat. Previous studies have reported increased growth and density in vegetated habitats compared to non-vegetated habitats (Heck and Thoman 1984; Thomas and Zimmerman 1990; Perkins-Visser et al. 1996; Lipcius et al. 2005). These structured habitats provide greater food supply relative to bare sediment (Harrod 1964; Heck and Wetstone 1977, see Chapter III of this thesis) and may also provide protection from predation (Heck and Thoman 1981), although we found no significant differences in mortality rates in the tethering experiments conducted in this study. Interestingly, we did not observe a significant effect of percent plant cover on juvenile crab densities in vegetated habitats. This suggests that the presence of vegetation is more important than the amount of vegetation present. Even at low percent cover, marsh edge and SAV likely provide a greater food supply and greater protection than do bare sediment habitats (Heck and Thoman 1984; Heck and Wilson 1987; Canion and Heck 2009).

Juvenile blue crab size did not vary across a range of marsh fragmentation but did vary between different habitats. Although model results contrasted with the patterns seen in the raw means (likely due to the significant habitat × month interaction and to the unbalanced nature of the CW analysis), model results show that juvenile blue crabs in marsh edge habitat were larger than those in bare sediment habitat. It is important to note that the difference in CW between the habitats is quite small, ≈ 0.14 mm, and thus may be only minimally relevant biologically. This study also found that juvenile crabs in

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marsh edge were larger than juveniles in SAV. The difference between juvenile blue crab size in marsh edge and bare sediment can be the result of greater food availability in marsh edge habitats, compared to bare sediment, as higher animal abundances are associated with vegetated habitats (Heck and Wetstone 1977; R.J. Orth et al. 1984). The difference in juvenile blue crab size in marsh edge and SAV can be the result of active substrate selection by the juvenile crabs, where smaller crabs are selecting the SAV habitat, possibly for increased protection against predation (Heck and Thoman 1981; Heck and Coen 1995). On the other hand, the size differences this study found between marsh edge, bare sediment, and SAV can be the result of a habitat filter effect, where smaller crabs in bare sediment are better able to hide in a minimally structured habitat than larger juveniles, which could be more vulnerable to predation.

Juvenile and adult blue crabs appear to respond similarly to a fragmenting marsh landscape. Neither adult nor juvenile crab abundances varied with marsh fragmentation, but both adult and juvenile crabs were in higher numbers in areas with SAV. The results from this study suggest that blue crab densities are not sensitive to landscape-level patterns of marsh fragmentation, but are instead sensitive to local-scale patterns of habitat availability, such as the presence of vegetation (Thomas and Zimmerman 1990; Lipcius et al. 2005). Essentially, if the preferred habitats are available, there will be crabs. It is, however, also possible that direct effects of marsh fragmentation will be seen at greater levels of marsh fragmentation than were assessed here. Perhaps levels of marsh fragmentation have not reached the threshold where extreme fragmentation leads to habitat loss as small patches of marsh disappear.

Although marsh fragmentation does not appear to directly affect blue crab abundance and density (at least at the levels of fragmentation assessed here), there is likely to be an indirect effect due to changes in the availability of the various habitats as marsh fragmentation (and marsh loss) progresses. As the marsh fragments, unless SAV is colonizing these newly bare habitats, there will likely be overall losses in populations because juvenile blue crabs might not have available nursery habitat. Megalopae will have farther to migrate to reach areas with suitable nursery habitat, or else density-dependent effects, like cannibalism or reduced growth, will increase because so many individuals are restricted within limited nursery habitat until they grow to a size where they are less vulnerable to predation and have greater mobility to further disperse into areas with fewer crabs. Under this scenario, the blue crab fishery will respond after a time-lag as the remaining adult blue crabs are harvested and the juveniles do not recruit successfully due to limited nursery habitat. Without new habitat being created (either SAV colonization, or marsh growth), blue crab populations and the fishery may experience an eventual decrease in yield if the marshes of coastal Louisiana continue to fragment.

CHAPTER III – ASSESSMENT OF BENTHIC INVERTEBRATE COMMUNITIES IN A

FRAGMENTING MARSH LANDSCAPE

Introduction

Habitat fragmentation, the breaking up of a continuous landscape, occurs

naturally and anthropogenically. This process is usually associated with negative effects

on biodiversity and ecological networks because fragmentation often occurs

simultaneously with habitat loss, which is documented as having severe negative effects

on biodiversity and ecosystem health (Fahrig 2003). However, there are positive effects

that can arise from habitat fragmentation: increased ecological network strength (Menke

et al. 2012), inhibited invasive species establishment (Alofs and Fowler 2010), and

increased habitat complexity, which in turn can promote positive edge effects (Macreadie

et al. 2010; Fonderflick et al. 2013). Coastal wetlands, such as tidal salt marshes, are

vulnerable to habitat fragmentation due to sea level rise, subsidence, and lack of

sedimentation and it is important to study the effects of marsh fragmentation on resident

faunas.

Habitat fragmentation can cause direct and indirect effects on species living in

and near the habitat. A direct effect would be to cause a species' abundance or density to

decline because there is not enough intact habitat to support that population (Lamberson

et al. 1992; Powell 2006). An indirect effect would be to strengthen the relationship

within a food web network because increased edge habitat allows greater access to

resources (Macreadie et al. 2010; Menke et al. 2012). There is also opportunity as one

habitat fragments, and subsequently disappears, for another habitat that is more tolerant

of the new conditions to expand its range and colonize the newly vacant area. In the case

of Mississippi River Delta coastal wetlands, land loss may be succeeded by expansion of submerged aquatic vegetation (SAV), where the SAV can colonize the newly bare substrate, as suggested by the results of past studies (Patriquin 1975; Orth and Moore 1988; Cho and May 2006).

These changes in plant regime may carry over to changes to the benthic invertebrate communities. Tidal marshes are very productive in terms of both primary and secondary production (Strange et al. 2008). Benthic invertebrates perform many important ecosystem functions including bioturbation of the sediment, sediment stabilization, substrate oxygenation, and secondary production (Algoni 1998). These organisms make up the diet for many animals, including the blue crab (*Callinectes sapidus* Rathbun), a species known to be voracious, opportunistic, generalist feeders. They are known to eat a wide range of prey organisms, including conspecifics (Millikin and Williams 1984, see citations within; Hines et al. 1990). In the face of increasing marsh fragmentation, the increased marsh edge created by initial low levels of fragmentation can be beneficial for habitat-generalist species, such as blue crabs, by providing them greater access to habitat that may serve as a refuge from predators and as a source of available prey.

It is unknown how the benthic invertebrate community change across varying levels of marsh fragmentation in the northern Gulf of Mexico. This study aims to rectify this knowledge gap by investigating the effects of marsh fragmentation and habitat type on benthic invertebrate community composition and biomass.

Methods

Study design

This research was conducted at three study sites in Terrebonne Basin, Louisiana. Each site (2×2 km) was centered around a Coastwide Reference Monitoring System station (CRMS 0369, 0345, and 0311) and contained three 500×500 m subsites selected to cover a range of levels of marsh fragmentation. Site selection was based on local occurrence of a range of marsh fragmentation, accessibility, and land-owner permission. Collaborators at the Water Institute of the Gulf quantified fragmentation at each subsite using satellite imagery, by delineating marsh and water boundaries on a 1-m scale. These delineations were used to calculate a unified, continuous fragmentation metric that included normalized measures of marsh perimeter, marsh area, and marsh patch number, following Bogaert et al. (2000). Each component is normalized relative to the maximum and minimum value possible for the geographic space analyzed and are independent of the used units of measurement (Bogaert et al. 2000). Although Bogaert et al. (2000) also included patch isolation in their fragmentation metric, we did not include patch isolation due to computational difficulties driven by the large number of marsh patches in some areas (up to 680 patches in a single 500×500 m subsite). This fragmentation metric was calculated for a 50 m $\times$ 50 m area surrounding each sample.

Benthic invertebrate survey

To assess potential prey availability for juvenile blue crabs, benthic cores were collected in May, July, and September 2016. These cores were collected in conjunction with juvenile blue crab abundance surveys described in Chapter 2. Four cylindrical benthic cores, 7 cm in diameter $\times$10 cm deep, were taken from the area immediately

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surrounding each throw trap, placed collectively into a labeled plastic bag and placed on ice. Upon return from the field, core samples were refrigerated. Within seven days of collection, cores were sieved with tap water over a 508-µm mesh sieve and subsequently preserved in 75% ethanol dyed with rose bengal (USGS 2010; USGS 2012). Core samples (i.e., the four combined cores) were sub-sampled via the fixed-fraction method. Each sample was drained of ethanol and spread evenly across a tray (22.9×33.0 cm) with a superimposed uniform grid (18 cells, each 5.72×6.99 cm). Any invertebrates visible to the naked eye at this time were removed from the sample, identified, counted, and preserved in plastic vials of 70% ethanol, and noted to have been sorted from 100% of the original sample (USGS 2010; USGS 2012). An online random number generator (www.random.org/sequences) was used to randomly select one-third of the grid cells containing sample matter. The contents of these selected grids were removed from the whole sample, after which the invertebrates within the subsample were sorted into broad taxonomic groups, enumerated, and preserved in plastic vials of 70% ethanol (USGS 2010; USGS 2012). Dry weight for each taxonomic group in each sample was measured after drying for 48 h at 60°C.

Analyses

Abundances and biomass of organisms were extrapolated to represent the entire benthic sample prior to analyses. Data were analyzed using generalized linear mixed-effects models (GLMM), permutational analysis of variance (PERMANOVA), and non-metric multidimensional scaling (nMDS, Table 9).

Total benthic invertebrate biomass (dry weight) in each sample, including that for rare taxon groups, was analyzed for effects of fragmentation and habitat using GLMMs

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(gamma distribution, log link). Although a gamma distribution fit the data best, a gamma-GLMM will not accept response values of 0. Prior to fitting GLMMs, a small constant (0.00000001, less than 1% of the lowest sample value) was thus added to all invertebrate biomass measurements. Total benthic invertebrate biomass was first analyzed for marsh edge and bare sediment samples from all three sites, using a GLMM (gamma distribution, log link) to test for effects of habitat type (marsh edge vs. bare sediment), marsh fragmentation, and month. Total benthic invertebrate biomass was then analyzed for the only site where SAV was present (CRMS 0369), using a GLMM to test the effects of habitat type (marsh edge. vs. bare sediment vs. SAV) and month.

Benthic community composition (abundance of individuals in each taxon group, excluding rare taxa) was then analyzed for all marsh edge and bare sediment samples from all three sites, using PERMANOVA (Bray-Curtis dissimilarity index) to test for effects of habitat type (marsh edge vs. bare sediment), fragmentation, and month. Benthic community composition was then analyzed for the only site where SAV was present and sampled (CRMS 0369), using PERMANOVA to test the effects of habitat type (marsh edge vs. bare sediment vs. SAV) and month. Taxon groups occurring in less than 5% of samples were excluded prior to analyses to avoid influences upon results by rare taxon groups.

Abundances of Polychaeta and Ostracoda, two of the most common taxon groups (Table 10), were analyzed using GLMMs (negative binomial family, log link), for marsh edge and bare sediment samples from all three sites to test for effects of fragmentation and habitat type (marsh edge vs. bare sediment) on taxon group abundances. Random effects included month and subsite nested within site, and a separate GLMM was used for

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each group. Finally, the effects of habitat type (marsh edge vs. bare sediment vs. SAV) and month on Polychaeta and Ostracoda abundances were analyzed using GLMMs, with a negative binomial family and log link specified, for the only site where SAV was present and sampled (CRMS 0369). Subsite was included as a random effect, and a separate GLMM was used for each group. Model selection occurred to determine the best way to include month: whether as a fixed effect with interactions, a fixed effect without interactions, or as a random effect. Models were compared using AIC scores, and the most parsimonious model was selected as the best model. *P*-values for fixed effects were obtained using Type II Wald Chi Sq. and Type III Likelihood Ratio tests. Insignificant interactions with continuous variables were removed and the analyses re-run prior to reporting. All analyses were run in R, v. 3.4.3, using the vegan, lme4, afex, car, multcomp, and ggplot2 packages.

Table 2

Details of models used in benthic community data analyses

Response variable	Subset of data used	Analysis	Independent variables/ Fixed Effects	Family (link)	Random Effects
Total Invertebrate Biomass + 0.00000001	Marsh and bare samples from all 3 sites	GLMM	Fragmentation, Habitat, Month	Gamma (log)	Site, Subsite (nested within Site)
Total Invertebrate Biomass + 0.00000001	Samples from CRMS 0369	GLMM	Habitat, Month, Habitat × Month	Gamma (log)	Subsite
Community composition	Marsh and bare samples from all 3 sites	PERMANOVA	Fragmentation, Habitat, Month, Habitat × Month	N/A	N/A
Community composition	Samples from CRMS 0369	PERMANOVA	Habitat, Month, Habitat × Month	N/A	N/A
Polychaeta Abundance	Marsh and bare samples from all 3 sites	GLMM	Fragmentation, Habitat	Negative binomial (log)	Site, Subsite (nested within Site), Month
Ostracoda Abundance	Marsh and bare samples from all 3 sites	GLMM	Fragmentation, Habitat, Fragmentation × Habitat	Negative binomial (log)	Site, Subsite (nested within Site), Month
Polychaeta Abundance	Samples from CRMS 0369	GLMM	Habitat, Month	Negative binomial (log)	Subsite
Ostracoda Abundance	Samples from CRMS 0369	GLMM	Habitat, Month	Negative binomial (log)	Subsite

Note: GLMM indicates Generalized Linear Mixed-effects Model and PERMANOVA indicates Permutational Analysis of Variance.

Sorted invertebrates were identified as belonging to thirteen different taxonomic groups (Table 10). These taxonomic groups represent four phyla: Arthropoda, Annelida, Mollusca, and Nematoda. All taxonomic groups identified in the samples were found to be items in juvenile blue crab diet analyses (Laughlin 1982; Alexander 1986; Mansour 1992; Cote et al. 2001).

Table 9

Taxonomic groups used to classify benthic invertebrates

Group	Taxonomic Level	Frequency of occurrence (% of total samples)
Insecta	Class	57.3
Polychaeta	Class	56.2
Ostrocoda	Class	39.3
Gastropoda	Class	37.1
Bivalvia	Class	30.3
Nematoda	Phylum	29.2
Tanaidacea	Order	25.8
Copepoda	Order	19.1
Amphipoda	Order	18.0
Acari	Sub-class	4.5
Cumacea	Order	2.2
Decapoda	Order	1.1
Hirudinea	Class	1.1

Effects of marsh fragmentation on benthic invertebrate biomass

Benthic invertebrate biomass varied significantly with marsh fragmentation, habitat and month across the three sites (Table 11). Across all three sites, benthic invertebrate biomass increased as marsh fragmentation increased and was significantly

higher in marsh edge (15.7 ± 7.5 mg dry weight per sample) than bare sediment (3.2 ±

0.9 mg dry weight per sample) habitats. Benthic invertebrate biomass also varied

significantly among months, being lower in September (2.4 ± 1.0 mg dry weight per

sample) than in May (8.2 ± 2.2 mg dry weight per sample) and July (17.3 ± 10.9 mg dry

weight per sample).

Table 10

Results of marsh fragmentation analysis on benthic invertebrate biomass

Effect	DF	χ^2	P
Fragmentation	1	4.24	0.04
Habitat	1	10.75	0.001
Month	2	10.96	0.004

Note: *P*-values are from a Type III Likelihood Ratio test.

Effects of habitat type on benthic invertebrate biomass

Benthic invertebrate biomass did not vary among habitat types in CRMS 0369

(the only site with SAV present) but was significantly influenced by month. There was

also a significant habitat × month interaction (Table 12), where biomass differed among

the three habitats in July (higher in marsh edge than bare sediment or SAV; Type III

likelihood ratio test, $P = 0.001$), but not in May (Type III Likelihood ratio test, $P = 0.69$)

or September (Wald χ^2 test [LRT failed to converge], $P = 0.110$).

Table 11

Results of habitat type analysis on benthic invertebrate biomass

Effect	DF	χ^2	P
Habitat	2	2.41	0.30
Month	2	7.74	0.02
Habitat × Month	4	12.04	0.02

Note: *P*-values are from a Type III Likelihood Ratio test.
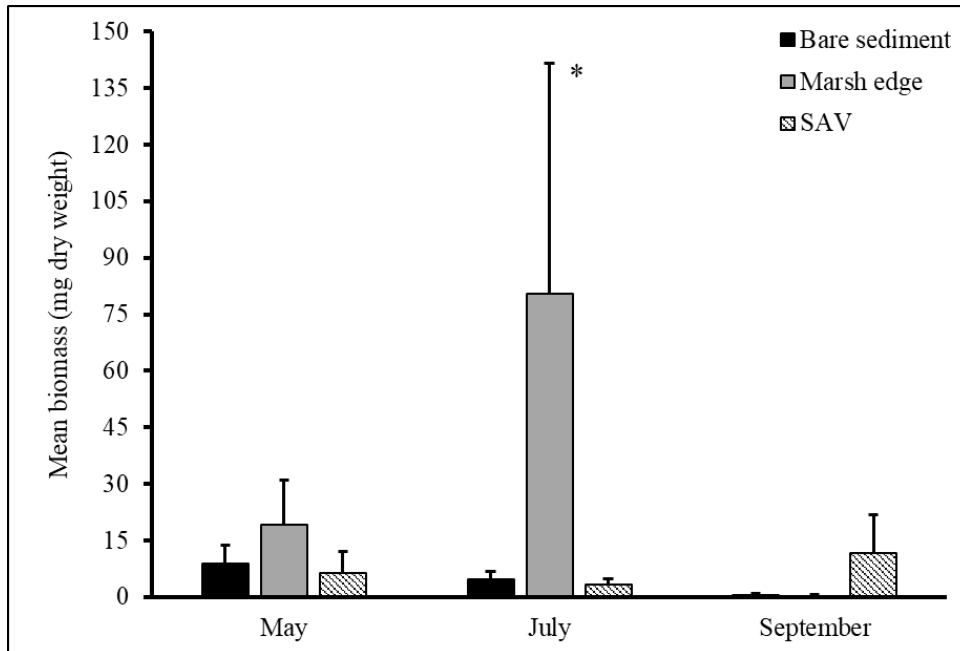
Figure 6 Benthic invertebrate biomass in different habitat types

Bars represent the mean biomass and the whiskers represent the standard error of the mean. Asterisks indicate a significant difference.

Effects of marsh fragmentation on benthic community composition

Benthic community composition across all three sites did not differ across the range of fragmentation values observed but was significantly different between marsh edge and bare sediment habitats and also across the months of this study (Table 13). There was no effect of fixed effect interactions on community composition. In marsh edge habitat, the benthic communities were composed largely of Tanaidacea, Polychaeta, and Amphipoda while benthic communities in bare sediment were heavily composed of Ostracoda, Nematoda, and Copepoda (Figure 6). Benthic community composition in the month of July is significantly different from community composition in May and September, where the benthic communities in July were largely composed of Copepoda and Nematoda (Figure 6).

Table 12

Results of marsh fragmentation, habitat, and month PERMANOVA on benthic community

composition

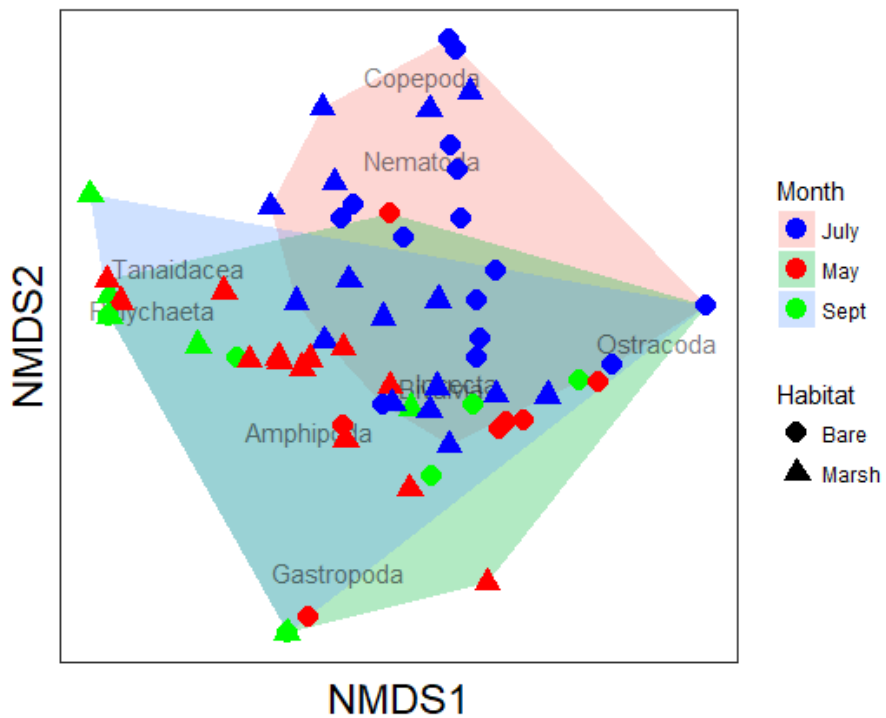| Source	DF	Sum of Squares	F	P
Fragmentation	1	0.321	0.902	0.552
Habitat	1	1.144	3.221	0.0002
Month	2	2.935	4.131	0.0001
Habitat × Month	2	0.634	0.892	0.612
Residual	67	23.802		

Figure 7 A nMDS plot of benthic community composition across all study sites

The circles represent samples from bare sediment, triangles are samples from marsh edge habitat. Blue shapes are samples from July,

red shapes are from May, and green shapes are from September. The colored polygons show the groupings of samples from each

month.

Effects of habitat type on benthic community composition

Benthic community composition was significantly dissimilar across months but was not dissimilar between the three habitat types (marsh edge, bare sediment, and SAV, Table 14) when considered only for the site where SAV was found (CRMS 0369). Benthic community composition in the month of May was significantly different from community composition in July, where communities in May were composed of Bivalvia, Polychaeta, Amphipoda, and Ostracoda while communities in July were composed of Nematoda, Insect, Copepoda, and Tanaidacea (Figure 7).

Table 13

Results of habitat type and month PERMANOVA on benthic community composition

Source	DF	Sum of Squares	F	*P*
Habitat	2	0.9070	1.3443	0.1550
Month	2	2.0451	3.0309	0.0002
Habitat × Month	4	1.4082	1.0435	0.3928
Residual	33	11.1334		
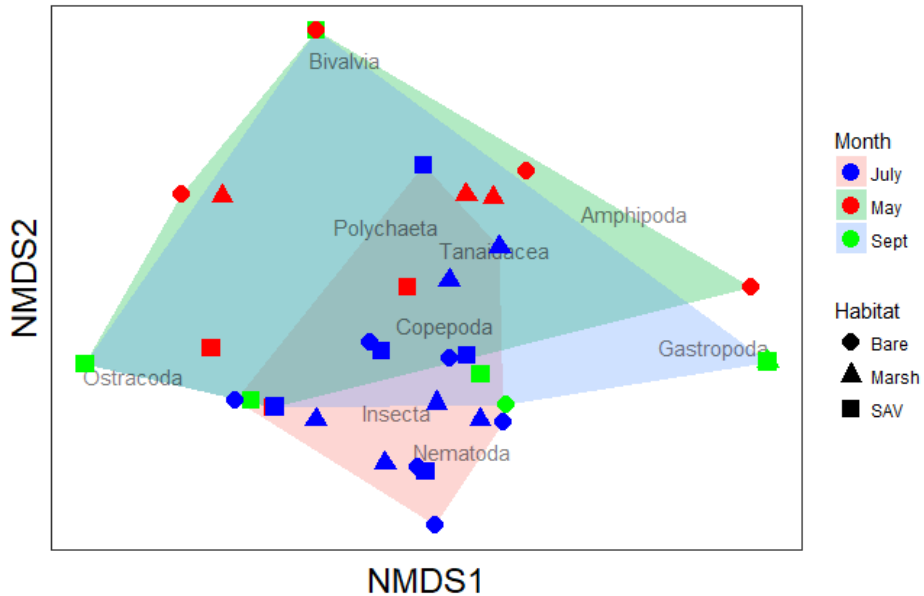
Figure 8 A nMDS plot of benthic community composition at CRMS 0369

Circles are bare sediment samples, triangles are marsh edge samples, and squares are SAV samples. The colored polygons represent the groups formed by samples in each month.

Effects of marsh fragmentation on common taxon abundances

        Abundances of polychaetes and ostracods, two taxon groups frequently encountered in samples, varied significantly between habitat types across the three sites (Table 15). Polychaeta abundance did not vary across marsh fragmentation but was significantly higher in marsh edge habitats than bare sediment habitat (Figure 8). Ostracoda abundance increased as marsh fragmentation increased and was significantly higher in bare sediment habitats than marsh edge (Figure 8). Ostracoda abundance was also seen to increase in marsh edge habitats as marsh fragmentation increased.

Table 14

Results of marsh fragmentation analyses on common taxon abundances in all study sites

Effect	DF	χ^2	P
Polychaeta			
Fragmentation	1	2.349	0.125
Habitat	1	19.520	< 0.0001
Ostracoda			
Fragmentation	1	1841.28	< 0.0001
Habitat	1	6847.76	< 0.0001
Fragmentation × Habitat	1	9.19	0.002

Note: *P*-values come from Type II Wald χ^2 tests.
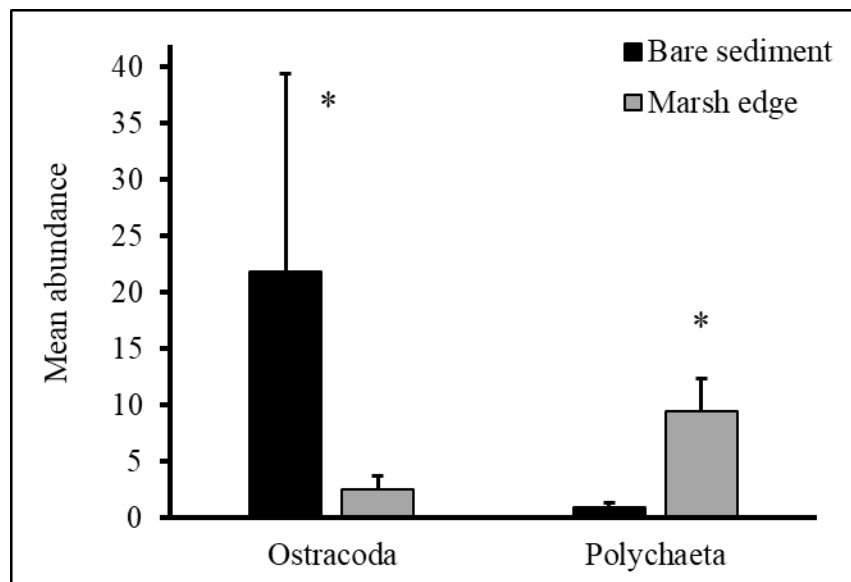
Figure 9 Polychaeta and Ostracoda abundance across all study sites

Bars represent mean abundance and the whiskers represent the standard error of the mean. Asterisks indicate a significant difference between habitats for a given taxon group.

Effects of habitat type on common taxon abundances

Polychaete and ostracod abundances were significantly different between habitats and months at CMRS 0369 (the only site with SAV present, Table 16). Polychaeta

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abundances were significantly higher in marsh edge than in bare sediment or SAV

(Figure 9). Ostracoda abundances were significantly lower in marsh edge than in bare

sediment or SAV, and abundances in September were significantly different from

abundances in July, but not significantly different from abundances in May (Figure 9).

Table 15

Results of habitat type analyses on common taxon abundances at CRMS 0369

| Effect	DF	χ^2	P
Polychaeta			
Habitat	2	9.46	0.009
Month	2	12.11	0.002
Ostracoda			
Habitat	2	6.79	0.03
Month	2	7.04	0.03

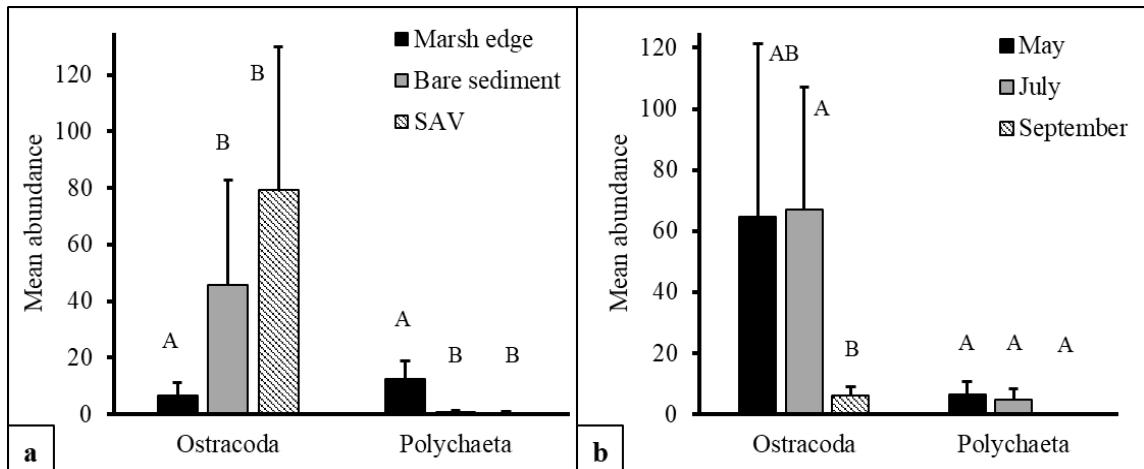Note: P-values are from Type III Likelihood Ratio tests.

Figure 10 Polychaeta and Ostracoda abundance at CRMS 0369

Bars represent the mean abundance and whiskers represent the standard error of the mean in a) different habitat types and b) months of

the study. Different letters within a taxon group indicate significant differences.

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Discussion

This study assessed benthic invertebrate communities across a fragmenting marsh landscape by examining benthic invertebrate biomass, community composition, and the responses of individual taxon groups. Benthic cores were used to sample benthic invertebrates across a gradient of marsh fragmentation and in different habitat types (marsh edge, bare sediment, and SAV).

Total benthic invertebrate biomass across all three sites varied across a range of marsh fragmentation, between marsh edge and bare sediment habitats, and across the months of the study. Total biomass increased significantly as marsh fragmentation increased, perhaps because of an increase in habitat complexity (increased edge habitat). Biomass was significantly greater in marsh edge habitats than bare sediment across all three sites. Biomass was also greater in marsh edge when compared to bare sediment and SAV habitats when considering only CRMS 0369 (the only site with SAV) but only in the month of July (when benthic biomass was highest). These findings are similar to past studies that have found greater benthic infaunal amounts in vegetated habitat than in unvegetated substrate (Harrod 1964; Heck and Wetstone 1977; Orth et al. 1984) and support the concept of vegetated aquatic habitats acting as nursery habitats due to increased prey availability. The similarities in benthic invertebrate biomass between bare sediment and SAV habitats could be related to the species of SAV that was sampled. Invasive Eurasian milfoil, *Myriophyllum spicatum*, was the dominant SAV species present at CRMS 0369 and has been found to create nocturnal hypoxic events (C. Martin, University of Florida, personal communication), which could prevent invertebrate

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establishment in its vicinity. Species within the taxonomic groups found in this study, like Polychaeta and Bivalvia, exhibit a range in tolerance to hypoxic levels (Diaz and Rosenberg 1995; Vaquer-Sunyer and Duarte 2008) and it is reasonable to assume that the taxon groups found in greater abundance in the SAV habitat (like Ostracoda) are able to establish themselves within those SAV beds. However, because this study did not identify invertebrates beyond the levels specified (Table 10), we cannot make too many assumptions about hypoxia tolerance of the individuals collected.

Community composition also differed among the habitats sampled, with marsh edge habitat containing macrofaunal individuals belonging to Amphipoda, Tanaidacea, Polychaeta, and Insecta, while bare sediment communities were largely composed of meiofaunal groups including Nematoda, Copepoda, and Ostracoda. These differences in assemblage suggest that the differences in total biomass, as described above, are driven by the benthic community (taxon groups containing larger individuals vs. groups with smaller individuals). Benthic invertebrate community composition was not found to vary between the three habitat types present at CRMS 0369 (the only site with SAV present) but this may have been due to the smaller number of samples used in the analysis. The observed differences in the benthic invertebrate community composition is likely mainly due to factors known to influence benthic invertebrate distributions: non-random recruitment, differential mortality after recruitment (Rader 1984), density-dependent processes, and tolerance to physical factors (Kneib 1984).

The differences in polychaete and ostracod abundances in different habitat types reflect the differences in these taxon habitat preferences. Polychaetes are a diverse group

of organisms where two families, Nereidae and Capitellidae, are common in marsh habitat, forming burrows around plant roots (Heard 1982), while ostracods prefer to settle in soft sediments, like those present in the non-vegetated and SAV habitats at CRMS 0369 (Keyser 1977). Although ostracods were found at greater abundances than polychaetes, their smaller size may explain biomass measurements equivalent to the polychaetes sampled.

Although benthic infauna communities were quite different among the habitat types examined, within a habitat type benthic infauna communities were insensitive to landscape-scale patterns of marsh fragmentation at the range investigated, when considering total biomass and community composition. As with results observed for juvenile blue crabs (Chapter II of this thesis), this suggests that direct effects of fragmentation are minimal. Yet total invertebrate abundance and biomass are likely to be indirectly influenced by marsh fragmentation due to changes in the availability of different habitats, as implied by noted habitat differences. Given that these invertebrate organisms are commonly consumed by a number of fish and macroinvertebrate species, changes in distribution, abundance, and community composition may cascade up through the food web in coastal salt marshes as fragmentation increases and the relative extent of habitat changes.

Patterns observed in this study are similar to those observed for juvenile blue crabs (see Chapter II), with exception to abundances in SAV habitat. This difference could be explained by the relative greater mobility juvenile blue crabs have compared to benthic invertebrates that allows them to move to areas, either higher in the water column

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or to a different habitat altogether, with higher dissolved oxygen levels during hypoxic events. Benthic invertebrates and blue crabs did not appear to be influenced by a landscape pattern of marsh fragmentation at spatial scale sampled and instead were more affected by the habitats present. Benthic invertebrate biomass and juvenile blue crab density were greater in marsh edge habitats than bare sediment. Although causality cannot be determined using the results of this study, it is possible that the greater food availability in marsh edge may be one factor underlying the greater abundance of blue crabs in that habitat. It is also possible that both juvenile blue crabs and benthic invertebrates respond similarly to favorable habitat, due to environmental conditions. That benthic invertebrate biomass and community composition were not different between bare sediment and SAV habitats also suggests that greater juvenile blue crab densities in SAV habitats are driven by greater protection against predation and not food availability (Heck and Thoman 1984, Chapter II of this thesis). However, past studies investigating the nursery habitat properties of SAV beds (Heck and Wetstone 1977; Heck and Wilson 1987; Orth and van Montfrans 1987; van Montfrans et al. 2003) were conducted in seagrass beds while the SAV in this study was a freshwater/brackish species.

One reason for seeing lack of statistical significance between the three habitat types at CRMS 0369 could be the patchiness of benthic invertebrate distributions (Morrisey et al. 1992). Samples were collected such that one bare sediment, one marsh edge, and one SAV (if present) sample were collected in close proximity (2- 30 m) so one area with all three habitat types nearby could very much have similar communities,

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despite the different habitat types. This is seen in Figure 7 where several samples from bare sediment and SAV habitats are located very close together, indicating low assemblage dissimilarity. There were also a select number of samples that had very high abundances of taxa that could have mitigated the significance of effects on community composition and biomass. Increasing the sample size and duration of the study could have helped this issue.

This study found that benthic invertebrate communities varied with habitat type and with patterns in the broad landscape at the spatial scale sampled. Higher benthic invertebrate biomass in marsh edge habitats suggest that juvenile blue crabs utilize marsh edge as much because of increased food availability as for predator avoidance. This conclusion was also supported by the lack of habitat differences in predation mortality in this study (Chapter II of this thesis). Increased habitat complexity can explain the observed trend of higher benthic invertebrate biomass in areas with higher marsh fragmentation, as there is increased marsh perimeter in these areas. Habitat fragmentation is likely to continue to have significant effects on benthic invertebrate communities until a threshold is reached at very high levels of fragmentation where the loss of marsh habitat greatly decreases the relative amount of available habitat for these benthic invertebrate communities and the juvenile blue crabs that depend on them.

CHAPTER IV – SUMMARY AND CONCLUSIONS

The fragmentation of coastal salt marshes is of great concern not only because of potential changes in biodiversity but also because of potential impacts on fisheries supported by these habitats. Coastal salt marshes are experiencing extensive habitat fragmentation worldwide, including in the Mississippi River Delta (Barras et al. 2003; Coleman et al. 2008). Future projections for habitat loss, preceded by fragmentation, are expected to continue due to increasing sea level rise, high rates of marsh subsidence, and anthropogenic activity (Day et al. 2000; Coleman et al. 2008).

Currently, the fragmentation of salt marshes in coastal Louisiana does not appear to negatively affect blue crab populations (Chapter II of this thesis). Rather, blue crab populations respond primarily to the presence of available habitat. Blue crabs utilize marsh edge as a nursery habitat during the juvenile stage, as evidenced by high densities of juvenile blue crabs in the marsh edge. Marsh edges provide greater prey availability (i.e., greater invertebrate biomass, types and sizes of invertebrate prey) compared to bare sediment. As the marsh landscape fragments, initial increases in available marsh edge habitat likely follow; but once fragmentation reaches a certain level, marsh edge habitat will begin to decrease, with potentially negative impacts on juvenile blue crabs. Blue crab populations and fisheries may experience time-lagged decreases due to the failure of juvenile blue crabs to recruit into the adult population because of a lack of nursery habitat.

Effects of marsh loss on coastal species, including blue crabs, can be mitigated if submerged aquatic vegetation (SAV) colonizes newly-created open water areas. SAV

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beds support high densities of juvenile blue crabs, likely due to increased protection from predators (Chapter II of this thesis). Yet SAV habitat does not appear to provide a greater benthic invertebrate food supply for juvenile blue crabs, at least in the area studied here (Chapter III of this thesis). It may also be important to take into account the species of SAV that is colonizing newly-created open water areas, as invasive SAV species (e.g., Eurasian watermilfoil) are quite common in coastal Louisiana and can cause hypoxic events at night when photosynthesis ceases (C. Martin, University of Florida, personal communication). Future research should investigate the differences between SAV type (freshwater/brackish vs. saline species) nursery habitats that could influence juvenile blue crabs.

Marsh fragmentation and land loss can be mitigated by increased sedimentation from terrestrial systems. A reduction in sediment supply due to extensive engineering of the Mississippi River and associated levees has left these coastal marshes starving for sediment. Sediment diversions are currently being planned in several areas of coastal Louisiana, with the goal of diverting sediment from the Mississippi River and back into the coastal marshes. Increased sediment supply from these diversions may help mitigate land loss by allowing coastal salt marshes to keep up with rising sea levels, thus ensuring adequate marsh edge habitat for juvenile blue crabs and other species.

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