



Blue Crab Abundance and Survival in a Fragmenting Coastal Marsh System

Lennah M. Shakeri¹ · Kelly M. Darnell^{1,2} · Tim J. B. Carruthers² · M. Zachary Darnell¹

Received: 13 March 2019 / Revised: 20 March 2020 / Accepted: 24 March 2020
© Coastal and Estuarine Research Federation 2020

Abstract

Louisiana's coastal marshes are becoming increasingly fragmented due to sea level rise, subsidence, reduced sediment inflow from the Mississippi River, and saltwater intrusion. Many commercially and recreationally fished species rely on the marsh system as nursery habitat, and the resilience of species to further marsh loss and marsh fragmentation is uncertain. We examined the impacts of marsh fragmentation on the blue crab, *Callinectes sapidus*, a species supporting one of the largest fisheries in coastal Louisiana and which uses marsh edge as nursery habitat. Juvenile and adult abundances were quantified in multiple habitats (bare sediment, marsh edge, and submerged aquatic vegetation [SAV]) within an actively fragmenting coastal marsh. Adult blue crabs were sampled using crab pots, while juveniles were sampled using a throw trap. In general, blue crab density was unrelated to marsh fragmentation, but was instead related to local-scale patterns of habitat availability, including presence and type of vegetation. In tethering experiments to examine predation rates on juvenile blue crabs across habitats, predation rates were lowest in SAV compared with marsh edge or bare sediment. While direct effects of marsh fragmentation on local-scale patterns of blue crab abundance were not observed, marsh fragmentation will likely have indirect effects on blue crab populations through changes in habitat availability. Unless SAV expands into newly created open water areas, providing an alternative nursery habitat for blue crabs, continued marsh fragmentation and loss are expected to have negative impacts on blue crab populations and fisheries through a decrease in available nursery habitat.

Keywords Salt marsh · Habitat fragmentation · Blue crab · *Callinectes sapidus* · SAV · Louisiana · Gulf of Mexico

Introduction

Coastal wetlands are undergoing extensive fragmentation and land loss worldwide. Coleman et al. (2008) examined 14 river deltas across the world and found that 15,845 km² of coastal wetland was lost between the early 1980s and 2002, due to conversion into agricultural or industrial land and open water expansion. This loss represents > 50% of the total area of coastal wetlands in these systems and is due to a number of processes, both natural and anthropogenic, including sea level rise, subsidence, saltwater intrusion, reduced freshwater inflow, canal dredging, and land use conversion (Scavia et al.

2002; Coleman et al. 2008; Day et al. 2011; Dahl and Stedman 2013). As rates of sea level rise increase, the rate of coastal wetland loss is expected to accelerate (Scavia et al. 2002; Coleman et al. 2008). In areas where coastal wetlands are lost to shallow open water, this loss does not typically occur as a uniform retreat of the shoreline; instead, fragmentation occurs whereby the marsh landscape breaks into smaller patches surrounded by open water. The greatest rates of fragmentation occur in saline marsh, due to greater exposure to wave energy (relative to fresh, intermediate, or brackish marsh; Couvillion et al. 2016). This results in a reduction of marsh interior and an initial increase in marsh edge up to a tipping point, beyond which marsh edge begins to decrease as fragmentation progresses (Browder et al. 1985).

Louisiana contains ~40% of the wetlands in the mainland USA (Jankowski et al. 2017) and also supports some of the largest commercial fisheries (by biomass) in the mainland USA (NMFS 2017). Many of the harvested species rely on coastal wetlands as nursery habitat (Zimmerman et al. 2000; MacRae and Cowan 2010). Louisiana is experiencing rapid fragmentation and loss of wetlands. Between 1932 and 2016,

Communicated by Matthew D. Taylor

✉ M. Zachary Darnell
zachary.darnell@usm.edu

¹ Division of Coastal Sciences, School of Ocean Science and Engineering, The University of Southern Mississippi, 703 E. Beach Dr., Ocean Springs, MS 39564, USA

² The Water Institute of the Gulf, Baton Rouge, LA 70802, USA

coastal Louisiana lost $\sim 4833 \text{ km}^2$ of wetland area, representing a loss of approximately 25% of coastal wetlands, with rates of wetland loss ranging from 28.01 ± 16.37 to $83.5 \pm 11.8 \text{ km}^2 \text{ year}^{-2}$ (Couvillion et al. 2017). Along with a loss of area, wetlands in Louisiana are also fragmenting, with a coastwide reduction of marsh aggregation (Turner and Rao, 1990; Couvillion et al. 2016). A further 2118–4677 km^2 of emergent marsh in Louisiana is predicted to be lost by 2060 (Couvillion et al. 2011; CPRA 2012; Couvillion and Beck 2013), which will likely occur through fragmentation.

While some species rely entirely on marsh interior (Powell 2006), others rely on marsh edge, including many fish and macroinvertebrates, which utilize the marsh platform as nursery habitat during tidal inundation periods and rely on open water areas for survival when the marsh is not inundated (Thomas and Zimmerman 1990; Minello and Rozas 2002; Lipcius et al. 2005; Strange et al. 2008). When considering effects of marsh fragmentation on fish and macroinvertebrate species, it is critical to consider how an organism utilizes the marsh landscape, and to understand the particular microhabitats preferred by species of particular interest.

As coastal marshes fragment, areas of land are converted to shallow open water with bare substrate. It is possible that submerged aquatic vegetation (SAV) may colonize the newly available bare substrate between marsh patches. As SAV is also considered valuable nursery habitat (Thayer et al. 1975; Heck and Thoman 1984), colonization of newly created open water areas by SAV can potentially provide an alternate habitat for species traditionally dependent on marsh edge (Strange et al. 2008; Saunders et al. 2013), specifically juvenile crustaceans and fish, whose densities are higher, and predation rates are often lower in SAV relative to bare sediment (Heck and Thoman 1981; Wolcott and Hines 1990; Lipcius et al. 2005; Canion and Heck 2009; Jerabek et al. 2017). High relative sea level rise from rapid subsidence rates combined with eustatic sea level rise in coastal Louisiana continues to result in transition of continuous emergent marsh to fragmented marsh and large areas of shallow submerged habitat (Couvillion et al. 2016). While this increases the potential shallow submerged habitat areas appropriate for SAV, the dominant SAV species growing in the Mississippi River Delta occur more commonly and with greater biomass in oligohaline and mesohaline rather than polyhaline areas (Hillmann et al. 2016). Oligohaline and mesohaline areas are dominated by *Myriophyllum spicatum* and *Ruppia maritima*, both of which grow rapidly into available habitats and are highly variable in occurrence and distribution through space and time (Cho and Poirrier 2005; Hester et al. 2005; Cho et al. 2009; Cho et al. 2012).

The purpose of this study was to examine the impacts of marsh fragmentation on blue crab, *Callinectes sapidus* Rathbun, a species that utilizes both marsh edge and SAV as nursery habitat. This euryhaline crab is common along the Atlantic and Gulf Coasts of the USA and supports a valuable

commercial fishery (NMFS 2016). Blue crabs first enter estuaries as megalopae and generally settle into vegetated (emergent or submerged) nursery habitats before metamorphosing into the first juvenile stage (Orth and van Montfrans 1987; Boylan and Wenner 1993; van Montfrans et al. 2003). The recruitment period for blue crabs in the northern Gulf of Mexico is protracted and highly episodic (Rabalais et al. 1995; Perry et al. 2003). 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 can use marsh edge or SAV as nursery habitat, it is important to understand how marsh loss, the associated increase in marsh edge, and potentially the presence of SAV influence habitat use by blue crabs. Identifying the complex relationships between juvenile blue crab populations, marsh fragmentation, and SAV cover is vital to understanding how blue crab populations may respond to future coastal change.

This study was designed to quantify juvenile and adult blue crab abundances in different habitats (marsh edge, SAV, and bare substrate open water) along a marsh fragmentation gradient and to determine if predation rates on juvenile blue crabs differed among these habitats. Specific hypotheses tested included the following: (1) juvenile blue crab density varies as a function of the degree of marsh fragmentation and habitat type; (2) in vegetated habitats (marsh and SAV), juvenile density varies as a function of the percent cover of vegetation; (3) adult blue crab catch-per-unit-effort (CPUE) varies as a function of the degree of marsh fragmentation and is greater in areas with SAV present when compared with areas without SAV; (4) juvenile blue crab mortality rates differ across the three habitats examined (marsh, SAV, bare sediment); and (5) in vegetated habitats, juvenile blue crab mortality rate varies as a function of the percent cover of vegetation present.

Methods

Study Design

This research was conducted at three study sites in the Terrebonne Basin, LA. The Terrebonne Basin is a microtidal system, with an astronomical tidal range of $< 0.5 \text{ m}$ (CPRA 2018), and supports a large blue crab fishery, with annual landings averaging 12.2 million pounds between 2000 and 2013 (Bourgeois et al. 2014). The Terrebonne Basin has experienced the greatest decrease in wetland area of the Louisiana coastal basins, with 1302 km^2 lost from 1932 to 2016, and is currently experiencing land loss at a rate of $\sim 6.12 \text{ km}^2 \text{ year}^{-1}$ (Couvillion et al. 2017).

Each of the three study sites ($2 \times 2 \text{ km}$) was centered on a Coastwide Reference Monitoring System station: CRMS

0369 (29° 17' 40.49" N, 90° 41' 42.14" W); CRMS 0311 (29° 12' 51.46" N, 90° 47' 32.14" W); and CRMS 0345 (29° 10' 14" N, 90° 45' 45" W). Under the CRMS program, at each station, the percent cover of emergent vegetation is monitored annually, and salinity is measured continuously to provide long-term data on marsh classification types and salinity. CRMS 0369, the most northern site (hereafter referred to as the "north site"), is currently classified as brackish marsh with *Spartina patens* as the dominant emergent vegetation and both CRMS 0311 (hereafter "central site") and CRMS 0345 (hereafter "south site") are currently classified as saline marsh, with *S. alterniflora* as the dominant emergent vegetation (CPRA 2018). During the 2016 vegetation growing season (March 1–November 30), which spanned sampling for this study, mean salinities were 5.23, 11.77, and 15.45 for the north, central, and south sites, respectively (CPRA 2018). Each site contained three 500-m × 500-m subsites selected to cover the range of marsh fragmentation at the site.

Using 1-m resolution satellite orthoimagery from the United States Department of Agriculture Farm Service Agency (Davidson 1998; USDA:FSA 2015), marsh and water boundaries were delineated on a 1-m scale (Fig. 1). These delineations were used to calculate a unified, continuous fragmentation metric that included normalized measures of marsh area, marsh perimeter, and marsh patch number, using the

methods described by Bogaert et al. (2000). This approach involves normalizing each component to the maximum and minimum value possible for the geographic space analyzed, and is independent of the units of measurement (Bogaert et al. 2000). This fragmentation metric was calculated at spatial scales relevant to the crab life history stage being examined: at the 500-m × 500-m subsite level for subadult/adult blue crabs (collected using crab pots), and at the 50-m × 50-m level for juvenile blue crabs (< 100-mm carapace width, collected using a throw trap). Briefly, this fragmentation metric was calculated as

$$|\phi|' = \sqrt{\alpha^2 + \beta^2 + \gamma^2}$$

where α represents a normalized index of habitat retention after fragmentation, based on the observed marsh area normalized relative to the maximum and minimum possible marsh area given the spatial scale and resolution examined, and is higher for minimally fragmented landscapes. β represents a normalized index of habitat perimeter, based on the observed marsh edge length normalized relative to the maximum and minimum possible marsh edge length given the observed marsh area; greater edge lengths generate lower β values. γ represents a normalized index of patch number, based on the observed number of marsh patches normalized relative to the

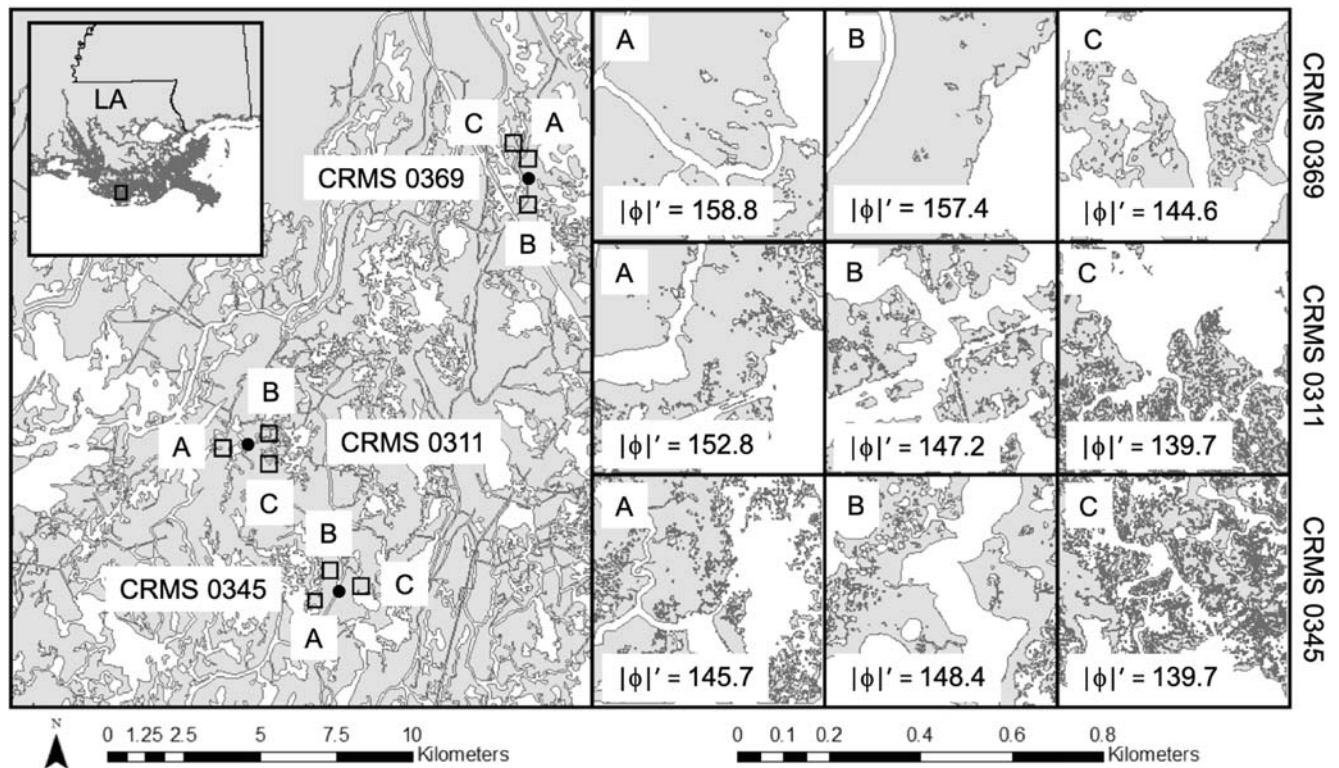


Fig. 1 Map of study site locations in Terrebonne Basin, LA. Gray represents land while white represents water. CRMS 0369 is the north site, CRMS 0311 is the central site, and CRMS 0345 is the south site. Panels on the right represent land-water delineations at the 1-m scale for

each subsite. 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

maximum and minimum possible patch number given the observed marsh area and the spatial scale and resolution examined; a low number of patches generates a high γ index. The resulting fragmentation metric was a continuous variable with higher values representing lower levels of marsh fragmentation and lower values representing higher levels of marsh fragmentation (Fig. 1). Additional details of these calculations are provided by Bogaert et al. (2000). Although Bogaert et al. (2000) also included patch isolation in their fragmentation metric, patch isolation was not included due to computational difficulties driven by the large number of marsh patches in some areas (up to 680 patches in a single 500-m \times 500-m subsite).

Juvenile Blue Crab Abundance

Juvenile crab densities were assessed monthly from May through September 2016, which represents the peak activity season for blue crabs and spans much of the growing season for SAV and emergent marsh vegetation in the study area. Juvenile crab densities were measured using a throw trap (1-m \times 1-m aluminum frame with 1.6-mm nylon mesh sides; Rozas and Minello 1997; Hitch et al. 2011; La Peyre and Gordon 2012) at two stations in each available habitat (marsh edge, bare sediment, and SAV [if present]) within each subsite. Stations were randomly selected each month. SAV was only present at the north site (CRMS 0369), and the SAV community was dominated by Eurasian watermilfoil *Myriophyllum spicatum* (present in 97% of throw trap stations). Throw trapping in the marsh habitat occurred on the marsh surface at the marsh edge, as juvenile blue crab density is greatest within 1 m from the marsh edge (Minello and Rozas 2002). The trap was deployed from a boat into the target habitat ensuring complete contact with the substrate. Water depth at throw trap stations ranged from 4 to 110 cm (mean \pm SD = 48 \pm 25 cm). For marsh and SAV habitat, total plant percent cover was estimated visually. A 1-m bar seine (1.6-mm nylon mesh) was swept through the trap 3 times from each side, for a minimum of 12 total sweeps, with sweeps continuing until 5 consecutive sweeps yielded no blue crabs. During sweeps, the net disturbed the sediment to capture any buried crabs. After each sweep, net contents were bagged, placed on ice, and later frozen. After thawing, blue crabs were sorted to species and counted. Crabs > 100-mm carapace width (4 crabs, 0.26% of all crabs caught in throw traps) were excluded from throw trap analyses, as the throw trap is not designed to catch large crabs and this size class was better represented in the data from crab pot surveys.

Adult and Subadult Blue Crab Abundance

Adult and subadult blue crab abundance was assessed monthly from April to September 2016 using commercial crab pots

(24" \times 24" \times 13.5" high, 1.5" mesh, 3 entry funnels) that were modified such that they did not contain escape rings but had terrapin-excluding devices installed in the entry funnels. The April–September sampling period represents the peak activity season for blue crabs and the season of greatest commercial landings in Louisiana (Bourgeois et al. 2014), and spans much of the growing season for SAV. Nine pots were deployed throughout each subsite each month. Pot deployment locations were randomly selected each month from a set of locations that had been surveyed in Spring 2016 for depth and SAV presence for another study (Darnell et al., in review). Depths where pots were deployed ranged from 38 to 220 cm. Each pot was baited with three previously frozen menhaden and collected 24 \pm 2 h after deployment. All crabs caught were sexed and measured for carapace width (CW). SAV presence or absence was assessed by raking the bottom substrate 6 times (3 on either side of the boat) at the location of the crab pot, following pot retrieval.

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 June and July of 2016 and 2017. Tethering was conducted in all three habitats at the north site only (the only site where SAV was present). Juvenile blue crabs (9–30-mm CW) were collected using a throw trap and randomly assigned to a habitat treatment (marsh edge, bare sediment, or SAV). A tether (100–110 cm long), constructed of 10 or 20-lb. test monofilament fishing line, was attached to the carapace of each crab using cyanoacrylate glue. The other end of the tether was tied through holes drilled near the top of a 2-ft-long 0.5" PVC anchor pole, with one tethered crab attached to each pole. The anchor pole was pushed completely into the sediment so the top end of the pole was flush with the sediment surface. Crabs tethered in the bare sediment and SAV habitats were tethered in patches (of bare sediment or SAV, respectively) that were at least as large as the range over which the crab could move while tethered. Crabs tethered in the marsh edge habitat were tethered at the marsh/open water interface, allowing these tethered crabs not only to enter the marsh but also to retreat from the marsh surface into open water during low-water events when the marsh surface was exposed. Although the marsh edge was occasionally characterized by a distinct drop-off, tether lengths were sufficient that the crab could reach the sediment surface of the marsh channel. Crabs were checked 24 \pm 2 h after tethering. The absence of a crab after 24 h was assumed to be mortality due to predation. Three to four crabs were tethered simultaneously in each habitat at 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 sampled, for a total of 83–90 crabs tethered in each habitat.

Data Analyses

Data were analyzed using generalized additive mixed-effects models (GAMMs) or generalized linear mixed-effects models (GLMMs), depending on the response variable in question. Analyses were structured to address specific hypotheses (Table 1):

Hypothesis 1: Juvenile blue crab density varies as a function of the degree of marsh fragmentation and habitat type. Negative binomial (log link) GAMMs were used to model juvenile crab density data (continuous; crabs m⁻²) from the throw traps. Fragmentation (continuous; calculated as described above in a 50-m × 50-m area surrounding the throw trap) and habitat type (categorical; bare sediment, marsh edge, or SAV) were included as fixed effects and subsite (categorical) and month (categorical) were included as random effects. Multiple candidate models were fit following Pedersen et al. (2019). All models included habitat as a parametric categorical fixed effect, but differed in the way the fragmentation smoother term(s) were specified: one included a single global fragmentation smoother for all observations, one included a global fragmentation smoother plus habitat-level smoothers corresponding, and one included habitat-level smoothers but no global smoother. Models were compared using AICc values, and the model with the lowest AICc value was selected.

Hypothesis 2: In vegetated habitats (marsh and SAV), juvenile density varies as a function of the percent cover of vegetation. Negative binomial (log link) GLMMs were used to model the effect of marsh and SAV (separately) on juvenile crab density (continuous; crabs m⁻²) from the throw traps. Total plant percent cover (continuous; measured within the throw trap) was included as a fixed effect. Subsite (categorical) and month (categorical) were included as random effects.

Hypothesis 3: Adult blue crab catch-per-unit-effort (CPUE) varies as a function of the degree of marsh fragmentation and is greater in areas with SAV present when compared with areas without SAV. A negative binomial (log link) GAMM was used to model blue crab CPUE (continuous; crabs pot⁻²) measured from crab pots, using data from all three sites but only samples where SAV was absent. Fragmentation (continuous; calculated as described above at the 500-m × 500-m subsite scale) was included as a fixed effect, and site (categorical) and month (categorical) were included as random effects. To compare between areas with and without SAV, a negative binomial (log link) GLMM was fitted using blue crab CPUE (continuous; crabs pot⁻²) from the crab pots as the response variable, using only samples from the north site. SAV presence/absence (categorical) at

Table 1 Details of models used in adult and juvenile blue crab data analyses. GLMM indicates generalized linear mixed-effects models, while GLMM indicates generalized linear mixed effects models. “s()” indicates a continuous variable included as a smooth term in a GAMM

Hypothesis	Response variable	Subset of data used	Model type	Family (link)	Fixed effects terms	Random effects terms
1	Juvenile crab density (crabs m ⁻²)	All throw trap data	GAMM	Neg. binomial (log)	Habitat + s(Fragmentation) + s(Fragmentation, Habitat)	Subsite, Month
2	Juvenile crab density (crabs m ⁻²)	All marsh throw trap samples	GLMM	Neg. binomial (log)	Percent cover	Subsite, Month
2	Juvenile crab density (crabs m ⁻²)	All SAV throw trap samples	GLMM	Neg. binomial (log)	Percent cover	Subsite, Month
3	CPUE (crabs pot ⁻¹)	All pot samples where SAV was absent	GAMM	Neg. binomial (log)	s(Fragmentation)	Site, Month
3	CPUE (crabs pot ⁻¹)	Pot samples from north site	GLMM	Neg. binomial (log)	SAV presence/absence	Subsite, Month
4	Fate (consumed or not consumed)	All tethering data	GLMM	Binomial (logit)	Habitat + CW + (Habitat × CW)	Subsite, Block
5	Fate (consumed or not consumed)	Tethering data from marsh	GLMM	Binomial (logit)	Percent cover + CW + (Percent cover × CW)	Subsite, Block
5	Fate (consumed or not consumed)	Tethering data from SAV	GLMM	Binomial (logit)	Percent cover + CW + (Percent cover × CW)	Subsite, Block

the trap location was included as a fixed effect and subsite (categorical) and month (categorical) were included as random effects.

Hypothesis 4: Juvenile blue crab mortality rates differ across the three habitats examined. A binomial (logit link) GLMM was used to model crab fate (categorical; consumed or not consumed). Habitat type (categorical; bare sediment, marsh edge, or SAV) and crab carapace width (continuous) were included as fixed effects and subsite (categorical) and block (a simultaneous round of tethering, categorical) were included as random effects.

Hypothesis 5: In vegetated habitats, juvenile blue crab mortality rate varies as a function of the percent cover of vegetation present. Separate binomial (logit link) GLMMs were fitted for marsh and SAV using crab fate (categorical; consumed or not consumed) as the response variable. Total percent plant cover (continuous; measured in a 1-m² area surrounding the tethering location) and crab carapace width (continuous) were included as fixed effects and subsite (categorical) and block (a simultaneous round of tethering; categorical) were included as random effects.

In all analyses, continuous variables were first standardized by subtracting the mean from each observation and dividing the difference by the standard deviation (Zuur et al. 2015). Fixed effect *P* values were obtained through Wald tests (for GAMMs) and likelihood ratio tests (for GLMMs). Tukey contrasts were used for post hoc comparisons when appropriate. All analyses were conducted in R v. 3.6.2 (R Core Team 2019), using the mgcv, lme4, afex, and multcomp packages. All R code used in analyses is available on Dryad (see Data Accessibility statement, below).

Results

Blue Crab Density Measured Using Throw Traps

A total of 1536 blue crabs were captured in the throw trap, with carapace widths ranging from 2 to 164 mm (median = 7.66 mm; Fig. 2). Four crabs with carapace widths > 100 mm were excluded from analyses. Juvenile blue crab densities in throw trap samples (excluding crabs > 100 mm) ranged from 0 to 104 crabs m⁻² (median = 1 crab m⁻²).

Marsh Fragmentation and Habitat Type Across all three sites, juvenile blue crab densities were independent of marsh fragmentation (Fig. 3), with non-significant global and habitat-specific smooth terms for fragmentation (Table 2). Juvenile blue crab densities did, however, differ significantly among the three habitats (Table 2). Both SAV and marsh edge supported greater juvenile blue crab densities than bare sediment (SAV vs. bare: $z = 6.596$, $P < 0.001$; marsh edge vs. bare: $z = 5.617$, $P < 0.001$), but although the median density was

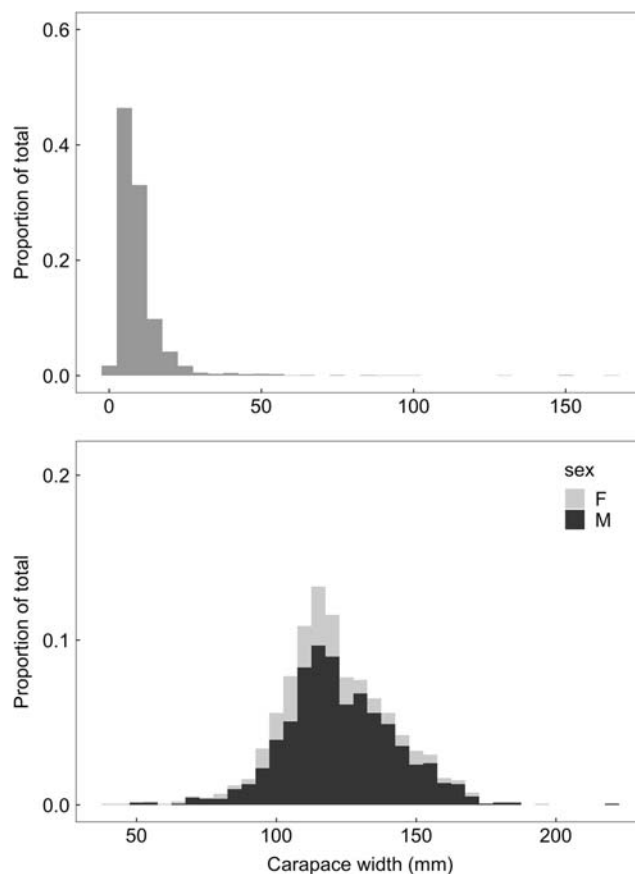


Fig. 2 Histograms of blue crab carapace widths captured in the throw trap (upper panel) and crab pots (lower panel)

greater in SAV compared with marsh edge, the difference was not statistically significant ($z = 2.070$, $P = 0.095$) (Fig. 4).

Percent Cover of Vegetation Each vegetated habitat (marsh edge and SAV) was dominated by a single plant species. Smooth cordgrass *Spartina alterniflora* was present at all

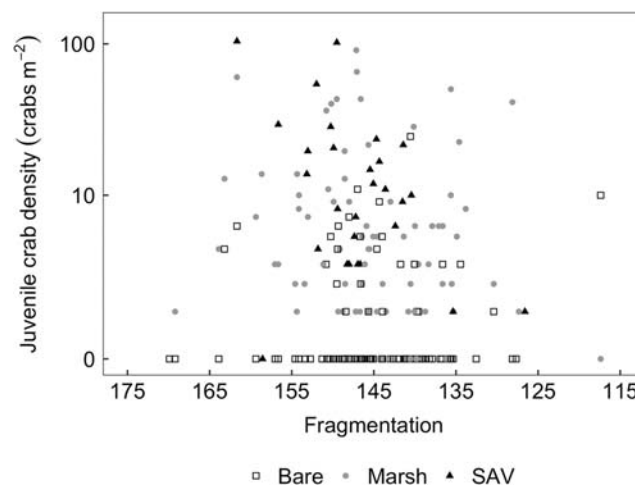


Fig. 3 Blue crab density across the range of marsh fragmentation sampled, from throw trap sampling. Note that the *y*-axis is on a log scale. Marsh fragmentation, on the *x*-axis, increases from left to right

Table 2 Results of Wald test with GAMM model using juvenile densities from throw trap samples across all three sites. Degrees of freedom (DF) are shown for parametric factor terms, while estimated degrees of freedom (EDF) are shown for smooth terms

Source	DF/EDF	χ^2	P
Habitat	2	52.230	< 0.001
s(Fragmentation)	0.002	0.001	0.366
s(Fragmentation, Habitat)	0.0002	< 0.001	0.410

marsh throw trap stations; 79% of all marsh edge throw trap stations were located in monospecific patches of *S. alterniflora*. Saltgrass *Distichlis spicata* was present at 6.7% of stations, with other species being present at < 5% of stations each. The dominant SAV species at throw trap stations was Eurasian watermilfoil *Myriophyllum spicatum* (present at 97% of SAV throw trap stations), followed by widgeon grass *Ruppia maritima* (present at 6% of SAV throw trap stations), and coontail *Ceratophyllum demersum* (present at 6% of SAV throw trap stations). In both marsh edge and SAV habitats, blue crab density was independent of percent plant cover (marsh edge: DF = 1, $\chi^2 = 0.26$, $P = 0.61$; SAV: DF = 1, $\chi^2 = 1.53$, $P = 0.22$).

Adult and Subadult Blue Crab CPUE in Crab Pots

A total of 1345 blue crabs were captured in the crab pots, with carapace widths of 41–222 mm (median = 119 mm; Fig. 2). Of the 1345 blue crabs collected in crab pots, 77.5% were male and 22.5% were female. CPUE in pot samples ranged from 0 to 17 crabs pot⁻¹ (median = 3 crabs pot⁻¹).

Across the three study sites, blue crab CPUE (crabs pot⁻¹) was not related to the degree of marsh fragmentation at the sub-site level (EDF = 1.001, $\chi^2 = 2.507$, $P = 0.113$). Blue crab CPUE

was related to SAV presence (north site only, DF = 1, $\chi^2 = 11.55$, $P < 0.001$); pots set in SAV caught more crabs than pots set outside of SAV. On average, 4.22 ± 2.25 (mean \pm SD, median = 4) blue crabs were caught per pot when SAV was present, compared with 2.96 ± 2.47 (median = 2.5) crabs when SAV was absent.

Tethering Experiments

Mortality Rates Across Habitats Predation rates in the three habitats were 31.3% in SAV, 46.7% in bare sediment, and 48.3% in marsh edge (Table 3). Predation rate differed significantly among the three habitats (type II LRT, DF = 2, $\chi^2 = 6.42$, $P = 0.04$), but was independent of carapace width (type II LRT, DF = 1, $\chi^2 = 0.74$, $P = 0.39$), and there was no significant habitat \times carapace width interaction (type II LRT, DF = 2, $\chi^2 = 1.03$, $P = 0.60$).

Mortality Rates and Percent Cover of Vegetation In marsh edge habitat, predation rates were independent of percent cover (type II LRT, DF = 1, $\chi^2 = 0.01$, $P = 0.91$) and carapace width (type II LRT, DF = 1, $\chi^2 = 1.95$, $P = 0.16$), and there was no significant percent cover \times carapace width interaction (type II LRT, DF = 1, $\chi^2 = 0.03$, $P = 0.86$). In SAV habitat, main effects of percent cover and carapace width were non-significant (type III LRTs; percent cover: DF = 1, $\chi^2 = 2.35$, $P = 0.13$; carapace width: DF = 1, $\chi^2 = 2.02$, $P = 0.16$), but there was a significant percent cover \times carapace width interaction (type III LRT, DF = 1, $\chi^2 = 9.25$, $P = 0.002$). Where percent cover was low, predation rates decreased with increasing crab size, but this pattern was reversed above $\sim 70\%$ cover (Fig. 5). At small crab sizes (under ~ 13 mm), predation rates decreased with increasing percent cover, while at large sizes, predation rates increased with increasing percent cover (Fig. 5).

Fig. 4 Blue crab density in each habitat, from throw trap sampling. Note that the y-axis is on a log scale

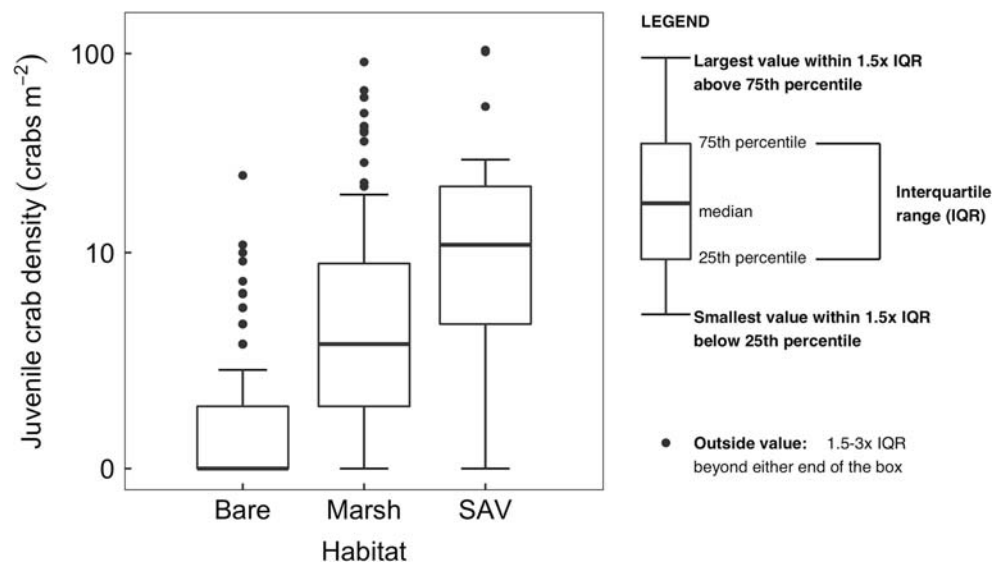


Table 3 Summary of results from tethering experiments examining mortality due to predation

Habitat type	Total no. of crabs	No. of crabs consumed	Proportion consumed
SAV	83	26	0.313
Marsh edge	89	43	0.483
Bare sediment	90	42	0.467

Discussion

We examined blue crab responses to coastal marsh fragmentation, assessing blue crab abundance and distribution among habitats across an actively fragmenting salt marsh landscape in the Terrebonne Basin, LA. Both juvenile and adult stages were sampled; during both stages, strong effects of habitat type were observed, with no discernable effect of marsh fragmentation.

Importance of Vegetated Habitats for Blue Crabs

Juvenile blue crab densities were independent of the degree of marsh fragmentation across the range of fragmentation conditions sampled here, but densities differed greatly among the three habitats sampled. The highest juvenile densities were observed in SAV, followed by marsh edge, then bare sediment. Previous studies have reported increased growth and density in vegetated habitats compared with 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 Weststone 1977) and also provide protection from predation, as observed in previous studies (e.g., Heck and Thoman 1981) as well as the results of the tethering experiments conducted here.

Although vegetated habitats supported higher juvenile blue crab densities than bare sediment, juvenile densities were independent of percent plant cover in both marsh edge and SAV habitats, suggesting that the presence of vegetation is more important than the density or small-scale (< 1 m⁻²) patchiness of vegetation at least in the vegetated habitats and range of percent covers sampled in this study (20–100% cover in marsh edge, 5–100% cover in SAV). Even at low percent cover, marsh edge and SAV likely provide a greater food supply than do bare sediment habitats. Blue crabs are generalist predators and scavengers at all stages, and juvenile blue crabs are primarily consuming small infaunal and epifaunal invertebrates, including other blue crabs (Lipcius et al. 2007). Vegetated habitats support substantially higher densities of these prey species than do nearby bare sediment habitats (Heck and Thoman 1984; Heck and Wilson 1987; Canion and Heck 2009), which explains the patterns observed here.

In vegetated habitats, the effect of percent plant cover on predation rates differed between habitats. In the marsh edge habitat, predation rate was independent of percent cover, again suggesting that the presence of vegetation is more important than the density or small-scale (< 1 m⁻²) patchiness of vegetation, at least over the range of percent cover sampled in the marsh edge during this study (20–100% cover). In SAV, we observed a complex relationship between predation rate and percent cover that differed across the range of crab sizes tested in this study. Small juvenile blue crabs are able to move efficiently through even dense SAV beds, and thus benefit from increased protection from predators in areas of high percent cover. At larger sizes, crabs are likely unable to move as efficiently through dense (high percent cover) SAV and may thus have to spend time moving near the top of the canopy, resulting in higher predation rates relative to those observed in less-dense (low percent cover) SAV. Alternatively, it is possible that the larger crabs disturb the canopy to a greater extent in dense SAV, thus pinpointing their location to visual predators. Previous studies in seagrasses have found that juvenile

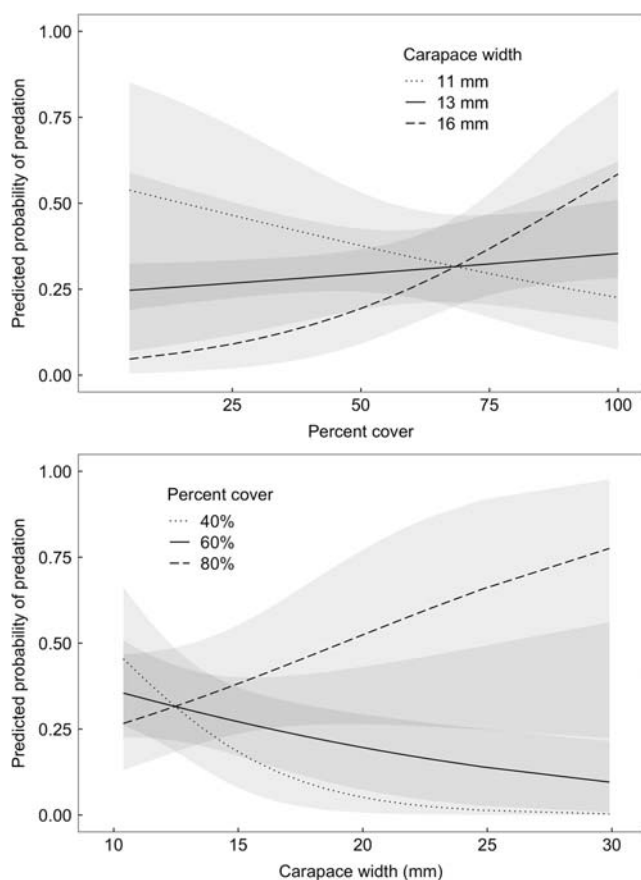


Fig. 5 Predicted probability of predation in SAV as a function of percent cover and carapace width. In each panel, the values of the grouping variable (CW in the upper panel, percent cover in the lower panel) represent the 1st quartile, median, and 3rd quartile of observed values

blue crab densities are positively related to seagrass percent cover (Ralph et al. 2013). The lack of an effect of SAV percent cover on juvenile crab densities observed here may reflect the greater structural complexity of the fresh and brackish water SAV species sampled, relative to most seagrasses (Hoyer et al. 1996; Larkum et al. 2006).

Similar to results observed for juvenile blue crabs, adult blue crab CPUE was independent of the level of marsh fragmentation, at least across the range of fragmentation conditions sampled in this study. We did, however, observe greater adult blue crab abundance and biomass in areas with SAV present compared with areas without SAV. Submerged aquatic vegetation offers greater prey availability, as densities of many organisms are higher in SAV than in adjacent bare sediment (Harrod 1964; Thayer et al. 1975; Heck and Wetstone 1977), so this difference likely represents a foraging effect, with blue crabs preferentially foraging in/around SAV beds. It should be noted, however, that the area of attraction of a baited blue crab pot (or any type of trap) is likely highly variable depending on a number of hydrographic and environmental parameters (e.g., McQuinn et al. 1988). Because the size and configuration of sampled SAV and bare sediment patches are unknown, it is possible that pots were attracting crabs from adjacent habitats. Differences in CPUE in crab pots between SAV and bare sediment areas must thus be interpreted with caution.

Landscape-Scale Implications of Marsh Fragmentation on Blue Crab Populations

Juvenile and adult blue crabs appear to respond similarly to a fragmenting marsh landscape. Neither adult CPUE nor juvenile density varied with marsh fragmentation, but abundances of both adult and juvenile crabs were higher in areas with SAV. The results from this study suggest that blue crab densities (at the local scale) may not be sensitive to larger-scale patterns of marsh fragmentation over the measured range of marsh fragmentation, but are instead sensitive to local-scale patterns of habitat availability, including the presence and type of vegetation present, supporting previous studies (Thomas and Zimmerman 1990; Lipcius et al. 2005). This implies that if the preferred habitats are available and abiotic conditions are suitable, crabs are likely to be present. Direct effects of marsh fragmentation may become apparent at greater levels of marsh fragmentation than were assessed here. It is possible that levels of marsh fragmentation in the three study sites sampled here have not reached the threshold where extreme fragmentation leads to habitat loss and small patches of marsh disappear. While marsh loss is a direct driver of marsh fragmentation, there is also a positive feedback mechanism, where fragmentation itself makes the landscape increasingly vulnerable to further marsh loss (Couvillion et al. 2016).

Although marsh fragmentation does not appear to directly affect blue crab abundance and density (over the scale of

fragmentation assessed in this study), 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. Initially, marsh fragmentation results in a transition to a more complex matrix of marsh and open water, with an increase in available edge habitat (Browder et al. 1985; Couvillion et al. 2016). Yet at higher levels of marsh fragmentation, the area of available marsh edge habitat will begin to decrease due to losses in marsh area (Browder et al. 1985) and the distance between patches will increase, isolating individual patches. Unless SAV is colonizing the newly created open water habitats, there will likely be decreases in blue crab populations, associated with the loss of marsh edge nursery habitat. Under such conditions, megalopae and early-stage juveniles will have to migrate farther to reach areas with suitable nursery habitat, and density-dependent effects such as cannibalism or reduced growth (Mansour and Lipcius 1991; Pile et al. 1996) could increase due to limited nursery habitat, at least until crabs reach a size where they are less vulnerable to predation and move into unstructured habitats (Pile et al. 1996). Under this scenario, any impacts on the blue crab fishery are likely to be observed after a time lag, as the remaining adult blue crabs are harvested and the recruitment of juveniles to limited nursery habitat declines. Within Louisiana coastal marshes, the dynamics of SAV communities and conditions under which SAV will colonize newly created open water areas is still being quantified. It is possible that increases in SAV area might buffer the effects of marsh loss by providing an alternative nursery habitat. Yet it is clear that without new habitat being created (either by SAV colonization or marsh expansion), blue crab populations and the blue crab fishery may experience an eventual decrease in yield if Louisiana's coastal marshes continue to fragment.

Future Research Directions

While this study found that marsh fragmentation does not appear to directly affect blue crab abundance and density, further research is needed to inform predictions of population-level responses of blue crabs to the continued fragmentation of coastal marshes. In particular, longitudinal studies observing changes over time during the process of fragmentation will provide critical insights. It is also important that future work considers the full range of fragmentation, from continuous marsh to extreme levels of fragmentation beyond those assessed here, to finally continuous open water, and also considers the likelihood of SAV colonization of newly created open water areas.

Acknowledgments The authors thank S. Cunningham, K. Ellsworth, A. Jerabek, A. Kemberling, L. Moss, and H. Olmi for assistance with field work, sample processing, and analyses.

Data Accessibility All data and model code are accessible at Dryad: <https://doi.org/10.5061/dryad.wwpzgm3>.

Funding Information This study was funded by the National Marine Fisheries Service award NA15NMF4270328 to TJBC, KMD, and MZD and an Early-Career Research Fellowship from the Gulf Research Program of the National Academies of Sciences, Engineering, and Medicine to MZD.

Compliance with Ethical Standards

Disclaimer The content is solely the responsibility of the authors and does not necessarily represent the official views of the Gulf Research Program of the National Academies of Sciences, Engineering, and Medicine.

References

- Aronson, R.B., K.L. Heck Jr., and J.F. Valentine. 2001. Measuring predation with tethering experiments. *Marine Ecology Progress Series* 214: 311–312.
- Bogaert, J., P. Van Hecke, D. Salvador-van Eysenrode, and I. Impens. 2000. Landscape fragmentation assessment using a single measure. *Wildlife Society Bulletin* 28: 875–881.
- Bourgeois, M., J. Marx, and K. Semon. 2014. *Louisiana blue crab fishery management plan*. Baton Rouge: Louisiana Department of Wildlife and Fisheries.
- Boylan, J.M., and E.L. Wenner. 1993. Settlement of brachyuran megalopae in a South Carolina, USA, estuary. *Marine Ecology Progress Series* 97: 237–246.
- Browder, J.A., H.A. Bartley, and K.S. Davis. 1985. A probabilistic model of the relationship between marshland/water interface and marsh disintegration. *Ecological Modelling* 29: 245–260.
- Canion, C.R., and K.L. Heck. 2009. Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. *Marine Ecology Progress Series* 393: 37–46.
- Cho, H.J., and M.A. Poirier. 2005. Seasonal growth and reproduction of *Ruppia maritima* L. s.l. in Lake Pontchartrain, Louisiana, USA. *Aquatic Botany* 81: 37–49. <https://doi.org/10.1016/j.aquabot.2004.10.002>.
- Cho, H. J., P. Biber, and C. Nica. 2009. The rise of *Ruppia* in seagrass beds: changes in coastal environment and research needs. In: *Handbook on environmental quality*, 333–47. Environmental Science, Engineering and Technology. Nova Science Publishers.
- Cho, H.J., A. Lu, P. Biber, and J.D. Caldwell. 2012. Aquatic plants of the Mississippi Coast. *Journal of the Mississippi Academy of Sciences* 57: 240–249.
- Coastal Protection and Restoration Authority (CPRA) of Louisiana. 2012. *Louisiana's comprehensive master plan for a sustainable coast*. Baton Rouge: Coastal Protection and Restoration Authority of Louisiana.
- Coastal Protection and Restoration Authority (CPRA) of Louisiana. 2018. *Coastwide reference monitoring system-wetlands monitoring data*. Retrieved from Coastal Information Management System (CIMS) database. <http://cims.coastal.louisiana.gov>.
- Coleman, James M., Oscar K. Huh, and DeWitt Braud Jr. 2008. Wetland loss in world deltas. *Journal of Coastal Research* 24: 1–14.
- Couvillion, B.R., and H. Beck. 2013. Marsh collapse thresholds for coastal Louisiana estimated using elevation and vegetation index data. *Journal of Coastal Research* 63: 58–67.
- Couvillion, B. R., J. A. Barras, G. D. Steyer, W. Sleavin, M. Fischer, H. Beck, N. Trahan, B. Griffin, and D. Heckman. 2011. Land area change in coastal Louisiana from 1932 to 2010. U.S. *Geological Survey Scientific Investigations Map 3164*.
- Couvillion, B.R., M.R. Fischer, H.J. Beck, and W.J. Sleavin. 2016. Spatial configuration trends in coastal Louisiana from 1985 to 2010. *Wetlands* 36: 347–359.
- Couvillion, B.R., H. Beck, D. Schoolmaster, M. Fischer. 2017. *Land area change in coastal Louisiana*. U.S. Geological Survey Scientific Investigations Map 3381, <https://doi.org/10.3133/sim3381>.
- Dahl, T.E., and S.M. Stedman. 2013. *Status and trends of wetlands in the coastal watersheds of the conterminous United States 2004 to 2009*. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service.
- Davidson, C. 1998. Issues in measuring landscape fragmentation. *Wildlife Society Bulletin* 26: 32–37.
- Day, J.W., G.P. Kemp, D.J. Reed, D.R. Cahoon, R.M. Boumans, J.M. Suhayda, and R. Gambrell. 2011. Vegetation death and rapid loss of surface elevation in two contrasting Mississippi delta salt marshes: the role of sedimentation, autocompaction and sea-level rise. *Ecological Engineering* 37: 229–240.
- Harrod, J.J. 1964. The distribution of invertebrates on submerged aquatic plants in a chalk stream. *Journal of Animal Ecology* 33: 335–348.
- Heck, K.L., and T.A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology* 53: 125–134. [https://doi.org/10.1016/0022-0981\(81\)90014-9](https://doi.org/10.1016/0022-0981(81)90014-9).
- Heck, K.L., and T.A. Thoman. 1984. The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. *Estuaries* 7: 70–92.
- Heck, K.L., and G.S. Wetstone. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *Journal of Biogeography* 4: 135–142.
- Heck, K.L., and K.A. Wilson. 1987. Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. *Journal of Experimental Marine Biology and Ecology* 107: 87–100.
- Hester, M.W., E.A. Spalding, and C.D. Franze. 2005. Biological resources of the Louisiana Coast: part 1. An overview of coastal plant communities of the Louisiana Gulf shoreline. *Journal of Coastal Research* 44: 134–145.
- Hillmann, E., K.E. DeMarco, and M. La Peyre. 2016. Establishing a baseline of estuarine submerged aquatic vegetation resources across salinity zones within coastal areas of the northern Gulf of Mexico. *Journal of the Southeastern Association of Fish and Wildlife Agencies* 3: 25–32.
- Hitch, A.T., K.M. Purcell, S.B. Martin, P.L. Klerks, and P.L. Leberg. 2011. Interactions of salinity, marsh fragmentation and submerged aquatic vegetation on resident nekton assemblages of coastal marsh ponds. *Estuaries and Coasts* 34: 653–662.
- Hovel, K.A., and R.N. Lipcius. 2002. Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance. *Journal of Experimental Marine Biology and Ecology* 271: 75–98.
- Hoyer, M.V., C. Morsburgh, K. Brown, and D. Canfield. 1996. *Florida freshwater plants: a handbook of common aquatic plants in Florida lakes*. Gainesville: University of Florida - Institute of Food and Agricultural Sciences.
- Jankowski, K.L., T.E. Tornqvist, and A.M. Fernandes. 2017. Vulnerability of Louisiana's coastal wetlands to present-day rates of relative sea-level rise. *Nature Communications* 8: 14792. <https://doi.org/10.1038/ncomms14792>.
- Jerabek, A., K.M. Darnell, C. Pellerin, and T.J.B. Carruthers. 2017. Use of marsh edge and submerged aquatic vegetation as habitat by fish and crustaceans in degrading Southern Louisiana coastal marshes. *Southeastern Geographer* 57: 212–230.
- La Peyre, M.K., and J. Gordon. 2012. Nekton density patterns and hurricane recovery in submerged aquatic vegetation, and along non-

- vegetated natural and created edge habitats. *Estuarine, Coastal and Shelf Science* 98: 108–118.
- Larkum, A.W.D., R.J. Orth, and C. Duarte. 2006. *Seagrasses: biology, ecology, and conservation*. Dordrecht: Springer Netherlands.
- Lipcius, R.N., R.D. Seitz, M.S. Seebo, and D. Colón-Carrión. 2005. Density, abundance and survival of the blue crab in seagrass and unstructured salt marsh nurseries of Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology* 319: 69–80.
- Lipcius, R.N., D.B. Eggleston, K.L. Heck, R.D. Seitz, and J. van Montfrans. 2007. Post-settlement abundance, survival, and growth of postlarvae and young juvenile blue crabs in nursery habitats. In *The blue crab, Callinectes sapidus*, ed. V.S. Kennedy and L.E. Cronin, 535–562. College Park: Maryland Sea Grant.
- MacRae, P., and J. Cowan. 2010. Habitat preferences of spotted seatrout, *Cynoscion nebulosus*, in coastal Louisiana: a step towards informing spatial management in estuarine ecosystems. *The Open Fish Science Journal* 3: 154–163.
- Mansour, R.A., and R.M. Lipcius. 1991. Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams. *Marine Ecology Progress Series* 72: 239–246.
- McQuinn, I.H., L. Gendron, and J.H. Himmelman. 1988. Area of attraction and effective area fished by a whelk (*Buccinum undatum*) trap under variable conditions. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 2054–2060.
- Minello, T.J., and L.P. Rozas. 2002. Nekton in Gulf Coast wetlands: fine-scale distributions, landscape patterns, and restoration implications. *Ecological Applications* 12: 441–455.
- Minello, T.J., K.W. Able, M.P. Weinstein, and C.G. Hays. 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth, and survival through meta-analysis. *Marine Ecology Progress Series* 246: 39–59.
- NMFS. 2016. *Fisheries of the United States, 2016*. Silver Spring: National Marine Fisheries Service.
- NMFS. 2017. *Annual commercial landing statistics*. National Marine Fisheries Service. http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html.
- Orth, R.J., and J. van Montfrans. 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Marine Ecology Progress Series* 41: 283–294.
- Pedersen, E.J., D.L. Miller, G.L. Simpson, and N. Ross. 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ* 7: e6876.
- Perkins-Visser, E., T.G. Wolcott, and D.L. Wolcott. 1996. Nursery role of seagrass beds: enhanced growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). *Journal of Experimental Marine Biology and Ecology* 198: 155–173.
- Perry, H., D.R. Johnson, K. Larsen, C. Trigg, and F. Vukovich. 2003. Blue crab larval dispersion and retention in the Mississippi Bight: testing the hypothesis. *Bulletin of Marine Science* 72: 331–346.
- Pile, A., R. Lipcius, J. Van Montfrans, and R. Orth. 1996. Density-dependent settler-recruit-juvenile relationships in blue crabs. *Ecological Monographs* 66: 277–300.
- Powell, A.N. 2006. Are Southern California's fragmented saltmarshes capable of sustaining endemic bird populations? *Studies in Avian Biology* 32: 198–204.
- R Core Team. 2019. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Rabalais, N.N., F.R. Burditt, L.D. Coen, B.E. Cole, C. Eleuterius, K.L. Heck, T.A. McTigue, S.G. Morgan, H.M. Perry, F.M. Truesdale, R.K. ZimmerFaust, and R.J. Zimmerman. 1995. Settlement of *Callinectes sapidus* megalopae on artificial collectors in four Gulf of Mexico estuaries. *Bulletin of Marine Science* 57: 855–876.
- Ralph, G.M., R.D. Seitz, R.J. Orth, K.E. Knick, and R.N. Lipcius. 2013. Broad-scale association between seagrass cover and juvenile blue crab density in Chesapeake Bay. *Marine Ecology Progress Series* 488: 51–63.
- Rozas, L.P., and T.J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries* 20: 199–213.
- Saunders, M.I., J. Leon, S.R. Phinn, D.P. Callaghan, K.R. O'Brien, C.M. Roelfsema, C.E. Lovelock, M.B. Lyons, and P.J. Mumby. 2013. Coastal retreat and improved water quality mitigate losses of seagrass from sea level rise. *Global Change Biology* 19 (8): 2569–2583.
- Scavia, D., J.C. Field, D.F. Boesch, R.W. Buddemeier, V. Burkett, D.R. Cayan, M. Fogarty, M.A. Harwell, R.W. Howarth, C. Mason, D.J. Reed, T.C. Royer, A.H. Sallenger, and J.G. Titus. 2002. Climate change impacts on U.S. coastal and marine ecosystems. *Estuaries* 25: 149–164.
- Strange, E.M., A. Shellenbarger Jones, C. Bosch, R. Jones, D. Kreeger, and J.G. Titus. 2008. Mid-Atlantic coastal habitats and environmental implications of sea level rise. Section 3. In *Background Documents Supporting Climate Change Science Program Synthesis and Assessment Product 4.1*, ed. J.G. Titus and E.M. Strange. Washington, D.C.: EPA 430R07004: U.S. EPA.
- Thayer, G.W., D.A. Wolfe, and R.B. Williams. 1975. The impact of man on seagrass systems. *American Scientist* 63: 288–296.
- Thomas, J.L., and R.J. Zimmerman. 1990. Abundance patterns of juvenile blue crabs (*Callinectes sapidus*) in nursery habitats of two Texas bays. *Bulletin of Marine Science* 46: 115–125.
- Turner, R.E., and Y.S. Rao. 1990. Relationships between wetland fragmentation and recent hydrologic changes in a deltaic coast. *Estuaries* 13: 272–281.
- USDA:FSA. 2015. 1-m resolution satellite orthoimagery. United States Department of Agriculture Farm Service Agency. Available: <https://gdg.sc.egov.usda.gov/GDGOrder.aspx>
- van Montfrans, J., C.H. Ryer, and R.J. Orth. 2003. Substrate selection by blue crab *Callinectes sapidus* megalopae and first juvenile instars. *Marine Ecology Progress Series* 260: 209–217.
- Wolcott, T.G., and A.H. Hines. 1990. Ultrasonic telemetry of small-scale movements and microhabitat selection by molting blue crab (*Callinectes sapidus*). *Bulletin of Marine Science* 46: 83–94.
- Zimmerman, R.J., T.J. Minello, and L.P. Rozas. 2000. Salt marsh linkages to productivity of penaeid shrimps and blue crabs in the Northern Gulf of Mexico. In *Concepts and controversies in tidal marsh ecology*, ed. M.P. Weinstein and D.A. Kreeger, 293–314. Springer Netherlands: Dordrecht.
- Zuur, A.F., A.A. Savaliev, and E.N. Ieno. 2015. *A beginner's guide to generalized additive mixed models with R*. Newburgh: Highland Statistics Ltd.