

Regional variation in seagrass complexity drives blue crab (*Callinectes sapidus*) mortality and growth across the northern Gulf of Mexico

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ABSTRACT: Seagrass meadows provide greater predator refuge and resource availability than unvegetated habitats and generally improve the survival and growth rates of associated animals. Few studies, however, have examined how these relationships might vary at a region-wide spatial scale. The blue crab (*Callinectes sapidus*) is a commercially important species that uses turtlegrass (*Thalassia testudinum*) habitats, but it is unclear if blue crab use of seagrass habitats varies across the northern Gulf of Mexico (GOM), USA. We conducted synoptic predation and growth experiments at six turtlegrass-dominated estuaries in the northern GOM to evaluate the role of seagrass structural complexity on juvenile (9.7–44 mm carapace width) blue crab mortality due to predation and growth. Relationships of blue crab mortality and growth rate with seagrass shoot density, canopy height, temperature, salinity, and seagrass leaf area index were evaluated using linear and generalized linear mixed effects models. Mortality rates due to predation (50 ± 9.6 [mean \pm SD] percent crabs eaten, $n = 291$) showed negative relationships with LAI across the northern GOM. Conversely, mean crab growth rate (0.52 ± 0.32 mm day⁻¹) was independent of seagrass shoot density or canopy height. We found that: 1) turtlegrass-dominated beds with a greater seagrass leaf area index provided more effective cover for juvenile blue crabs across the northern GOM, 2) blue crabs across multiple GOM estuaries responded similarly to changes in leaf area index, and 3) blue crab growth varied across the northern GOM and was likely dependent on regional factors unrelated to structural complexity.

Key words: habitat complexity, nursery hypothesis, seagrass, predation, blue crab, growth rate, turtlegrass, large-scale

1. INTRODUCTION

Habitat structure is an important driver of survival and growth in marine systems (Heck et al. 2003). Habitat complexity can be defined as the absolute abundance of all habitat structural components within a given habitat (McCoy & Bell 1991). Structurally complex habitats include reefs, marshes, macroalgae, and seagrass meadows, many of which function as nurseries for fish and invertebrate species, providing enhanced food and greater protection from predation than surrounding, unstructured habitats (Beck et al. 2001, Heck et al. 2003). Seagrasses in particular, provide critical nursery habitat for a diverse assemblage of commercially and recreationally important fish and invertebrates (Gillanders 2006). Plentiful food resources in seagrass habitats promote high growth rates (Bell & Pollard 1989, Heck et al. 1997) and 3-dimensional structure offers refuge from predation that can directly (Heck & Orth 2006) and indirectly (Fraser & Gilliam 1987) promote survival and growth rates of vulnerable juveniles.

The degree of protection provided by an environment is related to the complexity of the habitat (Heck & Crowder 1991, Heck & Orth 2006). At fine spatial scales (cm to m), nekton survival rates have been linked to variation in seagrass shoot density (Hovel & Lipcius 2002, Orth & van Montfrans 2002, Hovel 2003), surface area (Stoner 1982), and patch size (Hovel & Lipcius 2001, Hovel & Fonseca 2005). Likewise, nekton growth rate has been shown to vary with seagrass shoot density (Perkins-Visser et al. 1996, Spitzer et al. 2000).

Previous research in freshwater ecosystems indicates that changes in prey refuge availability and the outcome of predator-prey dynamics in structured systems is scale-dependent (Cooper et al. 1998). Because of differences in experimental scale and timing, however, few studies directly compare whether relationships between seagrass structure and nursery function are also scale-dependent (Gillanders 2006). McDonald et al. (2016) for example, compared

differences in seagrass features across the GOM and found spatial differences in seagrass morphology, growth, and reproduction that varied with environmental gradients of water temperature, salinity, and water clarity. However, whether such plasticity is associated with differences in nursery function or if nursery function varied at different spatial scales remains unclear. Understanding these relationships would allow resource managers to make decisions regarding the nursery value of their seascapes based on measurable, time-integrated attributes of seagrass habitats.

Further, a wide array of metrics are used to assess seagrass structural complexity (e.g., shoot density, leaf density, canopy height, leaf area index, aboveground biomass, and belowground biomass), which can complicate efforts to review and synthesize results from disparate studies (e.g., Mattila et al. 2008, Canion & Heck 2009, Hovel et al. 2016). Thus large-scale, synoptic studies incorporating a range of habitat complexity and environmental metrics are needed to improve our understanding of regional differences and drivers of nekton growth and survival in seagrass habitats.

Blue crabs are abundant inhabitants of seagrass and salt marsh throughout the western Atlantic and the GOM, where they support valuable commercial fisheries (NMFS 2021). Blue crab fisheries are managed as separate stocks by different states (VanderKoooy 2013), but it is unclear if interactions between crabs and seagrass differ across the region. Blue crab fisheries in the northern GOM have experienced a decline since the 1990s (NMFS 2021); this may be partially attributed to destructive hurricanes and anthropogenic events such as the *Deepwater Horizon* oil spill that closed harvests and potentially impacted stock production (VanderKoooy 2013), as well as the accelerating loss of seagrass nursery habitat in the GOM (Waycott et al.

2009). Juvenile blue crabs use seagrass as habitat, where predation is deterred (Orth & van Montfrans 2002, Hovel & Fonseca 2005) and food availability is high (Perkins-Visser et al. 1996), before moving into unstructured habitats such as salt and subtidal mud flats when they reach a size that reduces predation risk (Mense & Wenner 1989, Lipcius et al. 2005).

Blue crabs often use seagrass meadows dominated by turtlegrass (*Thalassia testudinum*), a sub-tropical and tropical seagrass species that in the US northern GOM occurs from the Laguna Madre to the Texas Coastal Bend, Texas; at the Chandeleur Islands, Louisiana; and along the Florida Gulf Coast. Throughout this range, turtlegrass exhibits high morphological, growth, and life-history plasticity (McDonald et al. 2016), which may affect its function as habitat for juvenile blue crabs. Previous work from Perkins-Visser et al. (1996) has demonstrated that juvenile blue crabs may experience higher growth rates in eelgrass (*Zostera marina*) beds compared to unstructured habitats due to increased food resources compared to bare sediment, but there is a lack of data available on relationships of juvenile blue crab growth to the structured habitat provided by other seagrass species such as turtlegrass. Changes in habitat complexity may alter prey availability, which in turn may impact blue crab growth and survival (Perkins-Visser et al. 1996).

Many studies that have evaluated seagrass complexity and blue crab mortality from predation (e.g. Hovel & Lipcius 2001, Hovel & Lipcius 2002, and Hovel 2003) have found a range of relationships depending on the focal seagrass metric and the study location. Hovel (2003) for example, reported that blue crab survival was negatively correlated with seagrass shoot biomass in North Carolina eelgrass meadows, whereas Hovel and Lipcius (2001) reported a positive correlation between crab survival and seagrass shoot density. These studies, however,

were conducted in eelgrass which has narrower leaves than turtlegrass, and thus results may not be directly applicable to the northern Gulf of Mexico. Additional research is needed to better understand how blue crab growth and predation differ along gradients of turtlegrass complexity (e.g., shoot density, canopy height). Given the ongoing decline of blue crab fisheries in the United States (NMFS 2021), it is imperative to understand what factors drive regional differences in blue crab growth and mortality so that managers can develop locally-targeted strategies to ensure future sustainable fisheries.

The purpose of this study was to examine regional patterns in drivers of blue crab (*Callinectes sapidus*) mortality and growth in seagrass habitats across the northern Gulf of Mexico (GOM). The objectives of this study were to (1) quantify regional differences in blue crab mortality due to predation and growth across the northern GOM, and (2) relate differences in crab mortality and growth to seagrass complexity and environmental variability. To address these questions, synchronous field experiments were conducted in turtlegrass-dominated seagrass beds across the northern GOM to quantify blue crab growth and predation. The following hypotheses were tested: (1) juvenile blue crab mortality due to predation is negatively related to seagrass shoot density, canopy height, leaf area index (LAI), and crab size because increasing seagrass complexity provides increased refuge from predators (Gillanders 2006) and larger crabs are better able to defend themselves from attack (Pile et al. 1996); (2) crab growth rate increases with increasing shoot density, canopy height, leaf area index (LAI), salinity, and mean water temperature throughout the growing season, because more complex seagrass habitat provides more protection from predators and more time for feeding on potential prey items, and juvenile

crab growth rate is coupled to temperature (Cunningham & Darnell 2015) and salinity (Guerin & Stickle 1997a).

2. MATERIALS AND METHODS

2.1. Study sites

Blue crab growth and predation risk experiments were conducted at six sites that span the distribution of turtlegrass across the northern GOM: two sites in Texas (LM: Lower Laguna Madre [26.14 N, -97.21 W] and CB: the Texas Coastal Bend [27.91 N, -97.12 W]), one site in Louisiana (LA: Chandeleur Islands [29.90 N, -88.83 W]), and three sites in Florida, (SG: St. George Sound [29.85 N, -84.61 W], CK: Cedar Key [29.08 N, -83.02 W], and CH: Charlotte Harbor [26.76 N, -82.12 W]) (Fig.1). These sites were chosen because they contain expansive turtlegrass meadows that exhibit a wide range of shoot densities and leaf morphologies (McDonald et al. 2016).

2.2. Predation experiments

A field experiment was conducted following Hovel and Lipcius (2002) to assess the role of turtlegrass structural complexity on crab mortality due to predation. Sampling stations at each of the six sites were selected using a stratified random sampling method in which a grid of tessellated hexagons was overlaid on the mapped extent of known seagrass cover at each site (Neckles et al. 2012, Wilson & Dunton 2012, Moore et al. 2014). Tessellated hexagon size varied between 500- to 750-m, on edge length depending on the site, to match the preexisting tessellated sampling design of Neckles et al. (2012). At each site, 10–15 hexagons with > 50%

turtlegrass cover were randomly selected and a random station was selected from the area within each hexagon to conduct experiments. In cases where no turtlegrass was found at a station or where stations were inaccessible, alternative hexagons were randomly selected and new stations randomly generated.

At each station in each site, 6–12 crabs were tethered for a total of 79–120 tethers per site (599 tethered crabs total). The number of crabs tethered at each station was based on crab availability at each site. All tethering experiments took place between 2 June and 20 July 2018. Crabs were tethered on multiple days at each site due to travel and tidal limitations and were spaced at least 2 m from each other, and from concurrent growth experiments. Juvenile crabs 9.7–38.8-mm carapace width (CW) were collected 24–96 h prior to the beginning of the experiment from seagrass habitat using trawl, benthic sled, throw trap, and dip net techniques, and transferred to the lab in aerated containers. To mitigate capture efficiency issues, all blue crabs used in both the growth and mortality experiments for CB, LM, and CH were collected at CB and then transported to their respective sites. A tether (75–100-cm long) of 20-lb test clear monofilament line was attached to each crab carapace using cyanoacrylate glue. Prior to placement in the field, blue crabs were acclimated to tethers for at least 24 h in aerated seawater. The free end of the tether was tied to a small PVC stake (3.3-cm diameter, 60-cm tall) that was inserted into the sediment until the top was flush with the sediment. Tethered blue crabs had the freedom to move within 1.5–2-m of the PVC stakes. Blue crabs were tethered at each station for ~24 h and then retrieved by hand. On retrieval, crabs were categorized as alive, molted (majority of carapace remaining on line), cut (knot was missing from end of line), or missing (no part of carapace remaining) following the categories of Hovel and Lipcius (2002). Previous field and

laboratory studies have indicated that crabs cannot easily escape from tethers, so it was assumed that all crabs missing from tethers after 24 h had been consumed by a predator (Hovel & Lipcius 2001, Hovel & Lipcius 2002).

Prior to blue crab tethering, seagrass structural complexity was measured near each tethering pole (6–12 measurements per station). Percent cover of seagrass by species and bare sediment were quantified in 1-m² PVC quadrats sectioned into 10-cm x 10-cm squares placed near the tethering area following methods from Belgrad et al. (2021). The presence of drift and attached macroalgae was also noted within each quadrat. Species-specific seagrass shoot counts were quantified in a randomly pre-selected cell within the quadrat, shoot density was calculated by multiplying species-specific percent cover and shoot count in that quadrat, and total seagrass shoot density was calculated by summing shoot density across all species present in the quadrat. If seagrass was not present in the pre-selected cell, shoot density was quantified in a second (or third) randomly pre-selected cell. In each quadrat, seagrass leaf length was also measured on three replicate plants of each species, and maximum canopy height was calculated as the maximum leaf length of all measured seagrass leaves.

At the end of the experiment, a single seagrass core (15-cm diameter, 10-cm deep) was collected in an undisturbed area near each tether. Cores were sieved in the field to retain the plants using either a 508- μ M sieve or a 2.5-mm mesh bag, stored on ice, and frozen for subsequent processing in the laboratory. Within each core, the number of seagrass shoots was counted for each species, leaves were gently scraped with a razor blade to remove epiphytes, and leaf lengths and widths were measured. Aboveground (leaves) and belowground (sheath, roots and rhizomes) material was separated visually based on the presence or absence of chlorophyll

(Duarte et al. 1998). Species-specific aboveground and belowground material, and total epiphytes for each core were dried separately in a drying oven at 60°C for at least 48 h, after which they were weighed. Leaf area index (LAI) was calculated as the total surface area of all leaves (length \times width \times 2 sides of the leaf) in a seagrass core and divided by the total surface area of the core (0.018 m²); seagrass shoot density (shoots m⁻²) was calculated as the total number of shoots in a core divided by core area; and epiphyte density (mg DW cm⁻²) was calculated as total dried epiphyte biomass divided by total seagrass leaf area in each core. Seagrass canopy height was calculated as the maximum seagrass leaf length in each core. All seagrass core morphology metrics were calculated separately for each seagrass species then combined for total seagrass complexity measurements. Water temperature, salinity, and dissolved oxygen (DO) were measured at the beginning of the experiment using a handheld multiparameter meter (YSI Inc.).

2.3. Growth experiments

To quantify relationships between blue crab growth and seagrass complexity, a field caging experiment was conducted at the same stations used for the tethering experiment. A single mesocosm was deployed at each station 24–48 h prior to the start of the experiment. Mesocosms were identical to those used by Rozas and Minello (2011) with cages consisting of a collapsible, bottomless cylinder (1.07-m diameter, 0.76-m tall) with 3.2 mm nylon mesh sides and top connected by two fiberglass rings, PVC pipe, and rebar (Fig. 2). A small closable sleeve (11.4-cm diameter, 15-cm long) sewn in the top allowed access to the inside of the mesocosm. During deployment, rebar was driven into the three PVC pipes supporting the mesocosm frame

to anchor it in place, and the bottom edge of the mesocosm was driven ~5 cm into the sediment using a rubber mallet to ensure there were no gaps between the cage and the sediment. Prior to crab deployment, visible macroalgae and fauna were removed from the cage by hand and dip nets.

Juvenile blue crabs (11–44 mm CW) were collected using the same collection methods as described for the predation experiments. To differentiate between individuals, crabs were tagged using visible implant elastomer tags (VIE tags; Northwest Marine Technologies) injected into the basal segments of the right or left swimming leg, the abdomen, or the body (Davis et al. 2004); each crab had a unique combination of tag placement location and color to enable identification of individuals. VIE tags do not adversely impact juvenile blue crab growth (Davis et al. 2004). After VIE implantation, all crabs were held overnight in the laboratory to monitor survival and tag retention prior to deployment.

Approximately 24 h after VIE tagging, tagged blue crabs were transported to the study site in aerated buckets and eight randomly selected individuals were placed in each mesocosm to start the experiment. This stocking density was chosen to standardize density across sites and ensure a high enough recovery rate to conduct statistical analysis. Blue crabs were not fed during the experiment, but instead relied on prey items within the mesocosm. Mesocosms were deployed for approximately 30 days to allow sufficient time for a blue crab to molt 1–2 times (Cunningham & Darnell 2015). Deployment was staggered across sites between 2 June and 19 July 2018; experiments were terminated between 27 June and 13 August 2018.

Environmental characteristics thought to influence blue crab growth were measured throughout the experiment. Water depth was measured using a pole marked in 5-cm increments,

and salinity, water temperature, and dissolved oxygen (DO) were measured using a handheld multiparameter meter (YSI Inc.) at the beginning, middle, and end of the experiment.

Additionally, five randomly assigned cages at each site were fitted with water temperature loggers (HOBO Pendant temperature/light 64 K Data logger, ONSET Computer Corporation) which recorded at one hour intervals.

At the end of the experiment, blue crabs were removed from each mesocosm. A 1-m x 1-m open-top, rectangular drop sampler frame lined with 0.32-cm mesh was placed around the mesocosm to ensure that crabs could not escape, and the mesocosm was then removed. The area enclosed by the drop sampler was swept with a bar seine and dip nets to collect all blue crabs within each mesocosm. Each crab was measured for carapace width (mm CW). Mean blue crab growth rate (mm day^{-1}) was calculated by subtracting initial carapace width from final carapace width for each individual, dividing by the duration (days) of the experiment, and averaging for all crabs retrieved from each mesocosm. Recovery rate was defined as the total number of crabs recovered in each mesocosm at the end of the experiment. Turtlegrass structural complexity was measured at each mesocosm at the end of the experiment using the same seagrass quadrat survey techniques described for the predation experiments. One seagrass core (15-cm diameter, 10-cm deep) was also collected from the periphery of the caged area and processed using the methods described above.

2.4. Analysis

To quantify the effect of different seagrass complexity measurements on blue crab mortality due to predation and growth, generalized linear mixed effects models (GLMMs) and

simple linear regression models (LMs) were used. Prior to linear regression analyses, violations of normality and homogeneity of variance for response variables were tested and corrected, when possible, using square root transformations.

To evaluate differences in sampling precision and to inform which sampling method was most appropriate to use in our statistical models, we plotted shoot density and canopy height against each other for each sampling method (quadrat and core) separately for each experiment (growth and predation) and conducted Pearson's correlation coefficient tests. Results from these correlation plots indicated that seagrass canopy height was similar between the quadrat and core metrics whereas shoot density tended to have larger shoot density ranges in the cores than the quadrats (see results section below for full description). Based on these preliminary results we decided to only include seagrass core metrics in our statistical models. Specific models were fitted to test the following hypotheses:

Hypothesis 1: Juvenile blue crab mortality due to predation will decrease with increasing seagrass complexity and crab size. A binomial GLMM model (logit link function) was fitted with crab mortality (categorical: consumed or not consumed) as the response variable and station as a random effect (categorical). Fixed effects included site (categorical), carapace width (continuous), seagrass maximum canopy height (continuous), shoot density (continuous), and seagrass LAI (continuous), with interaction terms for carapace width x site and carapace width x LAI.

Hypothesis 2: Juvenile blue crab growth rate will increase with increasing seagrass complexity, temperature, and salinity, and decrease with larger initial crab sizes and higher crab recovery rate. A linear model was fitted with the square root transformed mean crab growth rate

per mesocosm (continuous) as the response variable. Fixed effects included site (categorical), mean initial crab carapace width per cage (continuous), crab recovery rate (continuous), seagrass maximum canopy height (continuous), seagrass shoot density (continuous), seagrass LAI (continuous), salinity (continuous), and temperature (continuous), with an interaction term for starting carapace width x LAI. Crab recovery rate was included in the model to account for the potential of conspecific cannibalism occurring in mesocosms which could potentially increase blue crab growth rates (Hines & Ruiz 1995). We chose not to include dissolved oxygen as a predictor variable in the blue crab growth model as the dissolved oxygen variation across sites was minimal (see results section). To distinguish between site and temperature effects, we used the YSI-measured mean temperature values for the initial test, and to account for within-mesocosm temperature variability we reran the analysis using only mean temperature and crab growth data from mesocosms fitted with HOBO temperature loggers (n = 21).

For all analyses, continuous variables were first standardized following methods from Shakeri et al. (2020) by subtracting the mean from each observation and dividing by the standard deviation. Fixed effect *P*-values were calculated for GLMMs using type 2 likelihood ratio tests (LRTs) and for linear models using type 2 Analysis of Variance (ANOVA) tests. Tukey Honest Significant Difference (HSD) contrasts were conducted for significant main effects as post-hoc comparisons, when appropriate. All analyses were conducted in R v.4.0.3 (R Core Team 2020), using the *afex* (Singmann et al. 2015), *car* (Fox & Weisberg 2018), *multcomp* (Hothorn et al. 2008), *lmerTest* (Kuznetsova et al. 2017), and *lme4* (Bates et al. 2014) packages.

3. RESULTS

3.1 Environmental data

Environmental characteristics reflected regional variability across the northern GOM. During the tethering experiment, water temperatures ranged between 27.1 and 39.4 °C ($\bar{x} = 30.99$ °C), water depth ranged from 0.28 to 1.75 m ($\bar{x} = 1.02$ m), DO ranged between 2.5 and 14.5 mg L⁻¹ ($\bar{x} = 7.91$ mg L⁻¹), and salinity ranged between 10.53 and 40.1 ($\bar{x} = 30.29$, Table 1). Mean salinity was highest at LM and CB and lowest at CH (Table 1). Environmental characteristics measured during the growth experiment were similar to those reported for the predation experiments. During the crab growth experiment, water temperatures ranged between 24.2 °C and 40.1 °C ($\bar{x} = 30.24$ °C), water depth ranged between 0.5 and 1.4 m ($\bar{x} = 1.0270$ m), DO ranged between 4.4 and 12.4 mg L⁻¹ ($\bar{x} = 7.46$ mg L⁻¹), and salinity varied between 13.7 and 37.8 ($\bar{x} = 29.22$) (Table 2). Water temperature (30.24 ± 1.59 °C [mean \pm SD]) recorded by the HOBO loggers was similar across all sites but slightly higher at CH (Table 2).

Seagrass structural complexity metrics, as measured in the tethering experiment, varied across sites (Table S.1, Table S.2). Sites were dominated by turtlegrass, but also included shoal grass (*Halodule wrightii*), and manatee grass (*Syringodium filiforme*). Canopy heights tended to be lower at LM compared to other sites except CH, regardless of sampling method (quadrat or core) or experiment (predation or growth), and LAI was similar across sites but more variable and higher on average in the western GOM (LM and CB) than in the eastern GOM (Fig. 3, Fig. 4, Table S.3, and Table S.4). Seagrass shoot density was strongly correlated between quadrat and core sampling methodologies for both the predation (DF = 569, $r = 0.62$; $P < 0.01$) and growth (DF = 62, $r = 0.83$, $p < 0.01$) experiments (Fig. 5c and Fig. 5d), but seagrass canopy height was not for either the predation (DF = 569, $r = 0.14$, $P < 0.01$) or growth (DF = 62, $r = 0.28$, $P =$

0.02) experiments (Fig. 5a and Fig. 5b). Seagrass shoot density measurements tended to be higher in the cores than in the quadrats (Fig. 5).

3.2. Predation experiments

A total of 599 tethers were deployed and 594 tethers were successfully recovered. Of the recovered tethers, 21 tethers were removed from analysis because the tether line was cut during deployment ($n = 12$) or the crabs molted during the experiment ($n = 9$) resulting in 573 tethers being included in the analysis (Table 3). Tethered crabs ranged between 9.7 and 38.8 mm CW and had similar size ranges across sites (Table 3). Predation rate varied significantly with crab carapace width (Type II LRT, $DF = 10$, $\chi^2 = 16.69$, $P < 0.001$) and LAI ($DF = 10$, $\chi^2 = 11.91$, $P < 0.001$), with the likelihood of predation decreasing with increasing carapace width (mean $m = -0.86$, Fig. 6) and LAI (mean $m = -0.51$, Fig. 7). Predation rate did not differ significantly among sites ($DF = 5$, $\chi^2 = 10.04$, $P = 0.07$), with shoot density ($DF = 10$, $\chi^2 = 0.66$, $P = 0.41$), or with canopy height ($DF = 10$, $\chi^2 = 0.43$, $P = 0.51$), and there was no site \times carapace width interaction ($DF = 12$, $\chi^2 = 7.91$, $P = 0.16$) or LAI \times carapace width interaction ($DF = 16$, $\chi^2 = 0.3$, $P = 0.54$).

3.3 Growth experiments

A total of 125 blue crabs were recovered from mesocosms across all sites, representing an 18% total crab recovery rate (range: 14.25 – 22.50%, total stocked crabs = 698) with 64% of all mesocosms ($n = 64$) having at least one crab recovered. Mean duration of mesocosm growth experiments was 26.9 ± 0.63 SD days, and mean crab growth rate was 0.5 mm day^{-1} (Table 4).

There was a significant effect of site ($F_{(5,50)} = 6.02, P < 0.001$), and crab starting size ($F_{(1,50)} = 5.54, P = 0.02$) on crab growth, but no effect of crab recovery rate ($F_{(1,50)} = 0.16, P = 0.69$), seagrass shoot density ($F_{(1,50)} = 0.55, P = 0.46$), canopy height ($F_{(1,50)} = 0.21, P = 0.65$), LAI ($F_{(1,50)} = 1.19, P = 0.28$), salinity ($F_{(1,50)} = 2.38, P = 0.13$), or temperature ($F_{(1,50)} = 0.64, P = 0.43$), and there was no LAI and carapace width ($F_{(1,50)} = 2.00, P = 0.16$) interaction. Tukey pairwise comparisons indicated that mean crab growth rate was higher at CH than at all other sites (Table 5), and reanalysis of the model after removing the single crab with a very high growth rate at CH (1.88 mm d^{-1}), indicated that this difference was only statistically significant for crabs at the CH and LM sites (Table S.5). Crabs at all sites except CH had similar growth rates (Fig. 8, Table 5). Reanalysis using the HOBO logger data to account for within-mesocosm temperature variability indicated no effect of temperature on blue crab growth ($F_{(1,12)} = 0.10, P = 0.76$).

4. DISCUSSION

We examined regional differences in juvenile blue crab mortality due to predation and measured crab growth across six estuaries in the northern GOM. We related spatial patterns in mortality and growth to regional differences in seagrass complexity and environmental variability. Our findings demonstrate the value of conducting synchronous studies to reveal regional-specific drivers of nekton mortality and growth across broad spatial scales. Crab mortality due to predation was similar across estuaries and exhibited a strong association with changes in seagrass LAI and crab carapace width; however, crab growth rate tended to be highest

at our most eastern site, Charlotte Harbor, but exhibited no relationship with seagrass complexity metrics.

Juvenile blue crab mortality due to predation showed an inverse relationship with seagrass LAI that was consistent in shape and direction across sites, despite LAI being generally higher at estuaries in the western GOM than in the east, suggesting a Gulf-wide pattern rather than a localized trend. Seagrass habitats with higher LAI may increase refuge availability for blue crabs from predators by providing more leaf surface area per substrate that can inhibit predator movement and reduce prey visibility, mechanisms that have been reported elsewhere for a variety of small aquatic organisms, (e.g., Stoner 1982, Hovel 2003, Yeager & Hovel 2017, Shakeri et al. 2020). Stoner (1982) for example, reported that predation on the amphipods *Cymadusa compta* and *Melita elongate* by pinfish *Lagodon rhomboides* decreased with increasing seagrass total leaf surface area.

Remarkably, the relationship observed here between blue crab predation and LAI was evident across estuaries that support diverse assemblages of blue crab predators, including numerous fish and invertebrate species (Guillory & Elliot 2001). This suggests that predatory rates on blue crabs may be similarly impacted by changes in seagrass habitat structure in a wide variety of habitats across the northern GOM and illustrates the role of fine-scale plant metrics in driving important large-scale ecological processes. While a number of studies have evaluated the effect of seagrass LAI on blue crab mortality due to predation, most studies measure seagrass complexity using metrics such as canopy height, shoot density, and habitat complexity (Hovel & Lipcius 2001, Hovel 2003, Heck & Orth 2006). Thus additional research is needed to better understand the specific mechanisms driving the observed Gulf-wide trend. We found that LAI is

a useful, albeit currently underutilized, habitat quality metric that managers should consider when monitoring the refuge provided by seagrass.

In this study, we focused specifically on turtlegrass-dominated meadows, however it is important to note that the relationship between juvenile blue crab mortality and LAI may vary in seagrass beds dominated by other seagrass species exhibiting different leaf and canopy structures. Stoner (1982) reported that monospecific beds of shoal grass (*Halodule wrightii*) provided less protection for amphipods than either turtlegrass or manatee grass (*Syringodium filiforme*) beds, despite shoal grass having a higher surface to biomass ratio. Stoner attributed this species-specific difference to a mismatch between the size of the amphipod prey and the structure it was using as refuge; the narrow (< 1 mm wide) shoal grass leaves provided less protection for the amphipods than the wider turtlegrass leaves (> 6 mm) or the cylindrical manatee grass leaves (Stoner 1982). Turtlegrass is considered a climax seagrass species and an indicator of ecosystem stability (Williams 1990). Shifts in seagrass species composition are occurring across the northern GOM due to changes in water quality, storm events, and sea level rise with regional replacement of turtlegrass by earlier successional and “boom and bust” species such as shoal grass and widgeon grass (Cho et al. 2009). It is unknown, however, if blue crabs exhibit seagrass species-specific relationships to leaf area or if shifts in seagrass species compositions may alter protection provided to juvenile blue crabs in the northern GOM.

Although there was a clear relationship between crab mortality and LAI, there was no relationship between, crab mortality and shoot density. This contrasts with numerous previous studies that reported relationships – either negative or positive – between seagrass shoot density and crab mortality due to predation (Hovel & Lipcius 2001, Hovel & Lipcius 2002, Hovel 2003).

Our study was conducted in seagrass beds with high turtlegrass cover (> 50% cover) during the middle of the seagrass growing season in the northern GOM, so our results are biased for higher turtlegrass shoot densities than may have been found in studies of seagrass complexity that took place over multiple seasons (e.g., Hall et al. 1999). If predation on blue crabs follows the threshold model of seagrass density proposed by Nelson and Bonsdorff (1990) and supported by experimental work from Bartholomew et al. (2000) and Canion and Heck (2009), then it is possible that the high shoot densities observed in the current study were above a critical threshold and thus shoot density effects on mortality were not evident.

In our study, crab mortality was also affected by the size of the crab, where predation was lower on larger crabs than smaller crabs. Size-dependent predation effects are common in tethering studies (e.g. Hines et al. 1995, Heck & Spitzer 2001, Shakeri et al. 2020) as larger juvenile crabs are better able to defend themselves from potential predators or they may reach a size greater than the gape size of predators (Pile et al. 1996). Conversely, larger crabs may outgrow the protective function of the habitat, as their body size may no longer match the interstitial space available between the seagrass leaves (Bartholomew 2002), or they may be unable to move as efficiently through dense seagrass leaves (Shakeri et al. 2020). Additionally, blue crab growth rates in this study may be biased by the low crab recovery rates at each site (2 ± 1 crabs per mesocosm), which are likely related to high rates of conspecific cannibalism among crabs in each cage (Hines & Ruiz 1995, Moksnes et al. 1997). Cannibalism may lead to reduced resource competition and increased growth rates for the victorious individuals which can positively bias the average growth rates for each estuary.

Juvenile blue crab growth rate, unlike mortality, was independent of seagrass complexity, and water quality parameters, but varied among estuaries across the northern GOM, suggesting that factors other than habitat complexity, salinity, and water temperature may drive blue crab growth rates. Previous studies have found positive relationships between the growth rate of juvenile blue crabs and water temperature (Tagatz 1968, Seitz et al. 2005, Cunningham & Darnell 2015). In the current study, however, temperature variability between sites was low across the study period and water temperatures fell within blue crab thermal optima (Tagatz 1969), so it is unsurprising that we did not observe a clear relationship between crab growth rate and temperature.

Previous studies have found that the effect of salinity on blue crab growth rate is more variable and indirect than temperature (Cadman & Weinstein 1988, Guerin & Stickle 1997a, Guerin & Stickle 1997b). Some studies have indicated that crab growth rate may be positively associated with salinity (Cadman & Weinstein 1988, Guerin & Stickle 1997a) because of lower osmoregulatory costs at higher salinities (Guerin & Stickle 1997a, Guerin & Stickle 1997b), whereas other studies report that lower salinity habitats (0–20) in river-dominated systems may compensate for metabolic demand with greater input of labile organic matter and prey resources (Posey et al. 2005). In the present study, the site with the lowest salinity (Charlotte Harbor, 20.18 ± 5.5) had the highest growth rate (0.92 ± 0.39 mm day⁻¹) and the site with the highest salinity (Laguna Madre, 36.88 ± 0.44) had the lowest growth rate (0.27 ± 0.13 mm day⁻¹), however there was no significant effect of salinity on crab growth, suggesting that other factors, such as prey abundance may be driving the observed patterns.

Blue crabs are opportunistic scavengers that feed on a wide variety of epibenthic invertebrates, detrital matter, plant material, and small fish (Hines 2007), and the diet of blue crabs may vary spatially within (Laughlin 1982, Mansour 1992) and across estuarine systems (Stoner & Buchanan 1990, Stehlik et al. 2004). Abundance and quality of food can influence crab growth rate (Seitz et al. 2005) as well as physiological condition, and behavior (Belgrad & Griffen 2016). In the current study differences in potential prey abundance at each site may have contributed to differences in crab growth. Recent work from Hayes (2021), has indicated that turtlegrass-dominated beds in Charlotte Harbor support higher densities of palaemonidae shrimp (a common blue crab prey item) compared to turtlegrass-dominated beds in Laguna Madre (CH: 413.1 ind⁻¹ m⁻², LM: 10.9 ind⁻¹ m⁻²), suggesting that crabs in Charlotte Harbor may have more access to more abundant food sources. In this study, however, we did not quantify differences in food availability between sites or mesocosms or relationships between habitat complexity and food availability. We suggest that future studies investigate the quantity and quality of prey availability to juvenile blue crabs in turtlegrass-dominated systems and the relationship between habitat complexity, food availability, and crab growth.

This study examined regional differences in juvenile blue crab mortality due to predation and growth across six estuaries in the northern GOM and related differences in mortality and growth to regional differences in seagrass complexity and environmental variability. We identified consistent relationships between blue crab mortality and seagrass LAI across the northern Gulf of Mexico. Turtlegrass-dominated seagrass beds with greater LAI provided more effective cover for juvenile blue crabs. Our results also indicate that blue crab growth is variable across systems and is likely dependent on factors other than seagrass complexity, such as prey

availability. This study illustrates the value of conducting synchronous field-based experiments across broad spatial scales to identify regional patterns and the influence of regional versus local drivers.

Acknowledgements. We thank all the graduate students, post-docs, technicians, research scientists, lab managers, and undergraduate students who aided in the field and lab, especially Samantha Smith and Dr. Jessica Lunt. We also thank Jennifer Doerr for providing the mesocosms for the crab experiments. This paper is a result of research funded by the National Oceanic and Atmospheric Administration's RESTORE Science Program under award # NA17NOS4510093 to The University of Southern Mississippi, Dauphin Island Sea Lab, University of Florida, and Florida Fish and Wildlife Conservation Commission.

LITERATURE CITED

- Bartholomew A (2002) Total cover and cover quality: predicted and actual effects on a predator's foraging success. *Marine Ecology Progress Series* 227:1-9
- Bartholomew A, Diaz RJ, Cicchetti G (2000) New dimensionless indices of structural habitat complexity: predicted and actual effects on a predator's foraging success. *Marine Ecology Progress Series* 206:45-58
- Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1-48
- Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51:633-641
- Belgrad BA, Correia KM, Darnell KM, Darnell MZ, Hayes CT, Hall MO, Furman BT, Martin CW, Smee DL (2021) Environmental drivers of seagrass-associated nekton abundance across the northern Gulf of Mexico. *Estuaries and Coasts*, <https://doi.org/10.1007/s12237-021-00927-0>
- Belgrad BA, Griffen BD (2016) The influence of diet composition on fitness of the blue crab, *Callinectes sapidus*. *PloS one* 11:e0145481
- Bell JD, Pollard DA (1989) Ecology of fish assemblages and fisheries associated with seagrasses. In: Mcomb AJ, Larkum AWD, Shepherd SA (eds) *Biology of Seagrasses: An Australian Perspective*. Elsevier, Amsterdam, pp. 536-564

- Cadman LR, Weinstein MP (1988) Effects of temperature and salinity on the growth of laboratory-reared juvenile blue crabs *Callinectes sapidus* Rathbun. *Journal of Experimental Marine Biology and Ecology* 121:193-207
- Canion CR, Heck KL (2009) Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. *Marine Ecology Progress Series* 393:37-46
- Cho HJ, Biber P, Nica C (2009) The rise of *Ruppia* in seagrass beds: changes in coastal environment and research needs. In: Drury E, Pridgen T (eds) *Handbook on environmental quality*. Nova Science, New York, pp. 1-15
- Cooper SD, Diehl S, Kratz K, Sarnelle O (1998) Implications of scale for patterns and processes in stream ecology. *Australian Journal of Ecology* 23:27-40
- Cunningham SR, Darnell MZ (2015) Temperature-dependent growth and molting in early juvenile blue crabs *Callinectes sapidus*. *Journal of Shellfish Research* 34:505-510
- Davis JLD, Young-Williams AC, Hines AH, Zmora O (2004) Comparing two types of internal tags in juvenile blue crabs. *Fisheries Research* 67:265-274
- Duarte CM, Merino M, Agawin NS, Uri J, Fortes MD, Gallegos ME, Marbá N, Hemminga MA (1998) Root production and belowground seagrass biomass. *Marine Ecology Progress Series* 171:97-108
- Fox J, Weisberg S (2018) *An R companion to applied regression*. Sage publications, Thousand Oaks CA
- Fraser DF, Gilliam JF (1987) Feeding under predation hazard: response of the guppy and *Hart's rivulus* from sites with contrasting predation hazard. *Behavioral Ecology and Sociobiology* 21:203-209

- Gillanders BM (2006) Seagrasses, fish, and fisheries. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrasses: Biology, Ecology, and Conservation. Springer, Dordrecht, Netherlands, pp. 503-536
- Guerin J, Stickle W (1997a) Effect of salinity on survival and bioenergetics of juvenile lesser blue crabs, *Callinectes similis*. Marine Biology 129:63-69
- Guerin JL, Stickle WB (1997b) A comparative study of two sympatric species within the genus *Callinectes*: osmoregulation, long-term acclimation to salinity and the effects of salinity on growth and moulting. Journal of Experimental Marine Biology and Ecology 218:165-186
- Guillory V, Elliot M (2001) A review of blue crab predators. Proceedings of the Blue Crab Mortality Symposium Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi
- Hall MO, Durako MJ, Fourqurean JW, Zieman JC (1999) Decadal changes in seagrass distribution and abundance in Florida Bay. Estuaries 22:445-459
- Hayes C (2021) Patterns of Habitat Use and Trophic Structure in Turtle Grass (*Thalassia testudinum*)-Dominated Systems across the Northern Gulf of Mexico. PhD dissertation, The University of Southern Mississippi, Hattiesburg, MS
- Heck Jr KL, Spitzer PM (2001) Post settlement mortality of juvenile blue crabs: patterns and processes. In: Guilroy V, Perry HM (eds). Proc Blue Crab Mortality Symposium, Lafayette, LA
- Heck K, Nadeau D, Thomas R (1997) The nursery role of seagrass beds. Gulf of Mexico Science 15:50-54

- Heck KL, Crowder LB (1991) Habitat structure and predator—prey interactions in vegetated aquatic systems. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat Structure Population and Community Biology Series*, vol 8. Springer, Dordrecht, Netherlands
- Heck KL, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253:123-136
- Heck KL, Orth RJ (2006) Predation in Seagrass Beds. In: Larkum AWD, Orth RJ, Duarte CM (eds) *Seagrasses: Biology, Ecology, and Conservation*. Springer, Dordrecht, Netherlands, pp. 537-550
- Hines AH (2007) Ecology of juvenile and adult blue crabs. In: Kennedy VS, Cronin LE (eds) *The Blue Crab: Callinectes sapidus*. Maryland Sea Grant College College Park, Maryland, pp. 565-630
- Hines AH, Ruiz GM (1995) Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. *Bulletin of Marine Science* 57:884-901
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical Journal: Journal of Mathematical Methods in Biosciences* 50:346-363
- Hovel KA (2003) Habitat fragmentation in marine landscapes: relative effects of habitat cover and configuration on juvenile crab survival in California and North Carolina seagrass beds. *Biological Conservation* 110:401-412
- Hovel KA, Fonseca MS (2005) Influence of seagrass landscape structure on the juvenile blue crab habitat-survival function. *Marine Ecology Progress Series* 300:179-191
- Hovel KA, Lipcius RN (2001) Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. *Ecology* 82:1814-1829

- Hovel KA, Lipcius RN (2002) Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance. *Journal of Experimental Marine Biology and Ecology* 271:75-98
- Hovel KA, Warneke AM, Virtue-Hilborn SP, Sanchez AE (2016) Mesopredator foraging success in eelgrass (*Zostera marina* L.): Relative effects of epiphytes, shoot density, and prey abundance. *Journal of Experimental Marine Biology and Ecology* 474:142-147
- Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software* 82:1 - 26
- Laughlin RA (1982) Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. *Bulletin of Marine Science* 32:807-822
- Lipcius RN, Seitz RD, Seebo MS, Colón-Carrión D (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
- Mansour R (1992) Foraging ecology of the blue crab in lower Chesapeake Bay. PhD dissertation, College of William and Mary Williamsburg, VA
- Mattila J, Heck KL, Jr., Millstein E, Miller E, Gustafsson C, Williams S, Byron D (2008) Increased habitat structure does not always provide increased refuge from predation. *Marine Ecology Progress Series* 361:15-20
- McCoy ED, Bell SS (1991) Habitat structure: The evolution and diversification of a complex topic. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat Structure: The Physical Arrangement of Objects in Space*. Springer, Netherlands, Dordrecht
- McDonald AM, Prado P, Heck KL, Fourqurean JW, Frankovich TA, Dunton KH, Cebrian J (2016) Seagrass growth, reproductive, and morphological plasticity across environmental gradients over a large spatial scale. *Aquatic Botany* 134:87-96

- Mense DJ, Wenner EL (1989) Distribution and abundance of early life history stages of the blue crab, *Callinectes sapidus*, in tidal marsh creeks near Charleston, South Carolina. *Estuaries* 12:157-168
- Moksnes PO, Lipcius RN, Pihl L, van Montfrans J (1997) Cannibal–prey dynamics in young juveniles and postlarvae of the blue crab. *Journal of Experimental Marine Biology and Ecology* 215:157-187
- Moore LJ, Patsch K, List JH, Williams SJ (2014) The potential for sea-level-rise-induced barrier island loss: insights from the Chandeleur Islands, Louisiana, USA. *Marine Geology* 355:244-259
- Neckles H, Kopp B, Peterson B, Pooler P (2012) Integrating scales of seagrass monitoring to meet conservation needs. *Estuaries and Coasts* 35:23-46
- Nelson WG, Bonsdorff E (1990) Fish predation and habitat complexity: are complexity thresholds real? *Journal of Experimental Marine Biology and Ecology* 141:183-194
- NMFS (2021) National Marine Fisheries Service Annual Landing Statistics. www.st.nmfs.noaa.gov (accessed 23 July 2021)
- Orth RJ, van Montfrans J (2002) Habitat quality and prey size as determinants of survival in post-larval and early juvenile instars of the blue crab *Callinectes sapidus*. *Marine Ecology Progress Series* 231:205-213
- Perkins-Visser E, Wolcott TG, Wolcott DL (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
- Pile AJ, Lipcius RN, van Montfrans J, Orth RJ (1996) Density-dependent settler-recruit-juvenile relationships in blue crabs. *Ecological Monographs* 66:277-300

- Posey MH, Alphin TD, Harwell H, Allen B (2005) Importance of low salinity areas for juvenile blue crabs, *Callinectes sapidus* Rathbun, in river-dominated estuaries of southeastern United States. *Journal of Experimental Marine Biology and Ecology* 319:81-100
- R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rozas LP, Minello TJ (2011) Variation in penaeid shrimp growth rates along an estuarine salinity gradient: implications for managing river diversions. *Journal of Experimental Marine Biology and Ecology* 397:196-207
- Seitz RD, Lipcius RN, Seebo MS (2005) Food availability and growth of the blue crab in seagrass and unvegetated nurseries of Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology* 319:57-68
- Shakeri LM, Darnell KM, Carruthers TJB, Darnell MZ (2020) Blue crab abundance and survival in a fragmenting coastal marsh system. *Estuaries and Coasts* 43:1545-1555
- Singmann H, Bolker B, Westfall J, Aust F, Ben-Shachar MS (2015) Afex: analysis of factorial experiments. R package version 013–145
- Spitzer PM, Mattila J, Heck KL (2000) The effects of vegetation density on the relative growth rates of juvenile pinfish, *Lagodon rhomboides* (Linnaeus), in Big Lagoon, Florida. *Journal of Experimental Marine Biology and Ecology* 244:67-86
- Stehlik LL, Pikanowski RA, McMillan DG (2004) The Hudson-Raritan Estuary as a crossroads for distribution of blue (*Callinectes sapidus*), lady (*Ovalipes ocellatus*), and Atlantic rock (*Cancer irroratus*) crabs. *Fishery Bulletin* 102:693-710

- Stoner AW (1982) The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 58:271-284
- Stoner AW, Buchanan BA (1990) Ontogeny and overlap in the diets of four tropical *Callinectes* species. *Bulletin of Marine Science* 46:3-12
- Tagatz ME (1968) Growth of juvenile blue crabs, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fishery Bulletin* 67:281-288
- Tagatz ME (1969) Some relations of temperature acclimation and salinity to thermal tolerance of the blue crab, *Callinectes sapidus*. *Transactions of the American Fisheries Society* 98:713-716
- VanderKooy KE (2013) Gulf of Mexico blue crab stock assesment report. Gulf States Marine Fisheries Commission, Ocean Springs, MS,
<https://www.gsmfc.org/publications/GSMFC%20Number%20215.pdf>
- Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* 106:12377-12381
- Williams SL (1990) Experimental Studies of Caribbean Seagrass Bed Development. *Ecological Monographs* 60:449-469
- Wilson CJ, Dunton KH (2012) Assessment of seagrass habitat quality and plant physiological condition in Texas coastal waters. Coastal Bend Bays and Estuaries Program, Corpus Christi, Texas,
<http://texasseagrass.org/doc/Final%20Seagrass%20Report%20Tier%20202%202012.pdf>

TABLES

Table 1. Environmental characteristics for tether experiments across the northern GOM.

Site	No. Tethers	Depth (cm)	Temp (°C)	Salinity	DO (mg L ⁻¹)
		Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
L	120	99.55 ± 27.95	29.72 ± 1.11	38.72 ± 0.7	7.77 ± 2.44
M					
CB	96	74.66 ± 21.53	30.94 ± 2.22	37.87 ± 0.34	8.19 ± 2.57
LA	78	88.59 ± 16.44	30.7 ± 1.14	29.77 ± 2.68	7.53 ± 2.79
SG	100	126.86 ± 20.92	31.12 ± 0.54	29.28 ± 1.42	8.66 ± 1.87
C	100	109.4 ± 34.62	30.49 ± 1.59	23.33 ± 4.89	6.78 ± 1.6
K					
C	100	111.22 ± 23.07	33.18 ± 1.06	20.64 ± 6.16	8.53 ± 1.71
H					

Sites: (LM) Laguna Madre, Texas; (CB) Coastal Bend, Texas; (LA), Chandeleur Islands, Louisiana; (SG) St. George Sound, Florida; (CK) Cedar Key, Florida; and (CH) Charlotte Harbor, Florida.

Table 2. Environmental characteristics for crab growth experiments across the northern GOM.

Temperature was measured from continuous water temperature loggers (HOBOs) at each site.

Site	No. Cages	Depth (cm)	Temp (°C)	Salinity	DO (mg L ⁻¹)
		Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
L	13	108.67 ± 27.34	29.88 ± 1.52	36.88 ± 0.44	7.06 ± 1.14
M					
CB	13	88.87 ± 20.39	29.76 ± 1.60	34.52 ± 1.35	9.74 ± 1.65
LA	9	97.56 ± 9.04	30.59 ± 1.76	25.92 ± 0.38	8.71 ± 1.44
SG	8	117 ± 13.61	30.19 ± 1.46	29.73 ± 2.39	5.92 ± 0.78
CK	11	116.55 ± 6.64	30.08 ± 1.64	24.42 ± 2.6	6.45 ± 1.16
CH	10	90.85 ± 13.74	30.76 ± 1.26	20.18 ± 5.5	6.26 ± 1.01

Sites: (LM) Laguna Madre, Texas; (CB) Coastal Bend, Texas; (LA), Chandeleur Islands, Louisiana; (SG) St. George Sound, Florida; (CK) Cedar Key, Florida; and (CH) Charlotte Harbor, Florida.

Table 3. Results of tethering experiment evaluating differences in crab predation for six sites across the northern GOM. Predation rate is calculated as the total number of crabs consumed divided by the total number of crabs minus the number of crabs molted and crabs with cut tether lines.

Site	Total crabs	Crab size (CW) Mean \pm SD	No. crabs consumed	No. crabs alive	No. crabs molted	No. crabs cut line	Predation rate (%)
LM	120	19.77 \pm 5.16	55	64	0	1	46.22
CB	96	21.41 \pm 5.00	37	58	1	0	38.95
LA	78	17.13 \pm 5.14	36	38	0	4	48.65
SG	100	23.76 \pm 4.70	56	37	6	1	60.22
CK	100	23.34 \pm 5.17	41	55	2	2	42.71
CH	100	21.36 \pm 3.88	61	35	0	4	63.54

Sites: (LM) Laguna Madre, Texas; (CB) Coastal Bend, Texas; (LA), Chandeleur Islands, Louisiana; (SG) St. George Sound, Florida; (CK) Cedar Key, Florida; and (CH) Charlotte Harbor, Florida.

Table 4. Total crabs recovered in blue crab growth experiments, crab growth rate (mean \pm 1 SD), mean change in carapace width (mm CW), and mean experiment time (days) for six sites across the northern GOM.

Site	Total crabs	Crabs recovered	Recovery rate (%)	Growth rate (mm day ⁻¹) Mean \pm SD	Change CW (mm) Mean \pm SD	Exp time (days) Mean \pm SD
LM	120	23	19.17	0.27 \pm 0.13	6.68 \pm 3.26	25.23 \pm 0.35

CB	120	27	22.50	0.52 ± 0.2	13.42 ± 5.25	25.65 ± 0.53
LA	112	16	14.29	0.39 ± 0.13	11.04 ± 3.55	28.14 ± 1
SG	120	19	15.83	0.47 ± 0.2	11.55 ± 4.94	24.76 ± 0.41
CK	120	19	15.83	0.56 ± 0.36	14.77 ± 9.86	25.95 ± 1.08
			19.91		28.79 ±	
CH	106	21		0.92 ± 0.39	11.85	31.41 ± 0.4

Sites: (LM) Laguna Madre, Texas; (CB) Coastal Bend, Texas; (LA), Chandeleur Islands, Louisiana; (SG) St. George Sound, Florida; (CK) Cedar Key, Florida; and (CH) Charlotte Harbor, Florida.

Table 5. Tukey's HSD pairwise comparisons of blue crab growth rate for six sites across the northern GOM.

Compariso n	diff	lwr	upr	p.adj
LA-LM	0.0	-0.1	0.3	0.82
	9	3	1	
AP-LM	0.1	-0.1	0.3	0.76
	0	2	3	
CK-LM	0.1	-0.0	0.3	0.24
	6	5	6	
CB-LM	0.1	-0.0	0.3	0.16
	6	3	6	
CH-LM	0.3	0.17	0.5	<
	8		9	0.01*
AP-LA	0.0	-0.2	0.2	1.00
	1	3	6	
CK-LA	0.0	-0.1	0.2	0.95
	7	6	9	
CB-LA	0.0	-0.1	0.2	0.92
	7	5	9	
CH-LA	0.2	0.06	0.5	0.01
	9		2	
CK-AP	0.0	-0.1	0.2	0.98
	5	8	9	
CB-AP	0.0	-0.1	0.2	0.97
	6	7	9	
CH-AP	0.2	0.04	0.5	0.02*
	8		2	
CB-CK	0.0	-0.2	0.2	1.00
	1	0	1	
CH-CK	0.2	0.00	0.4	<
	2		4	0.05*

CH-CB	0.2	0.00	0.4	<
	2		3	0.05*

Asterisk (*) indicates significance at alpha = 0.05. Sites: (LM) Laguna Madre, Texas; (CB) Coastal Bend, Texas; (LA), Chandeleur Islands, Louisiana; (SG) St. George Sound, Florida; (CK) Cedar Key, Florida; and (CH) Charlotte Harbor, Florida.

FIGURES

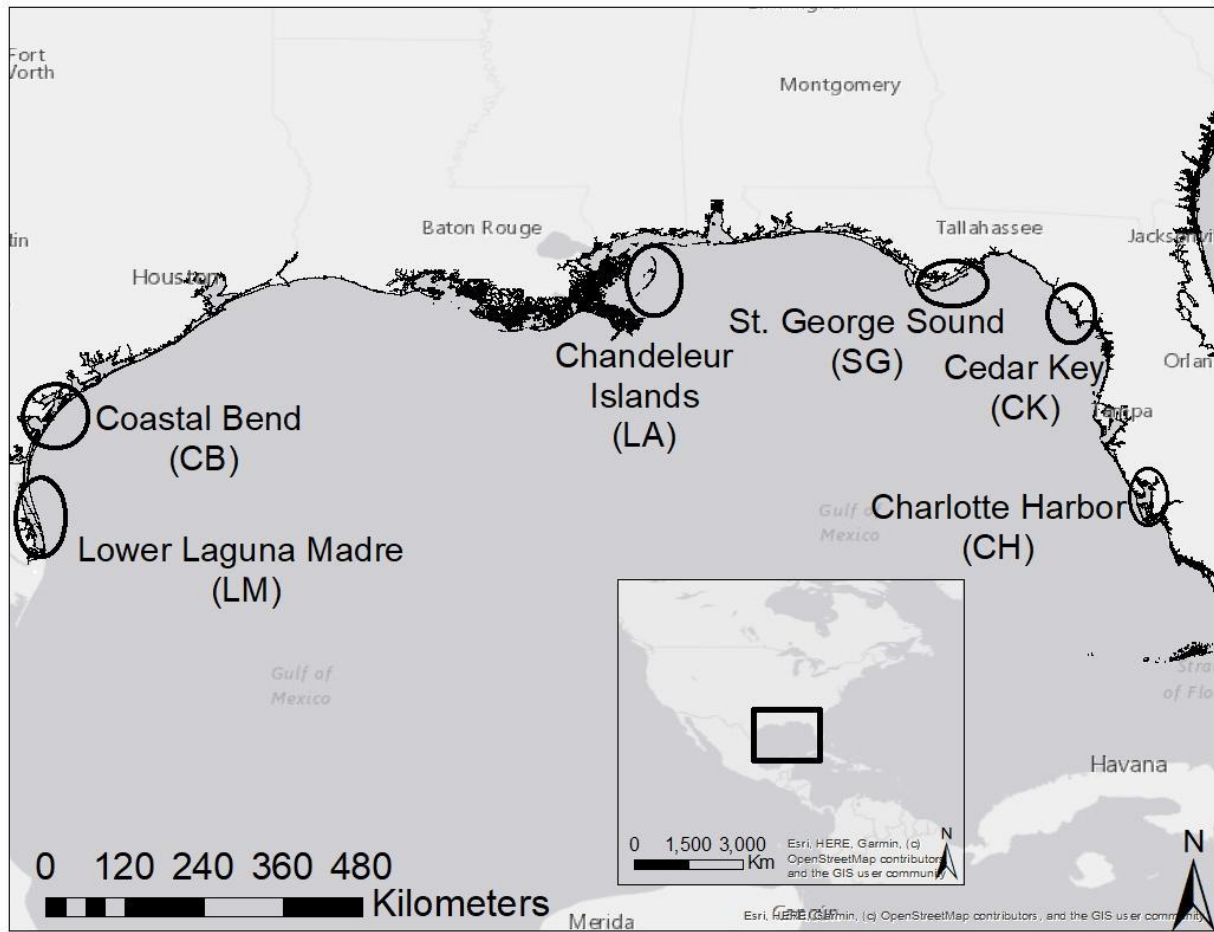


Fig. 1. Study sites across the northern GOM in Texas (Lower Laguna Madre [LM] and Coastal Bend [CB]), Louisiana (Chandeleur Islands [LA]), and Florida (St. George Sound [SG], Cedar Key [CK], and Charlotte Harbor [CH]).



Fig. 2. Mesocosm used for blue crab growth experiments.

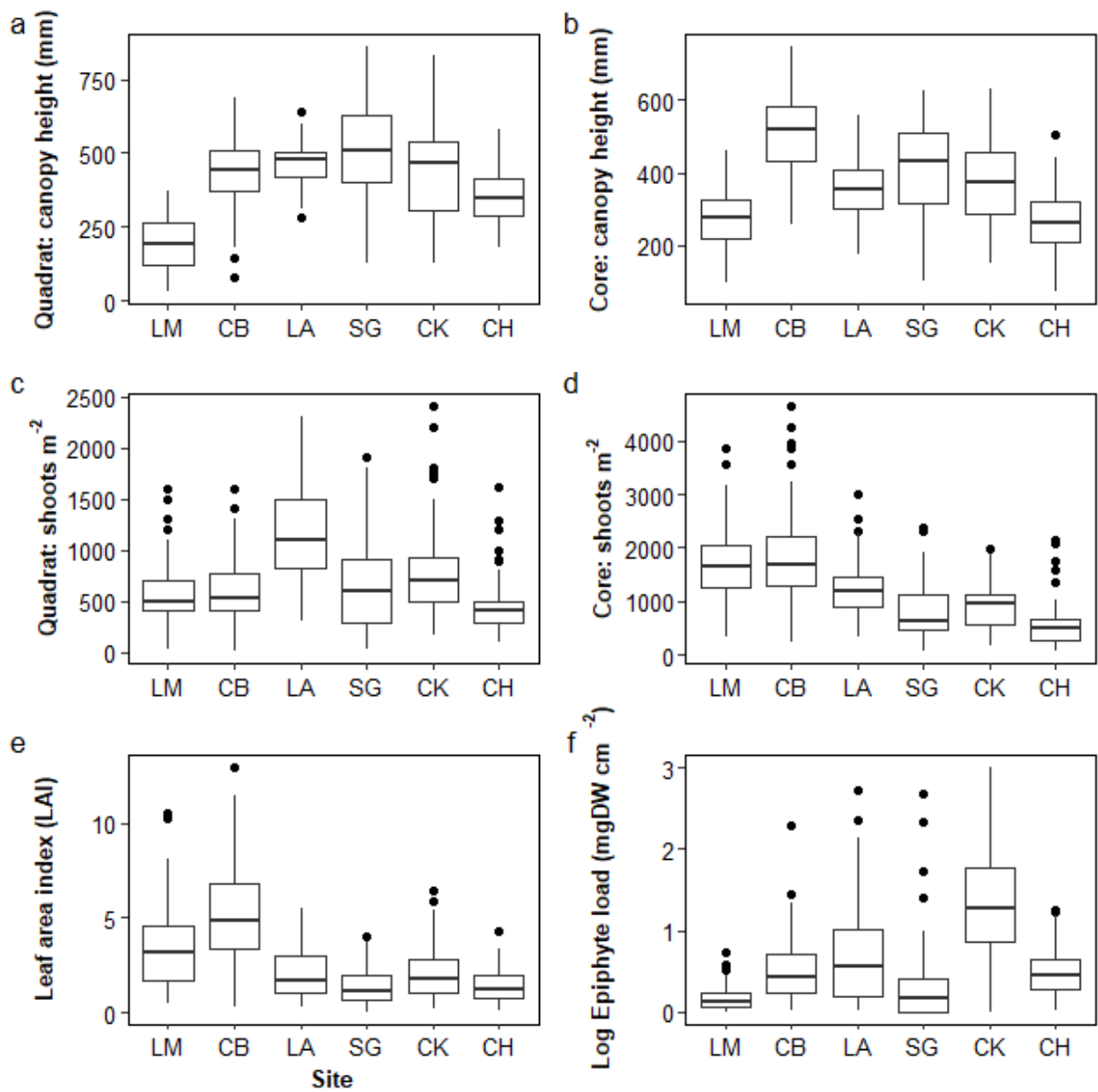


Fig. 3. Seagrass morphological traits for blue crab tethering experiments. (a) mean maximum leaf length, (b) core mean maximum leaf length, (c) quadrat mean shoot density, (d) core mean shoot density, (e) core mean leaf area index (LAI), and (f) core mean epiphyte weight over mean seagrass aboveground weight. Bold lines are medians, boxes represent 25th and 75th percentiles, whiskers are largest values within interquartile range, and black circles indicate outliers 1.5–3 x outside the interquartile range. Sites: (LM) Laguna Madre, Texas; (CB) Coastal Bend, Texas;

(LA), Chandeleur Islands, Louisiana; (SG) St. George Sound, Florida; (CK) Cedar Key, Florida; and (CH) Charlotte Harbor, Florida.

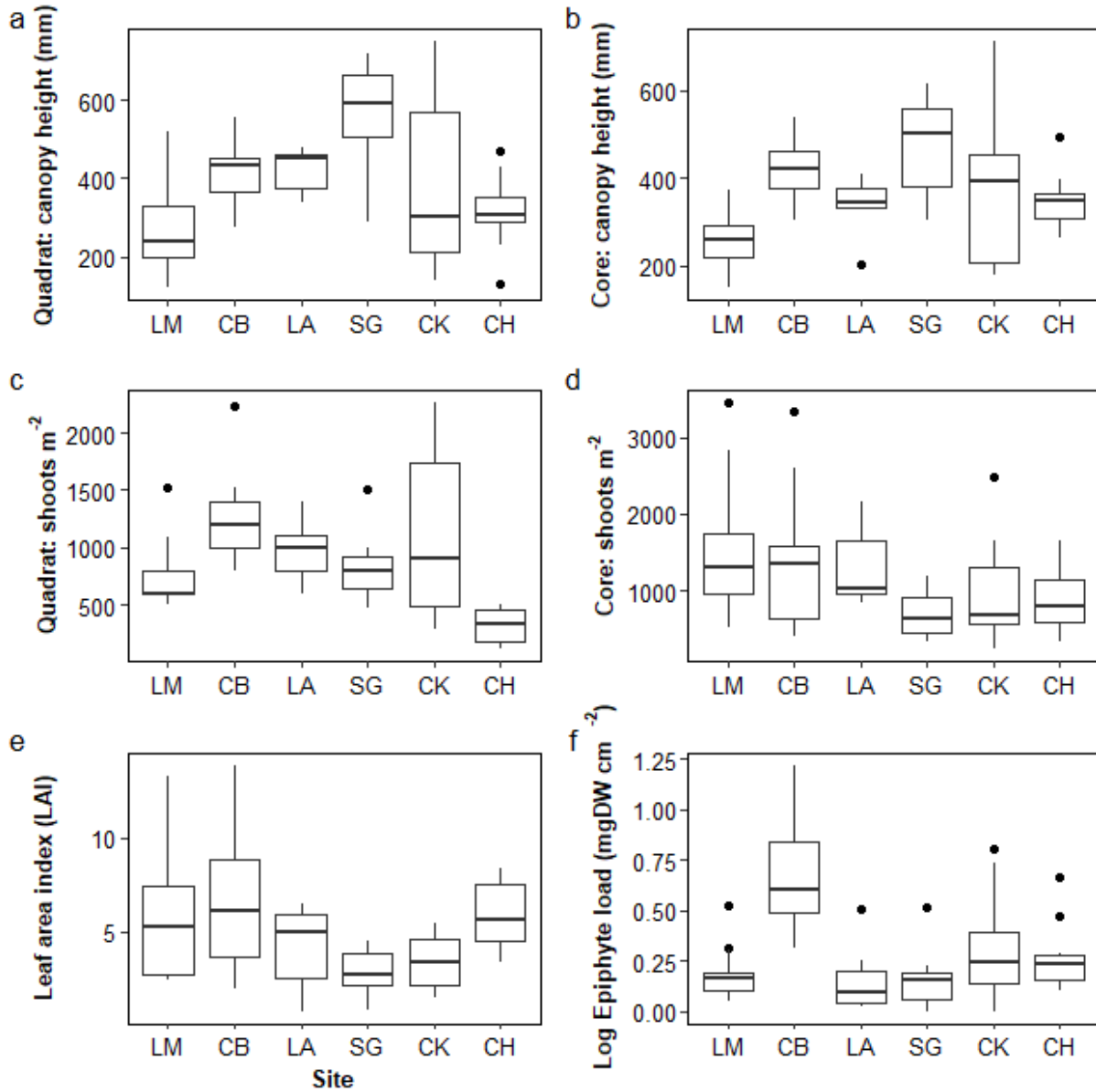


Fig. 4. Seagrass morphological traits for blue crab growth experiments. (a) quadrat mean maximum leaf length, (b) core mean maximum leaf length, (c) quadrat mean shoot density, (d) core mean shoot density, (e) core mean leaf area index (LAI), and (f) core mean epiphyte weight

over mean seagrass aboveground weight (One LA value > 10 outlier removed). Bold lines indicate median, boxes represent 25th and 75th percentiles, whiskers are largest values within interquartile range, and black circles indicate outliers 1.5–3 x outside the interquartile range. Sites: (LM) Laguna Madre, Texas; (CB) Coastal Bend, Texas; (LA), Chandeleur Islands, Louisiana; (SG) St. George Sound, Florida; (CK) Cedar Key, Florida; and (CH) Charlotte Harbor, Florida.

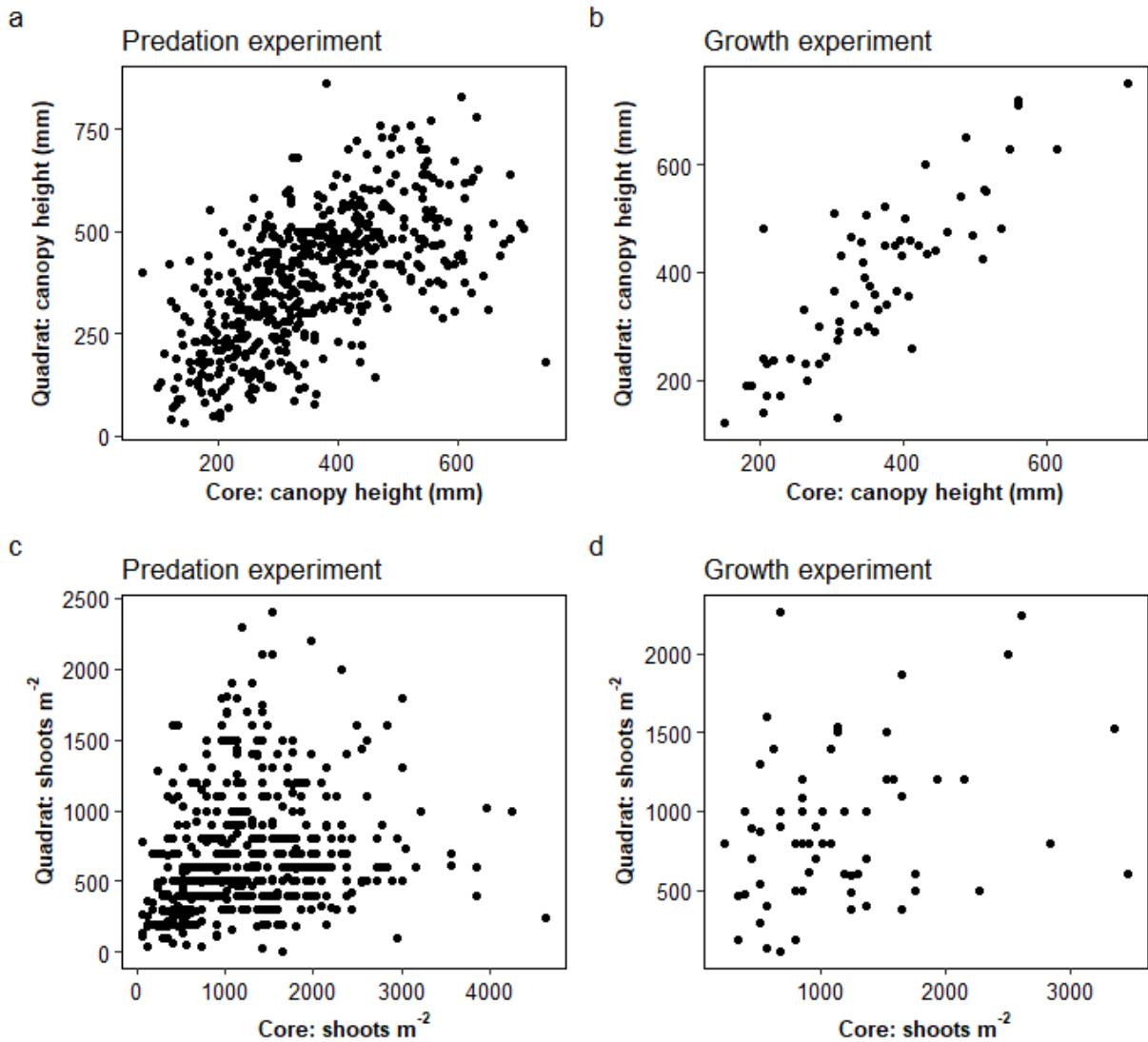


Fig. 5. Seagrass morphological comparisons for data collected from quadrats and cores for crab growth and predation experiments. (a) Core canopy height vs. quadrat canopy height for predation experiment (Note: core shoot density outliers $> 7500 \text{ m}^{-2}$ have been removed to allow for comparisons with growth shoot density), (b) core canopy height vs. quadrat canopy height for growth experiment, (c) core shoot density vs. quadrat shoot density for predation experiment, and (d) core shoot density vs. quadrat shoot density for growth experiment.

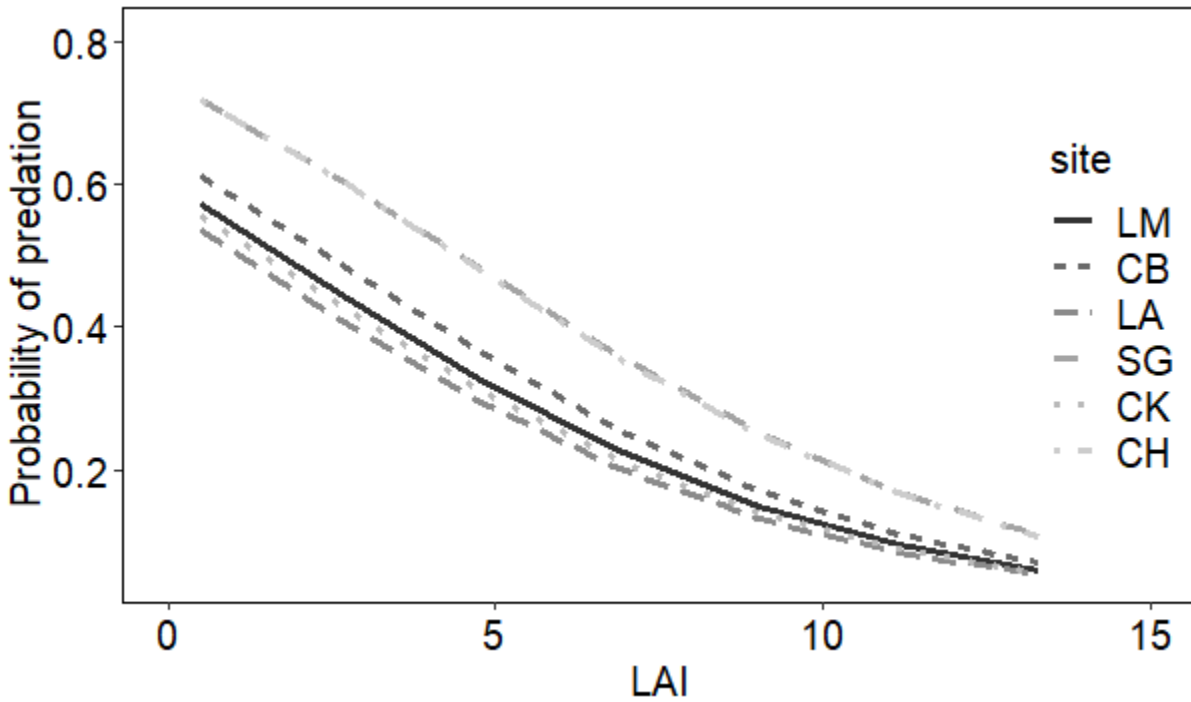


Fig. 6. Crab predation risk as a function of seagrass leaf area index (LAI) for six sites across the northern GOM. Lines indicate estimated marginal means from fixed effects of generalized mixed effects models for each site. Note: Two lines (LA and SG) have almost complete overlap. Sites: (LM) Laguna Madre, Texas; (CB) Coastal Bend, Texas; (LA), Chandeleur Islands, Louisiana; (SG) St. George Sound, Florida; (CK) Cedar Key, Florida; and (CH) Charlotte Harbor, Florida.

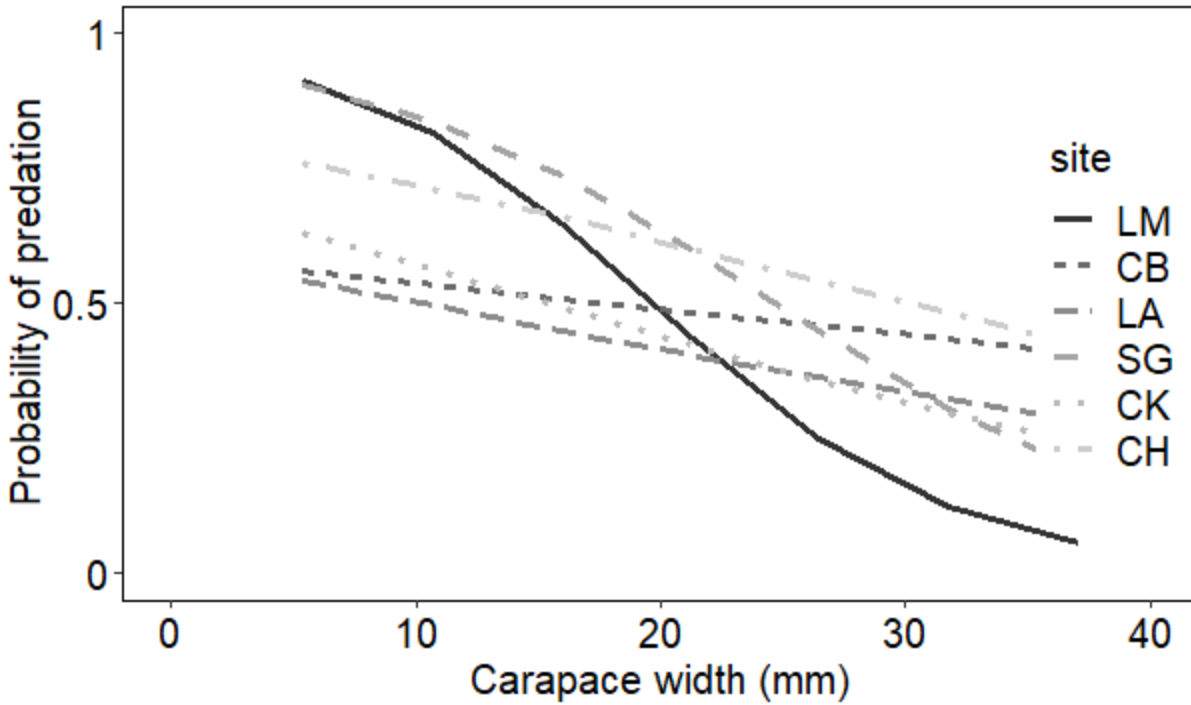


Fig. 7. Crab predation risk as a function of crab carapace width for six sites across the northern GOM. Lines indicate estimated marginal means from fixed effects of generalized mixed effects models for each site. Sites: (LM) Laguna Madre, Texas; (CB) Coastal Bend, Texas; (LA), Chandeleur Islands, Louisiana; (SG) St. George Sound, Florida; (CK) Cedar Key, Florida; and (CH) Charlotte Harbor, Florida.

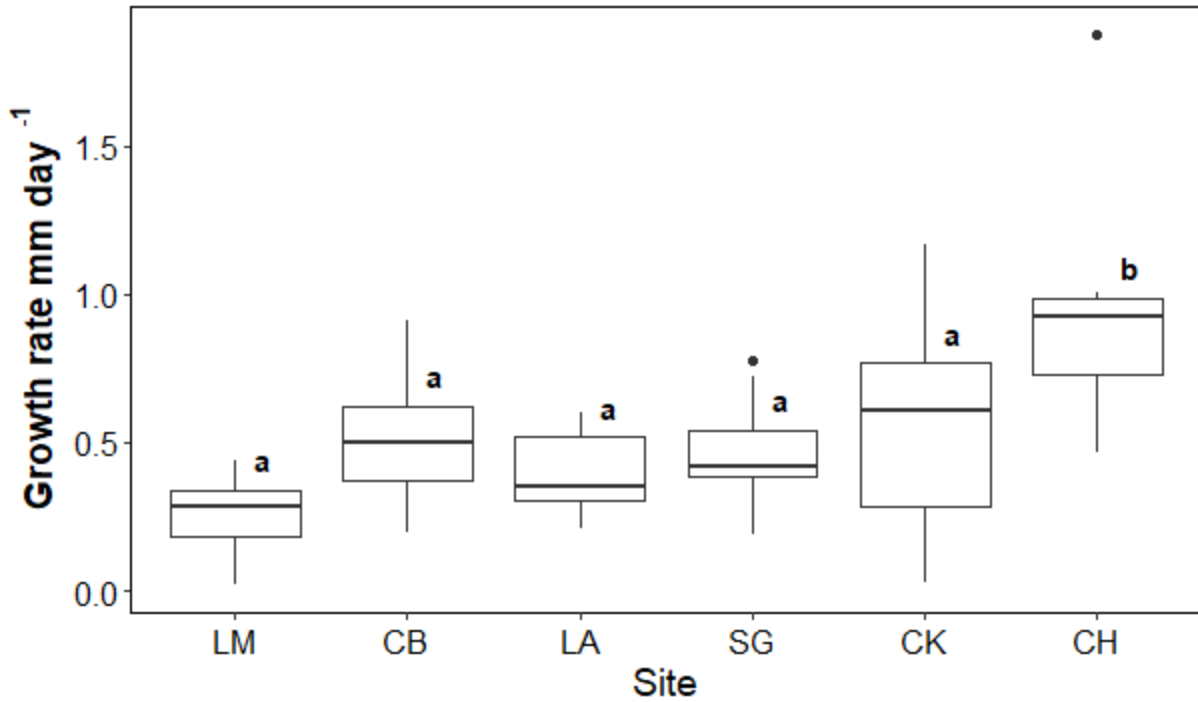


Fig. 8. Blue crab growth rate for six sites across the northern GOM. Bold lines indicate median, boxes represent 25th and 75th percentiles, whiskers are largest values within interquartile range, and black circles indicate outliers 1.5–3 x outside the interquartile range. Letters indicate significant differences from Tukey HSD tests. Sites: (LM) Laguna Madre, Texas; (CB) Coastal Bend, Texas; (LA), Chandeleur Islands, Louisiana; (SG) St. George Sound, Florida; (CK) Cedar Key, Florida; and (CH) Charlotte Harbor, Florida.