



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 6 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 predation and growth rate with seagrass shoot density, canopy height, temperature, and seagrass leaf area index (LAI) were evaluated using linear and generalized linear mixed effects models. Mortality rates due to predation ($50 \pm 9.6\%$ [mean \pm SD] crabs eaten, $n = 286$) showed negative relationships with LAI across the northern GOM. Conversely, mean crab growth rate (0.513 ± 0.317 mm d⁻¹) varied across the northern GOM but was independent of seagrass shoot density or canopy height. We found that: (1) turtlegrass-dominated beds with a greater seagrass LAI provided more effective cover for juvenile blue crabs across the northern GOM, (2) blue crabs across multiple GOM estuaries responded similarly to changes in LAI, and (3) blue crab growth varied across the northern GOM and was likely dependent on regional factors unrelated to structural complexity. 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.

KEY WORDS: Habitat complexity · Nursery hypothesis · Seagrass · Predation · Blue crab · Growth rate · Turtlegrass · *Thalassia testudinum* · Large-scale

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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,

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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 varies with seagrass shoot density (Perkins-Visser et al. 1996, Spitzer et al. 2000).

Previous research in freshwater ecosystems has indicated 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 have directly compared whether relationships between seagrass structure and nursery function are also scale-dependent (Gillanders 2006). For example, McDonald et al. (2016) compared differences in seagrass features across the Gulf of Mexico (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 whether nursery function varies 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, above-ground 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 habi-

tat 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 *Callinectes sapidus* are abundant inhabitants of seagrass and salt marsh habitats 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 occurs in the US northern GOM 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. Perkins-Visser et al. (1996) 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 on the 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, 2002, Hovel 2003) have found a range of relationships depending on the focal seagrass metric and the study location. For example, Hovel (2003) reported that blue crab survival was negatively correlated with seagrass shoot biomass in

North Carolina eelgrass meadows, whereas Hovel & Lipcius (2001) found a positive correlation between crab survival and seagrass shoot density. However, these studies were conducted in eelgrass, which has narrower leaves than turtlegrass, and thus the 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 USA (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 mortality and growth in seagrass habitats across the northern 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, 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 6 sites that span the distribution of turtlegrass across the northern GOM: 2 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]),

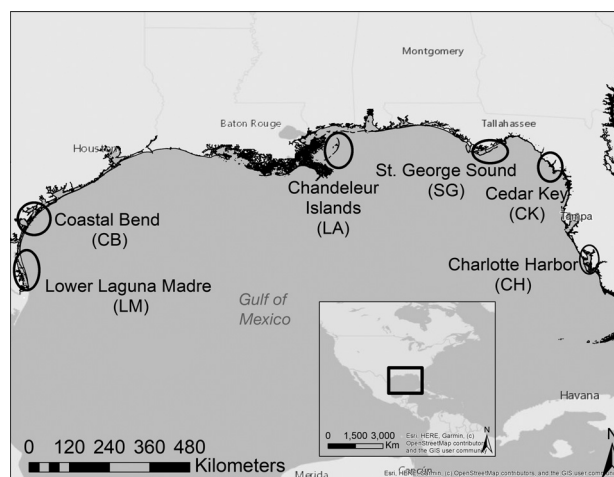


Fig. 1. Study sites across the northern Gulf of Mexico in Texas (Lower Laguna Madre; Coastal Bend), Louisiana (Chandeleur Islands), and Florida (St. George Sound; Cedar Key; Charlotte Harbor)

1 site in Louisiana (LA: Chandeleur Islands [29.90° N, 88.83° W]), and 3 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 & Lipcius (2002) to assess the role of turtlegrass structural complexity on crab mortality due to predation. Sampling stations at each of the 6 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 and 750 m 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 at each site, 6–12 crabs were tethered for a total of 79–120 tethers per site (599 teth-

ered 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 sites CB, LM, and CH were collected at CB and then transported to their respective sites. A tether (75–100 cm long) of 20 lb (9.1 kg) 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 0.75–1 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 the line), cut (knot was missing from the end of the line), or missing (no part of the carapace remaining) following the categories of Hovel & 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, 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 × 10 cm squares placed near the tethering area following the methods of 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 3 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 µm 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. Above-ground (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. LAI was calculated as the total surface area of all leaves (length × width × 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 dry weight 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).

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 & 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 2 fiberglass rings, PVC pipe, and rebar (Fig. 2). A small closable sleeve (11.4 cm diameter, 15



Fig. 2. Mesocosm used for blue crab growth experiments

cm long) sewn in the top allowed access to the inside of the mesocosm. During deployment, rebar was driven into the 3 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 (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 8 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 d 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 DO were measured using a handheld multiparameter meter (YSI) at the beginning, middle, and end of the experiment. Additionally, 5 randomly assigned cages at each site were fitted with water temperature loggers (HOBO Pendant temperature/light 64 K Data logger, Onset Computer) which recorded at 1 h intervals.

At the end of the experiment, blue crabs were removed from each mesocosm. A 1.25 m × 1.15 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 CW (mm). Mean blue crab growth rate (mm d^{-1}) was calculated by subtracting initial CW from final CW for each individual, dividing by the duration (in d) 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 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 ranges in the cores than in the quadrats (see Section 3 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:

H_1 : Juvenile blue crab mortality due to predation will decrease with increasing seagrass complexity and crab size. A binomial GLMM (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), CW (continuous), seagrass maximum canopy height (continuous), shoot density (continuous), and seagrass LAI (continuous), with interaction terms for CW \times site and CW \times LAI.

H_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 CW 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 CW \times 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 DO as a predictor variable in the blue crab growth model, as the DO variation across sites was minimal (see Section 3). 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 the methods of 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 ANOVA tests. Tukey 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 packages '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).

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 (mean = 30.99°C), water depth ranged from 0.28 to 1.75 m (mean = 1.02 m), DO ranged between 2.5 and 14.5 mg l⁻¹ (mean = 7.91 mg l⁻¹), and salinity ranged between 10.53 and 40.1 (mean = 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 and 40.1°C (mean = 30.24°C), water depth ranged between 0.5 and 1.4 m (mean = 1.027 m), DO ranged between 4.4 and 12.4 mg l⁻¹ (mean = 7.46 mg l⁻¹), and salinity varied between 13.7 and 37.8 (mean = 29.22) (Table 2). Water temperature (30.24 \pm 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 (Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m693p141_supp.pdf). Sites were dominated by turtlegrass, but also included shoal

Table 1. Environmental characteristics for blue crab tether experiments across the northern Gulf of Mexico. Data are given as mean \pm SD. LM: Laguna Madre, Texas; CB: Coastal Bend, Texas; LA: Chandeleur Islands, Louisiana; SG: St. George Sound, Florida; CK: Cedar Key, Florida; CH: Charlotte Harbor, Florida

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

Table 2. Environmental characteristics for blue crab growth experiments across the northern Gulf of Mexico. Temperature was measured from continuous water temperature loggers (HOBOS) at each site. Data are given as mean \pm SD. DO: dissolved oxygen. Site abbreviations as in Table 1

Site	No. cages	Depth (cm)	Temp ($^{\circ}$ C)	Salinity	DO (mg l $^{-1}$)
LM	13	108.67 \pm 27.34	29.88 \pm 1.52	36.88 \pm 0.44	7.06 \pm 1.14
CB	13	88.87 \pm 20.39	29.76 \pm 1.60	34.52 \pm 1.35	9.74 \pm 1.65
LA	9	97.56 \pm 9.04	30.59 \pm 1.76	25.92 \pm 0.38	8.71 \pm 1.44
SG	8	117 \pm 13.61	30.19 \pm 1.46	29.73 \pm 2.39	5.92 \pm 0.78
CK	11	116.55 \pm 6.64	30.08 \pm 1.64	24.42 \pm 2.6	6.45 \pm 1.16
CH	10	90.85 \pm 13.74	30.76 \pm 1.26	20.18 \pm 5.5	6.26 \pm 1.01

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 (Figs. 3 & 4; Tables S3 & S4). 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,d), 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,b). 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 2 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 LAI (Fig. 6) and CW (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 CW interaction (df = 12, $\chi^2 = 7.91$, $p = 0.16$) or LAI \times CW 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 1 crab recovered. Mean \pm SD duration of mesocosm growth experiments was 26.9 ± 0.63 d, and mean crab growth rate was 0.513 ± 0.317 mm d $^{-1}$ (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 CW ($F_{1,50} = 2.00$, $p = 0.16$) 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 S5). 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 6 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 CW; however, crab growth rate tended to be highest at our most eastern site, CH, but exhibited no relationship with seagrass complexity metrics.

Juvenile blue crab mortality due to predation showed an inverse relationship with seagrass LAI

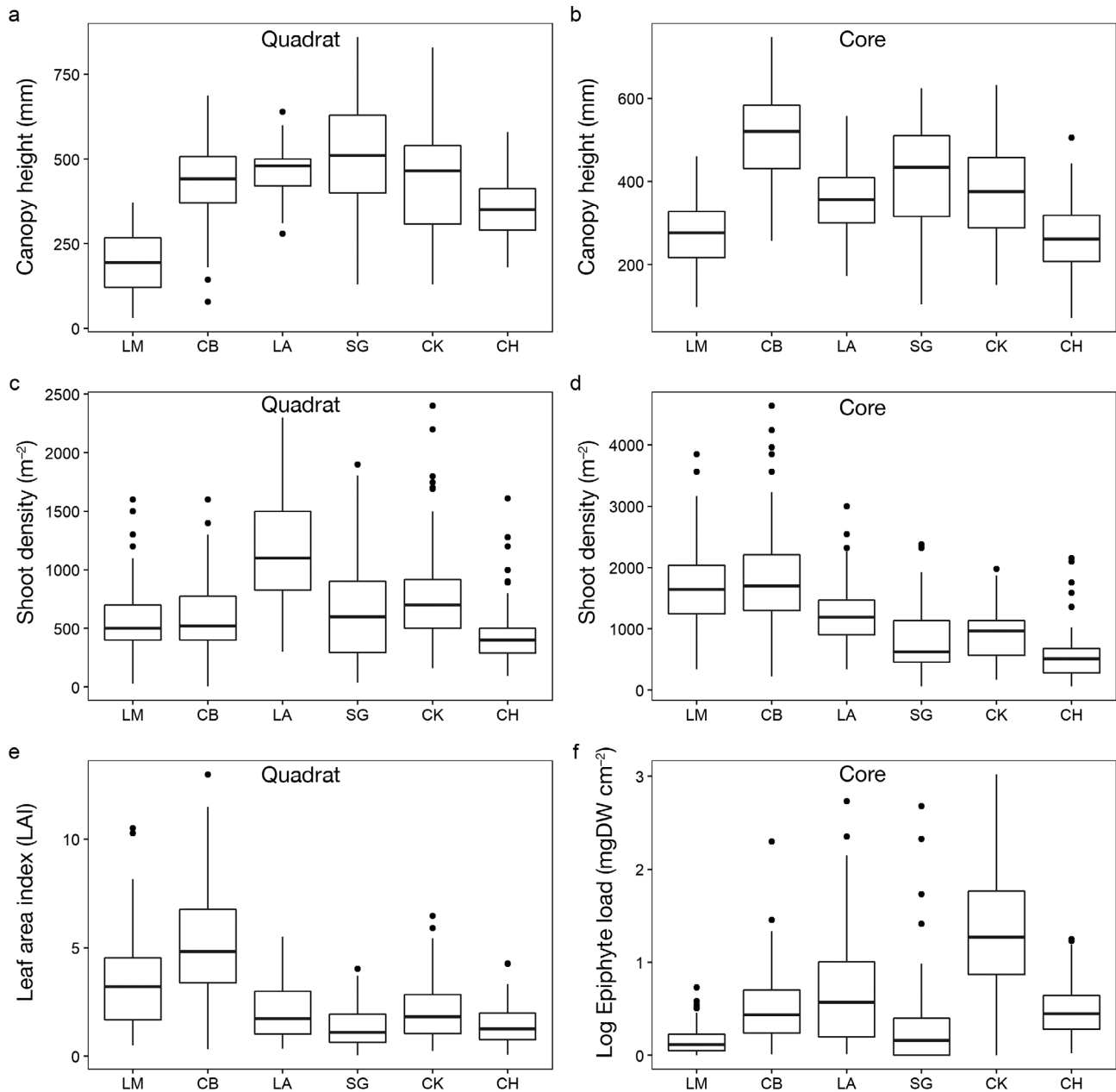


Fig. 3. Seagrass morphological traits for blue crab tethering experiments. Mean maximum leaf length in (a) quadrats and (b) cores. Mean shoot density in (c) quadrats and (d) cores. (e) Core mean leaf area index (LAI). (f) Core mean epiphyte weight over mean seagrass aboveground weight. Bold lines are medians, boxes represent 25th and 75th percentiles, whiskers are largest values within the interquartile range, and black circles indicate outliers 1.5–3× outside the interquartile range. Site abbreviations as in Fig. 1

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 GOM-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 visi-

bility, 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). For example, Stoner (1982) reported that predation on the amphipods *Cymadusa compta* and *Melita elongata* by pinfish *Lagodon rhomboides* decreased with increasing seagrass total leaf surface area.

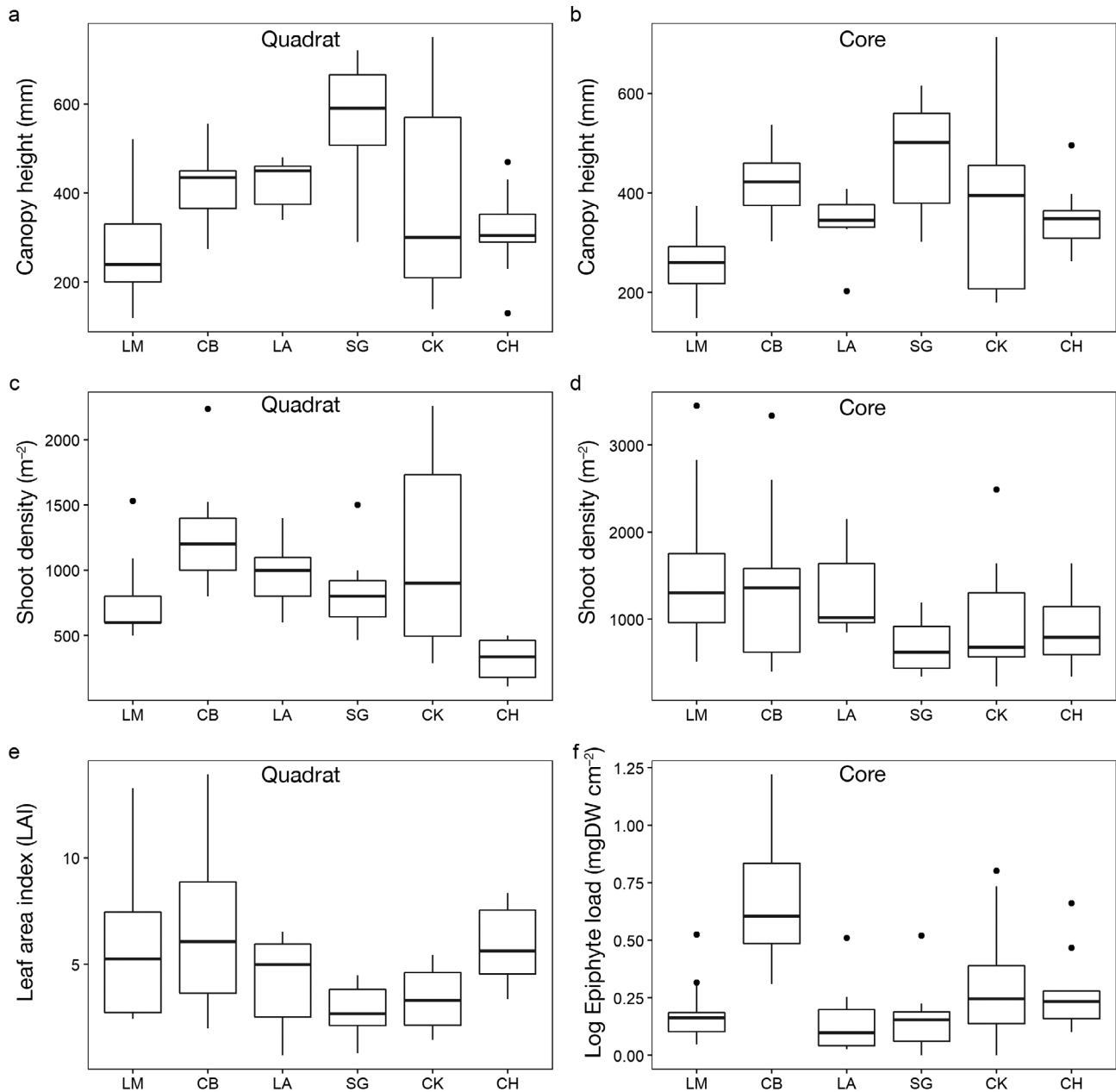


Fig. 4. Seagrass morphological traits for blue crab growth experiments. Mean maximum leaf length in (a) quadrats and (b) cores. Mean shoot density in (c) quadrats and (d) cores. (e) Core mean leaf area index (LAI). (f) Core mean epiphyte weight over mean seagrass aboveground weight (1 outlier >10 was removed for site LA). Site abbreviations as in Fig. 1; box plot parameters as in Fig. 3

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 GOM-

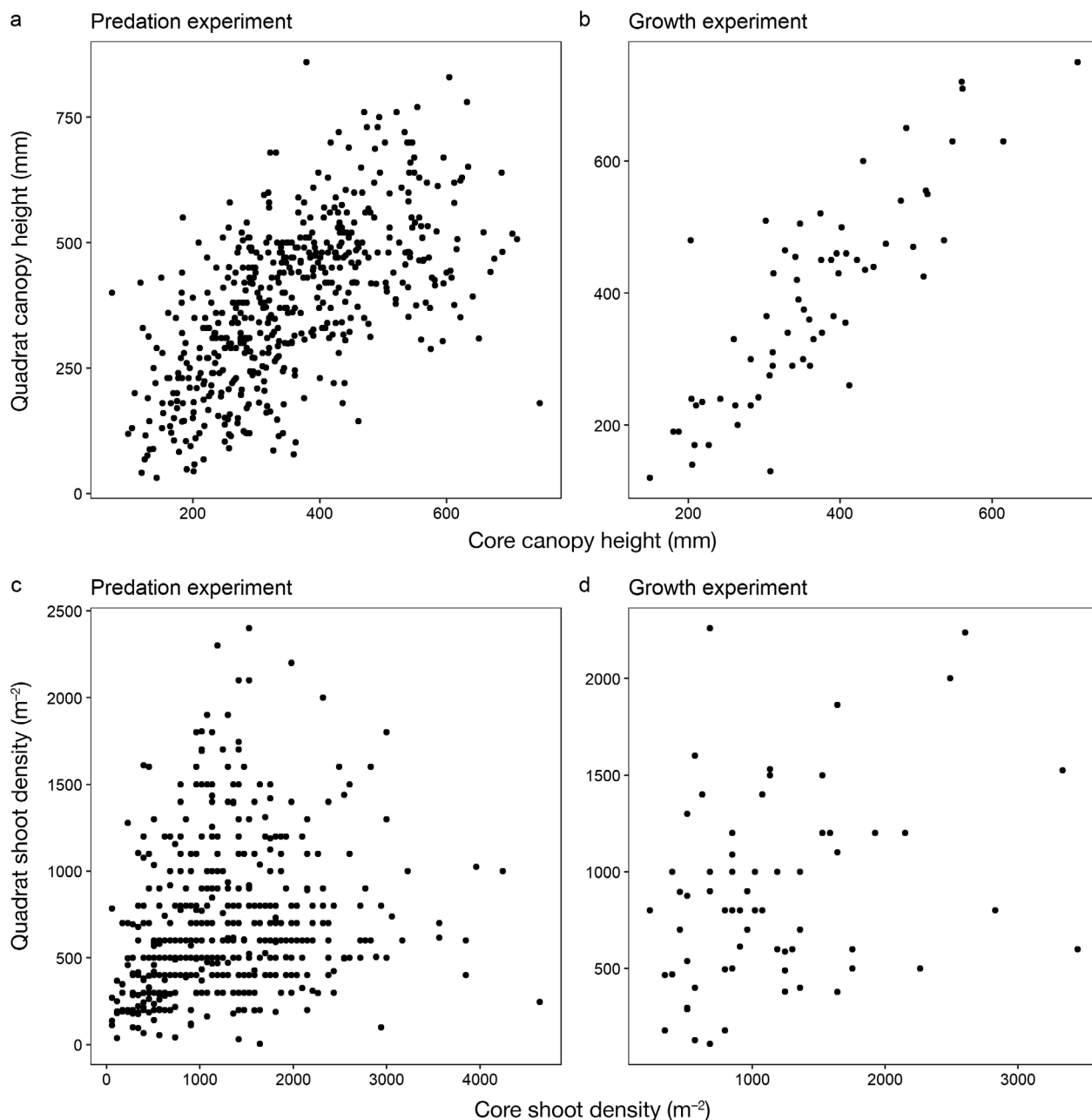


Fig. 5. Seagrass morphological comparisons for data collected from quadrats and cores for blue crab growth and predation experiments. Core canopy height vs. quadrat canopy height for the (a) predation experiment (note that core shoot density outliers $>7500 \text{ m}^{-2}$ were removed to allow for comparisons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

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, but 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 provided less protection for amphipods than either turtlegrass or manatee grass beds, despite shoal grass having a higher surface to biomass ratio. Stoner (1982) attributed this species-specific difference to a mismatch between the size of the amphipod prey and the structure it

Table 3. Results of a tethering experiment evaluating differences in predation on blue crabs at 6 sites across the northern Gulf of Mexico. Predation rate is calculated as the total number of crabs consumed divided by (total number of crabs minus the number of crabs molted and crabs with cut tether lines). CW: carapace width. Site abbreviations as in Table 1

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

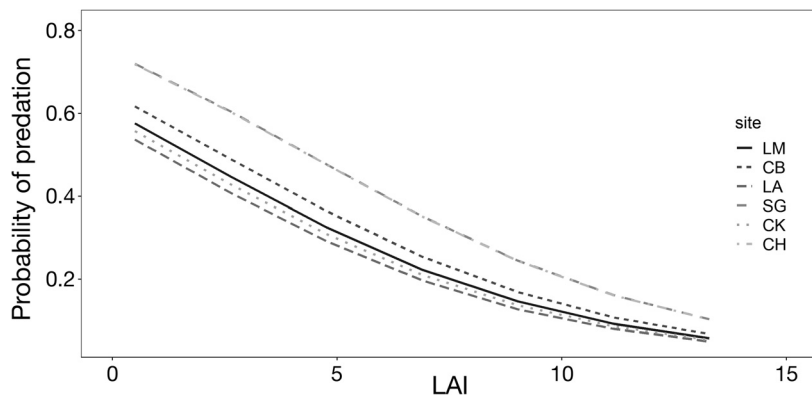


Fig. 6. Blue crab predation risk as a function of seagrass leaf area index (LAI) at 6 sites across the northern Gulf of Mexico. Lines indicate estimated marginal means from fixed effects of generalized mixed effects models for each site. Note: Two lines (sites LA and SG) have almost complete overlap. Site abbreviations as in Fig. 1

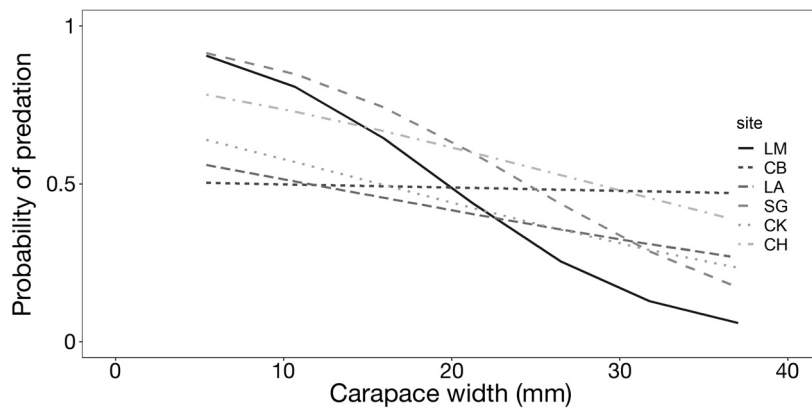


Fig. 7. Blue crab predation risk as a function of crab carapace width at 6 sites across the northern Gulf of Mexico. Lines indicate estimated marginal means from fixed effects of generalized mixed effects models for each site. Site abbreviations as in Fig. 1

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 *Ruppia maritima* (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, both negative and positive, between seagrass shoot density and crab mortality due to predation (Hovel & Lipcius 2001, 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 & Bonsdorff (1990) and supported by experimental work from Bartholomew et al. (2000) and Canion & Heck (2009), then it is possible that the high shoot

Table 4. Total blue crabs recovered in the growth experiments, crab growth rate, change in carapace width (CW), and experiment time for 6 sites across the northern Gulf of Mexico. Site abbreviations as in Table 1

Site	Total crabs	Crabs recovered	Recovery rate (%)	Growth rate (mm d ⁻¹) Mean ± SD	Change in CW (mm) Mean ± SD	Exp time (d) Mean ± SD
LM	120	23	19.17	0.27 ± 0.13	6.68 ± 3.26	25.23 ± 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
CH	106	21	19.91	0.92 ± 0.39	28.79 ± 11.85	31.41 ± 0.4

densities observed in the current study were above a critical threshold and thus shoot density effects on mortality were not evident.

Table 5. Tukey's HSD pairwise comparisons of blue crab growth rate at 6 sites across the northern Gulf of Mexico. Diff indicates mean difference in mean growth rate between sites, lower and upper are 95% confidence intervals of each comparison, and p.adj is the adjusted p-values for each comparison. Asterisk (*) indicates significance at alpha = 0.05. Site abbreviations as in Table 1

Comparison	Diff	Lower	Upper	p.adj
LA-LM	0.09	-0.13	0.31	0.82
AP-LM	0.10	-0.12	0.33	0.76
CK-LM	0.16	-0.05	0.36	0.24
CB-LM	0.16	-0.03	0.36	0.16
CH-LM	0.38	0.17	0.59	<0.01*
AP-LA	0.01	-0.23	0.26	1.00
CK-LA	0.07	-0.16	0.29	0.95
CB-LA	0.07	-0.15	0.29	0.92
CH-LA	0.29	0.06	0.52	0.01
CK-AP	0.05	-0.18	0.29	0.98
CB-AP	0.06	-0.17	0.29	0.97
CH-AP	0.28	0.04	0.52	0.02*
CB-CK	0.01	-0.20	0.21	1.00
CH-CK	0.22	0.00	0.44	<0.05*
CH-CB	0.22	0.00	0.43	<0.05*

In our study, crab mortality was also affected by crab size, whereby predation was lower on larger crabs than smaller crabs. Size-dependent predation effects are common in tethering studies (e.g. Hines & Ruiz 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 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

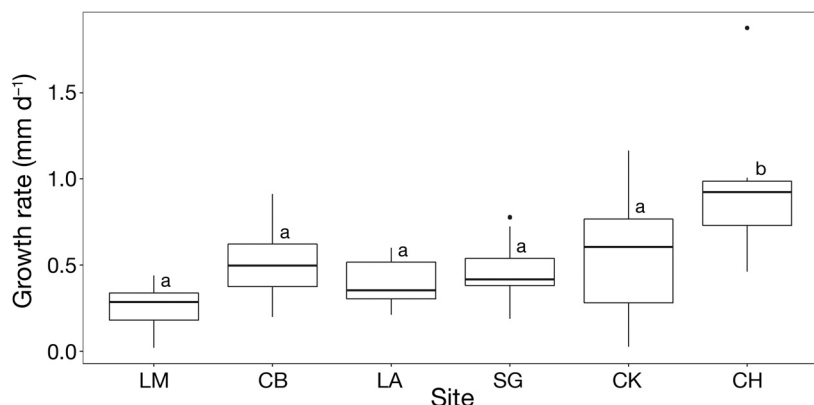


Fig. 8. Blue crab growth rates at 6 sites across the northern Gulf of Mexico. Letters indicate significant differences from Tukey HSD tests. Site abbreviations as in Fig. 1; box plot parameters as in Fig. 3

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,b). 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,b), whereas other studies reported 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 (CH, 20.18 ± 5.5) had the highest growth rate ($0.92 \pm 0.39 \text{ mm d}^{-1}$) and the site with the highest salinity (LM, 36.88 ± 0.44) had the lowest growth rate ($0.27 \pm 0.13 \text{ mm d}^{-1}$); 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 by Hayes (2021) indicated that turtlegrass-dominated beds in CH support higher densities of palaemonid shrimp (a common blue crab prey item) compared to turtlegrass-dominated beds in LM (CH: $413.1 \text{ ind. m}^{-2}$, LM: 10.9 ind. m^{-2}), suggesting that crabs in CH 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 6 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 GOM. 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.

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