

**Juvenile Blue Crab Survival in Nursery Habitats:
Predator Identification and Predation Impacts in Chesapeake Bay**

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Amanda Marie Bromilow

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Amanda Marie Bromilow

Approved by the Committee, August 2017

Romuald N. Lipcius, PhD
Committee Chair / Advisor

Mary C. Fabrizio, PhD

Rochelle D. Seitz, PhD

Matthew L. Kirwan, PhD

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THESIS ABSTRACT

Predator populations can have significant impacts on prey recruitment success and prey population dynamics through consumption. Young, inexperienced prey are often most vulnerable to predation due to their small size and limited evasion capabilities. To reduce the risk of predation, new recruits and young juveniles typically settle in structured nursery habitats, such as seagrass beds, which promote higher survival by acting as refuges from predators. Thus, successful recruitment to the adult portion of the population is often dependent on the availability of suitable nursery habitat. In this thesis, I used field tethering experiments and gut content analyses to assess the role of habitat, body size, finfish predation, and cannibalism on the survival of one of the most ecologically and economically important species in Chesapeake Bay: the blue crab *Callinectes sapidus*.

In field tethering experiments, survival probability of juvenile blue crabs in York River nursery habitats (i.e. seagrass beds, sand flats) increased significantly and additively with crab size and SAV cover. Images of predation events during tethering experiments revealed cannibalism by adult blue crabs to be a major source of juvenile mortality. Gut content analyses from three field studies identified seven predators of juvenile blue crabs in lower Chesapeake Bay nursery habitats: adult blue crabs, striped bass *Morone saxatilis*, red drum *Sciaenops ocellatus*, silver perch *Bairdiella chrysoura*, weakfish *Cynoscion regalis*, Atlantic croaker *Micropogonias undulatus*, and oyster toadfish *Opsanus tau*. Using frequency of consumption and diet proportion metrics, I determined striped bass, red drum, and silver perch to be the most impactful finfish predators on juvenile mortality, in addition to cannibalism. Atlantic croaker and oyster toadfish play minor roles in juvenile mortality in Chesapeake Bay nursery habitats. The probability of juvenile crabs being present in a predator's gut was also significantly higher in seagrass beds than in unvegetated sand flats.

Food web dynamics are an important aspect of ecosystem-based fisheries management. Understanding the ecological interactions between populations, and their environment, can provide insight into natural population fluctuations of valuable fishery species such as the blue crab. This thesis demonstrated the positive effects of body size and SAV cover on juvenile crab survival, indicating the importance of seagrass nursery habitat for blue crab population dynamics in Chesapeake Bay. However, despite the predator refuge offered by SAV, high densities of predators and prey in seagrass beds resulted in greater consumption of juveniles in those habitats. Key predators of juvenile blue crabs were also identified and their relative impacts were estimated. The predator-prey relationships revealed in this thesis were integrated into a revised food web for blue crabs in Chesapeake Bay, in the hopes of informing future ecosystem-based management efforts.

**Juvenile Blue Crab Survival in Nursery Habitats:
Predator Identification and Predation Impacts in Chesapeake Bay**

CHAPTER 1

**Drivers of nursery habitat selection:
Role of trade-offs, predation, and cannibalism for the blue crab**

ABSTRACT

Nursery habitats play a major role in the population dynamics of marine and estuarine species, with the blue crab *Callinectes sapidus* serving as a model invertebrate. The current paradigm of blue crab habitat use postulates that survival of juveniles decreases in submerged aquatic vegetation (SAV) due to a reduction in suitably scaled refuge as they grow, triggering an ontogenetic shift from SAV to unvegetated habitats. However, alternative mechanisms for this habitat shift have not been examined. We evaluated the paradigm of blue crab habitat use by conducting field tethering experiments in York River nursery habitats using a broad range of juvenile size and SAV cover. Cameras were deployed to identify key predators of juvenile blue crabs, and to assess the relative importance of predation and cannibalism as sources of juvenile mortality. Probability of survival increased significantly and additively with crab size and SAV cover. The absence of an interaction between crab size and SAV cover is inconsistent with the current paradigm. Rather, the ontogenetic habitat shift by juvenile blue crabs is likely driven by a density-dependent trade-off between predation risk and foraging efficiency. In images of predation events, adult blue crabs, northern puffers *Sphoeroides maculatus*, striped burrfish *Chilomycterus schoepfi*, and oyster toadfish *Opsanus tau* were identified as predators of juveniles in seagrass beds and sand flats. The high frequency of successful predation events by adult blue crabs suggests that cannibalism is a primary source of juvenile mortality, as or more influential to blue crab population dynamics than finfish predation.

INTRODUCTION

Nursery habitats and ontogenetic shifts

Coastal habitats are highly productive and provide foraging, spawning, and nursery grounds for commercially and ecologically important species (Seitz et al. 2014). Availability of suitable nursery habitat often determines recruitment success and population abundance, indicating that the nursery role is a valuable function of coastal habitats (Wahle & Steneck 1991, Gibson 1994, Juanes 2007, Sundblad et al. 2014). Nursery habitats promote greater densities, faster growth rates, and/or higher survival than other habitats, and thus provide a greater contribution of juveniles to the adult portion of populations (Beck et al. 2001).

Many species exhibit an ontogenetic shift between different habitats as they develop. Two primary mechanisms have been proposed to explain the purpose and timing of these ontogenetic habitat shifts. The first is based on the concept of fractal surfaces and predicts that the availability of and access to crevices or other types of refuge within a complex, fractal habitat decrease as body size increases (Caddy 1986, Eggleston & Lipcius 1992). Nursery habitats are typically structured habitats (e.g. seagrass beds, salt marshes, mangroves) that provide many interstices in which small juveniles seek shelter from predators (Heck & Thoman 1984, Wilson et al. 1987, Minello et al. 2003). Due to the limited availability of bigger sheltered spaces in a fractal habitat, larger animals may spend more time exposed to predators while searching for suitable refuge; they may even outgrow the protection afforded by the habitat completely (Eggleston & Lipcius 1992, Arsenault & Himmelman 1998, Lipcius et al. 1998). Thus, larger individuals reduce their risk of predation by migrating to other habitats.

The second mechanism proposed for ontogenetic habitat shifts involves trade-offs between growth and survival. Postlarvae and small juveniles often exhibit cryptic behavior to

avoid predators (i.e. hiding in nursery habitats), which can reduce their foraging efficiency by restricting the time spent foraging outside of the refuge or by foraging within suboptimal nursery habitats (Brown 1999). These smaller individuals may accept reduced food intake and slower growth rates for safety in less-productive nursery habitats, such as those with low prey availability. As animals grow, energetic demands increase and vulnerability to predators decreases (Werner & Gilliam 1984, Wahle 1992). Predator gape limitations (Hart & Hamrin 1988), increased aggression (Wahle 1992, Hines & Ruiz 1995, Stoner 2009), and increased physical defenses, such as a thicker carapace, shell, or spines (Stoner 2009, Pirtle et al. 2012), can reduce predation risk of large juveniles, allowing them to exploit energetically profitable habitats regardless of refuge availability. Food supply and the level of perceived risk in nursery habitats determine the size at which American lobsters *Homarus americanus* begin to forage in less-sheltered habitats (Wahle 1992).

Although many studies have examined the role of nursery habitats and the benefits they offer juveniles (Heck & Thoman 1984, Beck et al. 2001, Heck et al. 2003, McDevitt-Irwin et al. 2016), relatively few have examined the mechanisms underlying nursery habitat selection and subsequent migration to alternative habitats. In this study, we attempt to address these knowledge gaps of nursery habitat use, using the blue crab *Callinectes sapidus* as a model invertebrate species.

Blue crab nursery habitat use

Seagrass beds are the primary nursery habitat for many species in Chesapeake Bay, including the blue crab (Heck & Thoman 1984). After undergoing larval development in the coastal waters near the mouth of the Bay, blue crab megalopae (postlarvae) reinvade the estuary

and settle into seagrass beds, where they experience rapid growth and quickly transform into the first benthic juvenile instar (Orth & van Montfrans 1987, Metcalf & Lipcius 1992, Lipcius et al. 2007). The predator refuge provided by the structure of the submerged aquatic vegetation (SAV) enhances juvenile survival (Wilson et al. 1990, Perkins-Visser et al. 1996, Pile et al. 1996, Hovel & Lipcius 2001, Orth & van Montfrans 2002). Blue crabs remain in vegetated primary nursery habitats until they reach 20-30 mm carapace width (CW), at which point they start to move into unvegetated secondary nursery habitats such as sand or mud flats (Orth & van Montfrans 1987, Pile et al. 1996, Lipcius et al. 2005, 2007).

The current conceptual model of blue crab habitat use posits that juveniles exhibit an ontogenetic habitat shift from seagrass beds to unvegetated habitats at 20-30 mm CW because they have outgrown the size-specific refuge in SAV (Lipcius et al. 2007). The proposed mechanism follows the fractal habitat hypothesis for ontogenetic habitat shifts (Caddy 1986). While smaller juveniles can seek shelter among the grass blades and burrow into the sediment within the rhizome mat, larger individuals cannot effectively hide in the vegetation or sediment, and the structure may hinder their ability to evade predators (Lipcius et al. 2007, Johnston & Lipcius 2012). This hypothesis therefore predicts that small crabs <25 mm CW experience greater survival within SAV beds than larger crabs >25 mm CW, resulting in the migration of large juveniles to alternative nursery habitats. In these secondary nurseries, larger juveniles experience increased survival and growth because their bigger size allows them to exploit the abundant prey in these habitats with low risk of predation by gape-limited predators (Lipcius et al. 2005, 2007, Seitz et al. 2005).

The current blue crab habitat use paradigm was reinforced by a study in which survival of juvenile blue crabs was driven by an interaction between crab size and habitat type, such that

survival was positively related to crab size in unvegetated habitats, but negatively correlated with crab size in SAV (Johnston & Lipcius 2012). However, that study was conducted using a narrow range of seagrass shoot density, which could have biased the results. Furthermore, no studies have tested alternative hypotheses for blue crab habitat use or the drivers of the ontogenetic habitat shift.

Study objectives and rationale

The primary objectives of our study were to: (1) re-evaluate the current blue crab habitat use paradigm using a broad size range of juveniles and SAV cover; and (2) identify key predators of juvenile blue crabs in York River nursery habitats using innovative methods and technology (underwater camera systems).

To evaluate the blue crab habitat use paradigm, we generated six hypotheses (H_i) of juvenile blue crab survival with different combinations of crab size, SAV cover, time of day, and trial duration as independent variables. In H_1 (size), we expected larger juveniles to experience higher survival as a result of decreased susceptibility to gape-limited predators and increased aggression (Hines & Ruiz 1995, Pile et al. 1996, Orth & van Montfrans 2002). In H_2 (SAV cover), juvenile survival was expected to increase with SAV cover due to increased availability of structural refuge (Heck & Thoman 1981, Wilson et al. 1987, Hovel & Lipcius 2001, Orth & van Montfrans 2002). In H_3 (size, SAV cover), we considered the additive effects of crab size and SAV cover, and predicted that larger juveniles in densely vegetated areas experience the highest survival. The current paradigm of blue crab habitat was encompassed by H_4 (size x SAV cover), which posits an interaction between size and habitat, such that small crabs experience greater survival in SAV, whereas large juveniles survive better in unvegetated habitats (Lipcius

et al. 2005, 2007, Johnston & Lipcius 2012). H₅ (size, SAV cover, trial duration) predicted that survival decreases with trial duration due to prolonged exposure to predators. Finally, H₆ (size, SAV cover, duration, time) predicted that juveniles are more likely to survive at night due to lower foraging efficiency of visual predators. Experimental field studies were conducted to test the aforementioned hypotheses of juvenile blue crab survival, and to identify predators of blue crabs in York River nursery habitats.

MATERIALS AND METHODS

Study sites

Field experiments were conducted in July and August 2016 in vegetated and unvegetated habitats in the York River, a subestuary of Chesapeake Bay (Fig. 1). July experiments were conducted at Goodwin Islands (37° 13' N, 76° 23' W) and Sandy Point (37° 15' N, 76° 25' W); August experiments were conducted at Goodwin Islands only. Goodwin Islands and Sandy Point are shallow, tidal regions near the mouth of the York River with average depths <2 m and an average tidal range of 0.7 m. Throughout the study period, salinity ranged from 18-24, dissolved oxygen ranged from 3-13 mg l⁻¹, and water temperature ranged from 23-33°C (Virginia Estuarine & Coastal Observing System, Goodwin Islands Continuous Monitoring Station). The nearshore habitat in both locations is characterized by an extensive seagrass bed, adjacent to an unvegetated sand flat. The seagrass beds are dominated by eelgrass *Zostera marina* and widgeon grass *Ruppia maritima*, with occasional abundances of the exotic red alga *Gracilaria vermiculophylla* (A.M.B. pers. obs.). Each location contained a vegetated and unvegetated site.

Juvenile survival

Tethering is a common method used to measure relative survival rates of small benthic species, often crustaceans, across treatments (Heck & Thoman 1984, Pile et al. 1996, Hovel & Lipcius 2001, Moody 2003, Lipcius et al. 2005, Johnston & Lipcius 2012). In this study, tethering experiments were conducted to quantify relative survival rates of juvenile blue crabs in seagrass and sand habitats. Although tethered crabs are capable of normal movements (i.e. walking, swimming, burrowing), their ability to escape predators is limited to the length of the tether (Zimmer-Faust et al. 1994). Thus, tethering leads to inflated natural mortality rates and should only be used to determine relative rates of predation, not absolute rates.

Tethering may also introduce treatment-specific bias in survival (Peterson & Black 1994). For example, tethered crabs may experience lower survival in seagrass as a result of entanglement, but would not experience the same reduction in survival in sand such that relative survival rates could not be compared between these habitats. Previous studies have examined treatment-specific biases of tethering juvenile crabs in various habitats and found no significant interaction between tethering and habitat (Pile et al. 1996, Hovel & Lipcius 2001, Lipcius et al. 2005); therefore, we assumed there was no treatment-specific bias in our experiments, which used similar tethering methods as those in previous studies.

Juvenile blue crabs were collected from the York River by towing a crab scrape in seagrass beds adjacent to the study sites at Goodwin Islands and Sandy Point. Juveniles were held in an outdoor, flow-through seawater tank until tethering. To tether crabs, each juvenile was measured to the nearest 0.1 mm CW, and 20 cm of 11.3-kg monofilament fishing line was adhered to the carapace using cyanoacrylate super glue and Gorilla tape. A noose was tied around the carapace spines of juveniles >25 mm CW for additional security. A swivel was tied to

the other end of the fishing line. Individual tethered crabs were placed in small, plastic Tupperware containers to reduce the risk of cannibalism and entanglement prior to the experiment. The contained crabs were returned to the outdoor seawater tank overnight to ensure tether retention. Nearly all juveniles (95%) retained their tethers in the 24 h before deployment; thus, we assumed there was no effect of tether retention on survival estimates.

In the field, juvenile crabs 10-55 mm CW were randomly selected for tethering in either sand (Fig. 2A) or seagrass (Fig. 2B), and were deployed at the tether locations by fastening the swivel of the tether to a metal stake pushed into the sediment (Fig. 3). The stake was tied to a marker PVC pole with monofilament line to assist in tether retrieval at the end of each trial. The stake and marker PVC were 1 m apart to reduce the influence of structure in attracting predators. The tether locations were positioned along two transects parallel to shore, with each at least 3 m away from the nearest tether to maintain independence among tethers. Tether positions were constant throughout the experimental study.

At vegetated sites, percent cover of SAV was estimated using a 40-cm² quadrat placed on the seafloor with the tethering stake in the center. This ensured the percent cover estimation encompassed only the range of the tether, and reflected the available vegetation that the juvenile could use as refuge. Estimating percent cover for each tether before each trial allowed for a nearly random sample of SAV cover and accounted for changes in SAV abundance throughout the season (Fig. 4). Tethering trials were conducted during the day and at night to examine diel differences in predation. Only 8% of tethered juvenile crabs survived the 24-h pilot trials in the summer of 2015, and thus trial durations were limited to 3-13 h in the 2016 experiments. At the end of each trial, tethers were checked for crab survival, and pieces of carapace, a chewed line, or a cut line provided evidence of predation.

Predator identification

Predators of juvenile blue crabs were identified by using GoPro cameras to capture images of predator-prey interactions during tethering experiments. Cameras were mounted to the marker PVC poles and oriented such that the field of view encompassed the entire extent of the tether (Fig. 3). GoPro Battery BacPacs were used to extend battery life, and the cameras were programmed to take a photo every 2 s to limit battery use. Infrared camera lenses and infrared lights were used during night trials to capture images of crepuscular and nocturnal predators. A successful predation event was identified when a series of images showed a predator with the tethered juvenile in its mouth or claws; often, the crab was absent from the remaining photos of the trial and only a small piece of carapace or Gorilla tape was left attached to the tether. For predators identified in the tethering experiments, predation frequencies were calculated and compared to determine the relative impact of each species on juvenile blue crab mortality in York River nursery habitats.

Statistical analyses

To address our hypotheses about juvenile blue crab survival, we developed seven statistical models (g_1 - g_7) following an information-theoretic approach (Burnham & Anderson 2002, Anderson 2007), including the null model for comparison (Table 1). Juvenile survival was modeled as a binary response (1 = alive, 0 = dead), with crab size (mm CW), SAV cover (%), and trial duration (h) as continuous covariates, and time (day, night) as a fixed factor. Each model was analyzed using logistic regression to determine the probability of survival under those experimental conditions, and the bias-corrected Akaike's Information Criterion (AIC_C) values were calculated to determine the best model. Weighted model probabilities (w_i) based on Δ_i

values were used to determine the probability that a particular model was the best-fitting model. The Hosmer-Lemeshow goodness of fit test was used to assess the fit of the best model to the data (Hosmer & Lemeshow 1982).

The parameter estimates of the best-fitting model were used to calculate binomial survival probabilities as:

$$\theta = \frac{e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_i X_i}}{1 + e^{\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_i X_i}} \quad (1)$$

where θ is the probability of survival, β_0 is the parameter for the baseline condition (constant), β_i is the parameter representing increases or decreases in survival due to the effect of independent variable X_i . Crab size (X_1), SAV cover (X_2), and trial duration (X_3) are continuous and thus were represented by single variables. Time is categorical and thus night was represented as a dummy variable (X_4), and day was designated the constant (β_0); $X_4 = 0$ for day and 1 for night. The interaction term for crab size and SAV cover was $\beta_3 X_1 X_2$.

Multiple models were generated to determine the consistency of our data with the current blue crab paradigm using a categorical habitat factor. Again, juvenile survival was modeled as a binary response with crab size, trial duration, and time as independent variables, but SAV cover was replaced with habitat (vegetated, unvegetated). Unvegetated habitat was considered the baseline condition ($X_2 = 0$), and vegetated habitat was represented as a dummy variable ($X_2 = 1$). The models were analyzed using logistic regression to determine the effect of habitat on juvenile survival and the presence of an interaction between size and habitat.

RESULTS

A total of 145 independent trials was used to model survival in York River nursery habitats. Crabs that were missing when the tethers were checked were assumed to be eaten,

based on our tethering controls. In one case, the predator (oyster toadfish *Opsanus tau*) was identified because it had swallowed the juvenile crab whole and was still attached to the line. For the other trials in which crabs were assumed to be eaten, 36 were set up with GoPros, and 21 of those cameras (58%) captured images of the predator.

Juvenile survival

Juvenile blue crab survival was best explained by the additive model with crab size, SAV cover, and trial duration as predictors (g_5); model g_5 had the lowest AIC_C value and a weighted probability of 0.51 (Table 1). All other models except g_6 had weighted probabilities <0.01 and thus were eliminated from further consideration (Table 1). Although the probability of model g_6 was similar to g_5 , addition of time as a factor did not make a significant contribution in explaining the residual deviance and did not lower the AIC_C value (Table 1); thus, we selected g_5 as the most parsimonious model. The Hosmer-Lemeshow test indicated that model g_5 fit the data well ($\chi = 4.93$, $p > 0.05$).

Parameter estimates of model g_5 were significant (Table 2), with juvenile blue crab survival increasing with crab size (Fig. 5) and decreasing with trial duration (Fig. 6). Survival increased marginally with SAV cover (Table 2, Fig. 7). Parameter estimates of model g_5 were used to generate survival probabilities with the equation:

$$\theta = \frac{e^{0.6047+0.0556X_1+0.0095X_2-(0.3163X_3)}}{1+e^{0.6047+0.0556X_1+0.0095X_2-(0.3163X_3)}} \quad (2)$$

where X_1 = crab size, X_2 = SAV cover, and X_3 = trial duration. A value of 12 was used for trial duration (X_3) to standardize the survival probabilities. Equation 2 was used to create a 3D graph of the probability of survival as a function of crab size and SAV cover at a fixed trial duration of 12 h, a common interval for tethering experiments. In general, larger crabs in habitats with high

SAV coverage had the highest probability of survival (Fig. 8). At low SAV cover, predicted probability of survival increased with size from 7% at 12 mm to 45% at 54 mm CW (Fig. 8). At high SAV cover, juvenile survival probability increased with size from 17% to 68% (Fig. 8).

The model that best explained juvenile survival using habitat as a factor (vegetated, unvegetated) was the additive model with size, time, duration, and habitat as predictors. Similar to model *g5*, juvenile blue crab survival increased significantly with size and decreased with trial duration (Table 3). Vegetated habitat had a marginally significant, positive effect on crab survival relative to unvegetated habitat (Table 3). There was no interaction between size and habitat (Fig. 9).

Predator identification

GoPro photos of the tethering experiments identified four predator species of juvenile blue crabs in York River nursery habitats. Adult blue crabs were the primary predator, responsible for 79% of the predatory interactions that were captured in the images (Table 4, Fig. 10A). Northern puffers *Spherooides maculatus* and striped burrfish *Chilomycterus schoepfi* were also seen feeding on tethered juvenile crabs (Table 4, Fig. 10B,C). Additionally, an oyster toadfish was found on one of the tethers at the end of a trial, having swallowed the juvenile crab whole (Fig. 10D).

DISCUSSION

Juvenile survival

Our field experiments examined the relationship between juvenile blue crab survival, crab size, and SAV cover in York River nursery habitats. Our primary goal was to determine if

ontogenetic habitat shifts by juveniles between different habitats are driven by the fractal mechanism whereby the availability of and access to suitably scaled refuge decreases as body size increases, as observed in Caribbean spiny lobster *Panulirus argus* (Lipcius et al. 1998), or whether there is a trade-off between predation risk and foraging efficiency (*sensu* Werner & Gilliam 1984). The novel result of this study was the apparent lack of an interaction effect between crab size and habitat on juvenile survival, as hypothesized in the current paradigm of blue crab nursery use, which emphasizes suitably scaled refuges. Instead, juvenile survival increased additively with both blue crab size and SAV cover. Thus, the ontogenetic habitat shift by juvenile blue crabs is likely driven by a trade-off between predation risk and foraging efficiency, rather than a reduction of suitably scaled refuges as juveniles grow.

Seagrass beds are considered the primary nursery habitat for many estuarine and marine species because of the high abundances of juveniles found in these habitats (Heck & Thoman 1984, Beck et al. 2001, Heck et al. 2003). In Chesapeake Bay, abundance of juvenile blue crabs <20 mm CW is higher in seagrass beds than in unvegetated habitats, with densities as much as an order of magnitude higher in SAV (Orth & van Montfrans 1987, Pile et al. 1996, Lipcius et al. 2007). There are two primary functions that explain the high abundance of juveniles in seagrass beds. The first is predator refuge – the structural complexity of the vegetation inhibits predator detection and capture of prey, increasing juvenile survival (Wilson et al. 1990, Perkins-Visser et al. 1996, Pile et al. 1996, Hovel & Lipcius 2001, Orth & van Montfrans 2002). The second function is food supply (Orth et al. 1984, Seitz 2011, Glaspie & Seitz 2017) – the abundance and diversity of small prey items enhances energy intake and foraging efficiency, increasing juvenile growth (Beck et al. 2001, Perkins-Visser et al. 1996).

The current paradigm of blue crab habitat use posits that survival decreases in seagrass once juveniles reach a certain size because they have outgrown the small refuges offered by SAV (Lipcius et al. 2007, Johnston & Lipcius 2012). This conceptual model of habitat use requires an interaction effect between crab size and habitat on juvenile survival as demonstrated by Johnston & Lipcius (2012). Our results were consistent with previous studies, demonstrating that juvenile blue crabs experience increased survival in vegetated habitats compared to unvegetated habitats (Hines 2007, Lipcius et al. 2007). However, contrary to the current paradigm, there was no interaction between crab size and habitat, indicating that larger juveniles do not suffer increased mortality in vegetated habitats. Field observations of high abundances of juveniles >30 mm CW in seagrass beds support our results (Hines 2007). Furthermore, soft crabs (recently molted) of all sizes often seek refuge in seagrass beds during molting to reduce their risk of predation because they are vulnerable without the protection of a hard carapace (Ryer et al. 1997).

To further investigate the predator refuge role of vegetation, we examined the influence of SAV cover on juvenile blue crab survival. In general, survival increases with habitat complexity (i.e. shoot density, biomass) and areal cover because more SAV results in more barriers between predators and prey (Hovel & Lipcius 2001, Orth & van Montfrans 2002, Hovel & Fonseca 2005). Our study determined that vegetation cover has a marginally significant, positive effect on blue crab survival, and there was no interaction, indicating that increasing SAV cover is beneficial for juvenile blue crabs regardless of size. Limited observations for very small (<15 mm CW) and very large (>40 mm CW) crabs, particularly at low SAV cover (<50%), could have biased our model results; due to the absence of experimental plots with 5-45% cover, the form of the habitat-survival function could be nonlinear. However, the lack of observations at low-moderate SAV cover is representative of the available habitats at Sandy Point and Goodwin

Islands; SAV cover at these two locations was either very high (70-100%) or nonexistent (2016 Distribution of Submerged Aquatic Vegetation in the Chesapeake Bay and Tributaries and Coastal Bays).

The second function that contributes to high abundances of juveniles in seagrass beds is food supply (Orth et al. 1984, Seitz 2011), through augmented juvenile growth (Perkins-Visser et al. 1996, Beck et al. 2001, Seitz et al. 2005). In their early life stages (<30 mm CW), juvenile blue crabs feed primarily on bivalves, plant matter, detritus, polychaetes, amphipods, and shrimp (Laughlin 1982, Lipcius et al. 2007, Seitz et al. 2011). Not only does seagrass provide nutrition in itself, but increasingly complex vegetation can also increase food availability as the grass blades provide surface area on which epiphytes can grow (Orth et al. 1984). Additionally, seagrass beds support a diverse community of organisms, including epifauna (e.g. shrimp, gastropods), infauna (e.g. amphipods, bivalves), and mobile species (e.g. fishes, crabs) (Heck & Thoman 1984, Orth et al. 1984), all of which juvenile blue crabs consume. The large quantities of suitable prey support faster growth rates of small juveniles in seagrass than in unvegetated habitats (Perkins-Visser et al. 1996). Thus, blue crabs can optimize their foraging efficiency and growth in their early juvenile stages by settling in sheltered seagrass beds where small prey items are readily accessible.

Blue crab survival also increases with body size, a phenomenon that has been demonstrated for many marine species (Hart & Hamrin 1988, Morley & Buckel 2014, Long et al. 2015, Krueger et al. 2016, Tucker et al. 2016). Decreased predation mortality with size can be attributed to two mechanisms: physical capture limitations and handling difficulty. A relationship between jaw morphology and prey selectivity suggests that gape limitations of predators often restrict consumption of larger prey items (Hart & Hamrin 1988). Handling difficulty can also

reduce the likelihood of a successful predation event regardless of a predator's gape, as handling becomes increasingly difficult with larger prey. For example, juvenile bluefish (131-140 mm TL) capture efficiency is similar between small and large bay anchovy, but large anchovies are more likely to be lost during prey manipulation, and thus more likely to survive the encounter (Morley & Buckel 2014).

As juvenile blue crabs grow, they are less susceptible to gape-limited predators, and less palatable as their carapace hardens and their spines become more prominent. Larger crabs are also more likely to be aggressive and exhibit agonistic behaviors if threatened by a potential predator (Hines & Ruiz 1995). Thus, the probability of survival is higher for larger crabs than smaller ones, even without other physical forms of refuge such as structured habitats. Other studies have corroborated our results, suggesting that juvenile blue crabs experience a relative size refuge from predation once they reach 20-30 mm CW (Pile et al. 1996).

With increasing body size, energetic demands also increase (Werner & Gilliam 1984, Wahle 1992). For blue crabs, increasing energy requirements are reconciled by an ontogenetic diet shift; large juveniles and adults primarily feed on more substantial prey items such as clams and fishes (Laughlin 1982, Lipcius et al. 2007). Blue crab ontogenetic habitat shifts may partially result from ontogenetic diet shifts, as well as density-dependent migration (Pile et al. 1996), considering that both shifts occur at a similar developmental stage (20-30 mm CW). Distribution and growth of juvenile blue crabs >25 mm CW is driven primarily by clam density and accessibility, as some clam species have highest density in unvegetated sand and mud flats (Seitz et al. 2003, 2005), and juvenile crab densities are also an order of magnitude lower (Lipcius et al. 2005, 2007). Once juveniles reach 25 mm CW, the abundance of small prey items in seagrass beds may not be energetically efficient, resulting in migration to more profitable unvegetated

habitats where clams are abundant and accessible, and conspecific competitors are less dense (Mansour & Lipcius 1991, Seitz et al. 2003, 2005).

Our field experiments confirmed that complex SAV habitats increase juvenile blue crab survival, and that larger juveniles experience a size refuge from predation, reducing the need for structural refuge. We propose that small juvenile instars remain protected in SAV and forage on the abundant prey within the grass bed until they become so large that the food supply in the grass bed is no longer nutritionally sufficient for optimal foraging. Juvenile blue crabs 25-30 mm CW move into unvegetated sand or mud flats to avoid density-dependent growth and agonism (Mansour & Lipcius 1991) by exploiting higher densities and greater accessibility of more-profitable prey, such as the Baltic clam *Limecola balthica*, in areas where conspecific density is low. Therefore, it is likely that the abundance and diversity of both predators and prey influence the survival and habitat use of juvenile blue crabs, as occurs for the Caribbean spiny lobster (Mintz et al. 1994).

Predator identification

The second goal of our field experiments was to identify key predators of juvenile blue crabs within York River nursery habitats using advanced camera technology. In images of predation events, adult blue crabs, northern puffers, striped burrfish, and oyster toadfish were identified as predators of juveniles in seagrass beds and sand flats. The high frequency of successful predation events by adult blue crabs suggests that cannibalism is an important source of juvenile mortality, and may be as or more influential to blue crab population dynamics than predation by fish predators.

Over the last two decades, advances in camera technology have made quality, high-definition cameras easily accessible to a larger group of scientific investigators (e.g. students, NGOs) (Bicknell et al. 2016). Although camera technology is capable of providing novel insight into animal behavior in natural habitats, advanced cameras still have limitations, such as battery longevity and visibility (Bicknell et al. 2016). In some cases, these limitations could compromise the integrity of the study by introducing bias.

In our tethering experiments, we used GoPros to capture photographic evidence of predation events to identify predators of juvenile blue crabs in seagrass beds and sand flats. In 2016, predators were identified in 58% of the recorded trials. Dense vegetation and the limited range of the infrared lights used during the night trials were likely responsible for missed predation events. Additionally, GoPro battery life was limited to 6 h, and because some trials were >6 h, predation events could have easily occurred after the camera stopped taking pictures. All recorded trials in which predators were not identified were either conducted at night, in dense vegetation, or had a trial duration of 24 h.

The set-up of the camera may have also introduced a bias against fish or particular predator species due to differences in predatory behavior. Blue crabs are primarily benthic foragers, using chemosensory and tactile cues to locate prey, slowly searching the bottom and excavating buried prey with their walking legs (Blundon & Kennedy 1982, Lipcius & Hines 1986). Thus, blue crabs may have been more likely to be photographed than finfish predators that attack their prey swiftly, resulting in a higher proportion of observed predation events by blue crabs than other predators. Finfish such as striped bass *Morone saxatilis*, Atlantic croaker *Micropogonias undulatus*, and silver perch *Bairdiella chrysoura* were seen in images, swimming in the vicinity of the tethered crab, but a predation event was never witnessed. In addition to

actively foraging fish, the tethering set-up may have been biased against ambush predators such as summer flounder *Paralichthys dentatus*. Ambush predators often rely on prey movement to capture their prey, and the limited mobility of tethered crabs reduces the likelihood that an ambush predation event would occur during a tethering experiment.

Despite the potential biases of our experimental set-up, our results support previous findings that cannibalism is a primary component of juvenile blue crab mortality (Darnell 1958, Mansour 1992, Hines & Ruiz 1995, Ryer et al. 1997, Hines 2007). In field and laboratory tethering experiments, cannibalism by large blue crabs was the source of 75-96% of juvenile mortality (Hines & Ruiz 1995), which corroborates the 79% of predation events captured in images of our tethering experiments. Additionally, diet studies from both Louisiana and Chesapeake Bay confirmed that cannibalism has the potential to contribute significantly to juvenile mortality, with pieces of juvenile blue crabs in up to 45% of adult crab stomachs (Mansour 1992) and comprising an average of 13% of the diet by volume (Darnell 1958).

Northern puffers have also been identified as predators of juvenile blue crabs in prior studies, although Van Engel (1987) argued that puffers were only observed feeding on juvenile blue crabs when artificially confined; they had not been known to feed on crabs in natural circumstances. Another previous study conducted similar tethering experiments with underwater video and consistently observed northern puffers successfully preying upon tethered juvenile blue crabs (Moody 2003). However, these tethering experiments may not be representative of natural predation by puffers, as tethering limits a crab's ability to evade predators (Zimmer-Faust et al. 1994). Similarly, striped burrfish are slow-swimming predators, and thus may have only consumed juvenile blue crabs due to tethering constraints. A single review paper identified striped burrfish as a potential predator of blue crabs (Guillory & Elliot 2001), but the study

referred to in the review only found hermit crabs and unidentified crab pieces in the stomachs of several burrfish (Linton 1905). Although our results suggest that predation by northern puffers and striped burrfish may play a role in juvenile mortality in nursery habitats, diet studies of field-collected fishes should be conducted to confirm that they feed on juvenile blue crabs in nature.

A single oyster toadfish was found on a tether after an experimental trial, having swallowed the tethered juvenile whole. Similar events occurred during tethering experiments in seagrass beds near Manahawkin, New Jersey (Wilson et al. 1987), and unvegetated subtidal flats in upper (Schwartz & Dutcher 1963) and lower (Lipcius et al. 2005) Chesapeake Bay. Given their abundance in structured habitats throughout Chesapeake Bay tributaries (R.N.L. pers. comm.), oyster toadfish may contribute significantly to juvenile crab mortality in seagrass beds.

Our tethering experiments and accompanying GoPro imagery revealed cannibalism to be a major source of juvenile blue crab mortality, as well as some novel finfish predators. A comprehensive list of predators of juvenile blue crabs is necessary to determine the relative effects of predator species on the blue crab population, and to understand the role of predation and cannibalism in blue crab population dynamics.

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TABLES

Table 1. AIC calculations for the logistic regression models corresponding to the different hypotheses for juvenile blue crab survival represented by g_i . k is the number of parameters, including variance (σ^2), in model g_i ; AIC_C is the bias-corrected AIC value; Δ_i is the difference in the AIC_C value between model g_i and the best model; and w_i is the probability that model g_i is the best model in the set. Size is crab size in mm carapace width; SAV cover is the percent cover of submerged aquatic vegetation at the tether location; duration is the time interval of the trial in hours; and time is a categorical factor with day and night levels.

Model	Variables	k	AIC_C	Δ_i	w_i
g_1	Size (S)	3	185.09	23.86	<0.01
g_2	SAV cover (SC)	3	184.99	23.76	<0.01
g_3	S + SC	4	186.71	25.47	<0.01
g_4	S + SC + (S x SC)	5	187.75	26.51	<0.01
g_5	S + SC + Duration (D)	5	161.24	0	0.51
g_6	S + SC + D + Time (T)	6	161.32	0.08	0.49
g_7	Null	2	183.27	22.03	<0.01

Table 2. Parameter estimates from logistic regression model g_5 for juvenile blue crab survival.

Parameter	Variable	Estimate	SE	z	p
β_0	Intercept	0.6047	0.7511	0.805	0.4207
β_1	Size	0.0556	0.0257	2.165	0.0304
β_2	SAV cover	0.0095	0.0049	1.908	0.0564
β_3	Trial duration	-0.3163	0.0661	-4.785	<0.0001

Table 3. Parameter estimates from the best logistic regression model for juvenile blue crab survival using a categorical habitat factor.

Parameter	Variable	Estimate	SE	z	p
β_0	Intercept	0.4753	0.7645	0.622	0.5342
β_1	Size	0.0568	0.0266	2.136	0.0327
β_2	Habitat	0.8784	0.4703	1.868	0.0618
β_3	Trial duration	-0.3592	0.0760	-4.729	<0.0001
β_4	Time	0.6106	0.4143	1.474	0.1405

Table 4. Identified predators of juvenile blue crabs and their predation frequencies from the tethering experiments. Relative predation frequencies are given in parentheses as the proportion of all events.

Species	Predation Frequency
Blue crab (<i>Callinectes sapidus</i>)	27 (0.79)
Northern puffer (<i>Sphoeroides maculatus</i>)	4 (0.12)
Striped burrfish (<i>Chilomycterus schoepfi</i>)	2 (0.06)
Oyster toadfish (<i>Opsanus tau</i>)	1 (0.03)

FIGURES

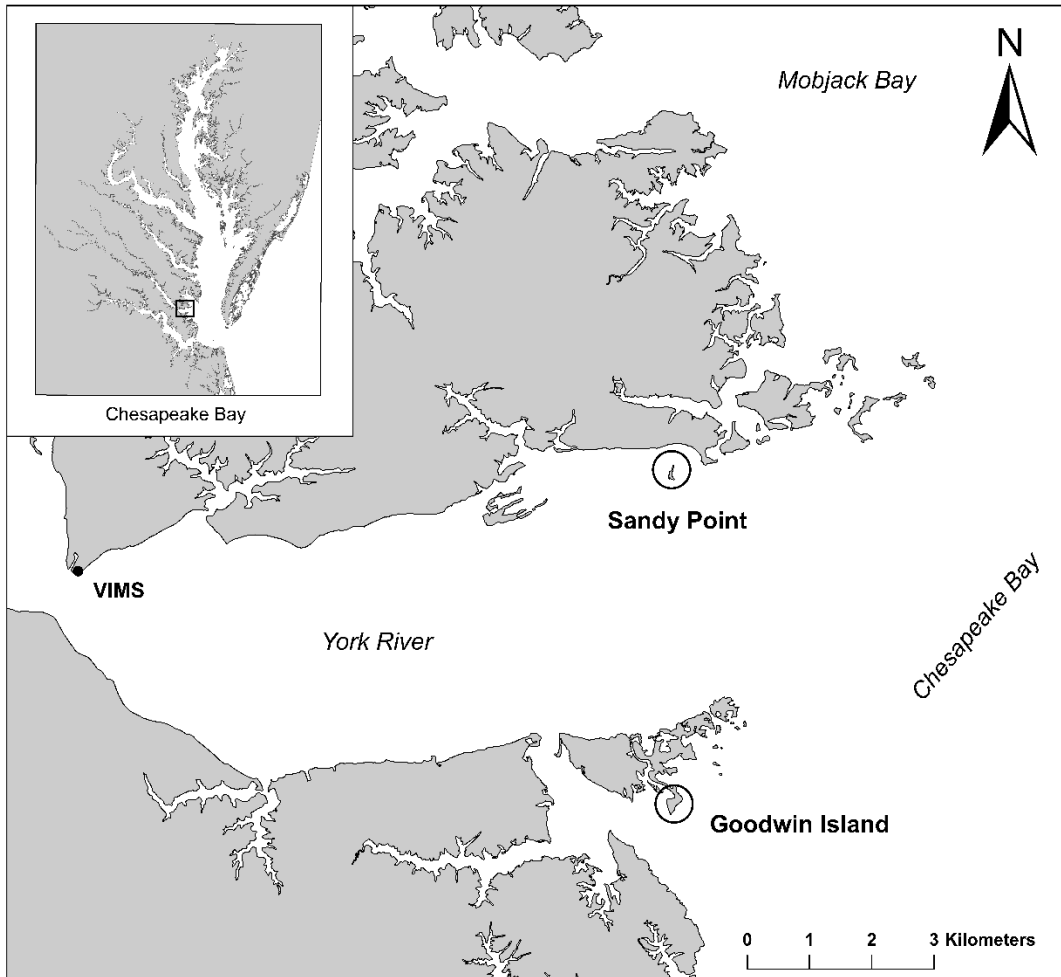
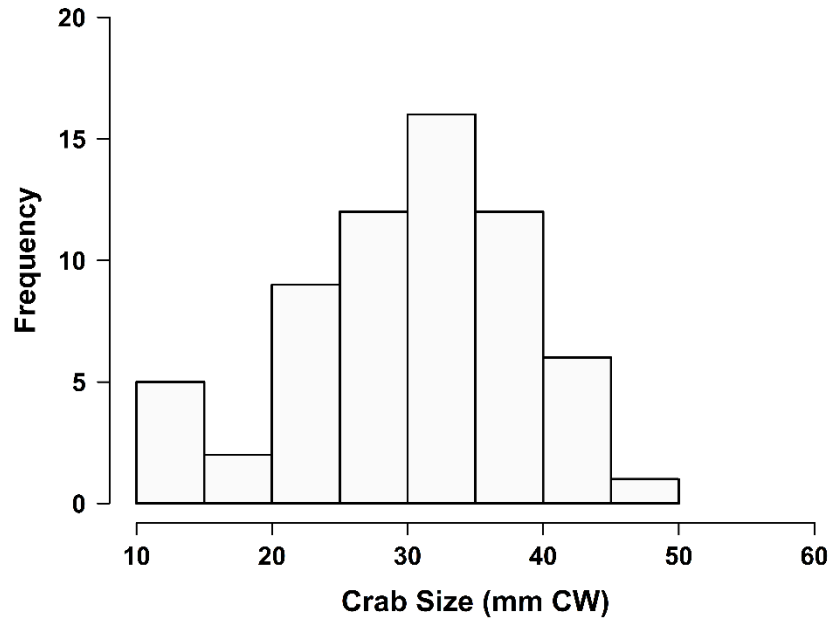


Figure 1. Map of the study areas in the lower York River, VA. Tethering experiments were conducted at a vegetated and unvegetated site at Sandy Point (July 2016) and Goodwin Islands (July-August 2016).

A) Sand



B) Seagrass

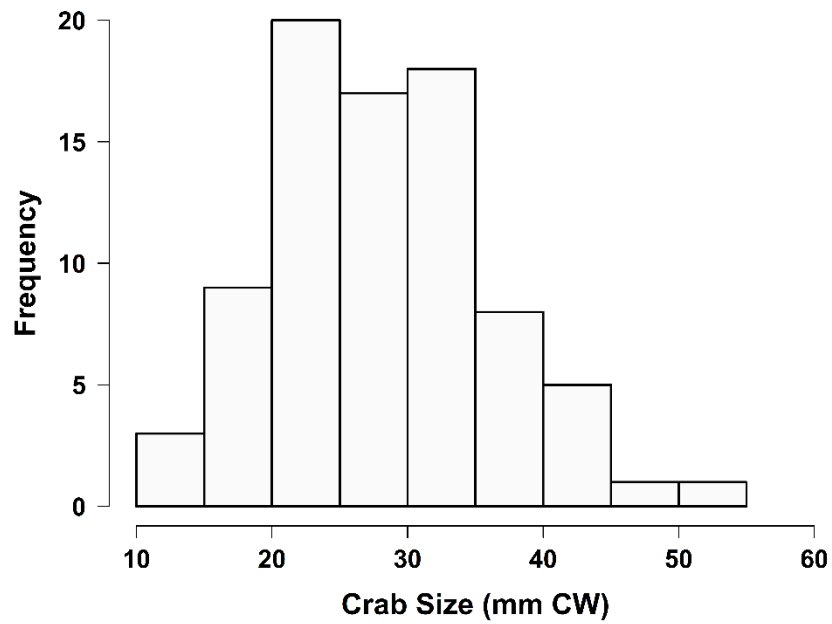


Figure 2. Size frequency of blue crabs tethered in (A) sand and (B) seagrass habitats in the 2016 field experiment.

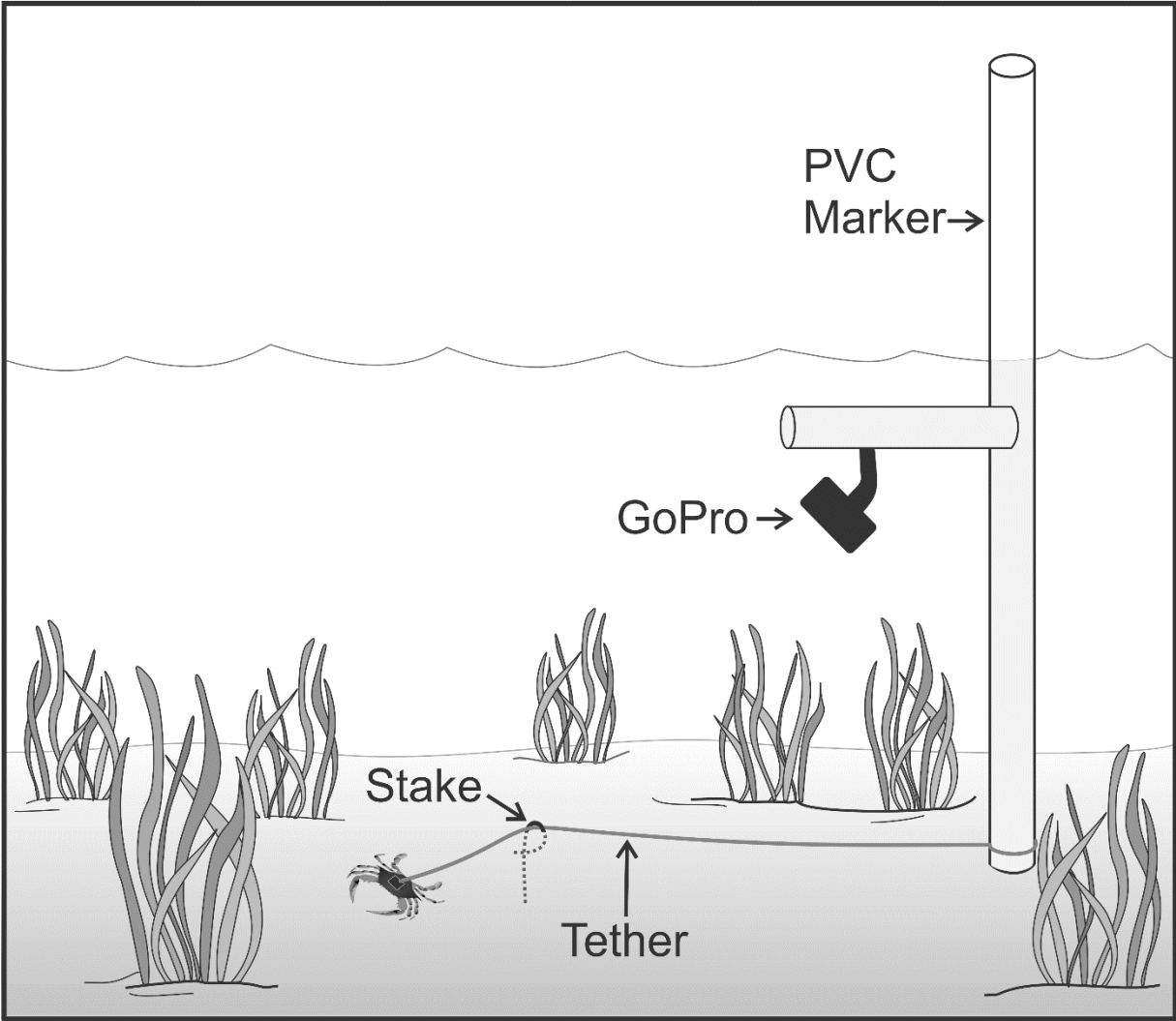


Figure 3. Schematic diagram of the tether set-up used in the experiments. The PVC marker was 1 m away from the tethering stake, and the crab was attached to a 20-cm tether. The GoPro camera was oriented such that the field of view encompassed the entire range of the tether. Juvenile crab not drawn to scale.

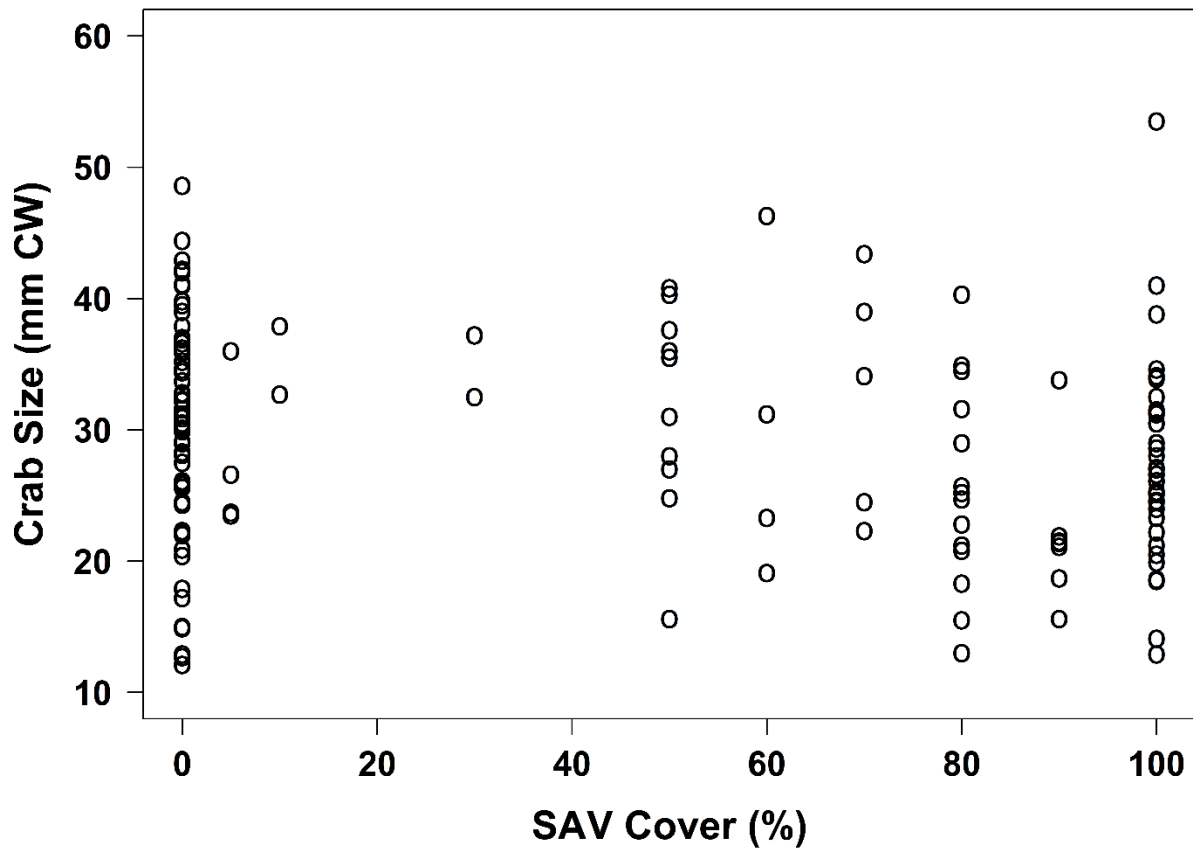


Figure 4. Crab sizes tethered in various levels of SAV cover during the 2016 field experiment.

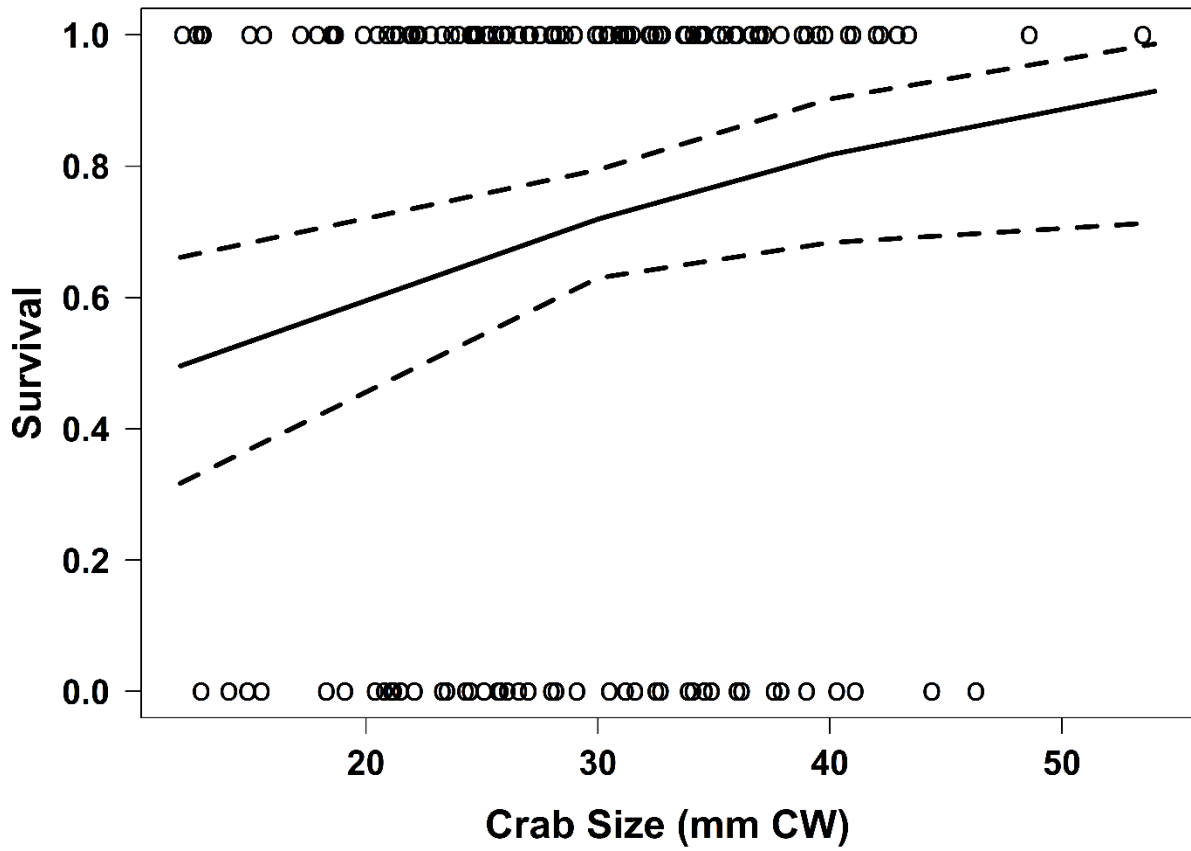


Figure 5. Effect of crab size on juvenile blue crab survival based on the best model (g_5). Circles represent observations of juvenile survival (1 = alive, 0 = dead). The solid line is the predicted survival probability; the dashed lines represent the 95% confidence interval.

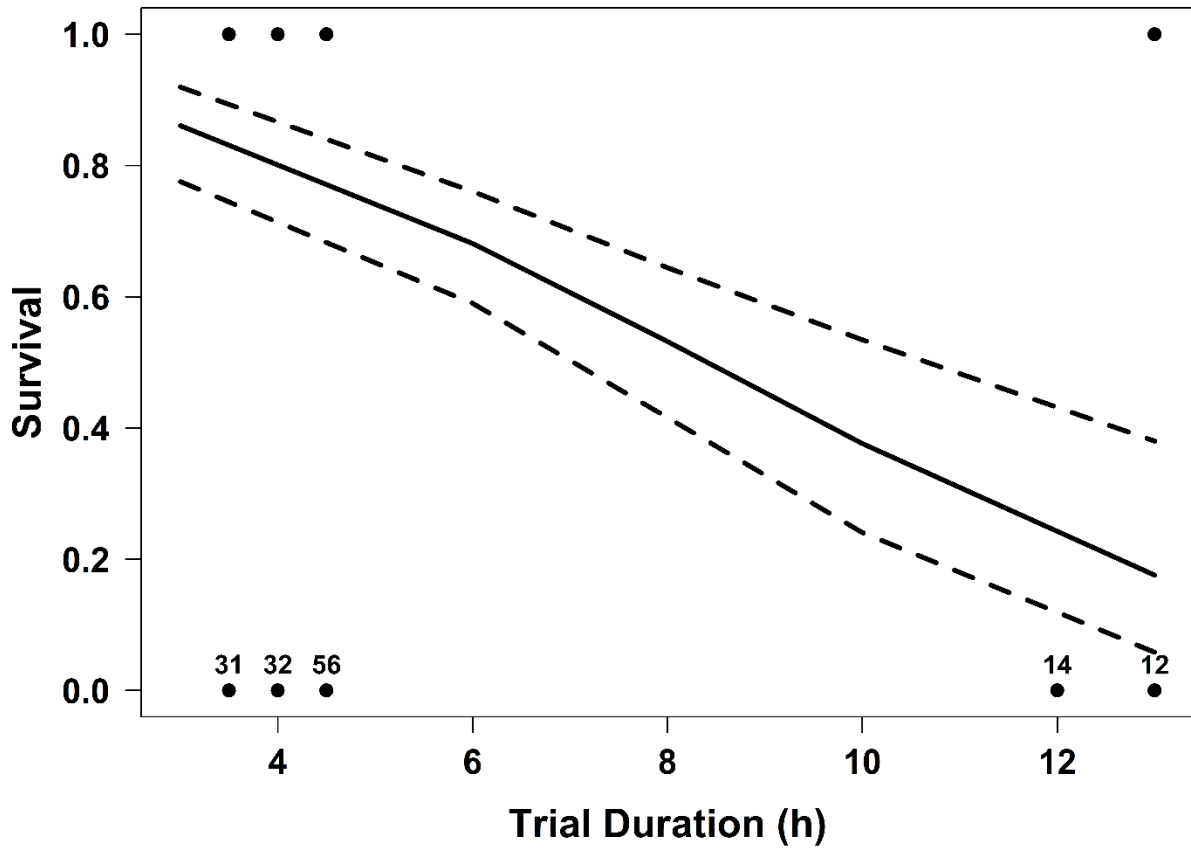


Figure 6. Effect of trial duration on juvenile blue crab survival based on the best model (g_5). Circles represent juvenile survival observed (1 = alive, 0 = dead) for the trial durations that were executed during the tethering experiments; the numbers represent the sample sizes of each duration. The solid line is the predicted survival probability; the dashed lines represent the 95% confidence interval.

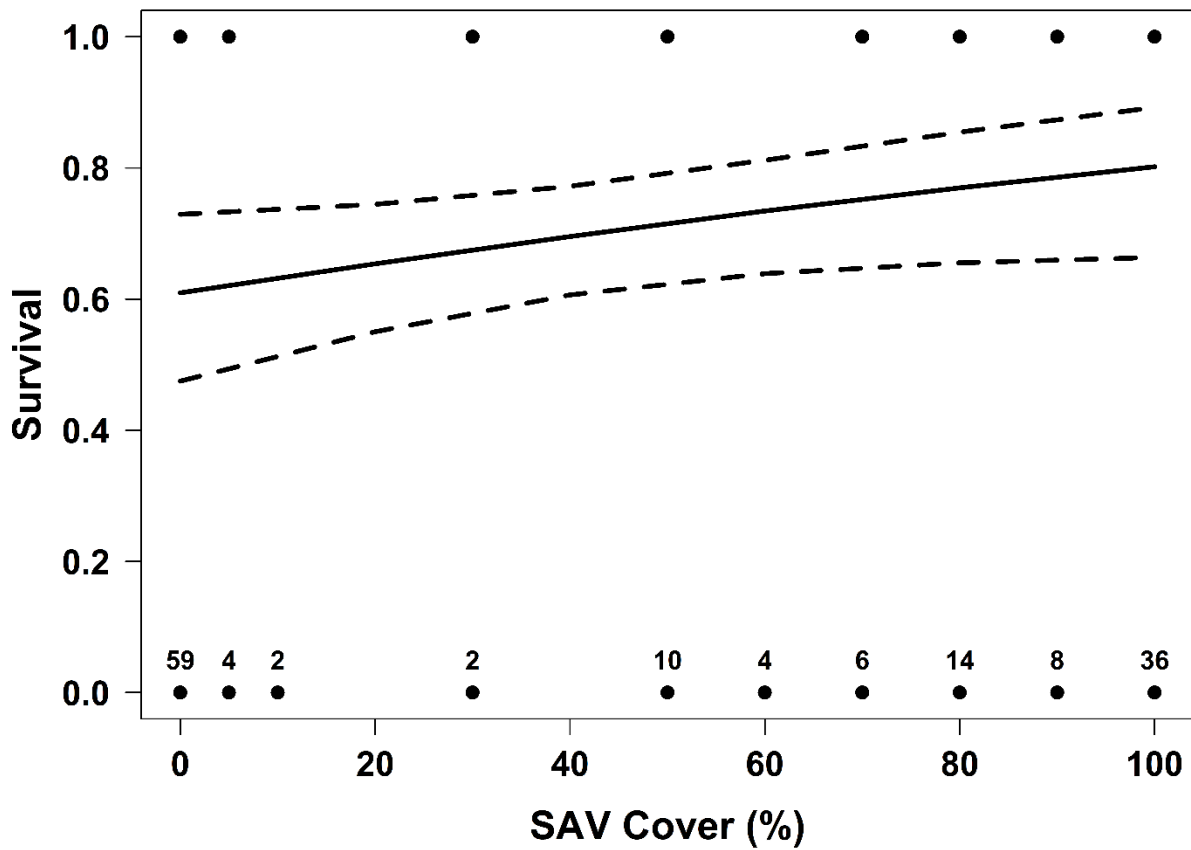


Figure 7. Effect of SAV cover on juvenile blue crab survival based on the best model (g_5). Circles represent juvenile survival observed (1 = alive, 0 = dead) for levels of SAV cover that were used during the tethering experiments; the numbers represent the sample sizes of each level of SAV cover. The solid line is the predicted survival probability; the dashed lines represent the 95% confidence interval.

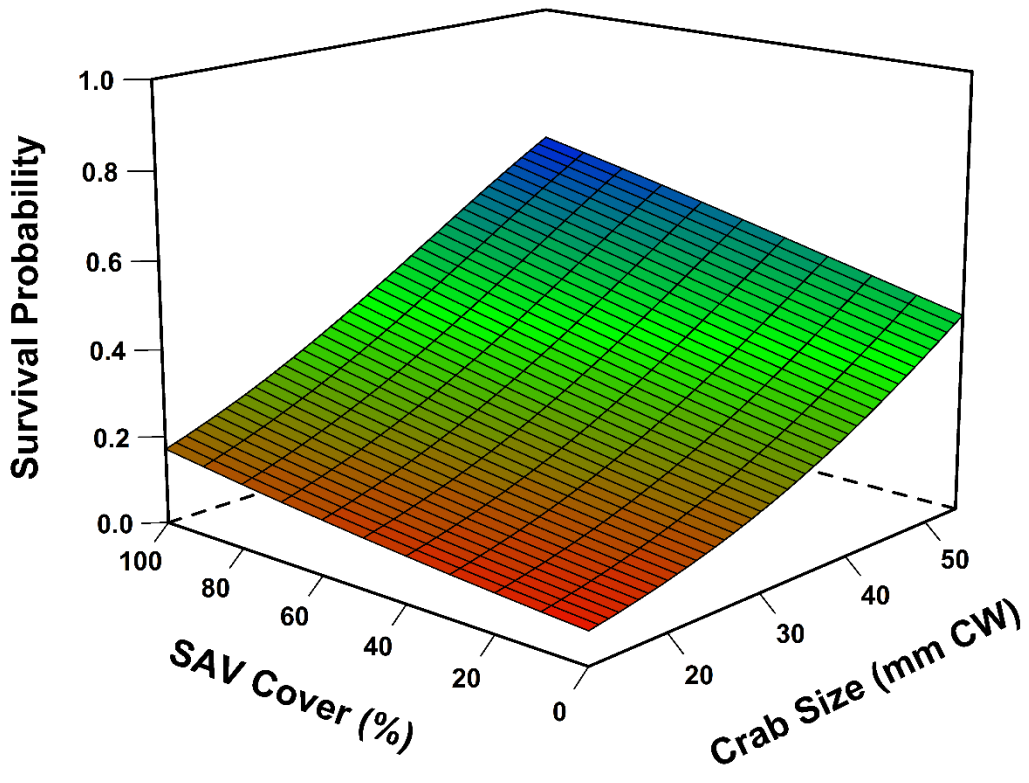


Figure 8. Juvenile blue crab probability of survival as a function of crab size and SAV cover at a standard trial duration of 12 h, derived from equation 2.

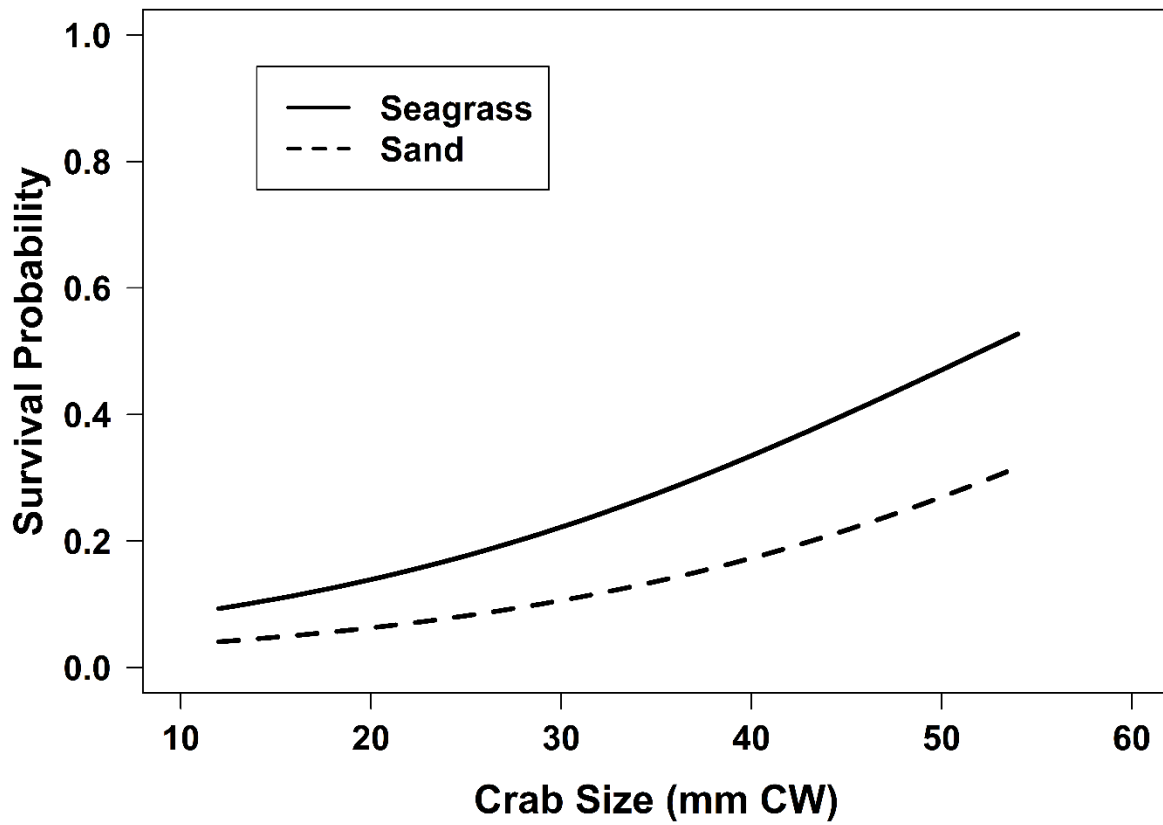


Figure 9. Juvenile blue crab survival probability as a function of crab size by habitat. The probabilities are derived from equation 1, using the parameter estimates from the best logistic regression model with the categorical habitat factor, holding time constant (day).

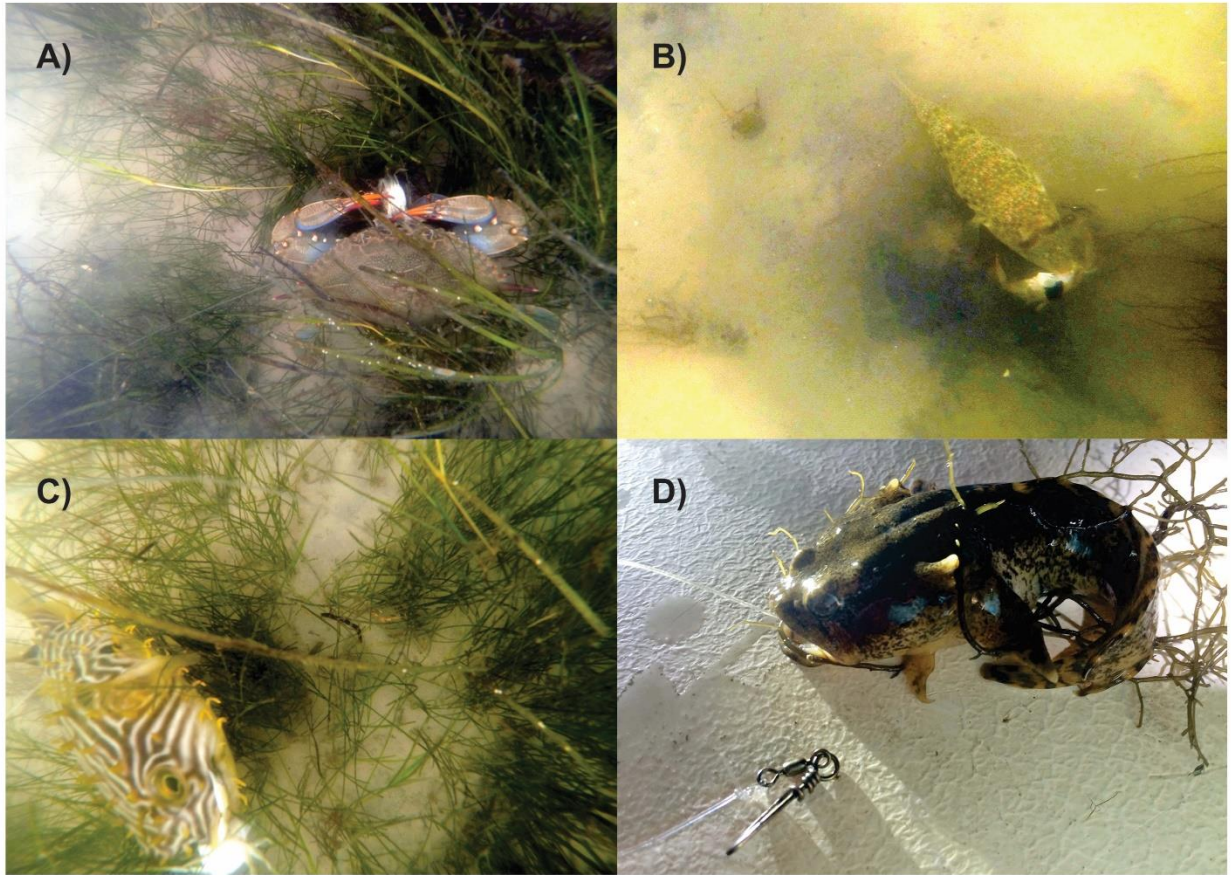


Figure 10. GoPro photos of predators of juvenile blue crabs in the tethering experiments: (A) adult blue crab; (B) northern puffer; (C) striped burrfish; (D) oyster toadfish. The tethered juvenile is seen in the mouth of predators A-C. The oyster toadfish (D) was stuck on the tether after swallowing the juvenile crab whole.

CHAPTER 2

Predator identification and predation impacts on juvenile blue crabs in Chesapeake Bay nursery habitats

ABSTRACT

Predator populations have significant impacts on prey recruitment success, and consequently, prey population dynamics. In Chesapeake Bay, the blue crab *Callinectes sapidus* is an ecologically dominant and economically valuable fishery species that has experienced substantial fluctuations in abundance since the 1990s. Low juvenile abundance and recruitment suggest that predation is a primary driver of blue crab population dynamics. We identified the key predators of juvenile blue crabs in Chesapeake Bay nursery habitats using gut content analyses. Adult blue crabs, striped bass *Morone saxatilis*, red drum *Sciaenops ocellatus*, silver perch *Bairdiella chrysoura*, weakfish *Cynoscion regalis*, Atlantic croaker *Micropogonias undulatus*, and oyster toadfish *Opsanus tau* were identified as predators of juvenile blue crabs. We also determined the relative impacts of these predators on juvenile mortality based on their frequency of consumption and diet proportions. Using these metrics, we identified adult blue crabs, striped bass, red drum, silver perch, and weakfish as major predators of juvenile crabs, while Atlantic croaker and oyster toadfish play minor roles in juvenile mortality in nursery habitats. Juvenile blue crabs were more frequently consumed in seagrass beds than in unvegetated sand flats. Despite the predator refuge offered by the structured habitat, the greater densities of foraging predators in grass beds lead to an increased probability of capturing predators containing juvenile blue crabs in these habitats. Based on our results, we created a revised food web for blue crabs in Chesapeake Bay that also includes silver perch and weakfish as key predators of juvenile crabs in Bay nursery habitats.

INTRODUCTION

Predator-prey population dynamics

Predator populations can have significant impacts on prey population dynamics through consumptive and non-consumptive effects (Estes & Palmisano 1974, Tonn et al. 1992, Gibson 1994, Carr & Hixon 1995, Kintzing & Butler 2014). A classic example of the consumptive effects of predators on prey populations is the trophic cascade involving sea otters and sea urchins in the Aleutian archipelago kelp forests (Estes & Palmisano 1974). High densities of sea otters *Enhydra lutris* lead to increased predation on sea urchins *Strongylocentrotus* spp., releasing the kelp forests from intense grazing pressure; the result is a substantial increase in the nearshore kelp beds and their associated communities. This example demonstrates how increases and decreases in predator (and herbivore) abundance influence prey (and algal) abundance through direct and indirect trophic interactions.

Non-consumptive predator effects occur when a predator's presence induces changes in prey behavior that are often suboptimal. For example, when long-spined sea urchins *Diadema antillarum* were exposed to the odor of one of their predators, spotted spiny lobster *Panulirus guttatus*, the urchins ceased foraging and instead exhibited predator avoidance behaviors (Kintzing & Butler 2014). These indirect interactions between predators and prey often result in suboptimal foraging through reductions in time spent searching for prey or foraging in energetically inadequate refuge habitats (Brown 1999). Assessing predator effects on prey populations can thus improve understanding of trophic structure and food web dynamics.

In marine and estuarine systems, recruitment is a crucial component of population dynamics that determines population abundance in subsequent years (Minchinton & Scheibling 1991, Lipcius & Stockhausen 2002). Larval recruitment is often regulated by consumptive and

non-consumptive predator effects (Tonn et al. 1992, Gibson 1994, Carr & Hixon 1995). New recruits and young juveniles are particularly vulnerable to predation due to their small size and limited experience and evasion capabilities (Hart & Hamrin 1988, Pile et al. 1996, Morley & Buckel 2014, Tucker et al. 2016). To reduce the risk of predation, new recruits and juveniles typically settle in structured nursery habitats, which, by definition, promote faster growth rates and higher survival than other habitats (Beck et al. 2001). Thus, successful recruitment to the adult portion of the population is often dependent on the availability of suitable nursery habitat (Sundblad et al. 2014).

Here we examine the influence of predators on one of the most ecologically and economically important fishery species in Chesapeake Bay: the blue crab *Callinectes sapidus*. The Chesapeake Bay blue crab population has experienced regular fluctuations in abundance since the fishery initially opened at the end of the nineteenth century (Stagg & Whilden 1997); however, severe declines in the late 1990s and early 2000s, and again in 2012-2013, suggested that reduced recruitment due to high juvenile mortality may be a key limiting factor of blue crab population size in the Bay. Increased fish abundances and watermen's anecdotal accounts of juvenile crab consumption by fishes motivated studies examining the role of natural mortality via predation on the blue crab population with a focus on nursery habitats, particularly seagrass beds.

Blue crab nursery habitat use

Seagrass beds are the primary nursery habitat for many species in Chesapeake Bay, including the blue crab (Heck & Thoman 1984). After undergoing larval development in the coastal waters near the mouth of the Bay, blue crab megalopae (postlarvae) reinvade the estuary and settle into seagrass beds, where they experience rapid growth and quickly transform into the

first benthic juvenile instar (Orth & van Montfrans 1987, Metcalf & Lipcius 1992, Lipcius et al. 2007). Despite higher abundances of foraging predators in submerged aquatic vegetation (SAV), the refuge provided by the structure of SAV enhances juvenile survival relative to unvegetated habitats (Wilson et al. 1990, Perkins-Visser et al. 1996, Pile et al. 1996, Hovel & Lipcius 2001, Orth & van Montfrans 2002). Blue crabs remain in vegetated primary nursery habitats until they reach 20-30 mm carapace width (CW), at which point they start to move into unvegetated secondary nursery habitats such as sand or mud flats (Orth & van Montfrans 1987, Pile et al. 1996, Lipcius et al. 2005, 2007). At this stage, juveniles have reached a size refuge and are less vulnerable to gape-limited predators (Pile et al. 1996, Bromilow & Lipcius in press).

Although seagrass beds provide some refuge from predation for juvenile blue crabs, mortality due to cannibalism and the diverse predators in seagrass beds may be severe (Lipcius et al. 2005, Johnston & Lipcius 2012). A prolonged period of low recruitment in the 1990s and 2000s (Lipcius & Stockhausen 2002) and a sharp decline in abundance of juvenile blue crabs in 2012 suggested predation as the culprit, particularly in 2012 when fishery management restrictions prevented overfishing from occurring. Consequently, we sought to advance our understanding of the role of predators in driving recruitment dynamics of the blue crab, which serves as a model system for benthic species.

Objectives

Our objectives were to: (1) identify predators of juvenile blue crabs in Chesapeake Bay nursery habitats (i.e. seagrass beds, sand flats) using gut content analysis; (2) synthesize data from three field studies to determine the relative impacts of predators on juvenile crab mortality; and (3) generate a revised food web for juvenile blue crabs in Chesapeake Bay using a

comprehensive list of key predators. The purpose of our studies was to provide insight into the ecological drivers of blue crab population dynamics, focusing on predation and juvenile mortality.

The first study was conducted in fall 1998, and assessed the feeding impacts of three recreationally and commercially important finfish predators (striped bass *Morone saxatilis*, Atlantic croaker *Micropogonias undulatus*, and red drum *Sciaenops ocellatus*) on juvenile blue crabs inhabiting a York River seagrass bed. The study aimed to quantify the abundance of the three species in the grass bed and to ascertain the feeding habits of those species as predators of blue crabs.

The second study was conducted in the spring and fall of 2004, and addressed the contention that reduced blue crab abundance in Chesapeake Bay in the early 2000s was a result of increased predation by finfish predators. The primary goal of the study was to quantify the impacts of fish predation on juvenile blue crabs inhabiting SAV throughout Chesapeake Bay by analyzing the gut contents of finfish predators (i.e. striped bass, Atlantic croaker, red drum) collected in SAV and by determining the density of juvenile blue crabs in those locations.

The third study was conducted in the summer and fall of 2016, and was prompted by the blue crab population decline and apparent increase in juvenile mortality in 2012-2013. This study aimed to identify a broader range of predators of juvenile blue crabs in nursery habitats and to determine their relative impacts on juvenile mortality. In addition to predator identification, effects of environmental factors (i.e. habitat, time of day) on the consumption of juvenile blue crabs by various predators were also examined.

MATERIALS AND METHODS

Study sites

The first study (Fall 1998) was conducted on October 20, 1998 at three sites at Guinea Marsh (Fig 1). Guinea Marsh is a shallow, tidal region at the mouth of the York River, a tributary of the lower Chesapeake Bay. The region is characterized by extensive seagrass beds adjacent to salt marsh patches. The seagrass beds are dominated by eelgrass *Zostera marina* and widgeon grass *Ruppia maritima*, with occasional abundances of the exotic red alga *Gracilaria vermiculophylla* (A.M.B. pers. obs.).

The second study (Spring and Fall 2004) was conducted in April-June (spring) and September-November (fall) of 2004 in three regions of Chesapeake Bay: Western Shore, Mid-Bay, and Eastern Shore. Western Shore sites included Goodwin Islands, Mobjack Bay, and Dameron Marsh (Fig. 1). Mid-Bay sampling sites included Tangier Island, Goose Island, and Smith Island (Fig. 1). Eastern Shore sampling sites were located at Hungars Creek, Parkers Island, and the Big Annemessex River (Fig. 1). Sampling locations in this study were established from aerial photography and onsite verification to ensure the presence of SAV.

In the third study (Summer and Fall 2016), predator sampling was conducted in August 2015 and July-October 2016 at Goodwin Islands and Sandy Point in the York River (Fig. 1). Sandy Point is on the northern shore of the river mouth, near Guinea Marsh, and Goodwin Islands is on the southern shore of the river. Similar to Guinea Marsh, these are shallow, tidal regions with substantial seagrass beds comprising eelgrass, widgeon grass, and red algae. The seagrass beds at both locations are adjacent to expansive unvegetated sand flats.

Field and laboratory procedures

Fall 1998

Six gill nets (30.5 m x 1.8 m; 8.9-cm mesh) were deployed in Guinea Marsh seagrass beds beginning at 0800-0900 h on October 20, 1998. Gill nets were fished every 3 h until 2100 h, yielding four samples from each of the six nets, three during the day and one at night. Sampling occurred on both the falling and rising tides. Only fish known to forage specifically on macroinvertebrates were selected for gut content analysis. Fish were removed from the nets, sorted into plastic bags, and immediately covered with a thick layer of ice in coolers for return to the laboratory.

In the laboratory, fish were identified and measured to the nearest 0.1 cm total length (TL). Stomach and intestines were removed from each individual and immediately frozen for detailed gut content analysis. Prey items were identified to species when possible and enumerated. For individuals containing dismembered and crushed prey items, body parts were categorized to estimate the total number of prey consumed.

Spring and Fall 2004

Predator sampling was conducted during 4-h periods encompassing nocturnal and daytime high tides to compare diel foraging activities throughout spring and fall. Fish predators were sampled by deploying a 180-m trammel net (~50% efficiency) from a fast-moving vessel (9-12 kn) in an arc along the shoreline. Net deployment was completed quickly, typically within 1-2 min, and the track was recorded using GPS to calculate the area sampled. The surface of the water within the arc was then aggressively disrupted with the boat (moving back and forth) and

with wooden poles to drive enclosed fish into the net. Captured fish were immediately removed from the net as it was retrieved and placed on ice for later processing.

Fish predators were processed in the laboratory within 12 h of capture. Length (cm fork length - FL) was recorded for each individual and stomachs were excised and preserved in Normalin for gut content analysis. Prey items were identified to species when possible, enumerated, and weighed to determine the diet composition by percent number and percent weight.

Suction sampling (~81% efficiency) was also conducted during low tide to quantify blue crab density in each SAV bed (Orth & van Montfrans 1987). Triplicate samples were collected at each site using a 1.5-m² cylindrical drop net with a mesh size of 0.05 mm. For each sample, the drop net was thrown haphazardly, suctioned for 6 min, and dipnetted for an additional 2 min. Samples were returned to the laboratory, frozen, and subsequently processed for blue crabs.

Summer and Fall 2016

Four multi-panel gill nets (30.5 m x 1.2 m; 5-cm, 7.6-cm, 10.2-cm stretched mesh) were deployed in a staggered formation perpendicular to shore in seagrass beds and sand flats at each sampling location to capture predators for gut content analysis. Gill nets were set during the day and at night to examine diel differences in predation. Sets were limited to 1-2 h to reduce the likelihood of prey digestion. A crab scrape (1 m wide; 1-cm mesh) was also towed for 3-5 min in each habitat to sample predators that may not enter a gill net. Sampling methods were not standardized because we were only interested in identifying predators of blue crabs, not estimating abundances. Predators were immediately removed from the gear, placed in an ice

slurry, and taken back to the laboratory. In the laboratory, predators were either frozen, or they were dissected and their guts placed in Normalin for later processing.

During processing, species were identified, and fish (TL) and crab (CW) size was measured to the nearest 1 mm and 0.1 mm, respectively. Stomach and intestines were excised from individuals and contents were sorted for whole or pieces of juvenile blue crabs (e.g. eye stalks, swimming legs, carapace spines). Due to the difficulty of identifying digested prey items, only blue crab presence/absence was recorded; measurements of prey weights and weight-based calculations of diet compositions would likely have resulted in biased estimates of prey importance in predator diets.

Statistical analyses

Fall 1998

Simple gut content analyses were conducted for this preliminary study. Percent frequency of occurrence of blue crabs was determined for each predator species (striped bass, Atlantic croaker, red drum) and mean number of crabs consumed per fish was calculated to determine the impact of each species on juvenile blue crab mortality.

Spring and Fall 2004

Mean blue crab density for each season was extrapolated to total SAV cover in the lower Chesapeake Bay (2003 data) to derive an estimate of total juvenile crabs N_{p_c} residing in SAV beds in time period p (spring or fall). Estimated total juvenile abundance was calculated as:

$$N_{p_c} = \frac{10,000\bar{N}_{p_c}A_{SAV}}{e_s} \quad (1)$$

where \bar{N}_{p_c} is the mean number of juvenile blue crabs m^{-2} in season p , A_{SAV} is the areal coverage of SAV in lower Chesapeake Bay (assumed to be 16,436 ha – Orth et al. 2004), and e_s is the efficiency of the crab suction sampling device (estimated as 0.81 – R.N.L. pers. comm.). A conversion factor of 10,000 was used to convert the SAV coverage from ha to m^2 . These seasonal abundance estimates represented the number of juvenile blue crabs available to fish predators in SAV beds and served as the basis for the overall determination of seasonal fish predation impacts.

Total estimated consumption of blue crabs by striped bass, Atlantic croaker, and red drum was calculated using the mean number of crabs consumed per fish for each season. Total consumption C_{p_i} of blue crabs (number eaten) by fish predator i during time period p was estimated as:

$$C_{p_i} = N_{p_i} A_{SAV} S_{p_i} d_p \quad (2)$$

where N_{p_i} is the mean number of fish i ha^{-1} , S_{p_i} is the stomach contents of predator i (mean number of crabs per fish per day), and d_p is the number of days in each time period p (season). Note that equation (2) assumes a gut evacuation time of ~24 h for crabs and a trammel net sampling efficiency of 50%. Predation impacts P_{p_i} of fish predator i during time period p was then estimated as:

$$P_{p_i} = \frac{C_{p_i}}{N_{p_c}} \quad (3)$$

Summer and Fall 2016

To identify key predators of juvenile blue crabs and determine the factors that influence consumption, we developed 12 statistical models (g_1 - g_{12}) of juvenile blue crab consumption with

various combinations of predictors, including the null model for comparison (Table 1). Juvenile consumption was modeled as a binary response (1 = present in gut, 0 = absent), with time (day, night) and habitat (seagrass, sand) as fixed factors. Due to small sample sizes, some species were placed into groups based on predator guild (i.e. benthopelagic, epibenthic); species with sufficient sample sizes were placed in their own groups. Predator guild (or group) was also included in models as a fixed factor. Each model was analyzed using logistic regression to determine the probability of crab presence (consumption) under those conditions. The bias-corrected Akaike's Information Criterion (AIC_C) values were calculated to determine the best model. Weighted model probabilities (w_i) based on Δ_i values were used to determine the probability that a particular model was the best-fitting model. The Hosmer-Lemeshow goodness of fit test was used to assess the fit of the best model to the data (Hosmer & Lemeshow 1982). A post-hoc Tukey test for multiple comparisons was conducted to examine the differences in mean consumption of blue crabs among predator guilds.

RESULTS

Fall 1998

Seven species of fish were collected during the 12-h sampling effort on October 20. Three species (striped bass, Atlantic croaker, and red drum) were selected for detailed analyses, including an assessment of feeding habits. Striped bass was the most abundant of the three species, followed by Atlantic croaker and red drum (Table 2). Mean sizes of striped bass, croaker, and red drum were 44.8, 27.7, and 15.4 cm TL, respectively. Higher percentages of the three species were captured during the nocturnal high tide (2100 h) than any other sampling period (Fig. 2). Of all fishes caught, red drum had the highest frequency of occurrence and mean

number of blue crabs present in guts, followed by striped bass and Atlantic croaker, respectively (Table 2).

Spring and Fall 2004

In spring 2004 ($n = 30$), blue crab density in seagrass beds varied from 1.6 (Goose Island) to 8.8 (Goodwin Islands) crabs m^{-2} , with an overall mean of 4.4 crabs m^{-2} (fall 2003 year class). Using equation (1), blue crab abundance during spring in lower Chesapeake Bay SAV beds was estimated at 890 million crabs. In fall 2004 ($n = 12$), blue crab density averaged 10.0 crabs m^{-2} (fall 2004 year class). Based on this density estimate, approximately 2.03 billion blue crabs were estimated to reside in lower Bay SAV beds in the fall.

In spring 2004, 33 trammel net samples (11 day, 22 night) were collected at the nine sampling locations. The total number of fish captured per set ranged from 0 to 73, with a mean of 12.53 (± 2.87 SE) fish. Overall, 14 species and 425 individuals were collected, but only striped bass, Atlantic croaker, and red drum were selected for detailed analyses. The mean number of fish ha^{-1} of SAV for striped bass, croaker, and red drum varied by time of day and across sites.

Of the 82 striped bass (mean FL: 45.4 cm) collected, 50 (~61%) had full stomachs and 32 (~39%) were empty. Of the 50 individuals that had prey in their stomachs, 29 (58%) consumed blue crabs in spring, with a mean of 3.41 (± 0.81 SE) crabs per fish (Fig. 3). Overall, striped bass consumed approximately 1.2 (± 3.0 SE) crabs per day on average, with blue crabs constituting almost 50% of their diet in spring. Using equation (2), the overall estimated consumption of blue crabs by striped bass in spring 2004 was 21,413,279 individuals. Using equation (3), striped bass consumed about 2.4% of juvenile blue crabs available to predators in lower Bay SAV beds. Striped bass also consumed a variety of fishes in SAV beds.

In spring 2004, 168 Atlantic croaker (mean FL: 35.3 cm) were collected. Of these, 105 contained prey in their stomachs and only three consumed juvenile blue crabs (Fig. 3). The estimated impact of croaker on blue crabs during spring was low at only 0.37% of crabs available. Atlantic croaker consumed few fish and fed primarily on polychaetes and infaunal bivalves. Only one red drum was caught in the spring and contained four blue crabs, resulting in a negligible impact on blue crabs overall.

In fall 2004, 44 trammel net samples (18 day, 26 night) were collected at the nine sampling locations. The total number of fish caught per set ranged from 0 to 88, with a mean of 15.05 (± 2.68 SE) fish. Overall, 22 fish species and 661 individuals were collected in SAV beds.

Of the 177 striped bass (mean FL: 37.2 cm) collected in the fall, 121 contained prey items and 78 individuals (64.5%) consumed a total of 436 blue crabs (Fig. 3). As in spring, the fall diet of striped bass primarily consisted of blue crabs and fishes. Overall, the estimated mean daily consumption of crabs by striped bass in fall was 2.4 crabs per fish. The estimated total number of crabs consumed over the fall sampling period was 77,380,216, or approximately 3.8% of crabs available in SAV beds in the lower Chesapeake Bay. Striped bass also consumed a greater variety of fish species in fall than in spring.

Atlantic croaker abundances declined during fall as water temperatures decreased. Only 31 individuals were collected and all had full stomachs. Although 22.6% (7 individuals) contained a total of 10 crabs (Fig. 3), Atlantic croaker were estimated to have consumed only 386,161 crabs overall. Predation impacts were estimated to be negligible at only 0.02% of the crabs available in SAV beds. Croaker continued to consume large quantities of polychaetes and infaunal bivalves and few fish prey.

Five red drum were collected during fall sampling, three of which (60%) consumed 19 blue crabs, with a mean of 6.3 crabs per fish (Fig. 3). The total estimated consumption of blue crabs by red drum in the fall was 4,464,383 individuals at an estimated predation impact of only 0.22% on the total segment of the juvenile population residing in SAV beds in the lower Chesapeake Bay. Red drum also consumed fishes that are typically associated with SAV beds.

In addition to the predators targeted in this study (i.e. striped bass, Atlantic croaker, red drum), 24 weakfish *Cynoscion regalis* were caught in the fall, 21 of which contained prey and 11 consumed juvenile blue crabs (Fig. 3). Predation impacts calculated for weakfish indicated that approximately 4,222,287 crabs were consumed, amounting to only about 0.21% of those available to predators in SAV beds during fall.

Summer and Fall 2016

Overall, 18 gill net sets were deployed throughout the sample periods, capturing a total of 221 predators and 17 different species (Table 3). Of the predators caught, 178 contained prey items in their guts and 36 contained blue crab remains (Table 3). Of all predators caught that contained prey, greater proportions had consumed juvenile blue crabs in seagrass (Fig. 4A) during the day (Fig. 4B). Seven species had juvenile blue crabs in their guts: Atlantic croaker, Atlantic sharpnose shark *Rhizoprionodon terraenovae*, blue crabs, oyster toadfish *Opsanus tau*, silver perch *Bairdiella chrysoura*, striped bass, and weakfish (Table 3).

Due to small sample sizes, some predator species were placed into feeding guilds (groups) for the statistical analyses; species that had sufficient samples were placed into their own group (Table 3). Only species that contained prey and had $N > 1$ were included in the groups and the analyses. Atlantic croaker, benthopelagics (cobia *Rachycentron canadum*,

speckled trout *Cynoscion nebulosus*, striped bass, and weakfish), blue crabs, and silver perch all contained blue crab remains, whereas bluefish and epibenthics (Atlantic spadefish *Chaetodipterus faber*, pigfish *Orthopristis chrysopterus*, pinfish *Lagodon rhomboides*, spot *Leiostomus xanthurus*, and striped burrfish *Chilomycterus schoepfi*) did not (Table 3). Thus, bluefish and epibenthics were not included in the statistical analyses.

Juvenile blue crab consumption was best explained by the additive model with predator guild and habitat as predictors (g_4); model g_4 had the lowest AIC_C value and a weighted probability of 0.35 (Table 1). All other model probabilities were <0.15 and thus were eliminated from further consideration (Table 1). Although the probability of model g_{10} was similar to g_4 , the interaction term (G x H) was not significant; thus, we selected g_4 as the most parsimonious model. Model g_4 fit the data well (Hosmer-Lemeshow test, $\chi = 1.47$, $p > 0.05$).

Parameter estimates of model g_4 were significant relative to the baseline condition (Table 4). Mean juvenile blue crab consumption by Atlantic croaker was significantly lower than that of benthopelagics, blue crab, and silver perch (Tukey test, $p < 0.05$), but there were no significant differences in mean consumption among any of the other predator guilds (Table 5). Predator consumption of juvenile blue crabs was also significantly higher in seagrass beds compared to sand flats (Table 4).

Probability of blue crab consumption for each predator guild was calculated based on the parameter estimates of model g_4 , holding habitat constant. The probability of Atlantic croaker consuming blue crabs was 0.22 (± 0.15 SE) (Fig. 5). The probability of benthopelagics, adult blue crabs, and silver perch consuming juvenile blue crabs was significantly higher at 0.82 (± 0.28 SE), 0.71 (± 0.27 SE), and 0.78 (± 0.20 SE), respectively (Fig. 5). Probability of blue crab consumption by habitat was also calculated based on model g_4 , holding predator guild constant.

Crab consumption probability was significantly higher in seagrass beds than in sand flats (Fig. 6). Due to small samples sizes and large standard errors, trends in blue crab consumption (i.e. habitat, time) for individual predator guilds could not be determined.

DISCUSSION

Our three field studies yielded a number of novel findings about the features of predation and cannibalism that drive juvenile blue crab mortality in nursery habitats (i.e. seagrass beds, sand flats) of lower Chesapeake Bay. In the Fall 1998 study, we (i) determined that red drum and striped bass were the major consumers of juvenile blue crabs. All red drum collected had eaten blue crabs, with 4.5 juveniles consumed per fish on average, while 81% of striped bass consumed a mean of about 2.3 juveniles per fish. Fewer Atlantic croaker consumed juveniles (59%), and only 1.4 crabs were consumed per fish on average. The results of the Spring and Fall 2004 study corroborated those of the Fall 1998 study. In the 2004 study, we (ii) determined that striped bass were the most impactful predators on juvenile mortality in seagrass beds, with 58-65% of striped bass consuming about 2-4% of all juvenile blue crabs residing in SAV beds in the lower Chesapeake Bay. Red drum (67%) and weakfish (52%) also consumed juvenile blue crabs in large quantities, but the low catches in the 2004 study resulted in low impacts of these species on the blue crab population. The estimated predation impacts of red drum and weakfish were 0.22% and 0.21% of blue crabs available to predators in seagrass beds in the fall, respectively. Atlantic croaker had negligible impacts on blue crabs, with 3-23% of fish consuming only 0.02-0.37% of the crabs available in the grass beds. In the Summer and Fall 2016 study, we (iii) found that silver perch is another major predator of small crabs in Chesapeake Bay nursery habitats, in addition to striped bass, weakfish, and adult blue crabs. More than 50% of the silver perch

caught contained young juvenile crabs in their stomachs. Similar to the 1998 and 2004 studies, high frequencies of crab consumption by striped bass (100%) and weakfish (60%) indicated that these species are major predators of blue crabs. Cannibalism by adult blue crabs also accounted for a substantial portion of juvenile mortality, with 44% of adult crabs sampled consuming juveniles. Few Atlantic croaker (7%) ate juvenile blue crabs. Our model results indicated that benthopelagic finfish species (i.e. striped bass, weakfish), silver perch, and blue crabs were significantly more likely to consume juvenile blue crabs than Atlantic croaker. A single Atlantic sharpnose shark and oyster toadfish were collected in the 2016 study and both had consumed juvenile blue crabs. Thus, these species may also be important predators of juveniles in Chesapeake Bay nursery habitats, but the small sample sizes in this study preclude any definitive conclusions. The predator-prey relationships revealed in these three studies were integrated into a revised food web for blue crabs in Chesapeake Bay nursery habitats (Fig. 10). Finally, based on the modeling results of our 2016 study, we (iv) identified habitat as an important predictor of juvenile blue crab consumption. Significantly higher proportions of fish caught in seagrass beds contained blue crabs compared to fish caught in unvegetated sand flats.

Key predators of Chesapeake Bay blue crabs

The current food web for blue crabs in Chesapeake Bay suggests that adult striped bass are one of the primary finfish predators of young juvenile blue crabs (Lipcius et al. 2007). Striped bass are large, predatory fish that use Chesapeake Bay as spawning and foraging grounds. A portion of the striped bass population resides in the Bay year-round, often migrating to the lower Bay after spring spawning in the upper tributaries. In previous diet studies, striped bass were a major consumer of juvenile blue crabs in Chesapeake Bay, particularly in mid to

lower Bay tributaries. Age 1 and 2 striped bass (350-650 mm) primarily fed on juvenile crabs in benthic habitats throughout the summer and fall (Hartman & Brandt 1995, Austin & Walter 2001, Overton et al. 2009). Approximately 30% of striped bass caught contained blue crab remains in their stomachs, with juvenile crabs making up nearly 30% of the diet by mass and over 40% of the diet by number (Hartman & Brandt 1995, Austin & Walter 2001, Overton et al. 2009).

Our gut content analyses revealed similar findings, with high frequencies of striped bass (52-100%) containing blue crabs. However, large juvenile crabs (>30 mm CW) were commonly found in striped bass stomachs in addition to smaller crabs; these results were incorporated into the revised Chesapeake Bay food web for blue crabs. Given the abundance and residency of the species within Chesapeake Bay, striped bass are likely one of the most influential predators on juvenile crab mortality in Bay nursery habitats, as suggested by the Spring and Fall 2004 study.

Red drum are opportunistic predators that are largely abundant in the Gulf of Mexico, where they are a voracious predator of juvenile blue crabs (Yokel 1966, Boothby & Avault 1971, Bass & Avault 1975, Levine 1980, Guillory & Prejean 2001). Juvenile red drum 150-350 mm (i.e. “puppy drum”) feed heavily on crabs along the coasts of Texas, Louisiana, and Florida, with up to 62% of fish consuming blue crabs, making up nearly 70% of their diet by volume (Yokel 1966, Boothby & Avault 1971, Bass & Avault 1975, Levine 1980, Guillory & Prejean 2001). Adult red drum also consume blue crabs, often larger juveniles, although less frequently than puppy drum (Guillory & Prejean 2001).

Red drum occur seasonally in Chesapeake Bay, visiting the shallows of the lower estuary from May to November. Our studies were the first to examine red drum feeding habits in Chesapeake Bay, and revealed that red drum forage in seagrass beds, consuming large numbers

of juvenile blue crabs. Red drum appear to be particularly active predators in the fall when new blue crab recruits are settling into the Bay grass beds. Although red drum are not consistently abundant from year to year, their high individual impacts (4.5 crabs per fish on average) make them particularly influential in blue crab population dynamics when they are abundant in the Bay. In the summer of 2012, there was an unprecedented influx of red drum into the Bay, which led to the theory that increased red drum predation depleted the 2011 year class of blue crabs and caused a sharp decline of the blue crab population. Thus, red drum should be considered a major predator of blue crabs not just in the Gulf of Mexico, but also in Chesapeake Bay.

Weakfish were not included in the original Chesapeake Bay food web for blue crabs, despite being one of the top carnivores in Bay seagrass beds (Lipcius et al. 2007). Similar to red drum, weakfish reside in the Bay from spring through fall, feeding in shallow grass beds. Age 1 and 2 weakfish occasionally feed on juvenile crabs in the spring (May-June), with crabs constituting only about 2% of the diet by mass (Hartman & Brandt 1995). However, our gut content analyses suggest that weakfish may have a greater impact on juvenile mortality than previously thought, with 50-60% of fish caught in seagrass beds containing blue crabs. In the prior study, weakfish were collected from mid-Bay sampling sites, which may account for the differences in juvenile blue crab consumption between the two studies; juvenile crabs primarily reside in shallow nursery habitats of Bay tributaries, not in the deeper waters of the main stem of the Bay. Additionally, weakfish consumption of blue crabs was prevalent during the fall blue crab recruitment of 2016, and the previous study only sampled fishes in the spring. Due to the relatively high percent frequency of crab consumption, weakfish are now included in the revised food web as a major predator of small blue crabs.

Prior to our gut content analyses, feeding habits of silver perch had only been assessed in the Gulf of Mexico, and thus were not considered in the Chesapeake Bay food web. Juvenile blue crabs occurred in only about 2% of silver perch stomachs in the estuarine community of Lake Pontchartrain, Louisiana (Darnell 1958, Levine 1980). However, percent frequency of crab consumption was much higher in our gut content analyses for Chesapeake Bay, with 52% of individuals consuming small juvenile blue crabs. The seasonal abundance of silver perch and the frequency of crab consumption warrant their inclusion in the food web as a key predator of juvenile blue crabs in Chesapeake Bay.

Cannibalism has been documented as a primary source of juvenile blue crab mortality in both Chesapeake Bay and the Gulf of Mexico. Field and laboratory tethering experiments revealed cannibalism by adult blue crabs to be the source of 75-96% of juvenile mortality in Chesapeake Bay (Hines & Ruiz 1995, Bromilow & Lipcius in press). Previous diet studies also suggested that cannibalism can significantly contribute to juvenile mortality, with juvenile crabs found in 45% of adult stomachs (Mansour 1992) and constituting an average of 13% of the adult diet by volume (Darnell 1958). Our gut content analyses corroborate prior studies, with 44% of adult blue crabs containing small juveniles. Therefore, cannibalism remains a primary component of juvenile blue crab mortality in the Chesapeake Bay food web.

Other finfish predators

In diet studies along the Gulf coast, Atlantic croaker fed on juvenile blue crabs, albeit rarely. Only an average of 4% of Atlantic croaker contained juvenile crabs across several studies along the coasts of Mississippi and Louisiana (Darnell 1958, Rogillio 1975, Overstreet & Heard 1978, Levine 1980). Although our gut content analyses revealed a higher mean frequency of crab

consumption by Atlantic croaker (23%) than prior studies, the relative impact on juvenile mortality was much lower than that of striped bass, red drum, silver perch, and weakfish. Thus, Atlantic croaker were incorporated into the Chesapeake Bay food web as a minor predator of blue crabs.

In prior studies, oyster toadfish consumed juvenile blue crabs in Chesapeake Bay. During summer sampling in the Patuxent River, 36% of toadfish contained small crabs, constituting 17% of the diet by volume (Schwartz & Dutcher 1963). In a more recent tethering study, an oyster toadfish was found still attached to a tethered juvenile after swallowing the crab whole (Bromilow & Lipcius in press). Only a single toadfish was collected in the Summer and Fall 2016 study, but the stomach contained a whole, small juvenile crab. Given the data from our study and those prior, oyster toadfish are a predator of juvenile blue crabs and should be included in the Chesapeake Bay food web, although not enough information exists to determine the relative impact of these predators on juvenile mortality and blue crab population dynamics.

Similar to the oyster toadfish, a single Atlantic sharpnose shark was captured with juvenile blue crabs in its stomach. However, the species was not included in the Chesapeake Bay food web as a primary predator of juvenile crabs due to the small sample size and the lack of supporting evidence in the literature.

Habitat effects

Seagrass beds are considered the primary nursery habitat for many estuarine and marine species given the high abundances of juveniles in these habitats (Heck & Thoman 1984, Beck et al. 2001, Heck et al. 2003). In Chesapeake Bay, juvenile blue crab abundance is higher in seagrass beds than in unvegetated habitats, with densities as much as an order of magnitude

higher in SAV (Orth & van Montfrans 1987, Pile et al. 1996, Lipcius et al. 2007). Juveniles, particularly smaller crabs, inhabit these grass beds because the structure of the SAV provides shelter from predators (Wilson et al. 1990, Perkins-Visser et al. 1996, Pile et al. 1996, Hovel & Lipcius 2001, Orth & van Montfrans 2002). However, densities of foraging predators are also often higher in seagrass beds than in sands flats (Orth & Heck 1980a, Orth & Heck 1980b).

The Summer and Fall 2016 study evaluated the influence of habitat type on juvenile blue crab consumption in Chesapeake Bay nursery habitats. In general, the probability of crabs being present in a predator's gut was higher in seagrass beds than unvegetated sand flats. This suggests that seagrass beds are important foraging grounds for fish predators, which may be a result of the higher prey densities in these habitats. Greater consumption of juvenile crabs in seagrass may seem counterintuitive considering that juveniles seek refuge from predators in vegetated habitats; however, increased crab consumption does not equate to decreased *per capita* survival in seagrass compared to unvegetated habitats. If juveniles preferentially settle in seagrass beds to avoid the high probability of mortality in unvegetated habitats (Bromilow & Lipcius in press) and predator densities are higher in seagrass (Orth & Heck 1980a, Orth & Heck 1980b), increased consumption of juvenile crabs in seagrass beds is expected.

A potential bias in examining the effect of habitat type on prey consumption is predator mobility. A fish or adult blue crab could easily consume a juvenile crab in a sand flat and then move into the seagrass bed to be captured (or vice versa). However, we are fairly confident that most of the fishes (and crabs) captured in seagrass were foraging within that habitat given the prevalence of seagrass found in the stomach contents.

Conclusions

Food web dynamics are an important aspect of ecosystem-based fisheries management. Natural mortality via predation plays a key role in the population dynamics of fishery species such as the blue crab. Understanding the ecological interactions between populations can provide insight into natural population fluctuations and help managers make informed decisions about overfishing issues. Based on the results of our gut content analyses, striped bass, adult blue crabs, and red drum are likely the top predators of juvenile blue crabs in Chesapeake Bay nursery habitats throughout the summer and fall, closely followed by silver perch and weakfish. Atlantic croaker appears to play a minor role as a predator of juvenile blue crabs in nursery habitats. Juvenile crabs were more likely to be eaten in seagrass beds than sand flats, likely due to the higher densities of predators and prey in those habitats. It is important to note that although a few species appear to be the dominant predators of blue crabs, annual variations in predator recruitment and abundance can alter the influence of predator species from year to year. Similarly, climate change will likely affect these ecosystem dynamics through increased water temperatures, and consequently, changes in species distributions. For example, with increasing water temperatures, red drum and other residents of the Gulf coast may reside in Chesapeake Bay for longer periods of time, which could increase juvenile blue crab mortality and reduce recruitment. Thus, it is critical to consider how climate change will influence not only individual species, but the entire ecosystem and interactions between species.

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TABLES

Table 1. AIC calculations for the logistic regression models, g_i , where k is the number of parameters, including variance (σ^2), in model g_i ; AIC_C is the bias-corrected AIC value; Δ_i is the difference in the AIC_C value between model g_i and the best model; and w_i is the probability that model g_i is the best model in the set. Group is a categorical factor representing the predator guilds or species caught; time is a factor with day and night levels; and habitat is a factor with seagrass and sand levels. Additions indicate additive models and multiplications indicate interaction terms. The epibenthic and bluefish groups were excluded from these analyses because of their zero values.

Model	Variables	k	AIC_C	Δ_i	w_i
g_1	Group (G)	3	120.97	2.37	0.11
g_2	Time (T)	3	137.12	18.53	<0.01
g_3	Habitat (H)	3	138.30	19.71	<0.01
g_4	G + H	4	118.60	0.00	0.35
g_5	G + T	4	121.64	3.04	0.08
g_6	T + H	4	135.34	16.75	<0.01
g_7	G + T + H	5	120.76	2.16	0.12
g_8	T x H	5	133.56	14.97	<0.01
g_9	G x T	5	126.76	8.17	<0.01
g_{10}	G x H	5	119.08	0.49	0.27
g_{11}	G + (T x H)	6	121.84	3.24	0.07
g_{12}	Null	2	146.48	27.88	<0.01

Table 2. Species captured in gill nets in Fall 1998 that were analyzed for gut contents with total number caught (N), number that contained prey, number that contained blue crabs, the proportion of individuals that contained prey items including blue crabs, total number of crabs consumed, and the mean number of crabs consumed per fish \pm 1 standard error (SE). Four other fish species were caught that were not included in the diet analyses.

Species	N	# w/ prey	# w/ crabs	Prop. w/ crabs	Total crabs	Mean crabs (\pm SE)
Atlantic croaker (<i>Micropogonias undulatus</i>)	28	17	10	0.59	13	1.4 \pm 0.7
Red drum (<i>Sciaenops ocellatus</i>)	20	20	20	1.00	89	4.5 \pm 2.8
Striped bass (<i>Morone saxatilis</i>)	76	57	46	0.81	106	2.3 \pm 1.6

Table 3. Species captured in gill nets in Summer and Fall 2016 with total number caught (N), number that contained prey, number that contained blue crabs, and the proportion of individuals that contained prey items including blue crabs. Species with N < 20 were assigned a predator guild unless N = 1; predators with N = 1 were excluded from analyses altogether. Bluefish was placed in its own guild considering that it was the only truly pelagic species caught in the samples.

Predator guild	Species	N	# w/ prey	# w/ crabs	Prop. w/ crabs
	Atlantic croaker (<i>Micropogonias undulatus</i>)	71	61	4	0.07
	Blue crab (<i>Callinectes sapidus</i>)	20	16	7	0.44
	Bluefish (<i>Pomatomus saltatrix</i>)	17	12	0	0.00
	Silver perch (<i>Bairdiella chrysoura</i>)	50	31	16	0.52
Benthopelagic	Cobia (<i>Rachycentron canadum</i>)	2	2	0	0.00
	Speckled trout (<i>Cynoscion nebulosus</i>)	2	2	0	0.00
	Striped bass (<i>Morone saxatilis</i>)	8	5	5	1.00
	Weakfish (<i>Cynoscion regalis</i>)	5	5	3	0.60
Epibenthic	Atlantic spadefish (<i>Chaetodipterus faber</i>)	4	4	0	0.00
	Pigfish (<i>Orthopristis chrysopterus</i>)	3	3	0	0.00
	Pinfish (<i>Lagodon rhomboides</i>)	4	4	0	0.00
	Spot (<i>Leiostomus xanthurus</i>)	24	24	0	0.00
	Striped burrfish (<i>Chilomycterus schoepfi</i>)	7	5	0	0.00

Table 3 continued...

Predator guild	Species	N	# w/ prey	# w/ crabs	Prop. w/ crabs
Not included in analyses	Atlantic sharpnose shark (<i>Rhizoprionodon terraenovae</i>)	1	1	1	1.00
	Oyster toadfish (<i>Opsanus tau</i>)	1	1	1	1.00
	Summer flounder (<i>Paralichthys dentatus</i>)	1	1	0	0.00
	White perch (<i>Morone americana</i>)	1	1	0	0.00

Table 4. Parameter estimates from logistic regression model g_4 for juvenile blue crab consumption. The baseline condition is Atlantic croaker in sand habitat.

Parameter	Variable	Estimate	SE	z	p
β_0	Intercept	-3.4157	0.6823	-5.006	<0.0001
β_1	Benthopelagic	2.7839	0.7625	3.651	0.0003
β_2	Blue Crab	2.1233	0.7471	2.842	0.0045
β_3	Silver Perch	2.5233	0.6402	3.942	<0.0001
β_4	Seagrass	1.1753	0.5809	2.023	0.0431

Table 5. Tukey multiple comparisons of predator guild (group) means based on logistic regression model g_4 for juvenile blue crab consumption. The null hypothesis for each comparison is that the difference between the group means is zero. BP is benthopelagic; AC is Atlantic croaker; BC is blue crab; and SP is silver perch.

Comparison	Estimate	SE	z	p
BP – AC	2.7839	0.7625	3.651	0.0014
BC – AC	2.1233	0.7471	2.842	0.0226
SP – AC	2.5233	0.6402	3.942	<0.001
BC – BP	-0.6606	0.7722	-0.855	0.8261
SP – BP	-0.2606	0.6674	-0.390	0.9796
SP – BC	0.4001	0.6527	0.613	0.9272

FIGURES

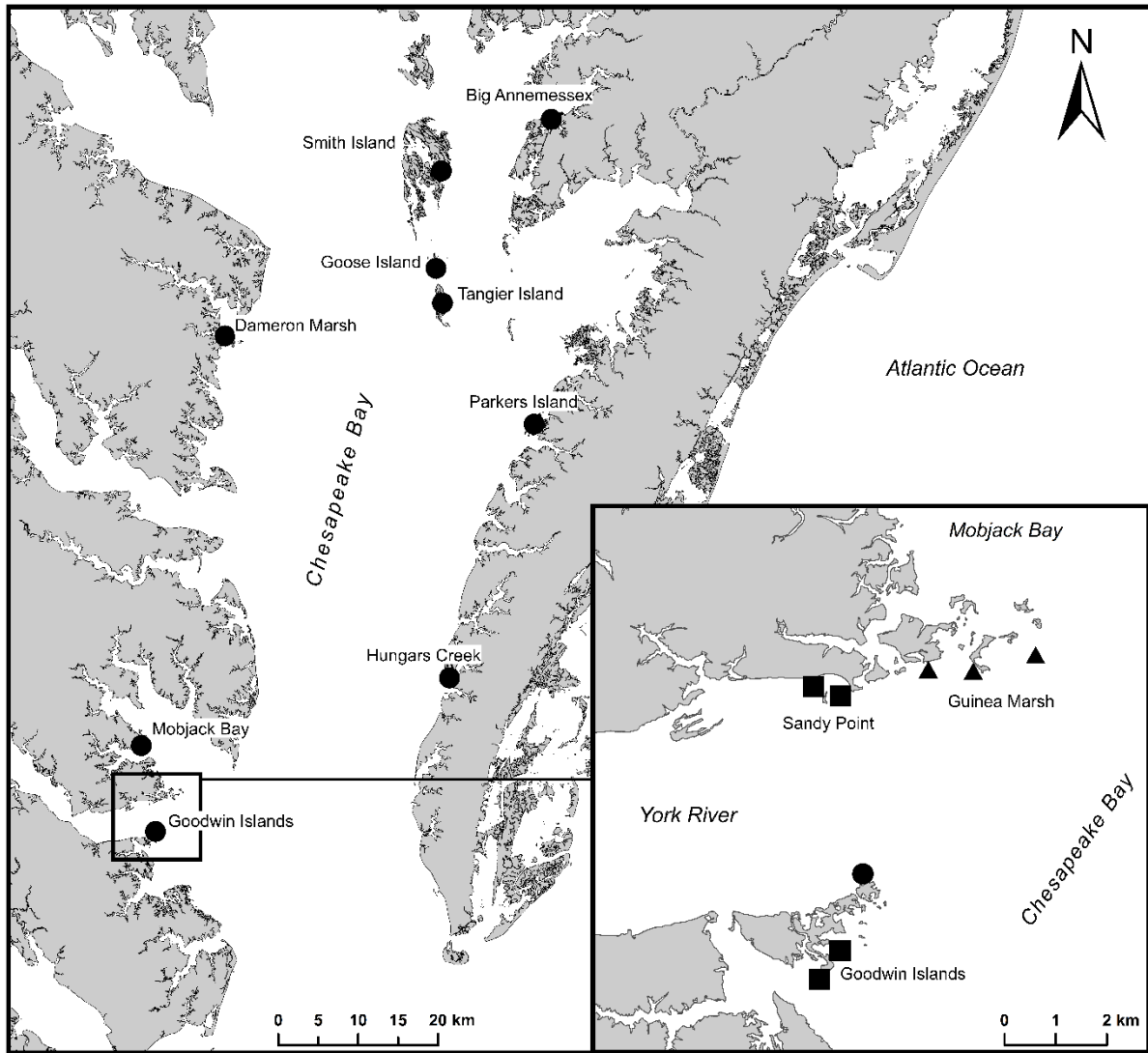


Figure 1. Map of the study sites across the Chesapeake Bay in Fall 1998 (▲), Spring and Fall 2004 (●), and Summer and Fall 2016 (■) studies.

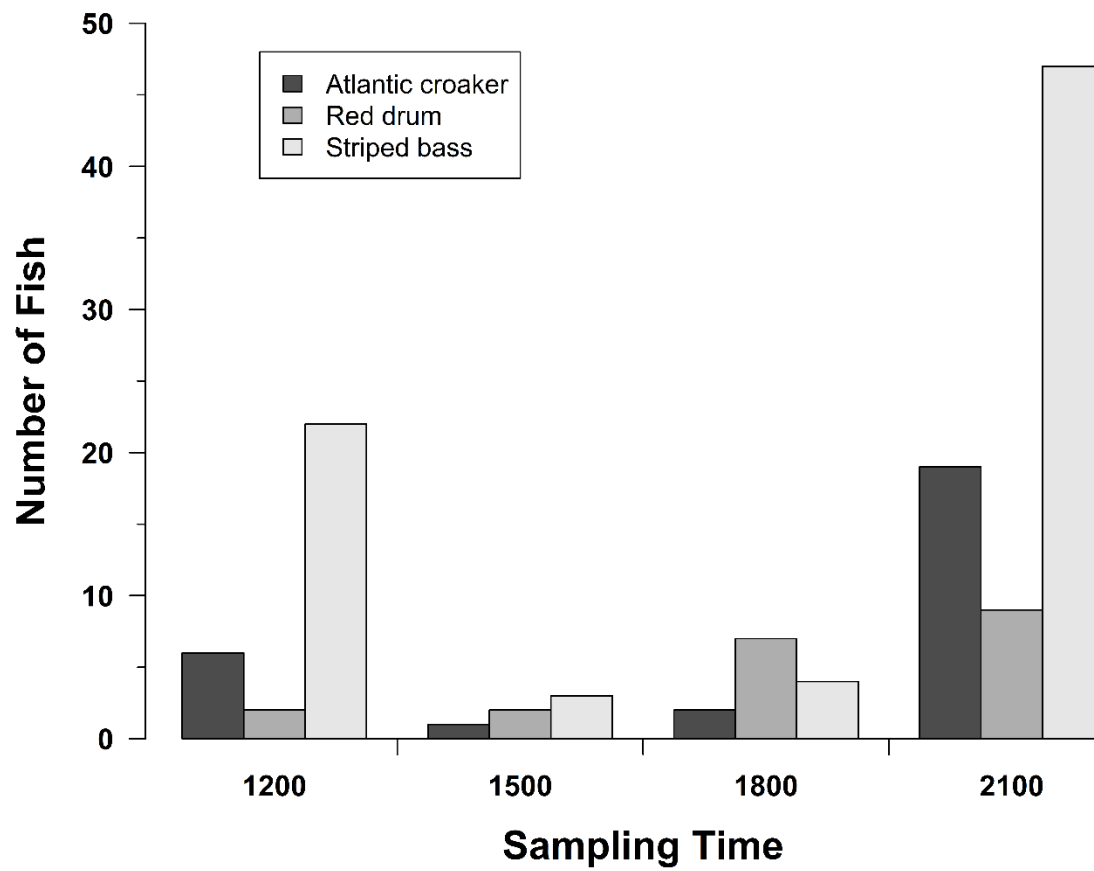


Figure 2. Number of fish caught for each species by sampling period in Fall 1998. The 1200-h sample occurred during the daytime falling tide; 1500 and 1800 h were at low tide; and 2100 was during the nocturnal high tide.

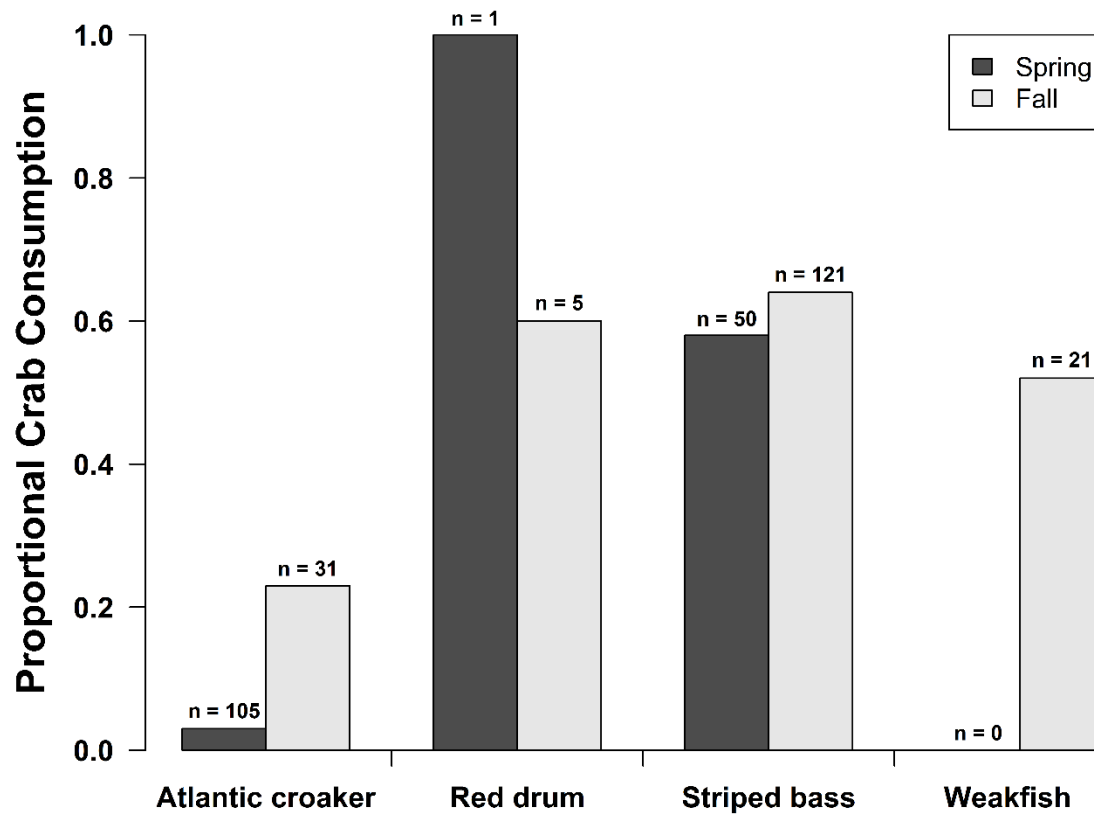


Figure 3. Proportion of individuals containing prey that consumed blue crabs for each species analyzed in Spring and Fall 2004.

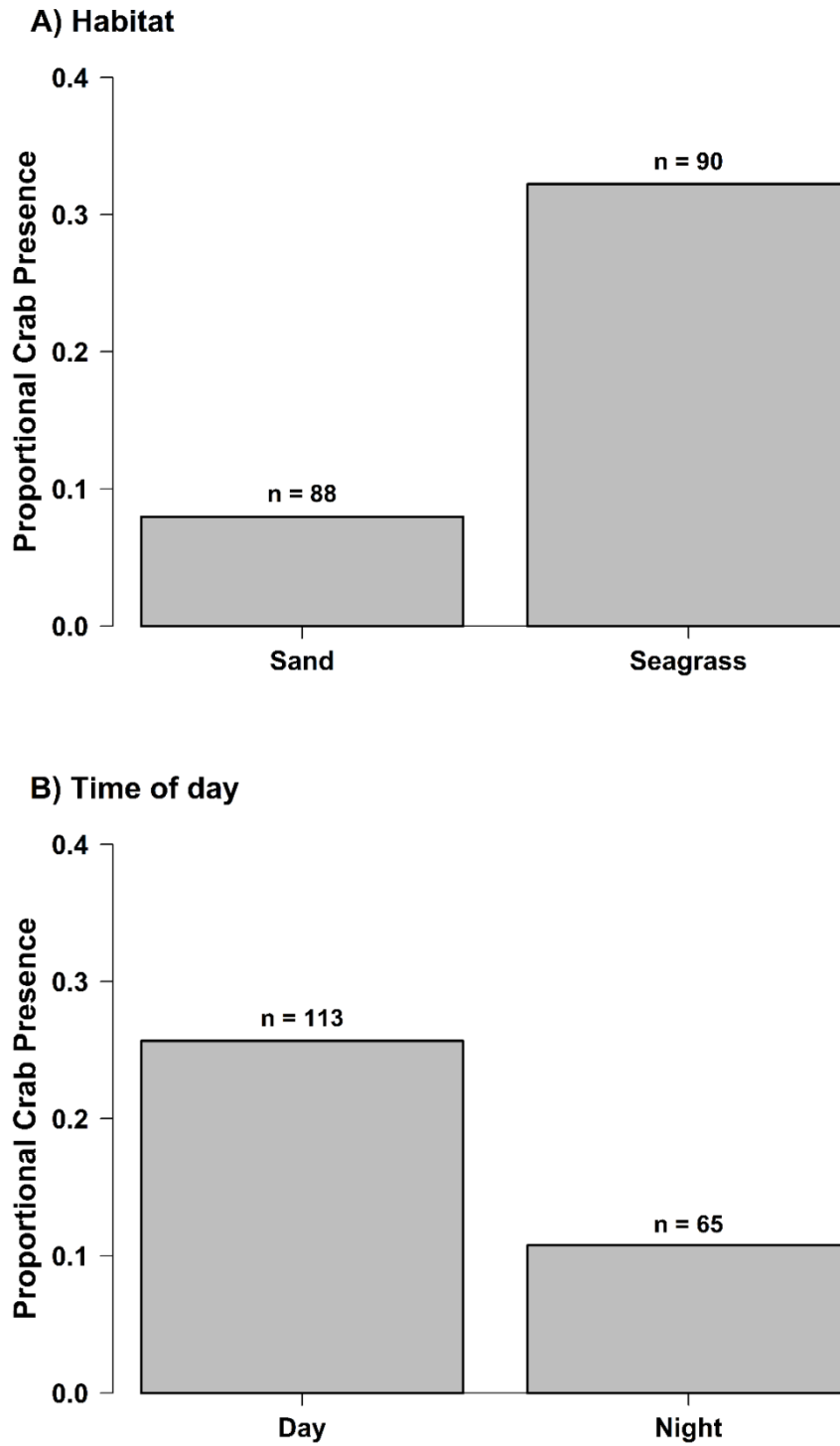


Figure 4. Proportion of predators containing prey that consumed blue crabs in Summer and Fall 2016 by A) habitat and B) time of day.

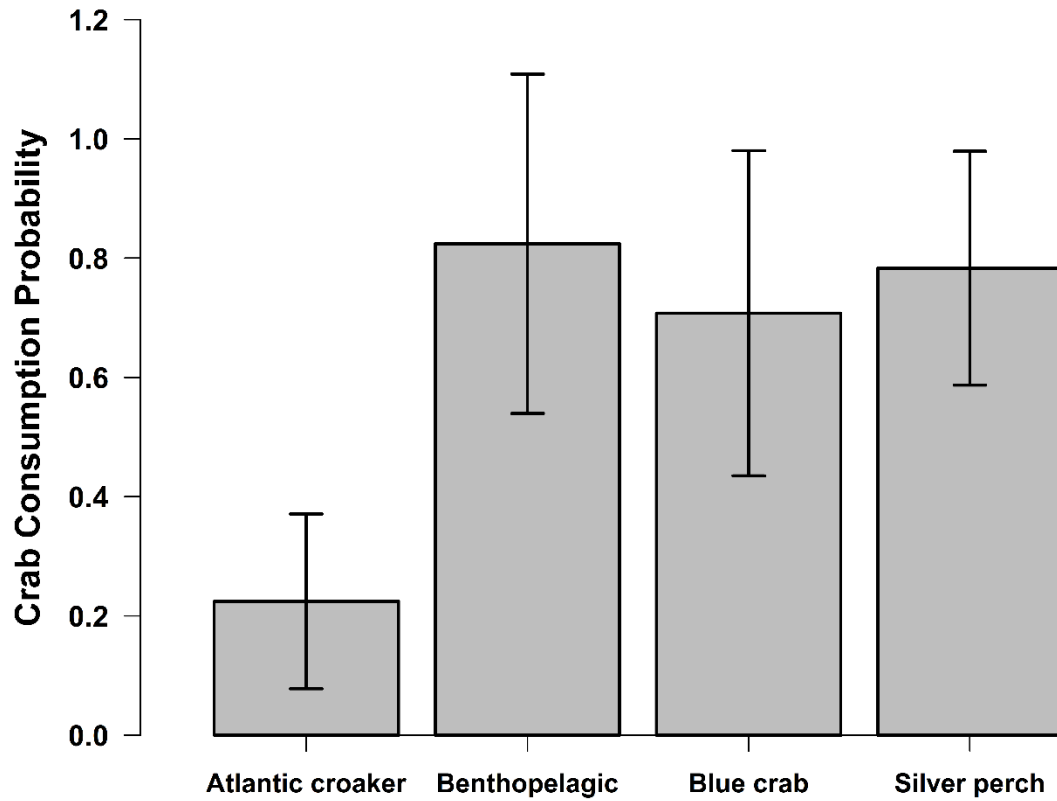


Figure 5. Probability of blue crab consumption (± 1 SE) for each predator guild based on logistic regression model g_4 . Bluefish and epibenthics were not included in these analyses because they did not consume blue crabs.

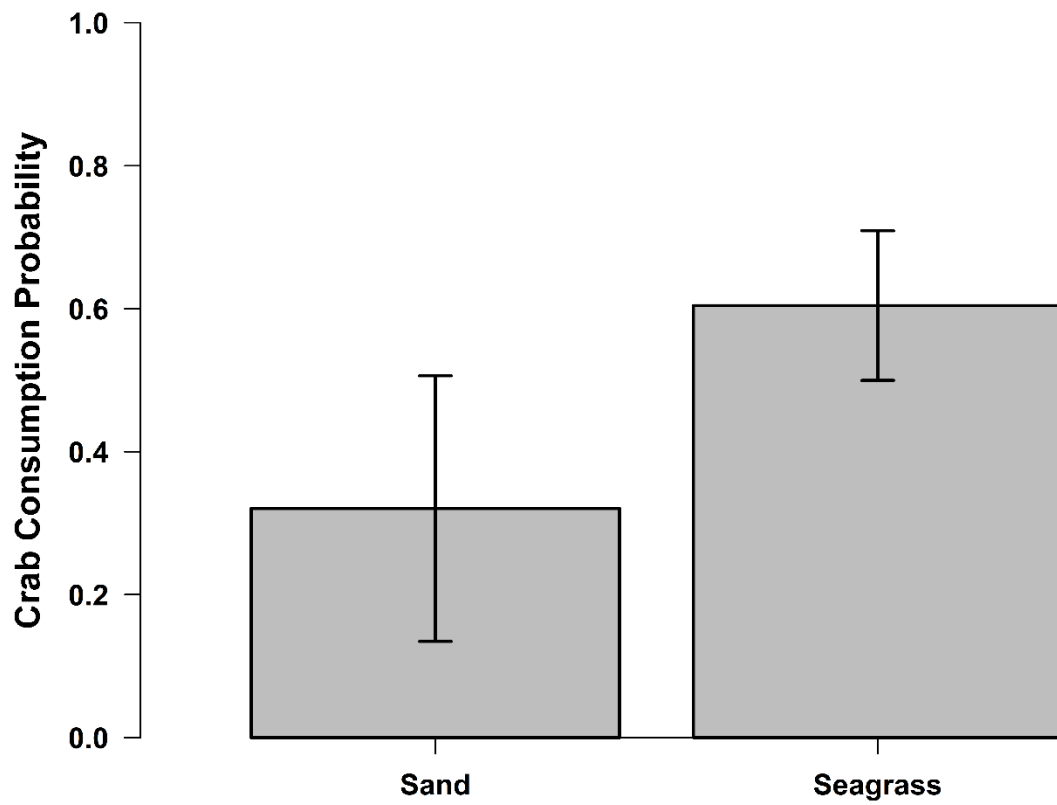


Figure 6. Probability of blue crab consumption (± 1 SE) by habitat based on logistic regression model g_4 .

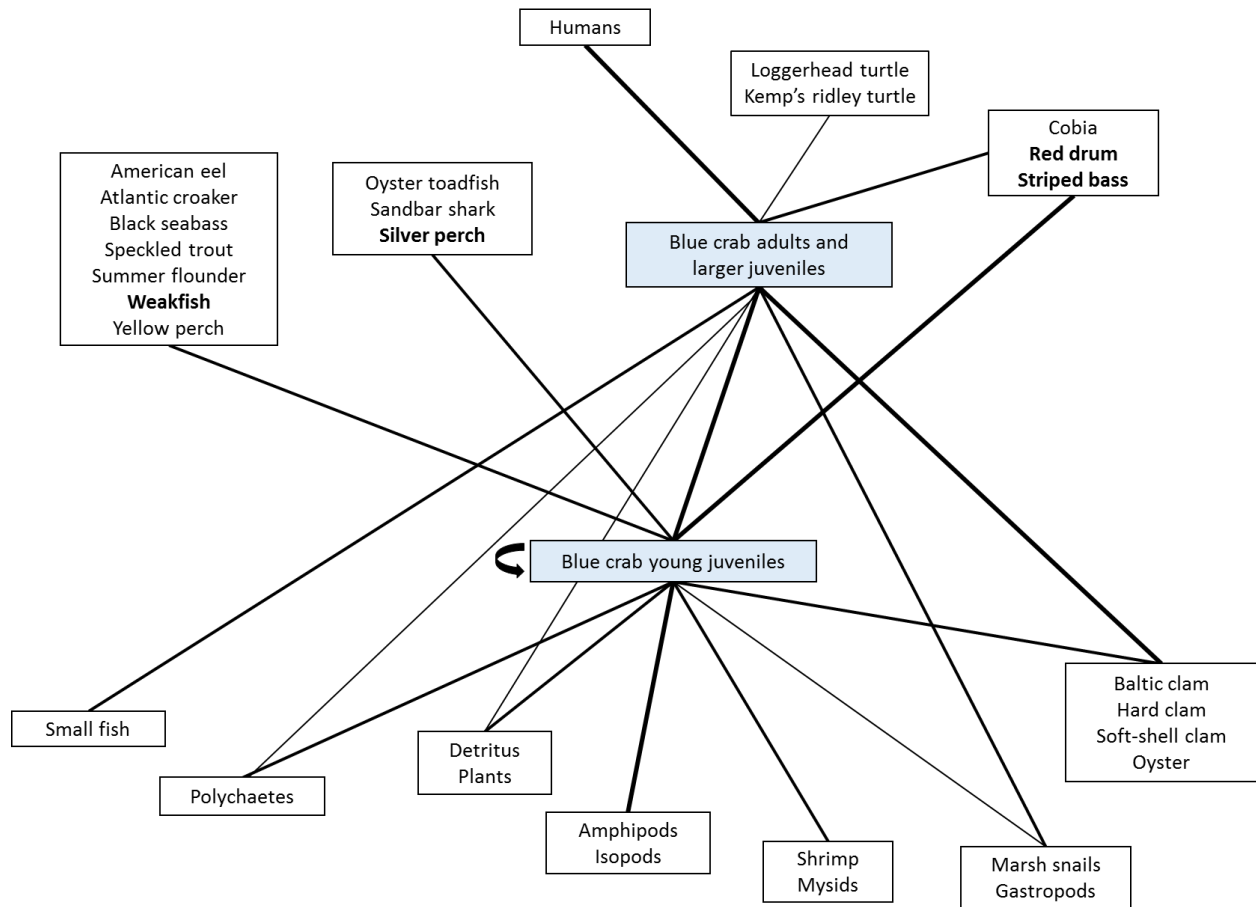


Figure 7. Food web of the blue crab in Chesapeake Bay revised from Lipcius et al. 2007, including linkages with blue crabs as predators and prey. Finfish predators are separated into three groups: fishery species that feed moderately on young juvenile crabs (far left; weakfish is highlighted as a particularly important predator in this group); non-fishery species that feed on young juveniles (middle; silver perch is a highlighted as a particularly important predator in this group); and fishery species that are voracious predators on both large and small juvenile crabs as well as adults (far right; red drum and striped bass are highlighted in this group as particularly important predators). “Blue crab young juveniles” refers only to crabs < 30 mm CW. Thicker lines represent stronger predator-prey connections determined from various studies including our three field studies.

VITA

Amanda Marie Bromilow

Amanda was born in Mt. Holly, New Jersey, on January 3, 1992. She graduated from Berrien Springs High School in Berrien Springs, Michigan, in 2010. Amanda attended the University of Michigan, Ann Arbor, where she completed an honors thesis on white shark behavior in South Africa. She graduated with honors and distinction from the University of Michigan in 2014, earning a Bachelor of Science in Ecology and Evolutionary Biology with a minor in Oceanography. Amanda entered the master's program at the Virginia Institute of Marine Science, College of William & Mary in 2014 under graduate advisor, Dr. Romuald Lipcius.