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Bromilow, Amanda and Lipcius, Romauld, Mechanisms governing ontogenetic habitat shifts: role of trade-offs, predation, and cannibalism for the blue crab (2017). *Marine Ecology Progress Series*, 584, 145-159. doi:10.3354/meps12405

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Mechanisms governing ontogenetic habitat shifts: role of trade-offs, predation, and cannibalism for the blue crab

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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 juvenile survival decreases with size in submerged aquatic vegetation (SAV) due to a reduction in suitably scaled refuge, 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 (Virginia, USA) 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 sea-grass 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 finfish predation.

KEY WORDS: Blue crab · Ontogenetic shift · Trade-offs · Size refugia · Survival · Predation impact · Habitat use

INTRODUCTION

Nursery habitats and ontogenetic shifts

Coastal habitats are highly productive and provide foraging, spawning, and nursery grounds for commercially and ecologically important species (Heck et al. 2003, Stål et al. 2008, Seitz et al. 2014, Abrantes et al. 2015, Kritzer et al. 2016). Availability of suitable nursery habitat often determines recruitment success and population abundance, indicating that the nurs-

ery role is a valuable function of coastal habitats (Wahle & Steneck 1991, Gibson 1994, Juanes 2007, Sundblad et al. 2014). By definition, 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.

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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. For example, 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, the study was conducted using a narrow range of seagrass shoot density and thus did not test the hypothesis over the full range of relevant conditions.

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 (Virginia, USA) nursery habitats using innovative methods and technology (underwater camera systems).

To evaluate the blue crab habitat use paradigm, we generated 6 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 than smaller juveniles 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 use was encompassed by H_4 (size \times 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). H_5 (size, SAV cover, trial duration) predicted that survival decreases with trial duration due to prolonged exposure to predators. Finally, H_6 (size, SAV cover, duration, time of day) 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 ($37^{\circ} 13' N$, $76^{\circ} 23' W$) and Sandy Point ($37^{\circ} 15' N$, $76^{\circ} 25' W$); 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 near-shore 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* (Wood 2017). Each location contained a vegetated and unvegetated site.

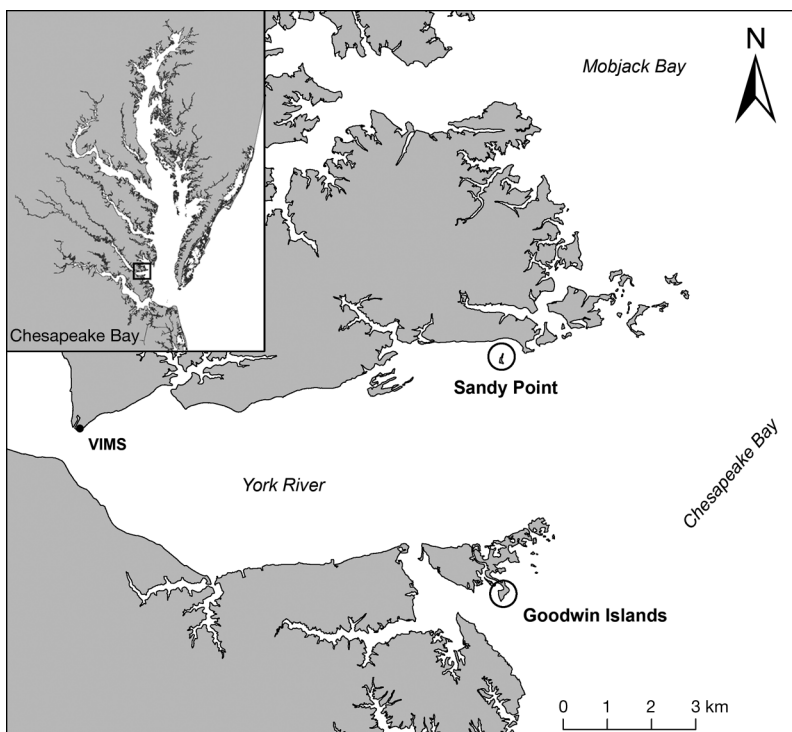


Fig. 1. Study areas in the lower York River, Virginia, USA. Tethering experiments were conducted at a vegetated and unvegetated site at Sandy Point (July 2016) and Goodwin Islands (July–August 2016)

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.

Within 2 or 3 wk of each tethering experiment, 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. The weight of the fishing line and the placement of the tether on the carapace prevented crabs from cutting their own tethers.

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. Similar results were

found in tether retention studies using the same methods (Lipcius et al. 2005, Johnston & Lipcius 2012); 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 2 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

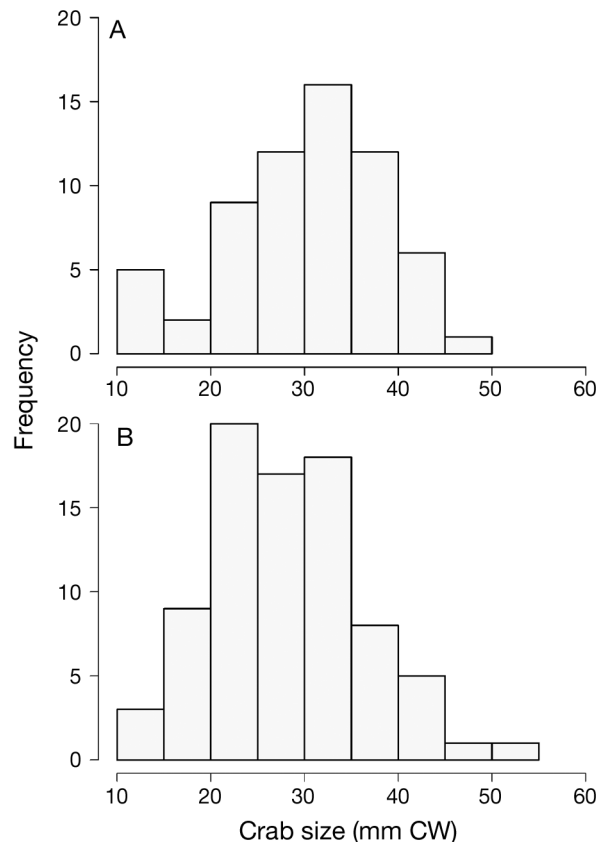


Fig. 2. Size distribution of juvenile blue crabs tethered in (A) sand and (B) seagrass habitats in the 2016 field experiment. CW: carapace width

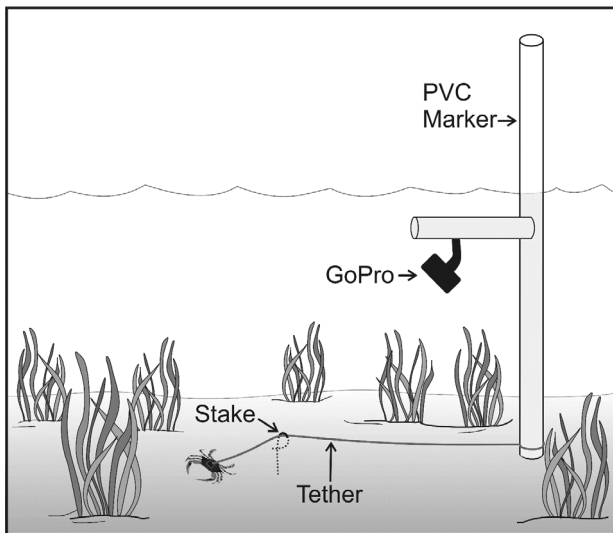


Fig. 3. Schematic diagram of the tether set-up used in the experiments with juvenile blue crabs. The PVC marker was 1 m away from the tethering stake, and the crab was attached to a 20 cm tether. The GoPro camera was oriented such that the field of view encompassed the entire range of the tether. Note that the juvenile crab is not drawn to scale and the submerged aquatic vegetation distribution is not necessarily representative of what was seen in the field

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

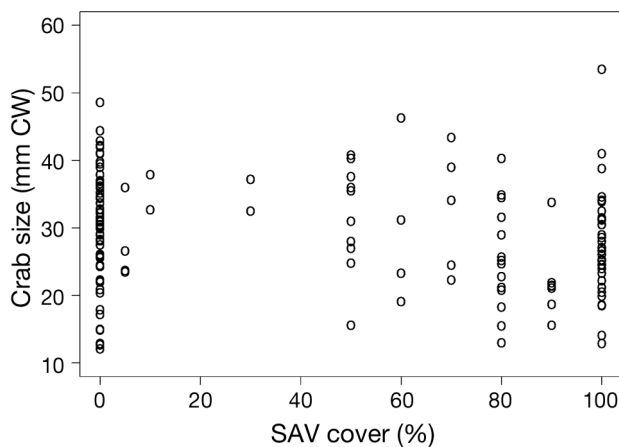


Fig. 4. Size distribution of tethered juvenile blue crabs at various levels of submerged aquatic vegetation (SAV) cover during the 2016 field experiment

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. The duration of a given trial was determined by logistical constraints (e.g. tides, weather). At the end of each trial, all tethers were checked for crab survival, and pieces of carapace, a chewed line, or a cut line provided evidence of predation. Individual crabs were only tethered for the duration of a single trial; surviving crabs were released upon trial completion.

Predator identification

Predators of juvenile blue crabs were identified by using GoPro cameras to capture images of predator–prey interactions during the 2015 pilot study and the 2016 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 7 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 bias-corrected Akaike's information criterion (AIC_c) values were calculated to determine

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

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 Stukel goodness of fit test (Stukel 1988) and coefficient of discrimination, a pseudo- r^2 statistic for binomial data (Tjur 2009), were used to assess model fit, rather than the Hosmer-Lemeshow test (Lemeshow & Hosmer 1982), due to their better statistical properties (Allison 2014). Model fit was further assessed by conducting likelihood ratio tests and checking for overdispersion. Statistical analyses were conducted using R (R Core Team 2014) and RStudio (RStudio Team 2016) statistical software. 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

Juvenile survival

A total of 145 independent trials was used to model juvenile blue crab survival in York River nursery habitats (Table 2). Juvenile 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 Stukel test indicated that model g_5 fit the data well (Table 3), and the likelihood ratio tests demonstrated that model g_5 was a better fit than the other models. The small ratio of the residual deviance to the residual degrees of freedom suggested that model g_5 was not overdispersed.

Parameter estimates of model g_5 were significant (Table 3), with juvenile blue crab survival increasing with crab size (Fig. 5A) and decreasing with trial duration (Fig. 5B). Survival increased marginally

Table 2. Design of the 2016 tethering experiments. N: number of juvenile blue crabs tethered in each treatment combination

Month	Habitat	Time	N
July	Sand	Day	32
		Night	31
	Seagrass	Day	31
		Night	25
August	Seagrass	Day	14
		Night	12

Table 3. Parameter estimates from logistic regression model g_5 (see Table 1) for juvenile blue crab survival. Stukel test indicated satisfactory goodness of fit ($\chi^2 = 0.455$, $df = 2$, $p = 0.80$), with the coefficient of discrimination = 0.20. SAV: submerged aquatic vegetation

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

with SAV cover (Table 3, Fig. 5C). 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. Eq. (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. 6). At low SAV cover, predicted probability of survival increased with size from 7% at 12 mm to 45% at 54 mm CW (Fig. 6). At high SAV cover, juvenile survival probability increased with size from 17 to 68% (Fig. 6).

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 g_5 , juvenile blue crab survival increased significantly with size and decreased with trial duration (Table 4). Vege-

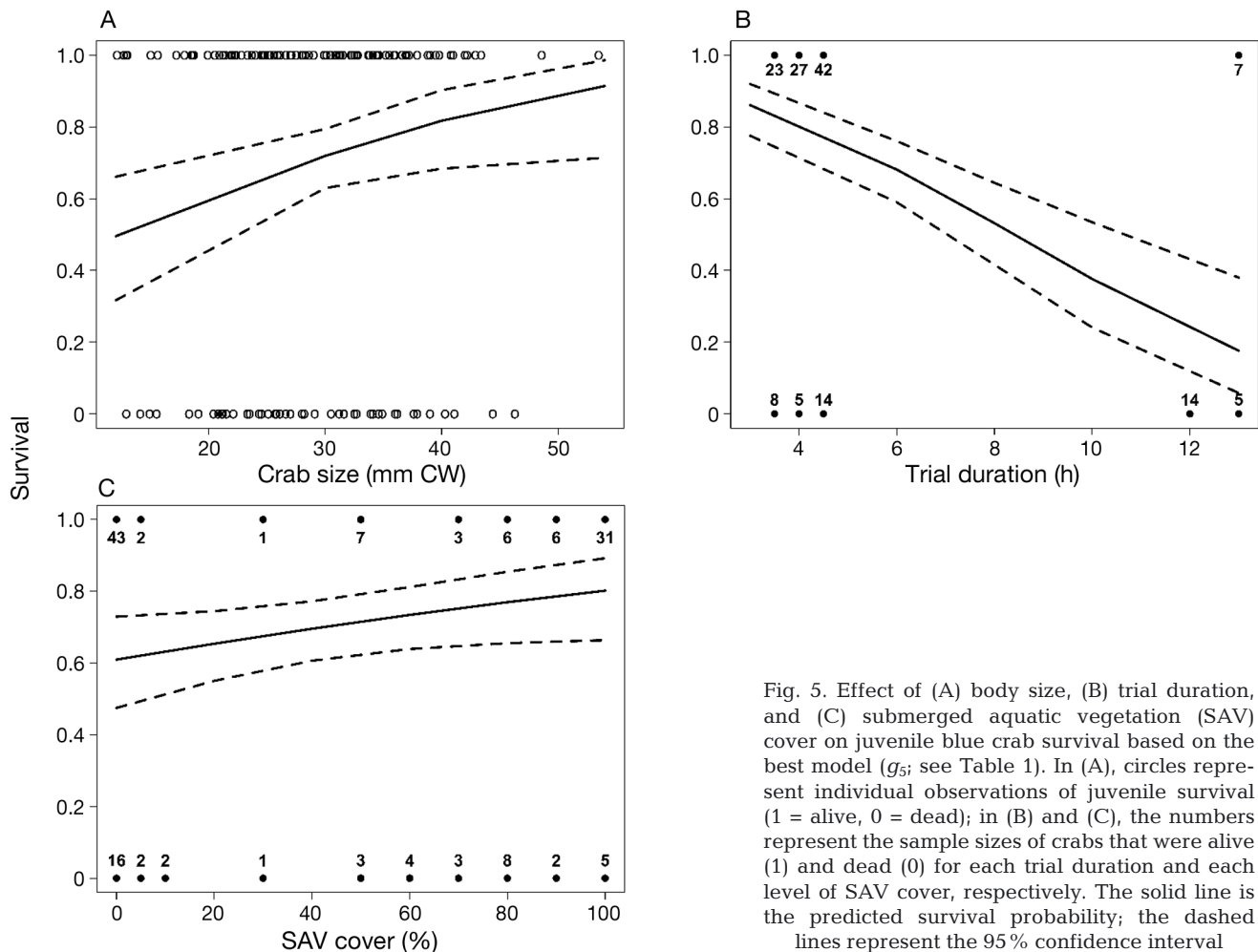


Fig. 5. Effect of (A) body size, (B) trial duration, and (C) submerged aquatic vegetation (SAV) cover on juvenile blue crab survival based on the best model (g_5 ; see Table 1). In (A), circles represent individual observations of juvenile survival (1 = alive, 0 = dead); in (B) and (C), the numbers represent the sample sizes of crabs that were alive (1) and dead (0) for each trial duration and each level of SAV cover, respectively. The solid line is the predicted survival probability; the dashed lines represent the 95% confidence interval

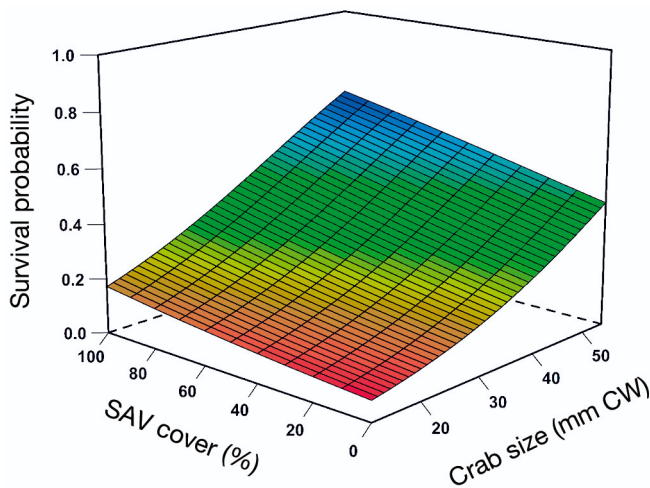


Fig. 6. Juvenile blue crab probability of survival as a function of crab size and submerged aquatic vegetation (SAV) cover at a standard trial duration of 12 h, derived from Eq. (2)

tated habitat had a marginally significant, positive effect on crab survival relative to unvegetated habitat (Table 4). There was no interaction between size and habitat (Fig. 7).

Predator identification

Juvenile blue crabs that were missing when the tethers were checked were assumed to be eaten, given the high tether retention. For the 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 predators. GoPro photos of the tethering experiments identified 4 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 5, Fig. 8A). Northern puffers *Sphoeroides maculatus* and striped burrfish *Chilomycterus schoepfi* were also seen feeding on teth-

Table 4. 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

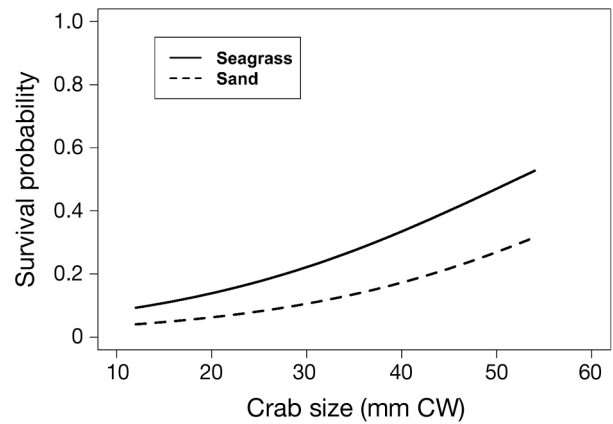


Fig. 7. Juvenile blue crab survival probability as a function of crab size by habitat. The probabilities are derived from Eq. (1), using the parameter estimates from the best logistic regression model with the categorical habitat factor, holding time constant (day)

Table 5. 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 adults <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)

ered juvenile crabs (Table 5, Fig. 8B,C). Additionally, an oyster toadfish *Opsanus tau* was found on 1 of the tethers at the end of a trial, having swallowed the juvenile crab whole (Fig. 8D). All predators identified in the GoPro images were seen at both the vegetated and unvegetated sites. Although tethered crabs at the unvegetated sites could not seek refuge in structured habitat, juveniles at both sites found refuge from predators by burrowing in the sediment.

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

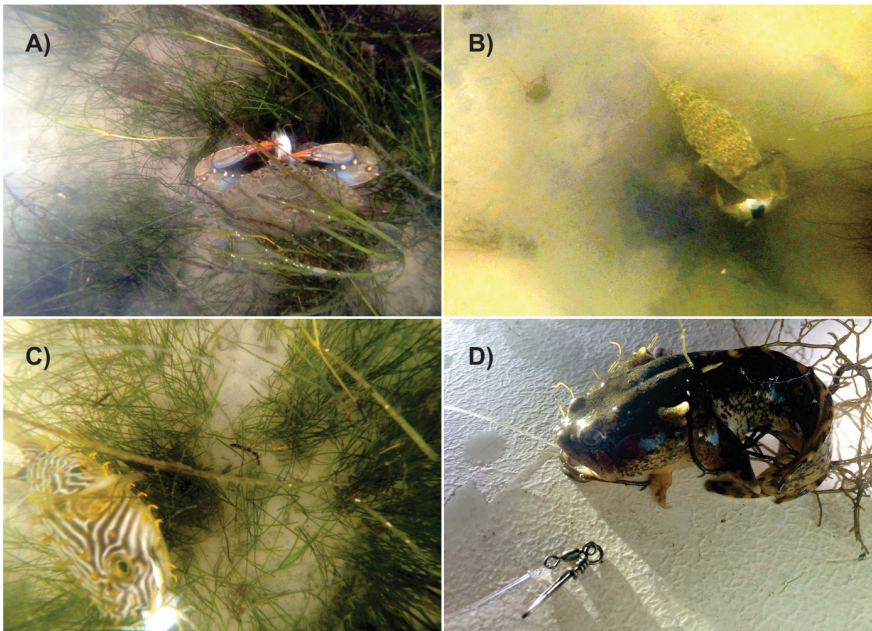


Fig. 8. GoPro photos of predators of juvenile blue crabs in the tethering experiments: (A) adult blue crab; (B) northern puffer; (C) striped burrfish; (D) oyster toadfish. Images show tethered juvenile crabs (A–C) or the tether line (D) in the mouths of predators

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 our 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 habitat 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,

Pardieck et al. 1999, Lipcius et al. 2007). There are 2 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 (Perkins-Visser et al. 1996, Beck et al. 2001).

The current paradigm of blue crab habitat use posits that survival decreases in sea-

grass 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). Most habitat–survival studies have used shoot density to quantify the structural complexity of a seagrass bed, often creating artificial seagrass mats of various densities to conduct the experiments (Hovel & Lipcius 2001, Orth & van Montfrans 2002, Hovel & Fonseca 2005). Measuring natural shoot densities requires partial removal of the grass bed; using artificial seagrass permits researchers to examine the effect of shoot density on survival without disturbing the environment, with the caveat that the artificial conditions may not be representative of the natural system. For this study, we were particularly interested in juvenile blue crab survival in York River nursery habitats, and thus opted to quantify available refuge habitat by estimating percent SAV cover at each tether location in the field. Estimating percent cover allowed us to conduct our tethering experiments at the same sites throughout the study period in naturally occurring patches of seagrass. Although vegetation cover is not a typical measure of structural complexity, its quantification can be a good representation of seagrass patchiness at small spatial scales and can provide information about the amount of habitat available as refuge within the proximity of a tethered juvenile blue crab.

Our study determined that dense SAV cover has a positive effect on blue crab survival, with a greater proportion of juveniles tethered in 100% SAV cover surviving than those in a completely unvegetated habitat. There was no interaction between percent cover and size, indicating that SAV cover is beneficial for juvenile blue crabs regardless of size. However, 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. For example, the absence of experimental plots with 5–45% cover may be concealing a non-linear habitat–survival function.

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. am-

phipods, 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 2 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 total length) 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 for 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 clams 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 dense cover of seagrass beds increases juvenile blue crab survival, and that larger juveniles experience a partial size refuge from predation, both in dense seagrass and in unvegetated sand habitats bordering seagrass beds. We propose that juvenile blue crabs remain protected in SAV and forage on the abundant prey within the grass bed until they become so large that density-dependent processes such as intraspecific aggression and competition for food drive them to disperse from SAV beds. In this manner, 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 lower. 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 2 decades, advances in camera technology have made quality, high-definition cameras easily accessible to a larger group of scientific investigators (e.g. students, non-governmental organizations; Bicknell et al. 2016). Although camera technol-

ogy 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 may significantly contribute 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).

Juvenile and adult blue crabs are spatially segregated in the winter, with adults, primarily females, overwintering in the deeper channels of the Chesapeake Bay main stem, while juveniles and mature males remain in the tributaries (Van Engel 1958, Heck & Thoman 1984, Orth & van Montfrans 1987). In the warmer months, however, adult and juvenile distributions overlap as adults move in and out of the tributaries to forage and mate within seagrass beds (Heck & Orth 1980), salt marshes (Fitz & Wiegert 1991), oyster reefs (Harding & Mann 2010), and unvegetated bottoms (Seitz et al. 2003). The abundance of foraging adults in Chesapeake Bay tributaries such as the York River (Heck & Orth 1980, Lipcius & Van Engel 1990) suggests that adult blue crabs have the potential to impact juvenile mortality through cannibalism in these critical nursery habitats.

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 observed feeding 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 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.

In addition to diet information, abundance data for northern puffers and striped burrfish are also lacking, as the species are not well-studied in Ches-

apeake Bay. However, fishery-independent data from the Virginia Institute of Marine Science (VIMS) Trawl Survey suggest that, despite some annual variation, northern puffers may be relatively abundant in lower Chesapeake Bay tributaries, with a total of up to 230 individuals caught in a season (Tuckey & Fabrizio 2012). Conversely, a total of only 16 striped burrfish were caught in the VIMS Trawl Survey in 2016 (Tuckey & Fabrizio 2016), suggesting an increase in abundance from previous years, but a relatively low abundance overall. Thus, it seems unlikely that striped burrfish would play a significant role in juvenile blue crab mortality even if they are capable of capturing juvenile crabs in the seagrass beds.

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. Oyster toadfish are common in seagrass beds and other shallow, structured habitats across the Bay, with as many as 747 individuals caught in the VIMS Trawl Survey in the summer of 2012 (Tuckey & Fabrizio 2012). Given their abundance in nursery habitats throughout the tributaries (Schwartz & Dutcher 1963, Tuckey & Fabrizio 2012, 2016), oyster toadfish may contribute significantly to juvenile crab mortality in Chesapeake Bay.

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.

Acknowledgements. We thank the students and staff of the Marine Conservation Biology and Community Ecology Labs at the Virginia Institute of Marine Science (VIMS) for field and laboratory assistance. We also thank Mary Fabrizio, Rochelle Seitz, and Matt Kirwan for their feedback and insight. This research was made possible through the support of the Willard A. Van Engel (WAVE) Fellowship in blue crab ecology and conservation, the VIMS GK-12 Short Trust Fellowship, VIMS student research grants, and a grant to R.N.L. from the National Oceanic and Atmospheric Administration, Chesapeake Bay Office (grant NA13NMF4570-205). This paper is Contribution No. 3702 of VIMS, College of William & Mary.

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*Submitted: May 2, 2017; Accepted: November 4, 2017
Proofs received from author(s): November 20, 2017*