



Saved by the shell: Oyster reefs can shield juvenile blue crabs *Callinectes sapidus*

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ABSTRACT: Juvenile blue crabs *Callinectes sapidus* use seagrass and other structured habitats as refuges from predation. Oyster reef habitats provide structural complexity that may offer refuge, but the value of these habitats for juvenile blue crabs has not been examined. We quantified survival of juvenile *C. sapidus* in structured oyster reef habitat versus unstructured soft-bottom habitat. In a field tethering experiment in the York River, lower Chesapeake Bay (USA), juvenile *C. sapidus* (10–50 mm carapace width [CW]) were tethered in sand (n = 40) or oyster reef (n = 39) habitats at subtidal sites 1–2 m deep. An underwater camera system was used to record predation activity during 24 h trials. Juvenile crab survival was significantly higher on the oyster reef habitat (53.8%) than on bare sand (15.0%), and tended to increase with crab CW in both habitats. The main successful predators on juvenile blue crabs were northern pufferfish *Sphoeroides maculatus* in the oyster reef habitat and adult blue crabs in the sand habitat. The high survival rate of juvenile *C. sapidus* in oyster reef habitats suggests that oyster reefs include physical habitat complexity that may offer refuge from predators. Restored and natural oyster reefs could provide an alternative nursery habitat for juvenile blue crabs, expanding the ecosystem services provided by restored oyster reefs.

KEY WORDS: Blue crab · Tethering · Oyster reef · Habitat refuge · Nursery habitat · Ecosystem services · Chesapeake Bay

1. INTRODUCTION

1.1. Nursery habitat

Structurally complex habitats can serve as nursery grounds for many invertebrates, including blue crabs *Callinectes sapidus*. Structured nursery habitats for blue crabs include seagrass beds (Heck & Thoman 1984, Heck et al. 2003, Lipcius et al. 2005, Seitz et al. 2005, Ralph et al. 2013), non-native algae (Johnston & Lipcius 2012), salt marshes (Minello et al. 2003), and coarse woody debris (Everett & Ruiz 1993). Structure can reduce the ability of a predator to find prey (Grabowski 2004), which may be key in reducing predator–prey and cannibalistic interactions of adult and juvenile blue crabs (Moksnes et al. 1997). Blue crab survival is enhanced in structured seagrass

habitats versus unstructured habitats, like sandy bottom, due to inhibition of predator detection (Wilson et al. 1990, Hovel & Lipcius 2001, 2002, Seitz & Ewers Lewis 2018). Oyster reefs provide protection from predation for mud crabs in Gulf Coast systems (Hill & Weissburg 2013), but their function in providing protection for juvenile blue crabs is unknown. Provision of habitat to increase survival of juvenile blue crabs could be an important ecosystem service of restored oyster reefs and is important to quantify.

1.2. Prey, predators, and crab size effects

The blue crab is a large portunid crab that is distributed along the Northwest Atlantic, Gulf of Mexico, and Caribbean coasts (Williams 1984, Lipcius

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& Van Engel 1990) and serves as predator and prey (Lipcius et al. 2007). It supports one of the most important fisheries in Chesapeake Bay (USA), with over 75 000 t landed per year, which is worth US\$81 million to the economy (NOAA 2019). This species is also vital ecologically, as it is a key component in the Chesapeake Bay food web (Baird & Ulanowicz 1989, Lipcius & Latour 2006). The main predators of juvenile blue crabs typically include conspecifics and epibenthic fishes (Bromilow & Lipcius 2017). Blue crabs are epibenthic generalists that forage on a wide variety of infaunal and epibenthic invertebrates as well as on plant material (Mansour 1992, Meise & Stehlik 2003, Stehlik et al. 2004). Ecologically, blue crab foraging has major effects on prey populations and benthic community structure (Hines 2007). The abundance and availability of prey, including eastern oysters (Eggleston 1990a,b,c) and hard clams (Van Engel 1958, Sponaugle & Lawton 1990), can be limited by blue crab predation. Blue crabs are central to Chesapeake Bay food web models (Baird & Ulanowicz 1989, Lipcius & Latour 2006); thus, blue crab predator–prey interactions are key to understanding the Chesapeake Bay ecosystem.

Prey size and habitat complexity are important in a predator–prey relationship. In unvegetated mud habitats, juvenile blue crab survival increases with carapace width (CW) (Johnston & Lipcius 2012), although the opposite is true in eelgrass habitats, leading to a predation-induced ontogenetic shift in habitats (Lipcius et al. 2007). Moreover, predators in structurally complex habitats are less successful than those in habitats that are not complex (Sih et al. 1985, Stoner 2009). Structurally complex habitats provide spaces and cover (i.e. shells, corals, and plants) in which animals can hide; thus, juvenile blue crabs are able to avoid multiple predators using habitat refuge. Therefore, the interstitial space provided by oyster reefs may serve as a refuge for juvenile blue crabs against predation and cannibalism.

Key components in predator–prey interactions involve aspects of the functional response of a predator, such as encounter time, handling time, and habitat (Holling 1959a,b). Handling time (HT), the time required for a predator to capture and consume prey, typically increases with armored prey (e.g. eastern oyster *Crassostrea virginica*), thereby reducing consumption rates (Hassell 1978). Time to first encounter, or encounter time (ET), can be defined as the initial predatory interaction between searcher (predator) and prey (Gurarie & Ovaskainen 2013). The effect of increased HT is typically a quantitative

reduction in predation rate allowing local persistence, whereas the effect of a reduced ET is a qualitative shift and decreasing predation rates at low prey densities, resulting in a low-density refuge (Seitz et al. 2001). A predator's ET changes with habitat when structural impediments to predators, such as decreased sediment penetrability (Lipcius & Hines 1986, Seitz et al. 2001) or increased vegetative cover (Lipcius et al. 1998, Hovel & Lipcius 2001), result in reduced accessibility of prey to predators. These structural impediments may thus enhance survival from cannibalism and predation (Lipcius & Hines 1986, Glaspie & Seitz 2018). Thus, examining ET and HT using field experiments can be insightful to aid further research on the effects of habitat on predator–prey interactions.

1.3. Ecosystem services of oyster reefs

Oyster reefs provide abundant ecosystem services, such as habitat and foraging grounds for recreationally and commercially valuable fish (Peterson et al. 2003, Coen & Grizzle 2007, Pfirrmann & Seitz 2019). Recently, oyster restoration has been employed not only to enhance oyster abundance but also to enhance production of other species (Peterson et al. 2003, Plunket & La Peyre 2005, Rodney & Paynter 2006, Coen et al. 2007). The habitat benefits of oyster reefs have been documented for finfish and some crab species in other ecosystems (Posey et al. 1999, Gregalis et al. 2009), such as in the southeast Atlantic (Meyer & Townsend 2000, Wilber et al. 2012) and the Gulf of Mexico (Thomas et al. 1990, zu Ermgassen et al. 2021); however, the function of eastern oyster reefs as habitat for blue crabs in Chesapeake Bay remains unknown. Crabs and fish may increase their production on oyster reefs depending on reef characteristics, environmental conditions, and season (Coen & Grizzle 2007, Gregalis et al. 2009, Robillard et al. 2010, Humphries et al. 2011, Yeager & Layman 2011). Thus, studies from one system may not necessarily apply to another. Studies from other systems suggest that small crabs, such as mud crabs, prefer oyster reef over vegetated marsh edge or unvegetated habitats, potentially due to the abundance of small refugia (Shervette et al. 2011). However, this preference for oyster-reef habitat over marsh or unvegetated habitats has not been documented for juvenile blue crabs.

Recent studies on restored oyster reefs using settlement trays demonstrated that larger juvenile and adult crabs utilized oyster reefs, but predominantly

as foraging grounds (Karp et al. 2018). Hence, studies are warranted to determine the role of oyster reefs as potential refuge habitat for juvenile blue crabs.

The objectives of the current study were to (1) examine survival of juvenile blue crabs on oyster habitat versus unstructured sand habitat; (2) determine changes in survival of juvenile crabs with crab size in the 2 habitats; (3) identify predators responsible for crab mortality; and (4) quantify ETs and HTs of different predators. We hypothesized that (1) oyster habitat would increase juvenile blue crab survival; (2) juvenile blue crab survival would increase with crab size; (3) predators of juvenile crabs would differ between oyster and sand habitats; and (4) ETs and HTs would differ significantly among predators.

2. MATERIALS AND METHODS

2.1. Site selection

This study was conducted in the York River at a subtidal (1–2 m water depth) location near the Virginia Institute of Marine Science (VIMS) in Gloucester Point, VA, from late July through early October 2017. Hydrographic conditions (water temperature, salinity, and dissolved oxygen [DO]) were obtained from a nearby VIMS Virginia Estuarine and Coastal Observing System (VECOS) monitoring buoy at Gloucester Point (CBNERR 2018). Hydrographic data from late July to early October 2017 indicated that water temperature averaged 26.0°C and ranged from 22 to 28°C, salinity averaged 20.6 (17–21), and DO averaged 6.6 mg l⁻¹ (2.9–17.5 mg l⁻¹).

Sites were muddy sand or oyster reef habitats, with the latter consisting of oyster reef communities that had grown naturally on plastic mesh aquaculture bags containing oysters and placed on racks (2.4 m × 1 m × 0.3 m) adjacent to VIMS (37° 14' N, 76° 30' W). These oyster reef communities grew on the tops and sides of the bags and resulted from natural settlement of wild oyster larvae on the bags over a few years. The oyster reef communities developed similar in structure to a natural oyster reef, and consisted of oysters, sponges including red beard *Microciona prolifera*, mud crabs (Xanthidae), gobies (Gobiidae), striped blennies *Chasmodes bosquianus*, and feather blennies *Hypsoblennius hentz*. Three sand sites and 3 oyster sites at least 5 m apart were chosen haphazardly and marked with PVC poles.

2.2. Blue crab survival

Juvenile *Callinectes sapidus* (10–50 mm CW) of both sexes were collected from the York River, VA, and kept in flow-through tanks. All crabs used in our experiments were immature; blue crabs do not reach sexual maturity until 82 mm CW for males (Williams 1984) and 90 mm CW for females (Van Engel 1958). Crabs were measured, then tethered with 20 cm lengths of monofilament fishing line by slip knots tightened and secured around the carapace spines of the crab. Monofilament length was shortened from 20 to 12 cm after the fourth trial to accommodate the field of view of the underwater camera system. This change in tether length did not significantly impact our results, with the short tether trials having a mean (\pm SE) proportional survival of 0.54 \pm 0.16 and the long tether trials having a mean proportional survival of 0.54 \pm 0.10. Crabs up to 30 mm CW were tethered with 5.4 kg test monofilament, while crabs measuring 30–50 mm CW were tethered with 6.8 kg test monofilament. These test monofilament weights were sufficient to tether the crabs used in this study and not break due to wave action (Heck et al. 2001, Moody 2003, Lipcius et al. 2005). A drop of cyanoacrylate adhesive and a small square of black duct tape were used to secure the knot of the crab tether. Black tape was chosen because it does not reflect light and would not likely attract predators. The monofilament line was then secured to a fishing swivel. Crabs were kept in individual plastic containers with air holes for at least 12 h in flow-through tanks, to ensure tether retention and crab survival, following methods from previous studies (Lipcius et al. 2005, Johnston & Lipcius 2012, Bromilow & Lipcius 2017).

Tethering is a common method to measure relative predation of small benthic species, including crustaceans (Heck & Wilson 1987, Pile et al. 1996, Hovel & Lipcius 2001, Moody 2003, Lipcius et al. 2005, Johnston & Lipcius 2012). Since the ability of tethered animals to escape predation is limited to the length of the tether (Zimmer-Faust et al. 1994), tethering can lead to inflated natural mortality rates. As such, the method can only be used to measure relative rates of predation, not absolute rates. Tethering also has the potential to introduce treatment-specific bias in survival (Peterson & Black 1994). However, previous studies found no significant interaction between treatment 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.

All tethered crabs were active and had both claws intact. At each sand site, a tethered crab was attached by a swivel to a metal garden stake pushed flush with the bottom. At each oyster habitat site, a zip tie was attached around the oyster rack structure, surrounded by the oyster community, and a tethered crab was attached by swivel to the zip tie (Fig. 1). Tethered crabs had full use of all of their limbs and could bury or hide in their respective habitats. Trials lasted 24 h, with a subset of trials under continuous video surveillance (see details in Section 2.3), at the end of which tethers were pulled up and checked to see if crabs were alive or had been eaten. Following previous studies, a piece of carapace, a chewed line, or a cut line indicated evidence of predation (Bromilow & Lipcius 2017). Because tethered crabs were held for at least 12 h prior to deployment, there is high confidence that crabs were not able to cut their line or escape their tether. Some trials did not use video and were only used for assessing survival. Fresh crabs were used at the start of each 24 h trial. In total, 21 trials were run at sand and oyster sites simultaneously, with 42 crabs tethered at sand sites, and 42 at oyster sites (Fig. 2). Crabs that molted during a trial (3 in oyster trials; 2 in sand trials) were excluded from analyses, resulting in 39 and 40 crabs in the oyster and sand trials, respectively.

2.3. Predator–prey interactions

A 4-channel underwater camera system (Ever-Focus SV-DVC4, Shark Marine Technologies) with

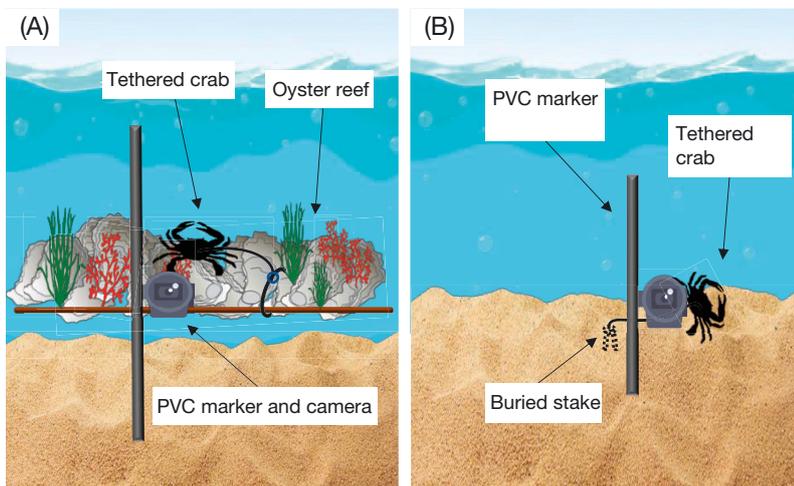


Fig. 1. Tether set-up used in the (A) oyster habitat and (B) sand habitat. The camera was oriented so as to encompass the entire range of the tether. Not drawn to scale

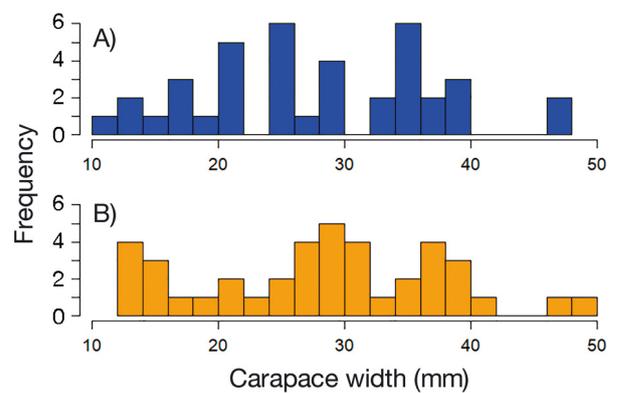


Fig. 2. Distribution of crab carapace width used for tethering in (A) oyster habitat and (B) sand habitat

DVR capabilities (ECOR264-4*1) was utilized to record predation activity for a subset of the 24 h trials. Recording rate was 30 frames per second. Cameras were positioned on numbered PVC poles at 4 of the 6 sites, such that the entire range of each tethered crab was in the camera's field of view (distance from the crab was 30–40 cm depending on water clarity and habitat type). Low light black and white cameras (SV-14R2) and infrared cameras for night filming (SV-16HR) were used. In total, 47 crabs in 14 trials were recorded (oyster habitat $n = 31$, sand habitat $n = 16$). Cameras were not used during trials that occurred during stormy weather due to poor visibility. Moreover, predator identification was only attempted in trials where visibility was adequate. Video footage was reviewed by fast forwarding until a predation event occurred and then that segment was analyzed slowly. ET was defined as the time from the start of the trial to the initial predatory interaction between a potential predator and a tethered crab (Gurarie & Ovaskainen 2013). HT was defined as time (h) from ET to when the prey was eaten, or the time spent feeding on a prey item (Giller 1980).

2.4. Statistical analyses

To address the hypotheses regarding juvenile crab survival, we developed 5 statistical models (g_1 – g_5) following an information-theoretic approach (Burnham & Anderson 2002, Anderson 2008), including the null model for comparison (Table 1). Each model represented a hypothesis and

Table 1. Akaike's information criterion (AIC) calculations for logistic regression models corresponding to the different hypotheses for juvenile blue crab survival represented by g_j . k : number of parameters, including variance (σ^2), in model g_j ; AIC_C : bias-corrected AIC value; Δ_i : difference in the AIC_C value between model g_j and the best model; w_j : probability that model g_j is the best model in the set; CW: crab carapace width; H: habitat in which juvenile crabs were placed (either sand or oyster reef)

Model	Variable(s)	k	AIC_C	Δ_i	w_i	% deviance explained
g_1	CW + H + (CW \times H)	4	94.51	2.54	0.13	15.6
g_2	CW + H	3	92.39	0.42	0.39	15.4
g_3	CW	2	104.63	12.66	<0.01	1.1
g_4	H	2	91.97	0.00	0.48	13.6
g_5	Null	1	103.63	11.65	<0.01	–

included different combinations of variables that could describe observed differences in the response variables.

Tethered crab survival was modeled as a binary response (1 = alive, 0 = dead), with crab CW (mm) as a continuous covariate and habitat (oyster, sand) as a fixed factor. Models were analyzed using logistic regression to determine the probability of crab survival, and bias-corrected Akaike's information criterion (AIC_C) values were calculated to determine the best model. Weighted model probabilities (w_j) based on Δ_i values were used to determine the probability that a particular model was the best-fitting model. Statistical analyses were conducted using R (R Core Team 2017) and RStudio (version 1.3.1093; RStudio Team 2017) statistical software. Parameter estimates of the best-fitting model were used to calculate binomial survival probabilities as:

$$\theta = \frac{e^{\alpha + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i}}{1 + e^{\alpha + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i}} \quad (1)$$

where θ is the probability of survival, α is the parameter for the baseline condition (constant), and β_i are parameters representing increases or decreases in survival due to the effect of corresponding independent variables x_i . Note that interaction terms are represented as $\beta_i x_i x_j$.

3. RESULTS

3.1. Juvenile crab survival

There was no bias between habitats in the mean CW of crabs used for tethering experiments or for the CW distri-

bution of crabs that survived after trials versus crabs that were eaten. The range of crab CW used in the experiments was 13.7–49.1 mm (mean \pm SE = 28.4 ± 1.5) in sand treatments and 11.6–47.4 mm (mean = 27.7 ± 1.5) in oyster treatments (Fig. 2), and did not differ significantly between treatments (Kolmogorov-Smirnov test, $p = 0.847$). The mean CW for crabs that survived ($n = 27$) was 29.6 ± 1.7 mm, whereas the mean CW for crabs eaten during trials ($n = 52$) was 27.3 ± 1.3 mm, indicating that these mean CWs did not differ significantly due to

the overlapping 95% confidence intervals.

For juvenile crab survival (crabs from both filmed and unfilmed trials), models g_2 (habitat and crab CW) and g_4 (habitat alone) had the highest weighted probabilities, 0.39 and 0.48, respectively (Table 1). Although model g_4 had a higher weighted probability, the effect of habitat was nearly equivalent in both models (Table 2), so we interpreted both model g_4 and model g_2 to include the effect of crab CW in the results. Models g_2 and g_4 both fit the data better than the null model and the global model with an interaction effect (likelihood ratio χ^2 test, $p > 0.1$), and explained 15.4 and 13.6% of the deviance, respectively. A Stukel test indicated the model fit the data satisfactorily (likelihood ratio χ^2 test, $p > 0.1$). Juvenile crab survival differed significantly between habitats, as indicated by the 95% confidence interval for the effect of sand habitat in model g_4 (Table 2). Mean crab survival, calculated from Eq. (1) and parameter estimates in Table 2 for model g_4 , was 53.8% in oyster habitat, which was over 3-fold higher than in the sand habitat (15.0%).

To assess the joint effects of crab CW and habitat (Fig. 3), parameter estimates of model g_2 (Table 2)

Table 2. Parameter estimates from logistic regression models g_2 and g_4 for juvenile blue crab survival. The sand habitat is compared to the oyster habitat (baseline). CW: carapace width

Model	Parameter	Estimate	SE	95% CI
g_2	Intercept = oyster reef	-0.905	0.862	-2.629, 0.819
	CW	0.038	0.029	-0.020, 0.096
	Effect of sand habitat	-1.966	0.561	-3.088, -0.844 ^a
g_4	Intercept = oyster reef	0.154	0.321	-0.488, 0.796
	Effect of sand habitat	-1.889	0.547	-2.983, -0.795 ^a

^aWhen a confidence interval excludes 0, a parameter estimate is considered to differ significantly from 0

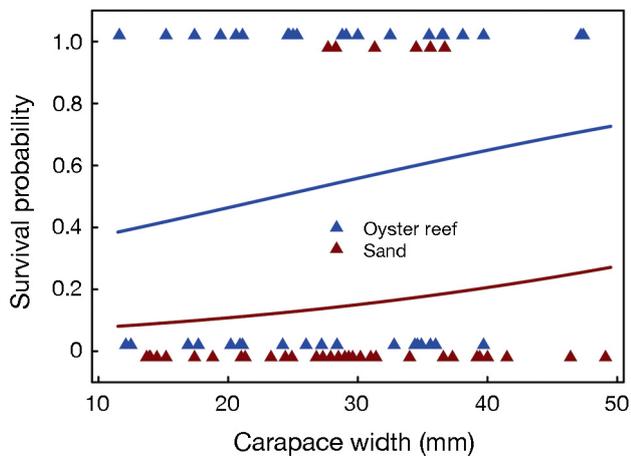


Fig. 3. Crab survival by habitat and carapace width. Eqs. (2) and (3) were used to generate the curves of survival probability

were used to generate survival probabilities using the following equations:

$$\theta = \frac{e^{-0.905 + 0.038x_1}}{1 + e^{-0.905 + 0.038x_1}} \quad (2)$$

$$\theta = \frac{e^{-0.905 - 1.966 + 0.038x_1}}{1 + e^{-0.905 - 1.966 + 0.038x_1}} \quad (3)$$

where x_1 = crab CW. These represent survival probabilities in oyster habitat (Eq. 2) and sand habitat (Eq. 3), although the estimated effect of crab CW had high variance (Table 2). In oyster reef habitat, survival ranged from 38.5% for a small 12 mm CW crab to 72.6% for a larger 50 mm CW crab (Fig. 3). Conversely, in sand habitat, survival was much lower, ranging from only 8.1% for a small crab to 27.1% for a larger juvenile (Fig. 3). To display the disparity in survival probability as a function of CW in the 2 habitats, we calculated the differences in survival probability between the habitats (cf. Figs. 3 & 4). The magnitude of the difference in survival probability ranged from 0.30 for small juveniles to 0.46 for larger juveniles (Fig. 4), but the percent difference was inversely related to CW. Oyster reef habitat increased survival probability by almost 400% for small juveniles but <200% for larger juveniles (Fig. 4).

3.2. Predator identity and behavior

In total, 47 individual juvenile crabs were filmed, of which 25 had instances of

predation that were filmed. Predators were positively identified in 16 instances, with adult blue crabs and the northern pufferfish *Spherooides maculatus* as the most common predators (Table 3, Fig. 5). The range in CW of tethered crabs with filmed instances of predation was 21.1–40.0 mm. The 2 main predators did not have sufficient ETs or HTs in both habitats to permit inter-predator comparisons. Thus, we limited the results to quantitative descriptions of ETs and HTs by habitat.

For ET in the sand habitat, 8 adult blue crabs encountered a tethered crab. Mean (\pm SE) ET was 8.5 ± 2.35 h, with a range of 0.15–16 h. No northern pufferfish encountered tethered crabs in the sand. In the oyster habitat, only 1 adult blue crab encountered a tethered crab, 13 h after the start of the trial. In contrast, 6 northern pufferfish encountered a tethered crab in oyster habitat. Mean ET was 6.75 ± 3.0 h, with a range of 1–21 h.

For HT in the sand, all 8 adult blue crab encounters led to consumption over 0.08–0.27 h with a mean HT of 0.13 ± 0.02 h. In the oyster habitat, the single adult blue crab consumed the tethered crab in 0.18 h. Meanwhile, all 6 northern pufferfish encounters led to consumption over 0.02–0.37 h with a mean HT of 0.08 ± 0.07 h.

Other fish including red drum, black drum, croaker, white perch, and yellow perch were recorded scavenging tethered crab remains, but they never made the initial attack (Table 3). In 1 instance, a blue crab scavenged the remains of a tethered crab eaten

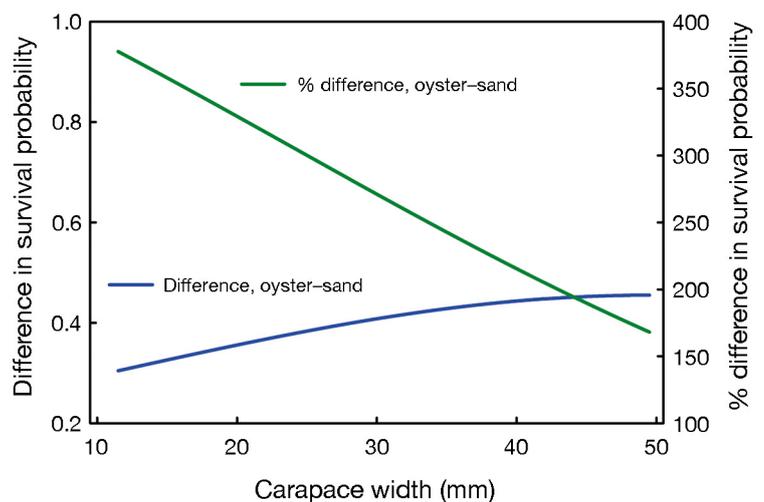


Fig. 4. Difference and percent difference in crab survival probability between oyster habitat and sand habitat. Eqs. (2) and (3) were used to generate the difference in survival probability, and reflect the distance between the curves in Fig. 3. Difference = (Eq. 2 – Eq. 3)/Eq. 3 either as a magnitude or percent difference

Table 3. List of predators and scavengers organized by total number of encounters, regardless of consumption. Oyster (sand) habitat encounter: number of times a predator/scavenger encountered a tethered crab in the oyster (sand) habitat; oyster (sand) habitat consumption: number of times a predator/scavenger consumed a tethered crab in the oyster (sand) habitat. Superscripts indicate which scavengers associated with which dominant predator (NP: northern pufferfish; BC: blue crab)

Species	Total encounters	Oyster habitat encounter	Oyster habitat consumption	Sand habitat encounter	Sand habitat consumption
Predators					
Blue crab (adult)	9	1	1	8	8
Northern pufferfish	6	6	6	0	0
Black seabass	2	2	1	0	0
Oyster toadfish	1	1	1	0	0
Scavengers					
White perch	3	3 ^{NP}	3 ^{NP}	0	0
Croaker	2	0	0	2 ^{BC}	2 ^{BC}
Black drum	1	1 ^{NP}	1 ^{NP}	0	0
Blue crab (adult)	1	1 ^{NP}	1 ^{NP}	0	0
Red drum	1	0	0	1 ^{BC}	1 ^{BC}
Yellow perch	1	0	0	1 ^{BC}	1 ^{BC}

when the crab tether was pulled at the end of an unfilmed trial.

4. DISCUSSION

4.1. Juvenile crab survival

Survival of juvenile blue crabs was over 3-fold higher in oyster habitat compared to sand. This is the first experimental demonstration of the potential for oyster reefs to serve as nursery habitat that reduces predator-induced mortality for this species. Juvenile crab survival also increased with crab CW, and though not significant, we included crab CW as an independent variable due to the extensive evidence for an effect of blue crab size on survival (Pile et al. 1996,

Hovel & Lipcius 2001, Lipcius et al. 2005, Johnston & Lipcius 2012, Bromilow & Lipcius 2017). The positive relationship between survival and crab CW is biologically important because the low survival of the smallest crabs may eliminate them from sand habitats in general (Pile et al. 1996). An ontogenetic shift in habitats has been proposed as a mechanism for blue crabs to improve survival as they grow (Bromilow & Lipcius 2017), with movement out of structured habitats as crabs grow larger than about 25 mm CW. The increased survival in structured oyster habitats for juvenile blue crabs is not surprising given the use of other structured nursery habitats by small juvenile crabs (Orth & van Montfrans 1987, Wilson et al. 1990, Everett & Ruiz 1993, Hovel & Lipcius 2001), and use of oyster habitats by other species (Brown et al. 2014). The efficacy of oyster habitats as nurseries for juvenile blue crabs in Chesapeake Bay might depend on the presence of competing species, such as shrimp (Eggleston 1998) and mud crabs, if they deter juvenile blue crabs from using oyster reef as habitat (Grabowski et al. 2008, Hill & Weissburg 2013). Mud crabs are prevalent in oyster reefs or shelly habitats (Williams 1984, Grabowski et al. 2008). Thus, areas with high densities of mud crabs may preclude use of oyster reefs by small juvenile blue crabs.

The increased survival of juvenile crabs in structured habitats presumably arises from the ability of the crabs to utilize small crevices among and between the structural elements, which protect small



Fig. 5. Dominant predators identified from video surveillance: (A) adult blue crab (on sand habitat) and (B) northern pufferfish (on oyster habitat). Images show tethered crabs being consumed

by a pufferfish. Two black seabass were recorded attacking a tethered crab, but only one successfully attacked and consumed the tethered crab. One oyster toadfish was caught consuming a tethered crab

crabs from either being seen or encountered by predators (e.g. Wilson et al. 1990, Pile et al. 1996, Hovel & Lipcius 2001, Orth & van Montfrans 2002). The percent increase in crab survival in oyster reef habitat as compared to sand was greatest for small juveniles compared to larger juveniles, suggesting that oyster reefs are most important for the smallest size classes. Our results regarding crab survival agree with our hypothesis and with previous studies showing high juvenile blue crab survival in structured versus unstructured habitats (Lipcius et al. 2007, Bromilow & Lipcius 2017). Vegetated habitats (i.e. emergent and submerged aquatic vegetation) are presumed to be the primary nursery habitat for juvenile blue crabs in other systems (Heck & Thoman 1984, Beck et al. 2001, Heck et al. 2003) as well as in Chesapeake Bay (Lipcius et al. 2007). However, the novel demonstration of oyster protection of juvenile blue crabs from predation suggests that restored oyster reefs may serve as alternative nursery habitats, like the exotic red alga *Agarophyton vermiculophyllum* in Chesapeake Bay (Johnston & Lipcius 2012) and oyster reefs in the Gulf of Mexico (zu Ermgassen et al. 2021).

4.2. Predator identity and behavior

Our video recordings allowed us to identify the main successful predators of juvenile blue crabs in different habitats, with adult blue crabs most common in sand habitats and northern pufferfish most common in oyster habitats. Cannibalism is a well-known source of mortality for juvenile blue crabs (Dittel et al. 1995, Hines & Ruiz 1995), but the northern pufferfish was only recently identified as a predator of juvenile blue crabs in video surveys (Moody 2003, Bromilow & Lipcius 2017). A few other predators were seen in our studies, including red drum, croaker, black seabass, and oyster toadfish, but these were secondary predators and were uncommon.

Blue crabs are olfactory (Weissburg & Zimmer-Faust 1993) and chemotactile foragers (Lipcius & Hines 1986, Keller et al. 2003), and they may have been able to detect prey in sand habitat more easily than pufferfish, which likely rely on visual cues since they commonly feed only during the daytime (Strand 2004).

4.3. Limitations

We suspect that juvenile blue crab survival on natural, large-scale oyster reefs would be similarly improved as compared to sand habitats, but this

needs experimental validation. Furthermore, predator identifications and encounter times were limited at times by poor water clarity in the York River during late summer. Of the 25 videos, 10 were excluded due to poor visibility. Nonetheless, in instances where predators were identified, predators were relatively habitat-specific. Issues with limited visibility could be remedied by replicating the experiment in the spring and late fall when water clarity is typically better but still warm enough for many predators, which may also identify any seasonal differences in predator activity. Finally, juvenile crabs in the mid-range size class (20–30 mm CW) were more heavily represented than the smaller and larger size classes (Fig. 2), which may have reduced the statistical power to detect a strong effect of crab size on survival (Pile et al. 1996, Hovel & Lipcius 2001, Lipcius et al. 2005, Johnston & Lipcius 2012, Bromilow & Lipcius 2017). Specifically, we had difficulty catching many crabs in the 40–50 mm CW size class for experiments. However, there was a general continuum of individuals from 10–50 mm CW used in trials for both habitats, and the CW relationship was apparent. Distributing the replicates more evenly would provide a stronger representation of juvenile crab survival and likely strengthen our confidence in the difference in survival by size.

4.4. Implications

The value of oyster reefs for supporting survival of juvenile crabs in our system suggests that restoration of oyster reefs could be beneficial for restoring the ecosystem service of providing alternative nursery habitat for juvenile crabs. This increased understanding of the ecosystem value of oyster reefs for blue crabs should help increase success in the economic valuation of ecosystem services provided by oyster reefs (Grabowski et al. 2012). Specifically, this work should increase economic valuation of habitat provisioning related to increased production of mobile fish and invertebrates (Peterson et al. 2003). Future work could focus on examining juvenile blue crab use of large (greater than 1 ha [10 000 m²]) restored reefs in the lower Chesapeake Bay (Karp et al. 2018) or natural oyster reefs, to improve our understanding of ecosystem services of restored and natural oyster reef habitats.

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