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# Density, abundance and survival of the blue crab in seagrass and unstructured salt marsh nurseries of Chesapeake Bay

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## Abstract

Structured benthic habitats such as salt marshes, seagrass beds and oyster reefs are recognized as critical nurseries for fish, crustaceans and mollusks in coastal and estuarine systems. Yet most estuaries and coastal habitats have extensive, relatively unstructured shallow-water habitats such as subtidal mud and sand flats, which are generally viewed as inconsequential nursery grounds. We tested this paradigm with the blue crab, *Callinectes sapidus* Rathbun, in shallow and deep benthic habitats of the York River, Chesapeake Bay. Juvenile blue crabs (<100 mm carapace width) were sampled quantitatively in deep channel muds (DCM, >2 m depth), in shallow unstructured subtidal mud flats (SMF) and sand flats (SSF) adjoining salt marshes, and in beds of submerged aquatic vegetation (SAV—eelgrass, *Zostera marina*, and widgeongrass, *Ruppia maritima*) in three river zones (Upriver, Downriver, Mouth) across 60 km of the river axis. Survival of juveniles 25–55 mm carapace width was examined experimentally in all shallow habitats. SAV habitats were examined only at the Mouth zone; SAV did not occur in the Downriver and Upriver zones. Juvenile blue crab density was nearly an order of magnitude lower in SMF and SSF than in SAV habitats; density was lowest in DCM. Density in Upriver SMF and SSF habitats was 4- to 10-fold higher than that in Mouth and Downriver SMF and SSF, and DCM. Consequently, the two areas harboring the greatest fractions of York River juveniles were shallow: Mouth SAV (~50%) and Upriver SMF and SSF (~40%). Upriver expanses of SMF and SSF adjoining extensive salt marshes near the turbidity maximum harbored an approximately equal abundance of juvenile crabs as the downriver SAV beds, despite the density difference. Survival of tethered juveniles was significantly higher in Upriver SMF and SSF habitats than in Mouth SAV, SMF and SSF habitats, despite the lack of structural refuge in SMF and SSF; crabs in Upriver SMF and SSF survived four times as long as crabs in SAV, Mouth SMF and Mouth SSF. We conclude that shallow subtidal mud and sand flats near upriver salt marshes and in marsh coves are vital nursery grounds for the blue crab, and thus warrant conservation and restoration efforts at the level provided to SAV. The production potential of the blue crab and other estuarine species that utilize salt marshes has likely been severely reduced due not only to direct salt marsh destruction, but also due to indirect degradation of shallow subtidal mud and sand flats fringing salt marshes.

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**Keywords:** Blue crab; *Callinectes sapidus*; Habitat; Nursery grounds; Predation; Survival

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## 1. Introduction

Structured shallow-water habitats such as seagrass beds, salt marshes and mangrove forests are considered the most valuable nurseries for marine and estuarine fish and invertebrates with complex life cycles because they enhance survival, movement and feeding rates relative to nearby unstructured (e.g., unvegetated) habitats (Heck and Thoman, 1984; Beck et al., 2001; Heck et al., 2003; Minello et al., 2003). For instance, several field and laboratory investigations have demonstrated that blue crab juveniles survive at substantially higher rates in seagrass or other structured habitats than in unvegetated subtidal habitats (Everett and Ruiz, 1993; Pile et al., 1996; Perkins-Visser et al., 1996; Moksnes et al., 1997; Ryer et al., 1997; Hovel and Lipcius, 2001, 2002). Consequently, there is currently a paradigm that the critical nurseries for marine and estuarine species such as the blue crab are structurally complex habitats such as seagrass beds and salt marshes (Heck et al., 2003; Minello et al., 2003).

However, most investigations comparing survival, growth and abundance in vegetated and unvegetated habitats were typically conducted at sites that were in close proximity, usually within a few 100 m (Fig. 1). A

few studies have indicated that abundance of blue crab juveniles may be relatively high in unvegetated, structurally simple habitats (e.g., subtidal mud flats) distant from the characteristic seagrass nurseries (Mense and Wenner, 1989; Lipcius and Van Engel, 1990; Rakocinski et al., 2003; Seitz et al., 2003), and survival of small juvenile blue crabs may be enhanced in such habitats, particularly in the extremely shallow zone of these habitats (Ruiz et al., 1993; Dittel et al., 1995; Hines and Ruiz, 1995). The worth of shallow unstructured habitats as nurseries may thus be undervalued. Hence, in this field study we sampled and conducted field experiments at broader spatial scales representative of the natural distribution of estuarine habitats (Fig. 1), and across a range of deep and shallow structured and unstructured habitats. In particular, we experimentally examined the hypothesis that blue crab survival and abundance are high in shallow unvegetated mud and sand flats bordering salt marshes, a commonly occurring and productive habitat in estuarine ecosystems (Seitz and Lipcius, 2001; Seitz et al., 2003), and contrasted the results with survival and abundance of juveniles in seagrass beds and deep unstructured habitats. Moreover, we dealt with the issue of whether or not these habitats should be viewed

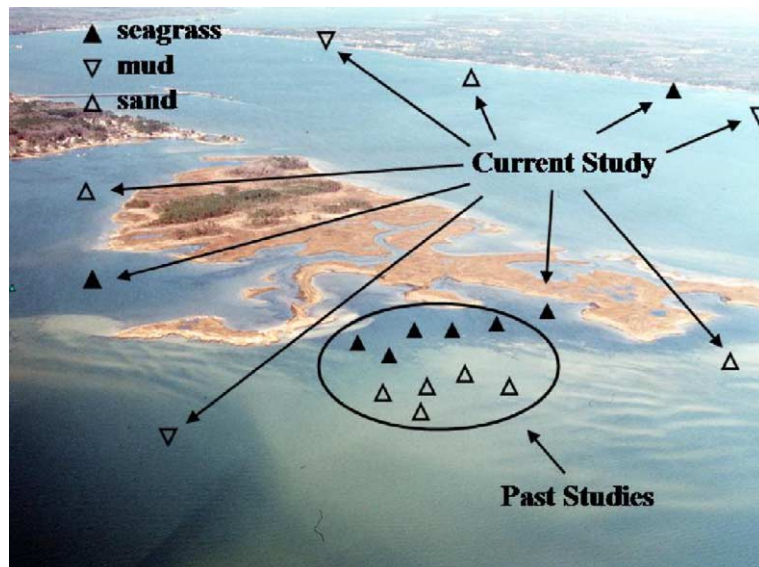


Fig. 1. Representation of the sampling and experimental layout in this investigation contrasted with that of prior investigations, in which survival and abundance in vegetated and unvegetated habitats were usually contrasted among sites in relatively close proximity, usually within 100 m. In this investigation, sampling and field experiments were conducted at the broader spatial scales representative of the natural distribution of experimental habitats (~100 m–60 km).

as critical nurseries for the blue crab, and potentially for other estuarine invertebrates and fish. To accomplish these general goals, our specific objectives were to quantify abundance and experimentally assess survival of blue crab juveniles in seagrass and in unvegetated subtidal flats adjoining salt marshes near (~10–500 m) and distant (~40–50 km) from seagrass beds.

## 2. Methods

### 2.1. Study system

Sampling and field experiments were conducted along a 60-km stretch of the York River (76°N

latitude, 37°W longitude), a tributary of lower Chesapeake Bay. We used three river zones (Upriver, Downriver, Mouth) along the axis of the river (Fig. 2); each zone was 10–15 km in length and separated from the adjacent zone by about 10–15 km. Within each zone, we randomly selected representative sites of three habitat types, subtidal mud flats (SMF), subtidal sand flats (SSF), and seagrass beds (SAV=Submerged Aquatic Vegetation); SAV beds were only present at the Mouth zone. SMF habitats were in coves, in tidal creeks, or along the shoreline at depths of 1–2 m. SSF habitats only occurred along the shoreline at 1–2 m depths (76–88% sand, 12–24% silt and clay content; Seitz et al., this volume). Sampling and experiments were conducted in summer and fall, 1999–2001. See

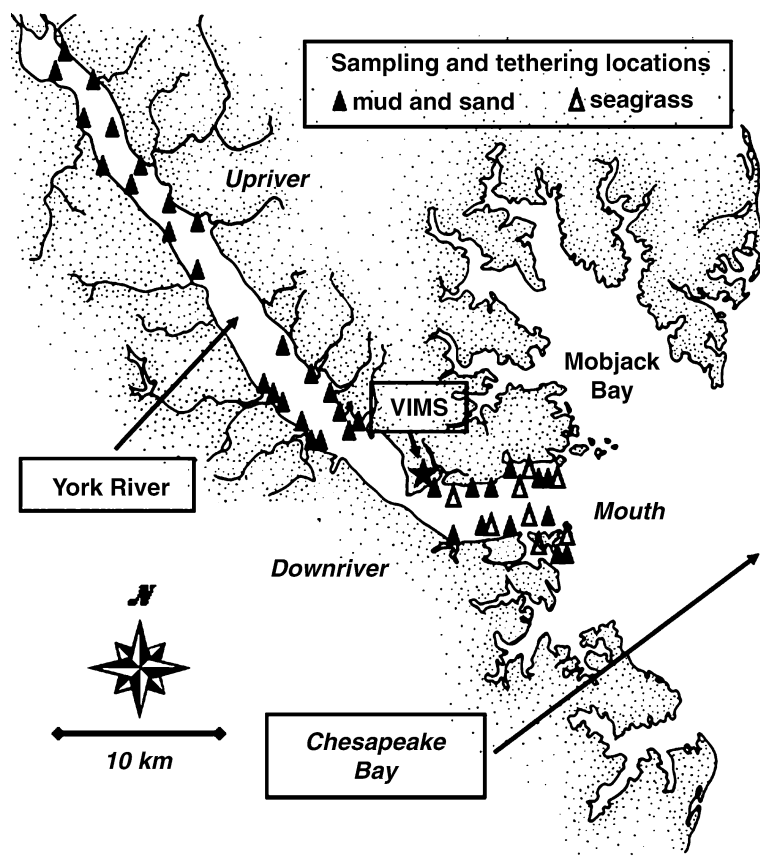


Fig. 2. Study sites in three zones (Upriver, Downriver and Mouth) along the axis of the York River, a relatively shallow (average depth <4 m) tributary of Chesapeake Bay. The York River has a deep channel (27 m at Gloucester Point) fringed by seagrass beds at the Mouth; salt marshes along its length, particularly in the Upriver zone where the turbidity maximum occurs; marsh-fringed muddy coves with little structure except for some coarse woody debris, oyster shell and seasonal algal growth; and, subtidal mud and sand flats throughout the river, but with a higher percentage of mud as one moves upriver. See Fig. 1 for examples at the Mouth zone.

Hovel and Lipcius (2001), and Seitz et al. (2003, this volume) for further descriptions of York River habitats.

## 2.2. Field sampling of density, abundance and distribution

GIS-based maps were used to delineate the area of each habitat type and to select four random sampling sites within each combination of habitat type and zone, except for SAV where we sampled six sites ( $N=30$  independent values). At each site, we chose areas with more than 50 m of shoreline, to allow unimpeded trawling and suction sampling. Measurements of water temperature, salinity, dissolved oxygen, turbidity, water depth, and sediment grain size are given in Table 2 of Seitz et al. (this volume).

To sample juvenile crabs (i.e., of carapace width <100 mm) in SAV beds, we used a suction dredge (1-mm mesh bag) to capture crabs within a 1-mm mesh cylinder (1.67 m<sup>2</sup>, 1.5 m high) weighted at the bottom to prevent escape by crabs. This sampling apparatus is 78% effective (Montane and Lipcius, unpublished manuscript) and has been used to sample juvenile blue crabs in SAV beds for two decades since Orth and van Montfrans (1987) established the technique. Each sample was suctioned for 6 min, followed by a 3-min

sweep of the area using a dip-net. Captured crabs were enumerated and measured with calipers. The data were corrected for the 78% efficiency of the suction.

To sample crabs in DMC, SMF and SSF habitats, we towed a 2-m-wide otter-trawl net with a 1-mm mesh liner along a 100-m transect bordering the marsh or shoreline. Trawls were conducted during the 3 h surrounding low tide to standardize sampling and to minimize the inaccessibility of crabs moving onto the marsh. All crabs caught in the samples were measured and counted. Data from the trawls were adjusted for the 22% efficiency (Homer et al., 1980), which accounts for size and density effects.

## 2.3. Field survival experiments

Two sets of survival experiments (summer–fall of 2000 and 2001) were conducted with juvenile crabs of 25–55 mm carapace width, using an established tethering technique (Fig. 3). In addition, we conducted pilot experiments in summer 2000 and 2001 to assess assumptions about the effectiveness of tethering in measuring survival of juvenile blue crabs. Tethering has been used frequently in survival experiments with the blue crab (Heck and Wilson, 1987; Wilson et al., 1990; Hines and Ruiz, 1995; Moksnes et al., 1997; Pile et al., 1996; Moody, 2001; Heck et al., 2001).

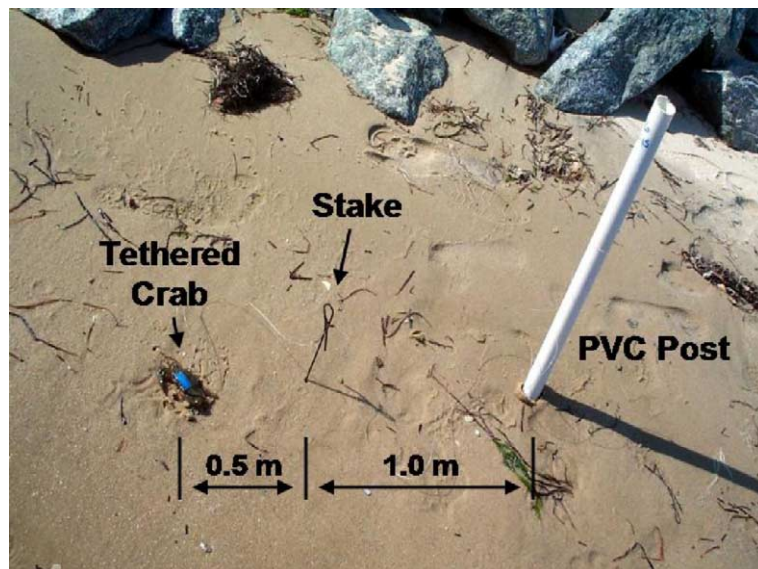


Fig. 3. Photograph of a crab tethered to the stake, which is tied to the PVC pole. In the field, the stake is completely buried in the sediment, and the pole is about 1 m away from the stake and crab.



Table 1  
Analysis of variance for 2001 pilot experiment examining treatment-specific bias of tethering

Source of variation	SS	df	MS	F	P
Habitat	4.867	1	4.867	5.16	0.028
Tether	0.293	1	0.293	0.31	0.580
Habitat×tether	0.202	1	0.202	0.21	0.646
Error	45.274	48	0.943		

Experimental crabs were caged with a larger, predatory blue crab in one of four treatments—tethered or untethered, and in sand or in seagrass.  $N=48$  individual trials. Note the non-significance of the interaction effect, and apparent absence of treatment-specific bias.

Tethering measures relative, not absolute, predation rates and has proven useful in comparing survival between different experimental treatments (Aronson and Heck, 1995; references above). Treatment-specific bias (Peterson and Black, 1994) has not been problematic with the habitat types used in our experiments (Pile et al., 1996; Hovel and Lipcius, 2001).

Tethering involved attaching a harness comprised of 20-cm monofilament or steel-leader fishing line to the crab's carapace with cyanoacrylate glue. The other end of the line was tied to a stake pushed into the bottom; the stake was tied to a location pole 1 m from the crab to minimize artificial structures that would attract predators to the tethered crab (Fig. 3). Tethered crabs were allowed to acclimate in laboratory aquaria for 24 h prior to placement in the field.

In the 2000 pilot experiments, 10 crabs were tethered and enclosed in predator-exclusion cages for 48 h in the field. In addition, 8 crabs were tethered separately for 48 h in laboratory aquaria containing a larger blue crab as a predator. All 10 field crabs were recovered still tethered and alive. Predation upon the laboratory crabs was evident by a missing crab and either pieces of carapace remaining on the line, chewed pieces of tape and monofilament line, or cut monofilament lines. These features were used to distinguish predation in the field experiments.

In the 2001 pilot experiments, 48 juvenile crabs of 40–60 mm carapace width were caged individually with a larger, predatory blue crab (>100 mm carapace width) in laboratory mesocosms with flowing seawater. Individual crabs were tethered or untethered, and caged in sand or in artificial seagrass at 400 shoots  $m^{-2}$ . Survival was checked at approximate 12-h intervals until all crabs had been killed. Survival times ranged from 12 to 36 h. Survival differed

significantly by habitat type (Table 1); crabs in sand had a 41% lower survival rate than those in artificial seagrass. Tethered crabs had a 12% lower survival rate than untethered crabs, but this difference was not significant (Table 1), probably due to the weak resolution of the observation schedule at the low end of the survival times (i.e., 12 h). The interaction effect was not significant, even at a marginal level of significance (Table 1), indicating that treatment-specific bias was not a strong influence. Given the results of the pilot experiments, and those of other studies (Pile et al., 1996; Hovel and Lipcius, 2001), we conclude that tethering provided a reliable measure of relative predation-induced mortality in our field experiments.

Tethering experiments were conducted in August 2000 and July–August 2001. Tethering sites were selected randomly from a GIS grid of potential sites in each of five habitat types: Mouth SAV, Mouth SMF, Mouth SSF, Upriver SMF, and Upriver SSF. Down-river sites were not examined in the tethering experiments because of the relatively low abundance of juvenile crabs in these habitats. Each tethering site was 50–200 m from the nearest tethering site, which permitted us to use each crab as an independent replicate in statistical analyses. All experimental crabs were collected from seagrass beds in the York River with a crab scrape, and sorted by size (25–55 mm carapace width). Healthy, intermolt crabs without multiple missing pereopods were kept in flow-through seawater tanks exposed to natural photoperiod and fed ad libitum until tethering trials.

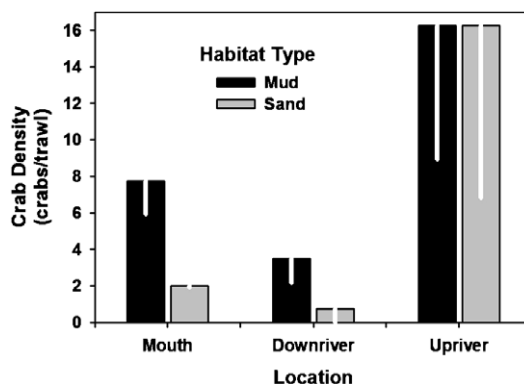


Fig. 4. Density of blue crab juveniles <100 mm carapace width in Mouth, Downriver and Upriver SMF and SSF shallow-water habitats sampled by trawl. Bars represent 1 S.E.

In 2000, we conducted three tethering trials, each with  $N=30$  independently tethered crabs (Fig. 1). For each trial we tethered 10 crabs in seagrass, 10 in Mouth unstructured habitats (5 in SMF, 5 in SSF), and 10 in Upriver unstructured habitats (5 in SMF, 5 in SSF), and assessed their survival after 48 h. Data (frequen-

cies surviving and dead by habitat type) were analyzed with a  $G$  test for each trial (Sokal and Rohlf, 1995).

In 2001, we conducted two tethering trials. For each trial, we tethered 40 crabs independently, 8 in each of the five treatments. Crabs were checked daily

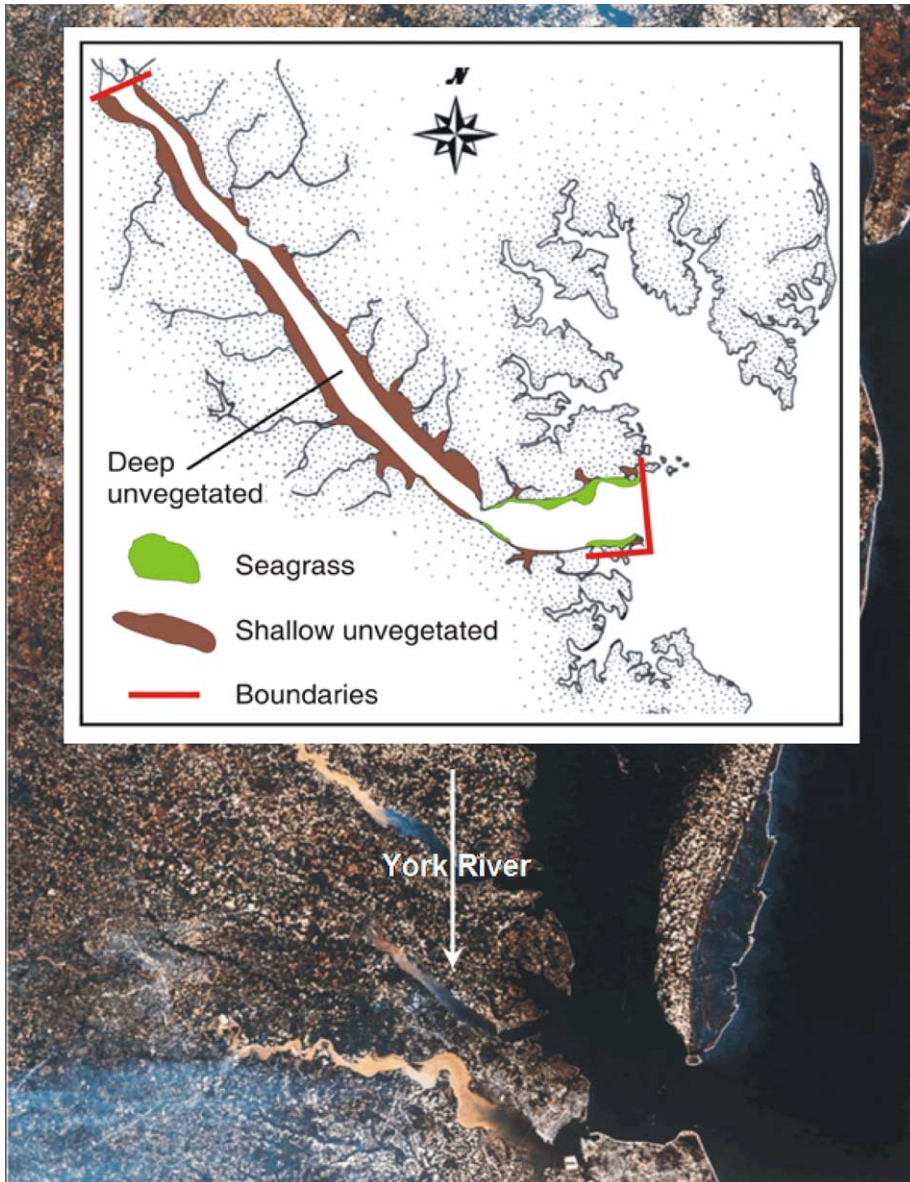


Fig. 5. Map of shallow unvegetated, deep unvegetated, and seagrass habitats in the York River. The background is a satellite image of Chesapeake Bay. The York River is visible in the satellite image above the James River and below the Rappahannock River. The mouth of Chesapeake Bay is in the lower right, which opens to the Atlantic Ocean.

until all crabs had been killed. The response variable (days until mortality) was approximately continuous, and therefore analyzed with fixed-factor analysis of variance models.

### 3. Results

#### 3.1. Field density, abundance and distribution

Juvenile crab density in unvegetated habitats differed significantly by Location (*L*) and Habitat type (*H*), but a significant *L*×*H* interaction effect (ANOVA, *P*<0.01) precluded singular interpretations of the main effects (Fig. 4). Crab density was significantly higher in Upriver SMF and SSF habitats than in all Downriver and Mouth unvegetated habitats (Student–Neuman–Keuls test, *P*<0.05); SMF habitats had the highest crab density Downriver and at the Mouth (SNK test, *P*<0.05).

To determine the river-wide distribution of blue crabs, we examined three major habitat strata—shallow unvegetated, deep unvegetated, and seagrass (Fig. 5). Juvenile crab density was highest in seagrass beds, followed by shallow unvegetated Upriver habitats (Fig. 6, SNK test, *P*<0.05). Crab density in shallow habitats, whether vegetated or unvegetated, was always higher than that in deep unvegetated habitats (Fig. 6, SNK test, *P*<0.05). We then assessed the area of each habitat stratum (Fig. 7) using

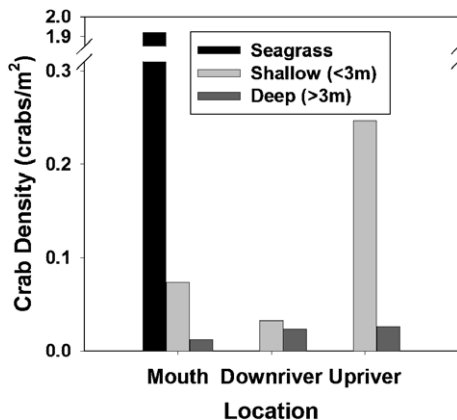


Fig. 6. Density of blue crab juveniles <100 mm carapace width in Mouth, Downriver and Upriver SMF and SSF habitats, deep-water mud habitats, and Mouth SAV habitats sampled by trawl and suction gear.

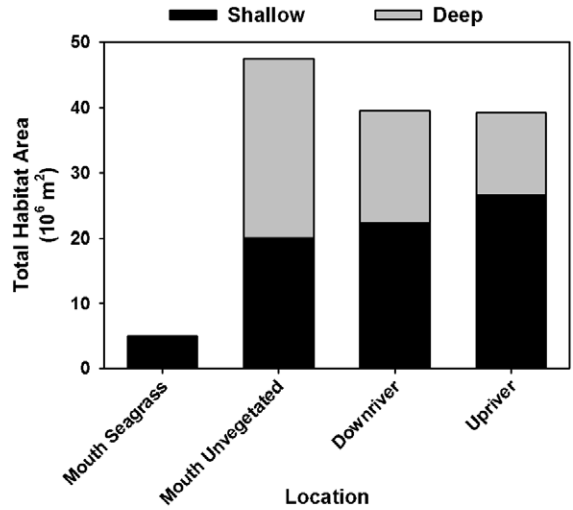


Fig. 7. Area of each of the major habitats in the York River, derived from a Geographic Information Systems grid. Shallow habitats are those <2 m water depth.

Geographic Information Systems technology (Fig. 5). Despite the much smaller area of seagrass beds (Figs. 5 and 7), about 47% of all crabs in the York River resided in seagrass (Fig. 8) due to the high crab density in this habitat type (Fig. 6). However, a major fraction (~36%) of all crabs in the York River inhabited shallow Upriver SMF and SSF habitats fringed by salt marshes (Fig. 8). Mud and sand habitats in the remaining segments of the river harbored less than 10% of all York River crabs per

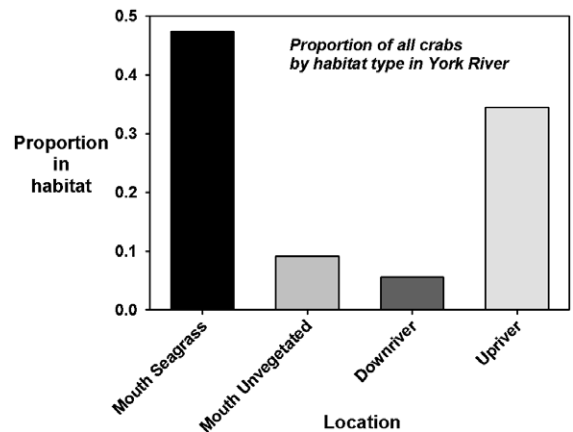


Fig. 8. Proportional abundance of juvenile blue crabs in each of the major habitats in the York River, derived from the product of the data in Figs. 6 and 7.

section (Fig. 8), even though these sections accounted for 2/3 of the habitat area (Fig. 7).

### 3.2. Field survival

In 2000, the three tethering trials yielded comparable results (Fig. 9). Lowest crab survival occurred in Mouth SSF (13% surviving crabs) and SAV (20%) habitats ( $G$  test,  $P < 0.05$ ). In contrast, 47% of the crabs tethered in Mouth SMF habitats survived; typically these were in muddy coves. Tethered crabs survived at significantly highest rates in Upriver habitats (Fig. 9,  $G$  test,  $P < 0.05$ ); the difference between SMF (80% surviving crabs) and SSF (87%) habitats was not significant ( $G$  test,  $P > 0.05$ ).

In 2001, the two sets of field survival experiments yielded statistically equivalent results (Fig. 10). Lowest juvenile crab survival occurred in Mouth SSF,

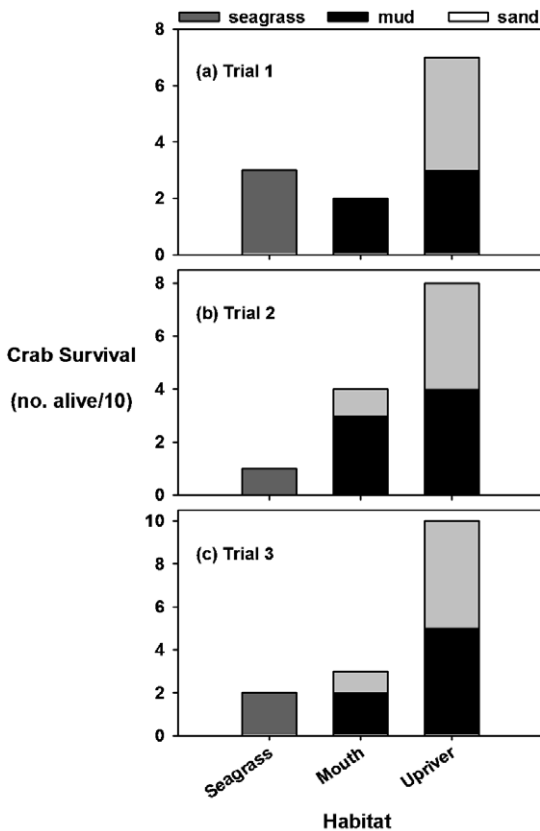


Fig. 9. Survival of tethered juvenile blue crabs 25–55 mm carapace width as a function of habitat type in three 2000 trials. The response in each trial is the number remaining alive out of 10 tethered crabs.

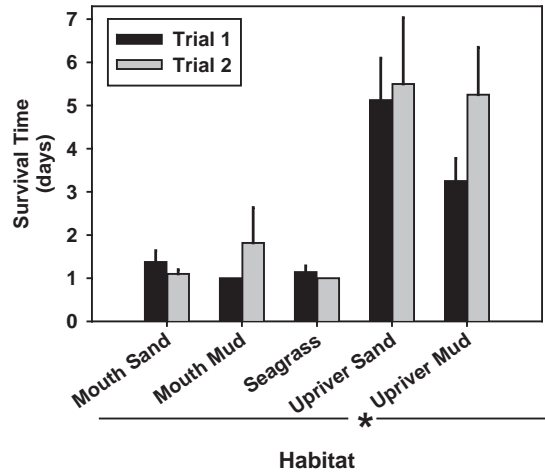


Fig. 10. Survival of tethered juvenile blue crabs 25–55 mm carapace width as a function of habitat type in two 2001 trials. Bars represent 1 S.E. The asterisk shows the significant difference between the two rightmost and three leftmost habitats (Student–Neuman–Keuls test,  $P < 0.05$ ).

Mouth SMF, and SAV habitats (ANOVA,  $P < 0.05$ ), where the average survival time was about 1 day (Fig. 10). There was no difference in survival time between any of the Mouth and SAV habitats (ANOVA,  $P > 0.05$ ). Significantly and substantially higher survival characterized Upriver SMF and SSF habitats, such that tethered crabs survived an average of approximately 5 days (Fig. 10, ANOVA,  $P < 0.05$ ). The difference in survival between Upriver SMF and SSF habitats was not significant (ANOVA,  $P < 0.05$ ).

## 4. Discussion

Our field investigation yielded two significant findings regarding abundance, distribution and survival of juvenile blue crabs in nursery habitats. First, a substantial fraction of the population's juveniles (~40%) inhabited shallow unstructured mud and sand habitats, which were in the subtidal zone fringing salt marshes in the upriver segment of the York River. Another 50% of the juveniles resided in SAV beds near the mouth, while only about 10% occurred in deep mud channels and the remaining shallow portion of the York River. Given that a combination of seagrass beds at the river mouth and subtidal mud and sand flats upriver encompass about 20% of all York River habitats, and that approximately 90% of



the population's juveniles reside in those habitats, then a relatively small fraction of potential nursery habitats comprise the functional nursery grounds of the blue crab in the York River. In addition, shallow mud coves throughout the river were valuable nurseries capable of supporting relatively high densities of juveniles. The major implications of these findings are that the abundance of juveniles in shallow-water habitats of the same type (e.g., mud coves) can differ radically depending on the location of those habitats, that a lack of structure per se (e.g., SAV) in potential nursery habitats does not prevent habitation by juveniles, and that a small percentage of potential nursery habitats serves as the functional nursery.

Second, juvenile crabs tethered in the unstructured upriver habitats survived at much higher rates than crabs tethered in SAV or in unstructured sand and mud habitats at the mouth of the York River; the difference was considerable—about 4-fold. The key implication of this finding is that an absence of significant structure in shallow-water habitats does not preclude high survival of juveniles in those habitats. Other factors besides habitat structure, such as predator and alternative prey abundance, must strongly influence the likelihood of predation in those habitats. Collectively, these findings indicate that particular unstructured shallow-water habitats (e.g., marsh-fringed mud coves) should be viewed as vital nurseries, complementary to structured nurseries such as seagrass beds and salt marshes (Beck et al., 2001; Heck et al., 2003; Minello et al., 2003).

That about half of all blue crab juveniles in the York River resided in seagrass beds is consistent with the paradigm that structured shallow-water habitats (e.g., seagrass beds, salt marshes and mangroves) are valuable nurseries for marine and estuarine fish and invertebrates in general (Beck et al., 2001; Heck et al., 2003; Minello et al., 2003) and for the blue crab in particular (Orth and van Montfrans, 1987; Pile et al., 1996; Perkins-Visser et al., 1996; Eggleston et al., 1998; Pardieck et al., 1999; Hovel and Lipcius, 2001, 2002). Second, survival of juveniles was often higher in seagrass than in adjacent unvegetated (sand) flats, similar to that typically observed in prior studies (Pile et al., 1996; Hovel and Lipcius, 2001, 2002). But, at broader spatial scales (i.e., upriver versus mouth habitats) and in different habitat types (i.e., mud

survival of juveniles did not fit the pattern of higher survival in structured habitats. Specifically, survival of moderately sized juveniles was higher in upriver unstructured habitats and in mouth mud habitats than in mouth seagrass and sand flats. How then can the findings of this study be made consistent with those of previous investigations? Why is it that a high abundance of juvenile blue crabs occurs and survives well in unstructured habitats?

We start with the current paradigm of ontogenetic shifts in habitat use by the blue crab, in this case as applied to the Chesapeake Bay ecosystem. After invading the estuary from the continental shelf, postlarvae settle in seagrass and metamorphose into the 1st benthic instar (J1), which is a few millimeters in carapace width. Many of the J1 juveniles remain in seagrass beds until reaching the J9 instar at about 25 mm carapace width, due to the higher survival and growth conferred by the structure and food in seagrass beds (Pile et al., 1996; Perkins-Visser et al., 1996; Eggleston et al., 1998; Pardieck et al., 1999; Hovel and Lipcius, 2001, 2002; Orth and van Montfrans, 2002). In some cases, the youngest instars (J1–J5) emigrate from seagrass beds, apparently to avoid density-dependent cannibalism (Etherington and Eggleston, 2000; Blackmon and Eggleston, 2001; Reyns and Eggleston, 2004). The remaining larger juveniles (>25 mm carapace width) disperse from seagrass beds to other shallow-water habitats such as subtidal mud and sand flats, as they have presumably reached a relative size refuge from predation and are able to leave the security of structured habitats. The larger juveniles are now less vulnerable to predation and thus able to utilize the ample prey occurring in the unstructured shallow-water mud and sand flats, which harbor benthic infauna such as the Baltic clam, *Macoma balthica* (Hines and Comtois, 1985; Hines et al., 1990; Seitz and Lipcius, 2001; Seitz et al., 2003, this volume).

This conceptual model thus posits that young juveniles reside in structured habitats (e.g., seagrass beds) safest from predation upon settlement and early growth; the corollary to this is that unstructured habitats are unsafe at this stage in the life cycle. Some of the youngest juveniles may disperse at an early stage to other structured or unstructured nurseries due to density-dependent mortality (Etherington and Eggleston, 2000; Blackmon and Eggleston,

ton, 2001; Reyns and Eggleston, 2004). As the juveniles grow (>25 mm carapace width) and become less susceptible to predation, they are able to leave the refuge of structured habitats and exploit the abundant prey in unstructured habitats. The corollary of this is that structured habitats such as seagrass beds remain safe for larger juveniles, but that larger juveniles can maximize their growth by dispersing from the structured habitats in a density-dependent fashion; otherwise they would be subject to negative density-dependent growth (Perkins-Visser et al., 1996).

Given our findings on survival and abundance of larger juveniles (25–55 mm carapace width), we propose that the conceptual paradigm on habitat use by larger juveniles needs modification. Specifically, we posit that larger juveniles (>25 mm carapace width) emigrate from seagrass beds and other structured habitats to unstructured mud and sand flats, not only to reduce density-dependent growth and mortality (Perkins-Visser et al., 1996), but because survival (this study) and food availability (Seitz et al., this volume) are substantially higher in many unstructured shallow-water habitats. In particular, mud and sandy mud coves or shores fringed by salt marshes in the upriver portions of riverine systems appear to be valuable nurseries for larger blue crab juveniles, even when there are seagrass beds in the system.

These findings are consistent with those of field investigations in upper Chesapeake Bay (i.e., Rhode River), which lacks seagrass beds, wherein abundance and survival of juvenile crabs (within the size range of those examined in our study) were substantially higher in shallow subtidal mud and sand flats than in deeper habitats (Ruiz et al., 1993; Dittel et al., 1995; Hines and Ruiz, 1995). A few studies in other systems have also indicated that abundance of blue crab juveniles may be relatively high in unvegetated, structurally simple habitats (Western Atlantic coast: Mense and Wenner, 1989; Gulf of Mexico: Rakocinski et al., 2003). These collective findings demonstrate that abundance and survival of juvenile blue crabs may be high in shallow unstructured habitats, whether in systems with or without seagrass beds, and that these habitats should therefore be viewed as beneficial nurseries.

The enhanced survival of larger juveniles in the shallow unstructured subtidal habitats relative to seagrass beds and other structured or deeper habitats is likely due to a combination of factors including

positive density-dependent survival, a reduction in the diversity and abundance of piscine and invertebrate predators, and lower cannibalism rates (Hines et al., 1990; Ruiz et al., 1993; Dittel et al., 1995; Hines and Ruiz, 1995; Moksnes et al., 1997), as potential cannibals can feed on abundant alternative prey (e.g., Baltic clam, *M. balthica*; Hines and Comtois, 1985; Mansour and Lipcius, 1991; Clark et al., 1999a,b; Seitz et al., 2003, this volume).

In some field survival studies, water depth has been shown to be crucial—survival of small juveniles was greatest in unstructured subtidal habitats at depths ca. 0.5 m deep and shallower, whereas juveniles in water >1 m were much more vulnerable to cannibalism (Ruiz et al., 1993; Dittel et al., 1995; Hines and Ruiz, 1995). Our field studies were conducted at 1–2 m depths to standardize water depth across all habitats. Had we conducted our studies at shallower depths, we suspect that the habitat-specific patterns in survival would have been qualitatively similar. Survival in SMF and SSF habitats might have been higher, except near SAV where SAV excludes SSF habitats from the extreme shallows.

The collective findings from our investigation and previous studies indicates that unstructured shallow-water nursery habitats, particularly subtidal mud and sand flats fringing salt marshes, be accorded protection from habitat degradation and that they be prioritized as essential blue crab nursery habitats for conservation and restoration (e.g., in spatial management and protected areas; Lipcius et al., 2003, 2005; Stockhausen and Lipcius, 2003). The production potential of the blue crab and other estuarine species that utilize salt marshes has likely been severely reduced due not only to direct salt marsh destruction (Peterson and Lipcius, 2003), but also due to indirect degradation of subtidal mud and sand flats fringing salt marshes, which may be playing a major role in the continuing decline of the blue crab in Chesapeake Bay (Lipcius and Stockhausen, 2002).

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