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Quantification of Nursery Habitats for Blue Crabs in Chesapeake Bay

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Quantification of Nursery Habitats for Blue Crabs in Chesapeake Bay

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A Dissertation

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

of the Requirements for the Degree of

Doctor of Philosophy

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by

Gina M. Ralph

2014

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

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ABSTRACT

The blue crab is an iconic species in Chesapeake Bay, supporting important commercial and recreational fisheries and functioning as a critical link in the food web. Structurally complex habitats are often cited as nurseries for the blue crab, and other commercially important fish and crustacean species, by providing enhanced growth and survival for juveniles. I quantified the value of shallow habitats as nurseries for blue crabs through field studies and a demographic model. In Chapter 2, I utilized a two-year juvenile survey in vegetated habitats of the lower Bay to examine the effect of habitat complexity on the density of juvenile blue crabs. The functional relationship between seagrass cover and juvenile density was exponential, such that there were proportionally more crabs per unit increase in cover of vegetated habitat at high percent cover than at low percent cover. The relationship varied spatially, with higher densities on the eastern shore, and between the two years. The high spatial and annual variability led to questions about how habitat utilization varied throughout the recruitment season. I addressed the timing of recruitment and migration between habitats in Chapter 3 through the development of a survey of shallow habitats in the York River with high temporal and spatial resolution. The study provided evidence for a carrying capacity of juvenile blue crabs in vegetated habitats at 10-15 crabs m^2. I found substantially higher densities of small juveniles in shallow unvegetated habitats than previously documented, which suggested that the current paradigm for blue crab recruitment requires modification to include the importance of shallow unvegetated habitats for small juveniles. In Chapter 4, I examined the effect of habitat utilization patterns as a function of age or ontogeny on the blue crab stock assessment by comparing juvenile density and abundance estimates from shallow vegetated and unvegetated habitats to estimates from deep habitats sampled by the primary survey for the stock assessment. Juvenile abundance was very high in both shallow habitats despite the relatively smaller area, thus suggesting that the winter dredge survey substantially underestimated the abundance of juvenile crabs. If this bias is inconsistent inter-annually, potentially as a function of temperature, then stock assessments may be producing biased reference points. Finally, I developed an exploratory habitat-specific demographic model to quantify the effects of habitat on population fitness in Chapter 5. Under all fishing mortality rates, including a complete fishing moratorium, the population growth rate was less than 1 when only unvegetated habitat was present; the increased survival of age-0 crabs provided by vegetated habitats led to increases in the population growth rates. The vegetated habitats provided a buffer from fishing mortality; that is, as the survival of juveniles increased in vegetated habitats, the population could sustain higher fishing mortality rates while still remaining stable or even increasing. Shallow vegetated habitats substantially influence juvenile blue crabs and the overall population growth rate. It is essential that these habitats be considered in future explorations of the dynamics of blue crabs, as well as other species that exhibit ontogenetic shifts in habitat utilization.

AUTHOR'S NOTE

The chapters of this dissertation were written in manuscript format for scientific publication. Thus, each chapter is written in the third person to represent my co-authors, and is formatted to align with the guidelines of the publication to which the manuscript was or will be submitted. At the time of writing, citations for individual chapters are as follows:

CHAPTER 2
Ralph, G.M., Seitz, R.D., Orth, R.J., Knick, K.E., and Lipcius, R.N. 2013. Broad-scale association between seagrass cover and juvenile blue crab density in Chesapeake Bay. Marine Ecology Progress Series, 488:51-63. [Contribution number 3278 of the Virginia Institute of Marine Science, The College of William and Mary, Gloucester Point, VA 23062]

CHAPTER 3
Ralph, G.M., Seebo, M.S., and Lipcius, R.N. *In prep*. Spatiotemporal patterns in juvenile blue crab recruitment to seagrass and unvegetated nursery habitats.

CHAPTER 4
Ralph, G.M., and Lipcius, R.N. *Accepted*. Critical habitats and stock assessment: age-specific bias in the Chesapeake Bay blue crab population survey. Transactions of the American Fisheries Society.

CHAPTER 5
Ralph, G.M., Miller, T.J., and Lipcius, R.N. *In prep*. Quantifying the role of nursery habitats for the Chesapeake Bay blue crab using population fitness.

Quantification of Nursery Habitats for Blue Crabs in Chesapeake Bay

CHAPTER 1

The Chesapeake Bay Blue Crab: Life History and Habitat Utilization

INTRODUCTION

The blue crab (*Callinectes sapidus*) is a dominant estuarine species, playing a major role in the coupling of the benthic and pelagic zones (Paolisso 2002, Hines 2007, Fogarty & Lipcius 2007, Lipcius et al. 2007, Paolisso 2002). In Chesapeake Bay, it supports one of the most valuable commercial fisheries, as well as a thriving recreational fishery (Miller et al. 2011). Currently, management of the blue crab relies on the bay-wide Winter Dredge Survey (WDS), which was designed in 1989 to provide estimates of total abundance and mortality. The WDS is a stratified random survey that samples 1500 stations deeper than 1.5 m annually using a 1.83 m wide Virginia crab dredge (see Sharov et al. 2003 for further details on the design of the survey).

While the abundance estimates garnered by the WDS have mirrored estimates from landings data, the survey does not adequately sample juvenile blue crabs (Miller et al. 2011). The mesh size of the dredge, minimum depth constraints of the vessels prevent an absolute estimate of juvenile abundance from the WDS. As such, much less is known about the distribution of juvenile blue crabs than adults at large temporal and spatial scales. A better understanding of juvenile life history and habitat utilization is essential for best management of the fishery, particularly in terms of longer-term forecasting of population abundance.

As an estuarine-dependent species with a complex life history, blue crabs utilize a variety of habitats. Adults exhibit seasonal sex-specific habitat preferences, with adult

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males generally found in the lower salinity waters of the upper Bay and tributaries. After pre-pubertal females complete the terminal molt and copulate, typically in the spring and fall in Chesapeake Bay, mature females migrate to the higher salinity waters near the mouth of the Bay to spawn (see Hines 2007 for a review). The zoea require warm, high salinity waters for proper development (Epifanio 2007), thus spawning near the mouth of the estuary provides the offspring with the best chance for survival. Eggs are hatched and zoea larvae are released near the mouth of the Bay; subsequently the zoea are advected onto the continental shelf. After 1-2 months of development, the zoea metamorphose into megalopae (i.e. postlarvae), which reinvade the estuary through wind-driven, geostrophic currents, inshore residual drift of bottom water, and vertical migration (Goodrich et al. 1989, Olmi 1994, Tankersley et al. 1995, Roman & Boicourt 1999, Forward et al. 2003, Epifanio 2007).

Megalopal settlement occurs episodically throughout the late summer and fall, with annual and latitudinal variability in the timing and magnitude of pulses (van Montfrans et al. 1995). In Chesapeake Bay, settlement generally occurs from July to November, with peaks usually occurring in August and September (van Montfrans et al. 1990). Significant pulses can occur into November, but these are much typically smaller in magnitude than the earlier pulses (van Montfrans et al. 1990). The current paradigm posits that megalopae preferentially settle in vegetated habitats, including seagrass beds, algal patches, and fringing marshes in the lower Bay (Orth & van Montfrans 1990, Lipcius et al. 2007). The youngest instars may exhibit density-dependent emigration from primary settlement habitats to alternative structured habitats when densities are high (Etherington & Eggleston 2000, Blackmon & Eggleston 2001, Reyns & Eggleston 2004).

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Juveniles remain within these structured habitats until they become outgrown the refuge from predation at 20-30 mm carapace width (cw; the distance between the lateral spines) provided by structured habitats (Pile et al. 1996, Lipcius et al. 2005, Johnston & Lipcius 2012). They then exhibit size-dependent dispersal to unvegetated habitats, as unvegetated habitats provide enhanced growth and survival rates for larger juveniles than vegetated habitats, likely due to the smaller suite of predators and high abundance of prey in unvegetated habitats (Seitz et al. 2003, 2005, Lipcius et al. 2005, 2007, Hines 2007).

Structurally complex habitats such as seagrass beds and salt marshes have often been described as nurseries for the blue crab, but debate remains as to what criteria should be used to designate a given habitat a nursery habitat. The concept of nursery habitats was originally invoked to describe a specific life history strategy of motile invertebrates and fishes in which juveniles develop in shallow, coastal habitats, followed by a migration to offshore adult habitats (Gunter 1967). It has recently been broadened to include all life history strategies with disjunct juvenile and adult habitats (Beck et al. 2001). Beck et al. (2001) recommended a criterion whereby nursery habitats contribute more adults *per unit area* on average to the population than other habitats. Dahlgren et al. (2006) coined the term "effective juvenile habitat" to describe juvenile habitats that are most important to maintaining adult populations in terms of their *total contribution* of adults to the population. Both of these terms rely on relative measures; i.e., the habitats with higher than average contribution are deemed most important. Both of these terms rely on relative measures; i.e., the habitats with higher than average contribution are deemed most important. The difference between these two criteria is whether the habitat contribution of adults to the population is calculated on a unit-area basis or as a habitat-

specific total.

However, in practice, these definitions are limited, as the number of successful recruits from a given habitat, either in relative or absolute terms, is very hard to determine. Not designed as integrated measures, neither can explicitly link the habitat-specific contributions to the persistence of the population. Fodrie and Levin (2008) and Fodrie et al. (2009) used the population growth rate (λ) as a measure of fitness to identify critical juvenile habitats for California halibut. By defining a nursery habitat as one that results in a λ greater than 1, the link between habitat and population growth rate is explicitly incorporated.

Despite the multitude of studies evaluating juvenile blue crab habitat at a local scale, there remains a question as to whether or not habitat is important at population scale. In this dissertation, I used large-scale field studies and a demographic model to indentify and quantify nursery habitat for juvenile blue crabs in Chesapeake Bay. In Chapter 2, I examined the effect of habitat complexity on juvenile blue crabs by developing a functional relationship between seagrass cover and juvenile density at a broad spatial scale. I addressed the timing of recruitment and migration between habitats in Chapter 3 by observing spatial and temporal trends in juvenile use of vegetated and unvegetated habitats. In Chapter 4, I provided an empirical example whereby inattention to habitat utilization patterns as a function of age or ontogeny may introduce significant error into stock assessments. Finally, I presented an exploratory demographic model to quantify the effects of nursery habitat on population fitness in Chapter 5.

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CHAPTER 2

Broad-scale association between seagrass cover and juvenile blue crab density in
Chesapeake Bay

ABSTRACT

Although numerous small-scale laboratory, mesocosm, and field experiments have demonstrated that abundance, survival, and growth of juvenile fish and invertebrates are higher in vegetated than in unvegetated habitats, the effect of habitat quality (i.e. habitat complexity) within vegetated habitats has not been documented at a broad spatial scale. We examined the relationship between percent cover in seagrass beds (eelgrass *Zostera marina*, widgeon grass *Ruppia maritima*, and associated macroalgae) and juvenile blue crab (*Callinectes sapidus*) density at a broad spatial scale. We quantified the functional relationship between juvenile density and percent cover of vegetation by sampling in Chesapeake Bay seagrass beds utilized by juvenile blue crabs in the fall of 2007 and 2008, following peak postlarval blue crab recruitment. Based on Akaike Information Criterion model comparisons, the most plausible model included both percent cover of vegetation and region of Chesapeake Bay. Juvenile crab density was a positive exponential function of percent cover of vegetation, and was augmented by 14–30%, depending on year, for every 10% increase in cover. Density was approximately two times higher on the western shore of Chesapeake Bay than on the eastern shore. Seagrass bed area, presence or absence of algae, and distance to the mouth of the bay did not significantly influence density. An expected threshold (i.e. sigmoid) response of juvenile density to percent cover of vegetation was not evident, probably because this study was undertaken when recruitment was low, such that habitats may not have been at carrying capacity. This study is the first to document the functional relationship between habitat quality and juvenile density at a broad spatial scale for a marine fish or invertebrate and suggests that the quality of seagrass habitat influences population dynamics.

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INTRODUCTION

The nursery role concept was introduced over a century ago to characterize the ecological function of near-shore shallow-water habitats, such as estuaries and lagoons, in species with complex life cycles that include ontogenetic shifts in habitat use. This early formulation offered the entire estuary as a nursery, but it was later suggested that specific habitats within the estuary were more important as nurseries than others (Beck et al. 2001). Typically these were structurally complex habitats, such as mangroves, marshes, and seagrass meadows, which usually have higher densities of juvenile fish and invertebrates than adjacent unvegetated habitats (Heck et al. 2003, Minello et al. 2003). For example, all of the 12 invertebrate species examined and 17, or 29%, of the taxa for which the International Council for the Exploration of the Sea (ICES) gives advice utilize coastal habitats as nurseries (ICES 2012).

Vegetated habitats, particularly marsh and seagrass, have often been described as nurseries for blue crabs (e.g. Orth & van Montfrans 1990), as most laboratory and field studies have found higher density, survival, or growth of young juveniles in seagrass habitats as compared to nearby unvegetated habitats (see Lipcius et al. 2007 for a review). Near Ono Island, Alabama, juvenile blue crab abundance was higher in vegetated habitats than unvegetated habitats throughout most of the year (Williams et al. 1990). This pattern decreased with size, as the abundance of juveniles > 10 mm carapace width (CW) was not significantly different between the habitats (Williams et al. 1990).

These patterns were also noted in a seagrass bed and an adjacent, unvegetated marsh creek in Chesapeake Bay (Orth & van Montfrans 1987). At two locations near Galveston Island, Texas, the density of juvenile blue crabs < 40 mm CW was higher in vegetated habitats, including seagrass and salt marsh, than in nearby unvegetated habitats (Thomas et al. 1990). Though there were no significant differences in juvenile density between vegetated and nearby unvegetated habitats at two locations in Great Bay, New Jersey, the low densities (0–3 crabs m^{-2}) may have obscured any trends (Wilson et al. 1990). Juvenile density was also positively correlated with seagrass shoot density at Goodwin Islands, Virginia (Hovel & Lipcius 2002).

Tethering experiments in Chesapeake Bay have indicated that survival of juvenile blue crabs is a function of both crab size and habitat (Pile et al. 1996, Schulman 1996, Lipcius et al. 2005, Hines 2007). Survival of juveniles 2–14 mm CW was higher in seagrass than unvegetated habitats (Pile et al. 1996), whereas survival of larger juvenile crabs, i.e. 14–16 mm CW (Pile et al. 1996) and 25–52 mm CW (Lipcius et al. 2005), was similar. In plots of artificial seagrass of varying shoot density, survival of juveniles was a function of size; survival of the smallest juveniles, ranging from 3–6 mm CW, was inversely related to shoot density, whereas survival of larger juveniles, 11–35 mm CW, was positively related to shoot density (Schulman 1996). Despite these numerous studies, few have addressed the role of habitat complexity within seagrass habitats (e.g. Hovel & Lipcius 2001, 2002), and the findings of these studies may not apply to the entire population because of their small spatial scale (i.e. one or two field locations).

Seagrass beds in Chesapeake Bay have undergone severe fluctuations in the last 80 years with the most dramatic losses occurring in the 1930s following the wasting

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disease pandemic and in the 1970s following significant water quality changes (Orth & Moore 1983). Full recovery after the wasting disease was evident by the 1960s. Although recovery from the 1970s' decline was observed through the 1990s, seagrass beds have once again been declining (Orth et al. 2010), prompting concerns that current declines could further compromise blue crab nurseries through reductions in the total seagrass bed extent and density. The area of individual seagrass beds and the presence of macroalgae, particularly the complex red macroalga *Gracilaria* spp., may also interact with the extent and density of seagrass beds to influence the density of juvenile blue crabs.

Given the absence of an evaluation of the relationship between features of seagrass habitats and juvenile blue crab density at a large spatial scale, we performed such an assessment across seagrass beds (and associated macroalgae) in Chesapeake Bay. The primary objective of this study was to quantify the relationship between density of recently settled blue crabs and the percent cover of vegetation. We also evaluated the effects of environmental factors, including region of Chesapeake Bay (eastern or western shore), seagrass bed area, distance to the mouth of the bay, and presence or absence of macroalgae, on juvenile blue crab density.

MATERIALS AND METHODS

Field surveys

In 2007 and 2008, we used a stratified random sampling survey in seagrass beds throughout lower Chesapeake Bay in the fall (October and early November), as postlarval recruitment to the bay typically occurs from August to November (van Montfrans et al.

1990). Sampling sites were randomly generated, using an algorithm in ArcGIS, across

shallow (< 2 m) seagrass beds in lower Chesapeake Bay (Figure 1), where primary blue

crab settlement occurs (Van Engel 1958, Heck & Thoman 1984, Lipcius et al. 2007) and

delineated from an annual aerial monitoring of all Chesapeake Bay underwater grass beds

(for detailed methodology, see Orth et al. 2011). Two species of seagrass were

encountered in the sampling, eelgrass *Zostera marina* and widgeon grass *Ruppia*

maritima, which generally co-occur in many areas of the lower Chesapeake Bay (Orth &

Moore 1988).

The study was designed to be representative of the population; thus samples were

allocated based on the area of seagrass on both the eastern and western shores during the

annual aerial seagrass monitoring, rather than equally across the shores. Approximately

twice as many samples were taken on the eastern shore than the western shore, as nearly

two-thirds of the seagrass beds in Chesapeake Bay are located along the eastern shore and

in Tangier Sound. In 2007, 43 samples were taken, with 33 and 10 on the eastern and

western shores, respectively; in 2008, 61 samples were taken with 40 and 21 on the

eastern and western shores, respectively (Figure 2). Samples were taken over a period of

eight days in 2007 and 30 days in 2008.

At each randomly selected sampling location, a 1.68-m^2 drop net was tossed off

the boat as close as possible to the randomly generated GPS coordinates. The net was

thrown from the bow of the boat while the engine was in neutral to minimize disturbance

of the juvenile crabs at the sampling location. Although multiple components of habitat

complexity, including shoot density, percent cover, and shoot height could potentially

influence the density of juveniles, we decided to utilize percent cover within the net

because it was the most consistent measurement and least likely to be influenced by observer bias (Dethier et al. 1993). Counting or measuring the length of each blade within a 1.68-m^2 area would influence density estimates, and taking a small core (e.g. 0.018 m^2, Hovel & Lipcius 2001, 2002) was unlikely to represent the entire area within the net given the patchy nature of seagrass beds in the fall. Percent cover of vegetation (i.e. seagrass and associated macroalgae) was visually estimated to the nearest 5% increment. Although the amount of macroalgae varied, it was rarely a dominant component, but was included in the estimates due to its prevalence and because it would increase habitat complexity within the sample. Of the 104 samples, macroalgae was present in 15, and comprised > 15% of the total cover in only 6 samples. A suction sampler, modified from Orth & van Montfrans (1987), was utilized to collect blue crabs to a sediment depth of about 5–10 mm. This method samples blue crabs with 80% efficiency in seagrass (R. Lipcius, unpublished data), but leaves most of the shoots intact. Each sample was pumped through a 1-mm-mesh collecting bag, then returned to the laboratory and frozen prior to processing. Each sample was sorted twice for quality assurance, and the blue crabs were counted, sexed, and measured for carapace width with Vernier calipers, then preserved in 70% ethanol. Only crabs ≤ 30 mm CW were included in the analysis, as this represents the size range of recruited juveniles in seagrass (Orth & van Montfrans 1987, Pile et al. 1996, Lipcius et al. 2007); there were relatively few crabs > 30 mm CW in the samples.

To evaluate landscape-level effects on juvenile density, two additional variables were calculated in ArcGIS 10.1. Nominal measures of seagrass bed area were calculated from the annual seagrass survey (Orth et al. 2008, 2009, 2010) for the spring prior to the

sampling season and for the spring after (e.g. for samples taken in 2007, we used the

2007 and 2008 spring aerial surveys). The distance from each sample to the mouth of

Chesapeake Bay via the deepest channels was also calculated, where the deepest channels

were delineated from a NOAA/NOS 30 m gridded digital elevation model (National

Oceanic and Atmospheric Administration 2006).

Statistical analyses and hypotheses

To address the shape of the relationship between vegetation cover and juvenile

crab density, we assessed whether the data met the assumptions of the linear model.

Three other plausible models, hyperbolic, exponential, and sigmoid, were considered

during analysis of the data. While additions of vegetation at low levels of cover may lead

to rapid increases in crab density (i.e. a hyperbolic function), high-density vegetation may

provide additional resources and refuge that can support much higher densities of

juveniles (i.e. an exponential function). However, newly settled blue crabs exhibit

density-dependent emigration from vegetated habitats (Blackmon & Eggleston 2001,

Etherington et al. 2003, Reyns & Eggleston 2004), suggesting an upper limit to the

number of juveniles within a given area (i.e. a sigmoid function).

Seagrass bed area and location may also influence crab density. The eastern and

western shores of the Chesapeake Bay exhibit two distinct morphologies: the western

shore is primarily composed of large tributaries, whereas the eastern shore is dominated

by small creeks and shallow sand bars. These differences and the greater area of seagrass

on the eastern shore were expected to result in lower densities of juveniles on the eastern

shore, where there are fewer impediments to migration. A positive relationship was also

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expected between bed area (Table 1) and juvenile density, as larger beds produce stronger chemical cues to which immigrating postlarvae or young juveniles may respond (Welch et al. 1997) and they have lower edge-to-interior ratios, which could limit emigration (Eggleston et al. 1998). As blue crab megalopae re-invade the bay from the coastal ocean, a negative relationship was expected between juvenile density and distance from the bay mouth. The presence of algae was expected to increase juvenile crab density, as it could provide additional structure and refuge.

We used Akaike's Information Criterion (AIC) within an information theoretic framework (Burnham & Anderson 2002, Anderson 2008) to evaluate which environmental variables were important in predicting juvenile blue crab density. This method relies on the development of multiple working hypotheses with associated mathematical models. The Kendall rank correlation coefficient (τ) was used to determine collinearity between the covariates, including juvenile density, percent cover of seagrass, bed area, and distance to the bay mouth. We proposed a total of 11 models comprised of the main effects and the interaction between shore and percent cover of vegetation (Table 2). All statistical analyses were run in the open-source statistical software package R (R Development Core Team 2008).

The benefit of using AIC as compared to other more traditional statistical methods is its ability to compare hypotheses against each other, through the likelihood of each model. To correct for a potential bias due to small sample sizes, the corrected AIC (AICc) was used (Anderson 2008). Each model was assessed by calculations that result in a weight (w_i), the probability that model i is the best model out of the candidate set of models (Anderson 2008):

$$AICc = -2\log(\hat{L}) + 2k + \frac{2k(k+1)}{n-k-1}$$

where n is the number of samples and k is the number of parameters;

$$\Delta_i = AICc_i - \min(AICc), \text{ and}$$

$$w_i = \frac{e^{-0.5\Delta_i}}{\sum e^{-0.5\Delta}}.$$

One caveat to the study is that sampling could not be synoptic due to logistical constraints. The survey was completed in October and November, but recruitment can occur episodically through November in the Chesapeake Bay (van Montfrans et al. 1990). Thus, there was some unknown variability in the samples that confounds year and month effects. However, given that the majority of pulses have generally occurred in the two months immediately prior to our sampling (van Montfrans et al. 1995), we are confident that our sampling represents a reasonable estimate of juvenile density in these habitats.

RESULTS

In 2007, the percent cover of vegetation ranged from 5–100%, with 6 of the 43 samples having < 20% cover; in 2008, percent cover ranged from 20–100%. Percent cover within the samples was not statistically different between eastern and western shores (Figure 3, Table 3).

Crab size was log-normally distributed with an overall mean of 7.4 mm CW (95% CI: 6.6–8.2 mm). Crabs were significantly smaller in 2008 than in 2007 and significantly smaller on the western shore than the eastern shore in both years. The difference between

the mean size of juvenile crabs on the eastern and western shores was greater in 2007 than in 2008, and the year x shore interaction was significant (Figure 4, Table 4).

Juvenile density was log-normally distributed with an overall mean of 24.0 crabs m^{-2} (SE = 2.7). Mean density of juvenile blue crabs in 2007 was 16.9 crabs m^{-2} (SE = 3.1); excluding the samples where seagrass cover was < 20% resulted in a density of 19.2 crabs m^{-2} (SE = 3.5). In 2008, the density was 29.0 crabs m^{-2} (SE = 3.9). Density of juveniles was significantly higher in 2008 than 2007 (t = 3.39, df = 58.7, p = 0.001).

The estimates of patch size from the year of the sampling and the year after were highly positively correlated in 2007 and 2008 (τ > 0.75). The correlations for all other pairs of environmental factors were weak ($|\tau|$ < 0.20). There was a small negative correlation between juvenile density and distance to the mouth of the bay (τ = -0.22 and -0.32 in 2007 and 2008, respectively).

Crab density vs. percent cover of seagrass

The linear function did not fit the data well, as evidenced by non-random residuals and heterogeneous variance, and was removed from further analysis. A polynomial fit to the data (LOWESS, Locally Weighted Scatterplot Smoothing) did not exhibit a peaked or asymptotic distribution, and indicated that an exponential or sigmoid model would be most appropriate. Given that the exponential model had randomly distributed residuals, that it did not exhibit heterogeneity of variance, and that the data did not approach an asymptote, the exponential model was used for the following analyses.

Based on the AIC model comparisons, models that contained only one of the predictor variables (models g_1–g_5) had virtually no support (i.e. w_i << 0.001). The

additive model of percent cover and shore, model g_6, received the highest weight in 2007, while the additive model of percent cover, shore, and distance to bay mouth, g_8, received the highest weight in 2008 (Table 5). However, including additional parameters, beyond percent cover and shore, added little in terms of goodness of fit, and in the supported models (i.e. with $w_i > 0.1$) only the parameter estimates for percent cover of vegetation and shore were estimated reliably (Table 6). Therefore, the most plausible model was the additive model of percent cover and shore (g_6; Figure 5). Specifically, juvenile density increased exponentially with percent cover but the steepness of the increase varied spatially (by shore) and temporally (by year).

We generated effect sizes for percent cover and shore based on model g_6. On average, there were 30% and 14% more crabs for every 10% increase in seagrass cover for 2007 and 2008, respectively. The addition of seagrass at the low range of percent cover had a relatively smaller effect on the total density than the addition of the same amount of cover at the high range, but the percent change was the same. The western shore had higher densities of juveniles than the eastern shore at equivalent percent cover, with 5.2 times more crabs on the western shore in 2007 and 2.8 times as many in 2008.

DISCUSSION

Crab density vs. percent vegetation cover

This study is the first to define the relationship between vegetation cover and density of juvenile blue crabs at a broad spatial scale (100s of km) representative of the population. We found an exponential relationship between vegetation cover and juvenile

density in Chesapeake Bay, rather than the expected sigmoid relationship. The relationship was not static; the shape of the curve varied both spatially (eastern vs. western shore) and temporally (by year), suggesting that the relationship is driven by differences in recruitment over space and time.

Previous studies have found higher density, survival, and growth of juvenile blue crabs in vegetated habitats relative to nearby unvegetated habitats (e.g. Heck & Orth 1980, Williams et al. 1990, Thomas et al. 1990, Lipcius et al. 2005, Seitz et al. 2005; see Lipcius et al. 2007 for a review); similar work has expanded this view to coarse woody debris (Everett & Ruiz 1993). The few previous studies that assessed the shape of the relationship between juvenile blue crab variables (i.e. density or survival) and features of vegetated habitats were at small spatial scales. In a field experiment in the York River, Virginia, there were size-specific differences in the relationship between juvenile density and shoot density of small artificial eelgrass patches for juveniles of three size classes (Schulman 1996), though the relationship between juvenile density and shoot density was approximately sigmoid. Crab density was positively correlated with percent cover of seagrass (eelgrass, widgeon grass, and shoal grass *Halodule wrightii*) in field surveys of Core and Back Sounds, North Carolina, for juveniles 5–50 mm CW (Hovel et al. 2002) and at the mouth of the York River, Virginia, for juveniles 10–30 mm CW (Hovel & Lipcius 2001).

This positive relationship may be a result of the ideal-free distribution, the theory that individuals are distributed to match the available resources (Fretwell & Lucas 1970). If juvenile blue crabs were distributed according to this theory, there should be higher densities of juveniles where resources are more abundant. For instance, foraging male

blue crabs (130–170 mm CW) more than doubled their consumption rates when prey resources doubled (Clark et al. 2000), and growth of juvenile blue crabs (25–52 mm CW) was highest in areas of the York River where clam densities were highest (Seitz et al. 2005). If structural complexity, such as vegetation cover, is a proxy for habitat quality, there should be a positive relationship between habitat complexity and juvenile density. Structurally complex habitats often have higher densities of prey items (Beck et al. 2001) and provide refuge from predation by visual predators for juvenile blue crabs (Heck & Thoman 1984, Orth & van Montfrans 2002, Lipcius et al. 2005).

Although we identified a positive relationship between habitat complexity and juvenile density at a broad spatial scale, it is important to differentiate between component and demographic effects (Stephens et al. 1999, Kramer et al. 2009). A component effect changes a single or multiple components of fitness (e.g. growth rate, survival) while a demographic effect changes the overall fitness and drives population growth rate (Stephens et al. 1999). A component effect can suggest that there is potential for a demographic effect, but it does not necessarily translate into a demographic effect (Stephens et al. 1999). Thus, while we demonstrated a component effect, further information is needed to determine if habitat complexity directly affects the population growth rate.

Spatial and temporal patterns

The relationship between percent cover of vegetation and juvenile crab density varied quantitatively, both spatially (higher on the western shore than eastern shore) and

temporally (higher in 2008 than 2007). Potential explanations for these differences include both physical and biological mechanisms.

Recruitment

One potential mechanism to explain spatial differences is variation in recruitment: i.e. more juveniles might be imported to the western shore of the Chesapeake Bay as compared to the eastern shore. In the York River, a tributary of the western shore of Chesapeake Bay, a coupled biological and hydrodynamic model suggested spatial differences in blue crab postlarval settlement (Stockhausen & Lipcius 2003). At the mouth of the river, predicted settlement was higher on the northern shore than on the southern shore. Additionally, the high predicted settlement at the mouth of the river created a settlement shadow upriver (Stockhausen & Lipcius 2003). Although it is possible that the coupling between postlarval behavior and transport processes results in higher densities of juveniles on the western shore as compared to the eastern shore, the evidence from circulation patterns is ambiguous. Advection into the estuary from the continental shelf occurs through wind-driven transport of surface waters (Epifanio 2007), and via high-density bottom water delivered via net nontidal flow below the outflowing surface waters on the western shore, and throughout the water column on the eastern shore (Tyler & Seliger 1978, Roman & Boicourt 1999). Thus, there are physical mechanisms that could deliver postlarvae earlier to the western shore than the eastern shore, but these are neither consistent nor conclusive.

Inter-annual differences in recruitment could also explain higher densities of juveniles in 2008 as compared to 2007. Consistent with this hypothesis, the Bay-wide

density of Age 0 crabs (i.e. juveniles < 60 mm in CW) was 11.6 crabs 1000 m^{-2} (95% confidence interval: 9.5–13.6 crabs 1000 m^{-2}) in 2007 and 17.6 crabs 1000 m^{-2} (95% confidence interval: 14.5–19.9 crabs 1000 m^{-2}) in 2008 (Miller et al. 2011), suggesting blue crab recruitment was higher in 2008.

Habitat

The overall amount of seagrass available for settlement could contribute to the estimates of juvenile density. If postlarvae were approximately equally distributed around the lower Bay, but the area of vegetated habitats into which the postlarvae could settle varied spatially, the densities of juveniles could also vary spatially. For example, if there were twice as much seagrass on the eastern shore than on the western shore, an equal number of juveniles recruiting to both shores would result in densities on the eastern shore half that of the western shore. The amount of seagrass estimated from aerial monitoring in the late spring during this sampling on the eastern shore was higher than that on the western shore in May and June (Orth et al. 2008, 2009), potentially because of a broader distribution across a greater depth range on the eastern shore than on the western shore (Orth & Moore 1988).

The spatial extent of seagrass could also explain differences by year. In the lower Bay, the area of seagrass increased 24% from 10,650 ha in early summer of 2007 to 13,225 ha in early summer of 2008 (Orth et al. 2008). This would suggest that, given constant recruitment, densities would decrease between 2007 and 2008. Instead, there was a 51% increase in juvenile crab density in seagrass, agreeing well with a 52% increase in recruitment as determined by the density of Age 0+ crabs in the Bay-wide

winter dredge survey (Miller et al. 2011). However, the two dominant seagrass species in Chesapeake Bay (eelgrass and widgeon grass) undergo spatially and temporally variable annual defoliation during the late summer and early fall, prior to our juvenile blue crab sampling. As there is no quantitative measure of the extent of seagrass during peak recruitment, this mechanism cannot be rigorously evaluated at present.

Growth and emigration

Juvenile blue crabs exhibit an ontogenetic shift in habitat use from seagrass to unvegetated habitats after ~ 20–30 mm CW (Orth & van Montfrans 1987, Hines 2007, Lipcius et al. 2007, Johnston & Lipcius 2012). Spatial variability in growth rates could result in juveniles moving out of seagrass beds faster in one region than another. Such a pattern of spatial variability in growth has been observed in other species. For example, spotted seatrout *Cynoscion nebulosus* growth differed between the eastern and western shores, and in wet and dry years (Smith et al. 2008). Under normal flow conditions, growth was higher on the eastern shore than on the western shore; under drought conditions, this trend was reversed (Smith et al. 2008). Previous studies found spatial differences in juvenile blue crab growth. Small juvenile blue crabs (mean CW = 2.65 mm) grew faster in seagrass as compared to unvegetated habitats in both field and laboratory experiments (Perkins-Visser et al. 1996). Larger juveniles (25–52 mm CW) grew at similar rates in downriver vegetated habitats and upriver unvegetated habitats (Seitz et al. 2005). If juveniles grow faster on the eastern shore as compared to the western shore, juveniles from a single recruitment pulse would leave vegetated habitats earlier on the eastern shore than on the western shore, and potentially contribute to the

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lower densities found on the eastern shore. This scenario agrees with our demonstrated larger average juvenile crab size on the eastern shore than the western shore.

The differences in sampling dates could also have contributed to the significantly smaller sizes and higher densities of juveniles collected on the western shore as compared to those on the eastern shore. In 2007, samples from the eastern shore were taken 4–8 d later than those from the western shore. The delay in sampling the eastern shore could have allowed the juveniles more time to grow, and die or emigrate from vegetated habitats, resulting in fewer, larger juveniles on the eastern shore. Newly settled juveniles grew an average of 1.5–2.1 mm CW week^{-1} in field enclosures (Perkins-Visser et al. 1996), which is close to the difference in size between the eastern and western shores in 2007. However, it is difficult to extrapolate those results to a more natural setting and larger crabs. Similar trends in density and size were observed in 2008. The samples were taken over a larger spatial and temporal extent in 2008, but again, most samples were taken earlier on the western shore than on the eastern shore.

Landscape effects

Previous studies have shown that juvenile blue crab survival can be influenced by landscape-level factors, such as patch size (Hovel & Fonseca 2005, but see Hovel & Lipcius 2001) and fragmentation type (Hovel & Lipcius 2002). The relationship between juvenile density and seagrass bed area may have been masked by a bias in the estimates of bed area from the aerial survey. These estimates may not reflect the actual habitat encountered by the postlarvae and young juveniles in late summer and fall, as seagrasses in Chesapeake Bay undergo an annual defoliation in late summer. Conversely, postlarvae

and young juveniles may not be responding to seagrass bed area at the scale measured by the aerial survey, and localized patchiness may be more important in controlling juvenile density.

Given the movement of postlarvae into Chesapeake Bay from the coastal ocean, the weak statistical relationship between distance to the bay mouth and juvenile density was surprising. The use of distance via deep channels may be biased, as currents and tides, strong drivers of postlarval recruitment, are not incorporated in this measure. Perhaps a better measure of distance could explicitly include hydrodynamic drivers of postlarval and juvenile advection.

Climate change and the future of vegetated habitat in Chesapeake Bay

Climate change will play a complex role in the life cycle of the blue crab, especially as it relates to the distribution and abundance of vegetated habitat. Whereas abundance of the temperate species, eelgrass, is likely to continue to decline given the expected increases in water temperature and phytoplankton abundance, the other abundant estuarine seagrass in Chesapeake Bay, widgeon grass, is more tolerant of higher water temperatures and may be more resilient to these changes (Evans et al. 1986). Other studies suggest that juvenile blue crabs can have similar survival and growth in emerging ecosystems such as *Gracilaria* spp., a complex red macroalga (Falls 2008, Johnston & Lipcius 2012). Juvenile blue crab densities in *Gracilaria* spp. patches in Rehoboth Bay (Epifanio et al. 2003) and in Chesapeake Bay were similar to those in seagrass patches (Johnston & Lipcius 2012). Larval abundance and postlarval recruitment decreased by an

order of magnitude between 1992 and 2000 as compared to earlier years (Lipcius &

Stockhausen 2002). Seagrass in Chesapeake Bay was recovering through the mid-1990s,

after which another prolonged decline began (Orth et al. 2010). While this period of

relatively high seagrass abundance and high juvenile abundance, followed by a period of

low seagrass and low juvenile abundance, suggests that there might be a relationship

between seagrass cover and crab density at the population level, other factors are likely at

play. For example, the blue crab population was classified as overfished with overfishing

occurring for most of the decade leading up to this study, and after reductions in fishing

pressure in 2008, there have been recent increases in the total population. Given the

continued ability of juveniles to utilize alternative vegetated habitats, it is unknown what

effect further declines of eelgrass in the Chesapeake Bay will have on the blue crab

population as well as the availability of alternative habitats.

Caveats and recommendations

This study was undertaken during a period of historically low blue crab

recruitment and should be repeated during a period of high recruitment to test the

generality of the findings. The lack of a threshold response of juvenile crabs to vegetation

cover could have been caused by low densities of juveniles overall. Perhaps the

exponential response would become a threshold response under higher recruitment.

Recently, abundances of adult female and juvenile blue crabs have increased (Miller et al.

2011) in waters > 1.5 m, but blue crab sampling in shallow waters is lacking. Continuing

to sample juveniles in shallow, vegetated habitats is critical and would provide more

information about the relationship between juvenile density and vegetation under

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different climate scenarios. Finally, the potential of the component effect of vegetation cover upon juvenile blue crab density to be a demographic effect demands assessment either through further Bay-wide population and vegetation sampling or by population modeling.

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Table 1: Area of vegetated habitat (km^2) within each region (1–10, see Figure 1). Distinct geographic regions are separated by rivers and sandbars (modified from Harwell & Orth 2002). Aerial extent of vegetated habitat was modified from the VIMS annual survey (Orth et al. 2008, 2009, 2010).

Region	2007	2008	2009
1	1.8	2.1	2.4
2	9.0	10.4	11.8
3	14.4	18.1	22.9
4	9.3	11.2	14.8
5	32.8	37.4	42.4
6	8.6	12.1	15.2
7	0.9	1.3	3.5
8	9.5	12.3	12.7
9	10.5	12.4	13.4
10	8.9	12.1	14.9
Total	105.7	129.4	154.1

Table 2. Models used in the AIC analysis of blue crab density. k = the number of parameters in each model. Cover refers to the percent of the sample ring that was covered with seagrass. $x_2 = 0$ if Eastern shore, $= 1$ if Western Shore. Bed Area refers to the area of the seagrass bed within which each sample was taken (i.e. patch size), based on the aerial seagrass survey from the May-June of the year after the sample was taken. Distance refers to the distance to the bay mouth along the deepest channels. $x_5 = 1$ if any algae was present in the sample, $= 0$ if algae was absent. If a β is located in a column then that variable was included in the model. All models were run using the exponential transformation, $\ln(y)$.

Model	k	Intercept	x_1 Cover	x_2 Shore	x_3 Bed Area	x_4 Distance	x_5 Algae	$x_1 * x_2$ Cover*Shore
g_1	3	β_0	β_1					
g_2	3	β_0		β_2				
g_3	3	β_0			β_3			
g_4	3	β_0				β_4		
g_5	3	β_0					β_5	
g_6	4	β_0	β_1	β_2				
g_7	5	β_0	β_1	β_2	β_3			
g_8	5	β_0	β_1	β_2		β_4		
g_9	5	β_0	β_1	β_2			β_5	
g_{10}	5	β_0	β_1	β_2				β_6
g_{11}	7	β_0	β_1	β_2	β_3	β_4	β_5	

Table 3. Two-way ANOVA results for the percent vegetation cover in Chesapeake Bay, Virginia, by year (2007 & 2008) and shore (Eastern & Western). Percent cover of vegetation estimates are from the visual inspections of the drop net at each sampling location.

Source	df	MS	F	P
Shore	1	0.48	0.08	0.57
Year	1	7.93	1.38	0.02
Shore X Year	1	1.79	0.31	0.74
Residuals	94	5.75		

Table 4. Two-way ANOVA results for the size of blue crabs in Chesapeake Bay, Virginia, by year (2007 & 2008) and shore (Eastern & Western).

Source	df	MS	F	P
Shore	1	20.67	73.62	<< 0.01
Year	1	66.84	238.10	<< 0.01
Shore X Year	1	4.29	15.29	<< 0.01
Residuals	3348	0.28		

Table 5. Results of the AIC analysis of blue crab density for 2007 and 2008. Δ_{AICc} and w_i are calculated from the log-likelihood of each model. Adjusted r^2 was used because it takes into account the number of parameters in the model. n = 43 for 2007 and n = 61 for 2008. All models were run using the exponential transformation, ln(y).

Model	k	2007			2008		
		Adj. r^2	Δ_i	w_i	Adj. r^2	Δ_i	w_i
g_1	3	0.382	14.3	<0.001	0.165	36.3	<0.01
g_2	3	0.186	26.2	<0.001	0.331	22.8	<0.01
g_3	3	-0.010	35.5	<0.001	0.004	47.1	<0.01
g_4	3	-0.012	35.6	<0.001	0.168	36.2	<0.01
g_5	3	0.024	33.0	<0.001	-0.016	48.4	<0.01
g_6	4	0.571	0.0	0.29	0.514	4.6	0.07
g_7	5	0.566	2.0	0.10	0.512	6.2	0.03
g_8	5	0.578	0.8	0.19	0.559	0.0	0.74

g_9	5	0.578	0.8	0.19	0.511	6.3	0.03
g_{10}	5	0.579	0.7	0.20	0.514	5.9	0.04
g_{11}	7	0.562	5.8	0.02	0.547	4.5	0.08

Table 6. Parameter estimates from the transformed data for models with $w_i > 0.01$ for (a) 2007 and (b) 2008. Parameter estimates with 95% confidence intervals that do not include 0 are in bold.

(a)

Model	k	Intercept	x_1 Cover	x_2 Shore	x_3 Bed Area	x_4 Distance	x_5 Algae	$x_1 x_2$ Cover*Shore
g_6	4	-0.08 (0.34)	**0.030 (0.005)**	**1.64 (0.38)**				
g_7	5	-0.21 (0.39)	**0.031 (0.005)**	**1.72 (0.40)**	~0			
g_8	5	-0.88 (0.71)	**0.030 (0.005)**	**2.04 (0.49)**		~0		
g_9	5	0.08 (0.36)	**0.03 (0.005)**	**1.63 (0.37)**			-0.50 (0.39)	
g_{10}	5	-0.28 (0.37)	**-0.034 (0.006)**	**2.58 (0.81)**				-0.016 (0.012)
g_{11}	7	-0.48 (0.91)	**0.030 (0.005)**	**1.90 (0.54)**	~0	~0	-0.30 (0.47)	

(b)

Model	k	Intercept	x_1 Cover	x_2 Shore	x_3 Bed Area	x_4 Distance	x_5 Algae	$x_1 x_2$ Cover*Shore
g_6	4	**1.68 (0.22)**	**0.01 (0.003)**	**1.04 (0.16)**				
g_7	5	**1.72 (0.23)**	**0.01 (0.003)**	**1.01 (0.16)**	~0			
g_8	5	**2.31 (0.32)**	**0.02 (0.003)**	**0.76 (0.18)**		~0		
g_9	5	**1.72 (0.23)**	**0.01 (0.003)**	**1.06 (0.16)**			-0.20 (0.24)	
g_{10}	5	**1.84 (0.27)**	**0.01 (0.003)**	0.60 (0.45)				0.006 (0.006)
g_{11}	7	**2.31 (0.32)**	**0.02 (0.003)**	**0.78 (0.19)**	~0	~0	-0.15 (0.23)	
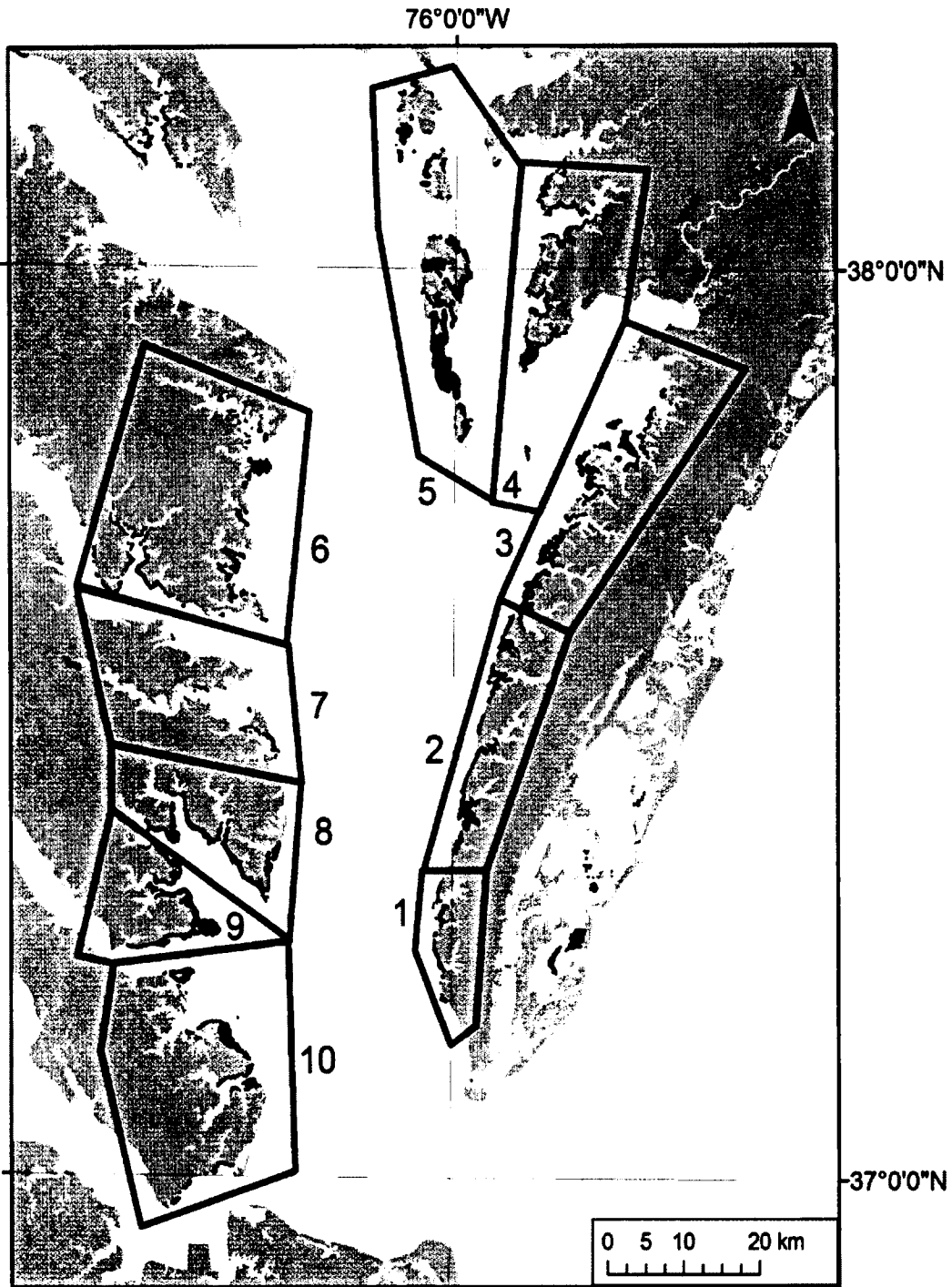
Figure 1. Map of aerial extent of vegetated habitats (widgeon grass, eelgrass and macroalgae) in the Chesapeake Bay in 2007 (dark gray patches). Black polygons represent distinct geographical regions separated by rivers and sandbars (modified from Harwell & Orth 2002). The distribution of vegetated habitats in 2008 was very similar, though the total area was slightly higher (Orth et al. 2008). See Table 1 for area of each polygon. Gray shading: land; white: water.

(a)
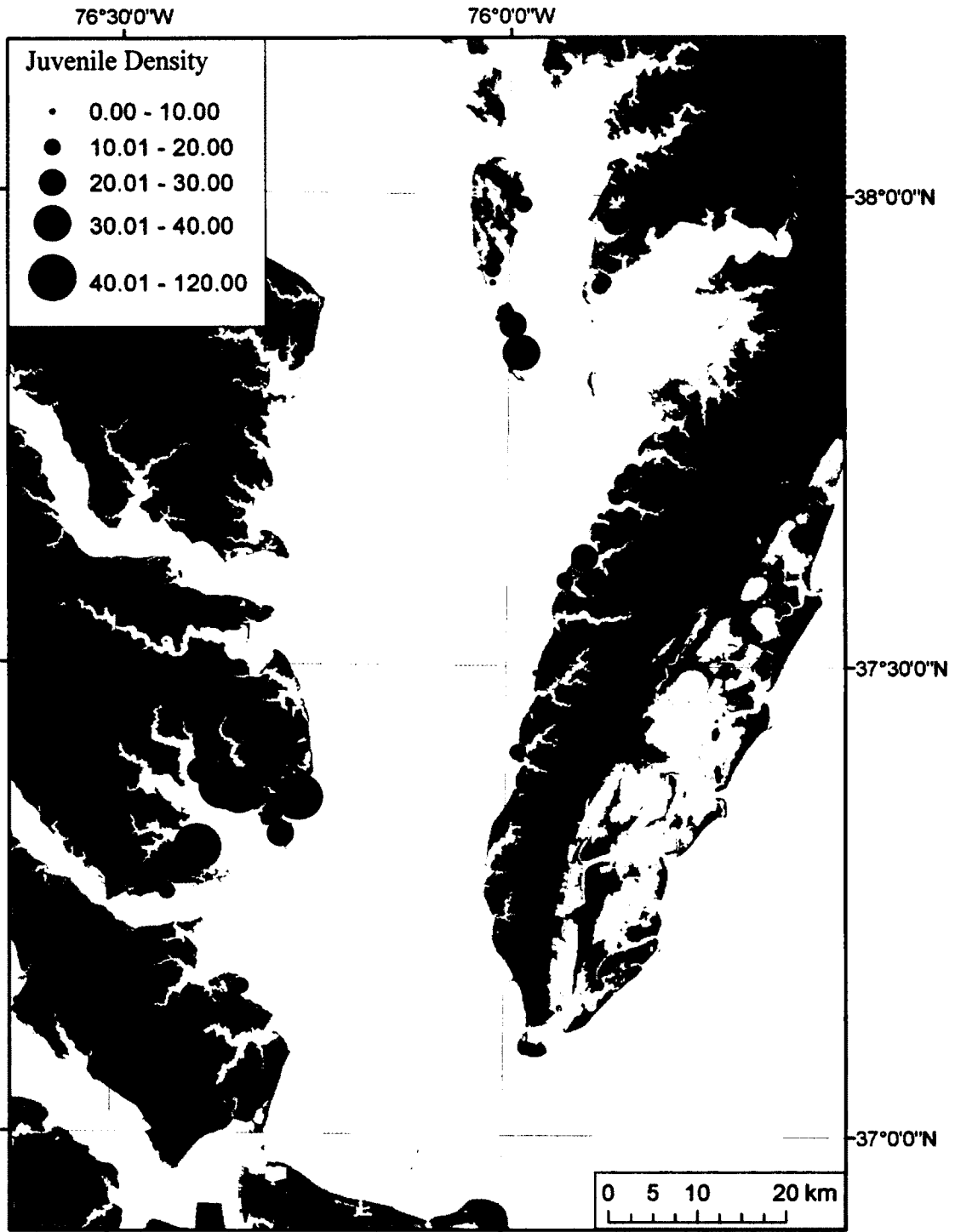
(b)
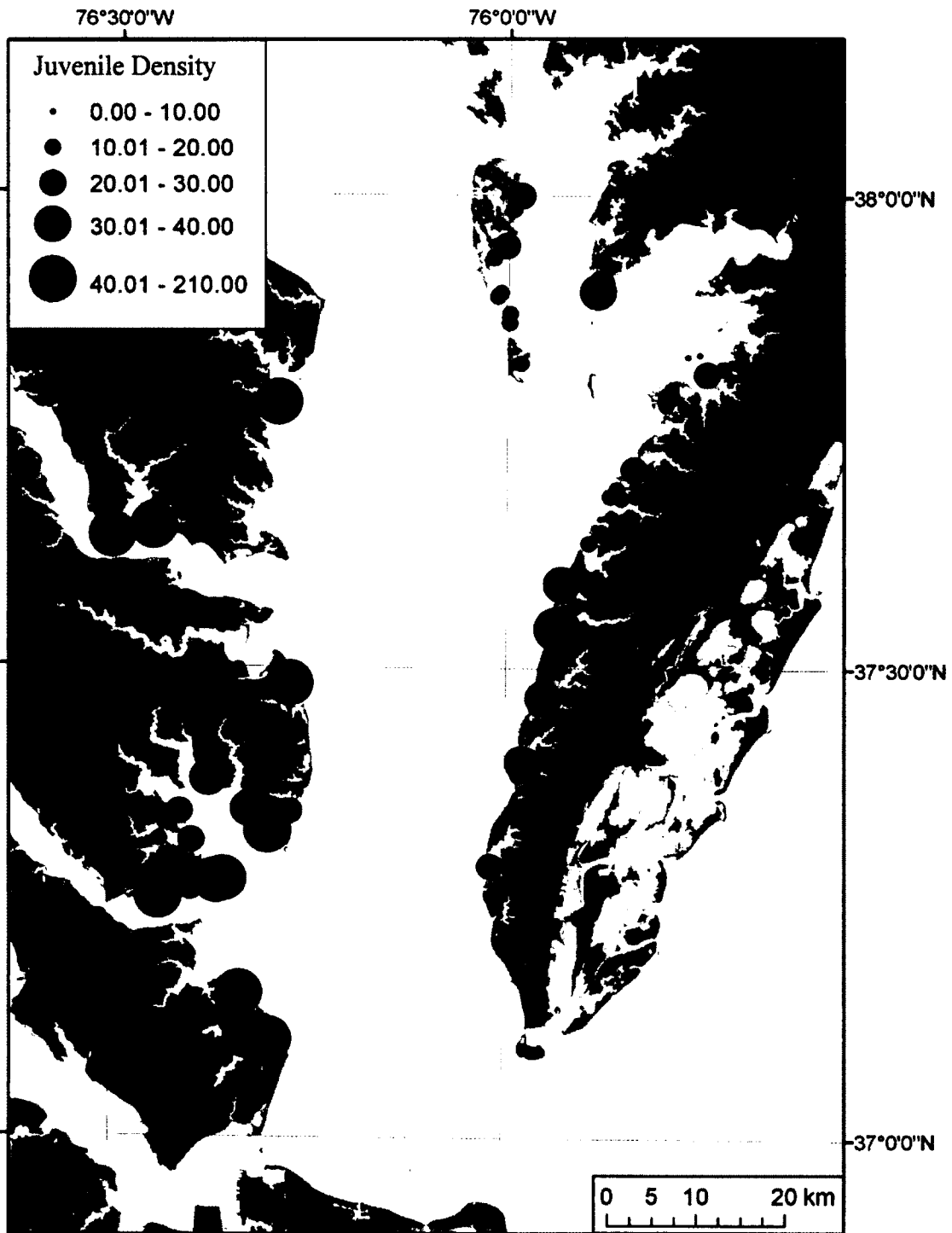
Figure 2. Map of sampling locations and crab density ($\leq$ 30 mm carapace width) for (a) 2007 and (b) 2008. In total, 43 samples were taken in 2007, 33 on the eastern shore and 10 on the western shore. In 2008, 61 samples were taken, 40 on the eastern shore and 21 on the western shore.
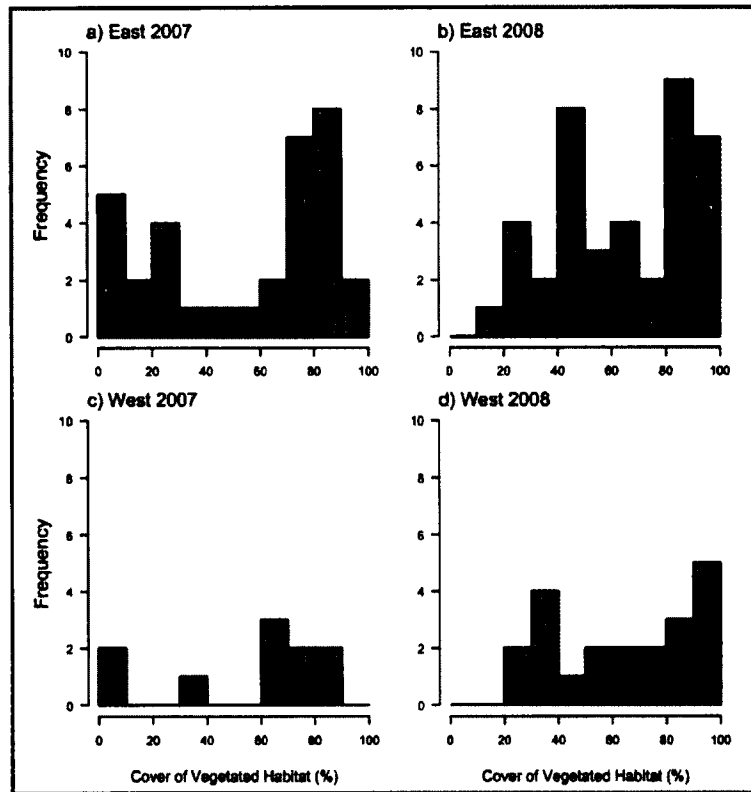
Figure 3. Frequency histograms for the percent cover of vegetated habitats (widgeon grass, eelgrass, and macroalgae) within each sample according to year and shore. In 2008, samples were not taken if the vegetation cover was < 20%.
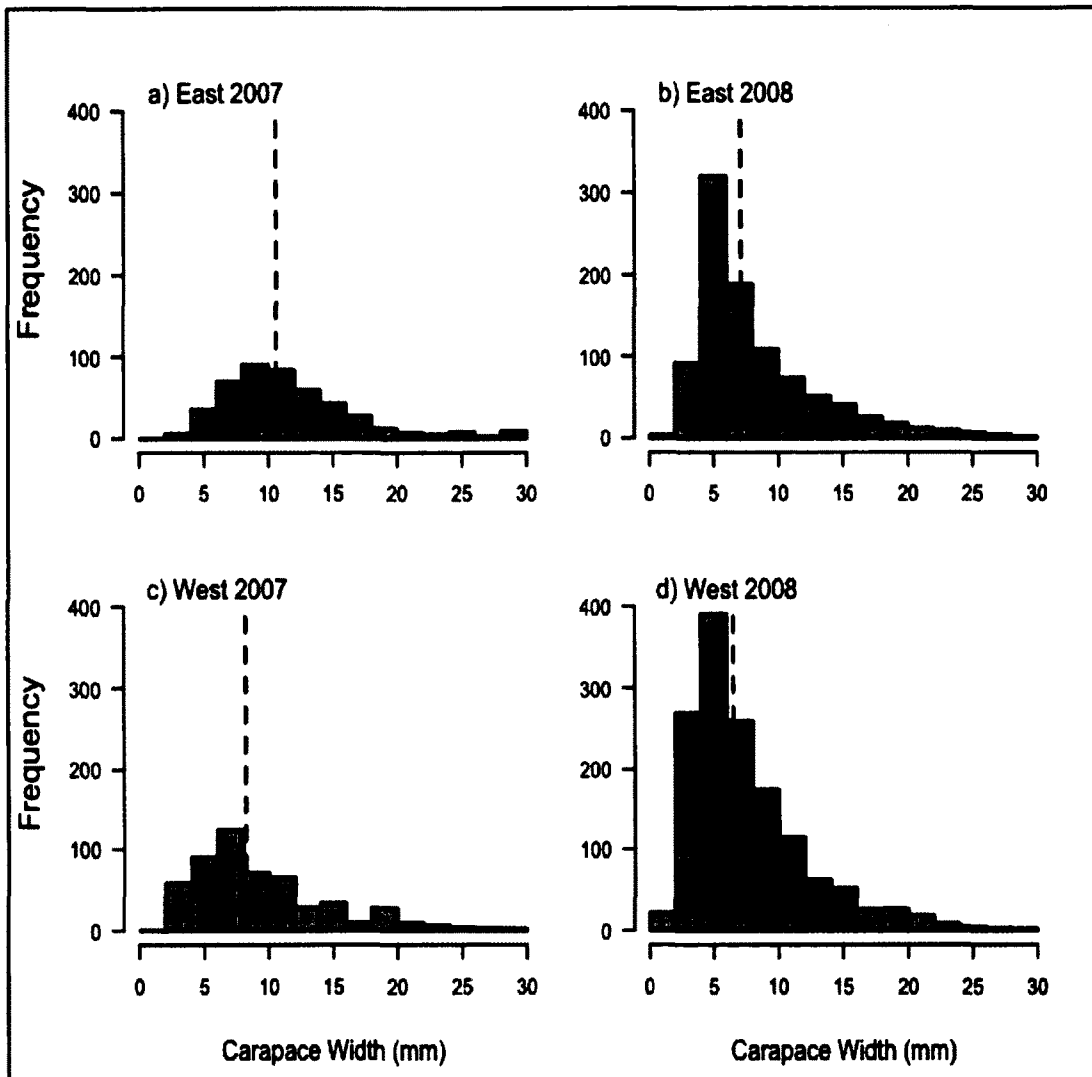
Figure 4. Size-frequency histograms for juvenile blue crabs (≤ 30 mm carapace width) according to year and shore. The dashed vertical line is the back-transformed mean size for each year by shore combination based on the natural log transformation: (a) East 2007 - 10.6 mm; (b) East 2008 - 7.1 mm; (c) West 2007 - 8.2 mm; (d) West 2008 - 6.5 mm.
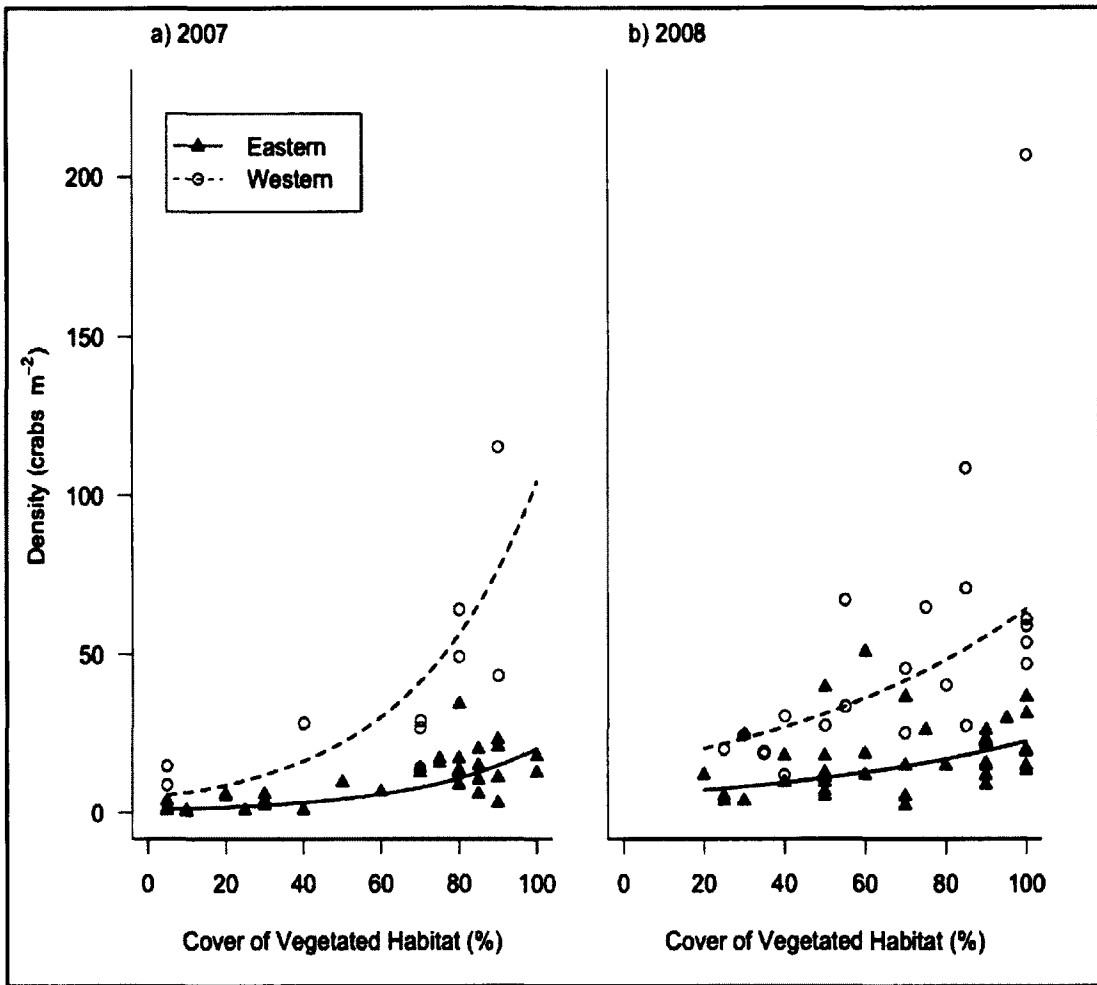
Figure 5. Raw data and model predictions for the best model as determined by AICc for (a) 2007 and (b) 2008. The predictions are based on the natural log transformation of the data.

CHAPTER 3

Spatiotemporal patterns in age-0 blue crab recruitment to seagrass and unvegetated
nursery habitats

ABSTRACT

Coastal habitat utilization is likely an essential component of the population dynamics of many exploited species. For the Chesapeake Bay blue crab, which supports one of the most important crustacean fisheries in the US, demographic rates are habitat-specific. In particular, age-0 crabs (i.e., <60 mm carapace width) appear to have widely variable mortality and growth rates depending on habitat. We examined spatiotemporal patterns in size-specific recruitment to shallow vegetated and unvegetated habitats throughout the York River, a sub-estuary of Chesapeake Bay, after new and full moons during the recruitment season in 2010 and 2011. Vegetated habitats at the mouth of the York River were sampled with a suction apparatus, while shallow unvegetated, marsh-fringe coves throughout the river were sampled with a benthic scrape. The density of age-0 crabs less than 25 mm carapace width was very high in vegetated habitats, and most were less than 10-15 mm carapace width. As expected, the density of juvenile crabs less than 25 mm cw was lower in unvegetated habitats than vegetated. These results support the ontogenetic shift from shallow vegetated habitats to shallow unvegetated habitats suggested by previous work, but provide evidence that the shift is occurring at a smaller size than would be predicted by differences in predation risk between vegetated and unvegetated habitats (25-30 mm carapace width). The current conceptual paradigm for recruitment of age-0 crabs to shallow water vegetated and unvegetated habitats must be revised to incorporate the importance of the extensive shallow unstructured habitats for small juvenile blue crabs (< 25 mm cw).

INTRODUCTION

The importance of coastal habitat is a poorly understood, but likely essential, component of the population dynamics of exploited species (ICES 2012). The limited demographic information on coastal habitat utilization available for most exploited species is not sufficient to determine if these habitats limit population growth and fishery production (ICES 2012). For species with complex life history strategies, in particular, understanding patterns in the timing and magnitude of movement between habitats is an essential first step to explicitly incorporating habitat utilization into demographic models.

The blue crab exhibits ontogenetic shifts in habitat utilization; for the purposes of describing these shifts, blue crabs are often classified by stage (i.e., larvae, postlarvae, juvenile) and by carapace width (cw: the distance between the lateral spines). In general, spawning occurs in estuaries, followed by larval development in the coastal ocean, and return to the estuary by the postlarvae (i.e., megalopae). In Chesapeake Bay, settlement occurs episodically; typically, megalopal settlement starts in early summer and continues through late fall on an approximately lunar cycle (Olmi 1995, van Montfrans et al. 1995). The current paradigm posits that megalopae preferentially settle in vegetated habitats prior to metamorphosis (Lipcius et al. 2007, Orth & van Montfrans 1990). The densities of megalopae and age-0 crabs less than 6 mm cw were not influenced by depth or seagrass species, suggesting fine-scale habitat selection does not occur in the water column and the initial age-0 distribution is mainly a function of larval supply and

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transport (Pardieck et al. 1999). However, field experiments found megalopae preferentially settled in seagrass compared to mud or oyster shell when substrates were located only 0.75 m apart (van Montfrans et al. 2003).

Vegetated habitats, including marsh and seagrass, often provide higher survival and growth rates blue crabs less than 25 mm cw (see Lipcius et al. 2007 for a review). Although there is evidence for density-dependent emigration from primary settlement habitats (Blackmon & Eggleston 2001, Etherington & Eggleston 2000, Reyns & Eggleston 2004), emigration from vegetated habitats is thought to occur when the refuge from predation provided by the habitat structure has been outgrown (Orth & van Montfrans 1987, Pile et al. 1996, Lipcius et al. 2005, 2007). Tethering experiments in Chesapeake Bay suggest seagrass beds provide the highest protection between 9-16 mm cw (Pile et al. 1996). The size-specific survival rates appear to be mediated by habitat: in vegetated habitats, survival decreases with size after some maximum, possibly due to increased visibility between seagrass blades; in unvegetated habitats, survival increases with size (Johnston & Lipcius 2012). Thus, survival may be maximized by immigrating to shallow, unvegetated habitats at 25-30 mm cw (Johnston & Lipcius 2012). At this larger size, the abundant prey resources in unvegetated habitats can be exploited (Seitz et al. 2005) while also experiencing increased survival (Lipcius et al. 2005).

Previous examinations of the movements of juvenile crabs have used direct and indirect methods. Small-scale tagging studies suggested that once dispersed, juvenile crabs tend to remain within sub-estuaries (Davis et al. 2005, Hines 2007, Johnston & Eggleston 2010). However, as mortality and growth rates are high, tagging studies are impractical for assessing large-scale movement patterns of juveniles. Instead, movement

has been inferred from size-specific trends in habitat utilization. For example, an ontogenetic shift in habitat utilization at 7 mm cw was concluded based on increased abundance in unvegetated habitats concurrent with decreased abundance in vegetated habitats (Pile et al. 1996).

We examined spatiotemporal trends in size-specific recruitment to shallow vegetated and unvegetated habitats throughout the York River. We also evaluated the effect of environmental variables on juvenile density (i.e., percent cover in vegetated habitats and depth in unvegetated habitats).

METHODS

Field sampling

Samples were collected in the York River, a 55-km sub-estuary on the lower western shore of Chesapeake Bay. The river was subdivided into three zones (up-river, mid-river, and down-river) similar to those used in previous studies of the York River (e.g., Lipcius et al. 2005, Seitz et al. 2005). Megalopal settlement into the York River occurs through the late summer and fall, with peak settlement typically occurring during and immediately after new and full moons (van Montfrans et al. 1990, Olmi 1995). To capture these episodic pulses, sampling was initiated 1-2 days after new and full moons between August and November of 2010 and 2011 (Table 1), for a total of six sampling events in 2010 and five in 2011. In 2010, samples were taken in vegetated habitat (seagrass beds of eelgrass *Zostera marina* and widgeon grass *Ruppia maritima* interspersed with patches of the exotic macroalga *Gracilaria vermiculophylla*) and

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unvegetated habitat (coves and creeks) fringed by salt marsh consisting predominantly of *Spartina alterniflora* and *S. patens*. In 2011, sampling was restricted to unvegetated habitats.

Sampling sites were randomly generated using an algorithm in ArcGIS for both vegetated and unvegetated habitats. Vegetated habitats were delineated from an annual aerial monitoring survey of Chesapeake Bay submerged aquatic vegetation. For details of the aerial survey, see Orth et al. (2011). Currently, the extent of seagrass habitat is limited to the down-river zone of the York River (i.e., below Gloucester Point, Virginia). During each sampling event, 15 - 27 samples were taken in vegetated habitat, for a total of 127 samples. Overall, 19 shallow, marsh-fringed coves throughout the York River were selected through visual examination of the shoreline, and the area was delineated digitally by drawing a straight line across the mouth of each cove. For each sampling event in 2010, nine shallow coves were sampled, three coves in each of the three river zones; four samples were taken per cove. To reduce variability between sampling events due to the random selection of coves, in 2011 we sampled the same six coves, two in each of the three rivers zones and sampled six random locations during each sampling event.

We utilized two sampling methods to survey the different habitats. Vegetated habitats were sampled using a drop net and suction sampler to evacuate a 1.68 m^2 area of debris and epifauna to a depth of 10-15 mm. This technique was modified from that of Orth & van Montfrans (1987) and collects blue crabs with 80% efficiency in vegetated habitats (R. Lipcius, unpublished data), but leaves most of the vegetation intact. The percent cover of vegetated habitat was visually estimated within the net to the nearest 5%

increment. Samples were pumped through a 1-mm-mesh collecting bag, then returned to the laboratory and frozen prior to processing.

However, suction sampling provides imprecise estimates of abundance in unvegetated habitats because of the small area of the drop net and comparatively low crab density. Further, previous studies suggested that crabs <6 mm cw do not utilize unvegetated habitats (Orth & van Montfrans 1987, Pile et al. 1996), so using a 1-mm-mesh net in unvegetated habitats was deemed excessive. Shallow unvegetated habitats were sampled by towing a 1-m-wide benthic scrape with a 6-mm-mesh net for 20 m. The larger mesh limited the times the net got clogged and stopped fishing, though it did limit direct comparisons for crabs < 6 mm cw. As the survival of crabs < 6 mm cw is low in unvegetated habitats (Pile et al. 1996, Johnston & Lipcius 2012), accurate density estimates for this size class may be irrelevant. Efficiency of the benthic scrape was not estimated directly in this study. Previous work with the same gear towed for 100 m suggested that efficiency is low, around 5.5% (Davis et al. 2005). Depth, a potentially important factor in determining age-0 crab distribution in unvegetated habitats, was estimated from the depth sounder on the vessel.

All blue crabs were counted, sexed, and the carapace width measured with Vernier calipers. The objective of this study was to examine habitat utilization of age-0 crabs, which are often not sampled well during large-scale surveys (e.g., Blue Crab Winter Dredge Survey and Juvenile Fish and Blue Crab Trawl Survey). In vegetated habitats, only small age-0 crabs (i.e., those <25 mm cw) were included in density estimates, as large age-0 crabs (i.e., those 25-60 mm cw) are typically not found in vegetated habitats. In unvegetated habitats, small and large age-0 crabs (i.e., those 6-25

mm cw and 25-60 mm cw, respectively) were separated to evaluate size-specific patterns. Density estimates in both habitat types were presented per m^2 by accounting for the area sampled and gear efficiency (vegetated habitats: 1.68 m^{-2} and 80% efficiency, unvegetated habitats: 20 m^{-2} and 5.5-50% efficiency).

Statistical analyses

All statistical analyses were performed using R (R Development Core Team 2011). One-way fixed factor analysis of variance (ANOVA) was used to compare density across sampling events in vegetated and unvegetated habitats separately to examine changes throughout the recruitment season. Density was natural-log transformed to meet assumptions of normality and homogeneity of variance. In unvegetated habitats, we qualitatively compared patterns in mean density in each river zone by sampling events.

The role of percent cover of vegetation on juvenile density was explored using linear regressions on transformed data. In the Croatan-Albemarle- Pamlico Estuarine System of North Carolina, newly settled blue crabs exhibited density-dependent emigration from vegetated habitats (Blackmon & Eggleston 2001, Etherington et al. 2003, Reyns & Eggleston 2004), suggesting an upper limit to the number of juveniles within a given area, or a sigmoid relationship. However, a previous study of small blue crabs in Chesapeake Bay found an exponential relationship with percent cover of vegetation (Ralph et al. 2013). Thus, both exponential and sigmoid relationships were evaluated.

In unvegetated habitats, shallow water (<0.7 m) may provide a refuge from

predation for juvenile blue crabs 30-70 mm cw in the upper Bay (Hines & Ruiz 1995).

We examined the effect of depth on density of juvenile crabs in unvegetated habitats in

2011. Samples taken in 0.5 m increments (i.e., 0.5-1.0 m, 1.0-1.5 m, 1.5-2 m) were

combined and a one-way fixed factor ANOVA was run on the natural log-transformed

data; although Hines & Ruiz (1995) used 0.7 m as the cutoff for shallow water, the

shallow, unvegetated habitats we sampled were mostly > 0.7 m.

Abundance estimation

The area of vegetated and unvegetated habitat in the York River was calculated in

ArcGIS. The estimate of vegetated habitat area was derived from the annual aerial

monitoring survey of submerged aquatic vegetation (SAV) in Chesapeake Bay during

May-June 2011 (Orth et al. 2012). All shallow creeks and coves in the York River were

included in the estimate of unvegetated habitats. However, this survey did not incorporate

shallow unvegetated habitats in the mainstem of the York River sampled by Lipcius et al.

2005, which may be important habitats for juvenile blue crabs greater than 25 mm cw.

Density for both habitats was estimated from the catch per sample (e.g., catch per

suction for vegetated habitats and catch per tow for unvegetated habitats). Density was

estimated for all age-0 crabs (1-60 mm cw) and for age-0 crabs vulnerable to the gear

deployed in the unvegetated habitats (i.e., 5-60 mm cw). Catch per sample in vegetated

and unvegetated habitats was averaged for each sampling region over all sampling

events, and scaled by the area of habitat in each region. Samples in vegetated habitats

were corrected for the 80% efficiency (R. Lipcius, unpublished data). Efficiency of the

scrape gear deployed in unvegetated habitats is not well known, so a range of plausible

values, between 5.5 and 50%, were utilized.

RESULTS

Vegetated habitats

The 2119 crabs collected in vegetated habitats ranged from 1.8 – 77.8 mm cw; nearly 99% were less than 20 mm and only 0.1% were greater than 60 mm. There were clear pulses, when more than 15% of the small juveniles collected were the first benthic instar, around September 8th, October 23rd, and November 6th (Figure 4). The mean size of age 0 crabs across all sampling events was 7.8 mm, and was not significantly different between sampling events (ANOVA: $F_{5, 116} = 0.88$, $P = 0.5$).

The maximum density of small juvenile crabs (≤ 25 mm cw) in vegetated habitats in 2010 was 192.3 crabs m^{-2}, with mean = 12.1 and standard error (SE) = 1.7. Density did not vary significantly by sampling event (ANOVA: $F_{5,121} = 0.569$, $P = 0.72$) or by lunar phase (ANOVA: $F_{1,125} = 0.211$, $P = 0.65$).

Both the exponential and sigmoid functions between juvenile density and percent cover of vegetated habitat were supported by the data, with an r^2 of 0.36 ($P < 0.001$) and 0.40 ($P < 0.001$), respectively. However, the shapes of the two best-fit lines were similar, as the sigmoid function did not display a threshold at high percent cover. Estimated density increased by 16% for every 5% increase in cover under the exponential model (Figure 3).

Unvegetated habitats

The 2943 crabs collected in unvegetated habitats in 2010 and 2011 ranged from 3.8-165.0 mm cw. The majority of juveniles collected in unvegetated habitats were between 10-40 mm cw; only crabs 6-60 mm cw were included in the analyses. There were often distinct peaks of crabs 8-15 mm cw; occasional peaks of larger crabs, 20-25 mm cw, were also discernible (Figures 10 & 11).

In 2010, the maximum density was 12.5 crabs m^{-2} assuming an efficiency of 10%, while in 2011, the maximum density was 21.0 crabs m^{-2}. The average density was 1.98 (SE = 0.14) and 3.76 (SE = 0.23) crabs m^{-2} in 2010 and 2011. However, the density estimate depends on the assumed efficiency; using efficiency estimates from 5.5-50% change the mean density to 0.40-3.60 in 2010 and 0.75-6.83 in 2011. There were no significant differences through time for both size classes in 2010, but there were in 2011 (Figures 5 & 6, Table 2). Overall, the trends through time for the river zones were very similar in both years for both size classes (Figures 7 & 8), despite the randomization of coves sampled in 2010. Depth did not have a significant effect on the medium juveniles in 2011 (ANOVA: $F_{2,176}$ = 1.89, P = 0.153; Figure 9), but it did have a significant effect on the small juveniles (ANOVA: $F_{2,176}$ = 4.23 , P = 0.016; Figure 9).

Abundance estimation

Based on 2010 density estimates, there were approximately 44 million age-0 crabs in vegetated habitats in the York River; however, this was dominated by first and second instars (<5 mm cw) and only about 26 million were 5-60 mm cw (Table 4). In unvegetated habitats, abundance varied by river region. Assuming a 10% efficiency, abundance ranged from 6 million crabs down river to 14-15 million crabs in the mid and

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up river regions (Table 4). The estimate of abundance in unvegetated habitats is highly dependent on the assumed efficiency of the gear, and ranges from 7-64 million age-0 crabs (Appendix I).

DISCUSSION

Although previous studies of megalopal ingress into the York River found significantly higher transport during full moons (Orth & van Montfrans 1987), there were no significant differences in juvenile density in vegetated habitats between sampling events after full and new moons. In terms of the sampling design, we may not have sampled frequently enough to capture temporal changes in density or our sample size may have been too small. However, there may be behavioral causes for the lack of trends as well. Patterns in megalopal abundance may be decoupled from juvenile abundance by density dependent processes, such as mortality or emigration. Further, although the moon phase may factor into larval megalopal ingress, it may not be affecting juvenile movement patterns.

Previous work suggested that shallow water (< 0.7 m) provides a predator refuge for 30-70 mm cw juveniles (Hines & Ruiz 1993); however, depth was not a significant predictor for abundance of 25-60 mm cw juveniles in unvegetated habitats in this study. Although there was a significant difference for 5-25 mm cw juveniles, the depth range in this study (0.5-2 m) may not have been sufficient to see an effect for the larger juveniles.

The similar spatial and temporal trends in crab density over a large spatial scale were consistent with previous findings that were limited to vegetated habitats in the down-river zone of the York River (Olmi et al. 1990). Despite the typically episodic and

variable ingress and settlement of megalopae (e.g., Orth & van Montfrans 1987, Olmi et al. 1990, van Montfrans et al. 1990), abundance of the juvenile stages in both vegetated and unvegetated habitats was not statistically different across temporal and spatial scales.

Juvenile density estimates in unvegetated habitats throughout the recruitment season, up to 21 crabs m^{-2} (assuming 10% efficiency), were substantially higher than what has been reported previously (e.g., 0.01-0.08 crabs m^{-2}: Lipcius et al. 2005). Shallow unvegetated habitats may be more important for juvenile blue crabs when recruitment is high. The estimates of annual recruitment from the bay-wide winter dredge survey (see Miller et al. 2011 for details) for 2010-2012 were about 4 times higher than the estimates for 1999-2002, when Lipcius et al. (2005) sampled. Assuming a set carrying capacity for vegetated habitats, we could expect more than 4 times as many juveniles in unvegetated habitats in 2010-2011 as compared to 1999-2002. However, other factors could also be contributing to this difference as well. Sampling locations in the current study were limited to inside shallow coves, while the previous study primarily sampled in shallow water of the York mainstem (Lipcius et al. 2005). There have also been considerable changes in the distribution and amount of vegetated habitat at the mouth of the York River since 1999, including extensive seagrass die-offs in 2005 and 2010 (Orth et al. 2006, 2011). This may have resulted in less vegetated habitat available for juveniles and thus higher densities in unvegetated habitats.

The gear that we used in unvegetated habitats was not designed to sample crabs <6 mm cw; however, these juveniles were typically not found in unvegetated habitats (Orth & van Montfrans 1987, Pile et al. 1996). Despite the larger mesh size used in unvegetated habitats, juveniles <6 mm cw were retained by the net, though the density

can not be determined. Further, the reduction in the quantity of vegetated habitats may result in more of these very small juveniles in unvegetated habitats than previously reported. As the survival of very small juveniles is likely to be low in unvegetated habitats (Johnston & Lipcius 2012), estimating the abundance may be irrelevant. However, to our knowledge, no mortality studies using juveniles less than 25 mm cw have been undertaken in the up-river zone, where predation intensity on the 25-55 mm cw crabs is lower (e.g., Lipcius et al. 2005).

Abundance estimation

Spatial patterns in abundance were not consistent with previous work in the mainstem of the York River, where the abundance was highest in the up river, followed by the down river and mid river regions (Lipcius et al. 2005). In the shallow creeks and coves, however, we found high abundances in both the mid and up river regions, and the lowest abundance in the down river section. This could partially be explained by variability in the estimates of habitat area. It was estimated that the area of upriver shallow habitat was slightly higher than the area of midriver shallow habitat (Lipcius et al. 2005), but the area of shallow creeks and coves was higher in the midriver than upriver regions. However, it may also be evidence for variation in habitat preferences as a function of both river region and location. The shallow creeks and coves are more protected than the mainstem, potentially providing additional refuge for the juveniles. Additionally, *Macoma balthica* density was similar in mud habitats (primarily found in creeks and coves) throughout the York River, but significantly different in muddy-sand (primarily found in shallow mainstem) between the up river region and mid and down

river regions (Seitz et al. 2003). This suggests that prey availability in the mainstem compared to the creeks and coves may be driving the differences in abundance determined in the two studies.

By excluding shallow mainstem habitats in this study, we may have underestimated the importance of shallow water habitats for age-0 blue crabs. There is approximately 80 million m^2 of shallow unvegetated habitat in the York River (Lipcius et al. 2005), but shallow creeks and coves only make up about a quarter of that. However, based on the density estimates from Lipcius et al. (2005) of 0.01-0.08 crabs m^{-2}, the shallow mainstem only accounts for 1-10% of the total abundance in the York River.

It is essential to keep in mind the importance of gear efficiency in shallow unvegetated habitats, as this substantially influences the estimate of abundance. Although previous work suggested that the gear is 5.5% efficient, the shorter tow distance likely results in a higher efficiency. Further, a similar gear, modified with a toothbar and deployed in the winter, was 24-34% efficient (Ralph & Lipcius, unpublished). This likely represents a maximum efficiency for the gear utilized in this study, as crabs are less active during the winter and the toothbar forces the gear deeper into the sediment. Additional efficiency experiments need to be conducted to improve estimates of total abundance in unvegetated habitats.

Paradigm of juvenile blue crab recruitment

The current paradigm for blue crab recruitment suggests that vegetated habitats are obligatory primary settlement sites, and that secondary dispersal of the crabs <20 mm cw typically occurs to other structured habitats. Juveniles typical emigrate from vegetated

habitats once a size-refuge from predation has been reached around 25 mm cw (Figure 12a, Lipcius et al. 2005). Given our findings and the results from the many previous studies of blue crab recruitment, we believe that the current paradigm for blue crab recruitment to shallow water habitats may require revision to account for the behavioral plasticity juvenile blue crabs exhibit in their secondary dispersal habitats.

In particular, this study provides evidence that shallow, unvegetated habitats are important recruitment sites for small juvenile blue crabs. The first alternative paradigm suggests that juveniles may be leaving vegetated habitat at a smaller size than would be predicted by the intersection of predation risk in vegetated and unvegetated habitats (i.e., 25-30 mm cw: Johnston & Lipcius 2012). Tethering was completed during the summer (Johnston & Lipcius 2012), and thus may not reflect the predation intensity during the majority of the recruitment season. Inter-cohort cannibalism can cause significant mortality in juvenile blue crabs (Moksnes et al. 1997), potentially resulting in higher mortality rates in the fall when juvenile crab density is higher. This could also be evidence for density-dependent emigration of the first stages of juveniles, as was found in North Carolina (Blackmon and Eggleston 2001, Etherington & Eggleston 2000, Reyns & Eggleston 2004). A second alternative paradigm posits that a substantial proportion of megalopae are not settling in vegetated habitats at all. A coupled biological and physical model of the York River suggested that simulated blue crab megalopae, released at the mouth, could reach the upriver zone within four days (Stockhausen & Lipcius 2002).

The alternate paradigms put forward here allow for the possibility of small juveniles to settle within unvegetated habitats, either at a smaller size than previously described or without settling in vegetated habitats at all (Figure 12b and c). Previous

studies may not have found these patterns due to lower overall recruitment, low spatial or

temporal resolution, and changes in the extent of vegetated habitat. Hence, under

different recruitment regimes and during different times in the recruitment season, crab

behavior may be governed by any of the three suggested paradigms.

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Table 1: Dates for sampling events in vegetated and unvegetated habitats in 2010 and 2011.

Year	Date of new/full moon	Sample dates	$N_{vegetated}$	$N_{unvegetated}$
2010	08/24 (full)	08/25-08/27	27	35
	09/08 (new)	09/09-09/13	26	35
	09/23 (full)	09/24-10/05	18	36
	10/07 (new)	10/08-10/11	23	36
	10/23 (full)	10/25-10/26	15	36
	11/06 (new)	11/08-11/10	18	36
2011	07/30 (new)	08/01-08/02	na	35
	08/13 (full)	08/15-08/16	na	36
	09/12 (full)	09/13-09/14	na	36
	09/27 (new)	09/28-09/29	na	36
	10/26 (new)	10/26-10/27	na	35

Table 2: Results from one-way fixed-factor ANOVA for number of crabs per tow in unvegetated habitat as a function of sampling event. The number of crabs per tow was natural log transformed, and analyses were run for each year and size class (small: 5-25 mm cw; medium: 25-60 mm cw) separately. P-values in bold denote significant differences at $\alpha = 0.05$.

Year	Size Class	df	F	p-value
2010	Small	5, 208	1.38	0.233
2010	Medium	5, 208	1.99	0.081
2011	Small	4, 174	2.79	**0.028**
2011	Medium	4, 174	3.21	**0.014**

Table 3: Estimated area of shallow water habitats within the York River.

Habitat	Area (million m^2)
DR vegetated	3.54
DR unvegetated	4.44
MR unvegetated	6.87
UR unvegetated	5.95

Table 4: Estimated abundance of juvenile blue crabs in shallow water habitats of the York River in 2010. Habitat specific density was corrected for gear efficiency (80% for vegetated habitats and 10% for unvegetated habitats), and multiplied by the habitat area from Table 3 to estimate abundance. Juvenile abundances based on a range of efficiency estimates are presented in Appendix I.

a) crabs 0-60 mm carapace width

Habitat	Density (crabs m^2)	Abundance (millions)
DR vegetated	12.56	44.49
DR unvegetated	1.44	6.39
MR unvegetated	2.03	13.95
UR unvegetated	2.49	14.82

b) crabs 5-60 mm carapace width

Habitat	Density (crabs m^2)	Abundance (millions)
DR vegetated	7.45	26.41
DR unvegetated	1.44	6.39
MR unvegetated	2.03	13.95
UR unvegetated	2.48	14.76
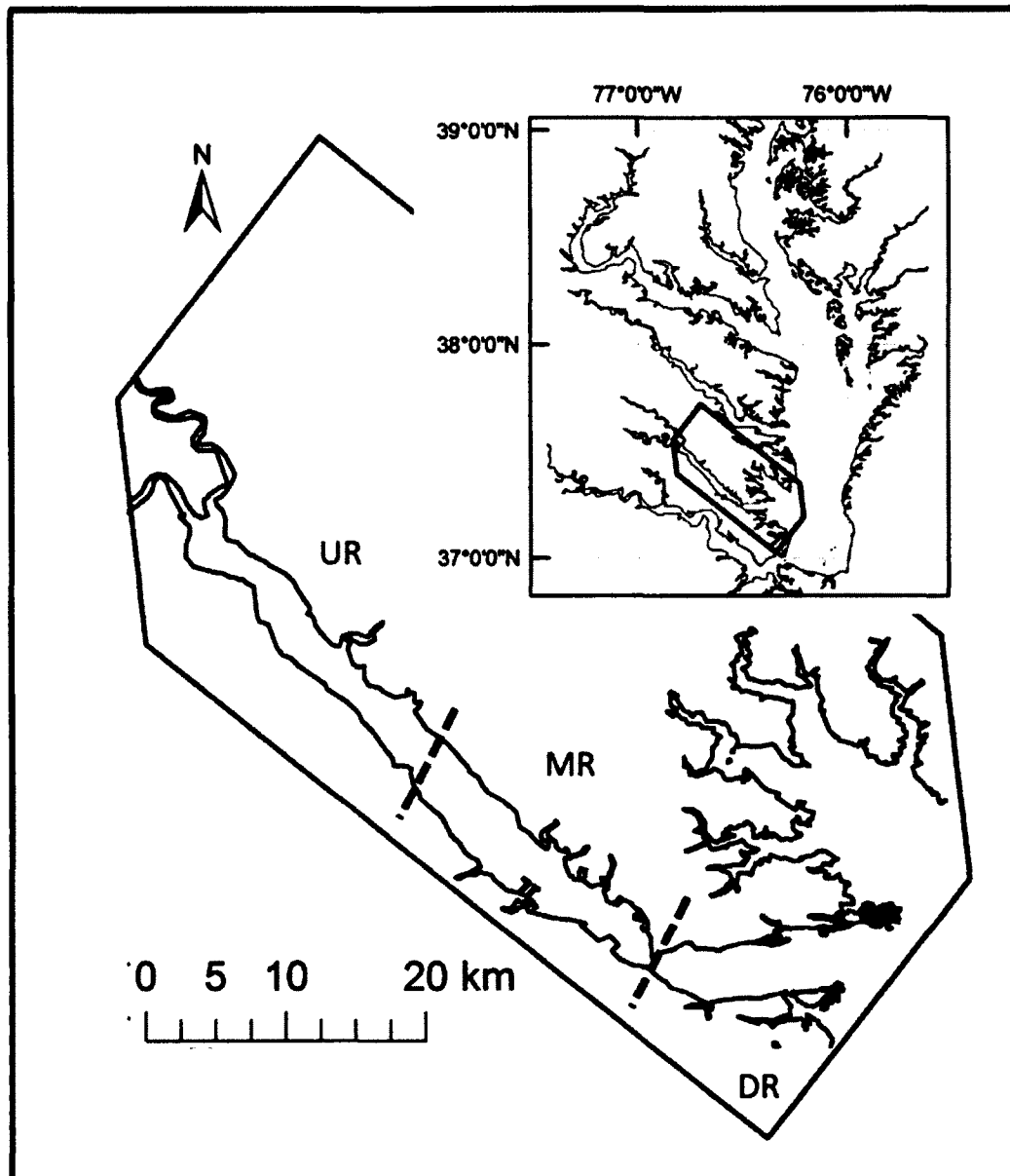
Figure 1: Map of vegetated and unvegetated habitats in the York River. Light gray shading at the mouth of the river depicts the extent of vegetated habitats in 2009 (modified from Orth et al., 2010). The dashed lines represent the borders of the down-river (DR), mid-river (MR), and up-river (UR) zones.
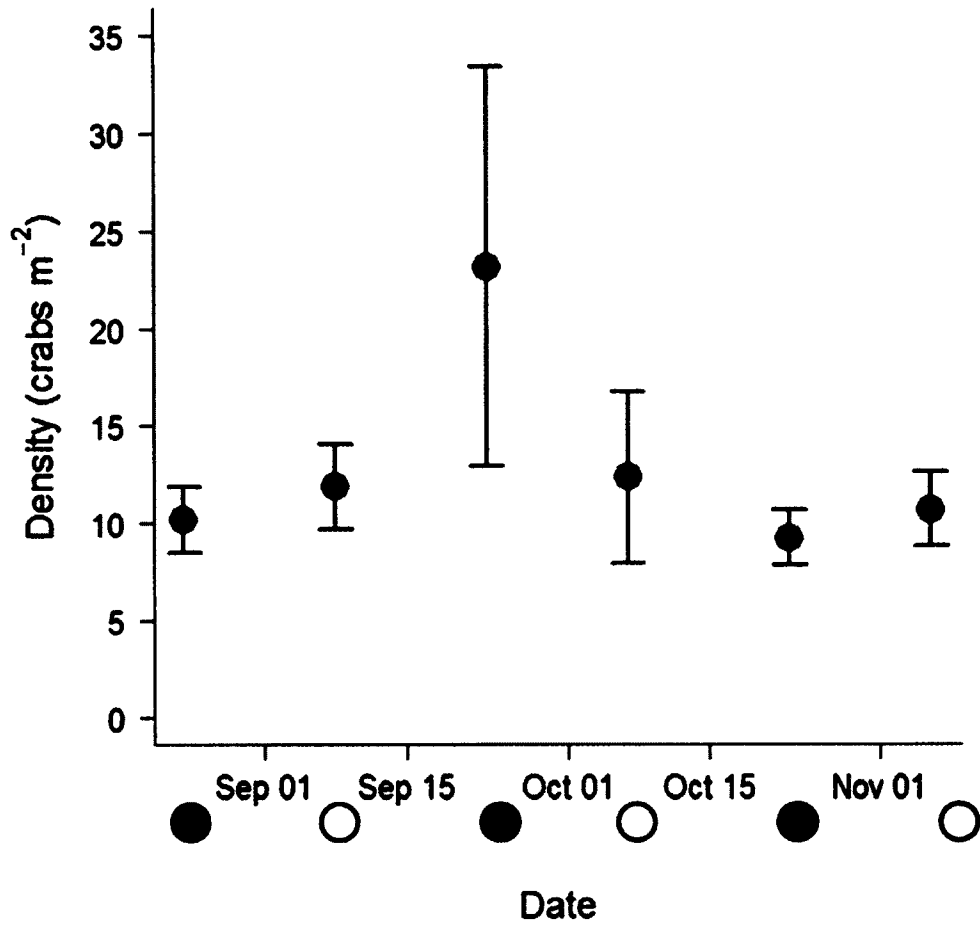
Figure 2: Density of juvenile crabs less than 25 mm cw in vegetated habitats of the York River in fall 2010 following new moons (open circles) and full moons (filled circles) during the recruitment season. Error bars are ±1 SE from the mean.
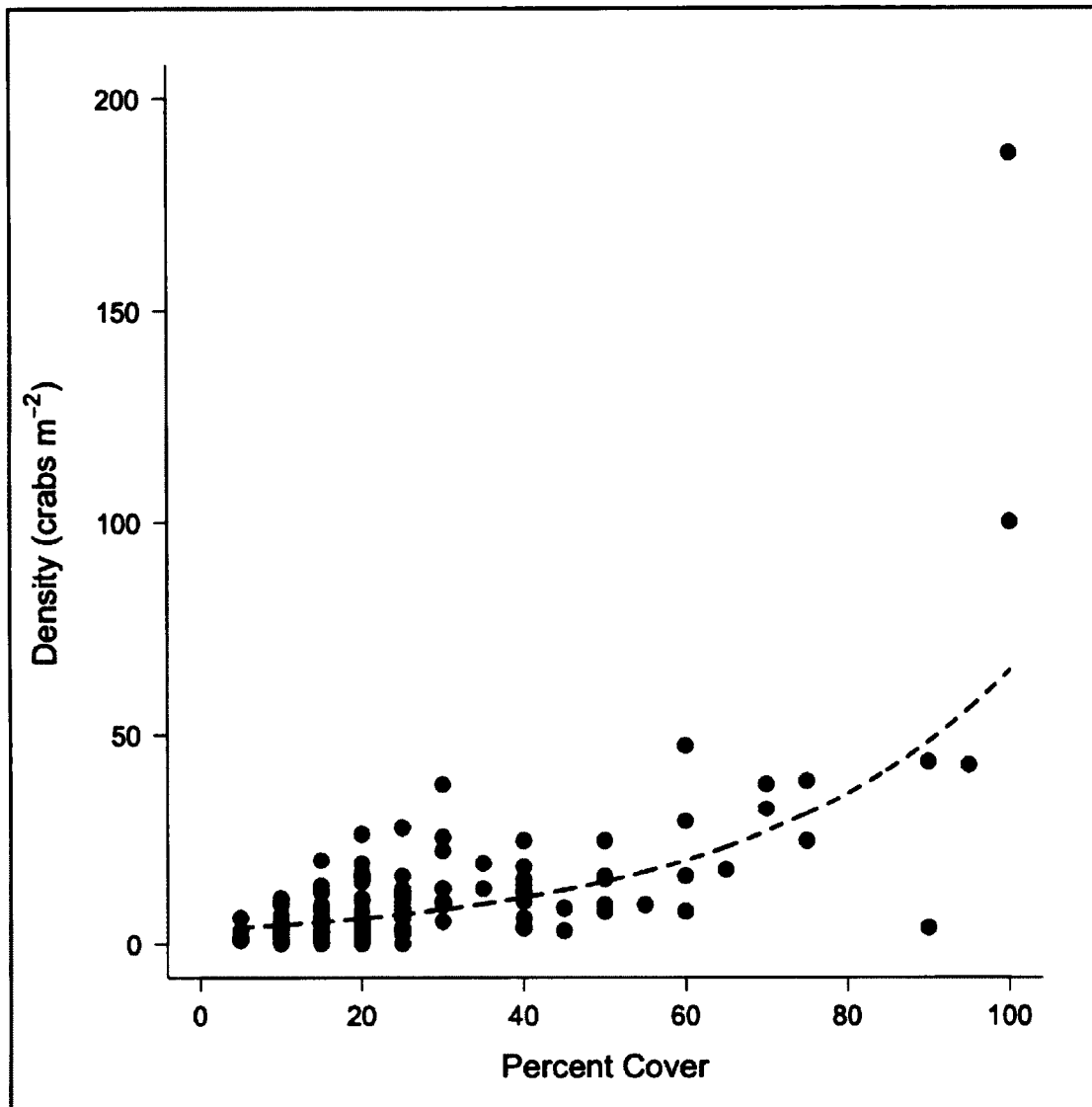
Figure 3: Relationship between density of juvenile crabs (≤ 25 mm cw) and percent cover of vegetated habitat. The dashed line represents the model predictions based on the natural log transformation of density.
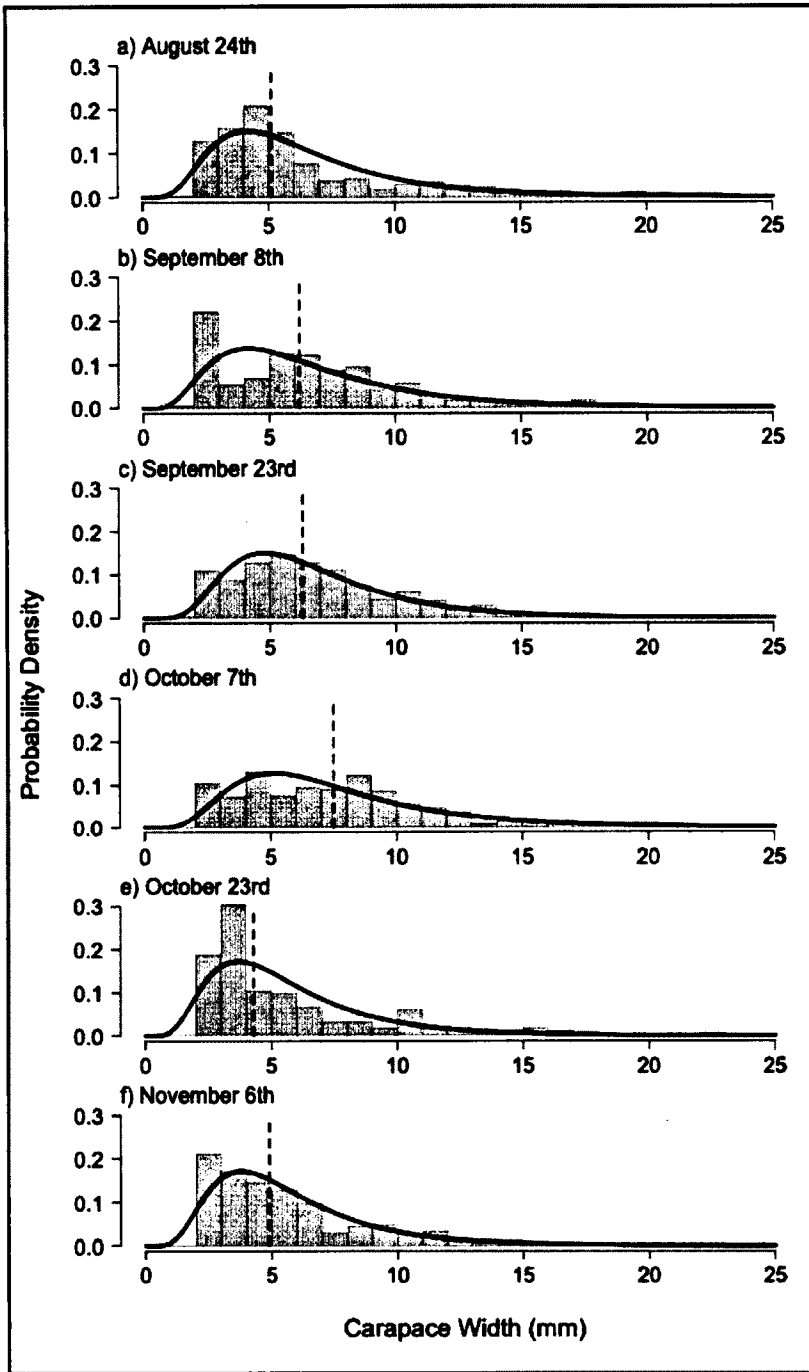
Figure 4: Size frequency distribution of small juvenile blue crabs (≤ 25 mm cw) in vegetated habitats following new and full moons during the recruitment season in 2010. The solid line depicts the theoretical lognormal size frequency distribution based on the mean and variance of the size from each sampling event. The dashed line is the median size for each sampling event.
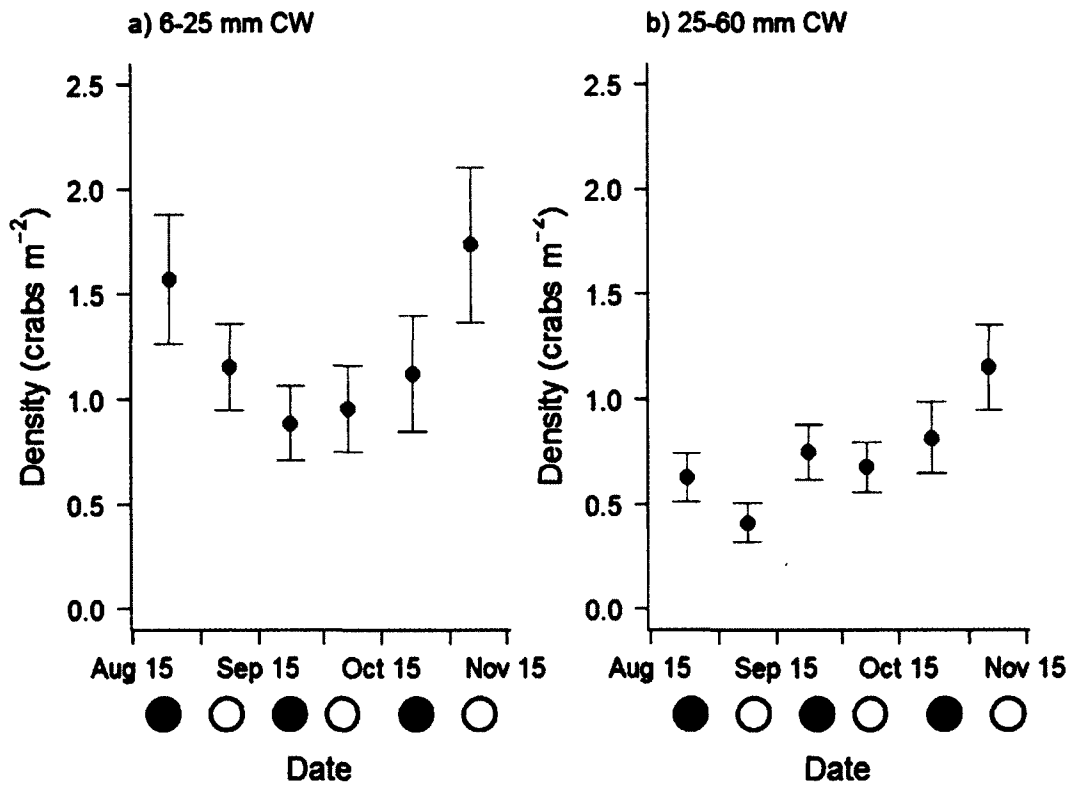
Figure 5: Juvenile crab density (assuming 10% efficiency) in unvegetated habitats of the York River following new moons (open circles) and full moons (filled circles) during the recruitment season in the fall of 2010. Error bars are ±1 SE from the mean.
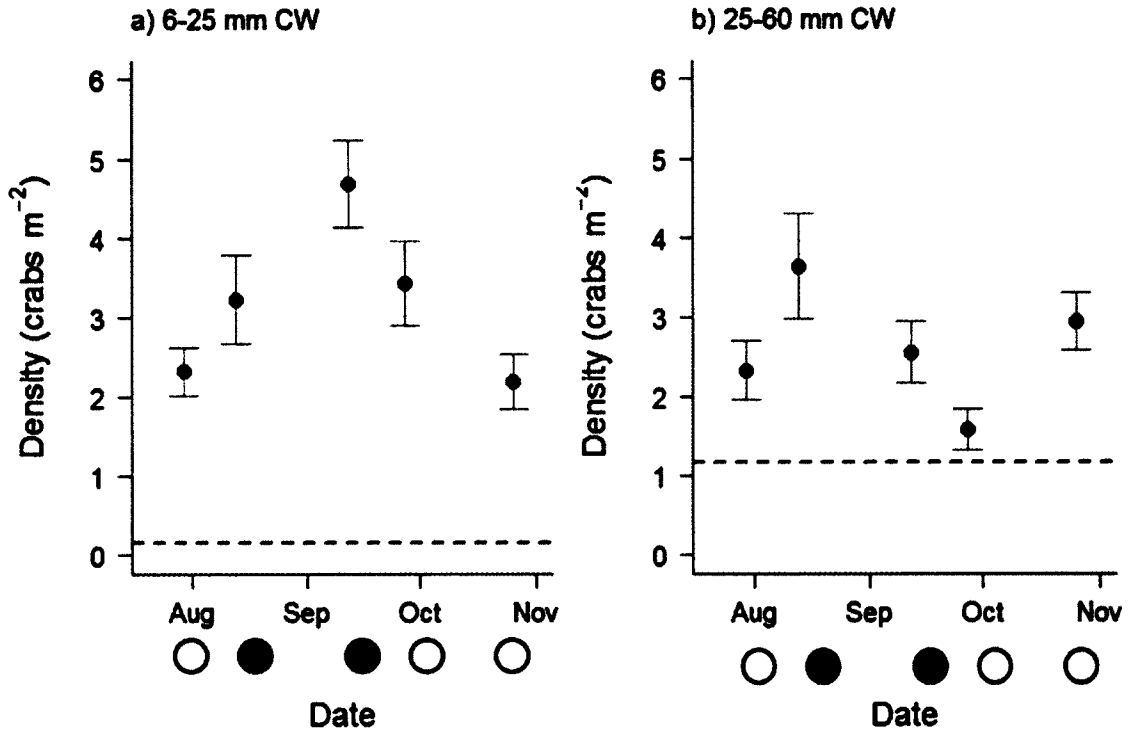
Figure 6: Juvenile crab density (assuming 10% efficiency) in unvegetated habitats of the York River following new moons (open circles) and full moons (filled circles) during the recruitment season in the fall of 2011. The dashed line represents the pre-recruitment juvenile density, determined from sampling in June 2011. Error bars are ±1 SE from the mean.
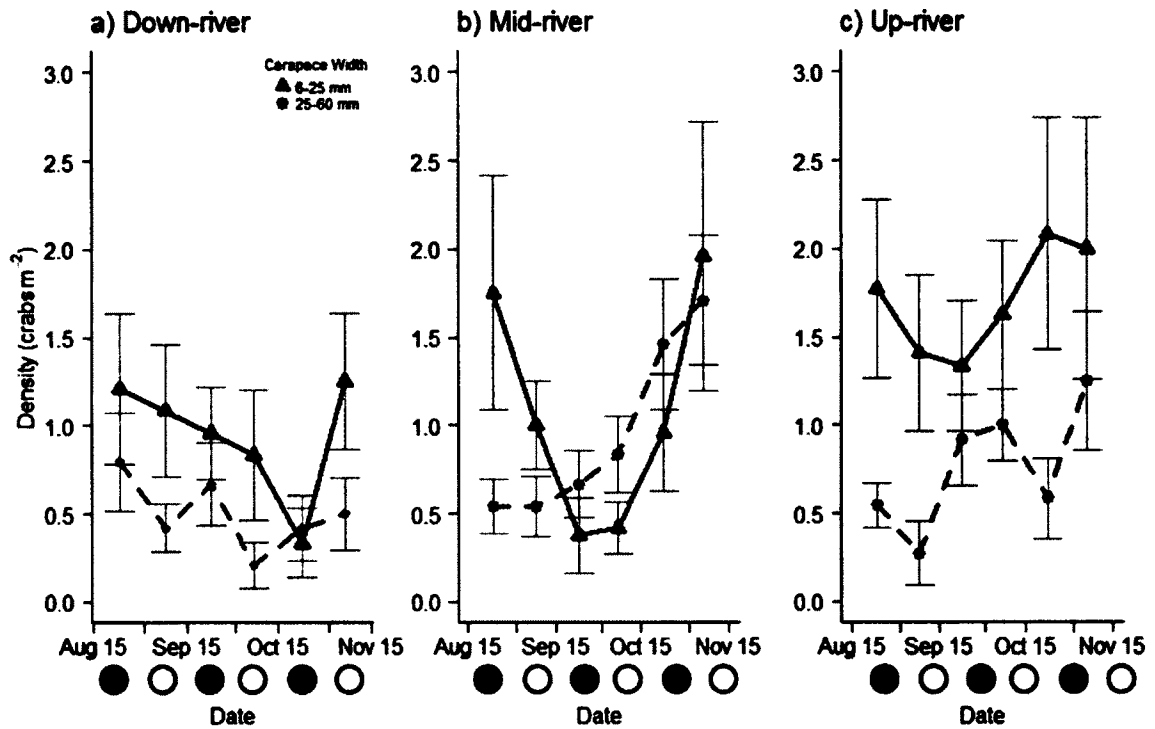
Figure 7: Density of juvenile crabs (assuming 10% efficiency) in unvegetated habitats of the York following new moons (open circles) and full moons (filled circles) during the recruitment season in the fall of 2010 by river segment. Error bars are ±1 SE from the mean.
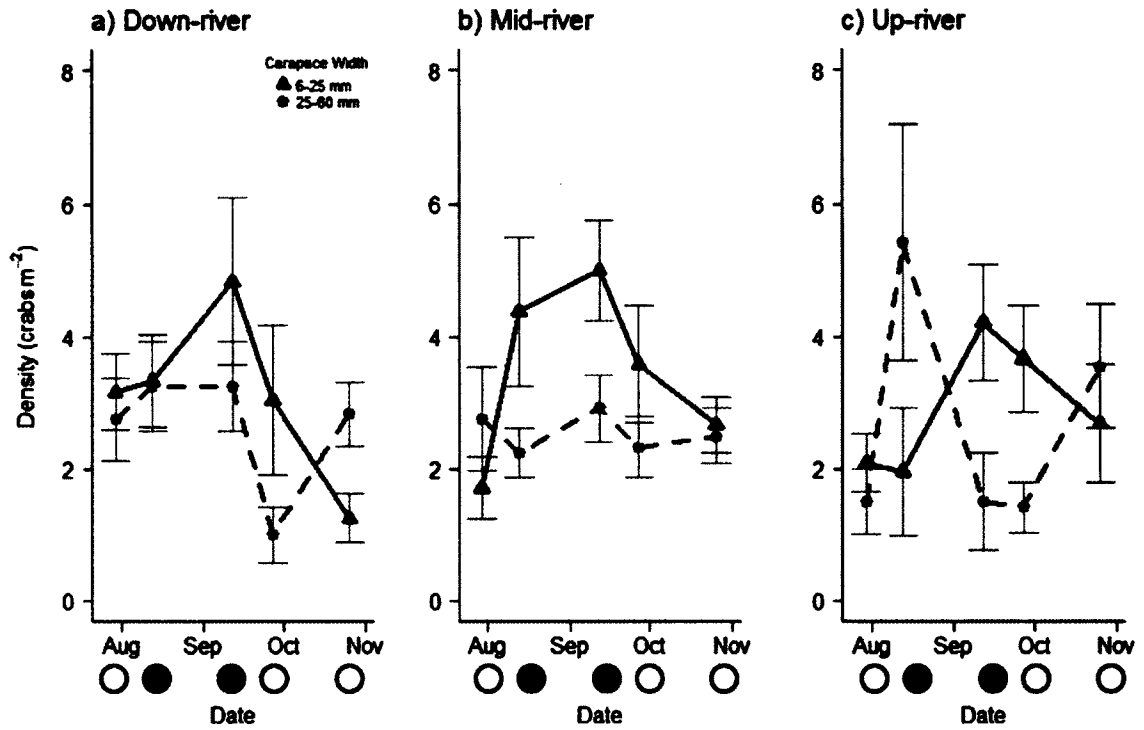
Figure 8: Density of juvenile crabs (assuming 10% efficiency) in unvegetated habitats of the York following new moons (open circles) and full moons (filled circles) during the recruitment season in the fall of 2011 by river segment. Error bars are ±1 SE from the mean.
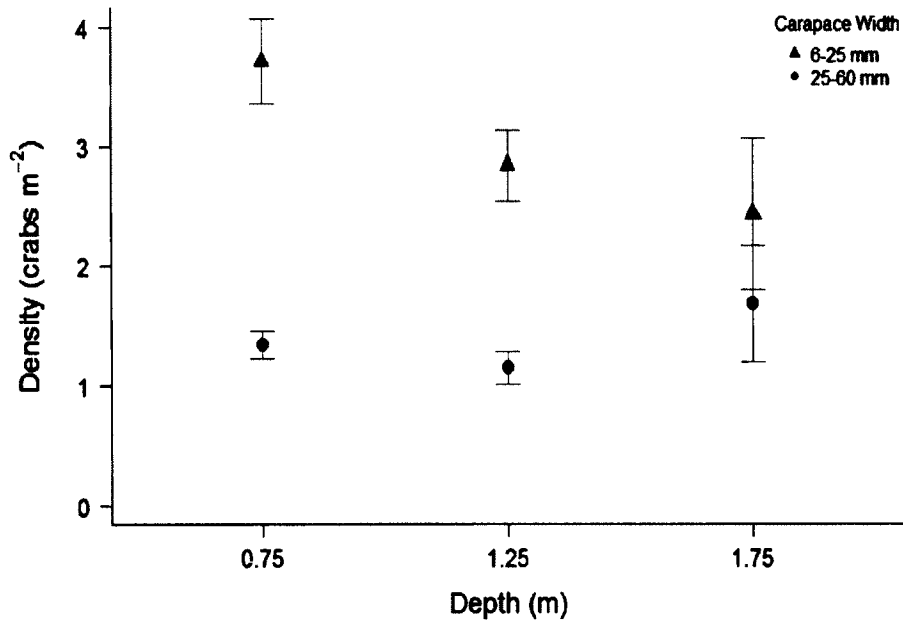
Figure 9: Density of juvenile crabs (uncorrected for efficiency) in unvegetated habitats of the York during the recruitment season in the fall of 2011 by depth. Samples were combined into 0.5 m increments (i.e., 0.5-1.0 m, 1.0-1.5 m, and 1.5-2.0 m), and averaged across all sampling events. Error bars are ±1 SE from the mean.
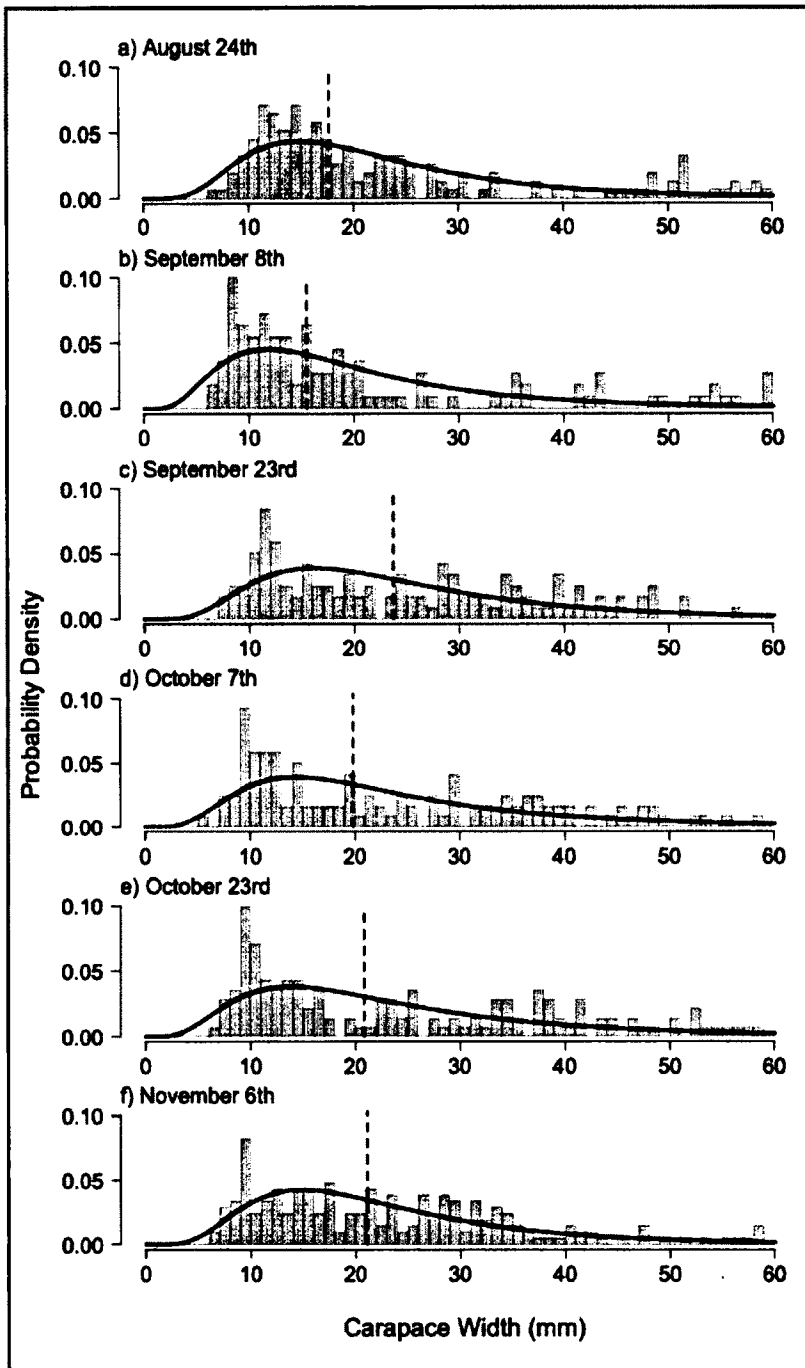
Figure 10: Size frequency distribution of small juvenile blue crabs ($\leq$ 60 mm cw) in unvegetated habitats following new and full moons during the recruitment season in the fall of 2010. The solid line depicts the theoretical lognormal size frequency distribution based on the mean and variance of the size from each sampling event. The dashed line is the median size for each sampling event.
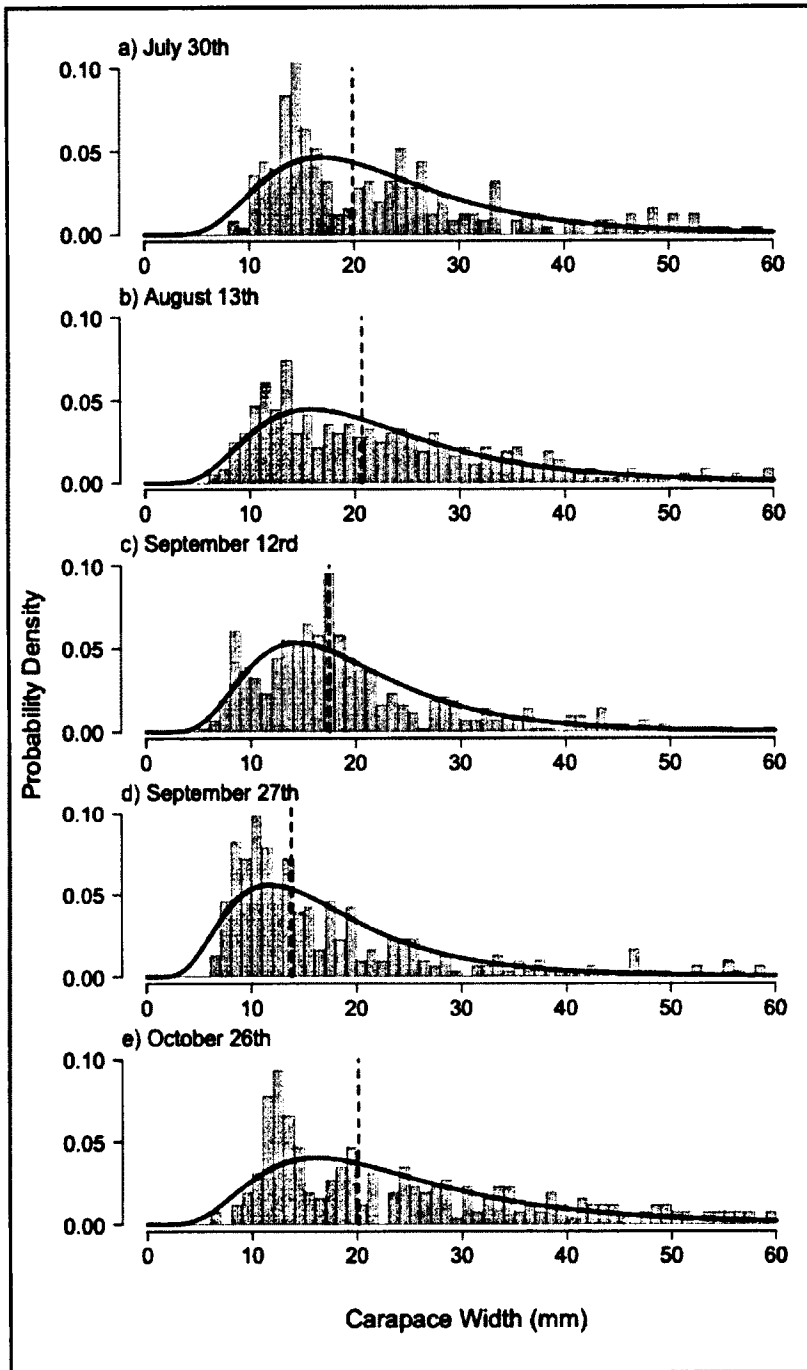
Figure 11: Size frequency distribution of small juvenile blue crabs (≤ 60 mm cw) in unvegetated habitats following new and full moons during the recruitment season in the fall of 2011. The solid line depicts the theoretical lognormal size frequency distribution based on the mean and variance of the size from each sampling event. The dashed line is the median size for each sampling event.

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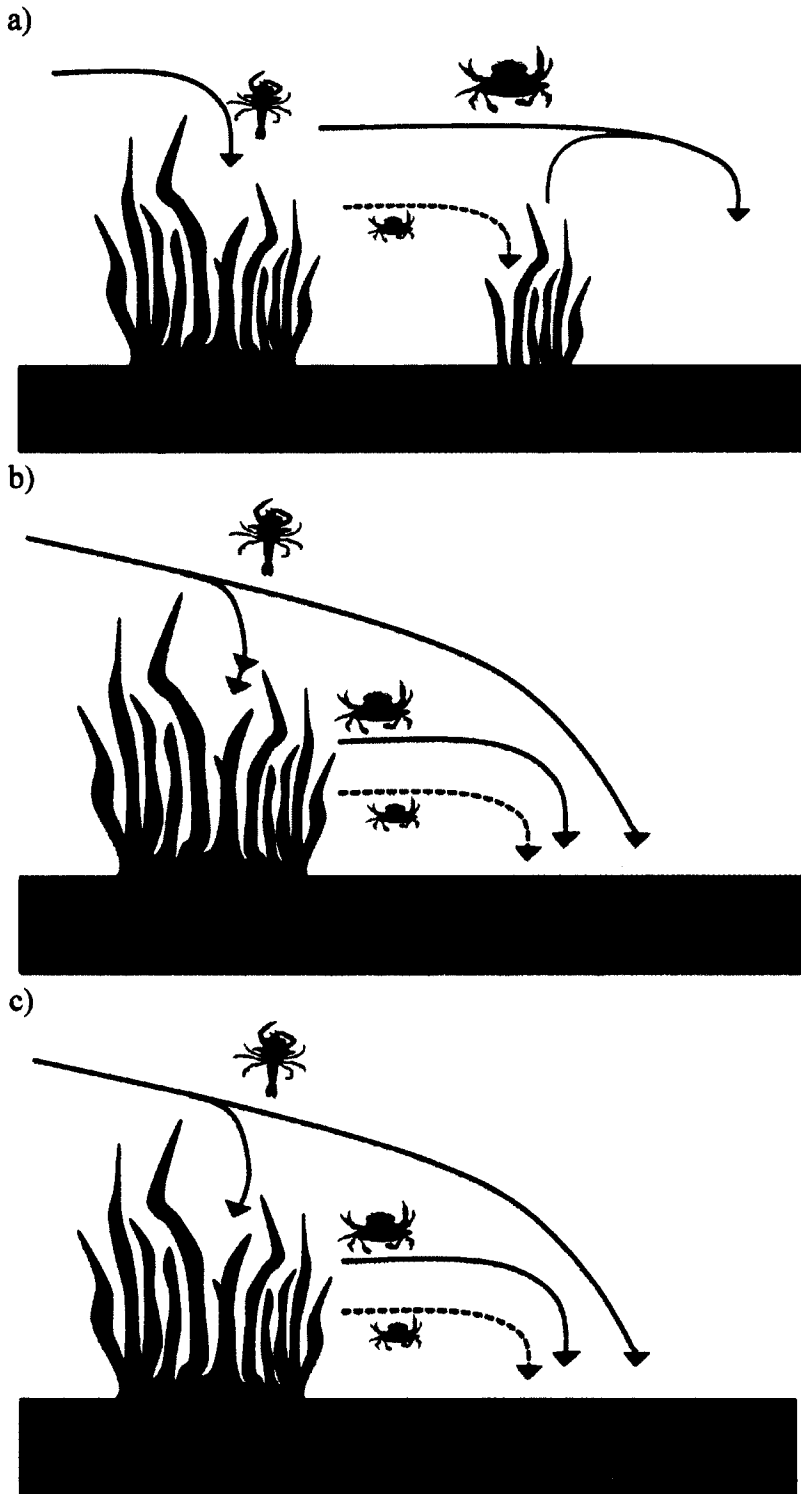
Figure 12: Conceptual diagrams depicting the current (a) and plausible alternative (b and c) paradigms for blue crab recruitment to vegetated and unvegetated habitats. The dashed line represents secondary dispersal from vegetated habitats by the first and second instars.

CHAPTER 4

Critical habitats and stock assessment: age-specific bias in the Chesapeake Bay blue crab
population survey

ABSTRACT

Population surveys used in stock assessment often ignore habitats that are difficult to sample under the assumption that these habitats harbor an inconsequential fraction of the population. We tested this assumption for the blue crab population in Chesapeake Bay, which numbers in the 100s of millions, supports one of the world's most productive crustacean fisheries, and is managed based on a rigorous stock assessment. The stock assessments rely on a bay-wide winter dredge survey (WDS), which produces an absolute estimate of abundance for age-1+ crabs. Although the WDS does not sample waters shallower than 1.5 m deep, where some number of juvenile age-0 crabs overwinter, it has been assumed that abundance of age-0 crabs in these shallow habitats is not substantial. We sampled shallow-water vegetated and unvegetated habitats not sampled by the WDS at four locations in lower Chesapeake Bay in February-April 2011. Age-0 density was about two orders of magnitude higher in shallow vegetated habitats than in deeper habitats sampled by the WDS; density in shallow unvegetated habitats was about 40 times higher than deep unvegetated habitats. Even after excluding juvenile crabs that would not be retained by WDS gear, juvenile density was still 50 and 32 times higher in shallow vegetated and unvegetated habitats, respectively, than in deep unvegetated habitats. Extrapolating these densities bay-wide, we estimated approximately 850 million to 1,500 million age-0 crabs in Chesapeake Bay, in contrast to the 2011 WDS estimate of about 205 million age-0 crabs. Thus, the WDS substantially underestimates age-0 crabs. If this bias in age-0 abundance is inconsistent inter-annually, then stock assessments may be producing biased reference points. Our findings provide an empirical example whereby inattention to habitat utilization patterns as a function of age or ontogeny may introduce significant error into stock assessments.

INTRODUCTION

Appropriate fishery management decisions can only occur when stock assessments, and the fishery-independent surveys on which they rely, are an adequate representation of the stock (Walters and Martell 2004). When fishery-independent surveys are logistically constrained (e.g., to certain depths or habitats), and the target species exhibits shifts in spatial distribution as a function of age or ontogeny, the survey may not accurately estimate the total population. For instance, the fishery-independent survey of the American lobster (*Homarus americanus*) in the Gulf of Maine was constrained to waters deeper than 50 m, and thus did not sample highly productive shallow waters where smaller lobsters were abundant (Chen et al. 2006). Stock assessment reference points based on such a restricted survey were likely too conservative, and thereby limiting fisheries yield (Walters and Martell 2004).

Coupled climate and population models suggest that large-scale, climate-induced changes in habitat-specific abundance (e.g., Atlantic cod: Fogarty et al. 2008) and distribution (e.g., Atlantic croaker: Hare et al. 2010) will continue for several decades. Further, given the likely increase in environmental variability, the timing and magnitude of shifts in spatial distribution as a function of age or ontogeny may vary annually. These patterns in abundance or distribution could introduce additional errors into stock assessments if the complementary fishery-independent surveys do not cover the entire range of the population.

In Chesapeake Bay, the blue crab stock assessment relies on the Bay-wide Winter Dredge Survey (WDS), which samples approximately 1500 sites annually. The WDS occurs during the winter, when temperatures are low and blue crabs are inactive (Sharov et al. 2003; Miller et al. 2005, 2011). The torpid state of blue crabs during winter allows the survey to sample the population effectively because immigration and emigration are minimal at this time. The WDS produces an estimate of abundance (N), which is used to determine stock status relative to the biological reference point of abundance. The estimate of N is also used along with an annual estimate of catch (C) to calculate the other key reference point, exploitation rate (u) = C/N (Miller et al. 2005, 2011).

The WDS produces an absolute estimate of abundance for age-1+ crabs (> 60 mm carapace width [cw]), but only a relative estimate of abundance for age-0 crabs ($\leq$ 60 mm cw) because the WDS does not sample shallow areas less than 1.5 m water depth (Sharov et al. 2003). Megalopal settlement into shallow, vegetated habitats of the lower Bay occurs throughout late summer and fall (van Montfrans et al. 1990, 1995), and is followed by ontogenetic shifts to unvegetated habitat (Lipcius et al. 2005, 2007). Although some age-0 crabs migrate to deeper waters to overwinter (Sharov et al. 2003, Hines 2007), there is evidence for high densities of age-0 crabs in shallow habitats at a local scale (Orth and van Montfrans 1987).

In prior stock assessments it was assumed that shallow-water habitats harbored a minor fraction of the population (Rugolo et al. 1998) or that the relative estimate of abundance for age-0 crabs was adequate because of the strong correlation between population abundance as estimated from the sum of age-0 and age-1+ crabs from the WDS and landings in any given year (Miller et al. 2005). In the most recent stock

assessment (Miller et al. 2011), however, the sex- specific population model required an absolute, not relative, estimate of age-0 abundance. To create an empirical estimate of absolute abundance, the model estimates a catchability coefficient to determine the percentage of age-0 crabs that are vulnerable to the survey. Although the model suggested that the estimates of age-0 abundance from the WDS were highly predictive of the values generated in the model, it estimated that approximately 60% of age-0 crabs are not being sampled by the WDS. If this percentage varies from year to year, it would introduce substantial error into the stock assessment model by ignoring age-specific differences in habitat utilization.

Given the empirical (Orth and van Montfrans 1987) and theoretical (Miller et al. 2011) evidence suggesting that a significant proportion of age-0 crabs resides in shallow-water habitats and is not susceptible to WDS gear, we sought to quantify utilization of shallow-water habitats by overwintering age-0 blue crabs. Ultimately, we seek to determine the potential bias in estimates of population abundance. The specific objectives of this study were to: (i) estimate the density of age-0 crabs in shallow-water vegetated and unvegetated habitats, (ii) derive variance estimates for these habitats to inform the effort necessary to sample age-0 crabs bay-wide, (iii) use the area of different strata to estimate population abundance of age-0 blue crabs in Chesapeake Bay, and (iv) compare these estimates with those derived from the WDS.

METHODS

Field survey

This survey was designed to quantify the density and variance of age-0 blue crabs in shallow habitats of lower Chesapeake Bay. Four representative locations were chosen, two each on the eastern (Onancock and Hungars creeks) and western (Dameron Marsh and Poquoson Flats) shores of the bay mainstem (Figure 1). Each location was composed of vegetated habitat (seagrass beds of eelgrass *Zostera marina* and widgeon grass *Ruppia maritima* interspersed with patches of the exotic macroalga *Gracilaria vermiculophylla*) in close proximity to shallow unvegetated habitat (coves and creeks) fringed by salt marsh consisting predominantly of *Spartina alterniflora* and *S. patens*.

Sampling sites were randomly generated using an algorithm in ArcGIS within the vegetated and unvegetated habitats at each location. Vegetated habitats were delineated from an annual aerial monitoring survey of Chesapeake Bay submerged aquatic vegetation (for details on the aerial survey, see Orth et al. 2011). At each location, 6-12 samples were taken in vegetated habitats and 47-53 samples in unvegetated habitats; sampling intensity was augmented in unvegetated habitats due to the higher variance in those habitats. Sampling occurred from February to April 2011, coincident with the WDS. Given the distances between locations, sampling could not be synoptic across all locations, but the low winter temperatures precluded temporal bias in abundance estimates.

It was necessary to utilize different sampling methods for vegetated and unvegetated habitats. In vegetated habitats we used a suction sampler and drop net to evacuate a 1.68 m^2 area to a depth of 10-15 mm. This technique was adapted from that of Orth and van Montfrans (1987) and collects blue crabs with 80% efficiency (R. N. Lipcius, unpublished), but leaves most of the vegetation intact. The percent cover of vegetated habitat was visually estimated within the net to the nearest 5% increment. Samples were pumped through a 1-mm-mesh collecting bag, then returned to the laboratory and frozen prior to processing. Each sample was sorted twice for quality assurance.

In vegetated habitats suction sampling is inefficient; assuming a density of age-0 crabs in shallow unvegetated habitats equivalent to that of the average WDS estimate (0.026 crabs/m^2, averaged over 1990-2011), 25 suction samples would have to be taken in unvegetated habitats to collect one crab. Thus, shallow unvegetated habitats were sampled with a gear designed to mimic the gear used in the WDS while also collecting smaller age-0 crabs. A commercial scrape (1-m wide), typically used to collect pre-molt crabs, was modified by adding a 10-cm toothbar and a 6-mm mesh liner. We did not use the scrape in vegetated habitats to minimize any destructive effects of our sampling. The scrape was towed for 20 m and processed immediately. Blue crabs from samples in both habitat types were counted, sexed, and the carapace width measured with Vernier calipers. All age-0 crabs (i.e., $\leq$ 60 mm cw) were included in this analysis, as this represents the size range of age-0 crabs as defined by the blue crab stock assessment (Miller et al. 2011). For ease of comparison with the WDS, age-0 density was scaled to a 1000 m^2 unit area.

Depth at each site was estimated from the depth sounder on the vessel. Suction samples were taken at depths ranging from 0.5-2.0 m; scrape samples were slightly deeper, ranging from 0.5-3.0 m deep. Mean scrape sample depth was 1.5 m in Dameron Marsh and 1.0 m at the other three sites. Although some of the scrapes were taken at depths sampled by the WDS (i.e., > 1.5 m), the locations chosen for this study, and similar shallow water creek and coves, are not sampled by the WDS as the vessels can not gain access to these nearshore locations.

Efficiency experiments

We conducted field depletion trials to estimate the efficiency of the scrape gear at three locations in the York River. At each location, PVC stakes were used to mark three corners of the sampling area, defined by a width of 3 m (three scrape widths) and a length of 20 m (one scrape tow length). The first tow was used to estimate the catch per tow, followed by additional tows until at least three tows had zero crabs. The total number of crabs collected was used to estimate the actual number of crabs in the area (60 m^2). Juvenile density estimated from the initial 20-m^2 tow was then divided by the total density of crabs collected over 60 m^2 to estimate gear efficiency.

Statistical analyses

All statistical analyses were performed using R (R Development Core Team 2011). A one-way, fixed-factor analysis of variance (ANOVA) was used to test whether mean density (age-0 crabs/unit area) varied by location in both vegetated and unvegetated

habitats. Tukey's test with a family-wise confidence level set at 0.95 was used for all post-hoc pairwise comparisons.

Comparison with the WDS

To compare the densities and abundances of juvenile blue crabs in shallow habitats with that in deep habitats, we defined four strata based on expected differences in age-0 abundance: (1) deep unvegetated, (2) upper bay shallow unvegetated, (3) lower bay shallow unvegetated, and (4) shallow vegetated.

The area of each stratum was calculated in ArcGIS. Bathymetric data were derived from hydrographic surveys collected by the National Oceanic and Atmospheric Administration - National Ocean Service (NOAA Ocean Service 1998). Soundings were interpolated using a Triangulated Irregular Network (TIN) and exported as a Digital Elevation Model (DEM) with a 3x3 arc second grid (for more details on the bathymetry data, see NOAA Ocean Service 1998). The linear extent of an arc second is 30.9 m in the N-S direction, but varies with latitude in the E-W direction. A 3x3 arc second grid is approximately 30.9 m by 24.8 m in Chesapeake Bay. The number of DEM cells within each depth and location strata was multiplied by the cell area (0.0066 km^2) to estimate the stratum area. Cells above mean lowest low water and outside of the WDS sampling domain were excluded. The estimate of vegetated habitat area was derived from the annual aerial monitoring survey of submerged aquatic vegetation (SAV) in Chesapeake Bay during May-June 2010 (Orth et al. 2011), and excluded SAV outside of the WDS sampling domain.

The density and size structure of age-0 crabs in deep unvegetated habitats were determined from the 2010-2011 WDS. The WDS utilizes a 1.83 m crab dredge with a 13-mm mesh liner to sample 1500 sites deeper than 1.5 m annually between November and March (Sharov et al. 2003). All sites from the 2010-2011 WDS were included in the estimate of the total abundance of age-0 crabs. However, megalopal settlement is generally limited to the lower bay, so only sites from the Virginia portion of the WDS were included in the comparison of density and size structure. Gear efficiency estimates from 1990-1999 were variable, ranging from 6-43% (Sharov et al. 2003); however, the jackknife mean from 88 experiments conducted during three surveys (1992-1995) was 15-16% (Vølstad et al. 2000).

The density and size structure of age-0 crabs in shallow habitats in the lower bay were determined in this study. The density of age-0 crabs in the upper bay was determined by a concurrent study (E. G. Johnson, University of North Florida, unpublished data). An identical 1-m-wide benthic scrape was used, but the tows were longer (75 m) to account for the lower densities of age-0 crabs typically found in shallow waters of the upper bay.

The non-parametric Kolmogorov-Smirnov (K-S) two-sample test (Young 1977) was used to compare size structure of age-0 crabs in the three habitats, as it is sensitive to both the mean and the variance of the distributions. Additionally, a one-way, fixed-factor ANOVA was used to test whether mean size varied by habitat. Comparisons were conducted under two scenarios: (1) including all age-0 crabs and (2) including only age-0 crabs fully recruited to the WDS sampling gear (i.e., 15-60 mm cw).

RESULTS

Vegetated habitats

The mean density (per 1000 m^2) of age-0 blue crabs in vegetated habitats ranged from over 500 to almost 7000 (Figure 2). Density was significantly different by site (ANOVA: $F_{3,38}$ = 7.06, P < 0.001); density in Hungars Creek was significantly lower than the other three sites (P < 0.001). The variability in density within location was comparable to the variability across all locations (standard deviation [SD] ~ 4000), except at Hungars Creek (SD = 887).

Crabs in vegetated habitats ranged from 4.8-36.1 mm cw, with most of the crabs less than 20 mm cw (Figure 3). Size distributions were similar in all locations, although fewer, slightly smaller individuals were collected at Hungars Creek. Cover of vegetated habitat within the sample ranged from 10-100%. Mean cover in Hungars Creek was about 70%, which was nearly twice as high as that at the other three locations, where mean cover ranged from 20-40%.

Shallow unvegetated habitats

Based on the depletion experiments, the efficiency of the benthic scrape ranged from 21-45% (mean = 34%; 95% confidence limits: 4-63%). These estimates are within the range of values for the WDS gear of 6-42% (Vølstad et al. 2000, Sharov et al. 2003) and are close to the efficiency estimate in the upper bay (24%: E. C. Johnson, unpublished data). When the mean correction factor was applied to shallow unvegetated habitats, the density of age-0 blue crabs (per 1000 m^2) ranged from almost 500 to over

95

1000 (Figure 4), with an overall mean density of 829. The minimum and maximum

efficiency estimates from the depletion trials resulted in the overall mean density ranging

from 626-1341; the 95% confidence limits were 447-7045. At Dameron Marsh and

Onancock Creek, the density at sites greater than 1.5 m deep was about half that at sites

less than 1.5 m deep.

There were no significant differences between locations for the natural log-

transformed density (ANOVA: $F_{3,194} = 1.58$, $P = 0.2$). Within-location variability was

comparable to the variation across all locations (SD ~ 1000) at Onancock Creek and

Poquoson; within-location variability was lower at Dameron Marsh and Hungars Creek

(SD = 504 and 645, respectively).

Crabs in shallow, unvegetated habitats ranged from 6.0-145.3 mm cw (Figure 5).

About 9% of the crabs collected were greater than 60 mm cw, and were excluded from

this analysis. The size distributions at the two western shore sites, Dameron Marsh and

Poquoson Flats, had peaks around 15 mm cw and similar numbers of juveniles greater

than 20 mm cw. At the eastern shore sites, the size distribution also peaked around 15

mm cw, but there were proportionally more juveniles greater than 20 mm cw than at the

western shore sites.

Comparison with WDS

Habitat type influenced size-frequency distributions. The size-frequency

distribution of age-0 crabs vulnerable to the WDS gear (i.e., 15-60 mm cw) was different

in vegetated habitats than in deep unvegetated (K-S test, D = 0.66, $P < 0.001$) and

shallow unvegetated (K-S test, D = 0.58, $P < 0.001$) habitats. The unvegetated habitats

were more similar to each other, but still differed significantly (K-S test, D = 0.11, P = 0.0016). These comparisons were more extreme for all age-0 crabs (K-S test, D = 0.25-0.76, P < 0.001). Larger age-0 crabs (> 20 mm cw) in both unvegetated habitats were rarely found in vegetated habitat. When including only age-0 crabs recruited to the WDS, the site-specific mean size varied by habitat (ANOVA: $F_{2,300}$ = 22.83, P < 0.001), with significantly smaller mean size in both shallow habitats as compared to the deep habitat (pairwise comparisons, p < 0.01).

Overall, age-0 blue crab densities in vegetated habitats were about two orders of magnitude higher than those in deep unvegetated habitats and five times higher than those in shallow unvegetated habitats (Figure 7). Age-0 crabs greater than 15 mm cw are vulnerable to all three gears, and provide an additional comparison that accounts for gear-specific selectivity. Compared to deep unvegetated habitats, age-0 density was 32 and 50 times higher in shallow unvegetated and shallow vegetated habitats, respectively.

The total area of the Chesapeake Bay was estimated to be approximately 9620 km^2, 86% of which is deep (> 1.5 m). Of the 1300 km^2 of water less than 1.5 m, approximately one-third is in the upper bay. The 870 km^2 of shallow water in the lower bay was comprised of 150 km^2 of vegetated habitat and 720 km^2 of unvegetated habitat in 2010.

In 2011, the density (per 1000 m^2) of age-0 crabs estimated by the WDS was 21.35, which equates to approximately 205.9 million age-0 crabs bay-wide. If the shallow water habitats surveyed in this study are representative and thus can be scaled up to the total area of shallow water in the bay, the estimated abundance of age-0 crabs bay-wide was almost an order of magnitude higher, about 1,500 million crabs (Table 1). Although

excluding age-0 crabs that would not be vulnerable to the WDS gear reduced the density in shallow habitats, the abundance estimate still increased three-fold to about 850 million. A substantial number of age-0 crabs 15-20 mm cw (~16%) appeared to be overwintering within the vegetated habitats, which represent only 1-2% of the total area of the bay.

DISCUSSION

Our findings provide a striking empirical example of the potentially severe bias that can be introduced into stock assessments through inadequate sampling of relatively inaccessible but critical habitats. To date, this is the first study to estimate abundance of age-0 blue crabs in shallow habitats at the temporal and spatial scale of the population in Chesapeake Bay, which is complementary to the population-wide sampling by the WDS. The results indicate that previously un-sampled shallow-water habitats, both vegetated and unvegetated, are important overwintering habitats for age-0 crabs. The WDS is likely underestimating the age-0 year class substantially, in this case by 75-90%, when not sampling shallow-water habitats and thereby introducing bias into abundance estimates of age-0 crabs. Given that the stock assessment estimated that 60% of age-0 crabs are not sampled by the WDS (Miller et al. 2011), then either the model estimate is wrong or the fraction of age-0 crabs unsampled by the WDS varies annually. If the latter holds, then bias in age-0 abundance is inconsistent from year to year, and stock assessment models may be producing inaccurate reference points of abundance and exploitation rate (Walters and Martell 2004).

The results from this study are consistent with previous studies demonstrating an ontogenetic shift in habitat use from shallow, vegetated habitats to shallow, unvegetated

habitats around 25 mm cw (Orth and van Montfrans 1987; Lipcius et al. 2007; Hines 2007; Johnston and Lipcius 2012). Within the Rhode River, a sub-estuary of Chesapeake Bay, age-0 crabs were primarily in waters less than 0.7 m deep during the summer (Hines et al. 1987, 1995; Ruiz et al. 1993; Hines and Ruiz 1995), suggesting that age-0 crabs utilize shallow habitats as refuge from predation. There may be a shift towards deeper unvegetated habitats during the fall (Sharov et al. 2003; Hines 2007). However, the substantially higher density in shallow unvegetated habitats than in deep habitats indicated that large numbers of juveniles were overwintering in shallow habitats.

Overall, the density of age-0 crabs in shallow unvegetated habitats was much higher than expected. A short-term survey coincident with the WDS in 1992-1993 found no differences between shallow and deep unvegetated habitats (Rothschild et al. 1992). However, that survey was restricted by low sample size and limited spatial coverage. Our survey found 15 times more age-0 crabs compared to the maximum age-0 density estimated by the WDS (52 per 1000 m^2). Uncertainty in the scrape efficiency yielded a minimum density of 325 per 1000 m^2 for age-0 crabs 15-60 mm cw, which is more than six times higher than the maximum density estimated by the WDS and more than 15 times higher than the density estimated by the 2010-2011 WDS.

Incorporating the use of shallow water habitats by age-0 crabs is essential to understanding the dynamics of the blue crab population. Although the most recent stock assessment (Miller et al. 2011) suggested that about 60% of age-0 crabs are not vulnerable to the WDS, these analyses indicate that as much as 80-90% of the age-0 crabs was not sampled in 2010-2011. This suggests that the proportion of age-0 crabs sampled

varies annually, which would reflect interannual bias in population surveys of age-0 crabs.

The mechanism underlying interannual variation in utilization of shallow-water habitats by age-0 crabs most likely involves changes in water temperature. Temperature plays an important role in regulating the growth (Churchill 1919, Brylawski and Miller 2003, Smith 2007), movement (Hines 2007), and spatial distribution (Saluta 2012) of blue crabs. During a cold winter that sets in quickly, we might expect that age-0 crabs would stop growing early and remain in the shallows, resulting in the WDS sampling only a small proportion of the total. During a warm winter, however, we might expect that the age-0 crabs would continue to grow and migrate into deeper waters, resulting in the WDS sampling a larger proportion of the total.

While the focus of this study was the blue crab, there are important implications for surveys of other species with age- or size-specific shifts in habitat use (e.g., Nassau grouper *Epinephelus striatus*: Eggleston 1995, Dahlgren and Eggleston 2000). The need for different gears to sample habitats or life-history stages presents a significant challenge to any analysis. While survey gears will likely perform differently in the same habitat, the habitat may also influence the efficiency of a single gear (e.g., scallop dredges are more efficient in soft sediment than hard sediment: Currie and Parry 1999). The gears chosen for this study targeted the sizes encountered in shallow habitats. However, a balanced approach between the differences in gear selectivity and bias should be developed. The methods developed in this study provide one possible solution for future monitoring of the blue crab population. Modifying surveys to encompass the entire population will

require thoughtful design dependent on the life history of the target species and potential

shifts in spatial distribution given drivers such as global climate change.

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Table 1: Estimates of the relative contribution of the four strata to a) all crabs < 60 mm cw and b) crabs 15-60 mm cw. Stratum area was estimated by GIS using bathymetry data from the National Ocean Service at NOAA. Age-0 density was estimated in this study (vegetated and shallow unvegetated habitats in the lower bay), in a collaborative study (shallow unvegetated habitats in the upper bay: Johnson, unpublished data), and from the WDS (deep unvegetated habitats).

a)

Stratum	Stratum area (km^2)	Age-0 density (per 1000 m^2)	Age-0 abundance (millions)	Percent of total abundance
Vegetated	150 lower Bay only	4234.0	635.1	41.5
Shallow unvegetated	720 lower bay	828.9	596.8	44.2
Shallow unvegetated	430 upper bay	204.0	87.7	4.7
Deep unvegetated	8320 bay-wide	21.4	178.0	9.6
Total	9620		1497.7	

b)

Stratum	Stratum area (km^2)	Age-0 density (per 1000 m^2)	Age-0 abundance (millions)	Percent of total abundance
Vegetated	150 lower Bay only	938.9	140.8	16.7
Shallow unvegetated	720 lower bay	603.8	434.7	51.7
Shallow unvegetated	430 upper bay	204.0	87.7	10.4
Deep unvegetated	8320 bay-wide	21.4	178.0	21.2
Total	9620		841.3	
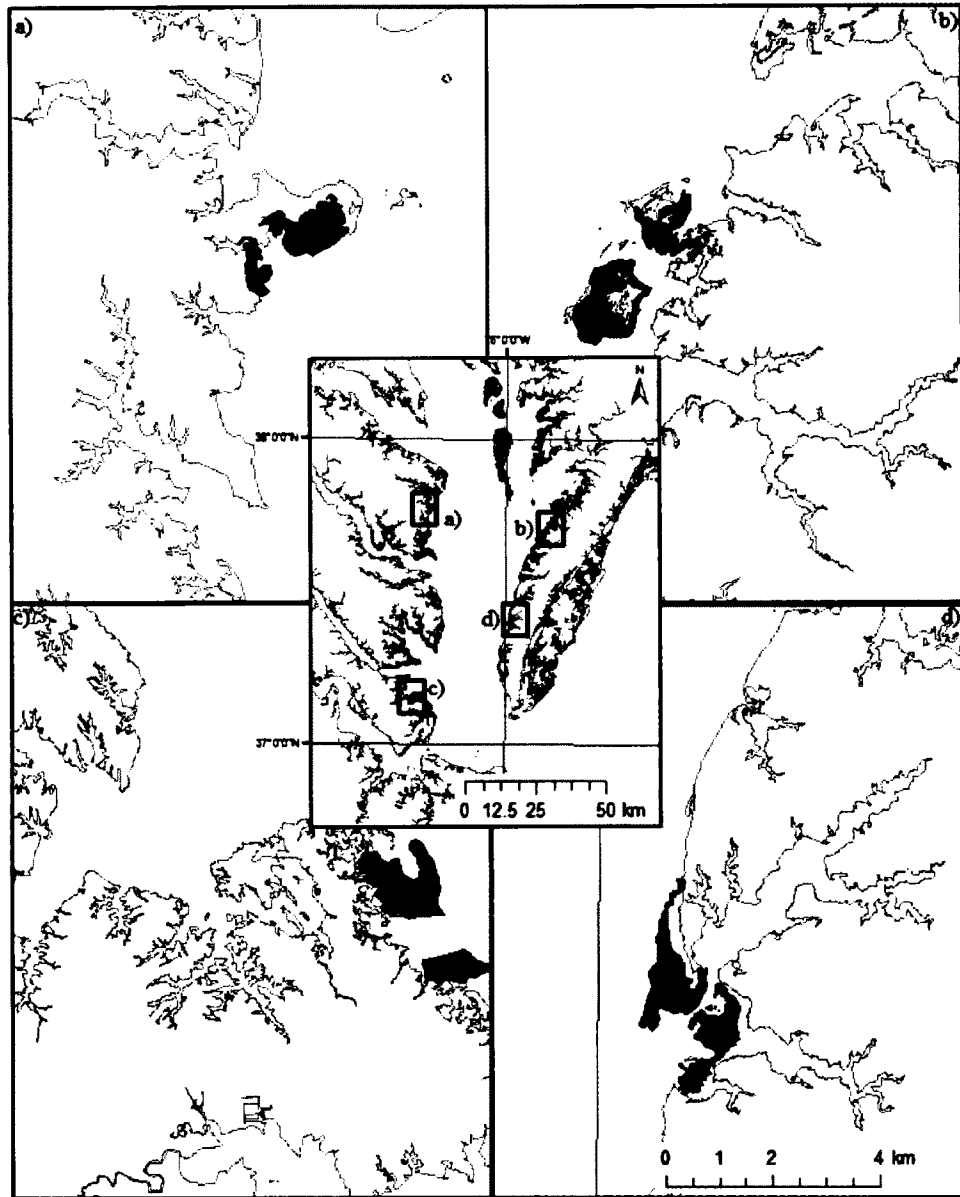
Figure 1: Sampling locations in the lower Chesapeake Bay: (a) Dameron Marsh, (b) Onancock Creek, (c) Poquoson Flats, and (d) Hungars Creek. At each location, samples were taken in shallow vegetated and unvegetated habitats. Gray shading depicts areal extent of vegetated cover (adapted from Orth et al. 2011).
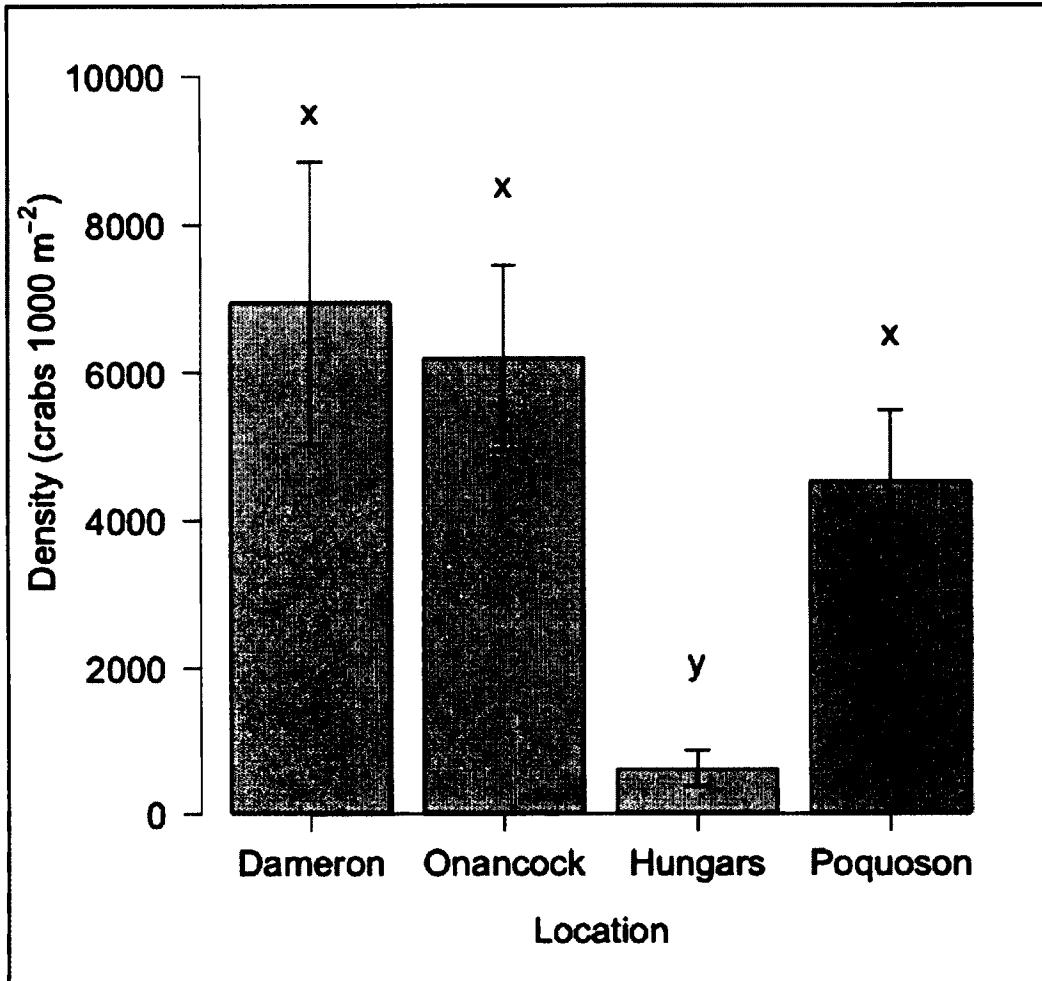
Figure 2: Density of age-0 crabs ($\leq$ 60 mm carapace width) in shallow, vegetated habitats. Error bars indicate standard error for each location. The x and y symbols denote differences in the pairwise comparisons that were significant at $\alpha = 0.05$.
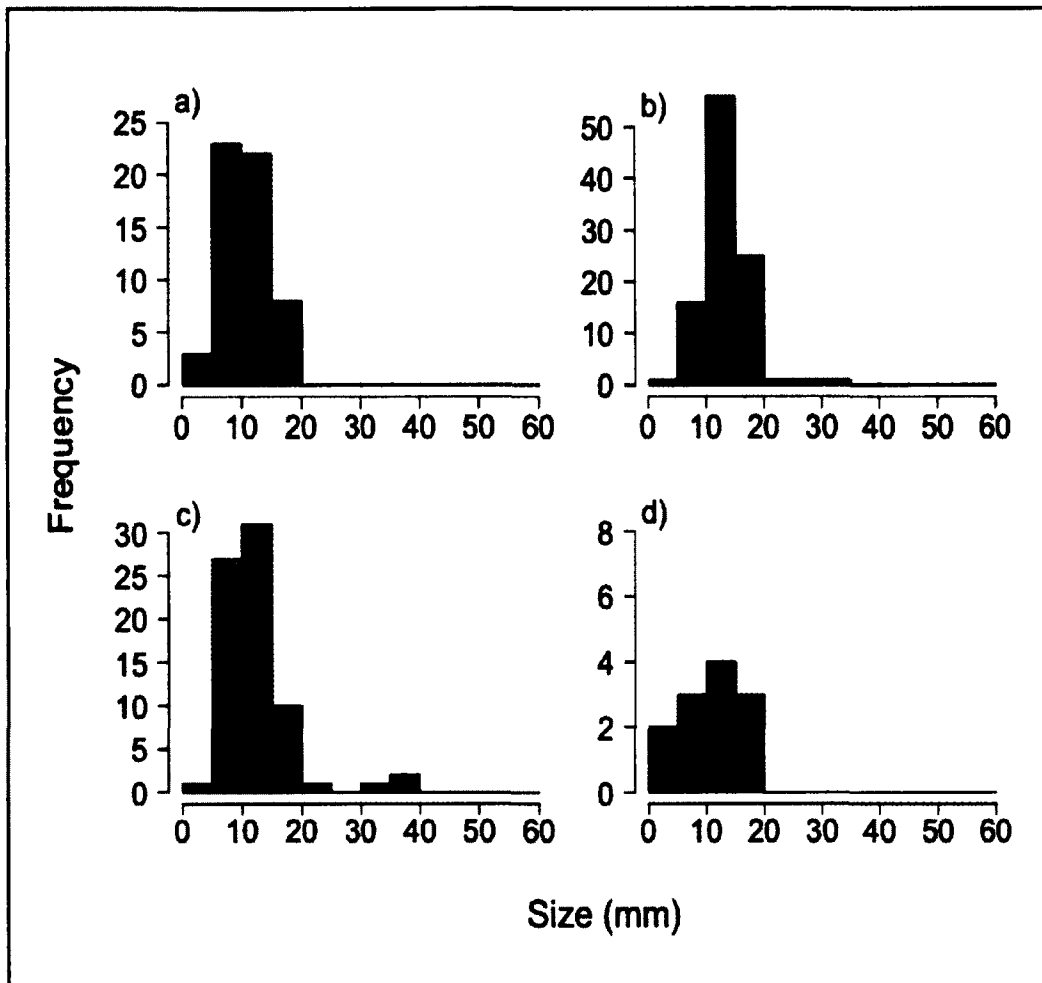
Figure 3: Size-frequency distributions for age-0 blue crabs in shallow, vegetated habitats at the four locations: (a) Dameron Marsh, (b) Onancock Creek, (c) Poquoson Flats, and (d) Hungars Creek.
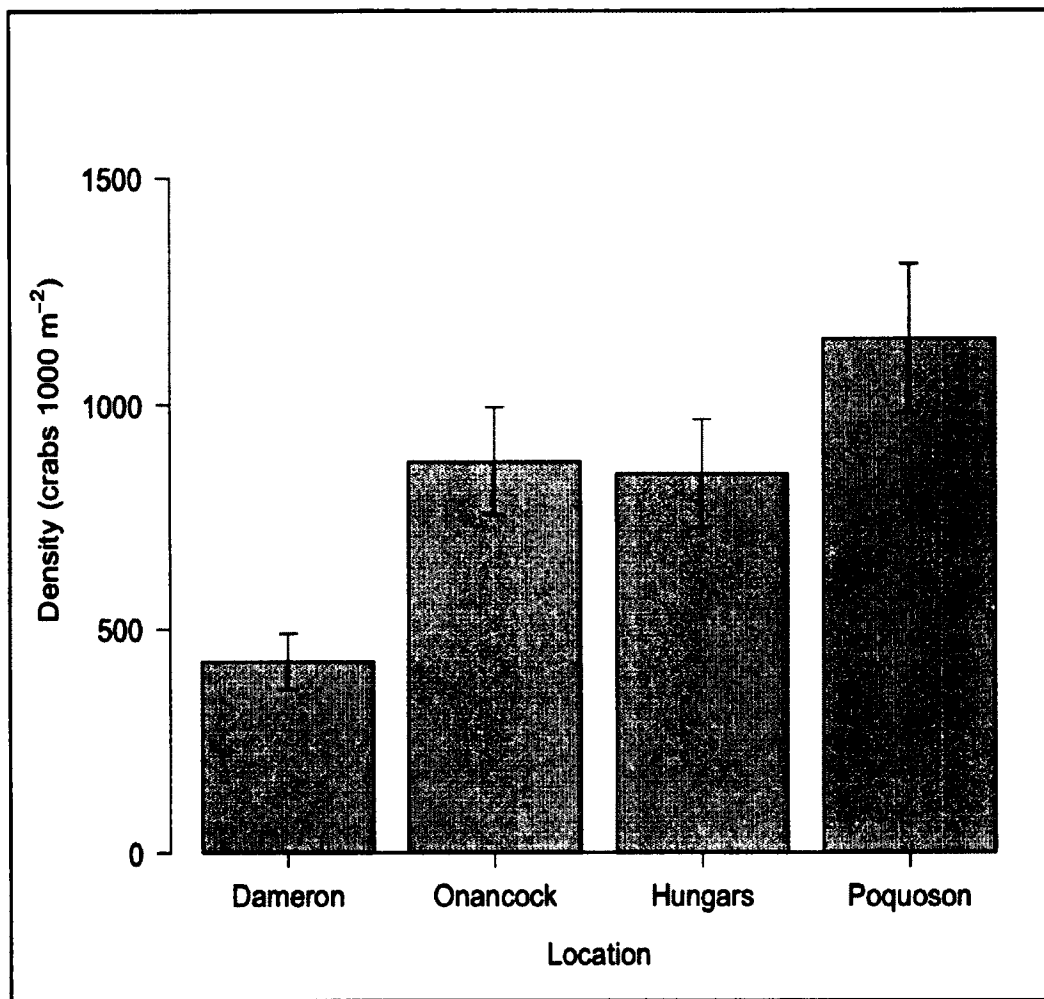
Figure 4: Density of age-0 crabs (≤ 60 mm carapace width) in shallow, unvegetated habitats. Error bars indicate standard error for each location.
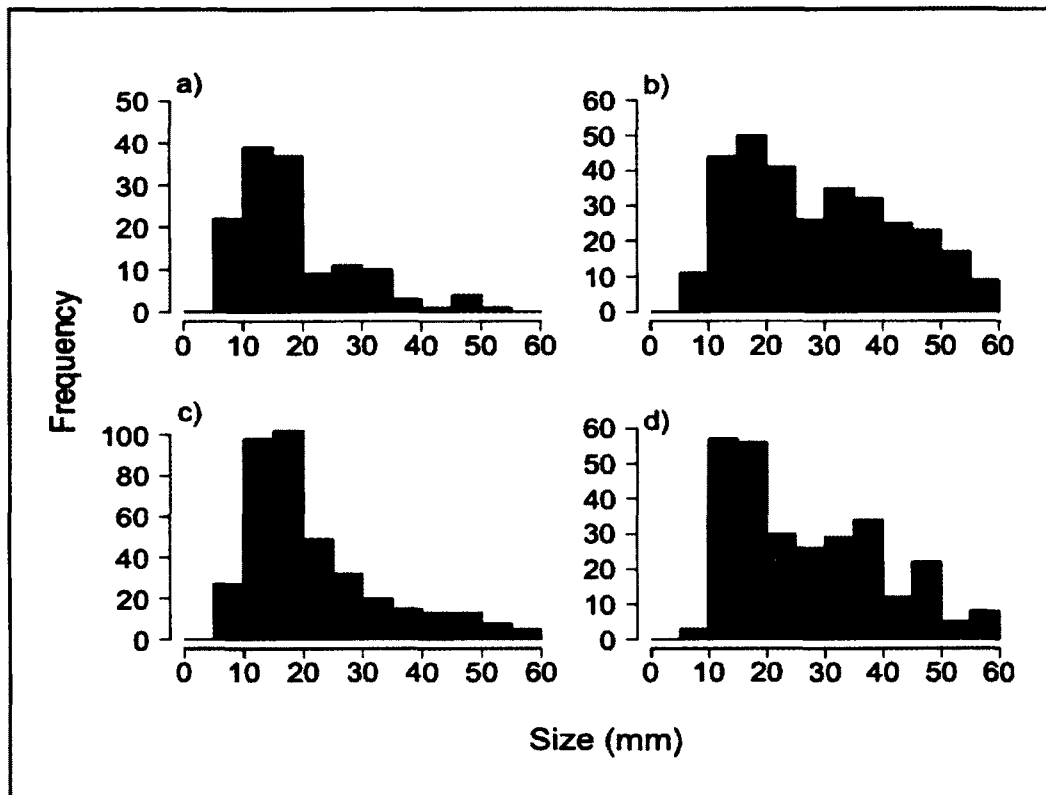
Figure 5: Size-frequency distributions for age-0 blue crabs (≤ 60 mm cw) in shallow, unvegetated habitats at the four locations: (a) Dameron Marsh, (b) Onancock Creek, (c) Poquoson Flats, and (d) Hungars Creek.
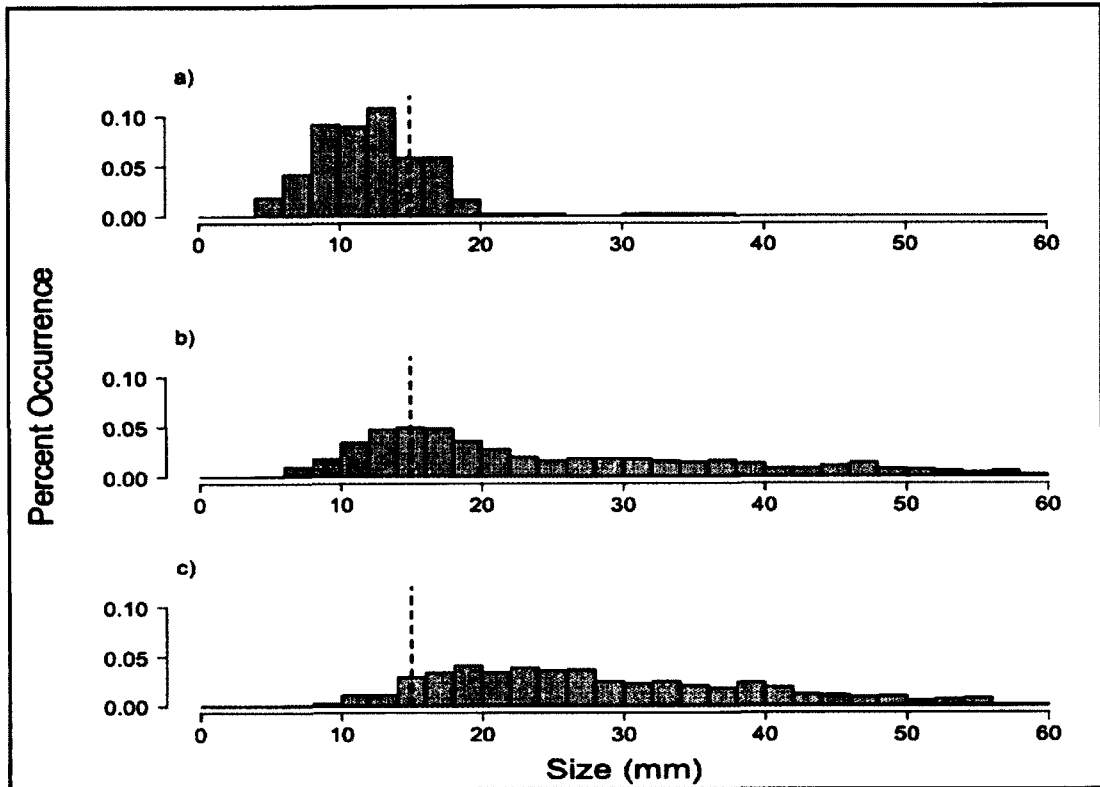
Figure 6: Size-frequency distribution of age-0 crabs ($\leq$ 60 mm cw) in (a) vegetated habitat, (b) shallow unvegetated habitat, and (c) deep unvegetated habitat. The horizontal dashed line at 15 mm cw represents the size at which crabs are susceptible to all gear types. Vegetated and shallow unvegetated estimates are from this survey; the estimate for deep unvegetated habitats is from the 2010-2011 annual blue crab WDS. Distributions were compared using Kolmogorov-Smirnov tests; p-values for all comparisons were < 0.001.
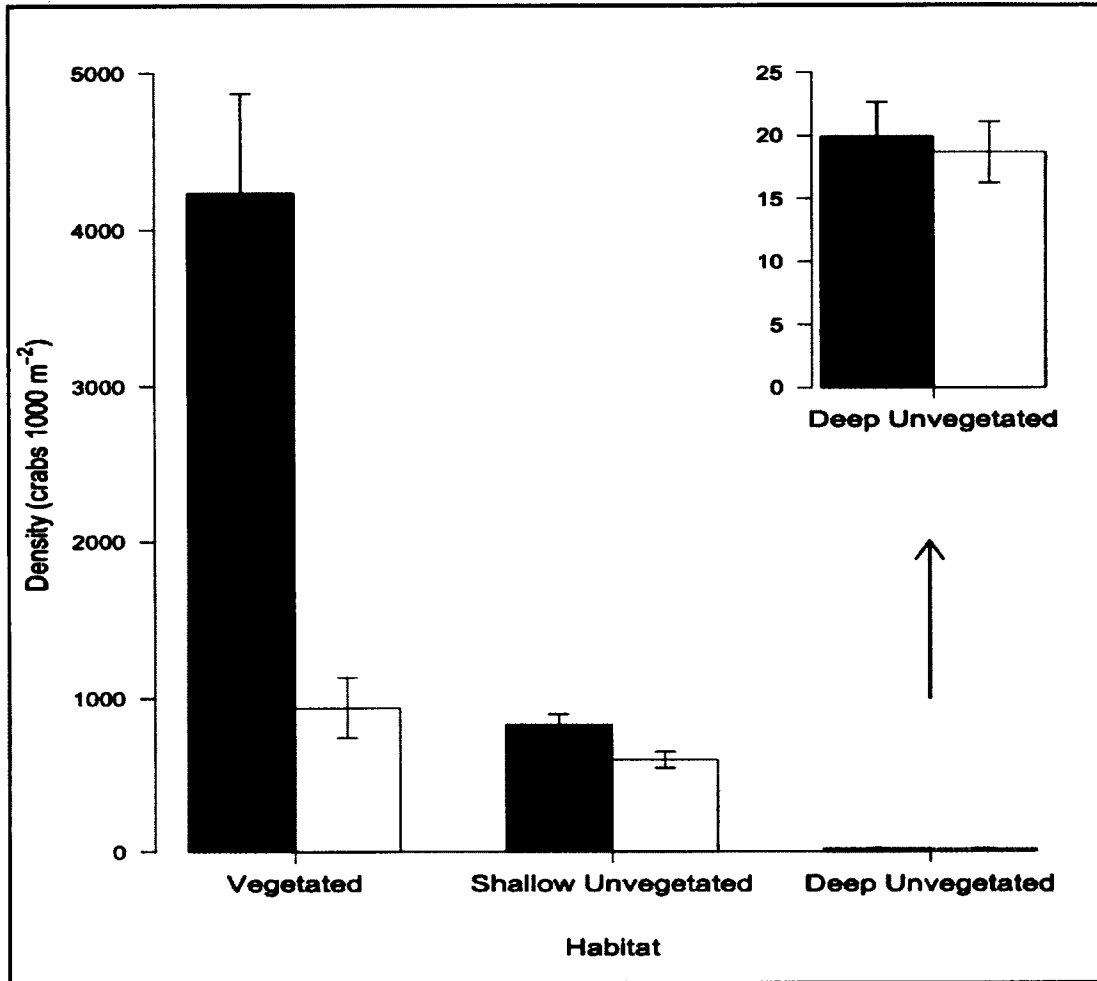
Figure 7: Average density of age-0 crabs (≤ 60 mm cw) by habitat. Grey bars represent the densities of all crabs less than 60 mm cw, white bars represent the densities of crabs vulnerable to all gears (i.e., crabs 15-60 mm cw). Vegetated and shallow unvegetated estimates are from this survey; the estimate for deep unvegetated habitats is from the 2010-2011 annual blue crab WDS. Error bars indicate standard error for each habitat type. Note the different y-axis scale for the deep unvegetated habitats.

CHAPTER 5

Quantifying the role of nursery habitats for the Chesapeake Bay blue crab using population fitness

ABSTRACT

As a dominant species, the Chesapeake Bay blue crab plays an important role in the food web and supports valuable fisheries. The life history is characterized by ontogenetic shifts in habitat use; however, most studies have focused on adults, with fewer and more localized studies on juvenile use of structured habitat. We modified an existing deterministic stage-based demographic model with the best available information on blue crab vital rates, with an emphasis on habitat-specific mortality rates of juveniles. The population growth rate (λ) was used as a measure of fitness to identify juvenile habitats critical to the persistence of the population. For the base simulations, we used a range of fishing mortality that represented realistic exploitation rates, and an unexploited scenario. Juvenile survival rates were estimated from two field studies and used to bracket the likely range of "benefit" juveniles derive from vegetated habitats; daily mortality rates were interpolated using a weight-based estimate for zoea and direct estimates of mortality for adults. For the scenarios where only unvegetated habitat was available, λ was consistently less than 1, regardless of the fishing mortality rate. However, the "vegetated benefit" scenarios provided a buffer from fishing mortality; that is, at higher levels of "vegetated benefit" the population could sustain higher fishing mortality rates while still remaining stable or even increasing. The population growth rate was strongly dependent on the juvenile survival, indicating that this stage is critical to the overall population trends. Although future modeling efforts for blue crabs should include additional information derived from a variety of juvenile habitats, this study provides further evidence that habitat characteristics must be incorporated in efforts to understand the dynamics of species with multiple juvenile habitats and ontogenetic shifts in habitat utilization.

INTRODUCTION

The original definition of nursery habitat described a specific life history strategy of motile invertebrates and fishes in which juveniles develop in shallow, coastal habitats, followed by a migration to offshore adult habitats (Gunter 1967). The current definitions include all life history strategies with disjunct juvenile and adult habitats (Beck et al. 2001). Structurally complex habitats such as seagrass beds and salt marshes are often described as nurseries for the blue crab. In the current paradigm for the Chesapeake Bay, megalopae (i.e., postlarvae) recruit to shallow, vegetated habitats in the lower Bay, and metamorphose to the first benthic instar. When densities are high, early juveniles may exhibit density-dependent emigration to alternative structured habitats. After reaching about 25 mm carapace width (cw: the distance between the lateral spines), juveniles have outgrown the size-specific protection in vegetated habitats, and migrate to lower salinity regions of the upper Bay and tributaries (Lipcius et al. 2007).

Many studies have attempted to address the role of structured habitats as nurseries for the blue crab in Chesapeake Bay through comparisons of survival, growth, or abundance in vegetated and unvegetated habitats at sites in close proximity to each other. Only a few studies have dealt with more than two of these characteristics, and none have followed the migration of juveniles from nursery habitats to adult habitats. The results of these investigations suggest that survival of the earliest juveniles is higher in vegetated habitats than in nearby unvegetated sediments (Johnston & Lipcius 2012, Lipcius et al.

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2005, Hovel & Lipcius 2001). Growth of small juveniles is also higher in seagrass than in nearby unvegetated habitats (Perkins-Visser et al. 1996), though larger juveniles have higher survival (Lipcius et al. 2005) and growth (Seitz et al. 2005) in upriver unvegetated habitats than any downriver habitats. Structurally complex habitats often have juvenile blue crab densities that are orders of magnitude higher than unstructured habitats (Lipcius et al. 2005).

Nursery habitats contribute relatively more adults than other habitats, through any combination of enhanced density, growth, survival, or movement to adult habitats (Beck et al. 2001). There has been some debate over what should be used to define "nursery" habitats. Beck et al. (2001) recommended a criterion whereby nursery habitats contribute more adults *per unit area* on average to the population than other habitats. Dahlgren et al. (2006) coined the term "effective juvenile habitat" to describe juvenile habitats that are most important to maintaining adult populations in terms of their *total contribution* of adults to the population. Both of these terms rely on relative measures; i.e., the habitats with higher than average contribution are deemed most important. The difference between these two criteria is whether the habitat contribution of adults to the population is calculated on a unit-area basis or as a habitat-specific total.

However, these two definitions could provide contradictory results. That is, a highly productive habitat that is small in total area might be designated a nursery habitat through the Beck et al. (2001) definition, but not an effective juvenile habitat through the Dahlgren et al. (2006) definition. Further, neither explicitly links the habitat-specific contributions to the persistence of the population. Fodrie & Levin (2008) and Fodrie et al. (2009) used the population growth rate (λ) to identify critical juvenile habitats for

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California halibut. By defining a nursery habitat as one that results in a λ greater than 1, the link between habitat and population growth rate is explicitly incorporated.

The goal of this study was to modify existing demographic models for the Chesapeake Bay blue crab to estimate the contribution of different habitats (i.e., shallow vegetated, shallow unvegetated, and deep unvegetated) to the persistence of the population. Specifically, we were interested in whether habitat-specific juvenile survival rate effected λ and how sensitive λ was to vital rates.

METHODS

Model Development

Matrix models can be used to examine the dynamics of structured populations, where subgroups within the population exhibit vastly different vital rates. Linear matrix models have been used in the past to explore the population dynamics of marine species (e.g., sea turtles, Crouse et al. 1987); the utility of these relatively simple methods can be seen in their continued use today (e.g., eastern hellbenders, Unger et al. 2013; Atlantic croaker, Diamond et al. 2013). Although more complex non-linear formulations can provide more realistic depictions of populations, linear models can provide important insights, despite the deterministic nature and the assumption of density-independence (Allman and Rhodes 2004). Given the specialized terminology used in this section, definitions can be found in the Appendix.

The blue crab exhibits seasonal and size-specific patterns in growth and mortality, which may influence the overall population trend. To capture these essential patterns, we

utilized a stage-based matrix modeling approach with two seasons based on Miller (2001). Following Miller (2001), we defined four stages: juvenile, small age-1, large age-1, and adult (Table 1). It is important to note that the two age-1 stages were differentiated by size; large age-1 crabs were defined as those vulnerable to crab fisheries. The year was divided into two seasons: summer, defined as June-November, and winter, defined as December-May (Miller 2001).

Based on the current understanding of blue crab growth and behavior, we developed a life cycle diagram for female crabs (Figure 1), which forms the basis of the seasonal transition matrices. The model tracked females only, as methods to analyze two-sex models are not well developed. Following an individual crab throughout its life cycle, we start with a summer juvenile. This summer juvenile must transition into an overwintering juvenile, but then can either transition into the small or large age-1 stage. It must then transition into an overwintering age-1 stage: if it is a summer small age-1, it can transition into either the small or large overwintering age-1, but if it is summer large age-1, it must overwinter as a large age-1. Whether it overwintered as a small or large age-1 crab, it must transition into the adult stage the following summer. Surviving adults will transition between the summer and overwintering adult stages every season. Sexually mature females, i.e., overwintering large age-1 and adult individuals, produce zoea on the last day of the winter season; zoea are present on the first day of the summer season.

For each season, a 4 × 4 population projection matrix (A) defined all seasonal dynamics (A_{summer} and A_{winter}) based on the life cycle diagram. The summer transition matrix (A_{summer}) is defined as:

$$
A_{summer} = \begin{vmatrix} as_{11} & 0 & 0 & 0 \\ 0 & as_{22} & as_{32} & 0 \\ 0 & 0 & as_{33} & 0 \\ 0 & 0 & 0 & as_{44} \end{vmatrix}
$$

and the winter transition matrix (A_{winter}) is defined as:

$$
A_{winter} = \begin{vmatrix} 0 & 0 & aw_{13} & aw_{14} \\ aw_{21} & 0 & 0 & 0 \\ aw_{31} & 0 & 0 & 0 \\ 0 & aw_{42} & aw_{43} & aw_{44} \end{vmatrix}
$$

Each transition element in the matrices described the growth, mortality, and fecundity associated with each stage. For example, the element as_{11} represents the survival of a zoea to the juvenile stage, while elements aw_{13} and aw_{14} represent the fecundity of a large age-1 crab and of an adult, respectively (see Table 2 for definitions of and equations for all elements in the seasonal matrices). To create a model with a yearly timestep, the two seasonal matrices were combined into a single matrix (A),

$$
A = A_{winter} \times A_{summer}.
$$

Using matrix algebra, the following general statements can be made:

$$
Av = \lambda v \text{ and}
$$

$$
uA = \lambda u,
$$

where A is a square matrix, v and u are non-zero vectors, and λ is a multiplier. The vectors v and u denote the right and left eigenvector, respectively, and λ denotes the eigenvalue associated with v and u. These terms describe important demographic

characteristics of the population projection matrix, A (see Appendix). The dominant eigenvalue of A, λ, is the finite rate of population increase; ln λ = r, the intrinsic rate of population increase. The right eigenvector of A, v, is the stable stage distribution, the expected number of individuals in a given stage class in a constant environment (Caswell 2000). The left eigenvector of A, u, describes the reproductive value of each stage, the expected reproductive contribution of each stage to the population growth rate (Caswell 2000). The stable stage distribution is typically presented relative to the expected total number of individuals in all stages, while the reproductive value is typically presented relative to the juvenile stage.

The effect of each transition element in the population projection matrix, A, on the population growth rate can be determined by sensitivity and elasticity analyses. The sensitivity of an element, a_{ij}, is the change in λ caused by a change in that element, and is defined by:

$$S_{a_{ij}} = \frac{\lambda}{a_{ij}}.$$

However, survival rates are inherently constrained to 0 – 1, while fecundity is not, so the numerical effects determined by sensitivity analyses are hard to compare. Elasticity analyses account for these differences in the scale of the vital rates. The elasticity of a_{ij} is the proportional change in λ caused by a proportional change in a_{ij}, and is defined by:

$$e_{a_{ij}} = \frac{a_{ij}}{\lambda}\frac{\lambda}{a_{ij}}.$$

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Elasticity is dependent upon the stable stage distribution, so the values should only be compared qualitatively. Elasticity analyses were performed for four scenarios representing the extreme values of both F and habitat benefit (i.e., F=0.25 and 1.67, unvegetated and high "vegetated benefit").

Parameter Estimation

The transition elements were calculated from six required parameters: natural mortality, fishing mortality, fecundity, early life history survival, and the fraction of age-1 crabs recruiting to the fishery (Table 3). Although the models developed by Miller (2001, 2003) also included a term for the dredge fishery, we accounted for dredge fishery mortality in a different manner (see below).

The first demographic model for blue crabs (Miller 2001, 2003) used the rule-of-thumb approach developed for the blue crab stock assessment (Rugolo et al. 1998) to estimate M, the instantaneous natural mortality rate. This method assumed the maximum life expectancy (α) was 8 years, and calculated $M \sim 3/\alpha = 0.375$. However, this rule-of-thumb approach likely substantially underestimates M; the estimate of M from a regression-based approach (Hoenig 1983) was 0.548, about 45% higher than the $3/\alpha$ approach (Hewitt and Hoenig 2005). A re-formulation of Miller (2001) to evaluate the effects of seascape structure on the blue crab population used $M = 0.548$ (Mizerek et al. 2011). However, a comparison of direct and indirect estimates of natural mortality suggested that M ranges from 0.7-1.1 for adult females (Hewitt et al. 2007). We set M =

0.9; for the model simulations, M/2 (= 0.45) was used for the seasonal transition matrices.

In the previous models (Miller 2001, 2003), the instantaneous rate of fishing mortality, F, was estimated by subtracting M from a time-series of total mortality (Z). Z was calculated from the average size of the catch (Hoenig 1987); the average Z was 1.255 for 1955-1997 (Rugolo et al. 1998, Miller and Houde 1999). Using the published time-series of Z and subtracting the rule-of-thumb estimate of M resulted in estimates of F that ranged from 0.62-1.26 (Miller 2001, 2003). However, given an annual exploitation rate (u) and M, F can be estimated numerically by solving u using the equation:

$$u = \frac{F}{F + M}(1 - e^{-(F+M)}).$$

Using M = 0.9 and a range of exploitation rates that bracket current and historical rates (u = 0.15, 0.30, 0.45, and 0.60), we estimated realistic values of F from 0.25-1.67. The range of F was similar to that presented by Miller (2001, 2003), but due to the higher M, resulted in higher total mortality rates (Z = 1.15-2.57). We also included a scenario where F = 0 to examine how the population might respond under unexploited conditions.

The models developed by Miller (2001, 2003) also included a term for the winter dredge fishery, which has been closed since 2008. We assumed that seasonal variation in F mirrored that of landings. The winter dredge fishery was typically responsible for about 10% of the harvest, and the crab pot fishery (open from late March through early December) was responsible for the majority of the annual landings. The seasonal activity levels of the crabs results in fewer crabs harvested during the colder months, so although about 30% of the potting season occurs during the winter months, it likely only accounts

for about 15% of F. Thus we allocated 25% of F in the winter and 75% of F in the summer.

We based our estimate of f, the proportion of age-1 crabs that entered the fishery, on the estimates in Miller (2001, 2003). Fishery-independent analyses performed by Rothschild et al. (1988) suggested that f = 0.15. Although previous studies have found habitat specific growth rates (e.g., Perkins-Visser et al. 1996, Seitz et al. 2005), accounting for the complexity of these size- and habitat-specific growth rates was beyond the scope of this study.

The estimate of fecundity used by Miller (2001, 2003) was based on the number of eggs produced in a single brood (Prager et al. 1990). Large age-1 females were assumed to have lower fecundity than that of adults based on the linear relationship between carapace width and number of zoea produced (Prager et al. 1990). Further, it was assumed that the average female only produces one brood each year. Although females in Chesapeake Bay are believed to spawn one to three times (Van Engel 1958), captive females in North Carolina produced up to seven broods, suggesting females can produce six to eight broods within the 25-week spawning season (Dickinson et al. 2006). We set the fecundity of large age-1 crabs to 66% of one adult brood (B_{age-1} = 1.056*10^6 female offspring), and assumed that the average female produced two broods (B_{adult} = 3.2*10^6 female offspring).

We modified the approach taken by Miller (2001, 2003) to estimate the early life history survival, μ, as the product of the daily survival. The estimate of daily mortality of the zoea was based on a linear relationship between weight and mortality rate (Peterson and Wroblewski 1984), and remained constant for the 40 days of the larval and postlarval

stages (Pletl 1992). We used the estimate of daily mortality during the zoeal and megalopal stages from Miller (2001, 2003), but the daily mortality of adults was increased to 0.00246 (i.e., 0.9/365) to reflect the higher estimate of M (Hewitt et al. 2007).

For the previous models, the estimated daily mortality rate was determined by a linear interpolation from the mortality of the postlarvae on day 41 to the daily mortality rate for an adult on day 182. This provides a simplified picture of the changing mortality rate as function of size in unvegetated habitat (Figure 2). However, it does not account for the reduced predation rates that have been found in vegetated habitats (e.g., Pile et al. 1996, Lipcius et al. 2005, Johnston & Lipcius 2012). We generated three scenarios to bracket plausible reductions of predation rates in vegetated habitats and thus benefits to the blue crab population. Under the low "vegetated benefit" scenario, the daily mortality rate was held constant at 0.072 for the two months that juveniles typically reside within vegetated habitats. The daily mortality rates in the mid and high "vegetated benefit" scenarios were estimated using a linear interpolation over the same two month as the low "vegetated benefit". The reduction in the daily mortality rates associated with the mid "vegetated benefit" was based on density estimates: in 30 days, about 25% of the 3rd instar juveniles survived to the 9th (Pile et al. 1996). A daily mortality rate of approximately 0.050 resulted in that decrease in density, and thus was used as the daily mortality rate for the first day of settlement. The reduction in the daily mortality rates associated with the high "vegetated benefit" was based on the relative survival of juveniles 5-25 mm carapace width in mud and seagrass (Johnston & Lipcius 2012). Based on a relative mortality rate in mud that was 6.5 times higher than in seagrass

(Johnston & Lipcius 2012), we estimated a daily mortality rate of 0.019 (= 0.1238/6.5) for the first day of settlement. In the three "vegetated benefit" scenarios, after residing within vegetated habitats for two months, juveniles immigrated to unvegetated habitats. For each scenario, the early life history survival was thus estimated as the product of the daily survival rates for 182 days.

RESULTS

The population growth rate, λ, ranged from 0.38-2.13 under all scenarios. The magnitude was strongly dependent on both fishing mortality rate and the habitat scenario; as F decreased and habitat benefit increased, λ increased (Figure 3). At low fishing mortality, all levels of habitat benefit result in positive population growth rates, while at high fishing mortality, only the highest habitat benefit results in a positive population growth rate. For the unvegetated scenarios, all fishing mortality rates used resulted in a decreasing population (i.e., $\lambda < 1$), even the unexploited scenario. Increasing F from 0.25 to 1.67 resulted in a decrease of 47% in the population growth rate. All fishing mortality rates resulted in positive population growth under the highest vegetated benefit scenario, though there was a 43% decrease in the population growth rate when F was increased from 0.25 to 1.67.

Under all scenarios of habitat and fishing pressure combinations, the juvenile stage dominated the stable stage distribution, representing more than 99% of the total population (Figure 4). As F increased, the proportion of juveniles decreased under all habitat benefit scenarios. The relative contribution of the small age-1 stage was

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consistently higher than both the large age-1 and adult stages, except for the unvegetated scenario with high F, where the adult stage was slightly higher. However, the relative contribution of the small age-1 stage increased quicker as a function of F as increasing habitat benefit scenarios.

For all scenarios, the relative reproductive value of the adults was the highest, ranging from about 2.5e5 to 3.1e6 times higher than the juvenile stage (Figure 5). The relative reproductive value of the adult and large age-1 stages decreased as F and habitat benefit increased. Although the relative reproductive value of the small age-1 stage also decreased with F, the decreases were much smaller than those associated with the adult and large age-1 stage.

The four scenarios for which elasticity analyses were performed represented combinations of the extreme values for F and habitat. As the elasticities represent the proportional effect each transition has on the overall population growth rate, they can be used as indicators for how the population will respond to changes in specific vital rates. The elasticity associated with the adult fecundity was the highest under all four scenarios; however, the elasticities associated with the transitions to and from the small age-1 stage were also high (Figure 6). Although overall the elasticities were similar across all four scenarios, the most important elasticities were higher under the high F scenario.

Only two of the transition matrices incorporate habitat-specific survival: the transitions that represent survival from the juvenile stage to the two age-1 stages. Of those, the juvenile to small age-1 transition was consistently higher than the juvenile to large age-1 transition. However, under both low and high F scenarios, the elasticity of the juvenile to large age-1 transition was higher under the high habitat benefit scenario than

the unvegetated scenario, while the elasticity of the juvenile to small age-1 remained fairly constant. The elasticity of the adult survival was much higher under the unvegetated scenario than the high vegetated benefit scenario.

DISCUSSION

The simple, flexible matrix modeling approach developed by Miller (2001) has been utilized previously to examine different aspects of blue crab population dynamics, including effects of the dredge fishery (Miller 2001), the large-scale spatial structure of blue crabs in Chesapeake Bay (Miller 2003), and the small-scale landscape structure of seagrass patches (Mizerek et al. 2011). In this study, we examined the interaction between fishing mortality and the benefit derived from reduced mortality rates in vegetated habitats on the population growth rate and stage structure. Both the fishing mortality rate and "vegetated benefit" had substantial effects on the population growth rate. The enhanced survival of juveniles provided in the three "vegetated benefit" scenarios created increasing population trends at all levels of fishing mortality.

As found by Miller (2001), increasing F decreased the population growth rate. Based on that model, it was suggested that the fishing mortality rates at the time were too high; the fishing mortality that produced a stable population was ~0.3 (Miller 2001). Under the unvegetated scenario in this study, which would be most similar to the conditions in Miller (2001), even the unexploited scenario resulted in a decreasing population. The population growth rate was driven primarily by three vital rates (adult fecundity, and transitions to and from the small age-1 stage); similar to Miller (2001), the adult survival became more important under lower fishing mortality rates. However,

changes in the parameter estimation, especially natural mortality, make direct comparisons between the two studies difficult.

The benefit derived from increased juvenile survival in vegetated habitats caused increased population growth rates under most realistic values for F. The fishing mortality rate that resulted in a stable population was about 0.5, 1.0, and > 1.7 for the low, mid, and high "vegetated benefit" scenarios, respectively. Further, under both low and high fishing mortality, the elasticity of the adult survival term was around four times higher in the unvegetated scenario than the high "vegetated benefit" scenario, though the magnitude was much lower in the high F scenarios. This suggests that vegetated habitats may provide a buffer against fishing mortality; that is, the quantity or quality of the vegetated habitat within the Chesapeake Bay may influence the level of fishing mortality that is sustainable. This model likely underestimated the benefit provided by vegetated habitats: only the survival varied in the different habitat scenarios, but field studies have suggested that vegetated habitats increase juvenile blue crab growth rates as well (Perkins-Visser et al. 1996, Seitz et al. 2005).

A previous modification of the Miller (2001) model varied age-1 survival as a function of seascape (Mizerek et al. 2011) through tethering studies performed in seagrass beds at the mouth of the York River (Hovel & Lipcius 2002). The seascape distribution influenced population persistence under the different fishing mortality scenarios (Mizerek et al. 2011), suggesting that the negative effects of fishing mortality on the population may be buffered by characteristics of the vegetated habitat present. Although the model formulation and parameter estimation varied substantially from what is presented here, together, these studies provide further evidence as to the importance of

including the presence and structure of vegetated habitats in studies of population dynamics.

The results from this model suggest that habitat and fishing mortality interact to influence the different life history stages. For example, the proportion of small age-1 individuals in the stable stage distribution increases non-additively with increasing fishing mortality and increasing "habitat benefit" scenarios. Increasing the "habitat benefit" increases the number of juveniles that survive to the small and large age-1 stages. However, F acts on the large age-1 stage, not the small age-1 stage. Similarly, the relative reproductive value of adult stage and both age-1 stages decreases non-linearly with increasing fishing mortality and "habitat benefit" relative to the juvenile stage. This suggests that the juvenile reproductive value is not increasing alone, but rather there must be some decreases to the reproductive value of the other three stages as well. However, under all scenarios the reproductive value of the juveniles is much lower than that of the other three stages; this is likely due to the very high mortality rates experienced by the juveniles. Although the reproductive value of the large age-1 stage is typically the higher than that of the small age-1 stage, at high fishing mortality rates, the reproductive value of the small age-1 stage surpasses that of the large age-1 stage.

Small age-1 stage

The small age-1 stage shows interesting trends due to being indirectly affected by both habitat and fishing. The proportion of individuals in the small age-1 stage is typically the highest, and increases quickly with increasing F and habitat benefit. The

juvenile stage is directly linked to the adult stage; therefore, decreases in adult abundance leads to a proportional decrease in the juvenile stage. However, the juveniles are linked to the adult stage through the small and large age-1 stages. The "habitat benefit" scenarios, relative to the unvegetated scenario, increase the number of juveniles that survive to be age-1 crabs. Thus, there is a build-up of individuals in the age-1 stages, particularly the small age-1 stage, because the large age-1 crabs are being fished as well as the adults.

Similar to Miller (2001), the transitions to and from the small age-1 stage were among the most important in determining the population growth rate. What is particularly interesting, however, is that high "habitat benefit" increased the elasticity of the transition from the juvenile stage to the small age-1 stage under the low F scenario, but decreased it under the high F scenario. Further, under higher fishing mortality rates, the transitions to and from the small age-1 stage become more important in driving the population growth rate. The factors driving juvenile survival are not well known, though there is evidence that structured habitats (Everett & Ruiz 1993, Pile et al. 1996, Lipcius et al. 2005, Johnston & Lipcius 2012) and shallow water (Hines & Ruiz 1995) can provide refuge from predation. This has substantial implications for management, as the small age-1 stage can not be directly managed, and provides additional evidence that we should move towards a ecosystem based fisheries management model.

Caveats

The linear matrix modeling approach used in this study can not account for density-dependent effects. The blue crab does exhibit density-dependence at some life

history stages (e.g., stock-recruit relationship: Lipcius and van Engel 1990 and cannibalism: Perkins-Visser et al. 1996). For the last decade, the blue crab population in Chesapeake Bay has been at very low abundances, so the assumptions of density-independence may not be too unrealistic. However, as the population responds to management actions aimed at increasing the abundance, this may need to be re-evaluated. The model developed here is also deterministic and the vital rates are assumed to be constant for all individuals in a given stage class. These two assumptions simplify the modeling approach, but are also restricting.

There are additional complications due to the nature of the blue crab and Chesapeake Bay that make using a simple matrix modeling approach less than ideal. First, we assumed there were only two habitats for the juvenile blue crabs to inhabit: vegetated and unvegetated. However, other available habitats may provide increased juvenile growth or survival (e.g., coarse woody debris: Everett & Ruiz 1993, complex macroalgae: Johnston & Lipcius 2012). Much less is known about role these habitats play in fostering increased survival or growth of blue crabs in Chesapeake Bay. There also may be differences in the connectivity patterns between juvenile and adult habitats that could change the overall population growth rates (see Gillanders et al. 2003). Finally, the blue crab population is inherently spatially structured, with certain life history stages occurring preferentially in different parts of the bay. Natural and fishing mortality are also likely to vary spatially, such that an individual's location within the bay could have consequences for its chance of survival. Incorporating these factors into future modeling efforts will allow a better understand of the dynamics of the blue crab population, and how best to manage them under increased natural and anthropogenic disturbances.

Future work

Although the blue crab is a relatively well studied species, there are still some aspects of the biology and ecology that need more study. This model suggests that the early life history plays an essential role in determining the overall population growth rate; unfortunately, this stage is also one of the most difficult to study. The daily mortality rates for zoea and megalopae have not been directly measured. Progress has been made in estimating the mortality rates of early juveniles, but, to date, there have been few studies to directly measure these rates (e.g., Etherington et al. 2003). Given how strongly the "vegetated benefit" scenarios influenced the population growth rate, it is essential that additional studies be undertaken to measure habitat-specific juvenile mortality.

Broader implications

The enhanced survival of juveniles in vegetated habitats made the difference between a decreasing and increasing population at all levels of F. However, currently the area of vegetated habitat within Chesapeake Bay, especially seagrass and marsh, is decreasing. If these trends continue or accelerate, the benefit provided by these habitats will be reduced and the buffer against population declines will be limited. Thus, an adaptive management strategy would be beneficial, with target fishing mortality rates higher when vegetated habitat is available and lower when it is not.

While this paper is limited in scope to the Chesapeake Bay blue crab, there are many species with life history stages dependent on specific habitats (e.g., Dungeness crab *Metacarcinus magister*, Spotted seatrout *Cynoscion nebulosus*, and Ocean surgeonfish *Acanthurus bahianus*). The approach developed in Fodrie & Levin (2008) and utilized here provides a simple approach to assessing juvenile habitats in terms of their importance in driving the overall population growth rate that can be used for many species with diverse life history characteristics.

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Table 1: The timing of the transitions between stages for an individual crab, beginning at hatching (month 0). OW = overwintering; S = summer. Overwintering adults that survive return to the summer adult stage.

Stage	Timing (months)	Natural Mortality Rate
S juvenile	0-5	Function of habitat
OW juvenile	6-11	0.45
S age 1 (small or large)	12-17	0.45
OW age 1 (small or large)	18-23	0.45
S adult	24-31	0.45
OW adult	32-36	0.45

Table 2: Definitions and equations for each of the elements within the seasonal matrices. Definitions for the fundamental parameters are provided in Table 3.

Element	Definition	Equation
as_{11}	Probability of a zoea surviving the summer and overwintering as a juvenile	μ
as_{22}	Probability of a small age-1 crab surviving the summer and overwintering as a small age-1 crab	$(1-f)\,e^{-M}$
as_{32}	Probability of a small age-1 crab surviving the summer and overwintering as a large age-1 crab	$f\,e^{-(M+F)}$
as_{33}	Probability of a large age-1 crab surviving the summer and overwintering as a large age-1 crab	$e^{-(M+F)}$
as_{44}	Probability of an adult crab surviving the summer and overwintering as an adult crab	$e^{-(M+F)}$
aw_{13}	Number of zoea produced by a large age-1 crab	$0.66B\,e^{-(M+F)}$
aw_{14}	Number of zoea produced by an adult crab	$2B\,e^{-(M+F)}$
aw_{31}	Probability of a juvenile surviving the winter and becoming a small age-1	$(1-f)\,e^{-M}$
aw_{31}	Probability of a juvenile surviving the winter and becoming a large age-1	$f\,e^{-M}$
aw_{42}	Probability of a small age-1 crab surviving the winter and becoming an adult	e^{-M}
aw_{43}	Probability of a large age-1 crab surviving the winter and becoming an adult	$e^{-(M+F)}$
aw_{44}	Probability of an adult surviving the winter	$e^{-(M+F)}$

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Table 3: Fundamental parameters used in the demographic model. Note that M and F were provided as annual rates; these terms were divided by two for use in the seasonal matrices.

a) Fundamental parameters

| Parameter	Definition	Estimate	Source
M	Instantaneous natural mortality rate	0.9	Hewitt et al. 2007
F	Instantaneous fishing mortality rate	$0 - 1.67$	Miller et al. 2011
f	Fraction of age-1 crabs entering the fishery	0.15	Miller et al. 2011
B	Fecundity	1.6×10^6	Prager et al. 1990
μ	Survival rate for juveniles during the summer:		Pile et al. 1996, Johnston and Lipcius 2012
	Unvegetated	9.01e-7	
	Low vegetated benefit	8.13e-6	
	Mid vegetated benefit	4.04e-6	
	High vegetated benefit	2.09e-5	
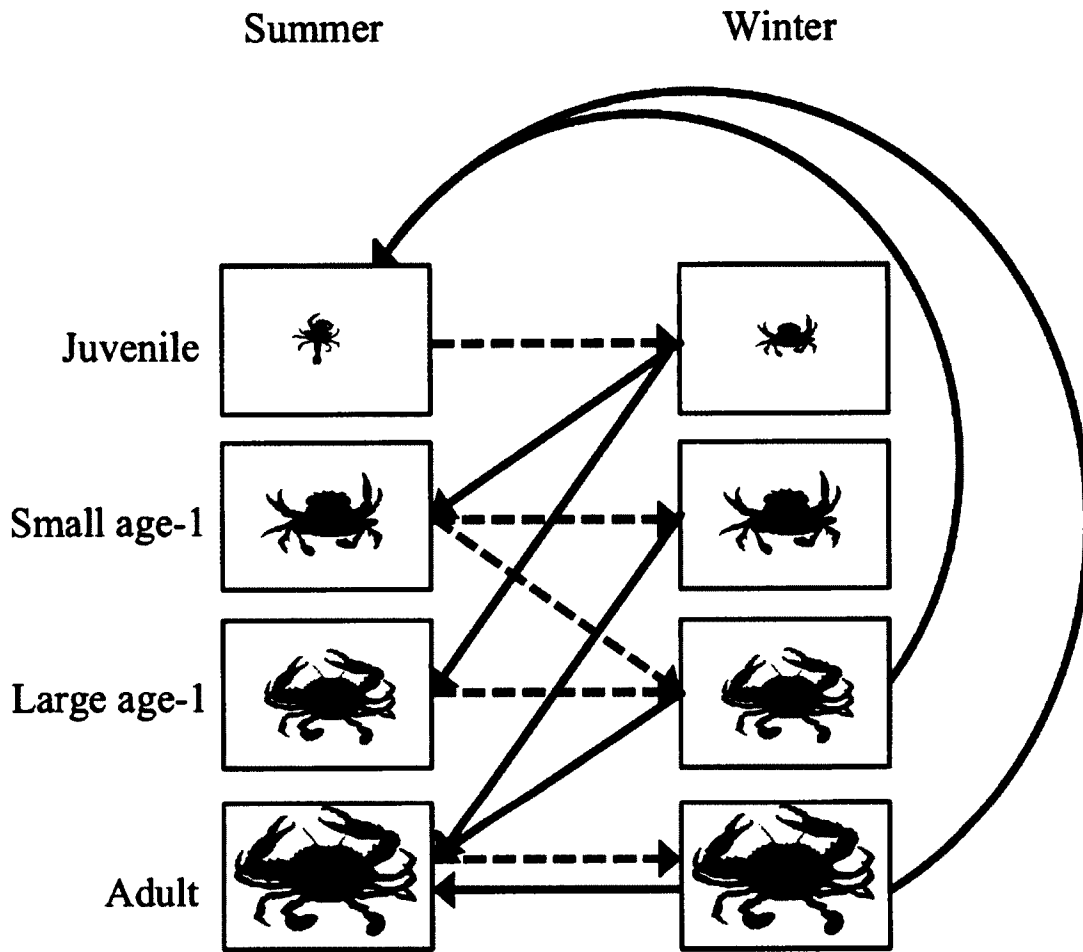
Figure 1: Life cycle diagram for the blue crab. An individual crab can be in one of four stages: juvenile, small age-1, large age-1, and adult during the summer and winter. Summer to winter transitions are represented by the dashed lines, while the winter to summer transitions are represented by the solid lines. Note that survival and growth probabilities are straight lines, while the fecundity terms are curved lines.
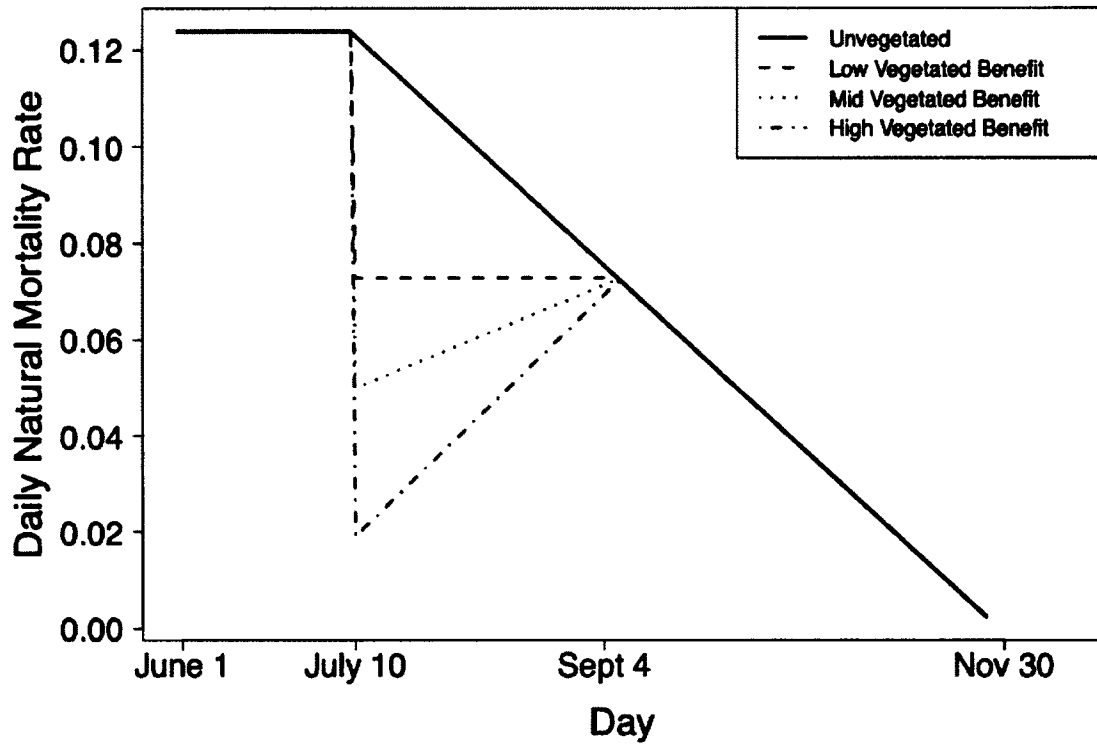
Figure 2: Estimated daily mortality rates for juvenile blue crabs during the summer. Unvegetated vs. three vegetated benefit scenarios. Low benefit = constant survival for 2 months. Mid benefit based on Pile et al. 1996 estimates of density of 9th and 3rd instar juveniles. High benefit based on Johnston & Lipcius 2012 relative survival in mud and seagrass. (see text for further details).
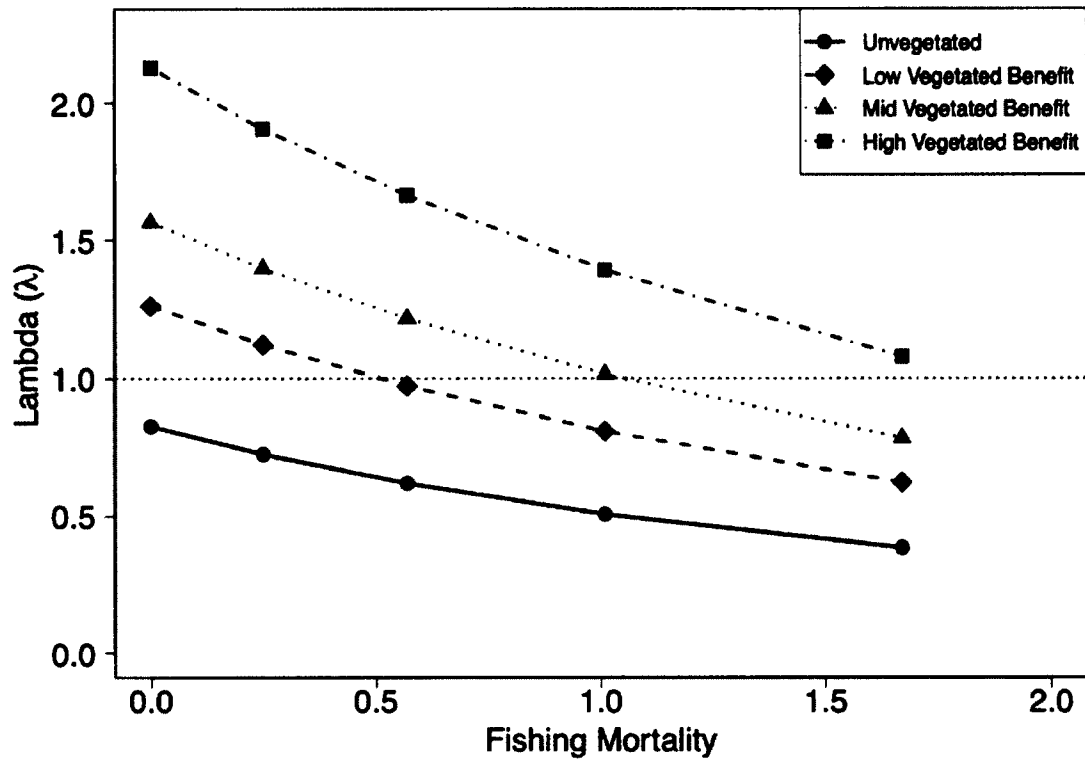
Figure 3: Estimated lambda for each fishing mortality and habitat scenario. Dotted line at lambda = 1 represents the lambda at which the population is stable.
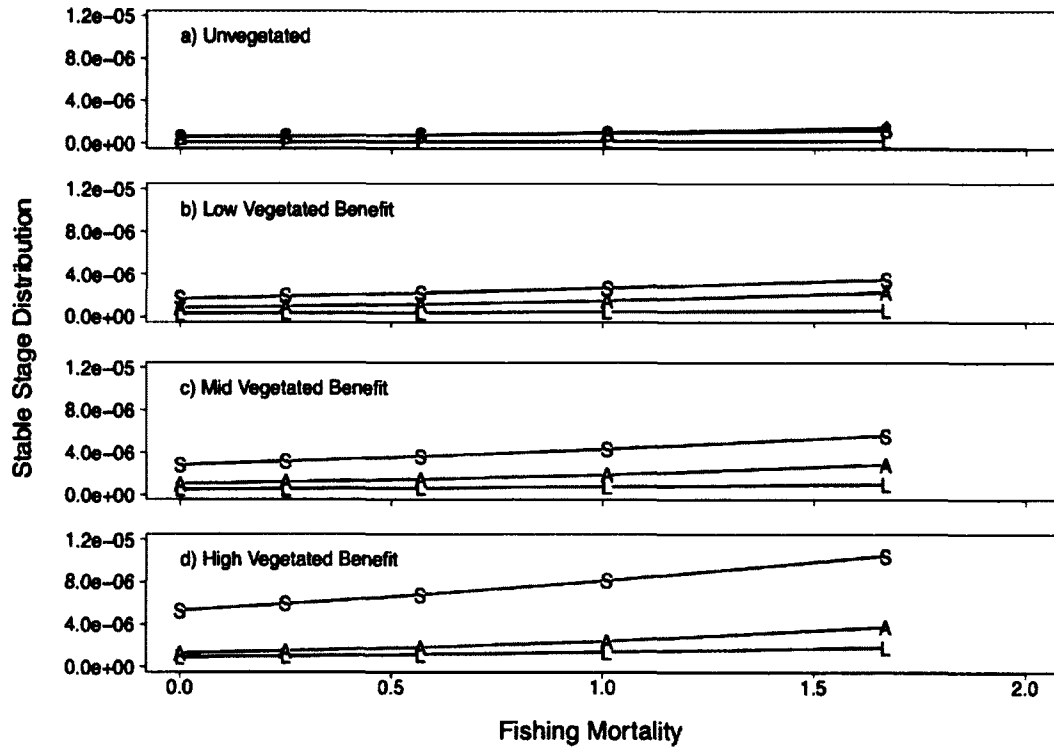
Figure 4: Stable stage distribution of small age-1 (S), large age-1 (L), and adult (A) stages for each habitat scenario. Stable stage distribution was calculated as a proportion of the total population. The juvenile stage (representing > 99% of the total population under all scenarios) was removed from these figures to allow for comparisons between the other three stages.
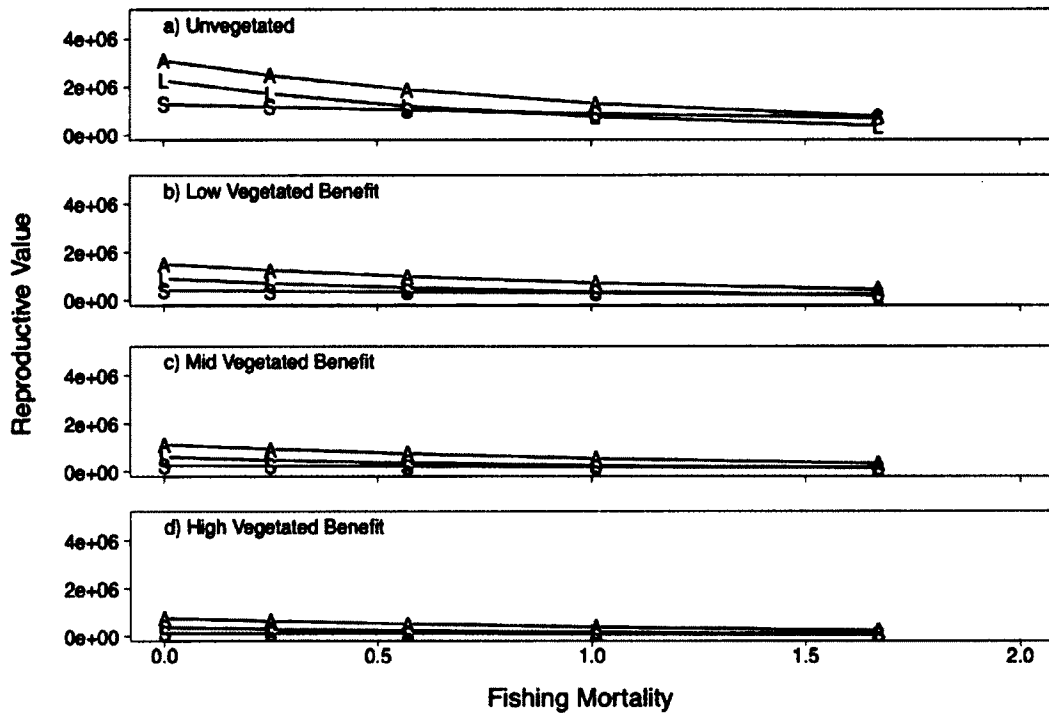
Figure 5: Reproductive value of small age-1 (S), large age-1 (L), and adult (A) stages for each habitat scenario. Reproductive value was calculated relative to the juvenile stage (= 1).

a)
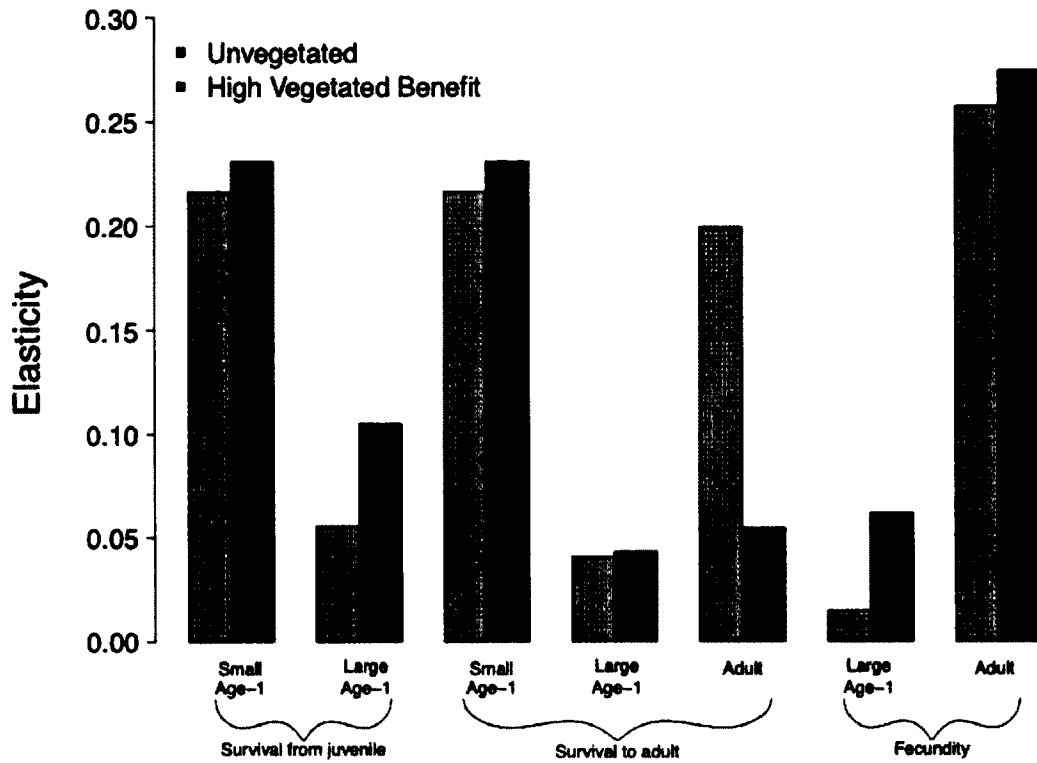
Figure 6: Elasticities of the combined projection matrix A for the unvegetated and high vegetated benefit scenarios under low (a) and high (b) fishing pressure. The first two pairs of bars represent the elasticities involving survival from the juvenile stage to the two age-1 stages. The third-fifth pairs represent the elasticies involving survival to the adult stage. The last two pairs of bars represent elasticies involving the stage-specific fecundity. Note that only the transitions involving the survival from the juvenile stage to the two age-1 stages incorporate habitat-specific survival.

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b)
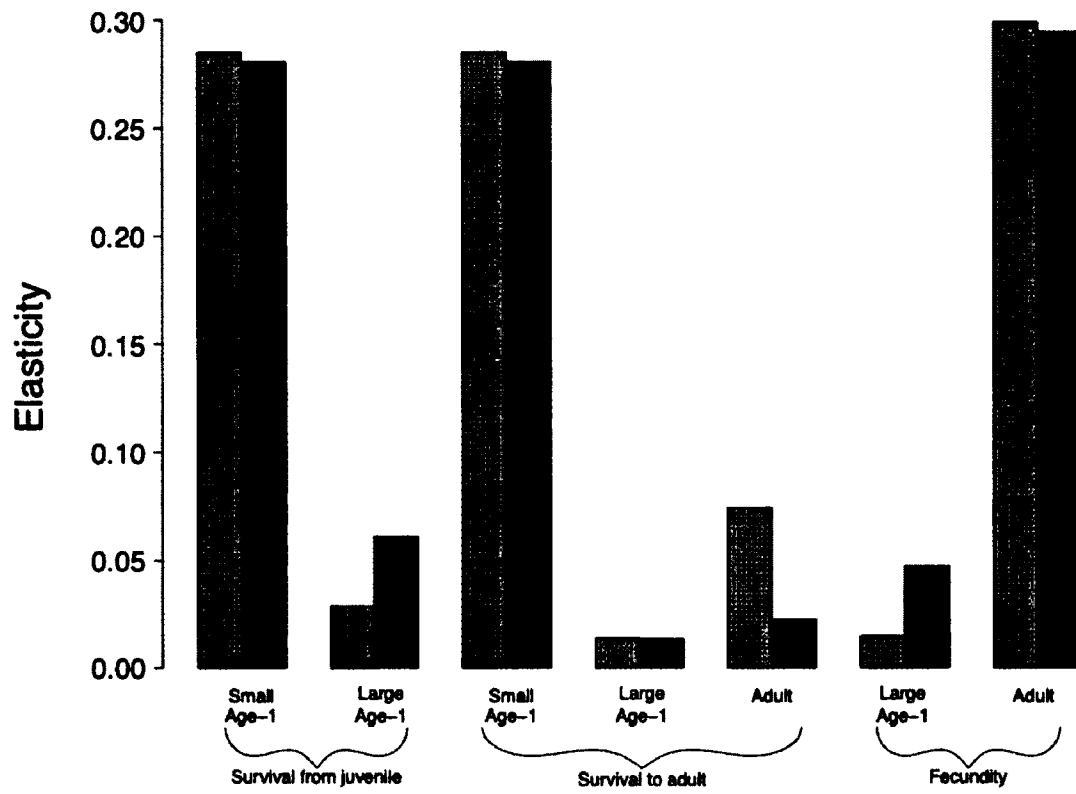
CHAPTER 6

Does seagrass matter?

CONCLUSION

The field and modeling studies within this dissertation represent an attempt to quantify the value of nursery habitats to the blue crab population in Chesapeake Bay at different temporal and spatial scales. The results of these studies have important implications for stock management and habitat restoration, particularly of submerged aquatic vegetation. Shallow water habitats, including vegetated and unvegetated habitats, appeared to impact juvenile blue crabs at multiple scales.

At a broad spatial scale, there was an exponential relationship between vegetation cover and juvenile density in Chesapeake Bay, rather than linear (Hovel & Lipcius 2001, Hovel et al. 2002) or sigmoid (Schulman 1996). This relationship may have been a function of the historically low recruitment during the survey, such that at higher recruitment, there would be a sigmoid relationship. Further evidence for recruitment as a driving force was the variability in the shape of the relationship between habitat cover and juvenile density; the shape of the curve varied both spatially (eastern vs. western shore) and temporally (by year). A similar exponential relationship was found in the York River throughout the entire recruitment season.

However, despite the typically episodic and variable ingress and settlement of megalopae (e.g., Orth & van Montfrans 1987, Olmi et al. 1990, van Montfrans et al. 1990), the abundance of the juvenile stages in vegetated habitats remained fairly stable over time, similar to previous findings at the mouth of the York River (Olmi et al. 1990).

The high densities of small juveniles collected in shallow, unvegetated habitats throughout the river suggested that these habitats were important recruitment sites for smaller juvenile blue crabs than was previously documented (e.g., Lipcius et al. 2005, Seitz et al. 2005). Taken together, these results signify the need for a revision of the paradigm of juvenile recruitment.

Our conceptualization of overwintering habitat for juveniles also required revisions. Previous studies suggested that juveniles typically inhabit deeper waters during the winter (Sharov et al. 2003; Hines 2007) and the most recent stock assessment (Miller et al. 2011) estimated that about 60% of age-0 crabs are not vulnerable to the WDS. However, a comparison of abundance of age-0 crabs in shallow vegetated and unvegetated habitats with that of deep habitats indicated that as much as 80-90% of the age-0 crabs were not sampled by the winter dredge survey in 2010-2011. If, as this study suggested, the proportion of age-0 crabs sampled varies annually, there are interannual biases in population surveys of age-0 crabs. A reasonable explanation for this variability, winter temperature, has been shown to significantly influence the distribution of both juvenile and adult blue crabs in Chesapeake Bay (Saluta 2012).

The benefit derived from increased juvenile survival in vegetated habitats caused increased population growth rates under most realistic values for fishing mortality rates. This suggests that vegetated habitats may provide a buffer against fishing mortality; that is, the quantity or quality of the vegetated habitat within the Chesapeake Bay may influence the level of fishing mortality that is sustainable. This model likely underestimated the effect of vegetated habitats on the population growth rate as only the survival varied in the different habitat scenarios. Field studies have suggested that

vegetated habitats increase juvenile blue crab growth rates as well (Perkins-Visser et al.

1996, Seitz et al. 2005), which would further increase the benefit of vegetated habitats.

However, currently the area of vegetated habitat within Chesapeake Bay, especially

seagrass and marsh, is decreasing. If these trends continue or accelerate, the benefit

provided by these habitats will be reduced and the buffer against population declines will

be limited.

There is substantial evidence that seagrass and other vegetated habitats are

preferred settlement habitats for megalopae and early juvenile blue crabs (e.g., Orth &

van Montfrans 1990), and that these structure habitats provide increased survival and

growth (e.g., Perkins-Visser et al. 1996), which can influence the overall population

dynamics. It is essential that shallow water habitats, both vegetated and unvegetated, be

incorporated into blue crab population surveys. Given the likelihood of increased

variability in environmental conditions in the coming decades, it is implausible that

spatially restricted surveys will provide an unbiased estimate of total population

abundance, especially in species with complex, ontogenetic shifts in habitat utilization.

Further, we need a better understanding of the demographic effect of habitat complexity,

for blue crabs as well as other species that exhibit ontogenetic shifts in habitat utilization.

This would be a massive undertaking, requiring substantial field efforts to directly

estimate habitat- and size-specific natural mortality rates for each species, which could

then be incorporated into demographic models. However, these data would in invaluable

for predicting species-specific responses to climate change, particularly changes in

habitat quality and availability.

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APPENDIX I

Abundance estimation for blue crabs in shallow water habitats of the York River.

Table 1: Abundance estimates by river region for all age-0 crabs. DR = down river, MR = mid river, and UR = up river. Samples in vegetated habitats were corrected for 80% efficiency; samples in unvegetated habitats were corrected for a range of plausible efficiencies: a) 50%, b) 25%, c) 10%, and d) 5.5%.

a)

Region	Density (per m^2)	Abundance (millions)
DR vegetated	12.40	43.93
DR unvegetated	0.29	1.28
MR unvegetated	0.41	2.79
UR unvegetated	0.50	2.96

b)

Region	Density (per m^2)	Abundance (millions)
DR vegetated	12.40	43.93
DR unvegetated	0.58	2.56
MR unvegetated	0.81	5.58
UR unvegetated	1.00	5.93

c)

Region	Density (per m^2)	Abundance (millions)
DR vegetated	12.40	43.93
DR unvegetated	1.44	6.39
MR unvegetated	2.03	13.95
UR unvegetated	2.49	14.82

d)

Region	Density (per m^2)	Abundance (millions)
DR vegetated	12.40	43.93
DR unvegetated	2.62	11.62
MR unvegetated	3.69	25.36
UR unvegetated	4.53	26.94

Table 2: Abundance estimates by river region for age-0 crabs 5-60 mm cw. DR = down river, MR = mid river, and UR = up river. Samples in vegetated habitats were corrected for 80% efficiency; samples in unvegetated habitats were corrected for a range of plausible efficiencies: a) 50%, b) 25%, c) 10%, and d) 5.5%.

a)

Region	Density (per m^2)	Abundance (millions)
DR vegetated	7.45	26.41
DR unvegetated	0.29	1.28
MR unvegetated	0.41	2.79
UR unvegetated	0.50	2.95

b)

Region	Density (per m^2)	Abundance (millions)
DR vegetated	7.45	26.41
DR unvegetated	0.58	2.56
MR unvegetated	0.81	5.58
UR unvegetated	0.99	5.90

c)

Region	Density (per m^2)	Abundance (millions)
DR vegetated	7.45	26.41
DR unvegetated	1.44	6.39
MR unvegetated	2.03	13.95
UR unvegetated	2.48	14.76

d)

Region	Density (per m^2)	Abundance (millions)
DR vegetated	7.45	26.41
DR unvegetated	2.62	11.62
MR unvegetated	3.69	25.36
UR unvegetated	4.51	26.83

Definitions of essential terminology for demographic modeling.

Elasticity: the proportional change in λ caused by a proportional change in a transition probability.

Eigenvalue (λ): the scalar multiplier that satisfies the equation: $Av = \lambda v$, where A is a square matrix and v is a non-zero vector. The dominant eigenvalue is the population growth rate.

Eigenvector, left: the non-zero vector that satisfies the equation: $uA = \lambda u$, where A is a square matrix and λ is a multiplier. The left eigenvector describes the reproductive value of each stage at equilibrium..

Eigenvector, right: the non-zero vector that satisfies the equation: $Av = \lambda v$, where A is a square matrix and λ is a multiplier. The right eigenvector describes the stable stage distribution of the population at equilibrium

Intrinsic rate of population increase (r): the rate at which a population increases in size if there is no density-dependence. Note that $r = \ln(\lambda)$.

Life cycle diagram: a depiction of all possible transitions between stages, which forms the basis for the population projection matrix.

Population growth rate (λ): the change in the number of individuals in a given population, typically over the course of one year. Note that this is the dominant eigenvalue of a matrix, A.

Population projection matrix: a square matrix that defines all of the possible transitions between life history stages.

Reproductive value: the expected contribution of each stage to the population growth rate. Note that this is the left eigenvector of a matrix, A.

Sensitivity: the absolute change in λ caused by a unit change in a transition probability.

Stable-stage distribution: the proportion of the population in each stage class at equilibrium. Note that this is the right eigenvector of a matrix, A.

Transition elements: 1) the probability that an individual in a given stage survives and remains within that stage or survives and moves to a different stage, or reproduces, or 2) the stage-specific fecundity of an average individual weighted by the survival probability. These elements form a population project matrix.

VITA

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