Ontogenetic patterns in juvenile blue crab density: effects of habitat and turbidity in a Chesapeake Bay tributary

A. Challen Hyman[1,*], Grace S. Chiu[2,3,4,5,6,7], Michael S. Seebo[2], Alison Smith[2], Gabrielle G. Saluta[2], Romuald N. Lipcius[2]

[1]College of Marine Science, University of South Florida, St. Petersburg, FL 33701-5016, USA
[2]Virginia Institute of Marine Science, William & Mary, Gloucester Point, VA 23062-2026, USA
[3]Institute for Climate, Energy & Disaster Solutions, Australian National University, Canberra, ACT 2601, Australia
[4]Department of Statistical Sciences and Operations Research, Virginia Commonwealth University, Richmond, VA 23284-9026, USA
[5]Department of Statistics, University of Washington, Seattle, WA 98195-0003, USA
[6]Department of Statistics & Actuarial Science, University of Waterloo, Ontario N2L 3G1, Canada
[7]Computational & Applied Mathematics & Statistics, William & Mary, Williamsburg, VA 23187-8795, USA

ABSTRACT: Nursery habitats are characterized by favorable conditions for juveniles, including higher food availability and lower predation risk, and disproportionately contribute more individuals per unit area to adult populations compared to other habitats. However, nursery habitat inference is complicated by changes in habitat preferences with ontogeny; individuals in early-life stages frequently inhabit different habitats than older juveniles or adults. In this field experiment, we modeled the density of 4 size classes of juvenile blue crabs *Callinectes sapidus* based on carapace width (CW) across multiple habitats at various locations within an estuarine seascape during the blue crab recruitment season. We examined 4 habitat types — unstructured sand, seagrass meadows, salt marsh edges (SME), and shallow detrital habitat (SDH). Results indicated that densities of small juvenile blue crabs (≤10 mm CW) were highest in seagrass, whereas densities of larger juveniles (16−25 mm CW) were highest in SME. Although densities of juveniles declined in seagrass habitat as a function of size, densities in SME remained consistently high, suggesting that secondary dispersal to SME by smaller juveniles after settlement and recruitment in seagrass may supplement losses in SME due to mortality. Turbidity was positively correlated with densities of both size classes, although our model did not address whether this was due to top-down (refuge) or bottom-up (food availability) mechanisms. Observed patterns in size-specific habitat utilization may result from changing requirements of juvenile blue crabs with size, as animals minimize mortality-to-growth ratios. Our findings emphasize the role of both seagrass and salt marsh habitat within juvenile blue crab ontogeny and emphasize the significance of structurally complex SME habitat in supporting juvenile blue crabs at sizes smaller than previously recognized, challenging past notions about the singular importance of seagrass habitat in this system. Our findings also underscore the need to quantify and preserve the complete chain of habitats used by juveniles.

KEY WORDS: *Callinectes sapidus* · Nursery habitat · Recruitment · Abundance · Seagrass · Salt marsh · Unstructured bottom · Bayesian modeling

1. INTRODUCTION

Nursery habitats are critically important for fish and invertebrates. Under the nursery role hypothesis (sensu Beck et al. 2001), nursery habitats are charac- terized by favorable conditions for juveniles, such as higher food availability and lower predation risk, and disproportionately contribute more individuals per unit area to adult segments of the population com- pared to other habitats (Beck et al. 2001, Gillanders et

*Corresponding author: achyman@usf.edu

al. 2003, Heck et al. 2003, Minello et al. 2003). Hence, nursery habitat availability is a major driver of commercially and recreationally exploited fisheries population dynamics. Consequently, a major research focus in fisheries science and estuarine ecology is identification of nursery habitats for commercially and recreationally exploited fish and invertebrate species both to prioritize conservation and restoration efforts as well as to guide management decisions (Seitz et al. 2014, Vasconcelos et al. 2014).

The nursery role hypothesis maintains that comparisons among all, or at least most, juvenile habitats are required prior to conferring nursery status to a habitat for a given species (Beck et al. 2001, Dahlgren et al. 2006, Litvin et al. 2018). Juveniles tend to utilize structurally complex habitats as nurseries in early life stages in part because of their superior refuge capacity (e.g. Heck et al. 2003, Minello et al. 2003, Lefcheck et al. 2019). The relative value of a given structurally complex habitat as a nursery may be dependent on availability of other habitats with similar characteristics. For example, submersed aquatic vegetation (SAV) or intertidal emergent vegetation (e.g. salt marshes) may seem less important as nurseries in regions where alternative structurally complex habitats are present and accessible (Nagelkerken et al. 2015, Litvin et al. 2018). However, many studies investigating nursery habitats only consider binary comparisons such as a structured habitat and an unstructured control. For example, approximately 50 percent of studies examined in 2 recent nursery habitat meta-analyses appear to be binary habitat comparisons (see supplemental material in McDevitt-Irwin et al. 2016; Lefcheck et al. 2019). This can limit inference on nursery function. In this study, we attempted to avoid this limitation by considering as many habitats as feasible.

Furthermore, characteristics of nominal nursery habitats (e.g. seagrass meadows or salt marshes) may fluctuate across space and time. The nursery function of these habitats can vary depending on the position within the seascape or season due to the influence of latent environmental, biological, or anthropogenic factors (Nagelkerken et al. 2015, Sheaves et al. 2015, Litvin et al. 2018). For example, predator composition and density vary seasonally in temperate estuaries (Dorenbosch et al. 2009) and may alter habitat use by prey (e.g. Crowder & Cooper 1982, Fraser & Emmons 1984, Crowder et al. 1997, Clark et al. 2003). In addition, spatial position within the seascape may modify the suitability of a habitat as a nursery, such as when habitats are positioned close to the site of larval ingress (Stockhausen & Lipcius 2003) or in areas with low predation pressure (Posey et al. 2005). Assessments

of habitats conducted over short temporal intervals or only in one spatial location may miss such phenomena and lead to spurious conclusions about nursery status (Litvin et al. 2018). Hence, these dynamic processes require careful consideration to ensure inferences on habitat comparisons are robust. Moreover, indirect comparisons of multiple habitats via meta-analyses and literature reviews of multiple studies — each considering different combinations of potential nursery habitats — are hindered by the potential influence of confounding, spatiotemporally fluctuating latent variables (e.g. Hyman et al. 2022). Thus, our work also provides a robust evaluation of nursery habitat to consider as many habitats concomitantly as possible, as well as other influential environmental factors.

Assessment of nursery habitat value is complicated by changes in habitat preferences with ontogeny. Individuals in early life stages frequently inhabit different habitats than older juveniles or adults (Jones et al. 2010, Nakamura et al. 2012, Epifanio 2019). Onto-genetic habitat shifts from one nursery to another can minimize mortality-to-growth ratios (sensu Werner & Gilliam 1984), and juvenile survival increases with size (Pile et al. 1996), such that larger juveniles can exploit habitats with less structural refuge and higher food availability (Dahlgren & Eggleston 2000, Lipcius et al. 2005, Seitz et al. 2005, Nakamura et al. 2012). Failure to consider ontogenetic habitat shifts may lead investigators to prioritize only a subset of habitats critical for maintaining healthy population abundances, while neglecting habitats that may be preferred by different stages (Sheaves et al. 2006, 2015, Nagelkerken et al. 2015). Quantitative assessments of nursery function must therefore consider nursery roles within the context of ontogeny, especially for organisms with complex life cycles (Epifanio 2007, 2019, Lipcius et al. 2007, Seitz et al. 2014, Vasconcelos et al. 2014, Litvin et al. 2018). In our work, we partitioned juveniles into multiple size classes and assessed each class concomitantly. This allows researchers to detect potential shifts in habitat utilization as juveniles grow and identify stage-specific nursery habitats throughout ontogeny (Lugendo et al. 2005, Aburto-Oropeza et al. 2009, Nagelkerken et al. 2015, Amorim et al. 2018).

Here, we focus on the blue crab *Callinectes sapidus*, a commercially and recreationally exploited species that relies on structurally complex nursery habitats throughout ontogeny. The blue crab opportunistically utilizes many habitats in early life stages, including seagrass (e.g. eelgrass *Zostera marina* and widgeon grass *Ruppia maritima* meadows in the Chesapeake Bay, USA), *Spartina alterniflora* salt marshes, and coarse woody debris (for a review, see Lipcius et

2007). After re-invading estuaries from the continental shelf, blue crab postlarvae settle into structurally complex nursery habitats, such as seagrass meadows, and rapidly metamorphose into first instar (j1) juveniles (Epifanio 2007, 2019). Although some early (j1—j5) juveniles emigrate from initial settlement locations to avoid adverse density-dependent effects associated with conspecifics (Etherington & Eggleston 2000, Blackmon & Eggleston 2001, Reyns & Eggleston 2004), many remain to exploit the high refuge quality afforded by primary nursery grounds. As juveniles outgrow the mouth-gape sizes of smaller predators, they emigrate to other habitats with lower-quality refuge but more abundant preferred prey (e.g. Baltic clam *Macoma balthica*; Seitz et al. 2003, 2005, Lipcius et al. 2005).

Several studies have posited different size thresholds for when emigration out of primary nursery grounds occurs. A mesocosm experiment examining the effects of simulated *S. alterniflora* shoots on survival estimated that juvenile blue crabs may shift their habitat preferences at sizes as small as 12 mm carapace width (CW), when they can achieve a size refuge from smaller predators abundant within salt marsh habitats (e.g. mummichog *Fundulus heteroclitus*; Orth & van Montfrans 2002). Subsequent field studies maintained that juveniles begin emigrating from seagrass meadows to utilize unstructured and salt marsh habitats only after reaching 25—30 mm CW (e.g. Pile et al. 1996, Lipcius et al. 2005, Johnston & Lipcius 2012, Hyman et al. 2022). Notably, these hypotheses are not mutually exclusive. Salt marsh habitat may represent an intermediate nursery, i.e. one with marginally lower refuge quality than seagrass but higher food availability (Seitz et al. 2003, 2005), before juveniles emigrate to unstructured or alternative nursery habitats (e.g. Stockhausen & Lipcius 2003, Mizerek et al. 2011, Ralph 2014, Wood & Lipcius 2022).

In this study, we investigated juvenile blue crab abundance across 4 distinct size classes, ranging from the smallest sizes hypothesized to emigrate from structured habitat (10 mm CW; Pile et al. 1996) to the largest sizes hypothesized to emigrate (25 mm CW; Lipcius et al. 2005). This research was conducted across diverse juvenile habitats situated within a dynamic estuarine seascape, focusing on the late summer—fall recruitment season for blue crabs. Specifically, our attention was directed towards 4 distinct habitat types, each possessing unique structural characteristics. These encompassed 3 habitats recognized for their importance as nursery grounds for juvenile blue crabs: seagrass meadows (hereafter referred to as seagrass), salt marsh edges (SME), and shallow detrital habitats (SDH) (e.g. Orth & van Montfrans 1987, Perkins-Visser

et al. 1996, Etherington & Eggleston 2000, Hovel & Lipcius 2002, Etherington et al. 2003, Hovel & Fonseca 2005, Lipcius et al. 2005, Bishop et al. 2010, Johnson & Eggleston 2010, Ralph et al. 2013, Ralph & Lipcius 2014, Hyman et al. 2022, Voigt & Eggleston 2023). Additionally, we estimated density in unstructured habitat of sand, which served as a control.

Building upon previous research (Hyman et al. 2022), we sought to complement large-scale spatio-temporal analyses with small-scale field sampling. This work was carried out within the York River, a tributary of Chesapeake Bay in Virginia, USA, encompassing spatial ranges on the order of tens of kilometers and temporal intervals of 2 wk. Our primary aim was to discern the impact of habitat type and environmental variables on the density of juvenile blue crabs across a range of sizes. To address this, we developed multiple Bayesian regression models (denoted as g_i), each incorporating different combinations of spatial positioning, habitat type, and turbidity as independent variables. The rationale and justification for these models, along with their corresponding independent variables, are elaborated upon in Text S1 in the Supplement at www.int-res.com/articles/suppl/m729p135_supp.pdf.

2. MATERIALS AND METHODS

2.1. Study area

Field work was conducted in the York River, a tributary in the lower portion of western Chesapeake Bay, between August and November 2020. The river is morphometrically characterized by depths generally between 5 and 10 m along the axes, but with deeper portions (>20 m) near the mouth (Smock et al. 2005). The York River has an average discharge of 47 m^3 s^{-1}, and is characterized by brackish salinities of 18—25 ppt at the mouth and 2—5 ppt near the confluence of the Mattaponi and Pamunkey Rivers. The system is mesotidal with an average tidal range between 0.5 and 1 m (Haas 1977). In addition, this system contains a range of seagrass, salt marsh, and unstructured sand habitat configurations ideally suited for investigating the relative importance of multiple habitat types (Hovel & Lipcius 2002, Lipcius et al. 2005). Seagrasses, primarily eelgrass and widgeon grass, vary from large, continuous meadows to areas with few small patches of variable shoot densities (Hovel & Lipcius 2002). Salt marshes, dominated by smooth cordgrass *Spartina alterniflora*, span extensive sections of the shorelines (CCRM 2019, Hyman et al.

2022), although areal coverage of marsh patches varies spatially along the shorelines. Secchi disk depth values, a proxy for turbidity, range from 0.5–1.5 m at the mouth of the system and 0–0.5 m upriver near the confluence of the Pamunkey and Mattaponi tributaries. Several latent variables, most notably predator composition, are strongly correlated with spatial position within the York River (Tuckey & Fabrizio 2022). As a result, we spatially stratified the river to account for the influence of any latent variables and improve inference on habitat variables. The river was divided into 3 approximately evenly split strata (nearly 17 km each) for a lack of an obvious stratification strategy, constituting downriver, midriver, and upriver strata (Fig. 1).

2.2. Sampling design

Site selection was achieved via a random sampling algorithm. Selection involved (1) extracting geographic coordinates using ArcGIS for the entire shoreline of the York River, (2) subsetting coordinates by habitat type and stratum, and (3) randomly select-ing a prespecified number of stations for each habitat within each stratum. Six SDH and sand stations were selected in each stratum, while 2 SME stations were randomly selected from the 6 SDH sites in each stratum. Finally, 6 seagrass stations were randomly selected from the downriver stratum, as seagrass is absent in midriver or upriver strata (Fig. 1). The number of sites per habitat in each stratum were the maximum logistically feasible to sample in a day given time constraints and tidal considerations.

Between August and November 2020, juvenile blue crabs were sampled in seagrass, SME, SDH, and sand at intervals of every 2 weeks. Four sampling trips were conducted to sample all 4 habitats. The first 3 sampling trips, targeting seagrass, SDH, and sand, were conducted 24–27 August (trip 1), 15–22 September (trip 2), and 5–8 October (trip 3). SME was also sampled on trips 2 and 3, as well as trip 4, which occurred 19–23 October. Hence, there is confounding between trip 4 and SME habitat (i.e. the effect of trip 4, should one exist, cannot be estimated separately from the effect of SME due to lack of replication in trip 4); otherwise, exploratory data analyses did not indicate interactions between habitat and trip.
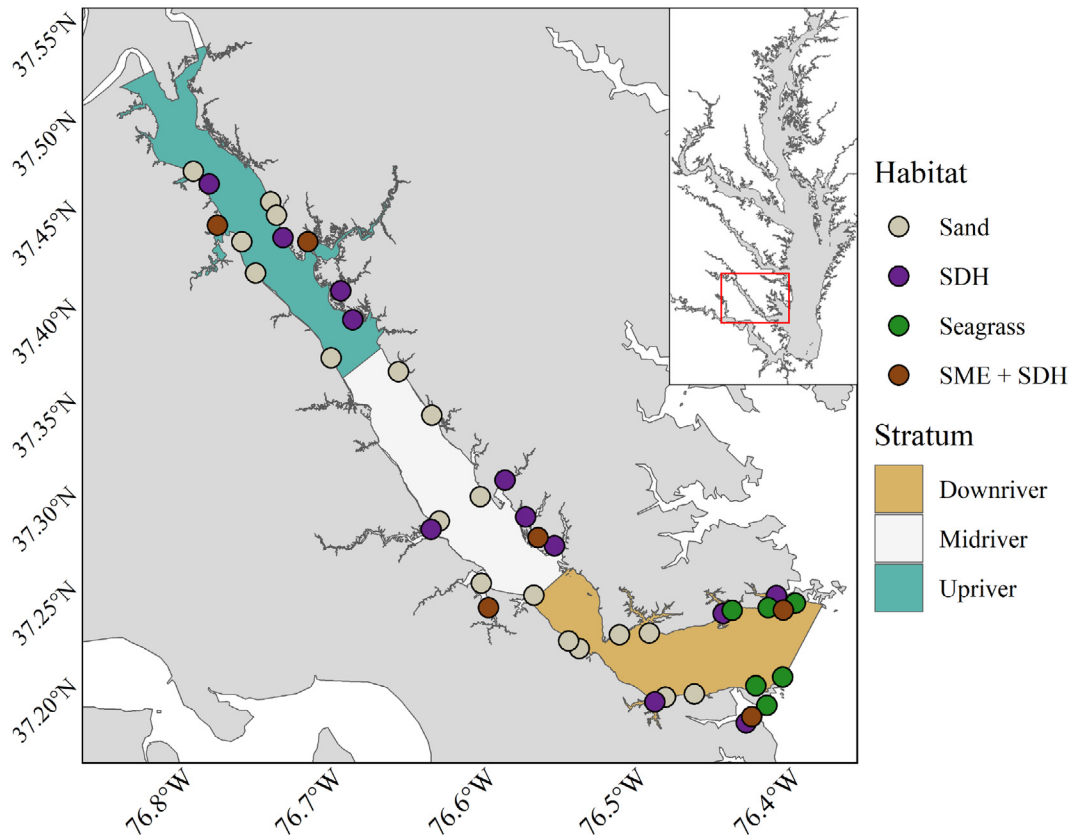

Fig. 1. York River (Virginia, USA, mouth located at 37.2476° N, 76.3824° W) displaying sampling sites colored by habitat type. Salt marsh edge (SME) sites are a subset of shallow detrital habitat (SDH) sites

This culminated in a total of 144 samples (Table S1), although 5 samples were later expunged due to missing predictor values (i.e. Secchi disk depth) in seagrass (2 sites) and SDH (3 sites).

Each habitat was sampled using gear and methodologies corresponding to habitat-specific structure and bottom types. All gear types used 3 mm hexagonal mesh netting to ensure that size-specific catchability was consistent after accounting for differences in gear efficiency. SDH and sand stations were sampled within ±3 h of high tide via benthic scrapes towed for 20 m along tidal salt marsh creek and beach shorelines, respectively (for details, see Ralph & Lipcius 2014). Meanwhile, SME stations were sampled using modified flume nets set at flood tide and collected at ebb tide (Fig. S1; McIvor & Odum 1986). Seagrass stations were similarly sampled within ±3 h of high tide. At seagrass stations, a 1.68 m² drop-cylinder and a 10 cm diameter PVC suction pipe attached to a sampling pump, modified from Orth & van Montfrans (1987), were employed to collect juvenile blue crabs (e.g. Orth & van Montfrans 1987, Heck et al. 2001, Hovel & Lipcius 2002, Ralph et al. 2013). Seagrass stations were suctioned within the drop-cylinders for 6 min continuously. For sand, SDH, and SME stations, immature juvenile crabs were counted, measured *in situ*, and released. The contents of each seagrass suction sample were frozen for storage and subsequently examined for juvenile blue crabs, double-checked, and all crabs counted and measured. Turbidity was recorded using a Secchi disk (water clarity, the inverse of turbidity) at each station on each trip.

2.3. Analyses

2.3.1. Size partitioning

To investigate how habitat utilization changes with ontogeny, we aggregated counts of juvenile blue crabs into 4 size classes based on carapace width: ≤10, 11−15, 16−20, and 21−25 mm. The smallest size class was chosen based on multiple lines of evidence suggesting that this was the lower bound upon which juveniles may begin emigrating from initial nursery habitats (Pile et al. 1996, Pardieck et al. 1999), to the upper bound proposed (Lipcius et al. 2005, Posey et al. 2005). We subsequently partitioned animals within this interval into 5 mm CW size classes, which was the minimum bin width that could be employed without introducing excessive numbers of 0 counts (particularly in sand and SDH) into the data. We recognize that these size classes are somewhat arbitrary, and

stress that ontogenetic shifts are likely a continuous process. Hence, inferences herein should be interpreted across size classes rather than focusing on environmental effects on any specific size class.

2.3.2. Basic model structure

All data analyses, transformations, and visualizations were carried out using the R programming language for statistical computing (R Core Team 2022). Relationships between both small and large juvenile blue crab abundance and environmental variables were evaluated using multivariate negative binomial linear mixed-effects models within a Bayesian framework. The negative binomial distribution was employed in lieu of a more conventional Poisson distribution due to substantial over-dispersion of juvenile crab counts. The predictor variables for juvenile abundance included habitat (seagrass, SME, SDH, and sand), spatial stratum (downriver, midriver, and upriver), and turbidity. Note that although we acknowledge that salinity may be an important predictor of juvenile abundance in other systems (e.g. Posey et al. 2005), salinity was highly collinear with turbidity. Recent evidence suggests that turbidity is an important predictor in juvenile blue crab abundance (Hyman et al. 2022), so we chose to focus on turbidity instead of salinity.

Transformations to turbidity values were applied prior to their inclusion in abundance models. Here, ln turbidity was defined as the natural log transformation of Secchi-disk depth, multiplied by −1 (turbidity (T) = −ln Secchi). The natural log transformation was applied based on the assumption that a threshold exists in water transparency. Assuming that effects of turbidity on juvenile abundance reflect refuge from visually oriented predators (top-down control), small changes in water transparency when water is relatively clear are not expected to substantially affect juvenile abundance as much as small changes in water transparency when water is turbid (e.g. predation rates by summer flounder on mysid shrimp; Howson 2000). Similarly, if associations between juvenile abundance and turbidity are related to elevated food availability near the estuarine turbidity maximum, juveniles would presumably remain more sensitive to fluctuations in turbidity at high values compared to clearer waters. Multiplying the variable by −1 facilitates inference on turbidity, instead of water transparency (inverse).

For the sth site on trip t in habitat h, the Bayesian model for juvenile blue crab abundance of size class i

is expressed as:

$$y_{hsti}|\mu_{hsti},\phi_i \quad \sim NB(\mu_{hsti},\phi_i) \tag{1}$$
$$\ln(\mu_{hsti}) = \boldsymbol{X}_{hst}\beta_i + \theta_{hsi} + A_h + E_h$$
$$\beta_i = [\beta_{i1}, \beta_{i2}, \ldots \beta_{ip}]$$
$$\begin{bmatrix} \theta_{hs1} \\ \theta_{hs2} \\ \theta_{hs3} \\ \theta_{hs4} \end{bmatrix} \Bigg| \Sigma \sim MVN\,(0, \Sigma)$$
$$\Sigma = \sigma_\theta^2(\boldsymbol{D} - \lambda\boldsymbol{W})^{-1}$$
$$\lambda \sim U(-1, 1)$$
$$\beta_{ik} \sim N(0, 1) \text{ for } k = 1,\ldots, p$$
$$E_{sand}, E_{SDH} \sim N(-1.20, 0.18)$$
$$E_{SME} \sim N(-0.083, 0.02)$$
$$E_{seagrass} \sim N(-0.13, 0.02)$$
$$\sigma_\theta^2, \phi_1, \phi_2, \phi_3, \phi_4 \sim \text{inverse-Gamma}(1, 1)$$

where $NB(\mu_{hsti}, \phi_i)$ denotes a negative binomial distribution with mean μ_{hsti}, while ϕ_i controls the over-dispersion for each size class such that $E[y_{hsti}] = \mu_{hsti}$ and $VAR[y_{hsti}] = \mu_{hsti} + \frac{\mu_{hsti}}{\phi_i}$. The response variables, juvenile crab counts for different size classes, are denoted by y_{hsti} where $i = 1, 2, 3$, and 4 denote the ≤ 10, 11–15, 16–20, and 21–25 mm size classes, respectively. Total area sampled (seagrass = 1.68 m^2, SME = 1 m^2, SDH and sand = 20 m^2) is included as an offset term A_h. In addition, due to varying requirements as a function of size, each size class was not expected to respond equally to predictor variables $\boldsymbol{X}_{hst}$ (habitat, turbidity, spatial position, and relevant interaction terms, see Text S1 for details). Hence, β_i refers to regression coefficients for each size class i associated with $\boldsymbol{X}_{hst}$. All fixed-effect regression coefficients were given a normal prior distribution with mean 0 and variance 1. Measurements of both the abundances of size classes and predictors $\boldsymbol{X}_{hst}$ were taken at the site-trip spatio-temporal resolution, such that predictors were not specific to any one size class i but to all sizes classes at a given site-trip. Here, θ_{hsi} denotes a site-specific random effect for a given size class i. The joint probability distribution of $(\theta_{hs1}, \theta_{hs2}, \theta_{hs3}, \theta_{hs4})$ is specified as multivariate normal (MVN) with a mean vector of 0s and variance–covariance matrix Σ. The Σ matrix describes dependence among size classes based on the nearest-neighbor structure specified by a 4×4 adjacency matrix, $\boldsymbol{W}$, and an autocorrelation parameter λ, which controls the degree of autocorrelation among size classes. We employed a binary weighting scheme for $\boldsymbol{W}$ where $w_{i,i'} = 0$ for all (i,i') unless size classes $i \neq i'$ were adjacent. For example, the smallest size class (≤ 10 mm CW) and the next largest $i = 2$ (11–15 mm CW) are considered adjacent because increases in size among individuals in $i = 1$ would shift them to $i = 2$,

whereas size classes $i = 1$ and $i = 3$ are not considered adjacent because individuals in size class $i = 1$ (≤ 10 mm CW) would need to move through size class $i = 2$ prior to reaching $i = 3$ (16–20 mm CW). Hence the 4×4 binary adjacency matrix employed here is expressed as:

$$\boldsymbol{W} = \begin{bmatrix} 0, & 1, & 0, & 0, \\ 1, & 0, & 1, & 0, \\ 0, & 1, & 0, & 1, \\ 0, & 0, & 1, & 0, \end{bmatrix} \tag{2}$$

The influence of an adjacent size class on a given size class was standardized by subtracting $\lambda\boldsymbol{W}$ from $\boldsymbol{D}$, a diagonal matrix where $\boldsymbol{D}_{i,i}$ is the number of neighbors for size class i (1, 2, 2, and 1 for size classes $i = 1$, 2, 3, and 4 respectively). The parameter λ was constrained between -1 and 1 through a uniform prior. This size class dependence structure was assumed to be homoscedastic through the variance parameter σ_θ^2, with an inverse-Gamma(1, 1) hyperprior. A similar parameterization is outlined by Hyman et al. (2022), although our nearest-neighbor structure refers to covariance among size classes instead of covariance across spatial polygons.

Informative prior distributions for gear efficiency E_h were supplied based on gear efficiencies from the literature (seagrass, SDH, and sand) and from the fall pilot study (SME). These prior distributions were subsequently converted to the ln-scale (see Text S2 and Table S2 for details). This incorporated increased uncertainty into habitat-specific estimates.

Bayesian inference required numerical approximation of the joint posterior distribution of all model parameters including the vectors of random effects. To this end, we implemented the model using the Stan programming language for Bayesian inference to generate Markov chain Monte Carlo (MCMC) samples from the posterior (Gelman et al. 2015). For each model, we ran 4 parallel Markov chains, each with 5000 iterations for the warm-up/adaptive phase, and another 5000 iterations as posterior samples (i.e. 20 000 draws in total for posterior inference). Convergence of the chains was determined both by visual inspection of trace plots (e.g. Fig. S2) and through inspection of the split statistic. All sampled parameters had a value less than 1.01, indicating chain convergence (Gelman et al. 2015). We considered covariates and interactions whose posterior distributions indicated a positive or negative effect with $\geq 80\%$ posterior probability, as scientifically relevant to juvenile blue crab abundance (Kruschke 2021). The International Panel on Climate Change (IPCC), an advocate of Bayesian approaches, defines probabilities of at least 66\% as 'likely' and probabilities of at least 90\% as 'very likely' (Chen et al. 2021). In

terms of practical significance, a credible level like 80% falls between these established ranges, indicating a reasonably dependable spectrum of parameter values. All CIs referenced here are the highest posterior density intervals (McElreath 2018).

Estimated log-pointwise predictive density (ELPD) and related Δ_{ELPD} values were used to evaluate the degree of predictive power for each model among the set of statistical models g_i (Vehtari et al. 2017). Values of ELPD are widely employed to measure out-of-sample predictive accuracy, while Δ_{ELPD} values refer to the difference in ELPD between a given model and the model with the best ELPD in the set. Values of ELPD and Δ_{ELPD} were estimated using the widely applicable information criterion (WAIC; Watanabe 2013, Gelman et al. 2015, Vehtari et al. 2017). Both WAIC and ELPD were estimated using the 'loo' package (Vehtari et al. 2022). When 2 models had comparable Δ_{ELPD} values (i.e. ≤4; Sivula et al. preprint doi:10.48550/arXiv.2008.10296), the simpler model was chosen as the more appropriate model under the principle of parsimony.

2.3.3. Alternative model structures

In our design, the downriver stratum was partially confounded with seagrass habitat, as seagrass is present only at the mouth of the York River (Fig. 1; Hyman et al. 2022). As a consequence, under this design it is not easily discernible whether spatial stratum interacted with seagrass habitat. To ensure that seagrass habitat and spatial stratum did not interact and influence results, we constructed 2 additional models — one with only SME, SDH, and sand across all strata and a second with all 4 habitats only in the downriver stratum — and compared the results to our best-fitting model, g_1. Posterior distributions of main effects (where present across models) strongly overlapped, indicating that interactions between spatial stratum and habitat were unlikely when other predictors were considered (Fig. S3).

2.3.4. Conditional effects

Conditional effects plots were used to visualize the relationship between response variables (juvenile blue crab abundance) and meaningful predictors both among habitats within a size class and within habitats between size classes. Herein, we refer to 'conditional effects'

as the effects of a given predictor (either continuous or categorical) while holding all random effects at 0 and fixing co-varying predictors. Specifically, we held ln turbidity at 0 to estimate habitat conditional effects and held habitat effects at the reference (i.e. sand; $h = 1$). Conditional effects were used to conceptualize mean effects of each level in a given categorical variable. Hence conditional linear contrast statements were used to determine whether differences in abundances among habitats were statistically meaningful. For the hth habitat (where $h > 1$), we considered pairwise difference between habitats $\beta_{hi} - \beta_{1i}$, where β_{1i} is the reference intercept (sand). Meanwhile, for comparisons of within-habitat abundances between ≤10 mm CW (i.e. $i = 1$) and the largest size class, 21–25 mm CW (i.e. $i = 4$), for the hth habitat, we considered the contrast $\beta_{h,10} - \beta_{h,25}$.

3. RESULTS

We collected and measured 975 juvenile blue crabs ≤25 mm CW from 139 samples. Herein, all abundance values for size classes refer to abundance per square meter, and are referred to as density. Size ranges of crabs are specified below as mm; these refer to CW measurements.

3.1. Model selection

The best fitting model was g_2, which posited juvenile blue crab abundance as a function of habitat, turbidity, and a habitat–turbidity interaction. However, models g_1, g_2, and g_5 had comparable ELPD values ($\Delta_{ELPD} \leq 4$) and standard errors of similar magnitude as Δ_{ELPD} (Table 1), indicating relative statistical equivalence.

Table 1. Model selection results from 5 Bayesian multivariate negative binomial regression models (g_i) using ln turbidity (T), habitat (H), and stratum (S) as predictors of juvenile blue crab abundance. Models are presented in order of predictive power based on collected data. WAIC: widely applicable information criterion; ELPD$_{WAIC}$: estimated log-pointwise density calculated from WAIC; Δ_{ELPD}: relative difference between the ELPD of any model and the best model in the set; SE$_{\Delta ELPD}$: standard error for the pairwise differences in ELPD between the best model and any given model; p$_{WAIC}$: estimated effective number of parameters. The selected model (g_1) values are presented in **bold** font. Model justifications are in Text S1

Model: Fixed effects	WAIC	ELPD$_{WAIC}$	Δ_{ELPD}	SE$_{\Delta ELPD}$	p$_{WAIC}$
g_2: H + T + H×T	1431.91	−715.96	0.00	0.00	54.33
g_5: H + T + S + H×T	1436.89	−718.45	−2.49	2.07	56.79
g_1: H + T	**1438.41**	**−719.21**	**−3.25**	**5.79**	**55.43**
g_3: H + T + S	1442.47	−721.23	−5.28	6.44	60.02
g_4: H + T + S + H×S	1449.71	−724.85	−8.90	5.36	62.18

Hence, we chose the simplest model, g_1, with additive habitat and turbidity effects, as the best model under the principle of parsimony. Hereafter, inferences are based on model g_1.

3.2. Habitat effects

3.2.1. Size class: ≤10 mm

Juvenile blue crab density among animals ≤10 mm was highest in seagrass (12.06 m^{-2} on the count scale), followed by SME (4.46), SDH (0.31), and sand (0.34) (Table 2, Fig. 2; Fig. S4). For pairwise linear contrasts among habitats SME–SDH, SME–sand, seagrass–SDH, seagrass–SME, and seagrass–sand, the posterior probability that a given contrast was positive exceeded 90%. Finally, the pairwise linear contrast among habitats SDH–sand strongly overlapped with 0. Taken together, these results indicated that differences in the expected density of small juvenile crabs among habitats were statistically meaningful with the exception of SDH–sand (Table 3; Fig. S5).

3.2.2. Size class: 11–15 mm

Among juveniles within the 11–15 mm size class, density was similarly highest in seagrass (5.40 m^{-2} on the count scale), followed by SME (3.54), SDH (0.60), and sand (0.41) (Table 2, Fig. 2; Fig. S5). Pairwise linear contrasts for the 11–15 mm size class were similar to those of the ≤10 mm size class. For contrasts among habitats SME–SDH, SME–sand, seagrass–SDH, and seagrass–sand, the posterior

Table 2. Posterior summary statistics (median and 80% CI) of habitat (SME: salt marsh edge; SDH: shallow detrital habitat) and turbidity effects for each juvenile size class based on model g_1 (see Table 1). Habitat values represent the expected juvenile density in a given habitat (abundance per m^2). The last column reflects the effect (i.e. regression coefficient) of ln turbidity on juvenile density, irrespective of habitat. Values are supplied on both the model (ln) and count scales. CW: carapace width

Size (CW, mm)	Scale	Quantile (%)	Sand	Seagrass	SME	SDH	Turbidity
≤10	Model	10	−2.21	0.96	0.26	−2.37	0.19
		50	−1.07	2.49	1.50	−1.18	0.46
		90	−0.14	3.74	2.72	−0.06	0.73
	Count	10	0.11	2.62	1.30	0.09	1.20
		50	0.34	12.06	4.46	0.31	1.59
		90	0.87	42.09	15.25	0.94	2.08
11–15	Model	10	−1.78	0.46	0.27	−1.54	0.00
		50	−0.89	1.69	1.26	−0.52	0.22
		90	0.11	2.90	2.36	0.50	0.47
	Count	10	0.17	1.59	1.32	0.22	1.00
		50	0.41	5.40	3.54	0.60	1.25
		90	1.12	18.17	10.58	1.64	1.60
16–20	Model	10	−1.67	−0.52	0.52	−2.36	0.01
		50	−0.71	0.93	1.68	−1.29	0.26
		90	0.26	2.17	2.84	−0.21	0.52
	Count	10	0.19	0.59	1.68	0.09	1.01
		50	0.49	2.53	5.39	0.27	1.30
		90	1.30	8.72	17.05	0.81	1.67
21–25	Model	10	−1.45	−1.85	0.59	−2.67	0.19
		50	−0.42	−0.38	1.88	−1.55	0.47
		90	0.56	1.06	3.11	−0.41	0.73
	Count	10	0.24	0.16	1.80	0.07	1.20
		50	0.66	0.68	6.55	0.21	1.59
		90	1.74	2.88	22.32	0.66	2.09

Fig. 2. Posterior distributions of habitat-specific conditional ln expected densities (holding random effects and ln turbidity at 0), from model g_1 for all size classes. Dots denote posterior median expected values, while thick bars represent 80% Bayesian CIs. The vertical red line denotes 0. CW: carapace width; SDH: shallow detrital habitat; SME: salt marsh edge
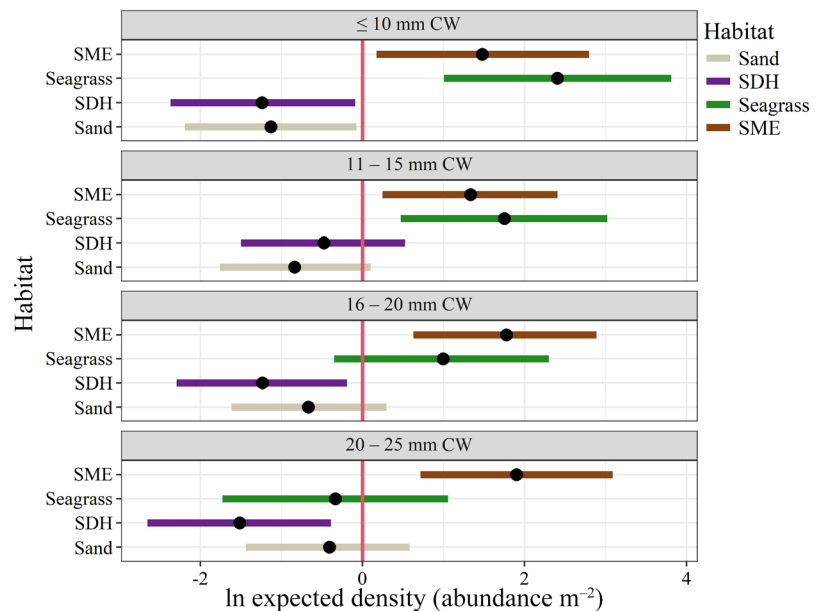
Table 3. Within-size class linear contrast depicting differences in expected juvenile blue crab density between habitats from Model g_1 (see Section 2.3.4). Percentages indicate 80% CI and median of differences in effect sizes, while the final 2 columns list the probability of a positive or negative effect. CW: carapace width; SDH: shallow detrital habitat; SME: salt marsh edge

Size class (CW, mm)	Contrast	10%	50%	90%	Pr > 0	Pr < 0
⩽10	SDH − sand	−0.80	−0.08	0.61	0.44	0.56
	Seagrass − sand	2.68	3.55	4.43	≈1.00	≈0.00
	Seagrass − SDH	2.78	3.67	4.44	≈1.00	≈0.00
	Seagrass − SME	−0.05	0.97	1.83	0.89	0.11
	SME − sand	1.80	2.65	3.43	≈1.00	≈0.00
	SME − SDH	2.00	2.72	3.39	≈1.00	≈0.00
11−15	SDH − sand	−0.17	0.37	0.88	0.80	0.20
	Seagrass − sand	1.77	2.54	3.34	≈1.00	≈0.00
	Seagrass − SDH	1.43	2.21	2.93	≈1.00	≈0.00
	Seagrass − SME	−0.42	0.41	1.16	0.74	0.26
	SME − sand	1.52	2.17	2.75	≈1.00	≈0.00
	SME − SDH	1.27	1.80	2.30	≈1.00	≈0.00
16−20	SDH − sand	−1.09	−0.57	−0.08	0.07	0.93
	Seagrass − sand	0.75	1.64	2.39	0.99	0.01
	Seagrass − SDH	1.38	2.23	2.98	≈1.00	≈0.00
	Seagrass − SME	−1.59	−0.77	0.02	0.11	0.89
	SME − sand	1.75	2.39	3.07	≈1.00	≈0.00
	SME − SDH	2.39	2.99	3.55	≈1.00	≈0.00
21−25	SDH − sand	−1.67	−1.14	−0.53	0.01	0.99
	Seagrass − sand	−0.86	0.04	0.92	0.52	0.48
	Seagrass − SDH	0.29	1.17	2.00	0.95	0.05
	Seagrass − SME	−3.19	−2.25	−1.32	≈0.00	≈1.00
	SME − sand	1.63	2.30	2.98	≈1.00	≈0.00
	SME − SDH	2.81	3.41	4.04	≈1.00	≈0.00

probability that a given contrast was positive all exceeded 90%, while the contrasts among habitats seagrass−SME and SDH−sand strongly overlapped with 0 (Table 3; Fig. S5).

3.2.3. Size class: 16−20 mm

Notably, density patterns began to shift for larger size classes. Juvenile density among the 16−20 mm size class was highest in SME (5.39 m^{-2} on the count scale), followed by seagrass (2.53), SDH (0.27), and sand (0.49) (Table 2, Fig. 2; Fig. S4). Pairwise linear contrasts for the 16−20 mm size class were similar to those of the 11−15 and ⩽10 mm size classes. For pairwise linear contrasts among habitats SME−SDH, SME−sand, seagrass−SDH, and seagrass−sand, the posterior probability that a given contrast was positive again all exceeded 90%, while for the contrast among habitats seagrass−SME, the posterior probability that the contrast was negative exceeded 90%. Similar to the 11−15 mm size class, the contrast among habitats SDH−sand strongly overlapped with 0 (Table 3; Fig. S5).

3.2.4. Size class: 21−25 mm

Juvenile densities of the 21−25 mm size class were notably higher in SME (6.55 m^{-2} on the count scale) than all other habitats (seagrass: 0.68; SDH: 0.21; sand: 0.66; Table 2, Fig. 2; Fig. S4). For pairwise linear contrasts among habitats SME−SDH, SME−sand, and seagrass−SDH, the posterior probability that a given contrast was positive again all exceeded 90%, while for the contrast among habitats seagrass−SME and SDH−sand, the posterior probability that the contrast was negative exceeded 90%. Finally, the contrast among habitats seagrass−sand strongly overlapped with 0 (Table 3; Fig. S5)

3.2.5. Comparisons among size classes

Within-habitat linear contrasts between the smallest (⩽10 mm) and largest (21−25 mm) size classes indicated changes in seagrass utilization with size (Fig. 2, Table 4; Fig. S6). Moving from the ⩽10 to 21−25 mm size classes, utilization decreased in seagrass meadows, but did not change appreciably in any other. The posterior probability of seagrass harboring fewer large crabs than small crabs was 90%,

Table 4. Within-habitat linear contrasts depicting differences in expected juvenile blue crab density between the smallest and largest size classes (i.e. the density of the smallest size class minus the conditional density of the largest size class, conditioned on holding ln turbidity and random effects at 0; see Section 2.3.4). Positive values indicate decreases in expected density as animals shift from ⩽10 to 21−25 mm (i.e. more ⩽10 mm than 21−25 mm individuals), while negative values indicate increases in expected density (i.e. fewer ⩽10 mm than 21−25 mm individuals). The first 3 rows indicate 80% CI and median values, while the final 2 rows list the probability of a positive or negative effect. SME: salt marsh edge; SDH: shallow detrital habitat

	Sand	Seagrass	SME	SDH
10%	−2.14	0.91	−2.13	−1.25
50%	−0.73	2.73	−0.41	0.28
90%	0.72	4.62	1.30	1.83
Pr > 0	0.26	0.97	0.38	0.59
Pr < 0	0.74	0.03	0.62	0.41

indicating strong statistical support. Meanwhile, the posterior probability of sand harboring more 21–25 mm crabs than ≤10 mm crabs was 74%, indicating weak to moderate support (Table 4; Fig. S6). Conversely, contrasts among size classes for SDH and SME were distributed approximately evenly across both negative and positive values, indicating considerable uncertainty and no discernible size effect.

3.3. Turbidity effects

Turbidity was positively associated with juvenile density across all size classes (Table 2, Fig. 3). Posterior distributions of regression coefficients for ln turbidity indicated a broadly positive effect, and the posterior probability that the effects of turbidity were positive exceeded 90% in all cases (Table 2, Fig. 3, right of red line).

3.4. Correlation between size classes

The posterior distribution of λ suggested that substantial dependence existed among size classes (Fig. 4). The posterior distribution of λ yielded a median (80% CI) of 0.97 (0.93–0.99), which indicated strong positive associations between size classes.
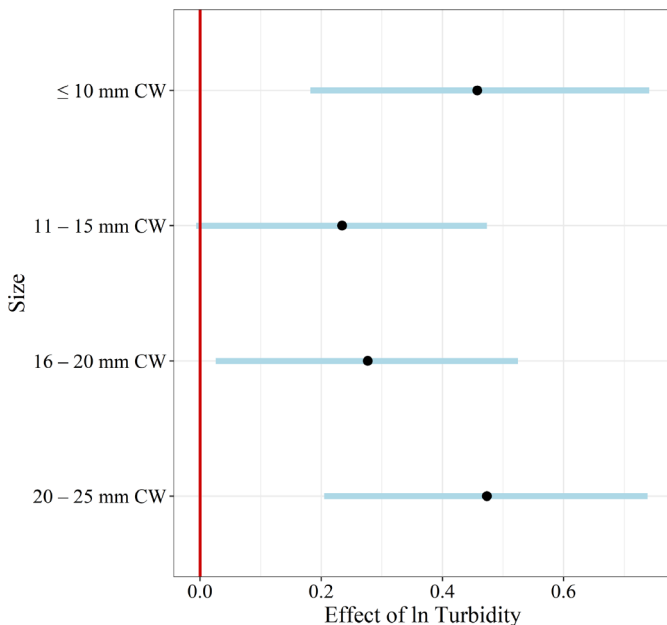

Fig. 3. Posterior summaries (median and CIs) for ln turbidity regression coefficients for all size classes. Dots denote posterior median difference in expected values, while thick bars represent 80% Bayesian CIs. The red line denotes 0. CW: carapace width
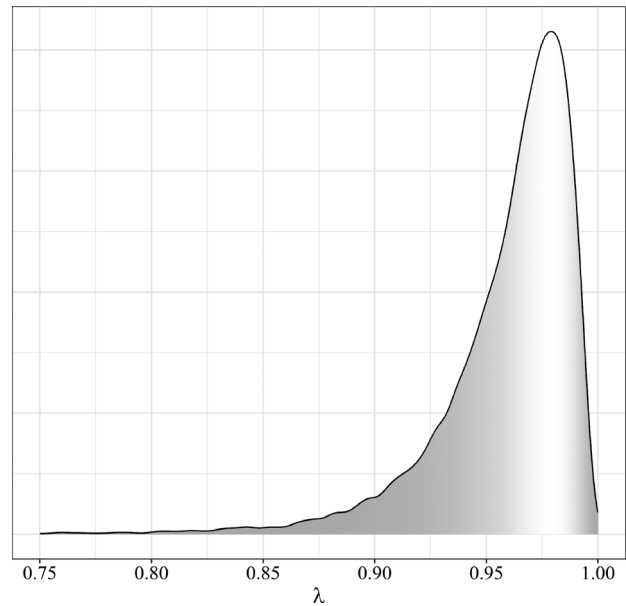

Fig. 4. Posterior distribution for the correlation parameter λ between juvenile size classes. Lighter colors denote areas of higher posterior probability

4. DISCUSSION

This study presents field- and model-based evidence of fine-scale differential habitat utilization among early juvenile blue crab stages and suggests that the current paradigm for blue crab early life history requires revision. Subsetting young-of-year juveniles into 5 mm size classes enabled us to deduce habitat shifts in density as juveniles grew, particularly among seagrass and SME. Our results are consistent with previous work emphasizing seagrass as an important nursery for the smallest juveniles (e.g. Lipcius et al. 2007), and suggest that SME represents an intermediate nursery habitat following secondary dispersal from seagrass beds but before occupying unstructured habitat commonly utilized by larger juveniles and adults (Lipcius et al. 2005). Our findings are novel in that they describe shifts in nursery habitats for juvenile blue crabs as a continuous process at smaller sizes than previously assumed (e.g. Lipcius et al. 2007). Moreover, after accounting for habitat-specific differences in density, turbidity was positively related to juveniles among all size classes. However, our experimental design could not address whether this effect is due to top-down (predation) or bottom-up (food availability) forces. Although more evidence (i.e. comparisons of survival and growth) is required to ascertain the exact role of structured marsh habitat in juvenile blue crab ecology, we posit that both sea-

grass and SME habitats are critical in maintaining adult populations and serve as nurseries across a continuum of juvenile sizes.

4.1. Size-specific habitat effects

In our study, juvenile blue crab density among the smallest size class was highest in structurally complex seagrass and SME habitats. Seagrass meadows harbored the highest densities of juvenile crabs in both the ≤10 mm and 11–15 mm size classes, which is consistent with previous work emphasizing this habitat as the preferred nursery for small juveniles (Orth & van Montfrans 1987, Perkins-Visser et al. 1996, Hovel & Lipcius 2002, Ralph et al. 2013, Voigt & Eggleston 2023). In addition, SME harbored high densities of juveniles in both the ≤10 mm and 11–15 mm size classes relative to sand and SDH. Postlarvae re-invading Chesapeake Bay likely encounter seagrass beds and other SAV such as the non-native macroalga *Gracilaria vermiculophylla* and preferentially choose these habitats for initial settlement (Stockhausen & Lipcius 2003, van Montfrans et al. 2003, Johnston & Lipcius 2012, Wood & Lipcius 2022). However, heterogeneity in hydrodynamic conditions can cause a substantial proportion of ingressing postlarvae to miss structurally complex SAV habitats (Stockhausen & Lipcius 2003). In addition, a proportion of early juveniles in SAV emigrate to alternative substrates to avoid adverse density-dependent effects (Etherington & Eggleston 2000, Blackmon & Eggleston 2001, Reyns & Eggleston 2004). High densities of juveniles observed in salt marshes at all spatial locations within the tributary likely reflect a combination of these 2 processes.

Densities of smaller juveniles (i.e. ≤15 mm) in SDH and sand were less than 1 m^{-2}, suggesting that these habitats were not readily utilized by juvenile blue crabs in these size classes. Although food availability can be high in sand, occupation by smaller juveniles in this habitat is likely discouraged by low structural refuge. Moreover, high densities of small juveniles were reported inhabiting SDH in North Carolina estuaries (e.g. Etherington & Eggleston 2000, Etherington et al. 2003, Voigt & Eggleston 2023), and small juveniles are also associated with high volumes of organic material in South American estuaries (Rodrigues et al. 2019). Yet we estimated far lower juvenile densities in similar habitat in the York River. It is unclear why SDH is an attractive habitat for juveniles in other locations but not within the York River, although differences in gear type or hydrodynamics as-

sociated with wind-driven vs. tidally driven estuaries may be responsible for these discrepancies. Specifically, logistical issues related to benthic scrapes may make this gear type inefficient when assessing abundance in SDH. Unlike sand, SDH is characterized by pitted surfaces and complex material, such that this gear type may be much less efficient in this habitat than efficiency estimates indicate. In addition, use of SDH may only occur at ebb tide. For example, the success of our flume nets was predicated on the notion that juveniles emigrate from the vegetated marsh surface to adjacent shallow water to remain inundated at ebb tide. However, we could not sample SDH at ebb tide using vessels due to depth limitations, and the soft mud substrate prevented the use of alternative methods (e.g. seine net) to assess the abundance of juveniles in SDH. Hence, it is conceivable that the use of SDH may be higher at ebb tide when juveniles cannot remain in SME. As a result, we caution that our abundance estimates may be overly conservative, and stress that additional studies using gear better suited to sample SDH (Voigt & Eggleston 2023) are required to validate our estimates.

Our estimated habitat-specific abundance patterns changed notably among juveniles at different size classes. Whereas juveniles ≤10 mm were more abundant in seagrass meadows than in SME, this pattern gradually reversed among larger juveniles. Decreases in habitat-specific density of progressively larger juveniles are understood to be a result of mortality or emigration. However, the degree to which either of these processes affects density is not clear. In contrast, the density of larger juveniles in SME did not change despite nearly certain losses from mortality, and is indicative of a possible shift in habitat utilization.

Patterns in size-specific habitat utilization observed here likely resulted from changing requirements of juvenile blue crabs with size. Seagrass meadows afford high survival to newly settled juveniles, particularly from smaller predators, due to the small interstitial spaces between shoots and rhizomes. In contrast, emergent salt marsh vegetation has higher interstitial space between shoots, allowing small predators such as the mummichog *Fundulus heteroclitus* to navigate and forage within the inundated marsh surface (Guillory & Elliot 2001). In the absence of juvenile density-dependent effects, smaller juveniles may prefer seagrass meadows because of the lower mortality risk when compared to salt marshes. However, upon reaching 10 mm CW, juvenile blue crabs begin to outgrow the mouth-gape sizes of many smaller predators, making salt marsh habitats increasingly favor-

able at progressively larger sizes (Orth & van Mont-frans 2002, Urban 2007). Furthermore, marsh shoots are dense enough to prevent larger predators from foraging effectively (Johnston & Caretti 2017, Miller et al. 2023). Salt marshes additionally harbor abundant detrital material, bivalves, and other invertebrates, which are consumed by juveniles to accelerate growth (Seitz et al. 2005). The combination of lower mortality risk from small predators and high food availability is consistent with mechanisms driving ontogenetic shifts in many marine species (Werner & Gilliam 1984, Dahlgren & Eggleston 2000), and accounts for shifts in utilization from seagrass to SME as juveniles grow.

Notably, an implication of our results is that small juveniles may traverse substantial distances to reach salt marsh habitat, particularly in upriver regions. Seagrass meadows currently only occur near the mouth of the York River, while salt marshes occur along shorelines as far as 50 km away. Yet we observed high abundances of juveniles in salt marshes regardless of spatial position within the tributary. This is consistent with previous work within the York River, which found high relative densities of 20–40 mm juveniles near upriver marsh habitat (Hyman et al. 2022), as well as work in the CAPES estuary system demonstrating the ability of small juveniles to utilize selective tidal stream transport and wind patterns to traverse long distances to alternative habitats (Reyns & Eggleston 2004, Reyns et al. 2006). Moreover, size distributions of juveniles within Chesapeake Bay among Maryland tributaries are consistently larger than those in Virginia (i.e. closer to the mouth of Chesapeake Bay), highlighting the ability of juveniles to emigrate long distances to find suitable intermediate habitats (Van Engel 1958).

Sand habitat utilization remained relatively consistent across different juvenile size classes; however, our findings hinted at statistically subtle upticks in sand utilization as the size of juveniles increased. Estimated densities of 21–25 mm juveniles in sand were nearly double those of juveniles ≤10 mm, although there was considerable uncertainty in these estimates, and the posterior probability that sand harbored more 21–25 mm juveniles was not high (i.e. <80%). Moreover, among all size classes, density in sand was much lower than in seagrass and SME. Results nonetheless suggested movement to unstructured sand by larger size classes, as densities among size classes in sand either did not appreciably change or subtly increased despite probable losses from mortality. If larger animals did not move into sand habitat to offset losses from mortality, we would have ex-

pected steady decreases in density from the smallest to the largest size classes. Hence, this pattern is consistent with movement to unstructured habitat after achieving a size refuge from predation at 21–25 mm (Lipcius et al. 2005, Rodrigues et al. 2019, Ortega et al. 2020).

Taken together with previous work and patterns observed in SME (Lipcius et al. 2005, Johnson & Eggleston 2010, Hyman et al. 2022), our results indicate a need to revise the current understanding of how juvenile blue crabs utilize habitats across multiple early-juvenile size classes. Although previous evidence supports shifts in blue crab habitat utilization at sizes exceeding 25 mm CW, our results suggest that juvenile blue crabs begin emigrating from seagrass meadows to salt marsh habitat as early as 10 mm CW, before potentially progressing to unstructured habitats at larger sizes (i.e. 25–55 mm CW; Lipcius et al. 2005). Emigration to SME by 21–25 mm juveniles would also explain patterns at larger spatial and temporal scales (Hyman et al. 2022), whereby density of juvenile blue crabs 20–40 mm CW was positively correlated with salt marsh habitat availability, especially in turbid areas. Although low densities of juveniles >30 mm CW prevented us from evaluating their use of salt marsh habitat, the present findings and related inferences would benefit from studies that consider additional size classes beyond those included here (e.g. 25+ mm CW size classes) to assess whether larger juveniles remain near marsh habitat or emigrate to adjacent unstructured habitats.

4.2. Turbidity

In our study, juvenile blue crab abundance was positively associated with turbidity across all size classes, although the magnitude of the association appeared to be size-class specific. The effect size of turbidity appeared strongest for the smallest (≤10 mm) and largest (21–25 mm) size classes, and had relatively weaker effects on intermediate (11–15 and 16–20 mm) size classes. High turbidity may increase juvenile abundance through both bottom-up and top-down forces. First, turbidity is positively associated with preferred food items of juvenile blue crabs: thin-shelled infaunal bivalves including the soft-shell clam *Mya arenaria* and Baltic clam *Macoma balthica* (Seitz et al. 2003, 2005). These species constitute a substantial proportion of juvenile blue crab diets and they aggregate near estuarine turbidity maxima within Chesapeake Bay tributaries (Seitz et al. 2003). Turbid upriver unstructured habitats are associated with

higher juvenile blue crab growth rates than those in downriver habitats (Seitz et al. 2005). Hence, association between turbidity and juvenile blue crab abundance may be a proxy for high prey abundance and bottom-up control. Second, turbidity may provide protection to juveniles from visual predators through a reduction in detectability (Cyrus & Blaber 1987, Ajemian et al. 2015, Marley et al. 2020), and it may also reduce cannibalism by larger congeners (O'Brien et al. 1976). However, many estuarine-dependent predators possess adaptations to forage using chemotactile sensors in low-visibility environments characteristic of estuaries, and as a result, it is unlikely that high turbidity provides more than a partial refuge from predation (Howson et al. 2022). The larger effect sizes at the ⩽ 10 mm size class suggest that at this size, turbid environments serve as a partial refuge, as the smallest juveniles likely prioritize survival over food. Moreover, the somewhat weaker positive effect of turbidity at intermediate sizes suggests that the refuge value of turbidity diminishes at larger sizes, and is consistent with animals increasingly achieving size refuges from predation. Finally, the relatively large positive effect size of turbidity in the 21−25 mm size class may suggest that at this largest stage, animals may be responding to increases in food availability associated with highly turbid environments.

5. CONCLUSIONS, LIMITATIONS, AND FUTURE WORK

Our results both underscore the value of salt marsh habitat for small blue crab juveniles and are consistent with the hypothesis that salt marshes represent a valuable intermediate nursery habitat as larger juveniles move from seagrass meadows to unstructured bottom through ontogeny (Werner & Gilliam 1984, Dahlgren & Eggleston 2000, Lipcius et al. 2005). Loss of salt marsh habitat may thus impose a bottleneck in population dynamics as small juveniles emigrate from seagrass beds.

However, this study comes with several caveats to be considered when interpreting the inferences drawn from the results. First, a major assumption of our work is that efficiency for all size classes was comparable. Although we included gear efficiency for each habitat in our analysis, gear efficiencies for different size classes may differ, particularly among the smallest animals. Unfortunately, data on gear efficiency as a function of juvenile blue crab size are unavailable. To ensure the robustness of our findings, future research should explore the viability of this assumption.

Second, our primary focus was on structurally complex habitats, but the vast majority of the York River consists of unstructured sand. Despite the low juvenile density in such areas, unstructured sand contributes significantly to adult populations in aggregate (Lipcius et al. 2005, Ralph 2014), aligning with the effective juvenile habitat hypothesis (Dahlgren et al. 2006). While our current study primarily examines ontogenetic patterns in juvenile blue crab habitat shifts, it would be ideal to incorporate the substantial contribution of unstructured sand at population scales.

Third, our study was not replicated spatially in other tributaries within Chesapeake Bay, nor was it replicated temporally at an annual scale. This lack of replication raises questions about the generality of our findings. Unfortunately, logistical constraints prevented us from expanding the replication beyond the York River on a biweekly temporal scale. Although our results appear to align with findings from a broad-scale study that examined salt marsh utilization patterns for larger juveniles across multiple tributaries in Chesapeake Bay (Hyman et al. 2022), we emphasize the need for future studies to replicate these investigations across multiple size classes and locations within Chesapeake Bay to ensure the broader applicability of our conclusions.

Fourth, we binned juveniles into 5 mm size classes based on other studies, but ontogenetic habitat shifts are likely a continuous function of size. Future work employing a continuous size model that is necessarily more complex, such as non-homogeneous Poisson-process, would more precisely describe ontogenetic shifts in blue crab habitat use with size.

Fifth, the uncertainty surrounding SDH sampling due to gear limitations and logistical challenges may be excessive. While we made efforts to sample this habitat, it is possible that it plays a significant nursery role similar to that described in other systems. Hence, future research should focus on evaluating the nursery role of shallow detrital habitats in Chesapeake Bay.

Finally, although juvenile abundance is a key metric when assessing the nursery function of salt marsh habitat, its role in population dynamics requires estimation of secondary production to the adult segment of a population by the use of additional metrics including survival, growth, and juvenile−adult linkage (Beck et al. 2001). For example, high juvenile abundance will not necessarily translate into high secondary production if survival of juveniles to adulthood is low. Further studies using additional metrics, such as growth and survival, concomitantly would help to clarify the role of salt marsh nursery habitats at the population level for blue crabs.

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