Population density, survival and movement of blue crabs in estuarine salt marsh nurseries

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ABSTRACT: The importance of a broad suite of complex structured habitats as nurseries for estuarine fauna is well recognized. In contrast, recent evidence indicates the nursery value of salt marshes and contiguous unvegetated mud flats for blue crabs are underestimated. To assess the nursery value of salt marsh tidal creeks for the blue crab *Callinectes sapidus* in coastal North Carolina, USA, we quantified population density, survival and movement patterns of juvenile blue crabs in 2 tidal salt marsh creeks during summer and fall. Survival rates of blue crab juveniles were high (0.98 d^{-1}) and similar in both creek systems. Juvenile crabs exhibited a high degree of site fidelity to a given marsh creek during summer–fall, suggesting that losses were predominantly due to mortality, not emigration. Our study provides critical information on the demographic processes underlying the importance of salt marshes as nurseries for estuarine-dependent species, and was novel in that it: (1) measured density, survival and emigration concurrently; and (2) enabled the identification of individuals, which allowed for the assessment of the relationship between blue crab size, survival and capture probability. We conclude that the observed patterns of abundance, survival and habitat utilization of blue crabs within tidal salt marsh creeks in North Carolina are consistent with the hypothesis that salt marsh creeks are important nurseries for blue crabs. Further, the relatively high use of the marsh surface by juvenile blue crabs, combined with a general lack of directed sampling within these complex habitats, suggests that crab densities may be even higher in salt marshes than previously thought.

KEY WORDS: Blue crab · *Callinectes sapidus* · Mark-recapture · Survival · Salt marsh

INTRODUCTION

Estuaries are composed of a mosaic of highly productive habitats. Within estuaries, structured shallow-water habitats such as seagrass, oyster reefs and salt marshes harbor high densities of fish and crustaceans and are thus recognized as important nurseries for many species (Nixon 1980, Boesch & Turner 1984, Zimmerman et al. 2000, Lipcius et al. 2005). The nursery function of estuarine habitats is of particular importance to conservation and management, and has received increasing attention in light of regulations that mandate the identification of essential fish habitat (EFH) for federally managed fishery species. Broadly defined, nurseries are those habitats that allow for

greater juvenile production as a result of a combination of factors favorable for: (1) high density, (2) growth, (3) survival and (4) efficient movement to adult habitats (Beck et al. 2001).

The blue crab *Callinectes sapidu* is a key benthic predator in the food web of estuarine and nearshore coastal habitats of the eastern United States and the Gulf of Mexico, and is capable of regulating populations of benthic and infaunal invertebrate prey (Eggleston et al. 1992, Seitz et al. 2001). The blue crab supports some of the most valuable fisheries on the Atlantic and Gulf of Mexico coasts of the US. Recent declines in blue crab stocks in Chesapeake Bay (Lipcius & Stockhausen 2002, Miller et al. 2005), Delaware Bay (Helser & Kahn 1999) and North Carolina (Eggle-

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ston et al. 2004), USA, have been largely attributed to overfishing, but also to habitat loss and fragmentation, indicating a vital need to understand the role of key nursery habitats for management and conservation efforts.

Like many estuarine-dependent species, the blue crab exhibits a complex life history which involves ontogenetic movements among marine and estuarine habitats. Although seagrass beds have long been considered the primary nursery areas for juvenile blue crabs because of their relatively high abundance and survival in these habitats (Orth & van Montfrans 1987, Etherington & Eggleston 2000, Etherington et al. 2003), the value of other estuarine habitats as nurseries for blue crab is currently unsettled. The importance of a broad suite of alternative habitats such as salt marshes, coarse woody debris, oyster reefs, unvegetated mud flats and shallow detrital habitats as secondary nurseries is becoming increasingly well understood (Everett & Ruiz 1993, Etherington & Eggleston 2000, Minello et al. 2003, King et al. 2005, Lipcius et al. 2005, 2007, Rakocinski & Drury McCall 2005, Seitz et al. 2005, Hines 2007). Further, these habitats may also serve as primary nurseries for young juvenile crabs that fail to settle in seagrass (Etherington & Eggleston 2000, 2003). In particular, recent evidence indicates that the value of salt marshes and shallow unvegetated mud flats as nurseries for blue crabs may be underestimated (Lipcius et al. 2005). This finding has prompted the development of a revised conceptual model of early blue crab life history (Lipcius et al. 2007).

To assess the nursery value of salt marshes for the blue crab in coastal North Carolina, we employed a series of complementary laboratory and field studies designed to quantify population density, survival and movement patterns of blue crabs in 2 tidal salt marsh creeks. Our investigation used well-established mark-recapture methods, but was novel in that it: (1) measured density, survival and emigration concurrently; and (2) enabled the identification of individuals, which allowed for the assessment of the relationship between blue crab size, survival and capture probability.

MATERIALS AND METHODS

Study sites. Juvenile blue crabs were sampled in 2 tidal marsh creeks, Prytherch Creek (PC) and Haystacks (HS), in the Newport River estuary near Beaufort, North Carolina, USA (Fig. 1). Intertidal zones within the study sites were composed mainly of the marsh grass *Spartina alterniflora*, while subtidal areas consisted of unvegetated mud with sparse macroalgae (predominately *Codium*) and small patch reefs of eastern oyster *Crassostrea virginica*. The study sites were

well suited for a mark-recapture study of mobile crabs because of the relatively high densities (0.1 to 1.2 crabs m^{-2}) of juvenile blue crabs and relatively small size of the study areas. Although only the unvegetated areas within each tidal creek could be sampled (PC = 1625 m^2, HS = 2028 m^2), we defined the total area our study site as the sum of the intertidal marsh and unvegetated areas within each system. The estimated area of intertidal marsh in each creek was 3275 m^2 in PC and 8270 m^2 in HS, for a combined total study area of 4900 m^2 (0.49 ha) in PC and 10 298 m^2 (1.03 ha) in HS. The actual area available to juveniles in each site is intermediate between these 2 measures since, although crabs clearly utilized the marsh edge, they were likely unable to access much of the high intertidal marsh.

Population sampling. During June to August 2001, PC was sampled on 10 occasions (mean sampling interval 4 d), while HS was sampled on 6 occasions during August to October 2001 (mean sampling interval 7.8 d). A 2 m beam trawl (0.76 cm mesh, 0.38 cm mesh codend) was used to collect juvenile and adult blue crabs (22 to 153 mm carapace width, CW). The beam trawl provides an efficient means of sampling blue crabs in shallow habitats because the width of the net is fixed and allowed for relatively accurate measures of animal densities, and the small size of the net and frame allowed manual towing immediately adjacent to the intertidal marsh in shallow water (<0.5 m). We focused our sampling effort to maximize the number individuals of captured to increase the precision of mark-recapture estimates. As a result, trawls were not standardized and gear efficiency not known, which precluded direct estimates of density from our trawls. A total of 1376 individual crabs was captured from PC over 10 sampling intervals and 1110 individuals from HS over 6 sampling intervals (Table S1 in the supplement at www.int-res.com/articles/suppl/m407 p135_app.pdf). Of these, 795 individuals were tagged and released in PC, and 347 individuals in HS. Three factors precluded the tagging and release of all captured crabs: (1) many crabs were smaller than the lower limit imposed by our tagging gear (22 mm); (2) crabs sustained damage from capture or interaction with conspecifics; or (3) recaptured crabs were sacrificed to obtain the coded microwire tag (CWT) which identified the initial date of capture and individual. An additional 386 crabs were collected from PC in late July and August to obtain length–frequency information; however, these data are not included in the Cormack-Jolly-Seber (CJS) modeling since sampling occurred after tagging had been terminated in PC. Captured crabs were sorted approximately by size (mm CW) and stored in dark holding containers filled with water to minimize agonistic encounters. Addition-
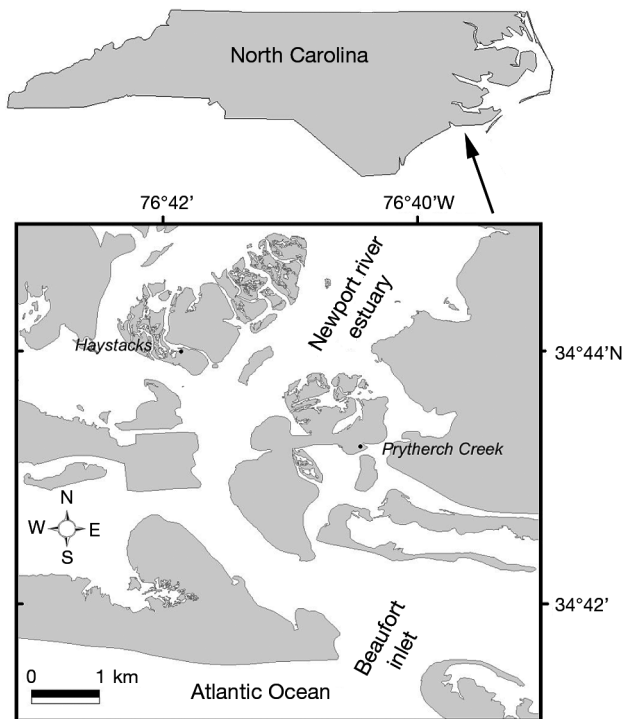
Fig. 1. Locations of salt marsh creek study sites at Prytherch Creek and Haystacks near Beaufort Inlet, North Carolina, USA

ally, containers were supplied with aeration to minimize physiological stress following capture. Both total and internal CW (Olmi & Bishop 1983), as well as sex, were recorded for each crab.

Crabs were tagged using stainless steel CWTs (Northwest Marine Technologies), which are numbered with a sequential numeric code and individually identifiable. CWTs have been previously used to quantify blue crab population size and survival in estuarine systems (van Montfrans et al. 1991, Fitz & Wiegert 1991b, 1992, Davis et al. 2005). Laboratory studies have demonstrated that CWTs have negligible effects on mortality and growth (van Montfrans et al. 1986, Fitz & Wiegert 1991a, Davis et al. 2004). CWTs were injected into the basal muscle of the 5th periopod, and were completely internal and retained through molting. After tagging, each crab was scanned using a magnetic moment detector to check for successful tag implantation and released in the approximate area of capture. During recapture efforts, captured crabs were checked for the presence of a CWT using a magnetic moment detector. Crabs with CWTs were not released, but were sacrificed and dissected in the laboratory to obtain the CWT for individual identification. Untagged crabs were tagged and released as described above. Capture histories were then used to generate CJS summary statistics for PC and HS (Table S1).

Mark-recapture analysis. Population abundance and maximum-likelihood estimates of apparent survival (ϕ) and recapture (p) probabilities were generated from individual capture histories using the CJS model framework (Cormack 1964, Jolly 1965, Seber 1965). The stochastic CJS model is useful for demographically open populations in which mortality, migration and recruitment occur (Manly 1984). Following standard CJS notation, ϕ_i is the probability of not dying or emigrating from the study site between periods i and $i + 1$, and p_i is the probability of being captured during period i. Estimates of population size ($\hat{N}_i$) for each sampling interval i were calculated as:

$$\hat{N}_i = n_i / \hat{p}_i$$

where n_i was the total number of individuals captured in period i and $\hat{p}_i$ was the probability of capture. The standard errors of $\hat{N}_i$ were calculated as:

$$\text{SE}(\hat{N}_i) = n_i / \text{SE}[\hat{p}_i] / \hat{p}_i^2$$

following the formula of Davidson & Armstrong (2002).

Goodness-of-fit and model selection. All CJS modeling used the program MARK (White & Burnham 1999) for parameter estimation and model selection. Goodness-of-fit (GoF) tests ensured that the CJS model provided an adequate fit to the data. Presently, there is no adequate method for assessing GoF with models containing covariates; therefore, GoF tests were performed on the most general model of time-varying survival and capture probabilities, with the size covariates omitted (Cooch & White 2008). To adjust for lack of fit, overdispersion in the data was quantified using $\hat{c}(\chi^2/df)$ from GoF testing (Lebreton et al. 1992) and, if necessary, used to transform Akaike's information criterion (AIC; Akaike 1973) values to quasi-likelihood adjusted AIC (QAIC$_c$) values. The preferred method to estimate $\hat{c}$, parametric bootstrapping (Cooch & White 2008), was inappropriate because tagged crabs were sacrificed at recapture.

Once an adequate fit to the fully time-dependent (ϕ_t, p_t) CJS model was established through GoF testing, reduced parameter models ϕ, p; ϕ, p_t; ϕ_t, p (model notation follows Lebreton et al. 1992), holding ϕ and p constant over all sampling intervals, were fitted to capture histories. Additionally, since crab size may affect the probability of capture and survival, CW was used as a covariate in some models. Survival and capture probabilities were constrained to linear and quadratic functions of CW. Individual covariates were standardized, $(x - \overline{x})/\text{SD}_x$, and estimators ($\phi$, p) were related to CW using a logit function with beta parameters estimated from MARK.

CJS model selection was based on QAIC$_c$, which was adjusted using $\hat{c}$ values generated from GoF testing. This is generally the preferred method for model selec-

tion, as it allows for comparison of a large number of candidate models without an inflation of experiment-wise error, and performs well when assumptions may be violated (Burnham et al. 1987). Models with $\Delta QAIC_c$ <7 are considered plausible, and models with a $\Delta QAIC_c$ <2 have approximately equal weight (Cooch & White 2008). Maximum likelihood estimates and standard errors of survival and capture probabilities were derived from model averaging of reasonably likely models ($\Delta QAIC_c$ < 7) for PC and HS.

Assumptions of the CJS model. Meeting the assumptions of capture-recapture models is critical to ensuring unbiased parameter estimates (Pollock & Mann 1983). The assumptions of the CJS model are: (1) all individuals in the population at a given sampling time have an equal probability of capture (this value can change over time); (2) every tagged individual has the same probability of survival; (3) tags are neither lost nor overlooked; (4) the duration of the sampling period is short (instantaneous) relative to the time between samples; and (5) animals are released immediately after sampling (Lancia et al. 1994). Below, we consider the assumptions of the CJS capture-recapture model employed in the present study and the degree to which these assumptions may have been violated.

Variation in capture probabilities among individuals (heterogeneity) can lead to positive or negative bias in estimates of population size (Pollock et al. 1990). When tagged individuals are more likely to be captured than untagged individuals, population size is underestimated since tagged individuals constitute a greater proportion of recaptured individuals than in the overall population. Conversely, if tagged individuals are less likely to be recaptured than untagged individuals, then population size will be overestimated. In the present study, we used a beam trawl to capture crabs within each study site. It is unlikely that the capture probabilities of tagged and untagged individuals differed because the efficiency of capture by actively trawling should be independent of tag status. Additionally, the shortest interval between sampling periods was 4 d, which should have been sufficient to allow for mixing of tagged and untagged individuals. A previous tagging study using blue crabs reported adequate mixing after several days (Fitz & Wiegert 1992).

Although the presence or absence of a tag is unlikely to affect capture rates, aspects of the ecology of blue crabs and large variations in size may lead to heterogeneous capture probabilities. Larger blue crabs are capable of faster movement rates, and may be more likely to evade sampling by the beam trawl than smaller crabs. This assertion was supported by field observations in which net avoidance by larger individuals was observed during field sampling within our study sites. Similarly, the smallest crab sizes are not sampled as effectively as larger crabs by trawl gear (Orth & van Montfrans 1987), leading to reduced capture probabilities for the smallest individuals. We addressed variation in capture probabilities by including CW as a model covariate, which allows the explicit estimation of capture probabilities as a function of size.

Survival rates are assumed constant for each tagged blue crab in the population. If tagging causes reduced survival of tagged individuals, then survival rates will be underestimated. Laboratory studies (van Montfrans et al. 1986, Fitz & Wiegert 1991a, present study) have demonstrated that microwire tagging has negligible effects on survival. Mortality rates may also vary as a function of body size since larger individuals attain a relative refuge from predation with size (Hines & Ruiz 1995). Smaller individuals also molt more frequently than larger crabs, and are particularly vulnerable to increased predation immediately following molting while in a soft-shell state (Ryer et al. 1997). Conversely, apparent survival of large crabs may be underestimated since large crabs are capable of relatively large daily movements (e.g. mean: 131 m d^{-1}; range: 0 to 569 m d^{-1}; Wolcott & Hines 1990), and are more likely to emigrate from study populations than smaller crabs. While we used CW as a covariate to assess size-specific differences in survival, a decrease in mortality with size may be balanced by an increase in emigration with size. The loss rates estimated in the present study likely represent mainly mortality, however, since smaller crabs composed 88 to 98 % of the study populations, and emigration rates for these sizes were extremely low.

The effects of tag loss include both direct and indirect consequences on parameter estimation. Most important is that tag loss will result in fewer recaptures and, consequently survival will be underestimated. Our estimate of tag retention (88 %) was similar to rates reported by van Montfrans et al. (1986), but lower than those (96 to 98 %) obtained by Fitz & Wiegert (1991a). High tag retention (Fitz & Wiegert 1991a) was likely a factor of the larger size of crabs used in their experiment (46.4 mm CW) versus the present study (27.6 mm CW). Both cases of tag loss in the present study were associated with the first molt following tagging, and occurred in the smallest individuals. In the present study, most tagged crabs were less than 40 mm CW, and therefore survival estimates were corrected for tag loss (Arnason & Mills 1981).

Laboratory estimation of tag retention and tag-induced mortality. A 37 d laboratory experiment (8 August to 12 September 2002) tested the effects of CWTs on blue crab mortality and estimated rates of tag retention (θ). A 2 m trawl was used to collect juvenile blue crabs (22.7 to 35.1 mm CW) from PC. This size range was representative of the population in both

Table 1. *Callinectes sapidus*. Mean (±SE) initial and final juvenile blue crab carapace width (CW), mortality and coded microwire tag retention estimates for tagged and untagged (control) crabs in a laboratory experiment. N = 15 crabs tagged and 15 crabs untagged (control). n/a: not applicable

	Initial CW (mm)	Final CW (mm)	Mortality (%)	Overall tag retention (%)	Tag retention between 1st and 2nd molts (%)
Tagged	27.6 + 1.1	41.2 + 1.6	7	88	100
Not tagged	28.0 ± 0.9	39.86 ± 1.95	13	n/a	n/a

study sites. Fifteen crabs were randomly selected and tagged, while 15 other crabs were not tagged and served as controls. Crabs were held in individual plastic containers in an aerated flow-through seawater table. Initial size of crabs did not differ significantly (Student's *t*-test, df = 28, p = 0.78) between tagged (27.58 mm CW ± 1.16 mm) and control (27.99 mm CW ± 0.88) individuals (Table 1). Crabs were fed to satiation at 1 to 2 d intervals with the snails *Littoraria irrorata* and fish, principally pinfish *Lagodon rhomboides* and killifish *Fundulus* spp. collected from local marsh creeks. Crabs were checked daily for mortality and molting. Recently molted crabs were allowed 1 to 2 d to harden prior to being measured and checked for tag retention. A Student's *t*-test was used to test whether or not tagging affected growth. The assumption of equal variances was tested using Levene's test. A χ^2 test was used to assess the effects of tagging on mortality.

Movement and habitat utilization. One disadvantage of the CJS model is the inability to separate the probability of loss $(1 - \phi)$ into mortality and emigration without additional information (Pollock et al. 1990). To quantify emigration rates of juvenile crabs from the marsh creeks and daily patterns of movement and distribution, individual crabs were externally tagged and tracked within PC and HS. Juvenile crabs (35 to 62 mm CW) collected from the study sites were fitted with numbered floats attached to the lateral spines by a short metal leader and 1 m of monofilament line (4 lb test). Floats were cylindrical (length: 25 mm, diameter: 11 mm) and weighed 0.45 g with vibrant reflective exteriors to facilitate relocation during night with approximately 5 mm of the float above the waterline during deployment. Due to the small size of the juvenile crabs in the present study, it was not feasible to use ultrasonic telemetry (e.g. Wolcott & Hines 1990) because of the relatively large transmitters required.

Crabs were highly mobile in pilot trials in the tidal creek systems, suggesting that the float did not significantly hamper movement in open water. While movement was not hampered in unvegetated habitats, crabs occasionally became tangled within the marsh grass; these crabs were removed from the analysis. The experiment was conducted in 4 batch releases (2 each at PC in June and HS in October), each consisting of 24 tagged crabs; the interval between trials at each site was no more than 4 d. Tagged crabs were released near slack flood tide at random locations within the subtidal non-vegetated areas of the study sites, and allowed 4 h to acclimate prior to tracking. Crabs were relocated visually every 1 to 2 h for 24 h. To track movement distance and direction, the location of each crab was plotted onto site maps relative to natural landmarks and PVC pipe stakes that were placed at 10 m intervals.

Two metrics were used to quantify movement distance within tidal creeks: (1) total distance traveled, defined as the sum of the linear distances between all sighting locations; and (2) net distance traveled, defined as the linear distance between the initial and final locations. An index of meander was also calculated as the ratio of net distance to total distance traveled. A meander value of 1 indicates directed movement, whereas 0 may indicate either random movement or a pattern of movement that varies in response to a periodic environmental forcing factor such as diel or tidal cycles. The fine-scale temporal resolution of our field observations (1 to 2 h) allowed for random and cyclical movement patterns to be differentiated, however, since the time between relocations was small relative to the period of diel and tidal cycles. Emigration rates were calculated as the proportion of crabs leaving the study area over 24 h. To determine microhabitat utilization, the habitat type (marsh vs. mud) was recorded for each resighting, and observations for individual crabs were stratified by tidal height relative to the marsh surface (flooded vs. exposed). The proportion of time each crab spent in each microhabitat was then calculated separately for periods when the marsh was flooded or exposed. Despite removing obviously entangled and immobile individuals from the analysis, the extent to which our tags impeded the travel onto marsh surface for those crabs not overtly entangled is not known. Thus, we refrained from performing statistical tests on the data and compare the observed proportions of habitat utilization during flood and ebb tides qualitatively.

RESULTS

Population structure

Blue crabs within the tidal marsh creeks consisted mainly of juveniles ranging from 6 to 79 mm CW; there

were few crabs greater than 120 mm CW (Fig. 2). Sex ratios (M:F) were 0.94 at PC and 1.03 at HS, and did not differ significantly from 1:1 at either PC ($\chi^2 = 0.859$, df = 1, p = 0.35) or HS ($\chi^2 = 0.16$, df = 1, p = 0.69).

Goodness-of-fit and model selection

Estimates of $\hat{c}$ were low (≤ 3) and indicate that the CJS model adequately fit the data sets from both locations (Lebreton et al. 1992), and that the assumptions of the CJS model were probably met. Estimates of $\hat{c}$ were 1.39 for PC and 0.34 for HS, and were used to correct

for overdispersion in the case of PC and calculate QAIC$_c$ (Burnham & Anderson 2002). Since correcting for underdispersion ($\hat{c} < 1$) is not suggested, a $\hat{c}$ of 1.0 was used for HS.

The full CJS model, allowing varying survival and capture probabilities over time, as well as reduced parameter models were fitted to the capture-recapture histories of crabs for PC and HS separately. QAIC$_c$ values for PC and HS were then used to rank the models from the candidate model set (Table S2 in the supplement; www.int-res.com/articles/suppl/m407p135_app.pdf). More complex models that allowed for capture and survival probabilities to covary with size
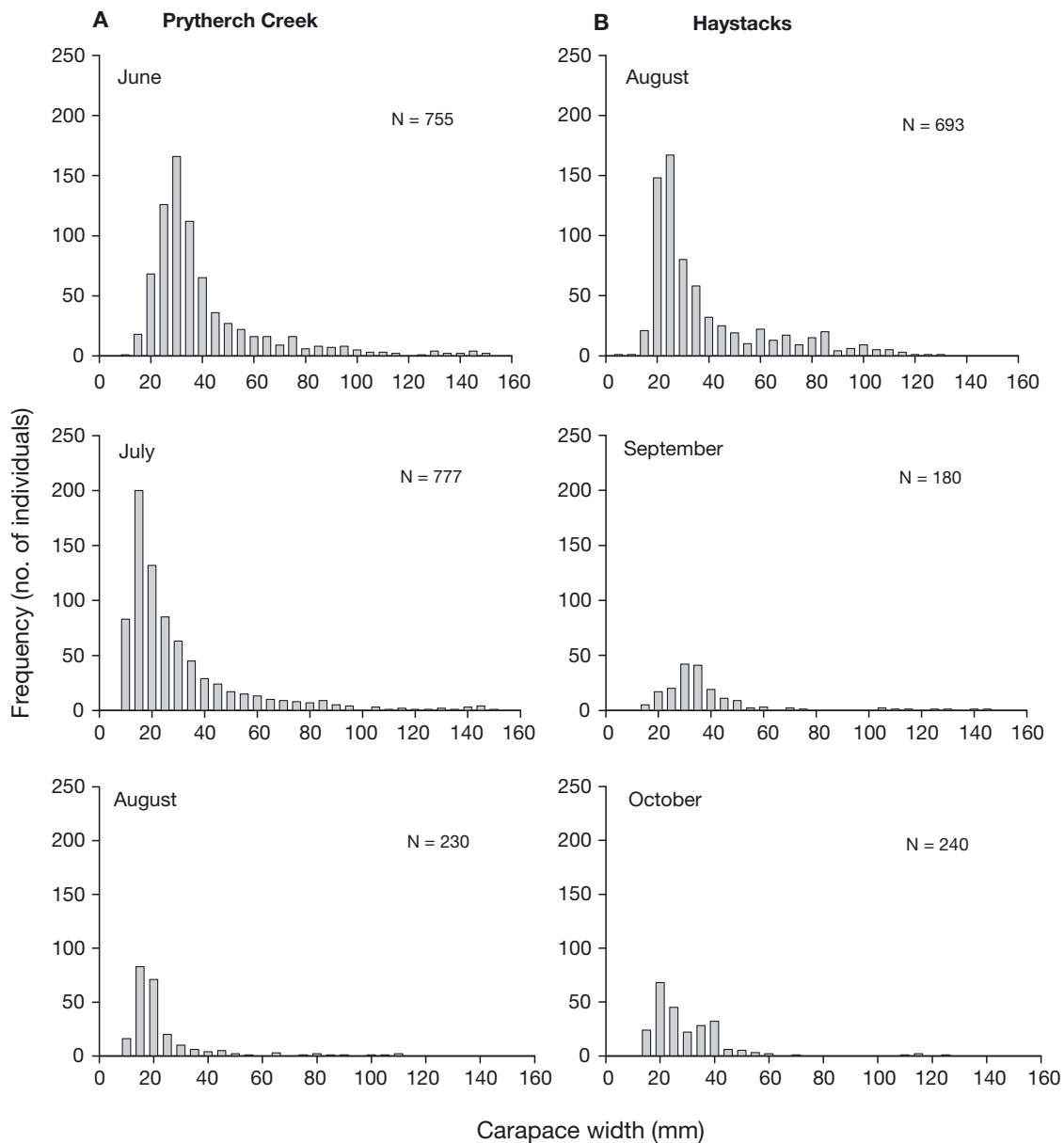

Fig. 2. *Callinectes sapidus*. Length–frequency distribution of blue crabs at (A) Prytherch Creek and (B) Haystacks study sites for each sampling month

(CW) were also fitted to the capture-recapture data. The smallest $QAIC_c$ for PC was obtained for the model with constant survival and time-specific probability of capture, where *p* was modeled as a quadratic function of size (CW) for the PC population (Table S2, Fig. 3). Because no single model clearly fitted the data better than another (Table S3 in the supplement; www.int-res. com/articles/suppl/m407p135_app.pdf), model averaging was used to generate apparent survival and capture probabilities (Burnham & Anderson 2002). For the HS population, the model with the best $QAIC_c$ assumed constant survival and time-specific capture probability, where survival was modeled as a linear function of CW, and probability of capture was modeled as a quadratic function of CW (Table S2, Fig. 3). As with PC, models with and without covariates generated similar overall estimates of survival and capture probability (Tables S3 & S4 in the supplement; www.int-res.com/ articles/suppl/m407p135_app.pdf), and model averaging was used to generate apparent survival and capture probabilities (Burnham & Anderson 2002).

Population size and demographic rates

Population size estimates at PC ranged from 1085 to 5096 crabs (Table 2) and were an order of magnitude larger than those from HS (range: 102 to 270 crabs). Mean crab density at PC was 12 000 crabs ha^{-1} (7000 to 33 000 crabs ha^{-1}) when considering only the subtidal
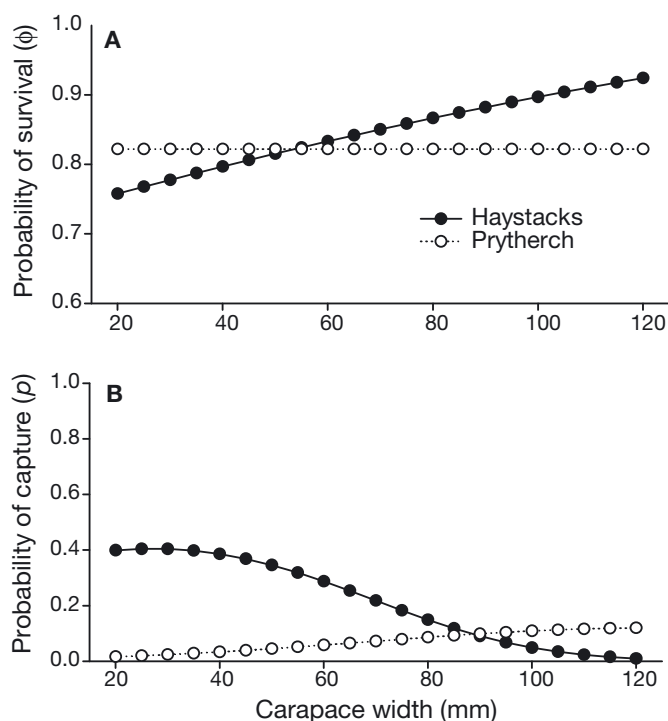

Fig. 3. *Callinectes sapidus*. Relationships between blue crab carapace width and Cormack-Jolly-Seber estimates of (A) survival and (B) capture probabilities for both Prytherch Creek and Haystacks study sites. Survival probabilities were modeled as linear functions of size, and capture probabilities were best described by quadratic functions. See 'Assumptions of CJS model' for justification for fitting linear and quadratic functions

Table 2. *Callinectes sapidus*. Estimates and approximate standard errors of juvenile blue crab population size (N), survival (ϕ) and capture probabilities (*p*) for populations in Prytherch Creek and Haystacks using Cormack-Jolly-Seber mark-recapture models. Estimates of tag retention (θ) were used to correct estimates of survival for bias due to tag loss ($\phi_i^c = \phi_i/\theta$)

Date	Period	N_i	SE	ϕ_i	SE	ϕ_i^c	SE	p_i	SE
Prytherch Creek									
11 Jun	1								
15 Jun	2	1085	363					0.17	0.05
19 Jun	3	1968	774					0.05	0.02
23 Jun	4	1447	424					0.10	0.03
27 Jun	5	1216	454	0.82	0.06	0.94	0.08	0.05	0.02
1 Jul	6	1866	797					0.04	0.02
5 Jul	7	1402	681					0.03	0.02
9 Jul	8	1548	552					0.03	0.02
13 Jul	9	5096	3995					0.02	0.01
17 Jul	10	2265	1315					0.03	0.02
	Mean	1988	1040	0.82	0.06	0.94	0.08	0.06	0.02
Haystacks									
22 Aug	1								
28 Aug	2	270	50					0.54	0.10
31 Aug	3	260	41	0.74	0.03	0.83	0.03	0.32	0.05
7 Sep	4	228	76					0.15	0.05
18 Sep	5	152	39					0.55	0.14
1 Oct	6	102	28					0.73	0.20
	Mean	202	47	0.74	0.03	0.83	0.03	0.50	0.05

area (0.16 ha) of the study site; however, when also including the area of the intertidal marsh that drained into PC (0.49 ha), mean density was 3918 crabs ha^{-1} (2214 to 10 400 crabs ha^{-1}). Estimates were an order of magnitude lower at HS, where mean density was 1000 crabs ha^{-1} (500 to 1300 crabs ha^{-1}) when considering the subtidal area (0.21 ha), and 202 crabs ha^{-1} (90 to 260 crabs ha^{-1}) when including both subtidal and intertidal marsh habitats within the study area (1.04 ha).

Apparent survival probabilities (ϕ) for each standardized sampling interval (4 d) were 0.82 ± 0.06 at PC and 0.72 ± 0.03 at HS (Table 2). Estimates of tag retention (θ) were used to correct estimates of survival (ϕ^c) for bias due to tag loss, and to calculate unbiased estimates of survival probabilities ($\phi^c = \phi/\theta$). After correction, survival probabilities increased to 0.94 ± 0.08 for crabs at PC and 0.83 ± 0.03 for crabs at HS for each 4 d sampling interval (Table 2). For comparison with estimated emigration rates (see below), which were daily probabilities, daily crab survival (ϕ_d) was calculated as $\phi_i = (\phi_d)^d$, where d is the time between sampling events in days. Mean survival probabilities corrected for tag loss were 0.98 ± 0.08 d^{-1} (0.94 = 0.98^4) for crabs at PC and 0.96 ± 0.03 d^{-1} (0.83 = 0.96^4) for crabs at HS. Coefficients of variation were 0.09 for PC and 0.04 for HS, indicating relatively precise parameter estimates. Following correction for tag loss, apparent survival, $\phi^c = 1 - $ (mortality + emigration), was partitioned using estimates of emigration from free-ranging blue crabs to calculate mortality.

There was no emigration from PC and the estimated emigration probability for HS was 0.02 d^{-1}, resulting in approximately equal estimated survival rates for both creeks (PC = 0.98 + 0.0 = 0.98; HS = 0.96 + 0.02 = 0.98). Estimates of capture probabilities were approximately 8-fold larger at HS, and more precise at HS (CV range at HS: 0.09 to 0.19; PC: 0.30 to 0.75). For example, mean recapture probability at PC was 0.06 ± 0.02 per sampling period, ranging from 0.02 to 0.17, whereas mean recapture probability at HS was 0.46 ± 0.10 per sampling period, and ranged from 0.15 to 0.73 (Table 2).

Tag retention and tag-induced mortality

Mortality of crabs in our 37 d laboratory experiment was low and did not differ significantly between tagged (7%) and control (13%) treatments ($\chi^2 = 0.28$, df = 1, p = 0.60). Of the 15 tagged individuals, 13 retained the tag through the 37 d laboratory experiment, resulting in a tag retention rate of 88% (Table 1). In both cases in which tags were shed, tag loss occurred during the first molt following tagging. All crabs that retained the tag through the first molt did so

through subsequent molts. Mean time to first molt, intermolt period and proportional increases in size after the first molt did not differ significantly between tagged and control treatments.

Movement in the field

Emigration rates of juvenile crabs from tidal creeks were low (0.02 crabs d^{-1} for HS, 0 crabs d^{-1} for PC), indicating high site fidelity in summer and fall. The mean total movement distance was 19 m d^{-1} at PC (range: 6 to 48 m) and 25 m d^{-1} at HS (range 4 to 50 m d^{-1}). Mean net movement was 12 m d^{-1} at PC (range: 6 to 23 m d^{-1}) and 18 m d^{-1} t HS (range: 4 to 37 m d^{-1}). The index of meander was 0.68 for PC and 0.73 for HS, indicating juvenile crabs exhibited relatively directed movement over a single day. Movement rates were slow, and averaged 0.77 and 1.09 m h^{-1} for PC and HS, respectively, and reflected the tendency of crabs to bury during low tide. There was no detectable relationship between movement rate and CW within the relatively small range of sizes tested in the present study.

While our objective was to quantitatively assess habitat use with our float-tagged crabs as a function of tidal inundation, the interpretation of the data was problematic due to statistical concerns and tangling of crabs in marsh. However, even after removal of entangled and immobile individuals from the analysis, several qualitative conclusions remained strongly supported by the data. Juvenile crabs demonstrated rapid and directed movement onto the vegetated marsh surface following release. Although all release locations were located in unvegetated areas of the study sites, most crabs were generally found in the marsh within hours of release and over 70% of subsequent crab relocations were on the marsh surface when the marsh was flooded. When the marsh was exposed, approximately equal numbers of crabs were observed to remain buried in the marsh (49%) versus entering subtidal muddy creek bottom (51%) at low tide. Despite a larger proportion of marsh edge at PC, we observed no clear differences in habitat utilization between sites.

DISCUSSION

Mark-recapture studies using microwire tags are a powerful tool for estimating demographic rates and habitat use of mobile crustaceans, information that is essential to quantifying the nursery value of a given estuarine habitat. The key findings from our complementary field and laboratory experiments were: (1) high survival of juvenile blue crabs in salt marsh

creeks; (2) juvenile crabs displayed a high degree of site fidelity with low emigration rates during summer and early fall; (3) crabs utilized the vegetated marsh surface during flood tide and often buried in mud during exposure of the marsh at during ebb tide; and (4) microwire tagging had negligible effects on crab growth and mortality. Our results indicate high survival rates and densities of juvenile blue crabs in salt marsh creeks and reinforce the current conceptual model that these habitats are important nurseries for this species (Lipcius et al. 2005, 2007). While there are many studies that report estimates of population density, mortality rates or movement rates for blue crabs, to our knowledge the present study is one of the first to estimate all quantities concurrently. It is also one of a few studies to apply mark-recapture techniques to juvenile blue crabs, and the first to allow for the identification of individual blue crabs and account for size-specific variation in capture and survival probabilities using mark-recapture modeling.

Population size and demographic rates

Densities of blue crabs estimated in the present study (7000 to 33 000 crabs ha^{-1} for PC and 400 to 1000 crabs ha^{-1} for HS) were similar to estimates from other salt marsh systems along the US East Coast during summer–fall: 800 to 48 000 crabs ha^{-1} (Orth & van Montfrans 1987, van Montfrans et al. 1991, Fitz & Wiegert 1992, Lipcius et al. 2005). Crab densities at PC were generally stable during the course of the study; however, estimates of population size near the end of the study at PC were extremely imprecise (particularly the estimate for 13 July 2001, which was 5096 ± 3995; Table 2) due to low recapture probabilities and associated large standard errors, making interpretation problematic. One advantage of CJS models is the ability to explicitly estimate capture efficiency within the model framework, and therefore provide estimates of absolute abundance. Estimates of population abundance are often difficult to obtain with traditional sampling regimes because they require that the sampling efficiency and selectivity of the sampling gear be known. Assuming catch efficiencies less than 100% (i.e. not all animals present are captured), densities will be underestimates of true abundance. Catch efficiency for the blue crab has been estimated for dredges (Volstad et al. 2000), trawls (Orth & van Montfrans 1987) and suction sampling (Orth & van Montfrans 1987), but interactions between gear type (Kneib 1997, Rozas & Minello 1997), habitat (Rozas & Minello 1997) and tidal stage (Kneib & Wagner 1994) make direct comparisons difficult.

Juvenile crabs at PC and HS were dominated by smaller size classes (6 to 39 mm CW). This finding is in contrast to size-specific patterns of relative abundance reported for blue crab populations in other marsh systems during summer and early fall. In Georgia marsh creeks, crab size ranged from 51 to 125 mm CW (Fitz & Wiegert 1991b, 1992), and crabs from 50 to 99 mm CW were most abundant in salt marsh systems within Chesapeake Bay (van Montfrans et al. 1991). These differences were apparent despite limiting our comparisons to those studies conducted during summer and fall to control for well-documented seasonal variation in size composition (Hines et al. 1987). However, key differences in sampling protocols may explain these differences in relative abundance. Fitz & Wiegert (1992) sampled exclusively in subtidal habitats (minimum depth 1.5 m), and van Montfrans et al. (1991) used block nets to capture crabs before they buried at low tide and uncovered buried crabs in the unvegetated intertidal mud flats by hand at low tide. An inverse relationship between crab size and distance traveled into the marsh has been reported (Arnold & Kneib 1983), with smaller individuals concentrated on the marsh surface relative to large crabs, which are restricted to the marsh edge at high tide (Kneib 1995). We sampled shallow areas immediately adjacent to the marsh edge (<0.1 m) until the study sites had completely drained of water at low tide, which likely allowed us to more effectively capture the smaller crabs found in these extremely shallow intertidal habitats.

The results from the present study indicate that densities of blue crabs in marsh systems may vary widely at local scales. Although the mechanisms underlying such differences remain unclear because sampling was not conducted concurrently, making direct comparisons between sites invalid, the differences in blue crab densities observed in the present study may reflect variability in recruitment, increased emigration from the HS site or differences in tidal creek morphology. In particular, several authors have noted the potential importance of creek morphology and microhabitat to overall habitat quality (Rozas et al. 1988, Hettler 1989). PC was smaller, composed of many pools and rivulets, and had a greater percentage of edge microhabitat relative to HS; 33% of the total marsh area in PC was classified as edge habitat (<3 m from unvegetated mud), while only 7% of the total marsh area in HS was edge habitat. Survival of blue crabs is higher along marsh edge microhabitats than the central channel of tidal creeks, and higher in small tidal creeks compared to large ones (Ryer et al. 1997). Other habitat features were qualitatively similar and probably did not contribute to differences in crab density. For example, creek bathymetry was similar and subti-

dal areas in both sites consisted of unvegetated mud with sparse macroalgae (predominately *Codium*) and small oyster patch reefs.

The probability of crab survival observed in the present study (98 % crabs d^{-1}) was similar to reported estimates for blue crabs using mark-recapture techniques in Chesapeake Bay during summer (92 to 94 % d^{-1}; van Montfrans et al. 1991), and to the highest loss rates observed in Georgia (60 % biweekly ≈ 97 % daily; Fitz & Wiegert 1992). Survival probabilities in our tidal marsh creeks were relatively constant over summer (PC, June to July) and early fall (HS, September to October), as has been reported for tidal creeks in Chesapeake Bay (van Montfrans et al. 1991, Ryer et al. 1997).

Survival increased linearly with size at HS, but not at PC, where survival was constant over all sizes (Fig. 3). The differing survival probability curves as a function of size for each creek may not be particularly surprising. First, while the best model differed between creek systems, models in which survival was assumed constant over all sizes and those that modeled survival as a linear function of CW were supported by the data in both creeks ($\Delta QAIC_c < 2$; Table S2). Second, the creeks were sampled during 2 different time periods; thus, the survival functions may have resulted from differing predator and cannibal suites or differences in habitat conditions. Nevertheless, the final estimates of survival did not differ significantly from models with and without covariates and weighted model averaging of survival across likely models reduced model selection bias (Burnham & Anderson 2002). Thus, we conclude that the survival rates estimated in the present study are representative of juvenile blue crabs in tidal creek systems since juveniles composed 88 to 98 % of the study populations.

The emigration rates observed in our movement study were extremely low, indicating that juvenile crabs display a high degree of site fidelity in tidal creeks during summer and early fall. Two additional sources of field sampling conducted at PC provided support for this finding: (1) beam trawling in areas immediately adjacent to the study sites failed to capture any tagged individuals; and (2) block netting at the entrance of PC, also failed to capture any blue crabs <100 mm CW leaving the site. Our findings are similar to those from experimental releases of hatchery-reared blue crab juveniles (~20 mm CW) in upper Chesapeake Bay, which generally remained within release coves of 0.4 to 8.0 ha in size (Davis et al. 2005, Hines et al. 2008). Further, the limited movement of juveniles in the present study is supported by telemetry studies in Georgia that reported male and immature female crabs (40 to 133 mm CW) utilized areas of 108 and 157 m^2, respectively, over a period

of 1 wk (Wrona 2004), areas significantly smaller than the total study areas used in our experiments (PC = 4900 m^2, HS = 10 358 m^2). Thus, the high site fidelity observed in the present study appears to be consistent for blue crab juveniles in shallow fringing marshes across estuarine systems of the eastern US. However, the low rates of emigration for juvenile blue crabs in low-energy salt marsh systems contrast sharply with the density-dependent and very rapid emigration rates of smaller juvenile blue crabs (2.1 to 9.1 mm CW) from seagrass beds near Oregon Inlet, NC (Etherington et al. 2003, Reyns & Eggleston 2004). Rapid emigration from submerged aquatic vegetation beds was also observed in pilot-scale translocation experiments with small juveniles (C1–C2) in Core Sound, NC (Eggleston et al. 2008). Thus, the probability of emigration is dependent on biotic and environmental factors including habitat, wind and currents, ontogenetic changes in blue crab dispersal behavior and crab density (Blackmon & Eggleston 2001, Reyns & Eggleston 2004, Reyns et al. 2006).

Utilization of marsh habitats

Juvenile crabs moved onto the marsh surface at high tide, a pattern consistent with earlier observations of habitat utilization in this species (Arnold & Kneib 1983, Fitz & Wiegert 1991a, Kneib 1995). We found that juvenile crabs were closely associated with the marsh edge, and rarely traveled more than 3 m into the marsh. While our method of tagging crabs impeded travel through the heavily vegetated marsh, Kneib (1995) also found that crabs rarely migrated far onto the marsh surface. Additional evidence that blue crabs migrate only partially into the marsh vegetation during high tide comes from data on predation rates by blue crabs on ribbed mussels *Geukensia dismissa* (Lin 1989, Stiven & Gardner 1992) and periwinkle snails *Littorina irrorata* (Lewis & Eby 2002), which decreased with intertidal elevation. Several authors have recognized the value of salt marshes as a refuge for juvenile fishes and crustaceans from predators (Boesch & Turner 1984, Zimmerman & Minello 1984, Rozas & Zimmerman 2000, Minello et al. 2003, Lipcius et al. 2005, Pallas et al. 2006). Juvenile crabs may experience a spatial refuge from cannibalism (Dittel et al. 1995, Hines & Ruiz 1995, Ryer et al. 1997) in the vegetated marsh, since adult conspecifics are physically impeded by dense vegetation and rarely move far into marsh habitats (Arnold & Kneib 1983, Kneib 1995, Kneib 1997). The marsh surface may also provide refuge to juvenile crabs by the exclusion of transient finfish predators that invade

inundated marsh creeks at high tide (Helfman et al. 1983, Rountree & Able 1992, Szedlmayer & Able 1993).

As the marsh became exposed at low tide, crabs buried within the marsh and unvegetated creek bottom. Burying behavior has been described for various life stages of the blue crab (Wilson et al. 1987, van Montfrans et al. 1991, Tankersley & Forward 1994). This behavior may represent a trade-off between predation risk and foraging behavior (Gilliam & Fraser 1987, Dahlgren & Eggleston 2000). Risk of predation in subtidal areas is likely increased, since greater densities of crabs are concentrated in subtidal habitats at low tide. Since crabs cannot actively forage while buried, the decreased risk of predation associated with burial may outweigh the benefits of continuous feeding. The ecological processes underlying size- and tide-specific habitat use of the marsh surface by juvenile crabs is unknown.

The patterns of high survival and abundance of blue crabs within tidal salt marsh creeks reported here are consistent with the findings of several authors (Minello et al. 2003, Lipcius et al. 2005, Lipcius et al. 2007), who concluded that salt marshes and associated unvegetated mud flats are important secondary nursery areas for decapod crustaceans, particularly blue crabs. Further, marshes may also serve as primary nurseries for young juvenile crabs that fail to settle in characteristic primary nurseries (e.g. seagrass; Lipcius et al. 2007), and may increase in value as the abundance of seagrass declines in many coastal estuaries (Lotze et al. 2006, Orth et al. 2006). The present study provides critical information on the key demographic processes underlying the importance of salt marshes as nurseries for estuarine-dependent species. Moreover, the observed use of the vegetated marsh surface by juvenile blue crabs, combined with a general lack of sampling within these complex habitats, suggests that crab densities may be even higher in salt marsh systems than previously thought.

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