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PARTITIONING LOSS RATES OF EARLY JUVENILE BLUE CRABS FROM SEAGRASS HABITATS INTO MORTALITY AND EMIGRATION

Lisa L. Etherington, David B. Eggleston and William T. Stockhausen

ABSTRACT

Determining how post-settlement processes modify patterns of settlement is vital in understanding the spatial and temporal patterns of recruitment variability of species with open populations. Generally, either single components of post-settlement loss (mortality or emigration) are examined at a time, or else the total loss is examined without discrimination of mortality and emigration components. The role of mortality in the loss of early juvenile blue crabs, *Callinectes sapidus*, has been addressed in a few studies; however, the relative contribution of emigration has received little attention. We conducted mark-recapture experiments to examine the relative contribution of mortality and emigration to total loss rates of early juvenile blue crabs from seagrass habitats. Loss was partitioned into emigration and mortality components using a modified version of Jackson's (1939) square-within-a-square method. The field experiments assessed the effects of two size classes of early instars (J1–J2, J3–J5), two densities of juveniles (low: 16 m⁻², high: 64 m⁻²), and time of day (day, night) on loss rates. In general, total loss rates of experimental juveniles and colonization rates by unmarked juveniles were extremely high (range = 10–57 crabs m⁻²/6 h and 17–51 crabs m⁻²/6 h, for loss and colonization, respectively). Total loss rates were higher at night than during the day, suggesting that juveniles (or potentially their predators) exhibit increased nocturnal activity. While colonization rates did not differ by time of day, J3–J5 juveniles demonstrated higher rates of colonization than J1–J2 crabs. Overall, there was high variability in both mortality and emigration, particularly for emigration. Average probabilities of mortality across all treatment combinations ranged from 0.25–0.67/6 h, while probabilities of emigration ranged from 0.29–0.72/6 h. Although mean mortality rates were greater than emigration rates in most treatments, the proportion of experimental trials in which crab loss from seagrass due to mortality was greater than losses due to emigration was not significantly different from 50%. Thus, mortality and emigration appear to contribute equally to juvenile loss in seagrass habitats. The difference in magnitude (absolute amount of loss) between mean emigration and mean mortality varied between size classes, such that differences between emigration and mortality were relatively small for J1–J2 crabs, but much larger for J3–J5 crabs. Further, mortality rates were density-dependent for J3–J5 juvenile stages but not for J1–J2 crabs, whereas emigration was inversely density-dependent among J3–J5 stages but not for J1–J2 instars. The co-dependency of mortality and emigration suggests that the loss term (emigration or mortality) which has the relatively stronger contribution to total loss may dictate the patterns of loss under different conditions. For older juveniles (J3–J5), emigration may only have a large impact on juvenile loss where densities are low, since the contribution of mortality appears to be much greater than emigration at high densities. The size-specific pattern of density-dependent mortality supports the notion of an ontogenetic habitat shift by early juvenile blue crabs from seagrass to unvegetated habitats, since larger individuals may experience increased mortality at high densities within seagrass beds. Qualitative comparisons between this study and a concurrent study of planktonic emigration of J1–J5 blue crabs (Blackmon and Eggleston, 2001) suggests that benthic emigration among J1–J2 blue crabs was greater than planktonic emigration; for J3–J5 stages benthic and planktonic emigration were nearly equal. This study demonstrates the potentially large role of emigration in recruitment processes and patterns of early juvenile blue crabs, and illustrates how juvenile size, juvenile density, and time of day can affect mortality and emigration rates as well as total loss and colonization. The components of population loss can have very different impacts at the population level on multiple spatial scales, which highlights the need to separate population loss into emigration and mortality.

Spatial and temporal variation in the recruitment of marine species with open populations (i.e., where local recruitment is uncoupled from local reproduction by a dispersive larval stage; Caley et al., 1996) is influenced jointly by events within the plankton, the settlement behavior of postlarval stages, and post-settlement mortality and emigration occurring before the time at which recruitment is measured by the observer. Thus, the factors underlying recruitment variability are a combination of physical and biological factors acting on the early life stages (Booth and Brosnan, 1995). Determining how post-settlement processes can modify patterns of settlement is vital in understanding the spatial and temporal patterns of recruitment variability.

Many studies have demonstrated a decoupled relationship between settlement and recruitment (review by Olafsson et al., 1994; Eggleston and Armstrong, 1995; Butler and Hernkind, 1997; review by Hunt and Scheibling, 1997; Steele, 1997), which suggests density-dependent post-settlement loss due to mortality or emigration. Rarely, however, has the impact of post-settlement immigration or emigration on population abundance been studied (but see Robertson, 1988; Iribarne et al., 1994; Lewis, 1997; Ault and Johnson, 1998). Further, the loss of individuals from a particular location over time is often measured as total loss, due to difficulty in separating loss into its two components, mortality and emigration (Manly, 1985), even though these components may have unique and independent population-level consequences. Thus, there is a need to separate population loss into the relative contribution of mortality and emigration to understand recruitment dynamics.

A density-dependent relationship has been identified between blue crab (*Callinectes sapidus*) juvenile settlers and recruits residing within seagrass habitats (Pile et al., 1996; Etherington and Eggleston, 2000). The process that regulates the population within these early juvenile stages, however, has not been identified. Pile et al. (1996) examined the role of predation in structuring this density-dependent relationship and found little evidence that predation-induced mortality was the source of density-dependent losses among these early juvenile stages from seagrass habitats. Instead, they suggested that emigration was the dominant process regulating early juvenile blue crab populations (Pile et al., 1996). In contrast, Perkins-Visser et al. (1996) demonstrated density-dependent mortality among early juveniles held in field enclosures, suggesting that cannibalism was the mechanism causing these patterns. In addition, Moksnes et al. (1997) detected increased agonistic interactions at high juvenile densities and suggested that this behavior could lead to increased emigration at higher densities. The relative contribution of emigration and mortality to overall loss of juveniles within seagrass habitats might be expected to change with juvenile size, whereby mortality decreases with increasing juvenile size (review by Hunt and Scheibling, 1997), and emigration increases with juvenile size, due to an ontogenetic shift in habitat use from seagrass to unvegetated habitats by older juveniles (Pile et al., 1996). In addition, demographic loss rates may vary between time of day due to behavioral responses of juveniles as well as their predators.

The present experiments were designed to separate the relative contribution of mortality and emigration in the loss of juvenile blue crab settlers (J1–J2) and recruits (J3–J5) within seagrass, and to examine the influence of conspecific density on these parameters. In addition, the experiments assessed the influence of time of day (day versus night) on relative rates of emigration and mortality among the two size classes. The objectives of this study were to 1) understand the relative contribution of emigration and mortality to loss of early juvenile blue crabs from seagrass habitats; 2) determine if these loss rates vary as a function of juvenile

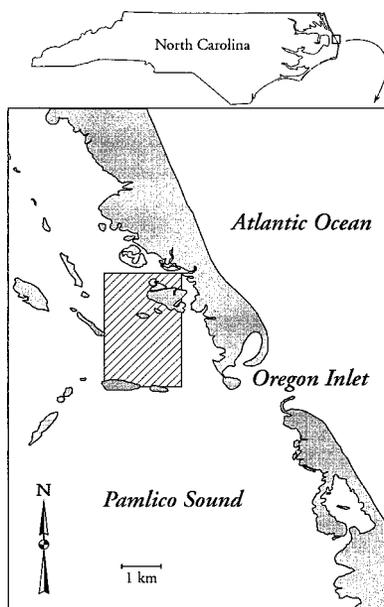


Figure 1. Study site of mark-recapture experiments in seagrass beds within Pamlico Sound, northwest of Oregon Inlet, North Carolina, U.S.A. The hatched rectangular area represents the region in which field mark-recapture experiments were conducted.

size class; 3) assess the influence of time of day on loss rates; 4) determine if emigration and mortality rates are density-dependent; and 5) examine juvenile rates of total loss and colonization in seagrass and determine how these rates vary over size class, time of day, and density.

MATERIALS AND METHODS

STUDY REGION.—Mark-recapture experiments were conducted within a 2 km \times 3 km region approximately 3 km northwest of Oregon Inlet, North Carolina, U.S.A. (Fig. 1). This region contained a mosaic of benthic habitats dominated by seagrasses and sandy bottom. Seagrass beds within this area were composed of *Zostera marina*, *Halodule wrightii*, and *Ruppia maritima*. The size of seagrass patches varied throughout the area, but was skewed towards larger (>1 ha) continuous beds (Etherington, pers. obs.). This region is influenced by both tidal and wind-driven currents, with a mean tidal range of 80 cm and an extremal range of 120 cm (Pietrafesa and Janowitz, 1991). Experiments were conducted from October 7–November 1, 1998. During this time period, temperatures ranged from 12 to 24°C and salinity varied between 21 and 34 psu. The water depth at the experimental plots ranged from 0.3 to 1.0 m.

EXPERIMENTAL THEORY.—The relative contribution of mortality and emigration to the population dynamics of early juvenile blue crabs was assessed with mark-recapture experiments using a new approach for the Jackson method of separating total loss from an area into these two components (Jackson, 1939; Manly, 1985; Stockhausen, unpubl. manuscript). Manly (1985) discusses the potential application of the Jackson method as a modification to standard methods of mark-recapture (e.g., Jolly-Seber method; Jolly, 1965; Seber, 1965), to allow for emigration when estimating survival. Overall, Manly (1985) concluded that the Jackson method of separating death and emigration with mark-recapture data is a relatively simplistic technique that can be used with confidence.

The general principle of the Jackson square-within-a-square method is that emigration has more of an effect on a small area than on a large area, thus allowing one to subtract survival estimates from two different sized areas to determine an estimate corresponding to no emigration (Manly, 1985). Using this technique, a square area is divided into four smaller squares. The assumption is that the emigration rate from the small square is twice that of the total area, since the relative periphery of the small square is twice that of the large area (Fig. 2). That is, for the large square, the area equals 4 and periphery equals 8; thus the periphery:area ratio is 2. For the small square, the area equals 1

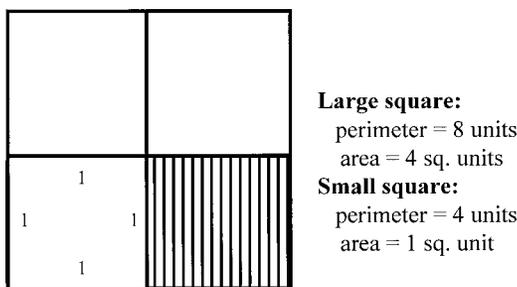


Figure 2. Schematic of mark-recapture experimental framework (Jackson, 1939). The shaded area represents one of the small squares. "1s" represent the perimeter units for the small and large squares, with an example given for the perimeter units for one small square. Each small square represented 0.25 m^2 in this experiment. See text and appendix for further details.

and periphery equals 4; thus the periphery : area ratio is 4. If the emigration rate is proportional to the periphery : area ratio, then the emigration rate in the small square is twice that of the large square ($4:2 = 2$). One assumption of this method is that the mortality rate is equal in both squares (small and large). It is also assumed that there is no directional bias in animal movement. Since there are two areas (small and large; Fig. 2), we end up with two simultaneous equations describing retention probabilities within the two different-sized areas which can then be solved for emigration and mortality.

Despite the apparent simplicity of the Jackson method, there are several problems associated with results obtained from such analyses (see Appendix). For example, when emigration is high, the expected ratio of emigration in the small and large squares is no longer 2, but approaches 1 as emigration increases, and therefore the method produces biased estimates (see Appendix). Also, where the number of marked individuals is small, nonsensical results can be obtained due to the stochastic nature of the estimated retention probabilities (see Appendix). To correct for these and other potential deficiencies of the Jackson method, we used a new approach based on Bayesian Analysis (Stockhausen, unpubl. manuscript) to partition loss of early juvenile crabs into emigration and mortality components using a single marking of a finite population of known density followed by a single recapture event [see Appendix for details].

EXPERIMENTAL DESIGN.—Experimental juvenile blue crabs were collected by dipnetting in seagrass areas. Individuals were first sorted by size class (J1–J2: juvenile instars 1&2 (2.1–4.2 mm CW) and J3–J5: juvenile instars 3–5 (4.3–9.1 mm CW); see Pile et al., 1996 for size class information). Juveniles were then placed in aerated tanks with one of two dyes, neutral red or methylene blue, where they remained for 12 hours. The concentration of neutral red solution was 1.43 g/l (Perkins-Visser et al., 1996), whereas the concentration of methylene blue was 0.12 g/l . The concentration of methylene blue was derived from preliminary staining trials designed to find the minimum concentration needed for juvenile crabs to retain their color for the 6 h experimental period. From observations of unstained and stained individuals after the 12 h holding period, we concluded that behavior, activity, and overall health appeared similar between the groups (Etherington, pers. obs.). Preliminary work has demonstrated that these size classes retain the two stains for over 24 h and can be easily distinguished from each other and unstained individuals through examination of the gills and antennules under a dissecting microscope (Etherington, unpubl. data).

To create the experimental plot, we marked out a 1 m^2 area with PVC stakes within a large seagrass bed, so that all sides of the plot were surrounded by continuous seagrass. The plot was further divided into four smaller squares (0.25 m^2 each) (Fig. 2). At the initiation of an experiment, the interior of the 1 m^2 plot was swept with a dipnet ($790 \mu\text{m}$) to remove juvenile crabs that were within the size class of the experimental treatment. The remaining macrofaunal community was replaced within the square. Four 0.25 m^2 wooden sieves with $500 \mu\text{m}$ mesh were then placed upside down on each of the four small squares and held into place with concrete blocks. Experimental treatments of juvenile crabs were then introduced under the sieves—three of the small squares received crabs dyed color 1 (red or blue chosen randomly) and one small square received crabs dyed color 2. The square that would serve as the "small" square, which would receive color 2, was chosen randomly. The entire 1.0 m^2 plot will be referred to as the "large" square. Each of the small squares (0.25 m^2) received either 4 or 16 juvenile crabs, depending on whether the treatment level of density was low (16 crabs m^{-2}) or high (64 crabs m^{-2}), respectively (see *Statistical Analyses*). The juvenile crabs were allowed to acclimate under the sieves for 15 min, after which time the sieves were carefully removed.

Preliminary trials of 12 h experimental periods yielded low recapture rates (Etherington, unpubl.

data); therefore, the experimental period was reduced to 6 h. Six hours after the juvenile crabs were introduced to the plot, sieves were quickly placed over each of the four small squares and held into place with concrete blocks. One at a time, a sieve was replaced by an open-ended metal recapture square and the area enclosed was sampled. Sampling consisted of suction sampling similar to the techniques described by Orth and van Montfrans (1987), with a modified 3.0 m extension hose to enable sampling within the 0.25 m² recapture area. The enclosed area was also swept by a dipnet to ensure complete recapture. From these recapture samples, we measured 1) the retention rate of juvenile crabs (color 2) within the small square (ψ_s) that were originally introduced into that same small square, and 2) the retention rate of all stained individuals (colors 1 and 2) within the large square (ψ_L). Retention rates represent the proportion of crabs which both survived and remained within the area (did not emigrate). These retention rates were then used to determine probability rates of mortality and emigration within each experimental plot using the modified approach for Jackson's square-within-a-square method (see Appendix).

STATISTICAL ANALYSES.—To test the assumption of the Jackson method that there was not a directional bias in juvenile movement within the experimental plots, Chi-square analyses were performed on the recapture data from each of the 1.0 m² experimental units before further analyses were conducted. The observed number of stained juveniles within each of the four small square quadrats was compared with expected values (one-quarter of the total number of stained individuals recaptured within the large square). We rejected the null hypothesis that the observed recaptures were no different than expected values in only one of the 48 experimental plots. This one replicate, therefore, failed to meet the assumption of the Jackson method and was removed from subsequent analyses.

The key response variables in this study were the probabilities of mortality and emigration relative to total loss from our experimental plots. Since the total loss varied between each experimental unit (plot), weighting emigration and mortality by this total loss would give us more confidence in the estimates than using each estimate as an independent response variable. Therefore, the probabilities of mortality and emigration were converted to their contribution to total loss by dividing the probability (emigration or mortality) for each observation by the total loss for that experimental plot. These two indices of contribution to loss were then used as separate response variables in ANCOVA analyses. A single multivariate ANCOVA was not used, since emigration and mortality were obtained jointly, and therefore were not independent. We tested whether the contribution of mortality and emigration to total loss rates of early juvenile crabs varied between time of day (day, night), juvenile size class (J1–J2, J3–J5) and juvenile density (low: 16 crabs m⁻², high: 64 crabs m⁻²) with two separate fixed factor, three-way ANCOVA models with seagrass characteristics, the potential predator guild, and density of unstained juvenile immigrants as covariates (see below for details of covariates). In addition to examining emigration and mortality separately, we were also interested in total loss rates of juveniles, as well as juvenile colonization rates within seagrass, and how these rates might vary as a function of the different experimental factors. Thus, three additional ANCOVAs were performed with the following response variables using the same factors and covariates as described above: 1) the proportion of stained experimental juveniles lost m⁻²/6 h, 2) the numbers of stained experimental juveniles lost m⁻²/6 h, and 3) colonization, which was the number of unstained juveniles of the same size class as the experimental treatment in the recapture sample (m⁻²/6 h). Crab loss was examined as both the proportion lost as well as the number lost so that we could evaluate differences between factors on a standardized scale, as well as observe general trends in loss over the different factors. The sample sizes for each treatment combination were unequal due to logistical constraints, and ranged between 4 and 8. Student-Newman-Keuls (SNK) a posteriori multiple comparison tests were conducted to interpret interaction effects.

Since mortality and emigration were calculated jointly from retention rates, and thus were not independent of one another, we could only examine qualitative differences in magnitude (absolute amount of loss) between mean emigration and mean mortality across experimental treatments. We also determined whether one process (mortality or emigration) was dominant; i.e., was the proportion of experimental trials for which crab loss due to mortality (or emigration) was greater than loss due to emigration (or mortality) significantly different than 0.5? To determine whether a particular loss term was dominant, we conducted binomial tests over all treatment combinations, examining the number of trials that had mortality rates greater than emigration rates, and vice versa, to determine if these values were significantly different from 0.5.

Juvenile size classes were selected to represent recent settlers (J1–J2: 0–16 days since settlement) and early recruits (J3–J5: 14–46 days since settlement) (Etherington and Eggleston, 2000) that are beginning to emigrate from seagrass to surrounding unvegetated habitats (Pile et al., 1996). Experimental densities represented low and high values in the ranges of natural juvenile densities within the region (Etherington and Eggleston, 2000), and were chosen to create a sufficiently large contrast in crab density to detect differences in responses between densities. Due to spatial and seasonal changes in abundance and species composition of the benthic community, a measure of potential predator abundance (obtained from recapture sampling) was included in the analyses as a covariate. The clas-

sification of potential predators was specific to each juvenile size class, based on size and behavioral characteristics of the predator and prey, as well as published literature on predation. The animals included as potential predators on J1–J2 blue crabs were: blue crabs (*Callinectes sapidus*) >J2 (Moknes et al., 1997), penaeid shrimp (*Penaeus* sp.), eels (*Anguilla rostrata*), toadfish (*Opsanus tau*) (McDermott, 1965; Bisker et al., 1989), croaker (*Micropogonias undulatus*), and skillettfish (*Gobiesox strumosus*). For the J3–J5 size class, potential predators were: blue crabs (*C. sapidus*) >J5, eels (*A. rostrata*), toadfish (*O. tau*), croaker (*M. undulatus*), and skillettfish (*G. strumosus*). Seagrass characteristics (shoot density, shoot length, shoot biomass), which were obtained from a 7.5 cm diameter core sample taken adjacent to the experimental plot, were also included as covariates since variation in habitat complexity could influence mortality and emigration rates (review by Heck and Orth, 1980a). Immigration of juveniles could also influence the response variables; therefore, the number of unstained juvenile immigrants recaptured within the large square was also used as a covariate.

Initially, the full ANCOVA models included all main factor \times covariate interaction terms to examine assumptions of homogeneous slopes of the regressions (Underwood, 1981). All of these interaction terms were non-significant ($P > 0.08$), and were therefore dropped from the final models. Where covariates did not explain a significant amount of variation in the response variable ($P > 0.05$), they were removed to simplify the model. As a result, all ANCOVA models were reduced to ANOVA models since covariates did not explain a significant amount of variation in the various response variables. Only in two cases did covariates have P values that were relatively low ($0.05 < P < 0.10$): 1) the influence of the number of juvenile immigrants on emigration and 2) the influence of the number of potential predators on numbers of juveniles lost. Thus, these specific covariates may be influential in juvenile blue crab loss, as indicated by lower P values, and therefore require further investigation.

Multiple experimental 1.0 m² plots were used in a single time period and were separated from each other by a minimum distance of 50 m. Haphazard dip-netting conducted throughout the seagrass beds between the 1.0 m² plots yielded no stained individuals, thus suggesting that there was no "leakage" of stained individuals between 1.0 m² plots, and that the experimental plots located 50 m from each other were statistically independent over a 6 h period. Variances were tested using Levene's test, which indicated that the assumptions of homogeneity were met. In only one analysis (number of juveniles lost) was the response variable log-transformed to meet the assumption of homogeneity of variances.

RESULTS

LOSS AND COLONIZATION OF JUVENILES IN SEAGRASS.—Overall, juvenile loss rates were very high, with average total losses of 0.86 and 0.79 (proportions of marked crabs lost m⁻²/6 h) for the small and large square, respectively. Proportional loss (proportions of marked crabs lost per 0.25 m²/6 h) within the small square ranged from 0.37 to 1.00, while loss from the large square ranged between 0.43 and 0.98. In 21 of the 48 experimental plots, no crabs were recaptured within the small square. For statistical analyses, we used both the proportion of marked crabs lost from each 1.0 m² experimental plot, as well as the number of juveniles lost within the 1.0 m² large square over the 6 h experimental period. The proportion of juveniles lost did not vary as a function of crab density (ANOVA; $F = 2.53$, $df = 1, 39$, $P = 0.120$) or crab size (ANOVA; $F = 2.82$, $df = 1, 39$, $P = 0.101$). In contrast, proportional loss varied according to time of day (Fig. 3; ANOVA; $F = 17.04$, $df = 1, 39$, $P < 0.001$) with higher loss at night than during the day (Fig. 3). None of the interaction terms were significant (all $P > 0.12$). The number of juveniles lost varied as a function of crab density (Fig. 4a, b; ANOVA; $F = 1,047.60$, $df = 1, 39$, $P < 0.001$) and time of day (Fig. 4a, b; ANOVA; $F = 16.16$, $df = 1, 39$, $P < 0.001$), with higher losses at high density compared to low density, and higher losses at night than during the day (Fig. 4a, b). Crab size did not influence juvenile loss (Fig. 4a, b; ANOVA; $F = 2.52$, $df = 1, 39$, $P = 0.12$). None of the interaction terms were significant (all $P > 0.10$).

Through the recapture sampling, we were also able to assess juvenile colonization (movement into the experimental plot) by measuring the number of unstained juveniles (of the same size class as that of the experimental crabs) recaptured within the 1.0 m² large square. Colonization rates over the 6 h experimental period were fairly high, ranging between 17–28 crabs m⁻²/6 h and 40–51 crabs

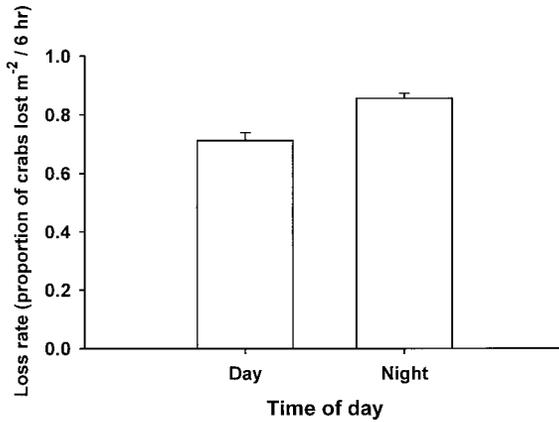


Figure 3. The effect of time of day (day, night) on the proportion of juveniles lost m⁻²/6 h. Values are means + 1 SE. n = 4 to 8.

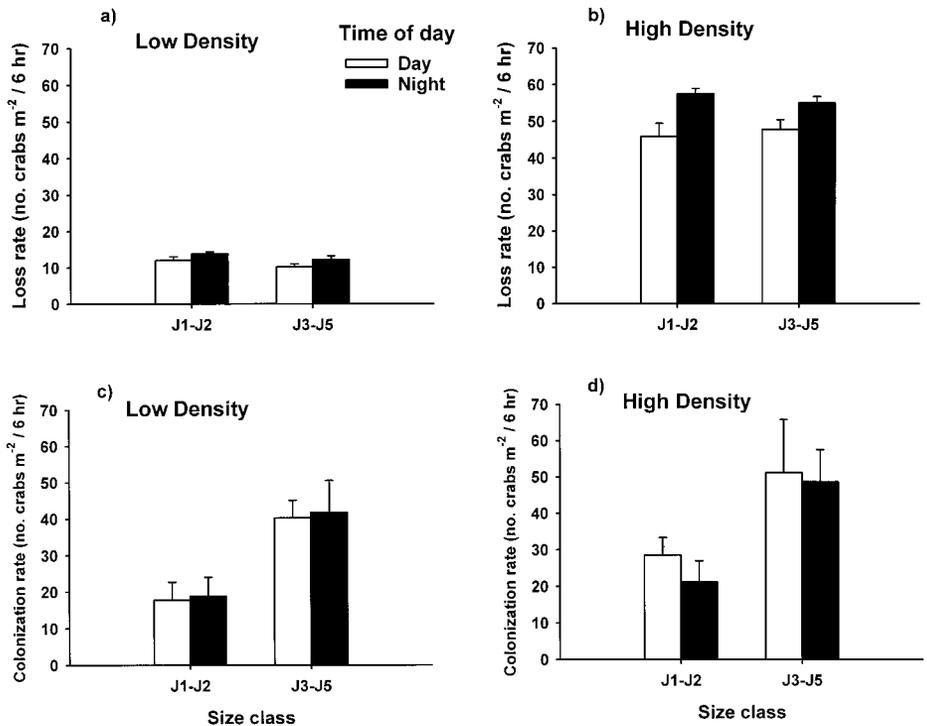


Figure 4. Comparison of loss (a & b) and colonization (c & d) rates of early juvenile blue crabs according to size class (J1–J2, J3–J5), crab density (low, high), and time of day (day, night). The rates represent the numbers of juveniles lost or colonized m⁻²/6 h. Note that the low-density treatment represents experimental plots where 16 crabs m⁻² were introduced, while the high-density treatment had 64 crabs m⁻². Therefore, one would expect higher loss rates at high than low density. Values are means + 1 SE. n = 4 to 8.

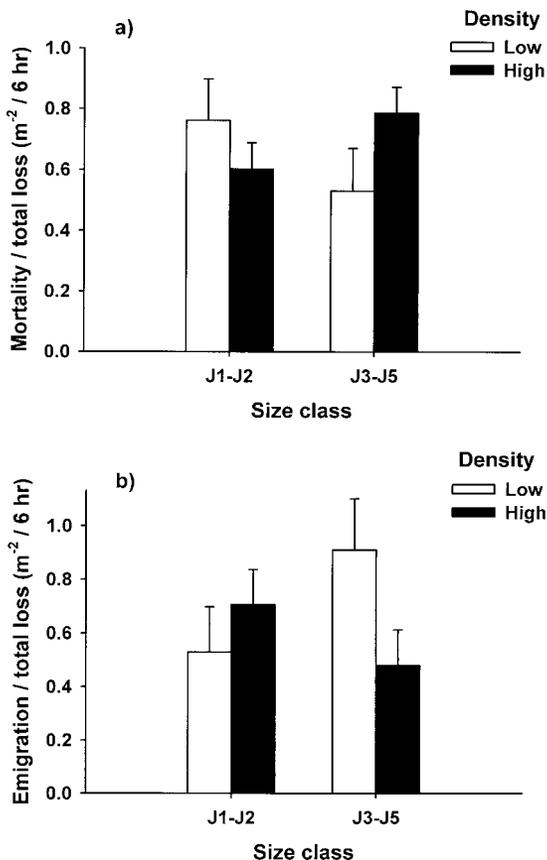


Figure 5. The effects of blue crab density (low: 16 crabs m⁻², high: 64 crabs m⁻²) and size class (J1–J2, J3–J5) on (a) contribution of mortality to total loss and (b) contribution of emigration to total loss. The responses represent probabilities over 6 h. Values are means + 1 SE. n = 4 to 8.

m⁻²/6 h for J1–J2 and J3–J5 size classes, respectively (Fig. 4c, d). Colonization rates did not vary by crab density (Fig. 3c, d; ANOVA; $F = 1.60$, $df = 1, 39$, $P = 0.213$) or time of day (Fig. 4c, d; ANOVA; $F = 0.09$, $df = 1, 39$, $P = 0.764$). In contrast, juvenile size influenced colonization rate significantly (Fig. 4c, d; ANOVA; $F = 15.21$, $df = 1, 39$, $P < 0.001$), with J3–J5 crabs exhibiting higher colonization than J1–J2 individuals. None of the interaction terms were significant (all $P > 0.61$)

EFFECTS OF JUVENILE DENSITY AND SIZE CLASS ON MORTALITY AND EMIGRATION.—Mortality did not vary by crab density (Fig. 5a; ANOVA; $F = 0.13$, $df = 1, 39$, $P = 0.721$) or crab size (Fig. 5a; ANOVA; $F = 0.01$, $df = 1, 39$, $P = 0.918$). The interaction effect between density \times size, however, was nearly significant (Fig. 5a; ANOVA; $F = 3.07$, $df = 1, 39$, $P = 0.087$), and resulted from a change in the relationship between mortality and density for the two size classes (Fig. 5a). There were similar rates of mortality between low and high densities for J1–J2 individuals, but significantly higher mortality rates at high densities than low densities for J3–J5 crabs (multiple comparison tests at alpha level of 0.11; Fig. 5a). All other interaction terms were non-significant (all $P > 0.20$).

Emigration did not vary by crab density (Fig. 5b; ANOVA; $F = 0.62$, $df = 1,$

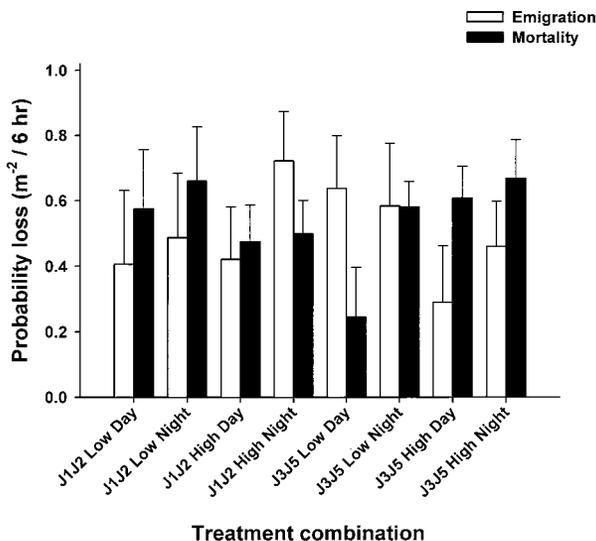


Figure 6. Comparison of mean emigration and mortality rates of early juvenile blue crabs across all treatment combinations of the factors size class (J1–J2, J3–J5), density (low, high), and time of day (day, night). The rates represent the probability of loss/6 h. Values are means + 1 SE. $n = 4$ to 8.

39, $P = 0.438$) or crab size (Fig. 5b; ANOVA; $F = 0.17$, $df = 1$, 39, $P = 0.681$). Once again, the density \times size interaction effect was nearly significant (Fig. 5b; ANOVA; $F = 3.42$, $df = 1$, 39, $P = 0.072$), and resulted from a change in the relationship between emigration and density for the two size classes (Fig. 5b). There were similar rates of emigration between low and high densities for J1–J2 individuals, but significantly higher emigration rates at low densities than high densities for J3–J5 crabs (multiple comparison tests at alpha level of 0.08; Fig. 5b). All other interaction terms were non-significant (all $P > 0.30$).

QUALITATIVE AND QUANTITATIVE COMPARISONS OF THE RELATIVE CONTRIBUTION OF EMIGRATION AND MORTALITY TO LOSS RATES.—Mean probabilities of emigration across all treatment combinations ranged from 0.29–0.72/6 h, while mean probabilities of mortality varied between 0.25–0.67/6 h (Fig. 6). The mean probability of mortality was greater than the probability of emigration across 5 of 8 treatment combinations (Fig. 6). These rates are expressed as probabilities, and thus the sum of emigration and mortality can be greater than 1.0, since it is the joint probability of these two rates that determines loss (retention is the joint probability of an individual remaining in area as well as surviving). For example,

$$p(\text{retention}) = p(\text{survival}) \cdot p(\text{remaining in square})$$

$$(1 - \text{loss}) = (1 - M)(1 - E)$$

$$\text{loss} = 1 - (1 - M)(1 - E)$$

$$\text{loss} = 1 - 1 + M + E - ME$$

$$\text{loss} = M + E - ME, \quad \text{which is why } M + E \text{ can be greater than } 1.$$

The dominance of either mortality or emigration was not significantly different than 0.5 for any of the treatment combinations. This lack of dominance may have been due to the small sample size ($n = 4$ –8), therefore, we pooled the trials across time of day, which also resulted in no difference in dominance of emigration or

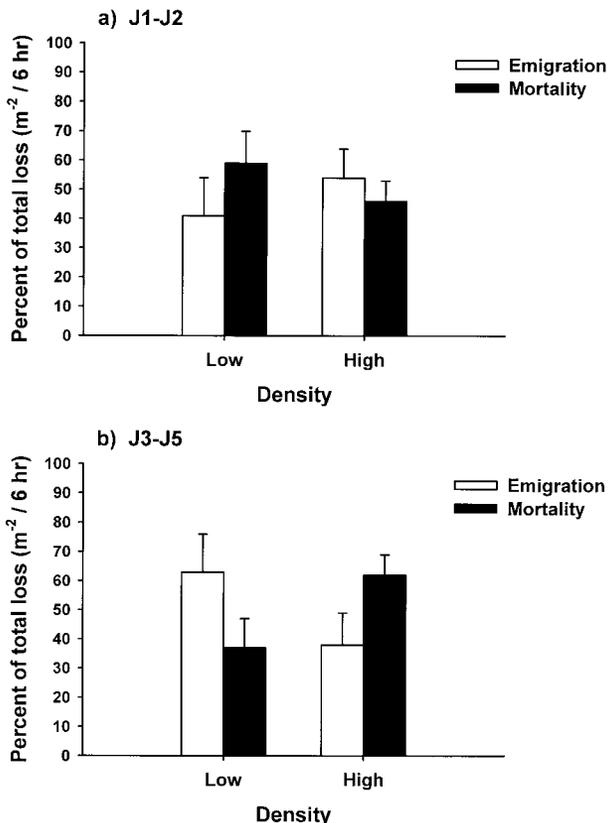


Figure 7. Comparison of emigration and mortality across blue crab density (low, high) according to juvenile size class (a) J1–J2 and (b) J3–J5. The responses represent the percent of total loss attributed to each of the loss components (emigration, mortality). Probabilities of the contribution of mortality and emigration to total loss were standardized to 1.0 so that they could be represented as components of total loss. Values are means + 1 SE. $n = 4$ to 8.

mortality. We also examined the potential differences in dominance across juvenile size class, and again, neither loss term could be considered significantly dominant over the other. Therefore, it appears that mortality and emigration contribute equally to juvenile loss in seagrass habitats.

The relative difference in magnitude (absolute amount of loss) of mean emigration and mortality varied according to the experimental treatments (Fig. 6). For J1–J2 crabs, the difference in the percent contribution of emigration and mortality to total loss was not very large (Fig. 7a). Under low density, the difference between emigration and mortality for J1–J2 was 18%, while at high density the difference was 8% (Fig. 7a). In contrast, J3–J5 crabs exhibited a larger difference between the contribution of mortality and emigration to total loss (Fig. 7b). Under low density, the contribution of emigration was much larger than the contribution of mortality, with a difference of 26% (Fig. 6b). Conversely, at high density the proportional loss due to mortality was substantially greater than that of emigration (difference of 24%) (Fig. 6b).

EFFECTS OF TIME OF DAY ON EMIGRATION AND MORTALITY.—Although total loss rates were significantly higher at night than during the day, the time of day did

not have a significant influence on mortality (ANOVA; $F = 0.46$, $df = 1$, 39 , $P = 0.504$) or emigration (ANOVA; $F = <0.01$, $df = 1$, 39 , $P = 0.956$).

DISCUSSION

Using a field mark-recapture technique with stained blue crabs of two different colors and a new analytical approach to Jackson's (1939) square-within-a-square experimental method, we were able to separate post-settlement loss of early juvenile blue crabs in seagrass beds into mortality and emigration components. Our results indicate that both emigration and mortality can be major components of early juvenile loss. Mortality rates were apparently density-dependent only for older juvenile crabs (J3–J5), suggesting a mechanism underlying an ontogenetic habitat shift of juveniles from seagrass to unvegetated habitats, or movement to other parts of the seagrass bed, as the probability of mortality increased with density among older juveniles within seagrass. Emigration rates were inversely density-dependent with particularly high emigration of J3–J5 under low density conditions, potentially as a means to redistribute populations before densities become high and mortality increases. The co-dependency of mortality and emigration suggest that the relatively stronger loss term (emigration or mortality) may dictate the patterns of loss under different conditions. For example, for older juveniles (J3–J5) emigration may only have a large impact on juvenile loss where densities are low; at high densities the contribution of mortality appears to be much greater than emigration. Rates of total loss were higher at night than during the day, potentially due to increased nocturnal activity of early juvenile blue crabs. Overall, rates of total loss and colonization were extremely high, with colonization being higher for J3–J5 than J1–J2.

LOSS AND COLONIZATION OF JUVENILES IN SEAGRASS.—The high rates of both total loss and colonization of juvenile blue crabs over a six hour period demonstrates the constant turnover of individuals within seagrass and highlights the dynamic nature of this environment. Our study demonstrated higher rates of turnover (overall mean of 77% $m^{-2}/6$ h; turnover defined as the percent of the total juveniles captured that were unstained) of blue crabs within seagrass beds than documented turnover rates of other crustaceans within seagrass (~25–60% turnover 0.56 $m^{-2}/6$ h for several crustacean species; Howard, 1985). Colonization appeared to be a relatively continual process that did not vary by time of day or crab density in our experimental plots, with colonization by J3–J5 crabs higher than that for J1–J2 crabs. This pattern could be a result of the available supply of these two size classes during this part of the recruitment period; however, higher colonization by J3–J5 crabs matched the results of the experimental stained crabs, whereby J3–J5 individuals showed particularly high emigration at low densities compared with the J1–J2 crabs under both densities. Rates of J3–J5 colonization nearly balanced the loss rates of J3–J5 crabs under high densities, but the lower rates of J1–J2 colonization could not replace the large numbers of J1–J2 individuals lost under high density conditions. Thus, larger juveniles may be more active and cover more area than the smaller early juveniles.

Diel variation in loss rates of both size classes of juvenile crabs might be due to increased activity at night. Increased activity by juveniles could cause higher encounter rates with predators at night, or blue crab predators may be more active or efficient at night. Increased activity could also inflate emigration rates. A previous study on late juvenile blue crabs (30–70 mm CW) did not detect diel variation in mortality rates (through tethering experiments); however, there was a trend of higher percent mortality at night than during the day across all water

depths (Hines and Ruiz, 1995), suggesting that predation pressure may be higher at night. Further, Sogard and Able (1994) found that smaller blue crabs (<50 mm CW) exhibited higher immigration (potentially due to higher activity levels) into artificial seagrass plots during the day, while larger individuals (>50 mm CW) were more likely to colonize the plots at night. Comparisons of blue crab abundance between day and night through trawl and seine surveys reveal no clear patterns of diel activity (Heck and Orth, 1980b; Summerson and Peterson, 1984). However, Blackmon and Eggleston (2001) found higher rates of planktonic emigration at night than during the day for J3–J5 crabs, suggesting increased nocturnal activity. Thus, diel activity of blue crabs may change during ontogeny due to changes in the risk of predation, the type of potential predators, as well as the conditions of optimal feeding. Although the separate analyses of emigration and mortality do not provide any insights as to what is responsible for the diel variation in total loss, our results of higher nocturnal loss of early juvenile blue crabs do stimulate questions regarding the diel activity levels of early juveniles as well as their predators, and how these behavioral patterns interact to determine predator-prey relationships within seagrass habitats.

QUALITATIVE AND QUANTITATIVE COMPARISONS OF THE RELATIVE CONTRIBUTION OF EMIGRATION AND MORTALITY TO LOSS RATES.—Mark-recapture methods have been used widely to estimate population sizes and rates of population loss and gain (Seber, 1982). It is often difficult to test mechanistic hypotheses about population dynamics using overall rates of population loss and gain, since it is not likely that the components of gain and loss are affected similarly by environmental and ecological factors (Nichols and Pollock, 1990). Thus, separating population loss into emigration and mortality is a challenge to obtaining a detailed understanding of the population dynamics of mobile animals. Although several methods have been proposed to correct for emigration in estimating survival rates (examples given by Manly, 1985), these often require extensive data from many recapture traps to determine the distribution of dispersal distances (e.g., Zeng and Brown, 1987). Rarely, however, has the relative contribution of mortality and emigration been examined experimentally.

In the present study, mortality and emigration contributed equally to total loss of early juvenile blue crabs within seagrass habitats. Of the relatively few studies that have jointly examined mortality and emigration, the relative importance of mortality and emigration on population abundance varied among systems and taxa (examples within Kratz, 1996). For example, Conroy and Bishop (1980) used the Jackson (1939) method to assess loss rates of the moth *Phigalia pilosaria*, and concluded that the greatest loss from the population was due to mortality (overall average = 0.32) compared with emigration (overall average = 0.03). Similar assessments of the population dynamics of a carabid beetle, *Calosoma sycophanta*, also yielded a greater effect of mortality (average = 0.16) than emigration (average = 0.08) (Weseloh, 1987). Using the Jackson (1939) method to examine the dynamics of the Heteropteran, *Clavigralla tomentosicollis*, emigration was more important than mortality in explaining decreases in adult populations (Dreyer and Baumgartner, 1997). Using a different method with two different sampling techniques, mortality of baetid mayfly nymphs (primarily *Baetis tricaudatus*) had a larger effect on population loss than predator-induced emigration (65% and 35%, respectively) (Kratz, 1996). Overall, mortality appears to have a greater effect on population loss than emigration; however, further studies across different taxa are needed to draw general conclusions.

Although neither mortality or emigration could be considered the dominant source of loss of early juvenile blue crabs across experimental treatments, the

relative contribution of mortality and emigration to total population loss of early juvenile crabs in seagrass varied as a function of crab density and size class. The magnitude of emigration and mortality appeared to be similar during the J1–J2 stages where density effects were not evident. The patterns of loss were more complex for the J3–J5 stages, where the magnitude of emigration was much greater than mortality under low density conditions, but mortality accounted for substantially more of the total loss than emigration under high density conditions.

Since rates of emigration and mortality were co-dependent (e.g., the number of crabs available to emigrate is dictated by the number that survive, and vice versa), we would not expect both emigration and mortality to be high. We therefore would not expect both density-dependent mortality and emigration. For example, in the absence of mortality, emigration may be directly density-dependent for J3–J5 crabs, but this relationship could be masked by large mortality. Similarly, the high emigration rates of J3–J5 crabs at low densities compared with high densities may not be a direct result of the low density condition on emigration, but could be a result of the reduced mortality at these low densities, which would allow for relatively high emigration rates. These high rates of emigration may represent background levels of movement due to foraging or refuge needs, even at these low densities. Alternatively, higher emigration at these low densities could redistribute the population so that high density conditions, and the attendant higher mortality rates, would not arise. In general, it appears that the contribution of mortality and emigration to population loss can change considerably with various ecological conditions, and that the expression of mortality and emigration depends on the dominant source of loss (Weseloh, 1987; Kratz, 1996; Dreyer and Baumgartner, 1997; this study).

ROLE OF MORTALITY IN EARLY JUVENILE LOSS.—Results from this mark-recapture study indicate that the role of mortality in early juvenile blue crab dynamics can vary according to size class and density, with density-dependent mortality occurring only among the J3–J5 size class. These results agree with a previous study which demonstrated lower survival rates of early juvenile blue crabs under high densities compared with low densities of juveniles held in field enclosures (Perkins-Visser et al., 1996). In contrast, Pile et al. (1996) concluded that mortality rates of early juveniles were not density-dependent. Two potential reasons for these contrasting results are that the experimental densities used by Pile et al. (1996) were not extreme enough (low density was not low enough) to detect density-dependent survival, or that relative rates of predation-induced mortality, as measured by tethering crabs, may have been too high to detect differences across density. High rates of mortality due to tethering may not be a possible explanation for the difference in results obtained by Pile et al. (1996) and the current study, since the rates of mortality in the current study were similar, if not slightly higher, than those reported by Pile et al. (1996) (see ‘*Experimental Considerations*’).

Density-dependent mortality among the older juvenile crabs (J3–J5) provides a mechanism for an ontogenetic shift in habitat use, which may occur among post-settlement juveniles beginning around the fifth instar stage (Pile et al., 1996; Moksnes et al., 1997), and could be a result of agonistic interactions among juveniles. For example, at high crab densities the frequency of agonistic interactions is greater, causing increased movements and decreased cryptic behavior resulting in an increased encounter rate with predators (Moksnes et al., 1997). Density-dependent mortality may also be a direct result of cannibalism, which has been suggested as a mechanism causing lower survival of early juveniles at high densities in field enclosures (Perkins-Visser et al., 1996). The functional

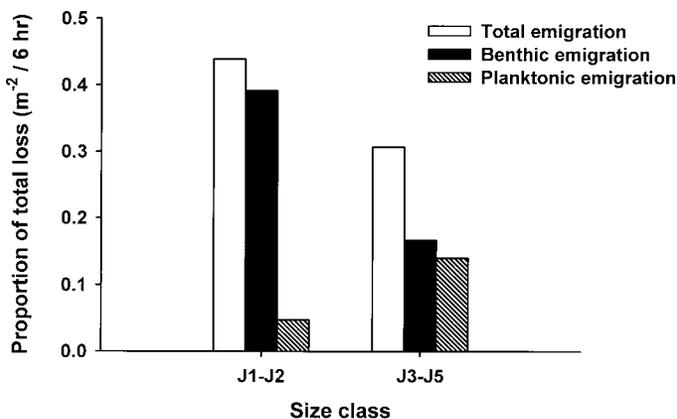


Figure 8. Qualitative comparison of the proportion of emigration to total loss for (1) total emigration (benthic and planktonic), (2) benthic emigration, and (3) planktonic emigration $m^{-2}/6$ hr across juvenile size class (J1-J2, J3-J5) under high-density conditions. Total emigration represents the mean percent of loss due to emigration multiplied by the proportion of experimental juveniles lost from the plot. Planktonic emigration is the mean proportion of experimental juveniles captured in planktonic nets surrounding a 1.0 m^2 experimental plot as measured in a concurrent study (Blackmon and Eggleston, 2001), and benthic emigration is calculated as total emigration minus planktonic emigration.

response of individual predators may also cause the observed density-dependent pattern, whereby predators exhibit higher per capita rates of consumption at high densities of juvenile crabs than at low densities (Holling, 1959). Density-dependent mortality may also result from an aggregative response, whereby predators aggregate in areas of higher densities of juveniles resulting in increased mortality rates (Holling, 1959). This mechanism of predator aggregation does not seem to be a possible explanation for the observed patterns of density-dependent mortality in this study, since adding 'potential predators' as a covariate in the analyses did not explain any significant variation in loss due to mortality. Further studies are needed to determine which mechanism (e.g., cannibalism, agonistic interactions, predator response), or combination of mechanisms, is responsible for the observed pattern of density-dependent mortality among J3-J5 crabs.

ROLE OF EMIGRATION IN EARLY JUVENILE LOSS.—The role of emigration in structuring juvenile blue crab population dynamics has received relatively little attention. Results from this study indicate that emigration is important in determining juvenile blue crab abundance within seagrass beds. The mode of emigration (benthic versus planktonic) could have different impacts on population dynamics since benthic movement is more restricted to a local level whereas planktonic emigration could have a regional influence. Both laboratory flume experiments (Blackmon and Eggleston, 2001) and field studies (Etherington and Eggleston, 2000; Blackmon and Eggleston, 2001) have demonstrated that early juvenile blue crabs disperse planktonically, and that this activity is due to an active behavioral response, primarily to increasing flow speed (Blackmon and Eggleston, 2001). A qualitative comparison between field rates of planktonic emigration (Blackmon and Eggleston, 2001) and total emigration (benthic + planktonic) (this study), that were measured in joint studies using the same experimental set-up and during the same time period, suggests that during high density conditions the benthic mode of juvenile dispersal is greater than planktonic dispersal, but that the relative importance of these modes of emigration is dependent on juvenile size class (Fig. 8). For J1-J2 juveniles, the majority of loss contributed by emigration was due

to benthic movement, whereas for the J3–J5 crabs, total emigration was almost equally divided between benthic and planktonic emigration. The nearly equal use of benthic versus planktonic forms of emigration for J3–J5 crabs emphasizes the potentially large role of planktonic emigration in determining post-settlement blue crab distribution and abundance patterns. Blackmon and Eggleston (2001) demonstrated that planktonic emigration was significantly greater for J3–J5 stages of blue crabs than J1–J2 stages, which differs from the lack of size class differences in total emigration (benthic and planktonic) measured in the present study. This difference in emigration patterns suggests that the form of juvenile dispersal (benthic vs. planktonic) might change during ontogeny, with older juveniles being more prone to planktonic dispersal than J1–J2 crabs.

EXPERIMENTAL CONSIDERATIONS.—In general, probability estimates of mortality and emigration were highly variable, particularly emigration. The variability in emigration rates could be a result of low retention rates. One way to improve the estimates of mortality and emigration would be to increase the probability of juvenile recapture. This can be done by decreasing the experimental period or increasing the size of the experimental plot. Decreasing the experimental period would be the logistically-easier option; however, increasing the experimental plot might represent more realistic conditions, since it appears that emigration rates of these crabs are high and interactions on a small time period can involve a larger area.

The high emigration and mortality rates in this study may have been an artifact of the experimental design due to the handling of crabs during capturing, staining, and releasing. However, mortality rates obtained during this study (mean of survival/24 h = 0.13 across juvenile sizes J1–J5; calculated as the proportion lost \times the percent of loss due to mortality) were comparable to those obtained by tethering studies of juvenile blue crabs (mean of survival/24 h \sim 0.17 for J3 crabs; Pile et al., 1996). High rates of colonization of unstained juvenile crabs of the same size class as the treatment (mean of 22.2 crabs $m^{-2}/6$ h and 46.2 crabs $m^{-2}/6$ h for J1–J2 and J3–J5 size classes, respectively) also suggest that the estimated rates of emigration (mean of 27.5 crabs $m^{-2}/6$ h and 23.6 crabs $m^{-2}/6$ h for J1–J2 and J3–J5 size classes, respectively) calculated by the Bayesian approach are reasonable. In addition, the acclimation period after crabs were introduced under the sieves should have alleviated inflation of emigration and mortality rates due to handling stress. Therefore, we feel that the high estimated rates of mortality and emigration are not an artifact of our experimental design, but represent realistic estimates of mortality and emigration rates of juvenile blue crabs in sea-grass beds.

IMPLICATIONS FOR POPULATION DYNAMICS.—Our mark-recapture experiments were conducted on a fairly small spatial scale and over relatively short time periods. The question remains as to how results from these experiments can be scaled up to represent population-level responses. It is possible that density-dependence tends to occur only at small local scales, where individuals interact with their immediate neighbors, but not on larger regional scales due to the potential dominance of density-independent processes (Forrester, 1995). In addition, density-dependence during the early juvenile stages may be exacerbated or canceled by processes at other stages (Harrison and Cappuccino, 1995). Nevertheless, examination of fishery-independent trawl survey data on juvenile blue crabs in North Carolina indicated strong density-dependent mortality on annual time scales and regional spatial scales (Eggleston, 1998). The data from the present study suggest that density-dependent mortality may occur within weeks of settlement.

The source of population loss (mortality or emigration) can have very different

impacts on the dynamics of mobile animal populations. On all scales (local and regional), loss due to mortality is permanent, and therefore mortality could be a factor regulating the population at both of these scales. Conversely, emigration can have different impacts on the population depending on the scale of observation, as well as the ultimate fate of dispersing juveniles. On a local scale, emigration could represent a permanent loss, or instead, individuals may emigrate and then move back into the original area. On a regional scale, emigration may redistribute the population to other potentially favorable habitats, therefore acting as a limiting factor causing additions or deletions within the population. Alternatively, emigration could cause increased regional mortality if individuals disperse to unfavorable habitats. Emigration can only act as a regulating factor if increased emigration at high densities leads to increased mortality (Harrison and Cappuccino, 1995). Further studies are needed to discern whether or not emigration is acting in a density-dependent manner, and whether it varies as a function of juvenile size class and time of day. In addition, studies that examine the fate of dispersing juveniles to determine whether emigration is acting as a regulating factor within these early stages would be beneficial in obtaining a better understanding of the role of emigration in population dynamics of early juveniles. In summary, the components of population loss can have very different population-level implications on multiple spatial scales, therefore highlighting the need to separate population loss into emigration and mortality components by size or age to examine their contributions to population dynamics of mobile animals.

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APPENDIX

The Jackson (1939) square-within-a-square method is a mark-recapture technique for partitioning observed losses of marked individuals from within a square area into mortality and emigration components. In this method, a “large” square area is subdivided into quarters—four equal-sized “small” squares. In one small square, some number of marked individuals are released, while in the other three small squares, an identical number of individuals bearing a different mark are released. After a fixed time interval, all marked individuals which remain within the four small squares are recaptured. Based on the location of recaptures of the two types of marked individuals within the large square, one can estimate the probabilities of retention within the large square (ψ_L) and within a small square (ψ_S). Although the Jackson (1939) method can be applied to multiple release/recapture data (and was, in fact, originally proposed in this context), in this study we applied Jackson’s method to single release/recapture data.

Two assumptions are integral to Jackson’s method: (1) survival rates are identical in all four small squares, and (2) there is no directional bias in individual movement (see validation in ‘*Statistical Analyses*’ section of Methods). Given these two assumptions, let ϕ be the individual probability of survival between release and recapture, ϵ_S be the individual probability of emigration from a small square between release and recapture, and ϵ_L be the individual probability of emigration from the large square between release and recapture. Then the retention probabilities ψ_L and ψ_S can be expressed as (Manly, 1985):

$$\psi_S = \phi(1 - \epsilon_S) \quad \psi_L = \phi(1 - \epsilon_L) \quad (1)$$

If ϵ_L is expressed as a function of ϵ_S , e.g., $\epsilon_L = \epsilon_S/r(\epsilon_S)$, where $r(\epsilon_S)$ is a known function, then this system of equations can be inverted to yield

$$\epsilon_S = \frac{r(\epsilon_S)(\psi_L - \psi_S)}{r(\epsilon_S)\psi_L - \psi_S} \quad \phi = \frac{r(\epsilon_S)\psi_L - \psi_S}{r(\epsilon_S) - 1} \quad (2)$$

At this point, the formula for ϵ_S in eq. 2 is not an explicit solution, since the solution depends on the value of $r(\epsilon_S)$ —and its value, in turn, depends on ϵ_S . However, if the functional dependence of r on ϵ_S is known (or assumed), it is possible to solve eq. 2 numerically for ϵ_S using an iterative approach (Stockhausen, unpubl. manuscript).

Jackson (1939) reasoned that the probability of emigration from a region was proportional to its perimeter-to-area ratio; thus, he made the further assumption that $r(\epsilon_S) = 2$, independent of ϵ_S . Under this assumption, eq. 2 constitutes a direct solution; no iteration is necessary. However, as Jackson

(1939) realized, the assumption that $r(\epsilon_s) = 2$ holds only when emigration rates are “low” relative to the spatial and temporal scales of the experiment. When emigration rates are “high,” it should be apparent that both ϵ_s and ϵ_L approach 1, so that $r(\epsilon_s) \rightarrow 1$ as $\epsilon_s \rightarrow 1$. Although it is possible, at least theoretically, to achieve “low” emigration rates by choosing the spatial and temporal scales (i.e., size of the square, time between release and recapture) for the experiment judiciously, this may not always be possible from a practical standpoint. In addition, such judicious selection requires previous estimates of emigration rates, perhaps from a pilot experiment, which may not be available.

One consequence of Jackson’s (1939) assumption that $r(\epsilon_s) = 2$ is that estimates of mortality are biased increasingly high as emigration rates increase (Stockhausen, unpubl. manuscript). Thus, when emigration rates are high, it becomes necessary to use the iterative solution of eq. 2 for ϵ_s , based on a functional form of $r(\epsilon_s)$, which depends on detailed assumptions about dispersal.

In addition to the problem of estimation bias when emigration rates are high, Jackson’s (1939) method also suffers from problems associated with the discrete and stochastic nature of the estimates for Ψ_L and Ψ_S when sample size is small (as is the case for this study; see Stockhausen, unpubl. manuscript). In particular, it is quite possible to obtain nonsensical estimates for ϵ_s (i.e., $\epsilon_s < 0$).

Consequently, we adopted an approach to estimating emigration and mortality based on Bayesian Analysis and Decision Theory (Berger, 1985; Ellison, 1996). This approach is appropriate for small sample sizes and reduces estimation bias when emigration rates are high by implicitly incorporating the dependence of r on ϵ_s (Stockhausen, unpubl. manuscript). Although computationally intensive, estimators based on Bayesian statistics have several advantages over estimators based on traditional statistical approaches (Berger, 1985; Ellison, 1996). In the present context, the two principal advantages are: 1) the estimation process incorporates the discrete and stochastic nature of the data, and 2) it generates a complete posterior probability distribution for the estimated parameters. A further advantage is that it is a simple matter to combine results from replicate experiments to improve estimation precision.

BAYESIAN ESTIMATION.—Bayesian estimators are based on Bayes’ Theorem (Bayes, 1783), which describes the relationship between posterior and prior probability distributions. Here, let θ denote the set of parameters which describe a system of interest, η denotes the results of an experiment using this system, and $P_{\eta,\theta}(\eta, \theta)$ describes the joint probability that the chosen system has parameter set θ and that results η were obtained. The joint probability, $P_{\eta,\theta}(\eta, \theta)$, can be decomposed in two ways:

$$P_{\eta,\theta}(\eta, \theta) = P_{\eta|\theta}(\eta|\theta)P_{\theta}(\theta) = P_{\theta|\eta}(\theta|\eta)P_{\eta}(\eta), \tag{3}$$

where $P_{\eta|\theta}(\eta|\theta)$ denotes the conditional probability of obtaining results η given that the system parameter set is θ , $P_{\theta}(\theta)$ denotes the probability that θ is the parameter set for the selected system *prior to the experiment*, $P_{\theta|\eta}(\theta|\eta)$ denotes the conditional probability that the system parameter set is θ given that experimental results η have been obtained, and $P_{\eta}(\eta)$ describes the probability of obtaining results η regardless of the system parameter set. The distributions $P_{\theta}(\theta)$ and $P_{\theta|\eta}(\theta|\eta)$ are referred to as the *prior* and *posterior* (i.e., *before* and *after* an experiment) distributions for θ , respectively (e.g., Berger, 1985).

Given experimental results η_e , Bayes’ (1783) Theorem allows one to calculate the posterior distribution $P_{\theta|\eta}(\theta|\eta_e)$ from the prior distribution $P_{\theta}(\theta)$ and the conditional distribution $P_{\eta|\theta}(\eta_e|\theta)$, such that (Berger, 1985; Ellison, 1996):

$$P_{\theta|\eta}(\theta|\eta_e) = \frac{P_{\eta|\theta}(\eta_e|\theta)P_{\theta}(\theta)}{\int P_{\eta|\theta}(\eta_e|\theta)P_{\theta}(\theta) d\theta} \tag{4}$$

Point estimates for the set of parameters θ , $\hat{\theta}$, can be defined using a maximum likelihood criterion, such that $\hat{\theta}$ is the parameter set which maximizes $P_{\theta|\eta}(\theta|\eta_e)$ (Ellison, 1996). However, unlike conventional statistical estimators, which also provide point estimates, the Bayesian approach yields a complete probabilistic description for the estimated parameters (Berger, 1985; Ellison, 1996). In addition, results from two experiments (e.g., replicate trials) can be combined using the posterior distribution from one experiment as the prior distribution for the other (Berger, 1985; Ellison, 1996).

To develop a Bayesian estimator, one must mathematically describe the prior and conditional distributions, $P_{\theta}(\theta)$ and $P_{\eta|\theta}(\eta|\theta)$ (Berger, 1985; Ellison, 1996). Here, we take $\theta = [\phi, \epsilon_s]$ and assume that no prior knowledge of θ is available before the start of the experiment (i.e., $P_{\theta}(\theta)$ is noninformative; Berger, 1985). Consequently, the prior distribution $P_{\theta}(\theta)$ is a constant; i.e., all ϵ_s and ϕ from 0 to 1 are equally likely prior to the experiment.

To develop an equation for the conditional distribution $P_{\eta|\theta}(\eta|\theta)$, we follow Jackson’s (1939) assumptions that survival is the same in the large and small squares and that movement is directionally unbiased. Let R be the probability that an individual which survives to be recaptured is retained within the small square in which it was released; thus, $R = 1 - \epsilon_s$. In addition, let A be the corresponding probability that the individual emigrated to a directly adjacent small square and let X be the corresponding probability that the individual emigrated to a diagonally adjacent small square. The param-

eters R , X , and A can be regarded as functions of ϵ_s . If N marked animals are released from one small square within the large square, the probability of recapturing $\{n, j, k, l\}$ individuals in the four small squares (starting with the release square and proceeding counter-clockwise around the large square) has a multinomial distribution:

$$P(n, j, k, l | \phi, \epsilon_s) = \begin{cases} 0 & \text{if } n + j + k + l > N \\ \frac{N!}{n!j!k!l![N - (n + j + k + l)]!} \times [\phi R(\epsilon_s)]^n [\phi A(\epsilon_s)]^j [\phi X(\epsilon_s)]^k [\phi A(\epsilon_s)]^l & \text{otherwise} \\ \times \{1 - \phi[R(\epsilon_s) + X(\epsilon_s) + 2A(\epsilon_s)]\}^{N-(n+j+k+l)} & \end{cases} \quad (5)$$

Consequently, the probability of recapturing m individuals somewhere within the large square (regardless of small square location) is

$$P(m | \phi, \epsilon_s) = \begin{cases} 0 & \text{if } m > 0 \\ \sum_{n+j+k+l=m} P(n, j, k, l | \phi, \epsilon_s) & \text{otherwise} \end{cases} \quad (6)$$

In Jackson's (1939) method, individuals released within three of the small squares are marked identically; as a consequence, emigration is apparent only when individuals move into the "small square" and are captured. There are a number of ways the experimental results could be recorded in this situation. In this study, the set of experimental results η consisted of the number of individuals released within the "small square" (designated as square 1, for convenience) and captured within each of the four small squares $\{n_1, j_1, k_1, l_1\}$, as well as the total number of individuals released in the other three small squares which were retained within the large square ($m = \sum_{i>1} (n_i + j_i + k_i + l_i)$). Thus, η was $\{n_1, j_1, k_1, l_1, m\}$. Consequently, the conditional probability is given by

$$P_{\eta|\theta}(\eta = [n_1, j_1, k_1, l_1, m] | \theta = [\phi, \epsilon_s]) = P(n_1, j_1, k_1, l_1 | \phi, \epsilon_s) \sum_{m_2+m_3+m_4=m} \prod_{i>1} P(m_i | \phi, \epsilon_s) \quad (7)$$

and the posterior distribution $P_{\theta|\eta}(\theta | \eta)$ is given by

$$P_{\theta|\eta}(\theta = [\phi, \epsilon_s] | \eta = [n_1, j_1, k_1, l_1, m]) = \frac{P_{\eta|\theta}(\eta = [n_1, j_1, k_1, l_1, m] | \theta = [\phi, \epsilon_s])}{\int_0^1 d\phi' \int_0^1 d\epsilon_s' P_{\eta|\theta}(\eta = [n_1, j_1, k_1, l_1, m] | \theta = [\phi', \epsilon_s'])} \quad (8)$$

MODELING DISPERSAL.—To evaluate eq. 8 numerically, one needs to express the relationships between ϵ_s and R , A , and X . This requires a mathematical model for dispersal. Although dispersal patterns have been described using a wide array of models (Manly, 1977; Turchin, 1998), we adopted the simplest: a two-dimensional, unbiased normal random walk. Under this model, the probability that an individual moves δx , δy along perpendicular axes in time t is described by a two-dimensional normal distribution; the variance in displacement, σ_d^2 , grows with time as $2Dt$, where D is a characteristic constant known as the diffusion coefficient.

In addition to accounting for the pattern of individual dispersal, the model must also incorporate the spatial pattern of releases. We assumed that marked individuals were randomly distributed within the small square in which they were released according to a two-dimensional uniform distribution.

As such, the probabilities ϵ_s , ϵ_L , R , X , and A are related to σ_d^2 by:

$$\begin{aligned} \epsilon_s(\sigma_d) &= 1 - \int_0^1 dx \int_0^1 dy \int_0^1 dx' \int_0^1 dy' \frac{1}{2\pi\sigma_d^2} \exp\left[-\frac{(x' - x)^2 + (y' - y)^2}{2\sigma_d^2}\right] \\ \epsilon_L(\sigma_d) &= 1 - \int_0^1 dx \int_0^1 dy \int_0^2 dx' \int_0^2 dy' \frac{1}{2\pi\sigma_d^2} \exp\left[-\frac{(x' - x)^2 + (y' - y)^2}{2\sigma_d^2}\right] \\ R(\sigma_d) &= \int_0^1 dx \int_0^1 dy \int_0^1 dx' \int_0^1 dy' \frac{1}{2\pi\sigma_d^2} \exp\left[-\frac{(x' - x)^2 + (y' - y)^2}{2\sigma_d^2}\right] \\ X(\sigma_d) &= \int_0^1 dx \int_0^1 dy \int_1^2 dx' \int_1^2 dy' \frac{1}{2\pi\sigma_d^2} \exp\left[-\frac{(x' - x)^2 + (y' - y)^2}{2\sigma_d^2}\right] \\ A(\sigma_d) &= \int_0^1 dx \int_0^1 dy \int_1^2 dx' \int_0^1 dy' \frac{1}{2\pi\sigma_d^2} \exp\left[-\frac{(x' - x)^2 + (y' - y)^2}{2\sigma_d^2}\right] \end{aligned} \quad (9)$$

In these equations, unit length is defined as the length of a side of a small square. The equations in 9 were numerically integrated (Mathcad, 1998) over a range of values for σ_d to implicitly define the functional relationships among ϵ_s and ϵ_L , R , X , and A .

ESTIMATING ϵ_s AND ϕ .—To estimate ϵ_s and ϕ from the recapture results for each experimental replicate, we numerically evaluated eq. 8 over a dense two-dimensional grid consisting of 41 values for ϕ (axis one from 0 to 1) and 51 values for ϵ_s (axis two from 0 to 0.99). We then used the values $\hat{\phi}$ and $\hat{\epsilon}_s$ which maximized the posterior distribution $P_{\theta|n}$ as point estimates of the probabilities of survival and emigration for that replicate. Finally, the probability of mortality was computed as $1 - \hat{\phi}$.