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Environmentally-controlled, density-dependent secondary dispersal in a local estuarine crab population

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Abstract The mechanisms driving the pelagic secondary dispersal of aquatic organisms following initial settlement to benthic habitats are poorly characterized. We examined the physical environmental (wind, diel cycle, tidal phase) and biological (ontogenetic, density-dependent) factors that contribute to the secondary dispersal of a benthic marine invertebrate, the blue crab (*Callinectes sapidus*) in Pamlico Sound, NC, USA. Field studies conducted in relatively large (0.05 km^2) seagrass beds determined that secondary dispersal is primarily undertaken by the earliest juvenile blue crab instar stages (J1 crabs). These crabs emigrated pelagically from seagrass settlement habitats using nighttime flood tides during average wind conditions (speed ~5 $m\ s^{-1}$). Moreover, the secondary dispersal of J1 crabs was density-dependent and regulated by intra-cohort (J1) crab density in seagrass. Our results suggest that dispersal occurs rapidly following settlement, and promotes blue crab metapopulation persistence by redistributing juveniles from high-density settlement habitats to areas characterized by low postlarval supply. Collectively, these data indicate that blue crab secondary dispersal is an active process under behavioral control and can alter initial distribution patterns established during settlement. This study highlights the necessity of considering secondary dispersal in ecological studies to improve our understanding of population dynamics of benthic organisms.

Keywords Blue crab · Density-dependence · Environmental cues · Post-settlement emigration

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Introduction

The degree to which populations are considered demographically open is often defined by an organism's dispersal capability, which is generally life-stage dependent. For example, many marine organisms undergo long-distance dispersal during a pelagic larval phase, before settling to benthic habitats where they remain as juveniles and adults (Scheltema 1986). While larval dispersal can have significant population-level consequences (e.g., maintain spatially-separated sub-populations, enhance gene flow, alter distribution and abundance patterns; Dieckmann et al. 1999), the same may be true of pelagic, post-settlement emigration (secondary dispersal) by juveniles or adults following initial settlement to the benthos (Caley et al. 1996). Similar to larval transport, secondary dispersal can occur over relatively large distances (Beukema and de Vlas 1989; Etherington and Eggleston 2003), and thus has the capacity to enlarge a species' distributional range (Armonies 1992), as well as restructure populations and communities (Caley et al. 1996; Palmer et al. 1996; Turner et al. 1997; Etherington and Eggleston 2000, 2003). Moreover, a rapidly growing body of literature suggests that secondary dispersal is more prevalent than previously believed in aquatic systems, with examples from diverse taxa including marine benthic macrofauna (Sigurdsson et al. 1976), marine meiofauna (Palmer 1988), marine and stream benthos (reviews by: Günther 1992; Palmer et al. 1996), and reef fishes (Hindell et al. 2003). The mechanisms underlying secondary dispersal, however, remain poorly understood.

The secondary dispersal of marine and stream benthic invertebrates may result from (1) a passive response to physical environmental conditions (e.g., resuspension due to storm event or downstream drift in high flow conditions), (2) an active behavioral response to biological (e.g., density-dependent effects) or abiotic environmental conditions, or more likely, a combination of both (Fegley 1987; Service and Bell 1987; Turner et al. 1997; Powers and Peterson 2000). The propensity for active or passive secondary dispersal will depend, in part, on the habitat characteristics where the organism resides. For example, in shallow coastal environments (<10 m) that experience relatively high bottom shear stresses, passive secondary dispersal is common for marine meiofauna and macrofauna that live near the sediment surface, as these organisms frequently become entrained with suspended sediments as flow increases, or during storm events (Palmer 1986; Wilson 1990; Emerson and Grant 1991; Hall 1994; Commito et al. 1995; Thrush et al. 2000). Likewise, passive entrainment with increasing flow has been observed for stream meiofauna (Palmer 1992) and macrofauna (Brittain and Eikeland 1988). While such passive dispersal is determined by local hydrodynamic forcing, secondary dispersal can also be actively promoted by behavioral responses such as swimming or emergence from the sediments during periods of increased current velocity (e.g., portunid crabs: Blackmon and Eggleston 2001; meiofauna: Hagerman and Rieger 1981; Fegley 1987), or by using morphological adaptations to increase hydrodynamic drag and remain suspended in the water column (e.g., thread-drifting bivalves: Sigurdsson et al. 1976; Beukema and de Vlas 1989). Other factors known to influence secondary dispersal include diel (Armonies 1992; Etherington et al. 2003) and tidal cycles (Beukema and de Vlas 1989; Armonies 1992), reflecting possible endogenous rhythms in activity (e.g., Forward et al. 2004), or adaptive behavioral responses to exogenous environmental variables associated with these cycles (e.g., Welch et al. 1999).

With the exception of a few studies described below, the factors initiating active secondary dispersal of marine benthic invertebrates have not been identified (but see review by Günther 1992). Active secondary dispersal can result from intra- and inter-specific interactions, such as competition for food or habitat resources, predator- or competitor-avoidance (Günther 1992), or habitat disturbances by other organisms (Dunn et al. 1999). For example, secondary dispersal by juvenile bivalves may be positively correlated with adult densities (Turner et al. 1997), or become density-dependent only in high flow conditions (Powers and Peterson 2000). Density-dependent secondary dispersal has also been observed for benthic meiofaunal harpacticoid copepods, where pelagic dispersal increases with infaunal density (Service and Bell 1987). Although evidence of density-dependent secondary dispersal implies that dispersal is an active process under behavioral control, the effects of density are seldom considered in studies of secondary dispersal. In this study, we examine the secondary dispersal of a local blue crab population in response to both physical environmental and biological conditions.

The blue crab, *Callinectes sapidus*, is an ecological and commercially important, estuarine-dependent species along the East and Gulf coasts of the United States. Following estuarine recruitment, postlarval blue crabs settle in beds of submerged aquatic habitat (e.g., seagrass or other structurally complex habitats) where they undergo metamorphosis to the first benthic instar (J1) (Heck and Thoman 1981; Orth and van Montfrans 1987; Etherington and Eggleston 2000). It has been generally accepted that juveniles remain in these habitats until they reach the fifth to seventh instar (J5–7) stage and begin to migrate benthically into non-vegetated habitats (Hines et al. 1987; Orth and van Montfrans 1987). Recent evidence, however, has demonstrated that pelagic, secondary dispersal from seagrass settlement habitats by earlier instars (J1–5) determines patterns of recruitment on a regional scale, and can mask density-dependent relationships among early juvenile life-history stages (Etherington and Eggleston 2000, 2003; Blackmon and Eggleston 2001; Etherington et al. 2003). Yet it remains unclear when juvenile blue crabs undergo such dispersal, and what factors underlie and mediate transport. Therefore, the objectives of this study were to (1) identify environmental factors (wind, diel cycle, and tidal phase) which may cue juvenile blue crabs to move into surface waters to undergo secondary dispersal, and to determine if this secondary dispersal varies with (2) ontogeny and/or (3) density.

Materials and methods

Study region

Two field studies were conducted in a region located near Oregon Inlet, NC, USA (35°47.5′N; 75°33.5′W). The area was characterized by relatively shallow (1 m deep), nearly continuous seagrass beds separated by deeper (4 m) unvegetated sandy channels. These seagrass beds typically harbor relatively high densities of post-settlement, early juvenile blue crabs during the fall blue crab recruitment months (August–October) (Etherington and Eggleston 2000; Blackmon and Eggleston 2001; Etherington et al. 2003). Within the region, two seagrass beds of similar size (~0.05 km^2) and habitat characteristics (97% *Zostera marina*, ~3% *Ruppia maritima* and *Halodule wrightii*) were selected for study. The seagrass beds, named North and South, respectively, were considered independent due to the distance separating them (~1.5 km) and negligible physical connectivity by tidal and wind-driven currents (Reyns, personal observation).

The study region experiences semidiurnal tides with a mean tidal range of 61 cm, but water levels are also influenced by wind-driven surface currents (Pietrafesa et al. 1986). In general, wind patterns during the blue crab recruitment months are characterized as being transitional between seasons, with winds shifting from southwesterly to northeasterly (Pietrafesa et al. 1986; Etherington and Eggleston 2003). While the magnitude of wind events experienced at our study site may be influenced by the episodic passage of frontal systems and tropical cyclones, the average wind speed during August–October is typically ~5 m s^{-1} (Etherington and Eggleston 2003).

Environmental cues study

To identify the environmental factors that correlate with secondary dispersal of blue crabs, we conducted a study at the North seagrass bed from 30 September–18 October 2001. We hypothesized that secondary dispersal of juvenile blue crabs would occur during nocturnal flood tides, because many estuarine organisms utilize cues associated with diel and tidal cycles to move up-estuary (reviews by: Boehlert and Mundy 1988; Forward and Tankersley 2001). The occurrence of secondary dispersal of juvenile blue crabs was defined by the concentration of crabs in the water column (no. crabs 100 m^{-3}), and was quantified using a channel net deployed outside the grass bed such that the top of the net frame was level with the water's surface. The channel net had 890 μm-mesh, a mouth dimension of 1 m (width)×0.5 m (height), and was equipped with a General Oceanics (Miami, FL, USA) flow meter to calculate the volume of seawater filtered. A preliminary study using passively and actively-towed channel nets determined net avoidance by J1–5 blue crabs to be negligible. In addition, flow meters mounted inside and outside of the channel net (e.g., Hodson et al. 1981) established that net capture efficiency was near 100%. To obtain a mean concentration of crabs in the water column during each treatment combination (see below), we conducted five sequential replicate, 5 min (~100 m^3 filtered) net sets.

The physical environmental factors examined in this study included wind intensity (wind speed and direction), diel cycle (day versus night) and tidal phase (flood versus ebb tide). We sampled under varying wind conditions because as wind intensifies, current velocity and exposure to wind waves in shallow seagrass beds may cause a resuspension of material from the seagrass canopy (Koch 1999), potentially enhancing secondary dispersal. Thus, sampling dates were initially picked qualitatively to alternate between storm ("windy") and calm conditions as predicted by NOAA weather forecasts. During sampling, the average wind speed was quantified 2 m above sea level from a small boat at the research site (and away from land obstructions) using a hand-held Kestrel 1,000 wind meter (Nielsen Kellerman, Chester, PA, USA). The influence of the diel and tidal cycles on secondary dispersal was examined by deploying the channel net during the following treatment combinations: day-flood tide, day-ebb tide, night-flood tide and night-ebb tide. Channel nets were set downstream of the seagrass bed during peak current velocity, which typically occurred 1–2 h before high or low tide. Upon collection, samples were preserved in 75% ethanol and transported to the laboratory where juvenile blue crabs were enumerated, measured for carapace width (CW; dorsal distance between lateral spines), and categorized by size class following Pile et al. (1996). Data collection was repeated during six separate 24-hr intervals, encompassing tides of both maximum (spring) and minimum (neap) amplitude.

Size-class distribution of crabs

In addition to relating secondary dispersal of juvenile blue crabs to potential environmental cues, we also tested the hypothesis that the propensity to undergo secondary dispersal changes with crab stage. Previous small-scale laboratory and field experiments suggested that secondary dispersal occurs primarily during later (J3–5: 4.3–9.1 mm CW), rather than early, instar stages (J1–2: 2.2–3.0 mm CW) (Blackmon and Eggleston 2001; Etherington et al. 2003). Therefore, we examined the size-class distribution of crabs collected in the water column during our environmental cues study.

While this study was conducted during the middle of the blue crab recruitment season when a range of blue crab instars (J1–9) is generally found within seagrass settlement habitats (Etherington and Eggleston 2000), conclusions regarding ontogenetic secondary dispersal could not be reached without first establishing if: (1) crabs were undergoing secondary dispersal (i.e. present in plankton), (2) not dispersing (i.e. present in seagrass but not in plankton), (3) or not available to disperse (i.e. absent from both seagrass and plankton). To address this, we compared the size-class distributions of pelagic and benthic crabs on two occasions (6 and 9 October 2001). Juvenile blue crab density within seagrass was quantified using standard suction sampling techniques (Orth and van Montfrans 1987; Pile et al. 1996; Etherington and Eggleston 2000). A suction dredge apparatus sampled seagrass within a 1.3 m-diameter drop net, and was equipped with a 790 μm-mesh collection bag. Samples were taken from five randomly selected areas within the North seagrass bed to obtain a mean density of juvenile blue crabs (no. crabs m^{-2}). Each sample was suctioned for 6 min and dip-netted until three consecutive sweeps of the net were free of crustaceans and fishes. Following collection, samples were preserved and processed for blue crabs as described above, and densities of crabs <25 mm CW corrected for the 88% efficiency of this method (Orth and van Montfrans 1987).

Statistical analyses

The influence of potential environmental cues on secondary dispersal was analyzed using a two-way, fixed factor ANCOVA model with time of day and tidal cycle as factors, and average wind speed during a trial as the covariate. Wind direction was not included as a covariate as winds were consistently out of the northeast on all sampling days. The covariate and all factor×covariate interaction terms were non-significant (all $P>0.16$). Therefore, we dropped these terms from the model and used a reduced two-way ANOVA model. Normality and homogeneity of variances were achieved after $\log(x+1)$-transformation of the response variable (mean concentration of crabs in the plankton).

To compare the size-class distribution of benthic and pelagic early juvenile blue crabs, we calculated the proportion of crabs that belonged to each size class as a function of habitat type (seagrass versus plankton). Differences in size-class distributions were tested using the two-sample Kolmogorov–Smirnov $_{n1n2}D$ statistic (Sokal and Rohlf 1995).

Density study

To determine if secondary dispersal of juvenile blue crabs is density-dependent, we conducted a second field study at the North and South seagrass beds from 6 September–9 October 2002. The objective of this study was to characterize the benthic density of juvenile blue crabs in seagrass and the corresponding pelagic concentration of crabs in surrounding waters. The density of crabs (no. crabs m^{-2}) in seagrass was quantified during the day using the suction sampling techniques described above (see 'Environmental cues study'). To obtain a mean crab density, five replicate suction samples were taken from each seagrass bed (North and South). In our study area, juvenile blue crabs reside within these grassbeds, and are absent from adjacent unvegetated benthic habitats (Etherington and Eggleston 2000). Therefore, crabs located in the water column surrounding the seagrass beds were assumed to have originated from these habitats, and were considered to be 'secondary dispersers'.

During the night following daytime suction sampling in seagrass, the mean concentration of crabs in the water column (no. crabs m^{-3}) was measured using replicate channel nets (same as methods previously described). Two nets were deployed at night and downstream of the seagrass bed at each site during flood tide (see 'Results' for justification of deployment time). Nets were set for approximately 1 h, 1–2 h prior to high tide (time of peak flow) to provide an integrated measure of secondary dispersal during this period. Suction and plankton samples were processed for blue crabs and corrected for efficiency, as described above. To obtain an average wind speed during the channel net deployments, we took wind measures at the time of net deployment, midway through the deployment, and at net retrieval.

By suction sampling the seagrass during the day and sampling plankton in nearby channels at night, we ensured that disturbances due to the suction pump did not enhance our measures of secondary dispersal. Prior to this study, we conducted preliminary trials that determined that sampling in this manner resulted in no difference in secondary dispersal measured on days of concurrent suction sampling, versus days when suction sampling was not performed. Collections were repeated on every fourth day for a total of seven times at both sites ($n=14$).

Statistical analyses

The relationship between secondary dispersal and the benthic density of crabs was analyzed using regression analysis to measure the fit of models that included the pelagic concentration of juvenile blue crabs as the response variable and the benthic density of crabs within a specific instar as explanatory variables. The majority of juvenile blue crabs collected in the plankton during the density study belonged to the J1 size class (see Results); therefore, the definition of the response variable was further refined as the pelagic concentration of J1 crabs. The explanatory variables in the regression model were defined as the benthic density of J1, J2, and J3 crabs because we hypothesized that these instars would be greater competitors (and predators via cannibalism) with J1 crabs (those undergoing dispersal) than later benthic instar stages. In addition, during our study, the relative abundance of J1–3 crabs in seagrass was greater than that of older instars (see Results). It was not possible to use the benthic density of all blue crab instars found in seagrass (J1, J2,..., J9) as separate explanatory variables, as the number of model possibilities with these variables would have exceeded our number of data points, likely producing spurious results (Freedman's paradox; Anderson and Burnham 2002). We did not consider wind speed as an explanatory variable because preliminary analysis of the wind data determined that average wind speed during the density study (3.8–7 m s^{-1}) did not differ significantly by sampling date (ANOVA results: $P>0.53$). Explanatory variables did not exhibit collinearity as identified using the variance inflation factor (VIF) and condition index, and no outliers were detected using Cook's D statistic (Rawlings et al. 1998). Finally, to meet assumptions of normality and homogeneous variances, response and explanatory variables were log(x+1)-transformed.

To identify which variables influenced the secondary dispersal of juvenile blue crabs, we used an information-theoretic approach (Burnham and Anderson 2002). This approach provides an objective way to select the 'best approximating model' for data analysis and inference using Akaike's information criterion (AIC), an extension of likelihood theory (Burnham and Anderson 2002). Furthermore, the relative importance of multiple variables can be assessed by examining a set of candidate models (Burnham and Anderson 2002).

Upon completion of the regression analysis, models were grouped by number of fitted parameters using R^2 and AIC. From these data, a second-order corrected AIC (AIC_c; used when $n<40$) and Akaike weights were calculated to select the most parsimonious regression model describing the relationship between secondary dispersal of J1 crabs and the density of early instars in seagrass. In addition, the relative importance of the explanatory variables was assessed by summing the Akaike weights of each variable (Burnham and Anderson 2002). Once we determined which explanatory variable exhibited the strongest relationship with secondary dispersal, the functional relationship between crab density and the pelagic concentration of J1 crabs was examined to determine if secondary dispersal was density-dependent. A density-dependent functional relationship would be characterized by an increase in the pelagic concentration of crabs with increasing crab density in nearby seagrass. Therefore, to characterize the functional relationship between our variables, linear and non-linear models were fit to the data. The distribution of model residuals was examined to verify that statistical assumptions were met, and the model that explained the most variability in the data was selected using AIC_c and Akaike weights (Burnham and Anderson 2002).

Results

Environmental cues

The mean concentration of crabs in the water column varied significantly by time of day (two-way reduced ANOVA: df=1,20, $F=11.04$, $P=0.003$) and tidal cycle (df=1,20, $F=4.36$, $P=0.049$). These variables displayed a significant time of day×tidal cycle interaction (df=1,20, $F=4.99$, $P=0.037$), whereby crabs exhibited secondary dispersal primarily during nighttime flood tides (Fig. 1). Although wind speed was non-significant in the initial analysis (two-way ANCOVA model), when winds exceeded 15 m s^{-1}, juvenile blue crabs were collected in the water column irrespective of time of day and tidal cycle (e.g., Day of year 273 in Fig. 1).

Size-class distribution

Of the juvenile blue crabs collected in the water column during the environmental cues study, approximately 98% were early-staged crabs (J1–2: 2.2–4.2 mm CW) with <2% belonging to larger size classes (J3–9: 4.3–16.1 mm CW). The distribution of blue crab size classes in the plankton differed significantly from the distribution of crabs in seagrass (Fig. 2a: $_{n1n2}D=0.98$, $P<0.01$; Fig. 2b: $_{n1n2}D=0.96$, $P<0.01$), whereby crabs in seagrass had a much broader distribution (J1–9) than crabs in the plankton. Size-class distribution patterns during the density study were similar to those observed in the environmental cues study (Fig. 2c), when crabs collected in the plankton and seagrass also exhibited significantly different size-class distributions ($_{n1n2}D=0.76$, $P<0.01$).

Explanatory variable selection

The secondary dispersal of juvenile blue crabs was influenced by the density of intraspecific crabs in seagrass (Table 1). The model with the benthic density of J1 and J2 crabs had the lowest AIC_c (Table 1) and was therefore considered the best approximation from all candidate

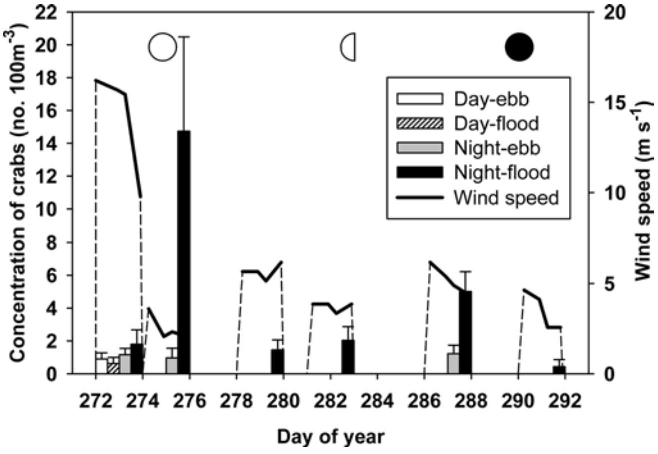

Fig. 1 Secondary dispersal of juvenile blue crabs in relation to time of day, tidal cycle and wind speed. The mean concentration of crabs during each environmental trial (+1 SE) is plotted over time. Lunar phase (*open circle* full moon; *closed circle* new moon), average wind speed measured during crab collections (*dark line*), and start and end of sampling periods (*dashed vertical lines*) are plotted for reference. Sampling took place on days: 273, 275, 279, 282, 287 and 291. The response variable was log(x+1)-transformed for statistical analysis, but raw data are presented for simplicity. See text for significance levels

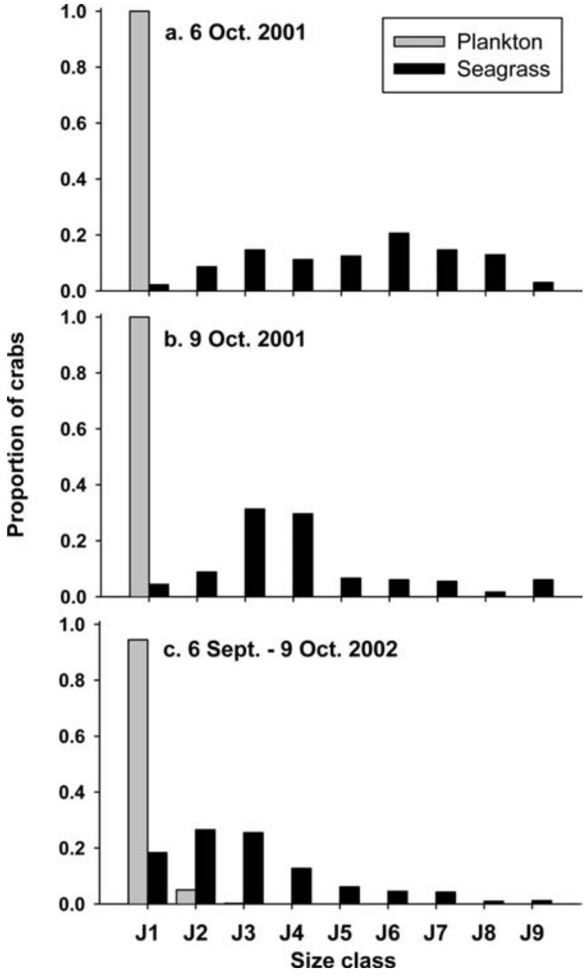

Fig. 2a–c Comparison of size-class distribution of juvenile blue crabs collected in the plankton and seagrass. Environmental cues study: **a** Sample sizes in plankton=49, seagrass=233; **b** plankton=27, seagrass=182. Density study: **c** plankton=616, seagrass=2,682; data were combined due to similar crab size-class distributions across study sites and sampling days. See text for significance levels

Table 1 Results of the explanatory variable selection using information-theoretic criteria

Explanatory variable	*K*	AIC$_c$	ΔAIC$_c$	Weights	Evidence ratio
J1	2	−48.03	1.07	0.3140	1.71
J2	2	−36.95	12.15	0.0012	447.75^b
J3	2	−36.76	12.34	0.0011	488.45^b
J1, J2	3	−49.10		0.5373	^{a}
J1, J3	3	−44.77	4.33	0.0616	8.72
J2, J3	3	−33.66	15.44	0.0002	2686.5^b
J1, J2, J3	4	−45.41	3.69	0.0845	6.36

Table values were calculated using model fits obtained from regression analysis on models that included the log(x+1)-transformed concentration of J1 crabs as the response variable, and the log(x+1)-transformed benthic densities of J1, J2, and J3 crabs as explanatory variables

K number of explanatory variables included in model+1, *AIC*$_c$ second-order corrected AIC for sample size <40,

Δ*AIC*$_c$ difference between model with lowest AIC$_c$, *weights* Akaike weight of evidence (probability) that model is best approximating model in a given set of candidate models, *evidence ratio* evidence supporting best approximating model

[a] Model with lowest AIC$_c$ against which all other models are compared

[b] Models with weights <0.054 have insufficient evidence to consider as plausible contributors to secondary blue crab dispersal

Table 2 Ranked relative importance of explanatory variables calculated from the Akaike weights in Table 1

Explanatory variable	Relative importance (%)
J1	99.74
J2	63.33
J3	14.74

models (Burnham and Anderson 2002). While this model had a 54% probability of being the right model for our data, it was only 1.71 times better at explaining variability in secondary dispersal than the one-parameter model with the density of J1 crabs as the explanatory variable (Table 1). Given the evidence ratio of <2.0, there was little basis to suggest that one model was better than another (Burnham and Anderson 2002). By ranking the relative importance of the explanatory variables, we determined that the density of J1 crabs was of greater relative importance in explaining the variability in secondary dispersal than the density of J2 crabs (99.7% versus 63.3%; Table 2). In addition, evidence for the relative importance of the J1 crab density variable (0.9979; Table 2) was substantially more than the weight of evidence for the next best approximating model (J1, J2: 0.5373; Table 1).

Models that included the benthic density of J2 and J3 crabs as explanatory variables (both separately and combined), had insufficient evidence of support (i.e. Akaike weights were less than 10% of the best approximating model weight, or <0.054; Table 1). Moreover, with respect to the other variables considered, the J3 explanatory variable was of low relative importance (~15%, Table 2). Thus, the density of J1 crabs explained more of the variability in secondary dispersal than the other explanatory variables considered in this study.

Functional relationship between pelagic and benthic juvenile blue crabs

In general, there was a non-linear increase in the pelagic concentration of J1 blue crabs with increasing benthic J1 crab density (Fig. 3). The benthic density of J1 crabs was used as the explanatory variable because of its relative importance in explaining variability in the pelagic concentration of J1 crabs (see above; Table 2). The model with the lowest AIC$_c$ was a sigmoid function, and had a 97% probability of being the right model given the set of candidate models (Table 3). The sigmoid model fit the data better than a linear model, which had no substantial evidence of support ($\Delta AIC_c > 10$, weights=0; Table 3; Burnham and Anderson 2002).

Discussion

The mechanisms driving secondary dispersal of aquatic benthic organisms are generally not well known, even though secondary dispersal can have significant implications to population and community dynamics (Caley et al. 1996; Palmer et al. 1996). For example, secondary dispersal by juvenile bivalves allow tide flats to be recolonized following disturbances and can determine adult distribution patterns in the North Sea (Beukema and de Vlas 1989). Secondary dispersal can also alter initial settlement patterns resulting in a decoupling between larval supply and later juvenile distributions. In Pamlico Sound North Carolina, for instance, secondary dispersal of early juvenile blue crabs links spatially-separated settlement habitats, thereby enhancing the nursery capacity of the entire sound (Etherington and Eggleston 2000, 2003). While small-scale field and laboratory studies have determined that secondary dispersal of early juvenile blue crabs is an active behavioral process, studies examining the effects of environmental cues and intraspecific crab density on secondary dispersal have been inconclusive (Blackmon and Eggleston 2001; Etherington et al. 2003). Results from this study suggest that secondary dispersal of early juvenile blue crabs from settlement habitats occurs rapidly following settlement in response to increasing conspecific density in seagrass, and is mediated by physical environmental conditions associated with diel and tidal cycles.

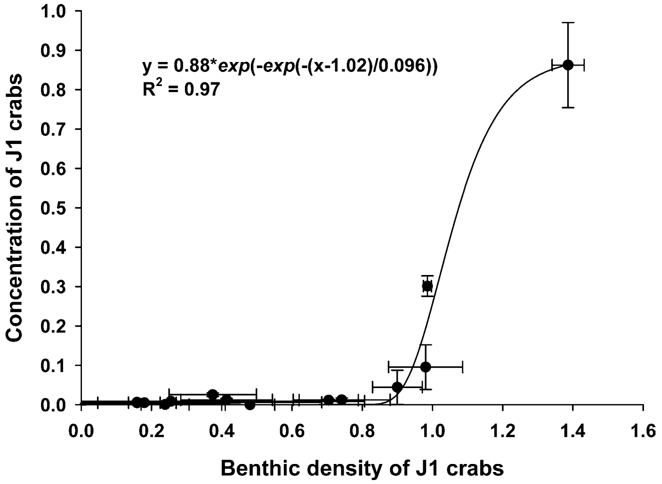

Fig. 3 Functional relationship between the pelagic concentration (no. m^{-3}) and benthic density (no. m^{-2}) of J1 blue crabs. Points represent means (±1 SE) of the log(x+1)-transformed concentration and density crab data. Regression line represents the best fitting function (see text and Table 3 for details). For reference, the concentration of juvenile blue crabs increased in the water column when benthic densities approximated 10 crabs m^{-2}

Table 3 Model selection results of the functional relationship between the log (x+1)-transformed pelagic and benthic abundances of J1 crabs

Model	K	AIC_c	ΔAIC_c	Weights
Linear	2	−48.03	35.57	0.0000
Sigmoid	3	−83.60		0.9687[a]

For simplicity, only criteria for the best approximating non-linear model are compared with those of the linear model.

K number of parameters included in model+1, AIC_c second-order corrected AIC for sample size <40, ΔAIC_c difference between model with lowest AIC_c, *weights* Akaike weight of evidence (probability) that model is best approximating model in a given set of candidate models

[a] Model with lowest AIC_c

Ontogenetic and density-dependent effects

Our results indicate that the relative abundance of early blue crab instars was greater in surface waters than those of later blue crab instars, suggesting that the propensity to use secondary dispersal is ontogenetic. This result is counter to previous findings where blue crab secondary dispersal occurred predominately by older (later) instars (Blackmon and Eggleston 2001; Etherington et al. 2003). The apparent discrepancy between our study and previous findings might be due to differences in the spatial scale over which secondary dispersal was examined. In our study, we quantified blue crab secondary dispersal from 0.05 km^2 seagrass beds, while other studies measured secondary dispersal from smaller-scale, 1 m^2 experimental seagrass plots (Blackmon and Eggleston 2001; Etherington et al. 2003) or in laboratory flumes (Blackmon and Eggleston 2001). Several reasons may explain why our results may be a more accurate depiction of which blue crab size classes undergo secondary dispersal. First, the secondary dispersal by older instars observed in other field studies was measured using plankton nets deployed over the seagrass bed (Blackmon and Eggleston 2001; Etherington et al. 2003). Such movements into the water column by larger juvenile crabs may represent redistribution of crabs within a seagrass bed rather than dispersal away from that habitat. In our study, the deployment of plankton nets over sandy areas downstream of the seagrass beds ensured that crabs collected in the water column were leaving these habitats through secondary dispersal (see assumptions in ‘Materials and methods’). Second, we know from concurrent sampling of the benthic and pelagic size-class distributions of blue crabs that J3 (and larger) instars were present in seagrass, but had low relative abundances in the plankton (Fig. 2a–c). Finally, because our field study was observational, we do not have artifacts associated with experimental field manipulations and laboratory studies.

Greater secondary dispersal of smaller rather than larger individuals (as we observed in this study) has been documented for other organisms living in aquatic habitats. For example, in marine bivalves, variation in the propensity to undergo secondary dispersal by stage likely reflects an ontogenetic difference in the burrowing depth between smaller and larger bivalves: smaller bivalves do not burrow as deeply as larger individuals, making them more susceptible to resuspension by wind waves (Thrush et al. 2000). In stream systems, competition among newly-hatched black fly neonates causes higher density-dependent dispersal of these stages than older larvae (Fonseca and Hart 1996). Early juvenile blue crabs also exhibit density-dependent secondary dispersal, implying that dispersal by J1 instars results from an active process under behavioral control rather than an ontogenetic susceptibility to passive dispersal.

Potential adaptive significance of density-dependent secondary dispersal by J1 crabs

Several studies examining the secondary dispersal of marine and stream benthic invertebrates have detected density-dependence in response to intraspecific or total infaunal density within a habitat (Service and Bell 1987; Fonseca and Hart 1996; Turner et al. 1997; Powers and Peterson 2000). Results from our study, however, indicate that secondary dispersal of early juvenile blue crabs was predominately influenced by intra-cohort density, rather than the total density of larger conspecifics. While the benthic density of J1 blue crabs was considered to be the most important determinant of density-dependent secondary dispersal in this study, the density of J2 instars (and their interaction with J1 crabs) might also enhance secondary dispersal and warrants further study. Nonetheless, density-dependent secondary dispersal by J1 instars demonstrates how local population regulation on the scale of a seagrass bed occurs rapidly following settlement.

The fact that conspecific density drives secondary dispersal is not surprising given that blue crabs are highly agonistic and cannibalistic (Moksnes et al. 1997). Furthermore, despite their small size, high movement rates of early juvenile blue crabs exhibited in seagrass (77% turnover m^{-2} in 6 h; Etherington et al. 2003) likely allows crabs to rapidly detect one-another within an initial settlement habitat. As such, density-dependent secondary dispersal is one mechanism by which early juvenile crabs can minimize predation by conspecifics, and may explain the non-linear relationships among blue crab settlers and recruits observed in the Chesapeake Bay (Pile et al. 1996) and North Carolina (Etherington and Eggleston 2000), as well as clarify why density-dependent predation of early juvenile blue crabs has not been identified (Pile et al. 1996). Lack of evidence for density-dependent mortality of blue crabs suggests that secondary dispersal may be of greater relative importance in structuring blue crab population dynamics than predation (e.g., Etherington et al. 2003).

Despite predictions of the ‘settle and stay’ hypothesis that high predation rates encountered in the plankton inhibit fishes and crustaceans from leaving initial settlement habitats (Bell and Westoby 1986), J1 blue crabs may experience a cannibalism refuge in the plankton by leaving habitats that harbor high conspecific densities. While this runs counter to the idea that mortality in the plankton is high (Thorson 1950), a recent study evaluating predation on planktonic coastal assemblages of marine invertebrate larvae measured relatively low predation rates (0–7% loss d^{-1}; Johnson and Shanks 2003). Predation rates for early juvenile blue crabs undergoing secondary dispersal in turbid estuarine conditions are unknown; however, preliminary tethering experiments suggest that while mortality of J1–2 blue crabs does not differ across habitat types (plankton versus seagrass), predation risk is slightly reduced at night (Reyns, unpublished data). A nocturnal reduction in mortality is not surprising, given that postlarval Caribbean spiny lobsters minimize predation by dispersing in surface waters during dark, new moon periods (Eggleston et al. 1998; Acosta and Butler 1999), and marine meiofauna (Hagerman and Rieger 1981), stream meiofauna (Palmer 1992), marine harpacticoid copepods (Service and Bell 1987), and some marine bivalve species (Armonies 1992) also undergo significantly greater secondary dispersal at night. Similarly, many estuarine and intertidal crabs have hatching rhythms that are synchronized with nighttime periods, as well as phases of the tidal cycle, to reduce larval predation by visual predators (Morgan 1995). For early juvenile blue crabs, the mechanism underlying nighttime transport appears to be due, in part, to an endogenous rhythm in swimming activity whereby juveniles become more active at night (Forward et al. 2004). We suggest therefore, that the timing of secondary dispersal by J1 blue crabs during nocturnal flood tides serves as an adaptive strategy to expedite transport from initial settlement habitats to alternative nursery habitats, while minimizing predation risk in the plankton.

The influence of environmental cues on secondary dispersal

Secondary dispersal can also be influenced by physical environmental conditions such as wind speed. Given the depth of the seagrass beds in our study area (1 m), the passive resuspension of juvenile blue crabs through wind-driven waves and currents is likely during strong wind events. Many marine and stream benthic invertebrates undergo passive secondary dispersal following storm or high-flow induced resuspension to the water column (Hagerman and Rieger 1981; Palmer 1992; Hall 1994). High flow conditions can also alter the rate at which density-dependent (active) secondary dispersal occurs in black fly neonates (Fonseca and Hart 1996). In our study, there was no statistically significant relationship between wind speed and the pelagic concentration of J1 blue crabs, suggesting that secondary dispersal is an active behavioral process regardless of wind speed. While crabs were collected during all diel and tidal phases during a relatively strong wind event (wind speed >15 $m\ s^{-1}$), and during nocturnal ebb tides (e.g., Day of year 275, 291: Fig. 1) corresponding to full and new moon periods when currents can reach 30 cm s^{-1} (Fonseca and Bell 1998), the size-class distribution of early juvenile blue crabs did not change during these periods (catch still dominated by J1 instars), as would be expected if secondary dispersal were passive. In addition, active secondary dispersal of juvenile blue crabs has been observed in laboratory flume conditions in flows between 20 and 30 cm s^{-1} (Blackmon and Eggleston 2001). Given that high wind conditions will enhance the concentration of suspended sediments in shallow environments and reduce light intensity, the presence of early juvenile blue crabs in surface waters during these events may instead reflect active secondary dispersal during low-light, high-flow conditions, rather than passive transport.

Conclusions and implications of secondary dispersal

Several studies have correlated the secondary dispersal of marine and stream benthic invertebrates with specific variables (e.g., wind speed, infaunal density, etc.; see reviews by Günther 1992; Palmer et al. 1996), but few have examined multiple, concurrent physical environmental and biological conditions as has been our approach in this study. This study, coupled with previous findings (Etherington and Eggleston 2000, 2003; Blackmon and Eggleston 2001; Etherington et al. 2003), demonstrates the ability of a juvenile marine benthic invertebrate to modify its regional distribution via dispersal in the water column by behaviorally responding to biological and physical environmental variables. Furthermore, because such secondary dispersal is density-dependent, blue crab metapopulation persistence is likely promoted through the redistribution of juvenile crabs from high-density settlement habitats to habitats characterized by low postlarval supply, which ultimately increases the regional nursery capacity (Etherington and Eggleston 2000, 2003). As such, secondary dispersal may be just as or even more important than pre-settlement (larval and postlarval) dispersal in linking regions of varying recruitment and habitat quality (Pulliam 1988). Consequently, predictions regarding the population dynamics of aquatic organisms, particularly for habitat conservation and fishery management applications, cannot be made without considering secondary dispersal and the degree to which it actually occurs.

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