Spatial dynamics of large-scale, multistage crab (*Callinectes sapidus*) dispersal: determinants and consequences for recruitment

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Abstract: We assessed determinants and consequences of multistage dispersal on spatial recruitment of the blue crab, *Callinectes sapidus*, within the Croatan, Albemarle, Pamlico Estuarine System (CAPES), North Carolina, U.S.A. Large-scale sampling of early juvenile crabs over 4 years indicated that spatial abundance patterns were size-dependent and resulted from primary post-larval dispersal (pre-settlement) and secondary juvenile dispersal (early post-settlement). In general, primary dispersal led to high abundances within more seaward habitats, whereas secondary dispersal (which was relatively consistent) expanded the distribution of juveniles, potentially increasing the estuarine nursery capacity. There were strong relationships between juvenile crab density and specific wind characteristics; however, these patterns were spatially explicit. Various physical processes (e.g., seasonal wind events, timing and magnitude of tropical cyclones) interacted to influence dispersal during multiple stages and determined crab recruitment patterns. Our results suggest that the nursery value of different habitats is highly dependent on the dispersal potential (primary and secondary dispersal) to and from these areas, which is largely determined by the relative position of habitats within the estuarine landscape.

Résumé : Notre étude porte sur les facteurs déterminants et les conséquences de la dispersion en plusieurs étapes sur le recrutement du crabe bleu, *Callinectes sapidus*, dans le système estuarien Croatan-Albemarle-Pamlico (CAPES) de la Caroline du Nord, É.-U. Un échantillonnage à grande échelle des jeunes crabes immatures pendant 4 ans a révélé que les patterns d'abondance spatiale sont reliés à la taille et sont causés principalement par une dispersion primaire des post-larves (avant l'établissement) et une dispersion secondaire des jeunes (tôt après l'établissement). En général, la dispersion primaire entraîne des abondances élevées dans les habitats situés plus vers la haute-mer, alors que la dispersion secondaire (qui est relativement constante) accroît la répartition des jeunes et augmente potentiellement la capacité de nursery de l'estuaire. Il y a de fortes relations entre la dispersion des jeunes crabes et certaines caractéristiques particulières du vent; cependant, ces patterns varient de façon nette selon les endroits. De nombreux processus physiques (e.g., épisodes de vents saisonniers, calendrier et importance des cyclones tropicaux) influencent par leur interaction les diverses étapes de la dispersion et déterminent les patterns de recrutement des crabes. Nos données laissent croire que la valeur des différents habitats comme nurseries dépend fortement du potentiel de dispersion (primaire et secondaire) vers ces régions ou à partir de ces régions, ce qui est en grande partie déterminé par la position relative des habitats dans le paysage estuarien.

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Introduction

Dispersal is a key element to understanding abundance patterns and population dynamics of organisms in spatially heterogeneous landscapes (Kareiva 1990; Wiens 1995). Exchange of individuals between groups can have various ecological impacts including increased flow of genetic information, enhanced metapopulation persistence, altered predator–prey dynamics, or modified population distribution and abundance patterns (Stenseth and Lidicker 1992; Dieckmann et al. 1999). Strong connectivity between groups through dispersal implies that local populations are partly dependent on processes occurring outside of the local environment (Caswell 1978; Roberts 1997). Thus, dispersal properties of organisms in spatially heterogeneous landscapes determine the scales at which processes act to control distribution and abundance patterns and population dynamics and the appropriate spatial configuration of conservation efforts (Crowder et al. 2000).

Dispersal properties of an organism are a function of the behavioral and morphological characteristics of the individual, as well as the characteristics of the environment. The degree of connectivity between isolated groups of individuals will be dependent on the life-history strategy of a given species (Horn 1983; Palmer et al. 1996) and the overall dispersal capabilities of the organism. Connectivity between habitat patches could occur during a limited period in the organism's life cycle (e.g., larval phase), or instead, large-scale dispersal may occur during multiple stages. For benthic marine species with open populations (i.e., where local recruitment is uncoupled from local reproduction by a dispersive larval stage; Caley et al. 1996), the importance of dispersal

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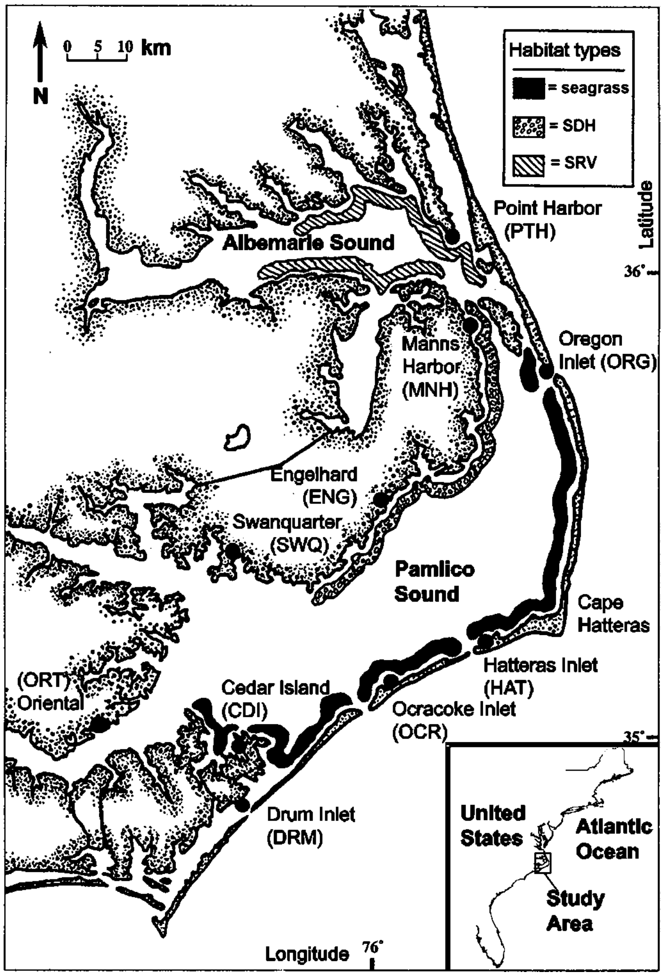
in determining population distribution and abundance has often been emphasized in the larval stages, before benthic settlement. There has been a relative lack of attention given to the role of dispersal of juveniles in the post-settlement phase and how this dispersal can influence local and regional population dynamics (Palmer et al. 1996). Nevertheless, there is a growing body of evidence demonstrating the importance of post-settlement dispersal in determining distribution and abundance patterns of diverse taxa including macrofaunal invertebrates (e.g., mollusks, crustaceans, and polychaetes; review by Gunther 1992), reef fish (Robertson 1988; Lewis 1997; Ault and Johnson 1998), and meiofauna (review by Palmer 1988). Post-settlement planktonic dispersal of early juvenile blue crabs (*Callinectes sapidus*) links spatially separated groups of organisms within the estuarine landscape and could be a key determinant of crab distribution and abundance patterns and population dynamics (Etherington and Eggleston 2000).

Patches of habitat can vary in their nursery value for a particular species because of differences in the their spatial pattern (e.g., habitat size, shape, fragmentation, connectivity), as well as their relative location (e.g., to larval supply, other juvenile habitats, or adult habitats; Beck et al. 2001). The relative position of a habitat within a landscape can influence its dispersal potential (both to and from a habitat; e.g., Stockhausen and Lipcius 2003) and therefore is crucial in defining which habitats are the most critical nursery areas requiring conservation. To determine the value of a particular habitat necessitates an understanding of how dispersal at multiple stages influences population abundance and distribution on various spatial and temporal scales.

The current study was conducted to determine how dispersal during multiple stages (both primary dispersal of post-larvae before settlement and secondary dispersal of juveniles soon after benthic settlement) interacts to determine distribution and abundance patterns of a marine invertebrate, the blue crab, within an estuarine landscape. Blue crab recruitment was examined within the Croatan, Albemarle, Pamlico Estuarine System (CAPES), North Carolina, U.S.A. (Fig. 1). The CAPES has two relatively isolated regions of shallow-water, structured habitats, differing in their proximity to oceanic larvae, that could serve as nursery habitats for blue crabs. A conceptual model was proposed by Etherington and Eggleston (2000) whereby, in the absence of tropical cyclones, post-larval blue crabs settle within the seagrass beds near the inlets of the CAPES (Fig. 1) and later disperse to more inland portions of the estuary either via the water column as early juveniles or through benthic dispersal as later-stage juveniles. We predicted that tropical cyclones could increase the nursery capacity of the estuarine system by delivering post-larvae to the sound region of the estuary, as well as facilitating juvenile post-settlement dispersal to areas that do not normally experience consistent settlement of post-larvae (Etherington and Eggleston 2000; D. Eggleston, unpublished data). The present study was conducted to test this model of blue crab recruitment over several years containing different patterns of tropical cyclone frequency to better understand the determinants of pre- (primary) and post-settlement (secondary) dispersal and the implications of this multistage dispersal on spatial dynamics of recruitment within the estuarine landscape.

Fig. 1. The Croatan, Albemarle, Pamlico Estuarine System (CAPES) in North Carolina, U.S.A., including all sites that were sampled for juvenile blue crab (*Callinectes sapidus*) density. Inlet sites: Oregon Inlet (ORG), Hatteras Inlet (HAT), Ocracoke Inlet (OCR), and Drum Inlet (DRM). Sound sites: Point Harbor (PTH), Manns Harbor (MNH), Engelhard (ENG), Swanquarter (SWQ), Cedar Island (CDI), and Oriental (ORT). Complex habitat types present in the CAPES: seagrass, shallow detrital habitat (SDH), and submersed rooted vasculars (SRV; primarily, *Myriophyllum spicatum*).



Our examination of juvenile blue crab recruitment dynamics within North Carolina focused on three main issues: (*i*) temporal variation in size-specific juvenile abundance in spatially separated estuarine regions; (*ii*) influence of wind forcing on multistage crab dispersal and subsequent initial and secondary recruitment; and (*iii*) spatial and temporal occurrence of post-settlement planktonic dispersal and its relationship with tropical cyclones.

Methods

Blue crab life history

The blue crab exhibits a complex life cycle whereby larval and post-larval stages reside in an oceanic environment, whereas juvenile and adults have a benthic existence, primarily in estuarine habitats. Mature females with egg masses migrate from lower salinity estuarine habitats towards oceanic waters where they release their larvae at the bay mouth or inlets (Van Engel 1958; Williams 1984). Larvae spend ~30 days in the oceanic environment before metamorphosing to the post-larval stage (McConaugha et al. 1983). Postlarvae then move back into the estuary using a combination of physical forcing mechanisms such as wind-driven surface currents and tidal currents (Epifanio et al. 1984; Goodrich et al. 1989). Once within the estuarine environment, post-larvae settle within complex benthic habitats such as seagrass (e.g., Heck and Thoman 1981; Orth and van Montfrans 1987), salt marsh (Thomas et al. 1990), or shallow detrital habitats (Etherington and Eggleston 2000) before metamorphosing to the first benthic juvenile stage (J1). Juvenile instars (molting stages) will subsequently be referred to as J1, J2, J3, etc.

Post-settlement planktonic dispersal of juvenile blue crabs from within seagrass beds has been documented in both field (Etherington and Eggleston 2000; Blackmon and Eggleston 2001) and laboratory studies (Blackmon and Eggleston 2001). This secondary juvenile dispersal appears to be an active behavior, primarily in response to increasing current speeds (Blackmon and Eggleston 2001) and induced by interactions between juveniles within seagrass beds (Etherington et al. 2003). Patterns of juvenile abundance indicative of post-settlement planktonic juvenile dispersal have been observed over large spatial scales (up to 50 km) in the CAPES (Fig. 1). Evidence of juvenile blue crabs within the water column away from structured habitats supports this notion of large-scale dispersal (Mense and Wenner 1989; N. Reyns, Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695, unpublished data). Thus, post-settlement planktonic juvenile dispersal has the potential to link groups of organisms that would otherwise be spatially separated (because of the amount of time that it would take juveniles to walk a great distance or because of unfavorable conditions such as a lack of refuge or an abundance of predators between habitat patches; Etherington and Eggleston 2000). Juvenile patterns representative of post-settlement planktonic dispersal of juvenile blue crabs have been documented during time periods associated with tropical cyclones (Etherington and Eggleston 2000). It is possible that this secondary dispersal only occurs during strong physical forcing events within the estuary, or instead, juvenile dispersal could be associated with a variety of environmental conditions.

Study system and sampling sites

We chose to examine recruitment of a marine benthic invertebrate to spatially isolated habitats within a large, primarily wind-driven estuary, the CAPES, North Carolina, U.S.A. (Fig. 1). The CAPES is a shallow lagoonal system that is enclosed by a strip of barrier islands, the Outer Banks. These physical attributes cause circulation within the system to be primarily driven by winds, with tidal influence only prevalent within 3–5 km of the inlets (Pietrafesa and Janowitz 1991; Tom Hopkins, Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695, personal communication). Therefore, different physical forcing mechanisms predominate in different regions of the estuarine system and could influence transport of post-larval and juvenile crabs.

We divided the CAPES into two main regions, inlet and sound, to define differences in proximity to oceanic sources of post-larval blue crabs. Within the inlet region, we identified four sites: Oregon Inlet, Hatteras Inlet, Ocracoke Inlet, and Drum Inlet (Fig. 1). The sound region consists of six sites that were distributed along the interior of the estuarine system: Point Harbor, Manns Harbor, Engelhard, Swanquarter, Oriental, and Cedar Island (Fig. 1). Overall, we had relatively wide sampling coverage of the CAPES, with sites located between 15 and 50 km apart along ~300 km of shoreline.

Spatial and temporal variation in crab abundance patterns

Juvenile sampling

Sampling of juvenile blue crabs consisted of replicated standardized suction sampling of a 1.674-m^2 area within a given structured benthic habitat (see Etherington and Eggleston (2000) for details). Habitat types varied across sites; most sites contained seagrass (*Zostera marina*, *Halodule wrightii*, and *Ruppia marina*), but some sites contained primarily shallow detrital habitats (SDH) and others were dominated by the freshwater macrophyte *Myriophyllum spicatum*, which we have categorized as SRV (submersed rooted vasculars, Fig. 1; Etherington and Eggleston 2000). Samples were taken from the complex habitat that was available at each site; densities of juvenile blue crabs do not differ significantly between these complex habitat types (Etherington and Eggleston 2000). Samples were taken at each site within a 5-day period beginning 3 days after the new moon in the months of August, September, and October in the years 1996–1999. Two sites were removed from the sampling protocol in 1998 (Oriental and Cedar Island) based on consistently low juvenile abundance, and one site was added to the sampling scheme in 1998 (Drum Inlet) to improve spatial coverage within the southern portion of the system. A core set of seven sites spanning the inlet and sound regions was sampled consistently over the 4-year period. Six replicate samples were taken at each site during a time period; however, the number of samples that were sorted in the laboratory ranged from 3 to 6 in an effort to reduce the amount of sorting time where categories had low variance between samples or extremely low numbers of juveniles (see Etherington and Eggleston (2000) for examples of sample size reduction and justification). From these samples, we quantified the density of juvenile instars 1 and 2 (J1–J2; carapace width 2.2–4.2 mm; 0–16 days since settlement) and the density of juvenile instars 3 through 5 (J3–J5; carapace width 4.3–9.1 mm; 14–46 days since settlement) (Etherington and Eggleston 2000). These size classes were chosen because (*i*) spatiotemporal patterns of J1–J2 recruitment are similar to patterns of post-larval settlement (measured with artificial settlement substrates; D. Eggleston, unpublished data); therefore, J1–J2 stages likely reflect processes influencing post-larval delivery and settlement; and (*ii*) post-settlement planktonic dispersal has been detected between J1–J2 and J5 stages (Etherington and Eggleston 2000); thus, patterns of distribution and abundance of J3–J5 stages are influenced by post-settlement juvenile dispersal. Thus, patterns of J1–J2 abundance are a reflection of primary dispersal occurring during the post-larval stage (pre-settlement), whereas J3–J5 abundance patterns incorporate the process of secondary dispersal by early post-settlement juveniles.

Statistical analyses

To examine spatial and temporal patterns of juvenile recruitment, we used a repeated-measures ANOVA (analysis of variance) model with month (August, September, October) as the within-subject factor and year (1996, 1997, 1998, 1999) and region (inlet, sound) as between-subject factors. Because a site was repeatedly sampled throughout a recruitment season, the repeated-measures design accounted for correlation in juvenile density between sampling months. Recruitment values between years were considered independent of one another; therefore, we blocked by year. We were primarily interested in spatial differences between regions (inlet and sound); therefore, we nested site within region. Significant interaction effects were interpreted with Ryan's Q multiple-comparison tests and lower-level ANOVA models.

Relationship between blue crab recruitment and wind components

Classification of wind

Wind data for Cape Hatteras National Weather Service Office (located at Cape Hatteras, N.C.; Fig. 1) were obtained through the N.C. State Climate Office. All wind variables in this study are described as the direction from which the wind was blowing. Daily averages of wind speed and direction were separated into east–west (u) and north–south (v) components. Thus, the u and v variables represented the magnitude of the wind from each of the orientations. Because recruitment to estuarine habitats may result from the stochastic likelihood that an offshore pool of post-larval crabs coincides with favorable winds, it is possible that the number of days with winds from a particular direction might better represent the influence of wind characteristics on recruitment than the average wind vectors over a period of time. To incorporate information on both wind vectors and number of days of a particular wind direction, these two variables were combined into a single independent variable. It is also likely that the speed of winds, irrespective of direction, could drive recruitment; therefore, we examined wind speed as a separate wind variable. Lastly, the number of tropical cyclones during a time period could impact recruitment levels to different regions. Tropical cyclones were defined as tropical storms or hurricanes that passed within 500 km of the North Carolina CAPES, because tropical cyclones within this distance can influence water levels within the system (L. Xie, Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695, personal communication; L. Etherington, personal observation). We examined the relationship between blue crab recruitment and eight wind variables: (1) u component (east–west); (2) v component (north–south); (3) percentage of days with winds from the east (days with an average east component, rather than west component); (4) percentage of days with winds from the north (rather than south); (5) u component and percentage of days from the east; (6) v component and percentage of days from the north; (7) wind speed; and (8) number of tropical cyclones.

Statistical analyses

The relationship between juvenile blue crab recruitment and wind variables was analyzed using multiple regression. Wind variables included in the model were examined for potential collinearity and were removed from the model when strong collinearity was detected. Plots of variances and predicted values versus residuals were examined to ensure that assumptions of normality and homogeneous variances were met. Outliers were detected using Cook's D statistic and were removed when necessary. The simplest model that explained the most variation in juvenile abundance was determined using Akaike's information criteria, Mallows' C_P statistic, and the adjusted R^2 values (Rawlings et al. 1998). The best fitting models were determined separately for J1–J2 and J3–J5 stages.

For J1–J2 crabs, wind variables were determined from 1 to 21 days before the juvenile sampling period. According to laboratory growth data (Millikin and Williams 1980), J1–J2 blue crabs are about 0–16 days since settlement (Etherington and Eggleston 2000), plus it takes ~5 days for post-larvae to metamorphose to juveniles in the presence of estuarine water (Wolcott and De Vries 1994). Thus, winds 0–21 days before juvenile sampling likely influenced post-larval delivery (primary dispersal) and settlement of individuals that would be sampled later as J1–J2 crabs. For J3–J5 stages, wind variables were determined from 1 to 25 days before the juvenile sampling period (i.e., all days in between the present juvenile sampling and the sampling 1 month prior). Winds during this time period would influence primarily post-settlement dispersal of juveniles (secondary dispersal), which would have settled before this time period, in addition to the delivery and settlement of post-larvae (primary dispersal), which would be later sampled as younger juveniles (J3) (J3–J5 blue crabs are about 14–46 days since settlement; Millikin and Williams 1980; Etherington and Eggleston 2000).

Initially, we examined the relationship between juvenile recruitment and the eight wind variables across all sites. This analysis resulted in a poor fit for both J1–J2 and J3–J5 recruits ($R^2 < 0.10$). Next, we determined the relationship between the various wind variables and juvenile recruitment separately for the inlet versus sound regions. For the inlet region, there was an overall lack of fit between wind characteristics and juvenile recruitment for both size classes (J1–J2, $R^2 = 0.05$; J3–J5, $R^2 = 0.03$). Therefore, we examined the inlet region on a finer spatial scale by analyzing the northern and southern inlets separately because of the difference in geographic orientation between these two coastlines (Oregon inlet, northeastward-facing, versus Hatteras, Ocracoke, and Drum Inlets, which are southeastward-facing; Fig. 1) and potential differences in the interaction of winds with the barrier island topography.

For the sound region, we removed Cedar Island and Oriental (Fig. 1) from our analyses because of consistently low levels of recruitment to these sites (see Results). The aggregation of all sites within the sound region led to a somewhat weak statistical fit between wind variables and juvenile recruitment (J1–J2, $R^2 = 0.15$; J3–J5, $R^2 = 0.15$). Because we were unsure of the specific spatial pathways of post-larval and juvenile transport from a specific inlet to a specific location within the sound region, we were unclear on how to group sites together for statistical analyses. Therefore, we assessed spatial coherence in J1–J2 and J3–J5 densities over time and sites within the sound using Pearson's correlation coefficients. For J1–J2 crabs, there was no clear separation of sites within the sound region, as many of the sites were correlated with one another (Table 1*a*). Thus, we examined the relationship between the density of J1–J2 crabs and wind variables with Engelhard and Swanquarter grouped together (based on relatively close proximity, similar distance from inlet sources of post-larvae, and geographic orientation (Fig. 1)), as well as separate analyses for Manns Harbor and Point Harbor (Fig. 1). For J3–J5 crabs, the correlation analyses indicated that temporal variation in the density of J3–J5 crabs was correlated between Engelhard and Swanquarter; however, density of J3–J5 crabs at Manns Harbor and Point Harbor was not correlated with any other sound sites (Table 1*b*). Thus, similar to our spatial analysis of J1–J2 crabs, we examined the relationship between wind variables and density of J3–J5 crabs at both Manns Harbor and Point Harbor independent of the other sites within the sound region, whereas Engelhard and Swanquarter were analyzed jointly.

Table 1. Spatial coherence of juvenile blue crab recruitment in the sound region as assessed with Pearson's correlation tests.

	PTH	MNH	ENG	SWQ
(*a*) J1–J2 crabs				
PTH	***	0.47	0.84	0.83
		(0.17)	(0.003)	(0.003)
MNH		***	0.13	0.60
			(0.68)	(0.04)
ENG			***	0.47
				(0.12)
SWQ				***
(*b*) J3–J5 crabs				
PTH	***	0.06	0.39	0.56
		(0.86)	(0.27)	(0.09)
MNH		***	0.05	–0.16
			(0.87)	(0.62)
ENG			***	0.80
				(0.002)
SWQ				***

Note: The top value is the Pearson's correlation coefficient and the bottom value in parentheses is the *p* value for the correlation between sites. The sample size ranged from 10 to12. PTH, Point Harbor; MNH, Manns Harbor; ENG, Engelhard; SWQ, Swanquarter.

Post-settlement planktonic dispersal

To determine the role of post-settlement planktonic dispersal in influencing large-scale juvenile blue crab distribution and abundance patterns, we examined site-specific cohorts over time to determine rates of juvenile loss or gain (see below). Laboratory growth data (Millikin and Williams 1980) were used to determine the time-since-settlement of different-sized juveniles, which, in turn, enabled us to define specific cohorts of juvenile blue crabs. Variable growth rates between field and laboratory conditions could alter our estimates of time-since-settlement. Nevertheless, our definition of a cohort is based on the only known data of juvenile blue crab growth and therefore represents the best estimate of a cohort. We examined the density of J1–J2 crabs of 1 month at a particular site and compared this with J5 density for the following month at the same site. As a result, we were able to follow two cohorts per year: (1) August J1–J2 – September J5; and (2) September J1–J2 – October J5 (see Etherington and Eggleston (2000) for further details). We would expect that the number of juveniles in a cohort would decrease over time as a result of mortality and emigration. In instances in which a cohort increased over time (i.e., density of J5 crabs at month $t + 1 >$ density of J1–J2 crabs at month t), we concluded that the cohort had been supplemented by planktonic immigrants. To distinguish an increase in the cohort size over time resulting from post-settlement planktonic dispersal versus an increase resulting from natural variability, we categorized a cohort as increasing only where the error bar of J1–J2 density did not overlap with the error bar of J5 density. It is unlikely that juvenile blue crabs moved from the inlet region to the sound region by walking because of (*i*) the potentially high predation rates of juveniles in unstructured bottom (Pile et al. 1996) and (*ii*) the speed necessary for juvenile crabs to move this distance (to move from the inlet to the sound region by walking, juveniles would have to travel at average speeds between 0.5 and 1.2 $\text{km}\cdot\text{day}^{-1}$, speeds far greater than those documented for adult blue crabs (0.25 $\text{km}\cdot\text{day}^{-1}$; Shirley and Wolcott 1991)). It also seems unlikely that juveniles are walking to locations within the sound region from nearby habitats, because benthic habitats within this region are very patchy (L. Etherington, personal observation); thus, juveniles would have to traverse large expanses of unstructured habitats where predation is expected to be high (Pile et al. 1996). We examined eight cohorts over the 4-year period (two per year) for juvenile patterns indicative of post-settlement planktonic dispersal. We were also interested in the potential physical forcing mechanisms that caused long-distance planktonic dispersal. To determine if post-settlement planktonic dispersal of juveniles occurred primarily during strong storm events (Etherington and Eggleston 2000), we examined the relationship between the number of tropical cyclones that occurred between the sampling periods for a cohort (cohort 1, August → September; cohort 2, September → October) and the percentage of sites within the sound region that demonstrated abundance patterns representative of post-settlement planktonic dispersal. Percentage rather than number of sites was used as the response variable, because during two time periods (1998, cohort 1; 1999, cohort 2), there were only three sites within the sound that were sampled (versus the other time periods when four sites were sampled).

Results

Environmental conditions

During 1996–1999, the general directional wind patterns at Cape Hatteras shifted during the blue crab recruitment season from an average southwest direction in August to a northeast direction in October (Figs. 2 and 3). There was a large amount of variability in the magnitude as well as direction of the winds during each 3-month blue crab recruitment period (Fig. 2). The 4-year study period contained a relatively high frequency of tropical cyclones, ranging from 2 to 4 per year (Fig. 2). During 1996–1999, tropical cyclones occurred in all months (August–October), with the number of tropical cyclones in a given month ranging from 0 to 2 (Fig. 2). Thus, there was considerable temporal variation in wind forcing with which to examine the response of blue crab recruitment.

Spatial and temporal variation in crab abundance patterns

For the inlet region, the mean density of all stages of early juvenile blue crabs was higher at Oregon and Drum inlets than at Hatteras and Ocracoke inlets (Fig. 4). For the sound region, mean density of J1–J2 crabs was highest at Manns Harbor, followed by Engelhard and Point Harbor, with lowest mean densities at sites in the southern portion of Pamlico Sound (Figs. 4 and 1). For J3–J5 crabs in the sound region, highest densities occurred at Manns Harbor and Engelhard, followed by Point Harbor and the southern sound sites. There was considerable variation in the density of early juvenile blue crabs across years and across months within a year (Fig. 5).

J1–J2 crabs

The density of J1–J2 blue crabs varied significantly according to region, month, and year; however a significant three-way interaction effect of region × month × year (Fig. 5*a*; repeated-measures ANOVA; F = 4.03, df = 6,48, p = 0.002) prevented clean interpretation of the main effects. In 6 of 12 months sampled, the density of J1–J2 crabs was significantly higher at the inlet region than the sound (Table 2*a*). The density of J1–J2 crabs was never significantly greater in the sound than in the inlets (Table 2*a*). Within the inlet region, September and October contained the highest densities of J1–J2 crabs during the 4-year study (Table 2*b*), whereas within the sound region, there was no particular month that contained significantly higher J1–J2 crab density than the other two months (Table 2*b*). Although annual variation in densities of J1–J2 crabs differed by region and month, 1996 had the highest densities in four of the six month × region combinations (Table 2*c*).

J3–J5 crabs

Densities of J3–J5 blue crabs varied significantly according to year and month; however, a significant year × month interaction effect (Fig. 5*b*; repeated-measures ANOVA; F = 4.35, df = 6,48, p = 0.001) prevented contrasts across the main effects. The highest density of J3–J5 crabs was in September or October of each year, similar to the pattern for J1–J2 crabs (Table 2 versus Table 3). In 1996, the density of J3–J5 in September and October was significantly higher than the density of J3–J5 in August, whereas in 1998, J3–J5 densities in September were significantly greater than in August and October. In 1997 and 1999 (years with low J3–J5 densities), there was no difference in the density of J3–J5 crabs between months (Table 3). Although there were higher densities of J3–J5 crabs in the sound than the inlet region (Fig. 5*b*), the trend was not significant (Fig. 5*b*; repeated-measures ANOVA; F = 0.47, df = 1,8, p = 0.51).

Relationship between blue crab recruitment and wind components

In general, the amount of variation in densities of juvenile blue crabs explained by wind forcing, as well as the specific wind variables that showed a positive relationship with juvenile density, varied according to juvenile size class as well as region (Table 4). When examining all sites together, there was a positive relationship between both J1–J2 and J3–J5 crabs and winds; however, winds explained very little of the temporal variation in juvenile density (Table 4). With finer spatial resolution, there was a much stronger relationship between juvenile blue crab density and wind forcing at several locations; however, at other locations, there was a lack of relationship.

At Oregon Inlet, there was a relatively strong relationship between the density of J1–J2 crabs and the strength and number of days of north winds; however, there was a lack of relationship between the density of J3–J5 crabs at Oregon Inlet and wind forcing (Table 4). In contrast to Oregon Inlet, there was no significant relationship between the density of juvenile blue crabs at the southern inlets (Hatteras Inlet, Ocracoke Inlet, Drum Inlet) and wind variables (Table 4). The relationship between the density of juvenile blue crabs and wind variables within the sound region was similar between size classes, but varied between sites within the region. Although juvenile abundance was significantly associated with wind forcing at Engelhard and Swanquarter (Table 4), it was most strongly related to wind forcing at Point Harbor. In contrast, at Manns Harbor, the densities of J1–J2 and J3–J5 crabs were not associated with wind variables (Table 4).

Influence of tropical cyclones on recruitment

We predicted that the spatial distribution of recruitment within the CAPES would increase during the passage of tropical cyclones because of increased primary and secondary dispersal to the sound region. Within the sound region, there did appear to be a positive relationship between the density of J1–J2 crabs and the number of tropical cyclones during September and October of 1996; however, outside of these two periods, densities of J1–J2 crabs in the sound region were extremely low, even during time periods influenced by tropical cyclones. The exception was Manns Harbor, where densities of J1–J2 crabs were moderate to high during most periods. The only site that showed a relationship between J1–J2 density and the number of tropical cyclones was Point Harbor (Table 4). This site is in the uppermost reaches of the CAPES; therefore, strong forcing events may be crucial in dispersal of post-larvae to this area. There was not a strong relationship between the density of J3–J5 crabs and the frequency of tropical cyclones (see below; although one multiple regression model did include the number of tropical cyclones as an explanatory variable; Table 4), suggesting a lack of relationship between secondary dispersal and the number of tropical cyclones. Overall, early juvenile crab abundance in the sound region is not driven solely by the presence or absence of tropical cyclones.

Post-settlement planktonic dispersal

Overall, post-settlement planktonic dispersal appeared to be an important component in juvenile blue crab population dynamics within North Carolina. In seven of the eight cohorts examined, we found evidence of post-settlement planktonic dispersal within at least one of the sound sites as indicated by increased density of crabs within a given cohort at a specific site (Fig. 6). Post-settlement planktonic juvenile

Fig. 2. Alongshore and cross-shelf components of wind velocity as measured at Cape Hatteras National Weather Service Office, N.C., from 1 July to 31 October (days of year 182 to 304) during the years of (*a*) 1996, (*b*) 1997, (*c*) 1998, and (*d*) 1999. The upper graph in each panel represents cross-shelf wind components and the bottom graph represents alongshore wind components. For cross-shelf winds, positive values are easterly winds and negative values are westerly winds. For alongshore winds, positive values are northerly winds and negative values are southerly winds. The direction is the direction from which the wind was blowing. The time periods of juvenile sampling are marked with asterisks, with one sampling period following the new moon in August, September, and October of each year. Tropical cyclones are marked with a letter: 1996, E = Hurricane *Edouard*, F = Hurricane *Fran*, H = Hurricane *Hortense*, J = Tropical storm *Josephine*; 1997, C = Tropical storm *Claudette*, D = Tropical storm *Danny*; 1998, B = Hurricane *Bonnie*, D = Hurricane *Danielle*; 1999, D = Hurricane *Dennis*, F = Hurricane *Floyd*. Wind data is missing from two time periods in 1999 because of the evacuation of the weather service office.

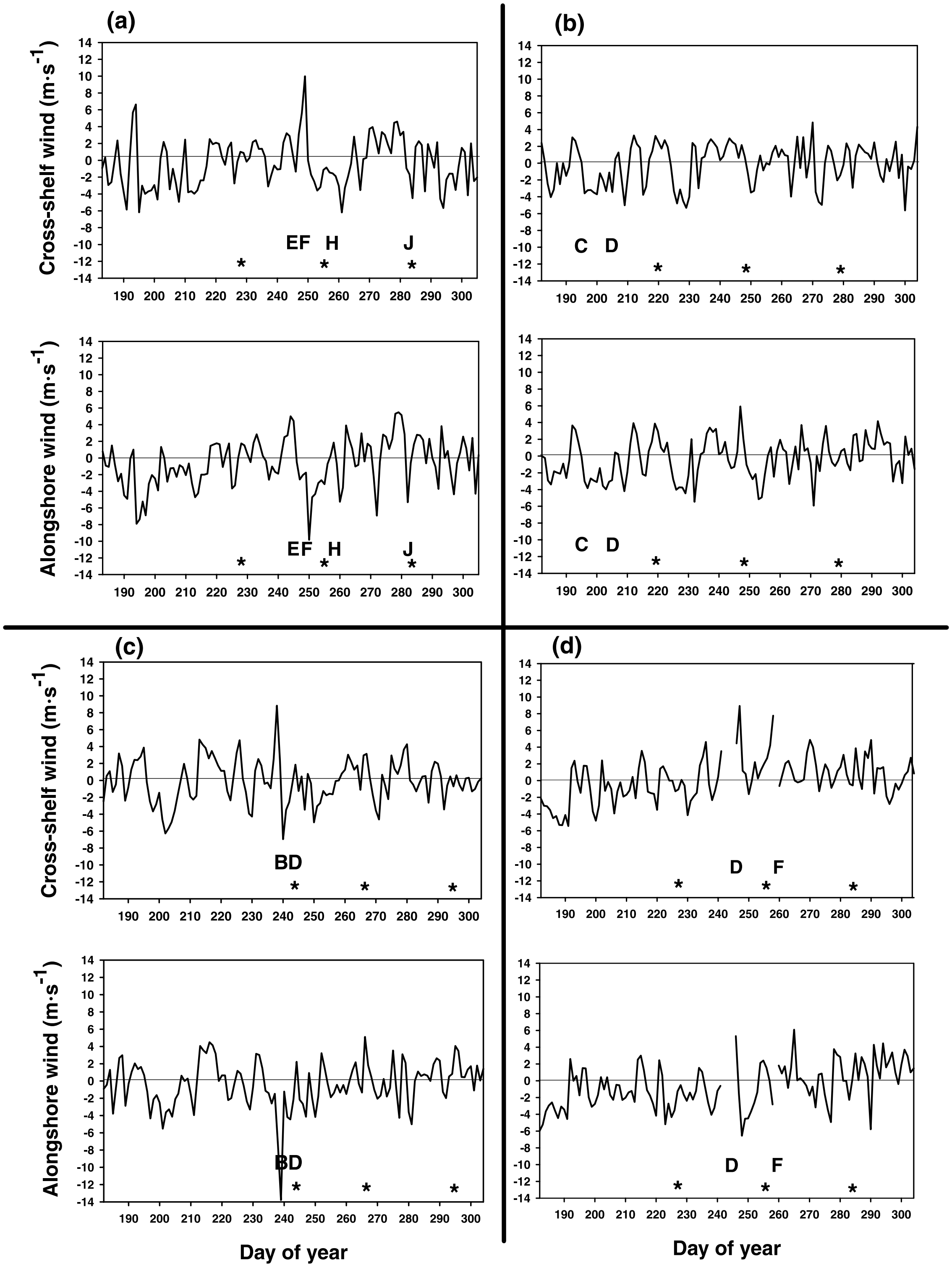
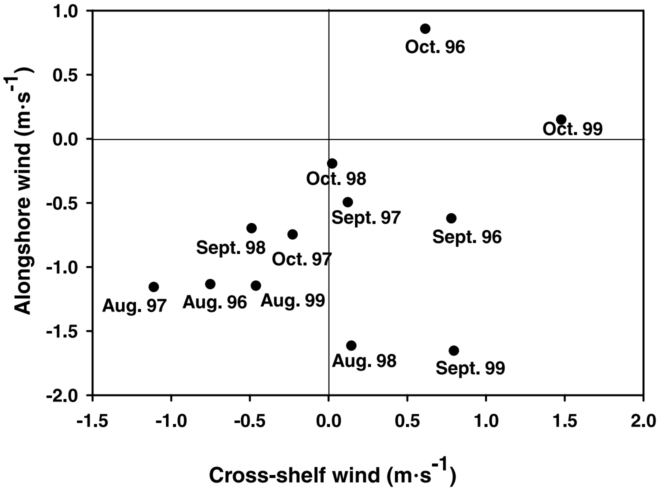


Fig. 3. Average alongshore and cross-shelf components of wind velocity as measured at Cape Hatteras National Weather Service Office, N.C. Wind characteristics were averaged over 25 days before juvenile crab sampling for August, September, and October of the years 1996–1999 (dates represented by two-digit years in the figure). For alongshore winds, positive values are northerly winds and negative values are southerly winds. For cross-shelf winds, positive values are easterly winds and negative values are westerly winds. The direction is the direction from which the wind was blowing. For example, average wind characteristics during August 1996, 1997, and 1999 were from the southwest, whereas winds during September 1996 and 1999 were strong from the southeast, and October 1996 and 1999 were characterized by northeasterly winds.



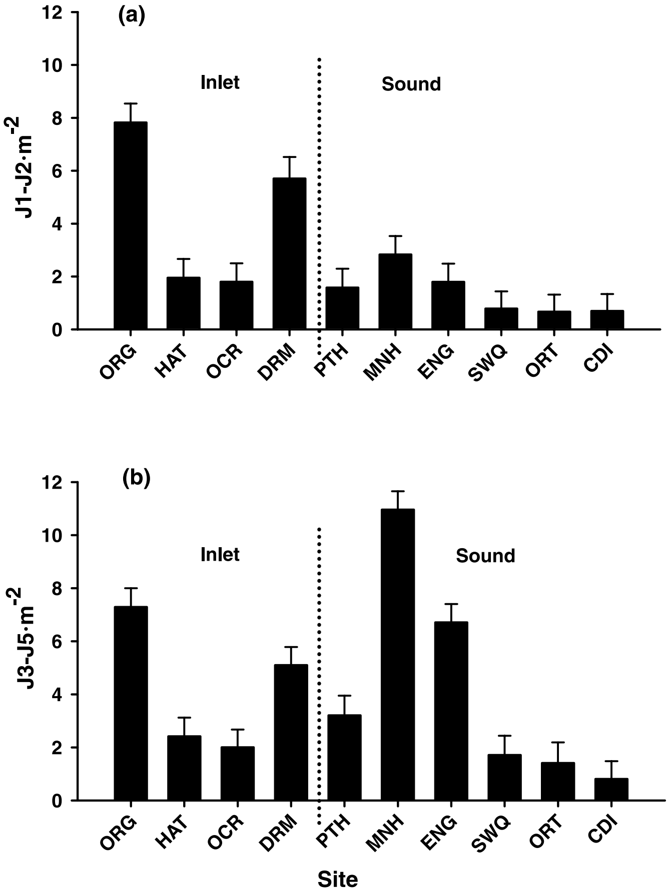
dispersal was detected only at sites within the sound region (except for one case (Cohort 1 of 1999 at Oregon Inlet); Fig. 6). Juvenile abundance patterns indicative of post-settlement dispersal were evident primarily at Engelhard (six of eight cohorts) and Manns Harbor (four of eight cohorts) but were also detected at Swanquarter (four of seven cohorts) and Point Harbor (three of six cohorts) (Fig. 6). The relative increase in cohorts over time was highest at Manns Harbor and Engelhard, suggesting that the magnitude of juvenile dispersal was highest to these sites (Fig. 6).

Contrary to our original hypothesis, there was not a relationship between the percentage of sites within the sound region that showed evidence of post-settlement planktonic dispersal and the number of tropical cyclones (Fig. 7). For example, 57% of the cohorts demonstrating patterns representative of secondary dispersal occurred during periods without tropical cyclones (Fig. 7). These results suggest that post-settlement planktonic dispersal was a consistent process that occurred during a variety of physical conditions, not just during tropical cyclones.

Discussion

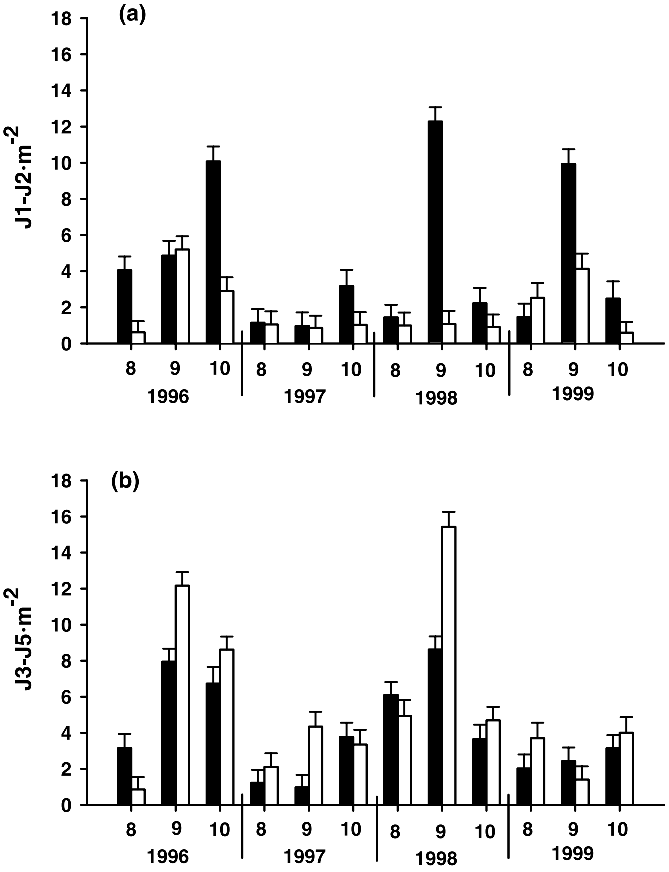
We demonstrated that juvenile blue crab distribution and abundance patterns reflect the interaction between primary dispersal of post-larvae and secondary dispersal of early benthic juveniles determined by a suite of wind events that act in a spatially explicit manner. Primary dispersal of post-larval crabs led to spatial clumping within the estuary, with highest densities at relatively seaward locations, particularly Oregon and Drum inlets. Secondary dispersal of post-settlement juveniles occurred soon after benthic settlement (less than 1 month) and increased the distribution of recruits throughout the estuary, potentially broadening the nursery capacity of the system.

Fig. 4. Spatial patterns of (*a*) J1–J2 crabs·m^{-2} and (*b*) J3–J5 crabs·m^{-2} according to site, averaged over all months and years. The vertical dotted line represents the division of the inlet region from the sound region. See Fig. 1 for site name abbreviations. The sites are arranged from north to south, reading from left to right, within each of the regions. Means (+ standard error) represent back-transformed values from means of log-transformed data.



The results from the present study led us to modify our original conceptual model of blue crab recruitment dynamics within the CAPES, whereby under a variety of weather conditions, most post-larvae settle within seagrass beds in the inlet region (donor habitats), with subsequent planktonic dispersal of juveniles to the sound region (receiver habitats). The particular wind events that facilitate primary or secondary dispersal to a particular habitat within the CAPES are highly dependent on the location of habitats within the estuarine system. The overall estuarine distribution of crabs is influenced by a combination of physical forcing processes such as seasonal wind events, the timing and magnitude of tropical cyclones within the recruitment season, and possibly El Niño conditions (predominantly weak offshore winds). Thus, the overall nursery value of different habitats is highly dependent on the dispersal potential (primary and secondary

Fig. 5. Juvenile blue crab (*Callinectes sapidus*) recruitment as a function of month (number under bars) and year for (*a*) J1–J2 crabs·m^{-2} and (*b*) J3–J5 crabs·m^{-2} for inlet (solid bars) and sound (open bars) regions. Means (+ standard error) represent back-transformed values from means of log-transformed data.



dispersal) to and from these areas, which is largely a function of the relative position of habitats within the estuarine landscape.

Spatial and temporal variation in crab abundance patterns

The results of this study provide a mechanistic understanding of spatial recruitment patterns that complements observational and simulation studies. For example, Bell et al. (1988) also found that particular locations of seagrass beds within the estuary contained higher settlement of many species of fish and decapod crustaceans than at other locations because of their relative proximity to spawning areas. Similarly, Heck and Thoman (1984) detected higher densities of blue crabs within seagrass habitats in the lower versus the upper Chesapeake Bay because of juvenile recruitment at locations closer to oceanic environments where they were spawned. A simulation modeling study of blue crab post-larval settlement within the Chesapeake Bay illustrated that the “value” of a particular seagrass habitat can depend on its location within the estuarine landscape because of the likelihood of post-larval settlement (Stockhausen and Lipcius 2003). These studies illustrate how the relative position of habitats within the landscape can influence their overall value as nursery habitats and emphasize the importance of hydrodynamics in marine systems in influencing individual responses to the spatial pattern of landscape mosaics (Robbins and Bell 1994).

The size- and region-specific patterns of intra-annual juvenile recruitment to the CAPES could result from the interaction between temporal variation in the oceanic pool of larvae with meteorological and physical–oceanographic conditions along the continental shelf of North Carolina. For example, J1–J2 crab density within the inlet region and J3–J5 densities across the CAPES were greatest in September and October, months that have favorable winds to deliver post-larvae into Oregon Inlet (see below). August and September represent a transition from spring–summer conditions, which typically exhibit variable winds from the south, to fall–winter conditions beginning in October, which typically involve northerly winds (Miller et al. 1982; Epifanio and Garvine 2001). In addition to more favorable winds in September and October, the occurrence of post-larval crabs in continental shelf waters may also be greater later in the fall (Epifanio et al. 1984) because of greater frequency of spawning in early fall than late summer. September and October also happen to be months in which the North Carolina coast experiences a large number of tropical cyclones, adding an additional mechanism to facilitate transport of post-larval crabs into the estuarine system. Thus, the intra-annual variation in juvenile blue crab abundance may reflect the interaction between the available larval pool and favorable winds.

The density of juvenile blue crabs also showed considerable variation between years. For example, the densities of J1–J2 crabs in 1996 and 1999 were relatively large, most likely because of the interaction of favorable winds and tropical cyclones. An unusually large peak of J1–J2 crabs is apparent in September 1998 that cannot be attributed to tropical cyclone delivery of post-larvae. Instead, the high abundance of J1–J2 in September of 1998 may represent a large recruitment pulse owing to a large spawning stock size that year, as detected in a fishery-independent trawl survey (1998 was one of the top two years in spawning stock biomass in the last 14 years, and there is a significant spawning stock–recruit relationship for the blue crab in North Carolina; Eggleston 1998). It is noteworthy that 1997 exhibited strong El Niño conditions, whereas the other years in this study were non-El Niño years (based on values of the standardized Southern Oscillation Index (SOI) found at www.cpc.ncep.noaa.gov/data/indices/). It is possible that the weather conditions associated with El Niño events (predominantly weak offshore winds) could influence overall juvenile recruitment and could have contributed to the particularly low densities of J1–J2 crabs in 1997. Overall, variation in juvenile blue crab abundance between years could be a reflection of meso- and large-scale meteorological processes (e.g., tropical cyclones and El Niño), as well as the size of the spawning stock.

Relationship between blue crab recruitment and wind components

When examined on an estuarine-wide scale, temporal variation in juvenile recruitment could not be explained by wind variables; however, when examined by site or region, wind characteristics were a fairly good predictor of juvenile density. For example, the relatively strong relationship between

Table 2. Ryan's *Q* test of the mean number of J1–J2-stage (log(x + 1)-transformed) blue crab instars per 1.67 m^2 for the region × month × year interaction effect.

(*a*) Month and year × region.

Month–year	Region	
August–1996	Sound	Inlet
September–1996	Inlet	Sound
October–1996	Sound	Inlet
August–1997	Sound	Inlet
September–1997	Sound	Inlet
October–1997	Sound	Inlet
August–1998	Sound	Inlet
September–1998	Sound	Inlet
October–1998	Sound	Inlet
August–1999	Inlet	Sound
September–1999	Sound	Inlet
October–1999	Sound	Inlet

(*b*) Region and year × month.

Region–year	Month		
Inlet–1996	8	9	10
Inlet–1997	9	8	10
Inlet–1998	8	10	9
Inlet–1999	8	10	9
Sound–1996	8	10	9
Sound–1997	9	10	8
Sound–1998	10	8	9
Sound–1999	10	8	9

(*c*) Region and month × year.

Region–month	Year			
Inlet–August	1997	1998	1999	1996
Inlet–September	1997	1996	1999	1998
Inlet–October	1998	1999	1997	1996
Sound–August	1996	1998	1997	1999
Sound–September	1997	1998	1999	1996
Sound–October	1999	1998	1997	1996

Note: Treatment levels that are not significantly different at α = 0.05 share an underline. Treatment levels are arranged in increasing order of density.

Table 3. Ryan's *Q* test of the mean number of J3–J5 (log(x + 1)-transformed) blue crabs per 1.67 m^2 for the month × year interaction effect.

Year	Month		
1996	8	10	9
1997	8	9	10
1998	10	8	9
1999	9	8	10

Note: Treatment levels that are not significantly different at α = 0.05 share an underline. Treatment levels are arranged in increasing order of density.

densities of J1–J2 and J3–J5 crabs and northerly winds at Oregon Inlet was consistent with the relationship between blue crab post-larval settlement to Oregon Inlet and northerly wind speed (D. Eggleston, unpublished data). Northerly winds, which are often associated with the passage of low-pressure systems in the early fall, cause onshore Eckman flow that facilitates transport of blue crab post-larvae into estuaries within the Mid-Atlantic Bight (Epifanio and Garvine 2001), as has been observed in several field studies along the western Atlantic (Goodrich et al. 1989; Little and Epifanio 1991; Jones and Epifanio 1995). On the continental shelf, blue crab post-larvae remain in the surface waters (Epifanio 1995); thus, post-larvae would be transported in the 5- to 15-m-thick surface layer during fall conditions (Miller et al. 1982). Within the CAPES, surface flow tends to be directed with the wind, with water current speeds approximately 0.01 of the wind velocity (Pietrafesa et al. 1986). Because of the shallow depth of the estuarine system and the influence of wind mixing, there is virtually no vertical stratification in the CAPES (Pietrafesa et al. 1986). Thus, the transport mechanism for primary and secondary dispersal, as well as cues initiating secondary juvenile dispersal, should be integrated over all depths. Computer simulations of surface and bottom currents demonstrate that north and northeasterly winds produce a strong exchange of water between the coastal ocean and the estuary; however, inwelling occurs primarily through Oregon Inlet, with outwelling at Hatteras and Ocracoke inlets (Xie and Eggleston 1999). Thus, northerly winds appear to be favorable in transporting post-larvae only through Oregon Inlet and may impede the transport of post-larvae through the southern inlets because of differences in the orientation of the coastlines. Transport of post-larvae into the southern inlets may be driven more by tidal forcing, owing to the lack of a southern-driven buoyancy current along this part of the coastline (Epifanio and Garvine 2001), which would have the potential to dampen tidal forcing, if present. Our results agree with a study of larval fish abundance in North Carolina that also detected differences between Oregon and Ocracoke inlets, with most fish species exhibiting different times of occurrence and peak abundance between Oregon Inlet and Ocracoke Inlet (Hettler and Barker 1993). Thus, temporal variation in wind conditions could create spatial variation in juvenile recruitment to inlet areas north and south of Cape Hatteras.

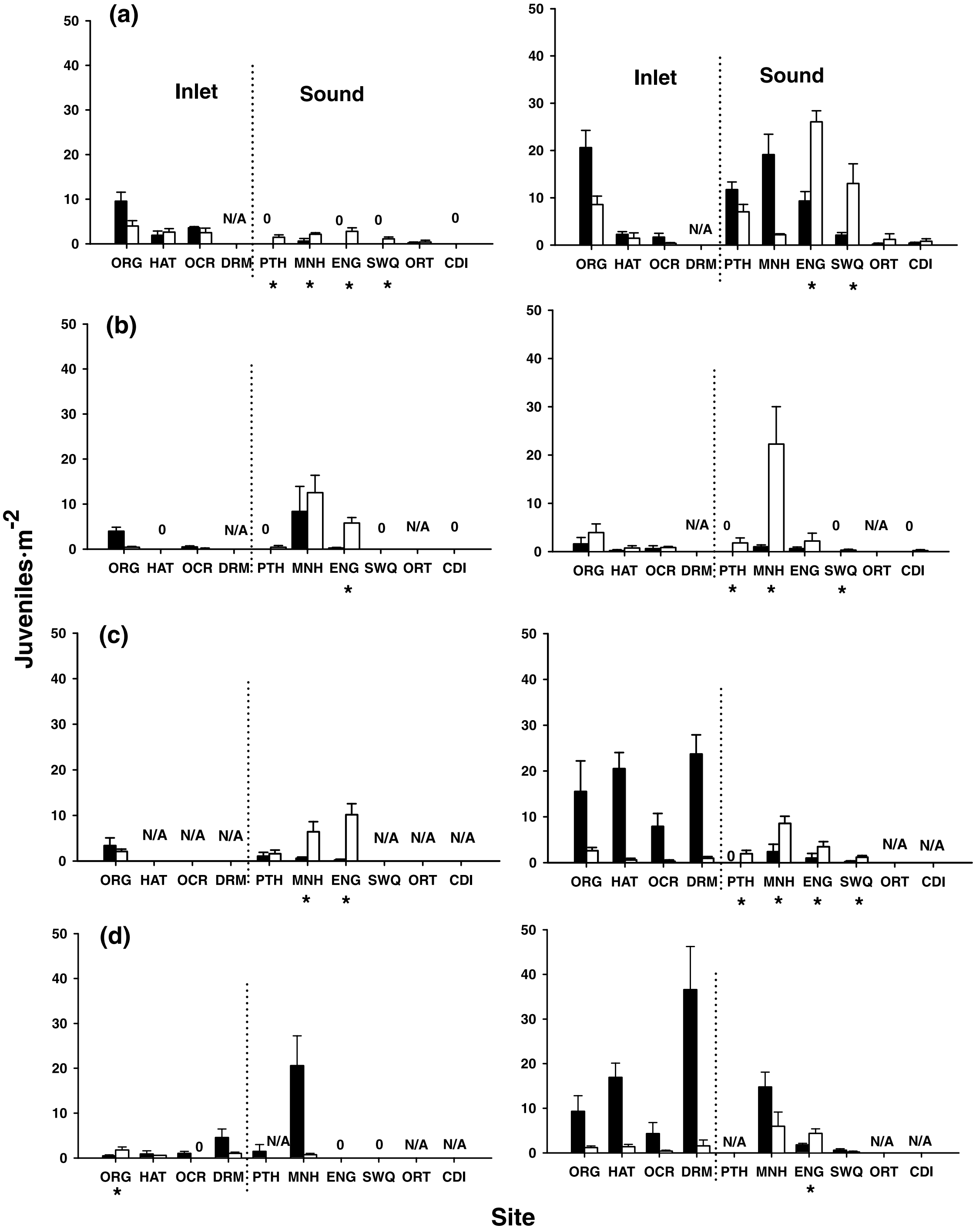
Although the wind characteristics that influenced the density of juvenile crabs within the sound region varied according to areas within the region, there were fairly consistent results between J1–J2 and J3–J5 size classes. At Point Harbor, the densities of J1–J2 and J3–J5 crabs were strongly dependent on the strength of east winds. Easterly winds relax the southward surface flow from Croatan Sound to Pamlico Sound that is present during most other wind events (Xie and Eggleston 1999), allowing primary post-larval dispersal and secondary juvenile dispersal northward into Albemarle Sound. There was also a relationship between J1–J2 stages and tropical cyclones, suggesting that primary dispersal of post-larvae into the Point Harbor area can occur during strong wind events. Recruitment variation of both J1–J2 and J3– J5 crabs at Engelhard and Swanquarter could also be explained by particular wind events, specifically the magnitude of northerly winds and strong forcing events (J1–J2, wind speed; J3–J5, tropical cyclones), which could be responsible for facilitating primary dispersal of post-larvae or secondary dispersal of post-settlement juveniles into these areas. These results match our findings of high post-larval settlement to Engelhard during strong forcing events (D. Eggleston, unpublished data). In contrast to the other sites within the sound region, the density of juvenile crabs within Manns Harbor could not be explained by particular wind characteristics. These results suggest that post-larval and juvenile dispersal to this area could occur during a variety of different wind events or, instead, that other forcing mechanisms, such as tidal flow (which may persist this far into the estuary), could play a role in dispersing crabs to the Manns Harbor area. The results from this study illustrate that the relation-

Table 4. Best-fit multiple regression models describing the relationship between wind variables and the density of J1–J2 and J3–J5 blue crabs within each study region.

	All sites (n = 88)	Oregon inlet (n = 12)	Southern inlets (n = 30)	PTH (n = 10)	MNH (n = 12)	ENG and SWQ (n = 24)
J1–J2	$R^2 = 0.07$	$R^2 = 0.71$	$R^2 = 0.10$	$R^2 = 0.75$	$R^2 = 0.19$	$R^2 = 0.29$
	$p = 0.01$	$p = 0.0006$	$p = 0.21$	$p = 0.008$	$p = 0.16$	$p = 0.03$
	Strength of east winds ($p = 0.01$)	Strength and % days of north winds ($p = 0.0006$)	% days of south winds ($p = 0.12$) % days of east winds ($p = 0.14$)	Strength of east winds ($p = 0.02$) No. of tr. cyclones ($p = 0.03$)	Strength and % days of north winds ($p = 0.16$)	Wind speed ($p = 0.02$) Strength of north winds ($p = 0.04$)
J3–J5	$R^2 = 0.06$	$R^2 = 0.03$	$R^2 = 0.08$	$R^2 = 0.64$	$R^2 = 0.23$	$R^2 = 0.35$
	$p = 0.02$	$p = 0.62$	$p = 0.13$	$p = 0.006$	$p = 0.11$	$p = 0.01$
	Strength of north winds ($p = 0.02$)	Strength of north winds ($p = 0.62$)	% days of west winds ($p = 0.13$)	Strength of east winds ($p = 0.006$)	"–" wind speed ($p = 0.11$)	Strength of north winds ($p = 0.01$) No. of tropical cyclones ($p = 0.10$)

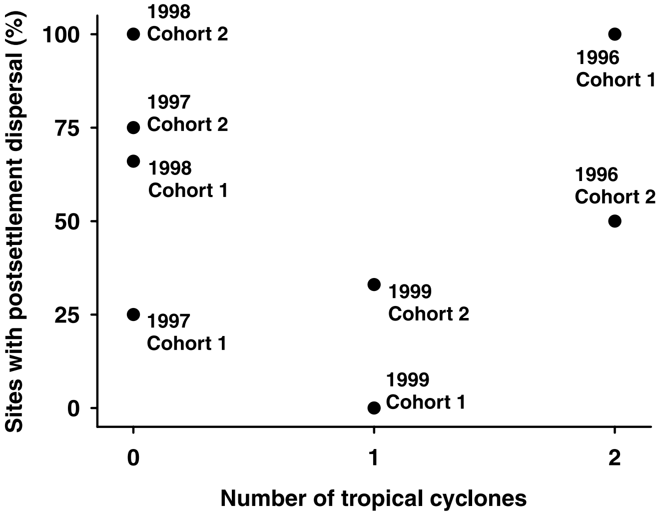
Note: Southern inlets: Hatteras, Ocracoke, and Drum. PTH, Point Harbor; MNH, Manns Harbor; ENG, Engelhard; SWQ, Swanquarter. Sample sizes for the models are given below the region title. p values are given for the whole model, as well as for each of the independent variables included in the model (p values for each of the variables included in model are in parentheses). All parameter estimates are positive, except where noted as "–".

Fig. 6. Analysis of site-specific cohort abundance over a 1-month period for two separate cohorts for the years (*a*) 1996, (*b*) 1997, (*c*) 1998, and (*d*) 1999. Cohort 1 (left panels) is defined by J1–J2 crabs in August and J5 stage crabs in September. Cohort 2 (right panels) is defined by J1–J2 crabs in September and J5 crabs in October. See Fig. 1 for site name abbreviations. Values are means + standard error. N/A denotes sites that were not sampled in that time period. Post-settlement dispersal within a cohort is evident where the abundance of J5 (open bars) is greater than J1–J2 (solid bars) at a given site and where the error bar of J1–J2 density does not overlap with the error bar of J5 density. Juvenile patterns indicative of post-settlement dispersal are marked with an asterisk (*) below the site name. Seven of the eight cohorts exhibited post-settlement dispersal (where at least one site within a cohort exhibited dispersal) to sites within the sound region. Cohort 1 of 1999 was the only cohort that did not exhibit post-settlement dispersal to the sound sites.



ship between recruitment and different wind characteristics can depend on the spatial location within the estuary, emphasizing the need to examine the influence of local topography on physical–biological coupling to understand spatial heterogeneity of dispersal between the oceanic and estuarine environments.

Fig. 7. Relationship between the number of tropical cyclones that occurred between the sampling periods of each cohort (cohort 1, August → September; cohort 2, September → October) and the percentage of sites within the sound region that exhibited evidence of post-settlement planktonic dispersal of juvenile crabs.



Relationship between recruitment and tropical cyclones

The timing of tropical cyclones within an organism's recruitment season may influence the overall impact of strong storm events on dispersal of post-larval and juvenile stages. Strong water forcing by hurricanes occurring early in the blue crab recruitment season (August) may not have much influence on overall recruitment because blue crab post-larvae are not as common in shelf waters during this time period (compared with September and October) (Epifanio et al. 1984). In our 4-year study, the two years that had hurricanes later in the season (September and October) had higher densities of J1–J2 crabs compared with years with tropical cyclones in August. It was also apparent that the cohorts in 1999 generally demonstrated the lowest percentage of sites with post-settlement dispersal, with cohort 1 of 1999 being the only cohort during the 4 years that did not exhibit patterns indicative of post-settlement dispersal at any of the sound sites. It is noteworthy that freshwater floodwaters from three sequential hurricanes (Dennis, Floyd, Irene) in September 1999 displaced three-quarters of the volume of Pamlico Sound (Paerl et al. 2001), which may have disrupted across-sound transport mechanisms. Finer-scale current data and planktonic sampling are needed within the CAPES to understand blue crab dispersal trajectories during tropical cyclones of various magnitudes, directions, and temporal occurrences within the recruitment season.

Post-settlement planktonic dispersal

In this study, secondary dispersal of early post-settlement juveniles modified initial distribution and abundance patterns of J1–J2 blue crabs. It is well known that secondary dispersal occurs in the blue crab (e.g., dispersal away from nursery areas, movement towards lower salinity mating areas, female migration towards oceanic waters to spawn; Van Engel 1958). The unique contribution of the present study is that a large amount of secondary dispersal is occurring very early in the life history of post-settlement crabs and that a substantial amount of it occurs in the plankton. As a result, processes in the water column assume a greater importance, because planktonic dispersal is a mechanism causing high connectivity between initial settlement and adult habitats. Moreover, distribution and abundance patterns established after secondary dispersal of early juvenile crabs match subsequent distribution and abundance patterns of later-stage juveniles (Eggleston 1998). These results suggest that secondary dispersal soon after benthic settlement is a key determinant in blue crab distribution and abundance within the CAPES.

In conclusion, recognition that distribution and abundance patterns of benthic marine organisms can be jointly influenced by primary dispersal to initial settlement sites and large-scale secondary dispersal can aid in our understanding of life stage dependent habitat connectivity, population dynamics, and the scales at which local ecological processes operate (Palmer et al. 1996). For example, secondary dispersal of individuals soon after settlement indicates that initial settlement patterns are not fixed and that there is the potential for high connectivity between spatially separated regions. High connectivity between spatially separated habitats suggests that regions of varying recruitment and habitat quality may be linked as donor and receiver areas. Our results indicate that donor and receiver regions were fairly consistent between years; however, the degree of connectivity appeared to be influenced by large-scale meteorological forcing mechanisms. This study also demonstrated that planktonic secondary dispersal soon after benthic settlement is a key determinant of population distribution and abundance patterns of later stage juveniles, suggesting that local dynamics can be strongly influenced by regional processes. Dispersal can also alter population dynamics by aggregating individuals (primary dispersal) or broadening the distribution of recruits (secondary dispersal). Our results emphasize the need to consider the dispersal potential and the spatial position of habitats within the landscape to determine their value as nursery habitats (Beck et al. 2001). High connectivity between habitats emphasizes the dependence between multiple regions and advocates the need to consider multihabitat management at the scale of the estuary (e.g., Roberts 1997). Thus, studies of multistage dispersal will aid in our understanding of habitat loss, spatial isolation of habitats, and the scales at which conservation efforts should be directed. Physical forcing can determine the relative influence of primary and secondary dispersal, therefore, changing the degree of connectivity between regions, modifying local population dynamics, and altering spatial patterns of habitat use. This study identified how physical processes, which are acting on different spatial and temporal scales (from local events lasting hours or days, to interannual patterns), interact to influence dispersal during multiple stages of an organism's life cycle and the resulting consequences on recruitment.

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