

## Secondary dispersal of early juvenile blue crabs within a wind-driven estuary

Nathalie B. Reynolds<sup>1</sup>

Center for Marine Sciences and Technology, North Carolina State University, 303 College Circle, Morehead City, North Carolina 28557; North Carolina State University, Department of Marine, Earth and Atmospheric Sciences, Raleigh, North Carolina 27695-8208

David B. Eggleston

North Carolina State University, Department of Marine, Earth and Atmospheric Sciences, Raleigh, North Carolina 27695-8208

Richard A. Luettich Jr.

Institute of Marine Sciences, University of North Carolina at Chapel Hill, 3431 Arendell Street, Morehead City, North Carolina 28557

### Abstract

We used a coupled biophysical study to examine the processes underlying secondary dispersal of early juvenile blue crabs (*Callinectes sapidus*) within Pamlico Sound, North Carolina, a predominately wind-driven estuary. We quantified the spatiotemporal distribution of early juvenile blue crabs in the water column with vertically stratified plankton samples (during day–night cruises during two consecutive years) and used a hydrodynamic numerical simulation model to recreate dispersal trajectories and assess potential transport pathways connecting inlet (eastern) and western sound nursery habitats. Early juvenile blue crabs belonging to the first benthic instar stage (J1) were observed within the water column, indicative of secondary dispersal occurring rapidly following postlarval settlement and metamorphosis to the juvenile stage. Moreover, J1 blue crabs were most abundant in near-bottom waters at night. Particle-tracking dispersal simulations revealed that across-sound blue crab secondary dispersal only resulted from the combined use of flood-tides near the inlets and wind-induced bottom currents within the main body of Pamlico Sound. Thus, our results indicate that behavioral responses to multiple hydrodynamic conditions ultimately influence habitat connectivity, particularly in the northwest region of our study area where a distinct transport pathway was evident. As such, generalizations of recruitment dynamics based on systems with strong tidal signals cannot be used to accurately characterize patterns of estuarine recruitment in predominately wind-driven systems.

The population dynamics of many marine organisms are partly dependent on processes that influence dispersal during the pelagic larval phase (Roughgarden et al. 1988; Underwood and Fairweather 1989). What is less well recognized is the degree to which dispersal of early juveniles, following initial settlement to nursery habitats (i.e., secondary dispersal), influences population size and structure (Günther 1992; Caley et al. 1996; Palmer et al.

1996). An important component to understanding secondary dispersal is to determine why juveniles leave settlement habitats and how they are dispersed. Secondary dispersal from settlement habitats may be initiated by density-dependent interactions (e.g., Turner et al. 1997; Powers and Peterson 2000; Reynolds and Eggleston 2004), ontogenetic differences in habitat use (e.g., Fonseca and Hart 1996; Thrush et al. 2000), and hydrodynamic conditions (e.g., high wave energy, strong flow, storm effects, etc., Hall 1994; Commito et al. 1995; Blackmon and Eggleston 2001). Once within the water column, transport may be determined by endogenous rhythms in swimming activity (Forward et al. 2004b; Forward et al. 2005) and behavioral responses to environmental cues (Beukema and De Vlas 1989; Armonies 1992; Reynolds and Eggleston 2004). A gap in the present knowledge for organisms that actively undergo secondary dispersal is how hydrodynamic conditions and organism behavior interact to influence transport trajectories and, ultimately, patterns of nursery habitat use. This information is critical to understanding habitat connectivity and may enable prioritization of specific habitats or dispersal corridors for heightened conservation. In this study, we examined how circulation patterns within a predominately wind-driven estuary and behavior influence the secondary dispersal of the blue crab, *Callinectes sapidus*.

The blue crab is an important ecological and commercial species that resides within estuaries along the Atlantic and

<sup>1</sup> Corresponding author (nreyns@whoi.edu). Present address: Biology Department, MS # 50, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

### Acknowledgments

We thank S. Searcy, J. Breeden, B. Sweet, G. Bell, and A. Sidell for help with fieldwork and sample processing; J. Fleming, C. Fulcher, and S. Carr for assisting with modeling efforts; the U.S. Coast Guard group at Oregon Inlet for use of their dock facilities; J. Willey for use of her house; and C. Cudaback for providing software and input on the analysis of our hydrographic data. Comments by S. Searcy, R. Forward, D. Kamykowski, C. Cudaback, R. Cowen, and one anonymous reviewer greatly improved previous versions of the manuscript.

Funding for this research was provided by the National Science Foundation (OCE 97-34472, OCE-0221099, OCE-0094938), North Carolina Sea Grant (Blue Crab FRG-02-POP-04), Sigma-Xi, PADI-Foundation, Association for Women in Science, NC Beautiful, and the Department of Marine, Earth and Atmospheric Sciences at North Carolina State University.

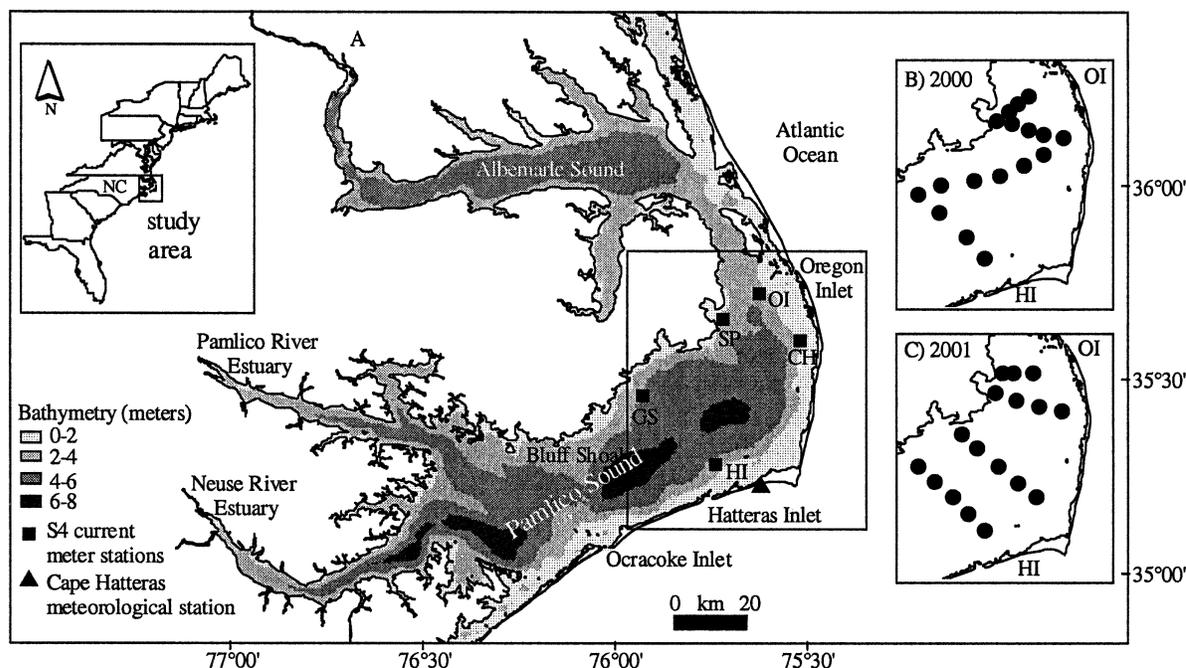


Fig. 1. Map of APES in North Carolina showing regional bathymetry and hydrographic stations within Pamlico Sound (A), OI = Oregon Inlet; SP = Stumpy Point; CH = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet. Blue crab plankton stations sampled in (B) 2000 and (C) 2001 are presented on enlarged maps of study area (northern basin of Pamlico Sound).

Gulf coasts of the United States. Larval development takes place in continental shelf waters, during which larvae molt through seven zoeal stages before metamorphosing to the postlarval (megalopal) stage (Costlow and Bookhout 1959). Postlarvae are transported onshore to coastal estuaries by across-shelf, wind-driven surface currents generated by Ekman circulation (reviewed in Epifanio and Garvine 2001). Once within the tidal prism of an estuary, postlarvae utilize flood-tide transport (FTT) for estuarine ingress and up-estuary movements (Forward and Tankersley 2001). Following entry into estuaries, postlarvae settle and metamorphose to the first benthic instar (J1) in nursery habitats generally composed of aquatic vegetation such as seagrass and salt marshes (e.g., Heck and Thoman 1981; Orth and Van Montfrans 1987; Etherington and Eggleston 2000). Although juveniles may remain in these habitats through the seventh instar (J7) (Hines et al. 1987; Orth and Van Montfrans 1987), recent studies have demonstrated that early juvenile blue crabs can return to the water column to undergo pelagic secondary dispersal (Blackmon and Eggleston 2001; Etherington et al. 2003; Reynolds and Eggleston 2004). Secondary dispersal by J1 blue crabs is density-dependent (driven by intracohort density in settlement habitats) and juvenile crabs use nighttime flood tides to rapidly disperse away from these areas (Reynolds and Eggleston 2004). The use of FTT, however, is only possible near tidal inlets or within tidal estuaries. It remains unclear how secondary dispersal of early juvenile blue crabs occurs within predominately wind-driven estuaries such as Pamlico Sound, North Carolina.

Pamlico Sound is the largest component of the Albemarle-Pamlico Estuarine System (APES) in North

Carolina (Fig. 1A) and serves as an important nursery for many commercially exploited finfish and crustacean species, including the blue crab. The eastern shore of Pamlico Sound comprises a barrier island chain that limits exchange with the coastal ocean to three relatively small (~1 km wide) inlets (Oregon, Hatteras, and Ocracoke Inlets, Fig. 1A). Thus, the relative magnitude of the principal semi-diurnal  $M_2$  tidal constituent is quickly dampened within a few kilometers of the inlet regions (Pietrafesa et al. 1986; Reynolds 2004). This lack of tidal influence, in addition to the relatively shallow depth of the system (mean depth ~4.5 m), enables circulation within Pamlico Sound to respond rapidly (within ~10–36 h) to wind forcing (Pietrafesa et al. 1986; Pietrafesa and Janowitz 1991).

Pamlico Sound is an ideal system in which to examine the secondary dispersal of blue crabs because it contains spatially distinct blue crab nursery habitats thought to differ in their relative importance as “donor” (high postlarval settlement through primary dispersal) and “receiver” (high juvenile recruitment through secondary dispersal) habitats (Etherington and Eggleston 2000; 2003). For example, seagrass beds located along the eastern shore of Pamlico Sound are nearest to postlarval inlet sources and typically experience relatively high postlarval settlement (Etherington and Eggleston 2000, 2003). In contrast, shallow detrital habitats located along the western shore of Pamlico Sound generally have low postlarval settlement rates, but relatively high early juvenile densities, suggesting that these habitats (i.e., receivers) are supplied by crabs through secondary dispersal from eastern shore habitats (i.e., donors) (Etherington and Eggleston 2000, 2003). To date, however, the connectivity of nursery

habitats via secondary dispersal has been inferred from habitat-specific early juvenile blue crab densities (Etherington and Eggleston 2000, 2003) without explicit measures of pelagic juvenile blue crab distributions within Pamlico Sound. Our objective, therefore, was to couple measures of currents and juvenile blue crab distributions in the water column to determine how circulation patterns within Pamlico Sound influence the secondary dispersal of early juvenile blue crabs from eastern to western sound nursery habitats.

## Methods

*Spatiotemporal distribution of early juvenile blue crabs*—The study was conducted within the northern basin of Pamlico Sound during peak blue crab recruitment months (September–October) in each of 2 years (2000 and 2001). Juvenile blue crabs, typically associated with benthic habitats (Heck and Thoman 1981; Orth and Van Montfrans 1987; Etherington and Eggleston 2000), are assumed to be undergoing secondary dispersal when collected in the water column in the middle of Pamlico Sound away from structured habitats. We hypothesized that juvenile blue crabs would disperse across-sound by moving into surface waters at night, as this behavior has previously been observed near the inlets in Pamlico Sound (Reyns and Eggleston 2004). To test this hypothesis, the vertical distribution of crabs within the water column was measured during day–night cruises by simultaneously towing a neuston net (surface measure) and plankton net mounted to a benthic sled (near-bottom measure) at 17 stations spaced ~6 km apart along four transects crossing the sound (Fig. 1B,C). Station locations were selected based on bathymetry of the sound (Fig. 1) and extended as close as possible to the western and eastern coastal boundaries while maintaining a minimum depth of 3 m to allow for simultaneous surface and bottom plankton tows. In 2000, we completed four day–night cruises (where all stations were sampled once during the day, and then re-sampled at night), whereas in 2001 we completed two day–night cruises and four night-only cruises because of the general paucity of crabs collected during the day (*see Results*). Sampling all 17 stations took ~8 h.

Surface and bottom nets had mouth dimensions of 1 m × 0.5 m, were fitted with 505- $\mu$ m mesh, and equipped with General Oceanics flow meters to calculate the volume of seawater filtered. Nets were towed for 5 min at about 1 m s<sup>-1</sup>, and had filtration efficiencies near 100% (N. Reyns unpubl. data). Following net retrieval, samples were preserved in 75% ethanol and transported to the laboratory where juvenile blue crabs were measured for carapace width ([CW] dorsal distance between lateral spines), and categorized by size class (J1–8, following Pile et al. 1996). Counts were standardized to concentrations (No. crabs 100 m<sup>-3</sup>).

To establish which blue crab size classes were undergoing secondary dispersal within the sound, we examined the size–class distribution of early juvenile blue crabs collected over all stations during both years. Differences in size–class distribution by year were tested using a two-

sample Kolmogorov–Smirnov  $n_1n_2D$  statistic (Sokal and Rohlf 1995). To determine if the concentration of early juvenile blue crabs varied by depth in the water column (surface vs. bottom) and by time of day (day vs. night), we used a two-way, fixed-factor analysis of variance model. We accounted for temporal variability in juvenile blue crab abundances by converting the response variable (concentration of crabs per net tow on a given cruise date) to relative concentrations, or proportions. Normality and homogeneity of variances were achieved after square-root transformation of the response variable (Sokal and Rohlf 1995).

*Hydrographic data*—Circulation was characterized by deploying five InterOcean S4 electromagnetic current meters at locations around the perimeter of the northern basin of Pamlico Sound during two periods: 17 September–8 November 2000 and 31 August–30 October 2001 (Fig. 1A). Instruments were configured to record current direction and velocity for 2 min every 20 min, and instruments were deployed near-surface (1 m below surface) because we initially hypothesized that early juvenile blue crabs would be in surface waters. Contrary to expectations, however, early juvenile blue crabs were primarily collected in near-bottom waters (*see Results*). Thus, to obtain near-bottom flow fields that corresponded to the depth of our crab collections, we used ADCIRC (ADvanced CIRCulation), a non-linear barotropic hydrodynamic model that solves the shallow water form of the momentum equations (Luettich et al. 1992, *see also* [http://www.marine.unc.edu/C\\_CATS/adcirc/](http://www.marine.unc.edu/C_CATS/adcirc/)). ADCIRC has simulated flow fields that are in good agreement with observed currents in the southern portion of the APES (e.g., Neuse River Estuary, Luettich et al. 2002), as well as observed surface currents measured within our study area (Reyns 2004). For example, cross-correlation coefficients between hourly-averaged, 40-h lowpass-filtered, modeled and observed surface currents were statistically significant at all sites (range of 0.39–0.90,  $p < 0.001$ , Reyns 2004), and modeled surface currents recreated both the variance (compare variance ellipses in Fig. 2A,B) and temporal fluctuations in observed surface currents (Fig. 3). As such, we assumed that ADCIRC realistically generates near-bottom flows.

Although the circulation in Pamlico Sound is generally characterized as being wind-driven (Pietrafesa et al. 1986; Pietrafesa and Janowitz 1991), early juvenile blue crabs utilize nocturnal flood tides in the vicinity of the inlets to initiate secondary dispersal (Reyns and Eggleston 2004). Thus, to determine which hydrodynamic conditions mediate early juvenile blue crab dispersal across Pamlico Sound, we used ADCIRC to generate circulation patterns resulting from the separate and combined affects of the wind and tides (i.e., wind-only, tide-only, and wind–tide simulations). In our wind-only simulations, we used the three-dimensional (3D) version of ADCIRC parameterized with a Mellor–Yamada level 2.5 turbulent closure and spatially constant quadratic slip bottom friction (0.0025) and lateral eddy viscosity (2 m<sup>2</sup> s<sup>-1</sup>) coefficients. We used a high-resolution triangular grid that encompassed the entire

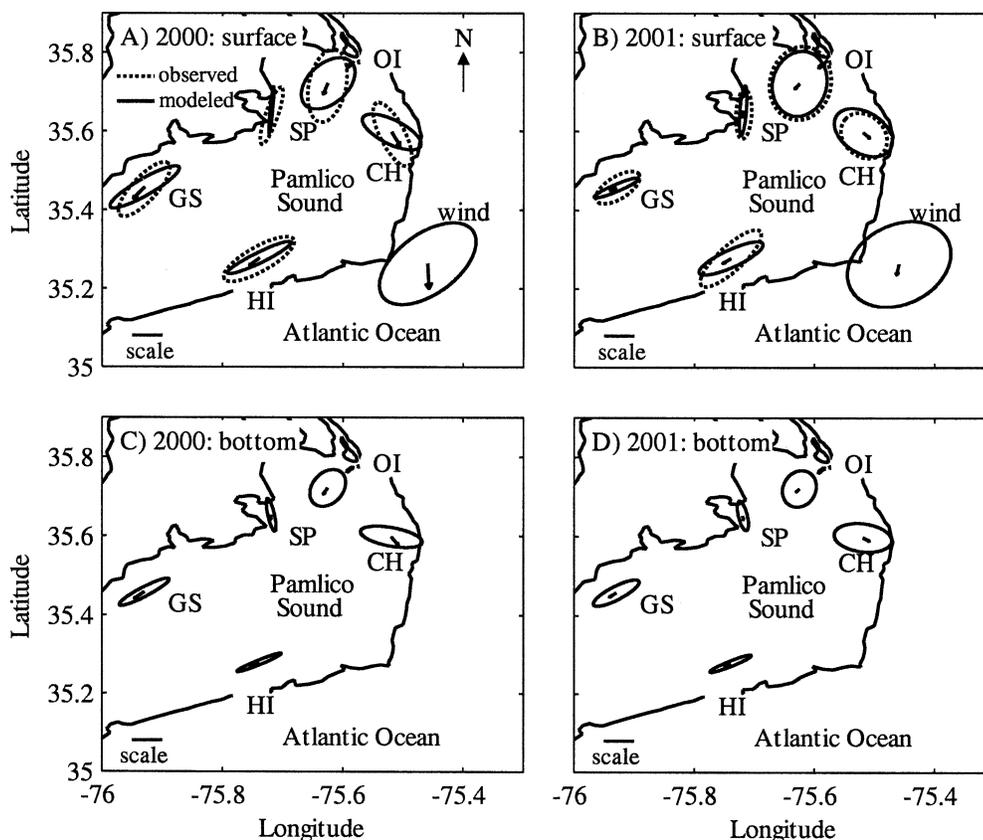


Fig. 2. Principal axes of variance of currents during the blue crab recruitment season (September–October). Comparison of observed and modeled wind-induced surface currents (shown within Pamlico Sound) with respect to wind (shown outside of sound) during (A) 2000 and (B) 2001. Modeled wind-induced bottom currents are also presented for (C) 2000 and (D) 2001. Arrows denote the mean direction of flow. Scale bar in bottom left corner represents  $1 \text{ m s}^{-1}$  for wind velocity and  $5 \text{ cm s}^{-1}$  for current velocity, respectively. OI = Oregon Inlet; SP = Stumpy Point; CH = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet.

APES domain as well as the Atlantic Ocean from the coast of Nova Scotia (northern boundary) to the coast of South America (southern boundary) to  $60^\circ\text{W}$  (eastern boundary). This portion of the Atlantic Ocean was included in the model grid to incorporate ocean–APES water exchange resulting from wind-induced pressure gradients that develop along the eastern (barrier island) boundary of the APES (Pietrafesa and Janowitz 1988). The model grid was composed of 54,543 nodes and 101,024 elements, producing a resolution within the APES between 300 m and 1 km, depending on the bathymetry and geometry of the estuarine system. Current velocities were computed over 11 variable depth layers.

We assumed that wind fields were spatially uniform over the entire APES domain (e.g., Weisberg and Pietrafesa 1983) and, therefore, forced the model with hourly wind velocities measured by the NOAA National Weather Service at the Hatteras Meteorological Station (made available by State Climate Office of North Carolina at North Carolina State University) (Fig. 1A). A 1-d ramp was applied to wind forcing, and the model was allowed a 3-d spin-up time before circulation patterns were compared with our juvenile blue crab distributions (see *Biophysical analysis*, below).

In tide-only simulations, we used a depth-integrated (2D) version of ADCIRC to compute tidal velocity fields for the APES, as the 3D version of ADCIRC was not currently configured to run with both wind and tidal inputs. Using the depth-integrated model for the tide-only case, however, was acceptable because the absence of vertical density stratification (Reyns 2004) and the shallow depths within the APES enable relatively strong tidal currents to effectively mix the water column (Luettich et al. 1999). In these tide-only simulations, the same boundary conditions described above for the wind-only simulations were used, but inputs included the  $K_1$ ,  $O_1$ ,  $M_2$ ,  $S_2$ , and  $N_2$  tidal constituents rather than the wind fields. A 10-d ramp was applied to the tidal forcing and, as with the wind-only simulations, current velocities were outputted at hourly intervals. Finally, to produce combined wind–tide flow fields, we added the individual wind-only velocity outputs for each depth layer to the depth-integrated tide-only velocity outputs.

*Biophysical analysis*—Wind and modeled current data were averaged into hourly and daily records, and decomposed into several components:  $u$  (east–west),  $v$  (north–

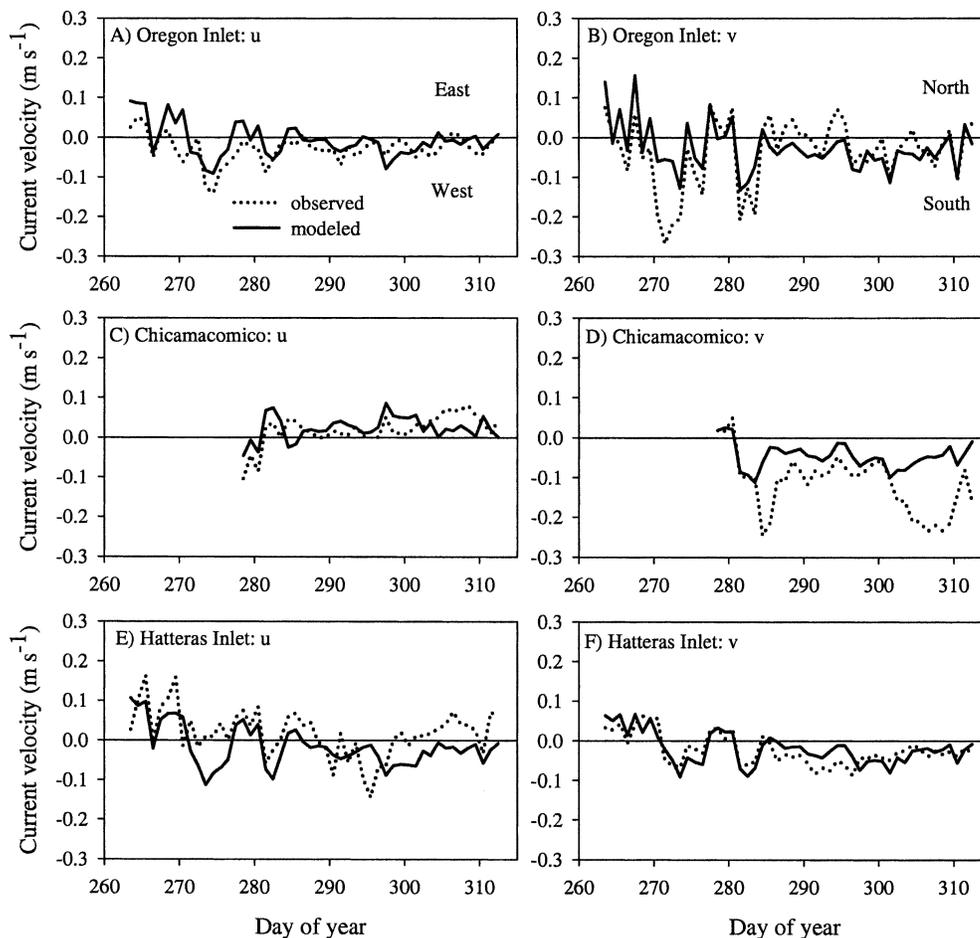


Fig. 3. Comparison of observed and modeled wind-induced surface currents for three sites located in the eastern portion of the study area (near sources of juvenile blue crabs): (A,B) Oregon Inlet, (C,D) Chicamacomico, (E,F) Hatteras Inlet during 2000. Left panels show east–west current velocities (u-component), and right panels show north–south current velocities (v-component), where positive values indicate currents flowing toward the east and north, respectively.

south), and principal axes of variance where velocity fluctuations are at a maximum and minimum along the major and minor axis, respectively (Emery and Thomson 2001). To assess how the concentration of early juvenile blue crabs varied spatially within Pamlico Sound, we compared crab distribution and abundance patterns on a given cruise date with winds and modeled wind-induced currents averaged over the 7-d period before plankton measurements. This 7-d period was selected because stage J1 blue crabs were most frequently collected in the plankton during our study (*see Results*) and crabs spend an average of 7 d in this stage before metamorphosing to the J2 stage (Millikin and Williams 1984). As such, J1 crabs collected on a specific cruise date could be 1–7-d old.

**Dispersal simulations**—To recreate the dispersal trajectories of early juvenile blue crabs collected during our cruises, we coupled a Lagrangian particle-tracking algorithm (Baptista et al. 1984; Foreman et al. 1992) with our different ADCIRC-generated flow fields. Dispersal was initially simulated using a passive dispersal (null) model,

where virtual crabs were released in wind-driven near-bottom ( $\sim 1$  m above bottom) flow fields (Table 1), because early juvenile blue crabs were predominately observed in near-bottom waters in our field study (*see Results*). Additionally, we incorporated juvenile blue crab behaviors into three active dispersal models (Table 1). In all active dispersal models, virtual crabs only dispersed at night (defined as 18:00 h to 06:00 h) and remained stationary during daylight hours because we collected more early juvenile blue crabs at night than during the day (*see Results*). These active dispersal simulations were conducted using: (1) a wind-only model where virtual crabs dispersed at night in near-bottom currents, (2) a tide-only model where virtual crabs dispersed at night using flood tides generated by the depth-integrated model (nighttime flood-tide transport, e.g., remained stationary during ebb tides as well as during daylight hours), and (3) a wind-tide model where virtual crabs dispersed at night using the combined near-surface wind-driven currents and depth-integrated flood tidal currents (to simulate nighttime flood-tide transport near the inlets) and switched to using near-

Table 1. Behavioral and hydrodynamic conditions used in particle-tracking model to simulate dispersal.

Dispersal simulation	Behavior and hydrodynamic conditions
Passive model	Dispersal using wind-driven bottom currents (no behavior)
Wind-only model	Dispersal at night using wind-driven bottom currents
Tide-only model	Dispersal at night using depth-integrated flood tide currents
Combined wind-tide model	Dispersal at night using: (1) combined wind-driven surface currents and depth-integrated flood tide currents near inlets, (2) wind-driven bottom currents when >10 km from inlets

bottom currents once they moved 10 km beyond the inlet regions. This 10-km distance was selected as the point where blue crab behaviors change as tidal currents become negligible beyond 10 km of the inlets (e.g., tidal amplitude decreases ~50–70% relative to amplitude at inlets, Pietrafesa et al. 1986). Flood tide periods were specified as the interval between slack water before flood and slack water before ebb and were determined by finding times when the magnitude of the velocity of the  $M_2$  tidal constituent was at a minimum.

In all dispersal simulations, we released 50 particles (i.e., virtual juvenile crabs) from both Oregon and Hatteras Inlets (where blue crab settlement habitats are located, Etherington and Eggleston 2000), and virtual crabs that left the APES boundaries were not allowed to re-enter the estuarine system. In all cases, the model time step was 2 min and particle positions were outputted at hourly intervals. To compare particle end-points with observed sound-wide early juvenile blue crab distributions, virtual crabs were released daily over the 7 d leading up to the plankton cruise dates ( $n = 350$  virtual crabs tracked from each inlet per cruise date).

Results

*Spatiotemporal distribution of early juvenile blue crabs*—We collected early juvenile blue crabs between the first and eighth instars (J1–8: CW = 2.2–14.1 mm) in our plankton collections during both years. Although crabs were more abundant in 2001 than 2000 (Fig. 4A), the size-class distribution of these crabs was not significantly different between years (Kolmogorov-Smirnov  $n_1n_2D = 0.07$ ,  $p =$  not significant), with J1 crabs (CW = 2.2–3.0 mm) comprising ~69% to 76% of the crabs collected in 2000 and 2001, respectively (Fig. 4B). Therefore, given that the majority of early juvenile crabs collected in the plankton belonged to the J1 size class, the remainder of this article focuses on the distribution and abundance patterns of J1 crabs.

The mean concentration of J1 crabs in the water column varied significantly by time of day ( $F_{1,534} = 50.95$ ,  $p < 0.0001$ ) and water depth ( $F_{1,534} = 26.86$ ,  $p < 0.0001$ ). There was also a significant day  $\times$  depth interaction ( $F_{1,534} = 20.86$ ,  $p < 0.0001$ ), whereby J1 crabs exhibited secondary dispersal at night in bottom waters.

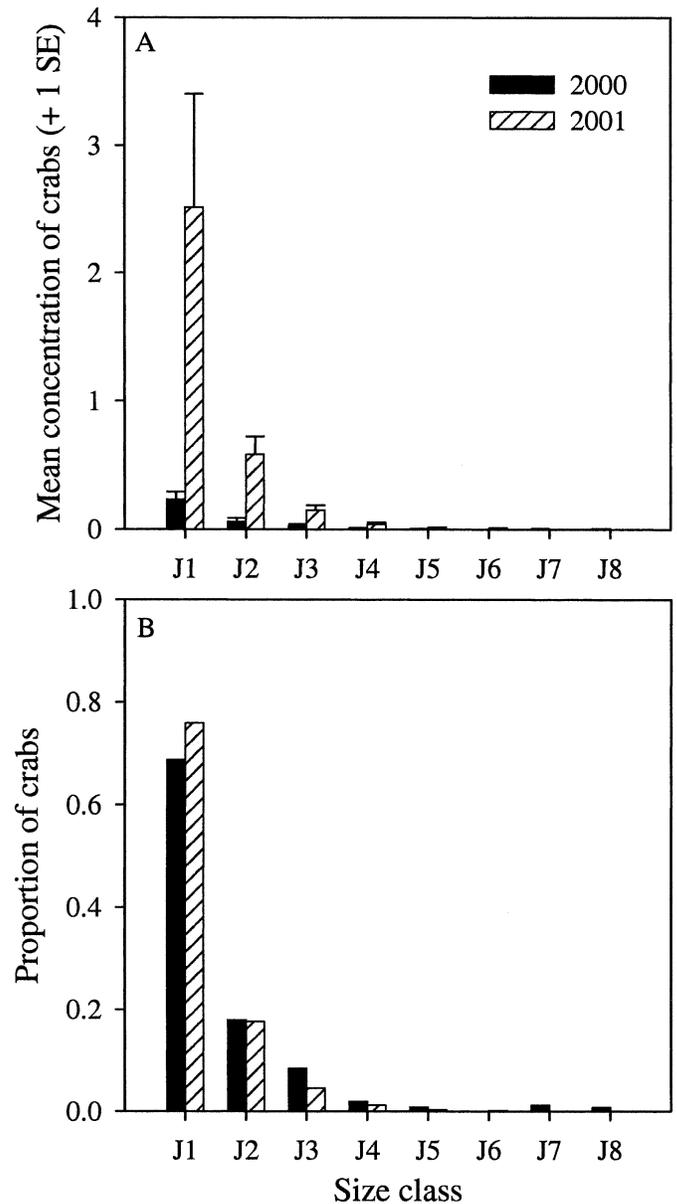


Fig. 4. Size-class distribution of juvenile blue crabs collected in the water column of Pamlico Sound during 2000 and 2001. (A) The mean concentration of crabs (No. 100 m<sup>-3</sup>) collected by size-class by year and (B) proportions of crabs. See text for significance levels.

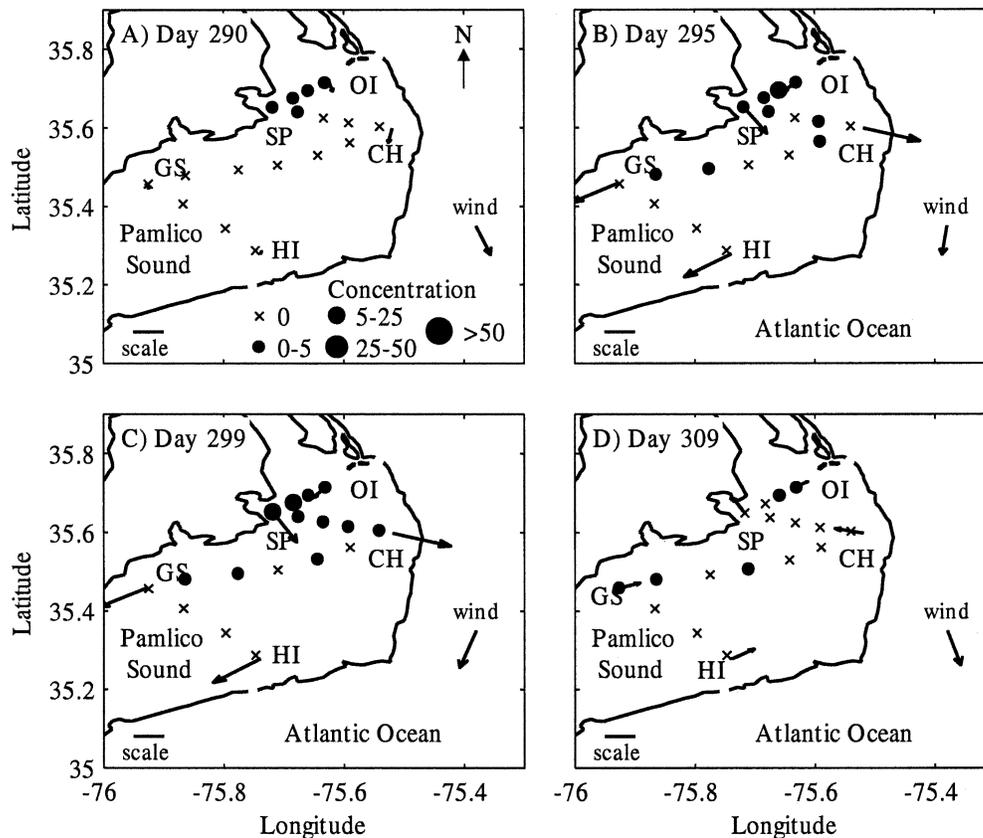


Fig. 5. (A–D) Concentration of J1 blue crabs (No.  $100\text{ m}^{-3}$ ) in bottom waters at night by cruise date during 2000. Arrows represent the mean direction of modeled wind-induced bottom currents (within Pamlico Sound) and mean direction of wind (outside of Pamlico Sound) during the 7-d period before each cruise date. OI = Oregon Inlet; SP = Stumpy Point; CH = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet. Scale bar in bottom left corner represents  $1\text{ m s}^{-1}$  for wind velocity and  $5\text{ cm s}^{-1}$  for current velocity, respectively.

In general, the concentration of J1 crabs in bottom waters was temporally variable across the spatial extent of the study area. The exception, where crabs were consistently collected, was at stations located between Oregon Inlet and Stumpy Point during both years (Fig. 5 and Fig. 6; see also Fig. 6D when J1 abundances were relatively low at all stations). Relatively high concentrations of J1 crabs were also located along the western shore of Pamlico Sound (e.g., Fig. 6C), and only once were crabs collected at nearly all plankton stations (Fig. 6B).

*Relationship between winds, currents, and crab concentrations*—During both years of the study, most variability in wind velocity occurred along a northeast–southwest axis, as shown by the principal axes of wind variance (Fig. 2A,B). Whereas wind fields were more variable during the study period in 2001 than 2000 (i.e., fatter ellipse in Fig. 2B than Fig. 2A), modeled wind-induced near-bottom currents at locations surrounding the plankton stations were similar in direction and variability during both years (Fig. 2C,D). Within the northern portion of our study area, bottom currents were aligned along a northeast to southwest axis at Oregon Inlet, along a northwest–southeast axis at Stumpy Point, and along a west/northwest to east/southeast axis at

Chicamacomico during both years (Fig. 2C,D). In the southern portion of our study area (Gibbs Shoal and Hatteras Inlet), bottom currents were less variable than at the northern stations and were aligned parallel to the shoreline along a northeast to southwest axis (Fig. 2C,D).

Modeled wind-induced bottom currents averaged over the 7-d period before the cruise dates were most frequently directed southward (Figs. 5, 6). During most cruises with average winds directed toward the southwest (Days 295 and 299 in 2000; Days 256, 262, and 288 in 2001), currents at Oregon Inlet, Gibbs Shoal, and Hatteras Inlet were also directed toward the southwest, while currents at Stumpy Point and Chicamacomico were directed toward the east–southeast (Fig. 5B,C and Fig. 6A,B,E). Bottom current patterns similar to those described during southwest-directed winds also occurred on one date when winds were toward the southeast (Day 276 in 2001, Fig. 6D). In contrast, during the other cruises with southeast-directed winds (Days 290 and 309 in 2000), bottom currents were variable (Fig. 5A,D). For example, on Day 309, bottom currents at all locations flowed northward in the opposite direction of the wind (Fig. 5D), potentially indicative of a near-bottom reverse flow. Bottom currents flowing in the opposite direction of the wind also occurred on Day 296 in

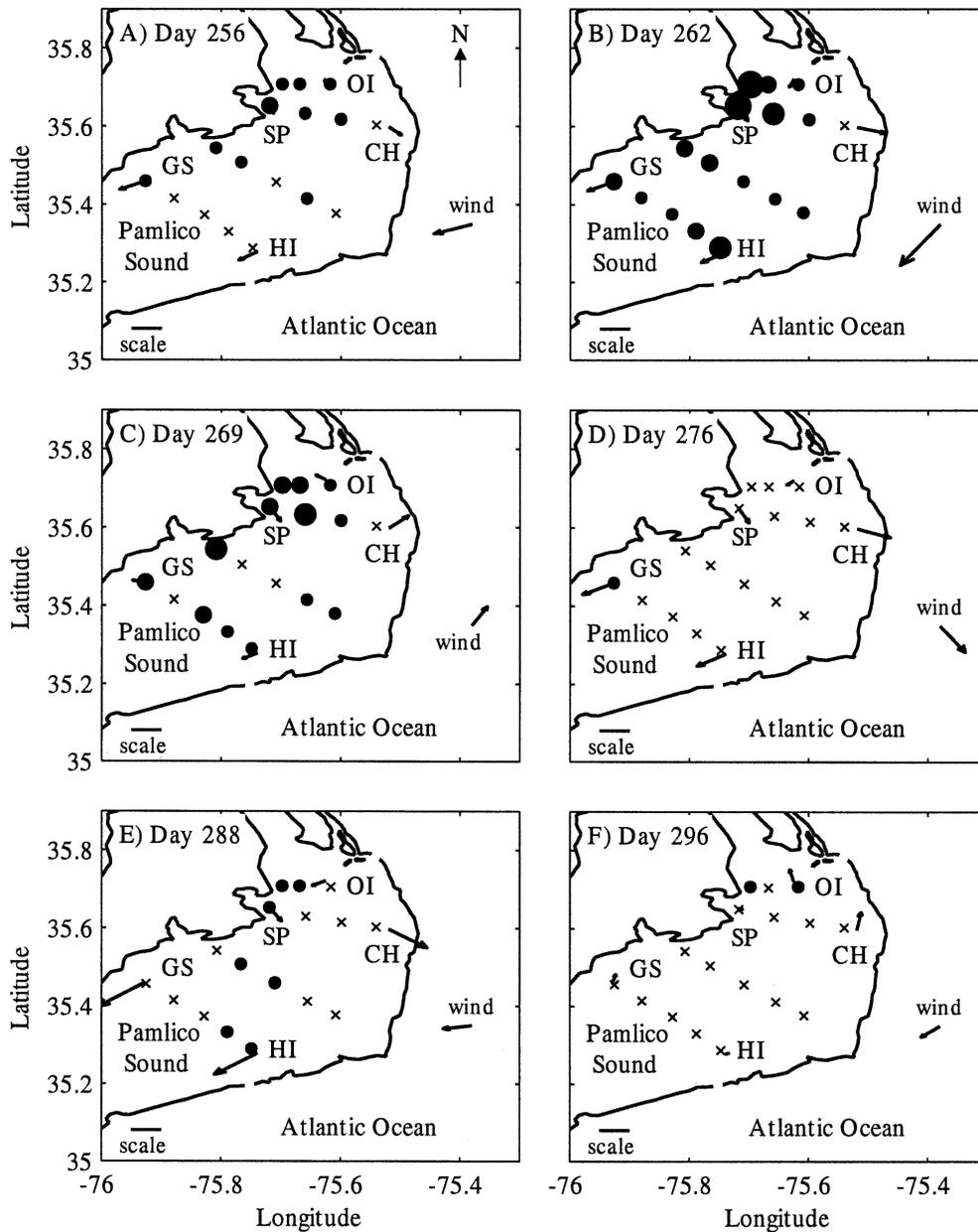


Fig. 6. (A–D) Concentration of J1 blue crabs (No. 100 m<sup>-3</sup>) in bottom waters at night by cruise date during 2001. Arrows represent the mean direction of modeled wind-induced bottom currents (within Pamlico Sound) and mean direction of wind (outside of Pamlico Sound) during the 7-d period before each cruise date. OI = Oregon Inlet; SP = Stumpy Point; CH = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet. Scale bar in bottom left corner represents 1 m s<sup>-1</sup> for wind velocity and 5 cm s<sup>-1</sup> for current velocity, respectively. Legend for crab concentrations is same as in Fig. 5.

2001 when winds were blowing toward the southwest (Fig. 6F). Only one cruise corresponded to a time period when winds were directed toward the northeast (Day 269 in 2001), and bottom currents at all locations were variable, with currents in the southern portion of the study area flowing southward in the opposite direction of the wind and currents at Oregon Inlet and Chicamacomico flowing northward (Fig. 6C). Thus, wind-induced bottom currents were spatiotemporally variable, and directions could not be

predicted based on average wind direction during the 7-d period before our cruises.

Examination of both years of J1 blue crab concentrations at the plankton stations, along with modeled wind-induced bottom currents, indicate that juvenile blue crabs undergoing secondary dispersal likely originated from Oregon Inlet (Fig. 5 and Fig. 6). For example, on cruise dates with the highest relative concentration of J1 crabs (Days 262 and 269 in 2001), bottom currents near Oregon

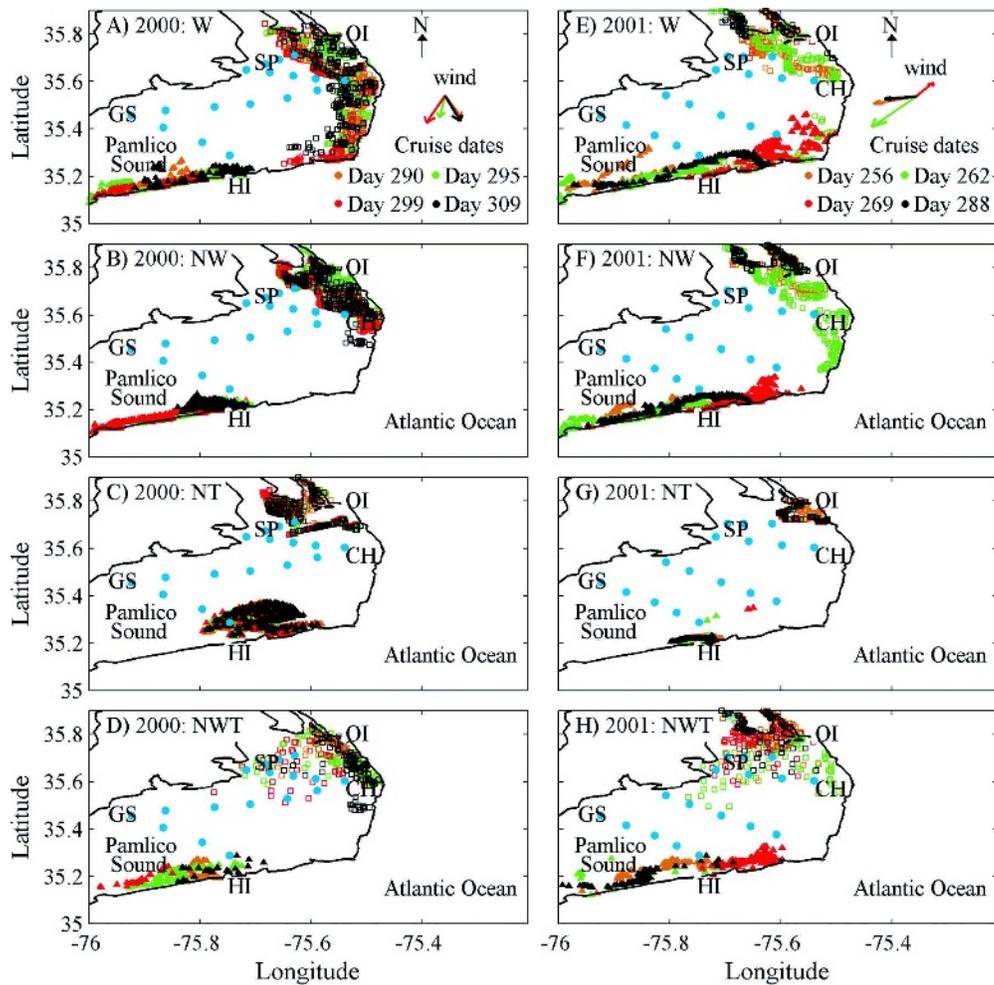


Fig. 7. End-points of virtual crabs released from Oregon and Hatteras Inlets during dispersal simulations corresponding to cruise dates in (A–D) 2000 and (E–H) 2001. (A,E) W = wind-only (null dispersal model using wind-driven near-bottom currents); (B,F) NW = night wind-only (active dispersal model using nighttime wind-driven near-bottom currents); (C,G) NT = night tide-only (active dispersal model using nighttime flood-tide currents); (D,H) NWT = night combined wind-tide dispersal simulations (active dispersal model using nighttime flood-tide and wind-driven surface currents near the inlets and wind-driven near-bottom currents in the sound). Symbol colors represent different cruise dates, with open squares denoting virtual crabs released from Oregon Inlet (OI), filled triangles denoting virtual crabs released from Hatteras Inlet (HI), and vectors denoting average wind direction during the 7-d period before each cruise date. For reference, early juvenile blue crab sampling stations are shown (filled blue circles); SP = Stumpy Point; CH = Chicamacomico; GS = Gibbs Shoal.

Inlet were directed toward the southwest or west, and currents at Stumpy Point were directed toward the southeast, allowing J1 crabs to disperse from Oregon Inlet toward the western and central regions of Pamlico Sound (Fig. 6B,C). Conversely, during this time, bottom currents at Hatteras Inlet were directed out of our study area toward the southwest. On the two sampling dates (Day 309 in 2000 and Day 296 in 2001) when average bottom currents at Hatteras Inlet were directed into our study area (toward the northeast), no crabs were collected at the plankton stations near this inlet (Figs. 5D, 6F).

*Dispersal simulations*—To determine which hydrodynamic conditions promoted across-sound secondary dis-

persal and to further test the hypothesis that Oregon Inlet acted as the primary supplier of early juvenile blue crabs to our study region, we examined the end-points of virtual crabs released near both inlets 1–7 d before each cruise date in the particle-tracking simulations. To simplify our findings, dispersal simulation results are presented for all cruises in 2000 and the four cruises with the highest juvenile blue crab abundances in 2001: Days 256, 262, 269, and 288.

In all dispersal simulations using the wind-only (null) model assuming passive blue crab transport in near-bottom wind-driven currents, virtual crabs predominately moved in the same direction as the wind and remained along the eastern shore of Pamlico Sound (Fig. 7A,E). In addition, there was some evidence of the development of bottom

return flows moving in the opposite direction of the wind; southwest-directed winds produced bottom currents that also moved virtual crabs from Oregon Inlet toward the north (e.g., Fig. 7E, see green squares for Day 262), and southeast-directed winds produced bottom currents that moved virtual crabs from Hatteras Inlet toward the west-southwest (e.g., Fig. 7A, see orange and black triangles for Days 290 and 309). In general, virtual crabs never dispersed beyond our eastern-most sampling stations during these simulations; therefore, regardless of wind direction, virtual crab end-points from our passive dispersal simulations were poor predictors of observed blue crab distributions (compare Fig. 7A with Fig. 5 and Fig. 7E with Fig. 6).

When dispersal was simulated using the nighttime wind-only model, virtual crab end-point distributions were similar to those generated by the passive model, although the range of transport was more limited because dispersal was restricted to nighttime periods only (Fig. 7B,F). In general, virtual crabs failed to move across Pamlico Sound beyond our eastern-most sampling stations (Fig. 7B,F), and as a consequence, these dispersal simulations were also unable to recreate our observed juvenile blue crab distributions. Similarly, virtual crab end-points generated by our nighttime tide-only dispersal simulations were generally poor predictors of observed J1 blue crab distributions (compare Fig. 7C with Fig. 5 and Fig. 7G with Fig. 6). Although virtual crabs released during these simulations moved partway into Pamlico Sound and reached the near-inlet sampling stations, virtual crabs also failed to reach the western sound (Fig. 7C,G). Thus, the use of flood-tide currents by early juvenile blue crabs during secondary dispersal, even over seven consecutive nights, is not likely to result in across-sound transport.

In contrast, virtual crab end-point distributions from our combined wind-tide active behavior dispersal simulations (where virtual crabs were released at night in near-surface tidal currents near the inlets and used wind-driven bottom currents when they moved beyond the inlet regions) provided a better match to observed J1 blue crab distributions than the virtual crab end-point distributions resulting from dispersal simulations using wind or tidal currents alone (compare Fig. 7D with Fig. 5 and Fig. 7H with Fig. 6). Regardless of wind direction, virtual crabs in the combined wind-tide dispersal simulations consistently reached western sound habitats in the vicinity of Stumpy Point, but only by crabs originating from Oregon Inlet. This northwestern region of Pamlico Sound also had the highest relative concentrations of J1 blue crabs (compare Fig. 7D with Fig. 5 and Fig. 7H with Fig. 6). Although our dispersal simulations failed to predict dispersal in the southern region of Pamlico Sound between Gibbs Shoal and Hatteras Inlet (e.g., where crabs were also collected in relatively high concentrations during some cruises: Day 262, Fig. 6B; Day 269, Fig. 6C), it is unlikely that crabs originating from Hatteras Inlet supplied this portion of our study area as virtual crabs released from this inlet never dispersed across-sound and only moved northward into our study area along the eastern shore of Pamlico Sound when winds were directed toward the northeast (Day 269: Fig. 7E–H). Collectively, the dispersal simulation results

suggest that most early juvenile blue crabs collected during our cruises originated near Oregon Inlet, from which across-sound transport was consistently possible as a result of the combined use of wind-induced and flood-tide currents (Fig. 7D,H).

## Discussion

A fundamental issue concerning the recruitment dynamics of marine organisms involves identifying pathways of dispersal connecting subpopulations and determining how spatiotemporal variation in the intensity of dispersal along these paths influences population dynamics. In this study, we demonstrate the potential for early juvenile blue crabs to use near-bottom wind-induced currents in combination with flood tides to undergo secondary dispersal within a relatively large, wind-driven estuary. Whereas our results indicate that juvenile blue crab behavior influences the outcome of such secondary dispersal, the prevailing hydrodynamic conditions promote dispersal along specific pathways to connect spatially-separated nursery habitats.

*Juvenile blue crab behavior*—In our study, J1 blue crabs (the earliest juvenile molt stage) were the most commonly observed crab stage within the water column, indicating that secondary dispersal occurred rapidly following postlarval settlement and metamorphosis to the juvenile stage. The propensity for J1 blue crabs to undergo secondary dispersal over later crab stages is likely caused by pulsed postlarval supply to settlement habitats (e.g., Van Montfrans et al. 1995; Forward et al. 2004a) that saturates these habitats with new recruits (J1 crabs) and increases the risk of cannibalism (Moksnes et al. 1997). Indeed, density-dependent intracohort interactions are known to drive the secondary dispersal of J1 blue crabs from seagrass settlement habitats (Reyns and Eggleston 2004), allowing these crabs to gain a potential cannibalism refuge within the plankton. Whereas, to our knowledge, our study is the first to explicitly examine the pelagic dispersal of early juvenile blue crabs in areas away from structured benthic habitats, other studies report collecting J1 blue crabs within the water column in Charleston Harbor (Mense and Wenner 1989) and Chesapeake Bay (Olm et al. 1990). Thus, the tendency for early juvenile blue crabs to undergo secondary dispersal may be more common than previously documented.

Our results demonstrate that the secondary dispersal of J1 blue crabs occurs primarily in bottom waters at night. This diel behavior supports our earlier findings of greater J1 secondary dispersal at night from near-inlet settlement habitats (Reyns and Eggleston 2004) and likely results from a circadian rhythm in vertical swimming activity (Forward et al. 2005). Nighttime dispersal is a common behavioral strategy employed by the early life stages of many estuarine organisms to reduce predation by diurnal visual predators (e.g., Morgan 1995).

Contrary to our hypothesis that early juvenile blue crabs would move into surface waters during secondary dispersal, J1 crabs were primarily collected in near-bottom waters throughout Pamlico Sound. Given that we never collected

J1 blue crabs within the water column during the day, regardless of depth, we assume that crabs were on the bottom during this time. In another study that examined vertical blue crab distributions, early juveniles were variably found in both surface and bottom waters depending on sampling station (Mense and Wenner 1989). The aforementioned study, however, was conducted within tidal creeks as shallow as 1 m, where depth-discrete sampling with plankton nets was likely hindered. While vertical swimming might allow crabs to reach the surface in shallow systems such as the one sampled by Mense and Wenner (1989), the same magnitude swim in Pamlico Sound (with shallowest stations ~3 m in depth) would likely result in crabs remaining near-bottom. Early juvenile blue crab swimming behaviors are not well known, but J1 blue crabs undergo a series of ascents and descents during vertical migrations rather than swimming continuously (Forward et al. 2005). Thus, remaining close to the bottom during secondary dispersal, as we observed, may be more energetically beneficial than moving into surface waters, where crabs would likely have to swim continuously to maintain their position within the water column. Furthermore, remaining near-bottom may be a behavioral adaptation to ensure up-estuary dispersal, as most estuaries are characterized as having a two-layer circulation with bottom waters flowing up-estuary and surface waters flowing seaward due to gravitational flow induced by freshwater input near the head and saltwater inflow near the mouth of the estuary (Dyer 1997). The environmental factors cueing such behaviors in Pamlico Sound, however, remain unclear; during our study period, the water column remained unstratified because of wind-mixing, and therefore, salinity or temperature cues potentially useful in other systems (e.g., Chesapeake Bay, Norcross 1991), could not have been operating here. Nonetheless, results from our dispersal simulations suggest that early juvenile blue crabs can use wind-driven bottom currents to disperse across-sound if tidal currents are initially used to move away from the inlets.

*Spatiotemporal variability in J1 blue crab distributions*—Temporal variability in the relative concentrations of J1 blue crabs during our cruises was likely caused by variability in the spawning stock biomass and environmental factors experienced during oceanic development and dispersal of the larval and postlarval stages. Blue crab spawning occurs during the summer and fall months, with peak blue crab recruitment in September–October in North Carolina (Eggleston et al. 2004). This fall period corresponds to a shift from summer to winter meteorological conditions (Pietrafesa et al. 1986) and spatiotemporal variability in postlarval supply to Pamlico Sound, and the subsequent delivery of postlarvae to nursery habitats within the sound has been related to such wind variability (Etherington and Eggleston 2003; Reyns 2004). Although wind and modeled bottom currents averaged during our study periods showed little year-to-year variability, when examined on a finer temporal scale (i.e., by cruise date) bottom flows within Pamlico Sound were variable with respect to wind direction. Such near-bottom current

variability was most prevalent in 2001, likely reflecting fluctuating wind fields.

Results from our dispersal simulations indicate that spatial variability in blue crab concentrations within Pamlico Sound was not solely driven by the wind. Based on the wind-only simulations, crabs in bottom currents primarily dispersed downwind along the eastern shore of Pamlico Sound from the inlet of release and rarely moved into the study area or dispersed across-sound. Although bottom flows develop when persistent winds cause surface currents to flow downwind, raising sea level at the downwind shore of Pamlico Sound and producing pressure gradient forces that drive upwind-flowing near-bottom currents (Pietrafesa and Janowitz 1991), only a few virtual crabs dispersed into our study via this mechanism. Rather, our results indicate that blue crab dispersal in wind-induced bottom currents to across-sound nursery habitats was only possible if tides were present to move crabs away from the inlets and into the sound. This result was unexpected as tidal currents within Pamlico Sound become minimal within ~10 km of the inlets (Pietrafesa et al. 1986), and Pamlico Sound circulation is predominately wind-driven (Pietrafesa et al. 1986; Pietrafesa and Janowitz 1991; Reyns 2004). Although across-sound transport did not result from our tide-only simulations, the use of tidal currents to facilitate up-estuary transport is a well recognized behavioral strategy employed by many estuarine fishes and crustaceans (see reviews by Boehlert and Mundy 1988; Forward and Tankersley 2001). Moreover, early juvenile blue crabs utilize flood-tide transport to rapidly disperse away from near-inlet high-density settlement habitats (Reyns and Eggleston 2004). This behavior, in addition to the results of our combined wind-tide dispersal simulations, suggest that at a very minimum, tidal transport away from the inlets is a critical phase during secondary dispersal of early juvenile blue crabs in Pamlico Sound. As such, secondary dispersal of early juvenile blue crabs within a wind-driven estuary is not necessarily downwind (as it is for bivalves in another wind-driven system, Commito et al. 1995), because of active behavioral responses to tidal hydrologic variables (near inlets) and, likely, a biological rhythm in vertical swimming (Forward et al. 2005) that allow blue crabs to vertically position themselves to mediate horizontal transport within wind-induced currents.

*Conceptual model of blue crab transport in a wind-driven estuary*—Based on results from this study and previous findings, we propose the following conceptual model for J1 blue crab secondary dispersal in Pamlico Sound (Fig. 8): First, J1 blue crabs leave initial near-inlet settlement habitats such as seagrass by utilizing nighttime flood tides when the intracohort density of conspecifics becomes relatively high (Reyns and Eggleston 2004). Whereas early juvenile blue crabs have an endogenous rhythm in vertical swimming behavior that underlies nighttime dispersal (Forward et al. 2004b; Forward et al. 2005), these crabs are predominately found near inlet regions in surface waters at night during flood tide (Fig. 8, part 1), suggesting that exogenous cues also mediate flood-tide transport (Reyns and Eggleston 2004). We hypothesize

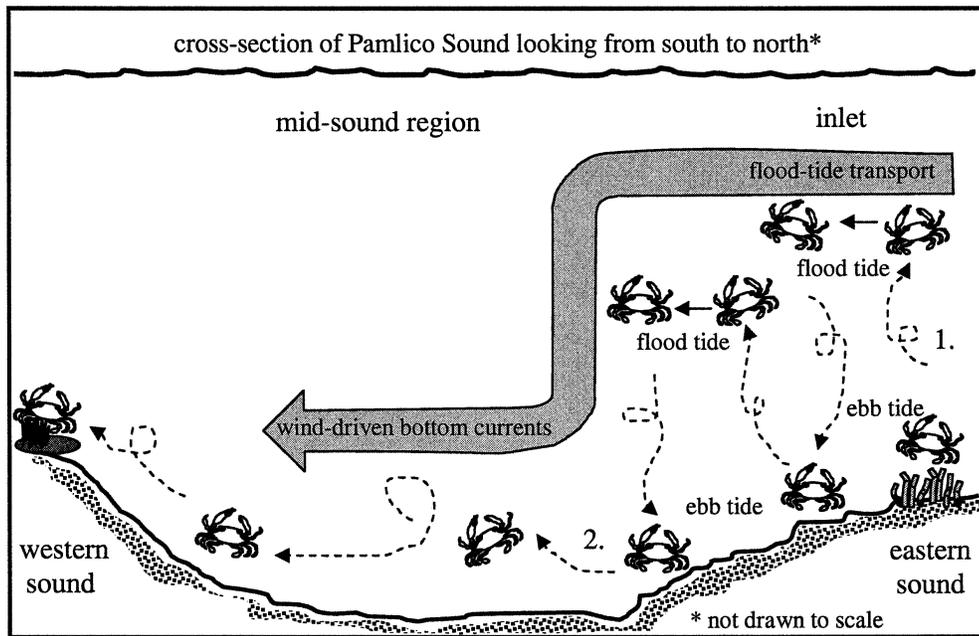


Fig. 8. Conceptual diagram of blue crab secondary dispersal within Pamlico Sound, North Carolina. Early juvenile blue crabs use flood-tide transport to move away from near-inlet settlement habitats (part 1), and wind-induced bottom currents to disperse across-sound (part 2). See text for details.

that rising salinity during nighttime flood tides causes juveniles to move into surface waters, and that turbulence from tidal currents cue juveniles to keep swimming (e.g., similar response as has been observed in postlarval blue crabs, Welch et al. 1999). As J1 blue crabs move away from the inlets, salinity signals and tidal currents weaken (Pietrafesa et al. 1986; Reynolds 2004); thus, in response to diminishing tidal cycle cues, crabs no longer move into surface waters (Fig. 8, part 2). Rather, J1 crabs undergo vertical swimming bouts at night in response to a biological rhythm and become entrained within the prevailing near-bottom currents. Over several days, such nighttime saltatory movements result in across-sound secondary dispersal, after which J1 crabs settle in shallow detrital habitats located along the western sound (Etherington and Eggleston 2000). Our results indicate that a dispersal pathway connecting eastern (inlet) and western sound habitats is evident between Oregon Inlet and Stumpy Point, suggesting that Oregon Inlet is of particular importance in supplying juvenile blue crabs to northwestern sound nursery habitats regardless of wind conditions. The existence of such a dispersal pathway also explains why we consistently observed early juvenile blue crabs at plankton stations between Oregon Inlet and Stumpy Point and why nursery habitats within northwestern Pamlico Sound typically have high relative abundances of late-stage juvenile blue crabs (Eggleston et al. 2004). As such, nursery habitats near Oregon Inlet (eastern shore, seagrass habitats) and the Stumpy Point region (northwestern shore, shallow detrital habitats) should be prioritized for habitat conservation and fisheries management.

*Model considerations*—This study demonstrates the value of using a numerical simulation model approach to examine the dispersal trajectories of organisms too small to track using available telemetry techniques (but see the example of method to track larval patches in Natunewicz et al. 2001). Our model outputted current velocities at spatial resolutions higher than what would have been possible to acquire using instrumentation. Our dispersal simulations illustrate the importance of taking a Lagrangian approach to examining the dispersal dynamics of benthic-oriented early juveniles within a wind-driven estuary as well as highlighting the need for high resolution information on near-bottom currents to better understand how nursery habitats are connected by dispersal.

Although our simulations were able to reproduce the general patterns of relatively high J1 blue crab distributions within the northwestern region of our study area, virtual crabs failed to reach the southwestern region of Pamlico Sound (near Gibbs Shoal), where J1 blue crabs were occasionally collected. One potential reason for this discrepancy is that the exclusion of early juvenile blue crab swimming behavior in our simulations underestimated the dispersal potential of J1 crabs. Including larval swimming behaviors within a simulation model greatly improved the fit between predicted and observed larval fish distributions along the Great Barrier Reef over model simulations that assumed passive larval dispersal (Wolanski et al. 1997). Postlarval blue crabs are relatively strong swimmers ( $5\text{--}20\text{ cm s}^{-1}$ ) capable of swimming in the same direction as the current (Luckenbach and Orth 1992), however, to our knowledge, swimming behaviors have not been documen-

ted for J1 blue crabs. Thus, although swimming can ultimately influence dispersal patterns, future studies are required to examine the horizontal swimming behavior of early juvenile blue crabs and incorporate such behavioral estimates into dispersal simulations. Nonetheless, our simulations provide a valuable step toward understanding the biophysical processes driving the secondary dispersal of blue crabs within Pamlico Sound and are also relevant to other estuarine organisms recruiting to the area during the fall months (e.g., Atlantic croaker). Furthermore, our findings indicate that generalizations of recruitment dynamics based on systems with strong tidal signals (e.g., Chesapeake Bay) cannot be utilized to accurately characterize patterns of estuarine recruitment in predominately large, wind-driven systems.

### References

- ARMONIES, W. 1992. Migratory rhythms of drifting juvenile molluscs in tidal waters in the Wadden Sea. *Mar. Ecol. Prog. Ser.* **83**: 197–206.
- BAPTISTA, A. M., E. E. ADAMS, AND K. D. STOLZENBACH. 1984. Eulerian-Lagrangian analysis of pollutant transport in shallow water. MIT RM Parsons Lab. Tech. Rep. No. 296, Massachusetts Institute of Technology.
- BEUKEMA, J. J., AND J. DE VLAS. 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. *Mar. Ecol. Prog. Ser.* **52**: 193–200.
- BLACKMON, D. C., AND D. B. EGGLESTON. 2001. Factors influencing planktonic, post-settlement dispersal of early juvenile blue crabs (*Callinectes sapidus* Rathbun). *J. Exp. Mar. Bio. Ecol.* **257**: 183–203.
- BOEHLERT, G. W., AND B. C. MUNDY. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *Am. Fish. Soc. Symp.* **3**: 51–67.
- CALEY, M. J., M. H. CARR, M. A. HIXON, T. P. HUGHES, G. P. JONES, AND B. A. MENGE. 1996. Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* **27**: 477–500.
- COMMITO, J. A., S. F. THRUSH, R. D. PRIDMORE, J. E. HEWITT, AND V. J. CUMMINGS. 1995. Dispersal dynamics in a wind-driven benthic system. *Limnol. Oceanogr.* **40**: 1513–1518.
- COSTLOW, J. D., AND C. G. BOOKHOUT. 1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. *Biol. Bull.* **116**: 373–396.
- DYER, K. R. 1997. *Estuaries: A physical introduction*. John Wiley.
- EGGLESTON, D. B., E. G. JOHNSON, AND J. E. HIGHTOWER. 2004. Population dynamics and stock assessment of the blue crab in North Carolina. Final report for contracts 99-FEG-10 and 00-FEG-11 to the North Carolina Fishery Resource Grant Program, North Carolina Sea Grant, and the North Carolina Department of Environmental Health and Natural Resources, Division of Marine Fisheries.
- EMERY, W. J., AND R. E. THOMSON. 2001. *Data analysis methods in physical oceanography*. Elsevier.
- EPIFANIO, C. E., AND R. W. GARVINE. 2001. Larval transport on the Atlantic continental shelf of North America: A review. *Estuar. Coast. Shelf Sci.* **52**: 51–77.
- ETHERINGTON, L. L., AND D. B. EGGLESTON. 2000. Large-scale blue crab recruitment: Linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. *Mar. Ecol. Prog. Ser.* **204**: 179–198.
- , AND ———. 2003. Spatial dynamics of large-scale, multi-stage crab (*Callinectes sapidus*) dispersal: Determinants and consequences for recruitment. *Can. J. Fish. Aquat. Sci.* **60**: 873–887.
- , ———, AND W. T. STOCKHAUSEN. 2003. Partitioning loss rates of early juvenile blue crabs from seagrass habitats into mortality and emigration. *Bull. Mar. Sci.* **72**: 371–391.
- FONSECA, D. M., AND D. D. HART. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos* **75**: 49–58.
- FOREMAN, M. G. G., A. M. BAPTISTA, AND R. A. WALTERS. 1992. Tidal model studies of particle trajectories around a shallow coastal bank. *Atmos.-Ocean* **30**: 43–69.
- FORWARD, R. B., JR., N. B. REYNs, H. DIAZ, J. H. COHEN, AND D. B. EGGLESTON. 2004b. Endogenous swimming rhythms of juvenile blue crabs, *Callinectes sapidus*, as related to horizontal transport. *J. Exp. Mar. Bio. Ecol.* **299**: 63–76.
- , ———, ———, ———, AND ———. 2005. Endogenous swimming rhythms underlying secondary dispersal of early juvenile blue crabs, *Callinectes sapidus*. *J. Exp. Mar. Bio. Ecol.* **316**: 91–100.
- , AND R. A. TANKERSLEY. 2001. Selective tidal-stream transport of marine animals. *Oceanogr. Mar. Biol. Annu. Rev.* **39**: 305–353.
- FORWARD, R. B., AND OTHERS. 2004a. Settlement of blue crab *Callinectes sapidus* megalopae in a North Carolina estuary. *Mar. Ecol. Prog. Ser.* **269**: 237–247.
- GÜNTHER, C.-P. 1992. Dispersal of intertidal invertebrates: A strategy to react to disturbances of different scales? *Neth. J. Sea Res.* **30**: 45–56.
- HALL, S. J. 1994. Physical disturbance and marine benthic communities: Life in unconsolidated sediments. *Oceanogr. Mar. Biol. Annu. Rev.* **32**: 179–239.
- HECK, K. L., JR., AND T. A. THOMAN. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Bio. Ecol.* **53**: 125–134.
- HINES, A. H., R. N. LIPCIUS, AND A. M. HADDON. 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **36**: 55–64.
- LUCKENBACH, M. W., AND R. J. ORTH. 1992. Swimming velocities and behavior of blue crab (*Callinectes sapidus* Rathbun) megalopae in still and flowing water. *Estuaries* **15**: 186–192.
- LUETTICH, R. A., JR., S. D. CARR, J. V. REYNOLDS-FLEMING, C. W. FULCHER, AND J. E. MCNINCH. 2002. Semi-diurnal seiching in a shallow, micro-tidal lagoonal estuary. *Cont. Shelf Res.* **22**: 1669–1681.
- , J. L. HENCH, C. W. FULCHER, F. E. WERNER, B. O. BLANTON, AND J. H. CHURCHILL. 1999. Barotropic tidal and wind-driven larval transport in the vicinity of a barrier island inlet. *Fisheries Oceanogr.* **8**: 190–209.
- , J. J. WESTERINK, AND N. W. SCHEFFNER. 1992. ADCIRC: An advanced three-dimensional circulation model for shelves, coasts and estuaries. Technical report DRP-92-6, Report 1: Theory and methodology of ADCIRC-2DDI and ADCIRC-3DL, U.S. Army Engineer Waterways Experiment Station.
- MENSE, D. J., AND E. L. WENNER. 1989. Distribution and abundance of early life history stages of the blue crab, *Callinectes sapidus*, in tidal marsh creeks near Charleston, South Carolina. *Estuaries* **12**: 157–168.
- MILLIKIN, M. R., AND A. B. WILLIAMS. 1984. Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. *FAO Fisheries Synopsis* **138**: 1–39.
- MOKSNES, P.-O., R. N. LIPCIUS, L. PIHL, AND J. VAN MONTFRANS. 1997. Cannibal-prey dynamics in young juveniles and post-larvae of the blue crab. *J. Exp. Mar. Bio. Ecol.* **215**: 157–187.

- MORGAN, S. G. 1995. The timing of larval release, p. 157–191. In L. R. McEdward [ed.], *Ecology of marine invertebrate larvae*. CRC Press.
- NATUNEWICZ, C. C., C. E. EPIFANIO, AND R. W. GARVINE. 2001. Transport of crab larval patches in the coastal ocean. *Mar. Ecol. Prog. Ser.* **222**: 143–154.
- NORCROSS, B. L. 1991. Estuarine recruitment mechanisms of larval Atlantic croakers. *Trans. Am. Fish. Soc.* **120**: 673–683.
- OLMI, E. J., III, J. VAN MONTFRANS, R. N. LIPCIUS, R. J. ORTH, AND P. W. SADLER. 1990. Variation in planktonic availability and settlement of blue crab megalopae in the York River, Virginia. *Bull. Mar. Sci.* **46**: 230–243.
- ORTH, R. J., AND J. VAN MONTFRANS. 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser.* **41**: 283–294.
- PALMER, M. A., J. D. ALLAN, AND C. A. BUTMAN. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends Ecol. Evol.* **11**: 322–326.
- PIETRAFESA, L. J., AND G. S. JANOWITZ. 1988. Physical oceanographic processes affecting larval transport around and through North Carolina inlets. *Am. Fish. Soc. Symp.* **3**: 34–50.
- , AND ———. 1991. The Albemarle-Pamlico coupling study. Final report to the Environmental Protection Agency.
- , ———, T.-Y. CHAO, R. H. WEISBERG, F. ASKARI, AND E. NOBLE. 1986. The physical oceanography of Pamlico Sound. UNC-WP-86-5, UNC Sea Grant Publication.
- PILE, A. J., R. N. LIPCIUS, J. VAN MONTFRANS, AND R. J. ORTH. 1996. Density-dependent settler-recruit-juvenile relationships in blue crabs. *Ecol. Monogr.* **66**: 277–300.
- POWERS, S. P., AND C. H. PETERSON. 2000. Conditional density dependence: The flow trigger to expression of density-dependent emigration in bay scallops. *Limnol. Oceanogr.* **45**: 727–732.
- REYNS, N. B. 2004. Biophysical dispersal dynamics of the blue crab in Pamlico Sound, North Carolina. Ph.D. thesis. North Carolina State University.
- , AND D. B. EGGLESTON. 2004. Environmentally-controlled, density-dependent secondary dispersal in a local estuarine crab population. *Oecologia* **140**: 280–288.
- ROUGHGARDEN, J., S. GAINES, AND H. POSSINGHAM. 1988. Recruitment dynamics in complex life cycles. *Science* **241**: 1460–1466.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*, 3rd ed. W. H. Freeman and Company.
- THRUSH, S. E., J. E. HEWITT, V. J. CUMMINGS, M. O. GREEN, G. A. FUNNELL, AND M. R. WILKINSON. 2000. The generality of field experiments: Interactions between local and broad-scale processes. *Ecology* **81**: 399–415.
- TURNER, S. J., J. GRANT, R. D. PRIDMORE, J. E. HEWITT, M. R. WILSON, T. M. HUME, AND D. J. MORRISSEY. 1997. Bedload and water-column transport and colonization processes by post-settlement benthic macrofauna: Does infaunal density matter? *J. Exp. Mar. Bio. Ecol.* **216**: 51–75.
- UNDERWOOD, A. J., AND P. G. FAIRWEATHER. 1989. Supply-side ecology and benthic marine assemblages. *Trends Ecol. Evol.* **4**: 16–20.
- VAN MONTFRANS, J., AND OTHERS. 1995. Settlement of blue crab postlarvae in western North Atlantic estuaries. *Bull. Mar. Sci.* **57**: 834–854.
- WEISBERG, K. H., AND L. J. PIETRAFESA. 1983. Kinematic and correlation of the surface wind field in the South Atlantic bight. *J. Geophys. Res.* **88**: 4593–4610.
- WELCH, J. M., R. B. FORWARD, JR., AND P. A. HOWD. 1999. Behavioral responses of blue crab *Callinectes sapidus* post-larvae to turbulence: Implication for selective tidal stream transport. *Mar. Ecol. Prog. Ser.* **179**: 135–143.
- WOLANSKI, E., P. DOHERTY, AND J. CARLETON. 1997. Directional swimming of fish larvae determines connectivity of fish populations on the Great Barrier Reef. *Naturwissenschaften* **84**: 262–268.

Received: 12 August 2005

Accepted: 25 April 2006

Amended: 25 May 2006