Dispersal dynamics of post-larval blue crabs, *Callinectes sapidus*, within a wind-driven estuary

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ABSTRACT

We examined how post-larval blue crab (*Callinectes sapidus*) dispersal occurs within Pamlico Sound, NC, USA, a predominantly wind-driven system. We sampled during multiple 24-h periods over 2 years (2000–01) to relate the spatial distribution of post-larvae in the water column with circulation patterns. A hydrodynamic model of the region was used to recreate dispersal trajectories and to assess potential transport mechanisms and pathways that link near-inlet and across-Sound nursery habitats. Most post-larval blue crabs were collected in surface waters at night, and were consistently distributed within the north-western region of Pamlico Sound. Particle-tracking simulations suggested that dispersal from the inlets to across-Sound nursery habitats only resulted from the combination of tidal and wind-driven currents. Our simulation results further indicated that the northernmost inlet (Oregon Inlet) was the primary supplier of post-larval blue crabs throughout the northern basin of Pamlico Sound, as crabs ingressing through Hatteras Inlet to the south were not retained within our study area. A dispersal pathway connecting Oregon Inlet and across-Sound settlement habitats was evident from field observations. Collectively, our results indicate how multiple forcing agents, coupled with post-larval vertical positioning within the water column, drive estuarine dispersal and connect spatially separated nursery habitats.

INTRODUCTION

Marine populations experience considerable year-to-year variability in abundance; understanding the processes contributing to this variability has long been a goal of marine ecology (or fishery scientists) (Rothschild, 1986). Although post-settlement processes are undoubtedly important in structuring marine populations (e.g. Sissenwine, 1984; Eggleston and Armstrong, 1995; Caley *et al.*, 1996), factors influencing the pelagic early life stages may ultimately drive population dynamics (e.g. Houde, 1987; Roughgarden *et al.*, 1988). Along the Atlantic and Gulf coasts of the US, most commercially exploited finfish and crustacean species undergo extensive larval migrations to move from oceanic development/spawning regions to nearshore estuaries (Houde and Rutherford, 1993). Great strides in elucidating transport mechanisms have been made, leading to the recognition that coastal oceanography and estuarine circulation (e.g. Crowder and Werner, 1999; Brown *et al.*, 2004; Miller and Shanks, 2004), coupled with behavioral responses to environmental conditions by larvae (e.g. DiBacco *et al.*, 2001; Queiroga and Blanton, 2005), influence the outcome of successful estuarine recruitment (herein defined as larval/post-larval settlement within a nursery habitat) (see also reviews by Norcross and Shaw, 1984; Boehlert and Mundy, 1988; Miller, 1988; Epifanio and Garvine, 2001).

A common behavioral strategy employed by many larval finfish and crustacean species to promote ingress and up-estuary transport is flood-tide transport (FTT), in which larvae migrate into the water column during flood tides and descend to the bottom during ebb tides (Boehlert and Mundy, 1988; Forward and Tankersley, 2001). Specific environmental conditions that may evoke FTT include changes in olfactory cues, currents, salinity, temperature and turbulence associated with

the tidal phase when mixing between shelf and estuarine waters occurs (reviewed by Boehlert and Mundy, 1988; Forward and Tankersley, 2001). An important consideration, however, is that the cues underlying FTT are driven by the tidal cycle, and it remains unclear how larvae reach nursery habitats in estuaries or systems that lack a predictable tidal signal, such as is the case in the main body of the Albemarle-Pamlico Estuarine System.

Study area

The Albemarle-Pamlico Estuarine System is the largest (area $\sim$6000 km^2) lagoonal estuary in the US, and is bounded by a barrier island chain that limits exchange with the coastal ocean to three main, relatively small ($\sim$1 km wide) inlets: Oregon, Hatteras and Ocracoke (Fig. 1a). Although these inlet regions experience semi-diurnal tides, tidal influence quickly diminishes with distance from the inlets, and circulation within the shallow (mean depth $\sim$4.5 m) main body of the Albemarle-Pamlico Estuarine System is predominately wind-driven (Pietrafesa et al., 1986b).

The Albemarle-Pamlico Estuarine System serves as an important nursery for many commercially exploited species including Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), Atlantic menhaden (*Brevoortia tyrannus*), southern flounder (*Paralichthys lethostigma*), summer flounder (*P. dentatus*), blue crabs (*Callinectes sapidus*) and penaeid shrimp (*Penaeus aztecus*, *P. duorarum*, *P. setiferus*). Previous investigators have hypothesized that following ingress through the inlets, demersal juvenile fish such as spot, Atlantic croaker, summer flounder and southern flounder reach nursery habitats along the western shore of Pamlico Sound by using wind-driven bottom currents (Miller et al., 1984). Based on a circulation model, Pietrafesa et al. (1986a) determined that winds directed toward the south-southeast to north-northeast generated near-bottom currents favorable for transport of juvenile fish from the inlets to western Sound nursery areas. While increases in juvenile spot within these nursery habitats coincided with eastward-blowing wind events (Pietrafesa et al., 1986a), the hydrography of the Sound and the distribution of spot within the water column were not measured, leaving across-Sound transport mechanisms to be inferred. Further, a plausible mechanism for the across-Sound transport of surface-oriented menhaden could not be determined (Pietrafesa et al., 1986a). Therefore, the physical mechanisms (e.g. wind- and tide-driven currents, or a combination of both) that promote across-Sound (from east to west) dispersal of

organisms within Pamlico Sound remain poorly understood.

In our study, we determined how biophysical factors (positioning within the water column, winds and currents) drive the dispersal of post-larval blue crabs. We focused our study on the blue crab because of its status as North Carolina's most commercially valuable fishery, and because 88% of landings in the state come from within the Albemarle-Pamlico Estuarine System (Henry and McKenna, 1998). Our findings, however, are relevant to the dispersal dynamics of other economically important species that utilize estuarine nursery habitats within predominately wind-driven systems.

Study species

The blue crab has a complex life history that is typical of many estuarine-dependent species. Females within estuaries migrate to ocean inlets to spawn (Van Engel, 1958; Millikin and Williams, 1984), and larvae are advected seaward to high-salinity continental shelf waters where they develop (Provenzano et al., 1983). Larvae complete their oceanic development after passing through seven to eight zoeal stages and metamorphosing to the post-larval (megalopal) stage (Van Engel, 1958; Sandifer, 1975). Post-larvae generally make the transition from shelf waters to coastal estuaries by using across-shelf wind-driven currents generated by Ekman circulation (Epifanio and Garvine, 2001), but must subsequently overcome the net seaward flow characteristic of estuarine circulation to move into and up estuaries to reach juvenile nursery habitats. Like many other crustacean and finfish species, post-larval blue crabs use FTT during estuarine ingress (Forward et al., 2003). While FTT by blue crabs mediates ingress through tidal inlets and dispersal within tidal estuaries (Forward and Tankersley, 2001), it is not known how post-larval transport occurs within the predominately wind-driven main body of the Albemarle-Pamlico Estuarine System. Understanding the spatiotemporal dynamics that drive post-larval dispersal from inlet source regions to western Sound habitats, however, is of particular importance for the prioritization of nursery habitats for fisheries management and conservation.

METHODS

Given the relatively large size of the Albemarle-Pamlico Estuarine System, we concentrated our research efforts on the northern basin of Pamlico Sound (bounded by Oregon Inlet to the north and Hatteras Inlet to the south; Fig. 1a). This area was selected

Figure 1. Map of Albemarle-Pamlico Estuarine System in North Carolina, USA showing regional bathymetry and hydrographic stations (■) within the northern basin of Pamlico Sound (a) (OI, Oregon Inlet; SP, Stumpy Point; CH, Chicamacomico; GS, Gibbs Shoal; HI, Hatteras Inlet). Blue crab plankton sampling stations (●) in 2000 (b) and 2001 (c) are presented on enlarged maps of study area. For reference, early juvenile blue crab nursery habitats are also shown (d) (SG, seagrass; SDH, shallow detrital habitat).
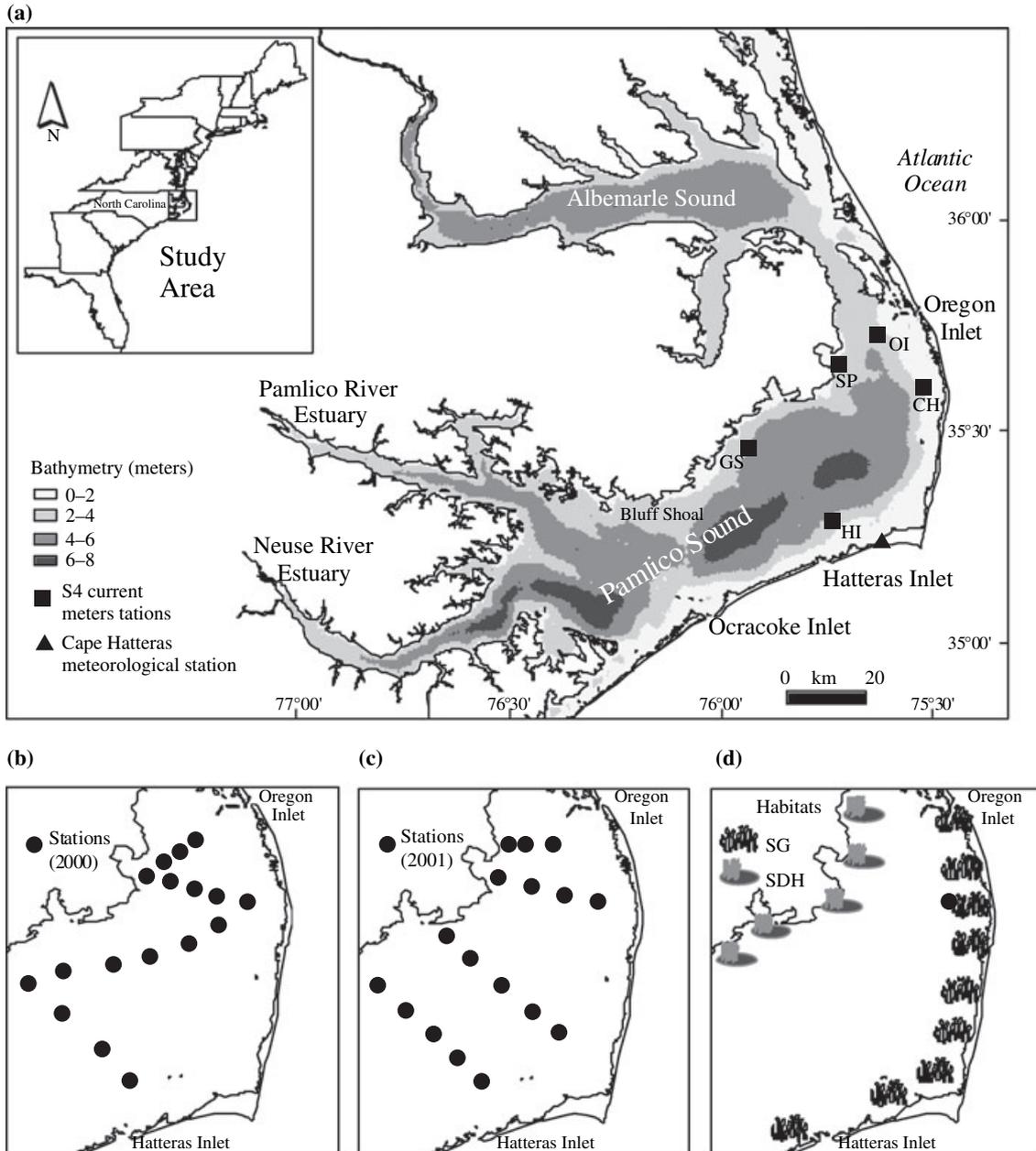
because it experiences relatively high post-larval supply of blue crabs (Eggleston *et al.*, 2004), and settlement habitats are extensive and well studied (Etherington and Eggleston, 2000, 2003). Early juvenile blue crab nursery habitats include seagrass (SG) located near the inlets and along the eastern shore of Pamlico Sound, as well as shallow detrital habitat (SDH) located along the western shore of Pamlico Sound (Etherington and Eggleston, 2000; Fig. 1d). The mid-Sound region is characterized by mud and sand and is devoid of structured aquatic vegetation (N. Reyns, unpublished data).

Post-larval patterns

To quantify the distribution and abundance of post-larval blue crabs throughout the northern basin of Pamlico Sound, we sampled 17 evenly spaced stations quasi-synoptically along four transects crossing the study area (Fig. 1b,c). All 17 stations were sampled within an 8-h period. To make day–night comparisons of blue crab distribution and abundance, we sampled all stations during the day and then re-sampled all stations at night. In 2000, we completed four day–night cruises, while in 2001 we completed two day–night cruises and four nighttime-only cruises.

At each station, the vertical distribution of crabs within the water column was measured by simultaneously towing a neuston net (surface measure) and plankton net mounted to a benthic sled (near-bottom measure). Both nets measured 1×0.5 m, had 505 μm mesh, and were equipped with General Oceanics flow meters (General Oceanics, Inc., Miami, FL). Nets were towed for 5 min at about 1 m s^{-1}. A pilot study following the methods described in Hodson *et al.* (1981) determined average filtration efficiency (± 1 standard error) for the neuston net and benthic sled to be 96.83% ($\pm 1.12\%$) and 95.82% ($\pm 1.62\%$), respectively. Furthermore, net efficiencies for the two gear types were not significantly different from one-another (*t*-test: d.f. = 17, $t = -0.05$, $P = 0.62$), allowing comparisons of vertical crab concentrations to be made. Following deployment, net collections were immediately sieved and preserved in 70% ethanol, and post-larval blue crabs were enumerated and identified in the laboratory. Counts were standardized to concentrations, defined as number of crabs 100 m^{-3}.

Physical oceanographic data

To characterize the circulation within our study area in Pamlico Sound, we deployed InterOcean S4 electromagnetic current meters (InterOcean Systems, Inc., San Diego, CA) during two periods: 17 September to 8 November 2000 and 31 August to 30 October 2001. Current meters were positioned near-surface (1 m below surface) at five locations surrounding our plankton stations (Fig. 1a), and current speed and direction were recorded for 2 min every 20 min. Instruments were cleaned weekly to minimize the effects of biological fouling. We also obtained hourly wind speed and direction data collected by the NOAA National Weather Service at Cape Hatteras (Fig. 1a; made available by State Climate Office of North Carolina at North Carolina State University).

Current meter and wind data were averaged into hourly and daily records, and decomposed into several components: u (east–west), v (north–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). In addition, to distinguish between tidal and non-tidal flows, current meter records were lowpass-filtered using a 40-h cut-off period. Given the variability in wind speeds observed during our study, we did not compute wind stress because of uncertainties in assigning the appropriate drag coefficient (Emery and Thomson, 2001). Furthermore, wind direction was not rotated to correct for the angle of the coastline because we compared winds with currents measured at multiple sites that were each oriented differently with respect to the coastline and true north.

Analyses

To determine if the mean concentration of post-larval blue crabs within Pamlico Sound varied vertically within the water column and by time of day, we tested the hypothesis that the concentration of crabs is affected by depth (surface versus bottom) and diel cycle (day versus night) using a two-way fixed-factor ANOVA. We accounted for temporal variability in post-larval settlement by converting the response variable (concentration of crabs per net tow on a given cruise date) to relative concentrations, or proportions, which were square root transformed (Sokal and Rohlf, 1995).

Given an average blue crab post-larval duration in estuarine water of 5 days (Wolcott and De Vries, 1994), post-larvae collected on a specific cruise date may have ingressed 1–5 days prior to a cruise. Therefore, to assess how the concentration of post-larval blue crabs varied spatially, we compared the distribution and abundance patterns of post-larval blue crabs on a given cruise date with winds and lowpass-filtered (non-tidal) currents averaged over the 5-day period prior to plankton measurements.

Hydrodynamic model

We used a 3D hydrodynamic model coupled with a Lagrangian particle-tracking algorithm to simulate crab dispersal trajectories to determine (i) the flow conditions that best explained observed post-larval blue crab distributions, and (ii) whether specific dispersal pathways connected inlet regions with western Pamlico Sound nursery habitats. Circulation was simulated using a nonlinear, finite-element barotropic 3D hydrodynamic model (ADCIRC: ADvanced CIRCulation model, Luettich *et al.*, 1992; Luettich and Westerink, 2004), which solved the shallow water form of the momentum equations over the entire Albemarle-Pamlico Estuarine System domain. ADCIRC

Figure 2. Comparison of observed and modeled east–west (a) and north–south (b) currents at Oregon Inlet during 2001. Positive values indicate currents flowing toward the east and north, respectively. *r* = cross-correlation coefficients taken from Reyns (2004).
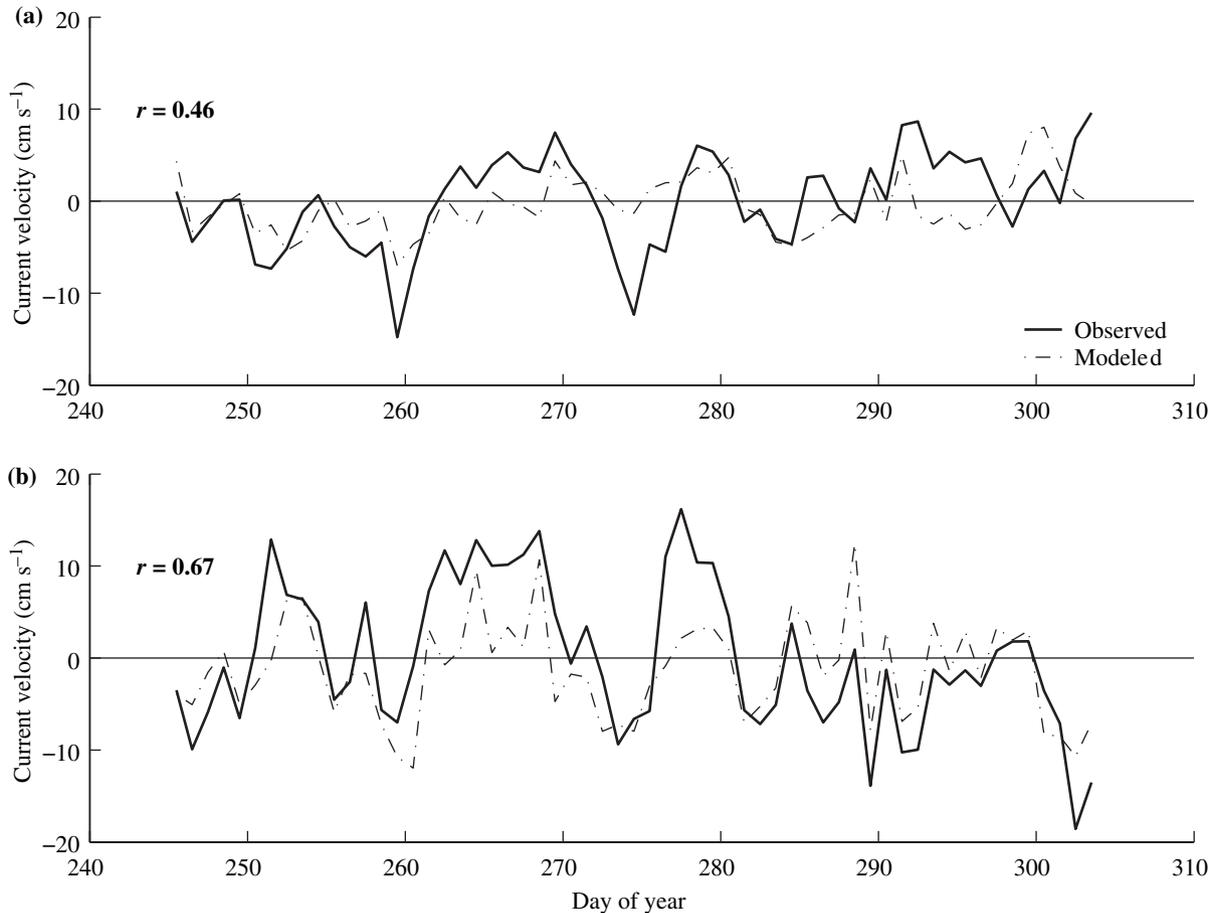
has produced flow fields that are in good agreement with observed currents in the southern portion of the Albemarle-Pamlico Estuarine System (e.g. Neuse River Estuary, Luettich *et al.*, 2002). In our study area within the northern basin of Pamlico Sound, cross-correlations between modeled and observed currents were statistically significant at all sites ($r = 0.39$–0.90, $N = 383$–1416, $P < 0.0001$: Reyns, 2004), and modeled currents reproduced both the magnitude and direction of our observed currents (Fig. 2).

To determine the flow conditions utilized by post-larval blue crabs to disperse across Pamlico Sound, we used ADCIRC to recreate circulation patterns under three different conditions: wind-only, tide-only and combined wind-tide conditions. In the wind-only simulations, the model was parameterized with a Mellor–Yamada level 2.5 turbulent closure. The quadratic slip bottom friction and lateral eddy viscosity coefficients were spatially constant, and specified as 0.0025

and 2 m^2 s^{-1}, respectively. We used a high-resolution triangular grid composed of 22 425 nodes and 41 330 elements, producing a grid resolution between 300 m and 1 km depending on bathymetry and geometry of the estuarine system (e.g. Fig. 3a,b). In the vertical domain, current velocities were computed over 11 variable depth layers. As spatial gradients in synoptic scale wind fields are minimal over the extent of our study area (Weisberg and Pietrafesa, 1983), and wind fields are generally correlated over the South Atlantic Bight (Weber and Blanton, 1980), we forced AD-CIRC with a spatially uniform wind field using hourly wind velocities measured at the Cape Hatteras Meteorological Station (Fig. 1a). A 1-day ramp was applied to wind forcing, and the model was allowed a 3-day spin-up time before particle-tracking simulations were run (see below). We assumed the Albemarle-Pamlico Estuarine System to be spatially isolated from the coastal ocean because when we expanded the model

Figure 3. Resolution of finite element grid in the Oregon Inlet (a) and Hatteras Inlet (b) regions. Particles (virtual crabs) were released from randomly selected locations near each inlet.

simulations, but had open boundaries at the inlets and was extended to include the Atlantic Ocean from the coast of Nova Scotia (northern boundary), to the coast of South America (southern boundary) to 60°W (eastern boundary). This grid was developed for eventual use in the 3D version of ADCIRC, where a large model domain will be necessary to appropriately model wind-driven ocean-estuary dynamics. Inputs to the depth-integrated model included the K_1, O_1, M_2, S_2, and N_2 tidal constituents. A 10-day ramp was applied to the tidal forcing and, as with the wind-only simulations, current velocities were output at hourly intervals.

To produce wind-tide flow fields, we also combined the velocity outputs from the wind-only and tide-only model simulations. In all three simulation types, baroclinic forcing was ignored as the water column within Pamlico Sound is typically well mixed (Reyns, 2004). To match our current meter deployment dates, model simulations ran for 57 days in 2000 and 64 days in 2001.

Simulated post-larval dispersal

A Lagrangian particle-tracking algorithm with a fourth-order Runge–Kutta scheme (Baptista *et al.*, 1984; Foreman *et al.*, 1992) was used to simulate post-larval blue crab transport within the three different ADCIRC-generated flow fields. Diffusion coefficients were not included in this model because of uncertainties in the physical mechanisms that cause dispersion within our study area. In all particle-tracking simulations, we incorporated active post-larval blue crab behaviors. All simulations used an algorithm where dispersal was restricted to nighttime only (defined as 18.00 to 06.00 hours) because we collected more post-larval blue crabs at night than during the day (see Results). In addition, given that post-larval blue crabs were predominately located in surface waters during our field study (see Results), particle-tracking simulations using the wind-only flow fields were conducted with current velocities corresponding to the near-surface (~1 m below surface) depth layer. In the particle-tracking simulations using the tide-only flow fields, dispersal was restricted to flood-tide periods to simulate post-larval FTT (as has been observed in tidal estuaries, see review by Forward and Tankersley, 2001). Finally, in the combined wind-tide particle-tracking simulations, dispersal occurred in surface waters during flood tide.

In all dispersal simulations, we released 40 particles at randomly selected locations within a 10 km^2 area surrounding both Oregon and Hatteras Inlets to represent variability in post-larval ingress through the inlets. The model time step was 2 min and particle

domain to include the continental shelf region, unrealistic depth values in our study area had to be used to accommodate wetting and drying. As such, this 3D version of ADCIRC did not consider wind-driven ocean-estuary exchange through the inlets, but still reproduced features of the local wind-driven circulation (e.g. vertical return flows).

In our tide-only simulations, we used the depth-integrated version of ADCIRC to compute tidal velocity fields in the Albemarle-Pamlico Estuarine System. A depth-integrated model was appropriate to use in this case as strong tidal currents effectively mix the water column due to the shallow water depths and absence of vertical stratification in our study area (Luettich *et al.*, 1999; Reyns, 2004). Tidal amplitude and phase generated by this version of ADCIRC have previously been shown to be in good agreement with observed data collected in the region (Luettich *et al.*, 1999; Hench and Luettich, 2003). The grid used for our tide-only simulations was the same grid used in the wind-only

positions were output at hourly intervals. To compare particle end-points with observed Sound-wide post-larval blue crab distributions, particles were released daily over the 5 days leading up to our plankton cruise dates ($N = 200$ particles tracked from each inlet per cruise date).

RESULTS

Wind and currents

During both 2000 and 2001, the major axis of wind variance was generally aligned along the northeast–southwest axis (Fig. 4a,b). The principal axes of variance of the lowpass-filtered (non-tidal) currents were aligned with the wind ellipses and the Albemarle-Pamlico Estuarine System shoreline (Fig. 4a,b). In both years, $\sim$70–96% of the variance in non-tidal current velocities occurred along the major axes (Table 1). With respect to tidal currents, as expected, velocities were greatest at the near-inlet current meter stations (see OI and HI, Fig. 4c,d). Near Oregon Inlet, tidal currents were aligned in an east-northeast to west-southwest direction during both years, while tidal currents near Hatteras Inlet were aligned in a north–south direction (Fig. 4c,d). Again, percentage variability associated with the major axes of tidal currents was relatively high ($\sim$69–99%, Table 1).

Post-larval distributions and relation to wind and currents

In both years, post-larval blue crabs were collected during all plankton cruises. On a vertical spatial scale in the water column, the concentration of post-larval blue crabs varied significantly by water depth ($F_{1,534} = 14.33$, $P = 0.0002$) and diel cycle ($F_{1,534} = 8.59$, $P = 0.0035$); the interaction effect was not significant ($F_{1,534} = 0.11$, $P = 0.7419$). In general, the concentration of post-larval blue crabs was greatest in surface waters and at night (Fig. 5).

Over the spatial extent of Pamlico Sound (horizontal scale), the concentration of post-larval blue crabs varied by station over time. During 2000, post-larvae were predominately concentrated within north-west Pamlico Sound, in the region between Oregon Inlet and Stumpy Point (Fig. 6). Winds during the 5 days prior to each cruise in 2000 had a southward component. In general, mean currents near Oregon Inlet were directed toward the west (Fig. 6a,b) and south-west (Fig. 6c,d), while at Stumpy Point, currents were mainly directed toward the east-southeast (across-Sound in opposite direction of Oregon Inlet, Fig. 6). Mean currents near Hatteras Inlet were directed toward the south-east or south-west, promoting transport toward the barrier island boundary or out of our study area, rather than across-Sound (Fig. 6a–d).

Figure 4. Principal axes of variance of current and wind velocities during the blue crab recruitment season (September–October 2000 and 2001). Hourly averaged, lowpass-filtered (non-tidal) current ellipses (shown within Pamlico Sound) and wind ellipse (shown outside of Sound) during 2000 (a) and 2001 (b). Scale bar in bottom left corner represents 1 m s^{-1} for wind velocity and 5 cm s^{-1} for current velocity, respectively. Compass directions are shown for reference in top-right corner of panel a. Tidal currents are shown for 2000 (c) and 2001 (d). Major axis is denoted by line extending along length of each ellipse. OI, Oregon Inlet; SP, Stumpy Point; CH, Chicamacomico; GS, Gibbs Shoal; HI, Hatteras Inlet.
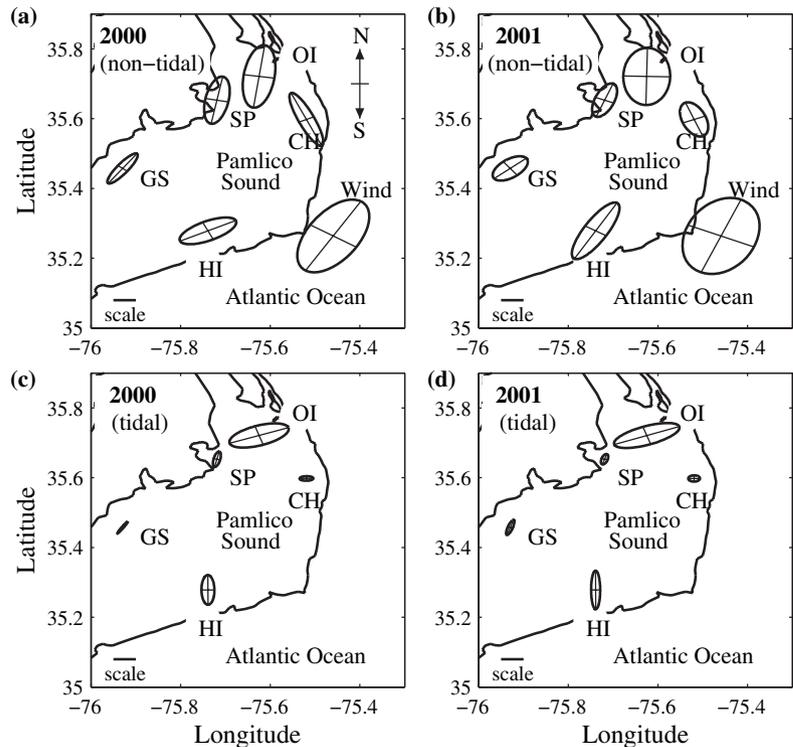
Station	Wind		Non-tidal		Tidal	
	2000	2001	2000	2001	2000	2001
Hatteras Meteorological Station	86.0	64.7	–	–	–	–
Oregon Inlet (OI)	–	–	87.3	70.9	85.9	89.5
Stumpy Point (SP)	–	–	87.1	83.4	90.4	83.3
Chicamacomico (CH)	–	–	96.1	78.8	85.3	68.7
Gibbs Shoal (GS)	–	–	95.5	76.4	98.9	94.2
Hatteras Inlet (HI)	–	–	88.4	94.8	89.6	99.1

Table 1. Percentage variability associated with the major axes of variance of hourly averaged wind, non-tidal currents, and tidal currents during 2000 and 2001 at each sampling station. Current meter station abbreviations are noted in parentheses for reference.

Figure 5. Mean concentration (no. $100 \, \text{m}^{-3}$) + 1SE of post-larval blue crabs within the northern basin of Pamlico Sound in relation to water depth (surface versus 1 m above bottom) and diel cycle (day versus night). Although post-larval crab concentrations were converted to proportions and square root transformed for analysis (see text), raw data are presented for simplicity.
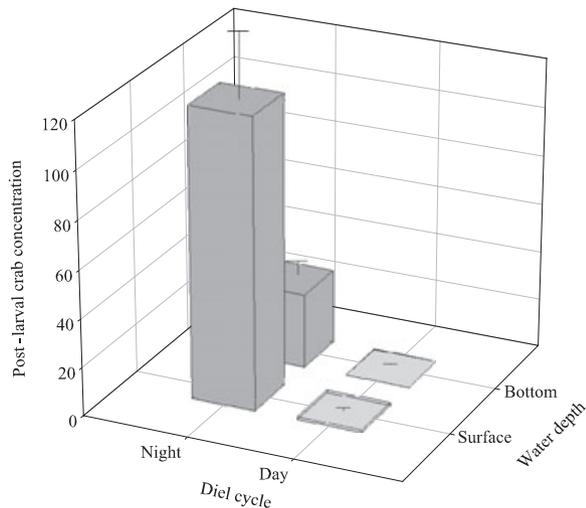
During 2001, Sound-wide post-larval blue crab concentrations were greater than in 2000, and were more variable spatially (compare Fig. 7 with Fig. 6). Blue crabs were consistently collected in the north-western region of Pamlico Sound during 2001 as in 2000 (Fig. 7), but were also collected more often in mid- and southern-Sound regions than in 2000 (Fig. 7b–e). Although wind conditions also were more variable in 2001 than in 2000, current patterns between years were similar. With the exception of one cruise date when winds were directed toward the north-east (Fig. 7c), currents generally exhibited a southward component, with flow predominately toward the south-west near Oregon Inlet and aligned along the main axis of Pamlico Sound. Only current patterns at Stumpy Point differed between years, with

mean currents primarily oriented toward the south-west and not toward the east-southeast as in 2000 (Fig. 7). Similar to 2000, flow near Hatteras Inlet was typically toward the south-east and directed out of our study area (Fig. 7). Unfortunately, annual comparisons of current patterns at Gibbs Shoal could not be made because of lengthy gaps in the data record during 2000.

On cruise dates with relatively high post-larval blue crab concentrations in the north-west region of Pamlico Sound (e.g. days 262 and 276 in 2001, Fig. 7), currents at Oregon Inlet were relatively strong and directed toward Stumpy Point (Fig. 7b,d). The area between Hatteras Inlet and Gibbs Shoal also exhibited high concentrations of post-larvae during these days (Fig. 7b,d); however, wind-driven currents at Hatteras Inlet were not favorable for across-Sound transport.

Particle-tracking simulations and dispersal trajectories

All wind-only simulations, where virtual crabs were released near the inlets in near-surface flow fields at night, failed to result in across-Sound transport (from east to west) regardless of the direction the wind was blowing (Figs 8a and 9a). Rather, dispersal was directed southward from the inlets following the direction of the prevailing winds and currents, with particles moving along the eastern shore of Pamlico Sound (Figs 8a and 9a). Generally, only particles released from Oregon Inlet remained within our study area, and only on dates when winds were directed toward the north-east did particles released from Hatteras Inlet move northward (e.g. red triangles: Fig. 9a, see Fig. 7c for wind direction). As such, we were not able to recreate our observed blue crab distribution patterns with these wind-only simulations.

Particles also failed to reach the western shore of Pamlico Sound during the tide-only simulations where dispersal was restricted to nighttime flood-tide periods (Figs 8b and 9b). Particles in the tide-only simulations, however, dispersed partway into Pamlico
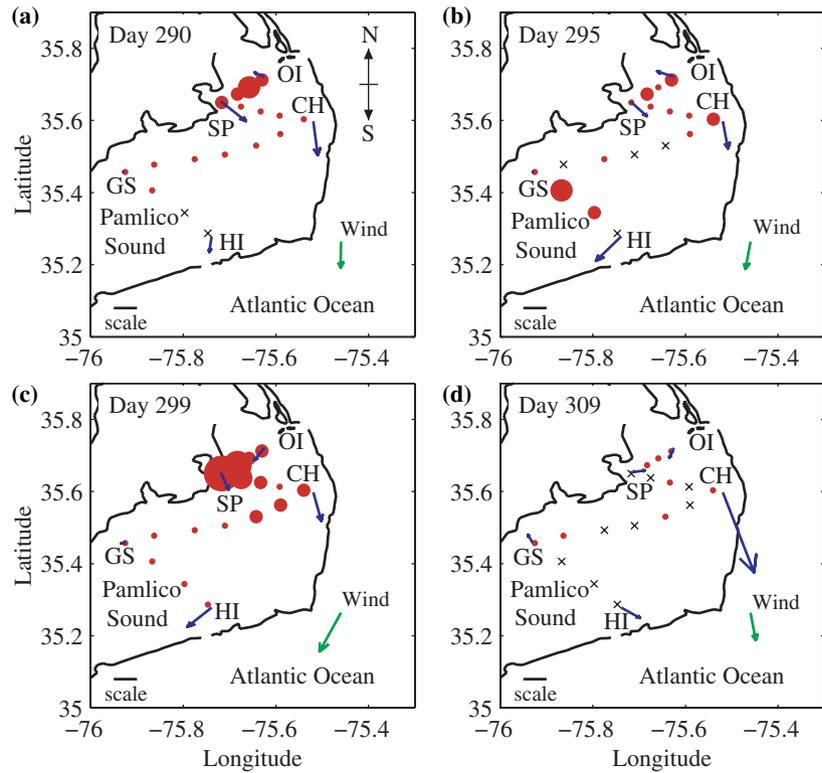
Figure 6. Concentration of post-larval blue crabs (no. 100 m^{-3}) in surface waters at night, by cruise date (a–d) during 2000. Arrows at current meter sites (in blue) represent the mean direction of current flow. The mean angle of the wind is plotted outside of Pamlico Sound in green. All mean directions were computed for the 5 days prior to 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^{-1} for wind velocity and 5 cm s^{-1} for current velocity, respectively. Compass directions are shown for reference in top-right corner of panel a.
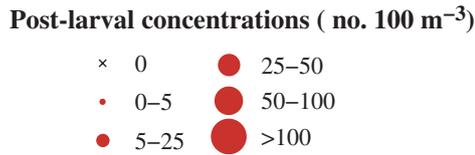
Sound reaching the plankton stations closest to the inlets.

Unlike the wind-only and tide-only simulations, across-Sound transport was achieved during the combined wind-tide simulations that incorporated movement into the Sound by both nighttime wind and flood-tide currents, but only by particles originating near Oregon Inlet (Figs 8c and 9c). When winds blew toward the south (e.g. day 290, Fig. 6a, see cyan symbols on Fig. 8c), south-west (e.g. day 262 Fig. 7b, see green symbols on Fig. 9c), or south-east (e.g. day 276 Fig. 7d, see magenta symbols on Fig. 9c), particles released near Oregon Inlet reached the western shore of Pamlico Sound, while particles released near Hatteras Inlet generally moved toward the south-west and out of our study area (Figs 8 and 9). Furthermore, particles released near Oregon Inlet typically dispersed over a greater extent of our study area than those released from Hatteras Inlet (Figs 8c and 9c). Only when winds were directed toward the north-east did particles from Hatteras Inlet move northward into our study area, although across-Sound transport was not achieved (day 269 Fig. 7c, see red triangles on Fig. 9c). Particles released from Oregon Inlet during periods with southward and westward winds, however, were favorable for such transport, with particles consistently reaching the north-western region of Pamlico Sound (Figs 8c and 9c). Indeed, particle end-points in this region corresponded to the post-larval blue crab distributions we observed during cruises with southward winds (compare simulation end-points in Figs 8c and 9c with observed distributions in Figs 6 and 7). Moreover, dispersal trajectories generated by the combined wind-tide simulations during southward winds were similar to those indicated by our observed currents under similar wind conditions, whereby currents moved toward the west from Oregon Inlet and generally southward in the vicinity of Stumpy Point and Hatteras Inlet (see Fig. 4 for variance ellipses and Figs 6 and 7 for mean flows).

Although there was good agreement between particle end-points and observed blue crab distributions in north-western Pamlico Sound when winds had a southerly component, our combined wind-tide simu-
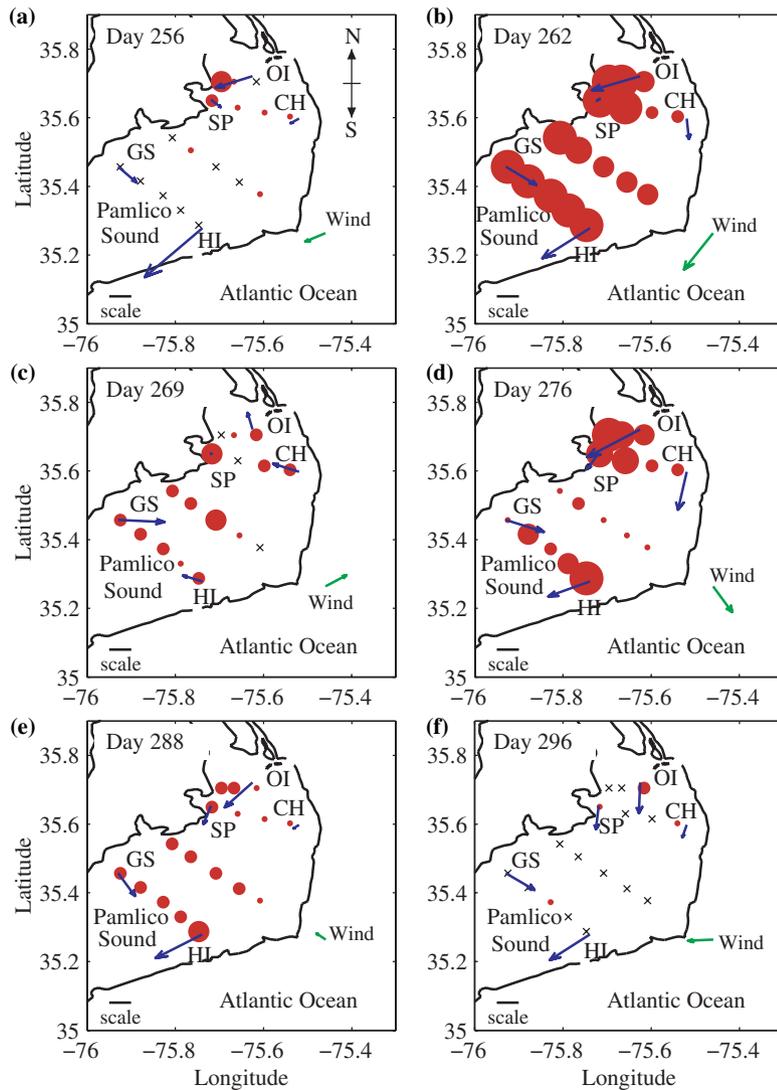
Figure 7. Concentration of post-larval blue crabs (no. 100 m^{-3}) in surface waters at night, by cruise date (a–f) during 2001. Arrows at current meter sites (in blue) represent the mean direction of current flow. The mean angle of the wind is plotted outside of Pamlico Sound in green. All mean directions were computed for the 5 days prior to 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^{-1} for wind velocity and 5 cm s^{-1} for current velocity, respectively. Compass directions are shown for reference in top-right corner of panel a. Legend for crab concentrations is shown in Fig. 6.

lations failed to predict post-larval blue crab distributions in the southern portion of our study area, where observed post-larval concentrations were relatively high in 2001 (e.g. compare Fig. 9c with observed distributions in Fig. 7).

DISCUSSION

Our study indicates that estuarine hydrodynamics (i.e. non-tidal and tidal flows) coupled with post-larval behavior (nighttime vertical positioning within the water column) drives blue crab dispersal within the northern basin of Pamlico Sound. In this study, post-larval blue crabs were primarily collected at night in surface waters. Nocturnal activity patterns in blue crabs are not surprising, as light inhibits swimming of post-larvae in estuarine water (Forward and Rittschof,

1994), and post-larval crabs move into the water column at the onset of darkness in laboratory experiments (Luckenbach and Orth, 1992) and in other field studies (e.g. Epifanio *et al.*, 1984; Mense and Wenner, 1989). Such behaviors are likely responses to avoid predation by visual predators during the day (Stich and Lampert, 1981).

Although we did not explicitly measure the vertical distribution of post-larval blue crabs near the inlets with respect to the tidal cycle, FTT is a common behavioral strategy employed by many estuarine species (including post-larval blue crabs) to migrate through tidal inlets from the coastal ocean (Boehlert and Mundy, 1988; Forward *et al.*, 2003). The tidal signal in Pamlico Sound diminishes with increasing distance from the inlets (Pietrafesa *et al.*, 1986b), however, making it unlikely that FTT over consecutive nights

Figure 8. End-points of particles released from Oregon and Hatteras Inlets during the wind-only (a), tide-only (b), and combined wind-tide (c) simulations for 2000. Symbol colors represent different cruise dates, with open squares denoting particles released from Oregon Inlet (OI), and filled triangles denoting particles released from Hatteras Inlet (HI). For reference, post-larval blue crab sampling stations are shown (filled blue circles).
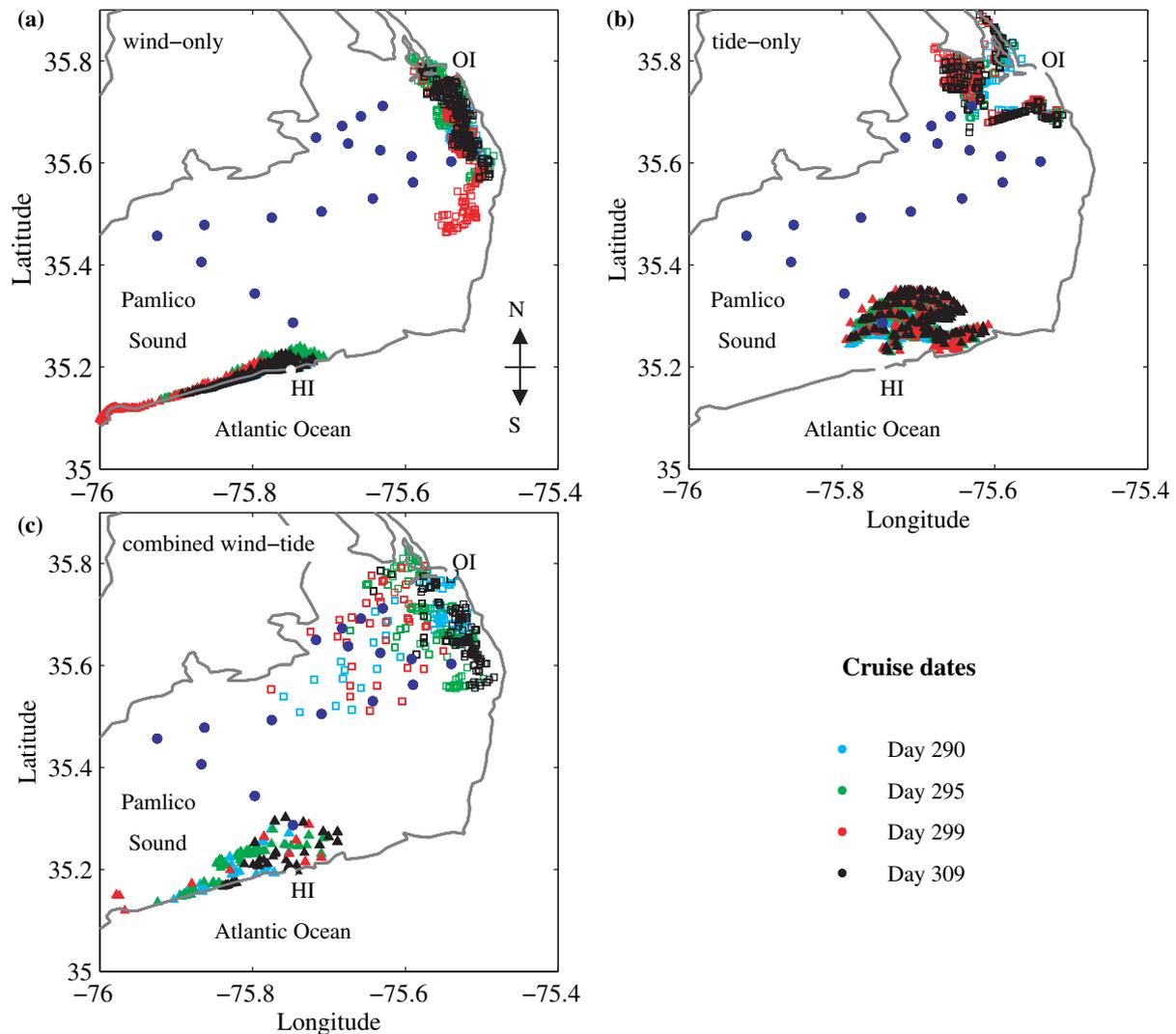
can be used to reach western Sound nursery habitats once organisms are within Pamlico Sound. Indeed, virtual crab (particle) end-point distributions from our tide-only dispersal simulations confirmed that within the 5-day stage duration reported for blue crab post-larvae (Wolcott and De Vries, 1994), across-Sound transport was not possible using tidal currents alone. Although little variability in post-larval duration has been observed in laboratory studies (<±0.4 days: Wolcott and De Vries, 1994), blue crabs may actually be developing faster in the field, as has been documented for other crustacean species (Welch and Epifanio, 1995). Thus, our dispersal simulations, which allow transport to occur over 5 days, likely produce

conservative estimates of blue crab dispersal potential within the northern basin of Pamlico Sound.

Despite the inability of post-larval blue crabs to use FTT to reach western Sound nursery habitats, our dispersal simulations suggest that tidal currents play an important role in transporting crabs at least partway across the Sound. This result was surprising; we expected that post-larval blue crabs would use wind-driven surface currents to mediate dispersal given that circulation within the Albemarle-Pamlico Estuarine System is generally characterized as being driven by the wind (Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1991), and that post-larval blue crabs were predominately collected in surface waters during this

Figure 9. End-points of particles released from Oregon and Hatteras Inlets during the wind-only (a), tide-only (b), and combined wind-tide (c) simulations for 2001. Symbol colors represent different cruise dates, with open squares denoting particles released from Oregon Inlet (OI), and filled triangles denoting particles released from Hatteras Inlet (HI). For reference, post-larval blue crab sampling stations are shown (filled blue circles).
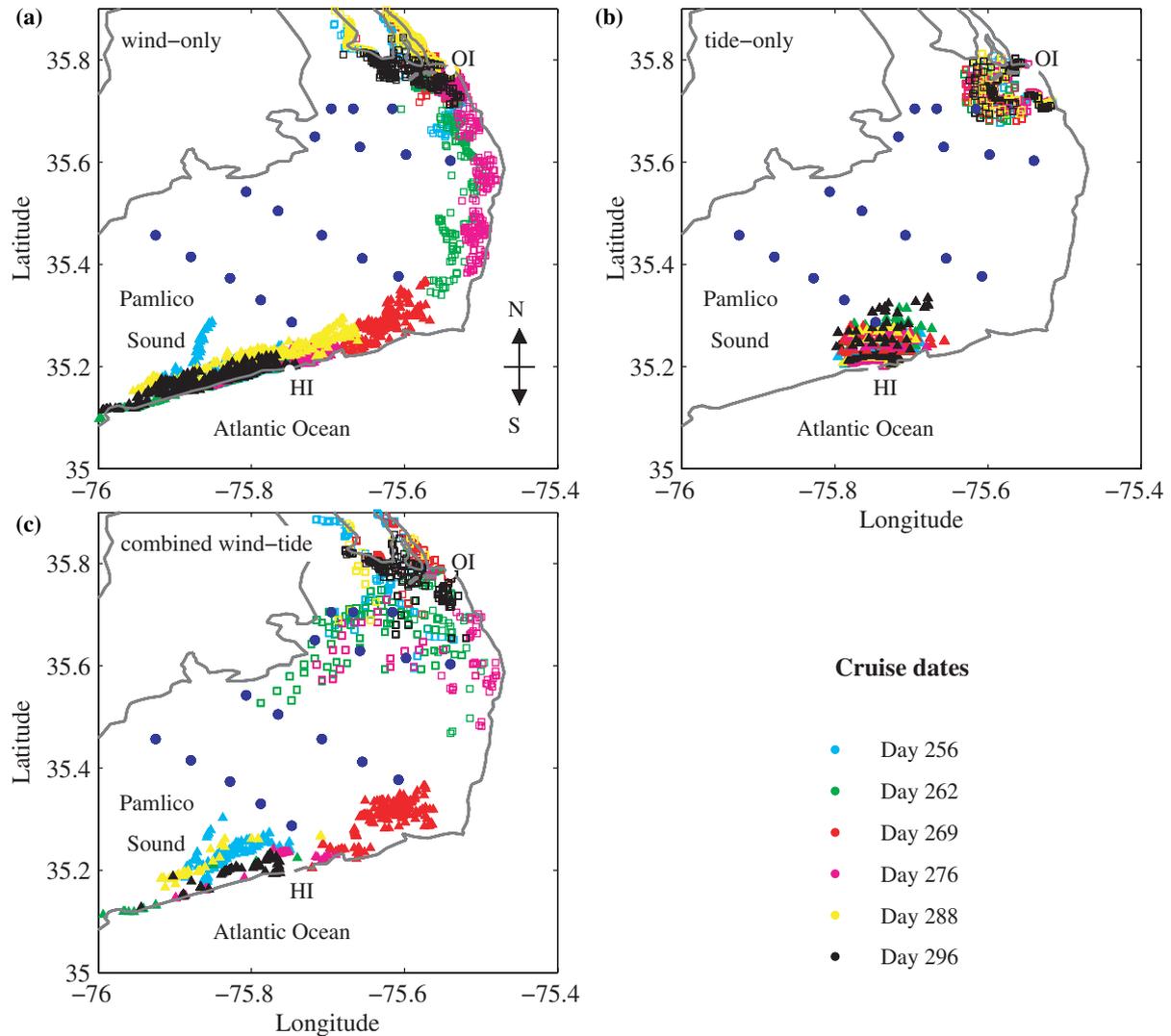
study. Yet, our wind-only dispersal simulations failed to reproduce observed blue crab distribution patterns within the northern basin of Pamlico Sound, suggesting that movement to western Sound nursery habitats from near-inlet source regions is also not possible using wind-driven surface currents alone. Rather, our dispersal simulations indicate that across-Sound transport and dispersal throughout the northern basin of Pamlico Sound only occur when crabs use combined wind- and tide-driven flow fields. Similarly, both wind-driven and tidal transport mechanisms contribute to the estuarine ingress of post-larval crabs and juvenile fish in Oregon (Miller and Shanks, 2004). Furthermore, local wind effects can have important

consequences for dispersal of organisms within estuaries dominated by tidal motions (e.g. blue crabs: Olmi, 1995; polychaetes: Thiébaut *et al.*, 1998). Thus, multiple forcing agents can contribute to the dispersal of organisms within estuaries, and transport of post-larval blue crabs within the northern basin of Pamlico Sound is not simply downstream of the prevailing wind direction.

Dispersal pathways from inlet source regions

Our dispersal simulations suggest that Oregon Inlet is the primary supplier of post-larval blue crabs to the northern basin of Pamlico Sound, as virtual crabs released near Hatteras Inlet rarely dispersed into our

study area, regardless of the flow conditions used in the model. The relative importance of Oregon Inlet as a source of post-larval blue crabs to the region may be a consequence of both the magnitude and alignment of non-tidal and tidal currents at this site. For example, currents at all our hydrographic stations were dominated by non-tidal (i.e. wind-driven) flows, with the exception of Oregon Inlet where non-tidal and tidal currents were of the same magnitude. Near Hatteras Inlet, tidal currents were slightly reduced in magnitude relative to non-tidal currents, but were still relatively strong when compared with tidal currents at the other non-inlet stations. Thus, the stronger combined non-tidal and tidal currents at Oregon Inlet may make this area more favorable for dispersal into Pamlico Sound than Hatteras Inlet. Additionally, due to the relatively short distance between Oregon Inlet and the western shore of Pamlico Sound (~20 km), organisms ingressing through this inlet have a greater probability of reaching western Sound nursery habitats than those ingressing through Hatteras Inlet where the distance to western Sound habitats is ~40 km (Fig. 1a).

A dispersal pathway linking Oregon Inlet to western Sound nursery habitats may be further enhanced by the similar alignment in direction of both non-tidal and tidal currents. General circulation patterns from our current meter records indicate that non-tidal surface currents predominately move in the direction of the wind, as has been observed in previous studies within the Albemarle-Pamlico Estuarine System (Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1991) and other wind-driven systems (Commito *et al.*, 1995). More specifically, during south-westward winds (the most common wind condition during our study), surface currents near Oregon and Hatteras Inlets were almost always directed toward the south-southwest. Such currents promote the dispersal of post-larval blue crabs from Oregon Inlet into our study area, but export post-larvae that originate from Hatteras Inlet out of our study area. Moreover, regardless of wind direction, tidal currents near Oregon Inlet were directly aligned along an axis that connected this inlet with the western Sound near Stumpy Point. In contrast, tidal currents at Hatteras Inlet were aligned north–south, which did not correspond to the northeast–southwest direction of the non-tidal currents. Thus, we propose that the alignment of non-tidal and tidal surface currents between Oregon Inlet and Stumpy Point, especially during south-westward winds, enhances the supply of blue crab post-larvae to the north-west region of Pamlico Sound, where relatively high concentrations of blue crabs were repeatedly observed during our cruises. Post-larval blue crab supply via the

'Oregon Inlet-Stumpy Point dispersal pathway' may also explain why the Stumpy Point region consistently experiences relatively high abundances of later-staged juveniles (Eggleston *et al.*, 2004). Given the evidence of a temporally consistent dispersal pathway between Oregon Inlet and Stumpy Point during our study, future studies are needed to evaluate the relative importance of nursery habitats in these regions in terms of their contributions to adult blue crab population dynamics.

Model considerations

Within the southern portion of our study region (near Hatteras Inlet), our dispersal simulations failed to predict observed post-larval blue crab distributions, suggesting that transport may be influenced by other factors not included in our model. One factor omitted from our model is the influence of wind-driven ocean–estuary exchange through the inlets. Winds can create water-level fluctuations which induce exchanges of water between the ocean and estuary (Queiroga and Blanton, 2004). Along the coast of the Albemarle-Pamlico Estuarine System, winds directed toward the south-west cause water to rise along the seaward-side of the barrier island coastline, and drop along the Sound-side of the coast, producing a pressure gradient force that drives currents through the inlets (Pietrafesa and Janowitz, 1988). More specifically, such wind conditions initiate inwelling of ocean water at Oregon Inlet and cause concurrent outwelling of estuarine water at Hatteras Inlet (Xie and Eggleston, 1999). This inwelling–outwelling dynamic balanced between the inlets changes when winds switch toward the north-northeast, as estuarine water exits from Oregon Inlet and oceanic water enters through Hatteras Inlet (Xie and Eggleston, 1999).

While wind-induced pressure gradients have been observed within our study area following synoptic wind events lasting 2–15 days (e.g. Pietrafesa and Janowitz, 1991), it remains unclear how or if the resulting currents influence across-Sound dispersal. Given that most of our cruises occurred during south-westward winds when inwelling at Oregon Inlet might have enhanced surface currents near this inlet, our dispersal simulations may be underestimating the dispersal potential of post-larval blue crabs ingressing through Oregon Inlet. As such, post-larval blue crabs originating from Oregon Inlet might have the capacity to reach plankton stations not attained by virtual crabs in our simulations (i.e. those within the southern region of our study area). Post-larval blue crabs originating from Hatteras Inlet, however, would have to swim against outwelling currents to reach our study

area. As mean current velocities observed near Hatteras Inlet approach 6.5 cm s^{-1} with maximum velocities exceeding 20 cm s^{-1} (Reyns, 2004), and post-larval blue crabs cannot swim against currents when velocities are 6.3 cm s^{-1} or greater (Luckenbach and Orth, 1992), it is unlikely that Hatteras Inlet would become a source of post-larval blue crabs to our study area if we incorporated wind-driven ocean-estuary dynamics within our hydrodynamic model.

We did not include blue crab swimming behaviors in our simulations, and this omission may also account for some of the discrepancy between observed post-larval crab distributions and virtual crab end-points. Horizontal swimming by the early life stages of fish (Leis *et al.*, 1996; Stobutzki and Bellwood, 1997) and crustaceans (Luckenbach and Orth, 1992; Fernandez *et al.*, 1994) has the potential to influence dispersal patterns. Unfortunately, it remains unclear if directed and sustained swimming by post-larval blue crabs occurs in the field (Luckenbach and Orth, 1992), and therefore, it is difficult to incorporate such behaviors in our particle-tracking algorithm at this time.

While the 3D version of ADCIRC is currently being revised, our hydrodynamic model in its current form provides a first approximation of the dispersal mechanisms and pathways that connect near-inlet source regions and western Sound nursery habitats within the northern basin of Pamlico Sound. The biophysical approach used in this study has allowed us to better understand the degree to which spatially separated nursery habitats are connected by dispersal; such information is critical for making recommendations regarding which nursery habitats should be prioritized for conservation to maintain (or maximize) the production of early juvenile blue crabs and fish within estuarine systems.

ACKNOWLEDGEMENTS

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