ABSTRACT

REYNS, NATHALIE BRIGITTE. Biophysical dispersal dynamics of the blue crab in Pamlico Sound, North Carolina. (Under the direction of David B. Eggleston).

For many species such as the blue crab, *Callinectes sapidus*, successful estuarine recruitment to juvenile nursery habitats is dependent on the biophysical processes experienced during dispersal of the early life stages. The goal of this study was to determine how blue crab primary (postlarval) and secondary (early juvenile) dispersal occurs within a predominately wind-driven estuary, Pamlico Sound, North Carolina, USA. We (1) characterized circulation patterns in Pamlico Sound during the fall blue crab recruitment months over two consecutive years using current meters (2) sampled during multiple 24 h periods to relate spatiotemporal water column distributions of postlarval and early juveniles blue crabs with circulation patterns, and used a hydrodynamic model to recreate dispersal trajectories from eastern (inlet) to western sound nursery habitats and (3) examined the environmental (wind, diel cycle, tidal phase) and biological (ontogenetic, density-dependent) factors that contribute to early juvenile blue crab secondary dispersal from near-inlet nursery habitats. During our study, surface currents responded synchronously to wind-forcing by generally flowing in the same direction as the wind. Particle-tracking simulations suggested that dispersal from Oregon and Hatteras Inlets to across-sound nursery habitats resulted from the combined use of tidal and wind-driven currents. Simulation results and observed crab

distributions further indicated that Oregon Inlet was the primary supplier of postlarval blue crabs (dispersing in surface waters at night) throughout Pamlico Sound, as postlarvae ingressing through Hatteras Inlet were not retained within our study area. Furthermore, Oregon Inlet supplied early juvenile blue crabs (dispersing in bottom waters at night) to northwestern sound habitats, while crabs from Hatteras Inlet dispersed to mid- and eastern-sound regions. Results from our study in near-inlet settlement habitats confirmed the importance of tides to mediating dispersal partway into Pamlico Sound, as early juvenile blue crabs responded to increasing conspecific density in settlement habitats by using flood-tide transport near the inlets to rapidly leave these habitats. Based on our findings, we make recommendations regarding the prioritization of nursery habitats for conservation and fisheries management.

BIOPHYSICAL DISPERSAL DYNAMICS OF THE BLUE CRAB
IN PAMLICO SOUND, NORTH CAROLINA

by

NATHALIE BRIGITTE REYNS

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PERSONAL BIOGRAPHY

Nathalie Reyns was born on June 9, 1972 in Louvain Belgium, but spent most of her childhood growing up in Arizona. Despite living in the desert, frequent family vacations to the beaches in Mexico and California exposed Nathalie to the marine environment, and at age 15 she became a certified diver. Later, it was her experiences while an undergraduate at the University of Arizona that helped promote her continued interest in the marine sciences, as Nathalie took frequent trips to the Sea of Cortez in Mexico where she led dive trips and participated in several marine ecology field courses. In addition, Nathalie's experience as an R.E.U. student at the Shannon Point Marine Center in Anacortes, Washington began to focus her interests on marine larval ecology. Upon her 1995 graduation with a Bachelor of Science degree in Ecology and Evolutionary Biology, she entered the graduate program at the Marine Sciences Research Center (SUNY at Stony Brook). There, she completed her Master's degree in Marine Environmental Sciences in 1998 after examining the biological and physical factors influencing the settlement of tropical crabs to Barbados, West Indies. In an effort to broaden her horizons beyond the tropics, Nathalie enrolled in North Carolina State University in 1999 to study blue crabs in a local estuarine system. While her time in North Carolina has produced the requisite appreciation for Carolina barbeque, she continues to drink her iced-tea unsweetened.

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In particular, I would like to thank my advisor, Dave Eggleston, for his continued support and guidance, and for keeping me focused on the "light at the end of

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CHAPTER 1

CIRCULATION CHARACTERISTICS OF PAMLICO SOUND, NORTH CAROLINA

ABSTRACT

Determining how physical forcing mechanisms drive circulation patterns can have important implications for the transport of organisms that use estuarine nursery habitats. We examined how the circulation of Pamlico Sound, North Carolina, USA responded to wind-forcing during the fall months (September-October, in 2000 and 2001), when commercially and ecologically important blue crabs (*Callinectes sapidus*) recruit to the estuary from the continental shelf. To examine spatial variability in currents, five InterOcean S4 electromagnetic current meters were deployed along the periphery of the northern basin of Pamlico Sound in near-surface waters, and one current meter was deployed near-bottom. Observed current meter data were used to validate a 3D circulation model developed for Pamlico Sound. Current meters were also configured to measure salinity and temperature. In addition, spatial variation in vertical distributions of salinity and temperature were measured synoptically during multiple cruises at 17 stations evenly-spaced across Pamlico Sound using a CTD. Wind data collected near Cape Hatteras were related to current and salinity patterns.

During both years of our study, winds were directed towards the southwest or towards the northeast. In general, surface currents responded synchronously within 1 d or less, to the north-south wind component. Southwestward-directed winds increased the inflow of salty, coastal water through Oregon Inlet and directed currents within Pamlico Sound towards the south. Northeastward-directed wind events were more variable in their influence on surface currents; however, for bottom currents, there was an inflow of salty water through Hatteras Inlet with northward transport in the middle of

the sound. Thus, larvae residing in surface waters are most likely to reach nursery habitats located within our study area when ingressing through Oregon Inlet, while those residing in bottom waters might be transported to such habitats if ingressing through Hatteras Inlet. Determining how organisms recruiting to Pamlico Sound nursery habitats are influenced by hydrodynamic processes ultimately entails identifying the inlet sources of these larvae, as well as understanding how larvae behaviorally respond to their estuarine surroundings.

INTRODUCTION

Most estuaries have traditionally been described as having a two-layered mean gravitational circulation with net outflow of low salinity water in the surface layer and net inflow of saltier (oceanic) water in the bottom layer. This mean circulation, however, can be altered by physical forcing mechanisms driven by tides, river outflow, terrestrial run-off, wind, as well as the geomorphology of the estuary (Dyer, 1997). It is widely accepted that the relative importance of different physical forcing mechanisms varies with respect to estuary classification. For example, in shallow coastal lagoons (defined as a body of water separated from the ocean by a series of barrier islands with inlets that allow estuary-ocean mixing), forcing mechanisms that operate at low frequencies (such as wind) are of particular importance to circulation patterns, as exchange with the coastal ocean via high-frequency tidal motions are often reduced by relatively narrow inlets (Janzen and Wong, 1998). The focus of this chapter is to examine how wind influences water circulation within the Albemarle-Pamlico Estuarine System (APES), the largest shallow lagoonal estuary in the United States (Fig. 1).

The APES is enclosed by a barrier island chain split by three main, relatively narrow (~1 km) inlets: Oregon, Hatteras, and Ocracoke Inlets (Fig. 1). Pamlico Sound comprises the largest component of the APES, and is approximately 120 km long (along NE-SW axis), 40 km wide (along NW-SE axis) and has a mean depth of 4.5 m. Sources of freshwater input include the Neuse and Pamlico River systems in the south and western regions of Pamlico Sound, as well as Albemarle Sound to the north. Shoaling occurs in the vicinity of the inlets and rivers, and across Pamlico Sound at Bluff Shoal,

which extends east to west from Ocracoke Inlet and bisects Pamlico Sound into two basins (Fig. 1).

Circulation within Pamlico Sound is predominately wind-driven, but may be influenced by other physical forcing mechanisms including tides, and riverine and freshwater inflow (Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1991). While the inlet regions experience semi-diurnal tides driven by the M_2 tidal constituent, tidal influence quickly diminishes with distance from the inlets and becomes negligible ($\pm$ 5 cm/s) within the main body of Pamlico Sound (Pietrafesa *et al.*, 1986b). During years with average rainfall, mean current velocities due to freshwater runoff and riverine discharge are also minimal (~ 3 cm/s) (Pietrafesa *et al.*, 1986b). Thus, tidal and freshwater effects appear relatively unimportant in driving circulation patterns within Pamlico Sound. Wind forcing, however, is believed to be the primary driver of sea level changes resulting in pressure gradient forces that set up circulation within Pamlico Sound (Giese *et al.*, 1979; Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1991). A conceptual model of wind-driven circulation in the APES (Pietrafesa and Janowitz, 1991) suggests that currents respond directly to wind forcing by flowing downwind at all depths. This downwind flow raises sea level at the downwind shore of the sound, while lowering sea level at the upwind shore. If the wind field persists in the same direction for 24 to 36 h, a strong pressure gradient develops, causing near bottom currents to flow in the opposite direction of the wind (i.e., upwind). Thus, although Pamlico Sound is a relatively shallow system, bottom currents in the deeper areas of the sound may be in opposition to surface currents. This conceptual model of wind-driven

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circulation is also supported by a numerical circulation model that depicts the response of the APES exposed to persistent (over 5 d) wind stress (Xie and Eggleston, 1999).

Characterizing the circulation patterns within Pamlico Sound is of particular importance as hydrodynamic processes influencing the delivery of larvae to nursery areas is generally believed to be a critical component to determining year-class strength (e.g. see Rothschild, 1986; Werner *et al.*, 1997 for reviews). Many commercially-important species including Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), flounder (*Paralichthys* spp.), blue crabs (*Callinectes sapidus*) and penaeid shrimp (*Penaeus* spp.) develop as larvae offshore before ingressing through the inlets and settling to nursery habitats located along the periphery of the northern basin of Pamlico Sound (Ross and Epperly, 1985; Epperly and Ross, 1986; Etherington and Eggleston, 2000; 2003). Despite the recognized importance of understanding hydrodynamic processes within Pamlico Sound, circulation patterns have not been extensively examined in the region surrounding these nursery habitats. Rather, pressure sensors, tide gauges, and current meters have been deployed at select sites within Pamlico and Albemarle Sounds (e.g. Singer and Knowles, 1975; Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1991). Moreover, predictions of basin-wide circulation using hydrodynamic models (e.g. Pietrafesa *et al.*, 1986b; Xie and Eggleston, 1999; Xie and Pietrafesa, 1999) remain untested. Therefore, the main objective of this study was to use a concentrated current meter deployment effort to examine the spatial variability of currents within the northern basin of Pamlico Sound under different wind conditions,

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to ultimately understand how organisms recruiting to Pamlico Sound are transported to estuarine nursery habitats.

While most wind variability is driven by synoptic wind events lasting two to fifteen days (Pietrafesa *et al.*, 1986b), the mean wind fields that drive Pamlico Sound circulation change seasonally. Winter conditions are characterized by winds blowing towards the southwest and an increased storm frequency, while summer conditions are characterized by winds blowing towards the northeast (Weisberg and Pietrafesa, 1983). Fall and spring are considered transitional periods as winds shift between these two primary directions. Given the two predominant wind directions (i.e., towards the southwest and northeast), we were interested in testing the following hypothesized circulation scenarios (assumed to develop when winds blow in the same direction for at least 24 h): (1) Winds blowing towards the southwest will push surface currents (along the coast and within Pamlico Sound) in the same direction as the wind, causing a set-up of sea level along the coast near Oregon Inlet and a set-down of sea level along the sound-side of the eastern shore of Pamlico Sound, thereby producing a divergence that drives an inflow of water from the ocean through Oregon Inlet (Fig. 2A). Furthermore, slight Ekman veering towards the west will cause a set-up of sea level along the western shore of Pamlico Sound, producing a northeastward bottom return flow (preferentially within the deeper mid-sound region) (Fig. 2A). (2) Winds blowing towards the northeast will push surface currents (along the coast and within Pamlico Sound) in the same direction as the wind, causing a set-up of sea level along the coast near Hatteras Inlet and a set-down of sea level along the sound-side of the southeastern shore of

Pamlico Sound, thereby producing a divergence that drives an inflow of water from the ocean through Hatteras Inlet (Fig. 2B). Slight Ekman veering towards the east will cause a set-up of sea level along the eastern shore of Pamlico Sound, producing a southwestward bottom return flow (preferentially within the deeper mid-sound region) (Fig. 2B).

METHODS

Hydrographic data

To characterize the circulation in Pamlico Sound, we deployed six InterOcean S4 electromagnetic current meters at five locations during two periods: 17 September – 8 November 2000 and 31 August – 30 October 2001 (Fig. 1). These time intervals were selected to coincide with the peak blue crab recruitment months (i.e., September-October) in North Carolina (Etherington and Eggleston, 2003), with the eventual goal of relating circulation patterns to the primary and secondary dispersal of blue crabs within Pamlico Sound (see Chapters 2 & 4). Current meter deployment locations were concentrated in the northern basin between Oregon and Hatteras Inlets (Fig. 1).

We were primarily interested in measuring surface currents as we expected postlarvae ingressing from the coastal ocean (i.e., primary dispersal) to remain in surface waters, and early juvenile blue crabs to move into the surface layer of the water column when undergoing secondary dispersal. Therefore, current meters were deployed near-surface (1 m below the surface) at all locations; however, we also positioned a current meter near-bottom (1 m above bottom) at Hatteras Inlet to determine the

relationship between surface and bottom flow (e.g., shear, flows in opposite directions, etc.). All current meters were configured to record current speed and direction, conductivity, temperature, and pressure for 2 min every 20 min. Further, to minimize the effects of biological fouling, instruments were cleaned weekly by divers using SCUBA.

To relate circulation patterns to wind-forcing, we obtained hourly wind speed and direction data from the State Climate Office of North Carolina at North Carolina State University (collected by NOAA National Weather Service at Hatteras, NC: 35.23˚N, 75.62˚W; Fig. 1). Using wind data from only one location is not likely to compromise our ability to make comparisons between circulation patterns and the wind, as wind fields are spatially coherent over the extent of our study area (e.g. Weisberg and Pietrafesa, 1983). Wind data from September-November 2000 and 2001 were used to coincide with the current meter deployment periods.

To clarify whether salinity (S) and temperature (T) gradients exist within Pamlico Sound, we measured vertical stratification in S and T throughout the sound. Previous work indicates that vertical stratification is minimal due to mechanical wind mixing within the main body of Pamlico Sound (Roelofs and Bumpus, 1953), and when stratification occurs it may be spatially and temporally variable (Pietrafesa *et al.*, 1986b). Although the NC Division of Marine Fisheries measures temperature and salinity at 52 randomly chosen trawl stations in Pamlico and Croatan Sounds and the Neuse and Pamlico Rivers each May and June (Eggleston *et al.*, 2004), we are unaware of any high resolution (in space and time) S and T data collections within Pamlico

Sound. Thus, we used a CTD to obtain water column profiles at 17 evenly-spaced stations along four transects crossing the northern basin of Pamlico Sound (Fig. 1B & C). CTD casts were performed using a Seabird SBE-19 CTD, and all 17 stations were sampled within an 8 h period. The CTD was configured to record conductivity, temperature, and density at 10 cm depth increments, and was lowered at a constant rate (~ 0.5 m/min). To determine if vertical profiles changed over a 24 h period, we sampled all stations during the day and then re-sampled all stations at night. A total of ten cruises were completed during the time the current meters were deployed: four day-night cruises in 2000, and during 2001, there were two day-night cruises and four nighttime-only cruises.

Hydrographic model

In addition to deploying current meters to examine the circulation during the fall blue crab recruitment months, we also developed a 3D hydrodynamic model to simulate circulation patterns on a relatively large spatial scale within Pamlico Sound. This model was subsequently used to recreate blue crab dispersal pathways in Chapters 2 and 4, and therefore, validation of the model with observed currents is presented here.

Pamlico Sound circulation was simulated using a nonlinear, finite-element barotropic 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 APES domain shown in Figure 1A. We parameterized the model with a Mellor-Yamada level 2.5 turbulent diffusion closure, a

free surface roughness of 0.033, and a bottom roughness 0.02. 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

comprised 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. In the

vertical domain, current velocities were computed over 11 variable depth layers. We

assumed that wind fields were spatially uniform over the entire APES domain, and

therefore, forced the model with hourly wind velocities measured at the Cape Hatteras

Meteorological Station (Fig. 1A). A 1 d ramp was applied to wind forcing, and the

model was allowed a 3 d spin-up time before comparisons were made between

predicted and observed currents (see 'Hydrodynamic model validation' below). Since

we were interested in specifically examining the potential for wind-driven flow fields to

generate across-sound dispersal pathways, tidal forcing was not included, and we

assumed the APES to be spatially isolated from the coastal ocean (i.e., inlets not open to

ocean). Furthermore, baroclinic forcing was ignored as the water column within

Pamlico Sound is typically well-mixed (see 'Results' below). To prevent elevation

errors, the modeling time step was reduced to 30 sec with currents outputted at 20 min

intervals to match the recording interval set on our current meters. To correspond with

the current meter deployment dates, model simulations ran for 57 d in 2000 and 64 d in

2001.

Data processing and analyses

Current and wind velocity data were decomposed into u (east-west) and v (north-south) components and analyzed using standard time-series analysis methods. First, periodicity in the current meter and wind records were examined using power spectral analysis following the steps outlined in Emery and Thomson (2001): Data records were de-meaned and de-trended, split into six evenly-sized pieces and smoothed with a Hanning window prior to computing the power spectra and 95 % confidence intervals. In addition, since the emphasis of this study was to examine how wind influences the circulation patterns within Pamlico Sound, we separated the low-frequency (subtidal) currents from the flow due to tides using a lowpass filter with a 40 h cutoff period. Finally, we used time domain Empirical Orthogonal Function (EOF) analysis to examine the temporal (over the duration of current meter deployment periods) and spatial (over all current meter stations) response of subtidal currents to wind-forcing. EOF analysis allows the variability of multiple data series to be described in terms of orthogonal functions known as statistical modes, whose patterns can then be related to possible physical forcing mechanisms (Preisendorfer, 1988; Emery and Thomson, 2001). For example, although it is clear that currents in Pamlico Sound respond to wind forcing (e.g. Pietrafesa *et al.*, 1986b), EOF analysis allowed us to examine the combined response of currents measured at multiple stations to winds.

During both years of our study, current meters were knocked free of their mountings, producing gaps in our time series (Table 1 and Table 2). Thus, we had to pick time intervals during which the majority of current meters were deployed

simultaneously to examine the temporal and spatial synchrony of the currents using EOF analysis. In 2000, temporal and spatial modes were calculated using data from five stations collected between 4 October – 7 November: Oregon Inlet, Stumpy Point, Chicamacomico, and Hatteras Inlet surface and bottom; current meter data from Gibbs Shoal was excluded from the analysis due to large periods of missing data (Table 1). In 2001, we used data collected between 27 September – 30 October so that all stations could be used in the analysis; we included Gibbs Shoal because the number of missing days at this station was relatively short (~ 5 d, Table 2).

To test our hypothesized circulation scenarios during southwestward and northeastward-directed winds (Fig. 2), we picked dates during both years of our current meter deployment periods when winds blew in a particular direction for at least 24 h. Although within 10 h of the onset of steady winds (blowing in the same direction), Pamlico Sound surface currents may start to respond by flowing in the same direction as the wind, pressure gradients causing flow reversals in bottom currents are predicted to develop when winds prevail for 24-36 h (Singer and Knowles, 1975; Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1991). Average current vectors were calculated at each station during time intervals greater than 24 h to examine the spatial response of currents to specific wind events, and were compared with our hypothesized current patterns (Fig. 2).

We examined CTD data collected during our cruises for evidence of vertical and horizontal stratification within Pamlico Sound by producing contour plots of the salinity and temperature profiles at each station along a cruise transect. Given that stations were

separated by ~ 6 km along each transect, we used linear interpolation, over 10 cm depth increments in the vertical, to fill salinity and temperature contours in the regions between stations. Therefore, our contour plots represent an approximation of the salinity and temperature fields across Pamlico Sound, but should still provide an indication of the prevalence of salinity and temperature gradients.

Hydrodynamic model validation

Modeled near-surface (0.8 depth layer) currents closest to our current meter deployment locations were picked to compare with observed surface currents, whereby Oregon Inlet corresponded to node # 4497 (on our high resolution grid), Stumpy Point corresponded to node # 4709, Chicamacomico corresponded to node # 5967, Hatteras Inlet corresponded to node # 7908, and Gibbs Shoal corresponded to node # 7255. We also used the modeled near-bottom (-0.8 depth layer) currents at Hatteras Inlet to compare with the bottom currents measured at this site.

Similar to data processing of the observed currents, modeled currents were decomposed into u- and v-components, and averaged into hourly records. We also applied a 40 h lowpass filter to the modeled current records so that cross-correlation analysis could be used to compare flow patterns with lowpass-filtered observed currents. In addition, to determine how well modeled currents recreated the variance of observed flows, we calculated the principal axes of variance where velocity fluctuations are at a maximum and minimum along the major and minor axes, respectively (Emery and Thomson, 2001). Furthermore, EOF analysis (as described above) was used to

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examine the temporal and spatial synchrony of modeled currents in response to wind forcing, and results were compared with the first EOF modes calculated using the observed currents.

RESULTS AND DISCUSSION

Temporal wind and current patterns

Despite temporal gaps in our current records, current meters were deployed at most stations for at least 50 d during both years (Table 1 and Table 2), allowing comparisons to be made with the wind. Examination of the vector diagrams of wind and subtidal (lowpass-filtered) currents indicated that surface currents generally flowed in the same direction as the wind (Fig. 3 and Fig. 4). The wind field was more variable in 2001 than 2000, with reversals in direction occurring approximately every five days (compare Fig. 3A with Fig. 4A). Surface currents at Oregon and Hatteras Inlet, and to a lesser degree at the other stations, tracked these reversals (Fig. 3 and Fig. 4). In some instances, surface currents did not reverse direction, but velocities became reduced in magnitude (see Oregon Inlet Days 281-303, Fig. 4B). Surface currents near the inlet sites likely had the best agreement with the wind record (over the western sound sites) as inflow and outflow exchanges with the coastal ocean are strongly linked with the wind (Xie and Eggleston, 1999). Regardless, surface currents from all stations were generally similarly directed over time.

With regard to bottom currents, we expected that in the deeper portions of Pamlico Sound, surface and bottom currents would flow in opposite directions, such

that surface flow driven by the wind would be compensated at depth by a return flow (Pietrafesa and Janowitz, 1991). While we only measured bottom currents at one station (Hatteras Inlet), bottom currents generally showed similar temporal patterns in direction as surface currents measured at the same station (Fig. 3E & F and Fig. 4E & F). A reduction in the magnitude of the bottom currents at Hatteras Inlet relative to those at the surface was only evident during periods of wind direction reversals (see reversals around Days 279, 289, and 299 in 2001, Fig. 4E & F). Contrary to expectations, bottom currents flowing in opposition to surface currents were apparent during one time interval in 2000: on Day 286, winds had a southward component (Fig. 3A) causing southward-flowing surface and bottom currents at Hatteras Inlet (Fig. 3E & F), two days later, bottom currents reversed and flowed towards the north for approximately four days (see Days 288-292, Fig. 3F), before reversing back towards the south. During the same time interval, both winds (Fig. 3A) and Hatteras Inlet surface currents (Fig. 3E) remained directed towards the south. In 2001, surface and bottom currents at Hatteras Inlet only flowed in opposition for brief periods (~ 24 h or less) following wind reversals (e.g. compare Day 268 in Fig. 4E with Days 268-269 in Fig. 4F), suggesting that it takes longer for bottom currents to respond to changes in the wind field than surface currents.

The fact that bottom currents were rarely observed flowing in opposition to surface currents may be because of our lack of spatial coverage of near-bottom current measurements (only one instrument deployed in this depth layer). Although we picked the deepest of our stations (i.e., Hatteras Inlet) to deploy the bottom instrument, this

instrument may not have been in the right location to measure bottom current reversals; such currents probably develop in the deeper mid-sound region running along the main axis of Pamlico Sound (see Fig. 1 for bathymetry). Thus, in this study, we are not able to definitively resolve the bottom circulation patterns using our current meter data (although see salinity results below for additional inferences on bottom circulation).

Periodicity in winds and currents

Wind effects

Spectra from wind data collected in Pamlico Sound during other studies show peaks in energy related to (1) seasonal changes, (2) the synoptic frequency band (2-15 day range), and (3) diurnal sea breeze (24 h) (Pietrafesa *et al.*, 1986b). Although our study was not conducted over a long enough time period to examine seasonal wind effects, we also observed energy peaks in winds at low frequencies (periods greater than 2 d) and around 24 h in our wind spectra (Fig. 5A and Fig. 6A). Similar energy peaks in the current spectra were also evident (Fig. 5 and Fig. 6), consistent with the notion that currents respond to wind forcing in Pamlico Sound.

In the synoptic wind frequency band (~ 2 d and greater), our results indicate that the v-component (north-south) of the currents dominates over the u-component (east-west) at all stations, with the exception of Hatteras Inlet surface and bottom records in 2000, Hatteras Inlet bottom records in 2001, and Gibbs Shoal records during both years (see Fig. 5 and Fig. 6). The dominance of the north-south component in the current

records is not surprising, as the wind and currents were mainly directed southward with occasional flow reversals directed towards the north (Fig. 3 and Fig. 4).

The diurnal sea breeze in Pamlico Sound is aligned slightly across-sound, with thermal winds blowing onshore towards the NNW during the day, and blowing offshore towards the SSE at night (Pietrafesa *et al.*, 1986b). Peaks in energy associated with the sea breeze (24 h) were evident in our current spectra, predominately at non-inlet stations such as Gibbs Shoal (Fig. 5E and Fig. 6E). While a diurnal signal is present in nearly all of the current spectra (see black lines, Fig. 5 and Fig. 6), Gibbs Shoal may respond most strongly to the sea breeze given its proximity to the mainland. A diurnal period in the Stumpy Point current spectra was also present, but stronger in the v-component (north-south) than the u-component (east-west) (Fig. 5C and Fig. 6C). There is likely more energy in the v-component of the currents in the diurnal frequency, because sea-level at Stumpy Point fluctuates diurnally in response to the north-south component of the wind (Pietrafesa *et al.*, 1986b). Thus, the diurnal sea breeze may induce some water motions within Pamlico Sound, particularly in the north-south currents along the western sound.

Tidal effects

As expected during both years, spectra of the current meter records near the inlets revealed energy peaks associated with the M_2 (12.42 h) semi-diurnal tidal constituent (Fig. 5B, F & G and Fig. 6B, F & G). Energy at this peak was more than an order of magnitude greater at Oregon and Hatteras Inlets than at all other current meter stations, both on the eastern (Chicamacomico) and western shores (Stumpy Point and Gibbs

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Shoal) of Pamlico Sound (Fig. 5 and Fig. 6). Our results are supported by observations within the APES that show the M_2 signal prevailing near the inlets, and rapidly diminishing as distance from the inlets increases (Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1991). Other tidal constituents may be contributing to energy in the current spectra, particularly at peaks ~ 24 h. While such peaks are likely partly related to the sea breeze (as discussed above), they may also result from diurnal tides.

Potential problems with instruments

Examination of the current velocity spectra also reveals potential discrepancies in the current meter data collected at our Hatteras Inlet station. For example, spectra from the Hatteras Inlet current meters failed to exhibit the typical rapid "roll-off" of energy with increasing frequency, as evident in the u-component (east-west) spectra from both surface and bottom instruments in 2000 (Fig. 5F & G). Although the v-component (north-south) showed some decreasing energy with increasing frequency, the u-component spectral energy remained relatively flat with respect to frequency when compared with the other spectra (Fig. 5). Moreover, in 2001, while both u- and v-components of the Hatteras Inlet spectra were better aligned with one-another at both depths (surface and bottom instruments), high-frequency (4 h or less) energy was still prevalent in the records (Fig. 6F & G). One possible explanation for these patterns includes simultaneous instrument failure; however, it is unlikely that two separate instruments, both of which were calibrated at the manufacturer prior to deployment, would record similar erroneous patterns. In addition, the same instruments were

deployed following this study and showed no such discrepancies in the data when compared to data collected by other instruments (J. Epps, NCSU, personal observation). Alternatively, the piling on which we deployed these instruments may have oscillated or vibrated at high frequency in response to the high current velocities experienced at this site (see Table 1 and Table 2 for Hatteras Inlet maximum current velocities). While a definite explanation remains elusive at this time, we believe that the data collected at Hatteras Inlet remain of value for two reasons. First, 40 h lowpass-filtered subtidal currents at Hatteras Inlet exhibited similar temporal patterns as those currents measured at our other stations (Fig. 3 and Fig. 4). Furthermore, our observed Hatteras Inlet currents were in good agreement with currents predicted at this location by a 3D hydrodynamic model for Pamlico Sound (see 'Hydrodynamic model' below). Therefore, we included Hatteras Inlet currents in our temporal and spatial EOF analyses and comparisons of circulation patterns with hypothesized flows during specific wind events (see below).

Temporal and spatial synchrony of currents

EOF analysis was used to examine the temporal and spatial synchrony of currents in response to wind forcing. We focused our analysis on the first EOF mode due to the difficulty in relating additional modes to physical forcing mechanisms (Emery and Thomson, 2001), and because during both years, the first EOF mode explained a relatively high percentage of the variance in the current velocities. In 2000, the first EOF mode for the u- and v-components accounted for 50 % and 47 % of the variance in

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current velocities, respectively. In 2001, variances were 39 % (u-component) and 53 % (v-component). Furthermore, the first temporal EOF modes were in good agreement with the u- and v-components of the wind (Fig. 7 and Fig. 8). In particular, the v-component EOF clearly tracked the wind v-component during both years (Fig. 7B and Fig. 8B). The u-component EOF also appeared to be in better agreement with the v-component of the wind velocity than the u-component wind velocity, especially in 2001 (Fig. 7 and Fig. 8). This dependence of the temporal EOF modes on the v-component of the wind velocity suggests that the currents in Pamlico Sound are more responsive to north-south winds than east-west winds. Likewise, water level fluctuations within the northern basin of Pamlico Sound are related to the north-south component of the wind (Pietrafesa and Janowitz, 1991).

In addition to responding to the north-south component of the wind velocity, peaks in the u- and v-component EOFs lagged those of the wind by a few hours in 2000 and 2001 (Fig. 7 and Fig. 8). This lag likely reflects the time it takes for circulation to set-up within Pamlico Sound, which can range between 10-36 h (Singer and Knowles, 1975; Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1991).

Spatial representation of the first EOF mode indicates that currents within Pamlico Sound are synchronous in their response to wind forcing, with mean flows at all stations directed towards the south during both years (Fig. 9). The relative magnitude of the current vectors at Hatteras Inlet suggest that near-bottom currents are slightly reduced in magnitude than those at the surface, although both surface and bottom mean currents were aligned in the same direction (Fig. 9). A reduction in bottom currents

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relative to those at the surface is consistent with the dissipation of current velocities with depth due to friction.

In addition to being directed towards the south, currents at all stations except for Chicamacomico also had a westward component to flow (Fig. 9). Conversely, currents at Chicamacomico had an eastward component to flow during both years, although the relative magnitude of the Chicamacomico vector was much smaller in 2000 when winds were consistently blowing towards the south (e.g. barely visible in Fig. 9A) than in 2001 when winds were more variable (Fig. 9B). The southeastward flow observed at Chicamacomico in comparison to southwestward currents observed at all other stations, may reflect spatial shearing in the u-component of the currents along the eastern shore of Pamlico Sound (C. Cudaback, NCSU, personal communication). In general, however, currents throughout the northern basin of Pamlico Sound appear temporally and spatially synchronous in their response to wind-forcing.

Circulation patterns with respect to wind events

Pamlico Sound circulation is predicted to take 10-36 h to set-up at the onset of persistent winds (Singer and Knowles, 1975; Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1991). During our fall study period, winds blowing towards the southwest were dominant over winds blowing towards all other directions (Chapter 2). In addition, southwest-directed winds had an average duration of ~ 22 h during both years, northeast-directed winds lasted for ~ 10 h, and southeast- and northwest-directed winds were generally shorter than 10 h (Fig. 10). Therefore, during our fall field season,

southeastward and northwestward wind events were not of sufficient duration to influence the circulation dynamics during the fall months (Fig. 10). Conversely, the relatively high frequency and long duration of southwestward and northeastward wind events provided adequate time for the circulation to develop (Fig. 10); therefore, we compared circulation patterns under these two contrasting (southwestward and northeastward) wind regimes.

To compare circulation patterns during southwestward and northeastward wind events, we picked time intervals when winds blew continuously in one direction for at least 24 h. During our study period, southwestward wind events lasting 24 h or more occurred five times in 2000 (min. duration = 55 h, max. duration = 131 h, mean duration = 83 h), and six times in 2001 (min. duration = 37 h, max. duration = 70 h, mean duration = 58 h). Consistent with our predictions under southwestward winds (Fig. 2A), currents were directed southward with the wind at all stations, except Gibbs Shoal in 2000 (Fig. 11A & B). It is not clear why current patterns at Gibbs Shoal changed between years, but may be due to the fact that this instrument was only deployed for a short time interval in 2000 (only 3 out of 5 wind events recorded). At Hatteras Inlet, surface and bottom currents were aligned in a similar direction, with no evidence of bottom currents flowing in opposition to surface currents (see 'HI', Fig. 11A & B).

Northeastward wind events greater than 24 h in duration were not as frequent as southwestward wind events. In 2000, northeastward wind events lasting 24 h or more only occurred once (duration = 70 h), while in 2001, occurred four times (min. duration = 24 h, max. duration = 97 h, mean duration = 45 h). Because of the relative few

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number of northeastward events to compare, current patterns were not as clear as during southwestward winds. For example, currents at Chicamacomico showed two distinct patterns, with flows directed towards the west or southwest (see 'CH', Fig. 12B). At Stumpy Point, currents were directed towards the northeast, east, southwest and southeast (see 'SP', Fig. 12B). Of consequence, however, is the observation that only during the northeastward wind event captured in 2000, were current vectors aligned in the same direction as the wind (Fig. 12A). In 2001, the response of the currents to northeastward wind events was more variable, and currents were often directed towards the south despite the northward wind component (Fig. 12B). Furthermore, surface and bottom currents at Hatteras Inlet were not aligned in the same direction, as was the case during southwestward wind events (see 'HI', Fig. 12B). Thus, our hypothesis that northeastward winds would cause currents to flow towards the north was not consistently supported (Fig. 2B). Conversely, our hypothesized flow predictions (Fig. 2) matched observed surface current patterns under southwestward winds during both years, but only during one northeastward wind event in 2000. To better understand the circulation patterns during northeastward winds more wind events of sufficiently long duration are needed.

Hydrodynamic model

Using ADCIRC, modeled currents recreated the variances in surface currents observed at all sites except Stumpy Point (SP) during both years (Fig. 13). The discrepancy between surface current variances at Stumpy Point (Fig. 13) is likely due to the poor fit

between the modeled and observed u-component of the currents at this site (Fig. 14 and Fig. 15, Table 3). Given the relatively high and statistically significant correlations between the modeled and observed u- and v-components at all of the other sites, including the SP v-component (Table 3, see also Fig. 14 and Fig. 15), model simulations using observed winds from Cape Hatteras are capable of reproducing observed surface currents within Pamlico Sound. ADCIRC has also produced wind-driven 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).

EOF analysis using the modeled currents produced similar results as the EOF analysis using observed currents (compare Fig. 7 with Fig. 16 and Fig. 8 with Fig. 17). During both years, the first temporal EOF modes were in good agreement with the u- and v-components of the wind (Fig. 16 and Fig. 17) and explained a relatively high percentage of the variance in current velocities. For example, in 2000, the first EOF mode for the u- and v-components accounted for 95 % and 84 % of the variance in current velocities, respectively, while in 2001, variances were 93 % (u-component) and 66 % (v-component). The first spatial EOF modes for both years also indicated that modeled currents were synchronous in their response to wind forcing. Mean modeled flows during both years were directed southward (as with the first spatial EOF mode of observed currents), although modeled surface currents at Stumpy Point had a more eastward flow than the observed currents at this site (compare Fig. 18 with Fig. 9). Generally, modeled surface currents throughout Pamlico Sound responded similarly to wind-forcing as observed surface currents.

Potential sources of error accounting for differences between our modeled and observed currents, includes the use of a spatially uniform wind field in our hydrodynamic model. Using wind data from one location is unlikely to be a large source of error, however, since 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; Blanton *et al.*, 1989). Further, in our model which used one source of wind data (Cape Hatteras), only one component of observed and predicted currents at Stumpy Point was in poor agreement. Stumpy Point is located along the western sound and experiences a southward freshwater flow due to riverine discharge and freshwater runoff from Albemarle Sound (Pietrafesa and Janowitz, 1991). While wind mixing prevents vertical salinity gradients from developing (see 'Spatial and temporal salinity patterns' below), horizontal salinity gradients may exist from the western (fresher) to eastern (saltier) regions of the sound (Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1991). Thus, the inclusion of baroclinic forces might further improve our circulation model predictions at Stumpy Point, especially during years with high freshwater outflow. Nonetheless, flow fields similar to those that we observed have been produced with a baroclinic model of the APES (Xie and Eggleston, 1999; Xie and Pietrafesa, 1999), suggesting that adding salinity gradients to our model would not greatly alter our results. In future model modifications, we plan to enlarge the model domain to include the coastal ocean and incorporate estuary-shelf exchange through the inlets. Our hydrodynamic model in its current form, however, appears robust in predicting flow fields within Pamlico Sound.

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Spatial and temporal salinity and temperature patterns

Previous studies conducted within Pamlico Sound have noted that salinity gradients generally occur from west to east, with fresher water along the western shore of Pamlico Sound due to freshwater runoff and riverine discharge, and saltier water near the inlets coming from the coastal ocean (Pietrafesa *et al.*, 1986b). A north-south salinity gradient may also persist along the main axis of the sound, due to the relatively less saline (31-34 PSU) Virginia Coastal Water (VCW) inflowing through Oregon Inlet and the higher salinity (34.5-37 PSU) Carolina Coastal Water (CCW) inflowing through Hatteras Inlet (Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1988). Furthermore, southward winds can influence the spatial patterns of salinity by pushing fresher Albemarle Sound water towards the south, or having the opposite effect when blowing towards the north (Pietrafesa *et al.*, 1986b).

To determine if salinity and temperature gradients exist across sound, we measured salinity and temperature during our cruises at stations located throughout Pamlico Sound and produced spatial maps to examine the salinity and temperature contours during each cruise. For brevity, we only present maps from our nighttime cruises, as salinity and temperature were spatially constant over day-night periods.

In 2000, all cruises were conducted when winds were blowing towards the south (see Fig. 19A for cruise dates relative to wind), and salinity and temperature patterns were relatively similar during most cruises. On Days 290 (Fig. 22), 299 (Fig. 24), and 309 (Fig. 25) horizontal salinity gradients were present across Pamlico Sound, with saltier water located in the bottom near the inlets (Fig. 22 and Fig. 24), or along the

eastern shore of Pamlico Sound (Fig. 25). During these cruises, temperature remained relatively homogenous horizontally (across-sound) and vertically (Fig. 22, Fig. 24, and Fig. 25). Salinity and temperature patterns during Day 295 (Fig. 23) were slightly different as some vertical stratification was evident throughout the sound. This vertical stratification, with saltier and colder water near-bottom, may have resulted from a recent switch in wind direction from blowing towards the north to blowing towards the south ~ 1 d prior to our cruise (Fig. 19A). Winds blowing towards the north would allow saltier CCW to inflow through Hatteras Inlet (station Q), and perhaps spread northward in near-bottom waters. A reversal in wind direction caused surface currents to move southward (Fig. 19 and Fig. 20), likely pushing fresher water from Albemarle Sound and the northern portion of our study area over the saltier bottom water. Saltier water may have also inflowed through Oregon Inlet (station A) after the wind reversal, however, instrument problems prevented us from obtaining complete vertical profiles along transect 1 during this cruise (Fig. 23).

In 2001, wind conditions during our cruises were more variable (Fig. 20A). When winds blew towards the south (during cruises on Days 256 [Fig. 26] and 269 [Fig. 28]), horizontal salinity gradients were again evident from east (saltier) to west (fresher), but the northern portion of our study area was also less salty than waters along the southern-most transect (Fig. 26 and Fig. 28). On Day 276 (Fig. 29), winds were also southward, and contrary to our expectations, horizontal salinity gradients were reversed, with saltier and warmer water located along the western shore of Pamlico Sound and fresher and colder water along the eastern shore of Pamlico Sound (see transects 2 & 3,

Fig. 29). Closer examination of the wind reveals that on Day 276 the wind was directed more towards the southeast than the south (see Chapter 2, Table 5), which may have pushed fresher Albemarle Sound water from the northern portion of our study area towards Oregon Inlet and southward along the eastern shore of Pamlico Sound, causing the relative drop in salinity and temperature we observed in this region.

When winds blew towards the north (Days 262 [Fig. 27], 288 [Fig. 30], and 296 [Fig. 31]), relatively salty water was located in the southern portion of our study area (transects 3 & 4), but also penetrated in near-bottom waters along transects 1 & 2, especially in the deeper, central region of Pamlico Sound (stations K, J, and I: Fig. 27, Fig. 30 and Fig. 31). It appears that this salty bottom water originated from Hatteras Inlet (station Q) and moved along the deeper contours of the sound towards the north (Fig. 27, Fig. 30 and Fig. 31). Water temperature during these cruises was more homogeneous than salinity, although there is evidence of differential heating at the surface of the sound (i.e., warmer water at surface than bottom), especially later in the season (Fig. 31).

With the exception of the near-inlet stations, vertical stratification was not common during our study, suggesting that mechanical wind forcing over the large surface area and shallow depth of Pamlico Sound is efficient at vertically mixing the water column. The extent to which salinity differences create fronts that may drive or alter circulation patterns within Pamlico Sound is not known; however, collecting CTD data at a higher spatial (stations < 6 km apart) and temporal frequency (sampling at <

weekly intervals), as well as current velocity profiles using an acoustic Doppler current profiler (ADCP), would better resolve this question.

To examine the temporal variability in salinity and temperature, we used time series of these parameters collected at our S4 current meter stations. Salinity, averaged over the duration of our study period, was lowest at Stumpy Point during both years and relatively high at the inlet sites (Table 1 and Table 2). Salinity was temporally variable, however, with changes influenced by the wind (Fig. 19 & Fig. 20). Wind-induced salinity changes were especially evident at Oregon Inlet, where spikes in salinity occurred during southward winds (Fig. 19B and Fig. 204B). Higher salinity water was also recorded at Chicamacomico on the order of hours (in 2001, see Fig. 20D) to days (in 2000, see Fig. 19D) after peaks were measured at Oregon Inlet. These spikes in salinity, in addition to our current meter data (Fig. 11), indicated that southward winds drive relatively high salinity water from the coastal ocean through Oregon Inlet, and southward to Chicamacomico along the eastern shore of Pamlico Sound (see also Pietrafesa and Janowitz, 1988). Southward winds, however, are not favorable for the inflow of coastal water through Hatteras Inlet (Xie and Eggleston, 1999), and it is not until these winds relax or reverse direction to the north that relatively salty CCW flows into Pamlico Sound via Hatteras Inlet (Fig. 19G and Fig. 20G) (Pietrafesa and Janowitz, 1988). Our lack of evidence for a salinity peak in Hatteras Inlet surface currents during northeastward winds is likely due to the fact that inwelling from the coastal ocean mainly occurs in bottom waters and is insignificant near the surface at this inlet (Xie and Eggleston, 1999). Moreover, spikes in salinity from the coastal ocean were not

recorded simultaneously at Oregon and Hatteras Inlets, because inflow through one inlet is generally compensated by outflow through the other inlet (Xie and Eggleston, 1999).

Along the western shore of Pamlico Sound, southward-directed winds caused decreases in salinity at Stumpy Point (Fig. 19C and Fig. 20C). This decrease in salinity at Stumpy Point is caused by low salinity water flowing out of Albemarle Sound along the northwest shore of Pamlico Sound (Pietrafesa and Janowitz, 1991). In the southwestern portion of our study area, salinity was more constant over time, as Gibbs Shoal showed only slight variations in salinity with no obvious relationship to the wind (Fig. 19G and Fig. 20G). Salinity is likely more constant near the surface at Gibbs Shoal than our other sites because of its distance from sources of riverine and oceanic inputs.

The sequence of wind-induced salinity changes throughout Pamlico Sound is evident during a representative 8 d period during 2001: (1) when winds blew continuously towards the south for at least 24 h, salinity increased near Oregon Inlet, followed by a spike in salinity less than one day later at Chicamacomico (also along the eastern sound, but south of Oregon Inlet), indicative of relatively high salinity water inwelling through Oregon Inlet from the coastal ocean (Fig. 21). (2) During this time, salinity near Hatteras Inlet slowly declined as lower salinity northern Pamlico Sound water was pushed southward (Fig. 21). (3). Along the western shore of Pamlico Sound, salinity at Stumpy Point dropped, indicative of low salinity Albemarle Sound water moving southward into the northern portion of Pamlico Sound. When winds reversed towards the north (~ Day 276, Fig. 21), salinity at Stumpy Point increased and leveled off, as Pamlico Sound water was pushed northward. (4) Likewise, salinity near Hatteras

Inlet spiked, likely due to inwelling of ocean water through this inlet (Fig. 21). (5) Salinities near Oregon Inlet and Chicamacomico began decreasing and leveled off as inwelling of ocean water ceased and well-mixed Pamlico Sound water was pushed northward (Fig. 21). Thus, salinities within Pamlico Sound can be spatially variable due to wind-induced circulation dynamics (e.g. inwelling through specific inlets, Albemarle Sound discharge, etc.).

Temperature measured at our S4 stations was more spatially constant than salinity, showing near-synchronous drops as the fall months progressed (Fig. 19 and Fig. 20). Although the passage of frontal systems during the fall months (generally out of the northeast or northwest) may have contributed to decreases in temperature over time, a direct connection between wind patterns and temperature at our stations was not visually apparent (Fig. 19 and Fig. 20). Thus, on the order of days (our sampling resolution in the middle of Pamlico Sound), spatial salinity profiles were variable, but temperature remained relatively constant.

CONCLUSIONS AND IMPLICATIONS FOR LARVAL TRANSPORT

It is widely recognized that wind events have considerable influence on the subtidal current variability in estuaries (Wong and Valle-Levinson, 2002 and references therein), and that this variability exists in systems ranging from well- and partially-mixed estuaries such as Delaware and Chesapeake Bays (e.g. Pritchard and Vieira, 1984; Wong and Garvine, 1984; Vieira, 1986), to highly stratified estuaries such as Mobile Bay (e.g. Noble *et al.*, 1996). In addition, many circulation studies in estuarine lagoons

with restricted access to the coastal ocean have observed wind-driven circulation patterns, where surface currents generally flow in the same direction as the wind (e.g. Wong and Wilson, 1984; Pietrafesa *et al.*, 1986b; Valle-Levinson *et al.*, 2001; Chiappa-Carrara *et al.*, 2003). Beyond the surface currents, however, circulation patterns are difficult to generalize across lagoonal systems because of complex interactions between the geomorphology of each system (e.g. bathymetry, size and location of openings to coastal ocean, alignment of estuary with respect to coastline, etc.) and the relative importance of physical forcing mechanisms (e.g., tides, wind, freshwater and riverine input in comparison to saltwater inflow, etc.) (Dyer, 1997).

Results from our hydrographic study in the northern basin of Pamlico Sound, North Carolina, demonstrated that surface currents primarily responded to the north-south wind component in synchrony and on the order of hours. During southwestward wind events lasting 24 h or greater (the most commonly directed wind events during the fall months in our region), our observed currents followed our hypothesized circulation scenario for surface waters, whereby surface currents were primarily directed with the wind, following the coastline of Pamlico Sound. Moreover, our results indicated that southwestward-directed winds increased the inflow of salty, coastal water through Oregon Inlet, and directed currents within Pamlico Sound towards the south. These wind events created salinity gradients across Pamlico Sound, from north to south (fresher water in northern portion of Pamlico Sound due to discharge from Albemarle Sound) and from west to east (saltier water near inlets due to exchange with coastal ocean).

Conversely, during northeastward wind events lasting 24 h or greater (second most common wind direction during fall months), our observed surface currents did not match our hypothesized flow scenario in surface waters. For example, surface currents did not consistently flow with the wind, and in some cases remained southward (as during southwestward wind events). Thus, more northeastward wind events of sufficient duration are needed to test our hypothesis under these wind conditions.

In addition to our hypothesized flows, northeastward-directed winds are predicted to cause outwelling of Pamlico Sound surface waters through Oregon Inlet, and inwelling at depth of coastal ocean water through Hatteras Inlet (Xie and Eggleston, 1999). This latter prediction was supported by examination of our across-sound salinity profiles which indicated that northward transport of relatively high salinity water (likely originating from Hatteras Inlet) occurred in the deeper region of the sound. As we did not measure bottom currents beyond the periphery of Pamlico Sound, however, an understanding of the bottom circulation patterns remains incomplete, and we could not adequately test our hypothesized flow scenarios for bottom waters.

Collectively our data have strong implications for understanding larval transport. Surface transport in the northern basin of Pamlico Sound was predominately from north to south. Thus, larvae in surface waters ingressing through Oregon Inlet have a higher probability of reaching nursery habitats located within our study area than those ingressing through Hatteras Inlet. Indeed, we have observed greater postlarval blue crab settlement at Oregon Inlet following southwestward winds (D. Eggleston, NCSU, unpublished data; Chapter 2), and the relative abundance of early- and late-stage

benthic juvenile blue crabs is higher in the northwest portion of Pamlico Sound than other regions (Etherington and Eggleston, 2003; Eggleston *et al.*, 2004). Conversely, larvae that are bottom-oriented may have a better chance of being transported into our study area when ingressing through Hatteras Inlet. Therefore, the vertical positioning of larvae in the water column during ingress has the potential to mediate dispersal and ultimately impact recruitment success to nursery habitats within the northern basin of Pamlico Sound. Once within Pamlico Sound, actively swimming larvae may be able to recognize and use the observed horizontal salinity gradients to navigate across-sound to nursery habitats (Miller *et al.*, 1984; Pietrafesa *et al.*, 1986a). Although more information on larval responses to hydrographic factors (which are variable by species and ontogeny) are needed, this study sets the framework for further development of coupled biophysical studies within Pamlico Sound.

ACKNOWLEDGEMENTS

LITERATURE CITED

Blanton, J.O., Amft, J.A., Lee, D.K. and Riordan, A. (1989) Wind stress and heat fluxes observed during winter and spring 1986. *J. Geophys. Res.* **94**:10 686-610 698.

Chiappa-Carrara, X., Sanvincente-Anorve, L., Monreal-Gomez, A. and Salas de Leon, D. (2003) Ichthyoplankton distribution as an indicator of hydrodynamic conditions of a lagoon system in the Mexican Caribbean. *J. Plankton Res.* **25**:687-696.

Dyer, K.R. (1997) *Estuaries: a physical introduction*. New York: John Wiley, 195 pp.

Eggleston, D.B., Johnson, E.G. and Hightower, J.E. (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 Thomson, R.E. (2001) *Data analysis methods in physical oceanography*. Amsterdam: Elsevier, 638 pp.

Epperly, S.P. and Ross, S.W. (1986) Characterization of the North Carolina Pamlico-Albemarle Estuarine Complex. *NOAA Technical Memorandum*: NMFS-SEFC-175,

Etherington, L.L. and Eggleston, D.B. (2000) Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. *Mar. Ecol. Prog. Ser.* **204**:179-198.

Etherington, L.L. and Eggleston, D.B. (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.

Giese, G.L., Wilder, H.B. and Parker, G.C., Jr. (1979) Hydrology of major estuaries and
sounds of North Carolina. *U.S. Geological Survey Water resources
Investigations*: 79-46,

Janzen, C.D. and Wong, K.-C. (1998) On the low-frequency transport processes in a
shallow coastal lagoon. *Estuaries* **21**:754-766.

Luettich, R.A., Jr. and Westerink, J. (2004) Formulation and numerical implementation
of the 2D/3D ADCIRC finite element model version 44.XX.
http://www.marine.unc.edu/C_CATS/adcirc/adcirc_theory_2004_05_14.pdf

Luettich, R.A., Jr., Westerink, J.J. and Scheffner, N.W. (1992) ADCIRC: An advanced
three-dimensional circulation model for shelves, coasts and estuaries. *Report 1:
Theory and methodology of ADCIRC-2DDI and ADCIRC-3DL*: Technical report
DRP-92-6, U.S. Army Engineer Waterways Experiment Station, Vicksburg,
MS.

Luettich, R.A., Jr., Carr, S.D., Reynolds-Fleming, J.V., Fulcher, C.W. and McNinch,
J.E. (2002) Semi-diurnal seiching in a shallow, micro-tidal lagoonal estuary.
Cont. Shelf Res. **22**:1669-1681.

Miller, J.M., Reed, J.P. and Pietrafesa, L.J. (1984) Patterns, mechanisms and
approaches to the study of migrations of estuarine-dependent fish larvae and
juveniles. In: *Mechanisms of migration in fishes*. J.D. McCleave, G.P. Arnold,

J.J. Dodson and W.H. Neill (ed) New York: Plenum Publishing Corporation, pp. 209-225.

Noble, M.A., Schroeder, W.W., Wiseman, W.J., Jr., Ryan, H.F. and Gelfenbaum, G. (1996) Subtidal circulation patterns in a shallow, highly stratified estuary: Mobile Bay, Alabama. *J. Geophys. Res.* **101**:25,689-625,703.

Pietrafesa, L.J. and Janowitz, G.S. (1988) Physical oceanographic processes affecting larval transport around and through North Carolina inlets. *Am. Fish. Soc. Symp.* **3**:34-50.

Pietrafesa, L.J. and Janowitz, G.S. (1991) The Albemarle-Pamlico coupling study. Final report to the Environmental Protection Agency,

Pietrafesa, L.J., Janowitz, G.S., Miller, J.M., Noble, E.B., Ross, S.W. and Epperly, S.P. (1986a) Abiotic factors influencing the spatial and temporal variability of juvenile fish in Pamlico Sound, North Carolina. In: *Estuarine Variability*. D.A. Wolfe (ed) New York: Academic Press, pp. 341-353.

Pietrafesa, L.J., Janowitz, G.S., Chao, T.-Y., Weisberg, R.H., Askari, F. and Noble, E. (1986b) The physical oceanography of Pamlico Sound. *UNC Sea Grant Publication*: UNC-WP-86-5, Raleigh, NC.

Preisendorfer, R.W. (1988) *Principal component analysis in meteorology and oceanography*. New York: Elsevier, 425 pp.

Pritchard, D.W. and Vieira, E.C. (1984) Vertical variations in residual current response to meteorological forcing in the Mid-Chesapeake Bay. In: *The estuary as a filter*. V.S. Kennedy (ed) Orlando: Academic Press, pp. 27-65.

Roelofs, E.W. and Bumpus, D.F. (1953) The hydrography of Pamlico Sound. *Bulletin of Marine Science of the Gulf and Caribbean* **3**:181-205.

Ross, S.W. and Epperly, S.P. (1985) Utilization of shallow estuarine nursery areas by fishes in Pamlico Sound and adjacent tributaries, North Carolina. In: *Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecosystem Integration*. Yáñez-Arancibia (ed) Mexico: UNAM Press, pp. 207-232.

Rothschild, B.J. (1986) *Dynamics of marine fish populations*. Cambridge, MA: Harvard University Press, 277 pp.

Singer, J.J. and Knowles, C.E. (1975) Hydrology and circulation patterns in the vicinity of Oregon Inlet and Roanoke Island, North Carolina. *Sea Grant*: UNC-SG-75-15, Raleigh, NC.

Valle-Levinson, A., Delgado, J.A. and Atkinson, L.P. (2001) reversing water exchange patterns at the entrance to a semiarid coastal lagoon. *Estuar. Coast. Shelf Sci.* **53**:825-838.

Vieira, M.E.C. (1986) The meteorologically driven circulation in mid-Chesapeake Bay. *J. Mar. Res.* **44**:473-493.

Weber, A.H. and Blanton, J.O. (1980) Monthly wind fields for the South Atlantic Bight. *J. Phys. Oceanogr.* **10**:1256-1263.

Weisberg, K.H. and Pietrafesa, L.J. (1983) Kinematic and correlation of the surface wind field in the South Atlantic bight. *J. Geophys. Res.* **88**:4593-4610.

Werner, F.E., Quinlan, J.A., Blanton, B.O. and Luettich, R.A., Jr. (1997) The role of hydrodynamics in explaining variability in fish populations. *J. Sea Res.* **37**:195-212.

Wong, K.-C. and Garvine, R.W. (1984) Observations of wind-induced, subtidal variability in the Delaware estuary. *J. Geophys. Res.* **89**:10,589-510,597.

Wong, K.-C. and Wilson, R.E. (1984) Observations of low-frequency variability in Great South Bay and relations to atmospheric forcing. *J. Phys. Oceanogr.* **14**:1893-1900.

Wong, K.-C. and Valle-Levinson, A. (2002) On the relative importance of the remote and local wind effects on the subtidal exchange at the entrance to the Chesapeake Bay. *J. Mar. Res.* **60**:477-498.

Xie, L. and Eggleston, D.B. (1999) Computer simulations of wind-induced estuarine circulation patterns and estuary-shelf exchange processes: The potential role of wind forcing on larval transport. *Estuar. Coast. Shelf Sci.* **49**:221-234.

Xie, L. and Pietrafesa, L.J. (1999) Systemwide modeling of wind and density driven circulation in Croatan-Albemarle-Pamlico estuary system part I: Model configuration and testing. *J. Coast. Res.* **15**:1167-1177.

Table 1. Summary of raw current meter data from 2000. Stations: Oregon Inlet (OI), Stumpy Point (SP), Chicamacomico (CH), Hatteras Inlet surface (HI-s), Hatteras Inlet bottom (HI-b), Gibbs Shoal (GS). u=east-west component and v=north-south component, where positive values indicate currents flowing towards the east and north, respectively.

Station	Position	Depth (m)	Record start (date)	Duration (days)	Comp.	Velocity Min. (cm/s)	Velocity Max. (cm/s)	Velocity Avg. (cm/s)	Sal. Avg. (PSU)	Temp. Avg. (˙C)
OI	35˚ 43' N 75˚ 37' W	1	18 Sept 2000	52	u	-36. 90	33.30	-2.79	18.80	19.38
					v	-55.18	30.87	-3.57		
SP	35˚ 39' N 75˚ 43' W	1	19 Sept 2000	51	u	-14.61	16.14	2.13	15.98	20.01
					v	-29.45	23.29	-3.26		
CH	35˚ 35' N 75˚ 31' W	1	3 Oct 2000	36	u	-19.72	19.97	1.85	20.26	17.63
					v	-44.43	15.85	-11.36		
HI-s	35˚ 16' N 75˚ 44' W	1	17 Sept 2000	53	u	-83.82	101.49	2.03	18.37	20.09
					v	-23.91	28.46	-2.45		
HI-b	(as above)	3	17 Sept 2000	53	u	-92.67	81.26	-5.18	20.15	19.99
					v	-40.34	37.54	-1.96		
GS	35˚ 27' N 75˚ 55' W	1	3 Oct 2000	5	u	-17.23	18.35	-0.81	18.95	18.68
			26 Oct 2000	13	v	-17.98	20.70	1.96		

Table 2. Summary of raw current meter data from 2001. Stations: Oregon Inlet (OI), Stumpy Point (SP), Chicamacomico (CH), Hatteras Inlet surface (HI-s), Hatteras Inlet bottom (HI-b), Gibbs Shoal (GS). u=east-west component and v=north-south component, where positive values indicate currents flowing towards the east and north, respectively. na =not available.

Station	Position	Depth (m)	Record start (date)	Duration (days)	Comp.	Velocity Min. (cm/s)	Velocity Max. (cm/s)	Velocity Avg. (cm/s)	Sal. Avg. (PSU)	Temp. Avg. (°C)
OI	35° 43' N 75° 37' W	1	1 Sept 2001	59	u	-37.11	23.47	-5.61	21.40	21.67
					v	-38.05	27.00	-5.25		
SP	35° 39' N 75° 43' W	1	1 Sept 2001	14	u	-18.52	19.97	-0.73	20.86	20.36
			27 Sept 2001	33	v	-32.02	21.30	-4.58		
CH	35° 35' N 75° 31' W	1	1 Sept 2001	59	u	-14.75	23.94	-2.42	22.77	21.34
					v	-32.93	12.20	-3.62		
HI-s	35° 16' N 75° 44' W	1	1 Sept 2001	59	u	-73.17	50.91	-8.40	na	na
					v	-70.86	64.94	-5.16		
HI-b	(as above)	3	1 Sept 2001	59	u	-52.34	54.31	-0.60	23.10	21.99
					v	-61.69	48.37	-6.05		
GS	35° 27' N 75° 55' W	1	1 Sept 2001	36	u	-7.89	23.37	6.47	22.71	22.85
			13 Oct 2001	17	v	-21.56	18.02	-4.37		

Table 3. Cross-correlation results between hourly lowpass-filtered observed and modeled currents. OI = Oregon Inlet; SP = Stumpy Point; CH = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet; N = sample size (not equal within each year due to different current meter deployment dates and servicing intervals); u = east-west velocity component; v = north-south velocity component; ns = not significant. All correlation coefficients presented are significant at $p < 0.0001$.

Station	Year	N	Component u	v
OI	2000	1176	0.51	0.59
	2001	1416	0.41	0.62
SP	2000	1176	ns	0.63
	2001	1127	-0.18	0.56
CH	2000	816	0.39	0.39
	2001	1416	0.90	0.81
GS	2000	383	0.54	0.70
	2001	1295	0.46	0.35
HI	2000	1176	0.58	0.81
	2001	1416	0.67	0.62

FIGURE LEGENDS

Figure 1. Map of Albemarle-Pamlico Estuarine System (APES) in North Carolina, USA showing regional bathymetry and hydrographic stations (■) within Pamlico Sound (A), OI = Oregon Inlet; SP = Stumpy Point; Ch = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet. CTD sampling stations (●) in 2000 (B) and 2001 (C) are shown (with station names in blue) on enlarged maps of our study area (northern basin of Pamlico Sound).

Figure 2. Hypothesized flows during southwestward (A) and northeastward-directed winds (B). Winds blowing towards the southwest will push surface currents (along the coast and within Pamlico Sound) in the same direction as the wind causing a set-up of sea level along the coast near Oregon Inlet (OI) and a set-down of sea level along the sound-side of the eastern shore of Pamlico Sound (A.1.), thereby producing a divergence that drives an inflow of water from the ocean through Oregon Inlet (O.I., A.2.). Furthermore, slight Ekman veering towards the west will cause a set-up of sea level along the western shore of Pamlico Sound (A.3.), producing a northeastward bottom return flow (preferentially within the deeper mid-sound region) (A.4.). Winds blowing towards the northeast will push surface currents (along the coast and within Pamlico Sound) in the same direction as the wind, causing a set-up of sea level along the coast near Hatteras Inlet (HI) and a set-down of sea level along the sound-side of the southeastern shore of Pamlico Sound (B.1.), thereby producing a divergence that drives an inflow of water from the ocean through Hatteras Inlet (HI, B.2.). Slight Ekman

veering towards the east will cause a set-up of sea level along the eastern shore of Pamlico Sound (B.3.), producing a southwestward bottom return flow (preferentially within the deeper mid-sound region) (B.4.).

Figure 3. Vector diagrams of hourly-averaged wind and S4 current meter time series collected during 2000. Current meter records have been 40 h low-pass filtered. Positive values indicate northward flow.

Figure 4. Vector diagrams of hourly-averaged wind and S4 current meter time series collected during 2001. Current meter records have been 40 h low-pass filtered. Positive values indicate northward flow.

Figure 5. Power spectra for wind and currents in 2000. For reference, the frequency of the M_2 tidal constituent (12.42 h) and diurnal period (24 h) are shown by the red and black vertical lines, respectively. Current meter stations plotted in left panels are located along the western shore of Pamlico Sound, while those stations plotted in right panels are located along the eastern shore of Pamlico Sound. Error bars represent 95 % confidence intervals, east-west velocities = u-component, and north-south velocities = v-component.

Figure 6. Power spectra for wind and currents in 2001. For reference, the frequency of the M_2 tidal constituent (12.42 h) and diurnal period (24 h) are shown by the red and

black vertical lines, respectively. Current meter stations plotted in left panels are located along the western shore of Pamlico Sound, while those stations plotted in right panels are located along the eastern shore of Pamlico Sound. Error bars represent 95 % confidence intervals, east-west velocities = u-component, and north-south velocities = v-component.

Figure 7. Time series of wind and first temporal EOF mode of observed currents in 2000. East-west (u-components) and north-south (v-components) are compared in A and B, respectively.

Figure 8. Time series of wind and first temporal EOF mode of observed currents in 2001. East-west (u-components) and north-south (v-components) are compared in A and B, respectively.

Figure 9. Spatial representation of first EOF mode of observed currents. In 2000 (A), Gibbs Shoal (GS) was not included in the analysis because the instrument deployment period was too short. All stations were included in 2001 (B). The relative length of vectors represents the strength of the flow and angles represent the mean direction of flow at each station. OI = Oregon Inlet; SP = Stumpy Point; Ch = Chicamacomico; HI = Hatteras Inlet. Two vectors are shown near HI, where top and bottom vectors represent surface and bottom currents, respectively.

Figure 10. Average length of time that winds blew towards a specific direction during September-October 2000 (A) and 2001 (B). Error bars represent ± 1 SE. During our study, winds never blew due north, due south, due east or due west.

Figure 11. Distribution of average subtidal (40 h low-pass filtered) currents during southwestward-directed wind events lasting 24 h or greater during 2000 (A) and 2001 (B). OI = Oregon Inlet (blue vectors); SP = Stumpy Point (light blue vectors); Ch = Chicamacomico (pink vectors); GS = Gibbs Shoal (green vectors); HI = Hatteras Inlet (surface = red vectors, bottom = black vectors). Wind is shown outside of Pamlico Sound (dark green vectors).

Figure 12. Distribution of average subtidal (40 h low-pass filtered) currents during northeastward-directed wind events lasting 24 h or greater during 2000 (A) and 2001 (B). OI = Oregon Inlet (blue vectors); SP = Stumpy Point (light blue vectors); Ch = Chicamacomico (pink vectors); GS = Gibbs Shoal (green vectors); HI = Hatteras Inlet (surface = red vectors, bottom = black vectors). Wind is shown outside of Pamlico Sound (dark green vectors).

Figure 13. Principal axes of variance of observed and modeled current and wind velocities during the blue crab recruitment season (September-October 2000 and 2001). Hourly-averaged, lowpass-filtered observed (blue) and modeled (red) current ellipses (shown within Pamlico Sound) and wind ellipse (shown outside of sound in green)

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. OI = Oregon Inlet; SP = Stumpy Point; Ch = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet.

Figure 14. Comparison between modeled (red) and observed (blue) hourly-averaged lowpass-filtered currents at western sound (left panels) and eastern sound (right panels) stations during 2000. SP = Stumpy Point; GS = Gibbs Shoal; OI = Oregon Inlet; CH = Chicamacomico; HI = Hatteras Inlet; u = east-west component where positive values indicate currents flowing towards the east; v = north-south component where positive values indicate currents flowing toward the north.

Figure 15. Comparison between modeled (red) and observed (blue) hourly-averaged lowpass-filtered currents at western sound (left panels) and eastern sound (right panels) stations during 2001. SP = Stumpy Point; GS = Gibbs Shoal; OI = Oregon Inlet; CH = Chicamacomico; HI = Hatteras Inlet; u = east-west component where positive values indicate currents flowing towards the east; v = north-south component where positive values indicate currents flowing toward the north.

Figure 16. Time series of wind and first temporal EOF mode of modeled currents in 2000. East-west (u-components) and north-south (v-components) are compared in A and B, respectively.

Figure 17. Time series of wind and first temporal EOF mode of modeled currents in 2001. East-west (u-components) and north-south (v-components) are compared in A and B, respectively.

Figure 18. Spatial representation of first EOF mode of modeled currents. In 2000 (A), Gibbs Shoal (GS) was not included in the analysis so that comparisons were similar to observed currents (see Fig. 9). All stations were included in 2001 (B). The relative length of vectors represents the strength of the flow and angles represent the mean direction of flow at each station. OI = Oregon Inlet; SP = Stumpy Point; Ch = Chicamacomico; HI = Hatteras Inlet. Two vectors are shown near HI, where top and bottom vectors represent modeled surface (0.8 depth layer) and bottom (-0.8 depth layer) currents, respectively.

Figure 19. Vector diagram of hourly-averaged wind and raw salinity and temperature time series from S4 current meters collected during 2000. For reference, filled circles in panel A represent dates when CTD cruises occurred.

Figure 20. Vector diagram of hourly-averaged wind and raw salinity and temperature time series from S4 current meters collected during 2001. Hatteras Inlet surface salinity and temperature were not recorded. For reference, filled circles in panel A represent dates when CTD cruises occurred.

Figure 21. Representative sequence of wind-induced salinity fluctuations within Pamlico Sound during 2001. The top panel shows the wind vector diagram, and the bottom panel shows salinity (by site) over time.

Figure 22. Contour map of salinity (right side) and temperature (left side) at cruise stations during rotation 1 (Day 290) in 2000. Each panel, from top to bottom, represents a cruise transect and letters are names along that transect (see Fig. 1 for map with station locations). Same color bar is used for salinity and temperature, but scale for salinity is in PSU, while scale for temperature is in degrees C. For reference, stations A = Oregon Inlet, D = Stumpy Point, H = Chicamacomico, N = Gibbs Shoal, and Q = Hatteras Inlet.

Figure 23. Contour map of salinity (right side) and temperature (left side) at cruise stations during rotation 2 (Day 295) in 2000. Each panel, from top to bottom, represents a cruise transect and letters are names along that transect (see Fig. 1 for map with station locations). Same color bar is used for salinity and temperature, but scale for salinity is in PSU, while scale for temperature is in degrees C. For reference, stations A = Oregon Inlet, D = Stumpy Point, H = Chicamacomico, N = Gibbs Shoal, and Q = Hatteras Inlet.

Figure 24. Contour map of salinity (right side) and temperature (left side) at cruise stations during rotation 3 (Day 299) in 2000. Each panel, from top to bottom, represents

a cruise transect and letters are names along that transect (see Fig. 1 for map with station locations). Same color bar is used for salinity and temperature, but scale for salinity is in PSU, while scale for temperature is in degrees C. For reference, stations A = Oregon Inlet, D = Stumpy Point, H = Chicamacomico, N = Gibbs Shoal, and Q = Hatteras Inlet.

Figure 25. Contour map of salinity (right side) and temperature (left side) at cruise stations during rotation 4 (Day 309) in 2000. Each panel, from top to bottom, represents a cruise transect and letters are names along that transect (see Fig. 1 for map with station locations). Same color bar is used for salinity and temperature, but scale for salinity is in PSU, while scale for temperature is in degrees C. For reference, stations A = Oregon Inlet, D = Stumpy Point, H = Chicamacomico, N = Gibbs Shoal, and Q = Hatteras Inlet.

Figure 26. Contour map of salinity (right side) and temperature (left side) at cruise stations during rotation 1 (Day 256) in 2001. Each panel, from top to bottom, represents a cruise transect and letters are names along that transect (see Fig. 1 for map with station locations). Same color bar is used for salinity and temperature, but scale for salinity is in PSU, while scale for temperature is in degrees C. For reference, stations A = Oregon Inlet, D = Stumpy Point, G = Chicamacomico, M = Gibbs Shoal, and Q = Hatteras Inlet.

Figure 27. Contour map of salinity (right side) and temperature (left side) at cruise stations during rotation 2 (Day 262) in 2001. Each panel, from top to bottom, represents a cruise transect and letters are names along that transect (see Fig. 1 for map with station locations). Same color bar is used for salinity and temperature, but scale for salinity is in PSU, while scale for temperature is in degrees C. For reference, stations A = Oregon Inlet, D = Stumpy Point, G = Chicamacomico, M = Gibbs Shoal, and Q = Hatteras Inlet.

Figure 28. Contour map of salinity (right side) and temperature (left side) at cruise stations during rotation 3 (Day 269) in 2001. Each panel, from top to bottom, represents a cruise transect and letters are names along that transect (see Fig. 1 for map with station locations). Same color bar is used for salinity and temperature, but scale for salinity is in PSU, while scale for temperature is in degrees C. For reference, stations A = Oregon Inlet, D = Stumpy Point, G = Chicamacomico, M = Gibbs Shoal, and Q = Hatteras Inlet.

Figure 29. Contour map of salinity (right side) and temperature (left side) at cruise stations during rotation 4 (Day 276) in 2001. Each panel, from top to bottom, represents a cruise transect and letters are names along that transect (see Fig. 1 for map with station locations). Same color bar is used for salinity and temperature, but scale for salinity is in PSU, while scale for temperature is in degrees C. For reference, stations A

= Oregon Inlet, D = Stumpy Point, G = Chicamacomico, M = Gibbs Shoal, and Q = Hatteras Inlet.

Figure 30. Contour map of salinity (right side) and temperature (left side) at cruise stations during rotation 5 (Day 288) in 2001. Each panel, from top to bottom, represents a cruise transect and letters are names along that transect (see Fig. 1 for map with station locations). Same color bar is used for salinity and temperature, but scale for salinity is in PSU, while scale for temperature is in degrees C. For reference, stations A = Oregon Inlet, D = Stumpy Point, G = Chicamacomico, M = Gibbs Shoal, and Q = Hatteras Inlet.

Figure 31. Contour map of salinity (right side) and temperature (left side) at cruise stations during rotation 6 (Day 296) in 2001. Each panel, from top to bottom, represents a cruise transect and letters are names along that transect (see Fig. 1 for map with station locations). Same color bar is used for salinity and temperature, but scale for salinity is in PSU, while scale for temperature is in degrees C. For reference, stations A = Oregon Inlet, D = Stumpy Point, G = Chicamacomico, M = Gibbs Shoal, and Q = Hatteras Inlet.

Figure 1

Figure 2

2000

Figure 3

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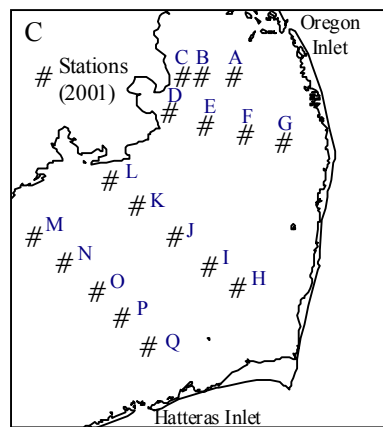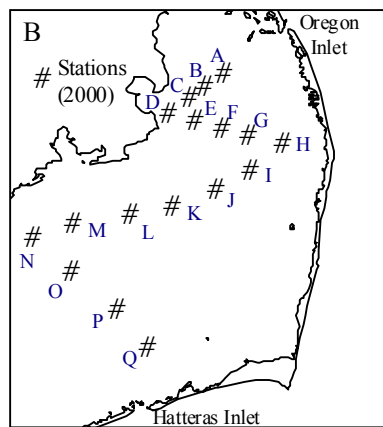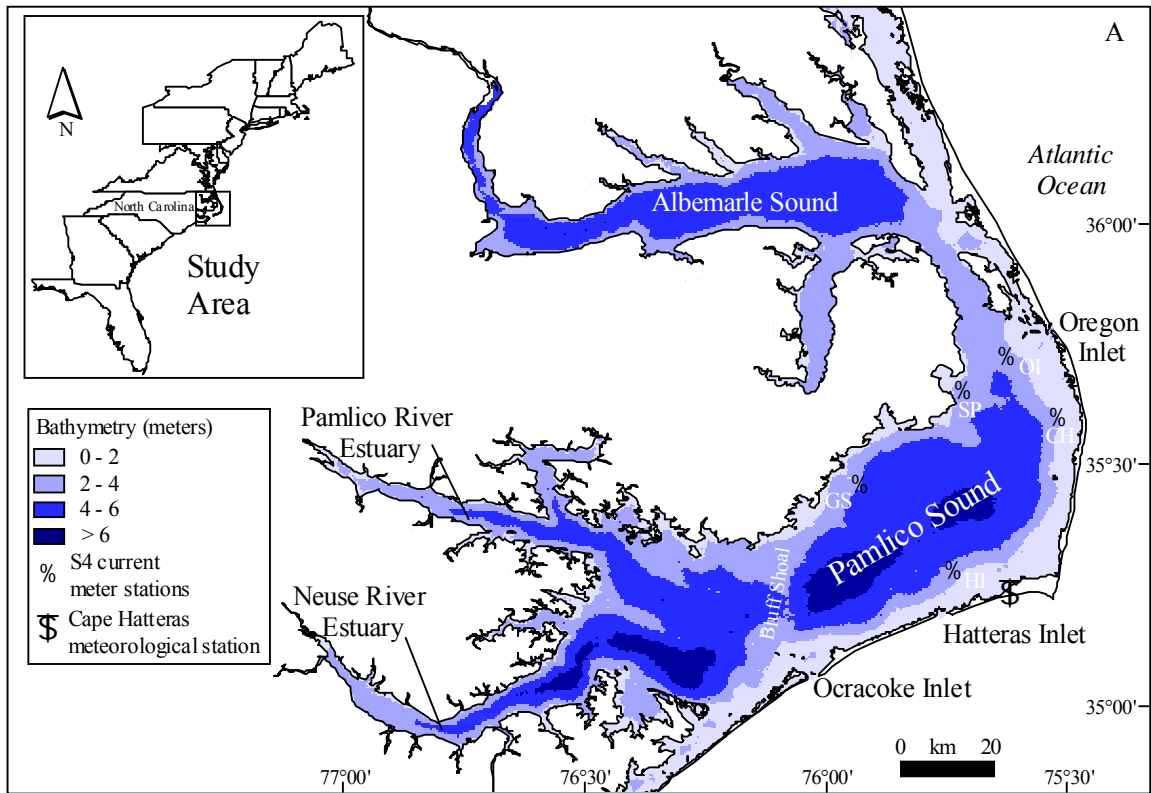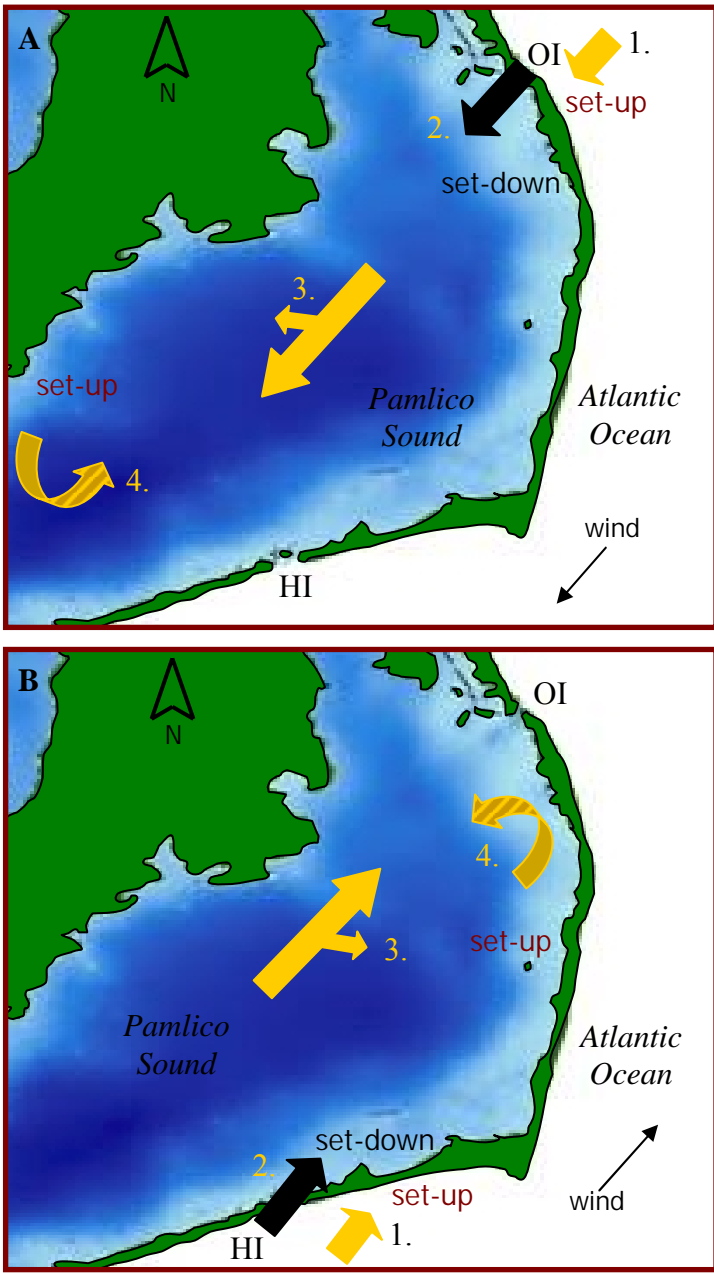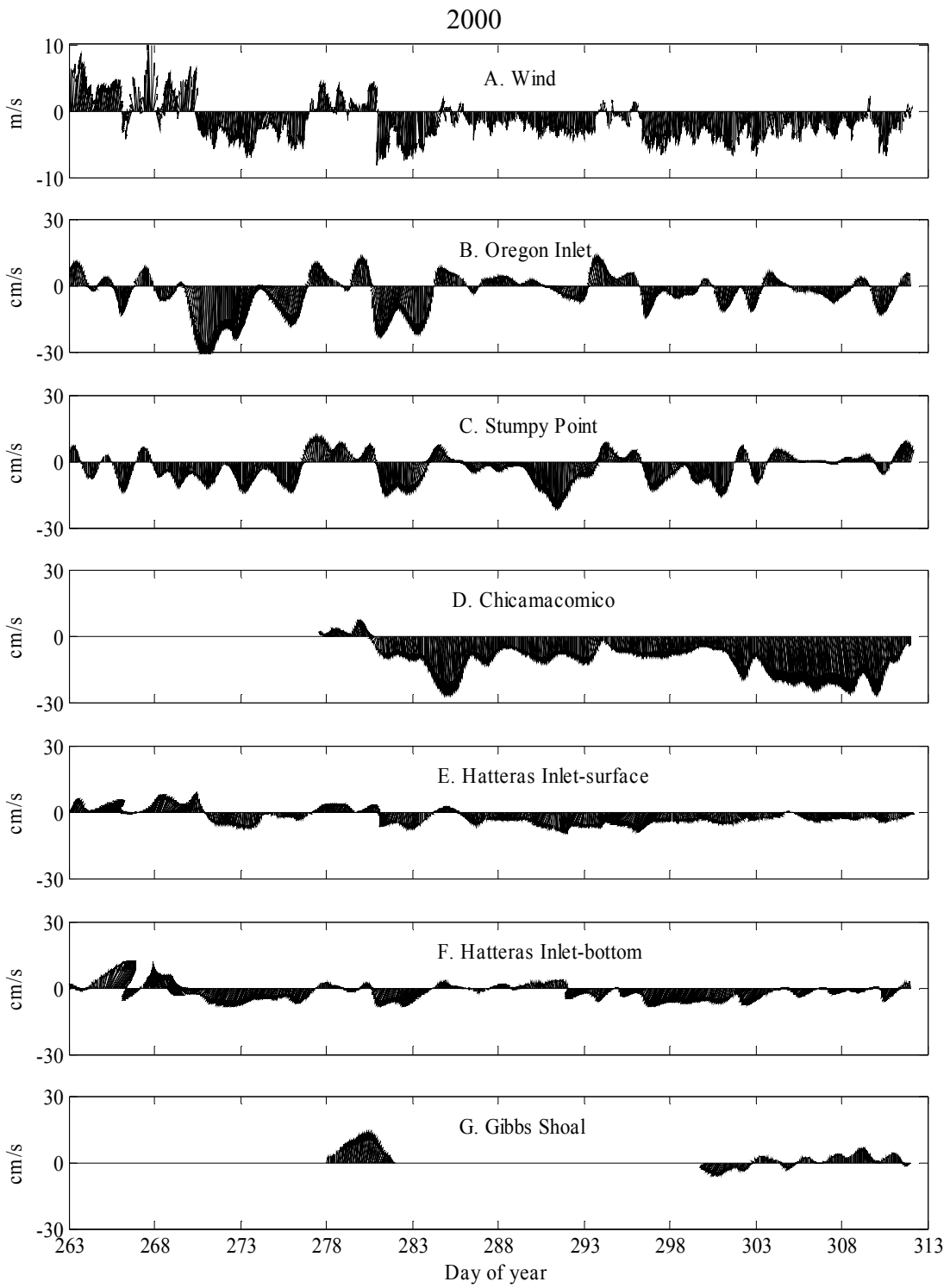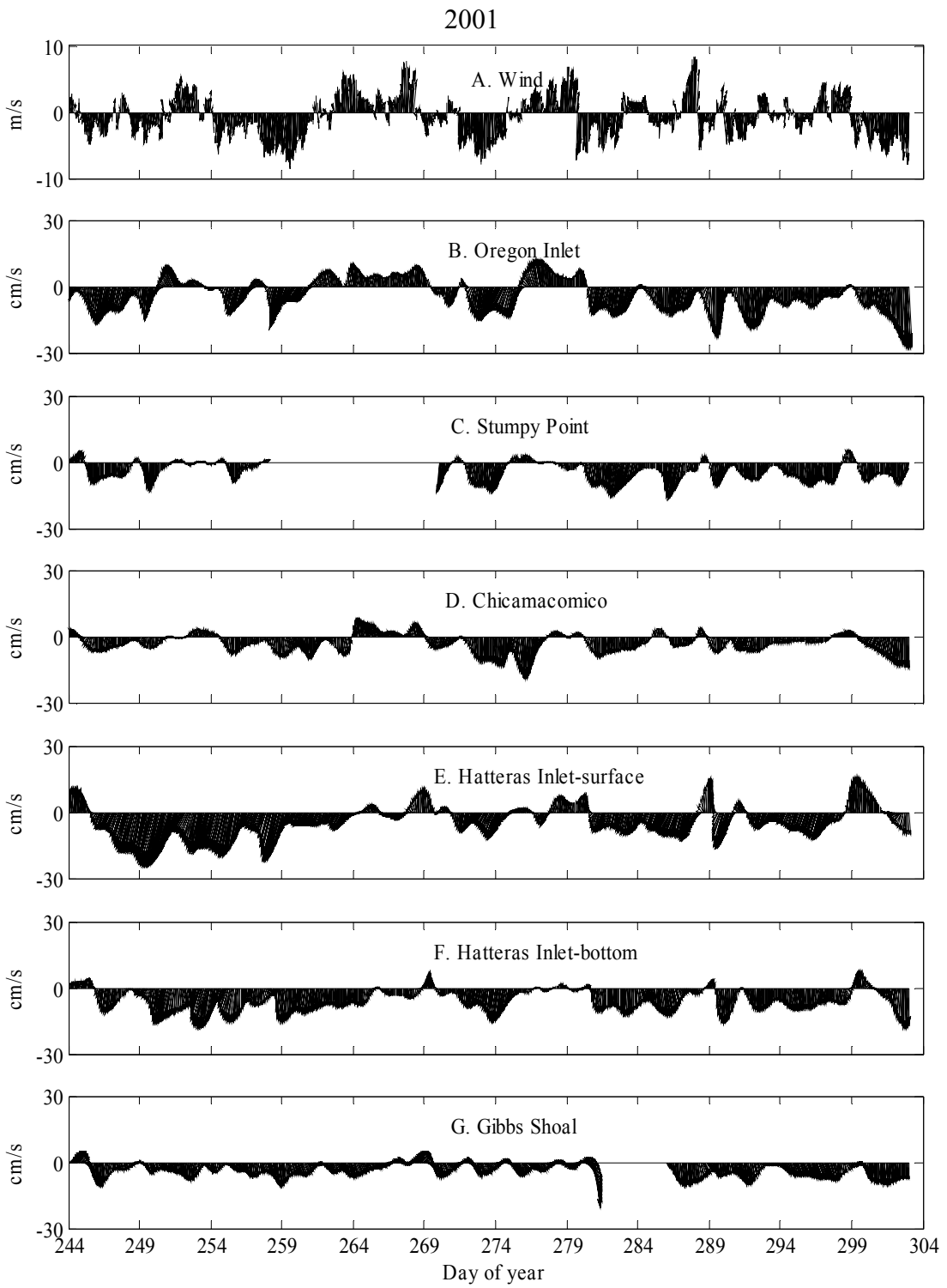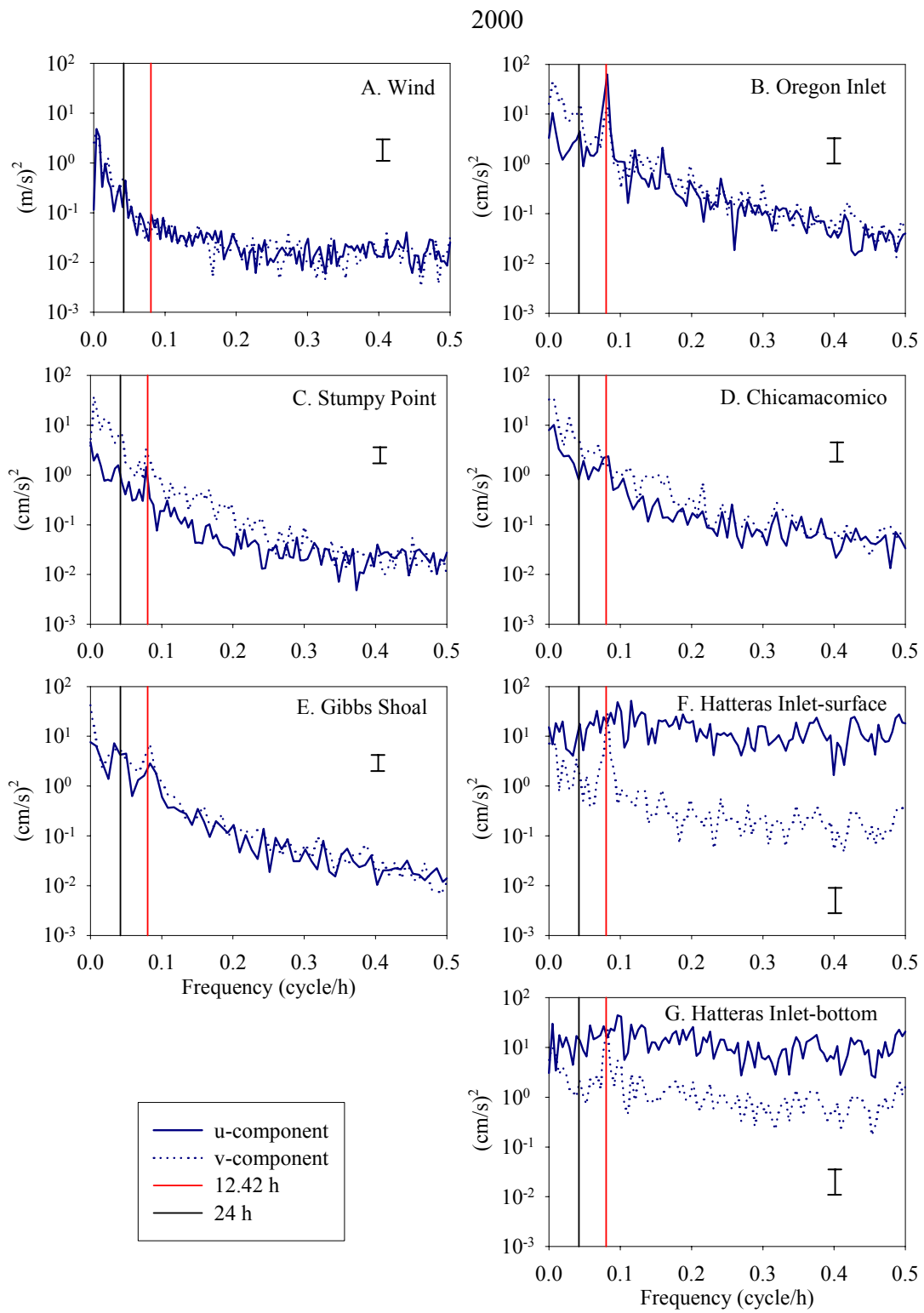
2001

Figure 4

2000

Figure 5

2001

Figure 6

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Figure 7

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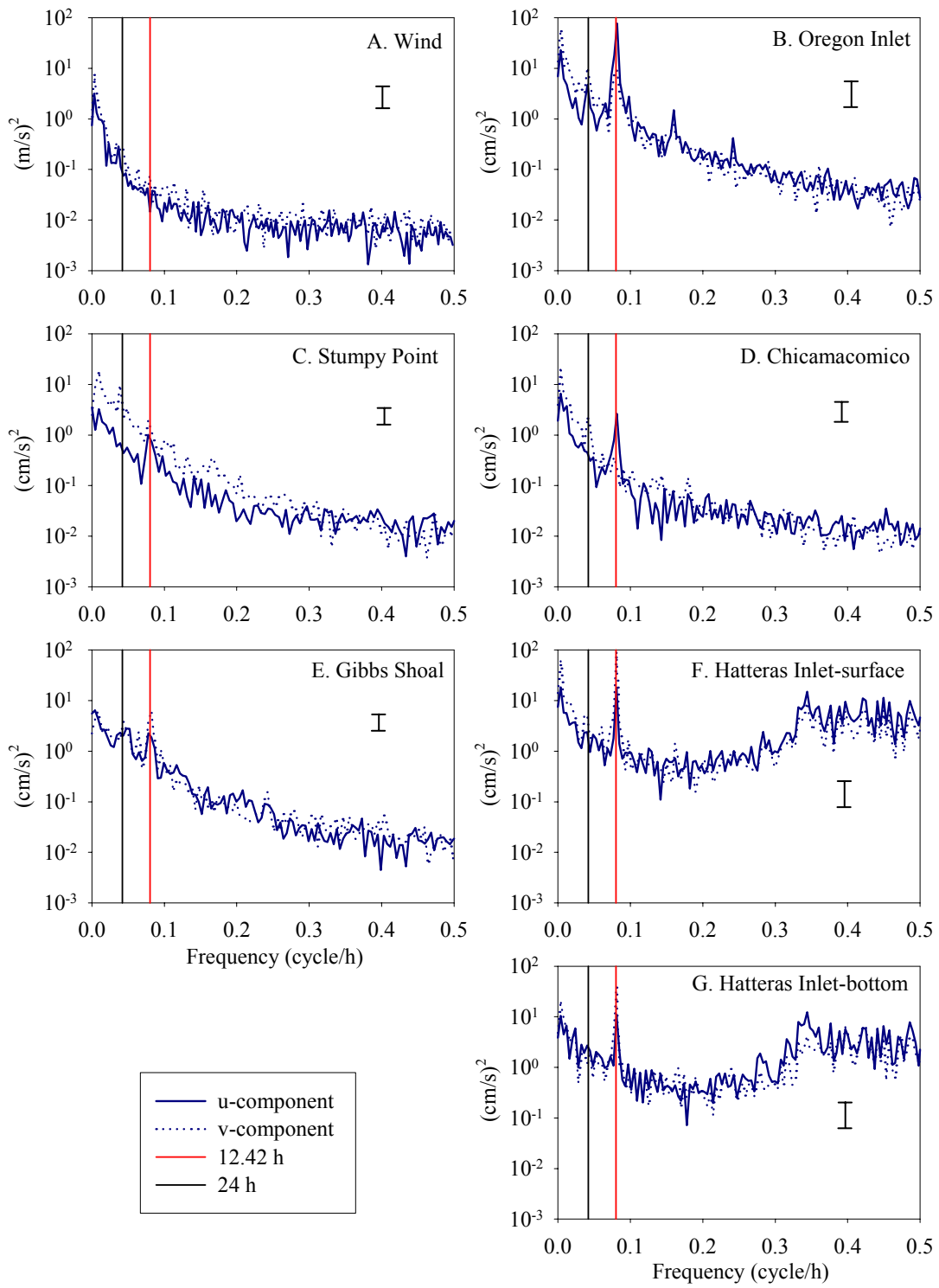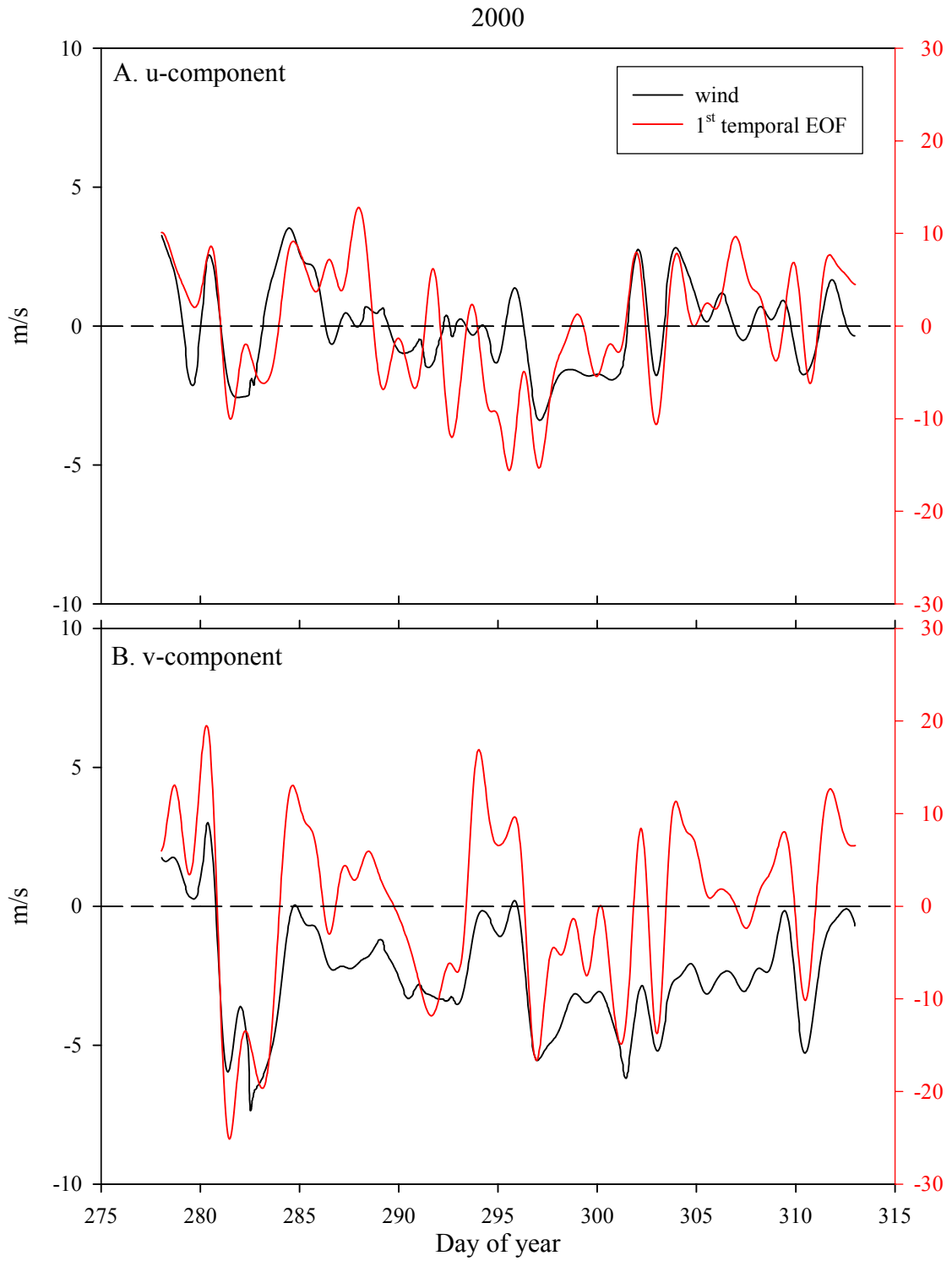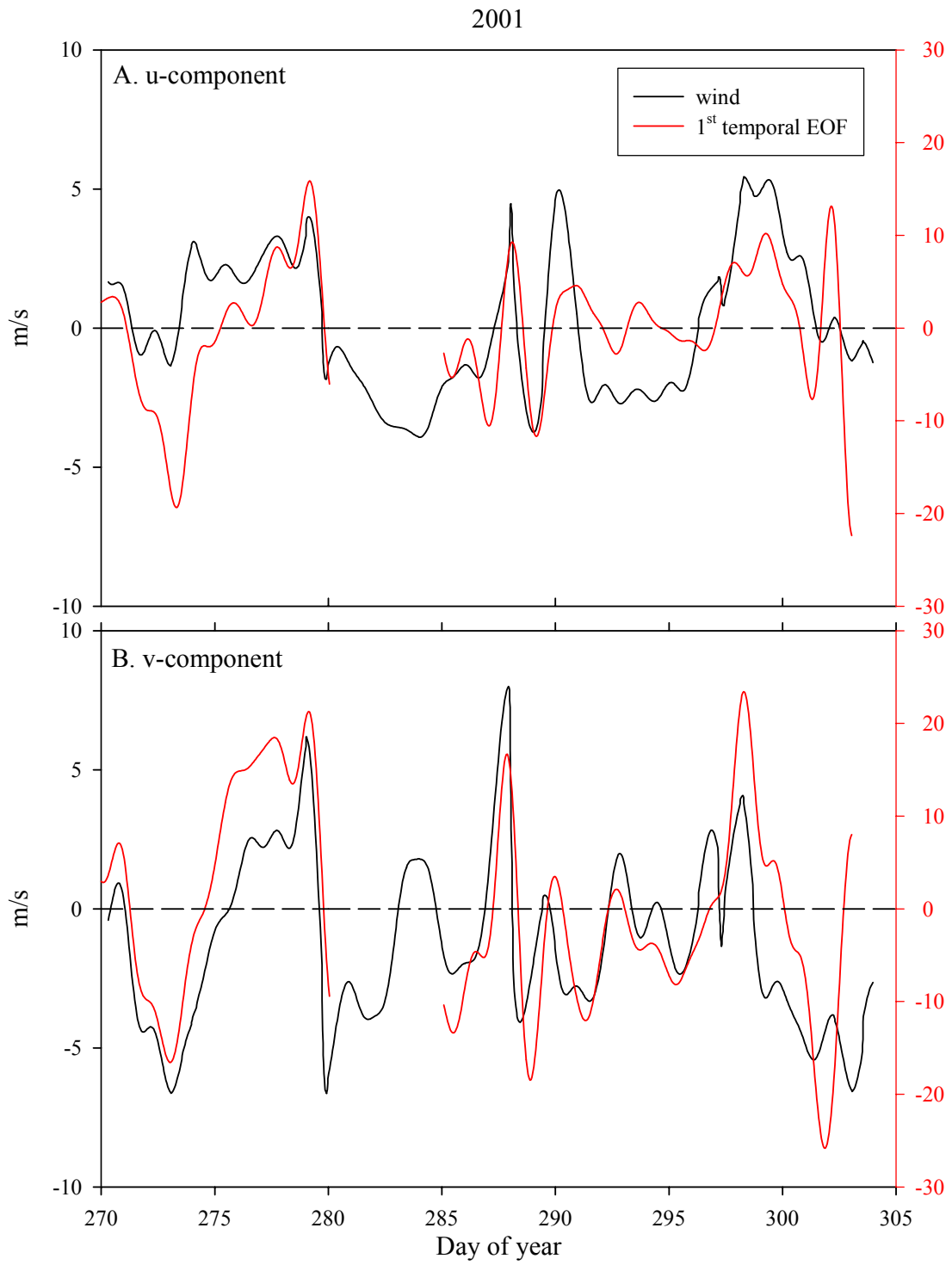
Figure 8

Figure 9

Figure 10

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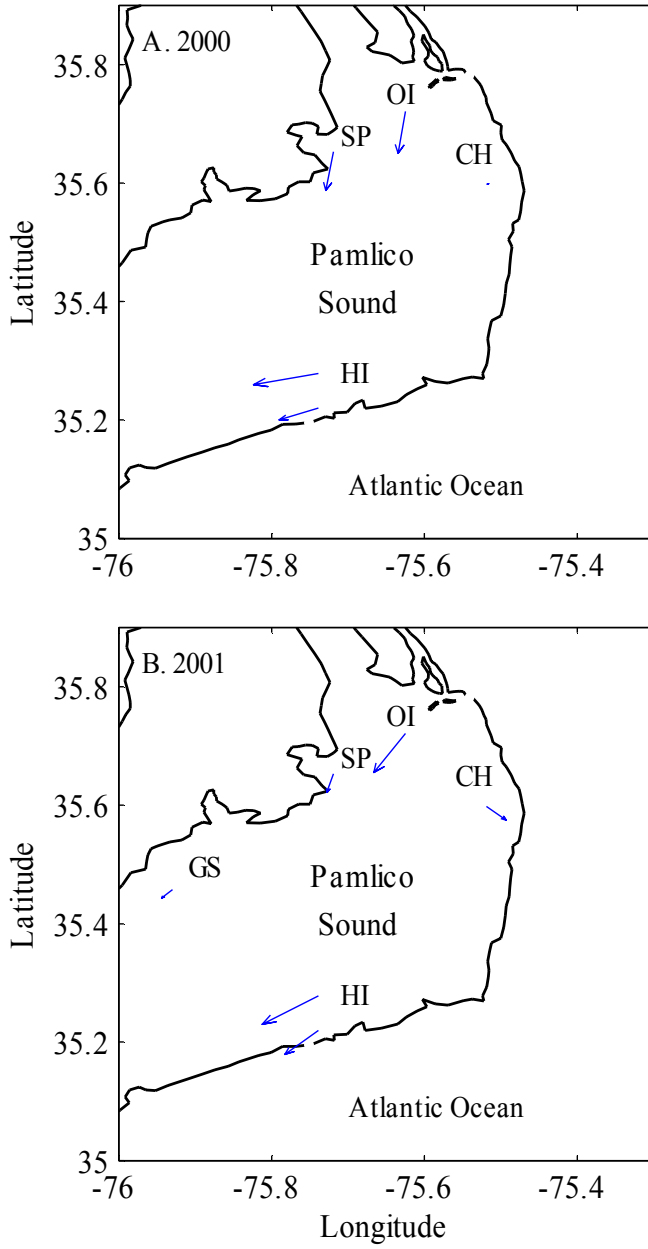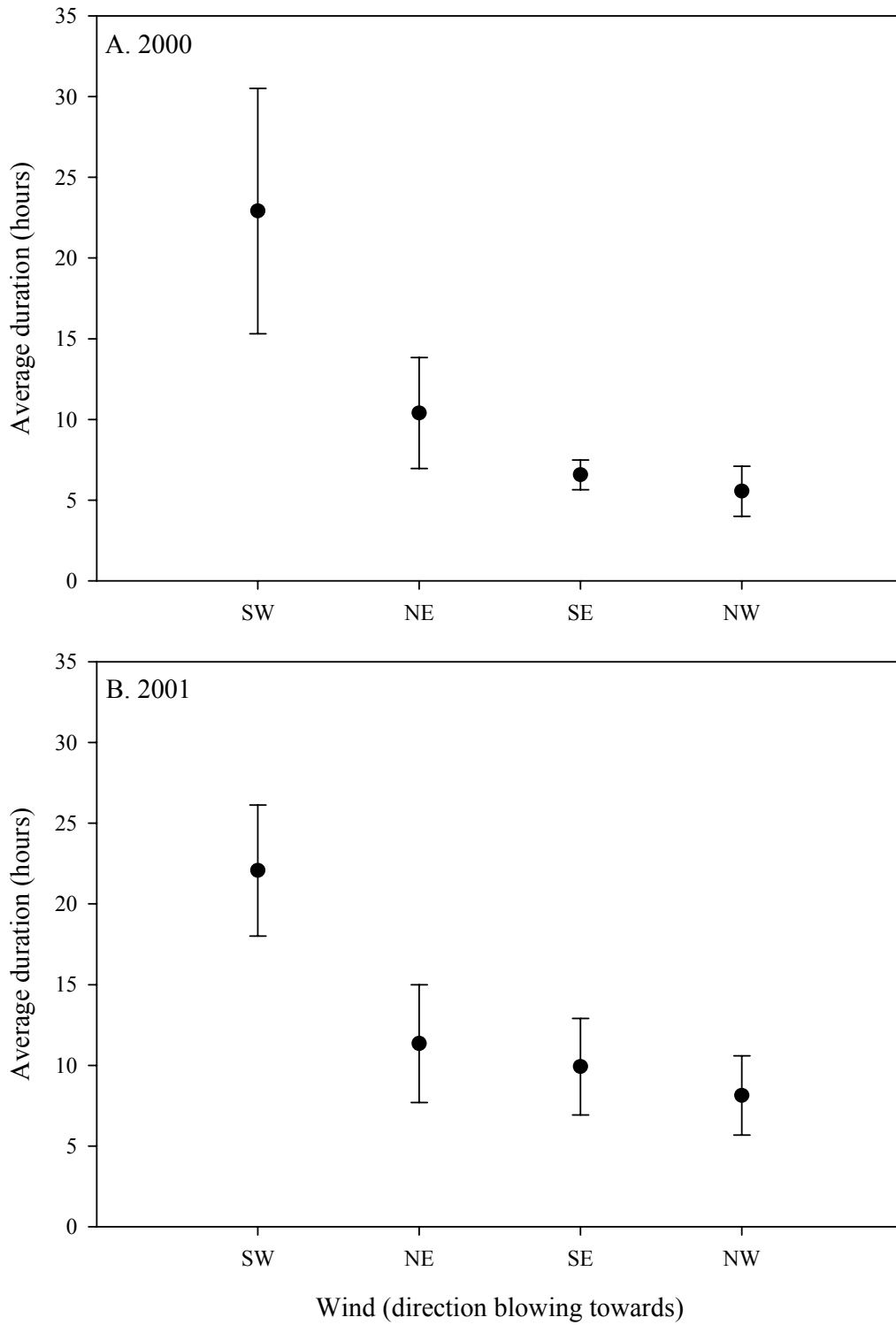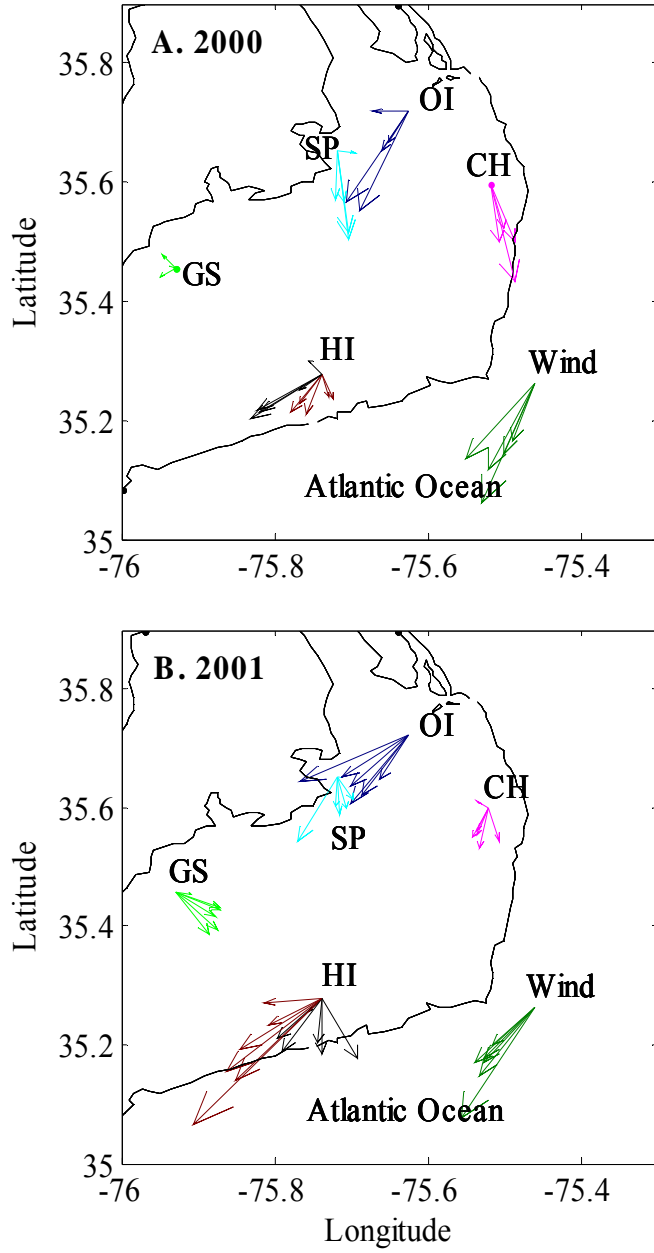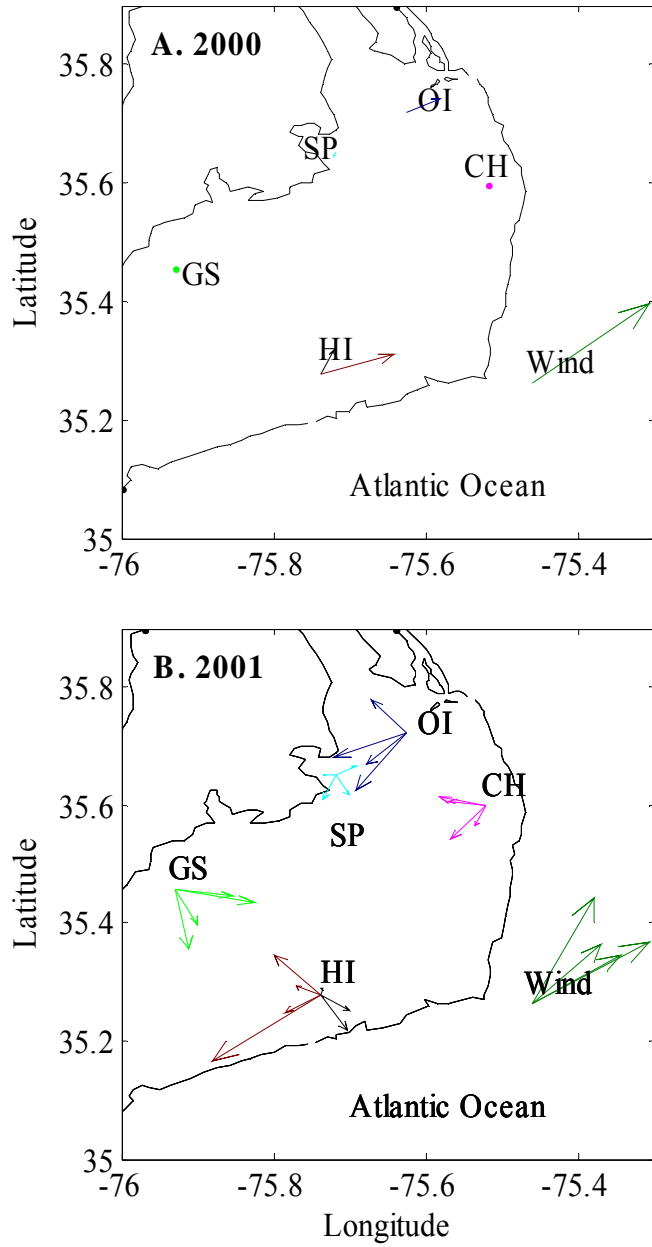
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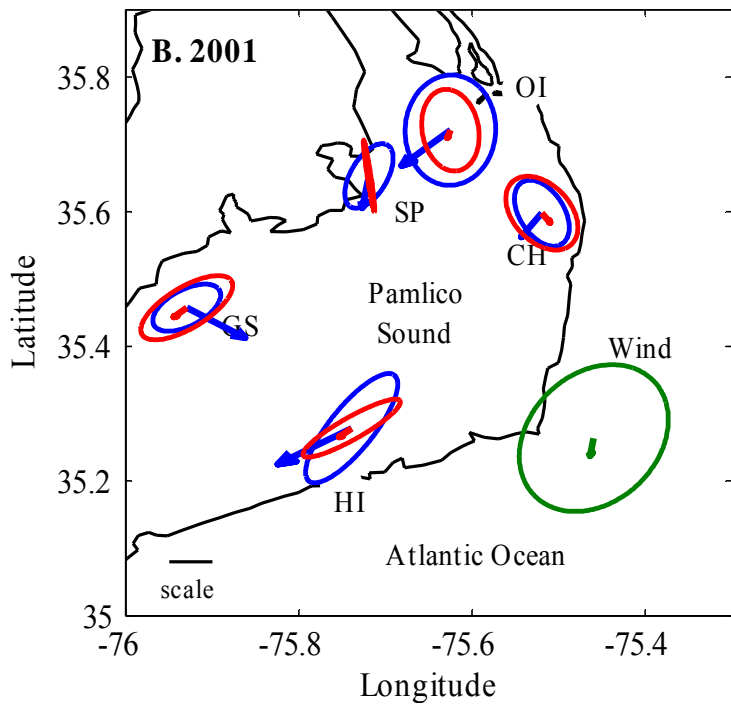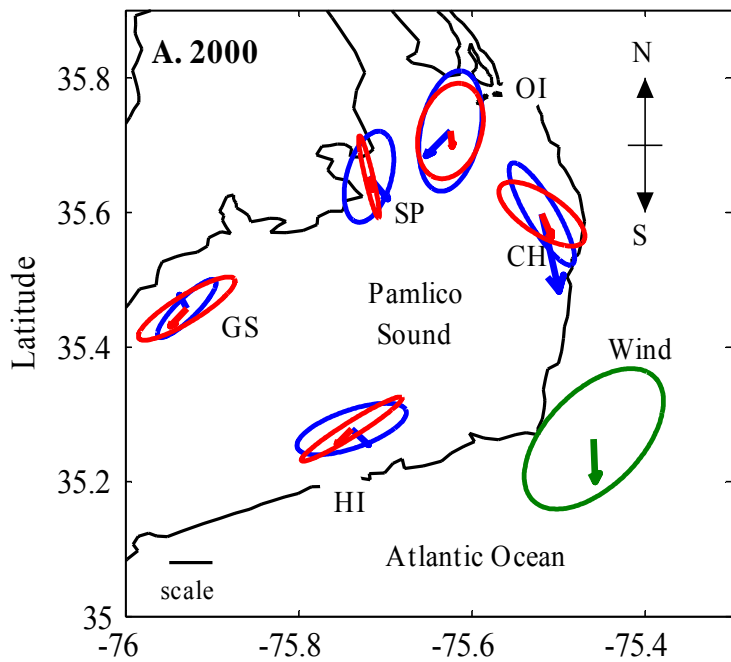
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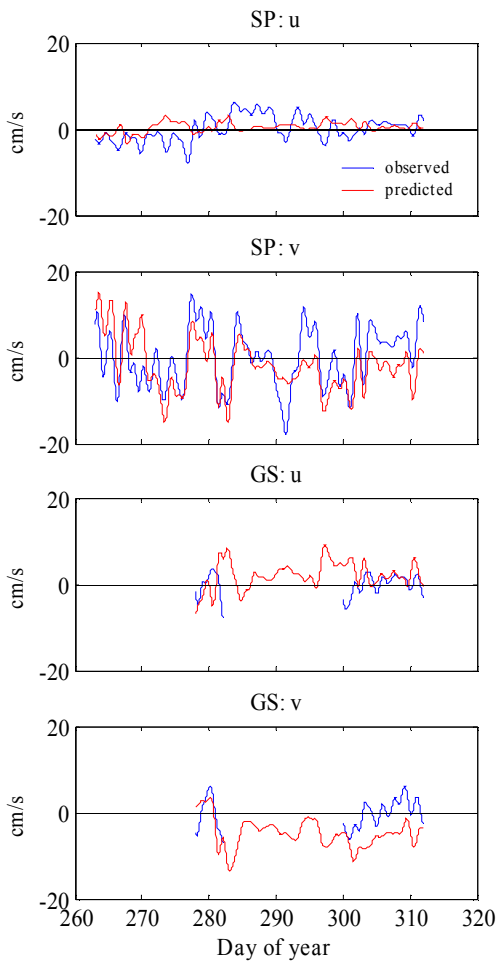
Western Sound   Eastern Sound

Figure 14

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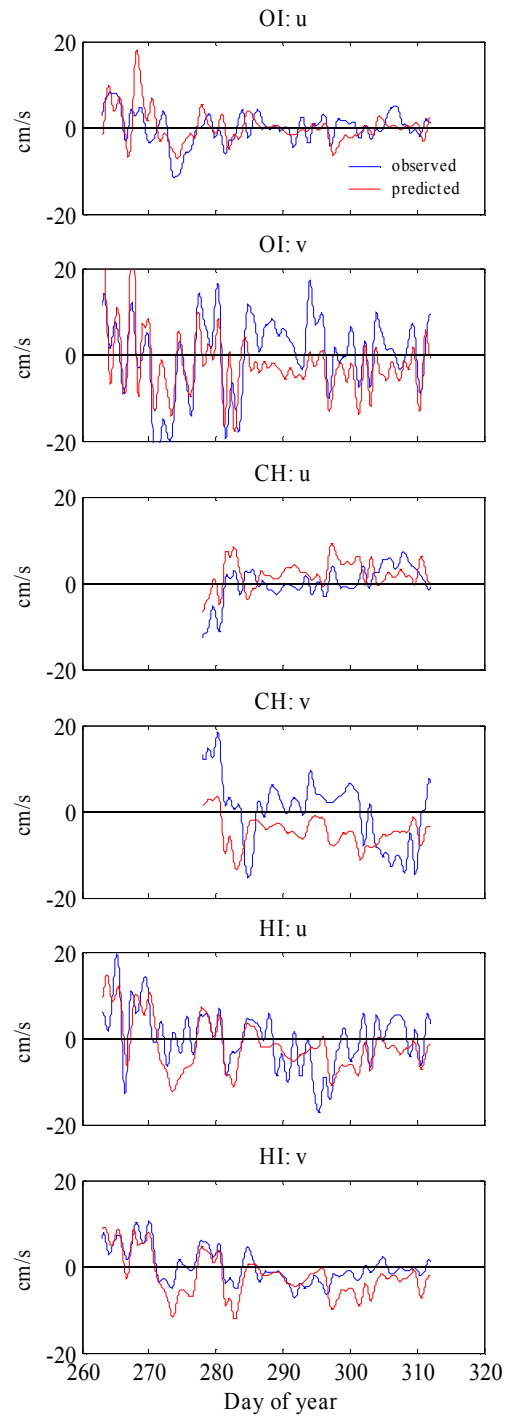
2001

Western Sound　　　　　　　　　　Eastern Sound

Figure 15

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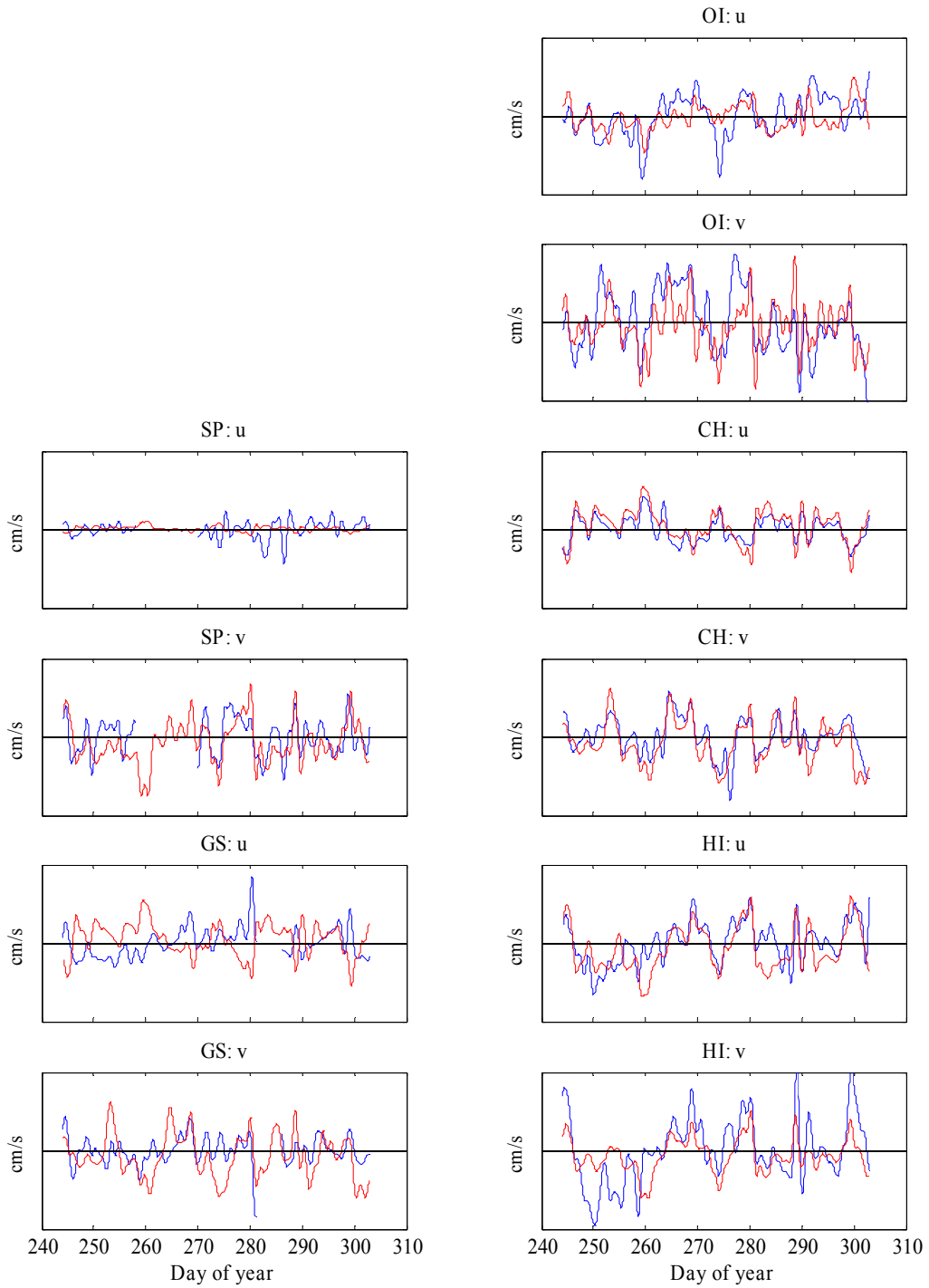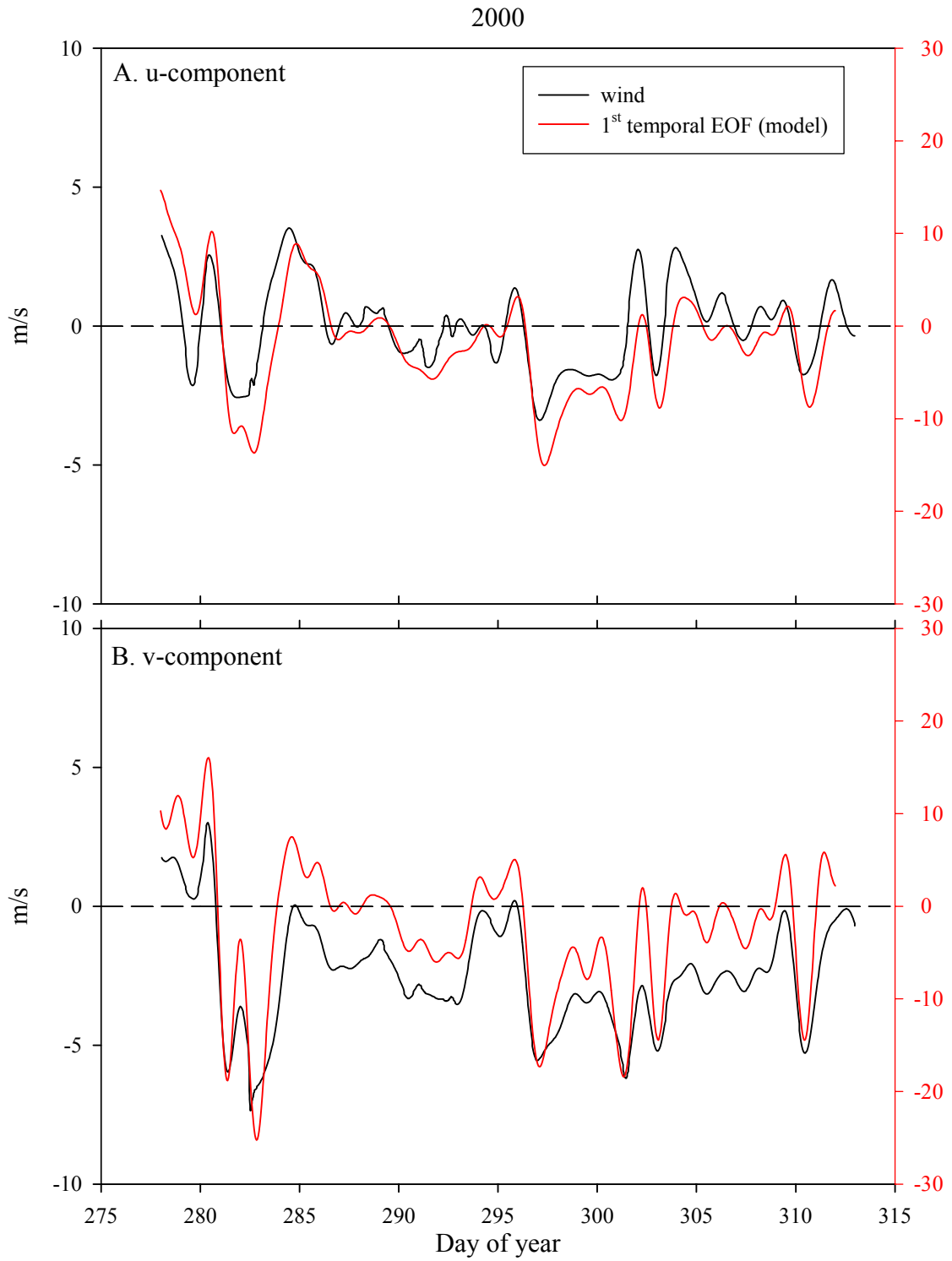
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Figure 17

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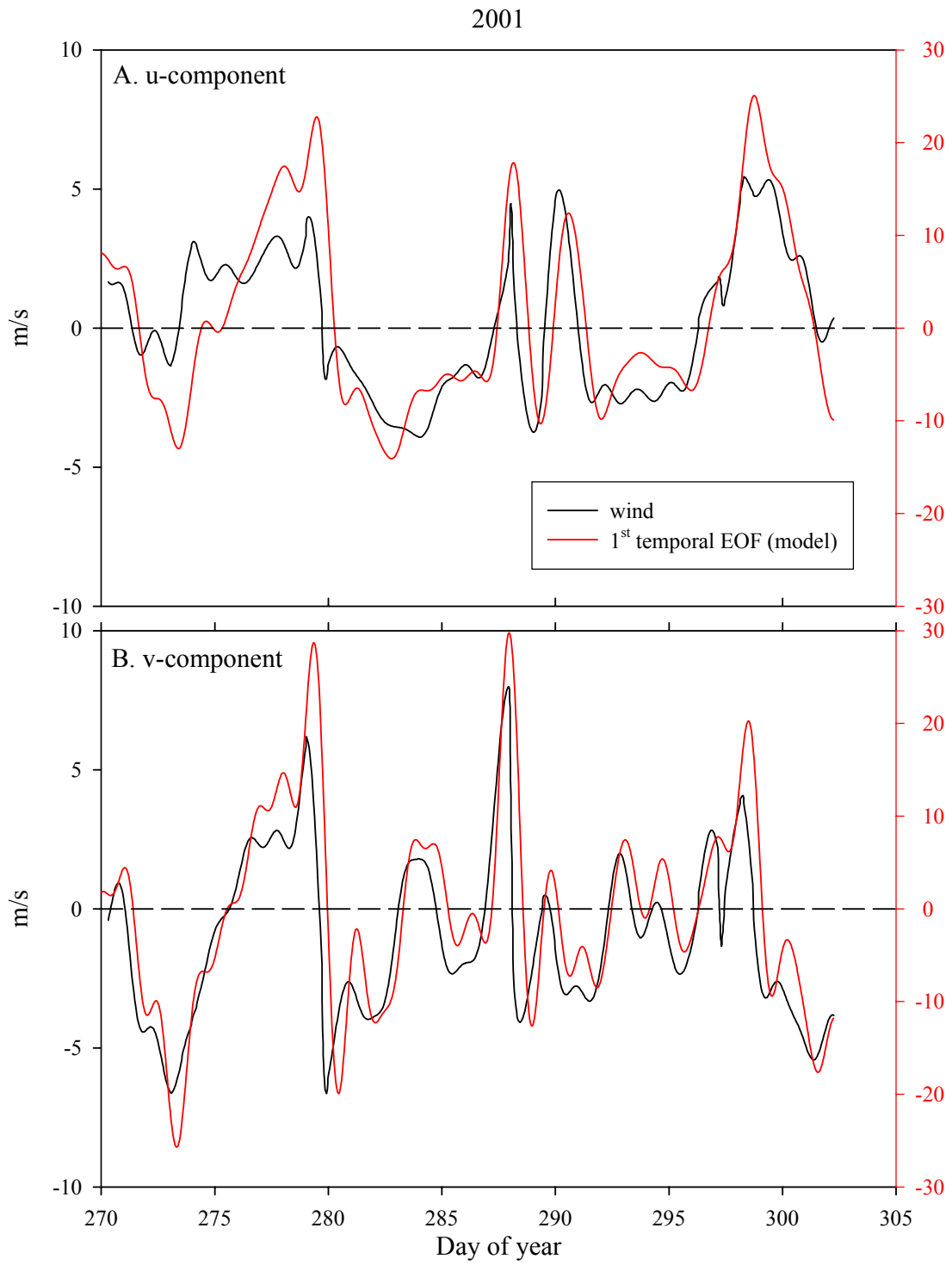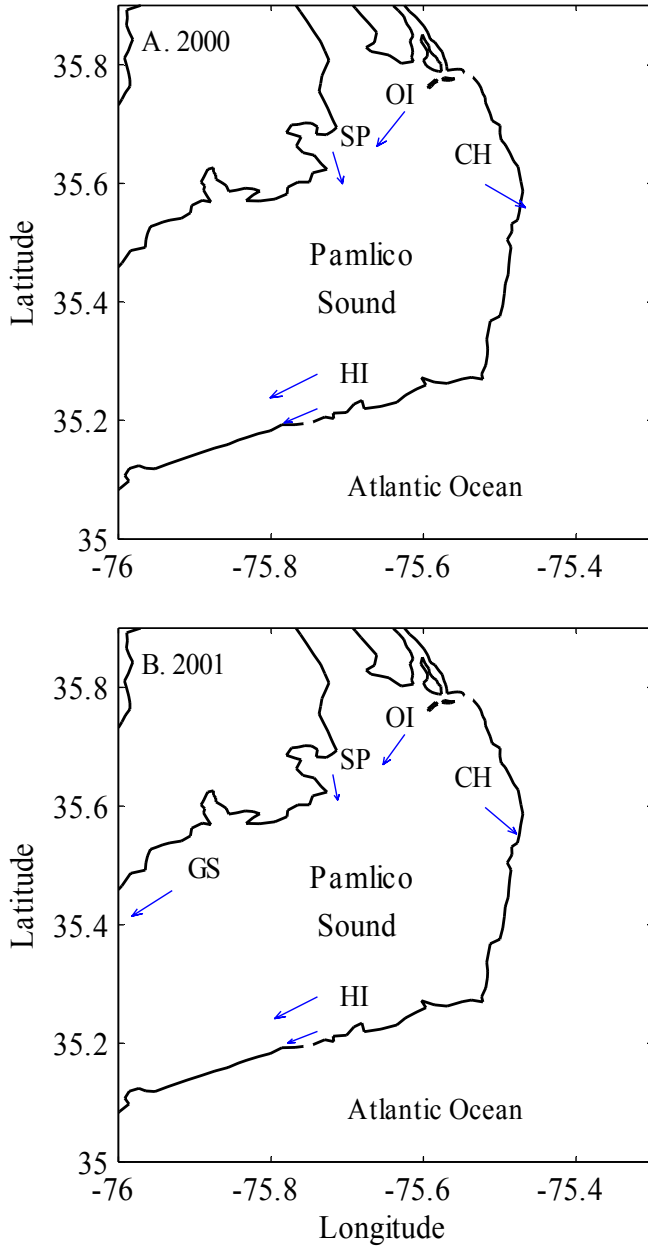
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Figure 19

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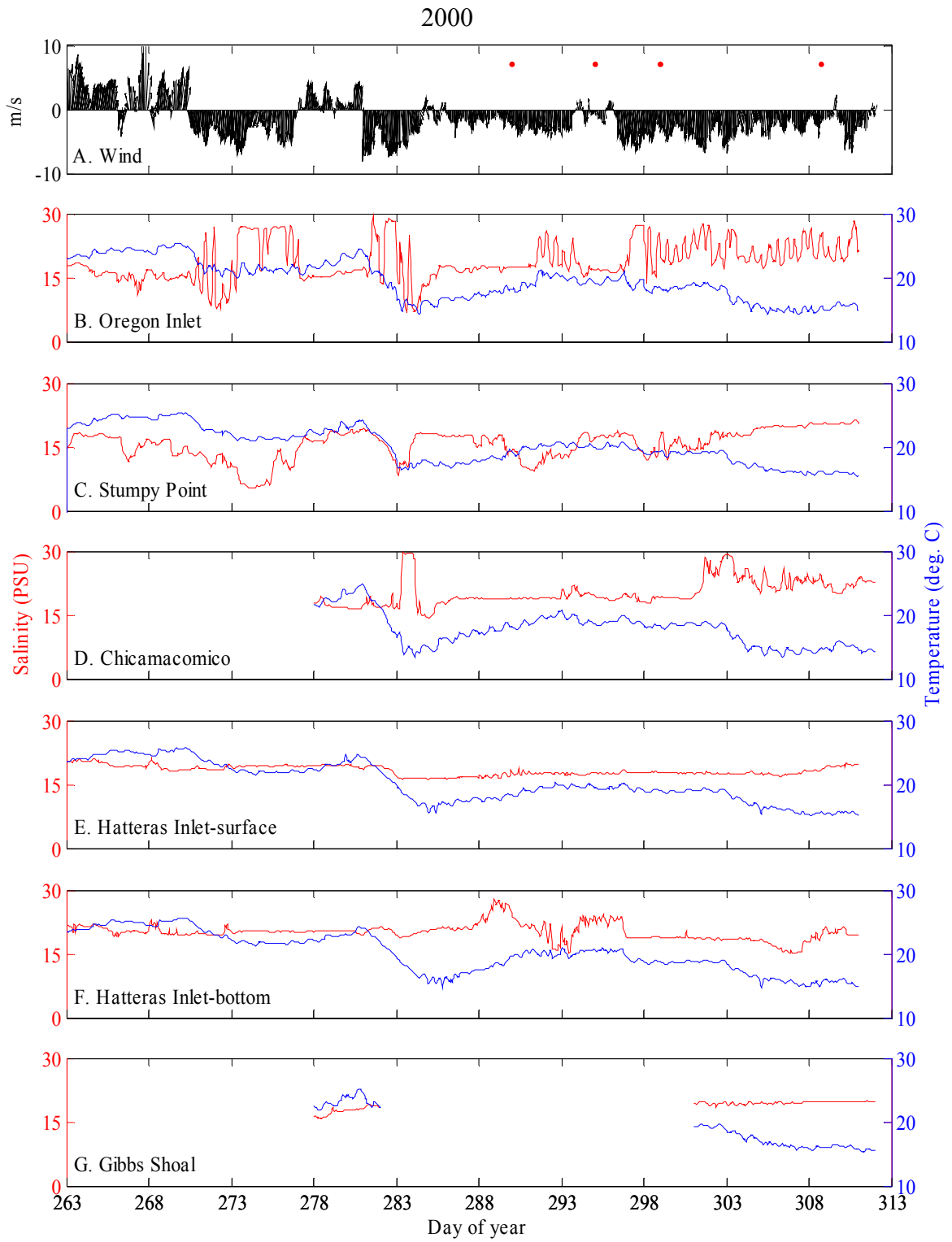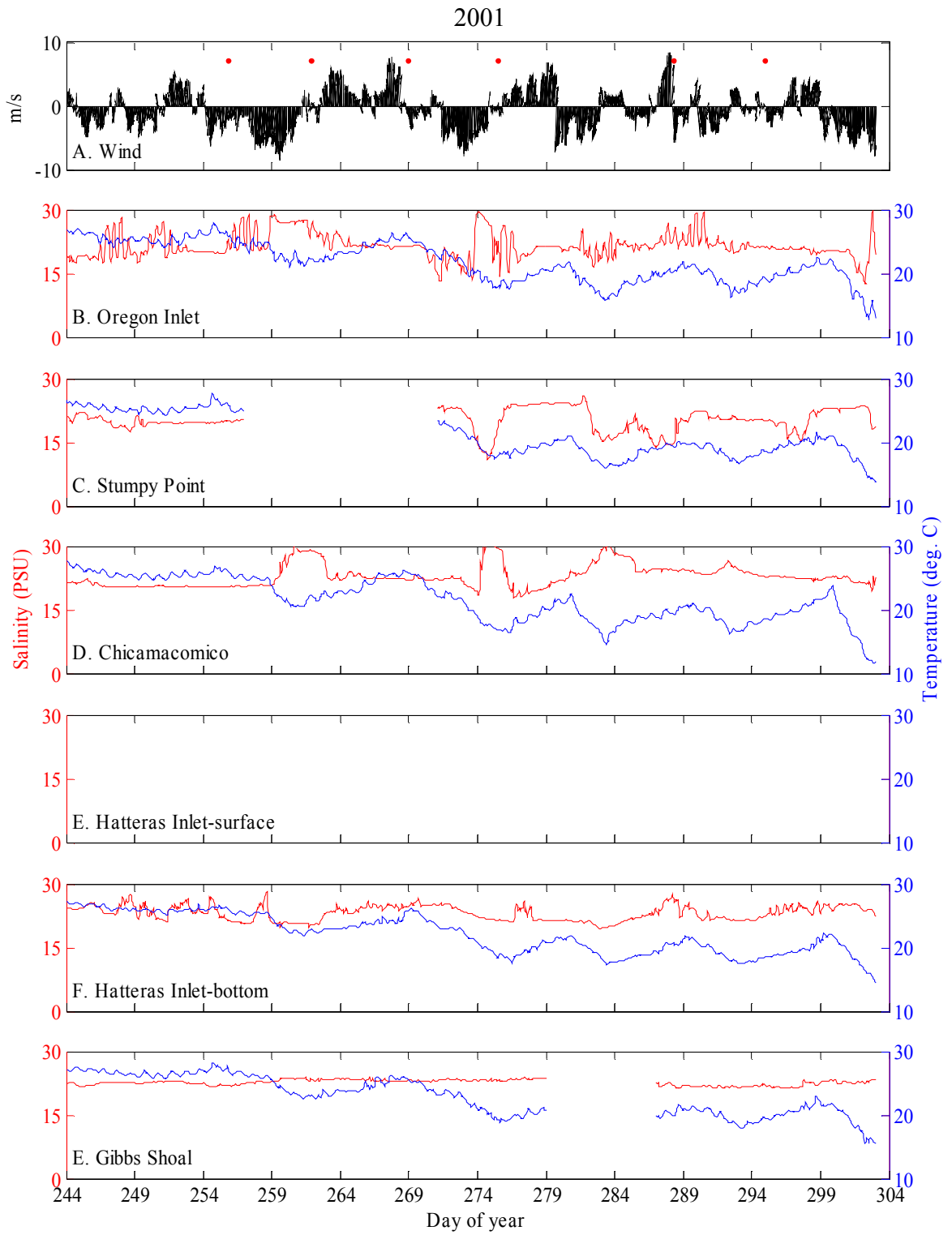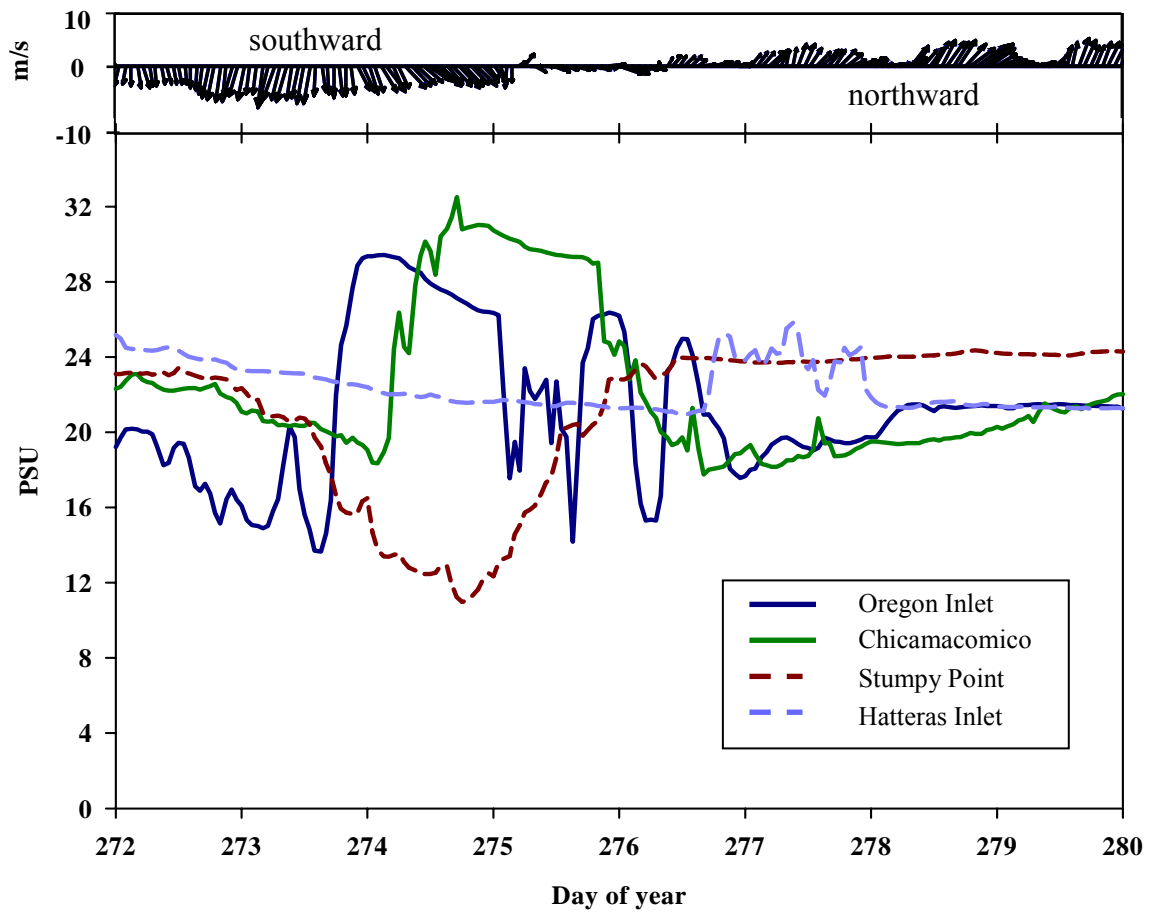
Figure 20

Figure 21

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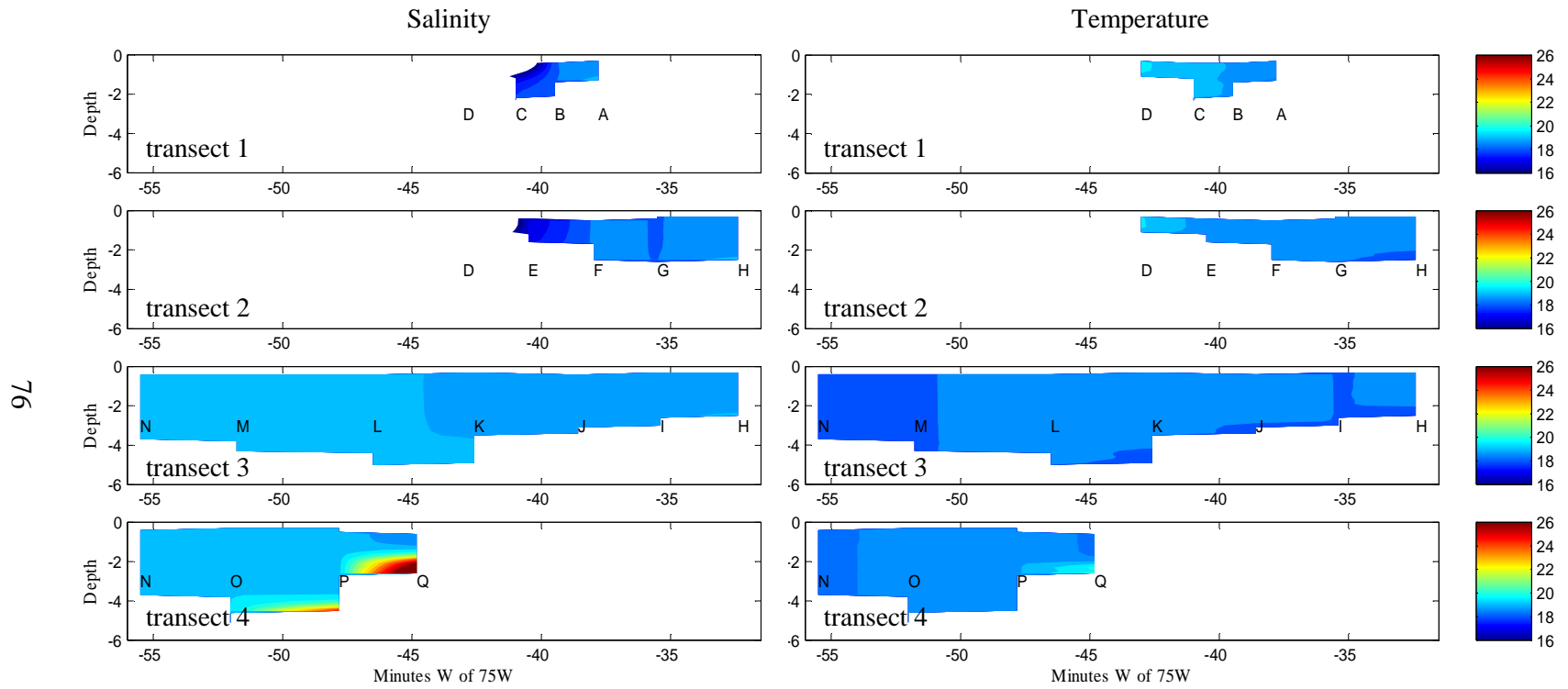
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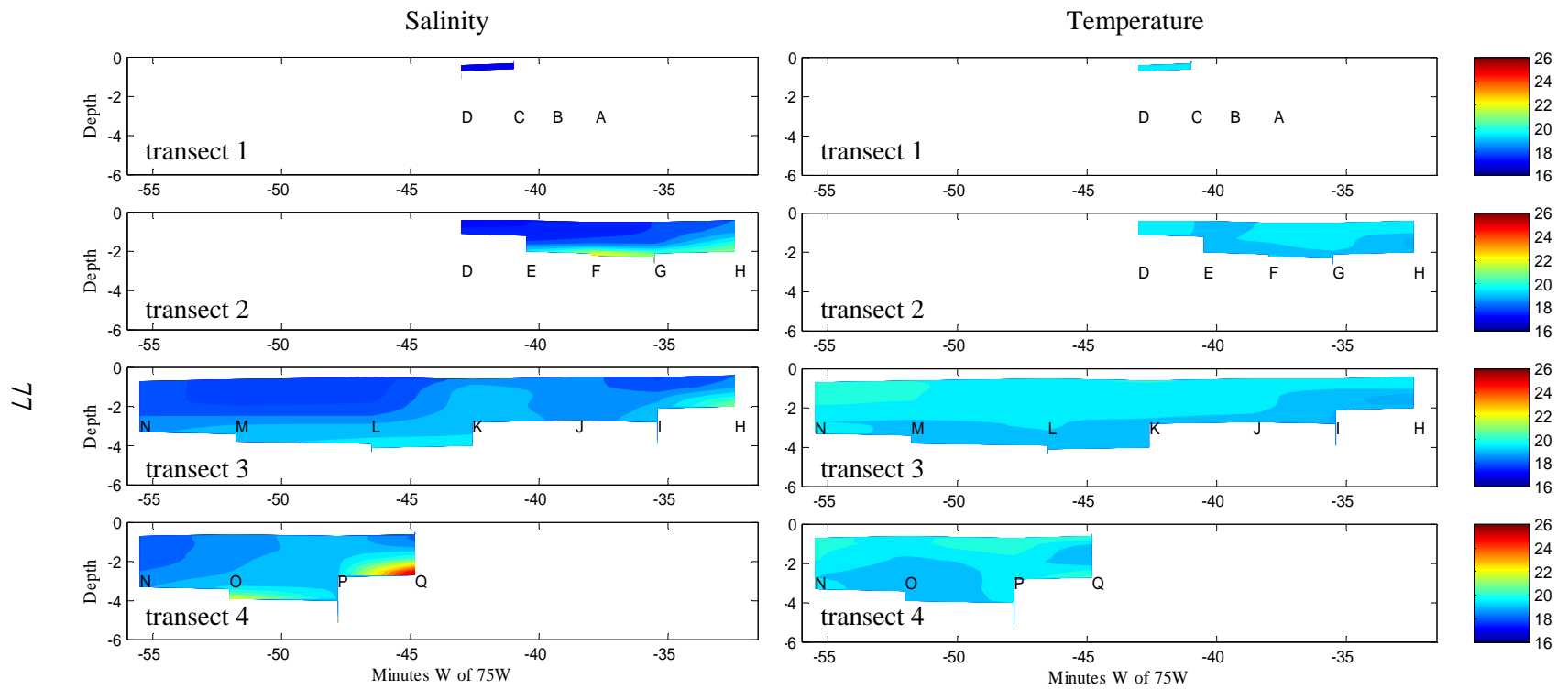
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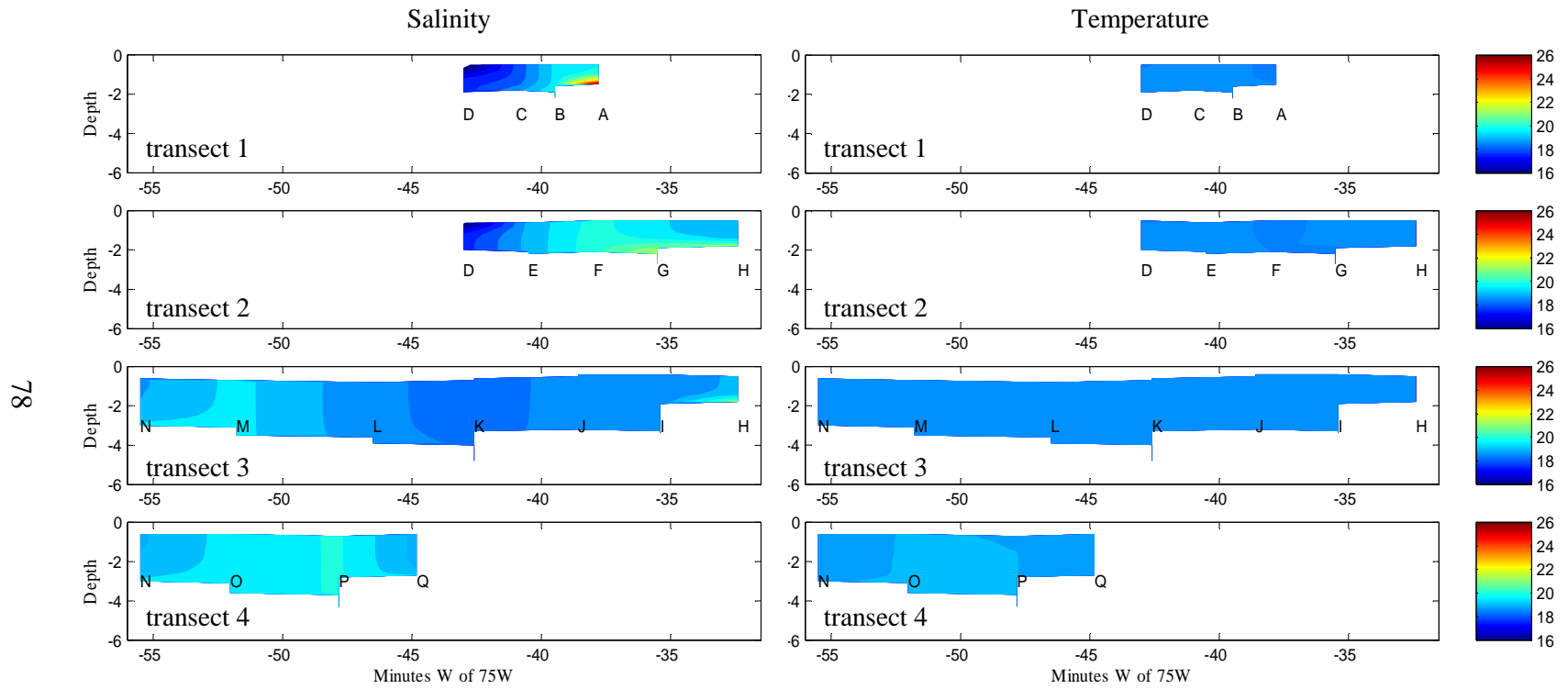
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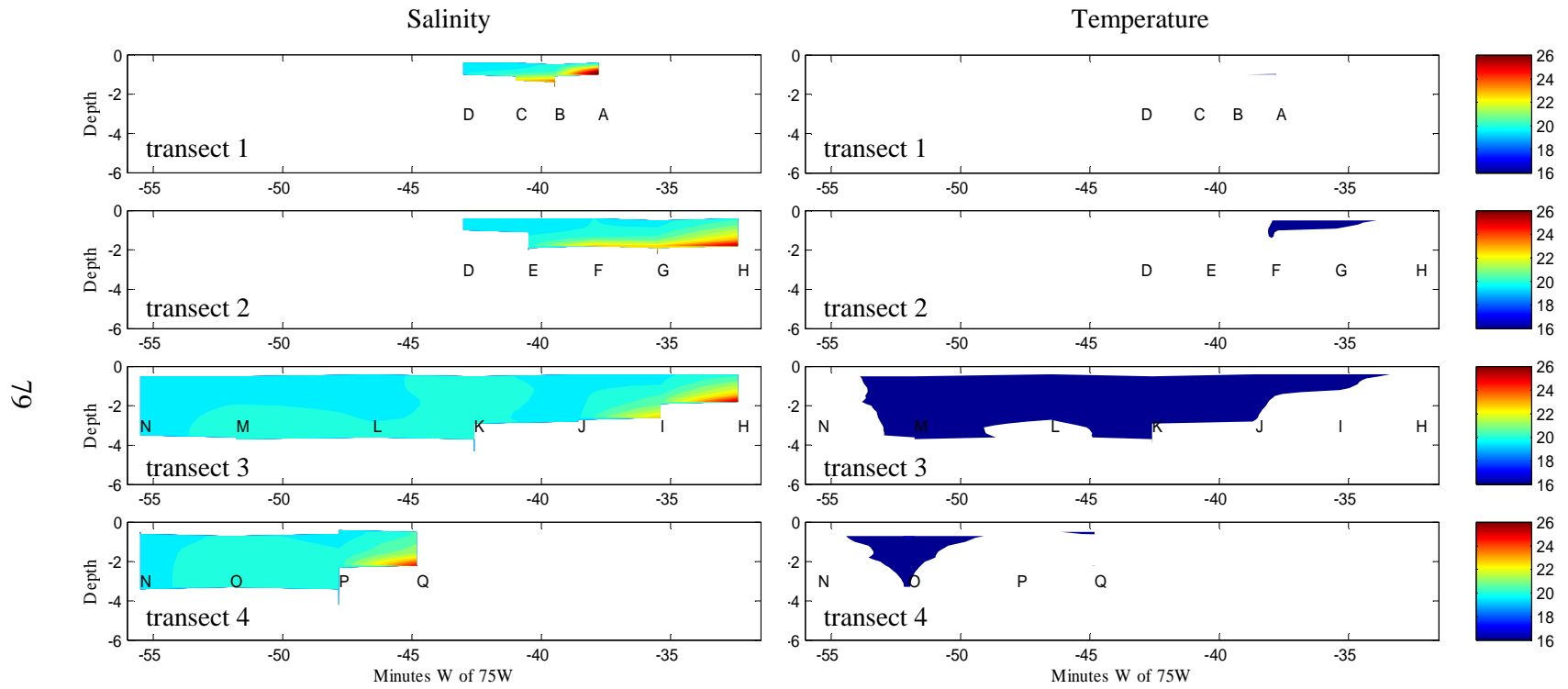
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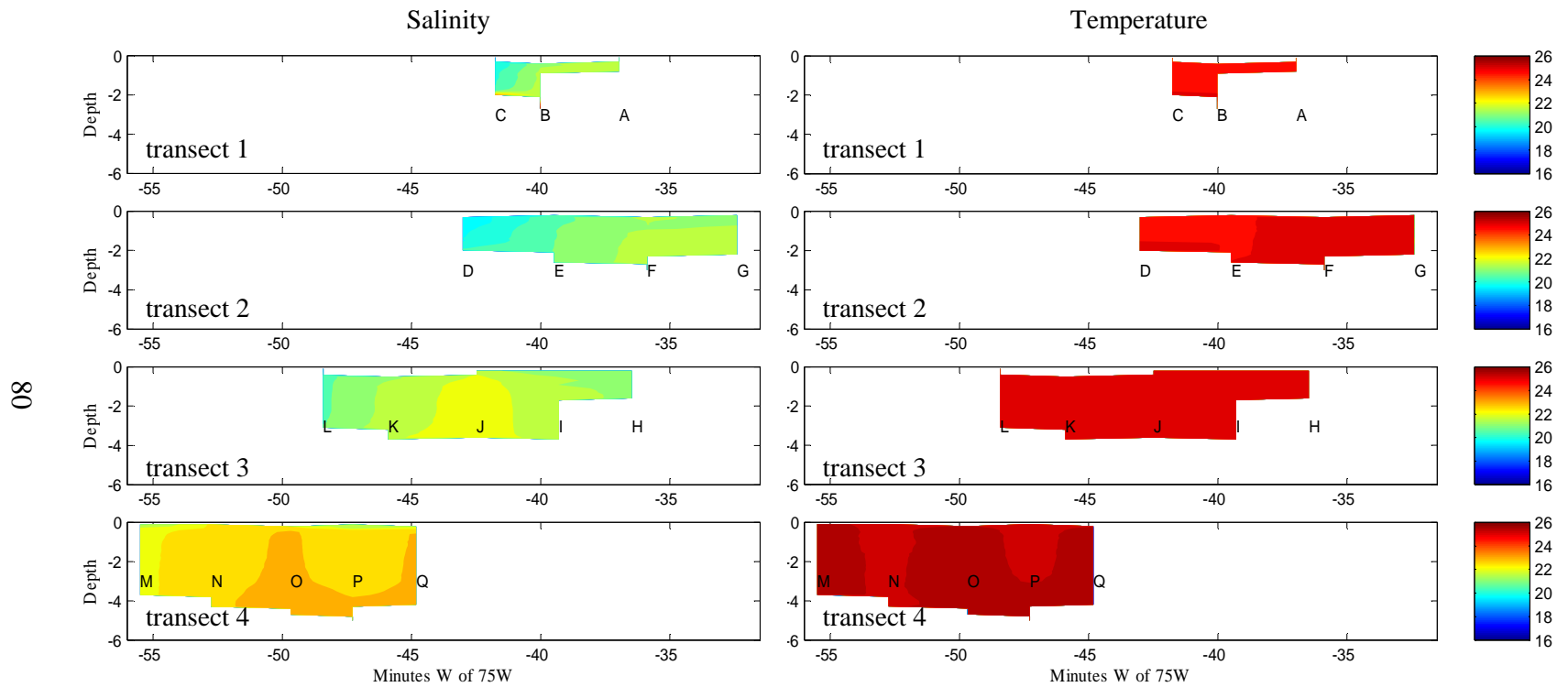
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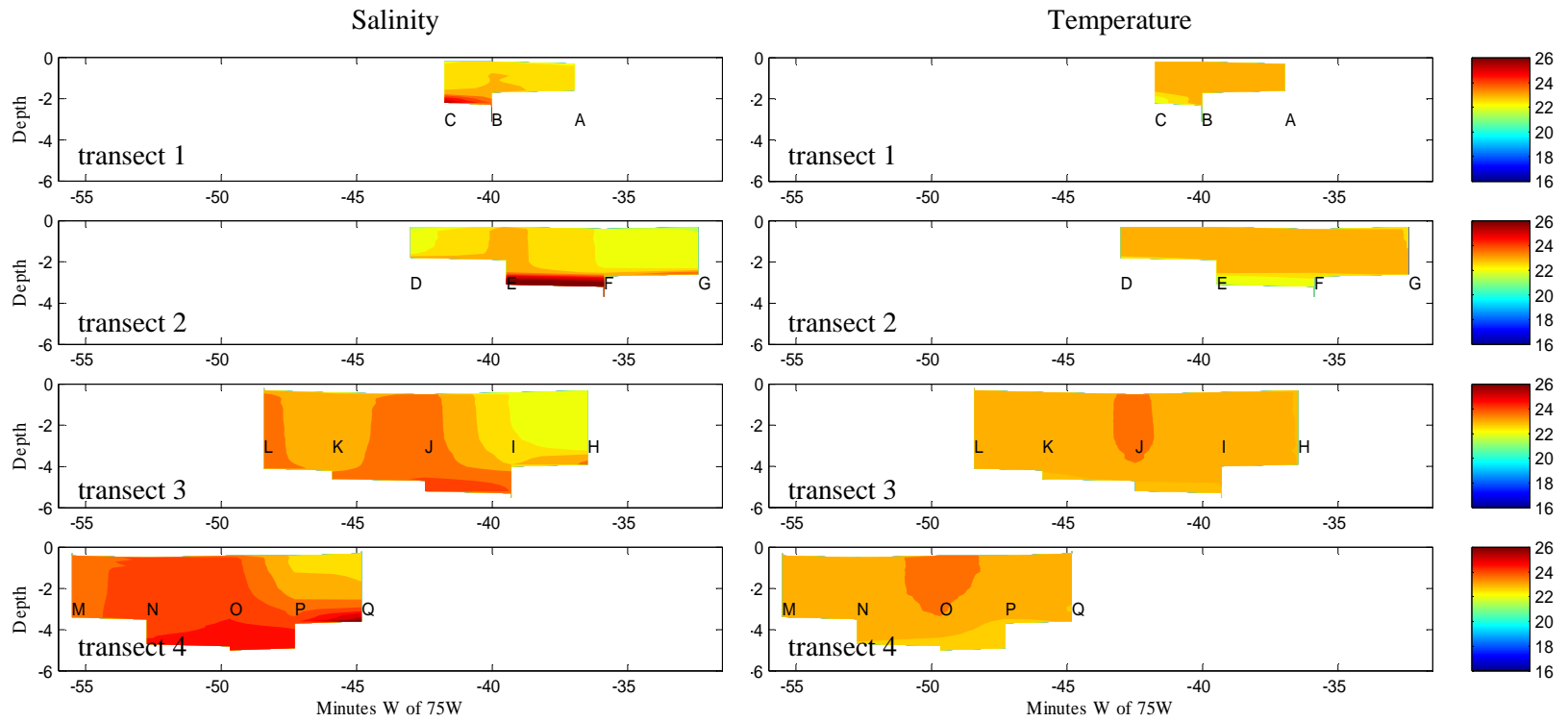
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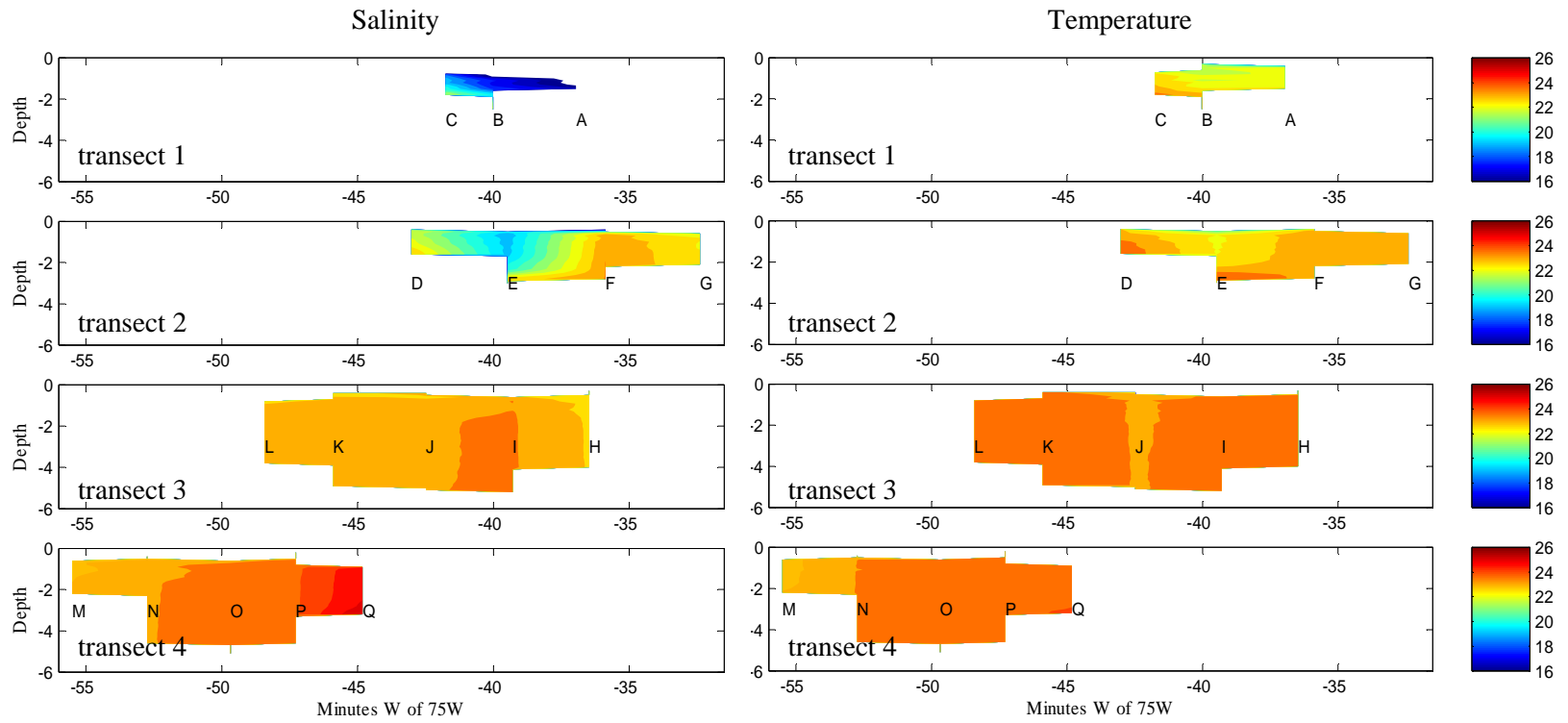
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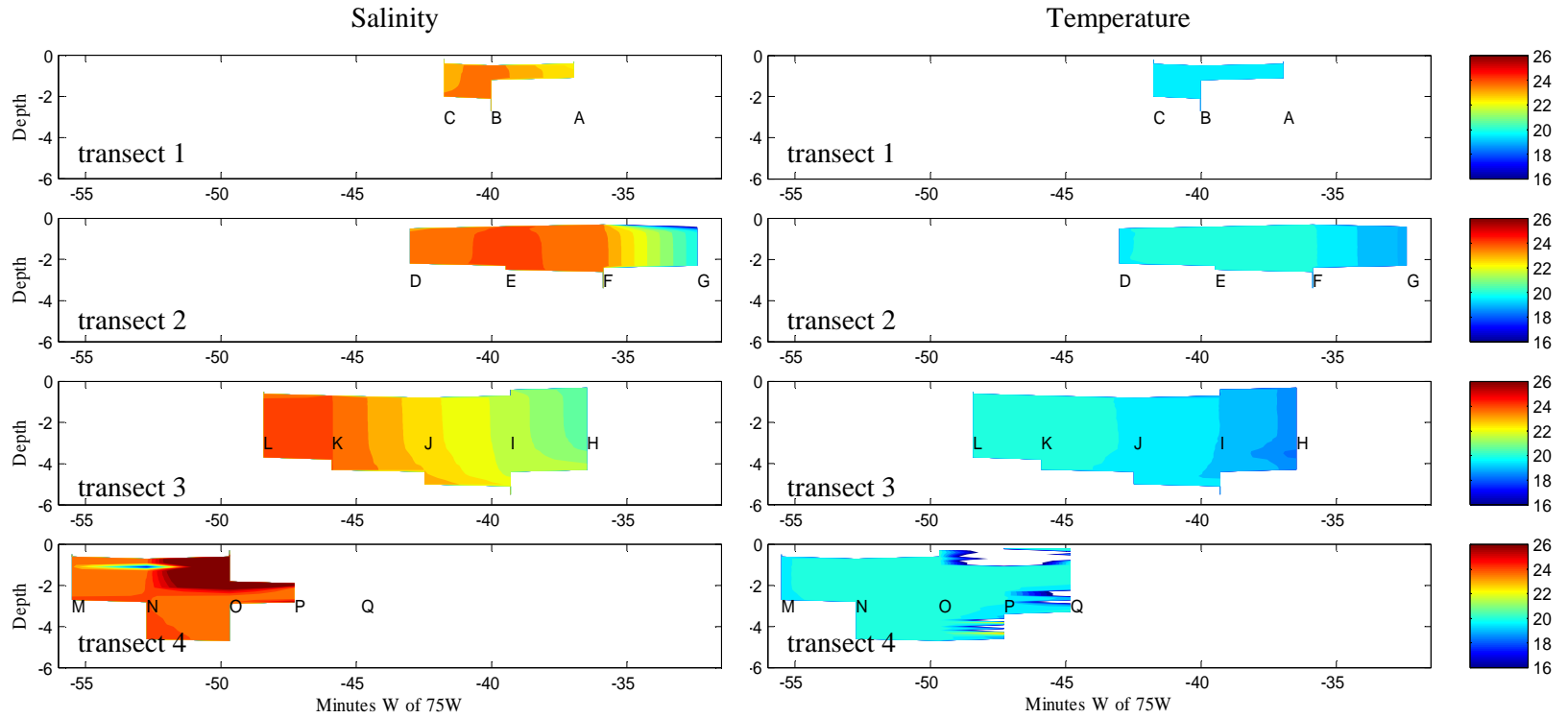
Figure 29

2001: Day 288 (night)

Salinity

Temperature

transect 1

transect 1

transect 2

transect 2

transect 3

transect 3

transect 4

transect 4
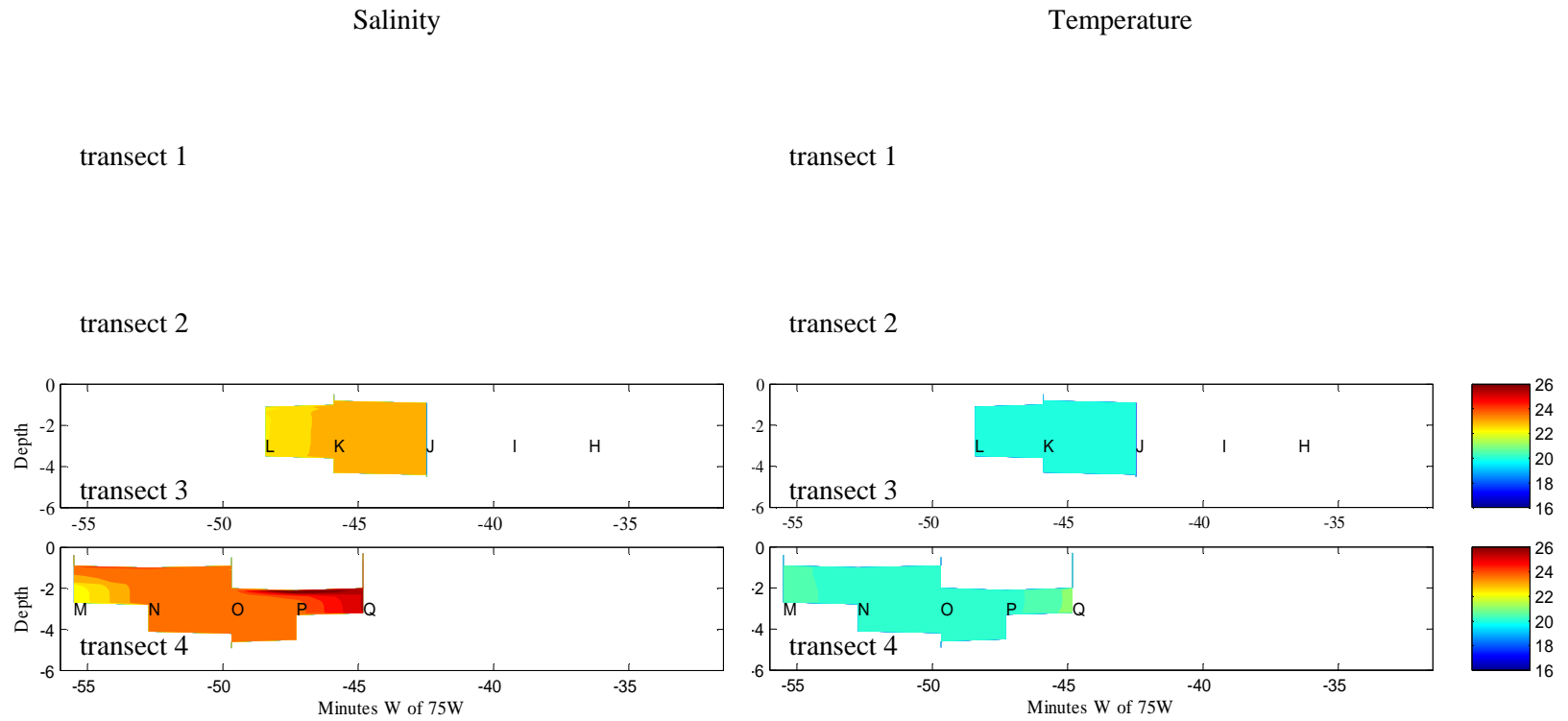
Figure 30

2001: Day 296 (night)
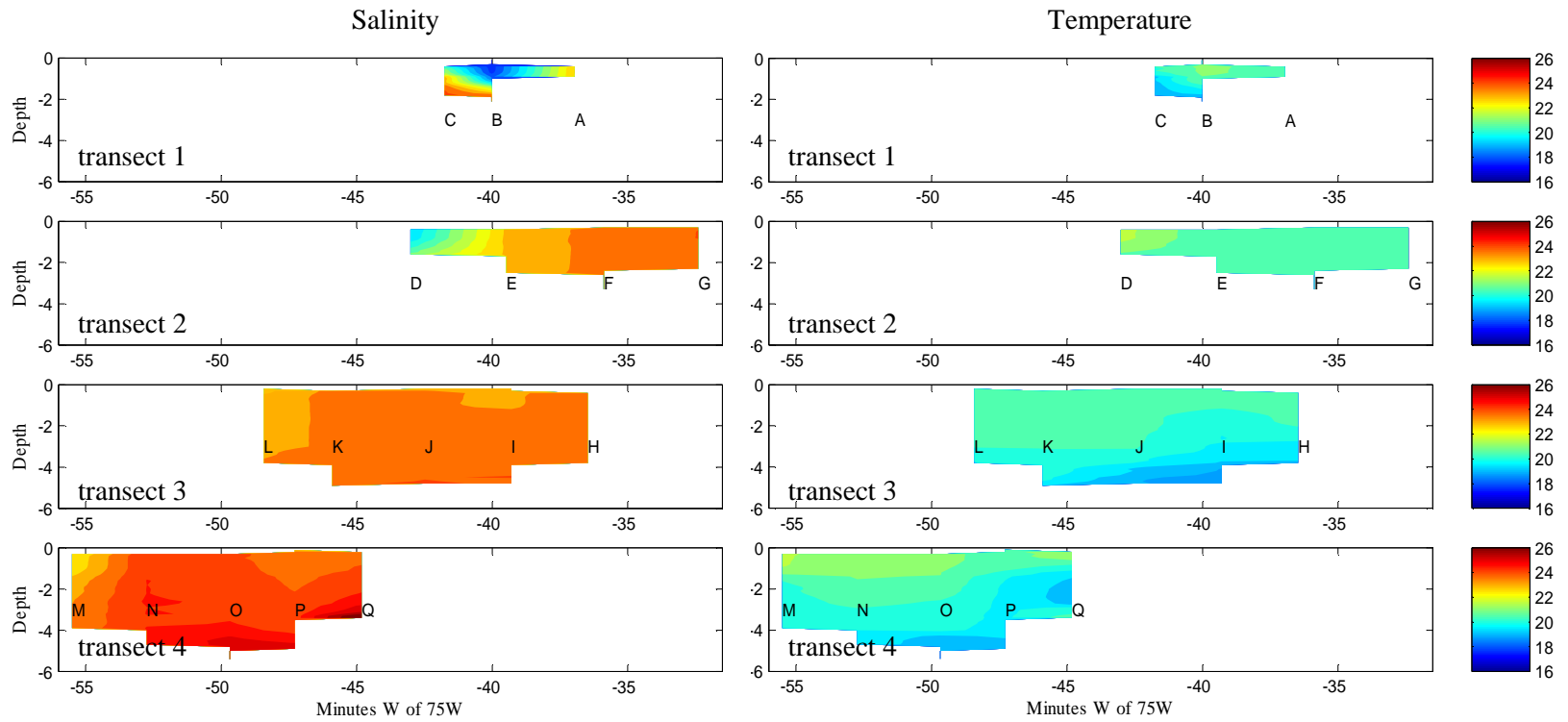
Figure 31

CHAPTER 2

DISPERSAL DYNAMICS OF POSTLARVAL BLUE CRABS, *CALLINECTES SAPIDUS*, WITHIN A WIND-DRIVEN ESTUARY

ABSTRACT

For many crustacean and fish species, successful estuarine recruitment to juvenile nursery habitats is dependent on the biophysical processes experienced during dispersal of the early life stages. To determine how postlarval blue crab (*Callinectes sapidus*) dispersal occurs within Pamlico Sound, NC, USA, a predominately wind-driven estuary, we quantified postlarval supply at two inlets, and sampled during multiple 24-hr periods over two years (2000-2001) to relate the spatiotemporal distribution of postlarvae in the water column (plankton tows) with circulation patterns (S4 current meters). A hydrodynamic model of the region was used to recreate dispersal trajectories and assess potential transport pathways that link near-inlet and across-sound nursery habitats. Blue crab postlarval abundance (supply) at both inlets was significantly correlated with southwestward winds, and also explained the sound-wide temporal variability in postlarval concentrations. Most postlarvae were collected in surface waters at night, and were consistently distributed within the northwestern region of Pamlico Sound. Particle-tracking simulations suggest that dispersal from the inlets to across-sound nursery habitats only results from the combined use of tidal and wind-driven currents. Our simulation results further indicated that the northern-most inlet (Oregon Inlet) was the primary supplier of postlarval blue crabs throughout 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 habitats was evident from field observations; nursery habitats surrounding these regions should

be prioritized for conservation to maintain the production of early juvenile blue crabs that utilize these habitats.

INTRODUCTION

Marine stocks experience considerable year-to-year population variability; understanding the processes contributing to this variability has long been a goal of fisheries managers (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 United States, most commercially exploited finfish and crustacean species spend a portion of their early life in estuaries (Houde and Rutherford, 1993), and population variability may be a consequence of the extensive larval migrations these species undertake to move from oceanic development/spawning regions to nearshore estuaries. Such larval migrations are generally considered a two-step process, whereby larvae first migrate across-shelf to the coast, and subsequently ingress and disperse up-estuary to reach juvenile nursery habitats (Boehlert and Mundy, 1988). Great strides in elucidating transport mechanisms on the continental shelf and within estuaries have been made, leading to the recognition that coastal oceanography and estuarine circulation, coupled with behavioral responses to environmental conditions by larvae, influence the outcome of successful estuarine recruitment (herein defined as larval/postlarval settlement within a nursery habitat) (see 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 flooding tides and descend to the bottom during ebbing tides (Boehlert and Mundy, 1988; Forward and Tankersley, 2001). Specific environmental conditions that may evoke FTT include changes in olfactory cues, currents, salinity, temperature, hydrostatic pressure and turbulence associated with the tidal phase when mixing between shelf and estuarine waters occurs (reviewed by: Boehlert & Mundy, 1988; Forward and Tankerlsey, 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 microtidal estuaries or systems that lack a predictable tidal signal. Our objective, therefore, was to determine how biophysical factors (postlarval supply, positioning within the water column, winds and currents) drive the dispersal of postlarval blue crabs (*Callinectes sapidus*) within a predominately wind-driven estuary, Pamlico Sound, North Carolina, USA.

The blue crab has a complex life history that is typical of many commercially important estuarine dependent species. Females within estuaries migrate to ocean inlets to spawn, 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 postlarval (megalopal) stage (Van Engel, 1958; Sandifer, 1975). Postlarvae 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, postlarval blue crabs use FTT during estuarine ingress (Forward *et al.*, 2003). More specifically, postlarvae respond to increasing salinity during flood tide by ascending into the water column (Tankersley *et al.*, 1995), and flood-tide associated turbulence keep postlarvae suspended in surface waters until decreasing turbulent kinetic energy at the end of flood tide cues them to descend (Welch *et al.*, 1999). While FTT by blue crabs mediates ingress through tidal inlets and dispersal within tidal estuaries, it is not known how postlarval transport occurs once tidal cues become negligible, such as is the case in the main body of the Albemarle-Pamlico Estuarine System (APES).

Study area

Our study was conducted within the APES, which is the largest (area ~ 6000 km^2) lagoonal estuary in the United States (Fig. 1A). The APES 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 and penaeid shrimp (*Penaeus aztecus*, *P. duorarum*, *P. setiferus*). Blue crabs support North Carolina's most commercially valuable fishery, with 88 % of landings in the state coming from within the APES (Henry and McKenna, 1998). The APES is bounded by a barrier island chain that limits exchange with the

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coastal ocean to three main, relatively small (~ 1 km wide) inlets: Oregon, Hatteras and Ocracoke (Fig. 1A). Although the inlet regions experience semi-diurnal tides, tidal influence quickly diminishes with distance from the inlets, and circulation within the shallow (mean depth ~ 4.5 m) main body of the APES is predominately wind-driven (Pietrafesa *et al.*, 1986b). Thus, for postlarval crustaceans and fishes that utilize estuarine nursery habitats, ingress through the inlets and dispersal within the APES must occur under a range of physical forcing mechanisms.

Within the APES, previous investigators have hypothesized that following ingress through the inlets, demersal juvenile fishes such as spot, croaker and 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 towards the south-southeast to north-northeast generated near-bottom currents favorable for transport of juvenile fishes 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 up-estuary (i.e., 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 are not well understood. Given that currents can directly influence recruitment and subsequent

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year-class strength (Norcross, 1991), understanding the spatiotemporal dynamics of dispersal during the early life stages is of particular importance for the prioritization of nursery habitats for fisheries management and conservation.

While one study has simulated estuarine circulation to identify patterns of estuary-coastal ocean exchange within the APES, with implications for larval transport of estuarine organisms (Xie and Eggleston, 1999), to our knowledge, researchers have yet to explicitly couple measures of dispersal and circulation to examine potential transport pathways within the APES. In our study, we quantified postlarval settlement of blue crabs at the inlets (as a proxy for supply), examined the abundance and distribution patterns of postlarvae within the sound, and characterized the circulation within our study area to determine how across-sound dispersal occurs within a wind-driven system. We then utilized a 3D hydrodynamic model coupled with a particle-tracking algorithm to establish which inlets serve as primary sources of postlarval blue crabs to Pamlico Sound, and to examine the dispersal trajectories of these crabs under specific wind conditions. While we focus on blue crabs, our results are relevant to the dispersal dynamics of other commercially important species that utilize estuarine nursery habitats within predominately wind-driven systems.

METHODS

All sampling took place during peak blue crab recruitment, between September and October, in 2000 and 2001. Given the relatively large size of the APES region, we concentrated our research efforts on the northern basin of Pamlico Sound (bounded by

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Oregon Inlet to the north and Hatteras Inlet to the south; Fig. 1A). This area was selected because it experiences relatively high postlarval supply of blue crabs (D. Eggleston, unpublished data), 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). The mid-sound region is characterized by mud and sand and is devoid of structured aquatic vegetation (N. Reyns, unpublished data).

Postlarval settlement at inlets

The spatial and temporal settlement dynamics of postlarval blue crabs within Pamlico Sound depends, in part, on postlarval supply to the region. We quantified postlarval settlement to our study area as a proxy for supply using standardized artificial settlement substrates constructed from 16.3 cm diameter x 37.5 cm length polyvinyl chloride pipes covered by sleeves of 'hogs-hair' air-conditioning filter material (as described in Metcalf *et al.,* 1995). These settlement substrates have been used extensively along the Atlantic and Gulf coasts of the United States to measure the relative magnitude of postlarval supply in blue crab settlement studies (e.g. Metcalf *et al.*, 1995; Rabalais *et al.*, 1995; van Montfrans *et al.*, 1995; Wrona *et al.*, 1995; Morgan *et al.*, 1996).

We deployed settlement substrates at U.S. Coast Guard facilities located within 4 km of Oregon and Hatteras Inlets (Fig. 1A). At each site, three replicate collectors were suspended below the surface of the water from docks, and deployed for a 24 h period. Deployment/retrieval generally occurred between 1500 h and 1700 h. Upon retrieval, each collector sleeve was rinsed with freshwater following standard protocols (Metcalf *et al.*, 1995), and postlarvae were sieved and preserved in 70 % ethanol for enumeration and identification in the laboratory.

The response variable, the average number of postlarvae per collector per site, was calculated for each 24 h period. During our study, gaps in sampling did not exceed 3 d. Blue crabs remain in the postlarval stage for about 5 d (Wolcott and De Vries, 1994); therefore, to account for the accumulation of postlarvae on days not sampled, daily postlarval abundance was estimated by averaging the number of postlarvae collected on the day sampling resumed, over the total number of sampling days missed.

Sound-wide spatiotemporal distribution of postlarvae

To quantify the distribution and abundance of postlarval blue crabs throughout 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 4 day-night cruises, while in 2001 we completed 2 day-night cruises and 4 nighttime-only cruises.

At each station, the vertical distribution of crabs within the water column was measured by simultaneously towing a neuston (surface measure) and plankton net mounted to a benthic sled (near-bottom measure). Both nets measured 1 m x 0.5 m, had 505 μm mesh, and were equipped with General Oceanics flow meters. Nets were towed for 5 min at about 1 knot, and a pilot study determined filtration efficiency of both nets towed in this manner to be near 100 % (N. Reyns, unpublished data). Following deployment, net collections were immediately sieved and preserved in 70 % ethanol, and postlarval blue crabs were enumerated and identified in the laboratory. Counts were standardized to concentrations, defined as number of crabs 100 m^{-3}.

Hydrographic data

To characterize the circulation within our study area in Pamlico Sound, we deployed six InterOcean S4 electromagnetic current meters at five locations surrounding our collector and plankton stations (Fig. 1A). Current meters were positioned near-surface (1 m below surface) at all locations except for Hatteras Inlet, which had an additional instrument positioned near-bottom (1 m above bottom). Current meters were configured to record current speed and direction, conductivity, temperature and pressure for 2 min every 20 min. Instruments were cleaned weekly to minimize the effects of biological fouling. Because we were interested in examining the relationship between wind-forcing and circulation within Pamlico Sound, we also obtained hourly wind speed and direction data collected by the NOAA National Weather Service at 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 principle 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.

Analyses

We used cross-correlation analyses to determine if settlement of blue crab postlarvae to Oregon and Hatteras Inlets was spatially synchronous, and to investigate the relationship between mean daily settlement at each inlet and daily-averaged wind components. Prior to analysis, settlement records were log(x+1)-transformed to equalize variances, and detrended. The autocorrelation function (ACF) was used to identify cyclical patterns in postlarval settlement and temporal dependence in settlement pulses (Jassby and Powell, 1990). We fit autoregressive moving average (ARMA) models to the postlarval and wind component time series to remove periodicity and autocorrelation, and to reduce each series to white noise (randomness) (Dunstan, 1993). Model residuals that passed a χ^2 test for white noise were used in the cross-correlations. We computed cross-correlations for lags of ± 5 d; positive lags for correlations between

settlement and wind components represent the number of days blue crab settlement peaked after wind events.

Given that the average blue crab postlarval duration in estuarine water is 5 d (Wolcott and De Vries, 1994), postlarvae collected on a specific cruise date may have ingressed 1-5 d prior to a cruise. Therefore, we averaged explanatory variables (postlarval settlement, wind and current components [see below]) over the 5 d period prior to a cruise date. To characterize the relationship between postlarval settlement at the inlets and the concentration of postlarval blue crabs within Pamlico Sound, we used a least-squares regression model. The concentration of postlarvae averaged over all stations by cruise date was defined as the dependent variable, and the average settlement of postlarvae to both inlets over the 5 d period prior to a cruise date was used as the explanatory variable. Both variables were $\log(x+1)$-transformed to stabilize variances.

To determine if the mean concentration of postlarval 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 would depend on depth (surface vs. bottom) and diel cycle (day vs. night) using a two-way fixed-factor ANOVA. We accounted for temporal variability in postlarval settlement by converting the response variable (concentration of crabs per net tow on a given cruise date) to relative concentrations, or proportions. Finally, to stabilize variances and normalize the data, we applied a square-root transformation to the response variable (Sokal and Rohlf, 1995).

To assess how the concentration of postlarval blue crabs varied spatially within Pamlico Sound, we compared the distribution and abundance patterns of postlarval blue crabs on a given cruise date, with winds and lowpass-filtered (non-tidal) currents averaged over the 5 d period prior to plankton measurements. In addition, because postlarval blue crabs ingressing through tidal inlets are known to utilize nighttime flood tides (NFT) to facilitate initial, up-estuary transport (e.g. Forward and Tankersley, 2001), we calculated the distance that postlarval crabs could potentially travel on flood tides over the five consecutive nights prior to our cruise dates (termed 'total potential NFT distance'). Distances traveled were calculated using tidal currents measured at our Oregon and Hatteras Inlet current meter stations, both of which were located approximately 10 km from the inlets (see Fig. 1A). Current meter records at these sites indicated that tidal currents remained dominated by the principal semidiurnal M_2 tidal constituent (Chapter 1). Given that tidal currents diminish with increasing distance from the inlets (Pietrafesa *et al.*, 1986b), our calculations represent a liberal estimate of the total NFT distance that postlarval blue crabs may travel from our Oregon and Hatteras Inlet current meter stations, and provide an indication of whether NFT can result in across-sound dispersal within Pamlico Sound.

Hydrodynamic model

We used a 3D hydrodynamic model coupled with a Lagrangian particle-tracking algorithm to simulate crab dispersal trajectories to determine (1) if observed postlarval blue crab distributions can be explained by wind-driven flow and (2) whether specific

dispersal pathways connect inlet regions with western Pamlico Sound nursery habitats. Circulation was simulated using a nonlinear, finite-element barotropic 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 APES domain shown in Figure 1A. ADCIRC has produced wind-driven 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 in our study region within Pamlico Sound (Chapter 1). For our simulations, the model was parameterized with a Mellor-Yamada level 2.5 turbulent diffusion closure, a free surface roughness of 0.033, and a bottom roughness 0.02. 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 comprised 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. 2A & B). In the vertical domain, current velocities were computed over 11 variable depth layers. We assumed that wind fields were spatially uniform over the entire APES domain, and therefore, forced the model with hourly wind velocities measured at the Cape Hatteras Meteorological Station (Fig. 1A). A 1 d ramp was applied to wind forcing, and the model was allowed a 3 d spin-up time before comparisons were made between predicted and observed currents. Since we were interested in specifically examining the potential for wind-driven flow fields to generate across-sound dispersal pathways, tidal forcing was not included, and we assumed the APES to be spatially isolated from the

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coastal ocean (i.e., inlets not open to ocean). Furthermore, baroclinic forcing was ignored as the water column within Pamlico Sound is typically well-mixed (Chapter 1). To match our current meter deployment dates, model simulations ran for 57 d in 2000, and 64 d in 2001.

Simulated postlarval dispersal trajectories

A Lagrangian particle-tracking algorithm (Baptista *et al.*, 1984; Foreman *et al.*, 1992) was used to simulate postlarval blue crab transport within ADCIRC-generated flow fields. All simulations were conducted using the modeled flow field corresponding to the near-surface (~1 m below surface) depth layer because our field results determined that postlarval blue crabs were predominately located within surface waters (see 'Results'). To simulate passive transport under strictly wind-driven conditions, we released 20 particles at randomly selected locations within 2 km of both Oregon and Hatteras Inlets (known as 'wind-only' simulations, Fig. 2A & B). Because postlarval blue crabs initially ingress through the inlets using flood tide-transport (Forward and Tankersley, 2001), we also released particles from start positions located further into the sound, representing positions that crabs could reach using tidal transport ('tide-wind' simulations). For simplicity, during each year, we designated these start positions (Fig. 2A & B) to be randomly located within the tidal ellipses calculated at our Oregon and Hatteras Inlet current meter stations (Fig. 3C & D). For the 'tide-wind' runs, we released 40 particles near each inlet (as tidal ellipses encompassed a larger area than the near-inlet region) within the same wind-driven flow field used above. Finally, because

we collected more postlarval blue crabs at night than during the day (see 'Results'), we incorporated a behavioral active transport component to the particle-tracking model by re-running 'tide-wind' simulations using an algorithm where dispersal was restricted to nighttime only. For all simulations, the model time step was 2 minutes with particle positions outputted at hourly intervals. To compare particle end points with observed sound-wide postlarval blue crab distributions, particles were released daily over the 5 days leading up to our plankton cruise dates ('wind-only' simulations, N = 200; 'tide-wind' simulations, N = 400 particles tracked per cruise date).

RESULTS

Hydrography

During both years of our study period, the winds primarily alternated between summer conditions (blowing towards the northeast) and winter conditions (blowing towards the southwest; Table 1). This pattern in wind direction was also confirmed with examination of the principal axes, showing the alignment of the major axis of wind variance along the northeast-southwest axis (Fig. 3A & B). Because a relatively high percent of the variability in wind velocity was associated with the northeast-southwest (major) axis of wind in both years (86 % variability explained in 2000, ~ 65 % explained in 2001, Table 2), we used this wind component in the cross-correlations with postlarval settlement at the inlets.

In general, the principal axes of variance of the lowpass-filtered (non-tidal) currents were aligned with the wind ellipses and the shoreline (Fig. 3A & B). In both

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years, ~ 70-96 % of the variance in non-tidal current velocities occurred along the major axes (Table 2). With respect to tidal currents, as expected, velocities were greatest at the near-inlet current meter stations (see OI and HI, Fig. 3C & D). Near Oregon Inlet, tidal currents were aligned in a east-northeast to west-southwest direction during both years, but tidal currents near Hatteras Inlet were more variable, with a north-south alignment of relatively low current velocities in 2000 changing to a less variable northeast-southwest alignment of relatively high current velocities in 2001 (Fig. 3C & D). Again, percent variability associated with the major axes of tidal currents was relatively high (~ 69-99 %, Table 2). Gaps in the current meter records occurred when instruments were knocked free of their moorings, once in 2000 (Gibbs Shoal: Day 282-300), and twice in 2001 (Stumpy Point: Day 258-270 and Gibbs Shoal: Day 280-285).

Postlarval settlement at inlets

Postlarval supply of blue crabs to Pamlico Sound, as inferred from settlement at Oregon and Hatteras Inlets was episodic over the blue crab recruitment season during both years (Fig. 4A & B). While the relative settlement of postlarvae at Hatteras Inlet was greater than that at Oregon Inlet during 2000 (Fig. 4A), in 2001, settlement at Oregon Inlet was considerably higher than at Hatteras Inlet, and an order of magnitude greater than during the same time period in 2000 (Fig. 4B). Based on autocorrelation analysis, peaks in postlarval settlement were temporally autocorrelated for 2 d at Oregon Inlet in 2000 ($p < 0.05$), but showed no temporal autocorrelation at Hatteras Inlet during the same year ($p > 0.05$). During 2001, peaks in postlarval settlement at both inlets exhibited

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temporal autocorrelations over 3 d (p < 0.05). These results indicate that peaks in postlarval settlement generally last 2-3 d.

During both years, postlarval settlement was spatially synchronous, with positive and significant correlations between Oregon and Hatteras Inlets, and settlement at Hatteras Inlet leading that of Oregon Inlet by 2 d (Table 3). There was also a significant negative correlation between the major axis of wind variance and postlarval settlement 1 d later at both inlets during 2001 (Table 3), indicating that postlarvae peak after winds blow towards the southwest for ~ 24 h. While settlement was not significantly correlated with the major axis of wind variance in 2000, there was a similar trend to patterns in 2001, with postlarval peaks associated with southwestward winds blowing for several days (Fig. 4A & B). For all cross-correlations, first-order autoregressive models reduced the postlarval and wind records to white noise (χ^2 test, p > 0.05).

Sound-wide spatiotemporal distribution of postlarvae

In both years, postlarval blue crabs were collected during all of our plankton cruises. Temporal variability in the concentration of postlarval blue crabs within Pamlico Sound, as measured during these cruises, was significantly related to settlement of postlarvae at the inlets over the five consecutive days prior to each cruise date (Fig. 5). In addition, for each year, dates with the highest average postlarval concentrations in Pamlico Sound corresponded to dates when the potential for nighttime flood tide

transport was greatest at both Oregon and Hatteras Inlets (e.g. highest total NFT distances, see Table 4: Day 299 in 2000 and Day 262 in 2001).

On a vertical spatial scale in the water column, the concentration of postlarval 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 postlarval blue crabs was greatest in surface waters and at night (Fig. 6).

Over the spatial extent of Pamlico Sound (horizontal scale), the concentration of postlarval blue crabs varied by station over time. During 2000, postlarvae were predominately concentrated within northwest Pamlico Sound, in the region between Oregon Inlet (OI) and Stumpy Point (SP) (Fig. 7). Winds during all cruises in 2000 had a southward component, and currents showed similar patterns over time. For example, currents near OI were variable in the across-sound direction, with mean flows directed towards the west (Fig 7A & B) and southwest (Fig. 7C & D). At SP, the major axis of non-tidal current variance was aligned with the coastline, with mean flows mainly directed towards the east-southeast (across-sound in opposite direction of OI, Fig. 7). Thus, currents within the northwest region of Pamlico Sound appear to form an 'S-shaped' pattern as currents at OI move towards the western sound and are reflected off SP to move towards the south. Within the southern region of our study site, currents near Hatteras Inlet (HI) were variable in the east-west direction with a mean flow oriented towards the southeast or southwest, promoting transport towards the barrier island boundary or out of our study area, rather than across-sound (Fig. 7A-D).

During 2001, sound-wide postlarval blue crab concentrations were greater than in 2000, but were also variable when examined by station over time (compare Fig. 8 with Fig. 7). Wind conditions were more variable in 2001 than in 2000, with variance ellipses positioned along the northwest-southeast and northeast-southwest axes. When wind ellipses were aligned with the northeast-southwest axis, current patterns were similar to those described above for 2000, regardless of the mean wind direction (Fig. 8 B, D & E). For example, all currents exhibited a southward component, with flow predominately downstream of OI and aligned along the length of Pamlico Sound. The mean current direction at SP, however, was primarily oriented along the western shore of Pamlico Sound and not across-sound as in 2000. Similar to 2000, flow near HI was typically alongshore and directed out of our study area (Fig. 8).

On cruise dates with the highest total sound-wide concentrations of postlarval blue crabs (Day 262 and 276 in 2001, Table 4), wind ellipses were oriented along the northeast-southwest axis, and produced relatively strong currents at OI that were directly aligned along an axis connecting OI and SP (Fig. 8B & D). This region of northwest Pamlico Sound adjacent to OI, had correspondingly high relative postlarval abundances (Fig. 8B & D). The area between HI and Gibbs Shoal (GS) also exhibited high concentrations of postlarvae during these days (Fig. 8B & D); however, wind-driven currents at HI were not favorable for across-sound transport. In this case, tidal transport may have contributed to the relatively high concentrations of crabs in southern Pamlico Sound, as potential NFT distances from HI were relatively high (see Days 262 and 276 in Table 4). Thus, regardless of the wind conditions, postlarval blue crabs

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appear to originate from Oregon Inlet most often, where currents are favorable for transport to the western and southern regions of our study area (but see exception on Day 269: Fig. 8C).

Particle-tracking simulations and dispersal trajectories

Dispersal patterns generated by our particle-tracking simulations could be categorized into three general groups based on whether the dominant wind direction was southward, northward, or westward (Table 5). Therefore, for brevity, we only present the details of simulation results from three specific model runs that are representative of dispersal during these three wind conditions: Day 262 (2001) for southward winds, Day 269 (2001) for northward winds, and Day 296 (2001) for westward winds.

All passive particle-tracking 'wind-only' simulations, where virtual crabs were released close to the inlets in near-surface flow fields, failed to result in across-sound transport (from east to west) regardless of the direction the wind was blowing (Fig. 9A, C & E). Rather, dispersal was directed downstream from the inlets of release following the direction of the prevailing winds and currents, with particles moving along the eastern shore of Pamlico Sound (e.g. southwestward winds: Fig. 9A, northeastward winds: Fig. 9C, and westward winds: Fig. 9E). As such, we were not able to recreate our observed blue crab distribution patterns with these simulations.

In contrast, across-sound transport was achieved during the 'tide-wind' simulations that incorporated initial movement into the sound by tidal transport, but only by particles originating near OI (Table 5). When winds blew towards the south

(e.g. Fig. 9B) or towards the west (e.g. Fig. 9F), particles from the OI region reached the western shore of Pamlico Sound, but particles released near HI generally moved southwestward and out of our study area. Furthermore, particles released near OI dispersed over the entire extent of our study area (e.g., Fig. 9B). During northward wind conditions, some particles released near OI were transported southward in the opposite direction of the wind towards the middle of the sound (Fig. 9D). Particles from HI moved downwind within an area between the middle and eastern boundary of the sound (Fig. 9D). Therefore, while our simulations did not produce across-sound flowing currents from HI, surface currents from OI during southward and westward winds were favorable for such transport.

When we limited dispersal during the 'tide-wind' simulations to nighttime periods (active dispersal algorithm), particles did not travel as far and resulted in clumped distributions near the regions of release (Fig. 10A, C & E). During southward and westward wind conditions, particles were concentrated in the northern portion of Pamlico Sound, especially in the region between OI and SP (Fig. 9A & E). Particle end-points in this region corresponded to the postlarval blue crab distributions we observed during cruises with southward winds (compare simulation end points in Fig. 10A with observed distributions in Fig. 7 & 8B & D). Our simulations during southward winds (both day and night 'tide-wind' runs) however, failed to predict postlarval blue crab distributions in the southern portion of our study area, where observed postlarval concentrations were relatively high (e.g. compare Fig. 9 & 10A with observed distributions in Fig. 8B & D).

Examination of the dispersal trajectories from the simulations revealed that potential transport from OI to the western sound does not follow a straight path, with trajectories meandering between OI and SP regardless of the wind direction (e.g. Fig. 10B, D & F). In the northwest Pamlico Sound region, dispersal trajectories under southward winds were similar to those indicated by our observed currents under similar wind conditions (see variance ellipses in Fig. 7), whereby currents moved towards the west from OI and then generally southward in the vicinity of SP (Fig. 10B). Near HI, observed current variance ellipses had an east-west alignment during 2000 (Fig. 7), which did not match the dispersal trajectories simulated under southward winds (Fig. 10B). In 2001, however, currents at HI were better aligned with the predicted dispersal trajectories (e.g. Fig. 8B), as transport was directed southward along the eastern shore of Pamlico Sound with the prevailing currents (Fig. 10B). During northward and westward winds, simulated dispersal trajectories from both OI and HI were in good agreement with the observed current variance ellipses (compare Fig. 8C with Fig. 10D and Fig. 8F with Fig. 10F). While dispersal trajectories from OI meandered in the general direction of the prevailing winds and currents, trajectories from HI were more linear, moving downwind along the eastern barrier island boundary of Pamlico Sound. Again, across-sound transport was possible when tidal and wind effects were combined in our simulations, but only from OI during southward and westward wind conditions.

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DISCUSSION

Postlarval settlement at the inlets: transport from continental shelf to estuary

Coastal and estuarine hydrographic processes can greatly influence the early life stages of finfish and crustaceans that utilize nursery habitats within estuaries (see Weinstein, 1988; Werner *et al.*, 1997; Eggleston *et al.*, 1998; Crowder and Werner, 1999 and references therein). The general weak horizontal swimming capabilities of these early life stages (Miller *et al.*, 1984; Metaxas, 2001), make them at least partly dependent on the prevailing currents to reach nearshore estuaries. Along the continental shelf of North America, dispersal from oceanic development/spawning grounds to nearshore estuaries may result from wind, tidal, and buoyancy-driven flows (reviewed by: Epifanio and Garvine, 2001). Weak tidal residuals along the North Carolina shelf, however, are not likely to impact shoreward larval/postlarval transport (Werner *et al.*, 1999), and buoyancy-driven currents during the fall blue crab recruitment months are reduced compared to late spring periods when low salinity estuarine discharge is at a maximum (Epifanio and Garvine, 2001). Therefore, onshore transport of early juvenile fishes and crustaceans from Middle and South Atlantic shelf development areas is generally believed to be associated with components of the wind-generated shelf circulation (e.g. Miller *et al.*, 1984; Checkley *et al.*, 1988; Goodrich *et al.*, 1989; Johnson and Hester, 1989; Blanton *et al.*, 1995; Mense *et al.*, 1995; Olmi, 1995; Wenner *et al.*, 1998).

We found that blue crab settlement to Pamlico Sound increased following southwestward wind events lasting several days (Fig. 4). Winds blowing towards the southwest have also been associated with settlement peaks of blue crabs in another

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study within the APES (Mense *et al.*, 1995). Such wind events, which parallel the coastline, advect shelf surface water towards the coast (westward) through Ekman transport. This produces a rise (i.e., set-up) in coastal sealevel, downwelling shelf water and driving a geostrophic alongshore current that flows southward (Blanton *et al.*, 1995). Within Pamlico Sound, southward winds cause a concurrent sealevel drop (i.e., set-down) along the sound-side of the barrier island coast, resulting in a pressure gradient force that drives a rapid current through the inlets (Pietrafesa and Janowitz, 1988). This coastal-estuarine circulation may develop within a day of persistent southwestward wind forcing (Pietrafesa and Janowitz, 1988; Blanton *et al.*, 1995). Given that postlarval blue crabs in coastal waters are generally found near the surface (McConaugha 1988), southward wind (downwelling) events provide a plausible across-shelf transport mechanism (Garland *et al.*, 2002), and favor dispersal into east-facing inlets (Pietrafesa *et al.*, 1986b).

Although both inlets where we quantified blue crab postlarval settlement in North Carolina are east facing to some degree, slight differences in the orientation of these inlets exist (Oregon Inlet faces east-northeast, and Hatteras Inlet south-southeast, see Fig, 1A). A 3D baroclinic circulation model of the APES has shown that differences in the response of Oregon and Hatteras Inlets to wind forcing in terms of shelf-estuary exchange may result from the respective orientation of these inlets, leading investigators to predict that larval transport would be greatest through Oregon Inlet during southwestward winds (Xie and Eggleston, 1999). In our field study, however, postlarval blue crab settlement pulses following southwestward wind events were not consistently

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greater at Oregon Inlet than Hatteras Inlet (see Fig. 4A). While differences in the magnitude of settlement pulses at each inlet may reflect different geographical sources of larvae (or blue crab spawning cycles), the fact that we observed nearly synchronous blue crab supply to Oregon and Hatteras Inlets suggests that temporal variability in postlarval blue crab abundance results, in part, from regional oceanographic processes occurring on the continental shelf, rather than localized processes specific to each inlet. In fact, the interaction between southward-wind generated shelf currents and the coastline, makes transport into both inlets possible: near-shore currents in the region north of Cape Hatteras (where Oregon Inlet is located within the Middle Atlantic Bight) move southward, and currents south of Cape Hatteras (location of Hatteras Inlet within South Atlantic Bight) are pushed towards the southwest (Werner *et al.*, 1999), such that currents are directed into Oregon and Hatteras Inlets, respectively.

As in a number of other blue crab studies along the Atlantic and Gulf coasts of the United States (e.g. van Montfrans *et al.*, 1990; Rabalais *et al.*, 1995; van Montfrans *et al.*, 1995; Forward *et al.*, 2004), settlement of blue crabs to Pamlico Sound was highly episodic, with pulses lasting for several days. Given that we observed increases in blue crab postlarval abundances at the inlets following southwestward winds, we suggest that variability in settlement reflects stochasticity in meteorological forcing. Although wind events are not temporally predictable, southwestward winds are associated with the passage of frontal systems (Epifanio and Garvine, 2001), and during each year of this study, occurred ~ 50 % of the time while increasing in frequency from fall to winter months. Previous work in the Chesapeake Bay, showed that wind-driven

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inflow events occur, on average, 10 times during any given blue crab season (fall months) (Goodrich *et al.*, 1989). Meteorologically-forced onshore flow therefore, represents a regular feature on the continental shelf that promotes the shoreward movement of organisms in surface waters, rather than a fortuitous transport mechanism (Goodrich *et al.*, 1989).

Regardless of the factors that influence postlarval settlement near estuary inlets, settlement variability at Oregon and Hatteras Inlets directly translated to variability in the sound-wide concentration of postlarval blue crabs. This was evident from the significant linear relationship we observed between the average number of postlarvae collected at the inlets during the 5 d period prior to each cruise date and the average concentration of postlarvae collected during a cruise in Pamlico Sound. Thus, blue crab settlement collectors positioned at the inlets provide an accurate, relative measure of postlarval supply to Pamlico Sound.

Inlet-to-sound transport

Once early life stages of crustaceans and fishes arrive from the shelf to nearshore estuaries, FTT generally mediates ingress through the inlets and dispersal up-estuary in tidal systems (reviewed by: Boehlert and Mundy, 1988; Forward and Tankersley, 2001). Only a few studies have examined larval/postlarval ingress through Pamlico Sound inlets, but have observed vertical migrations timed with the tidal cycle by larval fish species (Joyeux, 1998), and postlarval blue crabs are more abundant in surface waters during nighttime flood tides than at any other time of the diel or tidal cycles (N. Reyns,

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unpublished data). This implies that FTT is also an important transport mechanism for entry into our study system.

Given that the tidal signal in Pamlico Sound diminishes with increasing distance from the inlets (Pietrafesa *et al.*, 1986b), it is unlikely that FTT over consecutive nights can be used to reach western sound nursery habitats once larvae/postlarvae are within Pamlico Sound. Results from our study, however, suggest that tidal currents play an important role in transport at least partway across the sound. For example, the nights with the greatest concentration of postlarval blue crabs in Pamlico Sound corresponded to periods when the potential for nighttime FTT was relatively high at both inlets. During these nights, distances traveled over the 5 consecutive nights prior to our cruise dates varied from ~ 7-8 km at Oregon Inlet and ~ 4-11 km at Hatteras Inlet during 2000-2001 (see Table 4). Due to the relatively short distance between Oregon Inlet and the western shore of Pamlico Sound (~ 20 km), larvae/postlarvae ingressing through this inlet have a much greater chance of reaching western sound nursery habitats by using tidal currents alone, than those ingressing through Hatteras Inlet where the distance to western sound habitats is ~ 40 km (Fig. 1A). Further evidence in support of the importance of tidal currents to dispersal within Pamlico Sound, comes from our simulation results, which are discussed below (see '*Sound-wide spatiotemporal postlarval distributions and transport*').

Although we did not explicitly quantify the vertical distribution of postlarval blue crabs near the inlets, within the sound, postlarval blue crabs were primarily collected at night in surface waters. A nocturnal activity pattern is not surprising, as

light inhibits swimming of postlarval blue crabs in estuarine water (Forward and Rittschof, 1994), and postlarvae have been observed moving into the water column at the onset of darkness in laboratory experiments (Luckenbach and Orth, 1992). Postlarval blue crabs likely move into surface waters at night to avoid diurnal visual predators (Zaret and Suffern, 1976; Stich and Lampert, 1981). While greater abundances of blue crab postlarvae in estuarine surface waters have been observed at night during other field studies (e.g. Epifanio *et al.*, 1984; Mense and Wenner, 1989), postlarval abundances have also increased in near-bottom waters during the day (Mense and Wenner, 1989), suggestive of a diel vertical migration. We did not observe an increase in postlarval concentrations in bottom waters during the day; however, our sampling stations were deeper, on average, than those sampled by Mense and Wenner (1989). Thus, due to turbidity within Pamlico Sound, postlarvae descending from surface waters during the day may not need to reach the bottom to experience night-like, low-light conditions. As we did not conduct mid-depth plankton tows or turbidity measurements, this hypothesis remains to be tested.

Sound-wide spatiotemporal postlarval distributions and transport

Once postlarval blue crabs ingress through the inlets, our findings show that the outcome of dispersal within Pamlico Sound (i.e., direction and endpoint of transport) largely depends on the prevailing surface currents. Wind and tidal forcing within our study area, particularly near the inlets, can drive these surface currents. For instance, currents at all of 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 to tidal currents at the other non-inlet stations.

While we did not initially expect tidal currents to be an important determinant of dispersal within Pamlico Sound because circulation is generally driven by the wind, our simulation results indicate that it is the combination of non-tidal and tidal effects that promotes across-sound postlarval transport. For instance, particles (i.e., virtual postlarval crabs) released in wind-driven flow fields dispersed in the direction of the wind, but did not move into the sound beyond the inlet areas. Instead, these particles moved along the backside of the barrier island (eastern) shore, where extensive seagrass habitats are found. Given that we observed postlarval blue crabs throughout Pamlico Sound, however, these 'wind-only' particle end-point distributions suggest that transport by wind-driven currents alone does not result in movement to western sound nursery habitats. Across-sound transport and dispersal throughout Pamlico Sound was only achieved when we released particles within a region postlarvae could reach using FTT upon entry into Pamlico Sound ('tide-wind' simulations). As such, these simulation results demonstrate that transport within Pamlico Sound is not simply downstream of the prevailing wind direction, and imply that multiple forcing agents can contribute to the dispersal of organisms within estuaries classified as being predominately wind-driven. Similarly, Chesapeake Bay is considered a tidal estuarine

system, but local wind effects can have important consequences for postlarval transport (Olmi, 1995).

The combined influence of non-tidal and tidal currents on dispersal may be due to the alignment of these currents with respect to the inlets. General circulation patterns from our current meter stations show non-tidal surface currents predominately moving in the direction of the wind, as has been observed in previous studies within the APES (Pietrafesa *et al.*, 1986b; Pietrafesa and Janowitz, 1991) and other wind-driven systems (Commito *et al.*, 1995). More specifically, during southwestward winds (the most common wind conditions during our study), surface currents near Oregon and Hatteras Inlets were almost always directed towards the south-southwest. While such currents would push postlarvae downstream and out of our study region from Hatteras Inlet, they promote dispersal throughout our study region from Oregon Inlet. Furthermore, regardless of wind direction, tidal currents near Oregon Inlet were directly aligned along an axis that connects the inlet with the western sound near Stumpy Point. Thus, we propose that the alignment of non-tidal and tidal surface currents between Oregon Inlet and Stumpy Point, especially during southwestward winds, enhances the supply of blue crab postlarvae to the northwestern region of Pamlico Sound, where relatively high concentrations of blue crabs were repeatedly observed during our cruises. Postlarval blue crab supply via the 'Oregon Inlet-Stumpy Point dispersal pathway' may also explain why this region consistently experiences relatively high abundances of later-staged juveniles (Eggleston *et al.*, 2004).

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Within the southern portion of our study region (near Hatteras Inlet), our simulation results failed to predict our observed postlarval blue crab distributions, suggesting that dispersal is influenced by other factors not included in our particle-tracking simulations. While we expected postlarval blue crabs within the southern portion of Pamlico Sound to originate from Hatteras Inlet, the observed currents near this site were generally southward and not conducive to across-sound transport regardless of wind conditions. As such, postlarvae ingressing through Hatteras Inlet would have to swim against the currents to reach our sampling stations, including those nearest to the inlet. Yet, postlarval blue crabs cannot swim against currents when velocities are 6.3 cm s^{-1} or greater (Luckenbach and Orth, 1992), and mean current velocities observed near Hatteras Inlet in this study approached 6.5 cm s^{-1}, with maximum velocities exceeding 20 cm s^{-1}.

Swimming behavior by blue crabs, however, may account for some of the discrepancy between observed postlarval distributions and particle end-points, as horizontal swimming by the early life stages of fishes (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, because it remains unclear if directed and sustained swimming by postlarval blue crabs occurs in the field (Luckenbach and Orth, 1992), it is difficult to incorporate such behaviors in our particle-tracking algorithm at this time. Therefore, while the exclusion of directed swimming behaviors in our simulations likely underestimated the dispersal potential of postlarval blue crabs, especially when transport occurred only at night ('nighttime tide-

wind' runs), our 'tide-wind' simulations may still provide realistic dispersal estimates. Postlarval blue crabs found in the southern portion of our study area likely originated from Oregon Inlet rather than Hatteras Inlet, as a clear surface dispersal pathway between Hatteras Inlet and western sound nursery habitats is not apparent. Our findings are further supported by the results of another circulation model of the APES, where under all wind conditions except for those towards the northwest, across-sound dispersal is not possible from Hatteras Inlet (Xie and Eggleston, 1999).

CONCLUSIONS

Combined hydrodynamic and particle-tracking models have recently been used to examine the degree of connectivity between spawning populations via egg and larval dispersal within a semi-enclosed bay (Nahas *et al.*, 2003), colonization rates within a shallow tidal estuary (Lundquist *et al.*, 2004), larval supply and dispersal to a tidal inlet (Brown *et al.*, 2004), and the influence of vertical migration behaviors on estuarine transport in a tidal system (Carr *et al.*, in review). Results from these studies point to the relative importance of multiple physical factors, along with behavior, as driving dispersal patterns. For example, large-scale shelf physical processes can influence delivery of larvae to estuarine inlets (Brown *et al.*, 2004), but once within an estuary, organisms are subject to local dispersal processes (Lundquist *et al.*, 2004) that may result from behavioral responses to environmental conditions (Carr *et al.*, in review).

Our study indicates that wind affects the delivery of postlarval blue crabs from the continental shelf to nearshore estuary inlets; while estuarine hydrodynamics (i.e.,

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non-tidal and tidal flows) coupled with postlarval behavior (vertical positioning within the water column) drives dispersal and subsequent spatiotemporal abundance patterns of postlarval blue crabs within Pamlico Sound. More specifically, we demonstrate the importance of southwestward wind events, which enhance postlarval supply to the inlets, and along with tidal currents, facilitate south-southwestward dispersal within Pamlico Sound to western shore nursery habitats (Etherington and Eggleston, 2000). Our simulation results indicate that Oregon Inlet is the primary supplier of postlarval blue crabs throughout the northern basin of Pamlico Sound, as crabs ingressing through Hatteras Inlet were not retained within our study area. A dispersal pathway connecting Oregon Inlet and the western sound near Stumpy Point is evident during most wind conditions experienced during our study. Thus, nursery habitats surrounding these regions should be prioritized for conservation to maintain (or maximize) the production of early juvenile blue crabs and fishes that utilize these habitats. Finally, inlet modifications, such as dredging and jetty construction, especially near Oregon Inlet, have the potential for disrupting critical dispersal pathways of surface-oriented larvae/postlarvae within Pamlico Sound.

ACKNOWLEDGEMENTS

LITERATURE CITED

Baptista, A.M., Adams, E.E. and Stolzenbach, K.D. (1984) Eulerian-Lagrangian analysis of pollutant transport in shallow water. *Massachusetts Institute of Technology*: MIT RM Parsons Lab. Tech. Rep. No. 296, Cambridge, MA.

Blanton, J., Wenner, E., Werner, F. and Knott, D. (1995) Effects of wind-generated coastal currents on the transport of blue crab megalopae on a shallow continental shelf. *Bull. Mar. Sci.* **57**:739-752.

Boehlert, G.W. and Mundy, B.C. (1988) Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *Am. Fish. Soc. Symp.* **3**:51-67.

Brown, C.A., Holt, S.A., Jackson, G.A., Brooks, D.A. and Holt, G.J. (2004) Simulating larval supply to estuarine nursery areas: how important are physical processes to the supply of larvae to the Aransas Pass Inlet? *Fish. Oceanogr.* **13**:181-196.

Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P. and Menge, B.A. (1996) Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* **27**:477-500.

Carr, S.D., Hench, J.L., Luettich, R.A., Jr., Forward, R.B., Jr. and Tankersely, R.A. (in review) Spatial patterns in the ovigerous blue crab spawning migration: results from a coupled behavioral-physical model. *Mar. Ecol. Prog. Ser.*

Checkley, D.M., Jr., Raman, S., Maillet, G.L. and Mason, K.M. (1988) Winter storm effects on the spawning and larval drift of a pelagic fish. *Nature* **335**:346-348.

Commito, J.A., Thrush, S.F., Pridmore, R.D., Hewitt, J.E. and Cummings, V.J. (1995) Dispersal dynamics in a wind-driven benthic system. *Limnol. Oceanogr.* **40**:1513-1518.

Crowder, L.B. and Werner, F.E. (1999) Fisheries oceanography of the estuarine-dependent fishes of the South Atlantic Bight. *Fish. Oceanogr.* **8**:1-252.

Dunstan, F.D.J. (1993) Time series analysis. In: *Biological Data Analysis: A practical Approach.* J.C. Fry (ed) Oxford: Oxford University Press, pp. 243-310.

Eggleston, D.B. and Armstrong, D.A. (1995) Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. *Ecol. Monogr.* **65**:193-216.

Eggleston, D.B., Johnson, E.G. and Hightower, J.E. (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,

Eggleston, D.B., Armstrong, D.A., Elis, W.E. and Patton, W.S. (1998) Estuarine fronts as conduits for larval transport: hydrodynamics and spatial distribution of Dungeness crab postlarvae. *Mar. Ecol. Prog. Ser.* **164**:73-82.

Emery, W.J. and Thomson, R.E. (2001) *Data analysis methods in physical oceanography.* Amsterdam: Elsevier, 638 pp.

Epifanio, C.E. and Garvine, R.W. (2001) Larval transport on the Atlantic continental shelf of North America: a review. *Estuar. Coast. Shelf Sci.* **52**:51-77.

Epifanio, C.E., Valenti, C.C. and Pembroke, A.E. (1984) Dispersal and recruitment of blue crab larvae in Delaware Bay, USA. *Estuar. Coast. Shelf Sci.* **18**:1-12.

Etherington, L.L. and Eggleston, D.B. (2000) Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. *Mar. Ecol. Prog. Ser.* **204**:179-198.

Etherington, L.L. and Eggleston, D.B. (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.

Fernandez, M., Iribarne, O. and Armstrong, D. (1994) Swimming behavior of Dungeness Crab, *Cancer magister* Dana, megalopae in still and moving water. *Estuaries* **17**:271-275.

Foreman, M.G.G., Baptista, A.M. and Walters, R.A. (1992) Tidal model studies of particle trajectories around a shallow coastal bank. *Atmos.-Ocean* **30**:43-69.

Forward, R.B., Jr. and Rittschof, D. (1994) Photoresponses of crab megalopae in offshore and estuarine waters: implications for transport. *J. Exp. Mar. Bio. Ecol.* **182**:183-192.

Forward, R.B., Jr. and Tankersley, R.A. (2001) Selective tidal-stream transport of marine animals. *Oceanogr. Mar. Biol. Annu. Rev.* **39**:305-353.

Forward, R.B., Jr., Tankersley, R.A. and Welch, J.M. (2003) Selective tidal-stream transport of the blue crab *Callinectes sapidus*: an overview. *Bull. Mar. Sci.* **72**:347-365.

Forward, R.B., Jr., Cohen, J.H., Irvine, R.D., Lax, J.L., Mitchell, R., Schick, A.M., Smith, M.M., Thompson, J.M. and Venezia, J.I. (2004) Settlement of blue crab *Callinectes sapidus* megalopae in a North Carolina estuary. *Mar. Ecol. Prog. Ser.* **269**:237-247.

Garland, E.D., Zimmer, C.A. and Lentz, S.J. (2002) Larval distributions in inner-shelf waters: The roles of wind-driven cross-shelf currents and diel vertical migrations. *Limnol. Oceanogr.* **47**:803-817.

Goodrich, D.M., van Montfrans, J. and Orth, R.J. (1989) Blue crab megalopal influx to Chesapeake Bay: Evidence for a wind-driven mechanism. *Estuar. Coast. Shelf Sci.* **29**:247-260.

Henry, L.T. and McKenna, S. (1998) Status and management of the blue crab fishery in North Carolina. *J. Shellfish Res.* **17**:465-468.

Houde, E.D. (1987) Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.* **2**:17-29.

Houde, E.D. and Rutherford, E.S. (1993) Recent trends in estuarine fisheries: prediction of fish production and yield. *Estuaries* **16**:161-176.

Jassby, A.D. and Powell, T.M. (1990) Detecting changes in ecological time series. *Ecology* **71**:2044-2052.

Johnson, D.R. and Hester, B.S. (1989) Larval transport and its association with recruitment of blue crabs to Chesapeake Bay. *Estuar. Coast. Shelf Sci.* **28**:459-472.

Joyeux, J.-C. (1998) Spatial and temporal entry patterns of fish larvae into North Carolina estuaries: comparisons among one pelagic and two demersal species. *Estuar. Coast. Shelf Sci.* **47**:731-752.

Leis, J.M., Sweatman, H.P.A. and Reader, S.E. (1996) What the pelagic stages of coral reef fishes are doing out in blue water: daytime field observations of larval behavioural capabilities. *Mar. Freshwat. Res.* **47**:401-411.

Luckenbach, M.W. and Orth, R.J. (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. and Westerink, J. (2004) Formulation and numerical implementation of the 2D/3D ADCIRC finite element model version 44.XX. http://www.marine.unc.edu/C_CATS/adcirc/adcirc_theory_2004_05_14.pdf

Luettich, R.A., Jr., Westerink, J.J. and Scheffner, N.W. (1992) ADCIRC: An advanced three-dimensional circulation model for shelves, coasts and estuaries. *Report 1: Theory and methodology of ADCIRC-2DDI and ADCIRC-3DL*: Technical report DRP-92-6, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Luettich, R.A., Jr., Carr, S.D., Reynolds-Fleming, J.V., Fulcher, C.W. and McNinch, J.E. (2002) Semi-diurnal seiching in a shallow, micro-tidal lagoonal estuary. *Cont. Shelf Res.* **22**:1669-1681.

Lundquist, C.J., Thrush, S.F., Oldman, J.W. and Senior, A.K. (2004) Limited transport and recolonization potential in shallow tidal estuaries. *Limnol. Oceanogr.* **49**:386-395.

Mense, D.J. and Wenner, E.L. (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.

Mense, D.J., Posey, M.H., West, T. and Kincheloe, K. (1995) Settlement of brachyuran postlarvae along the North Carolina coast. *Bull. Mar. Sci.* **57**:793-806.

Metaxas, A. (2001) Behaviour in flow: perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. *Can. J. Fish. Aquat. Sci.* **58**:86-98.

Metcalf, K.S., van Montfrans, J., Lipcius, R.N. and Orth, R.J. (1995) Settlement indices for blue crab megalopae in the York River, Virginia: temporal relationships and statistical efficiency. *Bull. Mar. Sci.* **57**:781-792.

Miller, J.M. (1988) Physical processes and the mechanisms of coastal migrations of immature fishes. *Am. Fish. Soc. Symp.* **3**:68-76.

Miller, J.M., Reed, J.P. and Pietrafesa, L.J. (1984) Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. In: *Mechanisms of migration in fishes*. J.D. McCleave, G.P. Arnold, J.J. Dodson and W.H. Neill (ed) New York: Plenum Publishing Corporation, pp. 209-225.

Morgan, S.G., Zimmer-Faust, R.K., Heck, K.L., Jr. and Coen, L.D. (1996) Population regulation of blue crabs *Callinectes sapidus* in the northern Gulf of Mexico: postlarval supply. *Mar. Ecol. Prog. Ser.* **133**:73-88.

Nahas, E.L., Jackson, G., Pattiaratchi, C.B. and N., I.G. (2003) Hydrodynamic modelling of snapper *Pagrus auratus* egg and larval dispersal in Shark Bay, Western Australia: reproductive isolation at a fine spatial scale. *Mar. Ecol. Prog. Ser.* **265**:213-226.

Norcross, B.L. (1991) Estuarine recruitment mechanisms of larval Atlantic croakers. *Trans. Am. Fish. Soc.* **120**:673-683.

Norcross, B.L. and Shaw, R.F. (1984) Oceanic and estuarine transport of fish eggs and larvae: A review. *Trans. Am. Fish. Soc.* **113**:153-165.

Olmi, E.J., III (1995) Ingress of blue crab megalopae in the York River, Virginia, 1987-1989. *Bull. Mar. Sci.* **57**:753-780.

Pietrafesa, L.J. and Janowitz, G.S. (1988) Physical oceanographic processes affecting larval transport around and through North Carolina inlets. *Am. Fish. Soc. Symp.* **3**:34-50.

Pietrafesa, L.J. and Janowitz, G.S. (1991) The Albemarle-Pamlico coupling study. Final report to the Environmental Protection Agency,

Pietrafesa, L.J., Janowitz, G.S., Miller, J.M., Noble, E.B., Ross, S.W. and Epperly, S.P. (1986a) Abiotic factors influencing the spatial and temporal variability of juvenile fish in Pamlico Sound, North Carolina. In: *Estuarine Variability*. D.A. Wolfe (ed) New York: Academic Press, pp. 341-353.

Pietrafesa, L.J., Janowitz, G.S., Chao, T.-Y., Weisberg, R.H., Askari, F. and Noble, E. (1986b) The physical oceanography of Pamlico Sound. *UNC Sea Grant Publication*: UNC-WP-86-5, Raleigh, NC.

Provenzano, A.J., Jr., McConaugha, J.R., Philips, K.B., Johnson, D.F. and Clark, J. (1983) Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. *Estuar. Coast. Shelf Sci.* **16**:489-499.

Rabalais, N.N., Burditt, F.R., Jr., Coen, L.D., Cole, B.E., Eleuterius, C., Heck, K.L., Jr., McTigue, T.A., Morgan, S.G., Perry, H.M., Truesdale, F.M., Zimmer-Faust, R.K. and Zimmerman, R.J. (1995) Settlement of *Callinectes sapidus* megalopae on artificial collectors in four Gulf of Mexico estuaries. *Bull. Mar. Sci.* **57**:855-876.

Rothschild, B.J. (1986) *Dynamics of marine fish populations*. Cambridge, MA: Harvard University Press, 277 pp.

Roughgarden, J., Gaines, S. and Possingham, H. (1988) Recruitment dynamics in complex life cycles. *Science* **241**:1460-1466.

Sandifer, P.A. (1975) The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River Estuary and adjacent lower Chesapeake Bay, Virginia. *Estuar. Coast. Mar. Sci.* **3**:269-279.

Sissenwine, M.P. (1984) Why do fish populations vary? In: *Expoitation of marine communities*. R.M. May (ed) Berlin: Springer-Verlag, pp. 59-94.

Sokal, R.R. and Rohlf, F.J. (1995) *Biometry*. New York: W. H. Freeman and Company, 887 pp.

Stich, H.-B. and Lampert, W. (1981) Predator evasion as an explanation of diurnal
vertical migration of zooplankton. *Nature* **293**:396-398.

Stobutzki, I.C. and Bellwood, D.R. (1997) Sustained swimming abilities of the late
pelagic stages of coral reef fishes. *Mar. Ecol. Prog. Ser.* **149**:35-41.

Tankersley, R.A., McKelvey, L.M. and Forward, R.B., Jr. (1995) Responses of
estuarine crab megalopae to pressure, salinity and light: implications for flood-
tide transport. *Mar. Biol.* **122**:391-400.

Van Engel, W.A. (1958) The blue crab and its fishery in Chesapeake Bay. Part I.
Reproduction, early development, growth and migration. *Comm. Fish. Rev.*
20:6-17.

van Montfrans, J., Peery, C.A. and Orth, R.J. (1990) Daily, monthly and annual
settlement patterns by *Callinectes sapidus* and *Neopanope sayi* megalopae on
artifical collectors deployed in the York River, Virginia: 1985-1988. *Bull. Mar.
Sci.* **46**:214-229.

van Montfrans, J., Epifanio, C.E., Knott, D.M., Lipcius, R.N., Mense, D.J., Metcalf,
K.S., Olmi, E.J., III, Orth, R.J., Posey, M.H., Wenner, E.L. and West, T.L.
(1995) Settlement of blue crab postlarvae in western North Atlantic estuaries.
Bull. Mar. Sci. **57**:834-854.

Weinstein, M.P. (1988) Larval fish and shellfish transport through inlets. *Am. Fish. Soc.
Symp.* **3**:1-165.

Welch, J.M., Forward, R.B., Jr. and Howd, P.A. (1999) Behavioral responses of blue crab *Callinectes sapidus* postlarvae to turbulence: implication for selective tidal stream transport. *Mar. Ecol. Prog. Ser.* **179**:135-143.

Wenner, E., Knott, D., Blanton, J., Barans, C. and Amft, J. (1998) Roles of tidal and wind-generated currents in transporting white shrimp (Penaeus setiferus) postlarvae through a South Carolina (USA) inlet. *J. Plankton Res.* **20**:2333-2356.

Werner, F.E., Quinlan, J.A., Blanton, B.O. and Luettich, R.A., Jr. (1997) The role of hydrodynamics in explaining variability in fish populations. *J. Sea Res.* **37**:195-212.

Werner, F.E., Blanton, B.O., Quinlan, J.A. and Luettich, R.A., Jr. (1999) Physical oceanography of the North Carolina continental shelf during the fall and winter seasons: implications for the transport of larval menhaden. *Fish. Oceanogr.* **8**:7-21.

Wolcott, D.L. and De Vries, M.C. (1994) Offshore megalopae of *Callinectes sapidus*: depth of collection, molt stage and response to estuarine cues. *Mar. Ecol. Prog. Ser.* **109**:157-163.

Wrona, A.B., Wiegert, R.G. and Bishop, T.D. (1995) Initial report of settlement patterns of brachyuran megalopae at Sapelo Island, Georgia, U.S.A. *Bull. Mar. Sci.* **57**:807-820.

Xie, L. and Eggleston, D.B. (1999) Computer simulations of wind-induced estuarine circulation patterns and estuary-shelf exchange processes: The potential role of wind forcing on larval transport. *Estuar. Coast. Shelf Sci.* **49**:221-234.

Zaret, T.M. and Suffern, J.S. (1976) Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* **21**:804-813.

Table 1. Percentage of time wind blew towards a specific direction during study period in 2000 and 2001.

Wind Direction	2000	2001
SW	56 %	49 %
NE	19 %	20 %
SE	19 %	15 %
NW	6 %	16 %

Table 2. Percent 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.

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 3. Results of cross-correlation analyses of residuals of first-order autoregressive models fit to log(x+1)-transformed average daily postlarval settlement and the major axis of daily-averaged wind data. Significant ($p < 0.05$) cross-correlation R-values are reported, with days (in parentheses) by which factors in the column headings lead factors in the left rows. ns = not significant, na = not applicable, HI = Hatteras Inlet, OI = Oregon Inlet.

	HI settlement		Wind	
	2000	2001	2000	2001
OI settlement	0.73 (2d)	0.53 (2d)	ns	-0.30 (1d)
HI settlement	na	na	ns	-0.39 (1d)

Table 4. Mean concentration of postlarval blue crabs within Pamlico Sound over time (by cruise) as related to total potential nighttime flood tide (NFT) distance. Distances were calculated from Oregon and Hatteras Inlet current meter stations over the 5 d period prior to a given cruise date. For reference, maximum and average distances traveled by year are shown for each site in bold.

Year	Day of year	Postlarval concentration (mean no. 100m^{-3})	Oregon Inlet NFT distance (km)	Hatteras Inlet NFT distance (km)
2000	290	3.00	3.7	4.0
	295	1.80	5.8	2.9
	299	**9.71**	**7.4**	**4.5**
	309	0.53	4.3	2.9
			mean = 5.3	**mean = 3.6**
2001	256	3.21	3.3	6.8
	262	**338.14**	**8.8**	**11.5**
	269	8.86	2.9	7.3
	276	25.59	5.7	7.3
	288	7.94	6.6	8.8
	296	1.10	3.0	7.0
			mean = 5.1	**mean = 8.1**

Table 5. Summary of dispersal patterns during nighttime, 'tide-wind' particle-tracking simulations for the 5 d period prior to each cruise date. Wind component and wind dir. reflect the direction the wind is blowing towards. Inlet refers to inlet of origin for particles that achieved across-sound dispersal. OI = Oregon Inlet; SP = Stumpy Point. For reference, dates of simulation runs picked to represent dispersal results during specific winds (shown in Figs. 10 & 11) are denoted by *.

Wind component	Wind dir.	Year	Day	Across-sound dispersal?	Inlet	General dispersal patterns?
S	S	2000	290	Yes	OI	Particles cross from OI
	SSW	2000	295	Yes	OI	to SP and move
	SW	2000	299	Yes	OI	southward along
	SSE	2000	309	Yes	OI	western shore
	SW	2001	262*	Yes	OI	As above, but particles
	SE	2001	276	Yes	OI	also move southwards along eastern shore
N	NE	2001	269*	No	--	Particle pushed downwind from both inlets, but some particles from OI move southward into middle of sound
W	WSW	2001	256	Yes	OI	Most particles from OI
	NW	2001	288	Yes	OI	move north towards
	W	2001	296*	Yes	OI	Albemarle Sound, but some particles reach SP

FIGURE LEGENDS

Figure 1. Map of Albemarle-Pamlico Estuarine System (APES) in North Carolina, USA showing regional bathymetry and hydrographic stations (■) within Pamlico Sound, OI = Oregon Inlet; SP = Stumpy Point; Ch = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet (A). Blue crab plankton sampling stations (●) in 2000 (B) and 2001 (C) are presented on enlarged maps of our study area (northern basin of Pamlico Sound). Postlarval collector stations were located at Oregon and Hatteras Inlets during both years.

Figure 2. Resolution of finite element grid in the Oregon Inlet (A) and Hatteras Inlet (B) regions. During 'wind-only' simulations, particles were released within 2 km of the black circles (near-inlet releases). During 'tide-wind' and nighttime 'tide-wind' simulations, particles were released near the Oregon and Hatteras Inlet current meter stations (black squares; see text for more details).

Figure 3. 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

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along length of each ellipse. OI = Oregon Inlet; SP = Stumpy Point; Ch = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet.

Figure 4. Daily postlarval blue crab settlement to Pamlico Sound at Oregon and Hatteras Inlets in relation to the daily-averaged major axis of wind variance during 2000 (A) and 2001 (B). Positive wind speed values indicate winds blowing towards the northeast and negative values indicate winds blowing towards the southwest (oceanographic convention). For reference, plankton cruise dates are shown as filled circles, and day of year 250 = September 6, 2000. Note differences in the magnitude of blue crab settlement between years.

Figure 5. Relationship between the mean log(x+1)-transformed postlarval concentration of blue crabs (no. 100 m^{-3}) within Pamlico Sound, and mean log(x+1)-transformed postlarval supply (settlement measured as no. postlarvae collector^{-1}) to Oregon and Hatteras Inlets.

Figure 6. Mean concentration of postlarval blue crabs (no. 100 m^{-3}) within Pamlico Sound in relation to depth in the water column (surface vs. 1 m above bottom) and diel cycle (day vs. night). Although postlarval concentrations were converted to proportions and square-root-transformed for analysis, raw data are presented for simplicity.

Figure 7. Concentration of postlarval blue crabs (no 100 m^{-3}) in surface waters at night, by cruise date (panels A-D) during 2000. Ellipses at current meter sites (in blue) represent the principal axes of variance in current velocities, while arrows denote the mean direction of current flow. Wind ellipse and mean angle are plotted outside of Pamlico Sound in green. All principal axes calculations were computed for the 5 d 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.

Figure 8. Concentration of postlarval blue crabs (no 100 m^{-3}) in surface waters at night, by cruise date (panels A-F) during 2001. Ellipses at current meter sites (in blue) represent the principal axes of variance in current velocities, while arrows denote the mean direction of current flow. Wind ellipse and mean angle are plotted outside of Pamlico Sound in green. All principal axes calculations were computed for the 5 d 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 Figure 7.

Figure 9. End-points of particles released from Oregon Inlet (red squares) and Hatteras Inlet (green triangles) during 'wind-only' (left column) and 'tide-wind' (right column) simulations under different wind conditions. Southward winds represented by 2001 results from Day 262 (A & B), northward winds represented by Day 269 (C & D), and westward winds represented by Day 296 (E & F). For reference, modeled currents over the 5 d prior to each cruise date are shown in blue with the 'wind-only' simulation results (left column). Ellipses represent the principal axes of variance in modeled current velocities, and arrows denote the mean direction of current flow. Wind ellipse (in green) and mean angle are plotted outside of Pamlico Sound. OI = Oregon Inlet; SP = Stumpy Point; Ch = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet. Scale bar in bottom left corner (left column) represents 1 m s^{-1} for wind velocity and 5 cm s^{-1} for current velocity, respectively. Compass directions are shown in top-right corner of panel A.

Figure 10. End-points (left column) and dispersal trajectories (right column) of particles released from Oregon Inlet (red squares) and Hatteras Inlet (green triangles) during nighttime 'tide-wind' simulations under different wind conditions. Southward winds represented by 2001 results from Day 262 (A & B), northward winds represented by Day 269 (C & D), and westward winds represented by Day 296 (E & F). OI = Oregon Inlet; HI = Hatteras Inlet. Wind ellipse (in green) and mean angle are plotted outside of Pamlico Sound for reference. Compass directions are shown in top-right corner of panel A.
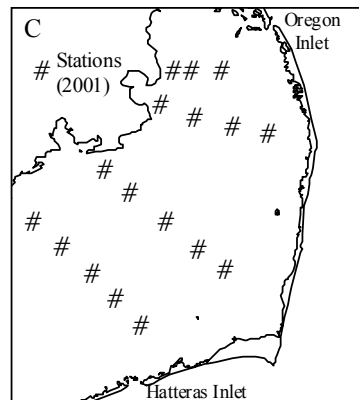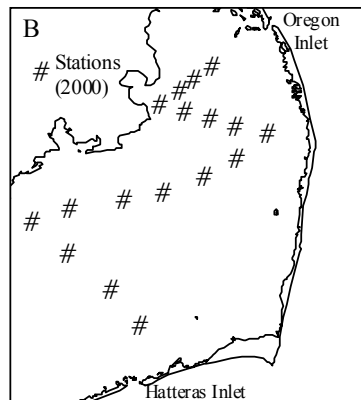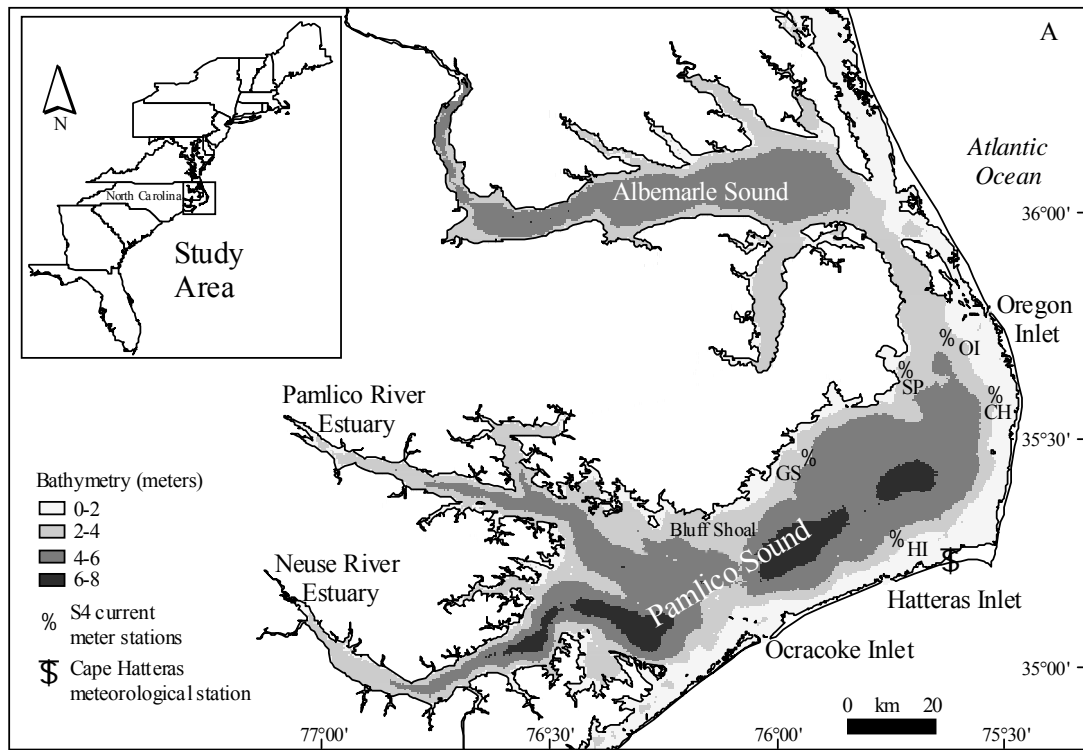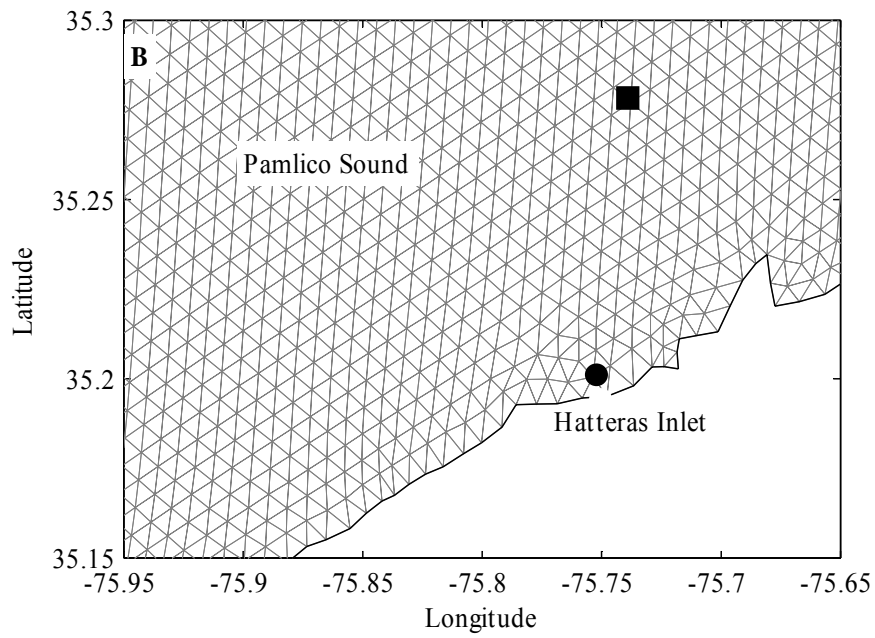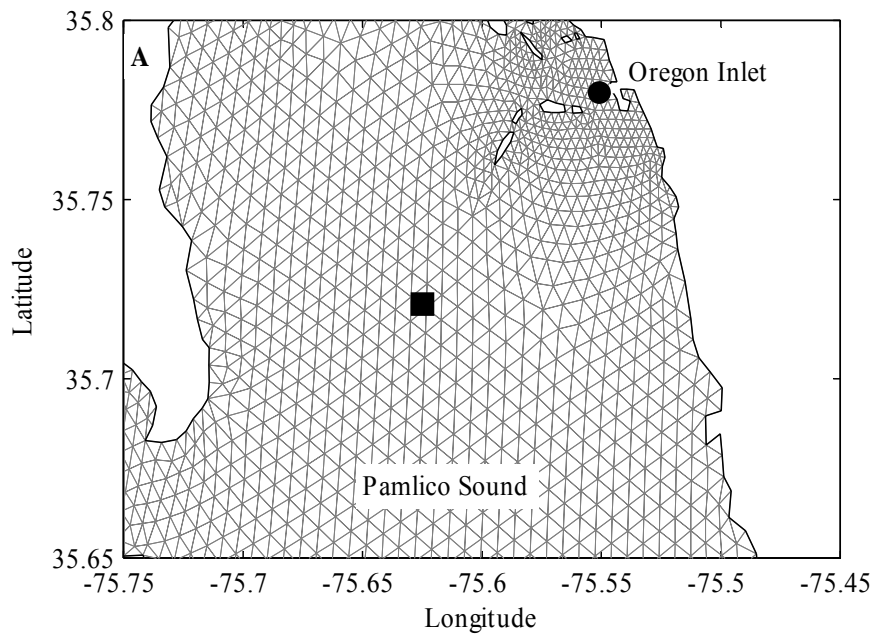
Figure 1

Figure 2
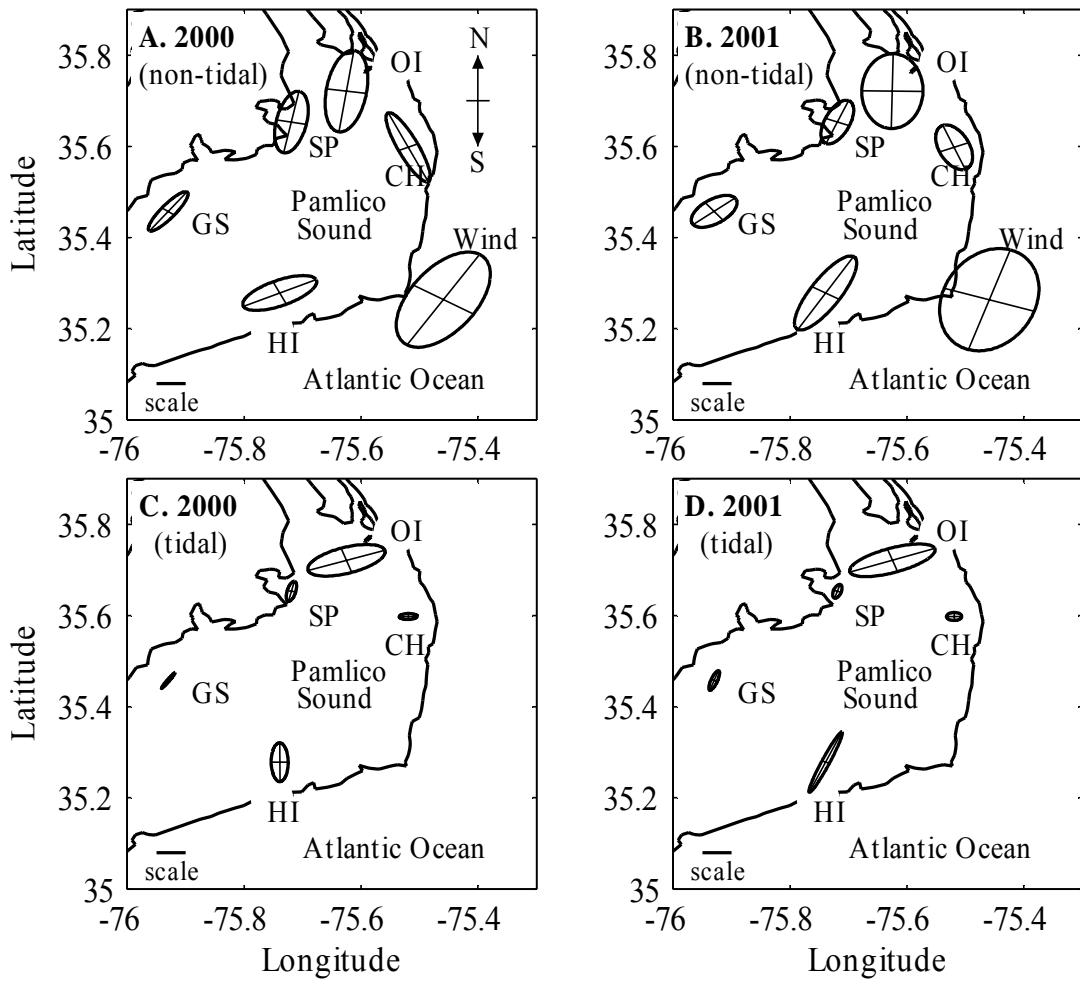
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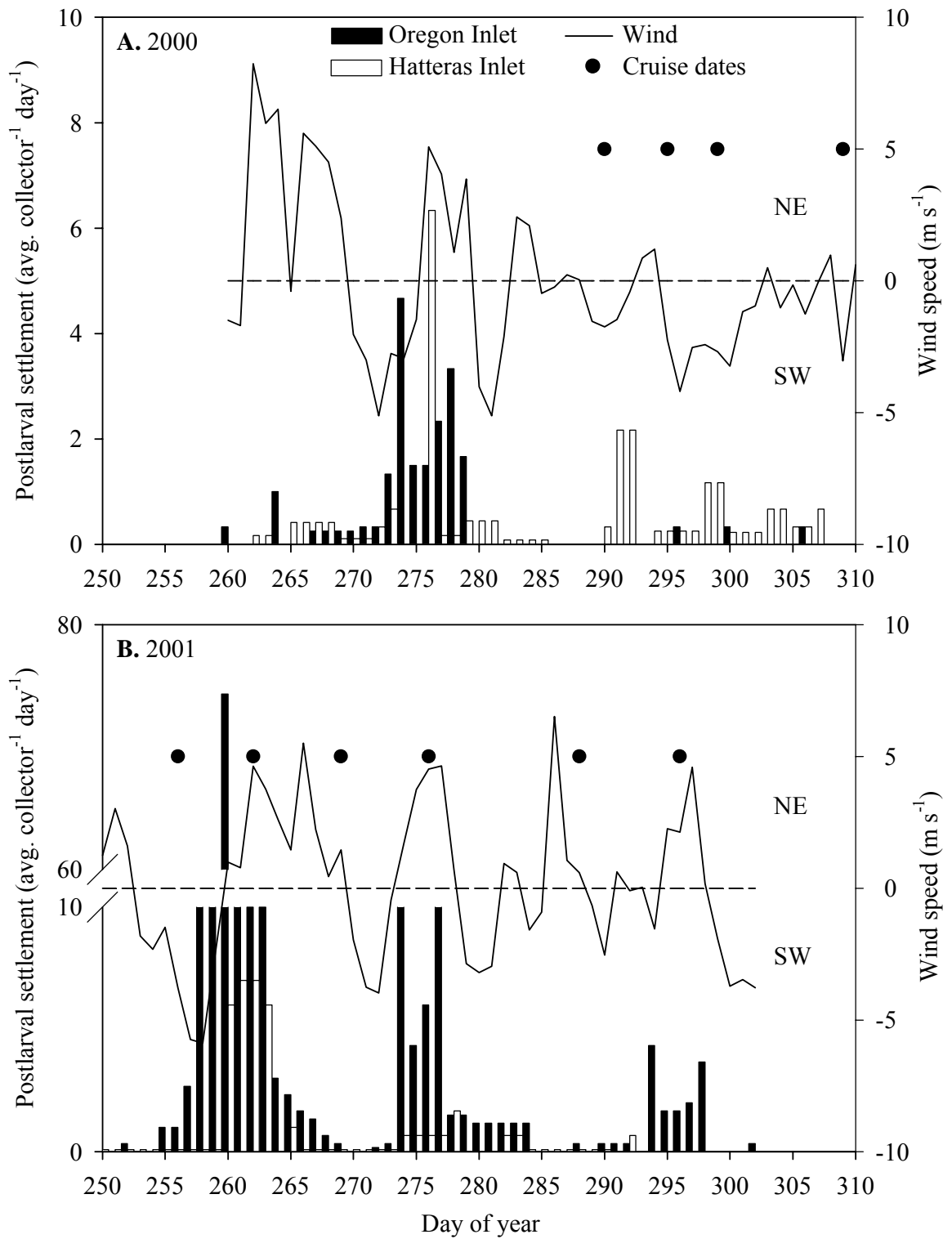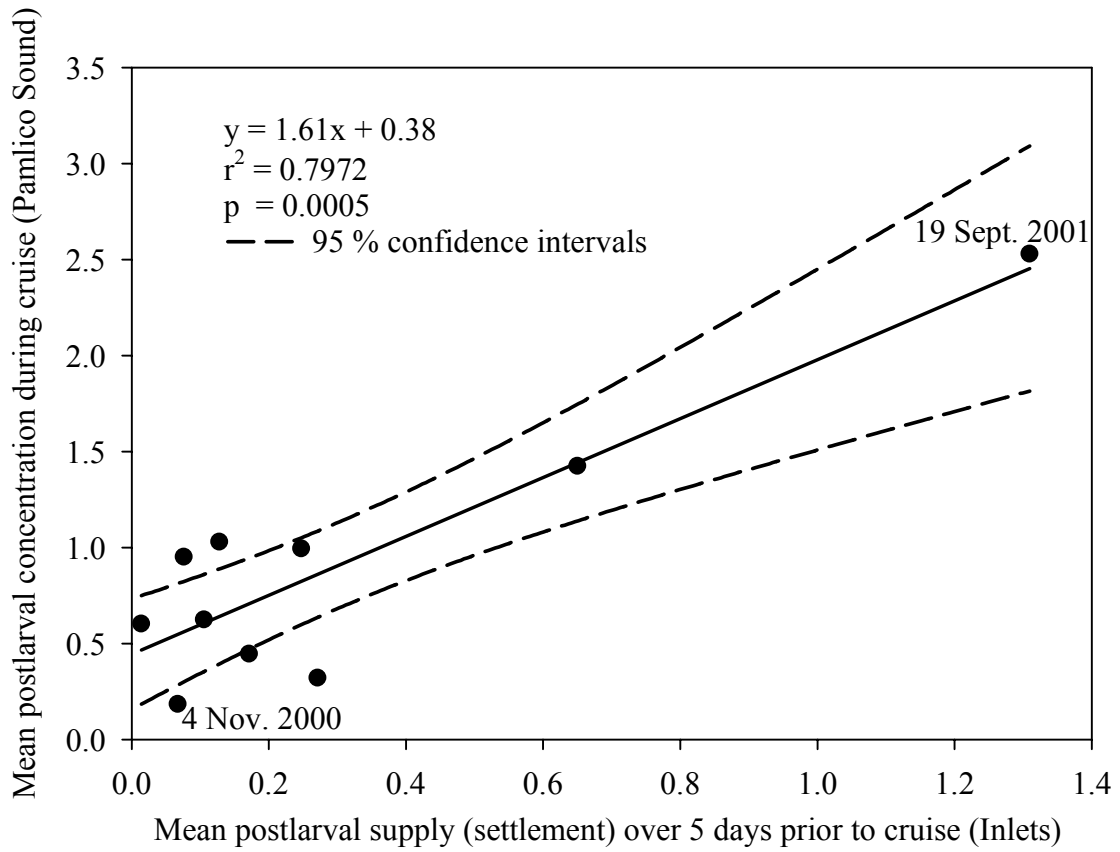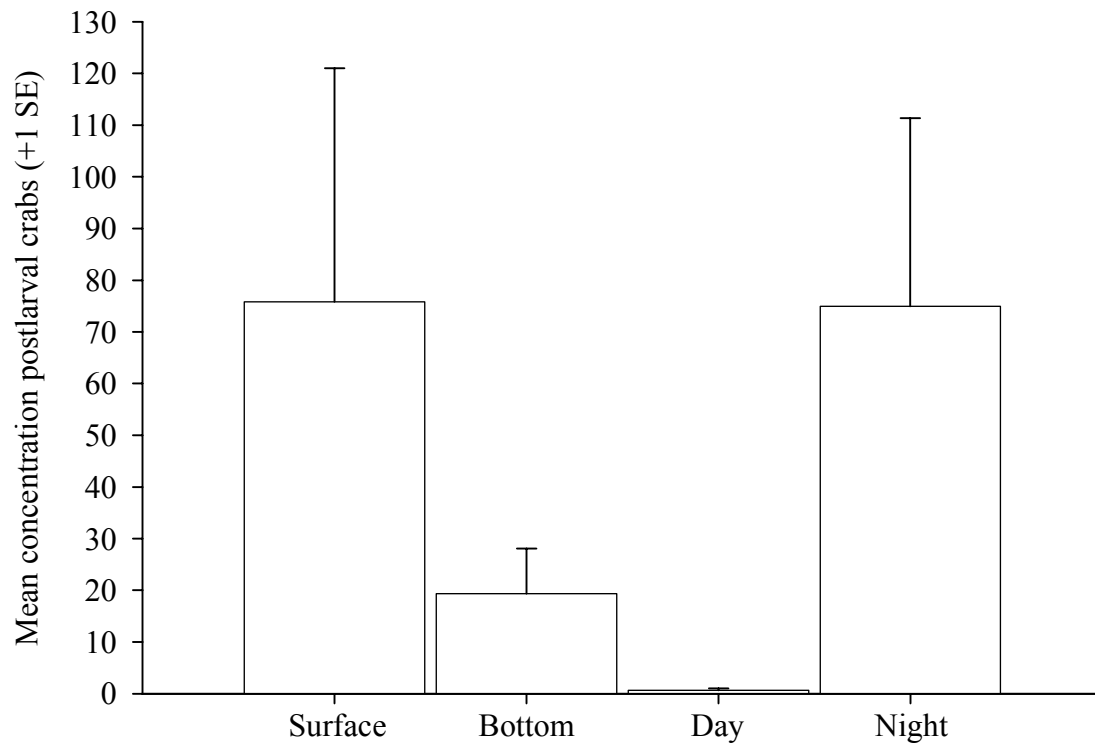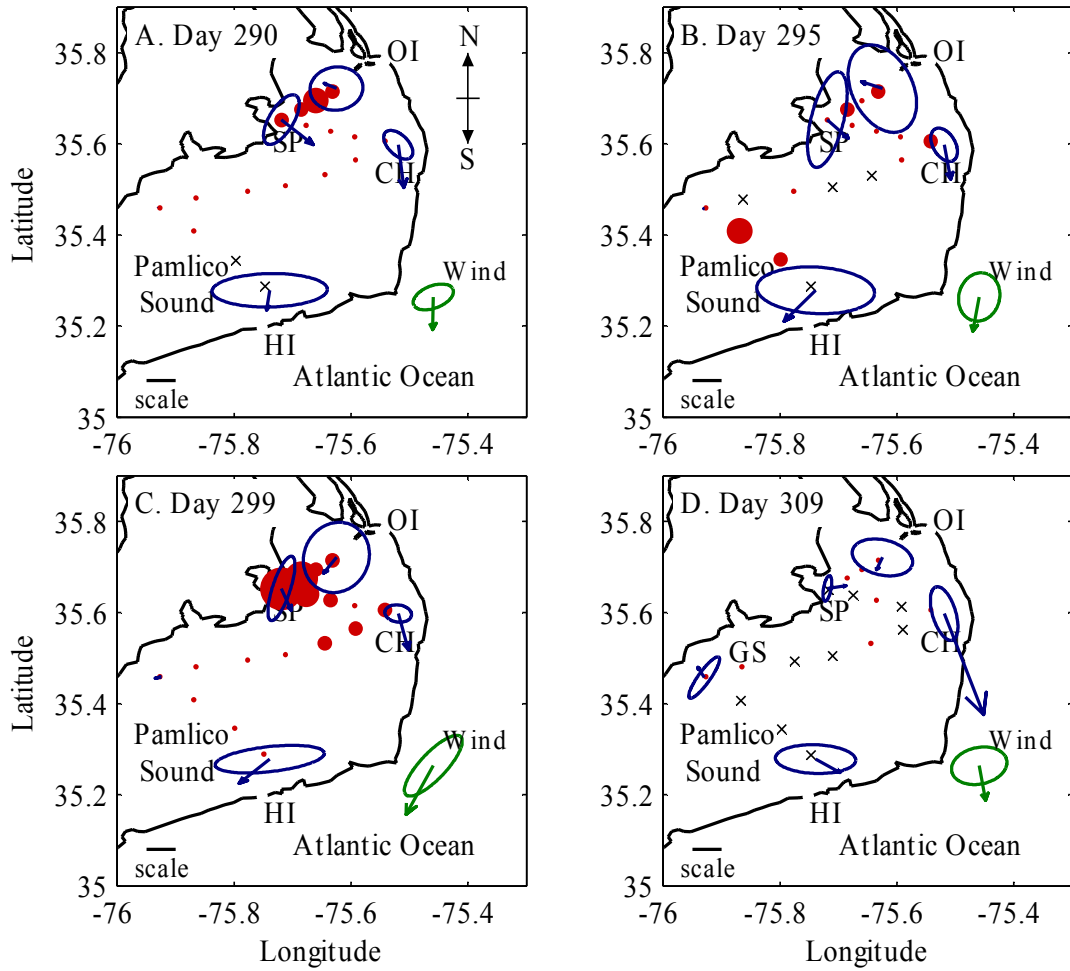
Figure 4

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Figure 5

Figure 6

Figure 7

Figure 8

Wind-only end-points   **Tide-wind end-points**

Figure 9

Nighttime tide-wind end-points

Nighttime tide-wind trajectories
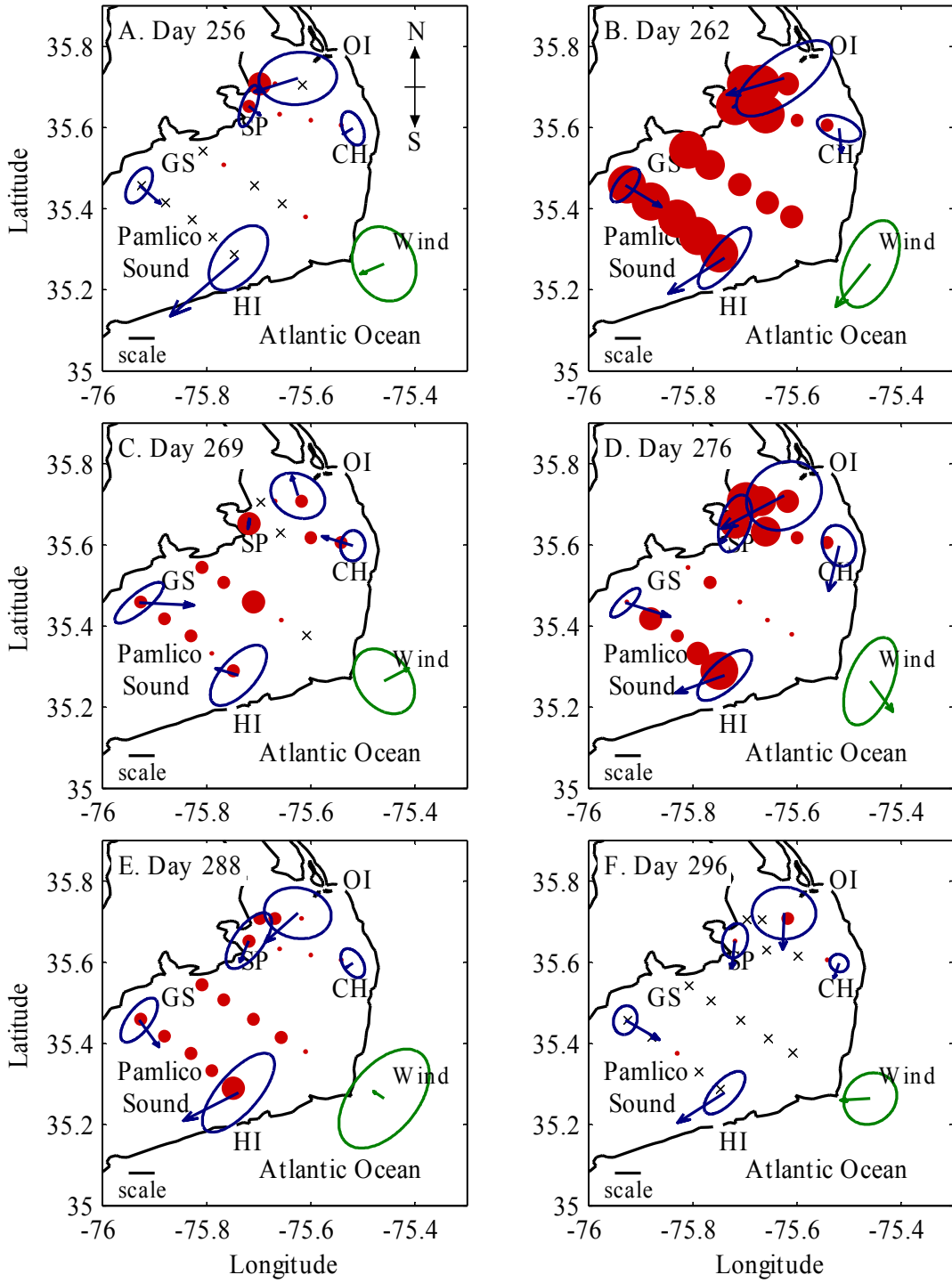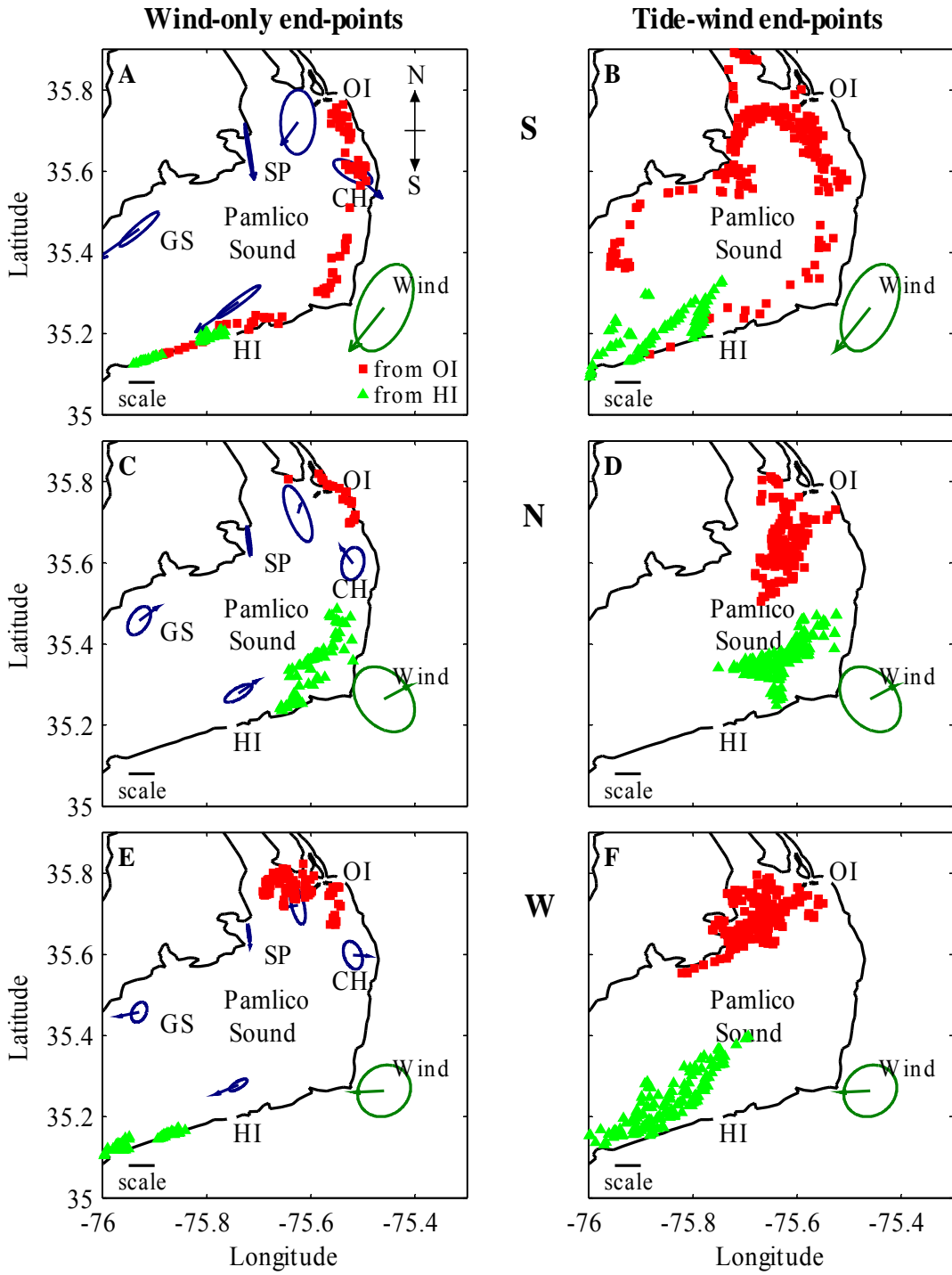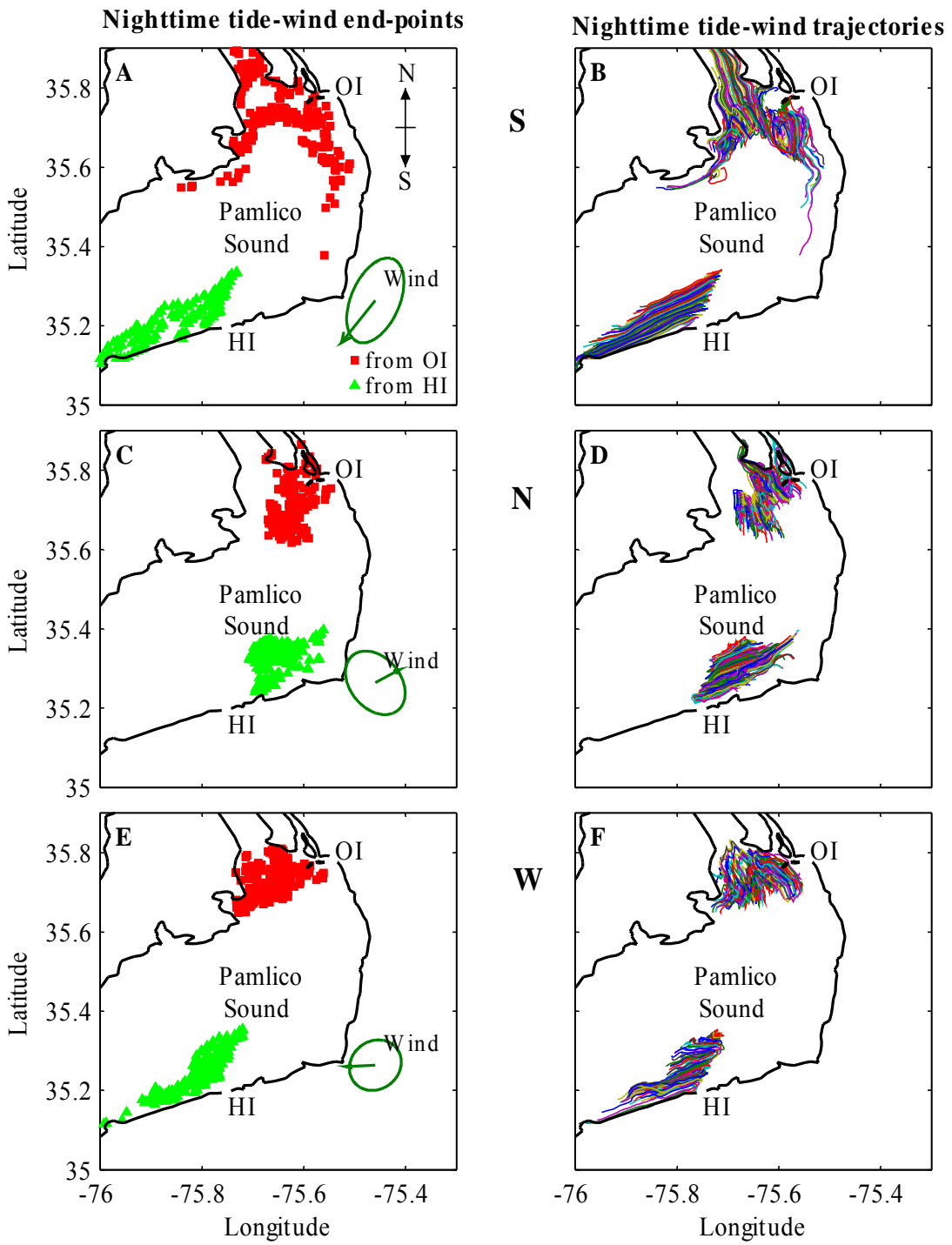
Figure 10

CHAPTER 3

ENVIRONMENTALLY-CONTROLLED, DENSITY-DEPENDENT SECONDARY DISPERSAL IN A LOCAL ESTUARINE CRAB POPULATION

ABSTRACT

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

INTRODUCTION

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

The secondary dispersal of marine and stream benthic invertebrates may result from (1) a passive response to physical environmental conditions (e.g., resuspension

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

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al., 2004), or adaptive behavioral responses to exogenous environmental variables associated with these cycles (Welch *et al.*, 1999).

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

The blue crab, *Callinectes sapidus*, is an ecological and commercially important, estuarine-dependent species along the East and Gulf coasts of the United States. Following estuarine recruitment, postlarval blue crabs settle in beds of submerged aquatic habitat (e.g., seagrass or other structurally complex habitats) where they undergo metamorphosis to the first benthic instar (J1) (Heck and Thoman, 1981; Orth

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and van Montfrans, 1987; Etherington and Eggleston, 2000). It has been generally accepted that juveniles remain in these habitats until they reach the fifth to seventh instar (J5-7) stage and begin to migrate benthically into non-vegetated habitats (Hines *et al.*, 1987; Orth and van Montfrans, 1987). Recent evidence, however, has demonstrated that pelagic, secondary dispersal from seagrass settlement habitats by earlier instars (J1-5) determines patterns of recruitment on a regional scale, and can mask density-dependent relationships among early juvenile life-history stages (Etherington and Eggleston, 2000; Blackmon and Eggleston, 2001; Etherington and Eggleston, 2003; Etherington *et al.*, 2003). Yet it remains unclear when juvenile blue crabs undergo such dispersal, and what factors underlie and mediate transport. Therefore, the objectives of this study were to (1) identify environmental factors (wind, diel cycle, and tidal phase) which may cue juvenile blue crabs to move into surface waters to undergo secondary dispersal, and to determine if this secondary dispersal varies with (2) ontogeny and/or (3) density.

METHODS

Study region

Two field studies were conducted in a region located near Oregon Inlet, North Carolina, USA (35º 47.5' N; 75º 33.5' W; Fig. 1). The area was characterized by relatively shallow (1 m deep), nearly continuous seagrass beds separated by deeper (4 m) unvegetated sandy channels. These seagrass beds typically harbor relatively high densities of post-settlement, early juvenile blue crabs during the fall blue crab

recruitment months (August-October) (Etherington and Eggleston, 2000; Blackmon and Eggleston, 2001; Etherington *et al.*, 2003). Within the region, two seagrass beds of similar size (~0.05 km^2) and habitat characteristics (97 % *Zostera marina*, ~3 % *Ruppia maritima* and *Halodule wrightii*) were selected for study (Fig. 1). The seagrass beds, named North and South, respectively, were considered independent due to the distance separating them (~1.5 km) and negligible physical connectivity by tidal and wind-driven currents (Reyns, pers. obs.).

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

Environmental cues study

To identify the environmental factors that correlate with secondary dispersal of blue crabs, we conducted a study at the North seagrass bed from 30 September-18 October 2001. We hypothesized that secondary dispersal of juvenile blue crabs would occur during nocturnal flood tides, because many estuarine organisms utilize cues associated

with diel and tidal cycles to move up-estuary (Boehlert and Mundy, 1988; Forward and Tankersley, 2001). The occurrence of secondary dispersal of juvenile blue crabs was defined by the concentration of crabs in the water column (no. crabs 100 m^{-3}), and was quantified using a channel net deployed outside the grass bed such that the top of the net frame was level with the water's surface. The channel net had 890 μm-mesh, a mouth dimension of 1 m (width) x 0.5 m (height), and was equipped with a General Oceanics (Miami, FL) flow meter to calculate the volume of seawater filtered. A preliminary study determined net avoidance by J1-5 blue crabs to be negligible and net capture and retention efficiency to be near 100 %. To obtain a mean concentration of crabs in the water column during each treatment combination (see below), we conducted five sequential replicate, five-minute (~100 m^3 filtered) net sets.

The physical environmental factors examined in this study included wind intensity (wind speed and direction), diel cycle (day versus night) and tidal phase (flood versus ebb tide). We sampled under varying wind conditions because as wind intensifies, current velocity and exposure to wind waves in shallow seagrass beds may cause a resuspension of material from the seagrass canopy (Koch, 1999), potentially enhancing secondary dispersal. Thus, sampling dates were initially picked qualitatively to alternate between storm ("windy") and calm conditions as predicted by NOAA weather forecasts. During sampling, the average wind speed was quantified 2 m above sea level from a small boat at the research site (and away from land obstructions) using a hand-held Kestrel 1000 wind meter (Nielsen Kellerman, Chester, PA). The influence of the diel and tidal cycles on secondary dispersal was examined by deploying the

channel net during the following treatment combinations: day-flood tide, day-ebb tide, night-flood tide and night-ebb tide. Channel nets were set downstream of the seagrass bed (see Fig. 1) during peak current velocity, which typically occurred one to two hours before high or low tide. Upon collection, samples were preserved in 75 % ethanol and transported to the laboratory where juvenile blue crabs were enumerated, measured for carapace width (CW: dorsal distance between lateral spines), and categorized by size class following Pile et al. (1996). Data collection was repeated during six separate 24-hr intervals, encompassing tides of both maximum (spring) and minimum (neap) amplitude.

Size-class distribution of crabs

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

While this study was conducted during the middle of the blue crab recruitment season when a range of blue crab instars (J1-9) is generally found within seagrass settlement habitats (Etherington and Eggleston, 2000), conclusions regarding ontogenetic secondary dispersal could not be reached without first establishing if: (1)

crabs were undergoing secondary dispersal (i.e. present in plankton), (2) not dispersing (i.e. present in seagrass but not in plankton), (3) or not available to disperse (i.e. absent from both seagrass and plankton). To address this, we compared the size-class distributions of pelagic and benthic crabs on two occasions (6 and 9 October 2001). Juvenile blue crab density within seagrass was quantified using standard suction sampling techniques (Orth and van Montfrans, 1987; Pile *et al.*, 1996; Etherington and Eggleston, 2000). A suction dredge apparatus sampled seagrass within a 1.3 m-diameter drop net, and was equipped with a 790 μm-mesh collection bag. Samples were taken from five randomly selected areas within the North seagrass bed to obtain a mean density of juvenile blue crabs (no. crabs m^{-2}). Each sample was suctioned for six minutes and dip-netted until three consecutive sweeps of the net were free of crustaceans and fishes. Following collection, samples were preserved and processed for blue crabs as described above, and densities of crabs < 25 mm CW corrected for the 88 % efficiency of this method (Orth and van Montfrans, 1987).

Statistical analyses

The influence of potential environmental cues on secondary dispersal was analyzed using a two-way, fixed factor ANCOVA model with time of day and tidal cycle as factors, and average wind speed during a trial as the covariate. Wind direction was not included as a covariate as winds were consistently out of the northeast on all sampling days. The covariate and all factor X covariate interaction terms were non-significant (all $P > 0.16$). Therefore, we dropped these terms from the model and used a reduced two-

way ANOVA model. Normality and homogeneity of variances were achieved after log(x+1)-transformation of the response variable (mean concentration of crabs in the plankton).

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

Density study

To determine if secondary dispersal of juvenile blue crabs is density-dependent, we conducted a second field study at the North and South seagrass beds from 6 September-9 October 2002. The objective of this study was to characterize the benthic density of juvenile blue crabs in seagrass and the corresponding pelagic concentration of crabs in surrounding waters. The density of crabs (no. crabs m^{-2}) in seagrass was quantified during the day using the suction sampling techniques described above (see 'Environmental Cues Study'). To obtain a mean crab density, five replicate suction samples were taken from each seagrass bed (North and South; Fig. 1). In our study area, juvenile blue crabs reside within these grassbeds, and are absent from adjacent unvegetated benthic habitats (Etherington and Eggleston, 2000). Therefore, crabs located in the water column surrounding the seagrass beds were assumed to have originated from these habitats, and were considered to be 'secondary dispersers'.

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

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

Statistical analyses

The relationship between secondary dispersal and the benthic density of crabs was analyzed using regression analysis to measure the fit of models that included the pelagic concentration of juvenile blue crabs as the response variable and the benthic density of

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

To identify which variables influenced the secondary dispersal of juvenile blue crabs, we used an information-theoretic approach (Burnham and Anderson, 2002). This

approach provides an objective way to select the 'best approximating model' for data analysis and inference using Akaike's information criterion (AIC), an extension of likelihood theory (Burnham and Anderson, 2002). Furthermore, the relative importance of multiple variables can be assessed by examining a set of candidate models (Burnham and Anderson, 2002).

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

RESULTS

Environmental cues

The mean concentration of crabs in the water column varied significantly by time of day (two-way reduced ANOVA: d.f. = 1,20, F = 11.04, P = 0.003) and tidal cycle (d.f. = 1,20, F = 4.36, P = 0.049). These variables displayed a significant time of day X tidal cycle interaction (d.f. = 1,20, F = 4.99, P = 0.037), whereby crabs exhibited secondary dispersal primarily during nighttime flood tides (Fig. 2). Although wind speed was non-significant in the initial analysis (two-way ANCOVA model), when winds exceeded 15 m s^{-1}, juvenile blue crabs were collected in the water column irrespective of time of day and tidal cycle (e.g., Day of Year 273 in Fig. 2).

Size-class distribution

Of the juvenile blue crabs collected in the water column during the environmental cues study, approximately 98 % were early-staged crabs (J1-2: 2.2-4.2 mm CW) with less than 2 % belonging to larger size classes (J3-9: 4.3-16.1 mm CW). The distribution of blue crab size classes in the plankton differed significantly from the distribution of crabs in seagrass (Fig. 3a: $_{n1n2}$D = 0.98, P < 0.01; Fig. 3b: $_{n1n2}$D = 0.96, P < 0.01), whereby crabs in seagrass had a much broader distribution (J1-9) than crabs in the plankton. Size-class distribution patterns during the density study were similar to those observed in the environmental cues study (Fig. 3c), when crabs collected in the plankton and seagrass also exhibited significantly different size-class distributions ($_{n1n2}$D = 0.76, P < 0.01).

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Explanatory variable selection

The secondary dispersal of juvenile blue crabs was influenced by the density of intraspecific crabs in seagrass (Table 1a). The model with the benthic density of J1 and J2 crabs had the lowest AIC_c (Table 1a) and was therefore considered the best approximation from all candidate models (Burnham and Anderson, 2002). While this model had a 54 % probability of being the right model for our data, it was only 1.71 times better at explaining variability in secondary dispersal than the one-parameter model with the density of J1 crabs as the explanatory variable (Table 1a). Given the evidence ratio of less than 2.0, there was little basis to suggest that one model was better than another (Burnham and Anderson, 2002). By ranking the relative importance of the explanatory variables, we determined that the density of J1 crabs was of greater relative importance in explaining the variability in secondary dispersal than the density of J2 crabs (99.7 % vs. 63.3 %; Table 1b). In addition, evidence for the relative importance of the J1 crab density variable (0.9979; Table 1b) was substantially more than the weight of evidence for the next best approximating model (J1, J2: 0.5373; Table 1a).

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

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Functional relationship between pelagic and benthic juvenile blue crabs

In general, there was a non-linear increase in the pelagic concentration of J1 blue crabs with increasing benthic J1 crab density (Fig. 4). The benthic density of J1 crabs was used as the explanatory variable because of its relative importance in explaining variability in the pelagic concentration of J1 crabs (see above; Table 1b). The model with the lowest AIC_c was a sigmoid function, and had a 97 % probability of being the right model given the set of candidate models (Table 2). The sigmoid model fit the data better than a linear model, which had no substantial evidence of support ($\Delta AIC_c > 10$, weights = 0; Table 2; Burnham and Anderson, 2002).

DISCUSSION

The mechanisms driving secondary dispersal of aquatic benthic organisms are generally not well known, even though secondary dispersal can have significant implications to population and community dynamics (Caley *et al.*, 1996; Palmer *et al.*, 1996). For example, secondary dispersal by juvenile bivalves allow tide flats to be recolonized following disturbances and can determine adult distribution patterns in the North Sea (Beukema and de Vlas, 1989). Secondary dispersal can also alter initial settlement patterns resulting in a decoupling between larval supply and later juvenile distributions. In Pamlico Sound North Carolina, for instance, secondary dispersal of early juvenile blue crabs links spatially-separated settlement habitats, thereby enhancing the nursery capacity of the entire sound (Etherington and Eggleston, 2000; 2003). While small-scale field and laboratory studies have determined that secondary dispersal of early juvenile

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blue crabs is an active behavioral process, studies examining the effects of environmental cues and intra-specific crab density on secondary dispersal have been inconclusive (Blackmon and Eggleston, 2001; Etherington *et al.*, 2003). Results from our new study suggest that secondary dispersal of early juvenile blue crabs from settlement habitats occurs rapidly following settlement in response to increasing conspecific density in seagrass, and is mediated by physical environmental conditions associated with diel and tidal cycles.

Ontogenetic and density-dependent effects

Our results indicate that the relative abundance of early blue crab instars was greater in surface waters than those of later blue crab instars, suggesting that the propensity to use secondary dispersal is ontogenetic. This result is counter to previous findings where blue crab secondary dispersal occurred predominately by older (later) instars (Blackmon and Eggleston, 2001; Etherington *et al.*, 2003). The apparent discrepancy between our study and previous findings might be due to differences in the spatial scale over which secondary dispersal was examined. In our study, we quantified blue crab secondary dispersal from 0.05 km^2 seagrass beds, while other studies measured secondary dispersal from smaller-scale, 1 m^2 experimental seagrass plots (Blackmon and Eggleston, 2001; Etherington *et al.*, 2003) or in laboratory flumes (Blackmon and Eggleston, 2001). Several reasons may explain why our results may be a more accurate depiction of which blue crab size classes undergo secondary dispersal. First, the secondary dispersal by older instars observed in other field studies was measured using

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plankton nets deployed over the seagrass bed (Blackmon and Eggleston, 2001; Etherington *et al.*, 2003). Such movements into the water column by larger juvenile crabs may represent redistribution of crabs within a seagrass bed rather than dispersal away from that habitat. In our study, the deployment of plankton nets over sandy areas downstream of the seagrass beds ensured that crabs collected in the water column were leaving these habitats through secondary dispersal (see assumptions in 'Materials and methods'). Second, we know from concurrent sampling of the benthic and pelagic size-class distributions of blue crabs that J3 (and larger) instars were present in seagrass, but had low relative abundances in the plankton (Fig. 3a-c). Finally, because our field study was observational, we do not have artifacts associated with experimental field manipulations and laboratory studies.

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

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

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

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

dependent predation of early juvenile blue crabs has not been identified (Pile *et al.*, 1996). Lack of evidence for density-dependent mortality of blue crabs suggests that secondary dispersal may be of greater relative importance in structuring blue crab population dynamics than predation (e.g., Etherington *et al.*, 2003).

Despite predictions of the 'settle and stay' hypothesis that high predation rates encountered in the plankton inhibit fishes and crustaceans from leaving initial settlement habitats (Bell and Westoby, 1986), J1 blue crabs may experience a cannibalism refuge in the plankton by leaving habitats that harbor high conspecific densities. While this runs counter to the idea that mortality in the plankton is high (Thorson, 1950), a recent study evaluating predation on planktonic coastal assemblages of marine invertebrate larvae measured relatively low predation rates (0-7 % loss d^{-1}: (Johnson and Shanks, 2003). Predation rates for early juvenile blue crabs undergoing secondary dispersal in turbid estuarine conditions are unknown; however, preliminary tethering experiments suggest that while mortality of J1-2 blue crabs does not differ across habitat types (plankton versus seagrass), predation risk is slightly reduced at night (Reyns, unpublished data). A nocturnal reduction in mortality is not surprising, given that postlarval Caribbean spiny lobsters minimize predation by dispersing in surface waters during dark, new moon periods (Eggleston *et al.*, 1998; Acosta and Butler, 1999), and marine meiofauna (Hagerman and Rieger, 1981), stream meiofauna (Palmer 1992), marine harpacticoid copepods (Service and Bell, 1987), and some marine bivalve species (Armonies, 1992) also undergo significantly greater secondary dispersal at night. Similarly, many estuarine and intertidal crabs have hatching rhythms

that are synchronized with nighttime periods, as well as phases of the tidal cycle, to reduce larval predation by visual predators (Morgan, 1995). For early juvenile blue crabs, the mechanism underlying nighttime transport appears to be due, in part, to an endogenous rhythm in swimming activity whereby juveniles become more active at night (Forward *et al.*, 2004). We suggest therefore, that the timing of secondary dispersal by J1 blue crabs during nocturnal flood tides serves as an adaptive strategy to expedite transport from initial settlement habitats to alternative nursery habitats, while minimizing predation risk in the plankton.

The influence of environmental cues on secondary dispersal

Secondary dispersal can also be influenced by physical environmental conditions such as wind speed. Given the depth of the seagrass beds in our study area (1 m), the passive resuspension of juvenile blue crabs through wind-driven waves and currents is likely during strong wind events. Many marine and stream benthic invertebrates undergo passive secondary dispersal following storm or high-flow induced resuspension to the water column (Hagerman and Rieger, 1981; Palmer, 1992; Hall, 1994). High flow conditions can also alter the rate at which density-dependent (active) secondary dispersal occurs in black fly neonates (Fonseca and Hart, 1996). In our study, there was no statistically significant relationship between wind speed and the pelagic concentration of J1 blue crabs, suggesting that secondary dispersal is an active behavioral process regardless of wind speed. While crabs were collected during all diel and tidal phases during a relatively strong wind event (wind speed > 15 m s^{-1}), and

during nocturnal ebb tides (e.g., Day of Year 275, 291: Fig. 2) corresponding to full and new moon periods when currents can reach 30 cm s^{-1} (Fonseca and Bell, 1998), the size-class distribution of early juvenile blue crabs did not change during these periods (catch still dominated by J1 instars), as would be expected if secondary dispersal were passive. In addition, active secondary dispersal of juvenile blue crabs has been observed in laboratory flume conditions in flows between 20 cm s^{-1} to 30 cm s^{-1} (Blackmon and Eggleston, 2001). Given that high wind conditions will enhance the concentration of suspended sediments in shallow environments and reduce light intensity, the presence of early juvenile blue crabs in surface waters during these events may instead reflect active secondary dispersal during low-light, high-flow conditions, rather than passive transport.

CONCLUSIONS AND IMPLICATIONS OF SECONDARY DISPERSAL

Several studies have correlated the secondary dispersal of marine and stream benthic invertebrates with specific variables (e.g., wind speed, infaunal density, etc.; see reviews by Günther, 1992; Palmer *et al*., 1996), but few have examined multiple, concurrent physical environmental and biological conditions as has been our approach in this study. This study, coupled with previous findings (Etherington and Eggleston, 2000; Blackmon and Eggleston, 2001; Etherington and Eggleston, 2003; Etherington *et al.*, 2003), demonstrates the ability of a juvenile marine benthic invertebrate to modify its regional distribution via dispersal in the water column by behaviorally responding to biological and physical environmental variables. Furthermore, because such secondary

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dispersal is density-dependent, blue crab metapopulation persistence is likely promoted through the redistribution of juvenile crabs from high-density settlement habitats to habitats characterized by low postlarval supply, which ultimately increases the regional nursery capacity (Etherington and Eggleston, 2000; 2003). As such, secondary dispersal may be just as or even more important than pre-settlement (larval and postlarval) dispersal in linking regions of varying recruitment and habitat quality (Pulliam, 1988). Consequently, predictions regarding the population dynamics of aquatic organisms, particularly for habitat conservation and fishery management applications, cannot be made without considering secondary dispersal and the degree to which it actually occurs.

ACKNOWLEDGEMENTS

LITERATURE CITED

Acosta, C.A. and Butler, M.J., IV (1999) Adaptive strategies that reduce predation on Caribbean spiny lobster postlarvae during onshore transport. *Limnol. Oceanogr.* **44**:494-501.

Anderson, D.R. and Burnham, K.P. (2002) Avoiding pitfalls when using information-theoretic methods. *J. Wildl. Manage.* **66**:912-918.

Armonies, W. (1992) Migratory rhythms of drifting juvenile molluscs in tidal waters in the Wadden Sea. *Mar. Ecol. Prog. Ser.* **83**:197-206.

Bell, J.D. and Westoby, M. (1986) Variation in seagrass height and density over a wide spatial scale: Effects on common fish and decapods. *J. Exp. Mar. Bio. Ecol.* **104**:275-295.

Beukema, J.J. and de Vlas, J. (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 Eggleston, D.B. (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 Mundy, B.C. (1988) Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *Am. Fish. Soc. Symp.* **3**:51-67.

Brittain, J.E. and Eikeland, T.J. (1988) Invertebrate drift- a review. *Hydrobiologia* **166**:77-93.

Burnham, K.P. and Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer-Verlag, 488 pp.

Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P. and Menge, B.A. (1996) Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* **27**:477-500.

Commito, J.A., Thrush, S.F., Pridmore, R.D., Hewitt, J.E. and Cummings, V.J. (1995) Dispersal dynamics in a wind-driven benthic system. *Limnol. Oceanogr.* **40**:1513-1518.

Dieckmann, U., O'Hara, B. and Weisser, W. (1999) The evolutionary ecology of dispersal. *Trends Ecol. Evol.* **14**:88-90.

Dunn, R., Mullineaux, L.S. and Mills, S.W. (1999) Resuspension of postlarval soft-shell clams *Mya arenaria* through disturbance by the mud snail *Ilyanassa obsoleta*. *Mar. Ecol. Prog. Ser.* **180**:223-232.

Eggleston, D.B., Lipcius, R.N., Marshall, L.S., Jr. and Ratchford, S.G. (1998) Spatiotemporal variation in postlarval recruitment of the Caribbean spiny lobster in the central Bahamas: lunar and seasonal periodicity, spatial coherence, and wind forcing. *Mar. Ecol. Prog. Ser.* **174**:33-49.

Emerson, C.W. and Grant, J. (1991) The control of soft-sediment clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. *Limnol. Oceanogr.* **36**:1288-1300.

Etherington, L.L. and Eggleston, D.B. (2000) Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. *Mar. Ecol. Prog. Ser.* **204**:179-198.

Etherington, L.L. and Eggleston, D.B. (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.

Etherington, L.L., Eggleston, D.B. and Stockhausen, W.T. (2003) Partitioning loss rates of early juvenile blue crabs from seagrass habitats into mortality and emigration. *Bull. Mar. Sci.* **72**:371-391.

Fegley, S.R. (1987) Experimental variation of near-bottom current speeds and its effects on depth distribution of sand-living meiofauna. *Mar. Biol.* **95**:183-191.

Fonseca, D.M. and Hart, D.D. (1996) Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos* **75**:49-58.

Fonseca, M.S. and Bell, S.S. (1998) Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Mar. Ecol. Prog. Ser.* **171**:109-121.

Forward, R.B., Jr. and Tankersley, R.A. (2001) Selective tidal-stream transport of marine animals. *Oceanogr. Mar. Biol. Annu. Rev.* **39**:305-353.

Forward, R.B., Jr., Reyns, N.B., Diaz, H., Cohen, J.H. and Eggleston, D.B. (2004) Endogenous swimming rhythms of juvenile blue crabs, *Callinectes sapidus*, as related to horizontal transport. *J. Exp. Mar. Bio. Ecol.* **299**:63-76.

Günther, C.-P. (1992) Dispersal of intertidal invertebrates: A strategy to react to disturbances of different scales? *Neth. J. Sea Res.* **30**:45-56.

Hagerman, G.M., Jr. and Rieger, R.M. (1981) Dispersal of benthic meiofauna by wave and current action in Bogue Sound, North Carolina, USA. *P.S.Z.N.I.: Mar. Ecol.* **2**:245-270.

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 Thoman, T.A. (1981) Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Bio. Ecol.* **53**:125-134.

Hindell, J.S., Jenkins, G.P., Moran, S.M. and Keough, M.J. (2003) Swimming ability and behaviour of post-larvae of a temperate marine fish re-entrained in the pelagic environment. *Oecologia* **135**:158-166.

Hines, A.H., Lipcius, R.N. and Haddon, A.M. (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.

Johnson, K.A. and Shanks, A.L. (2003) Low rates of predation on planktonic marine invertebrate larvae. *Mar. Ecol. Prog. Ser.* **248**:125-139.

Koch, E.W. (1999) Sediment resuspension in a shallow *Thalassia testudinum* banks ex Konig bed. *Aquat. Bot.* **65**:269-280.

Moksnes, P.-O., Lipcius, R.N., Pihl, L. and van Montfrans, J. (1997) Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. *J. Exp. Mar. Bio. Ecol.* **215**:157-187.

Morgan, S.G. (1995) The timing of larval release. In: *Ecology of marine invertebrate larvae*. L.R. McEdward (ed) Boca Raton: CRC Press, pp. 157-191.

Orth, R.J. and van Montfrans, J. (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. (1986) Hydrodynamics and structure: Interactive effects on meiofauna dispersal. *J. Exp. Mar. Bio. Ecol.* **104**:53-68.

Palmer, M.A. (1988) Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Mar. Ecol. Prog. Ser.* **48**:81-91.

Palmer, M.A. (1992) Incorporating lotic meiofauna into our understanding of faunal transport processes. *Limnol. Oceanogr.* **37**:329-341.

Palmer, M.A., Allan, J.D. and Butman, C.A. (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., Janowitz, G.S., Chao, T.-Y., Weisberg, R.H., Askari, F. and Noble, E. (1986) The physical oceanography of Pamlico Sound. *UNC Sea Grant Publication*: UNC-WP-86-5, Raleigh, NC.

Pile, A.J., Lipcius, R.N., van Montfrans, J. and Orth, R.J. (1996) Density-dependent settler-recruit-juvenile relationships in blue crabs. *Ecol. Monogr.* **66**:277-300.

Powers, S.P. and Peterson, C.H. (2000) Conditional density dependence: The flow trigger to expression of density-dependent emigration in bay scallops. *Limnol. Oceanogr.* **45**:727-732.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *Am. Nat.* **132**:652-661.

Rawlings, J.O., Pantula, S.G. and Dickey, D.A. (1998) *Applied regression analysis: a research tool*. New York: Springer, 657 pp.

Scheltema, R.S. (1986) On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bull. Mar. Sci.* **39**:290-322.

Service, S.K. and Bell, S.S. (1987) Density influenced active dispersal of harpacticoid copepods. *J. Exp. Mar. Bio. Ecol.* **114**:49-62.

Sigurdsson, T.B., Titman, C.W. and Davies, P.A. (1976) The dispersal of young juvenile molluscs by byssus threads. *Nature* **262**:386-387.

Sokal, R.R. and Rohlf, F.J. (1995) *Biometry*. New York: W. H. Freeman and Company, 887 pp.

Thorson, G. (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* **25**:1-45.

Thrush, S.E., Hewitt, J.E., Cummings, V.J., Green, M.O., Funnell, G.A. and Wilkinson, M.R. (2000) The generality of field experiments: interactions between local and broad-scale processes. *Ecology* **81**:399-415.

Turner, S.J., Grant, J., Pridmore, R.D., Hewitt, J.E., Wilinson, M.R., Hume, T.M. and Morrisey, D.J. (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.

Welch, J.M., Forward, R.B., Jr. and Howd, P.A. (1999) Behavioral responses of blue

crab *Callinectes sapidus* postlarvae to turbulence: implication for selective tidal

stream transport. *Mar. Ecol. Prog. Ser.* **179**:135-143.

Wilson, F.S. (1990) Temporal and spatial patterns of settlement: a field study of

molluscs in Bogue Sound, North Carolina. *J. Exp. Mar. Bio. Ecol.* **139**:201-220.

Table 1 (a). Results of the explanatory variable selection using information-theoretic criteria. Table values were calculated using model fits obtained from regression analysis on models that included the (log(x+1)-transformed) concentration of J1 crabs as the response variable, and the (log(x+1)-transformed) benthic densities of J1, J2, and J3 crabs as explanatory variables. K = number of explanatory variables included in model + 1. AIC_c = second-order corrected AIC for sample size < 40. ** = model with lowest AIC_c against which all other models are compared. ΔAIC_c = difference between model with lowest AIC_c. Weights = Akaike weight of evidence (probability) that model is best approximating model in a given set of candidate models. Evidence ratio = evidence supporting best approximating model. Models with weights < 0.054 have insufficient evidence to consider as plausible contributors to secondary blue crab dispersal and are denoted by ‡.

Explanatory Variable	K	AIC_c	ΔAIC_c	Weights	Evidence Ratio
J1	2	-48.03	1.07	0.3140	1.71
J2	2	-36.95	12.15	0.0012	447.75 ‡
J3	2	-36.76	12.34	0.0011	488.45 ‡
J1, J2	3	-49.10		0.5373	**
J1, J3	3	-44.77	4.33	0.0616	8.72
J2, J3	3	-33.66	15.44	0.0002	2686.5 ‡
J1, J2, J3	4	-45.41	3.69	0.0845	6.36

(b) Ranked relative importance of explanatory variables calculated from the Akaike weights in Table 1a.

Explanatory Variable	Relative Importance (%)
J1	99.74
J2	63.33
J3	14.74

Table 2. Model selection results of the functional relationship between the (log (x+1)-transformed) pelagic and benthic abundances of J1 crabs. For simplicity, only criteria for the best approximating non-linear model are compared with those of the linear model. K = number of parameters included in model + 1. AIC_c = second-order corrected AIC for sample size < 40. ** = model with lowest AIC_c. ΔAIC_c = difference between model with lowest AIC_c. Weights = Akaike weight of evidence (probability) that model is best approximating model in a given set of candidate models.

Model	K	AIC_c	ΔAIC_c	Weights
linear	2	-48.03	35.57	0.0000
sigmoid	3	-83.60		0.9687 **

FIGURE LEGENDS

Figure 1. Map of study region, near Oregon Inlet in Pamlico Sound, North Carolina, USA. During the environmental cues study (North site), the channel net was deployed during flood and ebb tide at locations denoted by 'a' and 'b', respectively. During the density study (North and South sites), channel nets (filled circles) were set downstream of the seagrass beds (hatched areas) during flood tide.

Figure 2. The effects of wind, time of day and tidal cycle cues on the secondary dispersal of juvenile blue crabs. The mean concentration of crabs (+ 1 S.E.) is plotted with respect to each environmental trial over time. Lunar phase (full moon: open circle; new moon: closed circle), and average wind speed (dark line) measured during crab collections are plotted for reference. Sampling took place on days: 273, 275, 279, 282, 287 and 291. The response variable was $\log(x+1)$-transformed for statistical analysis, but raw data are presented for simplicity. See text for significance levels.

Figure 3. Comparison of size-class distribution of juvenile blue crabs collected in the plankton and seagrass during the environmental cues study (a: 6 October 2001; b: 9 October 2001) and density study (c: 6 September-9 October 2002; data were combined due to similar crab size-class distributions across study sites and sampling days). Sample size (n) is shown in key; see text for significance levels.

Figure 4. Functional relationship between the pelagic concentration and benthic density of J1 blue crabs. Points represent means (±1 S.E.) of the log(x+1)-transformed concentration and density crab data. Regression line represents the best fitting function (see text and Table 3 for details). For reference, the concentration of juvenile blue crabs increased in the water column when benthic densities approximated 10 crabs m^{-2}.
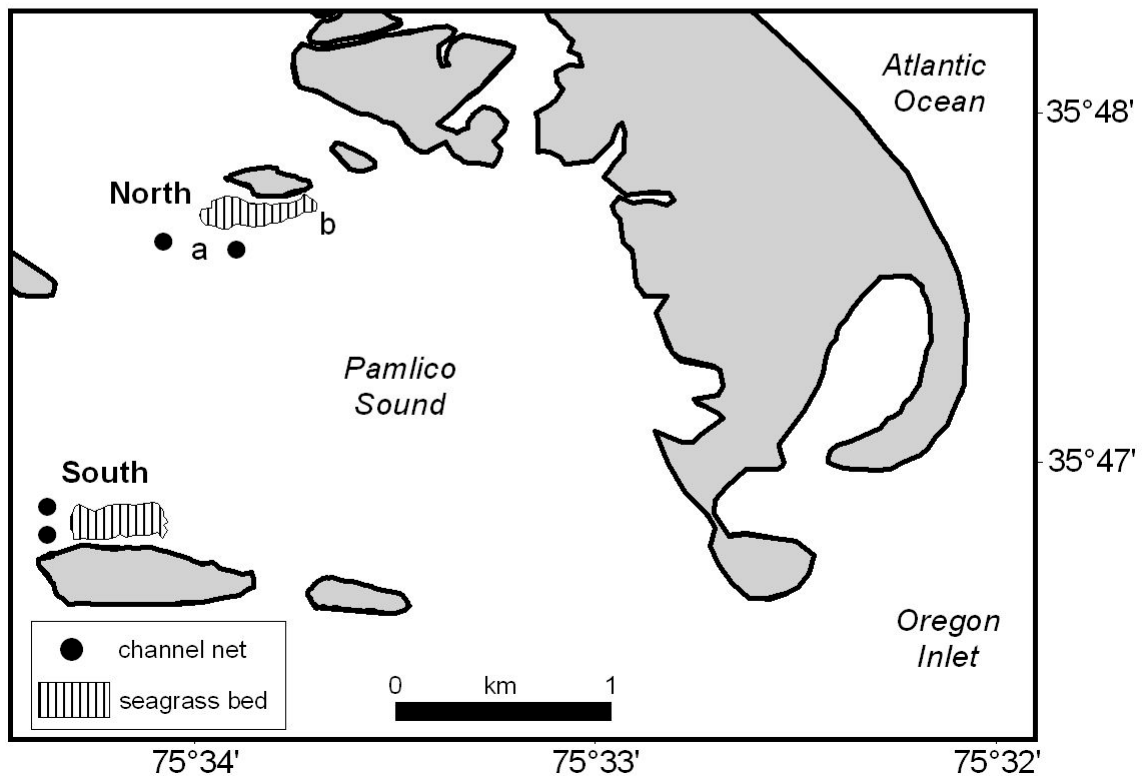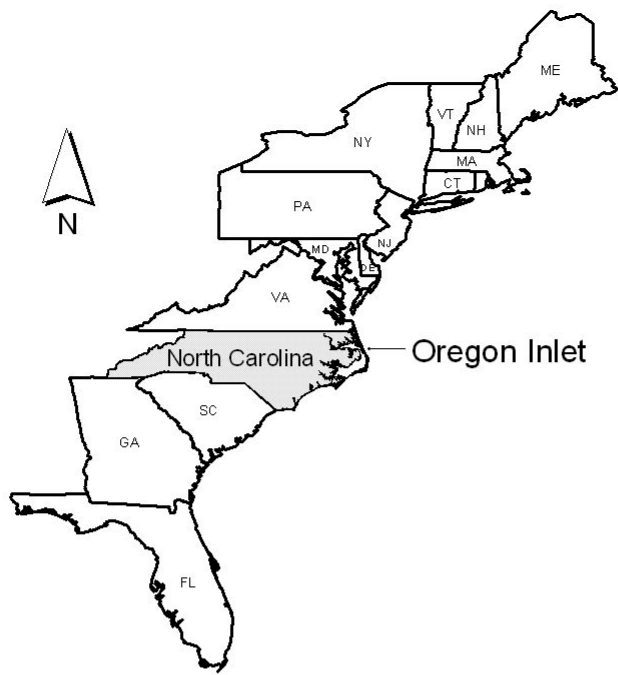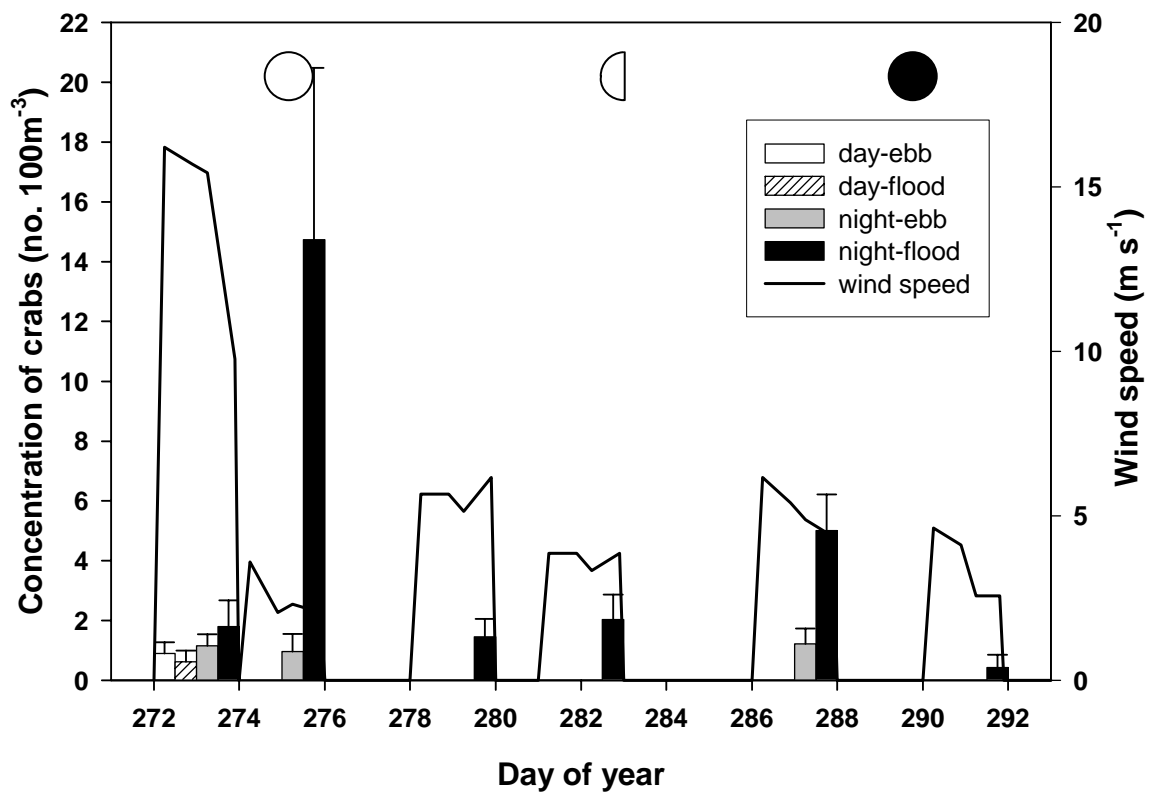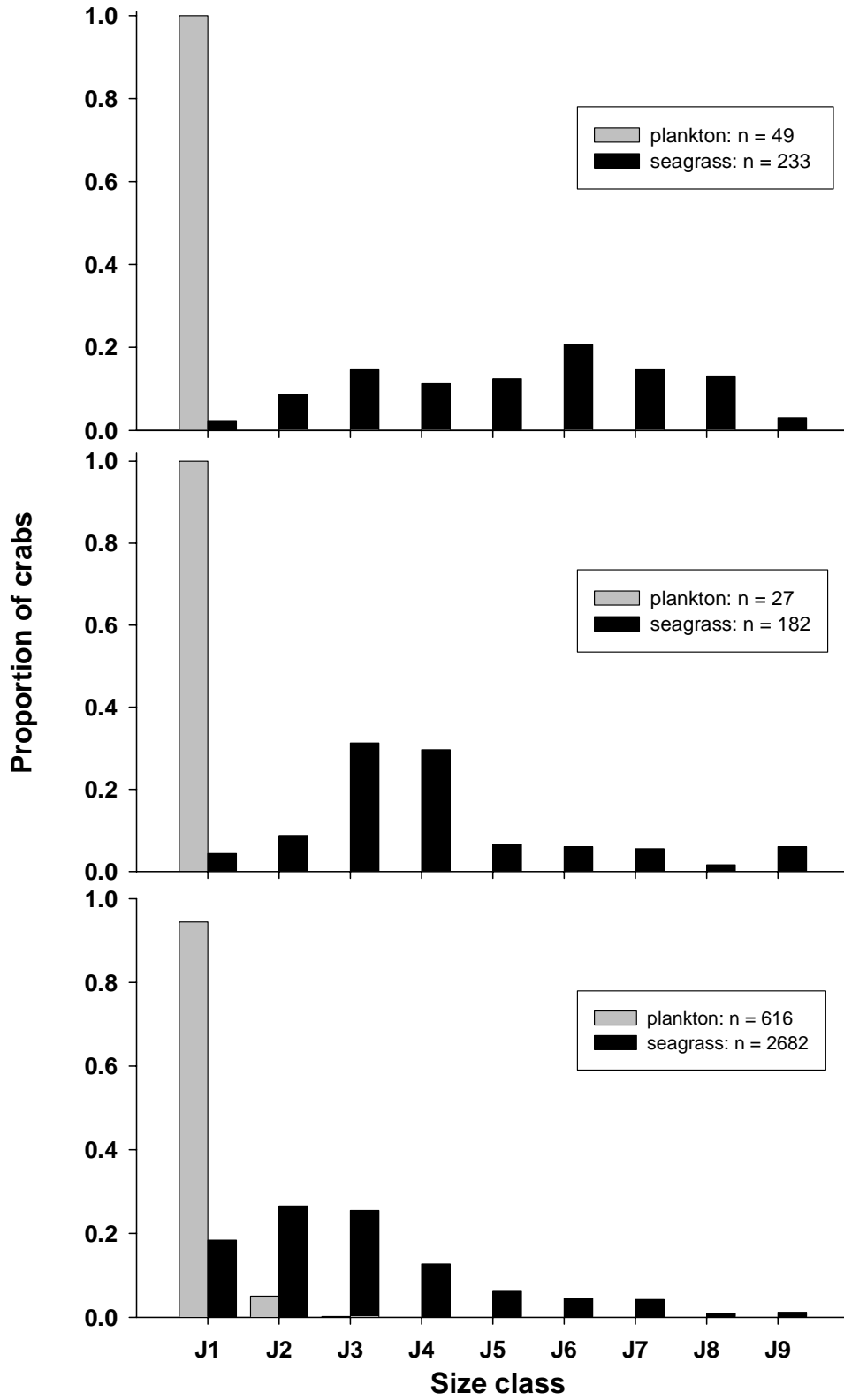
Figure 1

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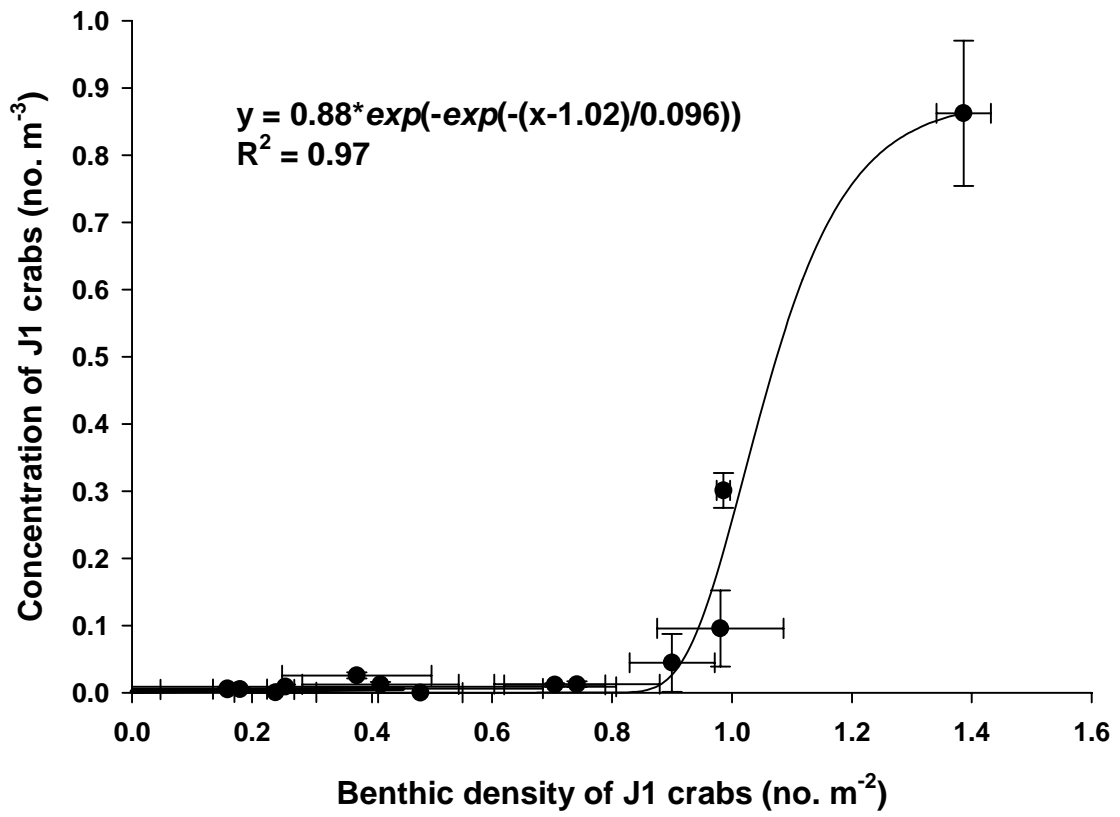
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CHAPTER 4

**SECONDARY DISPERSAL OF EARLY JUVENILE BLUE CRABS WITHIN
A WIND-DRIVEN ESTUARY**

ABSTRACT

A critical component to understanding the population connectivity of spatially-separated nursery habitats is to determine how organisms (following initial settlement to nursery habitats and metamorphosis) are dispersed during secondary dispersal. We used a coupled biophysical study to examine the processes underlying secondary dispersal of early juvenile blue crabs within Pamlico Sound, North Carolina, USA, 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 covering 17 stations, over two consecutive years [2000, 2001]) 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 throughout Pamlico Sound, indicative of secondary dispersal occurring rapidly following postlarval settlement and metamorphosis to the juvenile stage, presumably near inlet (eastern) regions. Moreover, J1 blue crab behavior influenced the distribution of crabs within the water column, whereby secondary dispersal was limited to nighttime periods in near-bottom waters. Such vertical positioning in the water column made wind direction alone a poor determinant of J1 blue crab transport trajectories, as bottom currents were variable within Pamlico Sound and occasionally developed as return flows that moved in the opposite direction of the wind. Particle-tracking simulation results suggest that J1 blue crab secondary dispersal from the inlets to across-sound nursery habitats only results from the combined use of

tides and wind-driven currents. Furthermore, secondary dispersal to the western sound occurred most often when J1 crabs originated from Oregon Inlet (especially during southwestward-directed winds), while transport to the middle and southeastern regions of the sound resulted from J1 crabs dispersing from Hatteras Inlet. Thus, both Oregon and Hatteras Inlets supply the northern basin of Pamlico Sound with early juvenile blue crabs, although the relative importance of each inlet as a crab source is partly dependent on the prevailing wind-induced bottom currents.

INTRODUCTION

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 (Turner *et al.*, 1997; Powers and Peterson, 2000; Reyns and Eggleston, 2004), ontogenetic differences in habitat use (Fonseca and Hart, 1996; Thrush *et al.*, 2000), and hydrodynamic conditions (e.g., high wave energy, strong flow, storm effects, etc., Emerson and Grant, 1991; 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.*, 2004a) and behavioral responses to environmental cues (Beukema and de Vlas, 1989; Armonies, 1992; Reyns and Eggleston, 2004). A gap in our 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 allow prioritization of specific habitats or dispersal corridors for protection. In this

study, we examine 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 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 comprised of aquatic vegetation (e.g. seagrass, salt marshes, etc.) (e.g. Heck and Thoman, 1981; Orth and van Montfrans, 1987; Etherington and Eggleston, 2000). While 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; Reyns and Eggleston, 2004). Secondary dispersal by J1 blue crabs is density-dependent (driven by intracohort density in settlement habitats) and juvenile crabs utilize nighttime flood tides to rapidly disperse away from these areas (Reyns and Eggleston, 2004). The use of flood-tide transport (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 a predominately wind-driven estuary such as Pamlico Sound, North Carolina, USA.

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. A barrier island chain makes up the eastern shore of Pamlico Sound, where exchange with the coastal ocean is limited to three relatively small 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, Chapter 1). Lack of tides, in addition to the relatively shallow depth of the system (mean depth ~ 4.5 m), allows 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 the postlarval sources (i.e., inlets) 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 have

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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 without explicit measures of pelagic juvenile blue crab distributions within Pamlico Sound (Etherington and Eggleston, 2000; 2003). Our objective, therefore, was to couple measures of currents and juvenile blue crab distributions within the water column to determine how wind-driven 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

We conducted our study examining the secondary dispersal of juvenile blue crabs in the northern basin of Pamlico Sound during peak blue crab recruitment months (September – October) in each of two 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. 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

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distribution of crabs within the water column was measured during day-night cruises by simultaneously towing a neuston (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). Both nets had mouth dimensions of 1 m x 0.5 m, were fitted with 505 µm mesh, and equipped with General Oceanics (Miami, FL, USA) flow meters to calculate the volume of seawater filtered. Nets were towed for 5 min at about 1 knot, and had filtration efficiencies near 100 % (N. Reyns, unpublished 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, Pile *et al.*, 1996). Counts were standardized to concentrations (no. crabs 100 m^{-3}). In 2000, we completed four day-night cruises (where all stations were sampled once during the day, and then re-sampled at night), while in 2001 we completed two day-night cruises and four nighttime-only cruises. Sampling all 17 stations took ~ 8 h.

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 $_{n1n2}D$ 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 ANOVA 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

To determine how early juvenile blue crabs undergo secondary dispersal in a wind-driven estuary, we examined the circulation patterns within the northern basin of Pamlico Sound. Circulation was characterized by deploying InterOcean S4 electromagnetic current meters at locations around the perimeter of the northern basin of Pamlico Sound (Fig. 1A). Because we initially hypothesized that early juvenile blue crabs would be in surface waters, we deployed five instruments near-surface (1 m below surface) and only one instrument near-bottom (1 m above bottom) (Fig. 1A). Contrary to expectations, early juvenile blue crabs were primarily collected in near-bottom waters (see 'Results'); therefore, our current meter data was not used in this portion of our study (but see Chapters 1 and 2 for discussion of surface currents). Instead, to simulate Pamlico Sound circulation patterns in near-bottom waters, we used ADCIRC (ADvanced CIRCulation), a 3D non-linear, barotropic hydrodynamic model that solves the shallow water form of the momentum equations (Luettich *et al.*, 1992; Luettich and Westerink, 2004). ADCIRC has produced wind-driven 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 surface currents measured by our current meters within our study area (Chapter 1).

For our simulations, ADCIRC was parameterized with a Mellor-Yamada level 2.5 turbulent diffusion closure. 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 encompassing the entire APES domain shown in Figure 1A, which was comprised 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 (see grid near inlets in Fig. 2 of Chapter 2). In the vertical domain, 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 below). Since we were interested in examining the potential for wind-driven flow fields to generate across-sound dispersal pathways, tidal forcing was not included in this first modeling exercise, and we assumed the APES to be spatially isolated from the coastal ocean (i.e., inlets not open to ocean). Furthermore, baroclinic forcing was ignored as the water column within Pamlico Sound is generally vertically well-mixed (Chapter 1). To match our current meter deployment dates and to encompass the period during our plankton cruises, model simulations ran for 57 d in 2000, and 64 d in 2001. Winds and modeled current data were averaged into hourly and

daily records, and decomposed into several components: u (east-west), v (north-south), and principle 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 currents averaged over the 7 d period prior to plankton measurements. This 7 d period was selected because J1 blue crabs were the stage 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), such that J1 crabs collected on a specific cruise date could be 1-7 d old.

To recreate 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 ADCIRC-generated flow fields. We simulated transport that could be experienced by crabs under three conditions: wind-driven transport ('wind-only' simulations), wind-driven transport with tidal flow near the inlets ('tide-wind' simulations) and wind-driven transport with tidal flow near the inlets that only occurred at night ('nighttime tide-wind' simulations). All particle-tracking runs were conducted using the modeled flow field corresponding to the near-bottom (~1 m below surface) depth layer. To simulate passive transport for the 'wind-only' simulations, we released 20 particles at randomly selected locations within 2 km of both Oregon and Hatteras Inlets. Next, 'tide-wind' simulations were used because early juvenile blue

crabs near the inlets employ flood-tide transport to initiate secondary dispersal into the sound (Reyns and Eggleston, 2004). Therefore, we released 40 particles from each inlet into the same wind-driven ADCIRC flow field used above, from start positions located further into the sound to represent positions that juvenile crabs could reach using tidal transport. More particles were released during the 'tide-wind' simulations than the 'wind-only' simulations because of the greater area that crabs can reach during tidal transport (see tidal ellipses in Chapter 2). Finally, because we collected more early juvenile blue crabs at night than during the day (see 'Results'), we incorporated a behavioral active transport component to the particle-tracking model by re-running 'tide-wind' simulations using an algorithm where dispersal was restricted to nighttime only. For all simulations, the model time step was two minutes with particle positions outputted at hourly intervals. To compare particle end points with observed sound-wide early juvenile blue crab distributions, particles were released daily over the 7 d leading up to our plankton cruise dates ('wind-only' simulations, N = 280; 'tide-wind' simulations, N = 560 particles tracked 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) in our plankton collections during both years. Although crabs were more abundant in 2001 than 2000 (Fig. 2A), the size-class distribution of these crabs was not significantly different between years (Kolmogorov-Smirnov $_{n1n2}D$ = 0.07, p = NS), with J1 crabs

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comprising ~ 69 % to 76 % of the crabs collected in 2000 and 2001, respectively (Fig. 2B). Therefore, given that the majority of early juvenile crabs collected in the plankton belonged to the J1 size class, we focus the remainder of this paper 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 x depth interaction ($F_{1,534}$ = 20.86, p < 0.0001), whereby J1 crabs exhibited secondary dispersal in nighttime bottom waters (Fig. 3).

In general, the concentration of J1 crabs in bottom waters was temporally variable over the spatial extent of our study area. The exception, where crabs were consistently collected, was at stations located between Oregon Inlet (OI) and Stumpy Point (SP) during both years (Fig. 4 and Fig. 5; but see also Fig. 5D 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. 5C), and only once were crabs collected at nearly all plankton stations (Fig. 5B).

Relationship between winds, currents and crab concentrations

During both years of our study, most variability in wind velocity occurred along a NE-SW axis, as shown by the principal axes of wind variance (Fig. 6). While wind fields were more variable during our study period in 2001 than 2000 (i.e., fatter ellipse in Fig. 2, see also Fig. 7), modeled near-bottom currents at locations surrounding our plankton stations were similar in direction and variability during both years (Fig. 6). Within the

northern portion of our study area, bottom currents were aligned along a N-S to N/NW-S/SE axis at Oregon Inlet (OI), along a NW-SE axis at Stumpy Point (SP), and along a W/NW to E/SE axis at Chicamacomico (CH) during both years (Fig. 6). In the southern portion of our study area (Gibbs Shoal [GS] and Hatteras Inlet [HI]), bottom currents were aligned with the wind ellipses and the shoreline (i.e., NE-SW; Fig. 6).

Wind and modeled bottom currents averaged over the 7 d period prior to our cruise dates more frequently had a southward-directed component to flow than a northward component to flow (Fig. 4 and Fig. 5). During most cruises with average winds directed towards the southwest (Days 295 and 299 in 2000; Days 256, 262, and 288 in 2001), currents at Oregon Inlet (OI), Gibbs Shoal (GS) and Hatteras Inlet (HI) were directed towards the southwest, while currents at Stumpy Point (SP) and Chicamacomico (CH) were directed towards the east-southeast (Fig. 4B & C and Fig. 5A, B & E). Bottom current patterns similar to those described during southwestward-directed winds were also observed on one date when winds were directed towards the southeast (Day 276 in 2001, Fig. 5D). In contrast, during the other cruises with southeastward-directed winds (Days 290 and 309 in 2000), bottom currents were variable (Fig. 4A & D). For example, on Day 309 in 2000, bottom currents at all locations had a northward component flowing in opposition to the wind (Fig. 4D), potentially indicative of a near-bottom reverse flow. In addition, bottom currents flowing in the opposite direction to the wind were observed on Day 296 in 2001 when winds were blowing towards the southwest (Fig. 5F). Only one cruise occurred when winds were directed towards the northeast (Day 269 in 2001), and bottom currents at all

locations were variable, with currents in the southern portion of our study area flowing southward, and currents at Oregon Inlet (OI) and Chicamacomico (CH) flowing northward (Fig. 5C). Therefore, while many cruise dates had similar mean wind directions, average modeled bottom currents were spatiotemporally variable.

Examination of both years of J1 blue crab concentrations from our plankton stations and modeled bottom currents indicate that juvenile blue crabs undergoing secondary dispersal likely originated from Oregon Inlet (OI) (Fig. 4 and Fig. 5). For example, on the cruise dates with the highest relative concentration of J1 crabs (Days 262 and 269 in 2001), bottom currents near Oregon Inlet (OI) were directed towards the southwest or west, and currents at Stumpy Point (SP) were directed towards the southeast, allowing J1 crabs to disperse from Oregon Inlet (OI) towards the western and central regions of Pamlico Sound (Fig. 5B & C). Conversely, bottom currents at Hatteras Inlet (HI) were directed out of our study area towards the southwest, and on the two sampling dates (Day 309 in 2000 and Day 296 in 2001) when average bottom currents at Hatteras Inlet (HI) were directed into our study area (towards the northeast), no crabs were collected at the plankton stations near Hatteras Inlet (HI) (Fig. 4D and Fig. 5F).

Particle-tracking simulations

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 prior to each cruise date in our particle-tracking

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simulations. Particle (virtual crab) end-points followed consistent patterns with respect to wind direction; therefore, for brevity, we grouped our results into four categories based on average wind direction during the 7 d period prior to our cruise dates: (1) southeastward, (2) southwestward, (3) west-southwestward and (4) northeastward. We only present results from simulations of one representative cruise date for each wind direction: Day 309 in 2000 for southeastward-directed winds, Day 262 in 2001 for southwestward-directed winds, Day 288 in 2001 for west-southwestward-directed winds, and Day 269 in 2001 for northeastward-directed winds (the only cruise date with this wind direction over both years). For each of the four wind directions examined, we also show the average currents and winds over the 7 d period prior to all cruise dates that fell into our wind categories. This allowed us to compare the general bottom circulation patterns with particle end-points during specific wind directions. For example, simulation results during southeastward-directed winds show particle end-points over the 7 d period prior to the cruise on Day 309 in 2000, and wind and currents averaged over the 7 d periods prior to all three cruise dates occurring during this wind direction (i.e., Days 290 and 309 in 2000 [Fig. 4] and Day 276 in 2001 [Fig. 5]; see Fig. 8A for example).

In our 'wind-only' simulations (where passive virtual J1 crabs used wind-driven bottom currents to undergo secondary dispersal from Oregon and Hatteras Inlets), particles predominately dispersed along the eastern shore of Pamlico Sound in the same direction as the wind (Fig. 8). A few examples also exist of particles moving in the opposite direction of the wind in bottom currents. We found particles released from

Hatteras Inlet (HI) moving into the mid-sound region (towards Gibbs Shoal [GS]) against the prevailing wind direction during southwestward-directed winds (Fig. 8A). Dispersal from Hatteras Inlet (HI) to this region was not confirmed with field results, however, as J1 blue crabs were never collected in this region during southeastward-directed winds (Fig. 4A & D and Fig. 5D). During northeastward-directed winds, particles released from Oregon Inlet (OI) were also transported in the opposite direction of the wind, and into the mid-sound region towards Stumpy Point (SP) (Fig. 8C); relatively high concentrations of J1 crabs were observed near this region (Fig. 5C). Overall, however, 'wind-only' simulations were generally poor predictors of observed blue crab distribution patterns (compare Fig. 8 with Fig. 4 and Fig. 5).

In contrast, particle end-point distributions during 'tide-wind' simulations (where virtual crabs were released away from the inlets to represent initial tidal transport into Pamlico Sound) provided a better match to observed J1 blue crab distributions than particle end-points without tides. During southeastward-directed winds, particles released near Oregon Inlet (OI) primarily dispersed southward along the eastern shore of Pamlico Sound, while those released near Hatteras Inlet (HI) moved in the opposite direction of the wind towards the northwest (Fig. 9A). Based on these particle end-point distributions, J1 crabs collected in the region between Oregon Inlet (OI) and Stumpy Point (SP) during cruises on Days 290 and 309 in 2000 likely originated from Oregon Inlet (Fig. 4A & D), whereas crabs distributed along the Chicamacomico (CH) to Gibbs Shoal (GS) transect on Day 309 likely originated from

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Hatteras Inlet (HI) (Fig. 4D). During southeastward-directed winds, J1 crabs within our study area were likely supplied from both Oregon and Hatteras Inlets.

During southwestward-directed winds, particle end-point distributions were similar to those generated by southeastward-directed winds (compare Fig. 9B with 9A), although a few particles released from Oregon Inlet (OI) also reached the western shore of Pamlico Sound south of Stumpy Point (SP) (Fig. 9B). Particles released from Hatteras Inlet primarily remained within the middle of the sound, and dispersed towards the northeast in the opposite direction of the wind (Fig. 9B). As such, J1 blue crabs collected in the northern and western regions of our study area likely originated from Oregon Inlet, and crabs collected in the middle of Pamlico Sound and at stations between Hatteras Inlet (HI) and Gibbs Shoal (GS) likely originated from Hatteras Inlet (HI) (Fig. 9B). Furthermore, particles released from Oregon Inlet (OI) were able to reach Hatteras Inlet (HI) during these simulations, suggesting that it is possible for mixing of crabs from both inlets to occur within 7 d (Fig. 9B).

When winds were directed towards the west-southwest (Days 256 and 288 in 2001; Fig. 5 A & E) or of relatively low magnitude towards the southwest (Day 296 in 2001; Fig. 5F), particles released in near-bottom currents from each inlet dispersed in opposite directions: Oregon Inlet (OI) particles moved to the north-northwest towards Albemarle Sound, whereas most particles from Hatteras Inlet (HI) moved towards the southwest in the same direction of the wind (with some particles also moving northward from Hatteras Inlet; Fig. 9D). The particle end-point distributions during west-southwest-directed winds did not match up well with observed J1 blue crab distributions

(Day 256, Fig. 5A). Relatively fewer crabs were collected on Days 288 and 296, but crabs within the middle of the sound south of the Stumpy Point (SP) to Chicamacomico (CH) transect (Fig 5E) likely originated from Hatteras Inlet, while those crabs collected along our northernmost transect originated from Oregon Inlet (OI) (compare Fig. 5E & F with Fig. 9D).

During northeastward-directed winds, particles released at Oregon Inlet (OI) dispersed in the opposite direction of the wind towards the southwest and into the middle of the sound while those released from Hatteras Inlet (HI) dispersed in the same direction as the wind (Fig. 9C). Thus, J1 blue crabs collected within the northwest region and along the western shore of Pamlico Sound originated from Oregon Inlet (OI), and crabs collected at the eastern-most stations along the two southern-most transects crossing Pamlico Sound may have originated from Hatteras Inlet (HI) (compare Fig. 5C with Fig. 9C). These simulations under northeastward-directed winds, however, failed to predict dispersal to the region near Gibbs Shoal (GS) where crabs were also collected in relatively high concentrations (Fig. 5C and Fig. 9C).

Finally, when dispersal during the 'tide-wind' simulations was limited to nighttime periods (active blue crab dispersal algorithm), particle end-points were grouped closer to the inlets of release, but had similar overall distribution patterns as during the passive 'tide-wind' simulations (compare Fig. 10 with Fig. 9). Similar to the transport simulations presented above, our 'nighttime tide-wind' simulation results suggest that the greatest possibility of mixing between crabs supplied from Oregon and

Hatteras Inlets occurs when winds are directed towards the southwest (compare Fig. 8B, Fig. 9B and Fig. 10B).

DISCUSSION

Secondary dispersal of early juvenile blue crabs enhances the nursery capacity of estuarine systems by redistributing crabs from high-density settlement habitats to habitats that receive low postlarval supply (Etherington and Eggleston, 2000; 2003). Our study was directed at understanding the biophysical processes underlying secondary dispersal of early juvenile blue crabs within a wind-driven estuary, Pamlico Sound, North Carolina. Increased recognition and understanding of processes underlying secondary dispersal should lead to a better understanding of nursery habitat use and ultimately estimates of recruitment.

Juvenile crab behavior

In our study, J1 blue crabs (the earliest juvenile molt stage) was the stage most often observed within the water column throughout Pamlico Sound, indicating that secondary dispersal occurs 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 due to pulsed postlarval supply to settlement habitats (e.g. van Montfrans *et al.*, 1995; Forward *et al.*, 2004b) that saturates these habitats with new recruits (J1 crabs), and increases the risk of cannibalism (Moksnes et al., 1997). Indeed, density-dependent intra-cohort interactions are known to drive the secondary dispersal

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of J1 blue crabs from seagrass settlement habitats (Reyns and Eggleston, 2004), allowing these crabs to gain a potential cannibalism refuge within the plankton. While to our knowledge our study is the first to explicitly examine the dispersal of pelagic 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 (Olmi 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.*, in review). Nighttime dispersal is a common behavioral strategy employed by 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,

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however, was conducted within tidal creeks as shallow as 1 m where depth-discrete sampling with plankton nets was likely hindered. Discrepancies in vertical blue crab distributions between studies may also be explained by J1 blue crabs having limited vertical swimming capabilities. For example, a 1 m vertical swim in a shallow system such as in the Mense and Wenner (1989) study would bring crabs to the surface, while the same magnitude swim at our plankton stations (with shallowest stations ~ 3 m in depth) would result in crabs remaining near-bottom. Although early juvenile blue crab swimming behaviors are not well known, J1 blue crabs undergo a series of ascents and descents during vertical migrations rather than swimming continuously (Forward *et al.*, in review). Thus, remaining close to the bottom during secondary dispersal, as we observed, may be more energetically beneficial that moving into surface waters where crabs would likely have to swim continuously to maintain their position within the water column. Furthermore, by remaining near-bottom, J1 blue crabs may attain a predation refuge from surface-oriented ctenophores (R. Forward, Duke University, personal communication).

Juvenile blue crabs may also remain in bottom waters in response to environmental cues such as salinity or temperature. For example, several benthic-oriented early juvenile finfish species are hypothesized to move from inlets to up-estuary nursery habitats within Pamlico Sound by remaining in relatively salty near-bottom waters (Miller *et al.*, 1984). This hypothesis, which remains untested, offers an attractive explanation for movement across-sound, as most estuaries are characterized as having a two-layer circulation with bottom waters flowing up-estuary and surface

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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). Indeed, the distribution of larval Atlantic croaker (*Micropogonias undulatus*) within the Chesapeake Bay is not uniform with depth, but related to hydrography such that larvae remain in up-estuary flowing water (Norcross, 1991). Thus, during stratified conditions, croaker larvae remained near-bottom, but were distributed throughout the water column during unstratified conditions when all depth layers moved up-estuary with the wind (Norcross, 1991). In Pamlico Sound during our study periods, two-layered gravitational flows do not appear as common, as the water column was unstratified due to wind-mixing (Chapter 1). Correspondingly, we observed that early juvenile blue crabs transport trajectories varied with wind conditions and were not always directed up-estuary as would be expected under gravitational flow (see below).

Spatiotemporal variability in J1 blue crab distributions

Temporal variability in the relative concentrations of J1 blue crabs during our cruises was likely due to variability in the spawning stock biomass, and environmental factors experienced during 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). Spatiotemporal variability in postlarval supply to Pamlico Sound, and the subsequent delivery of postlarvae to nursery habitats within the sound has been related to variability in wind conditions (Etherington and Eggleston, 2003, see also Chapter 2). Although

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wind and modeled bottom currents averaged over 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. For example, despite having average winds directed towards the southeast, bottom currents during cruises on Day 309 in 2000 and Day 276 in 2001 were not flowing in the same direction on both dates (Fig. 4D Fig. 5D). These circulation differences may reflect the more variable wind fields observed in 2001 than 2000 (Fig. 7). In 2000, the consistent wind direction over several days may have allowed the circulation time to set-up, while wind directions switched ~ every five days during 2001. Regardless, average wind direction does not appear to be a good predictor of bottom current direction; variability in the wind field prior to a date of interest (e.g. strength and percent of days with winds in a particular direction; Etherington and Eggleston, 2003) may also need to be considered.

While early juvenile blue crab transport trajectories within Pamlico Sound varied according to wind, the use of wind-driven bottom currents alone did not result in transport from Oregon and Hatteras Inlets to western sound nursery areas. Based on our '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 our study area. In these simulations, bottom currents that flowed in the opposite direction to the wind provided the only possibility for transport across-sound (e.g. see particles released from Hatteras Inlet, Fig. 8A, particles released from Oregon Inlet, 8C). Such bottom flows develop when persistent winds cause surface currents to flow downwind,

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raising sealevel at the downwind shore of Pamlico Sound, and producing pressure gradient forces that drive upwind-flowing near-bottom currents (Pietrafesa and Janowitz, 1991). While a few particles dispersed into our study area during the 'wind-only' simulations via the development of near-bottom return flows, particle end-points during these simulations were generally poor predictors of our observed J1 blue crab distributions, suggesting that secondary dispersal in Pamlico Sound does not result from the use of wind-driven currents alone.

Indeed, our results indicate that crab dispersal in wind-driven bottom currents to across-sound nursery habitats is only possible if tides are initially used 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 (Singer and Knowles, 1975; Pietrafesa *et al.*, 1986; Pietrafesa and Janowitz, 1991, Chapter 1). In general, however, 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 our modeled results suggests 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. Therefore, secondary dispersal of early juvenile blue crabs within a wind-driven estuary is not necessarily downwind (as it is for bivalves in another wind-

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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.

Assessing the relative importance of Hatteras and Oregon Inlet

Our study permitted us to assess the relative importance of Oregon and Hatteras Inlets in terms of their respective contributions to the juvenile blue crabs distributions in our study area. Our interpretation of how the two inlets supplied crabs to Pamlico Sound varied depending on whether we examined our modeled currents at select locations around the sound, or examined the particle-tracking simulation results. For instance, comparison of observed J1 blue crab distributions with modeled bottom currents at locations around the perimeter of Pamlico Sound (corresponding to our initial current meter deployment locations; see also Chapter 1 and Chapter 2), suggested that Oregon Inlet was the primary source of J1 blue crabs to our study area. This conclusion is based on the observation that during most cruises, modeled currents around the perimeter of the sound had southward-flowing bottom currents; therefore, currents were not conducive to northward dispersal from Hatteras Inlet to our study area. Results from our particle-tracking simulations, however, indicated that particles released from both inlets can reach our study area depending on the prevailing winds. In particular, particles released from Oregon Inlet had the potential for reaching western sound nursery habitats near Stumpy Point under southeastward-, southwestward-, and northeastward-directed winds during the 'tide-wind' and 'nighttime tide-wind' simulations, the latter of which is the most biologically reasonable period for dispersal. Particles released near Hatteras Inlet during southeastward-, southwestward-, and to a lesser degree,

northeastward-directed winds also moved into our study area, but remained within the southeast and mid-sound regions. During the fall blue crab recruitment months in North Carolina, winds are most often directed towards the southwest and northeast (Chapter 1 and Chapter 2). Thus, during these months, J1 blue crabs within the northwestern region of our study area are likely supplied by Oregon Inlet, while those within the southeastern region of our study area likely originate from Hatteras Inlet.

Given that J1 blue crab recruitment to southwestern sound nursery habitats is correlated with southward directed winds (Etherington and Eggleston, 2003), and our simulation results showing that particles reach the western sound from Oregon Inlet, Oregon Inlet appears to be the predominant source of early juvenile blue crabs to western sound nursery habitats. While Hatteras Inlet may also supply early juvenile blue crabs to the central portion of Pamlico Sound, the fate of these crabs is presently unknown.

Model considerations

This study demonstrated 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 method to track larval patches in: Natunewicz *et al.*, 2001). Our model outputted current fields at spatial resolutions higher than what would have been possible to acquire using instrumentation. Although using surface currents measured at select locations within Pamlico Sound can predict the general dispersal trajectories of surface-oriented organisms (i.e., postlarval blue crabs, Chapter 2),

comparisons of bottom currents at stations around the perimeter of Pamlico Sound with our particle-tracking simulation results suggest that bottom currents exhibit spatial variability that is not captured by current measures at a few locations. For instance, bottom currents can develop in the opposite direction of the wind (and surface currents; Chapter 1) within the central basin of Pamlico Sound, making wind direction alone a poor predictor of dispersal of bottom-oriented organisms. Thus, our study illustrates 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.

While our modeled results were able to recreate our observed J1 blue crab distributions within the northwestern and southeastern regions of our study area, particles in our simulations (especially during 'nighttime tide-wind' runs) failed to reach the southwestern region of Pamlico Sound near Gibbs Shoal, where crabs were sometimes 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. For instance, 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 (5-20 cm/s) capable of directed swimming in the same direction as the current (Luckenbach and Orth, 1992), but to our knowledge, such swimming behaviors have not been documented for J1 blue crabs. Thus, while

swimming behavior can ultimately influence within-sound 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.

CONCLUSIONS

Using a coupled biophysical study, we demonstrate the potential for early juvenile (J1) blue crabs to utilize tides in combination with near-bottom wind-driven currents to undergo secondary dispersal from near-inlet settlement habitats to alternative across-sound nursery habitats. Based on our findings, we propose the following conceptual model for J1 blue crab secondary dispersal: From the cross section of Pamlico Sound

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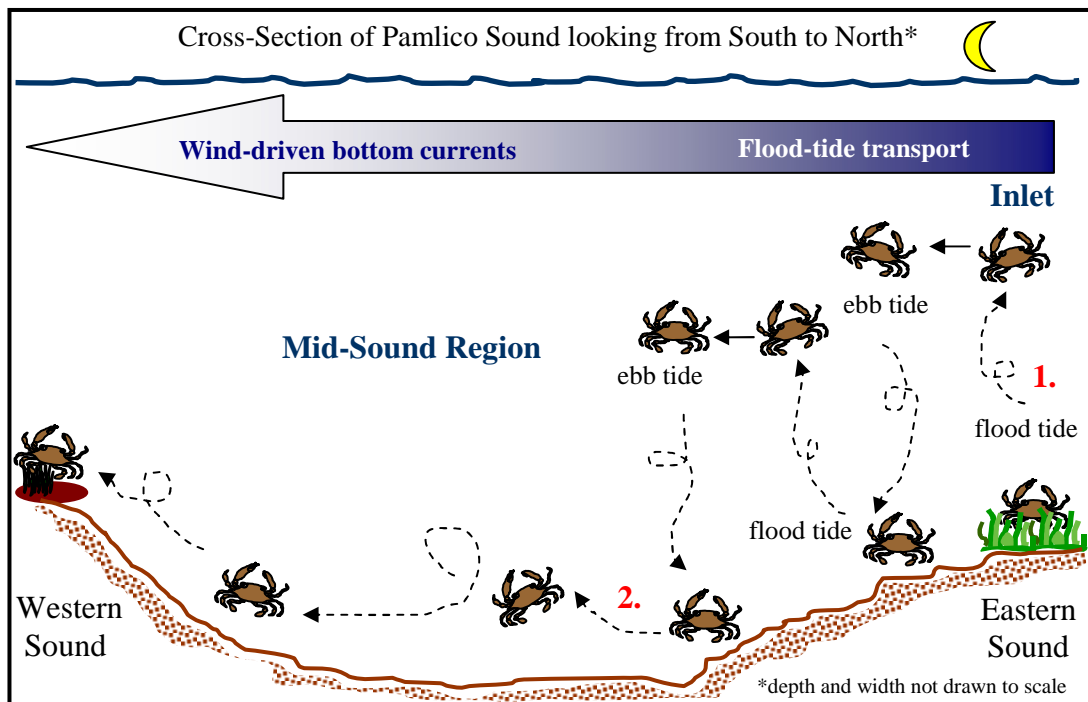
(looking from south to north), we start on the right side of the conceptual diagram near the inlets (shown above, at number 1). First, J1 blue crabs leave initial settlement habitats such as seagrass when the intra-cohort density of conspecifics becomes relatively high, by utilizing nighttime flood tides (Reyns and Eggleston, 2004). Early juvenile blue crabs have an endogenous rhythm in vertical swimming behavior that underlies nighttime dispersal (Forward *et al.*, 2004a; Forward *et al.*, in review); however, given that these crabs are only found near the inlets in surface waters during flood tide, it's likely that exogenous cues also mediate flood-tide transport (Reyns and Eggleston, 2004). We hypothesize 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 to postlarval blue crabs: Welch *et al.*, 1999). As J1 blue crabs move away from the inlets, salinity signals and tidal currents weaken (Chapter 1, Pietrafesa *et al.*, 1986); thus, in response to diminishing tidal cycle cues, crabs no longer move into surface waters (conceptual diagram, number 2). Instead, J1 crabs continue vertically swimming into the water column 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 across-sound detrital habitats. The degree of connectivity via specific dispersal corridors between eastern (inlet) and western sound nursery habitats will depend, in part, on the prevailing winds and their influence on bottom currents. For example, southwestward-directed winds are of particular importance in supplying J1 blue crabs from Oregon Inlet to northwestern

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sound nursery habitats. As these wind events are the most frequently experienced wind direction during the fall blue crab recruitment months (Chapter 1 and Chapter 2), nursery habitats near Oregon Inlet (eastern shore, seagrass) and the Stumpy Point region (northwestern shore, shallow detrital habitat) should be prioritized for habitat conservation and fisheries management.

In the broader context of dispersal within estuaries, our study provides valuable insight and serves as a model for future research in other systems. To date, many studies have found that estuarine organisms, from larval fishes (e.g. Weinstein *et al.*, 1980; Forward *et al.*, 1999) to postlarval penaeid shrimp and other crustaceans (e.g. Epifanio *et al.*, 1984; DeVries *et al.*, 1994; Wenner *et al.*, 1998) exhibit flood-tide transport, particularly near inlets of estuaries (see reviews by: Boehlert and Mundy, 1988; Forward and Tankersley, 2001). While the behaviors of these organisms, and consequently their distributions within the water column, are not well known once predictable tidal signals disappear (such as in the middle of Pamlico Sound), our study shows that vertical positioning at one site (i.e., inlets) does not necessarily translate to the same vertical positioning at sites further up-estuary. Differences in vertical positioning by a particular species may also be evident in different estuaries. For example, Atlantic croaker larvae utilize flood-tide transport in the Newport River Estuary, North Carolina to move up-estuary (Forward *et al.*, 1999), but in the Chesapeake Bay, their vertical distributions are related to hydrologic variables such that they remain in inflowing waters regardless of depth (Norcross, 1991). Thus, species-specific behaviors and estuary-specific hydrographic conditions likely interact to

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ultimately determine up-estuary dispersal (Boehlert and Mundy, 1988), making it difficult to generalize about dispersal mechanisms across estuarine systems.

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LITERATURE CITED

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., Adams, E.E. and Stolzenbach, K.D. (1984) Eulerian-Lagrangian analysis of pollutant transport in shallow water. *Massachusetts Institute of Technology*: MIT RM Parsons Lab. Tech. Rep. No. 296, Cambridge, MA.

Beukema, J.J. and de Vlas, J. (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 Eggleston, D.B. (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 Mundy, B.C. (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., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P. and Menge, B.A. (1996) Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* **27**:477-500.

Commito, J.A., Thrush, S.F., Pridmore, R.D., Hewitt, J.E. and Cummings, V.J. (1995) Dispersal dynamics in a wind-driven benthic system. *Limnol. Oceanogr.* **40**:1513-1518.

Costlow, J.D. and Bookhout, C.G. (1959) The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. *Biol. Bull.* **116**:373-396.

DeVries, M.C., Tankersley, R.A., Forward, R.B., Kirby-Smith, W.W. and Luettich, R.A., Jr. (1994) Abundance of estuarine crab larvae is associated with tidal hydrologic variables. *Mar. Biol.* **118**:403-413.

Dyer, K.R. (1997) *Estuaries: a physical introduction*. New York: John Wiley, 195 pp.

Eggleston, D.B., Johnson, E.G. and Hightower, J.E. (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,

Emerson, C.W. and Grant, J. (1991) The control of soft-sediment clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. *Limnol. Oceanogr.* **36**:1288-1300.

Emery, W.J. and Thomson, R.E. (2001) *Data analysis methods in physical oceanography*. Amsterdam: Elsevier, 638 pp.

Epifanio, C.E. and Garvine, R.W. (2001) Larval transport on the Atlantic continental shelf of North America: a review. *Estuar. Coast. Shelf Sci.* **52**:51-77.

Epifanio, C.E., Valenti, C.C. and Pembroke, A.E. (1984) Dispersal and recruitment of blue crab larvae in Delaware Bay, USA. *Estuar. Coast. Shelf Sci.* **18**:1-12.

Etherington, L.L. and Eggleston, D.B. (2000) Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. *Mar. Ecol. Prog. Ser.* **204**:179-198.

Etherington, L.L. and Eggleston, D.B. (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.

Etherington, L.L., Eggleston, D.B. and Stockhausen, W.T. (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 Hart, D.D. (1996) Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos* **75**:49-58.

Foreman, M.G.G., Baptista, A.M. and Walters, R.A. (1992) Tidal model studies of particle trajectories around a shallow coastal bank. *Atmos.-Ocean* **30**:43-69.

Forward, R.B., Jr. and Tankersley, R.A. (2001) Selective tidal-stream transport of marine animals. *Oceanogr. Mar. Biol. Annu. Rev.* **39**:305-353.

Forward, R.B., Jr., Reyns, N.B., Diaz, H., Cohen, J.H. and Eggleston, D.B. (2004a) Endogenous swimming rhythms of juvenile blue crabs, *Callinectes sapidus*, as related to horizontal transport. *J. Exp. Mar. Bio. Ecol.* **299**:63-76.

Forward, R.B., Jr., Reyns, N.B., Diaz, H., Cohen, J.H. and Eggleston, D.B. (in review) Endogenous swimming rhythms underlying secondary dispersal of early juvenile blue crabs, *Callinectes sapidus*.

Forward, R.B., Jr., Reinsel, K.A., Peters, D.S., Tankersley, R.A., Churchill, J.H., Crowder, L.B., Hettler, W.F., Warlen, S.M. and Green, M.D. (1999) Transport of fish larvae through a tidal inlet. *Fish. Oceanogr.* **8**:153-172.

Forward, R.B., Jr., Cohen, J.H., Irvine, R.D., Lax, J.L., Mitchell, R., Schick, A.M., Smith, M.M., Thompson, J.M. and Venezia, J.I. (2004b) 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 Thoman, T.A. (1981) Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Bio. Ecol.* **53**:125-134.

Hines, A.H., Lipcius, R.N. and Haddon, A.M. (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 Orth, R.J. (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. and Westerink, J. (2004) Formulation and numerical implementation of the 2D/3D ADCIRC finite element model version 44.XX. http://www.marine.unc.edu/C_CATS/adcirc/adcirc_theory_2004_05_14.pdf

Luettich, R.A., Jr., Westerink, J.J. and Scheffner, N.W. (1992) ADCIRC: An advanced three-dimensional circulation model for shelves, coasts and estuaries. *Report 1: Theory and methodology of ADCIRC-2DDI and ADCIRC-3DL*: Technical report DRP-92-6, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Luettich, R.A., Jr., Carr, S.D., Reynolds-Fleming, J.V., Fulcher, C.W. and McNinch, J.E. (2002) Semi-diurnal seiching in a shallow, micro-tidal lagoonal estuary. *Cont. Shelf Res.* **22**:1669-1681.

Mense, D.J. and Wenner, E.L. (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.

Miller, J.M., Reed, J.P. and Pietrafesa, L.J. (1984) Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. In: *Mechanisms of migration in fishes*. J.D. McCleave, G.P. Arnold, J.J. Dodson and W.H. Neill (ed) New York: Plenum Publishing Corporation, pp. 209-225.

Millikin, M.R. and Williams, A.B. (1984) Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. *FAO Fisheries Synopsis* **138**:1-39.

Moksnes, P.-O., Lipcius, R.N., Pihl, L. and van Montfrans, J. (1997) Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. *J. Exp. Mar. Bio. Ecol.* **215**:157-187.

Morgan, S.G. (1995) The timing of larval release. In: *Ecology of marine invertebrate larvae*. L.R. McEdward (ed) Boca Raton: CRC Press, pp. 157-191.

Natunewicz, C.C., Epifanio, C.E. and Garvine, R.W. (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, van Montfrans, J., Lipcius, R.N., Orth, R.J. and Sadler, P.W. (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 van Montfrans, J. (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., Allan, J.D. and Butman, C.A. (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 Janowitz, G.S. (1991) The Albemarle-Pamlico coupling study. Final report to the Environmental Protection Agency,

Pietrafesa, L.J., Janowitz, G.S., Chao, T.-Y., Weisberg, R.H., Askari, F. and Noble, E. (1986) The physical oceanography of Pamlico Sound. *UNC Sea Grant Publication*: UNC-WP-86-5, Raleigh, NC.

Pile, A.J., Lipcius, R.N., van Montfrans, J. and Orth, R.J. (1996) Density-dependent settler-recruit-juvenile relationships in blue crabs. *Ecol. Monogr.* **66**:277-300.

Powers, S.P. and Peterson, C.H. (2000) Conditional density dependence: The flow trigger to expression of density-dependent emigration in bay scallops. *Limnol. Oceanogr.* **45**:727-732.

Reyns, N.B. and Eggleston, D.B. (2004) Environmentally-controlled, density-dependent secondary dispersal in a local estuarine crab population. *Oecologia* **140**:280-288.

Roughgarden, J., Gaines, S. and Possingham, H. (1988) Recruitment dynamics in complex life cycles. *Science* **241**:1460-1466.

Singer, J.J. and Knowles, C.E. (1975) Hydrology and circulation patterns in the vicinity of Oregon Inlet and Roanoke Island, North Carolina. *Sea Grant*: UNC-SG-75-15, Raleigh, NC.

Sokal, R.R. and Rohlf, F.J. (1995) *Biometry*. New York: W. H. Freeman and Company, 887 pp.

Thrush, S.E., Hewitt, J.E., Cummings, V.J., Green, M.O., Funnell, G.A. and Wilkinson, M.R. (2000) The generality of field experiments: interactions between local and broad-scale processes. *Ecology* **81**:399-415.

Turner, S.J., Grant, J., Pridmore, R.D., Hewitt, J.E., Wilinson, M.R., Hume, T.M. and Morrisey, D.J. (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 Fairweather, P.G. (1989) Supply-side ecology and benthic marine assemblages. *Trends Ecol. Evol.* **4**:16-20.

van Montfrans, J., Epifanio, C.E., Knott, D.M., Lipcius, R.N., Mense, D.J., Metcalf, K.S., Olmi, E.J., III, Orth, R.J., Posey, M.H., Wenner, E.L. and West, T.L. (1995) Settlement of blue crab postlarvae in western North Atlantic estuaries. *Bull. Mar. Sci.* **57**:834-854.

Weinstein, M.P., Weiss, S.L., Hodson, R.G. and Gerry, L.R. (1980) Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary in Cape Fear River, North Carolina. *Fish. Bull.* **78**:419-436.

Weisberg, K.H. and Pietrafesa, L.J. (1983) Kinematic and correlation of the surface wind field in the South Atlantic bight. *J. Geophys. Res.* **88**:4593-4610.

Welch, J.M., Forward, R.B., Jr. and Howd, P.A. (1999) Behavioral responses of blue crab *Callinectes sapidus* postlarvae to turbulence: implication for selective tidal stream transport. *Mar. Ecol. Prog. Ser.* **179**:135-143.

Wenner, E., Knott, D., Blanton, J., Barans, C. and Amft, J. (1998) Roles of tidal and wind-generated currents in transporting white shrimp (Penaeus setiferus) postlarvae through a South Carolina (USA) inlet. *J. Plankton Res.* **20**:2333-2356.

Wolanski, E., Doherty, P. and Carleton, J. (1997) Directional swimming of fish larvae determines connectivity of fish populations on the Great Barrier Reef. *Naturwissenschaften* **84**:262-268.

FIGURE LEGENDS

Figure 1. Map of Albemarle-Pamlico Estuarine System (APES) in North Carolina, U.S.A. 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 sampling stations in 2000 (B) and 2001(C) are presented on enlarged maps of our study area (northern basin of Pamlico Sound). Postlarval collector stations were located at Oregon and Hatteras Inlets during both years.

Figure 2. Size-class distribution of juvenile blue crabs collected in the water column of Pamlico Sound during 2000 and 2001. The mean concentration of crabs (no. 100 m^{-3}) collected by size-class by year is shown in A, while proportions are shown in B. See text for significance levels.

Figure 3. Mean concentration of J1 juvenile blue crabs (no. 100 m^{-3}) collected at night in surface and bottom waters throughout Pamlico Sound. Crab collections for both years were combined due to similar patterns.

Figure 4. Concentration of J1 blue crabs (no 100 m^{-3}) in bottom waters at night, by cruise date (panels A-D) during 2000. Arrows represent the mean direction of modeled bottom currents (within Pamlico Sound in blue) and mean direction of wind (outside of Pamlico Sound in green) over the 7 d period prior to each cruise date. OI = Oregon

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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.

Figure 5. Concentration of J1 blue crabs (no 100 m^{-3}) in bottom waters at night, by

cruise date (panels A-D) during 2001. Arrows represent the mean direction of modeled

bottom currents (within Pamlico Sound in blue) and mean direction of wind (outside of

Pamlico Sound in green) over the 7 d period 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.

Figure 6. Principal axes of variance of modeled bottom current and wind velocities

during the blue crab recruitment season (September-October). Current ellipses are

shown within Pamlico Sound and wind ellipse is 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. OI = Oregon Inlet; SP = Stumpy Point; Ch =

Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet.

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Figure 7. Vector diagram of wind from Hatteras Meteorological Station during September-October study periods in 2000 (A) and 2001 (B). Filled red circles represent cruise dates during each year.

Figure 8. End-points of particles released from Oregon Inlet (filled red squares) and Hatteras Inlet (filled green triangles) during 'wind-only' simulations under different wind conditions. End-points during southeastward-directed winds (A) represent Days 290 and 309 in 2000 and Day 276 in 2001; during southwestward-directed winds (B) represent Days 295 and 299 in 2000 and Day 262 in 2001; during northeastward-directed winds (C) represents Day 269 in 2001; during west-southwestward-directed winds (D) represent Days 256, 288 and 296 in 2001. For reference, average winds and modeled bottom currents over all 7 d periods prior to cruise dates with the same wind conditions are shown. OI = Oregon Inlet; SP = Stumpy Point; Ch = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet. Compass directions and scale bar representing 1 m s^{-1} for wind velocity and 5 cm s^{-1} for current velocity are shown in panel A.
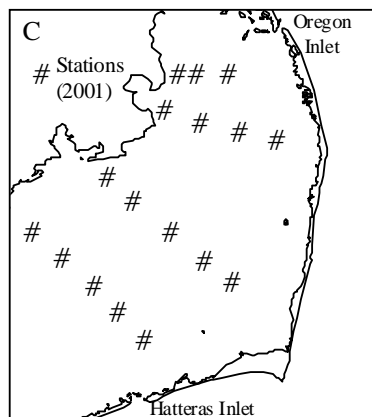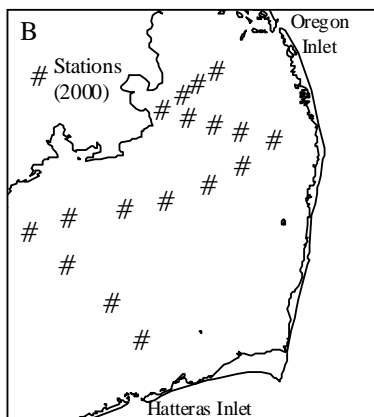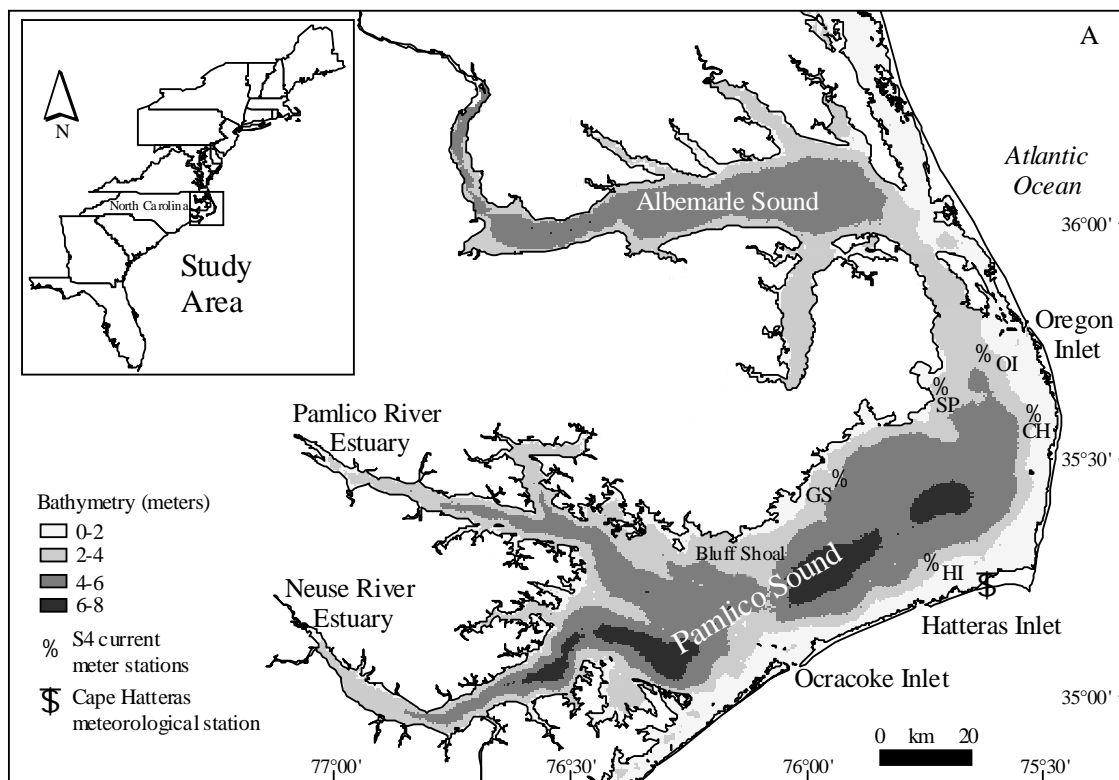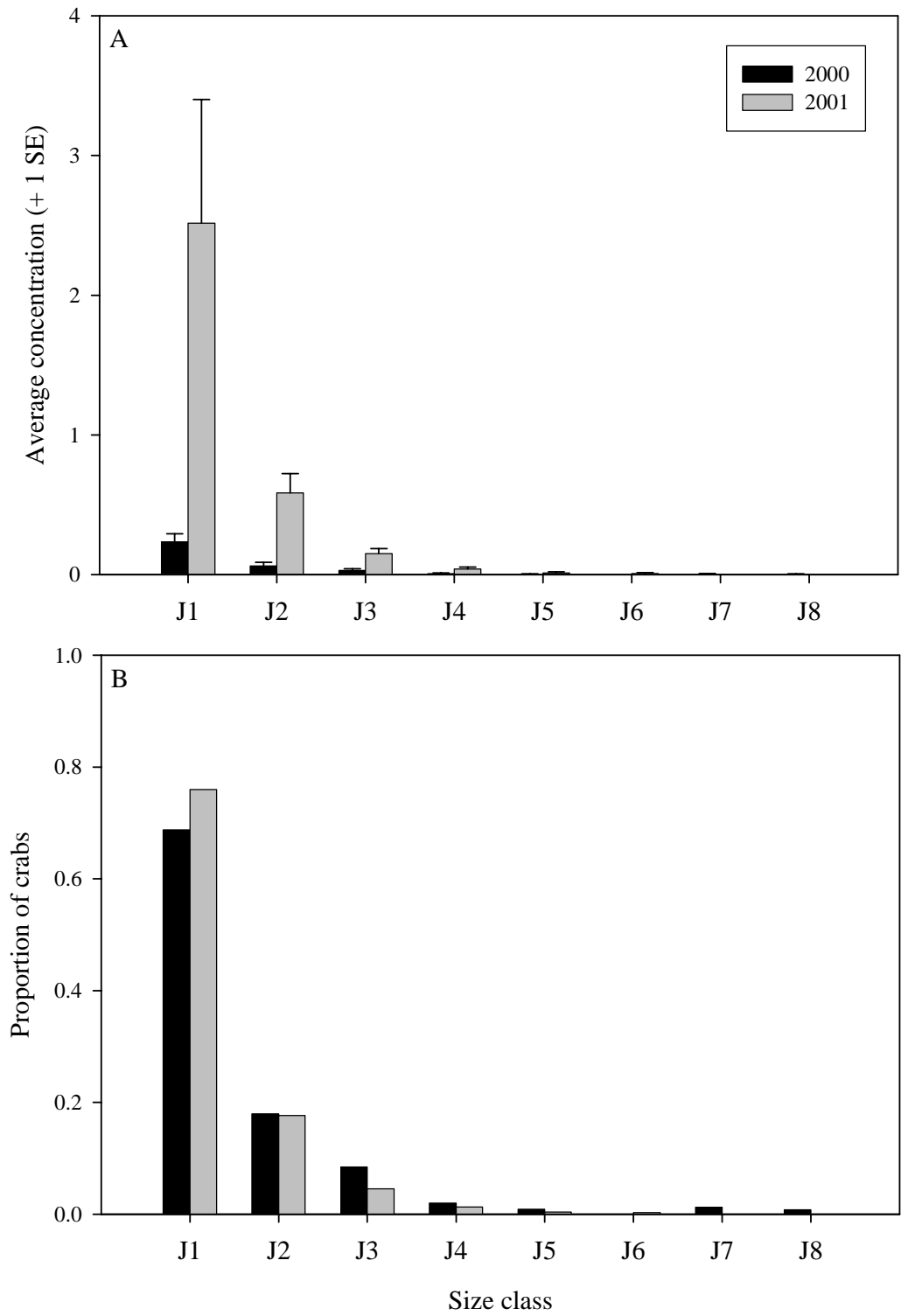
Figure 9. End-points of particles released from Oregon Inlet (filled red squares) and Hatteras Inlet (filled green triangles) during 'tide-wind' simulations under different wind conditions. End-points during southeastward-directed winds (A) represent Days 290 and 309 in 2000 and Day 276 in 2001; during southwestward-directed winds (B) represent Days 295 and 299 in 2000 and Day 262 in 2001; during northeastward-directed winds (C) represents Day 269 in 2001; during west-southwestward-directed

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winds (D) represent Days 256, 288 and 296 in 2001. For reference, average winds and modeled bottom currents over all 7 d periods prior to cruise dates with the same wind conditions are shown. OI = Oregon Inlet; SP = Stumpy Point; Ch = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet. Compass directions and scale bar representing 1 m s^{-1} for wind velocity and 5 cm s^{-1} for current velocity are shown in panel A.

Figure 10. End-points of particles released from Oregon Inlet (filled red squares) and Hatteras Inlet (filled green triangles) during 'nighttime tide-wind' simulations under different wind conditions. End-points during southeastward-directed winds (A) represent Days 290 and 309 in 2000 and Day 276 in 2001; during southwestward-directed winds (B) represent Days 295 and 299 in 2000 and Day 262 in 2001; during northeastward-directed winds (C) represents Day 269 in 2001; during west-southwestward-directed winds (D) represent Days 256, 288 and 296 in 2001. For reference, average winds and modeled bottom currents over all 7 d periods prior to cruise dates with the same wind conditions are shown. OI = Oregon Inlet; SP = Stumpy Point; Ch = Chicamacomico; GS = Gibbs Shoal; HI = Hatteras Inlet. Compass directions and scale bar representing 1 m s^{-1} for wind velocity and 5 cm s^{-1} for current velocity are shown in panel A.
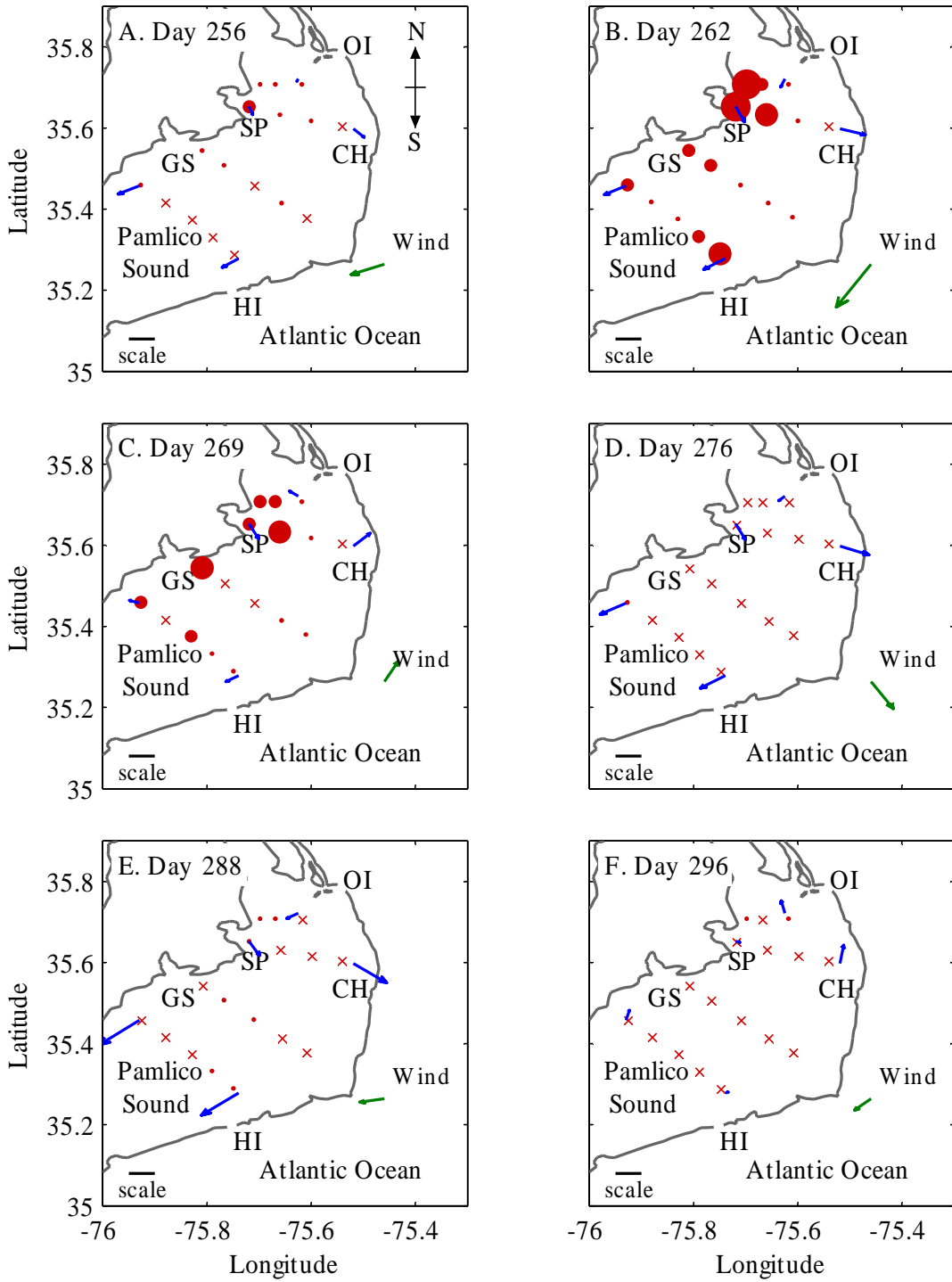
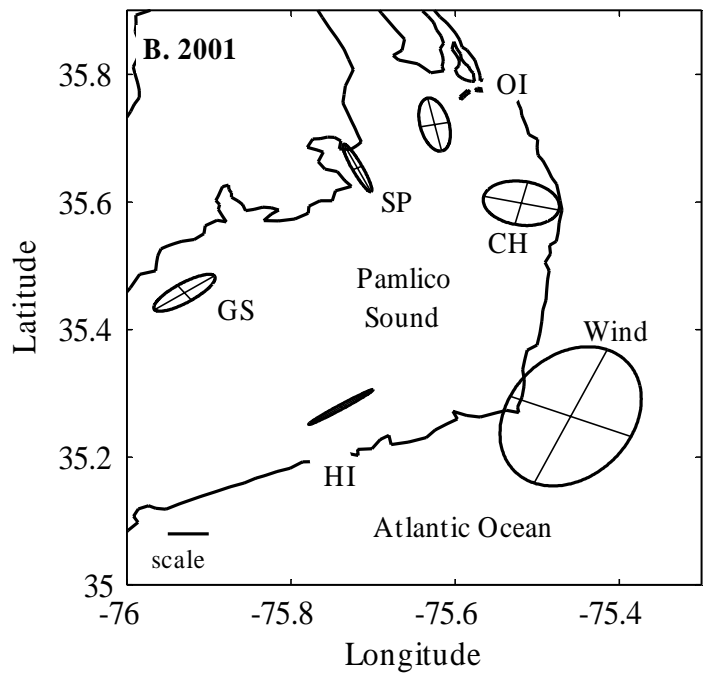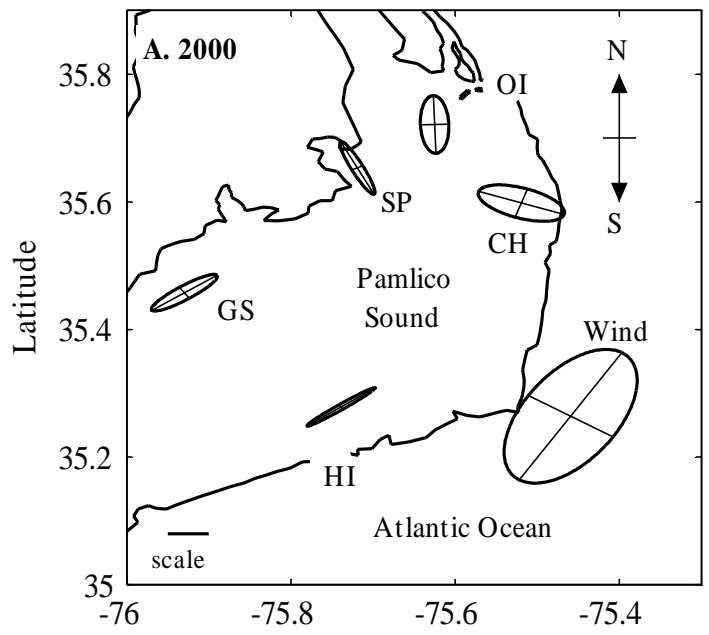Figure 1

Figure 2

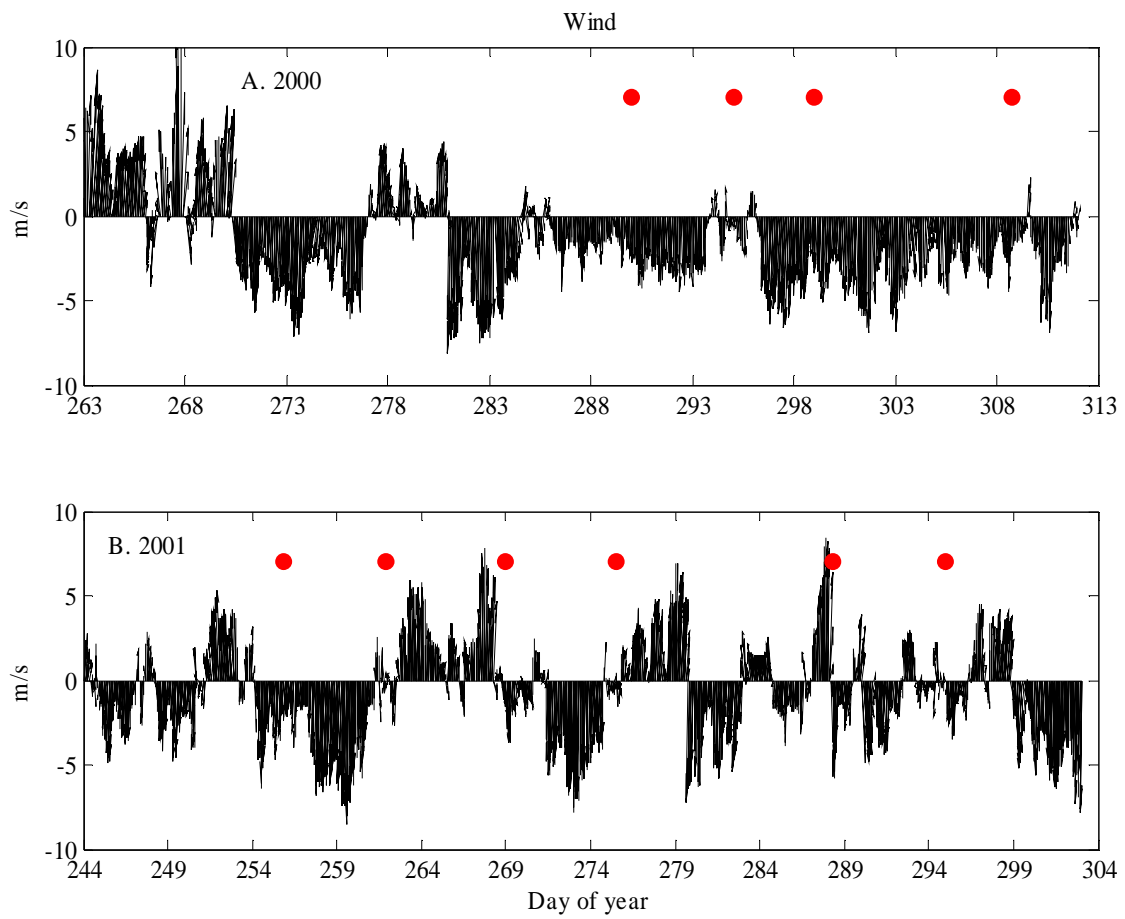238

Figure 3

Figure 4

Figure 5

Figure 6
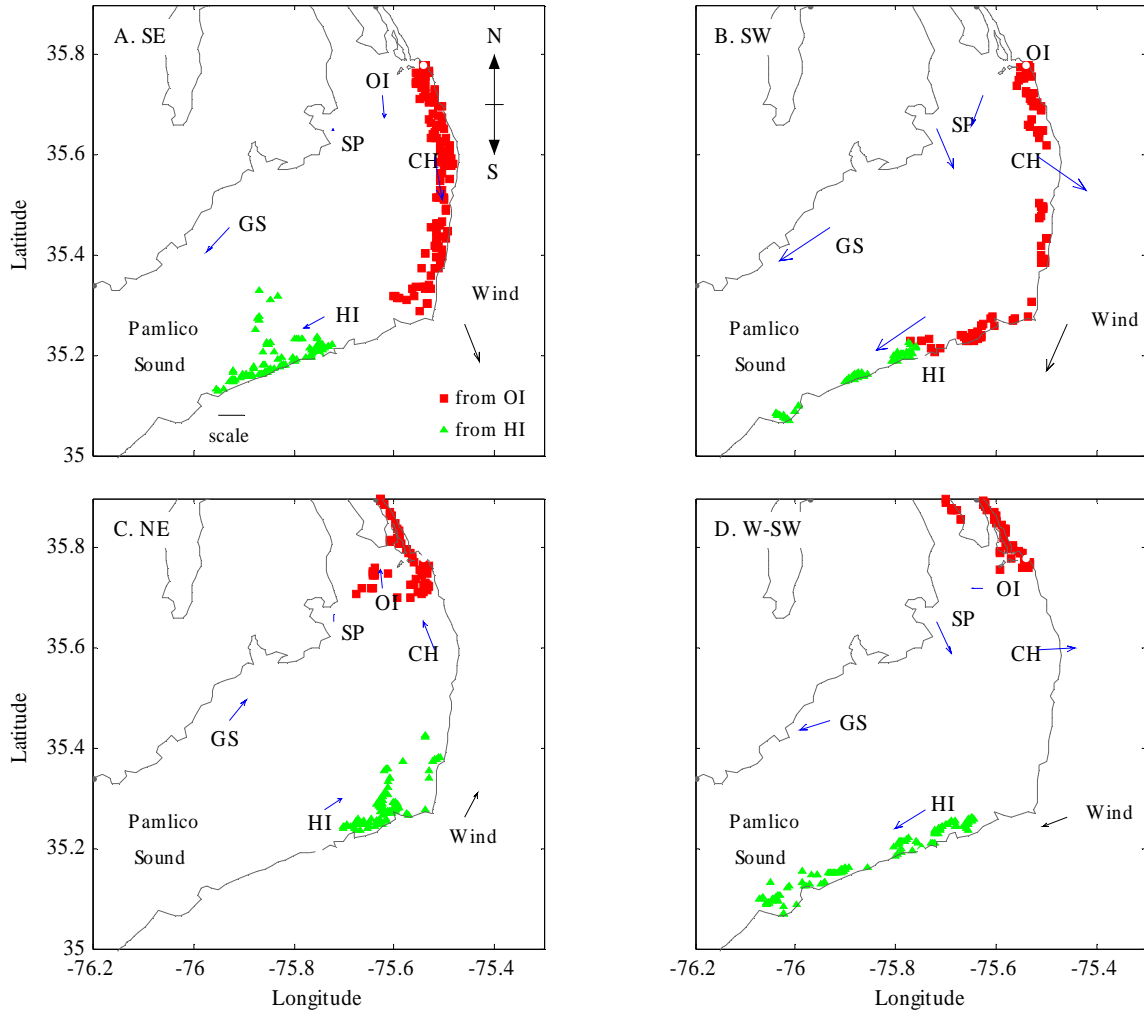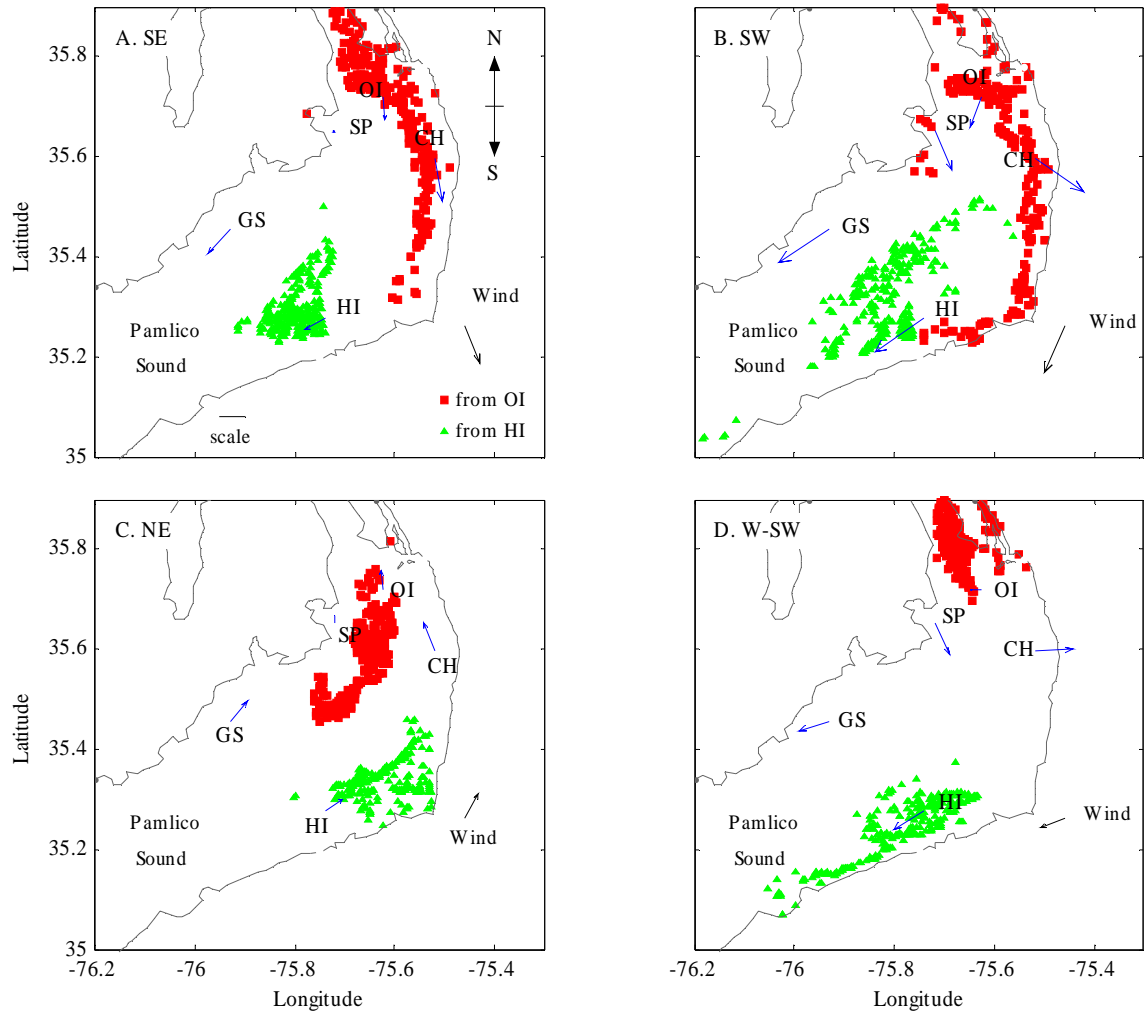
Figure 7

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Wind-Only Simulations

Figure 8

Tide-Wind Simulations

Figure 9

Nighttime Tide-Wind Simulations

Figure 10