ABSTRACT

HAASE, AMY TRESA. Circulation in Pamlico Sound and Predicted Oyster Larval Dispersal and Connectivity. (Under the direction of David B. Eggleston).

A critical component to understanding connectivity of spatially-separated populations of marine organisms is quantifying hydrodynamic paths of dispersal, and variation in the strength of these hydrodynamic connections. We mimicked larval dispersal of the Eastern oyster (*Crassostrea virginica*) by replicating wind-driven circulation patterns in Pamlico Sound (PS), NC using a numerical hydrodynamic model (ADCIRC, ADvanced CIRCulation) to produce 3-dimensional flow-fields, followed by predicted trajectories of virtual larvae using a particle-tracking model (PTM). Predicted larval trajectories were then used to estimate a larval connectivity matrix for PS to help guide oyster restoration efforts via a network of no-take oyster broodstock reserves. To force the ADCIRC model, we used wind observations during the time that oyster larvae would have been dispersing in PS, and used velocity observations from two bottom-mounted ADCP (Acoustic Doppler Current Profiler) instruments to validate velocities predicted from ADCIRC. Field observations of trajectories from 12 Pacific Gyre surface drift buoys released during the summer of 2007 were used to validate the paths of virtual larvae produced by the PTM.

The 3D ADCIRC model reliably predicted variation in velocities at different locations in PS, especially currents near-surface. The PTM also reliably simulated trajectories of surface drift buoys under varying wind regimes, thereby providing confidence in qualitative predictions of dispersal of virtual larvae, and potential larval
connectivity in PS. Potential oyster larval connectivity was not uniform among broodstock sanctuaries in PS, ranging from 20 to 65% connectivity from a given sanctuary. Moreover, potential self-recruitment to a given broodstock sanctuary also varied spatially. Thus, when spatial variation in the degree of potential oyster larval connectivity in PS identified in this study is combined with the results of related studies on spatial dynamics of oyster populations in PS (see below), there is strong evidence for an oyster metapopulation and possibly source versus sink population within PS.
Circulation in Pamlico Sound and Predicted Oyster Larval Dispersal and Connectivity

by
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BIOGRAPHY

Amy Tresa Haase was born on August 29, 1975 in Burien, Washington and grew up in Kent, a suburban of Seattle, Washington. After completing High School in 1994, Amy attended several colleges in pursuit of her passion for math, science and the environment. She received a Bachelor’s of Science degree from the University of Washington in Atmospheric Sciences in 2002 while interning from the National Weather Service at Sandpoint, WA. After graduation, she found employment with both the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) analyzing dual-doppler airborne radar data, and with the Northwest Weather and Avalanche Center developing her skills in mountain meteorology. Returning to academics, Amy received a Master’s of Science Degree in Meteorology from the Pennsylvania State University in 2005. Under the direction of Dr. Toby Carlson, Amy departed her study of the atmosphere and focused on a hydrological project developing a web-based interactive watershed evaluation tool to assess stream health. Continuing to shift into the diverse study of oceanography, Amy worked toward a Master’s Degree in Marine Sciences at North Carolina State University under the guidance of Dr. David Eggleston investigating wind-driven circulation, larval dispersal and connectivity in Pamlico Sound, NC. During this research program, Amy enjoyed numerous research experiences including chasing surface drift buoys with the NC Division of Marine Fisheries and the US Coast Guard Auxiliary, becoming a scientific diver, and supporting her colleagues in their field work. She recently took employment with the National Oceanographic Data Center, a division of the National Oceanographic and Atmospheric Administration in Silver Spring, MD.
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Introduction:

A fundamental issue concerning recruitment dynamics of marine organisms and marine conservation biology involves identifying the paths of dispersal connecting metapopulations, and how spatiotemporal variation in the intensity of dispersal along these paths influences population dynamics (Cowen et al. 2007 and references therein). Most benthic marine populations have limited mobility during their adult stages of life such that dispersal during the pelagic larval phase connects geographically isolated populations—our understanding of the spatial scales of connectivity is generally considered rudimentary (Cowen et al. 2006, Steneck 2006, Becker et al. 2007). The overall goal of this study was to estimate potential larval connectivity of Eastern oysters (*Crassostrea virginica*) in Pamlico Sound, NC, the second largest estuary in the U.S. and a primarily wind-driven system, within the context of a network of no-take, oyster broodstock reserves.

Study species

Oysters are important to the economy of North Carolina. “In 2003, more than 260,000 pounds of oyster meat was harvested at a value of more than $1.02 million compared to 724,000 pounds in 1983 valued at more than $1.12 million, according to the N.C. Division of Marine Fisheries (NC DMF)” (SeaGrant 2004). In addition to the value of the meat, oyster beds provide habitat for up to 300 other animal and plant species (SeaGrant 2004). Overfishing has reduced oyster populations sharply throughout their range, and Pamlico Sound is no exception. For example, annual oyster landings over the past century have
declined by over an order of magnitude (NC Fisheries Management Plan 2008). Poor water quality has also impacted oyster populations. For example, pollution from storm-water run-off and other point and non-point sources are the main cause for closure of harvest shellfish areas to human consumption, and oyster diseases (NCDMF 2001).

Oysters in PS spawn during the late spring to early summer when the water warms to about 20°C (Eggleston and Balance 2007, Mroch 2009). The duration of oyster larvae in a planktonic stage is about 14 to 25 days depending on water temperatures, salinity, turbidity, oxygen content and available nutrients (Dekshenieks 1993, and 1996). According to Dekshenieks, the optimal temperature range for oyster larvae development is from 15 °C to 35 °C, the salinity range from 17.5 to 25, and the optimal food concentration of 3.0 mg C l⁻¹. Young larvae begin at a size of 55 to 60 µm and gain swimming efficiency until their weight overcomes their swimming ability as their shells develop. This transition in vertical location within the water column takes place at a size of 220 to 270 µm, with settlement occurs at a size of about 335 µm (Dekshenieks 1996).

During this planktonic stage oysters are thought to disperse throughout the estuarine system. The mechanisms that dictate the distribution and retention of larvae are still under debate. According to Banse (1986), the swimming ability of oyster larvae is negligible and they are simply passive drifters guided only by the surrounding circulation. Though the swimming speeds of oyster larvae are not great enough to overcome horizontal advection by currents, recent studies indicate that oyster larvae migrate vertically through the water column and use various cues such as salinity gradients to direct this migration (Dekshenieks
et al. 1996, Newell et al. 2005). Vertical migration behavior of oyster larvae also influences dispersal. For example, dispersal simulations of two species of oyster larvae with known swimming behaviors, *Crassostrea virginica* who swim to remain above the halocline and *Crassostrea ariakensis*, who remain near bottom (Newell et al. 2005), result in significant differences in median dispersal distances and potential connectivity of subpopulations (North et al. 2008). The median dispersal distance of *C. virginica* was more than 20% farther than *C. ariakensis* for larval dispersal simulations conducted in the Chesapeake Bay (North et al. 2008).

Various larval and early juvenile stages of marine species use selective tidal stream transport (STST), whereby organisms migrate up in the water column at night to catch incoming flood tides, migrate down in the water column during ebb, and stay near bottom during the day, to migrate up-estuary (Forward and Tankersley 2001 and references therein). For estuarine-dependent species whose larvae are spawned and retained in tidal estuaries, larval dispersal is often governed by vertical migratory behavior phased differently with tides, or associated with a distinct halocline, and can vary by species or ontogenetically within a given species (Cronin and Forward 1979, Strathman 1982, Sulkin 1984, North et al. 2008). Teasing out the behavioral/physical interactions is vastly more difficult in systems where relevant physical cues are not as evident. Consequently, we know little about dispersal of weakly-swimming larvae in non-tidal estuaries, especially shallow, well-mixed estuaries, and estuaries in which tidal signals may be smaller than those caused by seiching (periodic “sloshing”), such as PS (Pietrafesa and Janowitz 1988, Luettich et al. 2002).
Study System

Pamlico Sound is located in the eastern coastal region of North Carolina and is sheltered from the Atlantic Ocean by a grouping of barrier islands known as the ‘Outer Banks’, and connected to the Atlantic Ocean via five major inlets. According to the North Carolina Division of Marine Fisheries (NC DMF), the Albemarle-Pamlico Estuarine System (APES) is the second largest estuarine system in the United States. Circulation is dominated by wind-driven currents and freshwater input (Pietrafesa and Janowitz 1988, Luettich et al. 2002), with little evidence of strong vertical shear flows at different locations in Pamlico Sound (this study). Average depth is 4 to 5 meters with the deepest basin only 7 to 8 meters (Pietrafesa and Janowitz 1988). Wind forcing is highly variable, changing direction and speed every few hours to days. It is also not predictable on hourly and daily temporal scales, but does sustain regular seasonal patterns. As a result, this variable wind-forcing significantly alters circulation patterns, potentially affecting oyster larval transport. Since oyster larval transport is primarily driven by horizontal currents, knowledge of these currents is important to understanding the dispersion patterns within their environment.

Objectives

The overall objectives of this study were to:

(1) assess the efficacy of 2D versus 3D ADCIRC hydrodynamic models in predicting variation in velocities as a function of vertical distance above-bottom and location in PS.
(2) integrate the best predictions of velocity under a given set of wind conditions into a Particle Transport Model (PTM) to predict oyster larval dispersal under realistic winds, and test observed versus predicted dispersal using surface drifters and the PTM.

(3) use the information from the first two goals to generate potential oyster larval settlement areas and a larval connectivity matrix among oyster broodstock reserves in PS.

**Methods:**

Our primary goal in this study was to assess potential oyster larval transport among broodstock sanctuaries in Pamlico Sound, NC. To accomplish this goal, we measured near surface currents using surface drift buoys, and current profiles with bottom-mounted ADCPs. We used the ADCP observations to help validate the ADCIRC circulation model for PS. We then created trajectories using a particle-tracking model driven by the predicted currents and used the drifter tracks to validate these trajectories. Our final products were potential oyster larval settlement areas using ensembles of virtual larval paths originating from oyster broodstock sanctuaries. We summarized our findings with a larval connectivity matrix based on potential oyster larval settlement areas.
Objective 1: Efficacy of 2D vs. 3D ADCIRC Hydrodynamic models

Numerical ADCIRC Hydrodynamic Models. — A numerical hydrodynamic model, ADCIRC (Advanced CIRCulation), was used to explain unique characteristics about the circulation in Pamlico Sound and was validated with field observations (Luettich et al. 1992 and 2002; Reyns et al. 2006, 2007). Using current meter data collected in the Neuse River Estuary, a riverine estuary connecting to the APES in the southwestern region, Luettich et al. (2002) replicated episodic flow patterns in PS. During their study, a modeled tidal signal captured only one percent of the variance in observed flow, and PS was described as a barotropic standing wave with a period of 13.2 h. Luettich et al. (2002) explained this non-tidal semi-diurnal velocity pattern as a seiche in shallow water governed by a wave speed $2L/T = (gh)^{1/2}$. Successful model replications were produced using a “seiche length”, $L$, of 139 km and “seiche depth”, $h$, of 3.5 m for the oscillation period, $T$, of 13.2 h, similar dimensions to Pamlico Sound (Luettich et al. 2002).

Various marine biological studies have benefited from model output from ADCIRC and particle tracking models. For instance, ADCIRC was used for studies conducted on larval and early juvenile species that migrated from inlets up-estuary in PS, such as blue crabs and various fish species (Luettich et al. 1999, Reyns et al. 2006, 2007). Model output predicted how circulation patterns in Pamlico Sound facilitated both primary and secondary dispersal of blue crabs across PS, and concluded that the northern region of Pamlico Sound serves as a consistent hydrodynamic corridor across PS (Reyns et al. 2006, 2007). ADCIRC was used in conjunction with a particle-tracking model to predict larval transport pathways.
for various fish species through Beaufort Inlet, NC (Luettich et al. 1999). Results of this study indicated the importance of tidal forcing and wind direction for optimal ingress.

Hydrodynamic models coupled with particle tracking models that include modeling biological behaviors are critical for understanding population connectivity (NSF 2002). One such behavioral model was recently developed by North, et al. (2006). This model used a new interpolation scheme for particle tracking called the ‘water column profile’ which replaced a linear interpolation scheme. This eliminated artificial aggregation of particles in regions of low diffusivity which is a major source of error in particle-tracking simulations. This water column profile scheme was developed to improve simulations near density gradients. Tested against a random walk model with both well-mixed conditions and dye releases, this interpolation scheme produced higher correlations between neutrally buoyant particle concentrations and vertical diffusivity over time and is recommended for investigating biological-physical interactions in estuaries (North et al. 2006).

We used both the 2D and the 3D ADCIRC, non-linear finite-element hydrodynamic model (Luettich et al. 1992, Atkinson et al. 2004, Reyns et al. 2006, 2007) in conjunction with a particle-tracking model to predict currents and simulate oyster larval dispersal in PS (Fig. 1). ADCIRC has produced flow fields that are in good agreement with observed currents in the Neuse River Estuary located in the southwestern portion of Pamlico Sound (Luettich et al. 2002), as well as in the northern basin of PS (Reyns et al. 2006, 2007) (Fig. 2). This study focused on model validation within both the southern and the northern basins.
of PS. Eulerian and Lagrangian observations were collected to “ground-truth” model output for both of these basins.

A triangular model grid (Reyns et al. 2006, 2007) for the entire Albemarle-Pamlico Estuarine System contained 22,425 nodes and 41,330 elements (Fig. 1) in the horizontal and was provided for this study by Dr. Rick Luettich at the University of North Carolina’s Institute for Marine Sciences. This grid contained a nodal spacing range of 300 m near inlets and adjacent river estuaries to 1 km in the northern and southern basins of PS. In the vertical, both a single layer (i.e. 2D) and seven variable depth layers (i.e. 3D) were selected to resolve the flow field.

Parameter settings used by Reyns et al. (2006 and 2007), such as slip and drag coefficients, bottom roughness, turbulence closure, and length of time-steps provided an initial set-up for model runs and were modified iteratively based on success of the model run and comparisons to observations. Coriolis force was neglected in the model runs because the characteristic time scale of motion in our small domain is less than a day, the minimum required for Coriolis acceleration to noticeably affect current velocities. Two formats of output velocities were possible. First, velocities at all depths from a single model grid node (the equivalent of time-series data collected from a unique geographic location) were generated, herein referred to as “station velocities”. Second, velocities from all model grid nodes for the entire domain at all depths were generated to produce a 3-dimensional flow field, herein referred to as “global velocities”. Global and station velocities were output at hourly time-steps. Geographic coordinates and output time intervals of these stations were
selected to match the locations where Eulerian observations were collected via moored instruments (Fig. 2). Global velocities were originally output as 2D matrices with the first column containing the model grid node number, followed by three columns per depth (U, V, and W velocity components), and rows for each model grid node repeating at each time interval. Two months of hourly output generated approximately 32 million rows of data, which was unwieldy. Thus, header lines were rewritten and the original 2D matrix was reshaped to a 3D matrix with time as the third dimension.

Global velocities were saved as a Matlab structure and formatted for use with a particle-tracking model (PTM). The PTM required input from a single water depth, therefore each depth used to drive the PTM was saved as a separate file. The PTM was designed to be used in conjunction with files from the ADCIRC model, including grids and global velocities. Specifications of the particle tracks to be generated were written in a parameter file that included: start time, duration, number of time steps, and number and initial locations of particles to be tracked. Particles simulated in the PTM were numerically advected to new locations with each time-step based on velocities at surrounding model grid nodes. This program did not resolve turbulence and therefore was limited in its ability to realistically disperse virtual “larval” particles released from a single location (e.g., North et al. 2008). A simple, though not ideal, solution to the lack of turbulence as a means to realistically disperse particles, was to position particles such that release locations were at least one model grid node apart. Particles were also limited to advection from velocities at a single depth, and
were constrained to a horizontal plain. For each particle released at each time step, the PTM output contained particle numbers, as well as latitude and longitude position reports.

**Meteorological Observations and Model Forcing.** Hourly wind observations were obtained from the National Weather Service (NWS) for the period May to November, 2007 for three stations: Cape Hatteras, Kill Devil Hills, and Manteo, NC (Fig. 2). These wind observations encompassed the active spawning period of oysters in Pamlico Sound (Eggleston and Ballance 2007, Mroch 2009). Wind speed was converted from mph as reported to m/s and re-formatted from direction and speed to east-west (U) and north-south (V) velocity components for consistency with other velocity datasets. The original format of the wind data provided by the NWS was modified to match the input requirements for use with the ADCIRC (Luettich et al. 1992). For example, the date format was changed from a 12-hour clock with six numbers, one each for year, month, day, hour, minute and second, to a single number containing eight digits--two digits for each year, month, day and hour. Minutes and seconds were not needed in the revised format. Several hours of missing data that were scattered throughout the time-period were replaced with an interpolation of neighboring observations. No data gaps were greater than a few hours in observations collected at Hatteras, but larger data gaps of up to several days occurred at Kill Devil Hills and Manteo. Cross-correlations, principal component analysis (PCA), and calculation of monthly means of wind observations were performed to determine spatial variation in the wind field over PS. Wind observations at Hatteras formed the most complete dataset of
prevailing winds out of three possible meteorological stations, and wind data from this station was used to force the numerical ADCIRC model.

**Hydrological Observations and Instrumentation.** -- Predicted flow fields produced by the 2D and the 3D ADCIRC models and simulated trajectories from the PTM were correlated with Eulerian and Lagrangian velocity observations collected in PS via two types of instruments: (i) moored Acoustic Doppler Current Profilers (ADCPs), and (ii) surface drift buoys. Moored instruments collected a time-series of Eulerian data from a fixed position, including velocity and water pressure. Surface drift buoys that were released and re-captured provided Lagrangian information on velocity and dispersal paths in PS under a variety of wind conditions during the oyster spawning season. The degree to which ADCIRC hydrodynamic model predictions fit observed data were tested with various statistical models discussed below.

(i) Eulerian observations via moored ADCP Instruments--Two RD Instrument ADCPs were deployed in each of two oyster broodstock sanctuaries, Crab Hole and Ocracoke, in PS during late spring to early fall of 2007 (Figure 2), and one at West Bluff in 2006. The ADCPs were fastened to aluminum frames at depths of 4 to 6 m and programmed to sample currents every 10 minutes from late spring until fall. ADCP settings, such as sample period and range, were modified to optimize data collection. For example, depth of each bin (sample volume as a function of range of the instrument), which determines the vertical resolution of data collection, was set to 0.2 m with 30 bins. This arrangement
yielded a total depth of data collection at 6 m. The deepest half meter and surface half meter
were not sampled because of instrument limitations (see below).

ADCP measurements of currents were collected at Crab Hole from early May to late
September 2007 and at Ocracoke from early May to mid-August 2007. Pre-processing of the
ADCP data included determining the surface-most useable depth bin (i.e., data collected
farthest from the instrument). In this case, return signal strength was a proxy for estimating
useable data, and was used to determine the range of observations available for analysis. If
the signal strength attenuated below the detection threshold of the receiver, velocity records
were likely erroneous. Additionally, data were truncated to exclude observations reported
above the surface of the water, such as pre- and post-deployment, and were also inspected for
gaps in time.

Filtering for tides and inertial oscillation was performed for model comparisons, but
was not performed when data was used in comparison to other observations, such as with
winds. Tides were removed using the T-Tide Matlab Software published by Rich Pawlowicz
at UBC (http://www.eos.ubc.ca/~rich/). Spectral Density Analysis was performed to identify
dominant frequencies such as tidal and inertial oscillations, and then used to verify that tides
were successfully removed from velocity datasets after applying T-Tide software. These
analyses included: ADCP east-west (U) and north-south (V) velocity components for surface
and bottom velocities at both ADCP locations in PS, and from the one pressure sensor on the
ADCP deployed at Ocracoke.
Cross-correlation analyses were used to determine the efficacy of 2D versus 3D ADCIRC hydrodynamic models by testing the relationship between observed versus predicted depth-specific velocities at Crab Hole and Ocracoke. Cross-correlations identified the lead or lag between predicted and observed hourly-averaged east-west (U) and north-south (V) velocity components from the ADCPs with correspondent station velocity output from the ADCIRC model. Additionally, PCA and calculation of monthly means of velocities were performed on the ADCP data to determine the mean flow field in these two sites in PS.

Initial parameter settings for the 2D and 3D ADCIRC models generated output values that correlated poorly (average R-values less than ~0.36 and lags up to 98 h) with observations of velocities both with and without tidal frequencies. Parameter settings were subsequently modified incrementally, for instance modifying slip coefficient values from 0.005 to 0.0025 by increments of 0.0005, until optimum correlation values were reached. A total of 30 model runs were conducted that resulted in final parameter settings (Appendix A) that were then used to generate global velocity output for two time periods: May 29 to June 29, 2007 and June 30 to July 31, 2007. These two time periods were selected to coincide with surface-drifter deployment dates (see below) and peak spawning periods for oysters in PS (Eggleston and Balance 2007). Splitting the output into two time-periods also enhanced processing efficiency.

(ii) Lagrangian surface drift buoys--Microstar surface drift buoys built by Pacific Gyre were deployed in PS during May -- September, 2007. Surface drift buoys, referred to hereafter as “drifters”, consisted of orange and white spherical plastic cases which housed
batteries, a temperature sensor, electronics and an antenna (Fig. 3). The tristar-configured drogue consisted of four drag-producing triangular nylon sails extending radially the entire length of a negatively buoyant polyvinyl chloride (PVC) tube centered at 1-m water depth and tethered by a nylon cord to the spherical case. Four horizontal tubes connected at a central joint supported the vertical sails. Additionally, four trapezoidal sails were attached to the horizontal tubes. Buoyancy for the entire system was provided by the spherical cases, thus no additional surface floats were required. The drifters were programmed to record their location every ten minutes, with three reports containing the following information transmitted every 30 minutes: locations, sea surface temperatures, and time of observations. Up to 144 position reports were recorded each day making re-capture and re-deployment in the field possible. Under these settings, the battery life of the drifters was eight to ten days.

During the summer of 2007, 17 drifter releases were conducted with 1-5 drifters per release (Table 1). A collection of concurrently released drifters is referred to hereafter as a “batch”. Over a 13-week period, four to nine drifters and up to two batches were deployed simultaneously and allowed to drift for up to one week along transects between oyster sanctuaries within Pamlico Sound (Fig. 2). Drifter deployment batch #s 21-29 were released into the northern basin, and batch #s 31-36 were released into the southern basin of Pamlico Sound (Table 1).

Several challenges were encountered when deploying drifters. These instruments would generally run aground in depths less than 1.5 m, which in PS includes large areas near the shoreline and over shoals. Drifters that ran aground were identified by notes in a log
made at the time of retrieval, plotted position reports, and zero velocity values. Drifter records were truncated for those running-aground by distance-differencing between position reports. For example, if the total change in position of each report was less than the accuracy of the GPS (<10 m) for the latter part of a record, it was deleted. In addition to running aground, there were several instances where drifters detached from their drogues, which was evident in the data when drifter velocities more than doubled within a single time-series. These data were also eliminated from analyses. Other instances where data were truncated included: (i) erroneous position reports, such as those several kilometers outside the study area or on land, (ii) reports separated by more than 12 hours, which were indicative of GPS signal loss, and (iii) duplicate reports. Temporal and spatial variation in drifter velocity cannot be treated with low-pass filters to remove inertial or tidal oscillations because the records are too short--tidal oscillations occur on a semi-daily and daily time scale. Drifter records needed to be at least a week in length for tidal-filtering. Currents within the study area, however, are not driven primarily by these oscillations but rather wind-driven (Pietrafesa et al. 1986, Luettich et al. 2002, Reyns et al. 2006); therefore the lack of filtering did not create a problem in analyzing data. Various drifter metrics, such as total and net distance traveled, were generated. Predicted oyster larval dispersal paths based on an ADCIRC particle-transport-model were tested against observed drifter tracks (see below).
Objective 2: Use PTM to predict oyster larval dispersal and test with drifters

Drifter paths were replicated with the Particle-Tracking-Model (PTM) driven by flow fields produced by the ADCIRC model. Twenty-five drifter deployments (deployment batch #s: 22, 23, 24, 25, 32 and 33, Table 1) were selected based on date of deployment (i.e., deployments corresponding to ADCIRC model output and peak oyster spawning) and duration (i.e., > 70 hours). All ten-minute drifter reports were hourly-averaged to create a consistent time interval with output from the PTM, also hourly, and to fill in short (< 2 h) data gaps.

Predicted drifter paths were simulated by entering the following data into the PTM parameter file: initial deployment time, duration, and drifter release locations and number of drifters for each deployment batch. When drifter releases and recoveries within one deployment batch lasted for several hours, the mean time of the release and duration of deployment was set into the parameter file. Typically, individual releases within a batch were completed in a couple hours. Conversely, drifter recoveries took significantly longer, sometimes in excess of six hours to recover all the drifters, which resulted in some drifter deployments being longer than the coincident PTM output; however, this discrepancy was negligible over several days of data collection.

Total and net distances transported (difference between the release and retrieval location) were calculated and compared for both observed and modeled paths (Table 2). Total distances transported were calculated by summing the individual changes in position at each time step (model) or report (observed). The net distance transported was calculated by
taking the difference in drifter recovery site with the drifter launch site for both observations and predictions. The selected observed drifter paths were then (i) qualitatively compared to those predicted by the PTM by plotting each on the same figure, and (ii) quantitatively compared by cross-correlations between the observed and predicted latitude and longitude. The average correlation values for both the latitude and longitude correlations, 25 pairs, were used as a final score to rank the performance of the PTM. For instance, if the correlation between observed versus predicted latitude was 0.7 and the correlation between observed versus predicted longitude was 0.9, then the average correlation used to rank model performance was 0.8.

**Objective 3: Oyster larval connectivity**

Potential paths of oyster larval dispersal from ten oyster broodstock sanctuaries in PS, nine existing and one presently under construction (Fig. 1), were generated to assess potential larval connectivity among sanctuaries using the PTM driven by the 3D ADCIRC global velocity fields. Model particles (i.e., non-swimming virtual larvae) were released from five initial starting locations within each oyster sanctuary, one at each of the four corners and one in the center. This technique varied from the previously mentioned PTM tests with drifters, which were released along transects between 2-4 sanctuaries for periods of 4-5 d in water depths greater than 1.5 m and away from the shoreline to avoid instrument damage. Testing potential larval paths was not constrained by these factors and was conducted for periods of 14-21 d with release sites located exclusively on the oyster sanctuaries. Ideally, the paths
taken by these particles would replicate the dispersal of oyster larvae produced by adult oysters on the sanctuary mounds. Model particles released from these initial starting locations, however, followed one path and did not deviate from the single trajectory/path during a 14 d trial simulation conducted at each sanctuary. The single particle trajectories from each sanctuary were likely due to the size of the sanctuaries, which were contained within a single model grid cell (cells enclosed by model grid elements connected at each node) and by PTM limitations since turbulence was not resolved in this model as suggested by North et al. (2008).

An alternate simulation scenario was adopted to overcome the omission of turbulent processes in the PTM and to artificially force particle dispersal. The initial starting locations were re-positioned in a ‘five dice’ pattern following the method used with drifters by Doble and Wedhams (2006) in or near each of the ten oyster sanctuary boundaries. The starting locations were then incrementally moved away from sanctuary corners at incremental distances of 0.01° latitude/longitude until independent transport paths were produced. All final particle release locations were about 0.03° from the center of a given sanctuary and located in separate model grid cells.

Using the final particle release locations, a total of 50 particles were released from 10 sanctuaries for a 21 d period to simulate a typical duration of oyster larvae in the water column (Dekshenieks 1993, 1996; North et al. 2006, 2008). This process was repeated every 24 h over 26 daily iterations during the period May 28-June 10, 2007 and from June 20-July 11, 2007. These simulations were set to correspond to the primary (May 28 to June 10) and
secondary (June 20 to July 11) oyster settlement peaks observed annually in PS (Eggleston and Ballance 2007) and also coincided with drifter deployment dates.

Figures were created by plotting the last 7 d of particle paths for each iteration according to their oyster sanctuary of release. This time-period was selected to simulate oyster larvae reaching the age in which they become competent to settle (North et al. 2006 and 2008; Fig. 12). Areas in which simulated oyster larvae traveled during the last 7 d of modeled dispersal were referred to hereafter as “potential settlement areas”. Plots were generated for each potential settlement area, and then they were qualitatively compared to one another. A connectivity matrix (Table 4) was also generated by visual inspection of the projected particle paths. If a particle traveled from one sanctuary to another, these sanctuaries were considered potentially connected biologically via the oyster larval phase. If a particle returned to the sanctuary in which it was released, that sanctuary was deemed self-recruiting.

Scores were given to particle tracks that either traveled from one sanctuary to within borders of another sanctuary (10%), back to the originating sanctuary (score of 10%), to within 0.01°, 0.02°, or 0.03° of a sanctuary border (score of 9%, 8%, 7%, respectively), or outside this range (score 0%). This scoring technique was developed based on the results of the particle paths. All particle paths located within 10 km of a sanctuary were scored. Sanctuary connectivity was calculated by summing the scores in each row (i.e., each individual sanctuary connection equals a maximum of 10% for a total score of 100% should it be connected to all sanctuaries). For example, if particles released from one sanctuary
returned to that original sanctuary and nine additional tracks from that original sanctuary entered the borders of the other nine sanctuaries, this set of 10 tracks would add-up to 100%.

**Results:**

**Objective 1: Efficacy of 2D vs. 3D ADCIRC Hydrodynamic models**

*Wind fields.*

Automated wind velocity observations among NWS stations (Hatteras, Manteo and Kill Devil Hills, NC; see Fig. 2 for locations) showed minimal spatial variance in the wind field over the study region. The major axis of variation in velocities (ellipses) at all stations was oriented along the northeast-southwest axis of PS (not shown). Mean velocity arrows were directed east of north at Hatteras, indicating predominant southwesterly wind. Mean velocity arrows were directed just slightly west of north for the sample period at Manteo and Kill Devil Hills, however, indicating a predominant southerly, versus southwesterly, wind. (Fig. 4). This 45° directional shift in predominant winds from Hatteras north to Manteo was the largest spatial variation in the mean winds during the study period. Monthly means of winds at all three stations indicated southwesterly winds during summer months (June, July and August) driving currents toward the northeast (Fig. 4). During May and September, the passage of cold fronts occurred every few days to a week causing a reverse in wind direction from southwesterly to northeasterly (Fig. 4, top) and resulting currents changed from northeastward to northwestward at Ocracoke (Fig. 4, bottom). At Crab Hole, little directional change was observed in the currents, northwest to west of northwest, but the
magnitude decreased from ~0.2 m/s to <0.1 m/s. Cross-correlation coefficients between wind velocities measured at Hatteras and the other wind stations ranged from 0.75 to 0.85 with lags ranging from 0 to 3 h. Due to the relatively high spatial coherence in winds measured at Hatteras versus Kill Devil Hills and Manteo, the ADCIRC model was forced by winds collected hourly from the Cape Hatteras Meteorological Station during the primary oyster spawning season in 2007 (May 1--September 18).

**Observed versus predicted currents.**

In general, there was good agreement between observed velocities measured with the ADCP instruments and currents predicted with the 3D ADCIRC model, but not with the 2D model. Predicted flow velocities were similar to, though less energetic, than observed velocities, and predicted currents from both 2D and 3D models were correlated with wind forcing (Fig. 5, and 6). Comparing velocity components at both sites, the strongest correlations between observed currents versus those predicted with the 3D ADCIRC model were found at Ocracoke in the U-component and at Crab Hole in the V-component (Fig. 7 and 8). Within a given site, correlations were strongest between observed and predicted near-surface currents, with highest correlation coefficients of 0.61 at Ocracoke and 0.67 at Crab Hole with lags < 2 hr (Fig. 9 and 10).

Predicted currents replicated changes in magnitude and direction of observed currents within each depth-specific velocity on a daily and weekly timescale, but did not recreate the higher magnitude velocity oscillations operating on hourly time-scales (sharp blue spikes;
Predicted surface velocities peaked near the water surface at a speed of 0.5 m/s and decreased to ~ zero near-bottom (Fig. 7 and 8). Conversely, observed velocities were more homogenous across water depths, with relatively little evidence of strong vertical shear. For example, observed velocities near the bottom of Pamlico Sound were nearly as strong at mid-depth as they were at the surface (both ~ 0.2 m/s, Fig. 7 and 8). Removing tidal constituents from the ADCP velocities did not improve correlations between observed and predicted velocities. Tidal-forcing was visible in the U-component of the observations at Ocracoke by the periodic oscillations matching those of only M2 and P1 tides; however, the model forcing did not include tides, and as expected, was not replicated. Spectral density analysis confirmed the removal of the tidal constituents, which slightly lowered all correlation coefficients by ~0.02. Based on these results, predicted velocities used to predict oyster larval transport were driven by winds from Hatteras and the 3D ADCIRC hydrodynamic model.

2. Objective 2: Evaluation of the PTM with drifters

Predicted particle tracks (i.e., latitudes and longitudes) produced by the PTM were highly correlated with the drifter deployment paths (Fig. 11) with an overall correlation score of 0.77 for longitude and 0.73 for latitude (Table 2); eleven of twenty-one possible correlations produced coefficients greater than 0.9 (Table 3). Correlations tended to be highest in areas with the greatest velocities that were produced by either strong wind velocities or by geographic location (i.e., near shore). Drifters deployed in near-shore
environments and that traveled along the western shore of PS (e.g., drifter batch #25, Table 3) had the highest correlation between predicted and observed latitude reports (Table 3).

The PTM did a good job of predicting the total and net distance transported by the drifters. Predicted total distances were highly correlated (R > 0.9) with observed distances, with correlation coefficients increasing with distance transported. Predicted total distances from the PTM, however, were generally 10% greater than total distance transported by the drifters. Predicted and observed total distances ranged from 5 to 58 km, and 1 to 63 km respectively (Table 3). Similar to predictions of total transport, predicted net transport was 20% greater than observed net transport (Table 3). Results from the comparison of trajectories from the PTM versus observed drifter paths was not consistent with the results from the ADCIRC comparisons to ADCP observations. This inconsistency is addressed in the Discussion section.

3. Oyster larval connectivity

**Potential Settlement Areas** -- Initial release location of particles influenced both the spread and distance traveled of virtual particles over 14-21 d periods (Fig. 12). During the first days of the first iteration of particle releases (May 28th- June 2nd, 2007), winds were light (<0.5 m/s), causing the particle to remain near ‘natal’ sanctuaries. A strong southwesterly wind event (>1 m/s) started on the fifth day forcing particles to the north. Most particles (90%) reached the model grid boundary (i.e., land) and terminated movement before the end of the test. Drifters released near shore also ran aground within a few days. Therefore, this
behavior was anticipated in the model given the close proximity of the oyster sanctuaries to land. In later iterations, numerous particle paths terminated in the center of the northern basin, such as those originating from Gibbs Shoal, West Bluff, and Ocracoke (Fig. 12c, d, and i). Particles released from the Neuse River and West Bay along the southern shore of PS traveled the greatest distances (~110 km) to Oregon Inlet near Croatan Sound in the north, crossing the entire sound along the western shore (Fig. 12g and h). Particles released at Ocracoke spread throughout the northern basin of PS, whereas particles released from Clam Shoals/Hatteras remained near the eastern shore until having traveled a significant distance north (Fig. 12i and j).

Qualitatively, the area of PS that served as potential settlement areas for virtual oyster larvae varied according to the sanctuary where larvae were released. For example, the largest potential settlement areas, filling two-thirds of PS, corresponded to virtual larvae released from Gibbs Shoal and West Bluff (Fig. 12c and d), both located on the western shore of PS. Conversely, the smallest potential settlement areas corresponded to virtual larvae released at Deep Bay and Middle Bay (Fig. 12e and f), both near the mouth of the Pamlico River. Virtual larvae released from the northern most sanctuaries, Croatan Sound and Crab Hole, were exported to Albemarle Sound (Fig. 12a and b) where salinities are likely too low for survival of oyster larvae (Dekshenieks et al. 1993, Xie et al. 1999, Pietrafesa et al. 1986). Potential settlement areas for virtual larvae released from Deep Bay and Clam Shoal/Hatteras were located primarily along-shore (Fig. 12e and j).
Assessment of Potential Connectivity Among Sanctuaries—Potential oyster larval connectivity was not uniform among broodstock sanctuaries in PS. The sanctuaries with the largest potential settlement areas, West Bluff and Gibbs Shoal, produced the greatest number of connections to neighboring sanctuaries, with percent connectivity of 65% and 59%, respectively compared to other sanctuaries (Table 4). Middle Bay, Deep Bay and Clam Shoals/Hatteras produced the fewest possible connections, 20% or less (Table 4). All sanctuaries, however, potentially self-recruit oyster larvae as indicated by a score of “10%” in the matrix cells along the main diagonal of the connectivity matrix, located equivalently to the diagonal of “ones” in a unit matrix (Table 4). Neuse River was an exception to this and scored a nine for connectivity with itself since particles did not re-enter the sanctuary, but came close.

Summing the columns of the Connectivity Matrix (Table 4) to interpret connection to the entire sound indicated that Crab Hole and Gibbs Shoal received the greatest supply of larvae from other sanctuaries, with percent connectivity scores of 56%. Conversely, Croatan Sound, though proximal to Crab Hole, scored 38%. Neuse River and West Bay were suggested to be sourced by the same sanctuaries due to there close proximity to each other: West Bluff, Neuse River, and West Bay. This was not the case, however, particles traveled into West Bay, but not into Neuse River.
Discussion and Conclusions:

A 3D numerical hydrodynamic model (ADCIRC) reliably predicted variation in velocities at different locations in PS, especially currents near-surface. A particle-tracking-model, using the ADCIRC currents, also reliably simulated trajectories of surface drift buoys under varying wind regimes, thereby providing confidence in qualitative predictions of dispersal of virtual larvae, and potential larval connectivity in PS. Potential oyster larval connectivity was not uniform among broodstock sanctuaries in PS, ranging from 20 to 65% connectivity from a given sanctuary. Moreover, potential self-recruitment to a given broodstock sanctuary also varied spatially. Thus, when spatial variation in the degree of potential oyster larval connectivity in PS identified in this study is combined with the results of related studies on spatial dynamics of oyster populations in PS (see below), there is strong evidence for an oyster metapopulation and possibly source versus sink population within PS.

Metapopulation theory integrates population ecology with principles from landscape ecology, where landscapes are viewed as a network of discrete but interconnected habitat patches (e.g., sanctuaries) with asynchronous demographic rates in space and/or time (Hanski 1998). Though the defining characteristics of a metapopulation are widely debated and non-quantitative (e.g., Grimm et al. 2003, Kritzer and Sale 2004), we consider the degree of connectivity within a metapopulation to range from relatively low, but nontrivial connections, to frequent, but asymmetrical connections (sensu Kritzer and Sale 2004, Lipcius et al. 2008). Integral to the metapopulation concept is the notion of source-sink dynamics, in which ‘sink’ populations have insufficient reproduction to balance local mortality and thus
are dependent upon an external supply of recruits from more productive ‘source’ populations (Pulliam 1988, Eggleston 1999). Source-sink and metapopulation dynamics have been considered in the design of marine reserves (e.g., Botsford et al. 2003), but with few empirical tests (but see Lipcius et al. 2003). Marine systems with spatially segregated sessile adult populations connected only by larval dispersal, such as oyster reserves in PS, are particularly amenable to testing metapopulation and source/sink concepts because of: (1) the presence of broodstock reserves that are separated by ~10 to 125 km, (2) spatial variation in the timing of spawning (Eggleston and Balance 2007), (3) spatial variation in oyster demographic rates such as fecundity, growth and survival (Mroch 2009, Puckett, Ph.D. dissertation, unpubl. data), and (4) variation in potential larval connectivity (this study).

**Efficacy of ADCIRC hydrodynamic model in predicting variation in velocities**

We tested the efficacy of 2D versus 3D ADCIRC hydrodynamic models in predicting observed velocities across a wide range of wind conditions and two geographically distinct areas in PS. Moored ADCP instruments, which collected Eulerian data on vertical distribution of velocities, were deployed in areas of PS where the model’s predictive abilities were presumed to be limited, for instance near complex terrain features such as Bluff Shoals, inlets and adjacent narrow sounds. The 3D model outperformed the 2D model by more accurately predicting surface velocities, particularly in magnitude of velocity. Velocities predicted with the 2D ADCIRC model were, in general, an order of magnitude slower than observed currents (predictions 0.01m/s when observed velocities were 0.1m/s per se),
whereas velocities predicted with the 3D model were in good agreement to the observations (see Results, and Figs. 5 and 6). Similarly, observations of currents in Beaufort Inlet, NC south of PS, collected with a combination of current meters and ADCP transects agreed well with 2D ADCIRC model predictions, especially in capturing both amplitude and phase of tidal constituents, and direction of flow, but under-predicted maximum current flux by as much as 50% (Luettich et. al 1999). Similarly, near-surface observations of currents in the northern region of PS during the fall recruitment period for blue crab (*Callinectes sapidus*) megalopae and early juveniles using S4 current meters were well-predicted by ADCIRC with statistical correlations between 0.39 to 0.9 (Reyns et. al 2006 and 2007). Other studies have validated ADCIRC model predictions, and generally found that the numerical analysis agreed with the observational analysis (Luettich et al. 2002), and reproduced storm surge with a mean error within 10% of surge height (Westerink et al. 2008).

**Efficacy of a Particle Transport Model (PTM) in predicting oyster larval dispersal**

We also tested the predictive ability of the PTM particle paths in a shallow estuarine environment to predict potential oyster larval dispersal. Tests were conducted to verify the model’s ability to replicate observed Eulerian and Lagrangian velocities in a computationally challenging environment, the wind-driven micro-tidal currents of PS. Additionally, we tested the PTM across a large spatial range, nearly the entire PS, using ADCIRC flow fields driven by spatially consistent winds. A collection of drifter observations were used to validate predictions from the PTM, which was then used to replicate potential larval larval paths. Through
analysis of the observations and modeled flow-fields, several unique features were discovered in PS that have implications for larval connectivity (see below).

Drifters were deployed in other studies off the Southeast US Continental Shelf which provided estimates of the retentive characteristic of the Southeast US Continental Shelf and showed overall good agreement between numerical and observed drifter tracks with statistical significance ($R^2$) ranging from 0.48 to 0.89 (Edwards et. al 2006). To date, no known published record exists of other drifter studies conducted within Pamlico Sound, NC.

Weekly drifter releases were conducted across the northern and southern basins of PS along transects during both the northeasterly and southwesterly wind regimes. Release sites were selected based on wind forecasts, southern release sites for southerly wind forecasts and northern release sites for northerly wind forecasts (Table 1 and Fig. 2). These release sites proved to be highly effective since drifters remained in PS during most deployments. On a few occasions, however, drifters deployed in the north exited the study area through Oregon Inlet and Croatan Sound. In the south, drifters exited PS through Neuse River, but not through Ocracoke Inlet. This only caused minor interruptions in the data collection (< 2 d).

Studies have used PTMs to estimate larval retention and export from estuaries and other coastal environments. These studies showed larval retention is higher for green crab in summer months versus spring month for Willapa Bay, WA (Banas et al. 2009). Similarly, differences in swimming behavior of two species of oyster larvae had significant consequences in dispersal distances (North et al. 2008), as did inter-annual variability of currents on shrimp larvae (Pedersen et al. 2003). Surface drift buoys have been used to
validate these PTMs, which also revealed skills and deficiencies for estimating Lagrangian dispersion with best predictions during spring and summer months and poor predictions during winter and autumn (Pizzigalli et al. 2007). In this study, the PTM was successful in replicating drifter tracks within PS producing cross-correlation coefficients between observations and predictions greater than 0.9.

Surprisingly, the predicted tracks generated by the PTM were generally longer than the Lagrangian observations, though the ADCIRC predicted flow fields were less energetic than the Eulerian observations. The mechanisms causing this unexpected result are not entirely known, though it could be attributed to slip velocities in the drifters which were reported to be 1 to 3 cm s\(^{-1}\) for the tri-star drogue configuration (Niiler et al. 1987 and 1995, Geyer et al. 1988). When drifter velocities were compared to ADCP velocities for concurrent observations, however, mean velocities for both instruments were within 1 cm s\(^{-1}\) of each other. Alternatively, the magnitude of the wind velocity and responding currents generally diminishes near dawn and are stronger during afternoon hours of the day (unpublished data from study). Time series predicted velocity plots did not show this relaxation during early morning hours. Virtual particles could then “catch-up” to and even pass drifter observations thereby producing longer tracks. Lastly, it is possible to hydrodynamic features not visible in the observations, such as density frontal boundaries, could have entrained drifters thereby slowing them down relative to predicted speeds and distances (e.g., Eggleston et al. 1998). A possible solution to this discrepancy between predicted and observed dispersal trajectories would be to create an interpolation of sigma
layers for the uppermost one meter depth. Observed tracks could then be compared to predicted tracks produced by velocities in the surface one meter rather than the uppermost layer of the model. This was not performed in this study because global velocities produced in the numerical model decreased significantly below the uppermost layer.

**Potential oyster larval settlement areas and connectivity among oyster sanctuaries**

The present study provides evidence that circulation in PS can support an oyster meta-population via larval connectivity of spatially-isolated broodstock sanctuaries. Connectivity, however, is not equal among reserves. A combination of winds and proximity to shores could be responsible for enhancing velocities which would facilitate connectivity among reserves. For instance, observed currents on the western shore in the northern basin of PS provide the most probable larval connection to neighboring sanctuaries on the western shore: Ocracoke, West Bluff, Gibbs Shoal, Crab Hole and Croatan Sound into Albemarle Sound (Fig. 13). Evidence of this current, with both southwesterly and northeasterly winds, was detected by drifters captured by this current in which they traveled twice as fast (0.4 m/s versus 0.2 m/s) and more than double the distance (12 km/d versus 5 km/d) than neighboring drifter deployments released outside this current. This strong current along the western shore of PS was reproduced by the 3D ADCIRC model. Also, PTM simulations for May 28 to June 17 and June 6 to June 28, 2007 (not shown) demonstrate the existence of this current and ability to provide a reliable larval connection between northern and southern areas along the western shore of PS.
A convergence zone near Bluff Shoals was produced in both southwesterly and northeasterly wind regimes in the surface currents, thereby increasing flow velocities three to four times that of nearby currents (Fig. 13 for southwesterly, and Fig. 14 for northeasterly). Divergence was produced in the bottom currents near Bluff Shoals (not shown). During southerly winds, surface currents flowing toward the shoal from the east or west were diverted to the north, and bottom currents were diverted to the south (Fig. 14). During a northerly wind, this pattern reversed and the surface flow was southward and the bottom flow was northward. Oyster sanctuaries located to the east or west of this shoal could have potentially limited connectivity with each other (Ocracoke to West Bay and Middle Bay, per se). Alternatively, sanctuaries located to the north or south of this shoal (Ocracoke to West Bluff, per se) could be well-connected.

The geometry of the narrow Croatan Sound connecting Pamlico Sound to Albemarle Sound could potentially facilitate oyster larval connectivity as well. During southwesterly winds, ADCIRC flow fields indicated surface waters originating in PS were pushed north into Albemarle Sound via Croatan Sound, while the bottom layer produced a weak return flow to the south. This bi-layer circulation continued until either the wind force decreased or the pressure gradient produced by the increased water depth exceeded the wind force. Once this balance of forces between the wind and the pressure gradient was interrupted, Croatan Sound acted like a venturi described by Bernoulli’s Principle (Hallidy and Resnick 1960). In Bernoulli’s experiments (1738), flow through a pipe was observed to increase in pressure and decrease in velocity up-stream of a restriction created by decreasing the pipe diameter, then
increased in velocity and decreased in pressure after passing through the restriction. Water from Albemarle Sound flowed south out of Croatan Sound into PS creating a strong southward flow (Fig. 15) at all depths. Velocities measured by the ADCP at Crab Hole exceeded 0.5 m/s, and this event is referred to as the “Albemarle Flush” hereafter. Drifters caught in the Albemarle Flush traveled up-wind (i.e. to the south when the winds were blowing southwesterly). Mean velocities and principle components from the ADCP moored at Crab Hole were dominated by a southward component likely caused by the Albemarle Flush. This behavior observed by the drifters and ADCP at Crab Hole could not be explained until the Albemarle Flush was detected in the global velocities produced by the 3D ADCIRC model (Fig. 15). Oyster larvae spawned from Croatan Sound or Crab Hole could be advected south toward Gibbs Shoal and West Bluff during occurrences of the Albemarle Flush, thereby enhancing potential larval connectivity between these northern sanctuaries and those located to the south.

Simulated particle tracks were also compared to shell-string settlement data from late spring of 2007 collected as part of this overall research program (Eggleston and Balance 2007). Adult oysters were believed to have spawned first in the Neuse River, as suggested by the water temperature data collected in conjunction with shell-string monitoring. Observed water temperature exceeded 20ºC (24.9ºC at Oriental, NC on May 20th, 2007), the minimum threshold for oyster spawning in PS (Mroch 2009). Other shell-string sites reported temperatures between 17ºC- 20ºC during this time, which was likely too cool for oyster spawning. Winds were southwesterly and simulated particle releases generated by the
PTM from the Neuse River traveled north along the western shore terminating on shorelines from Turnagain Bay to West Bluff. This finding agrees with observed peak oyster settlement in late May which occurred at Turnagain Bay (Eggleston and Balance 2007).

Assumptions and Applications

Oyster larvae are known to migrate throughout the water column (Dekshenieks et al. 1996, and North et al. 2008), however, we predicted larval dispersal using single-layer, vertically homogeneous velocity flow-fields. Our method did not allow for advantageous swimming behaviors in larvae, such as flood-tide transport. In Pamlico Sound, however, the water column is generally well-mixed and was demonstrated to behave frequently as a single layer where profile observations were collected. Therefore, this model limitation would have minimal effects in the study region. We also did not open our model to the Atlantic Ocean, constraining predicted flow-fields to within the boundaries of PS since the tidal influence on velocity diminishes significantly with distance from the inlets (Pietrafesa et al. 1986). It is possible that predicted particles, without these boundary limitations, would exit PS into the Atlantic Ocean through Oregon, Hatteras or Ocracoke Inlets as demonstrated by the drifters. This research project focused on retained species and accepted this minor limitation since most oyster sanctuaries are located away from inlets.

In conclusion, solving the larval dispersal challenge requires a diverse set of techniques, each with its own strengths and limitations for a given study system and space/time scale. These methods include field sampling of larvae and currents coupled with
bio-physical modeling, drifters, and genetic or geochemical tagging (NSF 2002). The results of this study provides confidence in existing tools and applications for studying larval dispersal in primarily wind-driven estuaries such as Pamlico Sound. For example, we demonstrated the efficacy of (1) ADCIRC in recreating 3D velocities in complex bathymetric and geo-morphological settings within the estuary, and (2) an ADCIRC-based PTM in recreating larval dispersal trajectories, which are critical in estimating larval connectivity among sanctuary net-works. Testing and refinement of numerical hydrodynamic models, particle-tracking models, and techniques for validating these predictions, such as bottom-moored ADCP and satellite drifters, will enhance decision support tools for improving the efficacy of net-works of sanctuaries for marine habitat and fisheries management and restoration purposes.
LITERATURE CITED


Doble, M.J., and P. Wadhams, 2006. Dynamical contrasts between pancake and pack ice,


Table 1. Summary of drifter batch releases. Deployment locations are identified by an abbreviation of the oyster sanctuary name or nearby landmark: Crab Hole (CH), West Bluff (WB), Hatteras (HA), Ocracoke (OK), and Neuse River (NR) (see Figure 2 for locations). Wind conditions were recorded at time of release while on site. Batch numbers in parentheses occurred simultaneously with batch number listed. Wind directions are listed by meteorological convention (i.e. s = southerly, n = northerly, etc.). Batches used in comparison to the PTM are in bold.

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Table 2. Summary of observed (drifters) and predicted (PTM) distances, cross-correlations and final latitude and longitude reports. Cross-correlations are between the mean observed (drifters) and predicted (PTM). Final latitude and longitude position reports for drifter deployments are highlighted in Table 1. The average, maximum and minimum cross-correlation coefficients (R-values) for 25 pairs of observed (drifters) and predicted (PTM) latitude and longitude position reports are listed. Cross-correlation coefficients for each pair of observed and predicted position reports are found in Table 3.

<table>
<thead>
<tr>
<th>Transport</th>
<th>Drifters (obs)</th>
<th>PTM (predicted)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Distance Transported:</td>
<td>746 km</td>
<td>824 km</td>
</tr>
<tr>
<td>Net Distance Transported:</td>
<td>411 km</td>
<td>496 km</td>
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<tr>
<td>R-values of Position Reports:</td>
<td>Mean</td>
<td>Max</td>
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<tr>
<td>Longitude:</td>
<td>0.77 (SE)</td>
<td>0.98</td>
</tr>
<tr>
<td>Latitude:</td>
<td>0.73 (SE)</td>
<td>0.99</td>
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</table>
Table 3. Summary of Total and Net Transport of observations (drifters) and predictions (PTM), and cross-correlations coefficients by deployment batch. Distances are in kilometers. Total distance was calculated by summing the individual changes in position for either observations or predictions. Net transport was calculated by differencing final position from the starting position. Difference in endpoints was calculated by differencing final positions reported by drifters and the last position produced by the PTM. R-values were calculated by cross-correlating longitude and latitude from the drifter position reports to the output of the PTM. R-values for longitude and latitude were averaged to produce mean R-values. Deployments containing insufficient data for statistical correlations are shown by NED due to instrument failure and error in data collection.

<table>
<thead>
<tr>
<th>Deployment Batch No.</th>
<th>Surface Drift Buoy</th>
<th>Model</th>
<th>Comparison</th>
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<tr>
<td></td>
<td>Number of Obs.</td>
<td>Total Distance</td>
<td>Net Transport</td>
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<tr>
<td>DB22</td>
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<td>17.93</td>
<td>16.45</td>
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<td>151</td>
<td>20.67</td>
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<tr>
<td></td>
<td>67</td>
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<tr>
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<td>136</td>
<td>9.59</td>
<td>8.38</td>
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<td>31.10</td>
<td>25.87</td>
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<td>114</td>
<td>26.91</td>
<td>24.45</td>
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<td></td>
<td>25</td>
<td>14.30</td>
<td>13.34</td>
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<tr>
<td></td>
<td>65</td>
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<td>20.04</td>
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<tr>
<td></td>
<td>82</td>
<td>15.91</td>
<td>3.43</td>
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</table>
Table 4. Connectivity Matrix. Potential larval connectivity is calculated between source sanctuaries (rows) and recipient sanctuaries (columns). Units are in percentages. Score of 10 indicates direct connectivity. Scores of 9, 8, and 7 indicate connectivity measured within 0.02, 0.03 and 0.04 degrees latitude/longitude of sanctuary boundaries, respectively. These values were selected as a simple measure of distance from the sanctuary boundary that partitioned the data. Zeros indicate no connectivity within 0.04 degrees (~4 km) of a sanctuary boundary.

<table>
<thead>
<tr>
<th>Connectivity Matrix</th>
<th>CS</th>
<th>CH</th>
<th>GB</th>
<th>WB</th>
<th>DB</th>
<th>MB</th>
<th>NR</th>
<th>WY</th>
<th>OK</th>
<th>CL</th>
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<tr>
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<td>9</td>
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<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Gibbs Shoal</td>
<td>GB</td>
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<td>10</td>
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<td>0</td>
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<td>0</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>West Bluff/ Bluff Point</td>
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<td>10</td>
<td>10</td>
<td>10</td>
<td>0</td>
<td>8</td>
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<tr>
<td>Neuse River</td>
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<td>9</td>
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<td>0</td>
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<tr>
<td>West Bay</td>
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<td>0</td>
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<td>10</td>
<td>0</td>
<td>0</td>
<td>9</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Ocracoke</td>
<td>OK</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Hatteras / Clam Shoals</td>
<td>CL</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10</td>
</tr>
</tbody>
</table>
Figure 1. Map of Pamlico Sound Oyster Sanctuaries and model grid nodes. This was used for running the ADCIRC Model. Oyster sanctuary names are abbreviated: Croatan Sound (CS), Crab Hole (CH), Gibbs Shoal (GB), West Bluff (WB), Deep Bay (DB), Middle Bay (MB), Neuse River (NR), West Bay (WY), Ocracoke (OK) and Clam Shoals/ Hatteras (CL). Every 5th model grid node was plotted to enhance readability.
Figure 2. Map of 2007 drifter releases locations and mooring sites for ADCPs and other relevant landmarks. Drifter release locations are indicated for the northern (closed circles) and southern (open circles) basins of Pamlico Sound, respectively. Drifters were released along transects in Pamlico Sound to maximize spatial coverage of data collected, as well as limit likelihood of running-aground. ADCP moorings in 2007 are shown (blue Xs).
Figure 3. Schematic of surface drift buoy courtesy of Pacific Gyre.
Figure 4. Monthly mean velocities of wind velocities and observed currents for 2007. Winds velocities are (top) at Hatteras (a), Manteo (b) and Kill Devil Hills (c). Monthly mean velocities (m/s) of observed currents measured with an ADCP during 2007 (bottom) at Ocracoke (a) and Crab Hole (b). Each month is represented by a color: Red = May, Magenta = June, Cyan = July, Blue = August, and Yellow = September. Axes are scaled to fit data; wind velocities are an order of magnitude greater than velocities. Larger arrows within each plot indicate stronger velocities relative to the other arrows. Winds during August were nearly identical to July at Kill Devil Hills, and representative arrows overlap. Currents were not measured at Ocracoke in September; therefore only four arrows are plotted.
Figure 5. Observed (blue) and predicted (red) surface velocities from the 3D ADCIRC model at the Ocracoke oyster sanctuary and winds measured at Cape Hatteras (black) in the U- and V-directions. Wind velocities were an order of magnitude greater than observed and predicted currents, therefore, to fit within the same plot only 20% of the magnitude of the wind velocity is shown.
Figure 6. Observed (blue) and predicted (red) surface velocities from the 3D ADCIRC model at the Crab Hole oyster sanctuary and winds measured at Cape Hatteras (black) in the U- and V-directions. Wind velocities were an order of magnitude greater than observed and predicted currents, therefore, to fit within the same plot only 20% of the magnitude of the wind velocity is shown.
Figure 7. Observed velocities measured with an ADCP at Ocracoke (blue at top three layers and bottom layer, multi-color: cyan to magenta for middle velocities near-top to near-bottom) and velocities predicted with ADCIRC (red) for a 2-week period during June 24-July 8, 2007. A 2-week time-series was chosen to illustrate depth-specific velocities over a short enough time-scale so as not to compress the data in a manner that prevented visual interpretation of the various depth velocities.
Figure 8. Observed velocities measured with an ADCP at Crab Hole (blue at top three layers and bottom layer, multi-color: cyan to magenta for middle velocities near-top to near-bottom) and velocities predicted with ADCIRC (red) for a 2-week period during May 31-June 14, 2007. A 2-week time-series was chosen to illustrate depth-specific velocities over a short enough time-scale so as not to compress the data in a manner that prevented visual interpretation of the various depth velocities.
Figure 9. Cross-correlations (Y-axis) between observed (ADCP) versus predicted (ADCIRC) velocities over time. Lag times are shown in hours (X-axis). Correlations for U-velocities are on the left and V-velocities are on the right.
Figure 10. Cross-correlation coefficients between depth specific observed and predicted depth-specific current velocities. U- velocities (squares) and V-velocities (triangles), with upper and lower limits (plus symbols) for Ocracoke (top) and Crab Hole (bottom).
Figure 11. Summary of 25 drifter tracks (colored) replicated by PTM (black). Deployment details are listed in Table 3. Drifter track colors correspond to deployment duration: Day 1 (blue), Day 2 (cyan) Day 3 (yellow), and Day 4 (magenta). Highest cross-correlations among observed and predicted paths occur when plots of tracks overlap.
Figure 12. Potential larval settlement areas in Pamlico Sound for virtual oyster larvae released from oyster sanctuaries. The following indicate oyster broodstock sanctuaries: Croatan Sound (a), Crab Hole (b), Gibbs Shoal (c), West Bluff (d), Deep Bay (e), Middle Bay (f), Neuse River (g), West Bay (h), Ocracoke (i), and Clam Shoals/ Hatteras (j). Lines represent the final 7 days of particle tracks where oysters are assumed competent to settle. Release sanctuaries are denoted with a black star.
Figure 13. Surface flow field output from ADCIRC model run on June 5, 2007. Box 1 highlights surface current along western shore. Box 2 highlights convergence zone between Ocracoke and West Bluff Oyster Sanctuaries (Fig.1). Winds were southwesterly at 7 m/s. Dots indicate zero velocities.
Figure 14. Surface flow field output from ADCIRC model on June 10, 2007. Box highlights convergence zone between Ocracoke and West Bluff Oyster Sanctuaries. Winds (right red arrow) were northeasterly at 4 m/s. Bottom velocities observed by ADCP at Ocracoke (OK, left red arrow) were northwestward at 0.17 m/s and at Crab Hole (CH, upper red arrow) were southward at 0.1 m/s. Blue dots indicate zero velocities.
Figure 15. Surface flow field output from ADCIRC model demonstrating the “Albemarle Flush” on June 2, 2007 06:00 (a); June 4, 2007 00:00 (b); June 4, 2007 01:00 (c); and June 4, 2007 15:00 (d). Winds were southerly 5-7 m/s (a-c) and veered to west-southwesterly at 5 m/s (d). Notice the surface currents were northeastward from Pamlico Sound into Albemarle Sound for several days, but within hours of a wind shift the flow reversed. Plots b and c are separated by only an hour.
APPENDIX

Appendix A. Fort 15 Parameter file for final 3D ADCIRC model run.

```
pamlico grid - Amy run   ! 30 CHARACTER ALPHANUM RUN DESCRIPTION
ADCIRC v48.36           ! 20 CHARACTER ALPHANUMERIC RUN IDENTIFICATION
1                      ! NFOVER - NONFATAL ERROR OVERRIDE OPTION
0                      ! NABOUT - ABREVIATED OUTPUT OPTION PARAMETER
1                      ! NSCREEN - UNIT 6 OUTPUT OPTION PARAMETER
0                      ! IHOT - HOT START PARAMETER
2                      ! ICS - COORDINATE SYSTEM SELECTION PARAMETER
1                      ! IM - MODEL TYPE (0 INDICATES STANDARD DEPTH INTEGRATED MODEL)
2                      ! NOLIBF - BOTTOM FRICTION TERM SELECTION PARAMETER
0                      ! NOLIFA - FINITE AMPLITUDE TERM SELECTION PARAMETER
0                      ! NOLICA - SPATIAL DERIVATIVE PORTION OF CONV. TERM SELECTION PARAM.
0                      ! NOLICAT - TIME DERIVATIVE PORTION OF CONV. TERM SELECTION PARAM.
0                      ! NWP - VARIABLE BOTTOM FRICTION AND LATERAL VISCOSITY OPTION
1                      ! NCOR - VARIABLE CORIOLIS IN SPACE OPTION PARAMETER
0                      ! NTIP - TIDAL POTENTIAL OPTION PARAMETER
3                      ! NWS - WIND STRESS AND BAROMETRIC PRESSURE OPTION PARAMETER
1                      ! NRAMP - RAMP FUNCTION OPTION
9.81                   ! G - ACCELERATION DUE TO GRAVITY - DETERMINES UNITS
-5.0                   ! TAU0 - WEIGHTING FACTOR IN GWCE
0.005 0.2              ! DT - TIME STEP (IN SECONDS) – REDUCED TO ELLIVIATE VELOCITY ERRORS
0.0                    ! STATIM - STARTING TIME (IN DAYS)
0.0                    ! REFTIM - REFERENCE TIME (IN DAYS)
07 05 01 00 00 00.      ! IREFYR,IREFMO,IREFDAY,IREFHR,REFSEC
2.2 36.4 -77.25 2.0 2.0 3600 !
NWLAT,NWLN, WLATMAX, WLONMIN, WLONINC, WTIMINC
138.0                  ! RNDAY - TOTAL LENGTH OF SIMULATION IN DAYS (138 would be full run)
2.0                    ! DRAMP - DURATION OF RAMP FUNCTION (IN DAYS)
0.35 0.30 0.35        ! TIME WEIGHTING FACTORS FOR THE GWCE EQUATION
0.5                    ! H0 - MINIMUM CUTOFF DEPTH
-76.0 33.0            ! SLAM0,SFEA0 - CENTER OF CPP PROJECTION IN DEGREES LONG/LAT
0.0020 1.0 10. 0.3333  ! FFACOR - BOTTOM FRICTION COEFFICIENT
2.0                   ! ESL - LATERAL EDDY VISCOSITY COEFFICIENT; IGNORED IF NWP =1
0.0                   ! CORI - CORIOLIS PARAMETER - IGNORED IF NCOR = 1
0                      ! NUMBER OF TIDAL POTENTIAL CONSTITUENTS BEING FORCED
0                      ! NBFR - TOTAL NUMBER OF FORCING FREQUENCIES ON OPEN BOUNDARIES
100.0                 ! ANGINN : INNER ANGLE THRESHOLD
1 0.0 138. 20        ! NOUTE,TOUTSE,TOUTFE,NSPOOLE:ELEV STATION OUTPUT INFO (UNIT  61)
2                      ! TOTAL NUMBER OF ELEVATION RECORDING STATIONS
-75.993933 35.177416  ! Ocracoke
-75.675083 35.72525   ! Crab Hole
```
Appendix A continued.

1 0.0 138. 90 ! NOUTV,TOUTSV,TOUTFV,NSPOOLV: VEL STATION OUTPUT INFO (UNIT  62)
2 ! TOTAL NUMBER OF VELOCITY RECORDING STATIONS
-75.993933 35.177416 !Ocracoke
-75.616666 35.72525 !Crab Hole
1 0.0 138. 90 ! NOUTM,TOUTSM,TOUTFM,NSPOOLM: MET STATION OUTPUT INFO (UNIT  71)
3 ! TOTAL NUMBER OF VELOCITY RECORDING STATIONS
-75.993933 35.177416 !Ocracoke
-75.616666 35.72525 !Crab Hole
-75.739 35.2333 !Hatteras - wind station
1 0.0 138. 360 ! NOUTGE,TOUTSGE,TOUTFGE,NSPOOLGE : GLOBAL ELEV OUTPUT (UNIT  63)
0 0.0 138. 120 ! NOUTGV,TOUTSGV,TOUTFGV,NSPOOLGV : GLOBAL VEL OUTPUT (UNIT  64)
0 0.0 138. 120 ! NOUTGW,TOUTSGW,TOUTFGW,NSPOOLGW : GLOBAL WIND OUTPUT (UNIT  74)
0 ! NHARFR - # FREQS IN HAR ANAL
0.0 0.0 40 0.000000 ! THAS, THAF, NHAINC, FMV
0 0 0 ! NHAZE, NHASE, NHAGE, NHAGV
0 1440 ! NHSTAR, NHINC
1 0 1e-5 25 ! ITITER, ISLDIA, CONVCR, ITMAX
0 ! IDEN: 0 = barotropic run, 1 = baroclinic run
2 0.0025 ! ISLIP, KP: slip code and slip coefficient
0.0334 0.001 ! Z0S, Z0B: free surface and bottom roughness
0.5 0.5 0.5 ! ALP1, ALP2, ALP3: time stepping coefficients (alpha1,3)
1 7 ! IGCF, NFEN: f.e. grid code, # nodes in f.e. grid
50 0.000001 0.0001 ! IEVC, EVMIN, EVCON: e.v. code, evmin, evcon coefficient
0.5 0.5 ! Theta1 and Theta2 for MY 2.5 closure
0 2 5 49 ! I3DSD, ... density station output parameters
0 1 0 138 90 ! I3DSV, ... velocity station output parameters
2
-75.993933 35.177416 ! Ocracoke
-75.675083 35.72525 ! Crab Hole
0 2 5 60 ! I3DST, ... turbulence station output parameters
0
0 2 5 49 ! I3DGD, ... density global output parameters
0 0 75 20 ! I3DGV, ... velocity global output parameters
0 2 5 49 ! I3DGT, ... turbulence global output parameters