



# Estuarine circulation and predicted oyster larval dispersal among a network of reserves

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## ABSTRACT

A critical component to understanding connectivity of isolated populations of marine organisms (i.e., metapopulations) is quantifying hydrodynamic paths of dispersal, and variation in the strength of these hydrodynamic connections. We replicated 3-dimensional wind-driven circulation patterns in Pamlico Sound (PS), North Carolina, USA using a numerical hydrodynamic model (ADCIRC, ADvanced CIRCulation) in conjunction with a particle-tracking model (PTM) to predict larval dispersal of the eastern oyster (*Crassostrea virginica*) and estimate connectivity among a network of ten no-take oyster broodstock reserves in PS to inform restoration efforts. ADCIRC was forced with wind observations, which were predominately southwesterly during May–November 2007 when oyster larvae were dispersing in PS. Acoustic Doppler Current Profilers and surface drifters were used to validate ADCIRC-predicted current velocities and PTM-predicted larval dispersal, respectively. ADCIRC reliably predicted current velocities at different locations in PS, especially currents near-surface ( $R = 0.6$ , lags  $< 2$  h). The PTM accurately predicted ( $R > 0.5$ ) the total and net distance transported by drifters, which ranged from 1 to 63 km and 0.3–42 km, respectively over  $\leq 7$  days. Potential oyster larval connectivity was not uniform among broodstock reserves in PS. Of the 100 possible connections, 24 were present. Eight of the 10 reserves provided  $\geq$  one inter-reserve connection, with 4 being the most. Self-recruitment occurred at all but one reserve. Spatial variation in the degree of potential oyster larval connectivity in PS, combined with evidence for spatiotemporal dynamics of oyster populations, provides strong evidence for an oyster metapopulation and possibly source-sink dynamics within the network of no-take reserves.

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## 1. Introduction

A fundamental issue concerning recruitment dynamics of marine organisms and marine conservation biology involves identifying the paths of dispersal connecting isolated populations, and how spatiotemporal variation in the intensity of dispersal along these paths influences population connectivity, the successful exchange of individuals among isolated populations, and, ultimately, population dynamics (Cowen et al., 2007; Cowen and Sponaugle, 2009 and references therein). Most benthic marine organisms have limited mobility as adults such that dispersal, the transport and spread of larvae from natal origin over the pelagic larval duration, connects geographically isolated populations that

often vary in their demographic rates, forming a metapopulation (Levins, 1969; Hanski, 1998). Due to asymmetrical population connectivity and variation in demographic rates, subpopulations within a metapopulation can be classified as sources, which contribute more births than deaths to the metapopulation, or sinks if the opposite is true (Figueira and Crowder, 2006; Lipcius et al., 2008).

Our understanding of marine population connectivity is generally considered rudimentary (Cowen et al., 2006; Steneck, 2006; Becker et al., 2007). Cowen and Sponaugle (2009) identified several challenges to improving our understanding of connectivity, three of which we address herein: (1) observations – determination of spatial scales of connectivity, (2) explanations – mechanisms underlying dispersal and connectivity, and (3) applications – issues of conservation and resource management. Several methods, including hydrodynamic modeling, geochemical and genetic markers, and drifters have been used to estimate dispersal and connectivity (Cowen et al., 2006; Becker et al., 2007; Hare and Walsh, 2007; Cudney-Bueno et al., 2009; Fodrie et al., 2011). Each

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method, however, has limitations. For instance, bio-physical models need rigorous empirical validation using geochemical markers or drifters, each of which are potentially constrained by spatial resolution and restricted dispersion compared to small larvae whose dispersal can be greatly influenced by diffusion (North et al., 2008; Cowen and Sponaugle, 2009). Consequently, integration of multiple methods and rigorous validation are required to enhance our ability to successfully predict larval dispersal and connectivity. In this study, we utilized a hydrodynamic modeling approach in conjunction with a particle-tracking model, each validated with Acoustic Doppler Current Profilers and surface drifters, respectively, to estimate dispersal patterns and potential larval connectivity of eastern oysters (*Crassostrea virginica*) within an estuarine network of no-take oyster broodstock reserves.

In marine systems, the protection, restoration, and management of species, including oysters, increasingly involves the establishment of no-take reserves closed to harvest (Briers, 2002; Spalding et al., 2008; Powers et al., 2009; Schulte et al., 2009). Reserve networks have been promoted as a viable solution because the boundaries of a single reserve are often much smaller than the protected species' geographic range and larval dispersal distance (Roberts et al., 2003). For isolated reserves to function as a network, inter-reserve connectivity is required and, thus, knowledge of larval dispersal and connectivity within the network is vital for informing management and restoration efforts (Gaines et al., 2010).

### 1.1. Study species

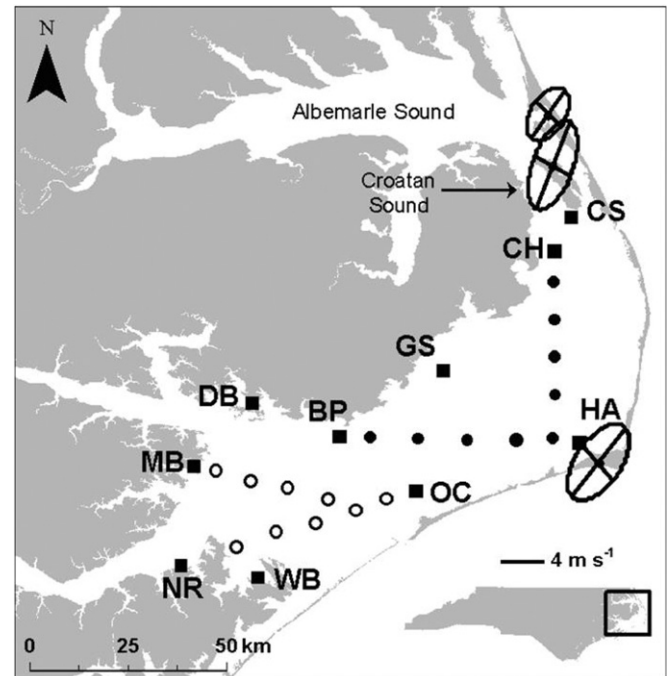
The eastern oyster is an economically and ecologically important species that inhabits estuarine and coastal waters from the Gulf of St. Lawrence to the Gulf of Mexico and West Indies (Stanley and Sellers, 1986; Beck et al., 2011 and references therein). Oysters are protandrous hermaphrodites, initially maturing as males several months post-settlement, and transitioning to functional females at ~40 mm shell height (Burkenroad, 1931; Mroch, 2009). In Pamlico Sound (PS), North Carolina, USA, oyster spawning occurs from May to October with fecundity and settlement peaks during May (Mroch, 2009) and June (Eggleston and Puckett, unpublished data), respectively. A smaller, secondary settlement peak typically occurs in July/August. Gametes are freely spawned into the water column where fertilized eggs develop into dispersing larvae with a pelagic duration of ~14–25 days depending on water temperatures, salinity, turbidity, oxygen content and available nutrients (Deksheniaks et al., 1993, 1996).

The overall objectives of this study were to (1) assess the efficacy of 2-dimensional (2D) versus 3-dimensional (3D) ADCIRC (ADVanced CIRCulation) hydrodynamic models in predicting current velocities in PS by validating predictions with Acoustic Doppler Current Profilers, (2) couple a Particle-Tracking Model (PTM) to ADCIRC to predict oyster larval dispersal under observed winds, and validate predicted dispersal paths using surface drifters, and (3) use the information from objectives (1) and (2) to estimate potential oyster larval settlement areas and population connectivity among oyster broodstock reserves in PS.

## 2. Methods

### 2.1. Study system

Pamlico Sound, the largest water body of the Croatan-Albemarle-Pamlico-Estuarine System (CAPES), is located in the eastern coastal region of North Carolina, USA and sheltered from the Atlantic Ocean by a grouping of barrier islands known as the 'Outer Banks' (Fig. 1). Connections to the Atlantic Ocean are limited



**Fig. 1.** Map of the Croatan-Albemarle-Pamlico-Estuarine System (CAPES). Location of oyster reserves in Pamlico Sound are depicted by closed squares (not to scale). Acoustic Doppler Current Profilers were deployed at CH and OC reserves. Circles represent drifter release locations for the northern (closed) and southern (open) basins of Pamlico Sound. Principal axes of variance of hourly wind velocities from May to November 2007 are shown for meteorological stations listed north to south at Kill Devil Hills (KFFA), Manteo (KMQL), and Hatteras (KHSE). CS, Croatan Sound; CH, Crab Hole; GS, Gibbs Shoal; BP, Bluff Point; DB, Deep Bay; MB, Middle Bay; NR, Neuse River; WB, West Bay; OC, Ocracoke; HA, Hatteras. Scale bars depicting wind velocity and distance as well as map of North Carolina are inset for reference.

to four narrow inlets (Lin et al., 2007). 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 PS (this study). Average depth in PS is 4–5 m with the deepest basin only 7–8 m (Pietrafesa and Janowitz, 1988). Wind forcing is highly variable, changing velocity at hourly to daily intervals, but does sustain regular seasonal patterns with winds predominately southwesterly in the late-spring/summer and northeasterly in late-summer/fall (Xie and Eggleston, 1999; Eggleston et al., 2010). Since oyster larval dispersal is primarily driven by horizontal currents, knowledge of these currents is important to explaining the mechanisms underlying dispersal and connectivity.

### 2.2. Numerical hydrodynamic model

We used both the 2D and 3D ADCIRC, a non-linear finite-element hydrodynamic model (Luettich et al., 1992; Reynolds-Fleming, and Luettich, 2004; Reyns et al., 2006, 2007), in conjunction with a particle-tracking model to predict currents and simulate oyster larval dispersal in PS. ADCIRC solves the governing equations of motion which are formulated using the traditional hydrostatic pressure and Boussinesq approximations. Momentum equations in the 2D and 3D form are used to obtain velocity solutions (Luettich and Westerink, 2004). ADCIRC has produced vector fields that are in good agreement with observed currents in the Neuse River Estuary located in the southwestern portion of PS (Luettich et al., 2002), as well as in the northern basin of PS (Reyns et al., 2006, 2007). To further validate ADCIRC, we collected Eulerian and Lagrangian observations of current velocities throughout PS.

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