

ABSTRACT

Title of Document: THE EXCHANGE OF EASTERN OYSTER (*CRASSOSTREA VIRGINICA*) LARVAE BETWEEN SUBPOPULATIONS IN THE CHOPTANK AND LITTLE CHOPTANK RIVERS: MODEL SIMULATIONS, THE INFLUENCE OF SALINITY, AND IMPLICATIONS FOR RESTORATION

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With limited funds available for restoration and management, information is needed that would enhance the objectives of restoration of the eastern oyster (*Crassostrea virginica*) in Chesapeake Bay. One challenge with choosing locations for *C. virginica* restoration is lack of information regarding larval exchange, which helps determine whether the reefs will be self-sustaining and/or enhance nearby populations. The goal of this research was to estimate the larval exchange between subpopulations within the Choptank and Little Choptank Rivers (Maryland, USA) and to determine the influence of low salinity on these patterns in connectivity. To this end, the Lagrangian TRANSport model (LTRANS) was coupled with a Regional Ocean Modeling System hydrodynamic model of Choptank River (ChopROMS) and applied to predict the exchange of simulated *C. virginica* larvae between 596 reefs within the system. Model results indicated that there is a high degree of connectivity among the subpopulations in this system. Most simulated larvae were transported down river (rather than upriver). Reefs in upper portions of the Choptank River and its tributaries

were in a position to produce the most larvae which encountered suitable habitat, whereas those in the lower Choptank River received the most simulated larvae. In addition, salinity-induced mortality of larvae substantially decreased transport success and self-recruitment, and changed patterns in reef-specific transport success throughout the estuary. Model results provide region-specific information that could be used to support restoration efforts in areas with low salinities like the Choptank River.

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SALINITY, AND IMPLICATIONS FOR RESTORATION

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Chapter 1: Modelling oyster (*Crassostrea virginica*) larval transport

Introduction

Crassostrea virginica (eastern oyster) populations are a critical component to a healthy Chesapeake Bay ecosystem: they improve water clarity by filtering sediment and phytoplankton (Newell 2004), they provide habitat for finfish and invertebrates (Coen et al. 2007), and historically they provided a valuable commercial fishery (Rothschild et al. 1994; Stevenson 1892). Current abundances of *C. virginica* in Chesapeake Bay are less than 1% of unfished levels (Wilberg et al. 2011) and *C. virginica* restoration efforts are being undertaken by private, state and federal agencies. The eggs and larvae of organisms with pelagic larval durations similar to *C. virginica* can be transported long distances, creating interconnectedness among populations (Roberts 1997). Restoration efforts could be enhanced by increasing understanding of the planktonic processes present in and around restoration areas, allowing for design of connected networks of populations that actively exchange individuals (Fogarty and Botsford 2007). The goal of this research is to estimate larval exchange between *C. virginica* reefs within the Choptank and Little Choptank Rivers (Maryland, USA) and to determine if low salinities, which cause larval mortality, could influence these patterns in connectivity.

Connectivity as defined by Cowen et al. (2007) is the exchange of individuals among geographically separated subpopulations. The processes involved in these exchanges are both biological and physical. One of these bio-physical processes is larval transport, which is defined as the horizontal translocation of a larva between two points (Pineda et al. 2007). The magnitude and direction of this transport is

influenced by vertical migration by larvae; the resulting exposure to variable current velocities alters the horizontal distribution of a larva (Pineda et al. 2007). Differences in larval vertical migration have been shown to significantly influence dispersal distance, self-recruitment rates, source-sink mechanisms, and patterns in connectivity (Cowen 2006; North et al. 2008). Exchange of individuals among marine populations requires dispersal from spawning sites to settlement sites; this dispersal is influenced by many factors including larval transport, suitable habitat, spawning time and location, fertilization success, predation and survival to settlement (Pineda et al. 2007). Together, all of these processes influence connectivity between populations (Pineda et al. 2007). If strong connectivity among separate regions is shown to exist, then processes taking place in one region will have direct impacts on the health of populations in another region (Roberts 1997). Understanding larval transport, larval dispersal, and ultimately connectivity will allow for better understanding and management of marine resources (Roberts 1997).

Larval connectivity among marine populations has been studied using a variety of techniques. For example, elemental fingerprinting has been used to identify differing connectivity and retention patterns of mussels *Mytilus californianus* and *Mytilus galaprovencialis* along the California coast (Becker et al. 2007) and with the *Pachygrapsus crassipes* (striped shore crab) in San Diego Bay (Di Bacco and Levin 2000). Also, genetic information has been used to determine connectivity (Benzie et al. 2003; Pujolar et al. 2013). For example, genetic connectivity was derived for the finfish *Diplodus sargus sargus* across vast distances inside and out of marine protected areas (MPAs) in the south Adriatic Sea (Pujolar et al. 2013). Another

strategy to discern connectivity is through the use of a larval transport model (Cowen et al. 2006; North et al. 2008; Hoffman 2012). For example, connectivity for *Pinctada margaritifera* (black-lip pearl oyster) among various regions in the Ahe atoll lagoon of French Polynesia was estimated with a larval transport model (Thomas et al. 2012). North et al. (2008) applied a larval transport modeling approach to investigate larval exchanges of *C. virginica* between major tributaries of this Chesapeake Bay. Yet, the hydrodynamic model used in that study did not have sufficient resolution to include many important subtributaries for *C. virginica* production within the model domain. This research focuses in detail and in high resolution on two river systems within Chesapeake Bay, the Choptank and Little Choptank Rivers, in order to simulate hydrodynamics and larvae transport at the scale at which restoration is conducted in these systems.

The Choptank and Little Choptank Rivers are tributaries on the eastern shore of Chesapeake Bay (Fig. 1). Chesapeake Bay, a partially mixed estuary, has a classic two layer density driven circulation pattern (Pritchard 1967). Moderate stratification in Chesapeake Bay is the result of moderate river outflow and moderate mixing (Valle-Levinson 2010). In the 114-km-long Choptank River (USGS 2015), salt penetration varies seasonally, with an average penetration of 70 km. Salt originates on the continental shelf and is moved up-estuary by two-layer estuarine circulation (Malone et al. 2003). Predominant circulation patterns in the Choptank vary from a well-mixed entrance channel, to a stratified, two-layer density driven middle portion, to a well-mixed freshwater-driven zone at its upper reaches (Malone et al. 2003). The Little Choptank is a small sub-estuary to Chesapeake Bay (~18 km long), with

circulation primarily driven by classic two-layer estuarine and wind driven patterns (pers. comm., William C. Boicourt, March 30, 2015).

C. virginica is meroplanktonic; it spends the larval period of its life in the water column. During this period, its transport is influenced by many physical forces including currents, tides, and mixing (Kennedy 1996). At the end of the 2-3 week dispersal period, *C. virginica* pediveligers (late stage larvae) begin to settle (i.e., find suitable substrate and affix themselves to it) (Kennedy 1996). The success of settlement is influenced by the biological requirement of *C. virginica* larvae to locate suitable hard habitat, preferably living *C. virginica* as demonstrated by Tamburri et al. (1996) through the detection of chemical cues given off by conspecifics. Once settled, *C. virginica* remain fixed in this settlement location for the duration of their lives (Stanley et al. 1986). In regions with low salinities (<10), outbreaks of the diseases due to *Haplosporidium nelsoni* (MSX) and *Perkinsus marinus* (Dermo) that affect juvenile and adult oyster are naturally depressed (Ewart 1993).

While in the plankton, the development success of *C. virginica* larvae is dependent on many biotic and abiotic factors including temperature, food availability, and salinity (Kennedy 1996). Salinities of 5.0 have been shown to induce high or complete mortality of larvae within 48 hours (Davis 1958). Successful development from the egg to pediveliger stage has been found between a wide range of salinities (7.5 – 35.0), with salinity tolerances increasing as larvae develop, differing between broodstock from different systems, and varying by the salinity in which adults develop gonads (Davis 1958; Davis and Calabrese 1964; Lough 1975). For example, development of larvae to ~2 d old from adult *C. virginica* from Long Island Sound

conditioned at salinities of 26.0 – 27.0 was unsuccessful at salinities ≤ 12.5 (Davis 1958; Davis and Calabrese 1964), whereas development of larvae from adult *C. virginica* from the upper Chesapeake Bay conditioned at salinities of ~ 8.5 developed successfully to straight-hinge stage in salinities as low as 7.5 (Davis 1958; Davis and Calabrese 1964). In the Choptank River, the Horn Point Oyster Hatchery (Fig. 1) operators routinely add salt to rearing tanks when ambient conditions drop below ~ 9.5 (pers. comm., Donald Meritt, March 11, 2015). When salinities are near or below the lower range of tolerances such as in the upper reaches of estuaries like the Choptank River, larval survival could be limited and could influence larval transport and subsequent connectivity.

Understanding the influence of salinity on connectivity between subpopulations in the Choptank would support restoration efforts. *C. virginica* restoration efforts are currently underway in the Choptank and Little Choptank Rivers. Harris Creek and the Tred Avon River (tributaries of the Choptank River) and the Little Choptank River (Fig. 1) have been designated sanctuaries and identified as targeted restoration areas, undergoing restoration efforts initiated in 2011. Current objectives are to restore 377 acres of reefs in Harris Creek, 400 acres of reefs in the Little Choptank, and 193 acres of reefs in the Tred Avon, with a combined cost of over 70 million dollars (MIORW 2013). Larval transport models were used as an aid to site selection for restoration efforts within Harris Creek (North et al. 2012), and are being applied to support site selection in the Tred Avon and Little Choptank Rivers (North and Spires in prep). Yet, the exchange of larvae between other regions in the Choptank that are important for harvest and restoration (e.g., Broad Creek, upper

Choptank) is not known, nor has the influence of salinity on connectivity patterns been assessed. Increased understanding of larval dispersal between subpopulations will help maximize restoration efforts by providing information on the predominant larval transport patterns present in and around restoration areas. This knowledge includes estimating larval supply from sanctuaries to areas open to harvest, the extent of retention of larvae within a sanctuary (i.e., self-recruitment) which would facilitate population enhancement, and conversely, whether a restoration area would not be a consistent producer of larvae because of salinity or transport patterns.

The goals of this project were to 1) estimate larval exchange among, and retention within, subtributaries and major oceanographic regions within the Choptank and Little Choptank Rivers, and 2) determine whether, and where, salinity-induced mortality could influence the predicted connectivity patterns. Three hypotheses guided this research: 1) a greater number of simulated larvae would be transported down river than upriver because of the net down-estuary flow of water at the surface and the near-surface orientation of larvae in early developmental stages, 2) reefs in the middle and upper Choptank would release the most larvae that successfully encountered suitable habitat due to availability of settlement habitat down-estuary, and 3) salinity-induced mortality of larvae will decrease transport success and influence connectivity patterns in the upper Choptank region. Although focused on the Choptank and Little Choptank Rivers, the techniques and findings are applicable to the many other systems where *C virginica* are found in low salinities (e.g., Louisiana, Mississippi and Florida)(Barnes et al. 2007; Butler 1949).

Methods

To estimate the connectivity of *C. virginica* populations within the Choptank and Little Choptank Rivers, a larval transport model was applied to simulate the trajectories of larvae between reefs, the results of which were summarized in a connectivity matrix for major regions within the model domain. Observations of salinity combined with freshwater discharge were used to estimate the frequency of occurrence of flows that resulted in low salinities in the Choptank River. The connectivity matrix was then adjusted with this information to estimate the influence of salinity-dependent larval mortality on larval exchange between regions. Results were used to develop maps highlighting regions with high probabilities of larval survival to guide restoration.

Estimating larval exchange. The larval transport model was applied to estimate larval exchange and was comprised of the LagrangianTRANSPORT model (LTRANS v.2b) (North et al. 2012; North et al. 2008; North 2014) coupled with the hydrodynamic model ChopROMS (Fig. 1). ChopROMS is a Regional Ocean Modeling System (ROMS) hydrodynamic model which uses boundary conditions from ChesROMS, a larger Chesapeake Bay ROMS model (North et al. 2012). Both ChopROMS and ChesROMS were forced with observed freshwater flow, wind, and air temperature from June to September, 2010. Streamflow into the Chesapeake Bay during 2010 was average, as determined by USGS (2015), nor were there major weather events in the Choptank region as recorded by NOAA (2015a) during the larval transport season (June –August). An extensive set of comparisons of salinity and temperature predictions from ChopROMS with measurements from 20 cruises on

the Choptank River indicates that the model simulated salinity quite well but had a slight bias predicting temperature (~1-1.5 degrees high), with most of the bias occurring in the up-river portions of the model domain (North et al. 2012). See Appendix A for more information about ChesROMS and validation plots.

LTRANS was a particle tracking model that uses stored predictions from ROMS hydrodynamic models to simulate the transport of larvae with *C. virginica* larvae-like swimming behaviors (North et al. 2008). The LTRANS model domain adopted the ChesROMS model domain, with open boundaries in the mainstem Chesapeake Bay (Fig.1). *C. virginica* larvae-like behaviors included vertical migration (Newell et al. 2005), age-specific swimming speeds (Mann and Rainer 1990, Kennedy 1996, Newell et al. 2005, J. L. Manuel et al. unpubl.), reactions to haloclines (Hidu and Haskin 1978; Newell et al. 2005), and an overall downward migration as the simulated larvae age (Andrews 1983; Baker 2003), and replicated methods and rationale used and described in North et al. (2006, 2008). Stages that were simulated were 1) fertilized gametes and early trochophores (0 to 0.5 d old), 2) veliger (0.5 to ~13.5 d old), and 3) pediveliger (~13.5 to ~21 d old) stages, with the durations of the veliger and pediveliger stages varying between individuals (see North et al. 2006, 2008 for details). Particles age 0 to 0.5 d old were assumed to be fertilized gametes and early trochophores that floated upward. From day 0.5 to the end of the veliger stage, swimming speeds varied for each individual in each time step, and were drawn from a normal random distribution which had a maximum swimming speed that increased linearly from 0.5 to 3 mm s⁻¹ as the age of the particle increased. Once larvae developed to the pediveliger stage their swimming speed was set to 3.0 mm s⁻¹

(North et al. 2008). The vertical direction of movement for simulated larvae was controlled by the stage of the larvae and the presence of haloclines. During the veliger stage, simulated larvae swam down unless they passed through a halocline which was defined as a vertical gradient in salinity $\geq 1.0 \text{ m}^{-1}$. In the presence of such a halocline, a veliger stage larva was cued to swim up during that time step. Pediveliger-stage larvae were directed to swim down until they were within 1 m of the bottom. Once inside 1 m of the bottom, their motion was randomly directed. Simulated pediveliger larvae maintained these behaviors until a simulated oyster reef was detected or they were deemed no longer capable to settle. Animations that visualize how these parameterizations of stage-specific behaviors change the vertical distribution of simulated larvae over time can be found here:

http://northweb.hpl.umces.edu/videos_animations/Oyster_Larvae_Animations.html

LTRANS was parameterized with the best available information on oyster habitat within the model domain. Most habitat polygons within the Choptank and Little Choptank systems were based on recent bottom mapping efforts (2010 – 2013) which involved video, acoustic surveys, and validation with sediment grabs and patent tong surveys (MIORW 2013, North and Spires *in prep*). The habitat polygons were areas that were deemed suitable for oyster restoration, and included “shell”, “shell and sand”, and “shell and mud” categories from bottom mapping efforts. In the mainstem Bay where recent bottom habitat surveys had not been conducted, the “cultch” layer data from the Maryland Bay Bottom Survey (MBBS) in the 1980s was used, after it had been reduced to 29.2% of its original size (Greenhawk 2005) to

account for habitat loss (Smith et al. 2005). Appendix B contains more details about the source of data used to create the habitat polygons used in the LTRANS.

Larval exchange was assessed between seven regions: Harris Creek, Broad Creek, Tred Avon River, Little Choptank River, and three regions of the mainstem Choptank River: the upper, middle, and lower (Fig. 1). These seven regions of interest were determined by taking into account geographical locations and prevailing circulation patterns. For the four sub-estuaries (Harris Creek, Tred Avon, Broad Creek and the Little Choptank), a line was projected between the points of land at each tributary's mouth to define the region. The boundaries of the upper, middle, and lower Choptank are approximately 16 and 27 km upriver from the river's mouth, respectively. These locations were selected at transition points in the predominate circulation patterns present in the Choptank River which were identified by Malone et al. (2003). In the upper Choptank (upriver of line A in Fig. 1), the river is predominantly well mixed with strong riverine influences driving circulation. Seaward of this boundary, in the middle Choptank region, the river becomes more stratified and two layer estuarine circulation patterns are present (between line A and B in Fig. 1). In the lower Choptank (between line B and C in Fig. 1), the shallower depths at the entrance sill induces vertical mixing which reduces stratification in this region (Malone et al. 2003). Any habitat polygon which was intersected by a line demarcating a region was assigned to the region which included greater than 50% of the habitat polygon area.

The timing of releases of simulated larvae was based on observed water temperatures in the Choptank River and the lower mass spawning temperature of *C.*

virginica, the water temperature which stimulates mass spawning of *C. virginica*. Because the lower mass spawning temperature of *C. virginica* in the Choptank River is not available, it was estimated to occur at 25 °C, coinciding with mass spawning events observed in Eastern Bay, a nearby tributary of Chesapeake Bay (Shumway 1996). Using observations of bottom temperatures in the Choptank River from Chesapeake Bay Program (CBP) monitoring stations, North et al. (2012) determined that water temperatures reached 25° C on June 18, 2010. This date was used as the initial release date for the simulations herein. Simulated larvae were released in five batches, the first starting on June 18, 2010, with subsequent releases on June 24, June 30, July 25, and July 31, 2010. This timing was the same as simulated larvae release dates conducted by North et al. (2012) and was designed to simulate observed peaks in settlement of *C. virginica* larvae in Chesapeake Bay (Kennedy 1996).

Simulated larvae were released from starting locations that were randomly assigned within habitat polygons in numbers proportional to the area of the habitat (9,417 simulated larvae km²). This method ensures random distribution and proportional representation of simulated larvae among all regions and is consistent with methods used in previous larval transport studies in this region (North et al. 2012; North and Spires *in prep*). The total number of simulated larvae released from each region for all five model runs were: 406,875 in the Tred Avon River, 606,645 in the Little Choptank, 527,575 in Harris Creek, 428,640 in Broad Creek, 475,520 in the upper Choptank, 557,050 in the middle Choptank, and 521,190 in the lower Choptank. A total of 3,523,495 simulated larvae were released in all simulations.

Once released, simulated larvae were competent to settle (could settle on habitat polygons) after 13 days on average, and remained competent until 21 days old on average, after which the simulated larvae were considered “dead” if suitable habitat was not encountered. These time frames were averages because each larvae was assigned a different duration for veliger and pediveliger stages using a random number generator to simulate individual variation in developmental times among *C. virginica* larvae (North et al. 2006; North et al. 2008). The change in location of each simulated larvae was predicted every 75 seconds from dispersal to settlement, “death”, or intersection with open ocean boundaries, at which point the simulated larva stopped moving. Simulated larvae settled if they encountered suitable habitat (i.e., crossed into a habitat polygon) once they became competent to settle (i.e., became pediveligers).

Model output was analyzed to estimate connectivity (i.e., exchange of simulated larvae) among the seven regions and to address the three hypotheses that guided this research. In addition, transport success, self-recruitment, and catching success from each reef were calculated. Transport success was defined as the percentage of simulated larvae that were released from a polygon and settled anywhere in the larval transport model domain. It indicated the ability of a reef or region to contribute individuals that successfully encounter suitable habitat. Self-recruitment was calculated as the percentage of simulated larvae that settled on the same polygon from which they were released and was a metric that revealed the ability of a reef or region to produce larvae that return to their reef of origin, which is important for self-sustaining reefs. Catching success was defined as the percentage of

successfully transported larvae that were released from a region and settled on each habitat polygon. It indicated how well a particular reef was positioned to receive larvae from other locations.

Estimating the occurrence of low salinities. Before being able to estimate the influence of salinity-induced mortality on connectivity in the Choptank and Little Choptank Rivers, the frequency of occurrence of salinities low enough to induce larval mortality was needed. Because no clear salinity threshold for larval mortality was available for the Choptank and Little Choptank Rivers, two salinity thresholds were used: 7.5 (based on Davis 1958) and 10 (based on the fact that 10 is the target salinity for larval cultures at the Horn Point Oyster Hatchery when ambient conditions drop below ~9.5 (pers. comm., Donald Meritt, March 11, 2015). Although Davis and Calabrese (1964) found 100% mortality of Long Island Sound eggs and early-stage larvae at salinities ≤ 12.5 , it is likely that salinities >10 do not result in decreased early-stage survival of larvae in the Choptank region based on Davis (1958) and the routine hatchery practices at Horn Point Laboratory.

To predict the frequency of occurrence of salinities >7.5 and >10 in the Choptank River, regression models were created that related freshwater flow to the average salinity at specific stations throughout the Choptank River during the time period of peak larval transport (June-August). (The Little Choptank was not included in this analysis due to a lack of data.) Salinity measurements were taken from the Bivalve Larvae TRANSPORT (BT) cruises (North 2013), Coastal Intensive Site Network (CISNET) program (Malone et al. 2003), Chesapeake Bay Program monitoring station ET 5.2 (CBP) (CBP 2015), a dataset of temperature and salinity in

the Tred Avon and Broad Creek from Roger Newell (Newell, R., pers. observation) and the Maryland Department of Natural Resources Eyes on the Bay vertical profiler (MDNR) (MDNR 2015) (Table 1, Fig. 1). Example contour maps of average salinities in 2010-12 can be found in Appendix Fig. C1. At each station, the salinity measurements <6 m deep (the deepest depth of oyster restoration activities (MIORW 2013) which were made from June-August were averaged by year and used as the dependent variables in the regression models. The independent variables in the models were freshwater flows observed at USGS gauging stations on the Choptank River (#01491000, Greensboro, MD) and the Susquehanna River (#01578310, Conowingo, MD). These gauging stations are downstream of the largest available watersheds that flow into the Choptank River and upper Chesapeake Bay, respectively. Monthly mean flow ($\text{ft}^3 \text{ s}^{-1}$) from February through August was summed for each year in the flow record at Greensboro (1948-2013) and Conowingo (1968-2013) gauging stations (Appendix Table C1). Summed flow records were paired with the corresponding salinity averages by year (Appendix Table C2) and were used in multiple regression analyses to predict salinity at each station with the following model:

$$\text{salinity at station } x = m_1 \times \text{Cono} + m_2 \times \text{Green} + b \quad \text{Equation 1}$$

Where x is a station in the Choptank River (Fig. 1), m_1 and m_2 are regression coefficients, Cono is the sum of mean monthly flows from February – August at the Conowingo gauging station, Green is the sum of mean monthly flows from February – August at the Greensboro gauging station, and b is the y-intercept. If the Cono or Green variable was not significant in the multiple regression model, it

was dropped from the model and results for the simple linear model were reported. All regression models passed assumptions of the Shapiro-Wilks test for normality and Levene's test for homogeneity of variance.

The regression equations were then used to predict the average salinity from June – August at each station for all years in the flow record using the summed monthly flow rates from February – August (Appendix Table C1) for each year. The percent occurrence of salinities >7.5 and >10.0 at each station was simply the number of years with salinities greater than the threshold salinity divided by the total number of years in the record, multiplied by 100.

Regression equations were not constructed for the upper reaches of Harris Creek, Broad Creek, and the Tred Avon because three or more years of salinity observations were not available. Instead, observations from two years (three cruises in each year) by the Midshore Riverkeeper Conservancy Creekwatchers (MRC 2015) (Table 2) were used to estimate frequency of occurrence of flows that resulted in salinities >7.5 and >10 in these subtributaries. Riverkeeper stations were selected that were close to stations for which there were regression equations. These Riverkeeper stations were located 1.0, 1.0, and 1.3 km from stations 4, 5, and 7 (Fig. 1) in Harris Creek, Broad Creek, and the Tred Avon River, respectively. The difference between salinities at these Riverkeeper stations and salinities at up-river stations were calculated for all cruises and then averaged. The average difference in salinity (S_{diff}) was used to adjust the regression equation. First, the regression equation was rearranged to solve for the flow rate at the threshold value for salinity. For example, for the threshold salinity of 7.5, the equation was:

$$FT=(7.5-b + S_{diff})/m_1$$

Equation 2

where FT is the ‘threshold’ flow rate. The threshold flow rate was then compared to the summed mean monthly flow rates for the full record of freshwater flow at Conowingo (1968-2014) or Greensboro (1948-2014). The frequency of flow rates which would give rise to salinities >7.5 and >10.0 at each station was simply the number of years with flows less than the threshold flow rate divided by the total number of years in the record, multiplied by 100. It was assumed that the frequency of flow rates which would give rise to threshold salinities was equivalent to the frequency of occurrence of threshold salinities.

Combining information from all sources, the frequency of occurrence of salinities >7.5 and >10.0 was visualized by creating contour plots using the Minimum Curvature method which allowed the use of ‘fault lines’ to prevent information flow across land in the contouring process (Surfer Software v.10).

Estimating the influence of salinity-induced mortality on connectivity. To estimate the influence of salinity-induced mortality, the percent occurrence of freshwater flows that resulted in salinities >7.5 and >10.0 was estimated at the centroid of each oyster habitat polygon using the grid residuals tool in Surfer Software v.10. These values were used to adjust transport success scores for each habitat polygon by simply multiplying the value times the transport success score after converting percentages to proportions. This technique assumed that all simulated larvae were considered dead when salinities were below the given salinity threshold.

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connectivity. To estimate the influence of salinity-induced mortality, the percent occurrence of freshwater flows that resulted in salinities >7.5 and >10.0 was estimated at the centroid of each oyster habitat polygon using the grid residuals tool in Surfer Software v.10. These values were used to adjust transport success scores for each habitat polygon by simply multiplying the value times the transport success score after converting percentages to proportions. This technique assumed that all simulated larvae were considered dead when salinities were below the given salinity threshold.

Results

Without salinity-induced mortality, the combined transport success of all simulated larvae released in the Choptank and Little Choptank rivers was 71.0%, whereas transport success scores were 53.1% and 34.1% when salinity-induced mortality was applied at salinity thresholds of <7.5 and <10.0 , respectively. Total transport success for regions in the Choptank River (excluding the Little Choptank) was 75.4%, and was reduced to 53.1 and 34.1% when salinity-induced mortality was applied at salinity thresholds of <7.5 and <10.0 , respectively. Changes in the spatial patterns in reef-specific transport success due to salinity-induced mortality were related to patterns in the occurrence of low salinities.

Estimating the occurrence of low salinities. Changes in salinity in the Choptank River were related to changes in freshwater flow. Summed monthly freshwater flow rates from February – August accounted for a significant amount of

variability in average salinities <6 m deep between June and August at all stations, with adjusted R^2 values ranging from 0.51 (n = 12) to 0.94 (n = 6) (Table 3) (although note that four out of the 11 stations only had three years of data available so strong relationships were not unexpected at those stations). Regression results indicate that salinity at stations 1-9 in the lower and middle Choptank River was significantly influenced by freshwater flow from the Susquehanna River because Conowingo flow was the only significant explanatory variable in the models at those stations. In contrast, flow from both Susquehanna and the Choptank River accounted for a significant amount of the variability in salinity at station 10. At the uppermost Choptank River station (station 11), regression analysis indicated that freshwater flow from the upper Choptank watershed was the only variable that accounted for a significant amount of variability in average salinities in this region during the time of larval transport. Although four of the 11 regression lines were based on only three data points, six regression lines were based on six or more data points, suggesting that the assumption of linearity was valid despite limited data at some stations.

The frequency of occurrence of salinities >7.5 and >10.0 had distinct spatial patterns (Table 4, Fig. 2). The lower Choptank region and the lower portions of Harris Creek, and Broad Creek, and the central portion of Tred Avon River were estimated to experience salinities >10.0 more than 60.8% of the time, and salinities >7.5 more than 91.3% of the time. In contrast, in the upper Choptank region and near the heads of Harris Creek and the Tred Avon River, the frequencies of occurrences of salinities >10 were between 2 and 10%, and the frequencies of occurrences of salinities >7.5 were between 64.6 and 85.1%, respectively. Only in Broad Creek was

salinity >10 and >7.5 estimated to occur throughout the tributary more than 65.9 and 90.1% of the time, respectively.

Estimating larval exchange. Larval exchange patterns among regions were first examined in model simulations with transport alone (i.e., without salinity-induced mortality).

Connectivity. Analysis of the starting and ending locations of simulated larvae indicated that there were distinct patterns in larval exchange and connectivity between regions. Simulated larvae were successfully transported from tributaries to the mainstem regions of the Choptank at high rates, with the Tred Avon, Harris Creek and Broad Creek sending 24.9, 19.4 and 23.7% of their respective simulated larvae to the lower Choptank region (Table 5A). Simulated larval exchange between tributaries was significantly lower, with highest exchanges between Broad Creek and Harris Creek at 8.1%, and from Harris Creek to Broad Creek at 3.9%. Upstream transport of simulated larvae was significantly lower than downstream transport: the lower Choptank transported 2.8 and 0.02% of its simulated larvae to the middle and upper Choptank, respectively, whereas the upper Choptank transported 39.4 and 29.7% of its simulated larvae to the middle and lower Choptank, respectively. The Little Choptank transported very few simulated larvae to regions in the Choptank River ($\leq 1.0\%$). Additionally, transport from regions in the Choptank River to the Little Choptank was low, with the lower Choptank region contributing the most simulated larvae of any region to the Little Choptank (3.8%).

Transport success. The highest and lowest transport success scores came from opposing ends of the mainstem Choptank River. The upper Choptank had the

highest overall transport success (96.2%) and the lower Choptank had the lowest overall transport success (49.6%) (Table 5A), likely because many more habitat polygons were located downstream of the upper Choptank region than the lower Choptank region. Total transport success of simulated larvae originating in the tributaries was highest in Broad Creek and the Tred Avon with 79.2% in both regions. Transport success from Harris Creek was 68.8%. In addition, there were distinct spatial patterns in transport success from individual reefs, with highest transport success in the upper reaches of the Choptank River, its tributaries, and the Little Choptank River and lower transport success in the lower portions of the river systems (Fig. 3A).

Self-recruitment. Self-recruitment was highest in the Little Choptank (38.9%) and lowest in the upper Choptank (13.2%) (Table 5A). Harris Creek, Broad Creek, and the Tred Avon River had predicted self-recruitment levels of 22.4, 27.7, and 27.1%, respectively, whereas self-recruitment in the mainstem Choptank River was <16.8%.

Catching success. Catching success (the percentage of all successfully transported larvae that settled in a region) was highest in downstream regions (Table 6, Fig. 4). The lower Choptank ‘caught’ the most simulated larvae, with 29.4% of all successfully transported larvae settling there (Table 6), having been contributed from a number of different regions (Fig. 5A). In contrast, catching success was lowest in the upper Choptank region (2.8%) (Table 6) which was its own source of most of the settled larvae in that region (Fig. 5A). Examining each region in detail, catching

success of simulated larvae released from each region was highest within and downstream of the region of origin (Fig. 6).

Estimating the influence of salinity-induced mortality. Patterns in connectivity and transport success, and the magnitude of self-recruitment and catching success were altered by the potential influence of salinity-induced mortality.

Connectivity. Connectivity among regions was affected when salinity-induced larval mortality was applied to model results, with the largest changes in the mainstem Choptank regions (see bold numbers in Table 5B,C). For example, when the salinity threshold was set at 7.5, 12.4% fewer simulated larvae were transported from the upper to the middle Choptank and 5.8-9.5% fewer simulated larvae were transported to the lower Choptank from all regions within the Choptank River (compare Tables 5A and 5B). When the salinity threshold was set at 10, 29.6% fewer simulated larvae were transported from the upper to the middle Choptank and 9.1-21.5% fewer simulated larvae were transported to the lower Choptank from all regions within the Choptank River (compare Tables 5A and 5C).

Transport Success. Total transport success in each region changed by 18.5-29.4% when the salinity-induced mortality threshold was 7.5, and by 27.8-71.4% when the threshold of 10 was applied (compare Table 5A with 5B,C). The upper Choptank region had the largest reductions in total transport success, from 96.2 to 66.8% (threshold of 7.5) and to 24.8% (threshold of 10) (Table 5C). When the threshold of 7.5 was applied, the upper Choptank remained the region with the highest transport success score (66.8%) but became the second lowest scoring region (24.8%) when the threshold of 10 was applied, while Broad Creek became the highest

scoring region (44.7%). When salinity-induced mortality was applied with a threshold of 7.5, the general spatial pattern in transport success from reefs was not substantially altered (i.e., transport success decreased from upstream to downstream), but the magnitude of the highest scores did decrease by 20-30%, with greatest reductions in the upper portions of the Choptank River, Harris Creek and the Tred Avon River (compare Fig. 3A and 3B). In contrast, the spatial patterns in transport success were substantially changed when salinity-induced mortality was applied with a threshold of 10, such that peak transport success scores occurred in the middle portion of the Choptank River, Harris Creek, and the Tred Avon River (Fig. 3C) instead of at the heads of the estuaries. These results suggest that determining the actual threshold of salinity-induced mortality in the Choptank River is important for understanding which regions and reefs would produce the most surviving larvae.

Self recruitment. Self-recruitment scores decreased by 4.0-7.5% and 8.0-12.3% when salinity-induced mortality was applied with thresholds of 7.5 and 10, respectively (compare Table 5A and 5B,C). While the magnitude of self-recruitment scores changed when salinity-induced mortality was applied, general patterns did not: self-recruitment scores remained higher for the tributaries than for the mainstem regions, and self-recruitment was highest in Broad Creek and lowest in the upper Choptank (Table 5). These results suggest that the tributaries have higher retention of larvae and greater chance to develop self-sustaining populations than mainstem regions.

Catching success. Catching success scores for each region decreased by a range of 0.1- 2.9% and 0.7-11.1% from transport alone scores, when salinity-induced

mortality was applied at the 7.5 and 10 thresholds, respectively (Table 6). Patterns in catching success however, remained consistent with or without salinity-induced mortality, with the upper Choptank having the lowest (0.7-2.8%) and the lower Choptank having the highest (18.3-29.4%) catching success scores (Table 6, Fig. 4). In addition, patterns in the source of larvae to each region were not substantially changed, with the lower Choptank receiving contributions from all regions in the Choptank (Fig. 5). These results suggest that reefs in the lower Choptank region are in an optimum location to ‘catch’ larvae from all regions upstream, regardless of changes in salinity, and that there is a high degree of connectivity among the subpopulations in the Choptank system.

Interactions with the model boundaries. Few (1.2%) simulated larvae encountered the northern boundary of the model domain (Table 7). In contrast, 24.4% of all simulated larvae contacted, and remained at, the southern boundary. The percentage of simulated larvae that contacted the southern boundary from each region decreased with distance from the boundary, with the lowest percentage of contact from simulated larvae released in the upper (1.2%) and middle Choptank (13.6%) regions, and the highest percentage of contact from simulated larvae released from Harris Creek (25.8%), the lower Choptank (46.7%), and Little Choptank (44.2%) regions. If simulated larvae had been transported south of the model domain (e.g., using a nested model), they could have had the opportunity to encounter reef habitat which would have resulted in higher transport success scores for these regions.

Discussion

Results indicate that salinity-induced mortality of larvae could substantially decrease transport success, self-recruitment, and catching success, and change patterns in reef-specific transport success throughout the estuary. In addition, more simulated larvae were transported down river (rather than upriver) and reefs in upper portions of the Choptank River and its tributaries were in a position to produce the most larvae which encountered suitable habitat. Successful transport of simulated *C. virginica* larvae from all regions in the Choptank River to the lower Choptank region (Fig.5) demonstrates a high degree of connectivity among the subpopulations in this system.

Prior modeling studies of *C. virginica* larvae in Chesapeake Bay predicted connectivity between Bay-wide populations (North et al. 2008). While this work lacked the resolution necessary to predict transport of simulated larvae among small tributaries, several noticeable similarities and differences between the studies can be discerned. Overall both modeling studies revealed a high degree of transport success from the Choptank River, with this study predicting an overall 75.4% transport success, compared to ~88% for the Choptank River (Fig. 7A in North et al. 2008). Additionally, spatial patterns in catchability were similar: a high percentage of larvae settled successfully at the mouths of the tributaries in both studies (compare Fig.6 with Fig. 9 in North et al. 2008). Similar patterns in larval settlement may be attributed to the high availability of suitable settlement habitat located at the mouths of tributaries, which are present in both studies. Patterns in connectivity to the mainstem Chesapeake Bay was another similarity between studies. This study predicted that 20.1% of simulated larvae released from the Choptank River settled

successfully in the mainstem Bay (Table 6), compared to 22.1% of simulated larvae in North et al. (2008) (their Table 5). Similarities in connectivity may be accounted for by the median (~11 km) and maximum (~21 km) dispersal distances of successfully transported particles from the Choptank River (Fig. 5A in North et al 2008). When applied to this study, these dispersal distances indicate that habitat located in portions of Harris Creek and most of the lower and Little Choptank were within ~11 km of mainstem reefs, and reefs from all seven regions were within ~21 km of mainstem reefs, suggesting that mainstem reefs are located close enough to Choptank River oyster populations to receive substantial subsidies from them.

In contrast with the predictions for the Choptank River, there were notable differences between transport success from reefs in the Little Choptank River between this study (51.1%) and that of North et al. (2008) (~79%). Model domains likely explain this difference: a large amount (44.2%) of simulated larvae released from the Little Choptank in this study encountered and “stuck to” the southern boundary, whereas 52.2% of the simulated larvae released from the Little Choptank in North et al. 2008 (Table 5) were able to encounter suitable habitat in the Maryland mainstem region which included reefs south of the this study’s model boundary. For both model studies, it is important to note that the percentages of larvae exchanged between regions do not reflect the true larval exchange present in the systems. Because the model projections do not take into account the number of adult spawners and fertilized gametes produced, the models do not predict how many larvae actually move along the simulated transport pathways. In addition, other physiological and

biological barriers to dispersal and connectivity are not accounted for, such as starvation, harmful algal blooms, and predation.

This research builds on the findings of prior studies of circulation patterns and *C. virginica* larval settlement rates in the Choptank River and its tributaries. One to two orders of magnitude difference in spat settlement rates have been observed between Broad Creek and the Tred Avon (Kennedy 1980). Spat settlement in Broad Creek was consistently higher than the Tred Avon, despite similarities in fresh water inflow, temperature, and salinity. Tributary-specific circulation patterns could account for the observed differences in spat settlement (Boicourt 1982). Broad Creek has stronger wind-driven and stronger two-layer gravitational circulation than the Tred Avon which results in Broad Creek having greater exchange with the mainstem Choptank River than the Tred Avon River (Boicourt 1982). Results of this study show comparatively high levels of predicted self-recruitment in Broad Creek (27.7%) and the Tred Avon (27.1%)(Table 5A) as well as similar levels of catching success (Broad Creek: 7.1%, Tred Avon: 7.5%)(Table 6) in the absence of salinity-induced mortality. The similarities between tributaries remained when salinity-induced mortality with a threshold of 7.5 was applied, but Broad Creek had slightly higher self-recruitment and catching success when the threshold of 10 was applied (Tables 5C and 6). Although differences in salinity, and hence better larval survival, could explain some of the differences in spat settlement between systems, it likely does not account for all of the orders of magnitude differences in spat settlement. The similarity between self-recruitment and catching success between the two systems

points to biological processes at work which were not included in the model, such as the abundance of adult oysters.

By incorporating and predicting salinity-dependent mortality in combination with transport, this research helps to improve our understanding of larval mortality and population connectivity. The larval transport model predictions by North et al. (2008, 2012) were limited because environmental-dependent survivorship was not simulated. By integrating salinity-induced larval mortality and transport success in this research, simulated larvae from some reefs experienced larval mortality as high as 90% in regions like the upper Choptank, which could help to explain part of the large mortality (95-99%) which is experienced in highly fecund marine species during larval dispersal (Thorson 1950). In addition, integrating transport and salinity-dependent mortality influenced patterns in connectivity. For example, connectivity between the upper Choptank and the middle Choptank was reduced by 29.6% when salinity induced-mortality was included (comparison of Table 5A and 5C), demonstrating that physical factors effect spatial patterns in connectivity.

While this study attempted to improve prediction of larval dispersal with the inclusion of salinity-induced larval mortality, limitations to its application were inherent. Lack of salinity data in the Little Choptank and portions of the major tributaries of the Choptank River did not allow for robust statistical relationships between stream flow and measured salinity in these regions, although salinity in the little Choptank was likely similar to conditions experienced in the lower Choptank, which are conducive to larval development. In addition, definitive thresholds for salinity-induced larval mortality in oligohaline regions were not present in the

literature and likely do not exist across broad distances between discrete populations. The tolerance of larvae to low salinities differs between populations and is dependent upon the salinity levels at which the adults develop gonads (Davis 1958; Davis and Calabrese 1964). While our study incorporated salinity-induced mortality similar to levels deemed suitable for larval survival and development in the Horn Point Oyster Hatchery, larval mortality likely occurs over a range of salinity units rather than at finite thresholds, and could occur throughout the larval and early juvenile stages, although is not as severe as early larval mortality which was simulated herein (Davis and Calabrese 1964; Lough 1975). Because reproductive population connectivity includes survival of individuals until reproduction (Pineda et al. 2007), prolonged exposure of low salinities to post-settlement oysters would affect survival rates, thus altering population connectivity between regions, and was not captured in this modeling study. Future studies investigating salinity-induced larval mortality in Choptank River broodstock will aid in optimization of larval transport models in oligohaline estuaries. Nevertheless, the salinity-induced mortality thresholds of 10.0 and 7.5 used in this study likely encompass the worst and best case scenarios for larvae in the Choptank region. Hence, the effect of salinity on patterns in connectivity and dispersal can be assumed to be represented in the analysis and these results can be applied to provide information useful for *C. virginica* restoration efforts.

The inclusion of salinity data at the heads of each major tributary (Harris Creek, Broad Creek, Tred Avon River) allowed for a more accurate description of the salinity gradients present in these regions, increasing our ability to make predictions of connectivity. The inclusion of such observations, although small in number,

revealed bottlenecks in the intrusion of salinity into the narrow upper reaches of these tributaries, and demonstrate the need for more routine monitoring of salinity in regions slated for oyster population restoration to enable selection of sites with salinities that are suitable for larval development.

Oyster populations in regions experiencing high frequencies of low salinities likely rely on a flux of older larvae from higher salinity areas for spat settlement (Davis 1958). Regions of Chesapeake Bay like the Chester River frequently experience salinities <10 during the larval transport season, and historically supported a commercial oyster fishery with hundreds of acres of named bars (CBP 2012) (MDNR 1997). Late-stage larvae have been shown to tolerate reduced salinities with observation of free swimming larvae in salinities as low as 5.17 (Nelson 1921) and successful settlement of late-stage larvae in salinities as low as 5.6 (Prytherch 1934). Larval supply in oligohaline regions like the Chester River and upper Choptank River may be dependent on infrequent droughts which result in favorable salinities for early stage larvae as well as transport of late-stage larvae up-estuary from high salinity areas by episodic wind events.

Results of this modeling study could be used to help guide site selection for restoration. For example, modeled results reveal a high degree of connectivity between the middle Choptank, the Tred Avon, Broad Creek, Harris Creek, and the lower Choptank. Restoration in the middle Choptank, Tred Avon, Broad Creek, and Harris Creek regions would establish reefs that could function well as larval sources, creating a subsidy of larval supply to reefs subject to harvest in the lower Choptank. To enhance local populations through self-recruitment, restoration efforts could be

targeted in Broad Creek and the Little Choptank, two regions shown to have high self-recruitment and low frequencies of salinities <10.0 (for Broad Creek).

Restoration efforts in regions experiencing high frequencies of low salinities, like the upper Choptank, may be best suited for habitat and ecosystem restoration benefits rather than restoring bay-wide *C. virginica* populations because of salinity-induced larval mortality and the low disease pressure on adults at reduced salinities (Ewart 1993). Catching success scores (Table 6) of reefs down estuary from regions of release show simulated larvae transport was highest from upper to lower estuary reefs. This understanding highlights the source-sink mechanisms at play in interconnected *C. virginica* populations, and supplies a blueprint for managers to place restored reefs in a regions that would enhance their objectives for oyster restoration.

Moving forward, model predictions in the Choptank River will be improved using in-situ observations of *C. virginica* larvae (e.g., Goodwin and North *in prep*), which can be used to verify vertical migration as done by Paris and Cowen (2004). Patterns in vertical migration have been shown to significantly affect dispersal distances, transport success, and connectivity of simulated oyster larvae in Chesapeake Bay (North et al. 2008). An important component of the simulated larval behavior in this study is the cue for veliger stage oyster to swim up if they encounter a salinity gradient $\geq 1.0 \text{ m}^{-1}$. This behavior results in aggregations of veliger stage oysters above halocline. If this value were to be reduced, greater numbers of oyster veligers would be simulated to remain in the upper water column, possibly altering dispersal direction and distance, ultimately affecting connectivity. The results of this

study are highly dependent on modeled behavior; future studies that validate simulated larval distributions with observed vertical distributions will greatly enhance confidence in larval transport model predictions.

Larval transport patterns predicted in this study rely on a hydrodynamic model predicting circulation for only one year (2010). Our ability to predict larval transport in this region would be strengthened with the inclusion of multiple years of hydrodynamic data. 2010 was an average year for freshwater inputs into Chesapeake Bay with no recorded hurricanes or floods during the larval transport season (June – August). Since 1980, 27 named storms have affected Maryland during the larval transport season (NOAA 2015). These storms contribute significant freshwater inputs, contain large wind events, and can lead to rapid changes in salinities which could increase salinity dependent larval mortality. Our ability to model larval transport and mortality during one of these events might result in more variable predictions. In addition to the inclusion of multiple years of hydrodynamic data, the performance of such hydrodynamic models influences the predictions of transport, especially for organisms whose modeled behavior is based on physical cues like the strength of haloclines. Improvements in the simulation of salinity and temperature in the hydrodynamic model could lead to more accurate predictions in the transport of organisms.

Oyster restoration is slated to take place in additional tributaries of Chesapeake Bay (USACE 2012) and around the United States (Barnes et al. 2007) with varying salinity levels and salinity gradients. Restoration plans in Chesapeake Bay were developed with input from a committee which included representatives

from the State of Maryland, the Commonwealth of Virginia, National Oceanic and Atmospheric Administration (NOAA), Environmental Protection Agency (EPA), U.S. Fish and Wildlife Service (USFWS), The Nature Conservancy (TNC), the Potomac River Fisheries Commission (PRFC), and Chesapeake Bay Foundation (CBF) (USACE 2012): The long term goal of the master plan developed by this committee and published by the USACE is to:

Throughout the Chesapeake Bay, restore an abundant, self-sustaining oyster population that performs important ecological functions such as providing reef community habitat, nutrient cycling, spatial connectivity, and water filtration, among others, and contributes to an oyster fishery. (USACE 2012).

Possible tributaries that will undergo targeted restoration efforts in Maryland are: the Severn River, the lower Chester River, and the St. Mary's River (USACE 2012).

Differing restoration objectives may be appropriate in these tributaries based on predominant summer salinity regimes and larval salinity tolerances.

When justifying site selection for targeted restoration efforts, each tributary mentioned above has advantages and disadvantages. The lower Chester and Severn Rivers are located in regions where average summer surface salinities are between 7.6 -10.0 (CBP 2012). Targeted oyster restoration in these regions would support development of large, long lived adult oysters, in regions that naturally suppress diseases (Ewart 1993), whose ecosystem services would provide habitat for benthic, demersal and pelagic organisms, as well as support benthic pelagic nutrient coupling, and seston reduction (Harding and Mann 2001; Newell et al. 2005). However, the prevalence of low salinities in these regions may reduce the frequency of successful spat settlement, limiting the ability to create self-sustaining reefs that are also subject to harvest, as outlined in the USACE (2012) master plan.

Restoration focused in regions with favorable salinities like St. Mary's River will produce larvae that survive well, contribute individuals to other locations subject to harvest, and enhance ecosystem services similar to those mentioned above. The St. Mary's River is located in a region where average summer surface salinities range between 12.6 and 15.0 (NOAA 2015b). However, disease pressure in regions of elevated salinities, like the St. Mary's River, may subject oysters to higher disease pressure than oysters in lower salinities, thus reducing the age and size class of oysters in these restoration areas, minimizing the availability of spawners and harvest size oysters due to increasing mortality rates as oysters age (Ewart 1993). These factors, among others, need to be weighed in the decision making process, as they directly influence the ability for restored oyster reefs to be self-sustaining, contribute individuals to other regions, and to produce individuals that will eventually recruit to the fishery.

This model successfully builds on previous larval transport studies by integrating salinity-induced mortality with larval behavior and by predicting larval transport in a high resolution hydrodynamic model domain. Moving forward, expanded simulations of larval transport across model boundaries will help to better understand connectivity between *C. virginica* communities in the Choptank and Little Choptank Rivers and reefs further south in Chesapeake Bay. In addition, future studies incorporating additional years of circulation patterns enhance understanding of the influence of inter-annual variations in physical conditions on larval exchange in this system. The predictions given in this study represent one step forward in the complex task of modeling bio-physical interactions. Future work which enhances

understanding of larval survival through post settlement also will strengthen the ability to design effective restoration strategies for dispersive organisms and improve our management of populations subject to human exploitation.

Tables

Table 1. Sources of salinity data. Station identification number (this study), data source, station identification number (from data source), year, latitude and longitude, number of station occupations per year (listed in order of year sampled). See Fig. 1. for location of stations. CISNET = Coastal Intensive Site Network report 1999-2001 (Malone et al. 2003), BT = Bivalve Larvae TRANSPORT Mapping Survey 2010-2012 (North 2013), CBP = Chesapeake Bay Program monitoring station ET 5.2 (CBP 2015), Newell, R.I.E = data collected by Roger I. E. Newell (unpublished data). NA is listed for Newell, R.I.E. because an Induction Salinometer RS5-3 was used.

Station	Data Source	Year	Latitude	Longitude	Number of CTD casts per year	Depth range (m)	Number of observations			
1	CISNET 3	1999	38.6363	-76.3274	3	6 - 0.50	35			
	“	2000			3	6 - 0.50	68			
	“	2001			3	6 - 0.50	68			
	BT station 1	2010	38.6363	-76.3267	12	6 - 0.75	235			
	“	2011			11	6 - 0.75	210			
	“	2012			9	6 - 0.75	190			
2	BT station 2	2010	38.6509	-76.2768	12	6 - 0.75	260			
	“	2011			11	6 - 0.75	229			
	“	2012			9	6 - 0.75	183			
3	BT station 3	2010	38.6869	76.28305	12	5 - 0.75	212			
	“	2011			11	5 - 0.75	176			
	“	2012			9	5 - 0.75	152			
4	BT station 22	2011	38.7432	-76.3033	11	5 - 0.75	210			
	DNR vertical profiler	2012	38.7359	-76.3040	2,010	2 - 0.50	6,031			
	“	2013			2,577	2 - 0.50	7,734			
	“	2014			2,955	2 - 0.50	8,830			
5	BT station 4	2010	38.7139	-76.2618	15	6 - 0.75	250			
	“	2011			12	6 - 0.75	224			
	“	2012			8	6 - 0.75	154			
6	Newell, R.I.E	1982	38.73778	-76.246	NA	0.5	3			
	"	1983			NA	0.5	3			
	"	1984			NA	0.5	3			
	"	1985			NA	0.5	3			
	"	1986			NA	0.5	25			
	"	1987			NA	0.5	13			
	"	1988			NA	0.5	8			
	"	1989			NA	0.5	15			
	"	1990			NA	0.5	10			
	"	1991			NA	0.5	11			
	CISNET 5	1999			38.6396	-76.197	2	6 - 0.5	35	
	“	2000					3	6 - 0.5	68	
	“	2001					3	6 - 0.5	68	
	7	BT station 6			2010	38.63967	-76.197	13	5.5 - 0.5	260
		“			2011			12	5.5 - 0.5	234
“		2012	10	5.5 - 0.5	215					

Table 1. (Cont.)

Station	Data Source	Year	Latitude	Longitude	Number of CTD casts per year	Depth range (m)	Number of observations
8	BT station 7	2010	38.6655	-76.1811	13	5.5 - 0.5	234
	"	2011			12	5.5 - 0.5	175
	"	2012			8	5.5 - 0.5	139
9	Newell, R.I.E	1982	38.73026	-76.1398	NA	0.5	3
	"	1983			NA	0.5	3
	"	1984			NA	0.5	3
	"	1985			NA	0.5	3
	"	1986			NA	0.5	25
	"	1987			NA	0.5	17
	"	1988			NA	0.5	8
	"	1989			NA	0.5	14
	"	1990			NA	0.5	10
	"	1991			NA	0.5	11
10	CBP ET 5.2	1999	38.5807	-76.0587	7	6 - 0.5	49
	"	2000			5	6 - 0.5	35
	"	2001			5	6 - 0.5	34
	"	2010			3	6 - 0.5	21
	"	2011			2	6 - 0.5	14
	"	2012			2	6 - 0.5	14
11	CISNET 11	1999	38.6341	-75.9828	3	6 - 0.5	35
	"	2000			3	6 - 0.5	69
	"	2001			3	6 - 0.5	68
	BT station 15	2010	38.6366	-75.9791	14	3 - 0.5	169
	"	2011			12	3 - 0.5	104
	"	2012			7	3 - 0.5	88

Table 2. Salinity observations taken from Midshore Riverkeeper Conservancy data set for which a handheld multimeter was used (MRC 2015). Station identification number (this study), data source, year, latitude and longitude, number of station occupations per year (listed in order of year sampled). See Fig. 1. for location of stations.

Station	Data Source	Year	Latitude	Longitude	Depth range (m)	Number of observations
4A	MidshoreRiverkeeper	2013	38.76338	-76.3044	0.5	3
	"	2014			0.5	3
4B	"	2013	38.77878	-76.2885	0.5	3
	"	2014			0.5	3
4C	"	2013	38.76338	-76.3044	0.5	3
	"	2014			0.5	3
4D	"	2013	38.8119	-76.2591	0.5	3
	"	2014			0.5	3
6A	MidshoreRiverkeeper	2013	38.73926	-76.2147	0.5	3
	"	2014			0.5	3
6B	MidshoreRiverkeeper	2013	38.7795	-76.2563	0.5	3
	"	2014			0.5	3
9A	MidshoreRiverkeeper	2013	38.7671	-76.0964	0.5	3
	"	2014			0.5	3

Table 3. Linear and multiple regression statistics for models that predict the average salinity at each station during summer given the average river flow (February-August), at Conowingo Dam on the Susquehanna River (stations 1-9) at Greensboro gauging station on the Choptank River (station 11), or at both locations (station 10). The table contains the values for regression coefficients, intercepts, *F* and *P* statistics, the adjusted R^2 for each model, and sample size (*n*) which corresponds to the number of years used in the analysis. NA indicates that the variable was not significant in the multiple regressions model and therefore was not included in the linear model.

	Coefficients Conowingo	Coefficients Greensboro	Intercept	<i>F</i>	<i>P</i>	Adjusted R^2	<i>n</i>
1	-0.000015	NA	16.75	0.0050	0.000032	0.82	6
2	-0.000013	NA	15.79	0.12	0.033	0.93	3
3	-0.000013	NA	15.24	0.13	0.040	0.91	3
4	-0.000013	NA	14.58	0.094	0.0099	0.73	4
5	-0.000014	NA	14.94	0.14	0.044	0.91	3
6	-0.000019	NA	16.87	0.0050	0.0000018	0.51	12
7	-0.000017	NA	16.42	0.0066	0.000065	0.80	6
8	-0.000014	NA	14.86	0.15	0.047	0.88	3
9	-0.000022	NA	17.44	0.0030	0.0000077	0.65	10
10	-0.000015	-0.0025	15.46	0.00069	0.00018	0.94	6
11	NA	-0.0037	12.52	0.015	0.00048	0.76	6

Table 4. Percent occurrence of salinities ≥ 7.5 or ≥ 10.0 based on regression models (Table 2) and freshwater flow records for the gauging station at Conowingo Dam on the Susquehanna River (February-August), and at Greensboro gauging station on the Choptank River (February-August). Region = region in which the station was located (see to Fig.1).

Station	Percent occurrence salinities ≥ 7.5	Percent occurrence salinities ≥ 10	Region
1	100.0	91.3	Lower Choptank
2	100.0	91.5	Lower Choptank
3	97.8	85.1	Lower Choptank
4	97.8	65.9	Harris Creek
4A	95.7	59.6	Harris Creek
4B	95.7	53.2	Harris Creek
4C	87.2	14.9	Harris Creek
4D	78.7	2.1	Harris Creek
5	97.8	73.9	Broad Creek
6	95.6	71.7	Broad Creek
6A	90.2	65.9	Broad Creek
6B	90.1	65.9	Broad Creek
7	97.8	82.6	Lower Choptank
8	97.8	76.6	Lower Choptank
9	91.3	60.8	Tred Avon
9A	85.1	10.6	Tred Avon
10	82.6	45.7	Middle Choptank
11	64.6	9.1	Upper Choptank

Table 5. Connectivity tables. Percent of simulated larvae that were successfully transported between regions in the Choptank and Little Choptank Rivers. Left hand column is the region in which simulated larvae started and the column headers indicate the region to which simulated larvae were transported. Shaded boxes indicate self-recruitment (the percentage of simulated larvae that were released in a region and settled in that same region). Model results with: (A) no salinity-induced mortality, (B) salinity-induced mortality using a salinity of 7.5 as a threshold, (C) salinity-induced mortality using salinity of 10.0 as a threshold. Bold numbers in B) and C) indicate a >5% change from corresponding cells in A).

A. Transport alone (i.e., no salinity-induced mortality).

Region	Upper Choptank	Middle Choptank	Tred Avon	Broad Creek	Harris Creek	Lower Choptank	Little Choptank	Mainstem Bay	Total transport success
Upper Choptank	13.2	39.4	6.0	0.8	0.9	29.7	0.3	5.9	96.2
Middle Choptank	1.1	15.5	5.4	2.0	3.0	35.1	1.9	18.2	82.2
Tred Avon	0.02	4.1	27.1	3.0	3.2	24.9	1.8	15.2	79.2
Broad Creek	0.002	1.3	1.3	27.7	8.1	23.7	2.0	15.1	79.2
Harris Creek	0.0009	1.2	0.6	3.9	22.4	19.4	2.7	18.6	68.8
Lower Choptank	0.02	2.8	1.7	3.7	3.8	16.8	3.8	17.0	49.6
Little Choptank	0.0	0.02	0.006	0.002	0.01	1.0	38.9	11.2	51.1

B. Transport and salinity-induced mortality using a salinity threshold of 7.5

Region	Upper Choptank	Middle Choptank	Tred Avon	Broad Creek	Harris Creek	Lower Choptank	Little Choptank	Mainstem Bay	Total transport success
Upper Choptank	8.8	27.0	4.2	0.5	0.7	20.8	0.2	4.6	66.8
Middle Choptank	0.8	11.5	4.0	1.5	2.2	25.8	1.3	13.4	60.5
Tred Avon	0.01	3	21.8	2.2	2.3	18.5	1.3	11	60.1
Broad Creek	0.002	1	1	21.8	6.1	17.9	1.5	11.4	60.7
Harris Creek	0.0006	0.8	0.4	2.6	16.3	13.0	1.8	12.4	47.3
Lower Choptank	0.01	1.6	1.0	2.2	2.1	9.3	1.7	8.8	26.7

Table 5 (Cont.).

C. Transport and salinity-induced mortality using a salinity threshold of 10.0

Region	Upper Choptank	Middle Choptank	Tred Avon	Broad Creek	Harris Creek	Lower Choptank	Little Choptank	Mainstem Bay	Total transport success
Upper Choptank	2.6	9.8	1.6	0.2	0.3	8.2	0.1	2.0	24.8
Middle Choptank	0.5	7.5	2.7	1.0	1.6	17.5	1.0	9.4	41.2
Tred Avon	0.001	2.2	14.8	1.6	1.7	13.5	0.9	7.1	41.8
Broad Creek	0.001	0.7	0.8	16.2	4.6	13.5	1.1	7.8	44.7
Harris Creek	0.0004	0.6	0.3	1.9	11.4	9.7	1.3	8.8	32.6
Lower Choptank	0.01	1.3	0.8	1.8	1.8	7.7	1.5	6.9	21.8

Table 6. Catching Success. Percentage of all simulated larvae which encountered suitable habitat and settled in each region based on model runs with A) transport alone (i.e., no salinity-induced mortality), B) transport and salinity-induced mortality using a salinity threshold of 7.5, and C) transport and salinity-induced mortality using a salinity threshold of 10.0.

	Transport alone	With salinity induced mortality (<7.5)	With salinity induced mortality (<10.0)
Upper Choptank	2.8	2.0	0.7
Middle Choptank	12.7	10.1	5.2
Tred Avon	7.5	6.7	4.4
Broad Creek	7.1	6.7	5.1
Harris Creek	8.1	7.8	5.7
Lower Choptank	29.4	26.5	18.3
Little Choptank	12.3	12.1	11.6
Mainstem Bay	20.1	19.1	14.9
Mainstem Bay(from Choptank River)	20.1	16.6	12.4

Table 7. Percentage of simulated larvae released from each region that encountered open water boundaries and stuck to northern or southern boundary, the percentage of simulated larvae released from each region that did not settle in the model domain (i.e., “died”), and the total transport success of simulated larvae released from each region. Region of origin is listed on the left hand column. Results reported for model with transport alone (i.e., salinity-induced mortality was not applied).

Region	Percent simulated larvae stuck to northern boundary	Percent simulated larvae stuck to southern boundary	Percent simulated larvae not settled	Total percent transport success
Harris Creek	2.7	25.8	2.8	68.8
Tred Avon	0.9	15.6	4.3	79.2
Broad Creek	1.0	15.5	4.3	79.2
Upper Choptank	0.1	1.2	2.5	96.2
Middle Choptank	2.9	13.6	1.2	82.2
Lower Choptank	1.3	46.7	2.5	49.6
Little Choptank	0.2	44.2	5.4	50.2
Whole domain	1.2	24.4	3.3	71.0

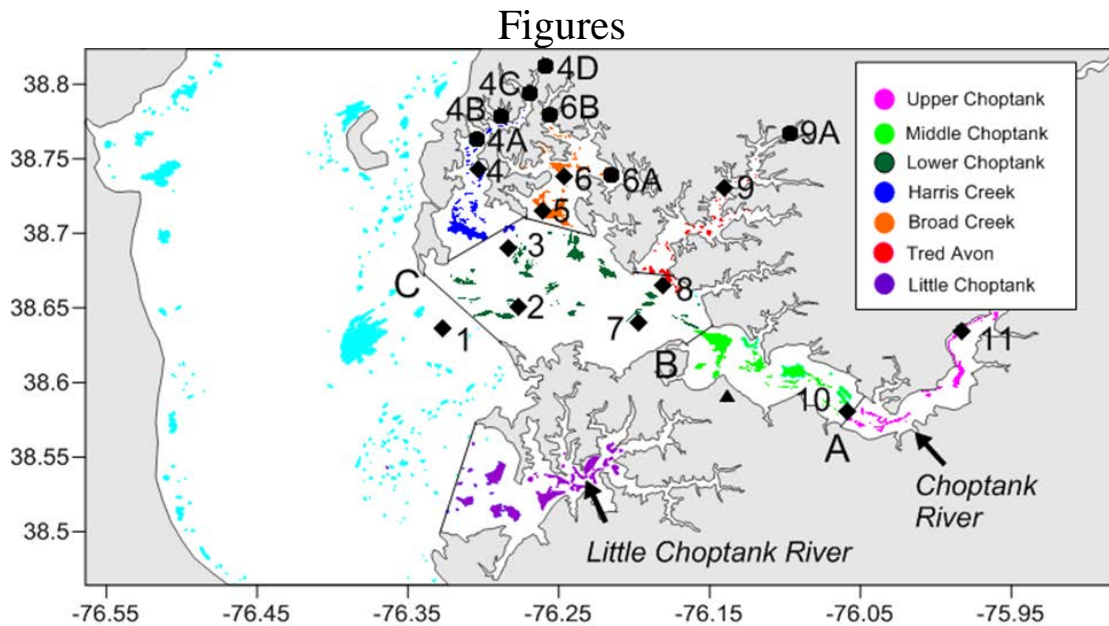


Fig. 1. Map of the larval transport and hydrodynamic model domains showing the Choptank and Little Choptank Rivers (right) and the adjacent mainstem Chesapeake Bay (left). The seven regions for which connectivity estimates were derived are indicated by different colors of oyster habitat within each region (see key). Black lines delineate the seven regions. The letters A, B, and C indicate the boundary lines between the A) upper and middle, and B) middle and lower Choptank regions, with C) indicating the seaward boundary of the lower Choptank region. Numbers representing the locations of salinity measurements that were used in regression analyses and are indicated by a “♦”, numbers representing the location of salinity measurements that were used for adjustment of regression equation predictions inside tributaries are indicated by a “•” (see Table 1). ▲ = Location of Horn Point Oyster Hatchery.

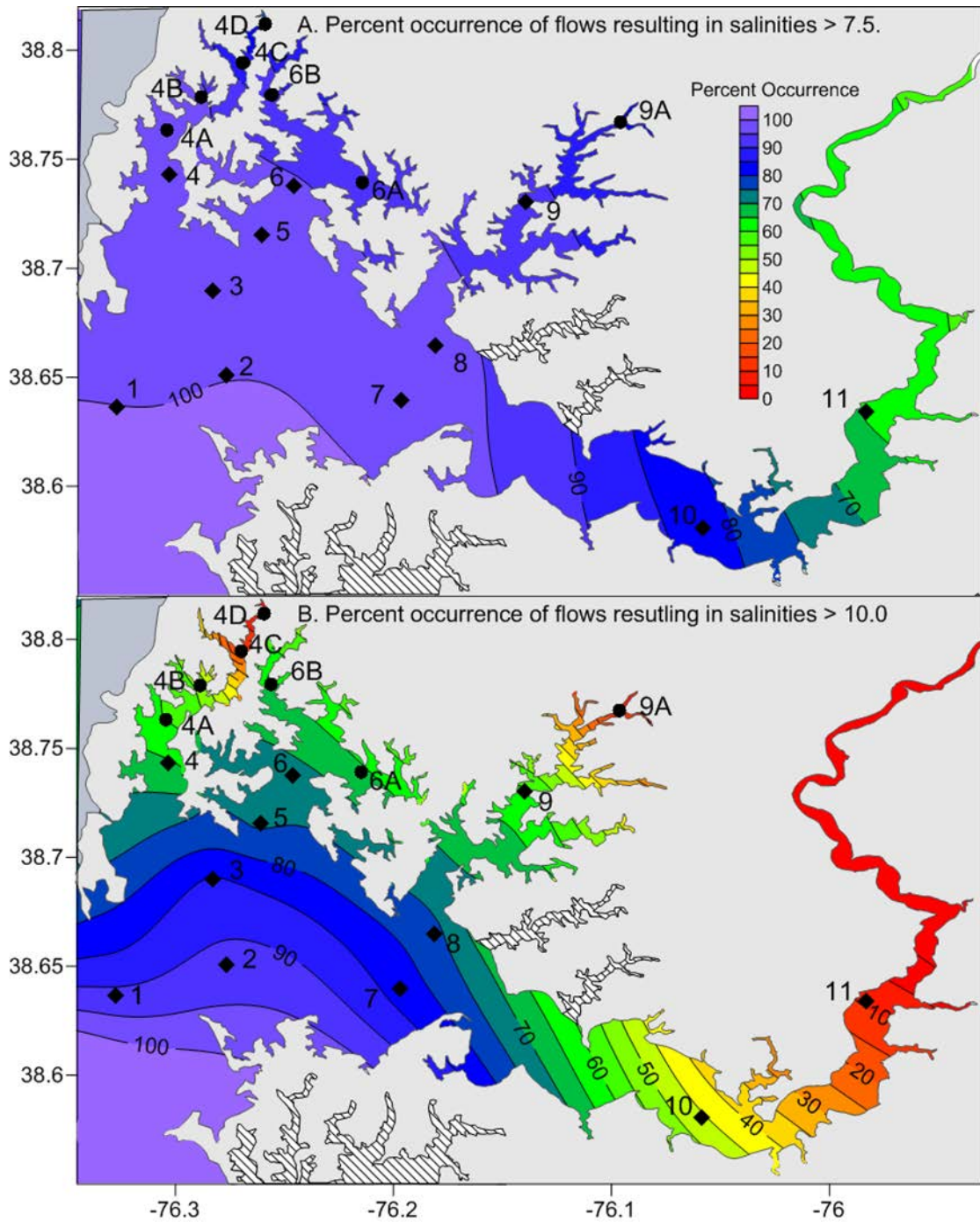


Fig. 2. Contour plots of the percent occurrence of flow rates which were predicted to result in salinities greater than A) 7.5 and B) 10.0. Regression equations based on Susquehanna and/or Choptank River freshwater flows were used to predict the flow rates which resulted in salinity of 7.5 or 10.0 at each station (♦) during the time of peak larval transport (June-August). Then the full record of freshwater flow for Susquehanna (1968-2014) and/or Choptank (1948-2014) Rivers were used to estimate the percent occurrence of the flow rate which would give rise to salinities of A) >7.5 and B) >10.0 at each station. Hatched regions indicate areas where salinity measurements were not available to make predictions.

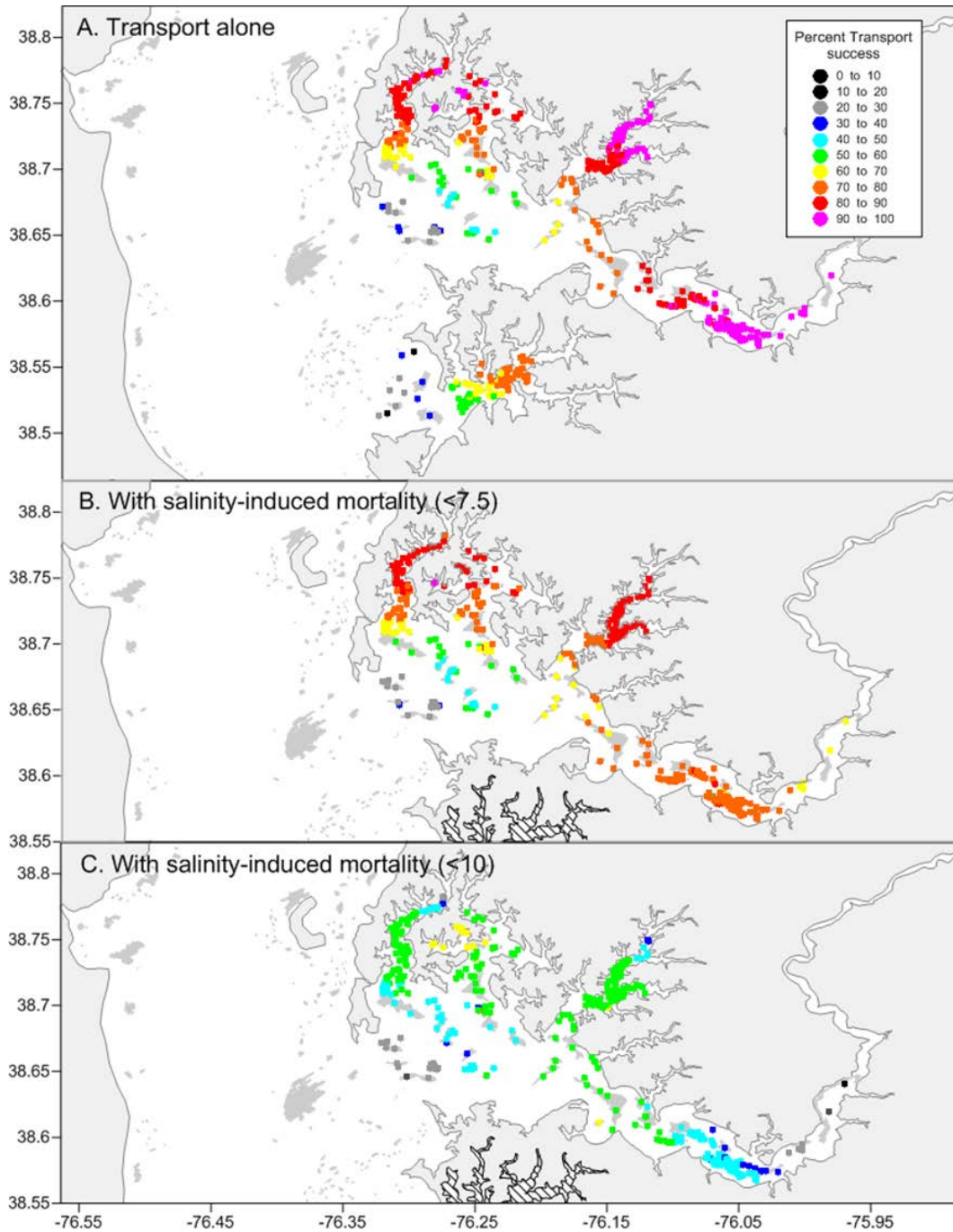


Fig. 3. Percent transport success scores for habitat polygons in the Choptank and Little Choptank Rivers based on A)transport alone (i.e., no salinity-induced mortality), B)transport and salinity-induced mortality using a salinity threshold of 7.5, and C)transport and salinity-induced mortality using a salinity threshold of 10.0. A colored circle over each habitat polygon indicates the percentage of simulated larvae that were released from that polygon and encountered suitable habitat anywhere within the model domain.

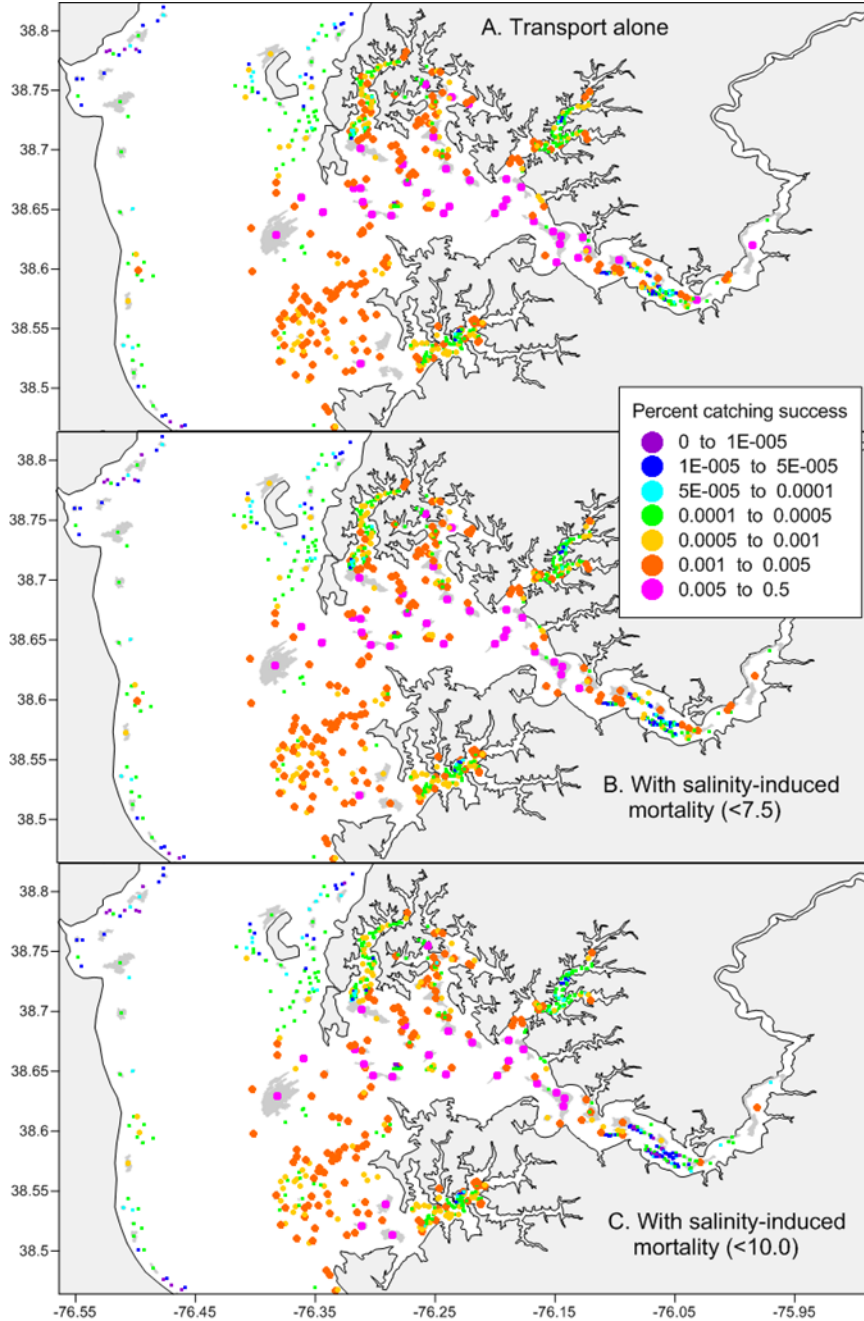


Fig. 4. Percent catching success combined for all model simulations. Percentage of all simulated larvae released to settle on any suitable habitat in model domain. A colored circle over each habitat polygon indicates the percentage of simulated larvae that were released from a given region and settled successfully on that polygon. A) transport alone (i.e., no salinity-induced mortality), B) transport and salinity-induced mortality using a salinity threshold of 7.5, and C) transport and salinity-induced mortality using a salinity threshold of 10.0.

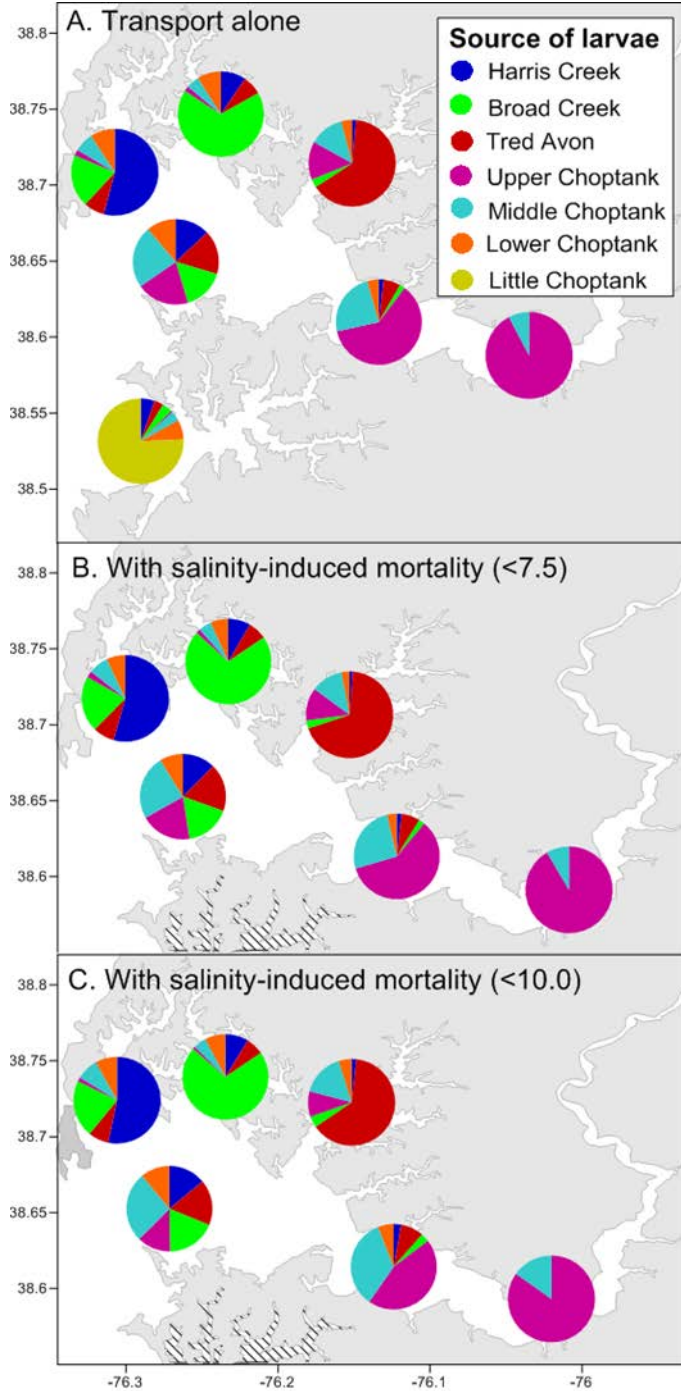


Fig. 5. The source of simulated larvae which settled in each region based on estimates of A) transport alone (i.e., no salinity-induced mortality), B) transport and salinity-induced mortality using a salinity threshold of 7.5, and C) transport and salinity-induced mortality using a salinity threshold of 10.0. Pie charts are displayed above the region where simulated larvae settled; colors represent the region from which the larvae were released (see key). The values in the pie charts are the percentages in the columns for each region in Table 5 and allow qualitative comparison of relative importance of the sources of larvae within each region.

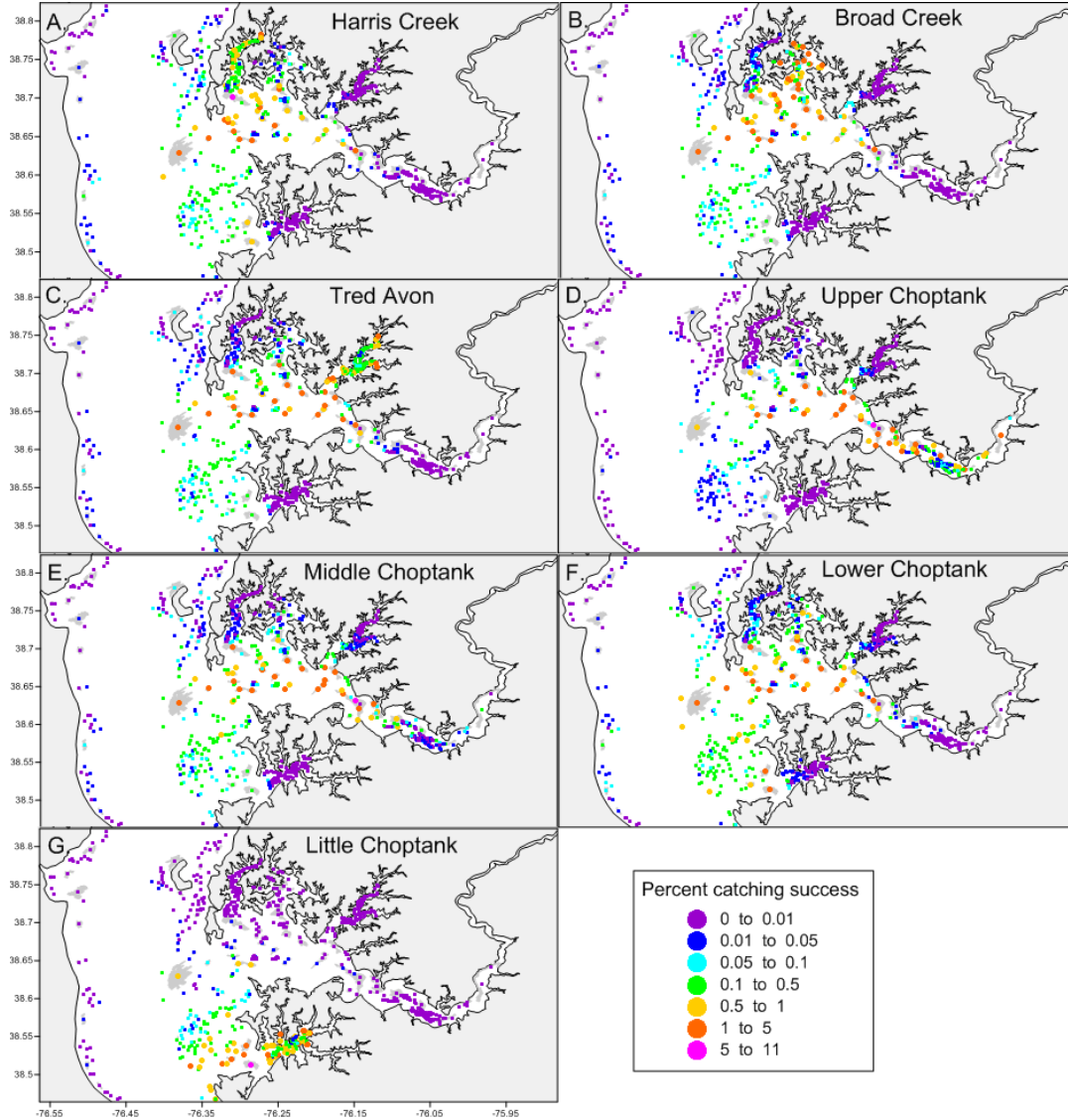


Fig.6. Percent catching success scores for simulated larvae released from A) Harris Creek, B) Broad Creek, C) Tred Avon, D) Upper Choptank, E) Middle Choptank, F) Lower Choptank, and the G) Little Choptank regions. A colored circle over each habitat polygon indicates the percentage of simulated larvae that were released from a given region and settled successfully on that polygon. Results are reported for transport alone (salinity-induced mortality was not applied).

APPENDIX A. ChopROMS model information and validation

The information below was excerpted from North et al. (2012) and was written primarily by Wen Long. Figures were produced by Wen Long and Steven Suttles. The text and figures are reproduced here to provide background information about the hydrodynamic model used in this thesis.

“ChopROMS (Choptank Regional Ocean Modeling System) is an open source 3D hydrodynamic model developed at the Horn Point Lab University of Maryland Center for Environmental Science by Dr. Wen Long. It is based on the Regional Ocean Modeling System (ROMS, <http://www.myroms.org/>, Shchepetkin et. al 2005), which is a numerical model based on curvilinear orthogonal horizontal grid system with a vertical terrain following S coordinate with finite difference method (FDM) to solve ocean dynamics with the assumption of hydrostatic pressure and flow incompressibility. The ChopROMS model is constructed based on a grid system with the dimension of 261x501 and resolution of approximately 120 m - 150 m (Fig. A1). Bathymetry and coastlines in the model were based on NOAA High Resolution (30 m) Estuary Bathymetry Data (based on mean lower low water level (MLLW)) adjusted to mean sea level (MSL) using datum info of NOAA tidal station #8571892 (http://tidesandcurrents.noaa.gov/epoch_datum_check.shtml?stnid=8571892) at Cambridge, MD with epoch 1983-2001.

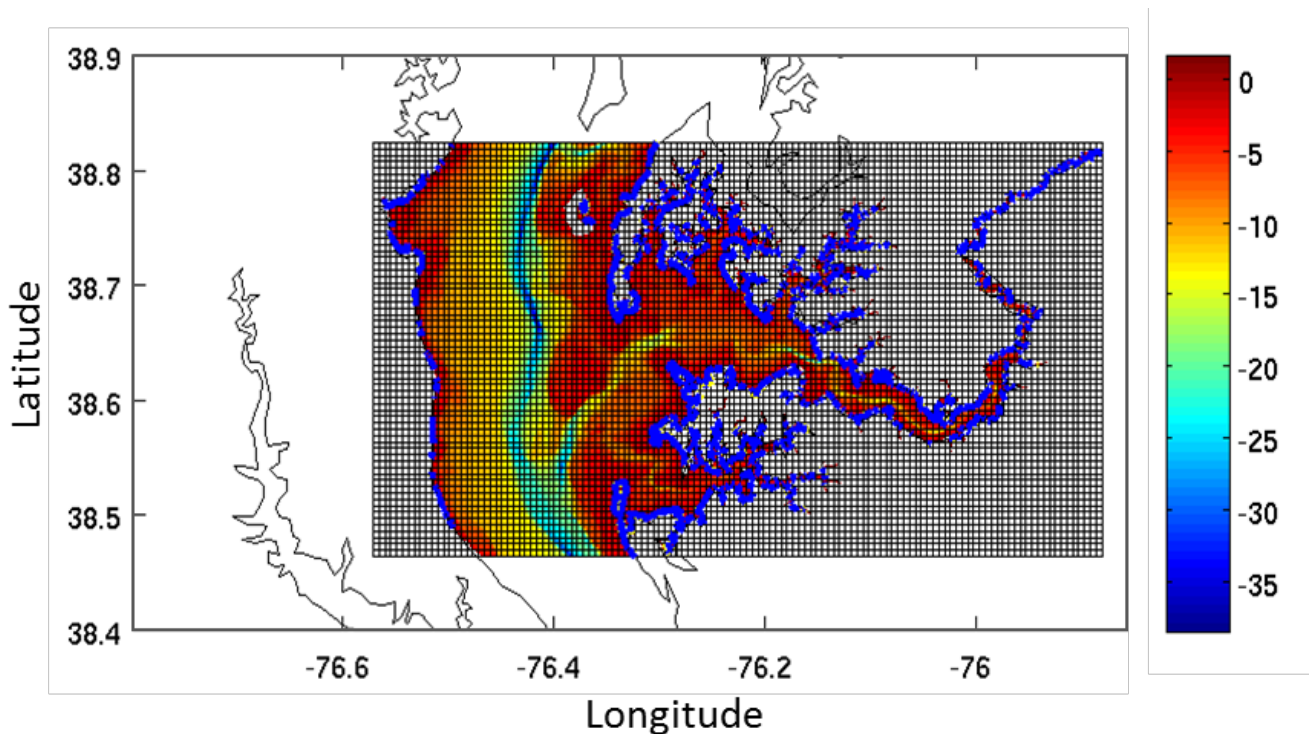


Fig.A1. ChopROMS grid with bathymetry (grid dimension: 261x501; grid size: 119-154 m; color scale: bathymetry (m) below MSL).

ChopROMS model is constrained by the following forcing conditions: 1) river discharge from the Choptank River at Greensboro adjusted by the fraction of the total watershed that this gauging station represents, 2) surface meteorological forcing including near surface wind speed, near surface air pressure and temperature, downward short wave radiation, long wave radiation and humidity, 3) boundary forcing conditions including tidal and subtidal water level, temperature and salinity at the outer boundaries located in the mainstem Bay. The data used in describing the upper forcing conditions for these hindcasts are as follows. For the river discharge, USGS daily mean discharge measurements (stream water gage #01491000) are used. For the surface meteorological conditions, the NARR (North American Regional Reanalysis) from NOAA NCEP program is obtained with a spatial resolution of 32 km and temporal resolution of 3 hours.

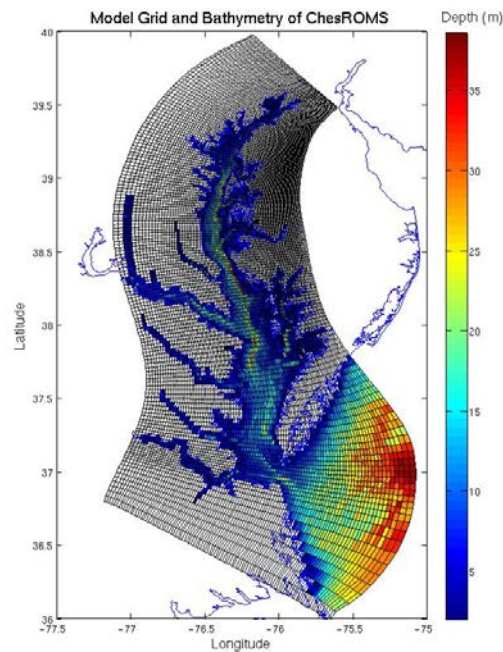


Fig. A2. ChesROMS model grid with dimension of 100x150 and depth indicated by color scale.

The total water level (tidal and subtidal), 3D temperature, salinity and depth averaged velocities (barotropic) and 3D velocities (baroclinic) are obtained from an outer model called ChesROMS (Chesapeake Regional Ocean Modeling System, Fig. A2 of ChesROMS) (Xu et al. 2002). ChesROMS is run operationally at NOAA Chesapeake Bay Office under the technical support of Wen Long and has been used to drive near-real time nowcasts and forecasts of harmful algal blooms (HABs, http://155.206.18.162/cbay_hab) in the Chesapeake Bay. Daily model outputs of ChesROMS are available at <http://155.206.18.162/ChesROMS/>. ChopROMS retrieves the ChesROMS results (temperature, salinity, velocity, sea surface height) from this URL automatically through a netcdf-java interface and interpolates them on to the northern and southern open boundary of the ChopROMS grid (Fig. A1).

ChopROMS was initialized with a cold-start (meaning that velocities were set to zero and surface elevation was set to mean sea level) and 3 months of spin-up was used before summer larval transport months were simulated. Time steps were 10 seconds for the baroclinic mode and 0.5 seconds for the barotropic mode in the model integration. There are 20 vertical sigma layers employed to resolve the vertical structure of the circulation. For the open boundaries, radiation and nudging conditions were used for temperature, salinity and barotropic velocity; radiation condition was used for baroclinic velocities; Chapman condition was used for surface elevation. These open boundary condition configurations force the model with the ChesROMS results. The k-omega turbulence model (Warner et al. 2005) was chosen to simulate the vertical turbulence structure due to shear and wind mixing.

The model was initially set up on a Linux workstation with 8 Dual-Core AMD Opteron(tm) 8220 processors, each of 2814.450 MHz cpu frequency. The model runs with MPI parallelization and it takes about 35 days wall clock time to finish one year of prediction using 6 processors on the workstation. In order to speed up the model testing and tuning process, ACOE provided access to a DOD high performance computer at chugach.arsc.edu which allowed the project to run the ChopROMS model with 48 processors in parallel and effectively finished one year of prediction within a week. Fourteen test runs of ChopROMS were conducted as part of model development and validation to ensure high-quality prediction.

A matlab toolbox was developed to compare the ChopROMS model results with CTD data (temperature and salinity) collected as part of the TRANSPORT program. Twenty 1-day cruises on the Choptank River were conducted from June through September of 2010. For each station within the model domain, the temporal and vertical variation of modeled and observed temperature and salinity were plotted. In addition, skill metrics were calculated and summarized with target diagrams (Jolliff et al. 2009). In target diagrams, a point above (or below) the center indicates model bias higher (or lower) than observations, a point to the left (or right) of center indicates more (or less) variation in the model compared to the observed variation, and a point inside (or outside) the black circle indicates whether the model does a better (or worse) job predicting the observations than the mean of observed values. Figures A3-A6 provide an example of these comparisons from a selected cruise during 2010. Overall, the skill assessment indicates that the model does an excellent job simulating salinity during the time period of larval transport (June 19 to August 24), with very little bias in June and July and slightly less or more variability than observed. The model captures the overall patterns in temperature change between cruises and from down-river to up-river, but was biased about 1 to 1.5 degrees higher than observations in model simulations in July and August. Most of the bias in both salinity and temperature occur in the up-river portion of the model domain, whereas the model tends to have less bias in the lower Choptank (the region with highest larval transport). Because salinity controls residual circulation patterns in estuaries (roughly 80% of density differences in estuaries are due to salinity), we conclude that the model is robust and that the bias in temperature does not significantly influence predicted circulation patterns.

ChopROMS model predictions were stored every 10-min to resolve changes in current velocities at tidal time scales. The following variables were stored for use in LTRANS: three-dimensional fields of temperature, salinity, density, and diffusivities, three components of velocity, and sea surface height. Each output file included 3 days of predictions and was 49 GB.”

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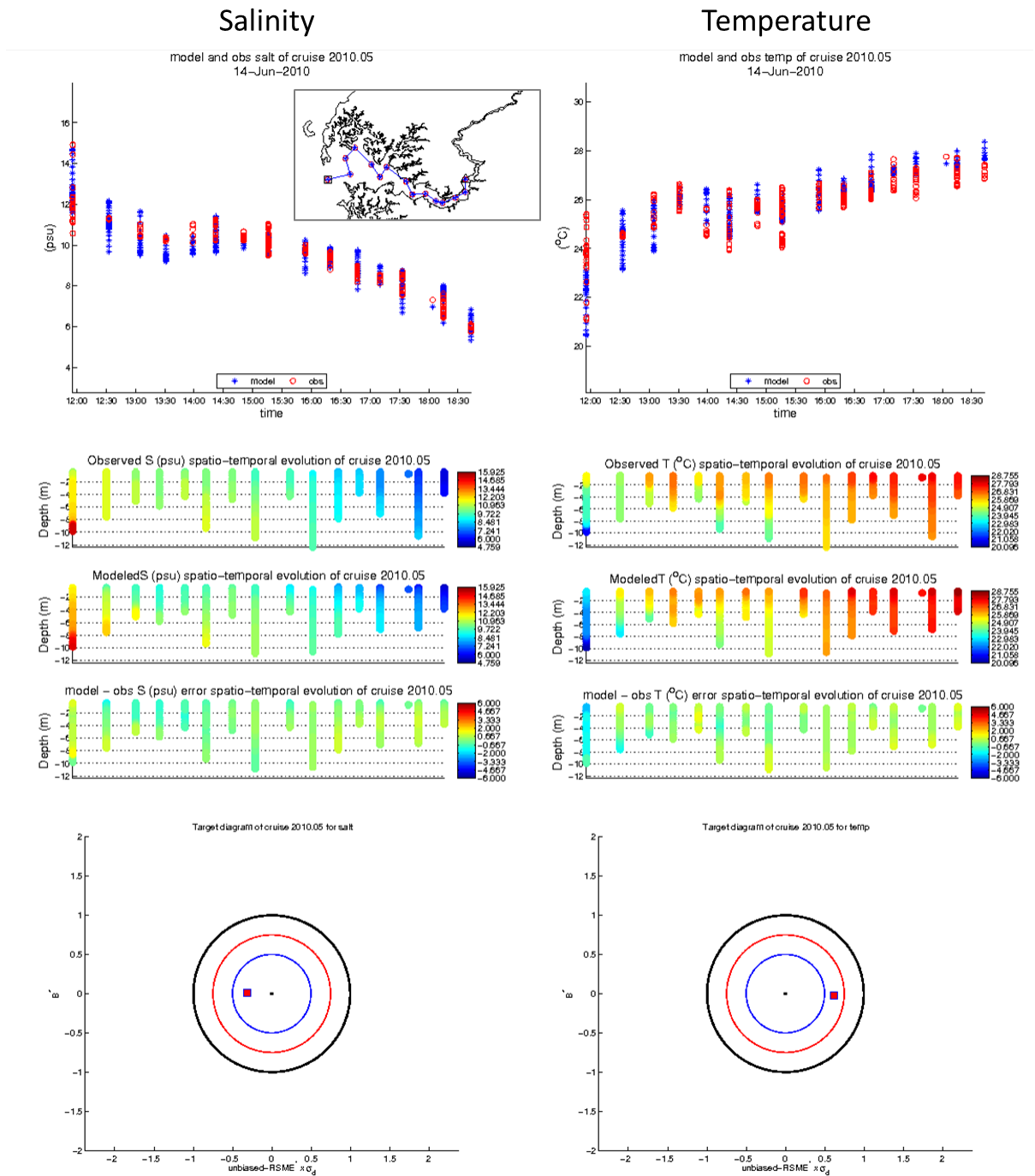


Fig. A3. Comparison of model predictions with observations of salinity (left panels) and temperature (right panels) from CTD casts on June 14, 2010. In the upper panels, scatter plots of observations (red) and model predictions at the same time and depth as observations (blue) are plotted versus time (which corresponds with the boat traveling from west to east). Middle panels show the profiles of observed values (top), predicted values (middle) and difference between them (bottom) over time with colors corresponding to salinity or temperature. Bottom panels show the target diagram score (red square). Inset in the upper left panel indicates the locations of the CTD measurements.

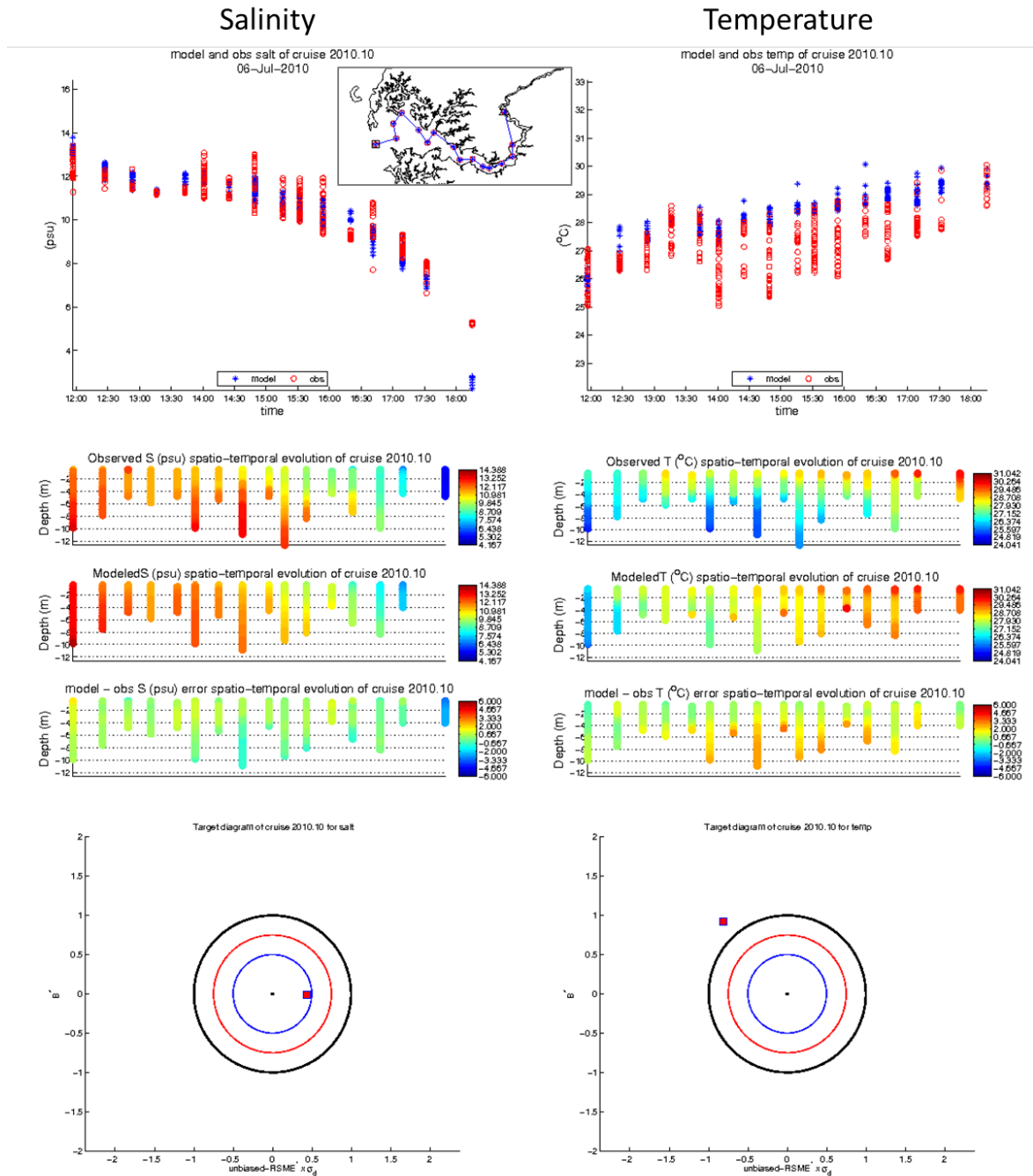


Fig. A4. Comparison of model predictions with observations of salinity (left panels) and temperature (right panels) from CTD casts on July 6, 2010. In the upper panels, scatter plots of observations (red) and model predictions at the same time and depth as observations (blue) are plotted versus time (which corresponds with the boat traveling from west to east). Middle panels show the profiles of observed values (top), predicted values (middle) and difference between them (bottom) over time with colors corresponding to salinity or temperature. Bottom panels show the target diagram score (red square). Inset in the upper left panel indicates the locations of the CTD measurements.

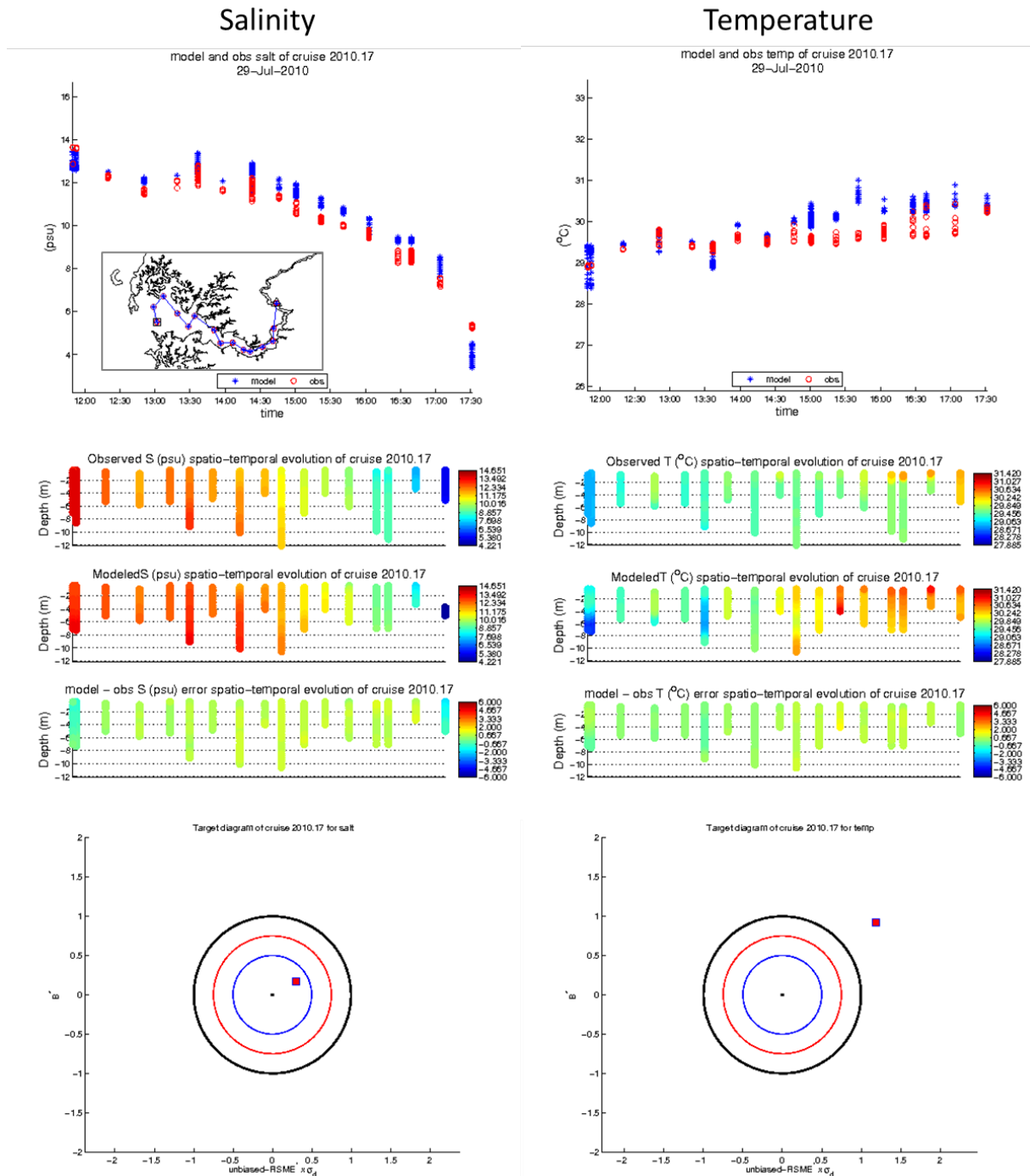


Fig. A5. Comparison of model predictions with observations of salinity (left panels) and temperature (right panels) from CTD casts on July 29, 2010. In the upper panels, scatter plots of observations (red) and model predictions at the same time and depth as observations (blue) are plotted versus time (which corresponds with the boat traveling from west to east). Middle panels show the profiles of observed values (top), predicted values (middle) and difference between them (bottom) over time with colors corresponding to salinity or temperature. Bottom panels show the target diagram score (red square). Inset in the upper left panel indicates the locations of the CTD measurements.

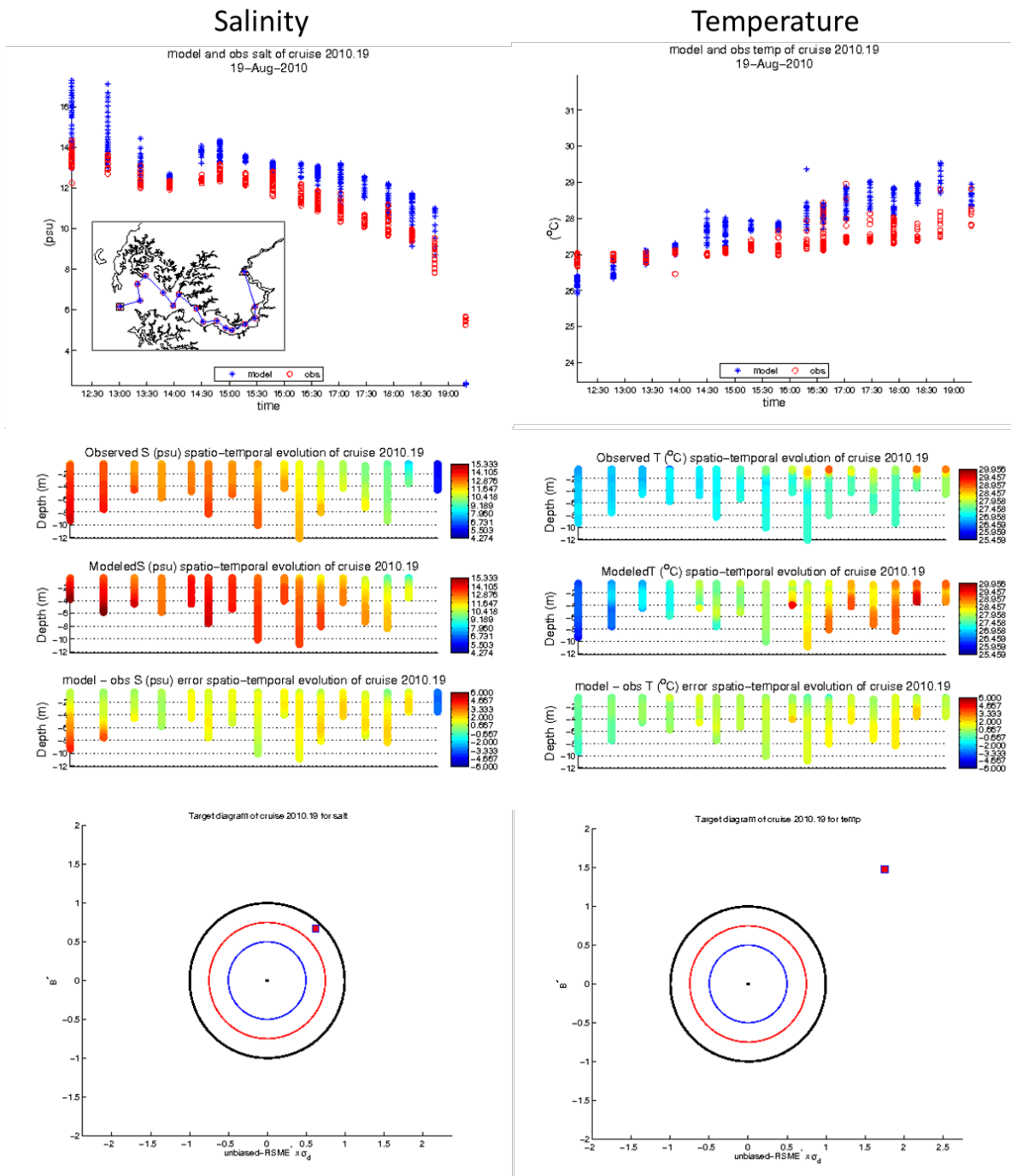


Fig. A6. Comparison of model predictions with observations of salinity (left panels) and temperature (right panels) from CTD casts on August 19, 2010. In the upper panels, scatter plots of observations (red) and model predictions at the same time and depth as observations (blue) are plotted versus time (which corresponds with the boat traveling from west to east). Middle panels show the profiles of observed values (top), predicted values (middle) and difference between them (bottom) over time with colors corresponding to salinity or temperature. Bottom panels show the target diagram score (red square). Inset in the upper left panel indicates the locations of the CTD measurements.

Appendix B. Oyster habitat used in larval transport model

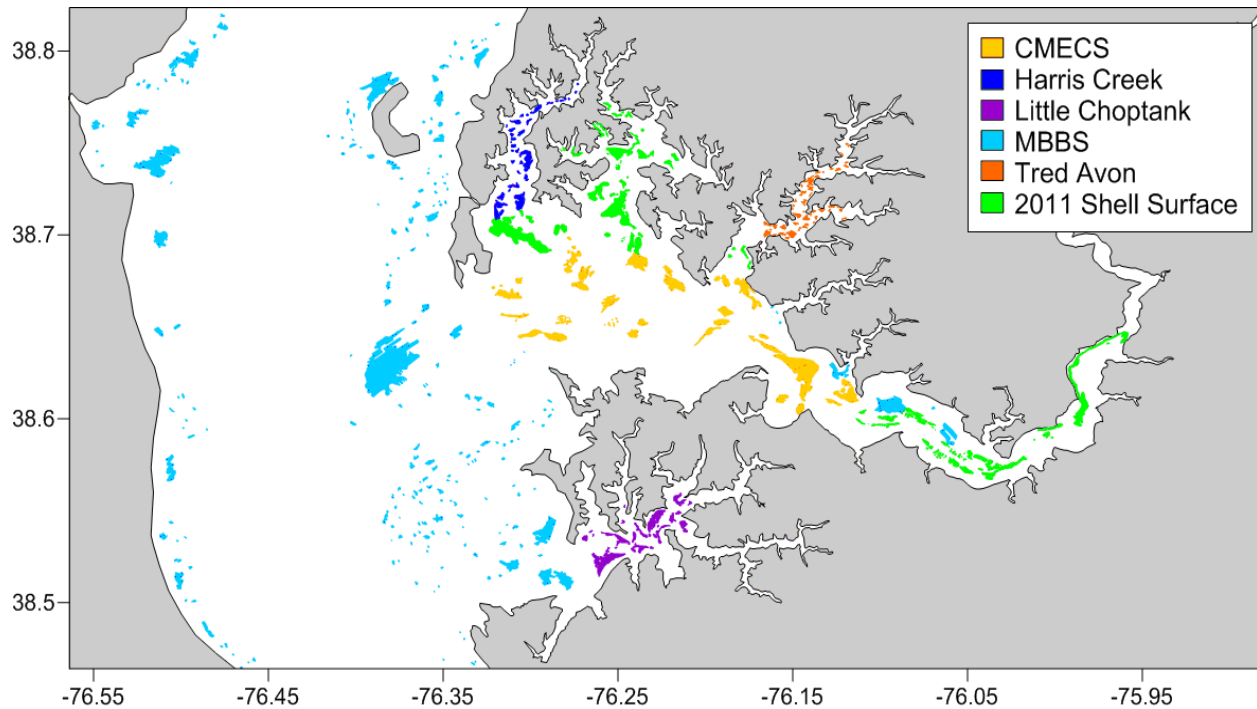


Fig. B1. Settlement habitat polygons used in the LTRANS larval transport model. Polygons are color-coded to reflect the source of the habitat information. CMECS = Coastal and Marine Ecological Classification Standard (planted reef, shell sand, shell mud); MBBS = Maryland Bay Bottom Survey; Harris Creek = targeted restoration areas in Harris Creek (MIORW 2013); Tred Avon = targeted restoration areas in the Tred Avon River (MIORW 2013); Little Choptank = targeted restoration areas the Little Choptank (MIORW 2013). In the region called the Coastal and Marine Ecological Classification Standard (CMECS) region, GIS polygons were created by combining Maryland Geological Survey side-scan sonar mosaics (2010), NOAA Chesapeake Bay Office video, ponar grabs, and acoustic classifications (2011), and patent-tong surveys (2011) by the Paynter Lab and Versar. The “planted reef”, “shell mud”, and “shell sand” polygons from the CMECS polygons were used. Outside of this region and outside of the regions with updated habitat in Harris Creek and the Tred Avon and Little Choptank Rivers, the habitat polygons which were implemented in the previous larval transport simulations were used (North et al. 2008, 2012). These polygons included the “shell surface” layers that were based on side-scan sonar surveys in 2010-2011 as well as the ‘cultch’ layer from the MBBS which had been reduced to 29.2% of their original area (Greenhawk 2005). More information about these polygons can be found in North et al. (2008, 2012). (Extracted from North and Spires *in prep*).

APPENDIX C. Flow and salinity analysis

Table C1. Sum of February through August monthly mean discharge $\text{ft}^3 \text{s}^{-1}$ at USGS gauging stations at Greensboro on the Choptank River (station identification number 01491000) and Conowingo Dam (station identification number 01578310) on the Susquehanna River.

Year	USGS Conowingo flow	USGS Greensboro flow
1948	NA	1,417
1949	NA	964
1950	NA	612
1951	NA	807
1952	NA	1,591
1953	NA	1321
1954	NA	650
1955	NA	735
1956	NA	679
1957	NA	740
1958	NA	2,096
1959	NA	656
1960	NA	871
1961	NA	1,441
1962	NA	941
1963	NA	682
1964	NA	1,058
1965	NA	509
1966	NA	244
1967	NA	1553
1968	266,458	900
1969	212,620	956
1970	367,550	979
1971	330,121	1,045
1972	584,940	1,560
1973	342,710	1,208
1974	296,190	955
1975	353,150	1,749
1976	328,710	581
1977	314,950	340
1978	388,260	1,316
1979	355,380	1,737
1980	276,270	1,053
1981	276,460	619

Table C1 (Cont.).

Year	USGS Conowingo flow	USGS Greensboro flow
1982	344,571	1,008
1983	358,031	1,849
1984	493,160	1,657
1985	204,758	419
1986	324,420	684
1987	240,138	818
1988	236,380	669
1989	368,790	1,952
1990	320,560	1014
1991	234,400	784
1992	255,970	673
1993	429,454	1,167
1994	485,530	1,939
1995	171,205	624
1996	363,040	1,943
1997	236,628	1,246
1998	379,247	1,500
1999	188,273	632
2000	324,620	1,363
2001	218,444	1,582
2002	276,553	389
2003	408,760	2374
2004	394,310	1,103
2005	291,372	1,225
2006	288,490	883
2007	259,529	1,029
2008	338,405	938
2009	246,380	1,129
2010	223,258	1,430
2011	497,320	1,548
2012	211,821	527
2013	263,920	1,907
2014	300,220	1,411

Table C2. Salinity and flow data used for regression analysis. Source of salinity data shown with sum of February – August monthly mean flow ft^3/s as measured at USGS Greensboro and Conowingo. Salinity value listed is the average seasonal salinity value for that given year and is the value used in regression analysis for that region. Data source CS = Coastal Intensive Site Network report 1999-2001 (Malone et al. 2003), BT = Bivalve Larvae TRANSPORT Mapping Survey 2010-2012 (North 2013), CBP = Chesapeake Bay Program monitoring station ET 5.2 (CBP 2015), Newell = Newell, R.I.E., pers. observation, MRC =Midshore Riverkeeper Conservancy (MRC 2015).

A. Station 1

Year	Data Source	Conowingo flow February- August $\text{ft}^3 \text{ s}^{-1}$	Greensboro flow February- August $\text{ft}^3 \text{ s}^{-1}$	Average Salinity	n
1999	CS 3	188,273	633	15.1	35
2000	CS 3	324,620	1,364	11.1	68
2001	CS 3	218,444	1,582	13.2	68
2010	BT 1	223,258	1,430	12.6	235
2011	BT 1	497,320	1,548	9.5	210
2012	BT 1	211,821	528	13.5	190

B. Station 2

Year	Data Source	Conowingo flow February- August $\text{ft}^3 \text{ s}^{-1}$	Greensboro flow February- August $\text{ft}^3 \text{ s}^{-1}$	Average Salinity	n
2010	BT 2	223,258	1,430	12.5	260
2011	BT 2	497,320	1,548	9.3	229
2012	BT 2	211,821	528	13.4	183

C. Station 3

Year	Data Source	Conowingo flow February- August $\text{ft}^3 \text{ s}^{-1}$	Greensboro flow February- August $\text{ft}^3 \text{ s}^{-1}$	Average Salinity	n
2010	BT 3	223,258	1,430	11.7	212
2011	BT 3	497,320	1,548	8.6	176
2012	BT 3	211,821	528	12.8	152

Table C2 (Cont.).

D. Station 4					
Year	Data Source	Conowingo flow February- August $\text{ft}^3 \text{ s}^{-1}$	Greensboro flow February- August $\text{ft}^3 \text{ s}^{-1}$	Average Salinity	n
2011	BT 22	497,320	1,548	8.3	294
2012	DNR	211,821	528	12.7	6030
2013	DNR	263,920	1,908	10.7	7,733
2014	DNR	300,220	1,411	9.8	8,865

E. Station 5					
Year	Data Source	Conowingo flow February- August $\text{ft}^3 \text{ s}^{-1}$	Greensboro flow February- August $\text{ft}^3 \text{ s}^{-1}$	Average Salinity	n
2010	BT 4	223,258	1,430	11.3	212
2011	BT4	497,320	1,548	8	176
2012	BT4	211,821	528	12.5	152

F. Station 6					
Year	Data Source	Conowingo flow February- August $\text{ft}^3 \text{ s}^{-1}$	Greensboro flow February- August $\text{ft}^3 \text{ s}^{-1}$	Average Salinity	n
1982	Newell	344,571	1,008	11.3	3
1983	"	358,031	1,849	9.0	3
1984	"	493,160	1,658	7.8	3
1985	"	204,758	420	13.6	3
1986	"	324,420	684	12.6	25
1987	"	240,138	819	13.7	13
1988	"	236,380	670	13.4	8
1989	"	368,790	1,952	10.1	15
1990	"	320,560	1,014	9.0	10
1991	"	234,400	784	11.5	11
2013	MRC	263,920	1,908	10.7	3
2014	MRC	300,220	1,411	8.7	3

Table C2 (Cont.).

F. Station 7

Year	Data Source	Conowingo flow February- August $\text{ft}^3 \text{ s}^{-1}$	Greensboro flow February- August $\text{ft}^3 \text{ s}^{-1}$	Average Salinity	n
1999	CS 5	188,273	633	14.7	35
2000	CS 5	324,620	1,364	10.4	68
2001	CS 5	218,444	1,582	12.5	68
2010	BT 6	223,258	1,430	11.7	260
2011	BT 6	497,320	1,548	8.5	234
2012	BT 6	211,821	528	12.9	215

G. Station 8

Year	Data Source	Conowingo flow February- August $\text{ft}^3 \text{ s}^{-1}$	Greensboro flow February- August $\text{ft}^3 \text{ s}^{-1}$	Average Salinity	n
2010	BT 7	223,258	1,430	11.3	234
2011	BT7	497,320	1,548	8.0	175
2012	BT7	211,821	528	12.5	139

H. Station 9

Year	Data Source	Conowingo flow February- August $\text{ft}^3 \text{ s}^{-1}$	Greensboro flow February- August $\text{ft}^3 \text{ s}^{-1}$	Average Salinity	n
1982	Newell	344,571	1,008	10.9	3
1983	Newell	358,031	1,849	8.7	3
1984	Newell	493,160	1,658	6.5	3
1985	Newell	204,758	420	13.2	3
1986	Newell	324,420	684	12.2	25
1987	Newell	240,138	819	13.2	17
1988	Newell	236,380	670	12.4	8
1989	Newell	368,790	1,952	8.9	14
1990	Newell	320,560	1,014	8.0	10
1991	Newell	234,400	784	10.5	11

Table C2 (Cont.).

I. Station 10

Year	Data Source	Conowingo flow February-August $\text{ft}^3 \text{s}^{-1}$	Greensboro flow February-August $\text{ft}^3 \text{s}^{-1}$	Average Salinity	n
1999	CBP	188,273	633	12.2	49
2000	CBP	324,620	1364	8.1	35
2001	CBP	218,444	1582	9.5	34
2010	CBP	223,258	1430	9.9	21
2011	CBP	497,320	1548	7	14
2012	CBP	211,821	528	12	14

J. Station 11

Year	Data Source	Conowingo flow February-August $\text{ft}^3 \text{s}^{-1}$	Greensboro flow February-August $\text{ft}^3 \text{s}^{-1}$	Average Salinity	n
1999	CS 11	188,273	633	11.1	35
2000	CS 11	324,620	1,364	6.4	69
2001	CS 11	218,444	1,582	5.9	68
2010	BT 15	223,258	1,430	7.4	169
2011	BT 15	497,320	1,548	5.2	104
2012	BT 15	211,821	528	9.1	88

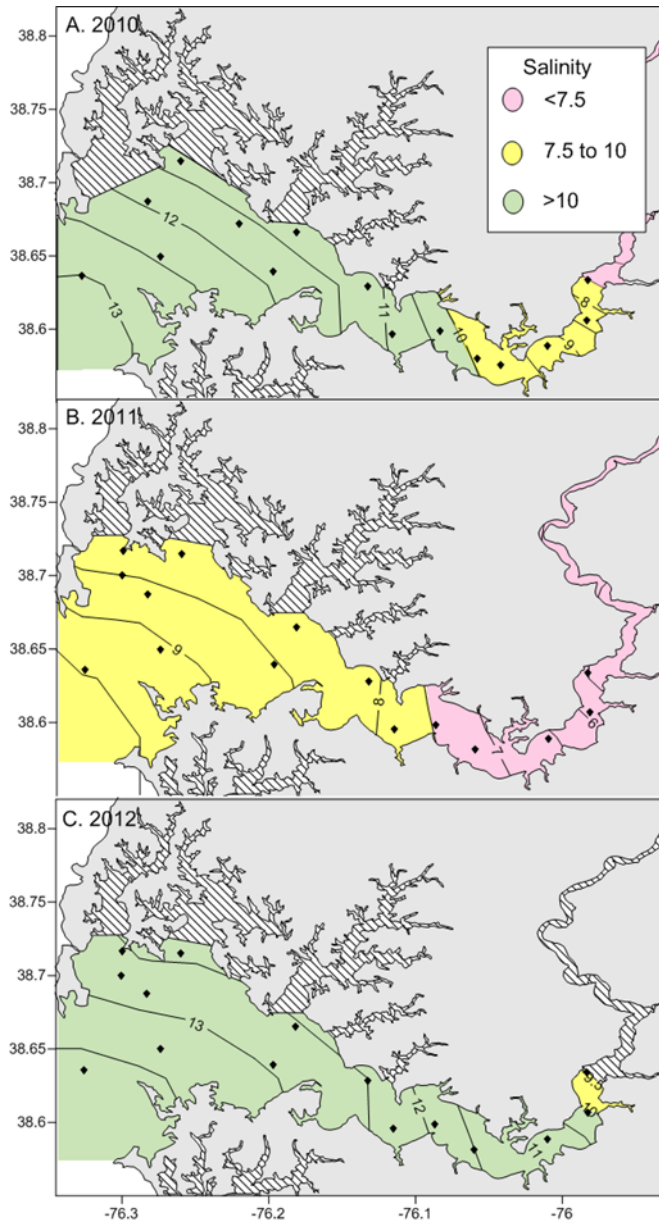
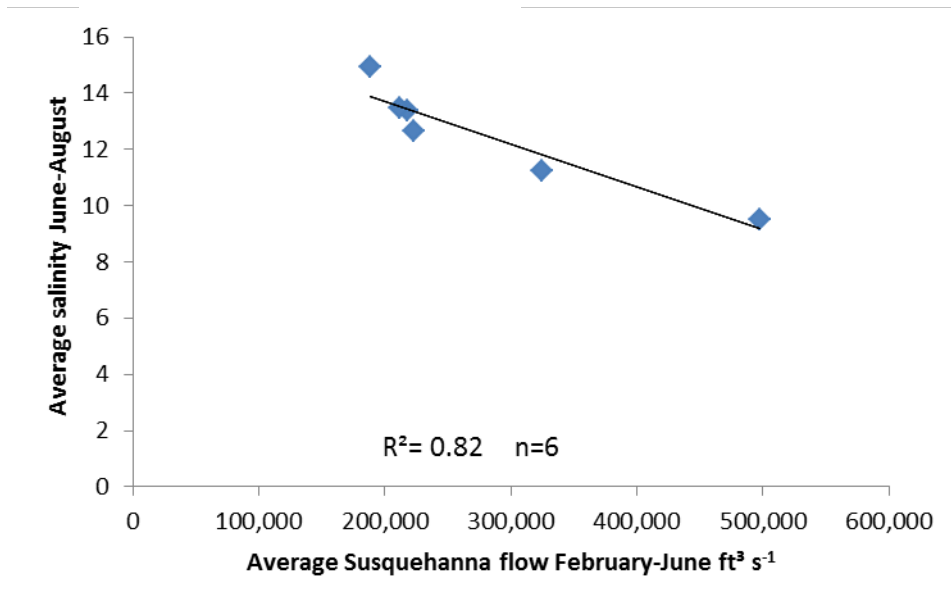
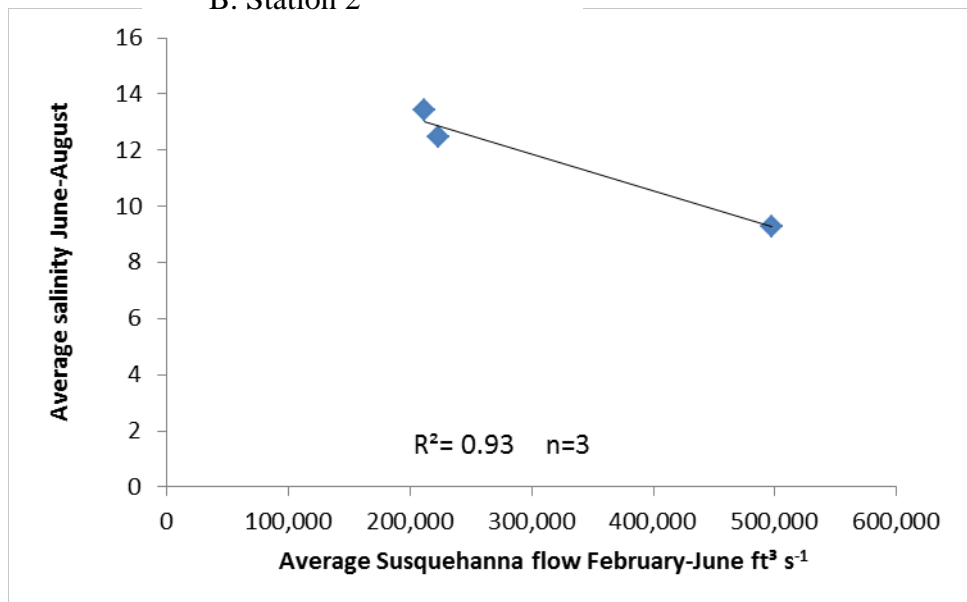


Fig. C1. Contour plots of average salinities at stations (•) in Choptank River during: A) 2010, B) 2011, C) 2012. Salinity observations were made during the Bivalve TRANSPORT Program (North 2013). Averages were composed of data collected between June- August and at depths between 6 - 0.75 m. The colors represent salinity values <7.5 (red) likely to be poor for larval survival, 7.5-10.0 (yellow) unknown effect on larval survival, and >10.0 (green) known to be good for larval survival. These plots indicate that there can be a large degree of variability in the average salinity during the time of larvae transport in the Choptank River from year to year. The summed monthly mean freshwater flows to the Susquehanna River were 7th, 46th and 4th percentiles in 2010, 2011, and 2012, respectively (based on Appendix Table C1). The summed flows to the Choptank River were 50th, 53rd and 6th percentiles in 2010, 2011, and 2012, respectively (based on Appendix Table C1).

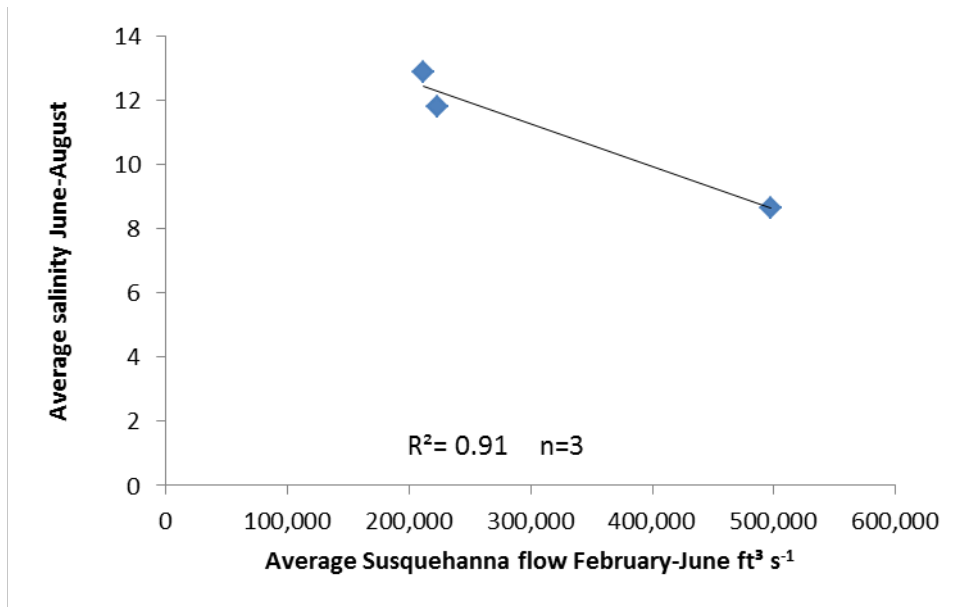
A. Station 1



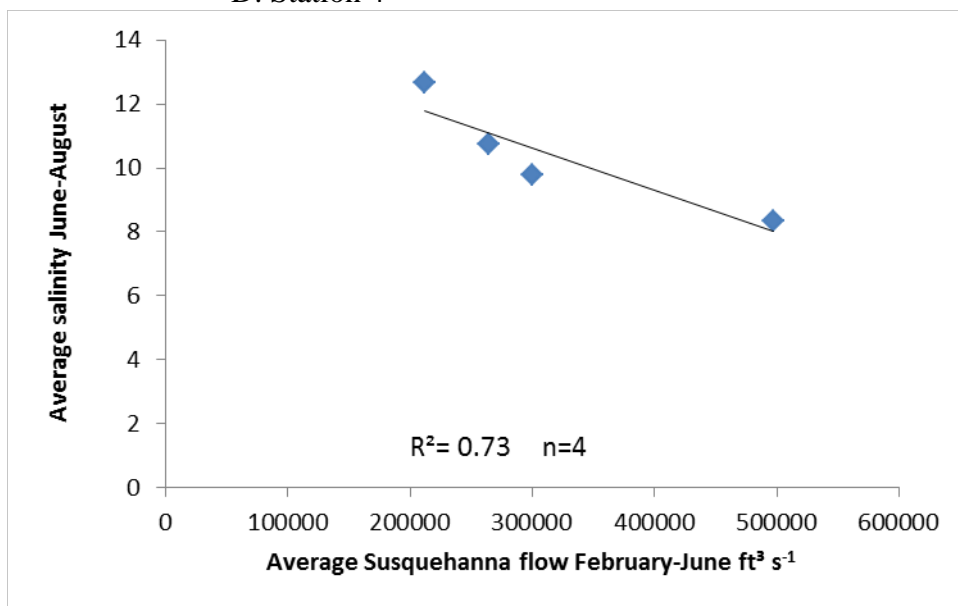
B. Station 2



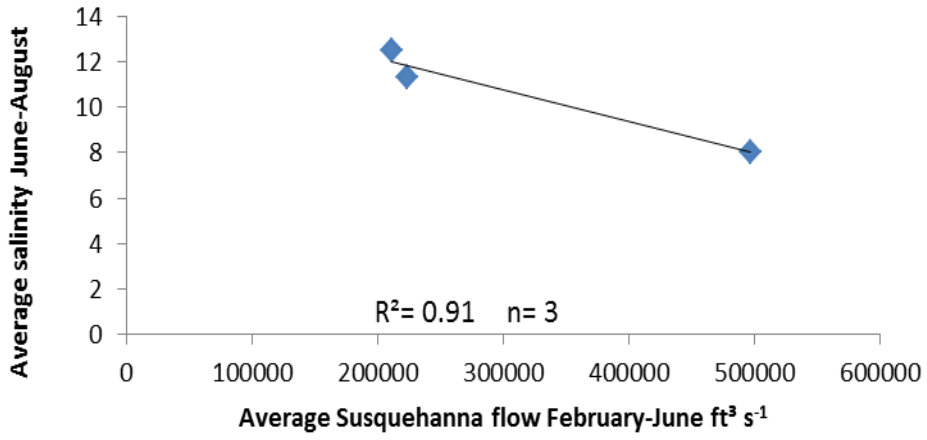
C. Station 3



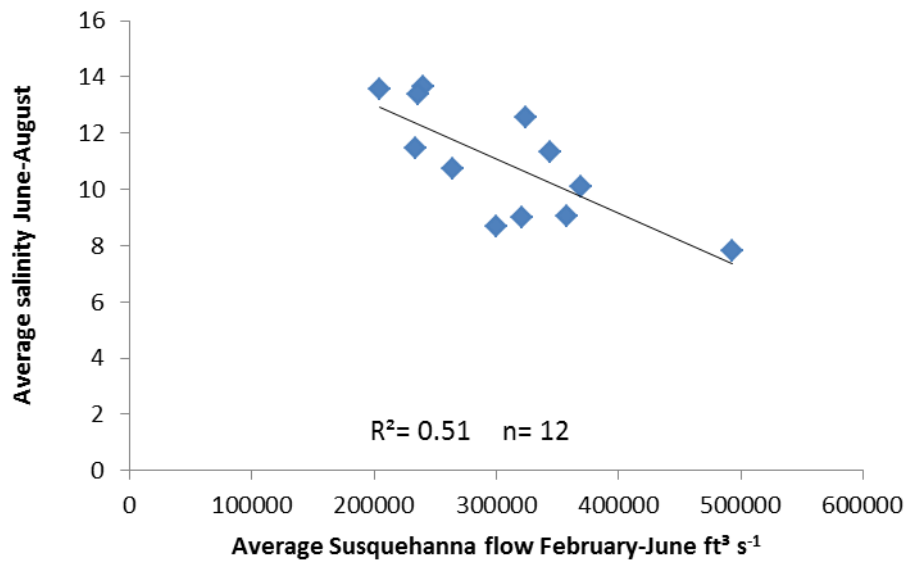
D. Station 4



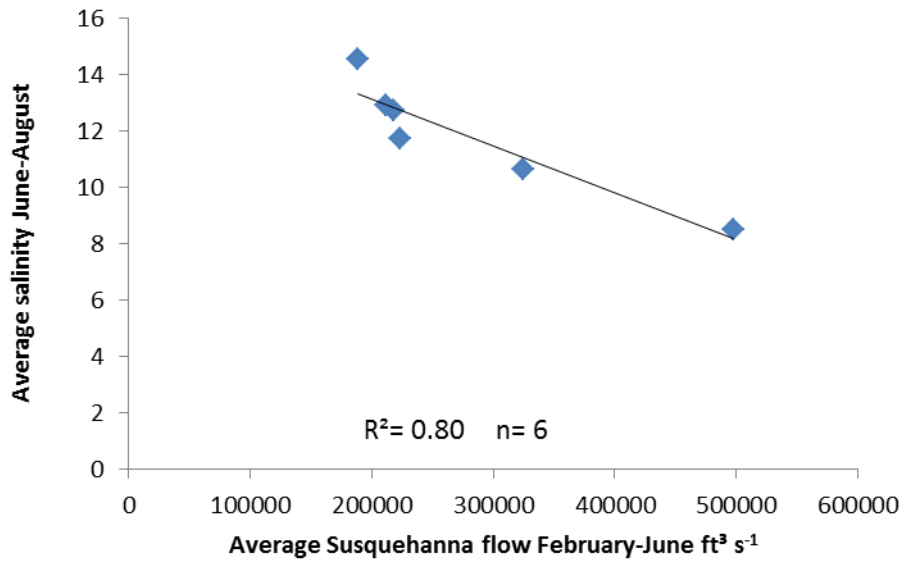
E. Station 5



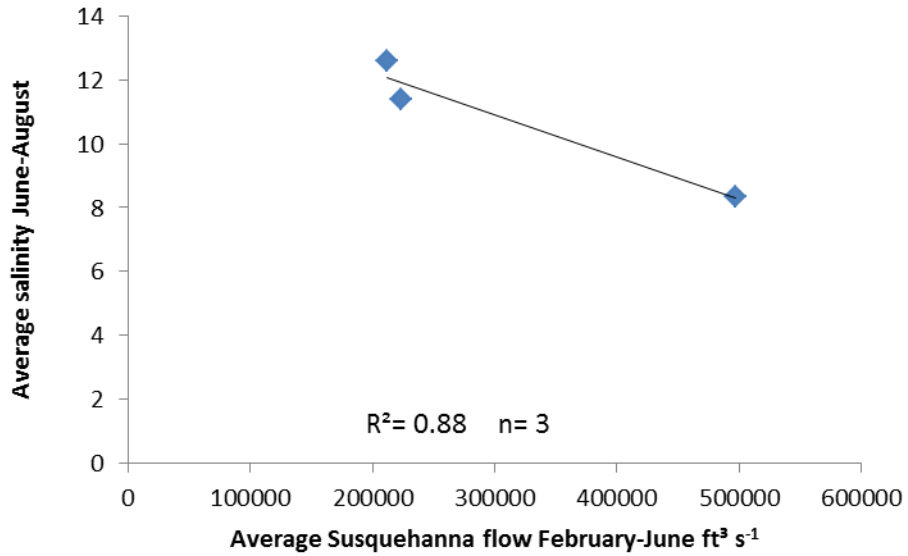
F. Station 6



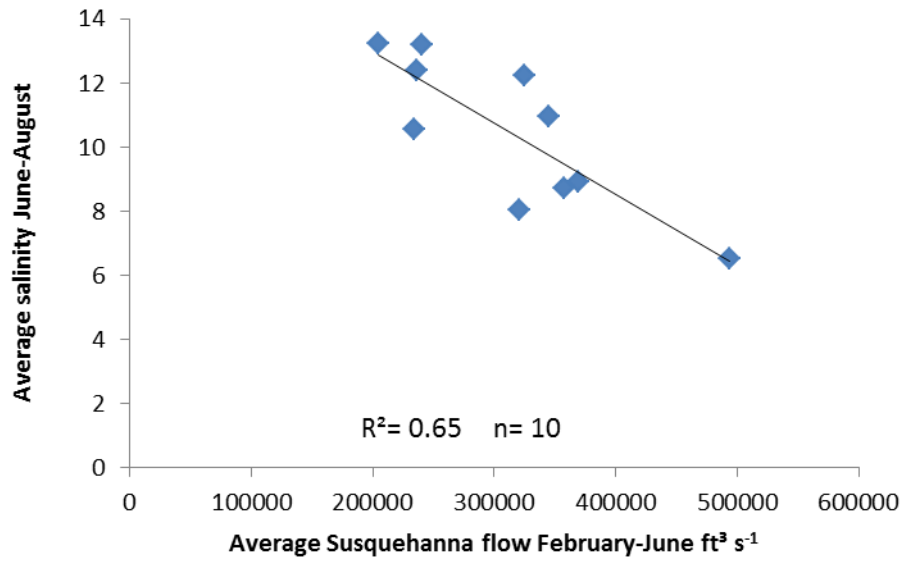
G. Station 7



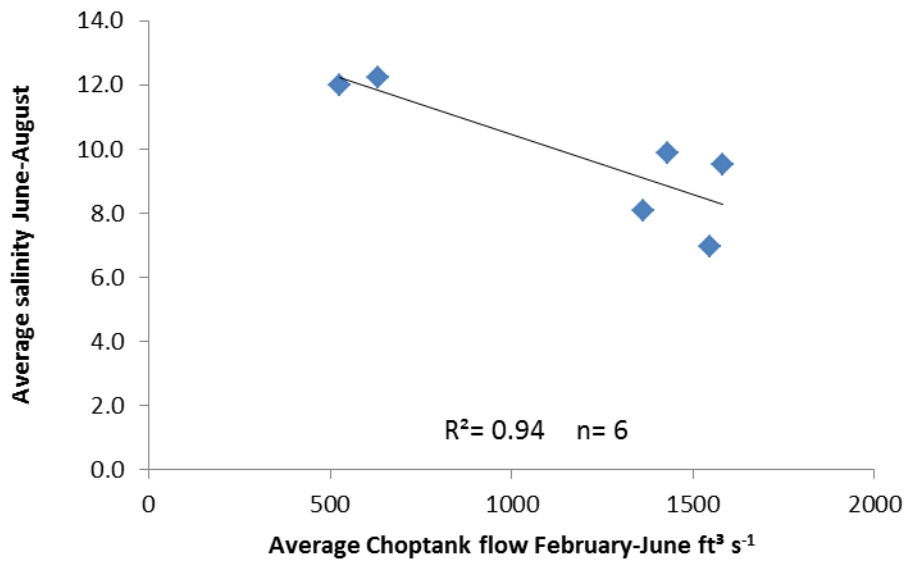
H. Station 8



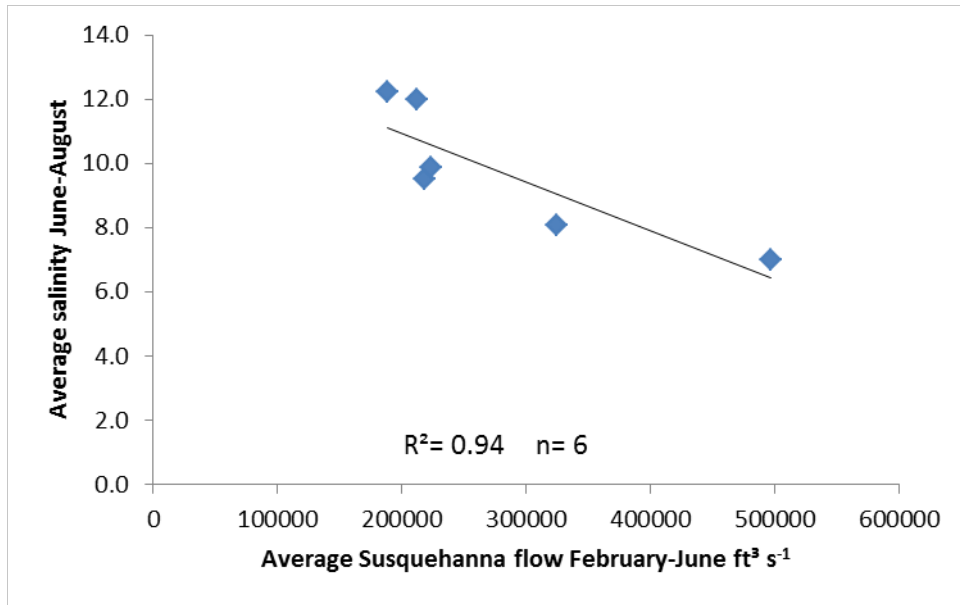
I. Station 9



J. Station 10



J. Station 10 (Cont.)



K Station 11

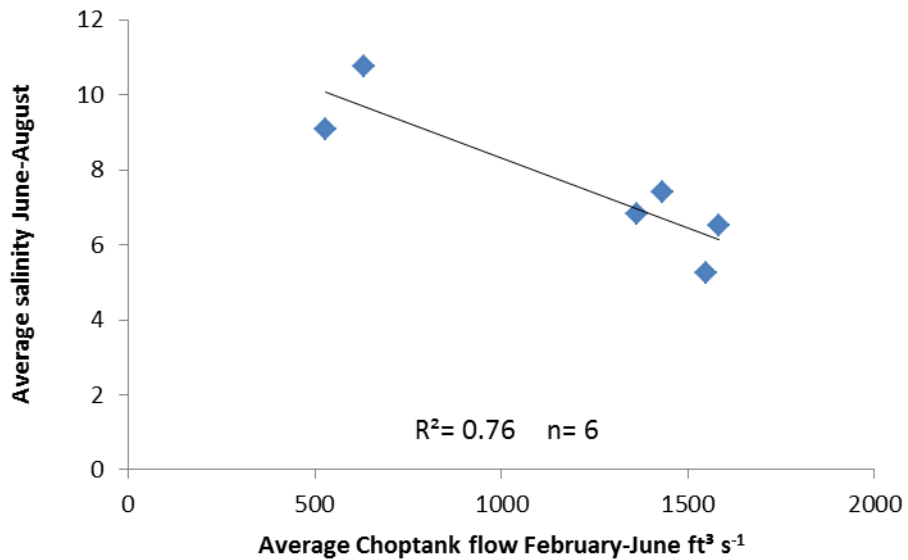


Fig C2. Sum of February through August monthly mean discharge ft³ s⁻¹ at USGS gauging stations at Greensboro on the Choptank River (station identification number 01491000) and Conowingo Dam (station identification number 01578310) on the Susquehanna River, plotted against average June –August salinities at stations 1-11. N= number of observations. R² values for station 10 are values from multiple regression analyses.

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