

The influence of mixing processes and behavior on larval transport and mortality estimates in a stratified wind- and tidally-forced system

E. W. North¹, R. R. Hood¹, L. Zhong¹, M. Li¹, and T. F. Gross²

¹University of Maryland Center for Environmental Science, Horn Point Laboratory
P. O. Box 775, Cambridge, MD, 21613, USA [tel: +1 410 228 8200, fax +1 410 221 8490, e-mail: enorth@hpl.umces.edu, raleigh@hpl.umces.edu, mingli@hpl.umces.edu, lzhong@hpl.umces.edu]

²NOAA/NOS/Coast Survey Development Lab and Chesapeake Community Model Program, Chesapeake Research Consortium, 645 Contees Wharf Road, Edgewater, MD 21037, USA [tel: +1 410-798-1283, fax +1 410 798-0816, e-mail: grosst@si.edu]

ABSTRACT

Coupled biological-physical models have been used to enhance understanding of fisheries recruitment, identify marine protected areas, and, in this case, determine the potential to establish or restore a self-sustaining population of oysters. The overall objective of our research program is to determine the potential distance and rate of larvae dispersal for two oyster species, *Crassostrea virginica* (native) and *C. ariakensis* (non-native), in Chesapeake Bay using a coupled biological-physical model. Predictions of the fate of larvae in coupled models may be highly dependent on simulated circulation patterns and mixing processes as well as biological factors like larval behavior. The goal of this paper is to assess the influence of these factors on predictions of larval transport. We used a particle-tracking model and output from a 3D hydrodynamic model (Regional Ocean Modeling System) implemented in Chesapeake Bay, a stratified wind- and tidally-forced estuary. We conducted two sets of model scenarios that focused on 1) turbulent processes and 2) larval behavior. Results of the turbulence sensitivity studies demonstrated that simulated vertical or horizontal turbulent particle motion resulted in both horizontal and vertical dispersal of particles. In addition, particle transport estimates were quite sensitive to the value of horizontal diffusivity used to parameterize sub-grid scale turbulence in the particle-tracking model. Model scenarios that included larval behavior demonstrated that even the particles with the slowest swimming speed (0.5 mm s^{-1}) influenced the direction of transport such that their distribution was significantly different from that of passive particles. In addition, there were stage-specific differences in particle dispersal, the magnitude of which differed between behavior types. Results indicate that proper parameterization of turbulent processes (for passive organisms like eggs) and behavior (for active organisms) is critical for predicting larval dispersal. In addition, results suggest that knowledge of the influence of stage-specific larval behaviors on transport is important for accurate estimates of mortality rates from field collections.

INTRODUCTION

Restoration of oyster populations in Chesapeake Bay is widely recognized by the scientific and management communities as a high priority goal (Chesapeake 2000 Agreement, <http://www.>

chesapeakebay.net/agreement.htm). The potential benefits include economic gain (restoring a valuable regional fishery), social gain (supporting an industry and a way of life) and environmental restoration (filtration and improved water quality). Efforts to restore the native oyster, *Crassostrea virginica*, are on-going in Chesapeake Bay but the results to date have been mixed; oyster populations are not flourishing and disease-related mortality rates are still high (NRC 2004). Maryland Department of Natural Resources (DNR) has proposed the introduction of a non-native oyster species, *Crassostrea ariakensis*, as an alternative strategy. It is believed that this species may be able to repopulate the Bay much faster than the native species because of their growth rates and resistance to disease (Calvo et al. 2001, NRC 2004). However, the introduction of *C. ariakensis* poses a number of potential risks that must be quantitatively assessed before an introduction is considered. These risks include potential disease transmission, unforeseen (and uncontrolled) growth and dispersal, and failure to establish a self-sustaining and harvestable population within a reasonable amount of time. *C. ariakensis* may have physiological tolerances, vital rates, and larval behaviors that could prevent it from establishing a viable population in Chesapeake Bay. These factors are being assessed in ongoing research programs funded by DNR, including our modeling study that focuses on transport of native and non-native oyster larvae.

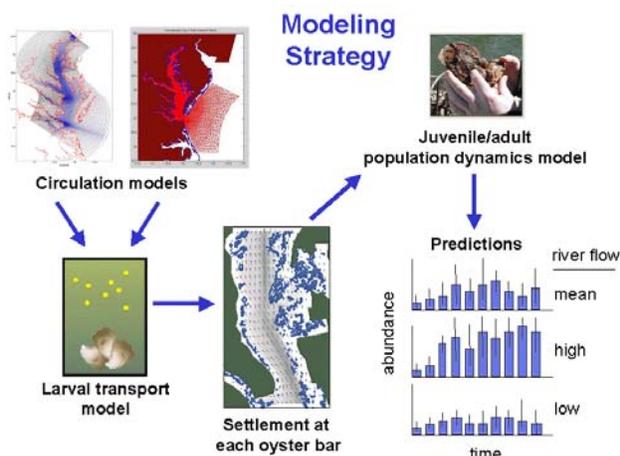


Fig.1. Overall modeling strategy. We will use output from two circulation models in the larval transport model to predict settlement success at each oyster bar. This information will be used in the DNR-funded juvenile/adult demographic model to make predictions about oyster population growth and dispersal under different climatic conditions.

settlement locations. Predictions from the larval transport model will be formatted for incorporation into the DNR-funded oyster demographic model (currently in development by M, Christman, J. Volstad and colleagues at University of Maryland College Park and Versar). In addition to enabling model-data comparisons of physical conditions and oyster spat settlement, our larval transport modeling approach will facilitate incorporation of uncertainty related to the interaction of circulation patterns and larval behavior into estimates of population growth and dispersal. The overall modeling strategy is depicted in Fig. 1.

The overall objective of our larval transport research program is to determine the potential distance and rate of *C. ariakensis* and *C. virginica* oyster larvae dispersal in Chesapeake Bay using coupled hydrodynamic and particle-tracking models with links to population models. Our goal is to implement an existing particle-tracking model (North et al. 2003, *in press*) as a stand-alone, open-source oyster larvae transport model that will utilize the output of two 3D hydrodynamic models (ROMS and QUODDY) to predict the movement of particles that simulate oyster larvae. The larval transport model will be run with 1) circulation patterns from both hydrodynamic models, 2) circulation patterns from years of different physical conditions, and 3) observed behaviors of *C. ariakensis* and *C. virginica*. The model will be used to track larval transport and pediveliger

The objective of this paper is to assess the sensitivity of larval transport predictions to the parameterization of mixing processes and larval behavior. Much of our understanding about the transport and dispersal of fish and shellfish early-life stages in coastal waters is based on large-scale advective processes (e.g., McConnaughey et al. 1994, Hare et al. 1999). Although advection is certainly an important factor in the transport of planktonic organisms, the influence of organism behavior and mixing processes may be substantial. As exemplified by Largier (2003), diffusive processes can significantly influence the range of a population's distribution, such that the dispersal of a population can be against mean advective flow. In addition, organism behavior such as selective tidal stream transport or diurnal vertical migration can result in directed movement, potentially in the opposite direction of mean flow (Miller 1988, Hill 1994, Rowe & Epifanio 1994).

We conducted a suite of sensitivity studies to identify the relative influence of advection, mixing processes, and larval behavior on predicted larval transport. We used a particle-tracking model and output from a 3D hydrodynamic model (Regional Ocean Modeling System) implemented in Chesapeake Bay, a stratified wind- and tidally-forced estuary. We conducted two sets of model scenarios that focused on 1) mixing processes and 2) larval behavior. The mixing sensitivity studies focused on comparisons in dispersal between particles whose movement was based on advection, vertical turbulence and/or horizontal turbulence. The larval behavior sensitivity studies focused on comparisons between four types of larval behaviors (passive, diurnal vertical migration, tidally-timed vertical migration, bottom oriented) and three stages (early, middle, late) simulated by varying vertical swimming speeds. In the following sections, we first describe the coupled bio-physical model then present methods and results of the sensitivity studies. Finally, we discuss results of the model scenarios and their implications for estimation of mortality rates from field collections.

MODEL DESCRIPTION

Our coupled bio-physical larval transport model has two components: a 3D hydrodynamic model and a particle-tracking model. The 3D hydrodynamic model provides circulation and hydrographic predictions that the particle-tracking model uses to determine particle movement through space and time.

Hydrodynamic model. We used predictions from the state-of-art Regional Ocean Modeling System (ROMS) implemented in the Chesapeake Bay estuary (Li et al., *submitted*) (Fig. 2). ROMS is a free-surface, hydrostatic, primitive equation ocean model that uses stretched, terrain-following coordinates in the vertical direction, and orthogonal curvilinear coordinates in the horizontal direction (Song and Haidvogel, 1994). The Chesapeake Bay implementation has a horizontal

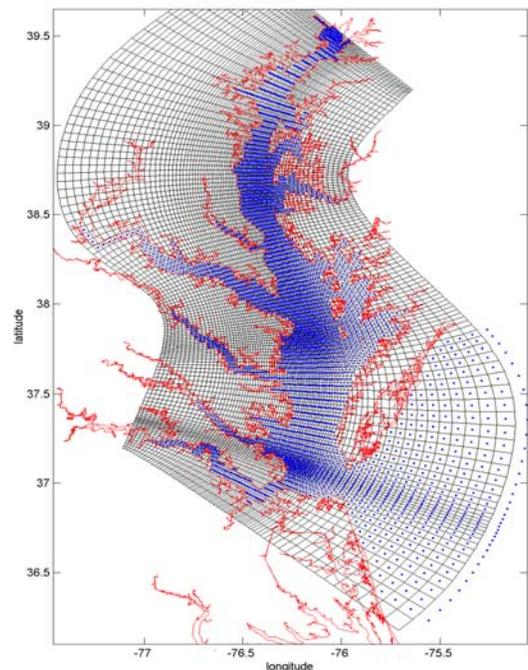


Fig. 2. Chesapeake Bay hydrodynamic model grid for the Regional Ocean Modeling System (ROMS) model.

resolution of about 1 km in the main stem of the Bay, 20 layers in the vertical direction, an internal time step of 120 s and an external time step of 2 s. Forcing conditions for ROMS include streamflow from USGS gauges at major Chesapeake tributaries (Susquehanna, Potomac, James, Choptank, etc.) as well as wind data that were assembled from regional airports. Tidal forcing was prescribed at the oceanic boundary by specifying 6 tidal constituents. We made a hind cast simulation for the high runoff year of 1996 and saved sea surface height (Fig. 3), current velocities, salinity, temperature, and vertical diffusivities at each grid coordinate at 6 min time steps in netCDF format.

Particle tracking model. The larval dispersal model is designed to predict the movement of particles based on advection, turbulence and larval behavior. It has an external and internal time step and boundary condition algorithms that keep particles from leaving the model domain. The external time step is the time step of hydrodynamic model output (6 min). The internal time step is the time step for which movement of particles is calculated and is much smaller (30 s) than the external time step so that particles do not move in large jumps that could cause inconsistency between hydrodynamic model and particle tracking model predictions.

For each particle, a triangulation search algorithm was used to determine the grid cell in which a particle was located and an interpolation scheme was used to estimate water properties at the particle location. The interpolation scheme was adapted from the existing North et al. (*in press*) particle-tracking model and enhanced to handle model domains with irregular bottoms (i.e., realistic bathymetries). Estimates of two-dimensional water properties (sea surface height, water depth) were calculated with 4-point linear interpolation weighted by the three-dimensional distance between the particle and each grid point. Estimates of three-dimensional water properties (current velocities in the x-, y-, z- directions, vertical diffusivity, salinity, temperature) at the particle location were completed with a ‘water column profile’ interpolation scheme (North et al., *in revision*). In this scheme, values were interpolated horizontally along each sigma level (using weighted distance interpolation) to create a vertical profile of values at the x-y particle location. Then a tension spline curve was fit to the vertical profile and used to estimate the water property (e.g., current velocity) at the particle location.

At each time step of the larval transport model, particle motion was calculated as the sum of movement due to advection, turbulence and larval behavior. The larval transport model contains sub-models for each of these components. A description of each follows.

Advection sub-model. A four-step procedure was used to calculate particle movement due to advection. First, current velocities were estimated at the particle location (x_n) at three time

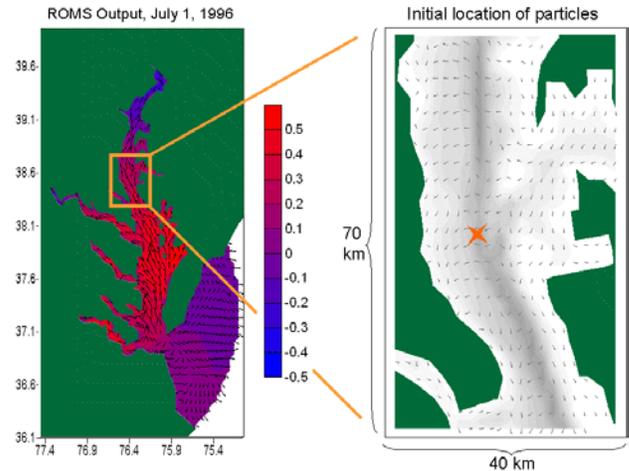


Fig. 3. Left: Chesapeake Bay sea surface height (color) and surface current velocities (arrows) predicted by ROMS model for July 1, 1996. Orange box indicates location of right panel. Right: location of model sensitivity studies including release location of particles (orange star), bottom depth (shading), and surface currents (arrows).

periods that correspond to the hydrodynamic model output (e.g., at 18 min, 24 min, and 30 min). Second, a polynomial curve was fit to the current velocities at the three time points and used to calculate the current velocity at the time of particle movement (e.g., 23 min) as well as just before (e.g., 22.5 min) and just after (e.g., 23.5 min). Next, a single value of current velocity at the particle location was calculated with these values using a 4th order Runge-Kutta scheme. Finally, the single value of current velocity (u) was multiplied by the duration of the internal time step (δt) to calculate the displacement of the particle and used to calculate the new location of the particle (x_{n+1}):

$$(1) \quad x_{n+1} = x_n + u \delta t$$

Turbulent particle motion sub-model. A random displacement model (Visser 1997) was implemented within the larval transport model to simulate sub-grid scale turbulent particle motion in the vertical (z) direction:

$$(2) \quad z_{n+1} = z_n + K'_v \delta t + R [2r^{-1} K_v \delta t]^{1/2}$$

where z_n = initial particle location, K_v = vertical diffusivity evaluated at ($z_n + 0.5K'_v \delta t$), δt = time step of the random displacement model, $K'_v = \partial K_v / \partial z$ evaluated at z_n , and R is a random number generator with mean = 0 and standard deviation $r = 1$. Unlike random walk models, random displacement models do not result in numerical artifacts (particle aggregation in regions of low diffusivity) if the vertical resolution is adequate to resolve sharp variations in vertical diffusivity (Visser 1997, Brickman and Smith 2002). The turbulent particle motion sub-model uses the same approach for determining K_v and K'_v at the particle location that is used in the advection model, except that a smoothing algorithm was applied to the water column profile of K_v to prevent artificial aggregation of particles in regions of sharp gradients in diffusivity (North et al. *in revision*).

A simple random walk model was implemented for turbulent particle motion in the horizontal direction (x - or y - directions). ROMS was implemented with a constant value for horizontal diffusivity ($K_h = 1 \text{ m}^2 \text{ s}^{-1}$). When K_h is constant, the random displacement model defaults to a random walk model (Visser 1997):

$$(3) \quad x_{n+1} = x_n + R [2r^{-1} K_h \delta t]^{1/2}$$

where K_h = horizontal diffusivity evaluated at (x_n).

Behavior sub-models. Several behavior sub-models have been adapted and/or developed for the larval transport model based on previous descriptions of *C. virginica* larval behavior. Swimming speeds of *C. virginica* larvae vary from 0 to 3.0 mm s⁻¹ over the course of the 2-3 week development from fertilized eggs to pediveligers ready for settlement (Mann and Rainer 1990, Kennedy 1996). Some researchers hypothesize that larvae undergo tidally-timed vertical migrations (i.e., swim up during flood and down during ebb) while others have found that larvae may aggregate in the halocline where salinity gradients are high (Kennedy 1996). In addition, pediveligers have been found to be sensitive to light, and avoid well-lit waters (Kennedy 1996). Little is known of the larval behavior of *C. ariakensis*, although preliminary observations indicate that they may swim toward the bottom. We have developed sub-models to simulate the following behaviors: passive, bottom-oriented, tidally-timed vertical migration, and diurnal vertical migration (swim away from light during the day). We are currently in the process of

developing a behavior sub-model that will allow particles to aggregate along the halocline, and a stress-response model that will allow particles to move away from salinities and temperatures that cause physiological stress.

Each behavior sub-model had a swimming speed component and a behavioral cue component. The behavioral cue component regulated the timing and direction of particle movement. The swimming speed component regulated how fast the particle moved. Physical conditions at the particle location (salinity, current speed, water temperature, depth, light) were used to cue behavior. For example, in the tidally-timed vertical migration sub-model, particles ‘swam’ up, when current velocities at the particle location were up-estuary (flood), and ‘swam’ down when current velocities at the particle location were down-estuary (flood). All physical conditions, except for light, are estimated by interpolating hydrodynamic model predictions at the particle location as described in the advection sub-model section. To estimate irradiance at the particle location, we adapted a light model that was developed by E. North, T. Fisher and R. Hood (unpublished). The light model used published light data for the Chesapeake region (Fisher et al. 2003), a series of predictive equations for instantaneous irradiance at the water surface for any given day of the year based on equations in Kirk (1994) and Meeus (1998), and a simple sub-surface light model (Kirk 1994) with average K_d values for July in mid-Chesapeake Bay (David Miller, personal communication).

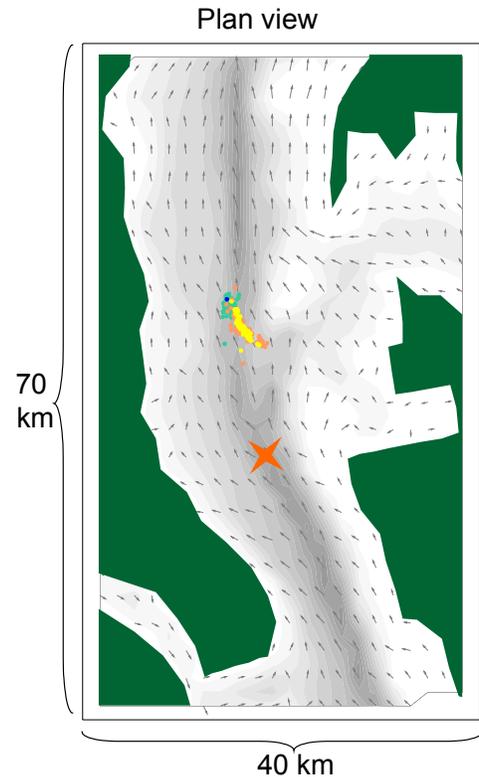


Fig. 4. Turbulence sensitivity study: comparison of particle locations 24 hr after release. Orange star indicates release location. Particle color corresponds to particle movement: advection (blue), advection plus horizontal turbulence (green), advection plus vertical turbulence (yellow), and advection plus horizontal and vertical turbulence (orange).

SENSITIVITY STUDIES: METHODS AND RESULTS

Numerical studies were conducted with the coupled bio-physical model to test sensitivity of larval transport predictions to turbulence parameterizations and larval transport. These studies were conducted in a subset of the model domain (Fig. 3) during summer when oyster larvae are found in the water column in Chesapeake Bay. All scenarios were initiated on July 1, 1996.

Advection and turbulence studies. Mixing processes could influence larval transport in a wind- and tidally forced system with two-layer estuarine circulation like Chesapeake Bay. Vertical mixing may move organisms between upper- and lower-layer water masses where along-channel residual current velocities are opposite in direction. Horizontal mixing can influence organism dispersal up- or down-estuary by moving organisms across channel where gradients in along-channel flow exist due to topographic steering and the earth's rotation. We conducted two simulations to determine the sensitivity of particle transport to turbulent motion in

the horizontal and vertical directions. In each simulation, 400 particles were released at 10 m depth at one location in the main channel of the Chesapeake Bay (Fig. 3) on July 1, 1996 and tracked for 24 hr.

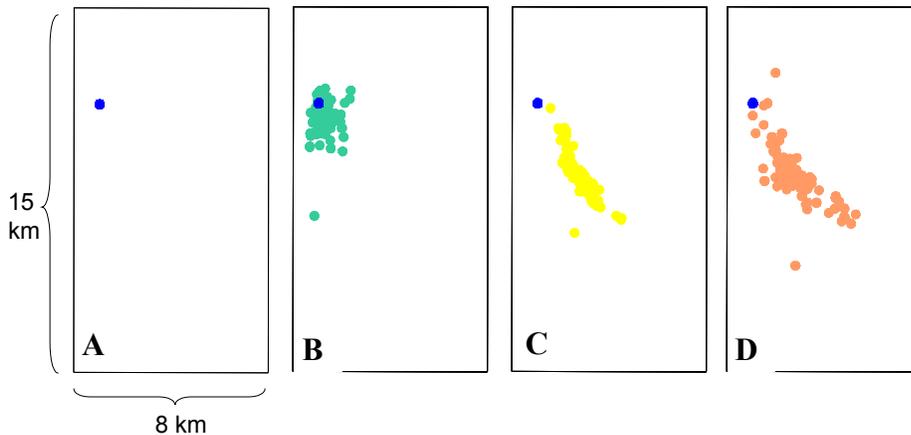


Fig. 5. Turbulence study: close-up comparison of particle locations from Fig. 4. Blue dot in all panels corresponds to particles whose movements were based on advection alone. Particle color corresponds to particle movement: A) advection, B) advection plus horizontal turbulence, C) advection plus vertical turbulence, and D) advection plus horizontal and vertical turbulence (orange).

In the first simulation, four types of particles were released, those whose motion were determined with 1) advection alone, 2) advection plus horizontal turbulence, 3) advection plus vertical turbulence, and 4) advection plus horizontal and vertical turbulence. Particle locations after 24 hrs were compared (Fig. 4,

5). Particles were separated by > 7 km when vertical turbulence was included in the particle motion, and by > 3 km with horizontal turbulence was included. In addition, particles with vertical turbulent motion were dispersed horizontally as well as vertically (Fig. 5C) and those with horizontal motion were dispersed vertically as well as horizontally (Fig 4, right panel). It was clear that turbulent particle motion was an important factor that affected the transport and dispersal of passive particles.

The goal of the second turbulence simulation was to determine how sensitive particle transport was to the value of horizontal diffusivity used in the horizontal turbulence model. When hydrodynamic models are implemented in shallow basins like Chesapeake Bay, modelers often set horizontal diffusivity to a small constant number (usually as small as possible yet maintaining model stability). Proper parameterization of horizontal mixing in particle-tracking models is therefore challenging because the horizontal diffusivities are user-defined instead of being based on first principles. In the simulation, the motion of all particles included advection and vertical turbulence as well as one of four types of horizontal turbulent motion by assigning horizontal diffusivity the value of 0 (no horizontal turbulence), 1, 10, or $100 \text{ m}^2 \text{ s}^{-1}$. These values span the range of horizontal diffusivities often found in shallow water hydrodynamic models.

All particles were released at 10 m depth at one location in the main channel of the Chesapeake Bay and tracked for one day (Fig. 6). After just one day, it was clear that predictions of particle transport were highly sensitive to the value of horizontal diffusivity used in the horizontal turbulence model. Particles whose motion was parameterized with $K_h = 100 \text{ m}^2 \text{ s}^{-1}$ dispersed laterally > 30 km in 24 hrs compared to lateral dispersal distances of ~ 8 and ~ 4 km for particles with $K_h = 10$ and $1 \text{ m}^2 \text{ s}^{-1}$, respectively. We plan to compare model estimates of horizontal dispersion to estimates from dye-release studies in order to properly parameterize the horizontal turbulent particle motion.

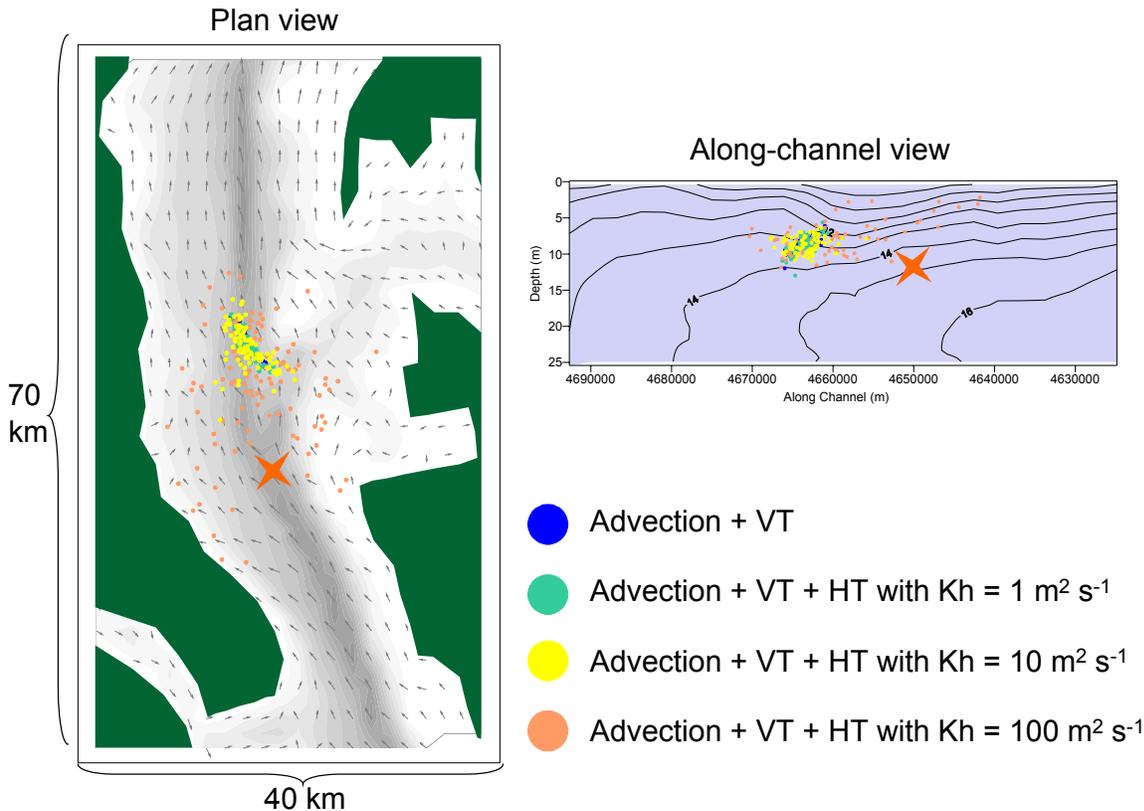


Fig. 6. Turbulence study: comparison of particle distributions after 24 hrs when different levels of horizontal diffusivity were used to calculate turbulent particle motion. Orange star indicates release locations. Left panel: plan view. Right panel: along channel view. VT = vertical turbulence, HT = horizontal turbulence.

Behavior studies. Simulations were conducted to determine how sensitive larval transport predictions were to different larval behaviors and swimming speeds. In each simulation, 400 particles were released at 10 m depth at one location in the main channel of the Chesapeake Bay (Fig. 7B) and tracked for 3 days. The motion of all particles included advection, vertical and horizontal turbulence, and behavior. Three behavior simulations were conducted: diurnal vertical migration, tidally-timed vertical migration, and bottom-oriented. For each behavior, four groups of 100 particles were released, each with a different vertical swimming speed (0, 0.5, 1.0, and 3.0 mm s^{-1}) to simulate differences in the swimming ability of larvae at various life stages. Particle locations were compared to identify potential differences in larval transport due to behavior.

After 3 days of model simulation, it was clear that behavior and swimming speed had a significant effect on the transport and dispersal of particles (Fig. 7). Comparison of passive particles (0 mm s^{-1} swimming speed) with actively swimming particles in all behavior scenarios demonstrated that transport of weakly swimming organisms could differ substantially from non-motile organisms, even those with swimming speeds as slow as 0.5 mm s^{-1} . Also, differences in location between the weakest and fastest swimming particles in each behavior group indicated that variations in swimming speed affected particle transport. The degree of dispersal between early-life stages depended on behavior type. For example, there were 2.7 km between the mid-

point location of the slowest and fastest swimming particles undergoing diurnal vertical migration (Fig. 7A) whereas the same ‘life stages’ were separated by 8.2 km when undergoing tidally-timed vertical migrations (Fig. 7B). Finally, a comparison between behaviors indicates that larval-like particles moved either up- or down-estuary (Fig. 7A vs. 7C), and within or across-channel (Fig. 7A vs. 7B), depending upon larval behavior type.

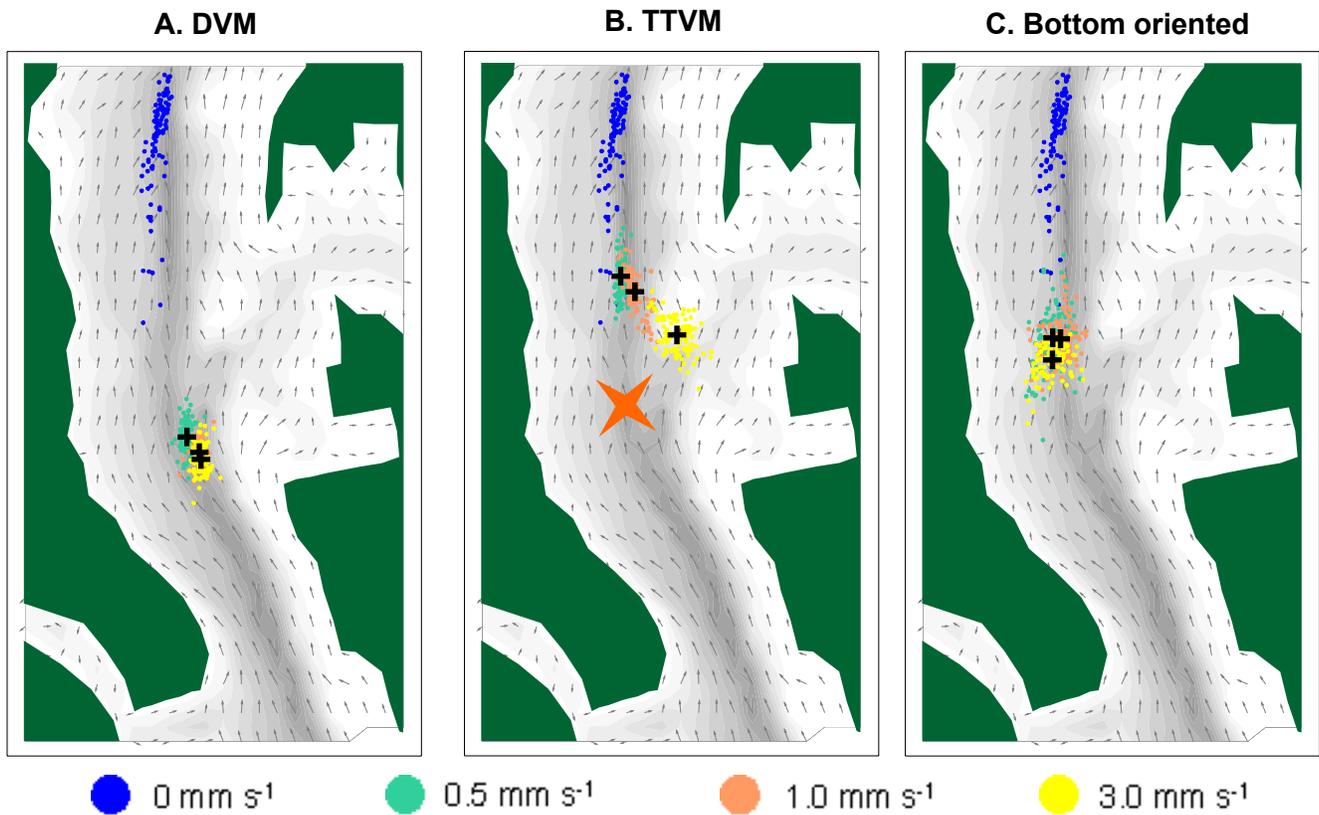
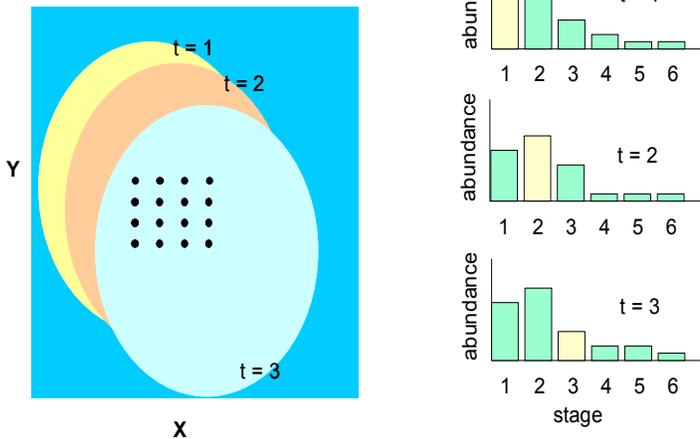


Fig. 7. Behavior study: comparison of particle locations 3 days after release with the following behavior types: A) diurnal vertical migration (DVM), B) tidally-timed vertical migration (TTVM), and C) bottom oriented. Color of particles corresponds to swimming speeds (key below panels). Black crosses indicate mid-point of swimming particle distributions. Orange star in center panel indicates release location for all behavior scenarios.

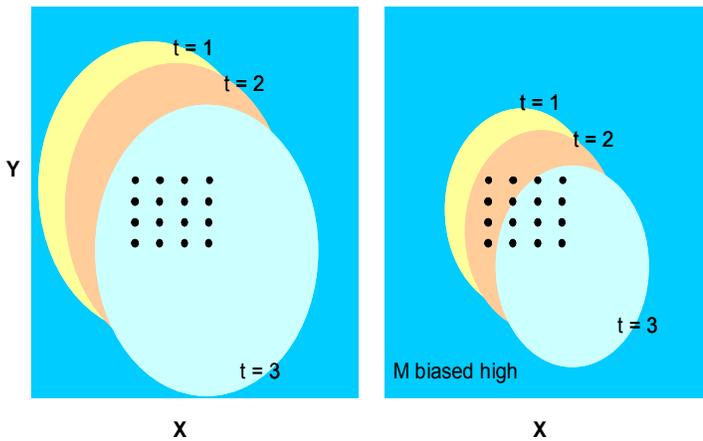
DISCUSSION

The results of all model scenarios demonstrated that predictions of larval transport are quite sensitive to turbulent particle motion and larval behavior. The effect of these factors on predictions of oyster larvae transport will be magnified because oyster larvae remain in the water column for 2-3 weeks, substantially longer than the 1-3 d analyses presented here. This suggests that proper parameterization of turbulence and behavior is essential for accurately predicting larval transport.

A. Mortality (M) calculated by tracking stage-specific abundance through time



B. Accurate mortality estimates depend on size of population in relation to sampling area



C. Accurate mortality estimates depend on larval behavior

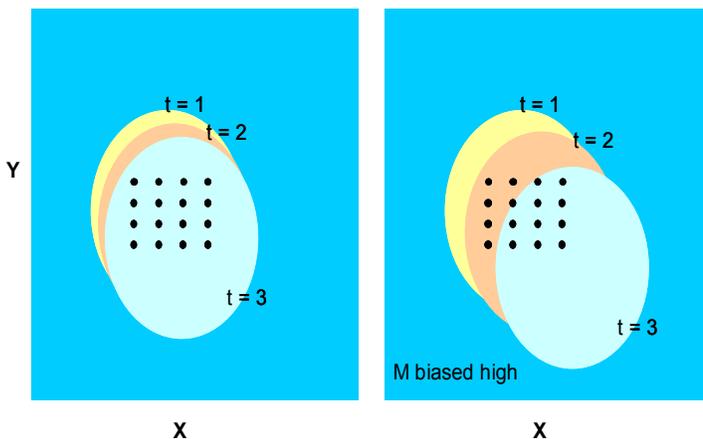


Fig. 8. Schematics depicting larval population location (ellipses) at 3 different sampling times (t) in relation to sampling stations (black dots). A) Technique for estimating mortality from field samples by calculating change in cohort abundance over time. B) The size and movement of cohort relative to sampling stations affects mortality (M) estimates, as does C) larval behavior.

The larval behavior sensitivity studies indicated that three relatively simple behaviors performed at relatively slow swimming speeds (0.5 mm s^{-1}) resulted in particle retention near the initial release location. These results support the long-standing theory that planktonic organisms can facilitate their own transport or retention within estuaries with simple behaviors that affect their vertical location in the water column (Boehlert and Mundy 1988, Miller 1988).

It is important to note that these studies were limited in scope because the location and timing of particle release likely affected particle transport. The mid-channel release location was chosen because we were interested in determining if passive particles were moving realistically in an area where we were familiar with the circulation patterns. In addition, the timing of particle release likely influenced the transport of particles, especially for the particles undergoing diurnal vertical migration. If particles were released at a time when the phase of tidal and light cycles were shifted, then transport would likely differ. We will be conducting further sensitivity studies with different release locations (e.g., on oyster bars) and times.

Results of the larval behavior studies have implications for estimating larval mortality rates from field collections. This is demonstrated pictorially in Fig. 8. One technique used to estimate mortality rates employs collection of larvae at fixed stations at separate times (Fig. 8A) and tracking decreases in cohort-specific abundances through time (Houde 2002). Advection and mixing processes move the cohort relative to the fixed stations, but as long as the fixed stations remain within the cohort population, the mortality estimates

can be considered reflective of loss processes happening within that cohort. As discussed by (Taggart and Frank 1990, Helbig and Pepin 1998), the size of the cohort relative to the fixed stations may influence mortality calculations (Fig. 8B). If the cohort is advected past the sampling stations, then calculations of mortality will be biased high; the decrease in abundance due to advective processes will be incorrectly ascribed to mortality. Results of our sensitivity studies suggest another factor could influence mortality estimates: larval behavior (Fig. 8C). Stage-specific differences in larval swimming speeds may result in little dispersal between stages (diurnal vertical migration, Fig. 7A) or significant dispersal (e.g., tidally-timed vertical migration, Fig. 7B). If there is dispersal between stages such that later-stage larvae move past the fixed sampling stations, then mortality estimates could be biased high and the effect of larval behavior could be incorrectly ascribed to mortality.

ACKNOWLEDGEMENTS

We extend our thanks to Charles Hannah, Wolfgang Fennel, and members of the ICES Working Group on Modeling Physical-Biological Interactions (WGPBI) for their helpful advice and discussions. EN appreciates support from the National Science Foundation for attending the WGPBI meeting (March 2004) during which these discussions occurred. This research was supported by the U. S. Maryland Department of Natural Resources.

LITERATURE CITED

- Boehlert, G. W., and B. C. Mundy. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* 3:51-67
- Brickman, D., and P. C. Smith. 2002. Lagrangian stochastic modeling in coastal oceanography. *Journal of Atmospheric and Ocean Technology* 19: 83-99.
- Calvo, G. W., M. W. Luckenbach, S. K. Allen, Jr., E. M. Burreson. 2001. A comparative field study of *Crassostrea ariakensis* (Fujita 1913) and *Crassostrea virginica* (Gmelin 1791) in relation to salinity in Virginia. *Journal of Shellfish Research* 20(1): 221-229
- Fisher, Gustafson, Radcliffe, Sundberg, Stevenson. 2003. A Long-term Record of Photosynthetically Available Radiation (PAR) and Total Solar Energy at 38.68N, 78.28W. *Estuaries* 26(6): 1450–1460
- Hare, J. A., J. A. Quinlan, F. E. Werner, B. O. Blanton, J. J. Govoni, R. B. Forward, L. R. Settle, D. E. Hoss. 1999. Larval transport during winter in the SABRE study area: results of a coupled vertical behaviour-three-dimensional circulation model. *Fisheries Oceanography* 8: 57-76.

- Helbig, J.A., and Pepin, P. 1998. Partitioning the influence of physical processes on the estimation of ichthyoplankton mortality rates. I. Theory. *Canadian Journal of Fisheries and Aquatic Science* 55: 2189–2205.
- Hidu, H., and H. H. Haskin. 1978. Swimming speeds of oyster larvae *Crassostrea virginica* in different salinities and temperatures. *Estuaries* 1: 252-255.
- Hill, A. E. 1994. Horizontal zooplankton dispersal by diel vertical migration in S2 tidal currents on the northwest European continental shelf. *Continental Shelf Research* 14(5): 491-506.
- Houde, E. D. 2002. Mortality. pp. 64-87. In: Fuiman, L. A., and R. G. Werner (eds), *Fishery Science. The Unique Contributions of Early Life Stages*. Blackwell Publishers. Malden, Massachusetts.
- Kennedy, V. S. 1996. Biology of larvae and spat. In: Kennedy, V. S., R. I. E. Newell, and A. E. Eble, eds. *The Eastern Oyster: Crassostrea virginica*. Maryland Sea Grant College, College Park, Maryland. 734 pp.
- Kirk, J.T.O. 1994. *Light and photosynthesis in aquatic ecosystems*, 2nd edition. Cambridge: Cambridge University Press. 509 pp.
- Li, M., L. Zhong and W.C. Boicourt. *submitted*. ROMS simulations of the Chesapeake Bay estuary: sensitivity to turbulence mixing parameterisation and comparison with hydrographic observations. *Journal of Geophysical Research*.
- Mann, R., and J. S. Rainer. 1990. Effect of decreasing oxygen tension on swimming rate of *Crassostrea virginica* (Gmelin, 1791) larvae. *Journal of Shellfish Research* 9(2): 323-327.
- McConnaughey RA, Armstrong DA, Hickey BM, Gunderson DR (1994) Interannual variability in coastal Washington Dungeness crab (*Cancer magister*) populations: larval advection and the coastal landing strip. *Fisheries Oceanography* 3: 22-38
- Meeus, J. 1998. *Astronomical algorithms*. Richmond, Virginia: Willmann-Bell, Inc. 477 pp.
- Miller JM (1988) Physical processes and the mechanisms of coastal migration of immature marine fishes. *American Fisheries Society Symposium* 3: 68-76
- North, E. W., R. R. Hood, S.-Y. Chao, and L. P. Sanford. *in press*. The influence of episodic events on transport of striped bass eggs to an estuarine nursery area. *Estuaries*.
- North, E. W., R. R. Hood, S.-Y. Chao, and L. P. Sanford. *in revision*. Using a random displacement model to simulate turbulent particle motion in a baroclinic frontal zone: a new implementation scheme and model performance tests. *Journal of Marine Systems*.

North, E. W., R. R. Hood, S.-Y. Chao, and L. P. Sanford. 2003. Combining Eulerian and Lagrangian numerical approaches to investigate the influence of hydrodynamic variability on the transport of sediment and fish eggs. *ICES CM/P:33*.

National Research Council. 2004. *Non-native oysters in the Chesapeake Bay*. The National Academies Press, Washington D.C. 326 p.

Rowe, P. M., and C. E. Epifanio. 1994. Tidal stream transport of weakfish larvae in Delaware Bay, USA. *Marine Ecology Progress Series* 110: 105-114

Song, Y.T. and D.B. Haidvogel. 1994. A semi-implicit ocean circulation model using a generalized topography-following coordinate system. *Journal of Computational Physics*. 115, 228-244.

Taggart, C.T., and Frank, K.T. 1990. Perspectives on larval fish ecology and recruitment processes: probing the scales of relationships. In: *Large marine ecosystems: patterns, processes, and yields*. Edited by K. Sherman, L.M. Alexander, and B.D. Gold. American Association for the Advancement of Science, Washington, D.C. pp. 151–164.

Visser, A. W. 1997. Using random walk models to simulate the vertical distribution of particles in a turbulent water column. *Marine Ecology Progress Series* 158: 275-281.