Retention of fish early-life stages and copepod prey in an estuarine nursery area: the influence of environmental variability

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Abstract

The estuarine turbidity maximum (ETM) is an important nursery area for anadromous fish in Chesapeake Bay where early-life stages can be retained in high prey concentrations and favorable salinities by the physics of the region. Episodic discharge, wind events and annual differences in river flow could influence the retention of striped bass (Morone saxatilis) early-life stages and their prey in the ETM. This hypothesis was evaluated with a coupled biological-physical model of a theoretical estuary. A particle tracking model was constructed within a numerical circulation model to simulate the transport of fish early-life stages and copepods in a 3-D flow field. Most neutrally buoyant particles released at depth within the ETM region were retained, while most released up-estuary of the ETM were transported down estuary, bypassing the ETM region within 10 days. Particles with the sinking speed of striped bass eggs were released up-estuary of the salt front. The number of egg-like particles located within the optimum ETM nursery area depended upon egg density and release site. Compared to steady-state conditions, a sudden increase in freshwater flow transported heavier egg-like particles to the optimum area and reduced the total number of particles within it by 12.9%. A down-estuary wind event resulted in a 72.4% reduction in the number of egg-like particles in the optimum area compared to steady-state conditions. Episodic river flow and wind events associated with storms during the striped bass spawning season may alter circulation patterns within the ETM region and cause loss of striped bass eggs from the ETM nursery area with negative consequences for survival. Results of preliminary scenarios with sub-grid scale turbulent motion suggest that inclusion and proper parameterization of sub-grid scale turbulence is critical for determining transport and retention of particles in the ETM.

Introduction

Estuarine turbidity maxima (ETMs) are characterized by elevated turbidity and suspended sediment concentrations compared to those up- and down-estuary (Figure 1). ETMs are found in coastal plain estuaries throughout the world (Schubel 1968), including the Tamar estuary in the UK (Uncles and Stephens 1993), the Gironde estuary in France (Allen et al. 1980), the Elbe and Weser estuaries in Germany (Kappenberg and Grabemann 2001), the St. Lawrence and Fraser River estuaries in Canada (D'Anglejan 1981, Kostaschuk 2002), and the San Francisco Bay/Delta, Columbia River, York River, Hudson River and Chesapeake Bay estuaries in USA (Schubel 1968, Jay and Musiak 1994, Burau et al. 1998, Geyer et al. 2001, Lin and Kuo 2001, Sanford et al. 2001). Fish eggs and larvae retained within the ETM region may be in 1) a zone of increased zooplankton biomass and production (Simenstad et al. 1994, Boynton et al. 1997, Kimmerer et al. 1998, Roman et al. 2001), 2) a predation refuge due to high turbidity (Chesney 1989), and 3) optimal temperature or salinity conditions (Strathmann 1982). In addition,

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retention within the ETM could prevent fish eggs and larvae from entering osmotically stressful, high salinity waters (Winger & Lasier 1994).
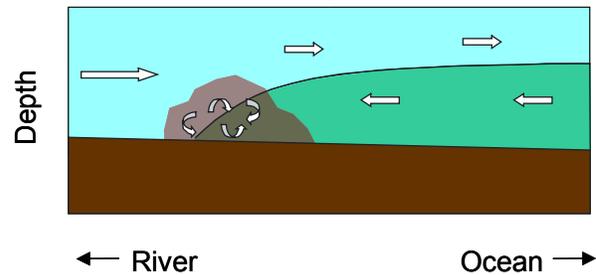

Fig. 1. Diagram of estuarine turbidity maximum that occurs where the salt front meets freshwater. Straight arrows represent residual current velocities. Brown cloud represents resuspended sediment.

The ETM region is an important nursery area for larval fish in the St. Lawrence River estuary (Dodson et al. 1989, Dauvin and Dodson 1990, Sirois and Dodson 2000) and potentially in the San Francisco Bay/Delta (Jassby et al. 1995). In Chesapeake Bay, the ETM is an important physical feature that forms the nursery habitat for anadromous fish like striped bass (Morone saxatilis) and its congener, white perch (M. americana). Elevated abundance of white perch larvae, striped bass larvae, and their potential prey were reported in and near the Chesapeake Bay ETM (Boynton et al. 1997, Roman et al. 2001, North and Houde 2001). Boynton et al. (1997) suggested that the ETM region could be an important nursery area for larval fish where biological conditions structured by the physics of the region could enhance recruitment potential. North and Houde (2001) demonstrated that physical characteristics of the ETM region were influenced by wind and freshwater flow, and concluded that the ETM region was an important nursery area for white perch and striped bass early-life stages. They also presented a hypothesis that linked variations in early-life-stage retention, larval survival and juvenile recruitment to annual differences in freshwater flow that alter the physical and biological characteristics of the ETM region.

Striped bass are anadromous fish that have important commercial, recreation, and ecological value along the coasts of North America. The majority of the Atlantic Coast population is derived from Chesapeake Bay stocks (Hornick et al. 1999). The largest and most productive striped bass spawning ground within Chesapeake Bay occurs at the head of the Bay (Hornick et al. 1999) where there is a persistent salt front and ETM (Schubel 1968, Sanford et al. 2001) (Figure 2). Spawning of Chesapeake Bay striped bass peaks in April and May (Mansueti 1964, Dovel 1971). Striped bass spawn pelagic eggs in tidal fresh water up-estuary of the salt front (Dovel 1971, Secor and Houde 1995). The spherical, slightly-heavy eggs (specific gravity = 1.0005 to 1.0066) are suspended by currents greater than 0.3 m s^{-1} (Albrecht 1964, Rulifson and Tull 1999). Eggs range in size from 2.0 to 3.7 mm depending upon individual spawner and spawning population (Mansuetti 1958, Stezler-Hamilton and Hall 1991). Striped bass larvae hatch in about 2 d at a size of ~3.1 mm and do not develop a swimbladder and absorb their yolk-sac until they are >5 d old and >5 mm in length (Mansueti 1958, 1964; Doroshev 1970). Striped bass larvae begin
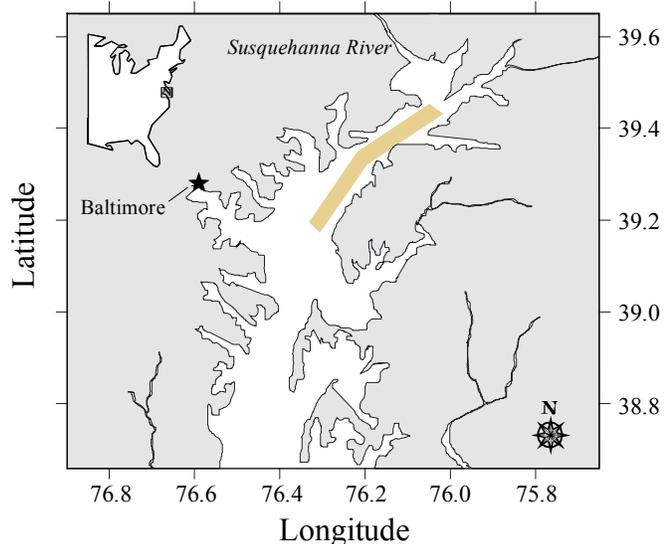

Fig. 2. Upper Chesapeake Bay, USA. Shaded area represents the region where the ETM occurs.

feeding on rotifers, copepodites, and <u>Bosmina</u> <u>longirostris</u> before shifting toward adult copepods (especially <u>Eurytemora</u> <u>affinis</u>) and larger cladocerans as they grow (Beaven and Mihursky 1980, Setzler-Hamilton et al. 1982).

Seasonal and annual changes in ETM properties may have consequences for striped bass larval survival and recruitment because the location and extent of the ETM nursery area is linked to the variable physics of the region. Although the ETM is a well-established feature of the upper Chesapeake Bay, its location, extent and intensity vary among hours, days, seasons, and years depending upon tidal excursion, wind forcing, and the amount of freshwater flow (Boynton et al. 1997, North and Houde 2001, Sanford et al. 2001). The ETM ranges from 10 - 30 km in extent and is generally associated with the tip of the 1 psu isohaline, but can be displaced from it by as much as 10 km due to tidal excursion (Boynton et al. 1997, Sanford et al. 2001). Changes in circulation patterns within the ETM region could influence egg and larval retention within the nursery area with significant consequences for larval survival and vital rates.

Episodic discharge, wind events and annual differences in river flow could influence the retention of fish early-life stages and their copepod prey in the ETM region. We are evaluating this hypothesis with a coupled biological-physical model of a theoretical estuary. This research is part of the BITMAX program (Bio-Physical Interactions in the Turbidity Maximum, www.BITMAX.org). BITMAX is a multiple-investigator, interdisciplinary program sponsored by the National Science Foundation that applies both field and modeling techniques to answer the question: How do estuarine turbidity maxima entrap particles, retain zooplankton, and promote fish recruitment?

Methods

Episodic river flow and wind events during the striped bass spawning season may alter the transport and retention of striped bass early-life stages and their copepod prey in the ETM nursery area. This hypothesis was tested with a three-dimensional hydrodynamic model of a theoretical estuary coupled with a Lagrangian particle tracking model. Particles were assigned sinking speeds of striped bass eggs or simple potential behaviors of copepods and released in the hydrodynamic model at different locations in relation to the salt front. The number of particles retained in the ETM nursery area was enumerated at steady-state, high river flow, and wind-event conditions.

Hydrodynamic and Sediment Transport Model. The three-dimensional hydrodynamic model, ETM203, is based on the code of the Princeton Ocean Model (POM) (Blumberg and Mellor 1987, Mellor 1998) under hydrostatic and Boussinesq approximations. Eddy viscosity and diffusivity is determined by the level-2.5 turbulent closure scheme of Mellor and Yamada (1974). Our enhancements to POM include building suspended sediment and sediment transport components that track bottom sediment concentrations, adding constant loading of suspended sediment at the up-stream boundary, parameterizing bottom sediment burial with a Newtonian dampening term, and constructing a more reasonable formulation for background diffusivity.

The ETM203 model domain (Figure 3) contains a 98-km long and 4.8-km wide channel with a gradually widening seaward reservoir that is 2141 km long and has a maximum width of 62.7 km. The entire basin is 12 m deep and contains 145 grid spacings in the x-direction (seaward) and 6 in the y-direction (across channel). Vertical resolution is provided by 12 sigma-coordinate layers. In the first 98 km of the channel, the longitudinal resolution (Δx) is 1 km and the lateral resolution (Δy) is 0.8 km. In the seaward reservoir, Δx and Δy gradually increase at a rate of 12 and 5.5 percent per grid, respectively. The seaward

Fig. 3. Schematic of hydrodynamic model domain.

reservoir, although of minor importance to the circulation and sediment transport within the channel, serves as a buffer zone to enhance the long term computational stability of the model. The temporal resolution of the model is split. Vertically averaged currents and sea level are resolved with a time step of 5 s, and salinity, sediment concentration, and vertically explicit current velocities are resolved with a time step of 40 s.
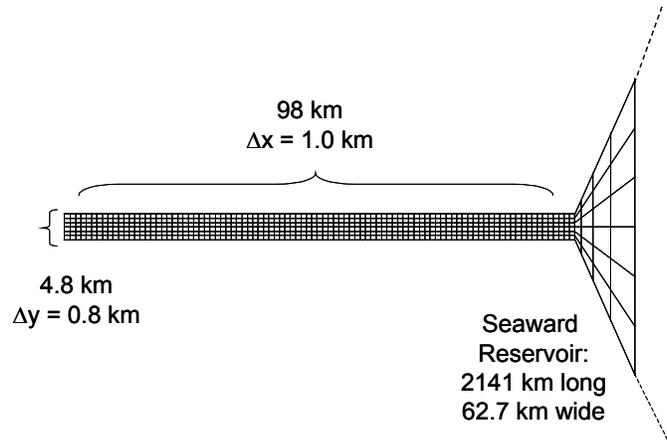
A barotropic tidal generation force is included in the longitudinal momentum equation to produce semidiurnal tidal currents in the channel. Tidal current speed and upstream dissipation are parameterized so that sea level height and tidal current velocities in the model are similar to those of predicted tides in upper Chesapeake Bay. Lateral walls bounding the channel are impenetrable, impermeable and free-slip. Further information regarding model parameterization and boundary condition in ETM203 is forthcoming (North et al. in prep) and can be obtained by contacting the authors.

All model scenarios presented in this paper are based on the steady-state scenario of ETM203. Initially, the channel was filled with motionless clear water of 12 practical salinity units (psu). The model was run with river inflow = 0.07 m s^{-1} and constant sediment loading until the model reached a quasi steady-state at day 350. In this quasi steady-state, sediment input equals sediment burial and the location of the salt front is stable: it oscillates with the tidal current in a repetitive cycle but does not progress up or down estuary.

Particle Tracking Model. A Lagrangian particle tracking model, PARTRACK, is coupled to ETM203. Particle trajectories are calculated every 40 s coinciding with the hydrodynamic model time step. Subject to perturbations by turbulent motions, changes in particle locations are calculated by multiplying U (along-channel), V (cross-channel), and W (vertical) current velocities (m s^{-1}) from the hydrodynamic model by the model time step (s):

$$\Delta x = U t \quad , \quad \Delta y = V t \quad , \quad \Delta z = W t$$

Current velocities at the particle locations are estimated using an 8-point linear interpolation scheme. For each velocity component, values at the 8 grid points nearest to the particle (Figure 4) are weighted by their distance from the particle to derive the component

velocity at the particle location. Near the bottom, the law-of-the-wall is applied so that U, V, and W-velocities decreased logarithmically to the depth of the roughness height (0.001 m) using linear interpolation. Between the bottom roughness height (0.001 m) and the bottom, a particle's velocity is either zero (when erosion rate = 0) or 0.00377 m s^{-1} upward (when erosion rate > 0). Erosion rate is derived in the sediment transport component of the hydrodynamic model and is passed to the particle tracking model. This approach allows particles to be resuspended if the critical erosion threshold is exceeded.
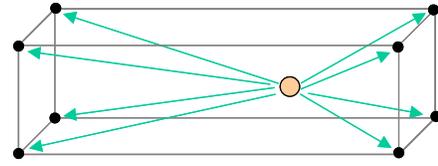

Fig. 4. Diagram of particle location and grid points used to calculate current velocities. Green arrows depict distances between the particle and grid points.

PARTRACK is formulated with simple boundary conditions. Particles that pass through the surface or bottom boundaries of the hydrodynamic model are placed 0.001 m from the boundary within the model domain. Particles that pass the up-estuary (rkm=1.5) or down-estuary (rkm=97) boundary of the particle tracking model remain fixed at the boundary. Particles that pass through the free slip, impenetrable and impermeable channel walls of the hydrodynamic model are simply placed back 10 m adjacent to the channel wall.

Striped bass egg parameterization. Striped bass egg sinking speed (m s^{-1}) depends upon egg density (specific gravity), egg diameter, and the density and viscosity of the water where the egg is located. Reynolds numbers for striped bass eggs are between 3 and 4 based on egg settling velocity and diameter measurements made by Schubel et al. (1974). Because Stokes Law does not apply when Reynolds numbers are > 1, we use a series of equations that describe the sinking speed of spherical particles at Reynolds numbers < 800 (Raudkivi 1990). First, Stokes Law is used to approximate egg sinking speed (w$_s$):

$$(1) \qquad w_s = \frac{g\ d^2\ (\rho' - \rho)}{18\ \rho\ \nu}$$

where g = gravity, d = diameter of sphere, ρ' = density of sphere, ρ = density of water, and ν = kinematic viscosity. Values for kinematic viscosity and water density at the particle location are derived from hydrodynamic model output. The Stokes sinking speed estimate (m s^{-1}) is used to calculate the Reynolds number (Re):

$$(2) \qquad Re = w_s\ d\ \nu^{-1}$$

which is used to calculate drag coefficient (C$_d$) using the Schiller and Naumann (1933) empirical equation for C$_d$ at Re < 800:

$$(3) \qquad C_d = \frac{24\ (1 + 0.150\ Re^{0.687})}{Re}$$

Initial values of Re and C$_d$ are inserted into the generalized terminal velocity equation:

$$(4) \qquad w_s = \left[\frac{4\ g\ d\ (\rho' - \rho)}{3\ C_d\ \rho} \right]^{1/2}$$

Equations 2, 3, and 4 then are iteratively solved until the sinking speed converges to a single value to produce a valid estimate of sinking speed at Reynolds numbers < 800 (Raudkivi 1990).

Sub-grid scale turbulence parameterization. The hydrodynamic model does not simulate sub-grid scale turbulence, an important physical feature that has significant effects on the distribution of planktonic organisms. Therefore, we added a sub-grid scale turbulence generator to the particle tracking model following Hood et al. (1999) and Dutkiewicz et al. (1993). The sub-grid scale turbulence model is based on the equation:

$$(5) \qquad TV_t = (-TV_{t-1} \ \Delta t \ TL^{-1} \ ) + R_t$$

where TV = sub-grid scale turbulence velocity in a component direction, Δt = time interval, TL = isotropic decorrelation time scale, and R_t = random velocity vector drawn from a normal distribution with zero mean and variance $\sigma = 2 \ \sigma_f \ \Delta t \ TL^{-1}$. The isotropic fluid velocity variance, σ_f, is derived with the relationship: $\sigma_f = K_e \ TL^{-1}$ where K_e = eddy diffusivity ($m^2 \ s^{-1}$). This equation is solved for each component velocity (U, V, W) to generate sub-grid scale turbulence in three dimensions. Equation (5) results in the particle loosing a fraction of its momentum due to turbulence decay ($-TR_{t-1} * \Delta t * TL^{-1}$) and receiving a random kick R_t from the surrounding fluid due to new turbulence.

The isotropic decorrelation time scale (TL) in equation (5) is calculated by converting turbulence length scales derived in the hydrodynamic model to time scales applicable to the sub-grid scale turbulence generator. The approximate length of time (T) turbulent diffusion takes over a distance (L) is specified by $T = L^2 \ K_e^{-1}$ (Mann and Lazier 1996). To determine TL, we add a scaling coefficient (*k*) to this equation:

$$(6) \qquad TL = k \ L^2 \ K_e^{-1}$$

For calculating turbulence velocities in the vertical direction, TL is calculated with vertical diffusivities and vertical turbulence length scales derived in the hydrodynamic model. For turbulence velocities in the horizontal directions, TL is calculated with horizontal diffusivity (K_h) from the hydrodynamic model and horizontal length scales (L_h) given by:

$$(7) \qquad L_h = \frac{K_h}{[\ 0.5 \ (\ \Delta U^2 + \Delta V^2 \ ) \ ]^{1/2}}$$

where U and V are along- and cross-channel velocities at the particle location. This allows the random motion of particles to differ in magnitude between the horizontal and vertical planes, and to be isotropic in the horizontal plane.

Model scenarios. Model scenarios were developed to determine the influence of egg density, spawning location and episodic river flow and wind events on retention of egg- and copepod-like particles in the optimum ETM nursery area. The optimum ETM nursery area (Figure 5) was defined as the low salinity area (0.5 to 3 psu) at the foot of the salt front where early-life stages could be retained in an area of high prey concentrations (Simenstad et al. 1994, Kimmerer et al. 1998, Roman et al. 2001, North and Houde submitted) and low salinities favorable for striped bass larval growth and survival (Lal et al. 1977, Winger and Lasier 1994).

Fig. 5. Along-channel section of hydrodynamic model output with salinity (psu) line contours, suspended sediment shaded contours (kg m^{-3}), and current velocity vectors. Area outlined in green is the optimum nursery area.
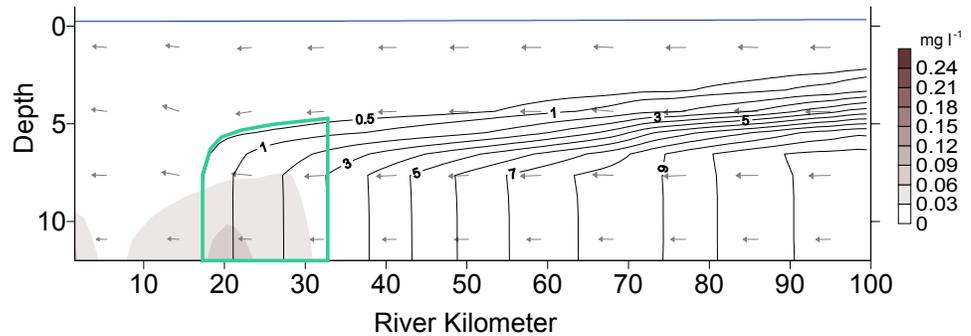
As a baseline for comparison with striped bass egg and copepod models, neutrally buoyant particles were released within the optimum nursery area and up-estuary of the salt front to demonstrate the fate of water parcels without egg-like characteristics (Figure 6). Releases up-estuary of the salt front occurred throughout the water column in increments of 2 km from 0 to 10 km up-estuary of the foot of the 1 psu isohaline. All particles are color coded with their initial release depth (orange = surface layer, green = mid-depth, blue = bottom waters). Neutrally buoyant scenarios were run for 10 d and the number of particles retained in the optimum nursery area were counted at day 2 and 10.

Fig. 6. Example of particle release locations up-estuary (at river km 16) and within the salt front. Line contours indicate salinity (psu) and color contours indicate suspended sediment concentrations (kg m^{-3}).
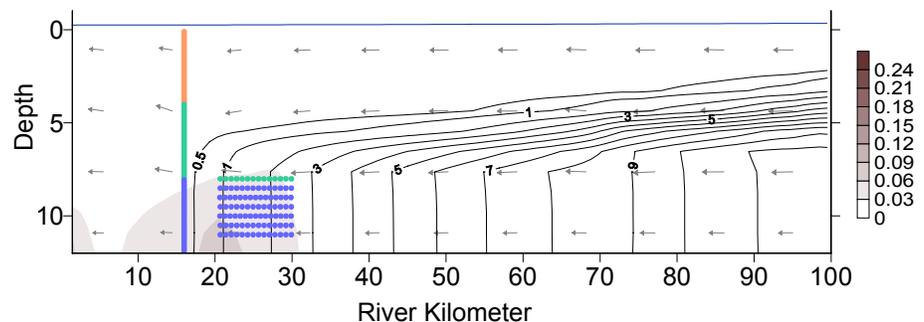
For the striped bass egg scenarios, both egg diameter and egg specific gravity (density) were held constant throughout model runs. Egg diameter was fixed at 2.5 mm to isolate the effects of egg density, spawning location, and water properties (ρ and ν) on the potential retention of eggs in the ETM nursery area. Egg specific gravity (s. g. = $\rho'\, \rho^{-1}$) was varied between model runs in increments of 0.0002. Release (spawning) location of egg-like particles was up-estuary of the salt front because striped bass eggs have been found to peak between 0 and 10 km from the intersection of the 1 psu isohaline with the bottom (Robichaud-LeBlanc et al. 1996, North and Houde 2001). In each scenario, 100 egg-like particles were released throughout the water column of the steady-state hydrodynamic model on day 350. Because striped bass eggs hatch in ~ 2 days, the number of particles suspended in the ETM nursery area after two days were counted. Particles that were transported down-estuary of the optimum ETM nursery area were considered lost. Likewise, particles that sunk to the bottom (where eggs can be smothered by sediment) and remained within 1 cm of the bottom were considered lost.

To determine the influence of river pulse and wind events, the egg density and release location scenarios were repeated with a sudden increase in river flow and with a wind event. For the river pulse scenarios, river flow was doubled (0.14 m s^{-1}) on day 350 and remained constant until 352. Freshwater pulse events that result in a doubling of river flow have been observed in

the upper Chesapeake Bay during striped bass spawning season, as have strong down-estuary wind events (North and Houde 2001). For wind event scenarios, a 1.6 dyne cm^{-2} down-estuary wind was initiated at day 350.5 and continued until day 352.

Steady-state, river pulse and wind event scenarios were conducted without sub-grid scale turbulence because tuning and validation of the sub-grid scale turbulence model was not complete. To estimate potential contributions from sub-grid scale turbulent motions, steady-state model scenarios were repeated with sub-grid scale turbulence. The sub-grid scale turbulence model was parameterized with the qualitatively reasonable values of $k = 1.0$ in the vertical and $k = 2.5 \times 10^{-5}$ in the horizontal directions. Description and results of scenarios with validated sub-grid scale turbulence generation and copepod-like particles will be presented at the 2002 ICES Annual Science Conference.

Results

Neutrally-buoyant particles. Most neutrally buoyant particles released up-estuary of the salt front were transported down estuary within 10 days in steady-state (> 75% loss from optimum nursery area), river pulse (100% loss), and wind event scenarios (93% loss) (Table 1). In contrast, most neutrally buoyant particles released within the optimum ETM nursery area within the salt front were located there after 10 days (75% retention) in steady-state scenarios, but not in river pulse or wind event scenarios. For all scenarios with neutrally buoyant particles, highest retention after 2 d occurred within the salt front.

Table 1. Number of neutrally buoyant particles located in the optimum nursery area after 2 d in steady-state, river pulse, and wind event scenarios. 100 particles were released in each scenario.

Release Location	Steady State		River Pulse		Wind Event	
(river kilometer)	2 d	10 d	2 d	10 d	2 d	10 d
10	0	3	19	0	14	0
12	22	4	17	0	4	3
14	39	5	16	0	7	3
16	47	9	20	0	9	3
18	42	15	22	0	12	3
20	43	25	23	0	10	3
Within salt front	100	72	98	0	40	5

Striped bass eggs: steady-state scenarios. The number of striped bass eggs that were located in the optimum nursery area after 2 d depended upon their release location and specific gravity (Figure 7, Table 2). Eggs with specific gravities of 1.0001 floated over the salt front and were transported down-estuary. Eggs with specific gravities > 1.0006 sunk to the bottom. Of the 4,200 particles released in all steady-state scenarios combined, a total of 1,267 particles (30.2%) were located in the optimum nursery area at day 352.
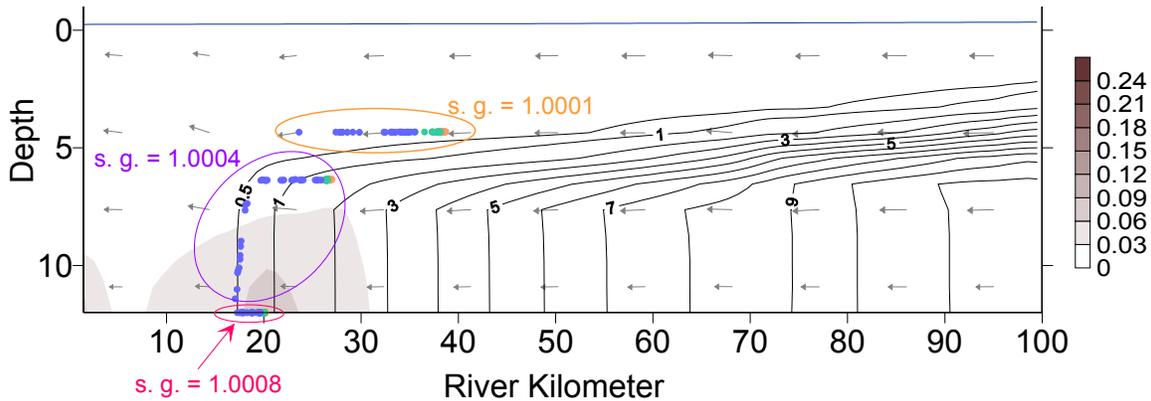

Fig. 7. Location of egg-like particles after 2 days in steady state conditions. Particles were released at river km 16. Eggs with similar specific gravities (s. g.) are circled. Line contours indicate salinity (psu) and color contours indicate suspended sediment concentrations (kg m^{-3}).

Table 2. Number of egg-like particles located in the optimum nursery area after 2 d in steady-state scenarios. Blue indicates all eggs floated above the salt front and were transported down estuary. Green indicates all eggs sunk to bottom and remained within 1 cm of bottom. 100 particles were released in each scenario.

Release Location	Specific Gravity						
(river kilometer)	1.0001	1.0002	1.0004	1.0006	1.0008	1.001	1.012
10	0	64	65	0	0	0	0
12	0	64	79	64	0	0	0
14	0	88	85	83	0	0	0
16	0	32	98	87	0	0	0
18	0	11	68	97	73	0	0
20	0	0	16	100	93	0	0

Striped bass eggs: river pulse scenarios. Two days of increased river flow (0.14 m s^{-1}) pushed the salt front and ETM region 6-km down estuary (Figure 8) compared to steady-state conditions (river flow = 0.7 m s^{-1}) (Figure 7). Like the results of steady-state scenarios, the number of striped bass eggs that were located in the optimum nursery area after 2 d of increased

river flow depended upon their release location and specific gravity (Figure 8, Table 3). In comparison to steady-state scenario results, the density distribution of the majority of particles located in the optimum area shifted during river pulse scenarios. More heavy particles (mostly with 1.0004 to 1.0008 specific gravities) were located in the optimum area during river pulse scenarios than those in steady-state scenarios (1.002 to 1.0006 s.g.). The mean specific gravity of egg-like particles located in the optimum nursery area increased from 1.00049 in steady-state condition to 1.00064 in river pulse scenarios. A total of 1,104 particles were located in the optimum area in river pulse scenarios, 26.3% of the total released. This represents a 12.9% reduction in the number of particles located in the optimum nursery area compared to steady-state scenarios. This reduction was mostly due to egg-like particles with low specific gravities (<1.0004) being transported down-estuary over the salt front in the increased river flow.
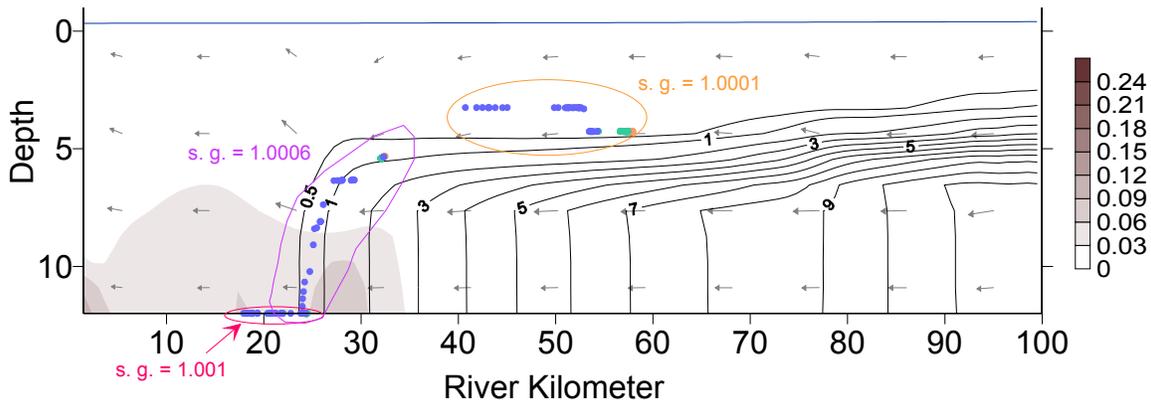

Fig. 8. Location of egg-like particles after 2 days in river pulse scenarios. Particles were released at river km 16. Eggs with similar specific gravities (s. g.) are circled. Line contours indicate salinity (psu) and color contours indicate suspended sediment concentrations (kg m^{-3}).

Table 3. Number of egg-like particles located in the optimum nursery area after 2 d in river pulse scenarios. Blue indicates all eggs floated above the salt front and were transported down estuary. Green indicates all eggs sunk to bottom and remained within 1 cm of bottom. 100 particles were released in each scenario.

Release Location	Specific Gravity						
(river kilometer)	1.0001	1.0002	1.0004	1.0006	1.0008	1.001	1.012
10	6	11	82	75	70	0	0
12	7	6	87	83	72	0	0
14	4	6	21	86	70	0	0
16	0	0	15	92	79	0	0
18	0	0	9	23	82	0	0
20	0	0	0	12	43	63	0

Striped bass eggs: wind event scenarios. The down-estuary wind event mixed the upper water column by day 352 and compressed the salt front (Figure 9). The intersection of the 0.5 psu isohaline with the bottom shifted ~2 km down-estuary and the 3 psu isohaline shifted ~ 4 km up-estuary compared to steady-state conditions (Figure 7). Substantially fewer egg-like particles were located in the optimum nursery area in wind event scenarios (350) than steady-state scenarios, a 72.4% reduction (Table 4). In general, eggs-like particles with specific gravities < 1.0008 were mixed up into the water column and were transported down-estuary. Egg-like particles with specific gravities that would have sunk to the bottom in steady-state conditions (s. g. = 1.001, 1.0012) were suspended and located in the optimum nursery area when released up-estuary of river kilometer 16. These egg-like particles were suspended by the strong upward velocities that occurred when the salt front was compressed and were heavy enough to resist being carried out of the optimum nursery area.
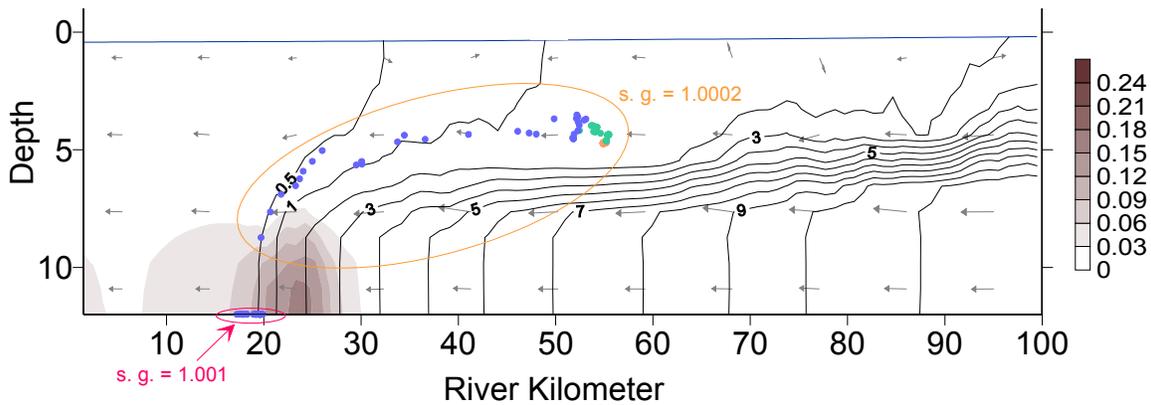

Fig. 9. Location of egg-like particles after 2 days in wind event scenarios. Particles were released at river km 16. Eggs with similar specific gravities (s. g.) are circled. Line contours indicate salinity (psu) and color contours indicate suspended sediment concentrations (kg m^{-3}).

Table 4. Number of egg-like particles located in the optimum nursery area after 2 d in wind event scenarios. Blue indicates all eggs floated above the salt front and were transported down estuary. Green indicates all eggs sunk to bottom and remained within 1 cm of bottom. 100 particles were released in each scenario.

Release Location	Specific Gravity						
(river kilometer)	1.0001	1.0002	1.0004	1.0006	1.0008	1.001	1.012
10	0	0	0	0	2	1	0
12	1	3	6	5	7	24	70
14	7	7	4	7	10	74	48
16	2	5	11	9	11	0	0
18	0	0	6	8	4	0	0
20	0	0	0	3	4	11	0

Striped bass eggs: steady-state scenarios with sub-grid scale turbulence. Results of steady-state scenarios that included sub-grid scale turbulence (Figure 10, Table 5) were markedly different from results of steady-state scenarios without turbulence. More than twice as many egg-like particles were located in the optimum nursery area with sub-grid turbulence (2,699) than without (1,267). Although the location of all particles was affected by the addition of turbulence (except those with s. g. = 1.0001), the addition of turbulence had the greatest effect on the location of the heaviest particles (s. g. > 1.0008). Instead of sinking to the bottom, the heaviest particles were found suspended in the optimum nursery area. Except for particles with specific gravities of 1.0001, 1.0002 (released at 18, 20 rkm) and 1.0004 (released at 20 rkm), the number of egg-like particles located in the optimum nursery area depended upon release location alone, as opposed to depending upon both release location and specific gravity.
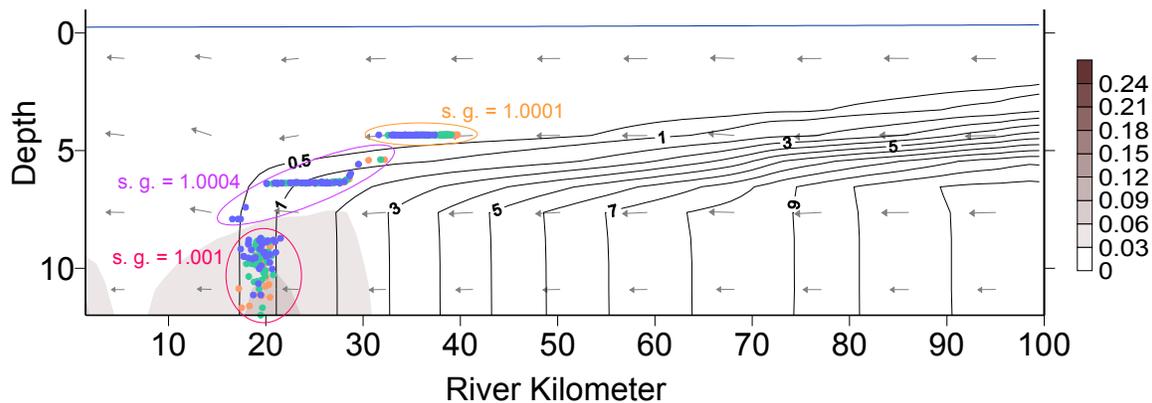

Fig. 10. Location of egg-like particles after 2 days in steady-stat scenarios with sub-grid scale turbulence. Particles were released at river km 16. Eggs with similar specific gravities (s. g.) are circled. Line contours indicate salinity (psu) and color contours indicate suspended sediment concentrations (kg m^{-3}).

Table 5. Number of egg-like particles located in the optimum nursery area after 2 d in steady-state scenarios with sub-grid scale turbulence. Blue indicates all eggs floated above the salt front and were transported down estuary. Green indicates eggs sunk to bottom and remained within 1 cm of bottom. 100 particles were released in each scenario.

Release Location	Specific Gravity						
(river kilometer)	1.0001	1.0002	1.0004	1.0006	1.0008	1.001	1.012
10	0	47	58	49	43	41	42
12	0	87	76	66	72	66	72
14	0	95	90	92	91	89	90
16	0	99	98	99	98	98	90
18	0	3	60	100	100	100	100
20	0	0	4	84	100	100	100

Discussion

Most neutrally buoyant particles released at depth within the optimum nursery area were retained in that region, even after 10 days in steady-state conditions. This suggests that the ETM region, the low salinity region at the foot of the salt front, is a retention area for planktonic organisms. Field collections confirm this: high concentrations of larval striped bass, larval white perch and Eurytemora copepods have been found in the ETM region in upper Chesapeake Bay (North and Houde 2001, North and Houde submitted). In contrast to those within the ETM region, most neutrally buoyant particles released up-estuary of the salt front were transported down estuary, bypassing the optimum nursery area. Particles with the sinking speed of striped bass eggs were retained within the ETM region (depending upon their density and release location). Striped bass may produce slightly-heavy eggs to facilitate transport to the optimum nursery area at the foot of the salt front where recently-hatched larvae could be retained in a region of favorable salinities, high prey concentrations, and refuge from predation.

Albrecht (1964) found that the eggs produced by San Francisco Bay striped bass had specific gravities that ranged from 1.0003 to 1.00065 with a mean of 1.0005. Model results suggest that striped bas eggs in the upper Chesapeake Bay may have a similar range of specific gravities. We plan to confirm this with field/laboratory work in 2003. In contrast, Rulifson and Tull (1999) found that striped bass eggs were significantly heavier in the Shubenacadie River, a tidal-bore river in Atlantic Canada. In this river, striped bass eggs increased in specific gravity with development, from 1.0016 for unfertilized eggs to 1.0066 for eggs with preflexion embryos. Atlantic coast striped bass populations produce heavier and larger eggs in high-energy river systems than those found in low-energy river systems (Bergey et al. in press). Greater egg density may be important for retention within high-energy estuaries like tidal bore Shubenacadie River (Rulifson and Tull 1999).

Kinetic energy in an estuarine system is related to the magnitude of tidal velocities and freshwater flow velocities. The range in sizes and densities of eggs produced by a striped bass population may be adapted to the range of freshwater flow velocities found in their natal river system during the spawning season. In our model simulations, the mean specific gravity of egg-like particles located in the optimum nursery was lower in the steady-state scenarios (1.00049) than in the river pulse scenarios (1.00064). This suggests that striped bass eggs with densities that are suitable for transport to the optimum nursery area at one flow velocity may not be as suitable at other flow velocities. Because flow patterns differ between river systems, the mean size and density of eggs may vary between striped bass populations to optimize transport to the ETM nursery areas in different flow regimes. We plan to use our coupled hydrodynamic-particle tracking model to test whether striped bass egg size and density may be an adaptation to the freshwater flow velocities of different river systems and to investigate the influence of tidal velocities and frequency of storm events on this potential relationship.

The river pulse and down-estuary wind event scenarios resulted in a 12.9 and 72.4% reduction in the number of egg-like particles located in the optimum nursery area. In wind event scenarios, the combination of egg density, wind mixing, and compression of the optimum nursery area resulted in a large portion of eggs being transported down-estuary. In river pulse scenarios, egg-like particles with low specific gravities (<1.0004) were transported down-estuary in the swift flow over the salt front. Storm events have resulted in episodic mortalities of eggs and newly hatched striped bass larvae, effectively eliminating >50% of a season's egg

production (Rutherford and Houde 1995). In addition to mortality due to sudden drops in temperature associated with storm fronts (Rutherford and Houde 1995), model results suggest that changes in circulation patterns associated with wind events during storms could result in the loss of a sizeable fraction of a larval cohort to transport down-estuary where mortality is likely (Secor et al. 1995).

The effect of including sub-grid scale turbulence in the model was profound: the number of egg-like particles located in the optimum nursery area more than doubled. Although results are preliminary, the potential error related to lack of sub-grid scale turbulence reinforces the importance of including turbulence in biological models (Rothschild and Osborn 1988, MacKenzie and Leggett 1991, Sundby 1997). Realistic turbulence may be especially important in models of stratified estuaries and shallow water bodies where the direction of transport of a particle is highly dependent on its vertical position in the water column. We intend to check our sub-grid scale turbulence parameterization by conducting dye-release experiments within the coupled hydrodynamic-particle tracking model. Sub-grid scale turbulence will be tuned so that it matches turbulent diffusion predicted by the hydrodynamic model.

In addition to exploring the effects of wind, freshwater flow and behavior on fish early-life stages and copepods within the ETM region on short time scales, our coupled hydrodynamic-particle tracking model has the potential to be used to explore the effects of environmental variability on trophic interactions and to link flow, temperature and wind fluctuations to fish recruitment variability on annual time scales. Our preliminary investigations suggest several research priorities that will facilitate quantitatively linking environmental conditions to early-stage survival and recruitment, including improved hydrodynamic modeling of turbulence in stratified flows, accurate parameterization of sub-grid scale turbulence in particle tracking models, and realistic representation of copepod and larval fish behavior.

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