

Larval Transport Model Peer Review and Lead Agency Response

Report Content and Charge:

This report describes the peer review process and presents the lead agencies response to the peer review. Also included are the names of the peer reviewers and their organizational affiliations, a compilation of all the peer review comments on the Larval Transport Model, and the principal investigators responses to the peer review.

The Larval Transport Model was developed as a supporting document for the Programmatic Environmental Impact Statement (EIS) for Evaluating Oyster Restoration Alternatives for the Chesapeake Bay, Including the Use of Native and Non-Native Oysters. The process followed for this peer review is consistent with the peer review plan that was developed by the Lead Agencies for the EIS project. This peer review plan was specifically designed to comply with the December 16, 2005 Office of Management and Budget's Peer Review Guidelines and was accepted by the US Army Corps of Engineers for this purpose.

Under the guidelines of the Peer Review Plan, the Project Delivery Team designated the Oyster Larvae Dispersal Peer Review Group (PRG) as the principal review group for the peer review of the Larval Transport Model. This group was specifically charged with the review of the application of larvae behavior data within the model. Since larvae dispersal is an interdisciplinary study, the Peer Review Group leader was asked to include as part of their review team individuals with expertise in larvae behavior and physical oceanography, as well as someone to assess whether the larvae dispersal dynamics have been incorporated into the model appropriately.

Because the larval transport data was used in the Oyster Demographic Model (ODM), the Independent Oyster Advisory Panel (OAP), the principal review group for the ODM, reviewed the Larval Transport Model results. The Project Delivery Team, the Scientific Advisory Committee, and the Atlantic States Marine Fisheries Commission (ASMFC), Interstate Shellfish Transport Committee were also provided opportunities to review and comment on the peer review report and the results from the Larval Transport Model. Comments received by the PRG, Project Delivery Team, Scientific Advisory Committee and ASMFC Interstate Shellfish Transport Committee were also provided to the OAP for their review and consideration.

A paper concerning the development and results of the Larval Transport Model will be published in a peer reviewed journal: North, E. W., Z. Schlag, R. R. Hood, M. Li, L. Zhong, T. Gross, and V. S. Kennedy. *in press*. Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. Marine Ecology Progress Series.

Study Objective:

The objective of the Larval Transport Model was to determine the spatial dispersal of *Crassostrea virginica* and *C. ariakensis* oyster larvae in Chesapeake Bay using coupled hydrodynamic and larval transport models and to transfer this information to a juvenile/adult demographic model.

The Lead Agencies Review and Response Process:

The PRG provided the lead investigators with preliminary comments in order to assist in making the assessment as scientifically sound as possible as well as to improve the clarity, cogency and credibility.

The Lead Agencies sent the Larval Transport Model draft report dated July 31, 2006 to the PRG for review on August 3, 2006. Peer review comments were provided to the Principal Investigators on September 25, 2006. Additional comments were received from the USACE – Baltimore District on August 21, 2006.

The revised Larval Transport Model report and the response to comments were submitted to the Lead Agencies on November 1, 2006. The Response to Reviews of the Larval Transport Model report summarized the manner in which the major PRG and USACE – Baltimore District comments were resolved in the revised Larval Transport Model report. The PRG provided a final peer review report to the study sponsor on February 22, 2007. The peer reviewers indicated that the principal investigator had adequately addressed the PRG concerns to the Larval Transport Model.

The Lead Agencies considered the Response to Reviews of the Larval Transport Model report and are satisfied that the key concerns raised by the PRG have been addressed.

Deposition of Peer Review:

Dr. Charles Epifanio, Ph.D (lead reviewer)
Professor and Associate Dean
College of Marine and Earth Studies
University of Delaware

Dr. Charles Tilburg, Ph.D
Department of Marine Sciences
University of Georgia

Stephen Sulkin, Ph.D
Director and Professor
Shannon Point Marine Center
Western Washington University

Peer Review Comments on the Draft Report dated July 31, 2006 (August 21, 2006)

4. Project 15: Modeling dispersal of *Crassostrea ariakensis* oyster larvae in Chesapeake Bay. E. North, R. Hood, M.Li, L Zhong, and T. Gross.

General Comments:

The rationale for this study was to model the physical transport of *Crassostrea ariakensis* and *Crassostrea virginica* larvae within Chesapeake Bay in attempt to determine how these two species disperse within the estuary. Specific objectives were: 1) to estimate the spatial dispersal of the two species using coupled hydrodynamic and larval transport models and 2) to transfer this information to a juvenile/adult demographic model. The initial package received by the panel included only two preliminary reports. However, the final report dated July 31, 2006 was delivered on August 3, 2006. Our comments deal with the final report.

In the introduction, the authors did an adequate job of providing context for the study. Their review of the literature was short (containing three references). But even in the absence of a substantial literature review, the authors were able to explain quite convincingly the need for the study.

The methodology consisted of coupling two previously validated hydrodynamic models of Chesapeake Bay with a larval behavioral model developed by the authors. This coupled model was used to examine the effects of varying larval behavior on the spatial dispersal and settlement success of oyster larvae spawned at various locations within the bay. The two hydrodynamic models were forced with actual physical conditions (wind, tides, river discharge and heat transfer) from five consecutive years that were characterized by very different buoyant discharges. The models were sufficiently described in the report. The two hydrodynamic models were validated using a number of different parameters and were used to examine the effects of different idealizations of the flow field on modeled larval transport and settlement. The larval behavioral model incorporated various aspects of behavior and was discussed in great detail. The authors highlighted both the techniques used and the limitations inherent in those techniques. As is the case in any numerical model of biological behavior, there are a large number of assumptions that may or may not be true. The authors discussed their assumptions and the effects of the assumptions on model results. The output necessary for the demographic model was discussed (although very briefly), but the actual demographic model was not mentioned, and we assumed that the demographic model had been developed separately from this project.

The results section was straightforward and provided sufficient detail. However, we found one troubling characteristic of the model output that was not discussed or even mentioned by the authors. The model was characterized by an almost complete lack of inter-annual variation. This is further discussed below:

- a) The range of years present in the model (1995-1995) was chosen because the freshwater discharge varied by a factor of five during this time. However tables 4 and 5 show that the largest difference in settlement between any two years was less than 7% for *C. virginica* (years 1999 and 1996) and less than 4% for *C. ariakensis* (years 1998 and 1995).
- b) The only noticeable inter-annual difference between the daily temporal structure of *C. virginica* settlement was the lag due to the starting-release date. Years 1995 – 1997 appear identical with only a slight lag in the beginning of settlement. Years 1998 and 1999 appear identical.

This lack of interannual variation in larval settlement is startling, indicating that larval transport and settlement within the Bay is almost completely unaffected by variations in freshwater discharge (and winds, which were not mentioned). The interannual variations present in both total larval settlement and in the temporal structure are so small that it is unclear if they could be due only to the random movement of larvae prescribed by the behavioral model. Because larval transport is largely governed by water velocities within the bay, one would expect a greater dependence of larval movement (and settlement) on those mechanisms that govern water movement. The conclusions do not mention this lack of variation, suggesting that the authors did not see this as a crucial outcome of the project. (Although the authors do quantify the variation, stating that the coefficient of variation for *C. virginica* was 27% and *C. ariakensis* was 16%; however we were not able to reproduce these values coefficients of variation.)

The lack of an explanation for this occurrence casts doubt on the entire project, which is unfortunate because the project as a whole is very good. Some recommendations to make this part of the project more credible are discussed below:

- a) Perform ensemble simulations of any one year to determine the variation due to random movement specified by the larval behavioral model.
- b) Demonstrate that the total annual larval settlement of each year is (or is not) statistically different from other years and discuss why this would be.
- c) Show the interannual variation of mean velocities within the bay and show how these affect larval settlement.
- d) Perform the simulation with no river discharge or winds to show that these mechanisms do indeed have no effect on the larval settlement as suggested by Figure 15 and Tables 3 and 4.

Review Criteria:

- 1) *Are conclusions adequately supported by evidence?* There were three main conclusions drawn from this study: (a) the differences in larval behavior result in significant difference in larval dispersal; (b) connectivity between basins was higher for *C. virginica* than *C. ariakensis*; and (c) the models were not able to quantitatively predict recruitment in any one year. All of the conclusions are supported by numerical output; however, the lack of discussion of the interannual variability casts some doubt on the veracity of the model output.
- 2) *Are uncertainties or incompleteness explicitly recognized?* Most parts of the study were carefully discussed; however, the lack of interannual variations was not recognized (or not deemed sufficiently important to be discussed).
- 3) *Are value judgments acknowledged?* The authors avoided value judgments.
- 4) *Are data and analyses adequately described?* No, since the larval transport is heavily dependent on flow within the bay, a better description of the velocities within the bay was warranted.

5) *Are statistical methods applied appropriately?* Overall, yes. However, we could not reproduce the coefficient of variation quoted in the annual larval settlements. In addition, the annual larval settlement should have been subjected to statistical analyses to determine if they were significantly different from each other.

6) *Is the report fair and impartial in tone?* Yes

Summary Statement:

The authors examined the effects of different behavior on larval dispersal of *C. virginica* and *C. ariakensis*. Their use of the numerical models and the appropriate larval behavior model was warranted and the description of the methods was complete. The text is very well organized, the figures clear (although there is no Figure 9 and two figures labeled 33), and the explanations complete.

The authors achieved their first objective in that they were able differentiate between the two species' potential for dispersal which suggests that the species would act differently if introduced to Chesapeake Bay. The report does not discuss in detail the necessary input for the demographic model, so we were not able to determine if the authors were successful in delivering the needed data to the demographic modelers.

The conclusions are hampered by questions concerning the model output. The lack of variation in larval settlement was unexpected and, if accurate, has profound ramifications on the modeling of oyster dispersal (e.g. it eliminates the need for running the hydrodynamic model over multiple years, since each year produces nearly identical results). This outcome was not mentioned by the authors and it is unclear if the authors felt that this was unimportant or did not notice it. Whether this outcome is due to the long residence time of the bay, the fact that the bay is tidally dominated, or an error in the modeling methods is unclear. Addressing this lack of variation and assuring the reader that this outcome makes physical sense would lend much credibility to the entire project.

USACE-Baltimore District Comments (September 25, 2006)

1. Figure 5, page 11- This is a good analysis. It may also be important to consider variance of the two hydrodynamic models with distance up estuaries. Based on Figure 4, it does not appear that ROMS boundaries extend as far into tributaries.
2. p18- What is the source of the presented probabilities for swimming behavior (paragraph 3)?
3. Is there any information about the probability of a pediveliger crossing an oyster bar and not setting in the wild?
4. p 20, last paragraph- 'reflective horizontal boundary condition'- Why isn't a particle that moves out of the boundary horizontally considered dead or lost? Is the thinking that these particles would be returned by flow or behavior into the domain? Has there been any analysis to understand what proportion of the particles actually did 'leave' and had to be reflected back into the domain?

5. p 26- Are there any estimates of how many gametes are actually released into the water column/year? In other words, do the number of particles released by this simulation represent 1%, 10%, 50%, etc. of natural release? Could the model be run on a subestuary scale with a number of particles that is representative of the magnitude of a) a historical release and b) a current typical release? Would it be worthwhile to compare the results of the whole Bay model run with the fewer number of particles with those of (b) to check if the model is capturing the transport of a typical release?

6. Figure 17- There appears to be very little, if any, loss of *C. ariakensis* to the Atlantic Ocean. This could be interpreted as a 'natural' barrier to *C. ariakensis* invasion of other Atlantic Coast estuaries. Chesapeake Bay is essentially acting as a trap estuary for *C. ariakensis*. Would this be an accurate conclusion if used to calm fears and complaints of those in Delaware Bay, North Carolina, the Gulf Coast, etc.?

7. Figure 24- How can this information be validated or field verified? If interpreted with respect to where the majority of good reefs exist today, does it hold up? Maryland and Virginia mainstem dots are confusing. The Maryland mainstem is shown as one dot in the northern Bay, but it actually stretches down to the Maryland line. Therefore, its high connectivity is not surprising, but how great a contribution do mainstem bars actually make today to the Bay population?

8. Table 6- The connectivity matrix does show connectivity, but no basins (except the mainstem) received any significant proportion of particles. Continuing on my thoughts of comment #7, does this make sense in the context of the role mainstem bars actually have in the current Bay population?

9. p38, first paragraph, last full line- Should the 1% be 100%?

10. Figure 26- 'Catching bars'- Only a few bars in the tributaries are identified as catching a high density. However, historically the prime beds are in the tributaries, not the mainstem. Have the habitat areas of tributaries bars been reduced in a greater proportion than those in the mainstem? Do you think a larger good habitat area in the tributaries affect the catch in the tributaries?

11. p 40, B. Validation and sensitivity studies- Why was Virginia data not included in the analysis?

12. p 41- Are there plans to compare the Maryland measured spatfall data with information produced by the demographic model?

13. Figure 33- lower left panel- The purple dots are very hard to recognize. Can a different color or symbol be used to present this information in a clearer way?

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Response to Reviews of the Larval Transport Model

November 1, 2006

Project Title: Modeling dispersal of *Crassostrea ariakensis* oyster larvae in Chesapeake Bay

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Funding: \$90,579 from Maryland Department of Natural Resources. Development of some model components was supported by NOAA/CBPO, NSF and UMCES Horn Point Laboratory.

Introduction

This report includes responses to review questions and comments on the larval transport model that was completed for the ongoing Environmental Impact Statement related to the introduction of a non-native oyster in Chesapeake Bay. The objectives of the larval transport research were to 1) determine the spatial dispersal of *Crassostrea virginica* and *C. ariakensis* oyster larvae in Chesapeake Bay using coupled hydrodynamic and larval transport models, and 2) transfer this information to a juvenile/adult demographic model.

Reviews of the larval transport model were conducted by the “Larval Transport Model Peer Review Team” and by Dr. Angela Sowers of the Army Corps of Engineers. Our responses to the comments, questions and recommendations of these reviewers are summarized below.

Response to Larval Transport Model Peer Review Team

Response to general comments. The Peer Review Team’s concerns with the larval transport model focused on one aspect of the model results: the lack of variation in total settlement success between years of different physical conditions. They wrote “*This lack of interannual variation in larval settlement is startling, indicating that larval transport and settlement within the Bay is almost completely unaffected by variations in freshwater discharge...*” The lack of interannual variability in total settlement success in the larval transport model was related to 1) the size and residence time of Chesapeake Bay, and 2) the settlement metric itself. As pointed out by the review panel, the residence time of water in the Chesapeake Bay (~26 weeks, North et al. *submitted*) is much longer than the duration of particle transport in the larval transport model (< 3 weeks). In addition, the average dispersal distance of all *C. virginica* particles in all years was 23.8 km, much less than the >300 km basin. The size and residence time of the system compared with the dispersal distance and larval stage duration indicates that most particles would not be rapidly flushed from the system into areas without

settlement habitat (hence the lack of a strong interannual signal in total settlement success). In addition to keeping in mind the dimensions of the Chesapeake Bay, it is important to clarify what the settlement metric represents and what factors influence settlement.

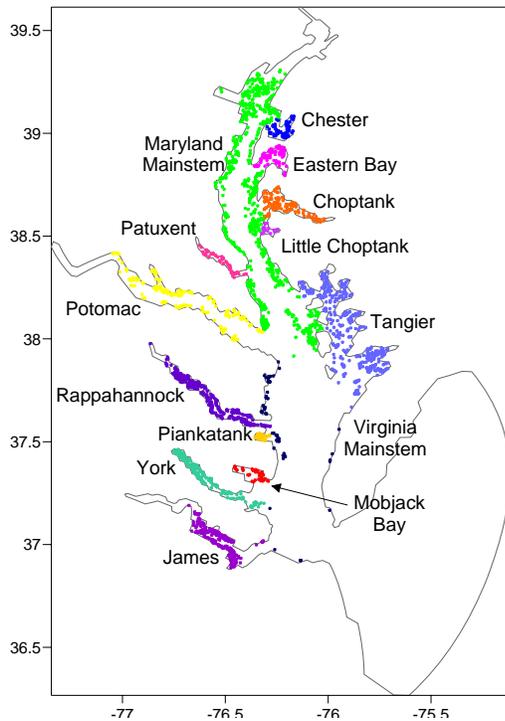


Fig. 1. Oyster bars (e.g. habitat polygons) and larval transport model boundaries. Oyster habitat is color coded by basin.

The settlement metric indicates whether a particle was able to ‘find’ suitable settlement habitat *anywhere* in the model domain during the ~7 d period when particles were competent to settle. It does not reflect the distance or direction that a particle traveled to ‘find’ the settlement location. A particle released from the same bar may settle on a different bar every year and retain the same settlement score. Settlement of any given particle is influenced by 1) the shape of the basin in which it is released because basin shape influences circulation patterns within the basin, 2) the amount and spatial arrangement of settlement habitat within the basin and in nearby basins, and 3) inter-annual differences in flow and wind. The basins within Chesapeake Bay are numerous and have different shapes and distributions of suitable settlement habitat (Fig. 1). Some basins contain habitat throughout (e.g., the Choptank River and Tangier Sound), so particles have ample opportunity to encounter suitable habitat during the ~1 week period when they are competent to settle. Other basins have large areas devoid of habitat (e.g., the Maryland mainstem) which reduces the chance of settlement success compared to other basins. In addition to differences in habitat, circulation patterns within the basins are expected to respond differently to

changes in freshwater flow and wind. Some rivers input more freshwater to the systems than others. For example, most of the average freshwater input to the Chesapeake originates from the following rivers: Susquehanna (48.2%), Potomac (13.6%), James (12.5%), Rappahannock (3.1%), Choptank (1.2%) and York (1.2%) (Schubel and Pritchard 1987). In addition, the basins do not have the same alignment and fetch in relation to the directions of wind events, so the effect of wind on circulation patterns would not be the same. For these reasons, it is reasonable to expect that circulation patterns and conditions that promote settlement success would differ between basins. It also is reasonable to expect that a metric that aggregates across many different basins (like total settlement success) would tend to dampen the degree of interannual variability that is inherent in model results if circulation patterns within basins do not respond in the same way to changes in flow and wind.

Because aggregating across many different basins likely masks interannual variability in settlement, basin-scale metrics should be applied to detect inter-annual variability in model predictions. In addition, other metrics may be more appropriate for detecting interannual signals that are related to changes in circulation patterns. For example, dispersal distance of particles

Table 1. Percent settlement success of *C. virginica* particles by basin and year for all simulations. The table also includes total settlement success in each basin ('All years'), the maximum difference in percent settlement success between years ('max difference'), and the P-values for ANOVA tests to determine if there is a significant difference in percent settlement success between years (bold values indicate a significant difference at $\alpha = 0.10$). Five releases of particles were conducted during each year. Each of these releases was used as a replicate within each year for the ANOVA analysis (n = 25).

Basin	All Years	1995	1996	1997	1998	1999	Maximum difference	ANOVA P-value
Chester River	84.0	85.6	82.3	80.8	85.8	85.5	5.1	0.06
Choptank River	87.8	88.1	88.9	89.9	86.8	85.2	4.7	0.53
Eastern Bay	82.4	82.2	81.6	84.0	83.9	80.0	4.0	0.68
James River	65.0	43.4	62.9	68.7	71.2	79.0	35.6	0.02
Little Choptank River	77.6	83.8	79.4	80.3	72.6	71.9	11.9	0.32
Maryland Mainstem	59.4	63.4	56.8	59.5	56.0	61.2	7.4	0.01
Mobjack Bay	49.2	55.4	42.5	52.2	51.3	44.7	12.9	0.45
Patuxent River	77.3	81.1	70.1	73.7	79.9	81.5	11.4	0.11
Piankatank River	58.5	58.5	68.5	41.9	52.3	71.3	29.4	0.08
Potomac River	48.0	49.4	43.3	50.4	48.6	48.5	7.1	0.33
Rappahannock River	80.7	71.1	78.5	83.3	83.5	86.9	15.8	0.06
Tangier Sound	77.9	80.5	78.3	76.5	77.4	76.7	4.0	0.05
Virginia Mainstem	14.4	13.7	13.8	11.6	16.5	16.5	4.9	0.55
York River	79.4	78.9	76.5	79.1	79.3	83.3	6.8	0.37
Chesapeake Bay	67.8	66.3	65.9	68.4	67.8	70.6	4.7	0.28

Table 2. Percent settlement success of *C. ariakensis* particles by basin and year for all simulations. The table also includes total settlement success in each basin ('All years'), the maximum difference in percent settlement success between years ('Maximum difference'), and the P-values for ANOVA tests to determine if there is a significant difference in percent settlement success between years (bold values indicate a significant difference at $\alpha = 0.10$). Five releases of particles were conducted during each year. Each of these releases was used as a replicate within each year for the ANOVA analysis (n = 25).

Basin	All Years	1995	1996	1997	1998	1999	Maximum difference	ANOVA P-value
Chester River	80.6	78.8	86.0	72.9	82.0	83.3	13.2	0.05
Choptank River	73.9	72.2	74.7	73.3	73.4	75.7	3.5	0.84
Eastern Bay	81.9	82.6	83.1	79.7	83.4	80.6	3.7	0.62
James River	84.2	65.4	89.0	90.6	84.8	91.4	26.0	0.02
Little Choptank River	75.3	83.2	78.3	71.3	75.2	68.2	15.0	0.15
Maryland Mainstem	67.9	66.9	68.3	66.7	70.5	67.0	3.7	0.68
Mobjack Bay	55.5	63.0	47.5	56.6	59.0	51.6	15.4	0.14
Patuxent River	48.4	52.2	40.5	46.6	49.3	53.2	12.7	0.25
Piankatank River	74.7	75.1	74.0	78.8	74.5	71.3	7.5	0.84
Potomac River	55.3	60.6	46.8	57.9	56.5	54.5	13.8	0.13
Rappahannock River	96.2	96.3	97.1	96.6	96.0	95.1	2.0	0.16
Tangier Sound	77.0	75.9	79.6	75.3	76.4	77.5	4.3	0.02
Virginia Mainstem	22.8	24.0	26.8	16.9	23.4	22.8	9.9	0.15
York River	87.4	88.8	87.5	87.8	86.5	86.2	2.6	0.57
Chesapeake Bay	73.9	72.1	74.5	73.9	74.8	74.4	2.7	0.36

incorporates spatial information that better reflects how larval transport is influenced by variations in circulation patterns between years.

At the basin-scale, the larval transport model does predict that there is interannual variation in settlement within basins. Basin-specific settlement success is reported in Tables 1 and 2 and is pictured in Fig. 22 of North et al. (2006b). For *C. virginica*, differences in percent settlement success between years was lowest in Eastern Bay (4.0%) and Tangier Sound (4.0%), and was highest in the James (35.6%) and Piankatank (29.4%) Rivers. For *C. ariakensis*, differences in percent settlement success between years was lowest in Rappahannock (2.0%) and York (2.6%) Rivers, and was highest in the James River (26.0%) and Mobjack Bay (15.4%). The difference between percent settlement success between years was significant for some basins and not for others (Tables 1 and 2), as would be expected due to differences in suitable habitat and the potential influence of wind and freshwater flow. Model results indicate that some basins could have more consistent spat settlement than others due to the shape and circulation patterns in the basin. This fact that some basins have better ‘trapping’ ability for larvae has been observed in sub-estuaries in Chesapeake Bay (Kennedy 1980, Boicourt 1982, Seliger et al. 1982, Andrews 1983). Model results suggest that ‘trapping’ circulation patterns may differentiate settlement success between larger systems. Results also suggest that basin shape and the amount and spatial arrangement of settlement habitat could influence the degree to which a population is impacted by interannual variability.

The Peer Review Team also stated that “*Because larval transport is largely governed by water velocities within the bay, one would expect a greater dependence of larval movement (and settlement) on those mechanisms that govern water movement.*” As stated above, settlement success is not the most appropriate metric for measuring the influence of interannual variability in water movement on larval transport. A better metric is dispersal distance which reflects the distance from the release site that a particle was transported by water movement. In this analysis, dispersal distance was calculated as the straight-line distance between release and settlement locations, regardless of whether the line crossed land boundaries in the model. As such, the dispersal distances presented should be regarded as the minimum potential distance that particles traveled. Mean dispersal distance was calculated for particles released within each basin for each of the five years of model simulation.

Mean dispersal distances differed between species, between basins, and between years within each basin (Table 3). Although there were instances of particles of both species settling as close as 1 m from their release site, the mean dispersal distance of all particles in Chesapeake Bay during all years was 16.9 km for *C. virginica* and 9.9 km for *C. ariakensis*. While minimum dispersal distances were similar between species (1 m), the maximum dispersal distance of a *C. virginica* settled particle (226.0 km) was more than 100 km greater than the maximum distance of the furthest traveling *C. ariakensis* particle (121.4 km). This is related to the vertical position of *C. virginica* veliger particles above the halocline where flow patterns would transport larvae down-estuary and where wind events would have a more direct impact on circulation patterns. In contrast, *C. ariakensis* veliger particles remained below the halocline and near bottom where friction with the bottom reduces current speed (and hence transport distance).

Table 3. Mean dispersal distance (km) of A) *C. virginica* and B) *C. ariakensis* settled particles by basin and year predicted by the larval transport model. The table includes the minimum (min) and maximum (max) dispersal distances and the standard deviation (std) of the mean for the entire Chesapeake Bay (bottom rows). Rightmost columns contain the maximum difference in mean dispersal distance between years, the R^2 values for the regression of dispersal distance versus freshwater discharge (June – August) in each year, the sign of the regression slope, and the river flow variable used in the regression (Sus = Susquehanna River, Pot = Potomac River, Rappah = Rappahannock River). Bold and starred R^2 values indicate that the regression slope was significant at the $\alpha = 0.1$ level.

A. *C. virginica*

Basin	All Years	1995	1996	1997	1998	1999	Maximum difference	R^2	Sign of slope	River Flow
Chester River	7.7	6.7	7.5	6.9	9.7	7.5	3.0	0.08	+	Sus
Choptank River	10.4	8.5	10.9	8.7	12.1	11.6	3.6	0.01	+	Choptank
Eastern Bay	12.3	10.3	12.6	11.3	15.4	12.0	5.2	0.15	+	Sus
James River	9.3	10.9	9.5	9.8	8.0	8.9	2.9	0.65*	+	James
Little Choptank R.	12.6	10.4	12.1	10.4	16.3	14.4	6.0	0.00	-	Sus
MD Mainstem	32.5	24.7	40.8	31.0	41.5	26.1	16.8	0.67*	+	Sus
Mobjack Bay	6.4	6.1	6.0	6.8	6.8	6.3	0.8	0.24	-	York
Patuxent River	17.7	14.6	23.1	21.9	15.5	14.6	8.5	0.56	+	Patuxent
Piankatank River	6.2	5.9	5.1	10.1	6.8	4.9	5.3	0.02	-	Sus + Pot
Potomac River	16.4	15.3	24.4	13.6	16.1	13.6	10.8	0.91*	+	Potomac
Rappahannock R.	10.9	16.5	11.9	9.9	8.4	8.9	8.1	0.87*	+	Rappah
Tangier Sound	6.1	6.0	5.9	6.0	6.4	6.1	0.5	0.01	-	Sus + Pot
VA Mainstem	20.7	17.9	20.9	24.8	20.8	20.0	7.0	0.00	+	Sus + Pot
York River	9.2	10.7	9.3	9.6	7.7	8.8	3.0	0.36	+	York
Chesapeake Bay	15.9	14.6	18.5	15.1	17.5	13.7	4.8	0.57	+	Total
Chesapeake std	20.8	16.3	24.4	18.8	24.7	18.3				
Chesapeake min	0.001	0.003	0.002	0.004	0.005	0.001				
Chesapeake max	226.0	155.3	226.0	162.6	223.4	225.4				

B. *C. ariakensis*

Basin	All Years	1995	1996	1997	1998	1999	Maximum difference	R^2	Sign of slope	River Flow
Chester River	5.8	5.0	5.9	6.0	6.2	5.6	1.2	0.15	+	Sus
Choptank River	7.8	7.7	7.6	8.5	8.7	6.6	2.1	0.00	+	Choptank
Eastern Bay	7.7	7.5	7.0	8.5	8.3	6.9	1.6	0.01	+	Sus
James River	7.0	9.8	6.5	6.7	5.9	6.6	3.9	0.78*	+	James
Little Choptank R.	6.7	6.3	7.8	7.1	6.5	5.7	2.0	0.72*	+	Sus
MD Mainstem	16.7	16.8	16.8	17.8	17.5	14.7	3.1	0.39	+	Sus
Mobjack Bay	5.9	6.3	6.5	5.8	5.3	5.7	1.2	0.61	+	York
Patuxent River	9.6	8.8	10.8	10.0	9.6	9.0	2.0	0.77*	+	Patuxent
Piankatank River	3.9	5.0	4.9	3.4	3.2	3.2	1.7	0.43	+	Sus + Pot
Potomac River	11.7	13.0	13.6	11.7	10.6	9.9	3.7	0.74*	+	Potomac
Rappahannock R.	7.2	8.7	7.5	7.0	6.4	6.3	2.4	0.91*	+	Rappah
Tangier Sound	5.7	5.8	5.6	5.5	5.8	5.6	0.3	0.00	+	Sus + Pot
VA Mainstem	16.7	19.4	17.2	15.8	15.9	14.8	4.6	0.20	+	Sus + Pot
York River	7.1	7.9	7.2	6.9	6.4	7.1	1.5	0.29	+	York
Chesapeake Bay	9.9	10.6	9.9	10.1	9.9	8.9	1.8	0.41	+	Total
Chesapeake std	9.9	10.3	10.1	10.0	10.0	9.0				
Chesapeake min	0.001	0.003	0.005	0.001	0.002	0.001				
Chesapeake max	121.4	113.8	113.5	98.6	121.4	103.8				

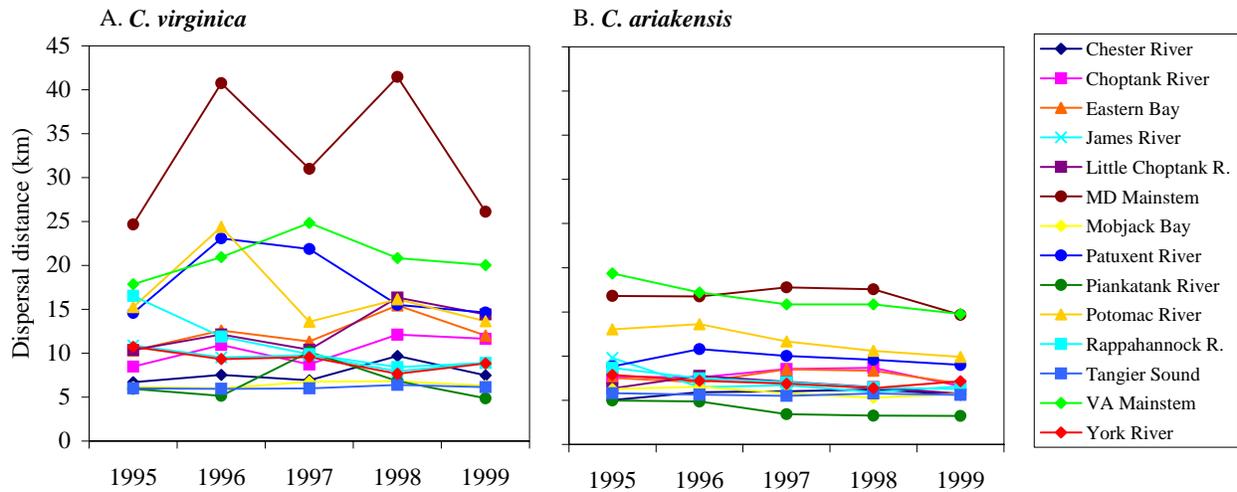


Fig. 2. Mean dispersal distance (km) of A) *C. virginica* and B) *C. ariakensis* particles released from basins in Chesapeake Bay for each year of model simulation.

Mean dispersal distance of settled particles differed between basins (Fig. 2, Table 3). Basin-specific *C. virginica* dispersal distances were greater than that of *C. ariakensis* and tended to be more variable with as much as 26.4 km and 12.8 km difference in mean dispersal between basins for *C. virginica* and *C. ariakensis*, respectively. *C. virginica* particles released in the Maryland mainstem had the highest mean dispersal distance (32.5 km) while those released in the Tangier Sound had the lowest (6.1 km). For *C. ariakensis*, highest mean dispersal distances for all years occurred in the Maryland and Virginia mainstems (16.7 km) and the lowest was in the Piankatank River (3.7 km).

Within basins, interannual variability in mean dispersal distances was apparent (Fig. 2, Table 3), especially for *C. virginica* particles. In the Maryland mainstem basin, mean dispersal distances differed by as much as 16.8 km between years. This basin is strongly forced by the Susquehanna River which delivers almost half of the freshwater input to Chesapeake Bay. Interannual variability in mean dispersal distance was smaller for *C. ariakensis* particles (maximum = 4.6 km), as expected based on their location in the water column during the veliger and pediveliger stages (i.e., near bottom). In several basins, freshwater discharge in that basin described a significant amount of the interannual variability in mean dispersal distance of particle released from that basin (Fig. 3, Table 3). All significant relationships ($\alpha = 0.1$, $n = 5$) had positive slopes for both *C. virginica* and *C. ariakensis*, indicating that longer dispersal distances were associated with increases in freshwater flow. The positive relationships ‘make sense’ physically, because increased freshwater flow can enhance down-estuary transport of water in the surface layer and up-estuary transport of water in the bottom layer in partially-mixed estuaries like Chesapeake Bay (Li 1999), but wind forcing could also influence the interannual variability in dispersal distance.

Wind-driven currents are usually larger than the gravitational circulation and may play an important role in driving particle dispersal at the time scale of days. Some of the interannual variability found in dispersal distance may be caused by differences in summer wind conditions.

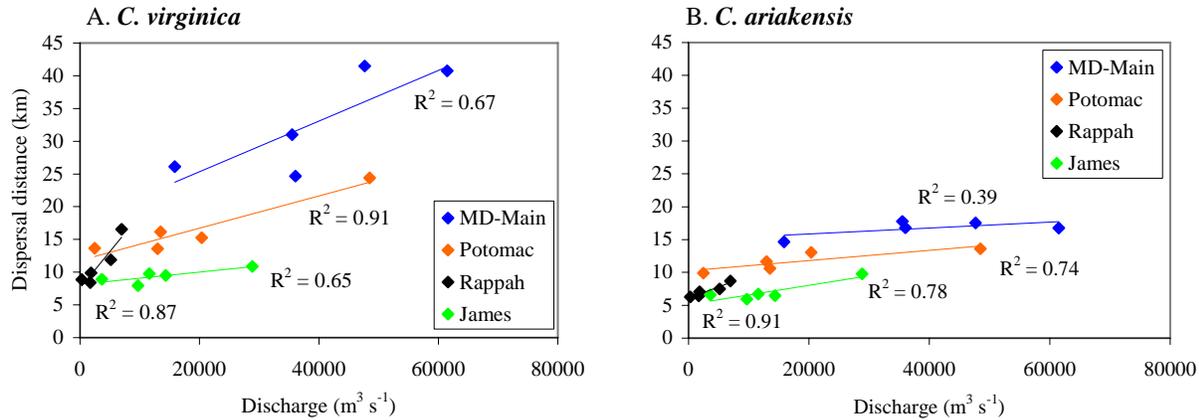


Fig. 3. Mean dispersal distance of A) *C. virginica* and B) *C. ariakensis* particles released from Maryland mainstem, Potomac, Rappahannock, and James River basins versus the sum of daily mean discharge for June, July and August from the Susquehanna, Potomac, Rappahannock, and James Rivers (1995 – 1999).

(see Li et al. 2005, 2006 for more information on how the ROMS model is able to capture changes in circulation patterns related to wind events). Although an extensive analysis of the influence of wind on particle dispersal distance is beyond the scope of this report, evidence does suggest that wind was also an influential factor. For example, when both wind and flow were included in the regression relationship predicting mean dispersal distance for *C. virginica* particles in the Maryland mainstem, the R^2 value increased from 0.67 (flow alone, Table 3a) to 0.93 (wind and flow, SAS 9.1). In this analysis, the wind index was calculated as the average of the summed absolute values of the north and east components of wind speed (measured at Patuxent River Naval Air Station or Thomas Point Light) during the time period of particle dispersal in the upper Chesapeake Bay. Another analysis indicates that basins without a strong relationship between flow and dispersal distance (e.g. Little Choptank), may be influenced by wind. The relationship between mean dispersal distance and flow in the Little Choptank had an R^2 of 0.00 (Table 3a), while the R^2 value with the wind index was 0.56 (SAS 9.1).

As can be seen, the results of the larval transport model do include interannual variability when viewed with the appropriate metrics and at the appropriate scale. Aggregated metrics like total settlement success may not display a strong interannual signal in large systems like Chesapeake Bay that have diverse basins that respond differently to changing physical conditions. This modeling study seeks to identify how physical factors influence larval transport in the absence of dynamic biological factors and is the first larval transport modeling study of oyster populations in the large Chesapeake system. Little evidence exists upon which to base expectations for the amount of variability that there should be in particle settlement due to physical conditions in a system as extensive and complicated as Chesapeake Bay. As stressed in the Final Report, the *larval transport model should not be expected to reproduce the orders-of-magnitude variability that is inherent in oyster recruitment* because it does not include many important nonlinear biological processes like adult spawner abundances, gamete fertilization success, and larval and juvenile mortality and growth. These processes are included in the demographic model where the expected juvenile production in any given year is a function of weather type (wet, average, dry as defined by freshwater discharge) and the spawning population, and is modeled by re-sampling from empirically-derived stock-recruitment

relationships (Jon Vølstad, pers. comm.). Preliminary validation analyses of the linked larval transport and demographic models suggest that biological factors (esp. adult spawner abundance) are important parameters for predicting juvenile oyster recruitment. Once the larval transport model is linked to the demographic model, each particle will represent the trajectory of different numbers of surviving oyster larvae depending upon the spawning populations on each oyster bar (from millions to hundreds of billions). Only when the link between the larval transport and demographic models are complete will we be able to determine if the interannual variability predicted by the linked model matches the variability in observed juvenile recruitment.

The Peer Review Team noted that they were not able to reproduce the Coefficients of Variation for annual total settlement success for *C. ariakensis* and *C. virginica*. The reported values, calculated in excel, were off by an order of magnitude. Here are the correct values: 1. 5% for *C. ariakensis* and 2.8% for *C. virginica* (SAS 9.1). Coefficient of Variation values reported on p. 41 of the Final Report were checked and confirmed to be reported correctly (SAS 9.1).

Response to specific recommendations. The Peer Review Team made specific recommendations to enhance their understanding of larval transport model results. The recommendations (a-d) and our responses to them are below:

“a) Perform ensemble simulations of any one year to determine the variation due to random movement specified by the larval behavioral model.”

This statement is related to the following general comment of the Peer Review Team: *“The interannual variations present in both total larval settlement and in the temporal structure are so small that it is unclear if they could be due only to the random movement of larvae prescribed by the behavioral model.”* In light of the fact that the larval transport model does predict interannual variability in basin-specific dispersal distances and settlement success, the need to conduct additional simulations is no longer necessary. But, this statement does suggest that member(s) of the Peer Review Team question the use of random movement in the larval transport model. There are two sources of random movement in the larval transport model: 1) the random components assigned to swimming speeds and direction in the larval behavior model to simulate individual variation, and 2) turbulent particle motion due to physical mixing processes that are on smaller scales than the hydrodynamic model grid resolution.

The random motions based on larval behavior are constrained to observed swimming speeds of oyster larvae (maximum 3 mm s^{-1}). The random component assigned to the direction of particle motion (up or down) was constrained by observations of oyster larvae and stage-dependent behaviors of oyster larvae inferred from recent laboratory (Newell et al. 2005) and past field studies (see Kennedy 1996 for review). Because the model is constrained by our best understanding of oyster larvae behavior, and because individual variation is fundamental characteristic of all life forms, the random component of the behavior model cannot be considered to introduce bias in, or confound, model predictions.

The second random component in the model is related to turbulent particle motion that is introduced to simulate physical mixing processes that are on smaller scales than the hydrodynamic model grid resolution. The use of turbulent particle motion in particle-tracking models is well-established in the oceanic particle-tracking literature (Werner et al. 1996, Visser

1997, Brickman and Smith 2002). One approach for determining how to parameterize particle motion is to complete a numerical ‘dye-release’ study that compares particle distributions with an Eulerian tracer (a ‘dye’) predicted by the hydrodynamic model (North et al. (2006a)). The particle distributions and dye should match if the particle tracking model correctly simulates the predictions of the hydrodynamic model. Figures 4 and 5 show the results of the dye-release studies (using the Princeton Ocean Model) when particles had no turbulent motion, turbulent motion specified by a random walk model, and vertical turbulent motion specified by a random displacement model. As can be seen, particles without turbulence underestimated the distribution of the dye as predicted by the hydrodynamic model, while turbulent particle motion simulated with a random displacement model provided the best match. Although it would have been ideal to complete this type of dye-release study with the larval transport model (based on ROMS hydrodynamic model), time constrains precluded this. Therefore, we parameterized turbulent particle motion in the larval transport model using the latest understanding available in the peer-reviewed literature (Visser 1997, Brickman and Smith 2002) and the best algorithms as found in the North et al. (2006a) study (i.e., panel D in Figs 4 and 5).

It is important to note that the ultimate validation of any particle tracking model requires *in-situ* dye-release experiments in regions of the Chesapeake that are simulated by the hydrodynamic model, preferably within several different size and shaped basins and during different wind and flow conditions. Although the particle-tracking model that we are using is state-of-art, we recognize the need for field validation and are in the process of planning proposals to request funds to do so. In addition to validating the circulation component of the larval transport model, measuring the *in-situ* vertical distribution of oyster larvae in different basins under various physical conditions would also be important for validating larval transport model predictions.

“b) Demonstrate that the total annual larval settlement of each year is (or is not) statistically different from other years and discuss why this would be.”

Statistical tests and discussion of the settlement metric are found in the ‘Response to general comments’ section above.

“c) Show the interannual variation of mean velocities within the bay and show how these affect larval settlement.”

Validation of current velocities predicted by the ROMS model in relation to different forcing conditions have been published in the peer reviewed literature (Li et al. 2005, 2006; Zhong and Li 2006).

“d) Perform the simulation with no river discharge or winds to show that these mechanisms do indeed have no effect on the larval settlement as suggested by Figure 15 and Tables 3 and 4.”

As can be seen in Fig. 3 above, river discharge does have an effect on larval settlement when model results are analyzed at the appropriate scale and with the metric dispersal distance. Our conclusion is that total settlement is not a good metric to use for discerning the influence of interannual variability on larval transport because it aggregates the responses of 14 very different basins in a >300 km estuary and it does not include information on the changes in spatial patterns in settlement between years. Based on these findings, there is no need to conduct further larval transport model simulations.

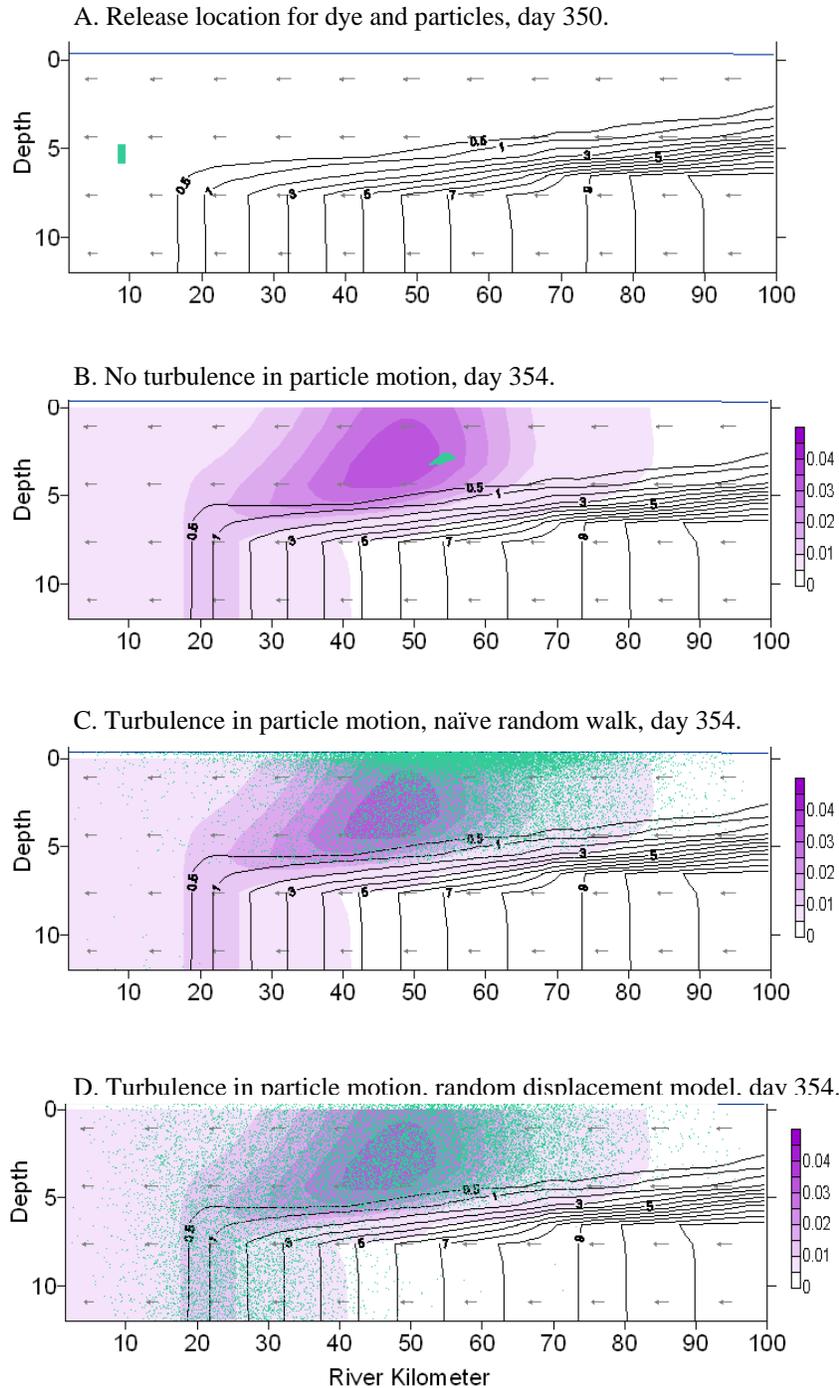


Fig. 4. Dye release study: passive tracer and particles released up-estuary of the salt front (lines are salinity contours). A) Location of particle and Eulerian tracer ('dye') release. Particles (green dots) and dye (purple contours) were neutrally buoyant. B) Location of tracer and dye after 4 days when particle motion was based on advection only (no turbulence). B) Location of tracer and dye after 4 days when particle motion included both advection and horizontal and vertical turbulence modeled with a naïve random walk model. C) Location of tracer and dye after 4 days when particle motion included both advection, horizontal turbulence (naïve random walk) and vertical turbulence modeled with a random displacement model. Panels A, C, D were reproduced in North et al. (2006a).

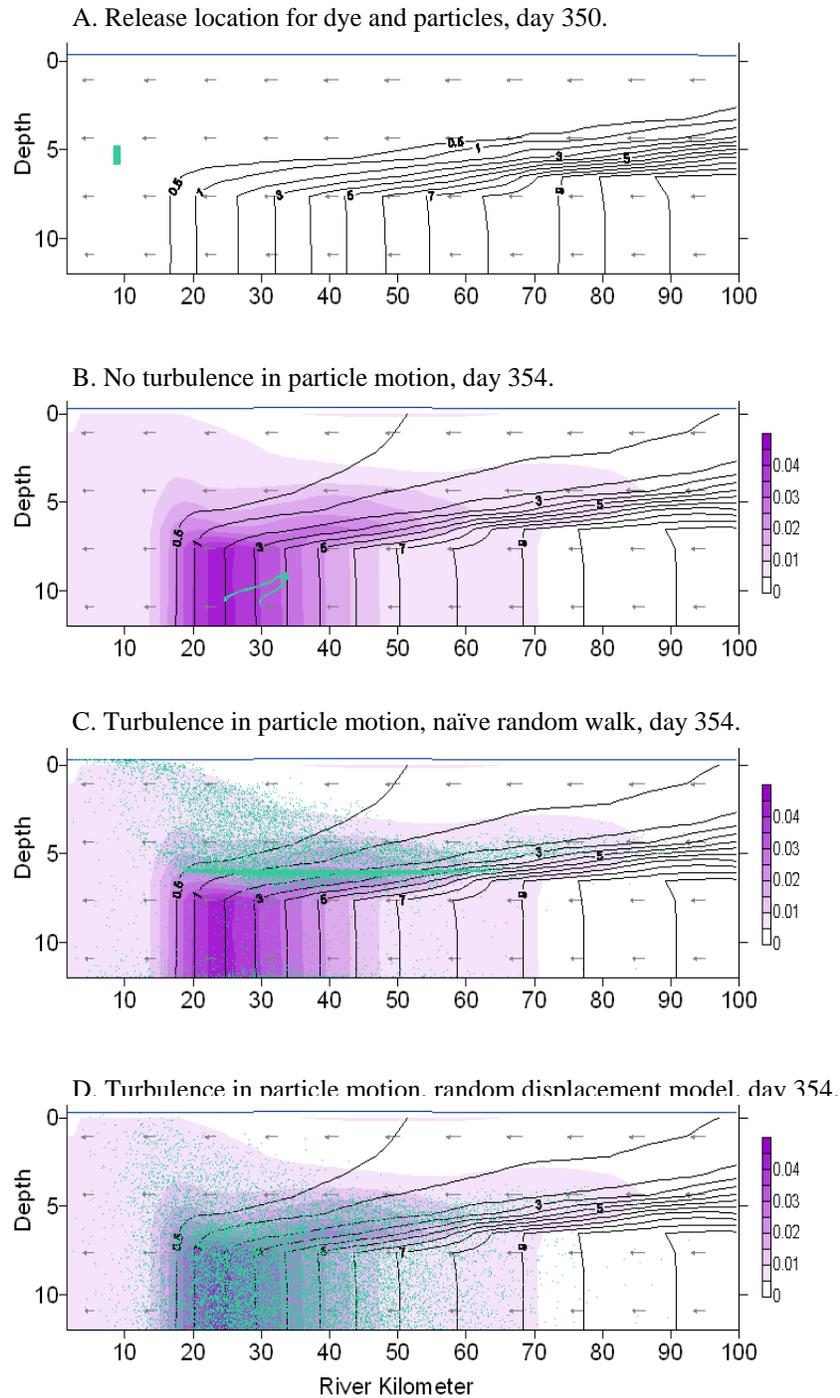


Fig. 5. Dye release study: sinking tracer and particles released up-estuary of the salt front (lines are salinity contours). A) Location of particle and Eulerian tracer ('dye') release. Particles (green dots) and dye (purple contours) were assigned a constant sinking speed of 0.3 mm s^{-1} . B) Location of tracer and dye after 4 days (during which there was a wind event) when particle motion was based on advection only (no turbulence). C) Location of tracer and dye after 4 days when particle motion included both advection and horizontal and vertical turbulence modeled with a naïve random walk model. D) Location of tracer and dye after 4 days when particle motion included both advection, horizontal turbulence (naïve random walk) and vertical turbulence modeled with a random displacement model. Panels A, C, D were reproduced in North et al. (2006a).

Response to Dr. Angela Sowers of the Army Corps of Engineers

Dr. Sowers comments and questions, and our responses to them, are below.

1. *Figure 5, page 11- This is a good analysis. It may also be important to consider variance of the two hydrodynamic models with distance up estuaries. Based on Figure 4, it does not appear that ROMS boundaries extend as far into tributaries.*

This is an important point. Because of the time constraints imposed by the EIS schedule, we were not able to build a hydrodynamic model ideally suited for predicting oyster larvae transport. To have finer resolution in tributaries, one could nest high-resolution tributary models within the Bay model or employ an unstructured-grid model, but these extensive model development efforts could not have been accomplished within the EIS time frame. In the hydrodynamic models that we used, the tributaries in both models were shorter than the actual river system, and the tributaries in the ROMS model domain were shorter than those in QUODDY (compare Fig. 5 and Fig. 16). In the ROMS model, oyster habitat extends to the tip of the following rivers: Chester, Choptank, and York. In these systems, particle settlement (esp. for *C. ariakensis*) could have been overestimated because particles were not able to be transported past suitable habitat into upstream reaches where suitable habitat would not exist. The best test for the potential effect of tributary length would be to extend the length of the tributaries in the ROMS model and compare particle settlement between the two ROMS models. Although any exploration of the sensitivity of model results to the structure of the model is important, this would be a significant effort that is likely outside the time line of the EIS.

2. *p18- What is the source of the presented probabilities for swimming behavior (paragraph 3)?*

The probabilities for swimming behavior were set by PI North so that the one-dimensional model of larval behavior (Fig. 10 in Final Report) would correspond to the behavior patterns inferred from laboratory and field studies, based on published literature and experts on oyster larvae behavior (see references in the Final Report, p. 16 - 18).

3. *Is there any information about the probability of a pediveliger crossing an oyster bar and not settling in the wild?*

Plankton collections of pediveligers over an oyster bar and newly settled spat would be required to calculate the probability of a pediveliger crossing an oyster bar and settling or not settling. In addition, measurements of the speed and direction of water currents at each oyster bar and the size and orientation of each individual oyster bar in relation to flow patterns would be needed to compute probabilities that were suitable for comparison with larval transport model predictions. This information has not been collected in the field.

4. *p 20, last paragraph- 'reflective horizontal boundary condition'- Why isn't a particle that moves out of the boundary horizontally considered dead or lost? Is the thinking that these particles would be returned by flow or behavior into the domain? Has there been any analysis to understand what proportion of the particles actually did 'leave' and had to be reflected back into the domain?*

First, it should be clarified that the particles do not leave the model domain. Particles are reflected off of the boundaries so that they stay inside the model domain. This keeps the particles

in the water and does not allow them to ‘jump’ out of the region where the hydrodynamic model makes predictions about water movement.

Second, reflective boundary conditions were chosen so that the particle tracking model predictions would be consistent with the hydrodynamic model. In the absence of larval behavior, particles should simulate water in the same manner that water is simulated by the hydrodynamic model. In the oyster larvae transport model, there is no larval behavior in the horizontal direction. Because the hydrodynamic model does not remove water when water encounters a horizontal boundary, particles should not be removed when they encounter a horizontal boundary. If particles were removed, then predictions of particle movement due to horizontal circulation patterns would not be consistent with the hydrodynamic model.

5. p 26- Are there any estimates of how many gametes are actually released into the water column/year? In other words, do the number of particles released by this simulation represent 1%, 10%, 50%, etc. of natural release? Could the model be run on a subestuary scale with a number of particles that is representative of the magnitude of a) a historical release and b) a current typical release? Would it be worthwhile to compare the results of the whole Bay model run with the fewer number of particles with those of (b) to check if the model is capturing the transport of a typical release?

The number of particles released is not intended to represent the actual number of gametes spawned. We released 1.3 million particles for all model runs. A single large adult female can produce 40 million eggs (Kennedy 1996). The particles are intended to estimate the spatial trajectory of surviving spat produced by spawners on a bar. The number of spat that are produced on each oyster bar will be predicted by the demographic model. Although it may be possible to run the larval transport model with the actual number of oyster gametes produced in a very (very) small basin on a super computer, the ‘super individual’ method (i.e., one particle represents multiple oyster larvae) is a more sensible approach given current computational constraints.

Although an extensive sensitivity analysis (e.g., Brickman and Smith 2002, North et al. 2006a) was not conducted due to the time constraints of the EIS process, we did conduct a sensitivity analysis to determine the number of particle releases that were needed to ensure that at least 98% of bars received particle settlement in any given year. We determined that at least five releases of particles were necessary (i.e., 313,865 particles each year).

6. Figure 17- There appears to be very little, if any, loss of C. ariakensis to the Atlantic Ocean. This could be interpreted as a 'natural' barrier to C. ariakensis invasion of other Atlantic Coast estuaries. Chesapeake Bay is essentially acting as a trap estuary for C. ariakensis. Would this be an accurate conclusion if used to calm fears and complaints of those in Delaware Bay, North Carolina, the Gulf Coast, etc.?

The larval transport model should not be used as evidence to suggest that *C. ariakensis* will not spread to other estuaries. This question was not addressed by the larval transport model. The ability of the model to resolve coastal circulation patterns was not assessed, nor did we include salinity-dependent mortality for *C. ariakensis* particles. Because the assessment of temperature- and salinity-dependent mortality of *C. ariakensis* larvae was not completed, it is impossible to determine if spawning populations could establish near the mouth of the Bay that would place larvae in ‘striking’ distance of other estuaries. In addition, it is possible that the most

likely means of oyster dispersal would be by humans. If *C. ariakensis* were to be established in Chesapeake Bay, there would be no way to guarantee that rouge introductions would not take place in nearby estuaries by ‘human’ rather than ‘larval’ transport.

7. Figure 24- How can this information be validated or field verified? If interpreted with respect to where the majority of good reefs exist today, does it hold up? Maryland and Virginia mainstem dots are confusing. The Maryland mainstem is shown as one dot in the northern Bay, but it actually stretches down to the Maryland line. Therefore, its high connectivity is not surprising, but how great a contribution do mainstem bars actually make today to the Bay population?

The dots are a symbolic tool to summarize model results. Figure 16 in the Final Report is presented so that the reader can understand the habitat distribution that the ‘dots’ represent in the summary figures like the connectivity plot. Given the size of the Maryland mainstem basin, the high connectivity of this basin is not surprising. The larval transport model does not predict spat settlement, so it is not appropriate to expect that the larval transport model can predict the actual contribution of the Maryland mainstem to bars within the mainstem or in other tributaries. Depending upon demographic model predictions, each particle could represent hundreds of thousands to hundreds of billions of spat. The larval transport model provides information on the spatial distribution of spat. It does not include adult spawner populations, the number of fertilized gametes that they produce, or the number of spat that survive to settlement. These parameters are critical for predicting spat settlement and are handled within the demographic model. Only with the linked demographic –larval transport model can the question of the contribution of mainstem bars be made (i.e., we can only address questions about the population that exists today with the linked model).

8. Table 6- The connectivity matrix does show connectivity, but no basins (except the mainstem) received any significant proportion of particles. Continuing on my thoughts of comment #7, does this make sense in the context of the role mainstem bars actually have in the current Bay population?

The fact that mainstem bars received the largest proportion of particles from other basins makes sense. All of the other basins empty into the mainstem so they are closer to the mainstem than to any other basin, therefore particles that leave these basins would be more likely to encounter suitable habitat in the mainstem before they would encounter it in any other basin. Again, population demographics are needed to assess the actual connectivity between basins.

9. p38, first paragraph, last full line- Should the 1% be 100%?

Yes.

10. Figure 26- 'Catching bars'- Only a few bars in the tributaries are identified as catching a high density. However, historically the prime beds are in the tributaries, not the mainstem. Have the habitat areas of tributaries bars been reduced in a greater proportion than those in the mainstem? Do you think a larger good habitat area in the tributaries affect the catch in the tributaries?

Habitat polygons were reduced uniformly in Maryland waters. “Catching bars” refers to bars that are located in a place where they catch more particles than are released from them. It does not indicate how many actual oysters would be located on the bar. “Prime beds” implies

that the largest and most commercially productive beds were located in tributaries. The larval transport model suggests that harvesting on “catching” bars may not have as great of an impact on the spawning stock because the adult oysters on these bars would contribute less surviving spat than other bars. It does not indicate that catches would be highest at those bars.

11. p 40, B. Validation and sensitivity studies- Why was Virginia data not included in the analysis?

Although we requested Virginia spatfall data, we did not (and still have not) received it.

12. p 41- Are there plans to compare the Maryland measured spatfall data with information produced by the demographic model?

Yes. Validation analyses with the linked larval transport and demographic models currently are being conducted.

13. Figure 33- lower left panel- The purple dots are very hard to recognize. Can a different color or symbol be used to present this information in a clearer way?

Yes. Fig. 6 is an alternate figure.

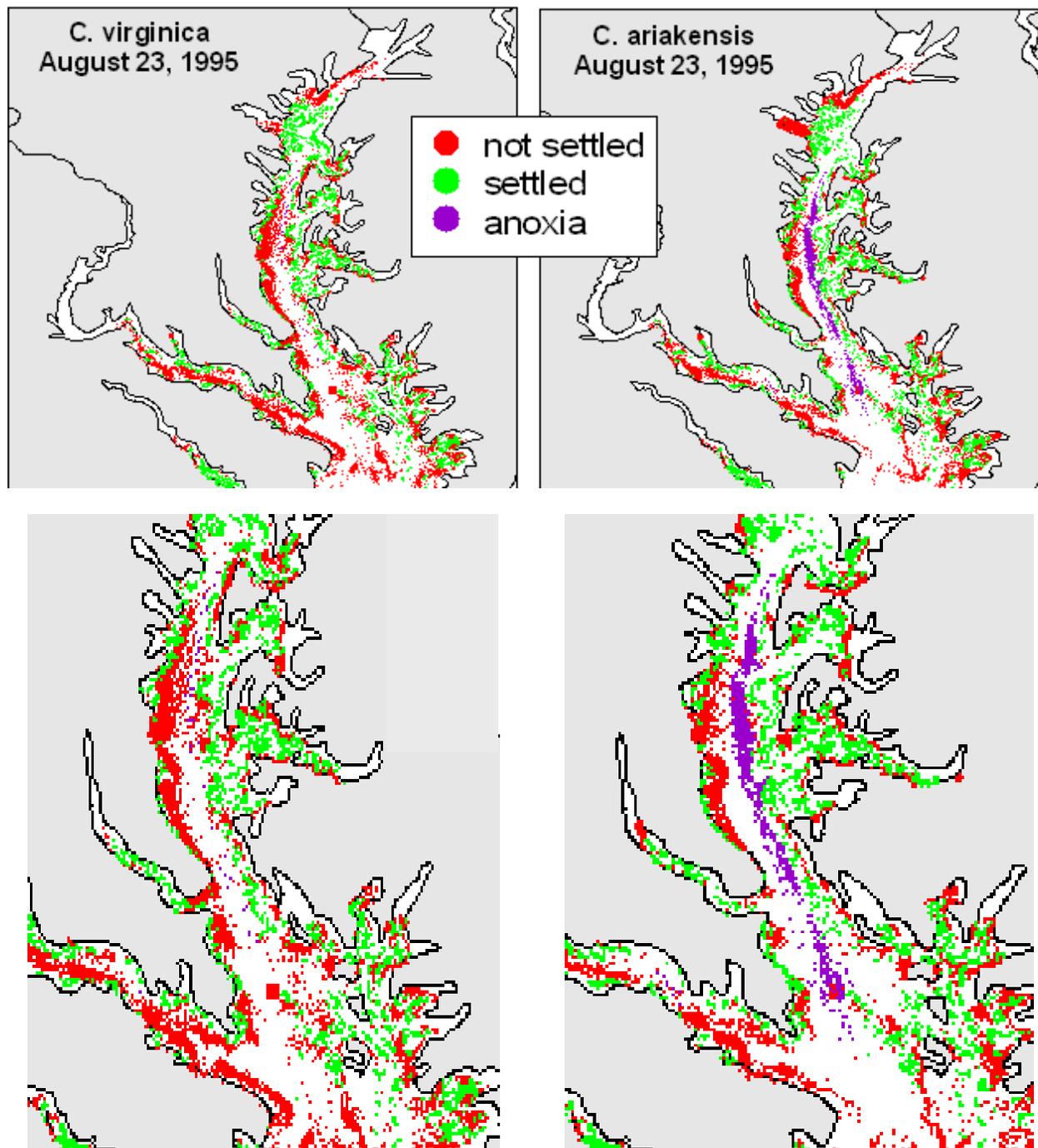


Fig. 6. Upper panels: post-processed larval transport model results at end of simulation (August 23, 1995) for *C. virginica* (left) and *C. ariakensis* (right) particles subjected to anoxia. Colors indicate whether particles were settled (green), dead due to anoxia (purple) or dead due to inability to find suitable substrate (red). Lower panels: enlargement of upper panels in region of anoxia.

Acknowledgements

We thank the review panel for their constructive comments, and Jon Vølstad, Roger I. E. Newell and Victor S. Kennedy for helpful information.

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PRG Final Peer Comments on the Revised Report dated November 1, 2006 (February 22, 2007)

Comments on the response to reviews: Modeling dispersal of *Crassostrea ariakensis* oyster larvae in Chesapeake Bay

General Comments:

The rationale for this study was to determine the spatial dispersal of *Crassostrea ariakensis* and *Crassostrea virginica* within Chesapeake Bay in attempt to determine how these two species disperse within the estuary. Specific objectives were 1) estimate the spatial dispersal of the two species using coupled hydrodynamic and larval transport models and 2) transfer this information to a juvenile/adult demographic model. Our earlier comments focused on the final report.

The methodology consisted of the coupling of previously validated hydrodynamic models of Chesapeake Bay with a larval behavioral model developed by the authors to examine the effects of varying larval behavior on the settlement success and spatial dispersal of spawned oyster larvae. The two hydrodynamic models were forced with actual physical conditions (wind, tides, river discharge and heat transfer) from five consecutive years that were characterized by very different buoyant discharges. Overall, the report provided all of the needed information. The review team was troubled by two major details: the seemingly lack of inter-annual variation in larval settlement and the lack of an explanation for this occurrence. In the original review, we stated that this combination casts doubt on the entire project (which we thought was unfair since the project as a whole was very good) and should be addressed. We had several recommendations for improvement of the report. These were:

- 1.) Perform ensemble simulations of any one year to determine the variation due to random movement specified by the larval behavioral model.
- 2.) Demonstrate that the total annual larval settlement of each year is (or is not) statistically different from other years and discuss why this would be.
- 3.) Show the interannual variation of mean velocities within the bay and show how these affect larval settlement.
- 4.) Perform the simulation with no river discharge or winds to show that these mechanisms do indeed have no effect on the larval settlement as suggested by Figure 15 and Tables 3 and 4.

In response to the comments by the review team, the authors have:

- 1.) Provided a valid physical (and biological) explanation for the lack of inter-annual variation in larval settlement, i.e. it was due to the use of an inappropriate metric.
- 2.) Discussed the limitations of the metric used and provided two metrics (i.e. basin-scale settlement success and mean dispersal distance) that did highlight the inter-annual variations
- 3.) Discussed the effects of wind events on the new metrics (this was not discussed in the previous report). This discussion revealed that wind events can have direct effects on one of the two metrics mentioned earlier, the larval settlement success at basin scales.

- 4.) Quantitatively related river-discharge to the new metrics. Again, this discussion revealed that variations in river discharge directly affect one of the two metrics, mean dispersal distance.
- 5.) Corrected errors in the calculation of Coefficients of Variation.

These additional explanations have eliminated the need to perform the tasks recommended by the review team. All of the recommended tasks were based on an apparent lack of inter-annual variation, which the authors have now shown was a consequence of an inappropriate metric and not a true lack of interannual variation.

In conclusion, the authors have addressed all of the review team's concerns.