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Linking larval transport and fisheries demographic models to study the influence of environmental variability and larval behavior on juvenile recruitment to oyster populations

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Abstract

Annual variations in freshwater flow and wind may influence the dispersal of oyster larvae (by affecting circulation patterns) and the survival of adults (by influencing salinity-dependent disease mortality) in Chesapeake Bay, a region whose oyster fishery has greatly declined. These observations suggest that environmental variability has important implications for rehabilitation efforts that involve enhancing native oyster broodstock. We tested this hypothesis for the eastern oyster *Crassostrea virginica* by linking larval transport and fisheries demographic models. Physical conditions in both models were based on five years with differing wind and freshwater flow patterns (1995-1999). The larval transport model predicted spatial settlement patterns by using a particle tracking model parameterized with larval behaviors discerned in preliminary analysis of ongoing laboratory studies. The demographic model incorporated estimates of stock-recruitment relationships, growth, natural mortality, disease mortality, fishing mortality, and the effect of extreme events such as freshets. A validation analysis of the linked models compared predictions of juvenile oyster settlement success with field observations from 1995 to1999. Larval transport model results indicated that settlement success of *C. virginica* larvae was influenced by freshwater flow conditions, with larval settlement higher in low freshwater flow years. The validation analysis indicated that including spawning stock abundance and mortality estimates in the linked larval-transport-demographic model may have improved predictions of juvenile recruitment. Our linked model could be used to assess risks associated with introducing a new species and guide oyster management activities such as locating brood stock sanctuaries and managing harvest in response to climate variability.

Keywords: biological-physical interactions, modeling, larval transport, demographic models, oysters

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Introduction

Restoration of native eastern oyster *Crassostrea virginica* populations in Chesapeake Bay is a high priority goal of regional scientific and management communities (Chesapeake 2000 Agreement, http://www. chesapeakebay.net/agreement.htm). Potential benefits include support of a revived commercial fishery, improved water quality through oyster filtration (Newell 2004), and enhanced fish habitat through reef restoration (Harding and Mann 2001). Efforts to restore *C. virginica* are on-going in Chesapeake Bay but oyster populations are not flourishing and disease-related mortality rates are still high (NRC 2004). In addition to continuing native oyster restoration efforts, the Maryland Department of Natural Resources is assessing the introduction of a non-native oyster *Crassostrea ariakensis* because of some evidence for this species' high growth rates and presumed disease resistance (Calvo et al. 2001).

Although *C. virginica* and *C. ariakensis* swimming speeds are similar, preliminary results of laboratory studies suggest that their behaviors differ (Newell et al. 2005). In the presence of a halocline, *C. virginica* veligers tend to be found above the halocline whereas *C. ariakensis* larvae tend to be found near bottom. Because such differences could influence the direction and rate of larval dispersal in Chesapeake Bay, it is necessary to incorporate larval transport into quantitative assessments of restoration strategies aimed at optimizing population growth and dispersal of either species.

We linked larval transport and demographic models together to determine the potential dispersal of native and non-native oysters in Chesapeake Bay under a suite of alternative management scenarios, some of which focus solely on the native oyster and others that include *C. ariakensis*. Although the larval transport model was built to quantify the influence of larval behavior on the potential dispersal of two oyster species in Chesapeake Bay, this paper focuses solely on the *C. virginica* larval transport model and its link to the *C. virginica* demographic model. We present 1) larval transport model results that demonstrate that environmental variability influences predicted settlement success and 2) a validation analysis that compares linked larval transport and demographic model predictions to observations of the relative abundance in nature of juvenile oysters (spat).

Methods

***Crassostrea virginica* larval transport model**. Our method of investigating larval dispersal was to use a coupled hydrodynamic and particle tracking modeling system. The hydrodynamic model numerically solved a series of equations to predict current velocities and water properties (salinity and temperature) at specific points in space and time. The particle tracking model used these predictions to move particles and cue their behavior to simulate the transport of individual oyster

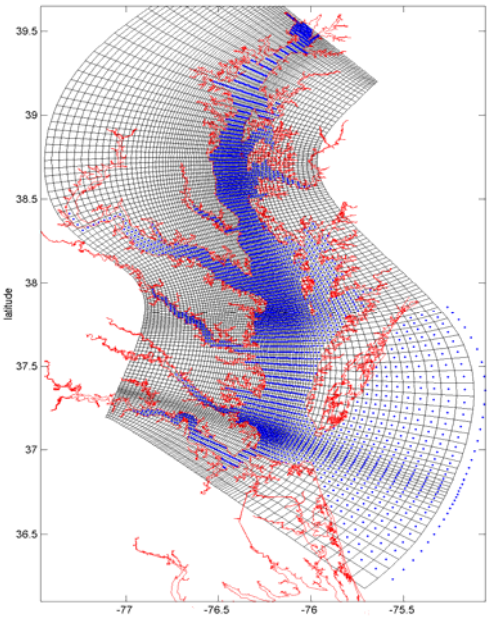

Fig. 1. Chesapeake Bay grids for the ROMS hydrodynamic model.

larvae. We used the North et al. (2005, 2006a) particle-tracking model and the output of a 3D hydrodynamic model to predict the movement of particles that simulate oyster larvae. The hydrodynamic model (Regional Ocean Modeling System (ROMS)) was implemented for Chesapeake Bay (Li. et al. 2005) (Fig. 1) with forcing conditions from 1995 to1999.

The larval transport model included algorithms that gave the particles "oyster larvae-like" behaviors that were constrained to observed swimming speeds and cued by salinity gradients that were deduced from laboratory experiments (Newell et al. 2005) and inferred from field studies (Andrews 1983, Mann and Rainer 1990, Baker 2003, and references summarized by Kennedy 1996). Particle stage durations were randomly assigned to mimic individual variation in oyster larvae using information from Carriker (1996), Kennedy (1996), Shumway (1996), and Thompson et al (1996). For particles from 0 to 0.5 day old, particles were assumed to be fertilized gametes and early trocophores that did not swim (i.e., swimming speed = 0). After 0.5 days, particles entered the late trocophore and veliger stages and began to swim. From day 0.5 to the end of the veliger stage (~14 d), their maximum swimming speed increased linearly from 0.5 mm s^{-1} to 3 mm s^{-1}. To simulate random variation in the movements of individual oyster larvae, the maximum swimming speed was multiplied by a number drawn from a uniform random distribution between 0 and 1 so that particle swimming speed varied in each time step. During the pediveliger stage, the swimming speed was 3 mm s^{-1} and no random component was added (although there was a random component to the direction as explained below).

The direction of particle movement was regulated with a behavioral cue sub-model. Preliminary analysis of laboratory studies (Newell et al. 2005) indicated that *C. virginica* larvae generally swam up in the presence of a halocline. Laboratory results of Hidu and Haskin (1978) also indicated that *C. virginica* oyster larvae changed behavior in response to salinity gradients. This information and discussions with R. Newell, J. Manuel, and V. Kennedy, was used to assign stage-dependent behaviors to *C. virginica* particles.

The direction of particle motion was determined by weighting output from a random number generator so that

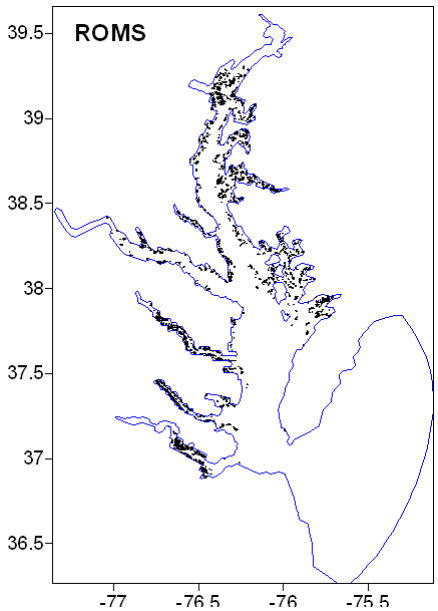

Fig. 2. Boundaries of the ROMS larval transport model (blue lines) with habitat polygons (i.e., oyster bars) (black shapes).

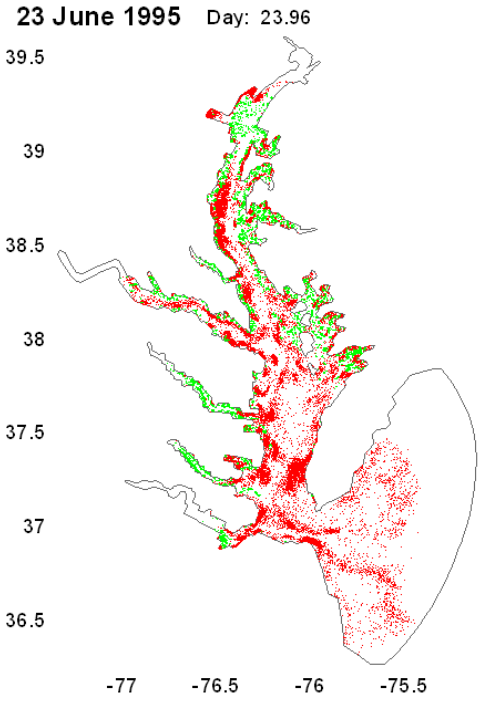

Fig. 3. End particle locations for *C. virginica* simulation with release date of June 23, 1995. Colors indicate whether particles are settled on an oyster bar (green) or dead (red).

particles had a tendency to move up or down depending on their age. In the late trocophore and early veliger stage (0.5 to 1.5 d), particles had a 90% chance of swimming up to simulate the initial near-surface distribution of larvae observed by Newell and Manuel (pers. comm.). Once in the veliger stage, larval behavior depended upon the presence or absence of a halocoline. In the absence of a halocline, veliger-stage particles were assigned probabilities that shifted their distribution from the upper layer to the lower layer as they increased in age. This resulted in a gradual shift in the depth distribution of older particles, as has been observed (Andrews 1983, Baker 2003) and modeled (Dekshenieks et al. 1996) in previous studies. In the presence of a halocline (determined by the change in the vertical gradient in salinity experienced by the particle), *C. virginica* velier-stage particles were cued to swim up with 80% probability in that time step. This response, combined with the slight bottom-oriented shift as particles increased in age, resulted in aggregation of particles above the halocline. Aggregations of *C. virginica* larvae above a halocline have been observed in several field studies (summarized by Kennedy 1996).

Pediveliger-stage particles were parameterized to swim down with 100% probability until within 1 m of bottom. Within 1 m of bottom, pediveliger particles had randomly directed motions (i.e., 50% probability of swimming up or down). Particles remained in the pediveliger stage until they either settled on a simulated oyster bar or reached the age at which they were no longer competent to settle (i.e. they died). At this point, the particle stopped moving.

The larval transport model contained a settlement sub-model to determine if a particle was inside or outside the boundaries of an oyster bar based on the best current information on oyster habitat in Chesapeake Bay (Fig. 2) (Greenhawk 2005). The model tracked the trajectories of oyster larvae in three dimensions and predicted the settlement locations of larvae on specific oyster bars in years of high, low, and average freshwater flow conditions. Model scenarios were conducted with hydrodynamic model predictions for the years 1995 to1999. Releasing multiple batches of particles within a year over several years of different physical conditions incorporated environmental variability that occurs between days, weeks, and years into estimates of larval transport.

To simulate observed pulses in spawning and settlement, we modeled five releases of 62,773 particles for each year (313,865 particles per year or 1,569,330 particles total) so that particle settlement occurred during the periods of peak *C. virginica* settlement in Chesapeake Bay (July-September) (Kennedy 1996, Southworth et al. 2000, 2001, 2002, 2003). Particles were released from the center location of each of the 2,776 oyster bars in the model in numbers that were proportional to the area of each bar (1 particle per acre or 10 particles if the bar was < 1 acre to ensure that potential trajectories from small bars were not underrepresented). The location of every particle was stored at 1-h intervals, and the starting bars (where particles were released), ending bars (where particle settled), and final locations (latitude/longitude) were recorded for every particle (e.g., Fig. 3). Details of the larval transport model formulation and predictions can be found in North et al (2006b).

The larval transport model provided the spatial trajectories of the offspring produced on each oyster bar that were used in the juvenile/adult demographic model. The demographic model estimated changes in oyster populations in Chesapeake Bay and incorporated growth, natural mortality, disease mortality, fishing mortality, and the effect of extreme events such as freshets.

It predicted the number of spawning adults on individual oyster bars. These predictions were then used with the results of the larval transport model and a stock-recruitment relationship to estimate the number of surviving spat (juveniles) produced by the adult oysters on each bar. The larval transport model supplied the information needed to assign the locations of the surviving spat (i.e., the bars on which they settled) and the demographic model provided the abundances of surviving spat to be assigned to those locations (Volstad et al. *in prep*).

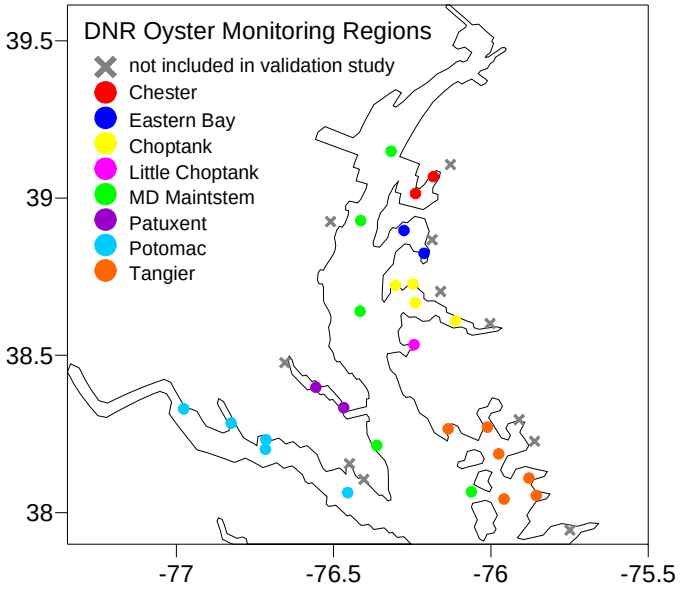

Fig. 4. Location of DNR oyster spatfall monitoring regions in the Maryland portion of Chesapeake Bay. Colors indicate basin classifications according to those of the larval transport model results (Fig. 4). Circles indicate regions used in the validation analysis; 'x's indicate regions excluded from the validation analysis.

Ultimately, the linked larval-transport-demographic model will be used to predict how different restoration strategies influence oyster populations from 1 to 15 years into the future and will incorporate environmental variability and uncertainty analyses. Linked model simulations are currently underway. In this paper, we present a validation analysis of a subset of the linked larval-transport-demographic model, namely the calculations used to predict *C. virginica* juvenile recruitment (i.e., 'spatfall').

Validation analysis. Predictions of the larval transport and demographic model were compared to spatfall observations (i.e., observations of successful recruitment of juvenile oysters) in 1995 to1999 in Maryland's portion of Chesapeake Bay. Maryland's Department of Natural Resources (DNR) conducts annual fall surveys of spat and adult abundances on reference oyster bars in the state's waters. Due to sampling design, this survey provides a relative index of spatfall (not an absolute estimate of recruitment) as measured by the number of spat (shell height < 40 mm) per bushel from the yearly fall surveys conducted by DNR. The fall survey is conducted during October or early November, using a standard oyster dredge to collect samples of oysters from 200 to 400 oyster bars (Tarnowski 2003) in 38 regions throughout Maryland waters. The number of spat (< 40 mm), small (shell height from 40 – 76 mm), and market-sized (shell height ≥ 76 mm) oysters per bushel is recorded for each bar. For a fixed set of 43 'disease bars', length frequency data in mm (from each size class) have

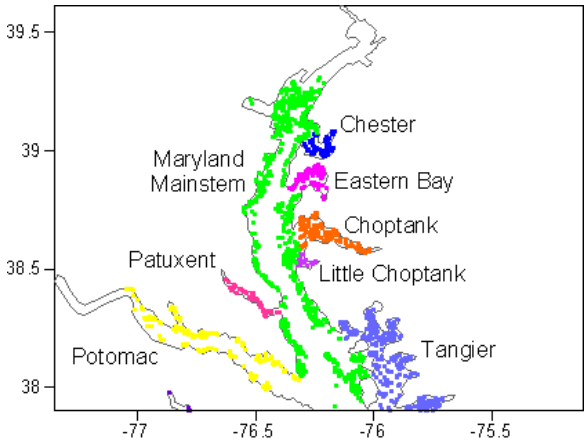

Fig. 5. Oyster bars color coded by basin in the Maryland portion of Chesapeake Bay.

been collected annually since 1991.

The spatfall data were formatted for comparison with larval transport model predictions. The mean latitude and longitude of bars within each region was used to determine the center of the region (Fig. 4). If the center coordinates were located outside the hydrodynamic model boundaries, the regions were not included in the analysis. Regions were assigned basin classifications that correspond with *C. virginica* management units in Chesapeake Bay (see Fig. 5 for names). A relative index of recruitment was calculated as the number of spat per tow within each basin for each year, then summed across basins to create an annual index of recruitment.

Larval transport model predictions were formatted for comparison with the DNR spatfall data. The number of particles that settled on bars within each basin (Fig. 5) was calculated with results from larval transport simulations using ROMS hydrodynamic model output. Basin classifications were the same as those used in the spatfall data. An index of settlement was calculated as the number of particles that settled in each basin divided by the summed acreage of bars in each basin. The number of settled particles per acre was summed across basins to create an index of particle settlement for each year.

Linking the demographic and larval transport models to predict spatfall entailed 1) deriving estimates of spawning stock populations in 1994 to 1998 on oyster bars in the larval transport model, 2) applying a stock-recruitment relationship to determine the number of juveniles produced, 3) allocating the production of each bar to other nearby bars (and back to itself) using predictions from the larval transport model, and 4) summing the number of spat produced per acre in each basin.

To derive estimates of spawning stock populations in 1994 to 1998 on the 1,000+ oyster bars in the larval transport model, we scaled spawning stock estimates from 2004 with spawning stock estimates from fall survey data in 1994 to 1998. This was necessary because estimates for spawning stock on the 1,000+ oyster bars in the larval transport model were only developed for 2004. Spawning stock populations in 2004 were estimated on the oyster bars in the larval transport and demographic model by Maryland Department of Natural Resources. The method developed by Jordan et al. (2002) and Jordan and Coakley (2004) was used to estimate mean density of oysters on oyster bars (regions with 'cultch') based on data from the 2004 dredge survey. Absolute abundance estimates were then obtained by expanding the mean density to the estimated area of the oyster habitat in Maryland (Smith et al. 2001; 2005). The high resolution estimates of spawning stock on each oyster bar were not undertaken for

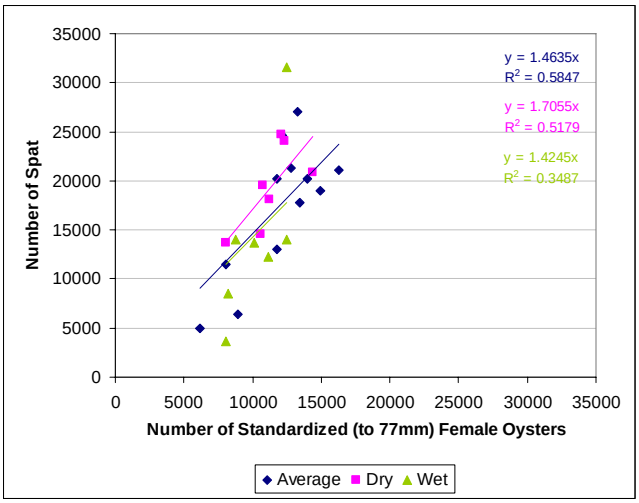

Fig. 6. Maryland oyster stock-recruitment relationship given a flow regime type (dry, wet, average flow year). Data from 1980 – 2005.

1994 to 1998, the years when fall surveys were conducted that provided estimates of spawner abundances corresponding to the spawning population assumed in the larval transport model simulations during the summer of 1995 to 1999. To create spawning stock estimates for 1994 to 1998 on the 1000+ oyster bars in the larval transport model, a conversion ratio was calculated using survey data collected on small and market-sized oysters for 1994 to1998 and 2004. These data were collected at the same locations and times as the spatfall survey data described above. For each year and basin, the mean numbers of small and market females per tow were calculated using a size-based sex ratio determined by Kennedy (1983). Total egg production per tow in each basin and year was estimated using length-weight and weight-specific fecundity equations (Mann and Evans 1998), then converted to the number of standardized female spawners per tow (e.g., a 'standardized' spawner is a female oyster that is 77 mm in length). A conversion ratio (R) for each year (y) and basin was calculated as:

$$(1) \qquad R_y = \frac{SS_y}{SS_{2004}}$$

where SS represents standardized female spawners per tow.

Spawning stock populations in 2004 on each bar were converted to number of standardized spawners using the methods described above. The conversion ratio (equation 1) for the appropriate basin and year was applied to the 2004 standardized spawners on each bar to create an index of spawning stock on each bar for the years 1994 to 1998.

Stock-recruitment relationships were applied to convert the number of standardized 77 mm female oysters on each bar to the number of surviving juveniles. To determine the stock-recruit relationship, Volstad et al. (*in prep*) used DNR annual fall oyster surveys (1980 – 2005) in conjunction with estimates of sex-ratios by size (Kennedy 1983) and egg-production by size (Mann and Evans 1998). Different stock-recruit relationship given a flow regime type (dry, wet, or average rainfall year) were determined and applied for the appropriate year (Fig. 6) of larval transport model predictions (1995 – 1999). Larval and early juvenile mortality was accounted for in the stock-recruitment relationships by estimating the average number of spat per spawner in the fall (median size of 30 mm spat). High predation mortality on oyster spat during the 1- to 2-week period after settlement may control a significant amount of recruitment variability (Newell et al. 2000) that is inherent in the spatfall data but not parameterized in the larval transport model. This mortality is parameterized in the linked larval transport-demographic model within the stock-recruitment relationship.

Once the number of juveniles produced on each bar was calculated, results of the larval transport model were applied to allocate the spatial distribution of spat production from each bar. The number of spat that each particle represented was calculated and allocated to appropriate settlement locations. Finally the total number of spat per acre in each basin was calculated, then summed to create predictions of annual juvenile recruitment for 1995 to 1999. Total annual predictions of settlement success (larval transport model) and juvenile recruitment (linked larval transport and demographic model) were compared to the relative index of observed spatfall to determine how well model predictions matched observations in 1995 to 1999.

Results and Discussion

Larval transport model. The larval transport model provided predictions of settlement success and self-recruitment in years of different physical conditions. Settlement success summarized how many particles find suitable settlement habitat per number of particles released. In this model, the only processes that reduce settlement (i.e., cause mortality) are changes in circulation patterns, the spatial distribution of settlement habitat, and differences in larval behavior in relation to salinity stratification. This allows us to understand how these factors could influence the larval dispersal stage.

Table 1. Summary of settlement success for *C. virginica* model results with ROMS hydrodynamic model predictions.

Year	Total particles	Total settled	Percent settled
1995	313,865	208,194	66.3%
1996	313,865	206,957	65.9%
1997	313,865	214,781	68.4%
1998	313,865	212,772	67.8%
1999	313,865	221,708	70.6%
1995 -1999	1,569,330	1,064,412	67.8%

On average, 68% of *C. virginica* particles successfully settled. Larval planktonic organisms that spend 14 to 25 d in the water column suffer 95% to 99% mortality (calculation based on Table 1 of Eckman (1996)). Annually, between 29 to 34% of *C. virginica* particles did not settle (Table 1). Note that the results of the larval transport model predict that it can capture only ~32% of the presumed 99% mortality during the *C. virginica* larval stage. This suggests that the interaction between circulation patterns and the ability of larvae to find suitable habitat may comprise about one third of the mortality that occurs in the larval stage of oysters.

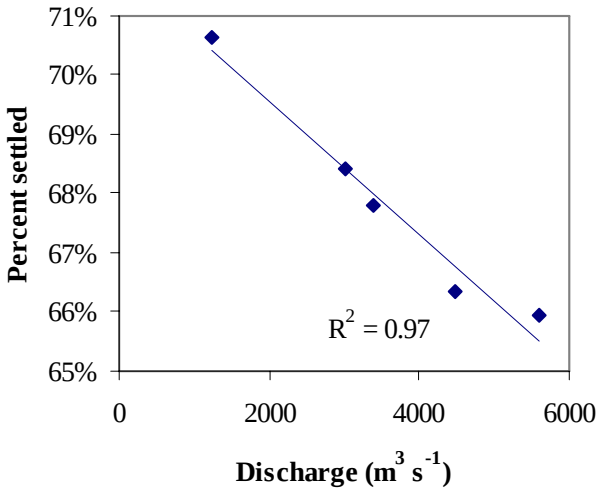

Fig. 7. Percent settled *C. virginica* particles in each year versus total freshwater discharge into Chesapeake during the main time period of larval transport (June-August). Flow data from (http://md.water.usgs.gov/publications/ ofr-68-Bue10/table9.html).

There was a significant negative relationship between annual settlement success of *C. virginica* particles and freshwater flow into Chesapeake Bay during the time period of larval transport (Fig. 7). This is likely a function of the vertical distribution of the larvae. The behavior of *Crassostrea virginica* veliger particles was parameterized so they particles would remain above the salinity gradient in the upper-layer which is more strongly forced by freshwater flow. In years of high flow, more particles were likely carried down-estuary away from regions with plentiful settlement habitat throughout the tributary (e.g., the Choptank) into regions with large expanses devoid of habitat (e.g., the central mainstem).

Measured spatfall in Maryland waters from 1980 to 2004 also displays a negative relationship with river flow (Fig. 8), as has been observed by Ulanowicz et al. (1980 here

precipitation, a factor in river flow, was the variable under consideration), Volstad et al. (*in prep*) and Kimmel and Newell (*in press*). The negative relationship between spatfall and freshwater flow in Fig. 8 is significant (P = 0.01) and accounts for 26% of the variability in spatfall in the 24-year time series.

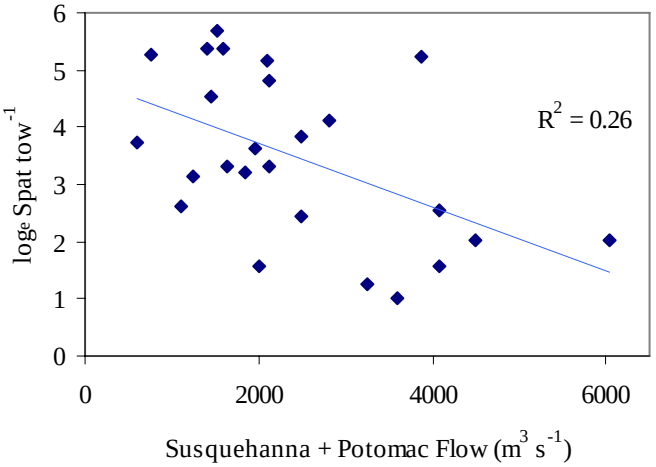

Fig. 8. Annual spatfall in Maryland waters versus freshwater flow from the Susquehanna and Potomac Rivers in June, July and August, 1980 – 2004.

Validation analysis. Predictions of particle settlement were compared with the observed spatfall index on an annual basis (Fig. 9). No relationship was found for data from 1995 to 1999. Spatfall in 1997 was the third highest in a 25-year time series (Fig. 10) and was mostly composed of an anomalously high spatfall in Eastern Bay and, to a lesser extent, the Choptank and Little Choptank Rivers. When data from 1997 were excluded, the relationship between model predictions and total observed spatfall in Maryland's waters was positive but weak. The variability in model predictions (Coefficient of Variation = 9.8%, n = 5) was many times lower than that for observed spatfall (Coefficient of Variation = 165.9%, n = 5), in part due to the fact that the same number of particles were released each year in the larval transport model. The larval transport model cannot be expected to capture the degree of natural variability, which is certainly driven by biological processes like spawner abundance, gamete fertilization success, and growth and mortality during the larval and juvenile stages.

The linked larval-transport-demographic model was better able to capture observed variations in spatfall (Fig. 11), most likely because it incorporated flow-dependent larval and juvenile mortality (from stock-recruitment relationships) and spawning stock abundances (based basin-specific survey data). The strong positive relationship in Fig. 11 was driven by the high

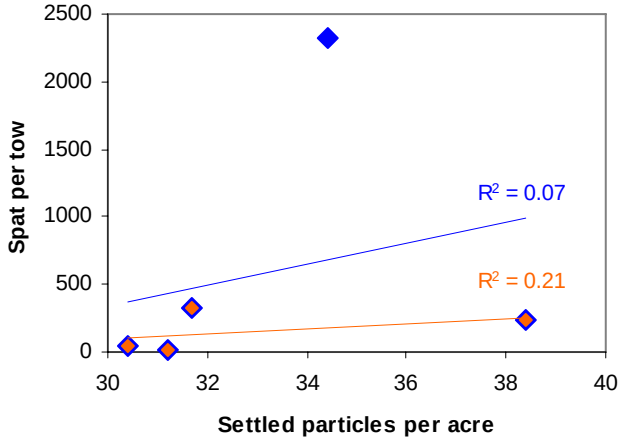

Fig. 9. Number of settled particle per acre versus observed spatfall in Maryland waters for 1995, 1996, 1998, 1999 (blue and orange diamonds) and 1997 (blue diamond).

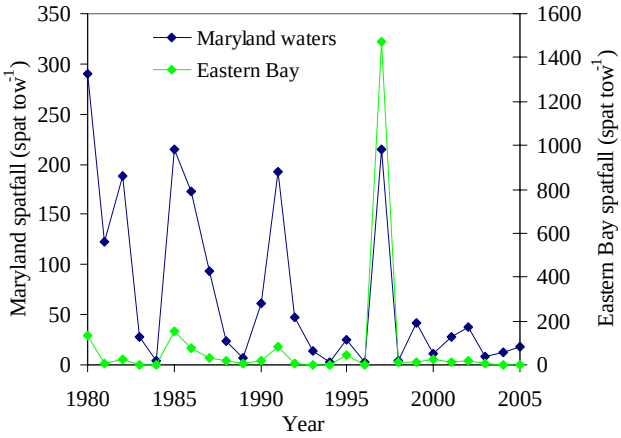

Fig.10. Twenty-five-year time series of spatfall in Maryland waters and in Eastern Bay (1980-2005).

spatfall in 1997 in three basins (Eastern Bay, Choptank River, Little Choptank River). When the 1997 data point was removed, the relationship was substantially weakened but remained positive ($R^2 = 0.47$). Although the peak in observed spatfall in 1997 was driven by recruitment in three basins (Eastern Bay, Choptank River, Little Choptank River), the peak in modeled spatfall was controlled exclusively by one basin, the Little Choptank River. The lack of accuracy in predictions at the basin scale (i.e., the linked larval-transport-demographic model did not predict high spatfall in Eastern Bay and Choptank Rivers) indicates that the strong relationship presented in Fig. 11 may not capture the true spatial dynamics of *C. virginica* recruitment in Chesapeake Bay. Additional work is needed on basin-specific recruitment dynamics and on the influence of salinity on larval mortality and the spatial distribution of successful settlement.

It is important to note that the links between the larval transport and demographic models are still undergoing development and validation. In addition, ongoing data analysis of recently completed laboratory studies will expand on the information on larval behavior given in Newell et al. (2005). Results presented here are preliminary and should not be cited without permission from the authors.

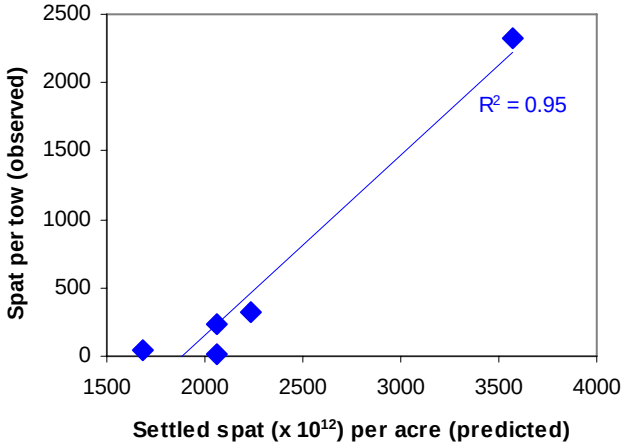

Fig. 11. Number of settled spat per acre predicted by the linked larval transport-demographic model versus observed index of juvenile recruitment (spat per tow).

Acknowledgements

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Literature Cited

Andrews, J. D. 1983. Transport of bivalve larvae in James River, Virginia. Journal of Shellfish Research 3(10): 29-40.

Baker, P. 2003. Two species of oyster larvae show different depth distributions in a shallow, well-mixed estuary. Journal of Shellfish Research 22(3): 733-736.

Calvo, G. W., M. W. Luckenbach, S. K. Allen, Jr., E. M. Burreson. 2001. A comparative field study of *Crassostrea ariakensis* (Fujita 1913) and *Crassostrea virginica* (Gmelin 1791) in relation to salinity in Virginia. Journal of Shellfish Research 20(1): 221-229

Carriker, M. R.. 1996. The shell and ligament. In: Kennedy, V. S., R. I. E. Newell, and A. E. Eble, eds. The Eastern Oyster: *Crassostrea virginica*. Maryland Sea Grant College, College Park, Maryland. 734 pp.

Dekshenieks, M. M., E. E. Hofmann, J. M. Klinck, and E. N. Powell. 1996. Modeling the vertical distribution of oyster larvae in response to environmental conditions. Marine Ecology Progress Series 136: 97-110.

Eckman, J. E. 1996. Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. Journal of Experimental Marine Biology and Ecology 200: 207-237.

Greenhawk, K. 2005. Development of a Potential Habitat Layer for Maryland Oyster Bottom. Maryland Department of Natural Resources, Fisheries Division Report. August 4, 2005.

Harding, J. M., and R. Mann. 2001. Oyster reefs as fish habitat: Opportunistic use of restored reefs by transient fishes. Journal of Shellfish Research 20(3): 951-959

Jordan, S. J., and J. M. Coakley. 2004. Long-term projections of eastern oyster populations under various management scenarios. Journal of Shellfish Research 23:63-72.

Jordan, S. J., K. N. Greenhawk, C. B. McCollough, J. Vanisko, and M. L. Homer. 2002. Oyster biomass, abundance, and harvest in northern Chesapeake Bay: trends and forecasts. Journal of Shellfish Research 21:733-741.

Hidu, H., and H. H. Haskin. 1978. Swimming speeds of oyster larvae *Crassostrea virginica* in different salinities and temperatures. Estuaries 1: 252-255.

Kennedy, V. S. 1983. Sex ratios in oysters, emphasizing *Crassostrea virginica* from Chesapeake Bay, Maryland. Veliger 25: 329-338.

Kennedy, V.S. 1996. Biology of larvae and spat. Pages 371-421 in V.S. Kennedy, R.I.E. Newell, and A. F. Eble (eds.). The Eastern Oyster, *Crassostrea virginica*. Maryland Sea Grant, College Park MD.

Kimmel, D. G., and R. I. E. Newell. *in press*. The influence of climate variation on eastern oyster (*Crassostrea virginica*) juvenile abundance in Chesapeake Bay. Limnology and Oceanography.

Li, M., L. Zhong and W.C. Boicourt. 2005. ROMS simulations of Chesapeake Bay estuary: sensitivity to turbulence mixing parameterizations and comparison with observations. Journal of Geophysical Research v.110, C12004, doi:10.1029/2004JC002585.

National Research Council (NRC), Committee on Nonnative Oysters in the Chesapeake Bay. 2004. Non-native oysters in the Chesapeake Bay. The National Academies Press, Washington D.C. 326 p.

Newell, R. I. E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalvae molluscs: a review. *Journal of Shellfish Research* 23(1): 51-61.

Newell, R. I. E., V. S. Kennedy, J. L. Manuel and D. Meritt. 2005. Behavioral responses of *Crassostrea ariakensis* and *Crassostrea virginica* larvae to environmental change under spatially realistic conditions. Final report to Maryland Department of Natural Resources, May 2005.

North, E. W., R. R. Hood, S.-Y. Chao, and L. P. Sanford. 2005. The influence of episodic events on transport of striped bass eggs to an estuarine nursery area. Estuaries 28: 106-121.

North, E. W., R. R. Hood, S.-Y. Chao, and L. P. Sanford. 2006a. Using a random displacement model to simulate turbulent particle motion in a baroclinic frontal zone: a new implementation scheme and model performance tests. Journal of Marine Systems 60: 365-380.

North, E. W., Z. Schlag, R. R. Hood, L. Zhong, M. Li, and T. Gross. 2006b. Modeling dispersal of Crassostrea ariakensis oyster larvae in Chesapeake Bay. Final Report to Maryland Department of Natural Resources, July 31, 2006. 55 p.

Mann, R., and D. A. Evans. 1998. Estimation of oyster, *Crassostrea virginica*, standing stock, larval production and advective loss in relation to observed recruitment in the James River, Virginia. Journal of Shellfish Research 17: 239-253.

Mann, R., and J. S. Rainer. 1990. Effect of decreasing oxygen tension on swimming rate of *Crassostrea virginica* (Gmelin, 1791) larvae. Journal of Shellfish Research 9(2): 323-327.

Shumway, S. E. 1996. Natural environmental factors. In: Kennedy, V. S., R. I. E. Newell, and A. E. Eble, eds. The Eastern Oyster: *Crassostrea virginica*. Maryland Sea Grant College, College Park, Maryland. 734 pp.

Smith, G. F., K. N. Greenhawk, D. G. Bruce, E. B. Roach, and S. J. Jordan. 2001. A digital presentation of the Maryland oyster habitat and associated bottom types in the Chesapeake Bay (1974-1983). Journal of Shellfish Research 20: 197-206.

Smith, G. F., D. G. Bruce, E. B. Roach, A. Hansen, R. I. E. Newell, and A. M. McManus. 2005. North American Journal of Fisheries Management 25: 1569-1590.

Southworth, M., J. M. Harding, R. Mann. 2000. The Status of Virginia's Public Oyster Resource 2000. Molluscan Ecology Program, Virginia Institute of Marine Science, The College of William and Mary, Gloucester Point, Virginia.

Southworth, M., J. M. Harding, R. Mann. 2001. The Status of Virginia's Public Oyster Resource 2001. Molluscan Ecology Program, Virginia Institute of Marine Science, The College of William and Mary, Gloucester Point, Virginia.

Southworth, M., J. M. Harding, R. Mann. 2002. The Status of Virginia's Public Oyster Resource 2002. Molluscan Ecology Program, Virginia Institute of Marine Science,The College of William and Mary, Gloucester Point, Virginia.

Southworth, M., J. M. Harding, R. Mann. 2003. The Status of Virginia's Public Oyster Resource 2003. Molluscan Ecology Program, Virginia Institute of Marine Science, The College of William and Mary, Gloucester Point, Virginia.

Tarnowski, M. 2003. Maryland Oyster Population Status Report: 2002 Fall Survey., Maryland Department of Natural Resources, Shellfish Program and Sarbanes Cooperative Oxford Laboratory.

Thompson, R. J., R. I. E. Newell, V. S. Kennedy, and R. Mann. 1996. Reproductive processes and early development. In: Kennedy, V. S., R. I. E. Newell, and A. E. Eble, eds. The Eastern Oyster: *Crassostrea virginica*. Maryland Sea Grant College, College Park, Maryland. 734 pp.

Ulanowicz, R. E., W. C. Caplins, and E. A. Dunnington. 1980. The forecasting of oyster harvest in central Chesapeake Bay. Estuarine Coastal and Marine Science 11: 101-106.

Volstad, J. M. Christman, D. Lewis, J. Dew. *in prep*. Modeling Population Growth and Dynamics of Oysters in the Chesapeake Bay under Different Management Scenarios. Draft Report to Maryland Department of Natural Resources.