Description of 1D Oyster Larvae Behavior Models

(This is a slightly revised excerpt from North et al. 2006).

The behavior model is parameterized with larval behaviors discerned in preliminary analysis of laboratory studies (Newell et al. 2005) and includes a swimming speed component and a behavioral cue component that depend upon species and developmental stage. The swimming speed component controls the speed of particle motion due to behavior. The behavioral cue component regulates the direction of particle movement. All particles begin swimming when they are 0.5 day old (as trocophores) and continue swimming during the veliger stage. After ~13.5 days, particles enter the pediveliger stage and remain competent to settle for another ~7 days during which they search for suitable substrate. If they do not find suitable substrate within this time period, they are considered 'dead'.

Particle stage durations are randomly assigned to mimic individual variation in oyster larvae using information from Carriker (1996), Kennedy (1996), Shumway (1996), and Thompson et al (1996). Although we planned to include temperature-dependent stage durations, the EIS timeline precluded this parameterization. Instead, each particle is assigned an age at which it becomes a pediveliger (when it would be competent to settle) and an age at which it would no longer be competent to settle (because pediveligers that do not find suitable substrate within a limited amount of time will not survive). Because ages vary among individual oyster larvae, we use a random number generator to assign ages in a normal distribution around 13.5 days (for the age at which transition to pedivelger occurs) and 21 days (age at which particles are no longer competent to settle). Resulting mean veliger and pediveliger stage durations are 13.5 d and 7 d, respectively (Fig. 1).

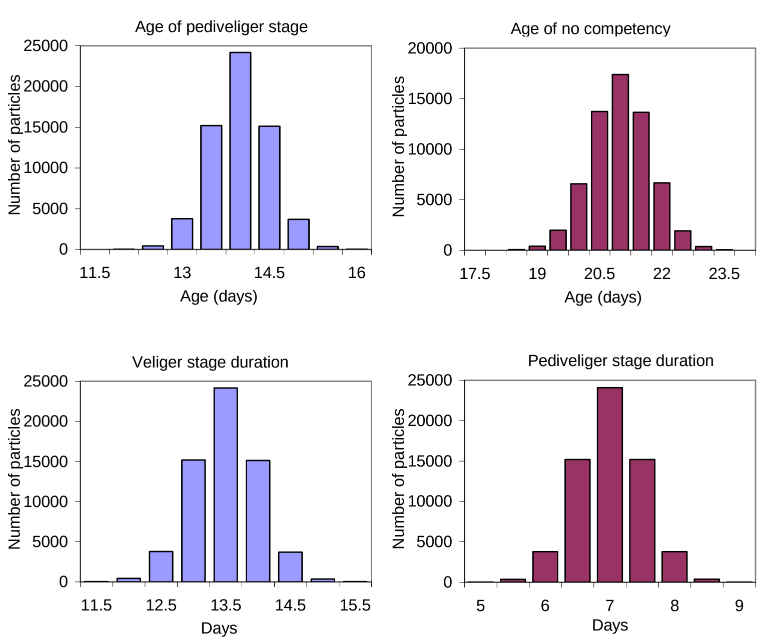

Fig. 1. Distribution of particle ages (upper panel) and stage durations (lower panels) used in the larval transport model.

Swimming speeds of *C. virginica* and *C. ariakensis* larvae vary from 0 to ~3.0 mm s^{-1} over the course of the 2-3 week development from fertilized eggs to pediveligers ready for settlement (Mann and Rainer 1990, Kennedy 1996, Newell et al. 2005). In the larval transport model, the swimming speed of a particle is determined by its age. For particles from 0 to 0.5 day old, particles are assumed to be fertilized gametes and early trocophores that do not swim (i.e., swimming speed = 0). After 0.5 days, particles enter the late trocophore and veliger stages and begin to swim. From day 0.5 to the end of the veliger stage, their maximum swimming speed increases 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 is multiplied by a number drawn from a uniform random distribution between 0 and 1 so that particle swimming speed would vary in each time step. During the pediveliger stage, the swimming speed is 3 mm s^{-1} and no random component is added (although there is a random component to the direction as explained below). The swimming speeds of *C. virginica* and *C. ariakensis* are treated with the same model formulation because laboratory results indicated that their speeds did not significantly differ (Newell et al. 2005).

The behavioral cue component of the behavior sub-model regulates the direction of particle movement. Preliminary analysis of laboratory studies (Newell et al. 2005) indicate that *C. virginica* larvae generally swim up in the presence of a halocline whereas *C. ariakensis* larvae swim down and remain near bottom. Laboratory results of Hidu and Haskin (1978) also indicate that *C. virginica* oyster larvae change behavior in response to salinity gradients. This information and discussions with R. Newell, J. Manuel, and V. Kennedy, is used to assign the stage-dependent behaviors to *C. virginica* and *C. ariakensis* particles. Although oyster larvae tend to swim in a helical trajectory, all behavioral motion of particles is limited to the vertical direction and is considered an integration of helical swimming pattern. In addition, the randomly assigned upward and downward motion of particles is considered to be an integration of observed swimming and sinking behaviors.

To simulate random variation in the movements of individual oyster larvae, the direction of particle motion is assigned a random component that is weighted so particles have a tendency to move up or down depending on species and age of particle. The change in depth distribution of *C. virginica* and *C. ariakensis* particles with development and in response to haloclines is summarized in Fig. 2.

In the late trocophore and early veliger stage (0.5 to 1.5 d), particles of both species have a 90% chance of swimming up to simulate the initial near-

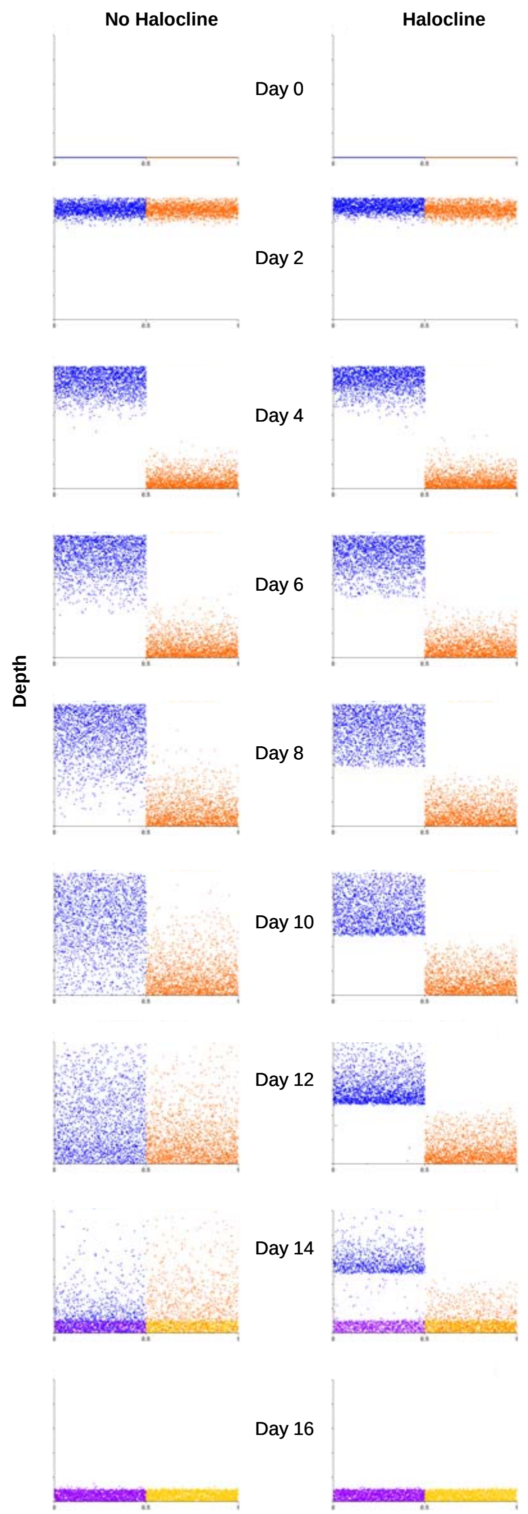

Fig. 2. Depth distribution of *C. virginica* veligers (blue) and pediveligers (purple), and *C. ariakensis* veligers (orange) and pediveligers (yellow) over time in the absence (left) or presence (right) of halocline.

surface distribution of larvae observed by Newell and Manuel (pers. comm.). Once in the veliger stage, the behaviors differed between species and in the presence or absence of a halocoline. In the absence of a halocline, *C. virginica* veliger-stage particles are assigned probabilities that shifted their distribution from the upper layer to the lower layer as they increase in age, from a 51% chance of swimming up in each time step to a 51.7% chance of swimming down. This results in a gradual shift in the depth distribution of older particles, as has been observed (Andrews 1983, Baker 2003) and modeled in previous studies (Dekshenieks et al. 1996). In the absence of a halocline, *C. ariakensis* veliger-stage particles between 2.5 and 3.0 days old are assigned probabilities of swimming down that decrease from 70% to 50.05% to gradually shift their distribution toward bottom (Fig. 10). After 3.0 days of age, particles are assigned 50.05% probability of swimming down to simulate broadly dispersed, but weakly bottom-oriented distributions in well-mixed conditions as observed by J. Manuel and R. Newell (pers. comm.).

In the presence of a halocline, the veliger-stage particles of the two species respond differently to the same salinity cue (Fig. 2). The presence of a halocline is determined by the change in the vertical gradient in salinity (ΔS) experienced by the particle. This is computed as the change in salinity (*s*) at the particle location divided by the change in depth of the particle (*z*) between the previous (*n-1*) and the present (*n*) time step:

$$(6) \quad \Delta S = \frac{(s_{n-1} - s_n)}{(z_{n-1} - z_n)}$$

If this gradient in salinity is greater than a threshold value then *C. virginica* velier-stage particles are 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, results in aggregation of particles above the halocline (Fig. 2). Aggregations of *C. virginica* larvae above a halocline has been observed in several filed studies (summarized by Kennedy 1996). If *C. ariakensis* veliger-stage particles pass through a salinity gradient, they are cued to swim down with 80% probability until they remained within 1 m of bottom or for 2 hrs, whichever comes first. If within 1 m of the bottom within the 2-hr time period, the probability of swimming up or down is 50%. This simulates the strong bottom-oriented behavior of *C. ariakensis* in the presence of a halocline as observed by Newell et al. (2005).

Pediveliger-age particles of both species have the same behavior: they swim down with 100% probability until within 1 m of bottom. Within 1 m of bottom, pediveliger particles have randomly directed motions with a 50% probability of swimming up or down (Fig. 2). Particles remain in the pediveliger stage until they either settle on a simulated oyster bar (which does not happen in the 1D Oyster Larvae Behavior Models) or reach the age at which they are no longer competent to settle (i.e. they die). At this point, particles are placed at the bottom, turn red, and stop moving.

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