

Larval Behavior and Protective Implications for Sea Scallops and Surf Clams within the Middle Atlantic Bight: Part One, a Sensitivity Study

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Abstract

*In this study, sensitivity studies of larval behaviors were performed, using numerical modeling and analytical methods, for sea scallops (*Placochelys magellanicus*) and surf clams (*Spisula solidissima*) in the Middle Atlantic Bight during 2006 and 2010. Based on multiple experiments, a regional ocean modeling system (ROMS) was implemented as the primary physical model, and larval individual behavior models (IBMs) for sea scallops and surf clam larvae were implemented and coupled to the ROMS. To simulate the physical environment and larval behavior using a series of numerical experiments, the coupled ROMS and IBMs were then employed and were driven by realistic dynamic forcing (e.g., winds, tides, and climatological mean boundaries), thermo-dynamic fluxes (e.g., solar radiation, sensible and latent heating), and hydrological forcing for larval behaviors such as vertical swimming and sinking, horizontal drifting with currents, growth, and settlement. Various growth patterns, release types, and larval behavioral parameters were analyzed and are summarized here, based on implications for the protection of sea scallops and surf clam larvae in the Middle Atlantic Bight.*

Keywords: Sea scallop larvae, surf clam larvae, Middle Atlantic Bight, larval behavior, ROMS, larval protection

1. Introduction

Sustainable populations of bivalves (e.g., sea scallops) are economically and ecologically important [1]. As the essential part of the population of bivalves, the larval population is generally determined by larval reproduction, settlement, fishing and predation, mortality, and area closure [2-6]. The initial stage for larval growth and the sustainable population of bivalves, larval settlement, is influenced by behaviors such as swimming with temperature-seeking behavior, sinking, and growth rates [7-12]. The favorable temperature range for (e.g., scallop) larval growth is generally very selective [13]. A fast growth rate (e.g., for surf clams) makes larvae settle over a shorter period of time (e.g., ~35 days) and reduces the chance for circulation to transport larvae out of the shallow shelf, while slowly growing larvae (e.g., scallops) that fail to settle sooner (e.g., longer than 45 days) more than likely lose their chance of survival. From 1994 to 2005, area closures have helped increase the biomass of sea scallops within the Middle Atlantic Bight (MAB) by approximately eight fold [6, 14].

Larval release and final settlement, following the growth rate and redistribution, are associated with the physical environment. As presented in this series, where sensitivity and mechanism studies were performed via modeling and analysis for relationships amongst larval settlements, dispersal, growth, and connectivity under different growth patterns, release mechanisms, and larval

behavioral parameters, as well as the physical environment, the physical environment is important for determining the observed biomass of sea scallops and surf clams within the MAB. Here, the physical model and larval behavioral models are outlined in Section 2. Numerical modeling results and analyses are provided in Section 3 and a summary is provided in Section 4. For clarification, the “shelf water column” (hence, the SWC) is defined as water with depths shallower than 60/100 m (used for larvae released via mechanism way3/way1, see Section 3 for details) without neighboring bays and rivers (sometimes written as 100 m SWC or 60 m SWC in the text that follows).

2. Model Implementation

A. Physical and bio-behavioral models: General configuration

The circulation model used in this study is a regional ocean modeling system (ROMS, www.myroms.org) that solves three-dimensional hydrostatic primitive equations in terrain following vertical coordinates and horizontal C-grids using split-explicit time stepping. Detail descriptions of the ROMS are provided in Wang et al. [15-17].

For this study, the ROMS was improved and coupled to scallop/surf clam individual behavior models (IBMs, as described in section 2b), hence ROMS-IBMs were used to couple the ROMS and IBMs. The implemented ROMS-IBMs were applied to the MAB (as depicted in Figure 2) using a model domain of 68-77 °W and 33.8-42 °N, a horizontal C-grid of 128 × 80 cells and a 5-8 km resolution, and bathymetry with depths of 5-4000 m (or deeper in some local

regions). To ensure the highest resolution near the sea surface where temperature and currents have larger vertical gradients, thirty-six vertical layers in the generalized topography coordinate system were weighted. The time step was 240 seconds and the barotropic mode was temporally integrated 30 times within each baroclinic time step.

Other settings included the following: 1) fourth-order centered vertical advection for momentum, 2) fourth-order Akima horizontal advection for tracers, 3) turbulent mixing using the Generic Length Scale scheme with k-kl closure parameters, and 4) radiation conditions at the open boundaries where salinity and temperature were treated using a zero-gradient condition [18-20]. To simulate more realistic temperatures and currents, ROMS-IBMs were forced by 3-hour atmospheric fluxes (i.e., solar radiation, winds, rain, air temperature, pressure, and moisture as obtained from the North American Regional Reanalysis-NARR) at the sea-surface. Tidal elevation and currents with seven tidal constituents (M_2 , N_2 , S_2 , K_1 , O_1 , M_4 , and M_6 , from the Global Advanced Circulation Model) drove the model at the domain perimeter. Daily river transport obtained from the U.S. Geological Survey was introduced into the MAB at the seven major neighboring rivers-Connecticut, Hudson, Delaware, Susquehanna, Potomac, Choptank, and James.

B. Bio-behavioral model: Major larval behavior and governing equations

Larval swimming behavior was applied at a rate of approximately 0.2-0.3 mm/s with temperature-seeking behavior, growth, sinking, and a settlement size of approximately 250 μm [7-12]. Using the parameters and variables defined in Table 1, the major governing equations for larval behaviors and for sensitivity studies were as described below.

i. The growth rate ($\mu\text{m/s}$) for larvae

Larval size by life span depends on larval growth rates. As indicated in Section 3, larval growth rate is highly sensitive to temperature and the determined larval settlement rate for a given circulation. Most (above 70%) of scallop larvae failed to grow to a settlement size

over their lifespan because they experienced a temperature higher than 17°C during June-August. Even a slight extension of the growth temperature window increased larval settlement (see Section 3 for details).

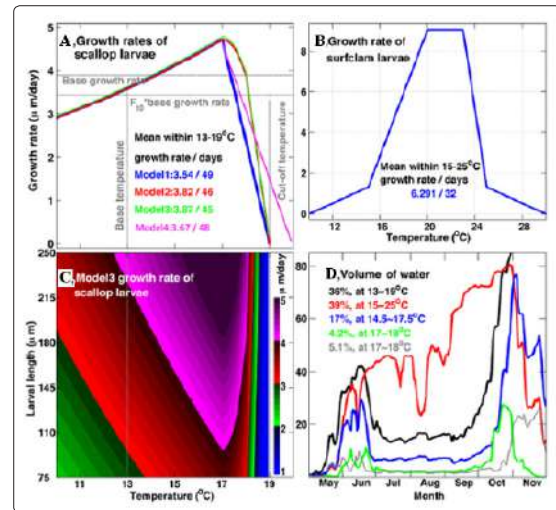


Figure 1: Larval growth rate versus temperature and larval size as defined in Equations 1-1A-C for scallop larvae (with Model1, Model2, Model3, and Model4 depicted with blue, red, green, and pink curves, respectively, in a and b) and in Equation 1-2 for surf clam larvae (c). Growth rates/day are provided in a and c, and were averaged within the temperature range of 13-19°C for scallop larvae and 15-25°C for surf clam larvae, based on the number of days for larvae to grow to their settlement sizes. (d) The volume percent (y-axis) of the shelf water whose temperature (°C) is 13-19 (black), 15-25 (red), 14.5-17.5 (blue), and 17-18 (green/gray, without/with a climate five degrees warmer), respectively, as computed from the model simulations for year 2006. For a temperature range of 15-25°C shelf water was no deeper than 60 m or 100 m for the other temperature ranges.

Table 1: The behavioral parameters of scallops and surf clam larvae

Par.	Unit	Scallop	Surf clam	Definition
D	μm			Larval size with a dD increment at one time (dt) prior to settlement
D_i	μm	75	58	Initial larvae size at 1.5 days old
D_{s1}	μm	240	260	Minimum settlement size, depending on motion and location
D_{s2}	μm	270	260	Maximum settlement size
G_r	m/s			Larval growth rate as a function of temperature (T) and foods
G_{r0}	$\mu\text{m/day}$	3.9	8.2	Initial larvae growth rate as basic growth
G_{r1}	$1/^\circ\text{C}$	0.069		Rate of increase of growth rate with temperature
M_1		0.828		Coefficient in the size-growth-rate correction
M_2	$1/\mu\text{m}$	1.198		Coefficient in the size-growth-rate correction
F_Q			1.2	Food quality for surf clam larvae: $FQ > 1$, sufficient food condition
T_0	$^\circ\text{C}$		10	The lowest temperature for surf clam larvae to grow
T_1	$^\circ\text{C}$	13		The base temperature for low temperature action on growth
T_2	$^\circ\text{C}$	17		Optimum growth temperature
T_3	$^\circ\text{C}$	198		Higher temperature above which growth drops faster
T_4	$^\circ\text{C}$	19		Highest temperature above which growth is zero Another experimental value is 19.5°C with $Tu1 = 18^\circ\text{C}$

T_{u1}	°C	16.5		Temperature at which half of the swimming time is spent swimming upward Additional experimental values included 15, 16, 17 and 18°C
T_{u2}	°C	0.9		Temperature coefficient that controls the fraction of swimming time spent swimming upward
F_t				Larval swimming time fraction
F_{t0}		0.92		Larvae swimming time fraction at the beginning
F_{ut}				Larval upward swimming time fraction
F_{u0}		0.5		Initial upward swimming time fraction/coefficient for scallop/surf clam larvae
W_t	mm/s			Larval vertical swimming speed
S_{kt}	mm/s			Larval sinking speed
S_{k0}		2.22×10^{-4}		Leading coefficient of sinking speed, with the unit changing with S_{kt} and S_{kl}
S_{kl}		1.744		Exponent of the power function of a sinking speed
S_{ut}	mm/s			Larval upward swimming speed
S_{u0}	mm/s	-0.381		Coefficients for a quadratic function providing upward swim speed as a function of larval length
S_{u1}	mm/s/ μm	9.262×10^{-3}		
S_{u2}	mm/s/ μm^2	-2.692×10^{-5}		
S_{dt}	mm/s			Larval downward swimming speed
S_{d0}	mm/s	-0.561	-0.9167	Coefficients of the quadratic function providing downward swim speed as a function of larval length
S_{d1}	mm/s/ μm	1.749×10^{-2}		
S_{d2}	mm/s/ μm^2	-6.538×10^{-5}		

As depicted in Figure 1 and defined in Equation 1-1, for sensitivity 111 studies of the effects based on growth-temperature patterns, four growth-temperature patterns for scallop larvae were applied. They were named Model1 (the basic model), Model2, Model3, and Model4. The models used for sensitivity studies were very close to one another, and were manipulated by quadratically (instead of linearly) changing temperature within a narrow band from 17-18°C (Model2), or by changing larval sizes based on Model2 (Model3), with a slightly extended cut off temperature of 19°C (in Model1) to 19.5°C (in Model4). The temperature band from 17-18°C used for the sensitive study on growth rates for scallop larvae are typical.

Simulated temperatures within the 100 m SWC were 10.9, 14.4, 17.2, 18.7, 18.9, and 17.3oC for May, June, July, August, September, and October during 2006, respectively. Up to 20% (mean 4.3%) of the 100 m SWC had a temperature of 17-18°C, and up to 58% (mean 16%) of the 100 m SWC had a temperature of 14.5-17.5°C (Figure 1d).

The small difference in growth rate between Model1, Model2, Model3, and Model4 should not compromise the experimental and observational basis on which Model1 was determined for scallops. Instead, Model2, Model3, and Model4 helped us explore possible behavioral effects induced by scallop larvae that may adapt better to a slightly (e.g., 0.5°C) higher temperature due to climate warming or other environmental changes.

As compared to scallop larvae, the “temperature adaption” effect should be smaller for surf clam larvae in that surf clam larvae grow within a broader temperature window with a higher growth rate, as shown in Figure 1 and defined in Equations 1-2. These growth-rate patterns (four for scallop larvae and one for surf clams) displayed both large and small differences in growth rate and provided an opportunity for sensitivity studies together with different larval

release strategies (see Section 3 for details).

Larval mortality was set to zero. Food and salinity were stated to be sufficient and did not change the growth patterns (in fact, the salinity was always higher than 30 psu and varied little below 3psu within the MAB according to the simulation). Based on related studies, the basic growth rates of Model1 for scallop larvae, with a growth rate increasing exponentially within $T \leq T_4 = 17^\circ\text{C}$ and decreasing linearly within $T \in (T_2 = 17, T_4 = 19)^\circ\text{C}$, were, as follows [7, 11, 8, 12].

$$G1_{rt} = U_t F_t G_{r0} \times \begin{cases} e^{G_{r1}(T-T_1)} \\ \max \left[e^{G_{r1}(T_2-T_1)} \frac{T_4-T}{T_4-T_2}, 0 \right] \end{cases} \begin{matrix} \text{if } T \leq T_2 \\ \text{if } T > T_2 \end{matrix} \quad (1-1A)$$

Where T is the temperature (°C) provided for scallop larvae, $U_t = 1/86,400$ (in days with the unit of G_{r0} in $\mu\text{m}/\text{day}$), and F_t is the swimming time fraction. $F_t = F_{t0} = 0.92$.

I assumed that scallop larvae would adapt better to a slightly higher temperature so that the larval growth rate did not drop suddenly at a temperature of 17°C as occurred in Model1 where it followed an exponential growth function for temperatures below 17°C and dropped linearly within a narrow temperature-band from 17-19°C. Instead, the growth rate decreased quadratically within $T \in (T_2=17, T_3 = 18)^\circ\text{C}$ then decreased linearly within $T \in (T_3 = 18, T_4 = 19)^\circ\text{C}$. The growth rate for Model2 was defined, as follows:

$$G2_{rt} = U_t G_{r0} \times \begin{cases} F_t e^{G_{r1}(T-T_1)} \\ (T-T_2)^2 - F_t(T-T_3) \\ \max \left[\frac{T_4-T}{T_4-T_3}, 0 \right] \end{cases} \quad \text{if } T \leq T_2$$

$$(T-2T_2+T_3)e^{G_{r1}(T_2-T_1)} \quad \text{if } T_2 < T \leq T_3$$

$$(T-T_3)e^{G_{r1}(T_2-T_1)} \quad \text{if } T_3 < T \leq T_4 \quad (1-1B)$$

Larvae grow at rates of approximately 3.1-3.5 $\mu\text{m}/\text{day}$ and 4.3-4.8 $\mu\text{m}/\text{day}$ during the final larval stage, implying that larvae grow faster in length as they become bigger, postponing growth to a warmer period [8, 12]. If the number of larval cells multiplies over a period $F(t)$ that changes with time, t , or growth stages, then the size (D) of larvae increases with time prior to larvae settlement. At an initial time when one larva has N_u cells and a volume, V_o , that is proportional to the total number of cells, volume can be written as insert equation $\frac{4}{3}\pi D^3 \propto V_o A^{F(t)}$ or $\frac{dD}{dt} \propto \frac{D}{3} \log A \frac{dF(t)}{dt}$. A is equal to a constant (typically, $A = 2$).

If cells split with a uniform frequency, $dF(t)/dt$ is equal to a constant. Hence, the basic conclusion is that the larval growth rate in length is proportional to larval length if no other factors (e.g., foods) are involved. Based on this idea and to test the size effect on growth rates and settlements, the growth rate within $T \in [T_1, T_4]$ for scallop larvae was written as follows (for Model3):

$$G3_{rt} = \frac{1}{D_{s1}-D_i} [M_1 D_{s1} - M_2 D_i + (M_2 - M_1) D] G2_{rt} \quad (1-1C)$$

Parameters M_1 , M_2 , D_{s1} , and D_i are provided in Table 1. The experimental Model3 was based on experimental Model2, with approximately the same mean growth rate but with growth timing slightly postponed due to slower growth during the early larval stage and faster growth during the late larval stage.

If scallop larvae adapt better to a slightly higher temperature by growing at a 0.5°C higher cut off temperature (i.e., $T_4 = 19.5^\circ\text{C}$, Tab.1), the result leads to Model4 using the same control equation (1-1A).

Surf clam larvae grow with a different growth pattern. With sufficient foods applied and with $T_0 < T < T_4$, the growth rate for surf clam larvae is given, as follows [21-23].

$$G_{rt} = G_{r0} F_t F_Q (1-p) T_p(i) + p T_p(j) \quad (1-2)$$

where

$$i = INT[1+(T-T_0)/dT], \quad j = MIN[i+1, 21], \quad p = [T/dT - (T_0/dT + i - 1)], \quad dT = 1^\circ\text{C},$$

and $T = [0, 0.288, .0576, .0864, .1152, .144, .3152, .4864, .6576, .8288, 1, 1, 1, .572, .144, .1152, .0864, .0576, .0288, 0]$

The up swimming time fraction for scallop larvae is as follows:

$$F_{ut} = F_{u0} \left(1 - \tanh \frac{T-T_{u1}}{T_{u2}} \right) \quad (2)$$

The sink speed (mm/s) for scallop and surf clam larvae is as follows:

$$S_{kt} = S_{k0} D^{S_{k1}} \quad (3)$$

The upward swimming speed (mm/s) for scallop and surf clam larvae is as follows:

$$S_{ut} = \max [S_{u0} + S_{u1} D + S_{u2} D^2, 0] \quad (4)$$

The downward swimming speed (mm/s) for scallop and surf clam larvae is as follows:

$$S_{dt} = \max [S_{d0} + S_{d1} D + S_{d2} D^2, 0] \quad (5)$$

The vertical swimming speed (mm/s) for both scallop and surf clam larvae is as follows:

$$W_t = -S_{kt} (1 - F_t) + F_t [S_{ut} F_{ut} - S_{dt} (1 - F_{ut})] \quad (6-1)$$

Without sinking:

$$W_t = S_{ut} F_{ut} - S_{dt} (1 - F_{ut}) \quad (6-2)$$

The larval size is very small prior to settlement (50–260 μm) and the density difference between larvae and the water could be small. The buoyancy (if from a neutral or non-neutral layer of the water column) should be too small to overcome the water tension stress surrounding the larvae. Therefore, the sinking effect on the settlement and growth rate can be ignored based on our modeling results (Figure omitted). During the modeling phase of our work, the vertical swimming speed was largely computed using equation (6-2), without sinking.

c. Some theoretical expectations

The temperature-averaged growth rate within $T \in [T_{str}, T_{end}]$ was derived for Model1 and Model4, as follows:

$$G_{rm} = \frac{U_t F_t G_{r0}}{T_{end}-T_{str}} \{ e^{G_{r1}(T_2-T_1)} [G_{r1}^{-1} + \frac{T_{end}-T_2}{2(T_4-T_2)} (2T_4 - T_2 - T_{end})] - G_{r1}^{-1} e^{G_{r1}(T_{str}-T_1)} \} \quad (7)$$

For Model2 and Model3, the temperature-averaged growth rate within $T \in [T_{str}, T_{end}]$ was derived based on the following:

$$G_{rm} = \frac{S_i U_t G_{r0}}{T_{end}-T_{str}} \left\{ \frac{F_t}{G_{r1}} \left[\left(1 + \frac{2G_{r1}(T_3-T_2)}{3} \right) e^{G_{r1}(T_2-T_1)} - e^{G_{r1}(T_{str}-T_1)} \right] + \frac{T_3^2 - 4T_3 T_4 + 6T_4 T_{end} - 3T_{end}^2}{6(T_4-T_3)} - \frac{T_2}{3} \right\} \quad (8)$$

$S_i = 1$ and $K_s(D)$ for Model2 and Model3, respectively.

For scallop larvae, a similar structure of growth rate against temperature was kept as Model1, with a slightly increased temperature-averaged growth rate as defined in Equations 1-1, 7, and 8 (also see Figure 1). If estimated statically for $T_{str} = 13^\circ\text{C}$, $T_{end} = 19^\circ\text{C}$, and $G_{rm} = 3.543, 3.822$ and $3.873 \mu\text{m}/\text{day}$, the growth time required for larvae to grow from $75 \mu\text{m}$ to a settlement size ($250 \mu\text{m}$) were 49, 46, and 45 days for Model1, Model2, and 210 Model3, respectively. For Model4, $G_{rm} = 3.673 \mu\text{m}/\text{day}$ and the growth time was equal to 48 days. Model4 improved little for the growth rate when the growth rate was higher than $2.91 \mu\text{m}/\text{day}$, the minimum growth rate for scallop larvae to grow to settlement size within its lifespan (60 days). As compared to scallop larvae, surf clam larvae

grow faster, $G_{m} = 6.291 \mu\text{m}/\text{day}$, and take less time, 32 days, to grow to the settlement size ($260\mu\text{m}$), with $T_{\text{sr}} = 15^\circ\text{C}$, $T_{\text{end}} = 25^\circ\text{C}$.

According to the simulated temperature during 2006, only ~36/39% of the SWC had a temperature of ~13-19/~15-25°C. Most water had an even larger temperature range (too cold during early spring or too hot during summer especially for scallop larvae), which would result in a lower mean growth rate. To some extent, the vertical motion of larvae helps them find a favorable temperature in the water, with a larger temperature range and an increased mean growth rate. As theoretically defined in Equations 2 and 6, when the surrounding water temperature is higher/lower than the favorite temperature (~17°C for scallop larvae), larvae tend to swim downward/upward to reach water of a lower/higher temperature within a temperature stratified water column.

d. Model improvement and validation

Circulations influence larval dispersion and settlement, and temperature is highly important to the growth of scallop larvae. Regional circulations are connected to the global circulation system. First, circulations simulated from regional models are not necessarily consistent with global circulations if the proper boundary conditions and processes are not included in the model. Additions were added to the relatively well-constructed dynamics of the ROMS. An accurate simulation of internal circulation helped us improve temperature simulations via accurate thermal advection across boundaries and within the entire modeling domain. For these reasons, a new nudging process with new coefficients was applied to open boundaries, forced by tracer and momentum climatology from a high-resolution (1/12 degree) global simulation, and validated using multiple data sources [24].

To accurately simulate temperatures, multiple experiments beyond the nudging-tests were further performed prior to the choice of a better scheme where 80% of NARR net solar shortwave radiation and water type 4 were used for the water column of the MAB [25, 26]. Based on multiple years of data at multiple locations in Delaware Bay, net solar shortwave radiation observed near the ground by the Delaware Environmental Observation System (<http://www.deos.udel.edu>) has been determined to be approximately 80% of the NARR net solar shortwave radiation, independent of season [15]. The difference in radiation was treated as a systematic error based on the reanalysis and improved the temperature simulation.

Modeling was also performed in an “on-line” manner (i.e., the ROMS and IMBs were coupled at each time step in order to embrace larval dispersion induced by all sub-scale dynamic processes including larval behaviors (swimming) and current mixing).

Also, for each of the cases, the ROMS-IBMs was run for three months for adjustments of circulations and traces prior to larval release in order to produce accurate simulations and to avoid “model choking” when any external initial conditions were initially fed into the model. Practically speaking, almost no initial condition automatically matched the model state, which was mainly determined by control equations, forcing factors, and, sometimes, boundary conditions. Simulations during the adjustment window could not be used as modeling conditions for larvae.

Temperatures were adjusted faster than salinity because they can play a significant role in the feedback of heat fluxes (e.g., sensible

heat flux) while salinity cannot. Currents can be adjusted faster with tidal mixing than without tidal mixing. The larger the fluid body or the slower the flow speed, the longer the time period required for initialized model adjustment.

Weeks of adjustment were used for Delaware Bay, but months were required for the MAB, based on many modeling experiments [15]. As a final point, the larval release strategy mattered to statistical significance. Large numbers of larvae were released and tested with released larvae covering the entire tidal-daily-seasonal cycle in order to increase the reliability of the statistics (see Figure 2 for the release description).

Physical model validation was performed between daily simulated and observed temperature and surface currents (data from CODAR and Glider) by employing system bias, Warner skill, and correlation. Still, there was less of a temperature observation available for validating the model in any single year, and the observed temperature reached a shallow water column (above 35m), covered a small spatial area, and had a shorter time window [27].

For a larger sample size with statistical significance, validation was based on the daily average within the time window from May–November of 2006–2012 (not just a single year), and temperature and its corresponding simulation at a given horizontal location were concatenated, if observed at different depths, to form one “time-space” series with a sample size of 150–200. Correlation between the data and the simulations was ~92%, the bias was under 0.8oC, and the WSK was 60–80%. Additional observed currents were available at the surface for most of the shelf water, with a large sample size (up to 1,700 days for 7 years). The correlation was ~70%, the bias was under 8 cm/s, and the WSK was equal to 60-90% (Figure 3).

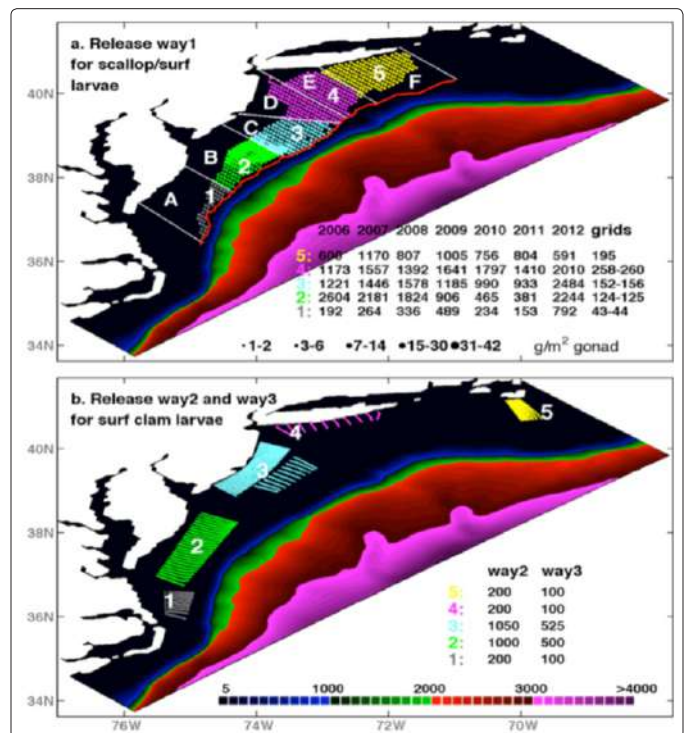


Figure 2: Model domain (i.e., 68–77°W, 33.8–42°N with 130×80 cells and a 5–8 km resolution), bathymetry (i.e., 5 – ~4000 m at 36 layers), and larval release strategies. Shelf water with depths

shallower than 100 m were separated into six regions: A–F circled by white lines with areas of ~1.50, 1.42, 0.98, 0.75, 0.70, and 1.44 ($\times 10^4 \text{ km}^2$), respectively. Larva were released in Groups 1–5 at the bottom in three ways, referring to the biomass of scallops using data provided by Dr. Burton Shank, as follows: Way1 for both scallops and surf clams; $192 + 2,604 + 1,221 + 1,173 + 600 = 5,790$ larvae were released at depths of 20.4–97.1 m at each of the 108 releases at 00:00, 04:08, and 08:17 on the 1st, 6th, 11th, 16th, 21st, and 26th of May–Oct, 2006 [28]. Way2 and 3 for surf clam; $200 + 1,000 + 1,050 + 200 + 200 = 2,650$ and a doubled number (5,300) of larvae were released at depths of 6.7–57.6 m near southern Virginia, Delmarva, New Jersey, Long Island, and southern New England (Regions 1, 2, 3, 4, and 5, respectively) and at each of the 126 releases. Red and white curves indicate the 70 and 100 m isobaths, respectively.

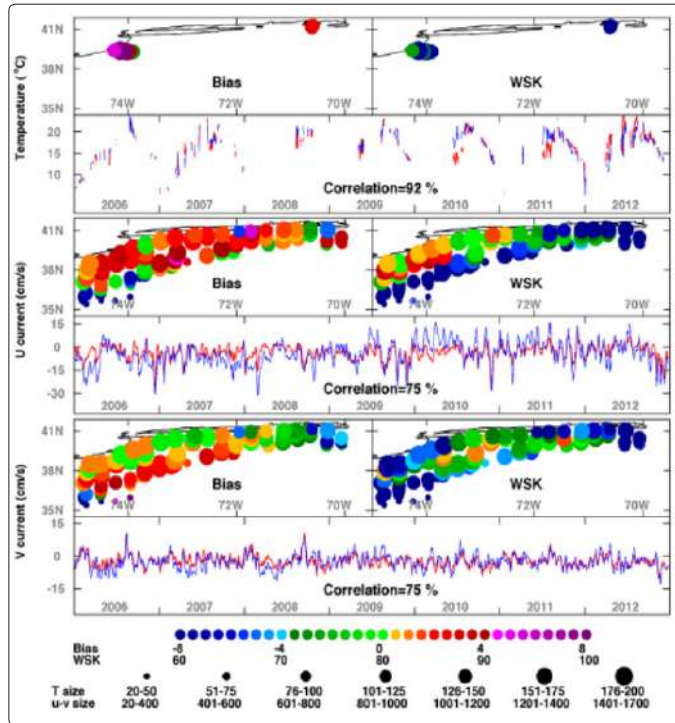


Figure 3: Model validation based on bias, Warner skill, and correlation [27]. CODAR and Glider data were used for validations of the “New” simulations of temperature with depth <35 m (rows 1–2) and u-v currents at surface (rows 3–6). The sizes, colors, and locations of the dots indicate the sample sizes, the Bias/WSK, and the locations of the data and simulations. Red and blue curves indicate the data and simulations, respectively. Temperature and its simulation are provided at a given horizontal location, concatenated if observed at different depths to form one series with a larger sample size.

Here a general evaluation was discussed for the IMB simulation. Settled scallop larvae released within regions B, C + D, and E + F are largely redistributed southward in Region A, Regions A and B, and Regions D, C, B, and even A (after June), respectively. A lower scallop biomass should be present in Regions E and F and a higher scallop biomass should be present in Regions A, B, C, and D (around Delmarva, Elephant Trunk, and Hudson Canyon south, respectively) due to the distribution of larvae. The percentage of settled larvae per unit area were 4.8 (2.7), 3.9 (2.8), 2.3 (2.0), 2.2 (2.3), 1.5 (1.2),

and 1.2 (0.7) ($\times 10^{-4}$, in $\%/ \text{km}^2$) during year 2006 (mean of years 2006–2012) in Regions A, B, C, D, E, and F, respectively.

The result was approximately consistent with observations obtained for mid-Atlantic sea scallop biomass during 2012 dredge surveys (Figure 4). The final settlement rate for all released larvae may serve as the relative initial number of larvae that may potentially grow up. Therefore, the simulated final settlement rate for all of the released larvae should be highly correlated to the observed recruits, as was the case for our simulations. The correlation coefficients were 92, 97, 88, and 86% between scallop recruits in Elephant Trunk (mostly within Region B) and for the simulated scallop larval recruitment rate averaged for all six regions, Region B, and Regions C and D, respectively, based on annual values from 2006 to 2011 (Figure 5).

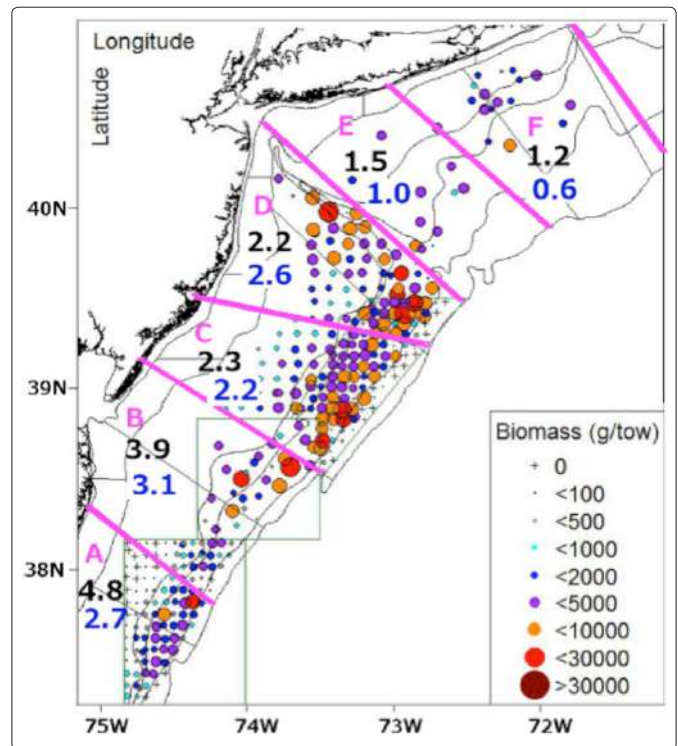


Figure 4: Total scallop biomass (g/tow, dots) and larval recruitment ($\times 10^{-4}$, in $\%/ \text{km}^2$, numbers) for the Mid-Atlantic. The figure was re-edited for biomass from Figure 4 published by the New England Fishery Management Council on website: <http://www.nefmc.org> from 2012 NEFSC dredge tows, as well as 2012 VIMS dredge tows in Hudson Canyon and inshore in NYB. The black/blue numbers indicate larval recruitment (%) settled in regions A–F from all released scallop larvae means for years 2006–2012, based on model simulations.

If correlated to the biomass in Hudson Canyon south 322 (near region C), the correlation coefficients decreased to 39, 54, 47, and 58%, respectively, in that the biomass mainly originated from mature scallops and, therefore, a long time duration existed for the time required for settled larvae to reach maturity. During the time requirement, other factors such as area closures, current transport, predation, and mortality may also have influenced the biomass.

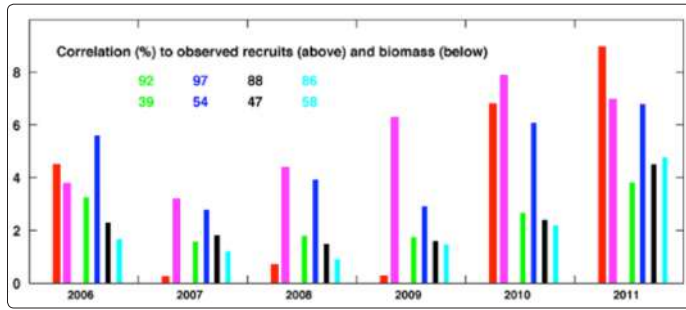


Figure 5: The simulated scallop larval recruitment rate versus the observed scallop recruits in Elephant Trunk (red bar top) and the biomass in Hudson Canyon south (red bar bottom). The scallop larval recruit rate was computed as a percent in unit area ($\times 10^{-4}$ % km²) for larvae successfully settled and redistributed within all regions (green bar), Region B (blue bar), C (black bar), and D (cyan bar). Scallop recruits are defined as those sea scallops with shell heights ranging from 40 mm to those with one year of growth from 40 mm [14]. Data for recruits and biomass were obtained from Munroe (2013).

3. Numerical modeling results and analysis

For sensitivity and mechanism studies, a series of simulations were conducted with a total of twenty cases performed (as described in Table 2), including four for scallops and one for surf clam larval growth patterns, different behaviors (e.g., vertical swimming, sinking, and no sinking), and three larvae release strategies with different release numbers, depths and locations, and different testing parameter values based on larval vertical swimming. Two target years (2006 and 2010) were applied, with 2006 used for major cases and 2010 used for different testing parameter values and for basic comparisons to 2006. Simulations for 2007, 2008, 2009, 2011, and 2012 were performed for a comparison of the models and the data.

Release mechanism way1 released scallop/surf clam larvae in depths of 20.4–97.1m, while release mechanisms way2 and way3 released surf clam larvae at shallower depths of 6.7–57.6 m (see Figure 2 for details).

Table 2: Experimental cases conducted for larval behaviors under different conditions

Case name	Description
Model1-2006	Scallop model for 2006, without larval sinking. The larval growth rate increased exponentially with $T < 17^\circ\text{C}$ then decreased linearly within $T \in [17, 19]^\circ\text{C}$ (Eq. 1-1A), as the basic case. $T_{ul} = 16.5^\circ\text{C}$ larvae were released via way1.
Model2-2006	Same as Model1-2006, but with the larval growth rate decreasing quadratically within $T \in [17, 18]^\circ\text{C}$ and linearly within $T \in [18, 19]^\circ\text{C}$ (Eq. 1-1B).
Model3-2006	Same as Model2-2006, but with the larval growth rate also indecreasing linearly with larval size.
Model4-2006	Same as Model1-2006, but with $T_4 = 19.5^\circ\text{C}$ (instead of 19°C). (This case made little difference to Model1-2006, but was a check.)
Passive-2006	Same as Model1-2006, but larvae did not actively move or sink.

PassiveS-2006	Same as Passive -2006, but larvae passively sink. (This case made little difference to case Passive-2006, but was a check.)
Model1-2010	Same as Model1-2006, but for 2010.
Model1-2010_15	Same as Model1-2010, but $T_{ul} = 15^\circ\text{C}$.
Model1-2010_16	Same as Model1-2010, but $T_{ul} = 16^\circ\text{C}$.
Model1-2010_17	Same as Model1-2010, but $T_{ul} = 17^\circ\text{C}$.
Model1-2010_18	Same as Model1-2010, but $T_{ul} = 18^\circ\text{C}$. (This case made little difference to case Model1-2010_17, but was a check.)
Passive-2010	Same as Passive-2006, but for 2010. (This case made no difference to case Passive-2006, but was a check.)
Other scallop cases	Same as scallop model1 but for 2007, 2008, 2009, 2011, and 2012 (These cases were used for model validation.)
Surf clam	Model for surf clam larvae with the same larval release strategy (way1) as the scallop larvae for comparison.
Surf clamA	Same as case Surf clam, but with larvae released via way2.
Surf clamB	Same as case Surf clam, but with larvae released via way3.

way1, way2, and way3 are described in Figure 2, and defined in Table 1.

Without considerations of larval mortality, released larvae were categorized into three groups, that is, those that successfully settled on the SWC within their lifespan (45/35 days for scallops/surf clam larvae) at a settlement size of 250 μm , those that still wandered within the SWC with a size smaller than the settlement size after their lifespan, and those that were lost into the deeper water column [6]. Settled larvae were generally analyzed for their settlement rate (percent of settled larvae in relation to all released larvae), drift distance, and redistribution percentage. The settlement rate plus the wandering rate (the percent of wandering larvae in relation to all released larvae), representing how many larva remained within the SWC, were used to study the relationship between dispersal and current conditions.

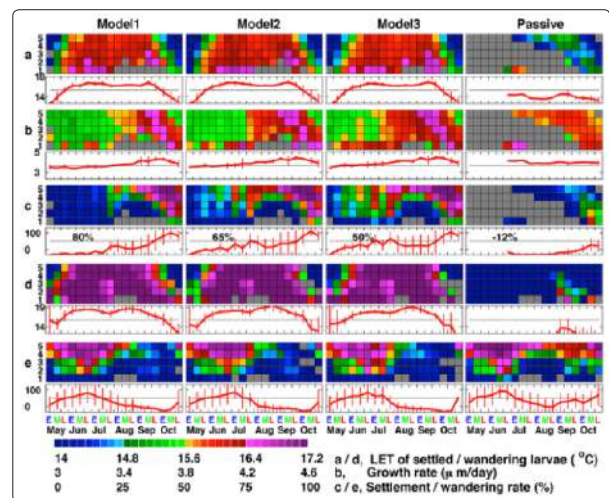


Figure 6 : General evaluations of behaviors and circumstances as

listed at the lower right corner and simulated for Model1, Model2, Model3, and Passive (Columns 1–4) for scallop larvae in 2006 with a settlement depth ≤ 100 m 45 days prior to release. Color contours were plotted for larvae released from May 1 to October 26 (x-axis, “E”, “M”, and “L” indicate the early, mid, and late portions of the months, respectively) in each of the five groups (y-axis). The mean and the error amongst the five groups and at a specific release time are depicted with a red curve and bars beneath the plots. The percent listed within row c is the correlation coefficients between the settlement rate and the growth rate.

For settled scallop larvae that grew in Model1 (Column 1 of Figure 6), the larval-experienced temperature (T_{LE}) was 14–17°C, lower during May and October but higher during July–September. The growth rate ranged from 3.5 to 4.2 $\mu\text{m}/\text{day}$, lower during May–August and higher during September. The settlement rate increased from 0 in May to up to 90% in September, and was highly (~80%) correlated to the growth rate. Most released larvae were lost during May and during August–September, if released near the southern areas (Groups 1 and 2). Most (50–90%) of the larvae released during May–August still wandered within the SWC because some of them went through a temperature that was too low (below 15°C) during May and most (above 70%) went through a temperature range that was too high (above 17°C) during June–August.

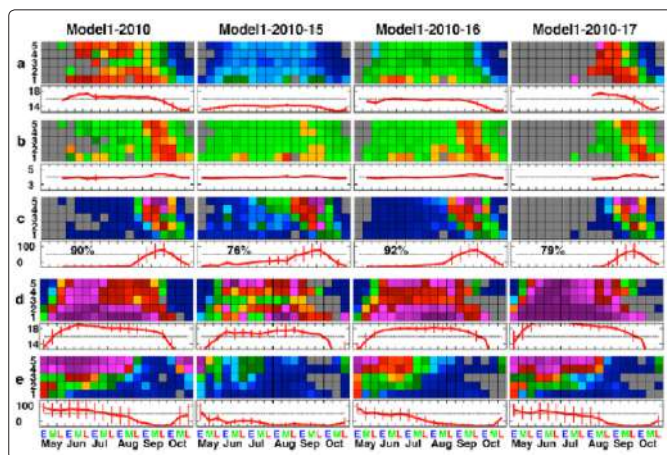


Figure 7: The same as for Figure 6 but for Model1-2010, Model1-2010-15, Model1-2010-16, and Model1-2010-17 (Columns 1, 2, 3, and 4, respectively).

For the target year 2006 (Figure6), the larval growth rate was highly sensitive to temperature and determined the larval settlement rate for given circulations. Even a slight extension of the growth temperature window increased larval settlement. For the settled scallop larvae that grew in Model2 and Model3, favorable patterns of T_{LE} , growth rate, and settlement rate extended or enhanced larvae that were released during June–August. Some of the wandering larvae released during June–August successfully settled with a slightly higher growth rate. If larvae grow slower during the earlier stage and faster during the later stage, favorable patterns for T_{LE} , growth rate, and settlement rate further extended to or enhanced larvae that were released during June–September. The settlement rate became slightly less dependent on the growth rate with smaller correlations (65–50%). The wandering rate was reduced during June–September.

Without vertical swinging behavior for scallop larvae, the T_{LE} , growth rate, and settlement rate would be much lower. Larvae were released at the bottom where the water temperature was generally low. No larvae released during May–June grew to the settlement size within their lifespan due to the low temperature. Some (mostly below 25%) settlement occurred amongst larvae released from September to October. More than 50% of the larvae released in Groups 4 and 5 were still wandering during September to October.

In target year 2010 (Figure7), more scallop larvae settled during June to October, 2010, based on Model1-2010 with a 16.5°C temperature, over which half of the swimming time was spent swimming upward. If the temperature was decreased to 15 and 16°C, settled scallop larvae moved through the lower temperature (14–16°C) by spending more time within water layers with a lower temperature and different currents. The growth, settlement, and wandering rates were all lower than those obtained at 16.5°C in Model1-2010. If the temperature was increased to 17°C, the lower temperature of the water during May to June could not support this warm environment. Scallop larvae only settled after July, following growth for 35–45 days. Therefore, it appears that scallop larvae “choose” an ideal temperature of 16.5°C so that half of the swimming time was spent swimming upward.

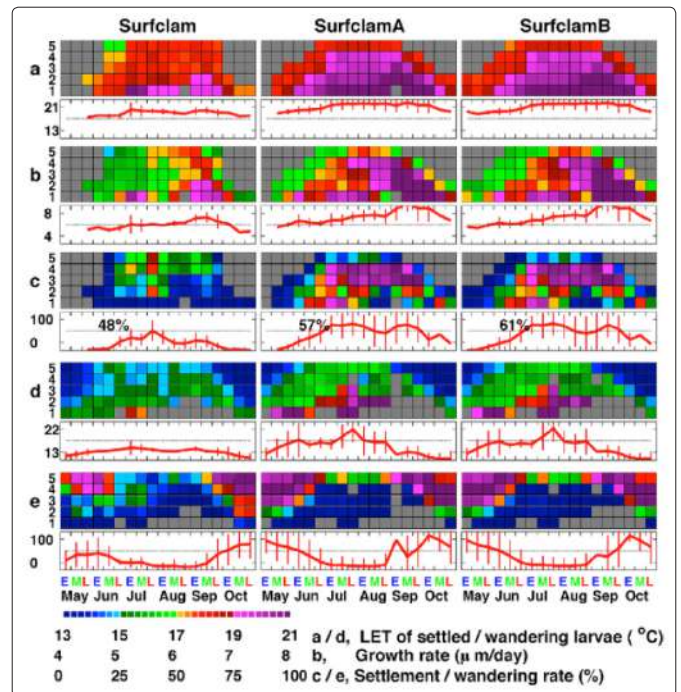


Figure 8: The same as for Figure 6 but for Surf clam, Surf clamA, and Surf clamB (Columns 1, 2, and 3, respectively) with a lifespan of 35 days for surf clam larvae.

As described in Section 2d and depicted in Figure 1, surf clam larvae had a different growth pattern (Figure 8). When compared to scallop larvae released at the same locations as scallop larvae, the T_{LE} of settled surf clam larvae was 16–23°C, higher than that of scallop larvae. The growth rate ranged from 5 to 8 $\mu\text{m}/\text{day}$, higher than that of scallop larvae. Larvae mainly settled during July–September, with a settlement rate higher and less dependent on the growth rate (with 46% correlated to the growth rate).

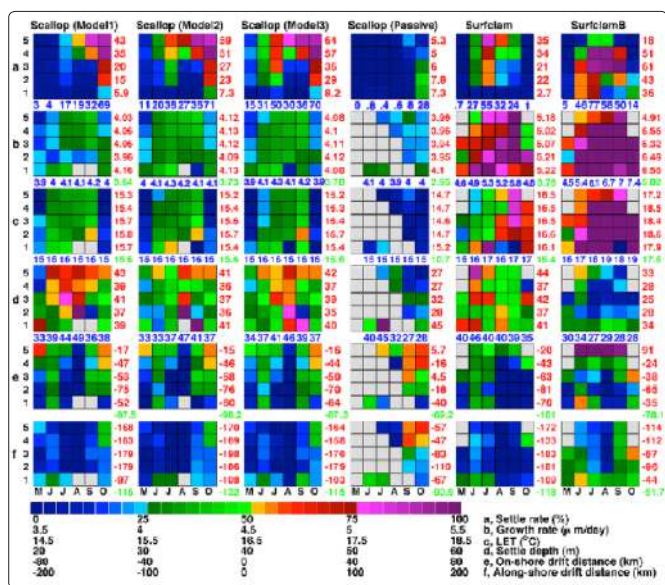


Figure 9: A summary and a comparison amongst the cases of Model1, Model2, Model3, Passive, Surf clam, and surf clamB (Columns 1–6, respectively) for larval behaviors and the circumstances as listed in the lower right corner. Behaviors and circumstances were averaged from those settled larvae released within each of the six release months from May–October (x-axis) and released from Groups 1–5 (y-axis). The life spans are 45/35 days and the settling depths are less than 100 m for scallop/surf clam larvae. The red, blue, and green numbers indicate the mean averaged over the entire period (May–October) for all groups or regions, and for all released larvae (for unsettled larvae, the settlement depth and drift distances were computed before they reached their lifespan).

Almost all of the larvae released during May and October were lost. Most (50–90%) of the larvae released during May and October still wandered in the SWC because they went through a temperature zone that was too low (below 16°C). Released in shallower water (shallower than 60 m) near southern Virginia, Delmarva, New Jersey, Long Island, and southern New England (Regions 1, 2, 3, 4, and 5, respectively), surf clam larvae behaved differently during July–September (with different release numbers), experienced a higher LET (19–23°C), a higher growth rate (7–9 μm/day), and a higher settlement rate (50–100%), almost independent of the release numbers of larvae. More larvae wandered in shallow water during May and October and experienced a higher T_{LE} during July and August.

Four more cases, Model4–2006, PassiveS–2006, Model1–2010_18, and Passive–2010 were conducted but their outcomes made little difference to those of Model1–2006, Passive–2006, Model1–2010_17, and Passive–2006. Among the fifteen experimented cases conducted six cases (i.e., Scallop Model1, Model2, Model3, Passive, Surf clam, and Surf clamB) for 2006 yielded typical results and were chosen for further analysis. Figure 9 summarizes modeling results for the six typical cases by averaging the settlement rate, the growth rate, the LET, the settlement depth, and the drift distances (a to f, respectively) from May to October over a 40/35day window for released scallop/surf clam larvae. In Surf clamB, larvae were released at depths of 6.7–57.6 m while for the other five cases they were released at depths of 20.4–97.1 m (as shown in Figure 2). Comparisons amongst

the cases shown in Figure 7 for settled larvae [all released larvae, if applicable] are listed below in the following formation: “the value range for release in Groups 1–5|the value range for release times during May–October|the total mean for settled larvae [for all released larvae if applicable]”.

1. Settlement rate (%): Model1: 6–43|3–69||24; Model2: 7–59|1–71||34; Model3: 8–64|15–70||39; Passive: 5–8|0–28||6; Surf clam: 3–35|0.7–55||23, Surf clamB: 18–61|5–77||42.
2. Growth rate (μm/day): Model1: 4–4.2|3.9–4.2||4.2 [3.64]; Model2: 4.1–4.1|4–4.3||4.1 [3.73]; Model3: 4.1–4.1|3.9–4.3||4.1 [3.78]; Passive: 4–4.1|3.9–4.1||4 [2.95]; Surf clam: 5–5.2|4.6–5.8||5.1 [3.76]; Surf clamB: 4.91–6.55|4.5–7.4||6.2 [5.02].
3. T_{LE} (°C): Model1: 15.3–15.8|15–16||15.6 [15.6]; Model2: 15.2–15.7|15–16||15.5 [15.6]; Model3: 15.2–15.7|15–16||15.5 [15.6]; Passive: 14.6–15.2|15–15||14.8 [10.7]; Surf clam: 16.1–16.6|16–17||16–17 [15.4]; Surf clamB: 17.2–18.6|16–17||16–19 [17.6].
4. Settlement depth (m): Model1–Model2–Model3: 35–43|33–49||39; Passive: 27–45|27–45||34; Surf clam: 37–44|35–46||40; Surf clamB: 25–34|27–34||29.
5. Off-shore drift distance (km, toward ocean): Model1–Model2–Model3: 15–76||51 [91]; Passive: -4.5–40||16 [69]; Surf clam: 20–81||58 [101]; Surf clamB: -91–65||23 [78].
6. Along-shore drift distance (km, southward): Model1–Model2–Model3: 97–198||165 [121]; Passive: -47–110||75 [91]; Surf clam: 109–183||154 [118]; Surf clamB: 44–114||82 [52].

For scallop larvae, the settlement rate generally increased from Groups 1 to 5 (6 to 43%), from May to October (3 to 69%), and from Model1 to Model2 to Model3 (24 to 39%). The mean growth rate for settled scallops was 3.9–4.3 μm/day. Model2 and Model3 slightly increased the growth rate of wandering larvae. The highest wandering rate occurred during June–July when the water temperature was high and strongly stratified. The size of wandering larvae was very close to the settlement size during their lifespan. If all of the released larvae were counted, the growth rate increased from 3.64 in Model1, to 3.73 in Model2, and to 3.78 in Model3, close to the theoretical expectations of 3.54 for Model1, 3.82 for Model2, and 3.87 for Model3 over the temperature range from 13–19°C (see section 2d). Scallop larvae experienced a mean temperature of ~15–16°C, lower than the ideal temperature of 17°C, due to the lower temperature of the water column. Without swimming behavior helping larvae reach the ideal temperature (mainly higher than the bottom temperature), the LET of “Passive” larvae was even lower, ~15°C for settled larvae and ~11°C for all released larvae because “Passive” larvae released at the bottom largely remained near the bottom where the temperature was lower.

For surf clam larvae, the settlement rate was higher during June–September for groups 2 to 5 if released via mechanism way1 (mean ~23%), and increased especially in southern locations if released via mechanism way3 (mean ~42%). The mean growth rate (μm/day) for settled larvae was 4.6–5.8 if released via mechanism way1, and increased significantly to 4.5–7.4, if released via mechanism way3. Averaged from settled/released larvae, the growth rate increased from 5.1/3.76 if larvae were released via mechanism way1 to 6.2/5.02 if they were released via mechanism way3. As compared to scallop larvae, settled larvae had a higher LET of 16–17 (mean 15.4)°C (still lower than the ideal temperature of 20°C) if released via mechanism way1 (on 100 m SWC), and even higher, 16–19

(mean 17.6)°C, if released via mechanism way3 (60 m SWC).

Settled scallop and surf clam larvae released via mechanism way1 had approximately the same mean settlement depths (35-49 m), cross-shore drift distance (15-81 km), and along-shore drift distance (97-198 km) although scallop larvae experienced larger ranges, with some larvae settling at slightly deeper depths and drifting longer distances because the lifespan of scallop larvae is approximately 10 days longer than that of surf clam larvae. If larvae lack swimming behavior, the settlement depth and the drift distance would be smaller, by approximately 5 m, for settlement depth, and by 35/90 km in the cross/along-shore drift distance because larvae without swimming behavior remain near the bottom where the currents are weaker. Surf clams released via mechanism way3 had smaller settle depths (25-34 m, mean 29 m) due to shallower release depths and drifted with currents over a shorter distance in the on-shore/along-shore direction (- 91-65 / 44-114 km), in that the generally weaker currents presented a shallower SWC. Some surf clam larvae released in southern New England even drifted toward shore for ~91 km under on-shore and, sometimes, along-shore currents.

The settlement-wandering-loss rate also changed with lifespan and settlement size. For the given surroundings, lifespan and settlement size matter to the larval settlement which increases with a longer lifespan within which larvae can grow, and for a smaller 504 settlement size which larvae can settle. Larval settlement, averaged for all released larvae is provided in Figure 10 using different life spans of 35, 40, 45, and 50 days and settlement sizes of 250 and 260 μm for scallop and surf clam larvae. In general, the larval loss rate did not change much with lifespan and settlement size, but was largely determined by currents. Remaining larvae either settled or were still wandering.

For scallop larvae, the major difference in settlement occurred from September to October when high settlement occurred, as follows: 1) within 35 days, no larvae were able to settle; 2) within 40 days, ~2.1% larvae were able to settle at the settlement size of 250 μm, but no larvae could settle at the settlement size of 260 μm; 3) within 45 days, ~14% larvae were able to settle at the settlement size of 250 μm, and ~7.7% larvae were able to settle at the settlement size of 260 μm; 4) within 50 days, ~18% larvae were able to settle at the settlement size of 250 μm, and ~15% of larvae were able to settle at the settlement size of 260 μm, based on Model1. Settlement could possibly increase in Model3 for life spans of 40 to 50 days.

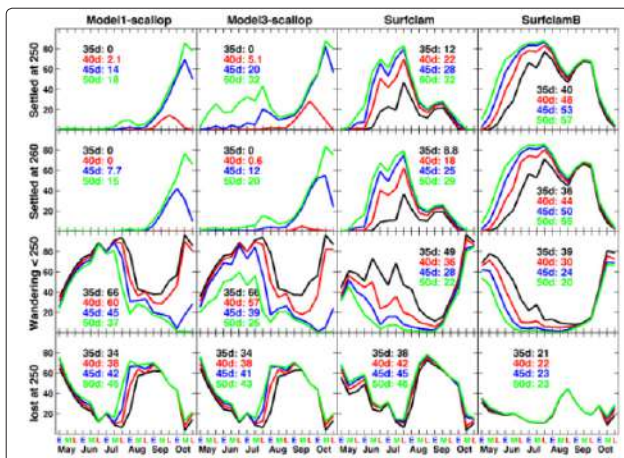


Figure 10: The settlement rate at a size of 250–260 μm (%), Rows

1–2), the wandering rate below a size of 250 μm (%), Row 3), and the loss rate at a size of 250 μm (%), Row 4) for scallops (Columns 1–2) and surf clam (Columns 3–4) larvae in Model1 and Model3; and surf clam and surf clamB (Columns 1–4, respectively), averaged from all of the larvae released within Groups 1–5 from May–October, 2006 (x-axis, “E”, “M”, and “L” indicate the early, mid, and late periods of the month, respectively) under life spans of 35, 40, 45, and 50 days (the black, red, blue, and green curves and numbers, respectively).

For surf clam larvae, the major difference in settlement occurred 526 from June to August when a high settlement occurred, as follows: 1) within 35 days, ~12%/8.8% of larvae were able to settle at the settlement size of 250 μm/260 μm; 2) within 40 days, ~22%/18% larvae were able to settle at the settlement size of 250 μm/260 μm; 3) within 45 days, ~28%/25% of larvae were able to settle at the settlement size of 250 μm/260 μm; and 4) within 50 days, ~32%/29% of larvae were able to settle at the settlement size of 250 μm/260 μm, based on the larval release mechanism way1. If released via mechanism way3, larval settlement could possibly increase by a factor of ~0.8 to 3.

4. Summary and discussion

Using numerical modeling and analytical methods, sensitivity studies of larval behavior under different circumstances were performed for sea scallops (*Placopecten magellanicus*) and surf clams (*Spisula solidissima*) within the Middle Atlantic Bight. The ROMS were tailored for the physical model of the Middle Atlantic Bight. Multiple individual behavior models (IBMs) were coupled to the ROMS, and modeling design and performance were acquired with improvements including the following:

- 1) implementation of a new nudging process with new coefficients,
 - 2) by applying 80% of NARR net solar shortwave radiation and water type four,
 - 3) using an “on-line” way (i.e., the ROMS and IBMs were coupled at each time step in order to embrace the larval dispersion induced by sub-scale dynamic processes including larval behaviors and current mixing),
 - 4) avoiding “model choking” when external initial conditions were initially fed into the model in order to yield a full pre-adjustment for circulations and traces prior to the release of larvae, and
 - 5) releasing larvae in large numbers in order to increase the statistical significance and to cover the entire swath of tidal-daily-seasonal cycles [24-26,15].
- Simulations of temperature and currents, as well as larval final settlement, were generally consistent with available observations.

The settlement rate (%) of released larvae and the redistribution (%) of settled larvae were determined by physical conditions, larval behaviors, larval release strategies, and experimental parameters.

Larval settlement increased for a longer lifespan, over which larvae could grow with a smaller settlement size and also settle. The average settlement rate for surf clam larvae was even higher if larvae were released shallower within the water column. While being carried by currents, larvae that settled over their life spans were able to drift southward up to ~500km (on average, 15–81 km cross-shore and 97–198 km along-shore). The larvae released in northern areas (e.g., Regions E and F) generally had a higher settlement rate than those released in southern areas (e.g., Regions A and B). Only 2–13% of scallop and surf clam larvae that 563 were released within Region A were retained in Region A.

Settled scallop and surf clam larvae released within Regions B, C + D, and E + F were largely redistributed southward to Region A, Regions A and B, and Regions D, C, B, and even A (after June), respectively. Surf clam larvae had a much higher settlement rate (%) and mainly settled in Regions E and F if released via mechanism way3, as compared to larvae released via mechanism way1, with the totally averaged settlement rate increasing by a factor of two to three.

For scallop larvae, the larval growth rate was highly sensitive to temperature and determined the larval settlement rate within the circulations provided. A slight extension of the growth temperature window increased the larval settlement rate. Most (50–90%) of the larvae released from May–August still wandered within the SWC because some were transported through an area that had a temperature that was too low (below 15°C) during May. Most (above 70%) were transported through an area with too-high of a temperature (above 17°C) during June–August.

If larvae are able to adapt to the temperature in a slightly better manner (e.g., with the growth rate decreasing quadratically instead of linearly over a narrow window of 17–18°C (Model2) or increasing with larval size (Model3 that also postponed growth to a warmer period)), the total mean growth rate ($\mu\text{m/day}$) increased from ~ 3.64 to ~ 3.73 for Model2 and to ~ 3.78 for Model3. The settlement rate (%) increased from 24 to 34 in Model2 and 39 in Model3.

A slightly increased growth rate resulted in significant increases for the settlement rate in that most (e.g., 50–90% during May–August) larvae still wandered within the SWC with their size very close to the settlement size during their lifespan and grew to the settlement size within their life span if they had a slightly higher growth rate. Model2 and Model3 slightly increased the upper limit of stratification during June and July when the temperature was high and stratification was stronger (the mean stratification experienced by settled scallop larvae was 0.373–0.437 °C/m for Model1, 0.398–0.469 °C/m for Model2, and 0.390–0.451 °C/m for Model3).

As compared to scallop larvae, the slight “temperature adaption” did not work for surf clam larvae in that surf clam larvae grew over a broader temperature window and with a higher growth rate. The size of wandering surf clam larvae was much smaller than the settlement size when the temperature was too low (during May). Instead, higher temperatures and weaker currents associated with the initial larval locations made a difference to larval settlement within a given general physical environment.

Additional studies for larval behavior and the physical environment were performed in parts two and three [29].

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and is coupled to the ROMS by Drs. Zhiren Wang; 3) the Surf clam IBM is coded by Drs. Fredric Castruccio and Zhiren Wang; 4) CODAR, Glider and Jason data are provided by Dr. Julia Levin and scallop biomass data are provided by Dr. Burton Shank.

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