Modeling larval dispersal and connectivity for Atlantic sea scallop (*Placopecten magellanicus*) in the Middle Atlantic Bight

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\textbf{A R T I C L E  I N F O}

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\textbf{A B S T R A C T}

Larval Atlantic sea scallops (*Placopecten magellanicus*) simulations in the Middle Atlantic Bight (MAB) from 2006 to 2012 were performed to investigate annual and inter-annual dispersal and connectivity patterns among stock regions. These simulations used a circulation model based on the Regional Ocean Modeling System (ROMS) and an individual-based larval model (IBM) that included larval behavior. The circulation model used realistic dynamical forcing (e.g., winds, tides, and open ocean boundary conditions), thermo-dynamical fluxes (e.g., solar radiation, sensible and latent heating), and hydrological forcing: the larval IBM included vertical swimming and sinking behaviour, temperature-dependent growth, and settlement. Simulated larvae that reach settlement size and suitable habitat in 45 days are considered ‘successful’, and two regions are considered ‘connected’ by larval dispersal when larvae successfully disperse from one region to the other. In general, simulated larval dispersal patterns varied seasonally (28% higher in September and October compared to May and June), among years (2007 through 2009 had 5% lower larval success during August and September compared to other years), and spatially, with larvae released from the northern regions like Long Island acting as a substantive larval source with 14% greater dispersal success and 15% greater connectivity with other regions than those released elsewhere. Over the seven years simulated, the MAB scallop stocks showed high rates of connectivity to regions to the south and more limited and variable connectivity to regions to the north. In species like sea scallops with limited adult mobility, larval dispersal supplies recruits, enables range expansion, and connects populations. Thus, appreciation of dispersal patterns are essential for fishery management of this economically valuable stock.

1. Introduction

Larval dispersal is important to understanding population dynamics (Possingham and Roughgarden, 1990; Pineda et al., 2007; Kerr et al., 2010; Munroe and Noda, 2010; Munroe et al., 2012), genetic connectivity (Scheltema, 1971; Munroe et al., 2015), and species range shifts (Zhang et al., 2015) in most marine invertebrates. This is particularly true for widely distributed, benthic species with limited adult mobility and long-duration planktotrophic larval stages, such as Atlantic sea scallops (*Placopecten magellanicus*). Larval dispersal brings the next generation of recruits into the overall population, is the mechanism by which range expansion can occur, and is the conduit by which different parts of sessile populations connect or mix with one another. Therefore, understanding larval dispersal and connectivity patterns within the larger population may be essential for fishery management (Kritzer and Sale, 2004) and predicting impacts of future climatic and oceanographic changes on species range distributions (Bernhardt and Leslie, 2013).

Simulation studies that include tracking of passive particles show that the Middle Atlantic Bight (MAB) shelf circulation can potentially disperse shellfish larvae hundreds of kilometers from their natal origins (Zhang et al., 2015). However, most marine larvae exhibit behavior, such as vertical swimming oriented to particular depths or conditions, and inclusion of this behavior with heterogeneous oceanographic currents has been shown to result in shorter dispersal and more retentive conditions (Metaxas, 2001; Metaxas and Saunders, 2009; Strathmann...
et al., 2002). Furthermore, larval growth and swimming are important components of larval dispersal models because behavior has been demonstrated to be important in determining dispersal distance, settlement success, and overall connectivity patterns (e.g., Xue et al., 2008; North et al., 2008; Tian et al., 2009; Kim et al., 2010; Narváez et al., 2012a,b; Zhang et al., 2015). The extent of larval dispersal away from or retention closer to their birthplace are important considerations for understanding the overall metapopulation structure in commercial fisheries for many shellfish and potentially other species with limited adult mobility (Kritzer and Sale, 2004).

The U.S. Atlantic sea scallop (Placopecten magellanicus) fishery is among the most valuable fisheries in the U.S., with an ex-vessel value in excess of $486 million USD in 2016 (National Marine Fisheries Service (NMFS, 2017). This fishery has shown a remarkable recovery from a severely overfished state in the early 1990s. Scallop biomass increased twelve-fold between 1994–2009, while landings more than tripled (Northeast Fisheries Science Center NEFSC, 2014). Though these increases are due to a combination of management measures and ecological factors (Hart, 2006; Hart and Rago, 2006; Shank et al., 2012), implementation of a rotation management program is viewed as an important contributor. In the U.S. scallop fishery management program, these rotational area closures are applied in part to stabilize and enhance the scallop population by preventing fishing on abundant cohorts of small scallops, allowing them to grow and reproduce in highly dense aggregations before they reach appropriate size for the fishery. An important mechanism underlying the success of such a strategy is larval supply (spillover) from high abundance regions or rotational closures to the wider stock. Sea scallop recruitment in the MAB is positively correlated with regional stock biomass, which suggests that increased larval supply tends to result in higher recruitment (Hart, 2013; Northeast Fisheries Science Center NEFSC, 2014). Similarly, recruitment of bay scallops (Argopecten irradians) in Peconic Bay improved following increases in the adult stock size (Tettelbach et al., 2013; see also Peterson et al., 1996).

Atlantic sea scallops are known to spawn in the spring (May), with a second spawn in the fall (DuPaul et al., 1989; Schmitzer et al., 1991). Additionally, larval scallops have been the focus of laboratory studies and field surveys and much is known about larval swimming behavior and vertical distribution in the water column (Tremblay and Sinclair, 1990; Manuel et al., 1996; Gilbert et al., 2010), response to temperature (Tremblay and Sinclair, 1988, 1990; Manuel et al., 2000; Pearce et al., 2004), and growth (Hurley et al., 1986; Manuel and Dadswell, 1991, 1993; Pernet et al., 2003; Gallagher et al., 1996). These behaviors and how they interact with heterogeneous oceanographic conditions throughout the spawning period and across the species’ range underlie patterns of connectivity that are important for understanding long-term population dynamics (Bryan-Brown et al., 2017). Moreover, a better understanding of larval dispersal among scallop stock regions (e.g. among rotational management areas or areas of high stock abundance) would help to improve overall management of the species and the fishery.

In this study, a coupled bio-physical individual-based model is implemented to estimate the patterns of connectivity among Atlantic sea scallop stock regions. Using this model, we quantify the inter-annual variability in dispersal and connectivity among broad management areas over seven years (2006–2012). The coupled model and dispersal simulation (connectivity) results are discussed in terms of their importance for understanding the ecology of the species and for management of this valuable fishery.

2. Model implementation

2.1. Circulation model

The circulation model used in this study is an implementation of the Regional Ocean Modeling System (ROMS, www.myroms.org; Shchepetkin and McWilliams, 2005) that was configured to simulate circulation on the MAB. Larval particle models that consider bivalve growth, development, and larval transport have been included in previous ROMS implementations (e.g., Narváez et al., 2012a,b; Zhang et al., 2015, 2016). For this study, a larval individual-based model (IBM) for the Atlantic sea scallop as described in Section 2.2 is embedded in the ROMS circulation model.

The coupled ROMS-IBM for a MAB model domain covering 68°–77°W and 33.8°–42°N (Fig. 1), with 130 x 80 cells and 5°–8 km horizontal resolution, and actual bathymetry with a minimum depth set to 5 m. Vertical resolution is provided by 36 layers that are non-uniformly distributed vertically such that more layers are used to increase resolution near the sea surface where temperature and currents have larger vertical gradients. The time step was set to 4 h (240 min), with the barotropic integration every 8 s. ROMS settings also used fourth-order centered vertical advection of momentum, fourth-order Akima horizontal advection of the tracer fields (temperature and salinity), turbulent mixing using the Generic Length Scale scheme (Umlauf and Burchard, 2003), and k-kl closure parameters (Mellor and Yamada, 1982).

The coupled ROMS-IBM model was forced every 3 h at the sea surface by atmospheric condition data (i.e., solar radiation, winds, rain, air temperature, pressure, and moisture) obtained from the North American Regional Reanalysis dataset (NARR, http://www.emc.ncep.noaa.gov/mmb/nreanl/). Tidal elevation and current data for the MAB were obtained from the Advanced Circulation Model (http://adcirc.org/products/adcirc-tidal-databases/) and input at the model domain perimeter. Daily river transport data from the U.S. Geological Survey is...
input into the MAB region at seven major rivers (Connecticut, Hudson, Delaware, Susquehanna, Potomac, Choptank and James). Open boundary segments use radiation boundary conditions (Marchesiello et al., 2001) and salinity and temperature are treated using a zero-gradient condition. Along the open boundaries, the circulation model is nudged to corrected and validated tracer and momentum fields from a high-resolution (1/12°) global simulation (Wilkin and Hunter, 2013; Zhang et al., 2015). In each year, the model was run for three months prior to larval release to allow for adjustment of the circulation and tracer fields.

2.2. Larval IBM

The IBM is based on an established coupled modeling platform developed to simulate dispersal of surfclam larvae in the MAB (Zhang et al., 2015, 2016), and dispersal of oyster larvae in the Delaware Bay (Narváez et al., 2012a,b; Munroe et al., 2012, 2013). In this case, the IBM simulates growth and swimming for Atlantic sea scallop larvae and is embedded in the circulation model so that high-frequency dynamical processes act on larval transport and dispersion.

Unlike many other bivalves that release eggs and sperm into the water column where fertilization occurs, fertilized scallop eggs are benthic and remain on the seabed for approximately one day as the embryo develops. The day-old trochophore stage enters the water column (Culliney, 1974; Tremblay et al., 1994); therefore, the larval model is initialized with trochophores that are 1.5 days old with a size of 75 μm (Culliney, 1974, Table 1).

Once the scallop larvae move into the water column, growth is simulated as a function of temperature. Scallop larval growth at 13 °C (grown under optimal laboratory conditions) was set to the average slope of linear growth functions for larval scallops obtained from experimental studies (Pernet et al., 2003; Gallacher et al., 1996; Gouda et al., 2006; Hurley et al., 1986, 1987). This relationship is used as the base growth rate at 13 °C (Gr0), and a temperature relationship was applied such that growth is zero at 0 °C, maximal at 17 °C, and decreases to zero at 19 °C, following results from incubation experiments (Culliney, 1974). Growth (change in length, L) over time (t) at a given temperature (T) is defined as:

\[
\frac{dL}{dt} = G_{r0}G_{rT}(T)
\]

with \(G_{rT}(T)\) modifying the base growth rate for \(T \leq T_1\) by:

\[
G_{rT} = \exp(G_{rT}(T - T_1)),
\]

and for \(T > T_1\) by:

\[
G_{rT} = \max \left[ 0, \frac{T - T_1}{T_1 - T_1} \right]
\]

where:

\[
T_{OP} = \exp(G_{rT}(T - T_1)).
\]

All parameter definitions and values used are provided in Table 1.

Net self-directed larval movement is a result of the combination of upward swimming, downward swimming, and sinking (larval scallops sink when their shell valves are closed). The speed of larval swimming is assumed to be 0.20 mm s\(^{-1}\) for a 250 μm veliger, an average based on helical trajectories reported in Gallacher et al. (1996). This rate is then modified by larval size, which is a function of temperature (Table 1). The amount of time spent swimming upward versus downward follows a hyperbolic tangent function such that at temperatures below ∼14.5 °C larvae will swim almost exclusively upward. A 50:50 balance of upward and downward swimming is assumed at 16.5 °C, and at temperatures above ∼18 °C larvae swim downward almost exclusively. Sinking rates of scallop larvae are based on reported values (Beaumont and Barnes, 1992; Chia et al., 1984; Gallacher et al., 1996) and change based upon the size of the larvae. At any given time, larvae can either swim or sink, and their activity is allocated so that 92% of the time they will swim and will sink 8% of the time; this parameter was set to allow simulated vertical distributions to match observations showing orientation within the pycnocline (Gilbert et al., 2010; Tremblay and Sinclair, 1990). In combination, these upward swimming \(U_s\), downward swimming \(D_s\), and sinking \(S\) behaviors result in net larval movement that tends to be upward in temperatures less than ∼16 °C and downward in temperatures greater than ∼16 °C. Varying the dependency of swimming and sinking on larval size means that net movement varies ontogenetically with larvae > 240 μm tending to move downward to the seabed for settlement.

The vertical movement (dZ) of larvae over time (t) is given as:

\[
\frac{dZ}{dt} = - Sk(L)(1 - Fu(T)) + (Us(L) \times Fu(T)) - Ds(L)(1 - Fu(T))
\]

where passive sinking (Sk) varies with length (L) as:

\[
Sk(L) = Sk_{0}L^{Sk_{1}}
\]

upward swimming speed \(Us\) varies with length (L) as:

\[
Us(L) = Us_{0} + Us_{1}L + Us_{2}L^{2}
\]

and downward swimming speed \(Ds\) varies with length (L) as:

Table 1 Parameters for simulating growth and swimming of sea scallop larvae.

<table>
<thead>
<tr>
<th>Par.</th>
<th>Unit</th>
<th>Value</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gr0</td>
<td>μm day(^{-1})</td>
<td>3.9</td>
<td>Initial basic larval growth rate, set as linear rate observed at 13 °C.</td>
</tr>
<tr>
<td>Gr1</td>
<td>°C</td>
<td>0.069</td>
<td>Rate of increase of growth rate with temperature.</td>
</tr>
<tr>
<td>T1</td>
<td>°C</td>
<td>13</td>
<td>Base temperature for growth.</td>
</tr>
<tr>
<td>T2</td>
<td>°C</td>
<td>17</td>
<td>Optimum growth temperature.</td>
</tr>
<tr>
<td>T3</td>
<td>°C</td>
<td>19</td>
<td>Highest temperature above which growth is zero.</td>
</tr>
<tr>
<td>Dus</td>
<td>mm s(^{-1})</td>
<td>-0.381</td>
<td>Initial upward swimming time fraction.</td>
</tr>
<tr>
<td>Us</td>
<td>mm s(^{-1})</td>
<td>9.262 × 10(^{-3})</td>
<td>Leading coefficient of sinking speed function.</td>
</tr>
<tr>
<td>Sk0</td>
<td></td>
<td>2.22 × 10(^{-4})</td>
<td>Exponent of the power function of sinking speed.</td>
</tr>
<tr>
<td>Sk1</td>
<td></td>
<td>1.744</td>
<td>Coefficients of the quadratic function giving upward swimming speed as a function of larval length.</td>
</tr>
<tr>
<td>Dus</td>
<td>mm s(^{-1})</td>
<td>-2.469 × 10(^{-5})</td>
<td>Coefficients of the quadratic function giving downward swimming speed as a function of larval length.</td>
</tr>
<tr>
<td>Tsw1</td>
<td>°C</td>
<td>16.5</td>
<td>Temperature at which half of swimming time is spent swimming upward.</td>
</tr>
<tr>
<td>Tsw2</td>
<td>°C</td>
<td>0.9</td>
<td>Temperature coefficient that controls the fraction of swimming time spent swimming upward.</td>
</tr>
<tr>
<td>Ds0</td>
<td>μm</td>
<td>75</td>
<td>Initial larval size at 1.5 days old.</td>
</tr>
<tr>
<td>Ds1</td>
<td>μm</td>
<td>240</td>
<td>Minimum settlement size, corresponds to the size at which larvae begin to move downward to the bottom.</td>
</tr>
<tr>
<td>Ds2</td>
<td>μm</td>
<td>270</td>
<td>Maximum settlement size.</td>
</tr>
</tbody>
</table>
than 220 over the release points within each region (Fig. 1) relative to the spatially explicit gonad biomass estimated from annual stock survey sampling (Northeast Fisheries Science Center NEFSC, 2014). The table below shows the total number of larvae released on each year over 36 total daily releases, occurring at 00:00, 04:08, and 08:17 daily on day 1, 6, 11, 16, 21 and 26 of May–October each year. In each year, the number of larvae are scaled spatially over the release points within each region relative to the spatially explicit gonad biomass estimated from annual stock survey sampling (Northeast Fisheries Science Center NEFSC, 2014).

<table>
<thead>
<tr>
<th>Region</th>
<th>Year 2006</th>
<th>2007</th>
<th>2008</th>
<th>2009</th>
<th>2010</th>
<th>2011</th>
<th>2012</th>
</tr>
</thead>
<tbody>
<tr>
<td>Long Island</td>
<td>32,693</td>
<td>32,688</td>
<td>32,866</td>
<td>32,599</td>
<td>32,686</td>
<td>32,416</td>
<td>32,735</td>
</tr>
<tr>
<td>NY Right</td>
<td>31,050</td>
<td>31,660</td>
<td>31,680</td>
<td>31,754</td>
<td>31,948</td>
<td>31,643</td>
<td>31,694</td>
</tr>
<tr>
<td>Delmarva Beach</td>
<td>14,658</td>
<td>14,709</td>
<td>14,632</td>
<td>14,727</td>
<td>14,517</td>
<td>14,602</td>
<td>14,604</td>
</tr>
<tr>
<td>Virginia Beach</td>
<td>38,57</td>
<td>38,23</td>
<td>37,48</td>
<td>37,69</td>
<td>34,91</td>
<td>37,30</td>
<td>38,11</td>
</tr>
</tbody>
</table>

\[ D_0(L) = D_0 + D_1L + D_2L^2. \] (8)

The fraction of time swimming upward \( (F_u) \) varies with temperature \( (T) \) such that:

\[ F_u(T) = F_{u0} \left(1 - \tanh \left( \frac{T - T_{mid}}{T_{bias}} \right) \right) \] (9)

All parameter definitions and values used are provided in Table 1. Scallops are capable of metamorphosis at shell sizes greater than 220 μm and have been observed to settle approximately 35 days post-hatch (Culliney, 1974), with the potential to delay metamorphosis or extend larval duration (Culliney, 1974; Gallaghier et al., 1996; Pearce et al., 2004). Thus, simulated larvae were assumed to settle (i.e., transition from a pelagic dispersive particle to a stationary bottom particle) when they reach a shell length > 250 μm and encounter suitable seabed habitat (defined by depth and adult distribution). Once the settlement length (250 μm) is reached, simulated larvae settle to the seabed at their existing horizontal location and remain fixed. Larvae that reach settlement length in 45 days and are in one of the designated regions are considered ‘successful’. Any of the following conditions result in ‘unsuccessful’ (nonviable) larvae: failure to reach settlement size within 45 days, settlement at a depth greater than 100 m, settlement outside the designated habitat, or larvae that leave the model domain. Two regions are considered ‘connected’ by larval dispersal when larvae successfully disperse from one region to the other.

Sensitivity simulations were performed to test dispersal of particles with IBM on (neutral particles without behavior). These simulations showed that passive particles were only 34% as successful as those with behavior, and that they travel only 45% as far alongshore. These results are due to the fact that without behavior, particles are unable to maintain position near the thermocline and are consistent with results obtained using a similar model domain and a slightly different IBM (Zhang et al., 2015). Further sensitivity simulations were performed to test whether larval behavior module produced expected vertical distributions under controlled (mesoscale mimicking) conditions. These simulations introduced larvae into a 50 m water column, with a bottom temperature of 8 °C, a thermocline at ~20 m depth, and a surface temperature of 21 °C. The larvae swam up to the thermocline in approximately 5 days and maintained their position near the thermocline through day 38. At day 38 (250 μm shell length) the larvae moved downward to the seabed to settle. Additional simulations tested the effects of turbulent mixing in which larvae were mixed above and below the thermocline during development. Larvae abruptly mixed 4–7 m above or below the thermocline were able to return to the thermocline within 3–5 h of displacement. Despite displacement and mixing, larvae were able to grow to settlement size within 38–40 days. Simulated larvae grew and moved as expected based on laboratory and field observations.

2.3. Simulations

The coupled ROMS-IBM was used to simulate physical conditions and scallop larval transport for the years 2006–2012, providing seven years of simulated scallop larval dispersal in the MAB. The shelf waters shallower than 100 m were separated into five regions that correspond to scallop management areas (Northeast Fisheries Science Center NEFSC, 2014) off Virginia Beach, Delmarva, New York Bight, Long Island, and Block Island (Fig. 1). The simulated larvae were released in the four southern regions, however, no larvae were released from Block Island because of low spawning stock density there (Fig. 1). All five regions received larvae. The total numbers of larvae released from each region was scaled each year to proportionally reflect the spatially-explicit observed scallop spawning biomass during that year (Northeast Fisheries Science Center NEFSC, 2014). As an example, in 2006, a total of 3857, 14,658, 31,050, and 32,693 larvae were released from each region (south to north, regional annual release totals for each year are provided in Table 2. Larvae were released on 36 days with three releases occurring at 00:00, 04:08, and 08:17 each day. Although scallops tend to spawn in spring and fall, release days occurred on day 1, 6, 11, 16, 21, and 26 of May through October each year for completeness of seasonal coverage.

3. Results

Success of larval dispersal varied among regions, seasonally, and by year (Fig. S2, Supplementary materials). On average over all release years, the greatest larval success occurred for larvae released from the northern region (Long Island) during September (Fig. 2 bottom right panel). On average, larvae released from Long Island had 14% greater success and 15% greater connectivity than those released from southern regions. Some years show larval success over a protracted range of regions and dates (e.g. 2010 and 2011, Fig. 2), whereas other years show a more constrained pattern of larval success over release dates and regions (e.g. 2007, Fig. 2). The period of 2007 through 2009 had 5% lower larval success for larvae released during August and September compared to other years.

Simulated larval success is the combined result of differences in growth rate, which is largely determined by temperature and dispersal to a habitable region. Like larval settlement success, larval growth rate varied among regions, seasonally, and by year (Fig. 3). On average over all years, fastest rates of larval growth were observed for the southern regions (Delmarva and Virginia Beach) and for the later releases in September and October (Fig. 3 bottom right panel). In some years, larval growth rate remained relatively high in the northern regions over a protracted period of release times, from July through October (e.g. 2009, 2011, Fig. 3).

The relationship between the median temperature experienced by a released group of larvae and the average growth rate over the same group’s pelagic life is relatively unimodal, with an optimum at 15 °C (Fig. 4). Temperature and growth tend to vary seasonally, with successful larvae released in the latter part of the year (September and October) experiencing relatively cooler temperatures (< 14 °C) and high growth (3.5–4.0 μm d⁻¹). Whereas in May, June, and July successful larvae tend to experience warmer and more variable temperatures on average and have correspondingly lower and more variable growth rates (Fig. 4).

Connectivity, a product of both larval success and oceanographic dispersal patterns, also varies seasonally and by year. In general, averaging over all larval releases and all years, connectivity is high among the regions, with each region supplying larvae most strongly to the region south of it and retaining some of its own larvae (Fig. 5). Connectivity tends to be stronger when larval success is higher later in the season. Spawning occurs most consistently in September for this species in the modeled region (Hart, unpublished data) and simulated connectivity for larvae released in September shows a general
downcoast pattern, with most regions highly connected to the region directly to the south (Fig. 6). Additionally, during the first four years of the simulations with larvae released in September, the Long Island and New York Bight regions supply a small percentage of larvae upstream to the region directly north (Fig. 6). The Long Island region is the most widely connected; in five of seven years, larvae released in September from the Long Island region successfully disperse to all other regions (Fig. 6). In contrast, the Virginia Beach region is the least connected to other regions with four of seven years having no larval dispersal to any other region (Fig. 6).

4. Conclusion and discussion

There is a general southward flow along the MAB (Lentz, 2008) which likely drives the somewhat downcoast larval dispersal pattern estimated from the coupled circulation-IBM simulations. The simulated patterns of connectivity among Atlantic sea scallop stock regions show that, in general, larval settlement success and connectivity patterns vary seasonally (28% higher in September to October compared to May–June), among years (2007 through 2009 had 5% lower larval success during August and September in comparison to other years), and spatially with larvae released in September from the Long Island region successfully disperse to all other regions (Fig. 6). In contrast, the Virginia Beach region is the least connected to other regions with four of seven years having no larval dispersal to any other region (Fig. 6).

Sea scallops in the MAB exhibit semiannual spawning with a spring spawn around May, followed by a second spawn in the fall in September through November (DuPaul et al., 1989; Schmitzer et al., 1991). This spawning pattern can vary annually and by scallop size, sex, and water depth and is likely associated with seasonal changes in bottom water temperature (DuPaul et al., 1989; Schmitzer et al., 1991). These simulations show a distinct difference in larval success between releases in the spring and those in the fall, with spring (May and June) releases generally being 28% less successful than those in the fall (September and October). This is consistent with Chute et al. (2012), who used stable isotope analysis of scallop shells to demonstrate that the adult sea scallops were primarily from fall spawns (13 out of 14 scallops overall, and 7 out of 8 in MAB). In our simulations, differences in larval success between spring and fall releases is largely due to differences in temperature that, in the larval model, generates different larval growth rates. Using a similar model for Atlantic surfclams in the MAB, Zhang et al. (2016) demonstrated seasonal differences in larval dispersal that were due to seasonal changes in wind patterns and stratification.

Interannual variability is also evident in our simulations, with 2007 through 2009 having ~5% lower larval success during August and September in comparison to other years. Observed recruitment from annual stock survey programs in the MAB during those years was also relatively poor (Northeast Fisheries Science Center NEFSC, 2014). Scallops, like many other species with high fecundity and dispersive larvae, experience highly variable population abundance among years that is often attributed to annually varying recruitment success (Hjort, 1914; Thorson, 1966; Levin, 2006; Gaines et al., 2007). Our simulations suggest that low larval success may have been a factor contributing to the low rates of recruitment observed during the 2007 through 2009 period; however, other factors controlling post-settlement success (e.g., predation, disease, etc.) also contribute to differences in recruit abundance among years (Ólafsson et al., 1994).

Larval success is also variable among the release regions. Larval
sources and sinks can vary over time (Munroe et al., 2014) and understanding the relative contributions of different portions of a population to overall source:sink dynamics is critical to management decisions about marine protected areas (Crowder et al., 2000) and fisheries (Kritzer and Sale, 2004). The Long Island region tends to have the highest larval success and consistently contributes larvae broadly to all other regions. Assuming these simulated results reflect the true spatial pattern of connectivity in this region, the Long Island region is important not only in local larval supply but also for supplying larvae regionally. Likewise, analysis of phytoplankton blooms and scallop recruitment strength (Northeast Fisheries Science Center NEFSC, 2014) showed that blooms are more strongly correlated to year 1 scallop recruit classes in Long Island than in other regions. Larval food (phytoplankton) is not included as model input; however, this empirical correlation may suggest that larvae from the Long Island region experience even greater success than predicted by the simulations because of synchronicity between larvae and their food.

From a management perspective, it is important to understand the dynamics of populations that are at the edge of a species’ range (Hampe and Petit, 2005), especially those that are larval sinks (Caddy and Gulland, 1983; Cowen and Sponaugle, 2009; Kritzer and Sale, 2004). Individuals at the range edge, particularly the southern end of the range, tend to be at higher risk for loss (Hampe and Petit, 2005) and populations that are a sink, or a net importer of individuals (Pulliam, 1988), face higher mortality risk because of their reliance on recruits from other sources. It should be noted that this species is distributed over a wider area than the management regions we have limited our simulations to, thus the range edges may not be entirely represented here. Likewise, the overall connectivity for the species may be higher if other areas outside the management areas we have included are considered. Nonetheless, the simulated larval connectivity patterns from our model suggests that the Virginia Beach region contributes the least larvae to other regions, and receives most of its settling larvae from regions northward. Thus, this region is a sink and is positioned at the southern edge of the stock range. This could have important implications in terms of vulnerability of this part of the stock (Hare et al., 2016; Kleiner et al., 2017), particularly with a changing climate and uncertainty about how changes in connectivity might manifest through changes to thermally-mediated larval behavior or changes to regional oceanography (Melillo et al., 2014; Rahmstorf et al., 2015; Saba et al., 2016). Qualities such as how strong a larval source or sink an area is are not only important to fisheries management, but are also relevant to
Fig. 5. Connectivity matrices among scallop regions, shown as percent of larvae successfully dispersing from the starting region to the settling region for all larvae released in a given year. The panel in the bottom right shows the average connectivity pattern across all releases for all years. Release regions are listed on the y-axis, destination regions listed along the x-axis. The shading within each grid cell is the proportion of all larvae released from a given region that successfully end in the given destination region. Region names are abbreviated as follows: Block Island: BI; Long Island: LI; New York Bight: NYB; Delmarva: DMV; and Virginia Beach: VB.

Fig. 6. Connectivity matrices among scallop regions, shown as percent of larvae successfully dispersing from the starting region to the settling region for all larvae released in September. Each panel shows the total larval connectivity over all releases in September for a given year (as labeled), with the panel in the bottom right showing the average connectivity pattern across all September releases for all years. Region names are abbreviated as follows: Block Island: BI; Long Island: LI; New York Bight: NYB; Delmarva: DMV; and Virginia Beach: VB.
marine spatial planning and restoration efforts. Decisions about marine protected areas, such as where they should be located or how large they should be, rely on understanding how populations are connected (Palumbi, 2003; Dawson et al., 2006; Cowen and Sponaugle, 2009). Similarly, strategic planning of restoration efforts should target locations that allow both survival of enhanced populations (adult shellfish) and support survival of larvae spawned from these populations which requires some information about how the larvae disperse both into and out of a restoration site. Simulation studies like this one can provide the type of dispersal pattern information needed for marine protected area or restoration planning, and can help in exploring potential evolutionary consequences of protected areas (Munroe et al., 2014).

Direct observation and tracking marine invertebrate larvae over their entire larval duration in a vast ocean remains a technical challenge (Gawarkiewicz et al., 2007) and tracking even in restricted water bodies is an arduous endeavor (Arnold et al., 2005; Thomas et al., 2012). Yet the importance of dispersal and connectivity to metapopulation dynamics and marine management is paramount (Possingham and Roughgarden, 1990; Kerr et al., 2010; Bryan-Brown et al., 2017). Although marine larvae are small, largely planktonic, and cannot overcome oceanic currents per se, many model-based particle tracking studies show that inclusion of simulated larval behavior produces patterns of dispersal and connectivity that differ from those with passive particles (Metaxas and Saunders, 2009; Narváez et al., 2012b; Paris et al. 2007; Gilbert et al., 2010; Zhang et al., 2015; Davies et al., 2015). As such, particle tracking in circulation models is now a standard tool for assessing connectivity within metapopulations for management purposes (Kritzer and Sale, 2004; Bryan-Brown et al., 2017). For example, this approach was used to define stock management units that span international borders in the valuable king scallop (Placopecten magellanicus) fishery in Europe (Nicolle et al., 2017). Narváez et al. (2012a,b) used a particle tracking simulations to estimate dispersal within an eastern oyster (Crassostrea virginica) metapopulation in the eastern U.S. and showed that both decadal variations in river discharge and tidal variability can influence the patterns of connectivity. Similarly, particle tracking simulations for the dispersal of larvae of the Atlantic surfclam (Spisula solidissima) showed seasonal patterns in connectivity that are related to regional stratification and wind stress (Zhang et al., 2016). In a study examining clam dispersal and recruitment in Northern Spain, Bidegain et al. (2013) incorporated both larval and settlement behavior to spawning and nursery areas of interest to restoration and management agencies. These previous studies are cases in which particle tracking simulation models have effectively demonstrated important mechanisms and conditions under which connectivity may vary in commercial shellfish stocks.

The simulations used herein build on these previous studies and provide insights into local, regional, seasonal, and interannual differences in larval success and population connectivity for the Atlantic sea scallop, one of the most important fisheries in the U.S. (van Voorhees, 2014; Northeast Fisheries Science Center NEFSC, 2014). Simulated patterns of connectivity suggest that fall spawners tend to produce more successful larvae, a period of poor larval success may explain a low stock recruitment observed from 2007 to 2009, and the Long Island region may function as an important larval source for other regions. These simulation results provide a basis for additional studies that incorporate environmental conditions such as food supply and post-settlement population dynamics and facilitate discussion about the management of this important fishery and its vulnerability to changing environmental conditions.

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Appendix A. Supplementary data

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References


