Northern quahog (*Mercenaria mercenaria*) larval transport and settlement modeled for a temperate estuary

M. Conor McManus[1*], David S. Ullman[2], Scott D. Rutherford[3], and Christopher Kincaid[2]

[1] Rhode Island Department of Environmental Management, Division of Marine Fisheries, Jamestown, RI, 02835, USA
[2] Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 02882, USA
[3] Roger Williams University, Bristol, RI, 02809, USA

*Corresponding author:
M. Conor McManus
3 Fort Wetherill Road
Fort Wetherill Marine Laboratory
Jamestown, RI, 02835, USA
phone: 401-423-1941;
fax: 401-423-1925;
email: conor.mcmanus@dem.ri.gov

David S. Ullman: dullman@uri.edu
Scott D. Rutherford: srutherford@rwu.edu
Christopher Kincaid: kincaid@uri.edu

Running head: Quahog larval transport modeling

Key words: quahog, larval transport, settlement, Narragansett Bay, fisheries management

ABSTRACT

Evaluating marine species' population connectivity through larval transport can provide insight into the reliance of geographically separated areas on each other's recruitment and metapopulation resiliency. Using larval transport modeling, we assessed the significance of different regions in supporting the Narragansett Bay Northern quahog (*Mercenaria mercenaria*) population. We aimed to identify how areas with varying adult quahog biomass and implemented management strategies (based on water quality and commercial harvest) contribute to the overall stock's larval supply. Larval trajectories were modeled by integrating the currents from a realistic physical circulation model with quahog larval behavior applied to particles during spawning periods of 2006, 2007, and 2014. Modeled larval transport suggested that settlement occurs throughout Narragansett Bay, with 35% of spawned larvae swept out of the Bay to the coastal ocean and leaving the stock bounds. Quahogs in areas where shellfishing is prohibited due to water quality concerns produce a significant portion of the Bay's spawned larvae, theoretically serving as *de facto* spawning sanctuaries. The Providence River, located at the head of the Bay with high mature quahog biomass and currently closed to fishing due to water quality, is a significant source of quahog larvae for the stock. Simulated larval quahog settlement locations corresponded predominantly to sandy bottoms, with less spatial correspondence to commercial fisheries landings. Our work provides insight into the population connectivity of quahogs in Narragansett Bay and highlights the importance of considering oceanography and species' life history characteristics when constructing effective fisheries management plans.

INTRODUCTION

Larval transport and dispersal are critical components of marine species' life cycles for ensuring population connectivity between successive life stages, maintaining recruitment, and sustaining populations (Pineda et al. 2007, Cowen et al. 2009, Llopiz et al. 2014). The life cycle for many marine benthic invertebrates consists of a demersal spawning stock releasing small pelagic eggs that hatch, and larvae transported by currents. For these benthic, sessile species, transport during planktonic stages serves as the sole dispersal mechanism and is critical in structuring local and metapopulation dynamics, maintaining genetic diversity, and contributing to the resiliency of populations to human exploitation (Cowen et al. 2007). For successful spatial management of these species, stock biomass, reproductive capacity, and dispersal of early life stages all must be considered (Fogarty and Botsford 2007). Thus, an understanding of these species larval transport and settlement patterns in areas that exhibit varying degrees of harvest pressure and natural population variability is necessary to develop effective, holistic, management plans.

The northern quahog (*Mercenaria mercenaria*) serves as an excellent example of a benthic sessile species of ecological and economic importance. Ubiquitous in coastal northwest Atlantic waters (Henry and Nixon 2008), the protandrous quahog typically displays aggregated distribution patterns over varying spatial scales: from less than a meter to hundreds of meters (Fegley 2001). The quahog serves important roles in the ecology, economy, and cultural heritage of New England, particularly in Rhode Island. Quahogs regulate benthic-pelagic coupling through suspension feeding organic matter and phytoplankton from the water column (Doering et al. 1986, Newell 2005), with their ecosystem services value having been suggested to exceed their fisheries value (Coen et al. 2007). In Rhode Island for example, the quahog supports

Narragansett Bay's largest fishery, which typically has an annual ex-vessel landings value over $5 million and supports over 500 active shellfishers (ACCSP 2018). As with many coastal shellfish species, quahogs have held cultural significance for centuries, with recreational harvest a cornerstone of Rhode Islanders' heritage (Schuman 2015).

Harvest regulations for suspension-feeding shellfish in coastal ecosystems often involves management plans that consider water quality to ensure human health and the species' population dynamics to avoid overfishing the stock. Certain areas of Narragansett Bay are closed to quahog harvest due to human health and water quality concerns associated with the consumption of quahogs taken from these areas (Fig. 1; Table 1; NBEP 2017). Commercial shellfishing is further managed spatially to enhance and sustain the shellfish stocks and harvest, respectively, with different management tools utilized, including size and possession limits, daily or seasonal closures, permanently closed areas with adequate water quality termed Spawner Sanctuaries, and the requirement that shellfishers report where their landings were harvested via designated 'tagging areas' (Fig. 1).

The benefits of water quality closures, particularly in preserving spawning stock and larval supply, have been debated. Closed or prohibited areas (Table 1) in Narragansett Bay have supported high quahog abundances where individuals can extend their life spans (Rice et al. 1989, Rice 2006), and as such have been considered by some as *de facto* quahog spawner sanctuaries that support greater larval production than areas open to fishing (Marroquin-Mora and Rice 2008). Other investigators, across various ecosystems, have argued that high quahog aggregations can lead to density-dependent effects that reduce larval supply due to competition for food and space and negative feedbacks on growth, survivorship, fecundity and adult predation on larvae (Krauter et al. 2005, Marroquin-Mora and Rice 2008). Gonadal condition in permanently closed areas due to water quality have also been reported to be poorer than those in conditionally-closed areas (Table 1, Marroquin-Mora and Rice 2008), yet how this translates to larval production has yet to be determined.

The objective of our work is to describe quahog larval transport and settlement in Narragansett Bay by coupling ocean circulation models with quahog larval behavior. Through modeling quahog larval transport and settlement, we describe prospective metapopulation connectivity between areas in Narragansett Bay, and identify particular regions' reliance on others to support settling larval quahogs within their area. The connectivity between various regions are evaluated in the context of the areas' management strategy designations, and how such designations help in supporting larval quahog production and the Bay's quahog stock. Lastly, through this analysis, we discuss whether closed or prohibited areas based on water quality or stock preservation could be significant in supporting the Narragansett Bay quahog stock based on larval transport dynamics, providing greater context for the *de facto* spawner sanctuary hypothesis.

METHODS

Study Area

Quahog larval transport was modeled within Narragansett Bay, Rhode Island (USA), an estuary with a mean depth of 8.3 m, and a north-south orientation from the Providence River to Rhode Island Sound (Fig. 1, Kremer and Nixon 1978, Oviatt et al. 2017). Narragansett Bay encompasses multiple sub-estuaries and rivers (including Mt. Hope Bay, Greenwich Bay, Providence River Estuary, and the Sakonnet River), and is highlighted by two distinct channels referred to as the East and West Passages (Fig. 1). Narragansett Bay is a partially mixed estuary

(Weisberg and Sturges 1976), with its circulation influenced by several factors including wind forcing, river runoff, and tidal fluxes (Kincaid et al. 2008, Balt 2014).

The Bay is generally dominated by tides in the sense that the depth-averaged tidal currents are larger than the non-tidal currents (Ullman et al. 2019). However, for particle transport on timescales of days, the non-tidal currents are the dominant factor. The mean, non-tidal, depth-averaged circulation is generally counter-clockwise within the Bay, with depth-averaged inflow (northerly) in the East Passage and outflow in the West Passage (Kincaid et al. 2008, Pfeiffer-Herbert et al. 2015). This pattern of mean circulation is strongly influenced by wind, with certain wind directions strengthening it and others weakening or reversing it. Superimposed on the depth-averaged circulation is a vertically sheared estuarine flow that, because the Bay is relatively wide in comparison to the internal deformation radius, varies laterally such that the vertical extent of the surface outflow (bottom inflow) layer is thicker (thinner) in the West Passage than in the East Passage. The average residence time for the Bay as a whole is 26 days (Pilson 1985). The combination of this circulation pattern and freshwater input from the major rivers near industrial areas in the north portion of the estuary creates down-Bay gradients in physical and biological oceanographic properties (Pilson 1985, Oviatt et al. 2002).

Ocean Circulation Modeling

The physical oceanography and circulation in Narragansett Bay was modeled using the Regional Ocean Modeling System (ROMS) (Haidvogel et al. 2008). The ROMS has been applied to Narragansett Bay previously to understand the water mass exchange between sub-regions and the prevalence of hypoxia (Bergondo 2004, Bergondo and Kincaid 2007, Rogers 2008, Kremer et al. 2010). The Narragansett Bay ROMS implementation uses a high-resolution grid (horizontal spatial resolution ~ 50-100 m in the upper Bay with 15 vertical levels) nested within a coarser grid that includes the Bay and extends out onto the continental shelf south of the Bay's mouth (Supplement 1). At its open southern boundary, the coarse grid model is forced with tidal constituents from the East Coast Tidal Constituent Database (Mukai et al. 2002) and non-tidal currents, temperature, and salinity from the hindcast version of the Northeast Coastal Ocean Forecast System (NECOFS), a regional model covering the northeast U. S. coastal ocean (Chen et al. 2006). Surface momentum and heat fluxes are derived from a combination of local meteorological measurements and output of a mesoscale atmospheric model run as part of NECOFS (Ullman et al. 2019). The model includes measured freshwater discharge forcing from the eight rivers gauged by the United State Geological Survey, as well as estimated discharge from several ungauged rivers, and measured discharges from multiple sewage treatment facilities (Ullman et al. 2019). The output of the coarse resolution model is used to force the high-resolution model at its southern open boundary (the mouth of the Bay) using the same river and meteorological forcing. Vertical mixing in both models is parameterized using the k-ε turbulence closure scheme (Umlauf and Burchard 2003, Warner et al. 2005).

Model skill, assessed by comparing model results with *in situ* current and hydrographic time series measurements from 2006 and 2007, is high in the mid- to upper-Bay region (Balt 2014, Ullman et al. 2019). For tidal currents, which dominate observed currents in the Bay, model skills (Willmott 1982) are in the range of 0.81-0.94 (a skill of 1 represents a perfect model). Model skills for non-tidal currents (low-pass filtered to remove tidal fluctuations) are somewhat lower, with a range of 0.51-0.85.

Larval Transport Behavior

In addition to physical oceanography, larval transport and settlement location are also dependent on early life history traits, such as the timing of spawning, the pelagic larval duration (Shanks et al. 2003), and swimming/sinking rates (Dekshenieks et al. 1996; DiBacco et al. 2001; North et al. 2008). Quahog larval behavior was parameterized in the modeling of larval trajectories using the Lagrangian TRANSport (LTRANS) model (North et al. 2008). This particle-tracking model coupled with ROMS output has previously been used to simulate larval bivalve transport in estuarine and coastal systems (Rasmussen et al. 2006; North et al. 2008; Li et al. 2013). LTRANS applies larval behavior characteristics that couple with the advective processes that are provided by the ROMS simulations. The behavior can include vertical swimming speed, swimming direction, and pelagic larval duration, with the latter two set as probabilistic functions.

Behavior for particles was set to reflect the development of quahog larvae (Carriker 1961, Eversole 1987, Hadley and Whetstone 2007). Larval transport was modeled for the early planktonic (including straight-hinged veliger and umboned stages) and the late-stage pediveliger, of which can be reached between 6 and 20 days old (Carriker 1954, Carriker 1961). Early-stage planktonic larvae tend to be found in the upper water column, and later-stage larvae in deeper portions of the water column as they prepare to settle (Carriker 1961). As such, vertical swimming behavior was constructed to align with these reports (Carriker 1961). From days 0-1, larvae were modeled as passive. Larvae between 1-2 days old had a 0.90 probability of swimming upward at each time step in the LTRANS model (30 seconds). From ages 2-6 days, larvae had a 0.51 probability of swimming up at each time step, and from 6-10 days old, larvae had a 0.50 probability of swimming up. After day 10 and until pediveliger age at day 12 ±0.25 (1SD), the probability of swimming up linearly decreased by 0.017 until the pediveliger age is reached. At pediveliger age, the larvae transitioned to having an 0.80 probability of swimming down. Whereas Arnold et al. (2005) modeled *Mercenaria* spp. larval transport using an 8-day pelagic larval duration, the longer stage duration was implemented to encompass both planktonic and pediveliger stages.

Few data on larval quahog swimming speeds exist, with none known for the pediveliger stage. Carriker (1961) and Turner and George (1955) report upward swimming speeds of approximately 0.0012 m s^{-1} for straight-hinged veligers. Directional swimming speeds have been reported for veliger and pediveliger stages for *Spisula* spp.; over varying salinities, Mann et al. (1991) found that there was an average decrease in swimming speed upon transition to the pediveliger stage. Based on this information, the initial larval swimming speed was set at 0.0018 m s^{-1}, representing the upward reported speed (Carriker 1961, Mileikovsky 1973) plus one-half the Stokes settling speed (to account for upward swimming larvae theoretically opposing the Stokes settling velocity). Swimming speed was then assigned to decrease by 15% at the onset of the pediveliger stage. The swimming speed linearly decreased over the life of the larvae from a maximum of 0.0018 m s^{-1} to a minimum of 0.0015 m s^{-1}. An increase in sinking rates with age that has been reported for shellfish larvae (Troost et al. 2008) was not directly incorporated, but the downward swimming speed and high probability of downward movement combined simulated the rapid vertical decent during the pediveliger stage.

Larval transport behavior did not include growth or mortality components because of the paucity of such information for the Northern quahog. Behaviors set in previous larval shellfish transport modeling work have implemented ontogenetic changes in swimming speed and direction (Munroe et al. 2018), whereas others have excluded it (North et al. 2008, Arnold et al. 2005), often based on the availability of deterministic growth functions for the species of interest. Without larval growth rates available for the Northern quahog, growth was not incorporated into the behavior parameterization and changes in swimming speed and direction were conditioned based on the age (i.e. days since spawned). Mortality rates have been shown to vary with ontogeny, as mortality tends to be higher for smaller individuals (McGurk 1986). However, such rates can vary substantially across marine taxa (Peck and Hufnagl 2012), and therefore other species' or metanalytic size-mortality functions were not incorporated in the quahog parameterization. Mortality was only accounted for via larval drift out of the stock bounds. Larvae transported out of Narragansett Bay to the coastal ocean (Rhode Island Sound) at any point of their larval duration were considered to have left the model domain and were incapable of reentering the Bay. This loss of larvae was assumed to represent either mortality or larval emigration.

Larval Settlement Behavior

Previous larval transport models for marine taxa have used various cues to indicate successful benthic settlement, including substrate type (North et al. 2008, Liu et al. 2015), depth (Decelles et al. 2015), and spawning zones or stock biomass (Liu et al. 2015, Munroe et al. 2018). In laboratory settings, quahog have been found to prefer sand over mud as a settlement substrate (Keck et al. 1974); however, quahogs have also been known as having a gregarious settlement behavior (Keck et al. 1972), with settlement occurring in mud, sand, a mud-sand mix, gravel, sand with rocks and shells, silt-clay substrate, and eelgrass beds (Pratt 1953, Pratt et al. 1992, Rice 1992.) Larval settlement preferences have been attributed to several factors, including representing areas with lower predators (Bricelj 1992), absence of organic matter and its associated bacteria, and presence of quahog pheromones (Keck et al. 1974.)

Benthic features (e.g. sediment type, depth, spawning stock biomass) were not used to inform settlement. If larvae were within one meter of the bottom upon descent, larvae swam randomly over the remaining larval duration, simulating their ability to search for a preferred settlement location. Sediment was not included as a cue given their ability to settle in different substrates and not knowing the probability of successful settlement across the substrates. Further, given the evidence of predation influencing sediment preferences and not knowing the predator fields, settlement parameterization using solely sediment may not have been appropriate.

Scenarios and Initialization

Lagrangian particles with assigned quahog larval behavior were released in 428 grid boxes across the Narragansett Bay model domain. The area of most grid boxes was 1 km^2; although several grid boxes were larger or smaller than $1km^2$ to accommodate land and model boundaries (Fig. 2.) Larvae were released between June 15 and July 15 to align with the major spawning period of quahogs in Narragansett Bay (Eversole 1987, Butet 1997). ROMS and LTRANS were run for the years 2006, 2007, and 2014 to provide a dataset useful in assessing interannual variability in larval transport in Narragansett Bay. Within each grid box, 1000 particles, or larvae, were released during the spawning season randomly in time and space, within 1 m of the bottom. LTRANS grid boxes' released particles were weighted to account for both non-uniform sized grid cells (G_s), and for non-uniform adult quahog abundance (a proxy for larval production) in Narragansett Bay (E_s) (Supplement 2). The E_s scalar was used to provide a realistic spatial supply of larvae (Munroe et al. 2018). Weighting based on the adult quahog abundance, used as a proxy for spawning production, was based on abundance estimates measured from the Rhode Island Department of Environmental Management (RIDEM) Division of Marine Fisheries' hydraulic dredge survey. Quahog abundances from 1993-2016 were spatially interpolated over the LTRANS grid to construct the E_s weights. The entire time series was used for interpolations to account for the survey design (i.e. most survey strata are sampled every other year) and to ensure the spatial interpolations captured the stock's spatial variability (Supplement 2). The final weight for each grid box was the product of the respective G_s and E_s scalars.

Analyses and Post-Processing

Larval transport results were aggregated over regions that corresponded to the Bay's spatial dynamics of water quality, fisheries management strategy, harvest removals, geography, or local significance (Fig. 2). Comparisons to spatial management were done relative to 2016 classifications to match the weighting scheme period and to best characterize the years where ROMS data used to inform ocean circulation were available. This work acknowledges that such modeled larval transport studies using Lagrangian particles do not completely represent complex marine larval organisms and individually-varying behaviors (North et al. 2008). However, hereafter, the particles with larval behavior in the LTRANS model are referred to as 'larvae'.

Source-sink relationships for quahog larvae in Narragansett Bay were evaluated to assess the magnitude of different regions' connectivity. Larvae weights were summed by their specific start and end regions, representing the larval production provided from one region to another. Larval production exported to Rhode Island Sound was calculated as the percent of larval production that left the Bay from all regions. Regions' connectivity results were then presented as relative percentages from two different perspectives: where do the larvae of a given region go, and where do the larvae settling in a given region come from? The former was calculated as percentages of larval production for a given source region based on the areas where its larvae settled, and the latter as a percentage of larval production for a given settling region based on the areas that contributed to its settled larvae. Source-sink relationships were presented using connectivity matrices. To account for the areas differing in size, regions' larval production remaining within the Bay were also presented by dividing the regions' production by the area they cover, producing estimates of larval production per square kilometer. The spatial dynamics of larval settlement were also compared to those of commercial fishing effort and benthic substrate types. Fishermen's reported landings by tagging area (Fig. 1) were obtained and compared to the modeled larval settlement of the corresponding tagging areas. Sediment comparisons were conducted to infer the dominant substrate types that larval may recruit to. Spatial sediment classification data for Narragansett Bay were obtained from McMaster (1960).

Sensitivity Analyses

Two sensitivity analyses were conducted to evaluate the uncertainties associated with the larval quahog model parameterizations. The first examined the impact of weighting larvae based on the adult quahog abundance (i.e. E_s scalars). The larval quahog transport results by regions' total larval production and connectivity with other regions were compared with and without the E_s scalars applied (Supplement 2). The second assessed the impact that larval behavior parameterization had on the transport and fate of larvae. Transport results with and without larval behavior (the latter representing passive particles) were compared (Supplement 3).

RESULTS

Larval Settlement in Narragansett Bay

Quahog larval transport in Narragansett Bay varied interannually with changes in circulation. Larval transport down-Bay was greater in 2006 (an unusually wet year with increased river flow) than 2014 (a dryer year). However, overall patterns emerged. In the years examined, the West Passage received the greatest number of larvae; the extent and magnitude of larval transport down the West Passage varied over the three years. Specific regions of significant larval settlement included the northern West Passage, Conditional Areas A and B, parts of Greenwich Bay, and the Providence River (Fig. 3). The source of larval production that remained in the Bay came primarily from the same regions: Providence River, Conditional Areas A and B, northern East and West Passages, and portions of Greenwich Bay (Fig. 4). LTRANS grids in the upper regions across Narragansett Bay proper (Mt. Hope Bay, Providence River, Conditional Areas A and B, Greenwich Bay, northern East Passage) had the highest proportion of their respective particles remaining in the Bay, suggesting the circulation patterns favor larval settlement from spawning in these grids (Fig. 4).

Over the three years' spawning period, an average of 35% ± 2.3% (mean ± standard error) of the larvae were transported out of the Bay. The Sakonnet River, southern East and West Passages, and portions of Mt. Hope Bay had the lowest proportion of their larvae settling within the Bay (i.e. greater amounts leaving the Bay than being retained), highlighting these regions' high flushing to Rhode Island Sound. When accounting for regions' sizes in larval production estimates, Greenwich Cove, the Providence River, and Apponaug Cove were the most productive in supplying larvae that remained within the Bay (Table 2). Other notably productive areas included Warwick Cove, the Warren River, and Conditional Area A. When evaluating spawning and settling locations by specific regions in the Bay (Fig. 2), the Providence River provided significant larval production to southern regions, including Conditional Areas A and B and northern portions of the East and West Passages (Fig. 5). Other regions contributing significant larval production included the northern East and West Passages, and Conditional Areas A and B (Fig. 5). On average over the three years, the prohibited areas of the Providence

River, Greenwich Bay coves, Potowomut River, and Warren River supplied roughly 39% ± 1.2% of the Bay’s larval production retained within the Bay.

Evaluating a region’s larval contribution to the other areas provides insight into which regions are supported by a given area’s larval productivity (Fig. 6). For the Providence River, 13.2% ± 2.3% of the larvae produced there settled within the area, with exports including 20.6% ± 0.5% to the northern West Passage, 16.3% ± 0.1% to Conditional Areas A and B, and 8.6% ± 0.2% to northern East Passage. Up to 24.1% ± 0.8% and 26.7% ± 1.1% of larval production from a given cove of Greenwich Bay (Greenwich Cove, Apponaug Cove, and Warwick Cove) were transported to Greenwich Bay proper or out to the northern West Passage, respectively (Fig. 6). The Spawner Sanctuary is relatively productive in providing retained larvae to Narragansett Bay compared to other regions (Table 2); however, approximately 31.7% ± 4.4% of its larval production left the Bay, with 28.5 ± 1.4% settling in the West Passage (Fig. 7).

Conversely, quantifying the origin of where settled larvae come from provides insight into the significance of external areas in supporting a given area's settlement larvae and recruitment (Fig. 7). Areas other than the Providence River received between 6.8% ± 1.5% and 79.4% ± 2.3% of their larvae from the Providence River, with the Providence River receiving 65.5% ± 0.4% of its larvae through self-recruitment (Fig. 7). The Conditional Areas A and B received 47.5% ± 0.7% to 42.6% ± 0.6% of their settled larvae from the up-bay Providence River. Conditional Areas A and B, northern East and West Passages, and the Warren River provided additional larval supply to the Providence River. The northern West Passage supported 1.2% ± 0.2% to 26.8% ± 2.8% of other regions total larvae supply, with 18.3% ± 1.6% of the settled larvae in the northern West Passage having spawned there. Greenwich Bay received 39.0% ± 0.9% of its settled larvae from Greenwich Bay and its adjoining coves, with 22.8% ±

1.5% and 10.7% ± 0.8% from the Providence River and northern West Passage, respectively. The Spawner Sanctuary received larvae primarily from Conditional Area A, the Providence River, and the northern West Passage (Fig. 7).

Settlement Results Compared to Sediment and Harvest Pressure

Tagging areas 3W (West Passage) and 4A (East Passage) received the most larvae spawned and settled than any other tagging area (Table 3). Area 3W represents the tagging area with the greatest larval settlement and second largest commercial harvest in Narragansett Bay. Conditional Area A typically has the greatest landings of tagging areas with settled larvae, but only 5.5% ± 1.7% of larvae settling in tagging areas settled in this region. Most of the larval settlement locations corresponded to sand and silty-sand, with these sediment types representing 41.5% ± 0.8% and 21.0% ± 1.7% of the quahog settlement locations, respectively (Table 3). Areas with sediments characterized as gravel or rock had substantially fewer larvae settling (Table 3).

Sensitivity Analyses

The connectivity between regions was similar between scenarios with and without the quahog abundance scaling, yet the magnitude or significance of the source-sink relationships was different (Supplement 2). Without weighting particles to reflect the quahog spawning stock, the northern West Passage and Mt. Hope Bay self-recruitment were the largest source-sink larval relations in the Bay, compared to the Providence River providing larvae for the northern West Passage when quahog abundance weights were applied (Supplement 2). The difference in results between scenarios with quahog larval behavior parameterized and assuming larvae are passive indicated that the assigned behavior had minimal effects on larval connectivity in Narragansett Bay's regions. Overall passive particle export was greater and more variable interannually than when applying quahog larval behavior to the transport model, but the connectivity pathways and their magnitudes were similar between the scenarios (Supplement 3).

DISCUSSION

Larval Transport and Settlement for a Sessile Marine Species

By coupling a realistically forced hydrodynamic model with larval behavior, we have provided insight into larval transport and settlement for an ecologically and economically significant species. Quahog larvae spawned in high adult density areas at the head of the Bay or deeper in sub-estuaries and coves were more likely to settle in the Bay than those from southern regions in closer proximity to the Bay's mouth. The dominant larval transport movement was down-Bay through the West Passage, corresponding to the mean, non-tidal, depth-averaged circulation within the Bay (Kincaid et al. 2008, Pfeiffer-Herbert et al. 2015) and as seen in physical and biological oceanographic properties of the West Passage (Pilson 1985, Oviatt et al. 2002). Coastal circulation has been found to influence larval transport across many estuarine systems through mechanisms including river flow, tidal fluxes, and basin topography (Norcross and Shaw 1984), with our results supporting this notion. These results underscore the importance of mean estuarine circulation in dictating transport and settlement of marine larvae.

The larval transport and settlement estimates highlight the importance of the pelagic larval stage for coastal sessile species in sustaining connectivity between geographically-separated regions within a population (Fig. 5-7). The importance of larval immigration to regions was particularly apparent for subregions of Narragansett Bay. For Greenwich Bay, a sub-estuary supporting an important winter fishery, a substantial portion of its settled larvae were from outside sources (Providence River, Conditional A and B, northern West Passage) and its coves (Apponaug Cove, Greenwich Cove) (Fig. 7). As evidenced here, quantifying larval transport connectivity between areas is vital in assessing local population maintenance, replenishments, and resiliency for species subjected to exploitation (Fogarty and Botsford 2007).

By analyzing the regions' sources and sinks for larval production, we hope to have provided insight into regions' quahog recruitment. The influence of larval transport to suitable habitats on marine fish and invertebrate populations' year-class success has long been deemed a significant contributor to prerecruit-survival and recruitment (Hjort 1914, Sinclair et al. 1985). Modeled larval settlement appears to be predominantly in sandy bottoms (Table 3), corresponding to reported suitable quahog settlement substrate (Kassner et al. 1991). The results have implications for recruitment dynamics in Narragansett Bay; however, other factors influencing fish recruitment were not incorporated, including predation, larval food supply, parental condition, and ecophysiology. Predation and food-limitation can be greater determinants for post-settlement shellfish abundances and recruitment than larval supply (Olafsson et al. 1994, Kraeuter et al. 2005), with predation hypothesized to be as important for settlement location as substrate (Bricelj 1992). Post-settlement quahog predator (such as mud crabs and blue crabs; Polyakov et al. 2007) data is sparse for Narragansett Bay, yet the down-Bay West Passage gradient in phytoplankton productivity (Oviatt et al. 2002, Oviatt et al. 2017) may regulate pelagic larval quahog survivorship. Predator and prey dynamics may contribute to the mismatch between high modeled larval settlement in the mid and lower West Passage and the reported decreasing down-Bay adult quahog standing stock (Pratt et al. 1992). These recruitment theories as well as commercial fishery challenges and impediments may be factors contributing to the spatial discrepancy between larval settlement and landings. For example, transit time, depth, tide, wind, and frequency of closures due to rainfall can influence fishing activity geographically, irrespective of local quahog densities. Aside from availability, fishery logistics and regulations also guide reported fishing effort.

Future Modeling Directions

The advent of biophysical models that incorporate accurate, fine-scale ocean circulation models have improved our understanding of larval transport and recruitment for marine species (Werner et al. 2007). However, many larval transport studies have not been validated with quantitative measurements of larval densities (Metaxas and Saunders 2009). Butet (1997) sampled quahog larvae during the 1995 spawning season, noting the down-Bay decrease in larval abundance from the major spawning source of the Providence River. Identification, time, and cost challenges with traditional larval sampling and microscopic identification remain; however, renewing these efforts would provide insight into the accuracy of the modeled transport and settlement. Furthermore, this research would benefit from a greater understanding of quahog larval behavior. The results appeared to be more influenced by the quahog abundance weighting than the parameterized larval behavior (Supplements 2 and 3), yet several behavioral characteristics were not accounted for. Previous research has documented quahog larval abundances associated with specific tidal currents (Carriker 1961), neap tides (Butet 1997), and affinity for euphotic zones (Carriker 1952). Such diel or tidal vertical movements can influence larval retention in nearshore zones (Paris et al. 2004) and should be further evaluated in field or laboratory settings.

Environmentally-explicit responses to growth, mortality, larval stage duration and behavior would provide more realistic spawning dynamics. In the case of temperature, warmer waters have been linked to shorter larval durations and dispersal distances (O'Connor et al. 2007), and changes in spawning dates and periods (Llopiz et al. 2014). The results from these dynamics may not be intuitive, as faster growth and increased larval mortality associated with increased temperatures may offset each other (Llopiz et al. 2014). The influence of temperature on larval growth and ontogenetic behaviors has been included in similar efforts, such as for Atlantic sea scallops (Munroe et al., 2018); however, such information is unavailable for quahogs. Incorporating ontogenetic drivers in larval life history rates have been advancements in larval dispersal modeling (Peck and Hufnagl 2012) and there is evidence for the need with quahogs (e.g. smaller and less developed quahog larvae have greater mortality and lower growth rates than larger and more developed larvae; Przeslawski and Webb 2009). Thus, functional relationships describing these dynamics over age or size would further improve these efforts.

As conducted in similar studies (Munroe et al., 2018), weighting the Lagrangian particles based on quahog standing stock abundance captured the spatial heterogeneity in spawning and provided more realistic estimates of regions' significance in Bay-wide larval production. However, how fecundity and larval production change across regions with varying water quality and abundance remains unclear. Quahog gonadal condition has been found to be higher in conditionally-closed areas than in permanently closed areas (Marroquin-Mora and Rice 2008), possibly due to density-dependent factors (i.e. overcrowding) or environmental conditions (e.g. hypoxia, poor water quality). If gonadal conditions vary spatially and temporally with environmental conditions and affect larval production, empirical relationships between fecundity and the contributing factors could improve this work.

Implications for Fisheries Management

Despite being relatively productive in relation to its size (Table 2), the Spawner Sanctuary was not a major contributor to the Bay's overall larval quahog production compared to other regions. The weak larval contribution of this protected area is not uncommon across marine systems, as the size, design and location of many early-established marine reserves have largely been the result of political or social processes with fewer biological considerations (Halpern 2003). The Spawner Sanctuary‘s efficacy in achieving its intended goal of sustaining the stock through an unperturbed larval supply should be further evaluated by fisheries managers and stakeholders. The sanctuary serves as an example for the need to use science (in this case, both physical oceanography and fisheries ecology) to construct effective fisheries management plans.

Prohibited areas appear valuable in supporting larvae for areas both closed and open to the commercial quahog fishery based on high standing-stock biomass and the physical oceanography of the Bay. If reduced gonadal quality from these prohibited areas translate to less fecund quahogs and larval production, gonadal quality reduction would likely need to be quite large to negate the value of these regions via their orders of magnitude larger adult standing stocks compared to open areas, and their favorable proximity allowing for larvae to be retained within the Bay. The large larval settlement throughout the Bay from prohibited areas supports the *de facto* spawning sanctuary hypothesis, and that these regions may serve as *de facto* sanctuaries in substantially contributing to Narragansett Bay’s overall quahog population (Rice et al. 1989, Marroquin-Mora and Rice 2008).

With permanently and intermittently closed regions to commercial fishing due to waste-water treatment effluent potentially important for population connectivity, future improvements to water quality have implications for both the quahog standing stock and larval supply. Multiple waste-water treatment facilities have upgraded to tertiary treatment in Rhode Island, reducing nitrogen inputs to the Bay and improving water quality in the Bay’s northern regions, such as the Providence River (Oviatt et al. 2017). Additional management measures have also been taken to reduce fecal coliform discharges in the Bay. Results from these management efforts have already been observed; in 2017, Conditional Area B was reclassified an open area (i.e. not conditionally-closed), and the criteria for closing Conditional Area A was reduced. As openings in these and other areas increase with improved water quality, commercially harvesting the spawning stock in these regions may reduce larval production for down-Bay areas that rely on northern-derived larvae. Such considerations are particularly important for the Providence River, which appears to be a significant larval source for many regions. This work serves as an example for coastal communities looking to improve waste water discharge into estuaries, and for the fishery considerations that should be made concurrently. In the absence of water quality closures, stringent quahog fisheries management plans in these regions would need to be considered to preserve the Narragansett Bay quahog population and fishery.

REFERENCES

Arnold, W.S., G.L. Hitchcock, M.E. Frischer, R. Wanninkhof, and Y.P. Sheng. 2005. Dispersal of an introduced larval cohort in a coastal lagoon. Limnol. Oceanog. 50: 587–597

Atlantic Coastal Cooperative Statistics Program (ACCSP). 2018. Commercial catch and effort data generated by Nicole Ares using ACCSP Data Warehouse [online application], Arlington, VA. Available at http://www.accsp.org. (last accessed on 6 April 2018).

Balt, C. 2014. Subestuarine circulation and dispersion in Narragansett Bay, Ph.D. thesis, University of Rhode Island, Narragansett, Rhode Island.

Bergondo, D. 2004. Water column variability in Narragansett Bay, Ph.D. thesis, University of Rhode Island, Narragansett, Rhode Island.

Bergondo D, and C Kincaid. 2007. Development and Calibration of a Model for Tracking Dispersion of Waters from Narragansett Bay Commission Facilities within the Providence River and Narragansett Bay, Narragansett Bay Commission Final Report, 46 pp.

Bricelj, V. 1992. Aspects of the biology of the Northern Quahog, *Mercenaria mercenaria*, with emphasis on growth and survival during early life history. In Proceedings of the second Rhode Island shellfish industry conference.

Butet, N.A. 1997. Distribution of quahog larvae along a North-South transect in Narragansett Bay. MS. Theses. University of Rhode Island. Narragansett, RI. 96 pp.

Carriker, M.R. 1952. Some recent investigations on native bivalve larvae in New Jersey estuaries. Proc. Natl. Shellfish. Assoc. 1950:69-74.

Carriker, M.R. 1954. Preliminary studies on the field culture, behavior, and trapping of the larvae of the hard clam, *Venus* (= *Mercenaria*) *mercenaria* L. Proc. Natl. Shellfish. Assoc. 1952:70-73.

Carriker, M.R. 1961. Interrelation of functional morphology, behavior, and autecology in early stages of the bivalve *Mercenaria mercenaria*. J. Elisha Mitchell Sci. Soc. 77: 168–241

Chen, C., Beardsley, R.C., and Cowles, G.W., 2006. An unstructured-grid, finite-volume coastal ocean model (FVCOM) system. Oceanography 19, 78–89.

Coen, L.D., R.D. Brumbaugh, D. Bushek, R. Grizzle, W.M. Luckenbach, M.H. Posey, S.P. Powers, and S.G. Tolley. 2007. Ecosystem services related to oyster restoration. Mar. Ecol. Prog. Ser. 341: 303-307

Cowen, R.K., G. Gawarkiewicz, J. Pineda, S.R. Thorrold, F.E. Werner. 2007. Population connectivity in marine systems: An Overview. Oceanography, 20(3): 14-21.

Cowen, R. K., and S. Sponaugle, 2009. Larval dispersal and marine population connectivity, Annual Reviews of Marine Science 1: 443-466

Decelles, G., Cowles, G., Liu, C., and Cadrin, S. 2015. Modeled transport of winter flounder larvae spawned in coastal waters of Gulf of Maine. Fish. Oceanogr., 24(5): 430-444.

Dekshenieks MM, Hofmann EE, Klinck JM, Powell EN (1996) Modeling the vertical distribution of oyster larvae in response to environmental conditions. Mar. Ecol. Prog. Ser. 136: 97-110.

DiBacco, C., D. Sutton, and L. McConnico. 2001. Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. Mar. Ecol. Prog. Ser. 217: 191-206.

Doering, P.H., C.A. Oviatt, and J.R. Kelly. 1986. The effects of the filter-feeding clam *Mercenaria mercenaria* on carbon cycling in experimental marine mesocosms. J. Mar. Res. 44: 839-861

Eversole, A.G. 1987. Species profiles: 1ife histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) -- hard clam. U.S. Fish Wildl. Serv. Biol . *Rep.* 82(11.75). U.S. Army Corps of Engineers, TR EL-82-4. 33 pp.

Fegley, S.R. 2001. Demography and dynamics of hard clam populations. In: J. N. Kraeuter & M. Castagna, editors. Biology of the hard clam. New York: Elsevier Science.

Fogarty, M.J., and L.W. Botsford. 2007. Population connectivity and spatial management of marine fisheries. Oceanography 20:112–123.

Hadley, N.H., and J.M. Whetstone. 2007. Hard clam hatchery and nursery production. Southern Regional Aquaculture Center, Publication 4301. Mississippi State, MS. 8 pp.

Haidvogel, D.B., H. Arango, W.P. Budgell, B.D. Cornuelle, E. Curchitser, E. Di Lorenzo, K Fennel, W.R. Geyer, and others. 2008. Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modeling System. J. Comput. Phy. 227: 3595–3624

Halpern, B.S. 2003. The impact of marine reserves: have reserves worked and does reserve size matter? Ecol. App. 13:S117–S137.

Henry, K.M., and S.W. Nixon. 2008. A half century assessment of hard clam, *Mercenaria mercenaria*, growth in Narragansett Bay, Rhode Island. Estuaries Coasts 31(4):755-766

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. - Comm. Int. Explor. Sci. Mer Mediterr. 20: 1–228.

Kassner, J.R., R. Cerrato, and T. Carrano. 1991. Toward and understanding and improving the abundance of quahogs (*Mercenaria mercenaria*) in the Eastern Great South Bay, New York. In: Proceedings of the first Rhode Island Shellfishers Conference, Rice, M.A., M.

Grady, and M.L. Schwartz (eds.), Rhode Island Sea Grant RIU-W-90-003, Narragansett, RI. pp 69-78.

Keck, R., Maurer, D., and Watling, L. 1972. Survey of Delaware's hard clam resources – Delaware Bay. 1971-72 Annu. Rep. U.S. Natl. Mar. Fish. Serv. 103pp.

Keck, R., Maurer, D., and Malouf, R. 1974. Factors influencing the settlement behavior of larval hard clams, *Mercenaria mercenaria*, Proc. Natl. Shellfish. Assoc., 64: 59-67.

Kincaid, C., D. Bergondo, and K. Rosenburger. 2008. Water exchange between Narragansett Bay and Rhode Island Sound, in *Science for Ecosystem-based Management*, edited by A. Desbonnet and B. A. Costa-Pierce, chap. 10, Springer, 2008.

Kraeuter, J.N., S. Bucknker, and E.C. Powell. 2005. A note on a spawner-recruit relationship for a heavily exploited bivalve: the case of northern quahogs (hard clams), *Mercenaria mercenaria* in Great South Bay New York. J. Shellfish Res. 24(4): 1043-1052.

Kremer, J.N., and S. Nixon. 1978. A Coastal Marine Ecosystem, Simulation, and Analysis. Springer-Verlag, New York, 217p.

Kremer, J.N., J.M.P. Vaudrey, D.S. Ullman, D.L. Bergondo, N. LaSota, C. Kincaid, D.L. Codiga, and M.J. Brush. 2010. Simulating property exchange in estuarine ecosystem models at ecologically appropriate scales. Ecol. Modell. 221: 1080-1088.

Li, Y., R. He, and J.P. Manning. 2013. Coastal connectivity in the Gulf of Maine in spring and summer of 2004–2009. Deep Sea Research Part II: Topical Studies in Oceanography 103: 199-209.

Liu, C., G.W. Cowles, J.H. Churchill, K.D.E. Stokesbury. 2015. Connectivity of the bay scallop (*Argopecten irradians*) in Buzzards Bay, Massachusetts, U.S.A. Fish. Oceanogr., 24(4): 364-382.

Llopiz, J.K., R.K. Cowen, M.J. Hauff, R. Ji, P.L. Munday, B.A. Muhling, M.A. Peck, D.E. Richardson, and others. 2014. Early life history and fisheries oceanography: New questions in a changing world. Oceanography 27(4):26–41.

Mann, R., B.M. Campos, and M.W. Luckenbach. 1991. Swimming rate and responses of larvae of three mactrid bivalves to salinity discontinuities. Mar. Ecol. Prog. Ser., 68:257-269.

Marroquin-Mora, D.C., and M.A. Rice. 2008. Gonadal cycle of northern quahogs, *Mercenaria mercenaria* (Linneas 1758), from fished and non-fished subpopulations in Narragansett Bay. J. Shellfish Res. 27(4): 643-652.

McGurk, M.D. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Mar. Ecol. Prog. Ser., 34:227-242.

McMaster, R.L. 1960. Sediments of Narragansett Bay and Rhode Island Sound, Rhode Island. Journal of Sedimentary Petrology 30(2): 249-274.

Mileikovsky, S.A. 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. Mar. Biol. 23: 11-17.

Mukai, A.Y., J.J. Westerink, R.A. Luettich Jr., and D. Mark. 2002. Eastcoast 2001: A tidal constituent database for the western North Atlantic, Gulf of Mexico and Caribbean Sea. U. S. Army Engineer Research and Development Center, Coastal and Hydraulics Laboratory, Technical Report, ERDC/CHL TR-02-24, September 2002, 201 pp.

Munroe, D.M., Haidvogel, D., Caracappa, J.C., Klinck, J.M., Powell, E.N., Hofmann, E.E., Shank, B.V., and Hart, D.R. 2018. Modeling larval dispersal and connectivity for Atlantic sea scallop (*Placopecten magellanicus*) in the Middle Atlantic Bight. Fish. Res., 208:7-15.

Narragansett Bay Estuary Program (NBEP). 2017. State of Narragansett Bay and Its Watershed (Chapter 24, Shellfishing Areas, pages 461-473). Technical Report. Providence, RI.

Newell, R.I.E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve mollusks: A review. J. Shellfish Res. 23(1): 51-61.

Norcross, B.L., and R.F. Shaw. 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. Trans. Am, Fish. Soc. 113: 153-165.

North, E.W., Z. Schlag, R.R. Hood, M. Li, L. Zhong, T. Gross, and V.S. Kennedy. 2008. Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. Mar. Ecol. Prog. Ser. 359: 99-115.

O'Connor, M.I., J.F. Bruno, S.D Gaines, B.S. Halpern, S.E. Lester, B.P. Kinlan, and J.M. Weiss. 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc. Nat. Acad. Sci. 104(4): 1266-1271.

Olafsson, E.B., C.H. Peterson, and W.G. Ambrose Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: The relative significance of pre-and post-settlement processes. Oceanogr. Mar. Biol. Ann. Rev. 32:65–109.

Oviatt, C.A., A. Keller, and L. Reed. 2002. Annual primary production in Narragansett Bay with no bay-wide winter–spring phytoplankton bloom. Estuarine, Coastal Shelf Sci. 54: 1013–1026

Oviatt, C., L. Smith, J. Krumholz, K. Coupland, H. Stoffel, A. Keller, M.C. McManus, and L. Reed. 2017. Managed nutrient reduction impacts on nutrient concentrations, water clarity, primary production, and hypoxia in a north temperate estuary. Estuarine, Coastal Shelf Sci. 199:25-34

Paris, C.B., and R.K. Cowen. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limnol. Oceanog. 49:1964–1979.

Peck, M.A. and Hufnagl, M. 2012. Can IBMs tell us why most larvae die in the sea? Model sensitivities and scenarios reveal research needs. J. Mar. Sys., 93: 77-93.

Pratt, D.M. 1953. Abundance and growth of *Venus mercanaria* and *Callocardia morrhuana* in relation to the character of bottom sediments. J. Mar. Res., 12: 60-74.

Pratt, S., A. Ganz, and M. Rice. 1992. A species profile of the quahog in Rhode Island. Rhode Island Sea Grant, University of Rhode Island.

Przeslawski, R., and Webb, A.R. 2009. Natural variation in larval size and developmental rate of Northern quahog *Mercenaria mercenaria* and associated effects on larval and juvenile fitness. J. Shellfish Res. 28(3):505-510.

Pfeiffer-Herbert, A.S. 2012. Larval transport in an estuarine-shelf system: Interaction of circulation patterns and larval behavior, Ph.D. Thesis, Graduate School of Rhode Island, University of Rhode Island, 227pp.

Pfeiffer-Herbert, A.S., C.R. Kincaid, D.L. Bergonndo, and Pockalny R.A. 2015. Dynamics of wind-driven estuarine-shelf exchange in the Narragansett Bay estuary. Cont. Shelf Res. 105: 42-59.

Pilson, M.E.Q. 1985. On the residence time of water in Narragansett Bay. Estuaries 8:2-14.

Pineda, J., J.A. Hare, and S. Sponaugle. 2007. Larval dispersal and transport in the coastal ocean and consequences for population connectivity. Oceanography 20(3): 22-39.

Polyakov, O., J.N. Kraeuter, E.E. Hofmann, S.C. Buckner, V.M. Bruchelj, E.N. Powell, and J.M. Klinck. 2007. Benthic predators and northern quahog (=hard clam) (*Mercenaria mercenaria* LINNAEUS, 1758) populations. J. Shellfish Res. 26(4): 995–1010

Rasmussen, L.L., B.D. Cornuelle, E. Di Lorenzo, J.L. Largier, L.A. Levin, and B.J. Becker. 2006. Modeling circulation and transport pathways of larval bivalve populations on a regional scale. EOS Trans. Am. Geophys. Union. 87:suppl.

Rice, M. 1992. The Northern quahog. Rhode Island Sea Grant, University of Rhode Island.

Rice, M.A. 2006. Quahog (*Mercenaria mercenaria*) spawner sanctuaries: does size or location matter? J. Shellfish Res. 25(2):671-672.

Rice, M.A., C. Hickox, I. Zehra. 1989. Effects of intensive fishing effort on the population structure of quahogs, *Mercenaria mercenaria* (L.) in Narragansett Bay. J. Shellfish Res. 8:445-454.

Rice, M.A., and J.A. Pechenik. 1992. A review of factors influencing the growth of the northern quahog, *Mercenaria mercenaria* (Linnaeus 1758). J. Shellfish Res. 11(2), 279-287.

Rogers, J. 2008. Circulation and transport in upper Narragansett Bay, University of Rhode Island, Master Thesis, Kingston, RI, 107 pages.

Schuman, S. 2015. Rhode Island’s shellfish heritage: an ecological history. University of Rhode Island. Narraganset, RI. 168 pp.

Shanks, A.L., B.A Grantham, and M.H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecol. App. 13(1), Supplement: The Science of Marine Reserves, S159-S169.

Sinclair, M., M.J. Tremblay, and P. Bernal. 1985. El Niño events and variability in a Pacific mackerel (*Scomber japonicus*) survival index: support for Hjort’s second hypothesis. Can. J. Fish. Aquat. Sci. 42: 602–608.

Troost, K., Veldhuizen, R., Stamhuis, E.J., and Wolff, W.J. 2008. Can bivalve veligers escape feeding currents of adult bivalves? J. Exp. Mar. Biol. 358: 185-196.

Ullman, D.S., C. Kincaid, C. Balt, and D.L. Codiga. 2019. Hydrodynamic Modeling of Narragansett Bay in Support of the EcoGEM Ecological Model, GSO Technical Report No. 2019-01 University of Rhode Island, 58pp.

Umlauf, L., and H. Burchard. 2003. A generic length-scale equation for geophysical turbulence models. J. Mar. Res. 61, 235-265.

Warner, J.C., C.R. Sherwood, H.G. Arango, and R.P. Signell. 2005. Performance of four turbulence closure models implemented using a generic length scale method. Oc. Mod. 8: 81-113.

Weisberg, R.H. and Sturge,s W. 1976. Velocity observations in the West Passage of Narragansett Bay: A partially mixed estuary, J. Phys. Oceanogr., 6, 345-354.

Werner, F.E., R.K. Cowen, and C.B. Paris. 2007. Coupled biological and physical models: present capabilities and necessary developments for future studies of population connectivity. Oceanography 20:54-69.

Willmott, C.J. 1982. Some comments on the evaluation of model performance. Bull. Am. Meteorol. Soc. 63:1309-1313.

ACKNOWLEDGEMENTS

We thank Jeff Mercer and Dale Leavitt for their contributions to this research during its early development, and their comments and reviews of this work. Comments from David Borkman, Dennis Erkan, two anonymous reviewers and the associate editor improved the manuscript. This work was supported by Rhode Island Sea Grant (Project Number 2014-R/F-1416-31.1-RES). The views expressed herein are those of the authors and do not necessarily reflect the views of their agencies.

FIGURE LEGENDS

Fig. 1. Water quality and shellfish management areas within Narragansett Bay, RI (left). Management types vary with color and reflect designations as of 2016. Region abbreviations used: Providence River (PR), Warren River (WR), Mount Hope Bay (MHB), Greenwich Bay (GB), Greenwich Cove (GC), Apponaug Cove (AC), Conditional Area A (CA), Conditional Area B (CB). GB is both a shellfish management area and conditionally closed area based on water quality criteria. Commercial shellfish harvest reporting areas (or “tagging areas”) for Narragansett Bay (right).

Fig. 2. Regions of Narragansett Bay over which the LTRANS results were aggregated. Region abbreviations used: Providence River (PR), Warren River (WR), Mount Hope Bay (MHB), Greenwich Bay (GB), Greenwich Cove (GC), Apponaug Cove (AC), Warwick Cove (WC), Conditional Area A (CA), Conditional Area B (CB), Potowomut River (PoR), northern West Passage (NWP), southern West Passage (SWP), northern East Passage (NEP), southern East Passage (SEP), Sakonnet River (SR), and the Spawner Sanctuary (SS).

Fig. 3. Settlement locations for larvae modeled during the spawning period of 2006 (top left), 2007 (top right), 2014 (bottom left), and the three years averaged (bottom right). Larvae that were transported out through the mouth of Narragansett Bay are not displayed. Scales are percent of total larval production retained in the Bay settling in each grid box.

Fig. 4. Average larval production of LTRANS grid cells (represented as the weighted number of Lagrangian particles) remaining within Narragansett Bay. Larval production is expressed as (a) the absolute number and (b) fraction of a grid cell’s total larval production remaining in the Bay. Averages are over the three years examined: 2006, 2007, and 2014.

Fig. 5. Average connectivity matrix of larval production (in number of simulated larvae) described by their start and end locations in Narragansett Bay. Averages are over the three years examined: 2006, 2007, and 2014. See Figure 2 legend for regions’ abbreviations.

Fig. 6. Average connectivity matrix of spawning area's ('Start Region') larvae transported to various areas ('End Region') in Narragansett Bay. Averages are over the three years examined: 2006, 2007, and 2014. This presentation highlights where larvae spawned in a given area ('Start Region') are transported to ('End Region'). Within a Start Region (along the x-axis, or columns), the percent values indicate the breakdown of where this region's larvae settled over all regions (along the y-axis). The dashed line represents the contribution of larvae that a region gives itself ('self-recruitment'). Columns may not sum to 100% given that some proportion of region's larvae leave the Bay. See Figure 2 legend for regions' abbreviations.

Fig. 7. Annual average connectivity matrix representing the percent of larvae settling in receiving areas ('End Region') by spawning origin ('Start Region'). This presentation highlights where a given settling area's ('End Region') larvae come from ('Start Region'). Within an End Region (along the y-axis, or rows), percent values indicate the relative importance of where larvae settling in the region came from (along the x-axis), with rows summing to 100%. The dashed line represents the contribution of larvae that a region received from itself ('self-recruitment'). See Figure 2 legend for regions' abbreviations.

TABLES

Table 1. General description of shellfishing area types in Narragansett Bay, RI.

Area Type	Area Description
Conditional Areas	Harvesting allowed except under conditions such as rainfall or wastewater discharge that increase indicator pathogens in the shellfish growing area.
Prohibited Areas	Harvesting prohibited due to water quality
Open Areas	Harvesting allowed year-round with set catch limits
Shellfish Management Areas	Harvesting allowed, with seasonal and daily closures, and reduced catch limit
Spawner Sanctuary	Harvesting prohibited to aid in replenishing the stock

Table 2. Average annual larval production from each starting region that remains within Narraganset Bay scaled to the acreage of the region (km^2).

Start Region	Larval Production km^{-2}
Greenwich Cove (GC)	5515.2
Providence River (PR)	3259.0
Apponaug Cove (AC)	2832.8
Warwick Cove (WC)	1607.5
Warren River (WR)	1518.4
Conditional Area A (CA)	1281.0
Spawner Sanctuary (SS)	1279.3
Greenwich Bay (GB)	1105.6
Conditional Area B (CB)	1090.3
northern East Passage (NEP)	782.9
Mt. Hope Bay (MHB)	590.7
northern West Passage (NWP)	551.1
Potowomut River (PoR)	451.5
southern East Passage (SEP)	288.7
southern West Passage (SWP)	71.3
Sakonnet River (SR)	65.1

Table 3. Larval settlement locations compared to commercial fishing areas (Tagging Areas) and their respective harvest (Commercial Landings Percent), and the sediment (Sediment Type). Larval settlement is based on annual average data from 2006, 2007 and 2014 model runs. Larvae settling outside commercial fishing areas or areas with sediment unclassified were not used in percentage calculations. Commercial landings percentages are based on average annual number of quahogs landed from 2012-2016.

Tagging Area	Larval Settlement Percent	Commercial Landings Percent	Sediment Type	Larval Settlement Percent
3W	45.7%	22.3%	Sand	41.5%
4A	26.6%	11.8%	Silty-Sand	21.0%
1A	5.5%	36.6%	Clay-Silt	20.1%
1B	5.4%	20.1%	Sand-Silt-Clay	12.6%
5A	4.2%	<0.1%	Sandy-Silt	3.4%
5B	4.0%	0.3%	Gravelly-Sand	0.6%
2C	1.9%	0.5%	Gravel-Sand-Silt	0.3%
1C	1.7%	0.1%	Rock	0.2%
2B	1.0%	3.8%	Silt	0.1%
5C	1.0%	<0.1%	Sandy-Gravel	0.1%
2A	0.9%	3.9%	Gravel	0.1%
3H	0.8%	0.2%	Gravel-Silt-Clay	0.0%
3A	0.6%	<0.1%		
5K	0.4%	0.2%		
3C	0.3%	<0.1%		
3F	0.1%	0.2%		
4B	<0.1%	<0.1%		