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Modeling larval connectivity of the Atlantic surfclams within the Middle Atlantic Bight: Model development, larval dispersal and metapopulation connectivity

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A R T I C L E I N F O

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A B S T R A C T

To study the primary larval transport pathways and inter-population connectivity patterns of the Atlantic surfclam, *Spisula solidiss*ima, a coupled modeling system combining a physical circulation model of the Middle Atlantic Bight (MAB), Georges Bank (GBK) and the Gulf of Maine (GoM), and an individual-based surfclam larval model was implemented, validated and applied. Model validation shows that the model can reproduce the observed physical circulation patterns and surface and bottom water temperature, and recreates the observed distributions of surfclam larvae during upwelling and downwelling events. The model results show a typical along-shore connectivity pattern from the northeast to the southwest among the surfclam populations distributed from Georges Bank west and south along the MAB shelf. Continuous surfclam larval input into regions off Delmarva (DMV) and New Jersey (NJ) suggests that insufficient larval supply is unlikely to be the factor causing the failure of the population to recover after the observed decline of the surfclam populations in DMV and NJ from 1997 to 2005. The GBK surfclam population is relatively more isolated than populations to the west and south in the MAB; model results suggest substantial inter-population connectivity from southern New England to the Delmarva region. Simulated surfclam larvae generally drift for over one hundred kilometers along the shelf, but the distance traveled is highly variable in space and over time. Surfclam larval growth and transport are strongly impacted by the physical environment. This suggests the need to further examine how the interaction between environment, behavior, and physiology affects inter-population connectivity. Larval vertical swimming and sinking behaviors have a significant net effect of increasing larval drifting distances when compared with a purely passive model, confirming the need to include larval behavior.

1. Introduction[2]

The Atlantic surfclam (hereafter, surfclam), *Spisula solidissima*, is a bivalve mollusk which lives on the continental shelf from shallow subtidal regions to depths of about 60 m, inhabiting the waters from the southern Gulf of St. Lawrence to Cape Hatteras, North Carolina (Ropes, 1980; Cargnelli et al., 1999). The general distribution pattern of surfclams from the Northeast Fisheries Science Center (NEFSC) survey (Fig. 1) indicates that the highest surfclam abundances occur along the New Jersey shelf (NJ), off the Delmarva Peninsula (DMV) and on Georges Bank (GBK). The surfclam is one of the most commercially important species along the Northeast U.S.

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[2] Abbreviations used in this article: MABGOM: Middle-Atlantic Bight and Gulf of Maine physical circulation model; MAB – Middle-Atlantic Bight; GBK – Georges Bank; GoM – Gulf of Maine; SVA – South Virginia; DMV – Delmarva; NJ – New Jersey; LI – Long Island; SNE – South New England; NEFSC – Northeast Fisheries Science Center of U.S; ROMS – Regional Ocean Modeling System; IBM – Individual-Based Model; Scl-IBM – Surfclam larval Individual-Based Model.

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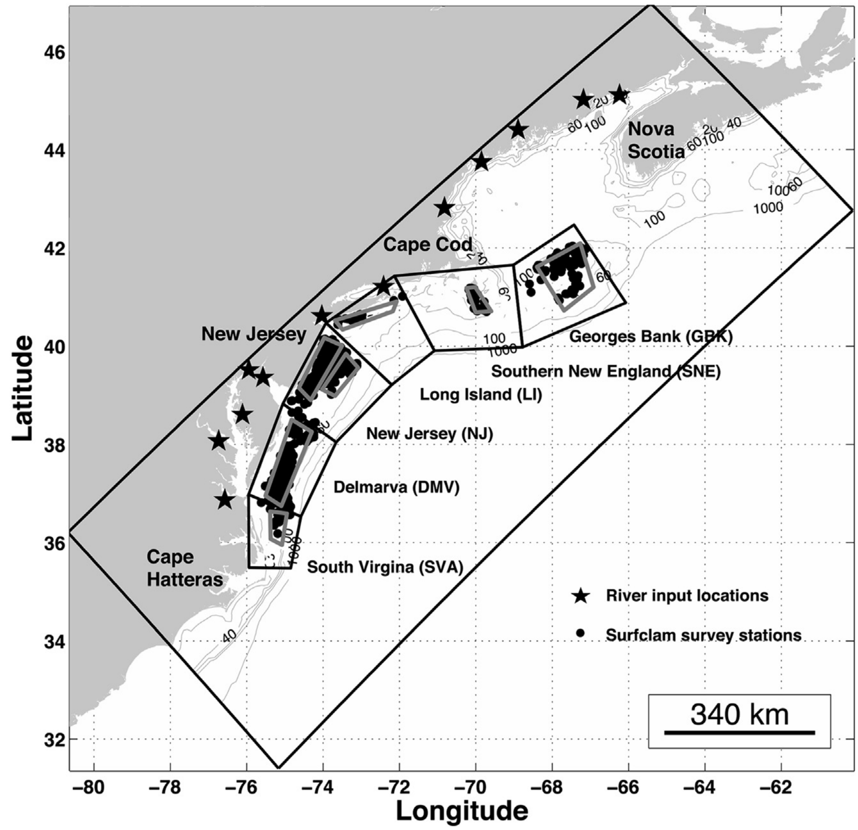

Fig. 1. Model domain and distribution of surfclam populations within the Middle Atlantic Bight and Georges Bank. The model domain (shown as the large black rectangular box) is defined by 160 × 120 grid cells and includes 12 rivers. Black stars indicate river input locations. The grid resolution is approximately from 6 to 12 km (the resolution varies about 15% from south to north). Distribution of surfclams in the domain was based on the NEFSC survey data from 1982 to 2008 (NEFSC, 2010) and is shown by black dots representing those survey stations with surfclam density higher than 80 number of clams per survey dredge tow. Black neighboring boxes along the coast represent conventionally used geographic regions for surfclam stock assessments (NEFSC, 2010); these are, from south to north: South Virginia/North Carolina (SVA), Delmarva (DMV), New Jersey (NJ), Long Island (LI), Southern New England (SNE) and Georges Bank (GBK). Gray boxes inside those black regions boxes denote regions of high surfclam density and are used as the larval release regions in the model. Isobaths of 20-, 40-, 60-, 100-, 1000 m are shown as gray solid lines.

coast. Total commercial landings of Atlantic surfclams in 2008 were approximately 28,000 metric tons (mt), with 22,000 mt from federal fisheries and the remainder from state fisheries (NEFSC, 2010).

Recent surfclam stock assessments (NEFSC, 2010) have shown that recruitment of surfclams into the fishable stock has been low in the southern portion of the range off DMV and to a lesser extent off NJ; commercial catch rates and stock biomass also have declined in recent years (1997–2005). In comparison, trends for large surfclam (>120 mm shell length) abundance in the north are either increasing on GBK or variable along the Long Island (LI) and Southern New England (SNE) shelves. These trends in growth and recruitment, particularly off DMV and NJ, remain unexplained; however possibilities include environmental interactions causing poor juvenile survival and slow growth after settlement, high fishing pressure, or discontinuities in larval transport into those areas. Fishing has been suggested to be an unlikely driver of the current period of poor recruitment (NEFSC, 2010); larval transport and connectivity, however, remains an important and as yet understudied aspect of this dynamic.

Similar to many other benthic invertebrates, surfclam life history includes a dispersive larval stage, followed by sessile juvenile and adult stages. Larval dispersal plays a key role in determining connectivity among geographically distinct populations, and is influenced by physical circulation and water properties (Levin, 2006; Cowen and Sponaugle, 2009). Quantitative observation of larval concentration in the ocean is challenging (Underwood and Keough, 2001) and therefore is rarely performed except under conditions that are ideally suited for tracking and observation of marked larvae (e.g., Arnold et al., 2005). As a consequence, numerical modeling has become the method of choice (Peck and Hufnagl, 2012). Numerical modeling has the ability to couple hydrodynamic and larval behavioral models to simulate larval transport, dispersal and growth (Werner et al., 1993; Lough et al., 2005; Savina et al., 2008; Ayata et al., 2009; Narváez et al., 2012a, b) and can therefore serve as a powerful tool for the study of larval dispersal and inter-population connectivity.

Numerical larval models have been in use for various invertebrate species and systems for many years (Leis et al., 2011), including applications examining larval transport on Georges Bank for sea scallops (Tian et al., 2009), the Gulf of Maine lobster (Incze and Naimie, 2000; Xue et al., 2008; Incze et al., 2010), and eastern oysters in Delaware Bay (Narváez et al., 2012a, b) and in Chesapeake Bay (North et al., 2008). Significant advances have been made in numerical modeling techniques; however, more detailed information concerning larval behavior and its interaction with the surrounding physical environment is necessary to further improve individual-based larval models (IBM) and thereby refine model simulations (Miller, 2007).

In this study, we introduce a coupled modeling system combining a physical circulation model and a biological individual-based model developed for Atlantic surfclam larvae. Specific research objectives focus on the development of the coupled modeling system and the determination of the main larval transport pathways and mean larval connectivity patterns for surfclam stocks in the MAB and GBK. These objectives are integral to