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Study of Atlantic salmon post-smolt movement in the Gulf of St. Lawrence using an individual-based model

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HIGHLIGHTS

- An individual-based model for movements of Atlantic salmon post-smolts (juveniles).
- Simulations of post-smolts' movement from north shore of Gulf of St. Lawrence.
- Swimming behavior and temporal changes in currents affect simulation results.
- Comparisons between observed and simulated travel times suggest possible behaviors.
- Prevailing circulation pattern may prevent post-smolts' migration to open ocean.

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ABSTRACT

This study examines the effect of environmental conditions and swimming behaviors on the movement of Atlantic salmon (*Salmo salar*) post-smolts (juveniles) in the Gulf of St. Lawrence (GSL) using an individual-based model (IBM). The IBM uses time-varying and three-dimensional currents and hydrography produced by an ocean circulation model combined with a numerical particle-tracking scheme where swimming behaviors can be specified. Various experiments are run using this IBM with the aim of gaining insight into the observed movements of post-smolts documented in a past field study. In that study, a post-smolt released from the Saint-Jean River on the north shore of the GSL in June 2010 was found to exit the GSL through the Strait of Belle Isle (SBI) to the northeast of the release area. Two other post-smolts, released later in June 2010, were detected near Anticosti Island (AI) to the southwest of the release area. The numerical results suggest that, for both the post-smolt(s) that moved to the SBI and towards AI, the ambient near-surface circulation patterns favored their movements. In the case of movement towards AI, the travel times simulated using the simulated circulation pattern and a variety of swimming behaviors agree well with observations. For movement towards the SBI, an efficient swimming strategy is necessary in addition to a favorable circulation pattern in order for simulated travel times to be similar to observations. This study suggests two successful strategies for movement towards the SBI: (a) swimming with currents in favorable directions and against currents in unfavorable directions, and (b) swimming towards a series of target locations that define a migration route. The possibility that Atlantic salmon post-smolts originating from rivers on the north shore of the GSL may sometimes be confined to the GSL instead of migrating to the open ocean is consistent with past observational studies.

1. Introduction

Populations of wild Atlantic salmon (*Salmo salar*) have declined in recent decades (Parrish et al., 1998). In the salmon's freshwater habitat, a possible reason for this decline is the presence of dams, which can lead to injuries, increased predation, and delayed migrations (e.g. Lawrence et al., 2016). In the salmon's marine habitat, changes in the marine ecosystem and ocean temperature, driven by climate change, may be contributing to the lower abundance (Mills et al., 2013).

Atlantic salmon exist in anadromous and non-anadromous (freshwater resident) forms (Klemetsen et al., 2003). Anadromous Atlantic salmon spend the first one to eight years of their lives in their natal rivers, migrate to the open ocean for feeding and growth, and return to their natal rivers for reproduction after one to four years at sea (COSEWIC, 2010). Juvenile Atlantic salmon migrating from their natal rivers to the open ocean are called smolts when they are still in freshwater environments, and post-smolts

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upon saltwater entry (Allan and Ritter, 1977). These two stages are thought to be especially vulnerable periods in the Atlantic salmon's life cycle, due to factors such as competition for food, likelihood of predation because of their small size, and the larger number of predators assumed to be in coastal waters than in the open ocean (Hansen et al., 2003). Kocik et al. (2009) estimated the survival rate for wild smolts traveling the 30-km distance between the Narraguagus River and the Gulf of Maine to be about 36%–47%.

To examine the ways in which marine species are affected by environmental conditions, reliable knowledge about the species' distributions and migrations is needed. The development of electronic tags in recent decades has greatly enhanced the abundance and variety of information that can be collected on marine animal movement (Cooke et al., 2011). A type of electronic tracking technology called acoustic telemetry uses tags that are small enough to be attached to relatively small marine animals such as Atlantic salmon smolts (e.g. Lacroix and McCurdy, 1996). These tags transmit signals that are detected by fixed or shipboard receivers (Nelson et al., 2013). Thorstad et al. (2004) and Økland et al. (2006) tracked Atlantic salmon smolts carrying acoustic tags while also measuring ocean currents, and combined the two types of measurements to calculate the smolts' swimming speeds and directions. Plantalech Manel-la et al. (2009) measured vertical profiles of temperature and salinity while tracking Atlantic salmon smolts, and found that they swam in the warmest waters but did not seem to have preferences for specific salinities. Although acoustic telemetry has increased our understanding of fish migration, it does have limitations. A limitation of acoustic telemetry with fixed acoustic receivers is that the locations of tagged animals are only determined when they are near receivers, and there is no information on the paths taken by animals when they are not within detection range of any receivers. Receiver arrays are often several hundred kilometers apart (e.g. Lefèvre et al., 2012). Following animals tagged with acoustic tags using a boat equipped with a receiver (and making concurrent measurement of oceanic conditions) is practical only over relatively short tracking distances.

Numerical simulations using individual-based models (IBMs) can complement observational studies and provide a very useful way to address the above-mentioned limitations of observations. Different from other numerical approaches such as population-based models, an IBM simulates biological processes at the level of individuals or small groups of individuals (Gentleman, 2002; Willis, 2011). When an IBM is used to study animal movement, a numerical particle-tracking scheme calculates the movement of particles that represent individual animals. The particles can be classified as passive or active depending on their type of movement. The movement of passive particles is solely due to the ambient ocean currents. The movement of active particles is due to both ocean currents and a pre-assigned swimming behavior. Using an IBM, experiments can be run with various environmental conditions and swimming behaviors, and the effects of these variations on the particles' travel times can be compared. A comparison between the observed and simulated travel times can be used to assess the relative likelihood of a given behavior.

Byron and Burke (2014) reviewed previous applications of various IBMs to the migration of salmon species in the Atlantic and Pacific Oceans. They noted that strategies used during migrations vary among species and are also dependent on oceanic conditions. Migration strategies can be divided into those that use navigation (in which migrating animals can determine their current positions without relying on cues from their surrounding environment) and orientation (in which the animals direct themselves relative to their surrounding environment). Examples of previous studies using IBMs for juvenile salmon migrations include investigations made by Booker et al. (2008), Mork et al. (2012), Burke et al. (2014), Byron et al. (2014), and Moriarty et al. (2016). Booker et al. (2008) and Mork et al. (2012) simulated the migrations of Atlantic salmon post-smolts in the northeast Atlantic Ocean towards the Norwegian Sea. Both studies suggested that giving virtual post-smolts a capability to swim in the direction of the ambient currents resulted in movements that were similar to observations. These two studies also suggested that preference for a certain range of temperature and/or salinity is an important orientation mechanism for post-smolts. Burke et al. (2014) simulated the seaward migration of juvenile Chinook salmon from the Columbia River. The simulated migrations of fish that navigated themselves with a sense of the compass direction (either to maximize northward passive movement or to actively swim northward) resulted in distributions that most closely matched observations.

Byron et al. (2014) and Moriarty et al. (2016) examined the migration of Atlantic salmon post-smolts from the Gulf of Maine towards the central Scotian Shelf using an IBM that combined a numerical particle-tracking scheme with the ocean circulation model of Xue et al. (2005). Moriarty et al. (2016) tested various swimming behaviors using this model and found that the one with the highest likelihood of successful migration was "directed swimming", in which simulated post-smolts navigated from their natal rivers in the Gulf of Maine towards a point on the Scotian Shelf while avoiding the coastline. The rate of successful migrations was negatively correlated with the strength of coastal currents, which are generally in directions opposite to those of the post-smolts' migration. Byron et al. (2014) added to this model a bioenergetics component that calculated the growth of fish as a function of water temperature, body mass, and swimming activity. Growth, in turn, resulted in faster swimming by the virtual fish. The "directed swimming" behavior defined by Moriarty et al. (2016) was used in all experiments. The movements of post-smolts simulated by this model suggested that interannual variability in the ocean circulation was an important factor in the duration and distance of post-smolts' migration, while interannual variability in sea surface temperature was not.

In this study, an IBM is used to assess the efficiency of various swimming strategies in replicating the observed travel times of post-smolts in the northern Gulf of St. Lawrence. We conduct numerical experiments among which particles' swimming behaviors are varied, with the aim of identifying behaviors that result in travel times that are consistent with field observations. We also vary the starting times of the experiments to examine the sensitivity of our experiments' results to differences in the currents encountered by the particles.

The next section presents descriptions of the study area, the IBM used in this study, and numerical experiments that were conducted using this IBM. The results of the experiments are presented in Section 3. In Section 4 we discuss our results in the context of previous studies of the Atlantic salmon and propose possible directions for future research.

2. Materials and methods

2.1. Study area

The study area is the northern part of the Gulf of St. Lawrence (GSL; Fig. 1). The GSL is one of the largest semi-enclosed seas in the world by surface area (about 2×10^5 km^2). Exchanges between the GSL and the northwest Atlantic Ocean occur through the Strait of Belle Isle (SBI) to the northeast and Cabot Strait (CS) to the south (Koutitonsky and Bugden, 1991). The SBI is about 15 km wide and has a cross-sectional area of 1 km^2, while CS is about 100 km wide and has a cross-sectional area of 35 km^2 (Koutitonsky and Bugden, 1991).

Previous observational studies suggested that the mean surface flow in the SBI is into the GSL (westward) along the north shore