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Could ocean currents be responsible for the west to east spread of aquatic invasive species in Maritime Canadian waters?

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ABSTRACT

The circulation in the shelf seas of Maritime Canada is predominantly in the northeast–southwest direction. Despite the mean northeast–southwest flow, a number of AIS invasions have been observed to proceed in the opposite direction – from the Gulf of Maine, around Nova Scotia, and into the southern Gulf of St. Lawrence. Flow fields from a numerical circulation model are used to investigate whether these invasions could be due to drift in ocean currents. Particle tracking experiments are performed and probability density functions (PDFs) derived that describe the probability of drifting a given upstream distance in a given drift time. Analysis of these PDFs revealed that for invasions that took 20–40 y to occur, propagule drift in ocean currents could be responsible for the upstream spread, while this was not the case for short timescale invasions (<10 y). Rafting could be responsible for both short and long timescale invasions.

1. Introduction

Aquatic invasive species (AIS) are non-indigenous animals and plants that are able to establish themselves in their introduced environment, usually with deleterious consequences. Due to the ecological and economical effects of invasions, the study of AIS has become one of primary interest in marine research.

There are 5 principal vectors for AIS. The primary one globally is via vessel ballast water – the process whereby organisms are transported in the ballast tank of a vessel and then released into the waters of the open-ocean or a different port. Mitigation regulations for ballast water transport are under the direction of the International Maritime Organization (see www.imo.org and IMO, 2004). Another vector can be called "direct human mediated", examples being due to the live bait trade, "disposal" of live exotic foods, and accidental release of Aquarium species (DFO, 2013). Hull fouling is the process by which organisms attach to the hull of a boat and are transported to another location where they can establish themselves. This is a vector of interest in coastal waters mostly mediated by recreational boating (Minchin et al., 2006; Darbyson et al., 2009a,b). Common to the above list is the human involvement in the process. Two other vectors of interest, rafting and egg/larval drift, are human-independent. The release of (potentially) viable offspring (eggs/larvae or seeds) into the water column and subsequent dispersion and settlement is part of the life history of many marine species. Rafting is a catch-all phrase that encompasses numerous possibilities of hitching a ride elsewhere on floating debris (e.g. seaweed, but also including self-fragments). Rafting can be an efficient vector as fragments may be better able to establish themselves compared to eggs or larvae. Common to these two vectors is their mediation by ocean currents.

The shelf circulation in the Maritime region of Atlantic Canada is characterized by a general northeast–southwest flow of water from the Labrador and Newfoundland Shelf areas through the Gulf of St. Lawrence (GSL), Scotian Shelf (SS) and Gulf of Maine (GoM) to the Mid-Atlantic Bight (Fig. 1). Principal current streams include a shelfbreak current flowing east–west from Newfoundland to southwest of Georges Bank, and a coastal current that travels through Cabot Strait, along the NS coastline (the NS coastal current) and around the GoM (the GoM coastal current). Numerous rivers enter the system with the primary source of freshwater coming from the St. Lawrence Estuary. Although small in volume flux ($\sim 10^4$ m^3 s^{-1}) the outflow from the St. Lawrence Estuary constitutes a characteristic low salinity pulse, with peak in the spring, which can be followed through the GSL and onto the SS as part of the NS coastal current, arriving at southwest NS in late summer. Although the flow in the region is generally from northeast to southwest, there is evidence that the flow in the coastal zone does occasionally reverse. For example, the current meter data presented in Smith (1983) (off southwest NS) and Anderson and Smith (1989) (from near Halifax) both show periods of northeasterly flow. This behaviour

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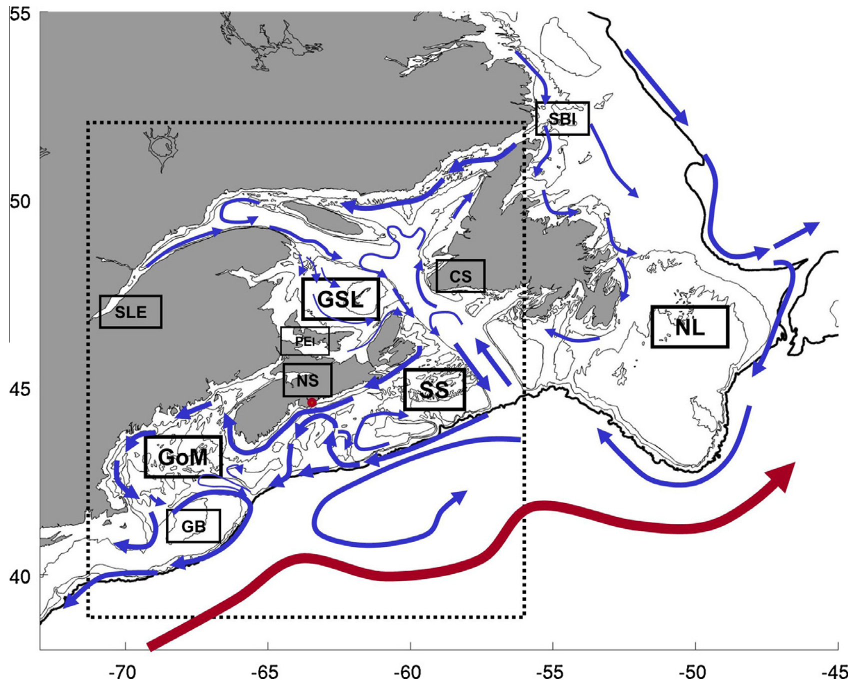

Fig. 1. Schematic of the circulation in the study region. The dashed box is the model domain. Place names are: GoM = Gulf of Maine, SS = Scotian Shelf, GSL = Gulf of St. Lawrence, SBI = Strait of Belle Isle, NL = Newfoundland/Labrador, CS = Cabot Strait, GB = Georges Bank, and SLE = St. Lawrence Estuary, NS = Nova Scotia, PEI = Prince Edward Island. Halifax is located at the red dot.

is also reported in a numerical circulation model of the region (Brickman and Drozdowski, 2012a; Hebert et al., 2012).

Despite the mean northeast–southwest flow, a number of AIS invasions have been observed to proceed in the opposite direction – from the GoM, around NS and into the (southern) GSL. The following examples are mostly based on the DFO AIS website (http://www.qc.dfo-mpo.gc.ca/publications/envahissant-invasive/index-eng.asp).

The European green crab (*Carcinus maenas*, hereafter "green crab") was observed in the GoM in 1950s and later in GSL in the mid 1990s. The colonial bryozoan *Membranipora membranacea* (or Coffin Box), was first found in the GoM in the 1980s, and spread to NS by the 1990s, and into the GSL by 2003. The Japanese green alga oyster thief (*Codium fragile* ssp. *fragile*) first appeared in southern Nova Scotia in 1989 and subsequently was found in the Gulf of St. Lawrence in 1996. The red alga *Heterosiphonia japonica* was reported near Rhode Island ca. 2007 and found in Mahone Bay (∼100 km southwest of Halifax) in 2012 (Savoie and Saunders, 2013). Japanese skeleton shrimp (*Caprella mutica*) was first reported in eastern Canada in the 1990s in the Bay of Fundy, and in the Gulf of St. Lawrence (Prince Edward Island) in 2000. Various invasive tunicates are reported in Maritime Canadian waters. Of those reported in multiple locations, the violet tunicate (*Botryllus violaceus*) was found in NS in the 1990s and Prince Edward Island in 2002 (Carver et al., 2006a), and outbreaks of the vase tunicate (*Ciona intestinalis*) were noted in NS in 1997 and Prince Edward Island in 2004 (Carver et al., 2006b) (although note that the latter species has historically been reported in other eastern Canadian locations (LeGresley et al., 2008)).

Even though the number of invasions documented above is small, they seem to reveal an interesting pattern. Green crab and *M. membranacea* are species whose eggs/larvae spend 30–90 days in the water column (Klassen and Locke, 2007; Caines and Gagnon, 2012). Their invasions took 20–40 y to move the roughly 1000 km from the GoM region to the GSL. The other species mentioned above are characterized by absent or short egg/larval durations (typically less than 7 days: ASLC, 2004; Husa et al., 2004; Husa and Sjøtun, 2006; Turcotte and Sainte-Marie, 2009; Carver et al., 2003; Clarke and Therriault, 2007; Daniel and Therriault, 2007; Locke et al., 2007; Vercaemer et al., 2011). Their invasions took less than 10 y to travel the 1000 km upstream distance.

This study investigates the potential for upstream drift of AIS by ocean currents in Maritime Canadian waters, in order to assess whether this vector could be responsible for the observed west-to-east spread of invasive species. The problem is a complicated one and the solution method will entail numerous simplifications.

The conceptual model is one of upstream propagule drift and subsequent establishment of a population – i.e. a cycle of spawning (or rafting), settlement, establishment, and growth. Progress upstream proceeds as a series of steps, typically occurring annually. The goal is to estimate the expected step distances for egg/larval drift and rafting, and determine whether these steps could account for the observed timescales for spread. To accomplish this, an ocean circulation model of the region is run to produce a set of flow fields in which particle release experiments are performed. These experiments are analyzed to determine probability density functions (PDFs) for upstream drift. These PDFs, which describe the probability of drifting a given upstream distance in a given time, are used to address the abovementioned question.

The outline of the paper is the following: The methods section provides details of the ocean circulation model simulations, the particle tracking experiments, and the computation of the drift PDFs, as well as basic results from the model and particle drift simulations. The Results and Interpretation section provides more details on the space/time characteristics of the drift PDFs and shows how they can be used to assess the effectiveness of ocean currents in producing the observed pattern of AIS spread. The last section is a discussion.

2. Methods

The model used in this study (the CANOPA circulation model, Brickman and Drozdowski, 2012a) is a version of the NEMO-OPA