



Hydrodynamics and spatial separation between two clades of a copepod species complex



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ABSTRACT

The purpose of this study was to explore the importance of hydrodynamics in the spatial distribution of a dominant calanoid copepod, *Eurytemora affinis*, in the middle St. Lawrence Estuary. To do this, we used a 3D numerical model of the region. We successfully compared modelled trajectories to real trajectories obtained from surface drifters. Multiple trajectories were then generated to compute finite-time Lyapunov exponents (FTLEs). A ridge of high FTLE values, which starts downstream close to the shoal between Île-aux-Coudres and Ste-Anne's Bay and reaches its upstream extremity on the south shore near Montmagny, separates two groups of modelled particles. This ridge seems to separate two distinct water masses that will not mix together. It appears 1 h after high tide and is persistent for 3 to 4 h during every ebb tide, suggesting that hydrodynamics is an important factor maintaining the separation between the two genetically different *E. affinis* clades.

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1. Introduction

The horizontal spreading and mixing of Lagrangian tracers governs the dynamics of many processes that occur in the ocean: the dispersion of pollutant spills, plankton patchiness, and population dynamics are examples of these processes (Hitchcock and Cowen, 2007; Martin, 2003; Perianez, 2004). It is natural to approach these problems in a Lagrangian framework because a Eulerian view does not provide information on the fate of Lagrangian tracers in time-dependent systems. By using numerical models (Haza et al., 2008; Mancho et al., 2008) or surface current speeds obtained from HF and VHF radar (Gildor et al., 2009; Lekien et al., 2005; Olascoaga et al., 2006), it has become easy to generate large amounts of Lagrangian trajectories in a given domain. While the trajectory of one passive tracer can be clearly deciphered, it rapidly becomes difficult to interpret the resulting entangled diagram of several Lagrangian tracers, given the chaotic nature of these paths. Lagrangian parameters, like finite-time Lyapunov exponents (FTLEs), can overcome this problem by extracting information from the trajectories and presenting it as a time-dependent scalar field in space. In a certain way, FTLEs (or other similar Lagrangian parameters, like finite-

scale Lyapunov exponent) present Lagrangian information in a Eulerian view. These Lagrangian parameters reveal structures, called Lagrangian coherent structures (LCSs), that govern the exchanges between distinct water masses (Shadden et al., 2005).

LCSs revealed by FTLE are being increasingly used to get a better understanding of the role the circulation plays in diverse oceanographic phenomena (Coulliette et al., 2007; Gildor et al., 2009; Lekien et al., 2005; Olascoaga et al., 2006, 2008). In our study, we computed FTLEs in the St. Lawrence Estuary (Fig. 1) to examine the importance of hydrodynamic processes in the separation of two clades of the *Eurytemora affinis* copepod species complex. The North Atlantic clade (non-invasive) largely occupies the central portion of the middle St. Lawrence Estuary while the Atlantic clade (invasive) is found predominantly in the upstream oligohaline part of the middle estuary (Fig. 2) (Winkler et al., 2008). This spatial separation was unexpected since highly energetic hydrodynamic processes were believed to produce a homogenous spatial distribution of the two clades, at least in the brackish part of the St. Lawrence Estuary. Physiological factors do not seem to be responsible for the two clades spatial segregation, since an experimental study showed that both clades have high survival rates in brackish water (Winkler, unpublished data).

FTLE fields were obtained from a 3D numerical model. FTLEs were computed using Lagrangian tracers that were tracked for 6 h. To evaluate the model capacity to compute accurately Lagrangian trajectory of this duration, surface drifter experiments of this time-scale were carried out to compare real and modelled trajectories.

Abbreviations: FTLE, Finite-time Lyapunov exponent; LCS, Lagrangian coherent structure.

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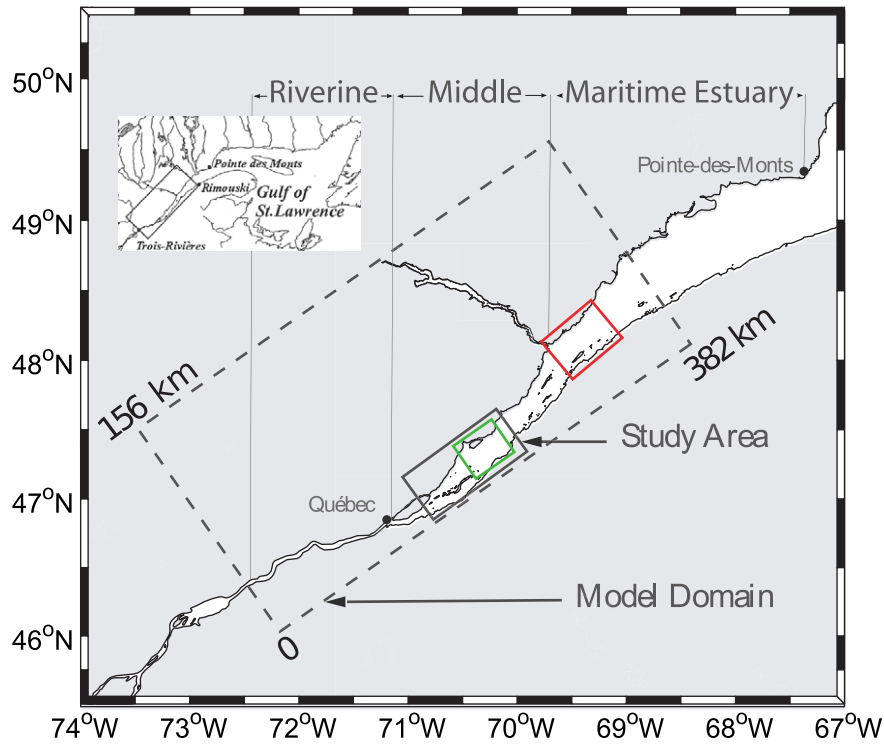


Fig. 1. Map of the St. Lawrence Estuary. The red rectangle corresponds to Fig. 4(a), the green one to Fig. 4(b). The dashed rectangle corresponds to the domain of the numerical model, where distances are given in km from the origin on the lower left corner. Distances on the subsequent figures refer to this grid.

The computation of FTLEs revealed a ridge of high FTLE values that separates the two genetically different *E. affinis* clades. This ridge seems to separate two distinct water masses that will not mix together.

1.1. Study region

Subregions of the St. Lawrence Estuary are defined differently by different authors. Based on its physical characteristics, we divide the estuary into riverine, middle, and maritime sections, with the riverine estuary extending from Trois-Rivières to the western point of Île d'Orléans, the middle estuary reaching the mouth of the Saguenay Fjord, and the maritime estuary ending at Pointe-des-Monts. These divisions took into account bathymetric features (maritime/middle estuary), the limit of salt intrusion (middle/riverine estuary) and weak tidal influence (riverine estuary/St. Lawrence River).

The middle estuary (Fig. 2) is 180 km long, up to 24 km wide, and up to 120 m deep. It consists of a mixture of fresh water from the St. Lawrence River (averaging $11000 \text{ m}^3 \text{ s}^{-1}$) and deep oceanic water from the Laurentian Channel. A series of shoals and islands divide the northern and southern parts. The northern part is generally deeper, with a channel extending for most of its length. In the southern part, the South Channel and Middle Channel are shallower than 30 m except in front of Kamouraska, where the South Channel is more than 40 m deep. A shallow (<10 m) shelf of variable width (5 km to 10 km) extends along the south shore (El-Sabh, 1988).

The salinity of the middle estuary ranges from ~0 upstream to 30 psu at the bottom of the Île-aux-Lièvres basin (El-Sabh and Silverberg, 1990; Saucier et al., 2009), and the strongest longitudinal salinity gradients are observed near the section of Île-aux-Coudres (Greisman and Ingram, 1977; Ingram and El-Sabh, 1990). The general circulation consists of a two-layer lengthwise circulation in which brackish water flows downstream over deeper, saltier water. The lateral salinity gradient can reach 8 psu.

The tides of this system represent 94% of its energy (Muir, 1982). The tidal range is maximum between Île-aux-Coudres and Île d'Orléans, where it can reach 7 m (Saucier and Chassé, 2000), and the M2 component is by far the most important (White and Johns, 1997). Because the tidal wave length decreases as it propagates upstream, the resulting tidal stream can be as much as 4 m/s (Silverberg and Sundby, 1979).

This study mainly focuses on the upstream part of the middle estuary, characterized by the limit of salt intrusion and the turbidity maximum. According to Pritchard's classification (Pritchard, 1967), El-Sabh (1988) described this region as vertically homogeneous around Île d'Orléans and partially mixed everywhere else.

1.2. Copepods

The study by Bousfield et al. (1975) was the first to describe the abundance and composition of zooplankton in the middle estuary. This study found that calanoid copepods constituted 60% of the mesozooplankton population with three dominant species: *E. affinis* (43%), *Acartia longiremis* (35%), and *Eurytemora herdmani* (17%). *E. affinis* was the dominant calanoid copepod and was mainly found in brackish waters between Île d'Orléans and Île-aux-Coudres. Due to its high abundance, *E. affinis* is the dominant grazer of autotrophs in the middle estuary. It was estimated that its population consumes approximately 50 tons of algal carbon per day, representing 20% of the net algal production of the estuarine transition zone; this illustrates the potential impact of copepod grazing on phytoplankton biomass. In turn, its (*E. affinis*) main predators are larval fishes and mysids, the latter being by far the most important (Winkler et al., 2003).

Laprise and Dodson (1994) noted that *E. affinis* could withstand large salinity fluctuations, reporting high abundances in waters with salinity varying from 0.5 to 23; this confirms *E. affinis* as a euryhaline species. Lee (1999, 2000) revealed that *E. affinis* is a cryptic species complex made up of six ancestral clades distributed over the Northern Hemisphere, with two sympatric clades found between Île d'Orléans

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