Journal of Great Lakes Research xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Predicting spread of aquatic invasive species by lake currents

Dmitry Beletsky [a,*], Raisa Beletsky [a], Edward S. Rutherford [b], Jennifer L. Sieracki [c], Jonathan M. Bossenbroek [c], W. Lindsay Chadderton [d], Marion E. Wittmann [e,1], Gust M. Annis [f], David M. Lodge [e,2]

[a] CILER, SNRE, University of Michigan, Ann Arbor, 48108, United States
[b] Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, Ann Arbor, MI 48108, United States
[c] Lake Erie Center, Department of Environmental Sciences, University of Toledo, Oregon, OH, United States
[d] The Nature Conservancy, South Bend, IN 46617, United States
[e] Environmental Change Initiative, and Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46656, United States
[f] The Nature Conservancy, Lansing, MI 48906, United States

ARTICLE INFO

Article history:
Received 14 December 2015
Accepted 2 February 2017
Available online xxxx

Keywords:
Aquatic invasive species
Lake Michigan
Lake Erie
Eurasian ruffe (*Gymnocephalus cernua*)
Golden mussel (*Limnoperna fortunei*)
Dreissenid mussels

ABSTRACT

Knowledge of aquatic invasive species (AIS) dispersal is important to inform surveillance and management efforts to slow the spread of established invaders. We studied potential dispersal of invasive Eurasian ruffe *Gymnocephalus cernua* and golden mussel *Limnoperna fortunei* larvae in Lakes Michigan and Erie using a three-dimensional particle transport model. Ruffe is currently in Lake Superior and northern Lake Michigan, while *Limnoperna* has not yet invaded the Great Lakes. We predicted larval transport during several spawning seasons (individual years) from several major tributaries and ports that are most prone to invasion because of their significant recreational and commercial usage. Depending on release location, larvae traveled distances ranging from <1 km to tens of kilometers (in some cases over 100–200 km, depending on species) during 2–3 weeks of drift time. Dispersal distances from nearshore locations (i.e. rivers and ports) were smaller than from offshore deballasting locations near ports. *Limnoperna* dispersal distances were larger than ruffe due to stronger seasonal currents and longer drift period. Settlement areas resulting from offshore releases were larger than for nearshore releases, and larger for *Limnoperna* than for ruffe. Model results compared favorably to observed spread of ruffe and *Dreissena* spp. mussels in Lake Michigan. Our modeling effort suggests that larval advection by lake currents is an important AIS dispersal mechanism in the Great Lakes. It also emphasizes the importance of effective surveillance programs that maximize early detection of new introductions before lake current dispersal obviates containment and prevention of spread and impacts.

Introduction

There have been many non-indigenous species introductions to the Great Lakes region, a small percentage of which have established and caused irreparable economic and ecological damage (Lodge et al., 2016; Mills et al., 1993; Rothlisberger et al., 2012). These introductions can be attributed to a wide variety of dispersal pathways, including canals, trade in live organisms, intentional releases and ballast water exchange from maritime vessels originating from ports outside the Great Lakes (Ricciardi, 2006). Currently, more than 180 non-native species have been detected in the Great Lakes (Pagnucco et al., 2015).

Species invasions are a multiple stage process comprised of transport and introduction of organisms to a novel habitat from the native range, establishment and growth of self-sustaining populations within the new environment, and secondary spread of the organism (Kolar and Lodge, 2001). While preventing introductions is the most efficient strategy to reduce the likelihood of negative effects of non-native species (Leung et al., 2002), even the most effective prevention efforts are not perfect. In recognition of this reality, and the advent and adoption of more effective genomic detection tools (Jerde et al., 2011; Lodge et al., 2012), there is growing interest in developing a basin-wide aquatic invasive species surveillance program for the Great Lakes basin as well as incursion response capabilities. Both outcomes are explicit commitments of the updated Great Lakes Binational Water Quality Agreement (2012; Annex 6 – Invasive Species, http://binational.net/annexes/a6/), and the Council of Great Lakes Governors Mutual Aid Agreement (2015; http://www.cglg.org/media/1564/ais-mutual-aid-agreement-3-26-15.pdf). Whereas eradication of novel populations is the preferred response outcome, the absence of acceptable and effective control tools for many potential invasive species will mean that managers will employ strategies to slow

---

[*] Corresponding author.
E-mail address: beletsky@umich.edu (D. Beletsky).
[1] Current address: University of California Natural Reserve System, University of California, Santa Barbara, CA 93106-6150, United States.
[2] Current address: Atkinson Center for a Sustainable Future, and Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853. United States.

http://dx.doi.org/10.1016/j.jglr.2017.02.001

Please cite this article as: Beletsky, D., et al., Predicting spread of aquatic invasive species by lake currents, J. Great Lakes Res. (2017), http://dx.doi.org/10.1016/j.jglr.2017.02.001

the rate of AIS spread until more effective control strategies can be developed. Thus the ability to predict where non-indigenous species will establish and spread becomes a valuable component to the development of invasive species management frameworks.

While hull fouling and ballast water exchange associated with commercial and recreational vessels are important mechanisms by which non-native species disperse within the Great Lakes (Carlton, 1985; Sieracki et al., 2014), transport by lake currents also may facilitate movement of species, particularly those with pelagic life stages. The physical properties of pelagic systems and their effects on biological populations have been explored through the use of hydrodynamic and particle transport models, including case studies of AIS spread in marine environments (Johnson et al., 2005; See and Feist, 2010; Tilburg et al., 2011). These models have shown that variability in circulation is an important component of the dispersal and recruitment in marine fish populations (Crowder and Werner, 1999; Heath and Gallego, 1998), freshwater fishes (Beletsky et al., 2007; Zhao et al., 2009) and invasive bivalves (Hoyer et al., 2014).

Currents in the Great Lakes vary over multiple temporal and spatial scales and may contribute to variability in the population dynamics of species in the nearshore and offshore regions (Beletsky et al., 2007; Höök et al., 2006). Advection by lake currents, along with turbulent diffusion and shear dispersion (Choi et al., 2015), is expected to affect the dispersal of non-indigenous species in the lake. In this paper we explore the effects of Great Lakes currents on dispersal of two non-indigenous species of significant concern: the Eurasian ruffe (*Gymnocephalus cernua*; hereafter ruffe) which is established in the Great Lakes region, and the golden mussel (*Limnoperna* fortunei, hereafter *Limnoperna*), which has been predicted as a potential future Great Lakes invader (Keller et al., 2011; Ricciardi, 1998).

We chose to model larval dispersal of ruffe because it has a documented history of expansion in the Great Lakes, and its reproductive life history is similar to that of other fishes considered to be potential invaders in the Great Lakes. Several of the AIS fishes identified as future invaders by NOAA's GLANSIS watch list (http://www.glerl.noaa.gov/res/programs/glansis/glansis.html) are cyprinids and gobies, and like ruffe have relatively short larval stages before becoming demersal. Ruffe is a spiny benthivorous percid fish first introduced to North America in the mid-1980s in the St. Louis River, a tributary of Lake Superior (Collette and Bănărescu, 1977; Pratt et al., 1992). Ruffe are native to Europe and Asia and their introduction to Lake Superior was accidental, most likely through ballast water discharge from transoceanic vessels (Pratt et al., 1992). Due in part to its high fecundity rate, ruffe became the most abundant fish in the St. Louis Estuary within five years of its discovery (Gunderson et al., 1998). The distribution of ruffe in Lake Superior remains quite limited; although now present along most of the southern shore, they are most abundant in the lower reaches of some rivers, but are largely absent in offshore waters owing to cold lake temperatures (Ogle, 1998). Ruffe also have established localized populations in Green Bay (northern Lake Michigan). In Lake Michigan, ruffe were first discovered in Escanaba, MI in 2002, and no specimens have been collected outside of Green Bay (Bowen and Keppner, 2013), although ruffe DNA was detected in southern Lake Michigan waters near Chicago in 2013 (Tucker et al., 2016).

Ruffe are highly fecund, batch and broadcast spawners, and are able to spawn several times each year, depending upon temperature conditions (Hokanson, 1977). Ruffe spawn in waters <20 m in depth (Pratt, 1988) on a variety of substrates between mid-April and July at temperatures ranging from 5 to 18 °C (Brown et al., 1998). Ruffe commonly mature at age two or three, but may mature at age one in populations experiencing high mortality or warm temperatures (Neja, 1988; Ogle, 1998). Eggs hatch in 5 to 12 days at 10 to 15 °C (Craig, 1978), and the embryos remain sedentary for up to 7 days near the bottom until reaching sizes of 4.5–5.0 mm, at which point they feed exogenously and become phototactic. Larval ruffe survival is poor below 10 °C and above 21.5 °C (Hokanson, 1977).

Ruffe can have indirect negative impacts on other Great Lakes fishes, such as yellow perch *Perca flavescens*, owing to their consumption and competition for benthic prey resources (Ogle et al., 1995; Savino and Kolar, 1996). Ruffe also have unwanted effects through direct predation on eggs of commercially important fish such as lake whitefish (*Coregonus clupeaformis*.) (DeSorcie and Edsall, 1995). Within the Great Lakes, the species" spread may have been augmented by inter- and intra-lake shipping transport (Pratt et al., 1992; Stepien et al., 1998), but it is unknown what role advective processes have played in the dispersal of this species. There is significant concern that this species may spread into the Mississippi River Basin from the Great Lakes through tributaries or manmade waterway connections (Tucker et al., 2016).

Limnoperna is an epifaunal bivalve native to mainland China. Since the mid 1960s, it has been unintentionally dispersed across the globe via ballast water; established populations are present in Hong Kong, Taiwan, Japan, Brazil, Paraguay, Uruguay, Bolivia and Argentina (Darrigran and Pastorino, 1995; Ricciardi, 1998). The rapid spread of *Limnoperna* throughout the Rio de la Plata basin in South America is due in part to advection of its pelagic veligers along the river system (Cataldo and Boltovskoy, 2000; Karatayev et al., 2007). *Limnoperna* is thought to have a similar life history and habitat preference as dreissenid mussels, which have a widespread distribution and unwanted impacts in the Great Lakes watershed (Karatayev et al., 2007).

The reproductive ecology and larval development of *Limnoperna* is fairly well known. *Limnoperna* begin reproducing in spring and cease reproducing in fall at temperatures around 16–17 °C, providing an extended period of reproduction in warm ecosystems. The mussels are dioecious and reproduce via external fertilization. Larvae undergo several pelagic development stages before settling and attaching to the substrate 11–20 days after spawning (Cataldo et al., 2005). *Limnoperna* feed on nanoplankton during larval development (Cataldo, 2015; Ernandes-Silva et al., 2016).

The main objective of this paper is to predict and compare the dispersal of larval ruffe and *Limnoperna* in Lakes Michigan and Erie using a particle transport model. These Great Lakes were chosen because they have thermal habitat suitable for *Limnoperna*. An additional objective is to compare dispersal of ruffe and *Limnoperna* when larvae of these species were released from different habitats and locations, specifically river mouths, ports, and offshore locations. These locations were chosen because their significant recreational and commercial usage makes them likely introduction points of AIS into the Great Lakes.

Methods

In this section we present details of the particle transport model, larval model parameters, substrate data and metrics used. We also provide background information on lake circulation that drives larval dispersal by summarizing results of previous hydrodynamic modeling.

Particle transport model

To predict larval transport and settlement of ruffe and *Limnoperna* in Lakes Michigan and Erie, we applied a particle transport model previously used in the Great Lakes by Michalak et al. (2013) and Fraker et al. (2015). The model is of Lagrangian type, i.e. it tracks trajectories of particles representing fish larvae over time (Hofmann and Lascara, 1998). The three-dimensional particle trajectory code is based on the second order accurate horizontal trajectory code described in Bennett and Clites (1987), with the addition of vertical position tracking. Particles in the model are assumed to be neutrally buoyant and passive (follow the local currents). Particles remain in the near shore zone after collisions with model boundaries. Although we realize that in reality this collision may lead to some mortality, the details of the process, including larval mortality rate, are unknown, so we chose to ignore mortality due to any boundary-related causes (or mortality caused by any other reason for that matter), and our results should be treated as the

Please cite this article as: Beletsky, D., et al., Predicting spread of aquatic invasive species by lake currents, J. Great Lakes Res. (2017), http://dx.doi.org/10.1016/j.jglr.2017.02.001