



Predicting spread of aquatic invasive species by lake currents



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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 debalasting 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.

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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

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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

upper boundary of dispersal (i.e., worst case scenario from a management perspective). The model includes horizontal and vertical diffusion, both introduced via random-walk approach. Horizontal diffusion is based on the Smagorinsky parameterization (with non-dimensional coefficient of 0.005), while vertical diffusion was set to $5 \times 10^{-4} \text{ m}^2/\text{s}$. The particle model was previously compared with drifter data and qualitatively matched observed surface drift patterns (Beletsky et al., 2006).

Hourly advection fields used by the particle model were produced by the three-dimensional finite-difference hydrodynamic model based on the Princeton Ocean Model (Blumberg and Mellor, 1987). The model went through rigorous skill assessment during development of the Great Lakes Operational Forecast Systems (Chu et al., 2011) and several other applications that involved large observational data sets (Beletsky et al., 2013; Beletsky et al., 2012; Beletsky and Schwab, 2008; Beletsky and Schwab, 2001). The hydrodynamic model uses uniform 2 km horizontal grids with 20 vertical levels in Lake Michigan and 21 levels in Lake Erie. The Detroit and Niagara Rivers are the only rivers in the two lakes that have appreciable influence on lake currents at 2 km grid resolution and are both included in the Lake Erie model (Schwab et al., 2009). The Lake Michigan model does not have tributaries. We used six years (2002–2007) of available current data output for Lake Michigan and six years (2004–2005, 2007 and 2009–2011) of available current data for Lake Erie for particle transport model runs, while temperature output for the lakes was used to determine spawning times of ruffe and *Limnoperna*.

AIS introduction points and larval transport model parameters

To predict the movement of larvae via currents through Lakes Michigan and Erie, larvae were released in the larval transport model daily at the lake surface (0 m) where ballast exchange takes place (or where hatched larvae swim up from lake bottom). The release points were at river mouths, major commercial shipping ports, and sites 10 km offshore from these ports (hereafter rivers, ports and offshore). For offshore releases, each larva was released in the middle of a grid cell, and for ports and rivers, each larva was released 200 m off the water cell boundary with land. Ruffe are known to spawn in shallow depths (<20 m), (Pratt, 1988) of lakes, in estuaries, and in large rivers over similar types of habitat (Ogle, 1998). Thus, for in-depth analysis, we selected eight ports for each lake and eight river mouths that have large drainage areas (>80 km²). The minimum catchment size was chosen for pragmatic reasons, but also based on the assumption and field observations (ruffe eDNA surveys – in Tucker et al. (2016)) that small creeks with catchments below this size seemed unlikely to support populations of ruffe that could contribute substantial numbers of larvae to coastal areas (overall there are 64 rivers in Lake Michigan and 29 rivers in Lake Erie that fit the selected drainage area criterion).

To estimate the impact of spawning period duration on larval dispersal (see explanation below) we picked four river mouths around Lake Michigan that are located near ports, i.e. Escanaba, Kinnickinnic, Grand, and Pine Rivers (Fig. 1). The remaining four rivers were chosen from those located between ports to maximize spatial coverage. For Lake Erie (Fig. 2) we also encountered several cases where river mouths coincided with port locations (e.g. Detroit or Maumee River cases), but each such AIS introduction point was treated as either a river or a port (e.g. we selected Port Detroit rather than Detroit River, and Port Toledo rather than Maumee River) to maximize spatial coverage. The reason for releasing larvae 10 km offshore of each port (except for Port Detroit where both kinds of introduction points coincided because the port is located about 10 km upstream of the river mouth) is to capture release events associated with the practice of ship deballasting prior to arrival in ports (David Reid, St. Lawrence Seaway Development Corporation, personal communication).

To predict when and where larvae are likely to settle in Lakes Michigan and Erie based on our larval transport model, we derived estimates from the literature of several parameters, including spawning dates,

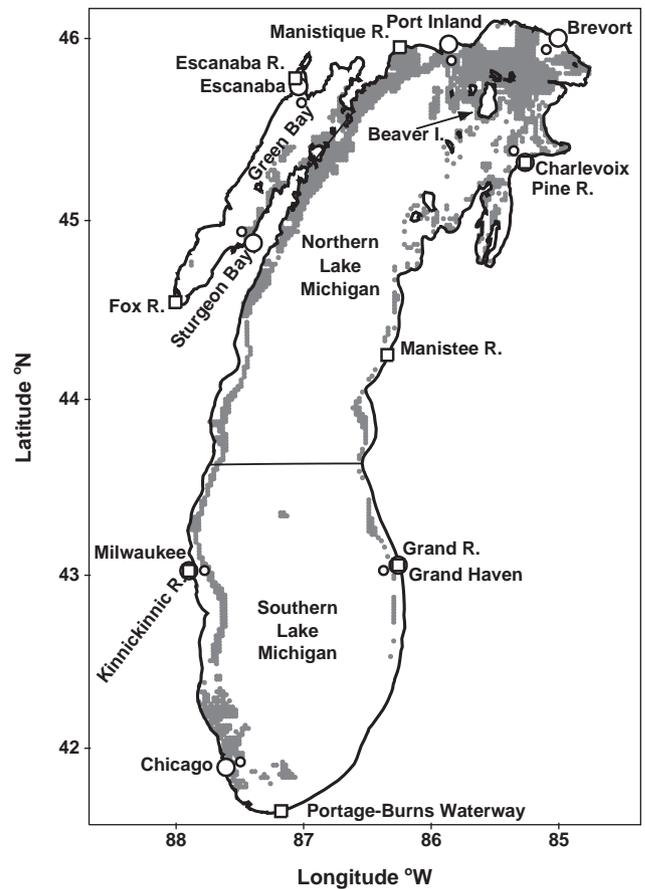


Fig. 1. Larval release locations in Lake Michigan: squares - rivers, large circles - ports, small circles - offshore. Hard substrate in areas <50 m deep is shown by gray shading.

days the larvae were in the drift, and the potential depth of settlement (Table 1). Larvae release time was dependent on published accounts of spawning temperatures for each species. To determine spawning dates for each species we used a time-series of bottom temperatures derived from multi-year average hydrodynamic model results (Beletsky et al., 2013; Beletsky and Schwab, 2001) for a variety of nearshore regions with depths ranging between 0 and 50 m with a 5 m increment. Although temperature varies between locations (and years) in each lake, in this study we use an identical release time in each lake for each species to ensure accurate comparison of dispersal across different release types (e.g. offshore versus nearshore). Analysis showed that for both species, the first two shallowest regions (0–5 and 5–10 m) covered the whole range of suitable spawning temperatures (Fig. 3). In particular, because temperatures in deeper (5–10 m) offshore areas warm up later than in shallow (0–5) nearshore areas, the spawning period for ruffe is extended, e.g. by about 20 days in Lake Michigan (Fig. 3a, Table 1). On the other hand, because temperatures in nearshore waters warm up in spring much faster in southern and shallow lakes than in northern and deep lakes, the spawning period for ruffe shortens; in Lake Erie the spawning period is shorter by about a month than in Lake Michigan (Fig. 3, Table 1). In addition, for *Limnoperna* we considered a scenario where larvae spawned in Lake Erie were transported to Lake Michigan via commercial vessel ballast exchange and released at Lake Michigan ports, essentially extending the natural spawning period (Fig. 3b, Table 1).

Although larval growth and development are temperature and prey dependent, a coupled biophysical model analysis was beyond the scope of this effort, so we chose to run simulations of larval dispersal using the maximum reported larval stage duration for each species. The pelagic

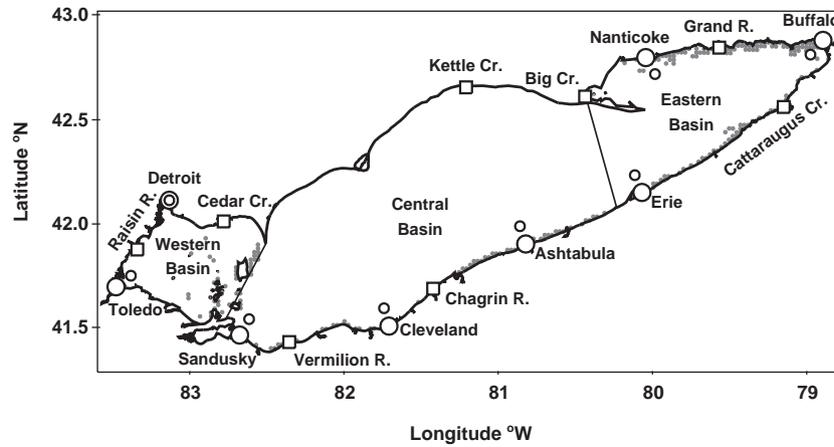


Fig. 2. Larval release locations in Lake Erie: squares - rivers, large circles - ports, small circles - offshore. Hard substrate in areas <50 m deep is shown by gray shading.

larval stage for ruffe can last up to 14 days (Brown et al., 1998), while *Limnoperna*'s pelagic phase is longer and can last up to 20 days ((Cataldo et al., 2005), Table 1). To assess dispersal distance and settlement, larval positions were tracked daily and larvae were considered settled if they were located within the settlement zone (i.e., the area between the coast and maximum settlement depth). For each drifting larva, multiple settlement locations were allowed throughout the drift period. Maximum settlement depth varied between species: 0–10 m for ruffe (Bauer et al., 2007) and 0–50 m for *Limnoperna* (T. Nalepa, personal communication) (Table 1). Data in Table 2 show calculated areas potentially available for settlement of ruffe and *Limnoperna* in both lakes. Calculations are based on bathymetric data in hydrodynamic model grids and maximum settlement depths of 10 and 50 m.

Substrate clipping (*Limnoperna* case)

Limnoperna veligers are known to settle on hard bottom substrates (Cataldo and Boltovskoy, 2000). To evaluate the potential effects of including substrate composition on *Limnoperna* spread, we compared model results with and without substrate composition as a modifying variable. Harmonized substrate composition data were derived for Lake Michigan and Lake Erie from the Great Lakes Aquatic Habitat Data (GLAHF; (Wang et al., 2015)). The substrate data for Lake Michigan were compiled from surveys conducted in the 1940s and 1980s. A composite map of substrate composition for Lake Michigan was created from two separate surveys of surficial sediments of Lake Michigan. For Lake Michigan south of Frankfort, a sediment survey map by Powers and Robertson (1968) essentially corroborated two earlier surveys by Hough (1935) and Ayers and Hough (1964). Sediment composition data for northern Lake Michigan were available from unpublished lake survey data of NOS-NOAA (Great Lakes Basin Framework Study 1976). A composite map was produced by overlaying the northern and

southern survey maps, and merging areas of like sediment type (http://gis.glin.net/ogc/services.php#lm_substclass_ifr, accessed 06/28/2016). Additional substrate data were available from Creque et al. (2010). For Lake Erie, substrate composition data were available from Thomas et al. (1976). Areas available for settlement of *Limnoperna* according to the criteria described above are shown for lakes Michigan (Fig. 1) and Erie (Fig. 2); numerical results are presented in Table 2.

Seasonal circulation patterns

In both lakes, circulation patterns and current speed have considerable seasonal variability thus impacting the dispersal patterns for ruffe and *Limnoperna*. We limit our discussion to the average surface circulation patterns during April–October (the period that spans larval drift in both lakes) because particles were released at the water surface and most of them tended to drift in the upper layer (0–20 m).

In Lake Michigan, circulation was weakest (<5 cm/s in most areas) in the spring and early summer seasons (Electronic Supplementary Material (ESM) Fig. S1) during periods of ruffe spawning, hatch and larval development. Lake-wide surface circulation was cyclonic (counter-clockwise) in spring (ESM Fig. S1, April panel), but by early summer (ESM Fig. S1, June panel), the pattern changed drastically and exhibited northerly currents along both coasts with relatively uniform eastward drift (Ekman transport) in the middle of the lake. During this period, anticyclonic (clockwise) circulation also began to develop in both the shallow southernmost and northernmost (Beaver Island area) parts of the lake. Beginning mid-summer, cyclonic circulation began to strengthen again due to deepening of seasonal thermocline and strengthening of nearshore-offshore (density related) pressure gradients (Beletsky et al., 2006). Overall current speed increased as well, especially towards the end of summer and fall (ESM Fig. S1, August and October panels), seasons important for dispersal of late spawners like *Limnoperna*. The

Table 1
Larval dispersal model parameters.

Species	Spawning temperature (°C)	Lake Michigan spawning period (days)	Lake Erie spawning period (days)	Drift time (days)	Settlement depth (m)
Ruffe	5–18 ^a	102 to 210 (mid-April to late July)	86 to 160 (late March to early June)	14	0–10
<i>Limnoperna</i>	16–28 ^b	170 to 275 ^c (mid-June to early October) 144 to 290 ^d (late May to mid-October)	144 to 290 (late May to mid-October)	20	0–50

^a Brown et al. (1998).
^b Cataldo and Boltovskoy (2000); Morton (1982); Xu et al. (2013).
^c Based on temperature and used for river mouths.
^d Using Lake Erie sources of *Limnoperna* larvae for ports and offshore ballast release locations.

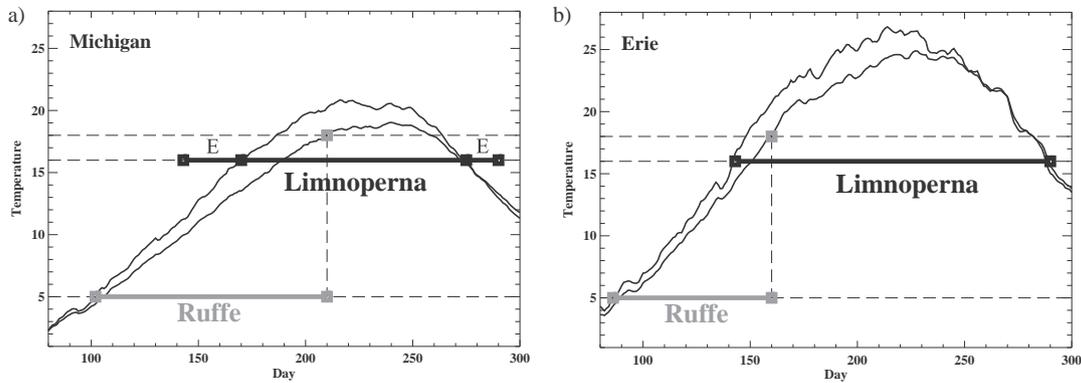


Fig. 3. Nearshore bottom temperature (multi-year average) in a) Lake Michigan, b) Lake Erie. Top curve is the 0–5 m region, bottom curve is the 5–10 m region. Thick black line – spawning period of *Limnoperna*, thick gray line – spawning period of ruffe. “E” indicates extended release period (port-related cases) of *Limnoperna* in Lake Michigan (see explanations in text).

typical speed of surface currents was 5–10 cm/s. In southern and middle Lake Michigan, circulation patterns tended to be cyclonic in the deep area but anticyclonic in the shallow nearshore areas (Beletsky and Schwab, 2008; Beletsky et al., 2006). Interestingly, because the southern anticyclonic gyre is rather narrow, in some areas nearshore currents are southward but turn northward a short distance offshore, providing conditions for contrasting dispersion patterns for nearshore and offshore release locations.

Seasonal circulation in Lake Erie had some notable differences from that in Lake Michigan. One area of the lake where circulation is rather stable on monthly or longer time scales is its shallow western basin where eastward flow is driven to a large extent by the Detroit River (ESM Fig. S2). In other basins, circulation was weak (<5 cm/s) in spring (period most pertinent for larval ruffe transport), with strongest eastward flows along the south coast in the central basin and along both north and south coasts in the eastern basin (ESM Fig. S2, April panel), while weak southerly flow was present offshore in the central basin. Lake circulation intensified by early summer (when *Limnoperna* begins spawning), with strong eastward coastal flows in the central basin and broad eastward flow in the eastern basin (ESM Fig. S2, June panel). By late summer (ESM Fig. S2, August panel) the whole central basin and most of the eastern basin were covered by strong (~10 cm/s) anticyclonic circulation (Beletsky et al., 2013). The remnants of this anticyclonic circulation are seen in most areas of the lake in the fall (ESM Fig. S2, October panel) but cyclonic circulation in the deepest part of the eastern basin became more pronounced.

Metrics used

To compare spread of larvae from different locations and between species, we employed several different metrics: settlement success, dispersal distance, settlement area and probability of settlement. Dispersal distance (km) for each release location was defined as the ensemble-average distance to daily positions of all released larvae (both that settled and not) during the allowed drift time (14 days for ruffe, 20 days for *Limnoperna*). Maximum distance (km) for each release location was defined as maximum of all distances to daily positions of all released larvae during the allowed drift time. Settlement area (%) originated from individual release location was defined as the number of grid cells (in

the 2 km × 2 km bathymetric grid of hydrodynamic model) within the settlement zone occupied by larvae divided by the total number of grid cells in the lake-wide settlement zone. In a sense, settlement area is an indicator of the relative importance of a particular introduction point for larval dispersal. The total settlement area (in either % or km²) then determines cumulative settlement from all release locations (with potentially overlapping individual settlement areas). Settlement success (%) is the number of daily releases resulting in settlement divided by the total number of release days. To calculate probability of larvae settlement in a particular grid cell within a settlement zone resulting from an individual release site, the number of larvae passing through that cell (first time only for each particle trajectory) is divided by the total number of larvae released from this site. Differences among source areas and species in settlement success, settlement area and dispersal distance were compared using ANOVA, or Wilcoxon non-parametric tests if assumptions of data normality and homogeneity of variance were violated. Differences were considered significant at the alpha ≤0.05 level.

Although we report settlement success results for all cases for completeness, we only apply statistical analysis for offshore release cases. The reason is that in reality, both ruffe and *Limnoperna* larvae released on the lake coast should be considered settled by the definition we adopted because their release depth (whether port or river) is already within the settlement zone depth range (at least 10 m), so settlement success should be 100% for all nearshore points. Because horizontal resolution in the model does not allow very precise description of the nearshore zone in areas of steep bathymetric gradients, in some nearshore locations (mostly in Lake Michigan) the depth of the releasing cell is over 10 m and settlement success is <100% in a few cases.

Results

Larval dispersal

In general, the larval transport model indicated that larval dispersal for both ruffe and *Limnoperna* would result in high levels of settlement for both Lakes Michigan and Erie (Tables 3 and 4). At the same time, maximum distances traveled by larvae varied greatly depending on release location, ranging from <1 km to tens of kilometers and in some

Table 2

Total surface area and areas (km²) available for settlement for ruffe (depth < 10 m) and *Limnoperna* (depth < 50 m) in Lakes Michigan and Erie.

Lake	Surface area	Settlement area for ruffe	Settlement area for <i>Limnoperna</i>	Settlement area for <i>Limnoperna</i> , substrate clipped
Michigan	57,750	4420	20,644	8040
Erie	25,657	4964	25,332	968

Table 3

Modeled larval dispersal from release sites in Lake Michigan. Dispersal distance and settlement success is an average of six individual years (no averaging of maximum distance). Settlement area is a combined settlement area from six individual years (with overlap). H-depth of release location in model. Ruffe larvae: D_R – dispersal distance, MD_R – maximum distance, A_R – settlement area, S_R – settlement success. *Limnoperna* larvae: D_L – dispersal distance, MD_L – maximum distance, A_L – settlement area, S_L – settlement success. A_{LC} – settlement area clipped by substrate; S_{LC} – settlement success clipped by substrate.

Source type	Site	H (m)	D_R (km)	MD_R (km)	A_R (%)	S_R (%)	D_L (km)	MD_L (km)	A_L (%)	S_L (%)	A_{LC} (%)	S_{LC} (%)
			Ruffe				<i>Limnoperna</i>					
River	Portage-Burns	9.0	14.2	96.0	6.5	100.0	26.1	204.6	21.0	100.0	4.1	40.1
River	Kinnickinnic	8.0	14.4	133.3	6.2	100.0	33.1	153.1	11.3	100.0	4.3	74.8
River	Fox	5.0	4.1	41.2	9.0	100.0	6.2	65.0	3.5	100.0	0.0	0.2
River	Escanaba	7.0	5.4	96.1	9.1	100.0	7.9	92.6	9.2	100.0	1.9	8.0
River	Manistique	5.0	13.1	98.5	6.9	100.0	20.4	173.6	15.0	100.0	11.6	99.4
River	Pine	27.0	6.6	55.6	1.3	17.9	10.1	157.9	7.1	100.0	4.9	89.5
River	Manistee	6.0	13.5	119.1	3.8	100.0	25.6	151.7	5.3	100.0	1.4	62.7
River	Grand	12.0	21.8	168.8	6.6	89.8	32.8	273.8	11.7	100.0	1.8	62.6
8 rivers average		9.9	11.6	101.1	6.2	88.5	20.3	159.0	10.5	100.0	3.8	54.7
8 rivers combined (with overlap)					49.0				71.6		25.5	
Port	Chicago	5.0	16.7	127.2	10.0	100.0	26.3	216.0	22.2	100.0	4.9	100.0
Port	Milwaukee	8.0	14.4	145.8	6.0	100.0	30.7	156.2	13.0	100.0	4.8	73.4
Port	Sturgeon Bay	8.0	9.9	95.8	8.0	100.0	12.1	119.9	12.2	100.0	3.3	100.0
Port	Escanaba	16.0	9.4	77.4	11.7	98.6	11.3	138.6	13.3	100.0	4.0	20.6
Port	Port Inland	5.0	15.5	93.9	13.8	100.0	22.5	154.7	22.7	100.0	16.6	99.5
Port	Brevort	5.0	10.5	84.6	12.7	100.0	11.7	80.8	13.5	100.0	9.0	81.1
Port	Charlevoix	27.0	6.7	48.9	1.9	19.9	9.6	132.2	7.8	100.0	5.5	88.1
Port	Grand Haven	12.0	21.7	182.4	6.8	89.1	32.4	277.2	13.2	100.0	1.8	58.5
8 ports average		10.8	13.1	107.0	8.8	88.5	19.6	159.4	14.7	100.0	6.2	77.7
8 ports combined (with overlap)					62.4				84.7		32.9	
Offshore	Chicago - 10 km	14.0	21.0	138.0	11.1	59.3	31.7	240.3	24.3	100.0	4.8	84.1
Offshore	Milwaukee - 10 km	38.0	26.1	139.8	8.1	57.6	44.6	156.3	16.4	100.0	5.6	100.0
Offshore	Sturgeon Bay - 10 km	25.0	14.5	85.2	15.4	77.5	17.3	118.7	15.4	100.0	4.4	100.0
Offshore	Escanaba - 10 km	18.0	14.6	81.0	13.8	93.7	18.7	205.2	17.7	100.0	6.2	48.5
Offshore	Port Inland - 10 km	46.0	18.5	128.0	12.9	55.2	26.7	226.0	24.4	100.0	17.9	100.0
Offshore	Brevort - 10 km	17.0	15.4	85.3	14.9	76.9	17.7	120.2	17.6	100.0	12.1	96.7
Offshore	Charlevoix - 10 km	26.0	12.0	54.4	2.2	26.3	17.3	184.2	11.1	100.0	8.2	100.0
Offshore	Grand Haven - 10 km	62.0	32.2	156.2	6.0	67.9	45.7	266.4	11.8	94.3	2.0	68.9
8 offshore average		30.8	19.3	108.5	10.5	64.3	27.5	189.7	17.3	99.3	7.7	87.3
8 offshore combined (with overlap)					74.3				88.6		34.2	

cases over 100 km. Highest maximum distance among all release sites in Lake Michigan reached 182 km for ruffe and 277 km for *Limnoperna*, in both cases released from Port Grand Haven (Table 3). In Lake Erie, maximum distance reached 151 km for ruffe and 241 km for *Limnoperna*, released offshore Ashtabula and Sandusky respectively (Table 4). The lowest maximum distance in both lakes (only 0.4 km for both species) was predicted for Port Buffalo in Lake Erie where most released larvae drifted into the Niagara River. In Lake Michigan, the lowest maximum distance was predicted for semi-enclosed Green Bay (when larvae were released from the Fox River site) and was 41 km for ruffe and 65 km for *Limnoperna*.

The direction of spread varied between lakes, species, and among release locations. In Lake Michigan (Fig. 4), dispersal of both species' larvae was bi-directional (and quite symmetric in both alongshore directions at northernmost locations like Manistique, Port Inland and Brevort) although in most areas one direction was dominant owing to a tendency for general cyclonic circulation (ESM Fig. S1). Drift of both species' larvae released in Green Bay was mostly confined to Green Bay although some larvae (especially *Limnoperna*) were able to drift into the northern basin of Lake Michigan.

In Lake Erie (Fig. 5), ruffe larvae released from Detroit and Toledo drifted southeast and northeast respectively. While ruffe larvae from release points on the south shore drifted primarily eastward reflecting prevailing spring surface circulation (ESM Fig. S2, April panel), larvae released on the north shore exhibited more bi-directional drift. Aside from a unidirectional spread from Detroit, *Limnoperna* dispersal from nearshore locations was generally bi-directional although eastward direction was dominant. Dispersal from offshore locations in the central basin was strongly affected by the presence of an anticyclonic gyre (Fig. S2).

Comparative analysis of settlement success, distance and area

We next present quantitative analysis of the differences in dispersal between 1) lakes, 2) species, and 3) nearshore and offshore release locations. In this quantitative analysis we used model results for six individual years for each individual site to retain interannual variability rather than using multi-year average data on dispersal distance and settlement success or six-year combined settlement areas (reported in Tables 3 and 4, Figs. 4 and 5).

Each species had similar rates of settlement success, distance spread and area settled in both lakes. We note that *Limnoperna* settlement success was 100% everywhere except at a single offshore release location in Lake Michigan where depth of release point was >50 m (% settlement = 94.3%, Table 3). The annual dispersal distances in the two lakes ranged from 0.2 km to 71.3 km with a statistically significant higher mean dispersal distance of 18.6 km (averaged over species and sites) in Lake Michigan compared to 16.1 km in Lake Erie ($p < 0.004$, $F_{1,575} = 8.610$). Annual settlement areas of larvae (averaged across individual release sites) were similar ($p = 0.11$, $F_{1,575} = 2.53$) in both lakes (6.2% for Lake Erie compared to 6.2% in Lake Michigan), as were settlement success rates ($p = 0.126$, $F_{1,575} = 2.346$) (Lake Erie = 92.8%; versus 90.1% in Lake Michigan).

In general, *Limnoperna* had larger dispersal distances, settlement area, and settlement success compared to ruffe. Mean settlement success for offshore locations was higher for *Limnoperna* than for ruffe ($99.9 \pm 0.1\%$ vs $83.0 \pm 1.6\%$, respectively) ($p < 0.0001$, $X^2 = 123.282$, d.f. = 1) (averaged over lakes and release sites). Annual distance traveled by *Limnoperna* was higher than ruffe ($p < 0.0001$, $X^2 = 43.695$, d.f. = 1) with mean dispersal distances of 20.4 ± 0.7 km and 14.2 ± 0.4 km respectively. Annual settlement area (averaged across individual

Table 4
Modeled larval dispersal from release sites in Lake Erie. Dispersal distance and settlement success is an average of six individual years (no averaging of maximum distance). Settlement area is a combined settlement area from six individual years (with overlap). H-depth of release location in model. Ruffe larvae: D_R – dispersal distance, MD_R – maximum distance, A_R – settlement area, S_R – settlement success. *Limnoperna* larvae: D_L – dispersal distance, MD_L – maximum distance, A_L – settlement area, S_L – settlement success. A_{LC} – settlement area clipped by substrate; S_{LC} – settlement success clipped by substrate.

Source type	Site	H (m)	D_R (km)	MD_R (km)	A_R (%)	S_R (%)	D_L (km)	MD_L (km)	A_L (%)	S_L (%)	A_{LC} (%)	S_{LC} (%)
			Ruffe		<i>Limnoperna</i>							
River	Cedar	4.1	5.8	54.8	12.3	100.0	12.7	194.3	17.2	100.0	0.4	15.2
River	Raisin	3.0	7.6	51.1	26.0	100.0	10.9	101.4	8.9	100.0	0.3	5.8
River	Vermilion	5.8	17.7	134.2	4.8	100.0	18.7	175.3	18.7	100.0	0.6	100.0
River	Chagrin	8.0	13.9	111.8	3.1	100.0	15.4	154.8	20.1	100.0	0.7	29.7
River	Cattaraugus	4.4	7.0	41.8	2.9	100.0	9.6	107.5	10.9	100.0	1.0	100.0
River	Grand	10.0	17.8	64.6	8.8	100.0	22.1	101.7	16.2	100.0	1.8	94.1
River	Big	3.0	2.5	98.6	3.1	100.0	2.7	72.9	1.9	100.0	0.0	0.3
River	Kettle	8.1	18.3	142.3	6.9	100.0	34.1	180.6	32.4	100.0	0.1	0.8
8 rivers average		5.8	11.3	87.4	8.5	100.0	15.8	136.1	15.8	100.0	0.6	43.2
8 rivers combined (with overlap)					64.5				85.9		3.4	
Port	Detroit	3.4	26.7	76.7	35.1	100.0	31.1	140.0	13.3	100.0	0.5	32.2
Port	Toledo	3.0	6.9	50.2	15.7	100.0	4.4	56.8	3.7	100.0	0.1	0.5
Port	Sandusky	3.0	5.1	72.8	6.0	100.0	10.5	216.4	17.1	100.0	0.6	26.0
Port	Cleveland	7.0	11.2	98.3	4.0	100.0	15.2	158.0	18.5	100.0	0.6	52.3
Port	Ashtabula	10.1	16.8	129.8	5.0	88.2	23.2	180.5	21.9	100.0	1.0	100.0
Port	Erie	4.1	8.8	98.4	3.1	100.0	11.3	147.6	15.6	100.0	0.8	58.4
Port	Buffalo	5.1	0.2	0.4	0.1	100.0	0.2	0.4	0.0	100.0	0.0	100.0
Port	Nanticoke	7.4	13.8	91.2	11.1	100.0	18.4	95.5	16.2	100.0	1.5	91.4
8 ports average		5.4	11.2	77.2	10.0	98.5	14.3	124.4	13.3	100.0	0.6	57.6
8 ports combined (with overlap)					68.5				68.2		3.5	
Offshore	Detroit - 10 km	3.4	26.7	76.7	35.1	100.0	31.1	140.0	13.3	100.0	0.5	32.2
Offshore	Toledo - 10 km	3.0	8.6	60.3	25.2	100.0	8.0	69.1	6.5	100.0	0.3	3.2
Offshore	Sandusky - 10 km	12.0	17.7	94.9	9.5	53.8	27.1	240.7	31.0	100.0	0.7	29.1
Offshore	Cleveland - 10 km	16.1	23.6	133.4	4.5	34.7	28.9	182.2	35.2	100.0	0.8	21.8
Offshore	Ashtabula - 10 km	20.2	16.9	151.0	4.2	22.4	37.1	163.9	37.6	100.0	0.9	22.0
Offshore	Erie - 10 km	19.4	28.5	123.8	4.7	34.7	31.2	199.6	32.1	100.0	1.6	42.0
Offshore	Buffalo - 10 km	15.7	8.4	17.4	2.6	99.8	9.0	127.7	1.4	100.0	0.3	99.7
Offshore	Nanticoke - 10 km	21.6	19.1	93.6	6.8	20.9	28.6	113.2	25.6	100.0	2.1	38.7
8 offshore average		13.9	18.7	93.9	11.6	58.3	25.1	154.6	22.9	100.0	0.9	36.1
8 offshore combined (with overlap)					71.2				87.9		3.7	

release sites) for *Limnoperna* in the two lakes was larger than for ruffe ($p < 0.0001$, $F_{1, 575} = 51.896$; 7.9 ± 0.3 versus $5.2 \pm 0.3\%$, respectively).

When comparing release locations, offshore sites had the highest dispersal distances, highest percent area of settlement, but lowest levels of settlement success. Although offshore sites had lower settlement success rates (Wilcoxon Test: $\chi^2 = 101.717$, d.f. = 2), the average (over lakes and species) annual distances that the larvae traveled when released offshore was approximately 55% larger (22.6 km) than releases in rivers (14.8 km) or ports (14.5 km) ($p < 0.0001$, $F_{2, 575} = 44.995$). Similarly, releases at offshore sites resulted in an average 47% larger annual settlement area from individual sites being settled (8.3%) compared to the rivers (6.2%) and ports (5.2%) ($p < 0.0001$, $F_{2, 575} = 23.923$).

Probability distributions

Although simulated dispersal by lake currents resulted in large areas covered by larvae (especially for *Limnoperna*), the concentration of larvae varied substantially between different areas. Therefore, it is useful to analyze spatial differences using the probability of settlement calculated for each release site (Figs 6 and 7). Probability of settlement is 100% at the source and often close to 100% near it, but dispersal (especially in multiple directions) leads to quick reductions in concentration of larvae, and hence lower probability values can be observed just 5–10 km away.

Because currents near shore are essentially bi-directional, the probability of settlement near a port or river source is relatively high in the alongshore direction and drops quickly in the offshore direction. For example, the probability of *Limnoperna* larvae released from Grand River, Lake Michigan to drift south or north is equally high (Fig. 6d); but at a location farther north (Manistee) where currents are more uniform in direction (primarily northward), the probability of larvae spreading north is several times higher than the probability of spreading south.

At offshore release locations, currents are more omni-directional (Beletsky et al., 2006) and dispersal is more effective, which is why the probability of larval settlement for release offshore Chicago was much lower than that of release in the port of Chicago itself (Fig. 6e and f).

In Lake Erie (Fig. 7), the fairly stable and unidirectional flow of Detroit River water in the western basin leads to extended areas of high settlement probability from the Detroit port and Cedar River for both species, spreading south-east and east to the middle of the western basin and central basin respectively. In the central basin, the probability is high that *Limnoperna* would settle east of Vermilion River (Fig. 7d), Ports Ashtabula and Erie (Fig. 7e) while larvae are more likely to settle west from offshore Ashtabula and Cleveland transported by the anticyclonic basin-scale gyre (Fig. 7f).

Interannual variability

Geographic patterns produced by settled larvae varied between individual years (not shown) due to interannual variability in circulation patterns, resulting in substantially higher 6-year cumulative settlement areas (Tables 3 and 4; Figs. 4 and 5) compared with that of any individual year (Figs. 8 b, e; and 9 b, e). At the same time, there were no statistically significant differences among years in dispersal distance, settlement area (which does not take into account geographic patterns of settlement) or settlement success in either lake or both lakes combined for either species. Settlement success of ruffe from offshore locations (Table 5) varied more in Lake Erie (53–66%) than in Lake Michigan (62–67%).

In Lake Michigan, the largest variability in dispersal distance among years for both ruffe and *Limnoperna* was observed for offshore releases (Fig. 8a and d), where the ratio of maximum to minimum distances

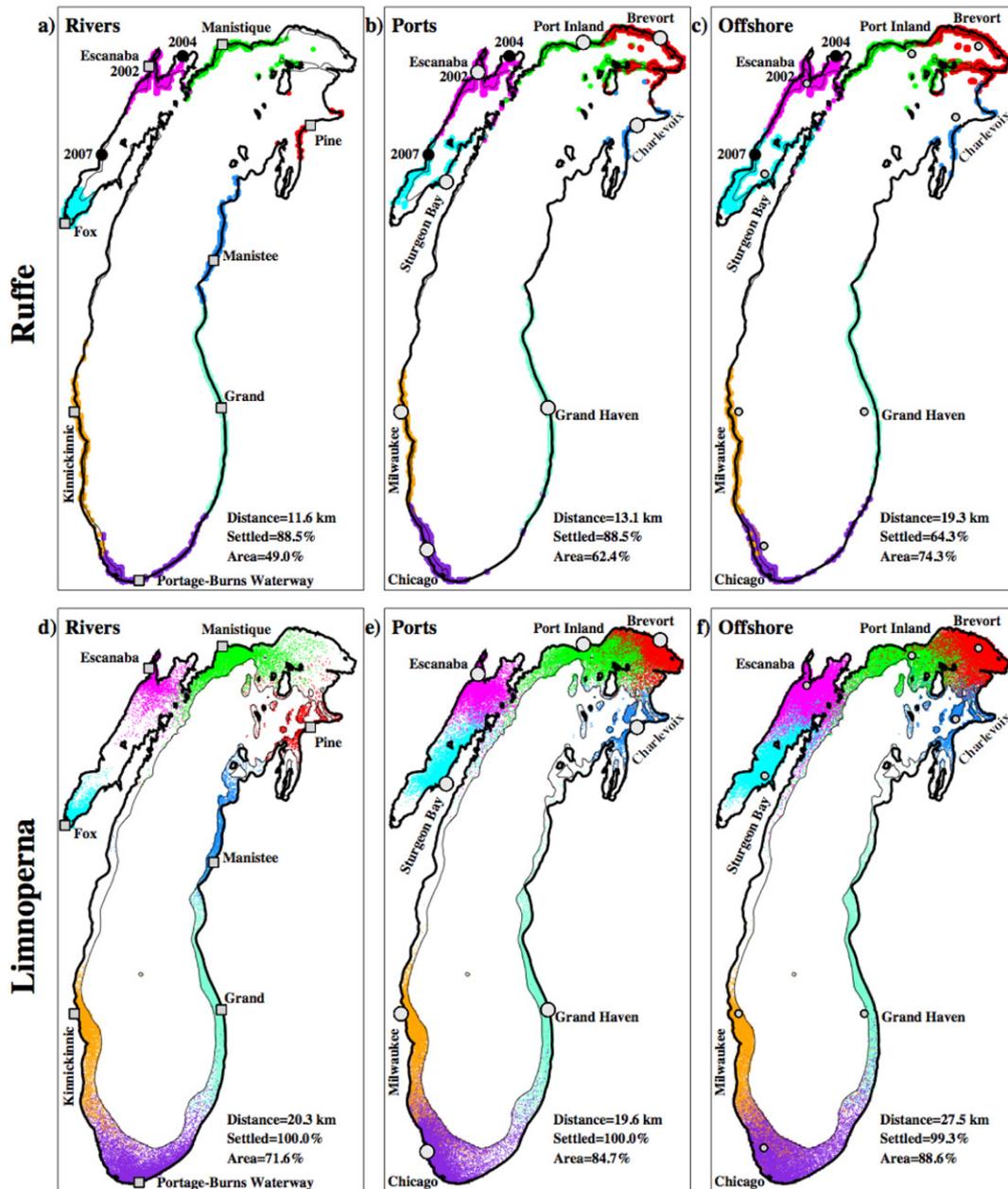


Fig. 4. Modeled larvae dispersal in Lake Michigan (daily positions within settlement zone) from individual sites (color coded) during six release years. Top row – ruffe dispersals assuming larvae release locations at a) rivers, b) ports, and c) offshore. The 10 m isobath is shown. Bottom row – *Limnoperna* dispersals assuming larvae release locations at d) rivers, e) ports, and f) offshore. The 50 m isobath is shown. Particle size is increased in case of ruffe to enhance visibility. Black filled circles: ruffe sightings in Lake Michigan in different years (Bowen and Keppner, 2013).

reached 122 and 148%, respectively (Table 6). Variability in settlement area was not pronounced for either species (Fig. 8b and e, Table 6).

In Lake Erie, the largest interannual variability in dispersal distances for ruffe larvae was for port releases (Fig. 9a) and for *Limnoperna* was for offshore releases (Fig. 9d) where the ratio of maximum to minimum distances reached 130% and 129%, respectively (Table 6). Variability in settlement area was more pronounced for ruffe than for *Limnoperna* in Lake Erie: the ratio of maximum to minimum areas reached 133% for ruffe (offshore releases, Fig. 9b) and 122% for *Limnoperna* (offshore releases, Fig. 9e) respectively.

Impact of increased spawning time

While an increase in spawning period duration does not necessarily increase dispersal distance, it may increase settlement area. For

example, results for *Limnoperna* spread in Lake Michigan show that settlement areas originating from four ports (Milwaukee, Grand Haven, Charlevoix and Escanaba) were generally higher than those from four adjacent (nearly co-located) rivers (Table 3). However, repeated calculations of settlement areas for all eight port locations in Lake Michigan that used shortened release times (matching rivers) revealed that while settlement area was slightly higher for ports the result was not statistically significant ($p > 0.65$, $F_{1,15} = 0.21$).

Regional settlement characteristics

To explore regional differences in settlement patterns (e.g. to locate preferred settlement zones in a lake) we calculated total settlement areas for the three major basins in each lake: south, north and Green Bay basins in Lake Michigan (Fig. 1) and west, central and east basins

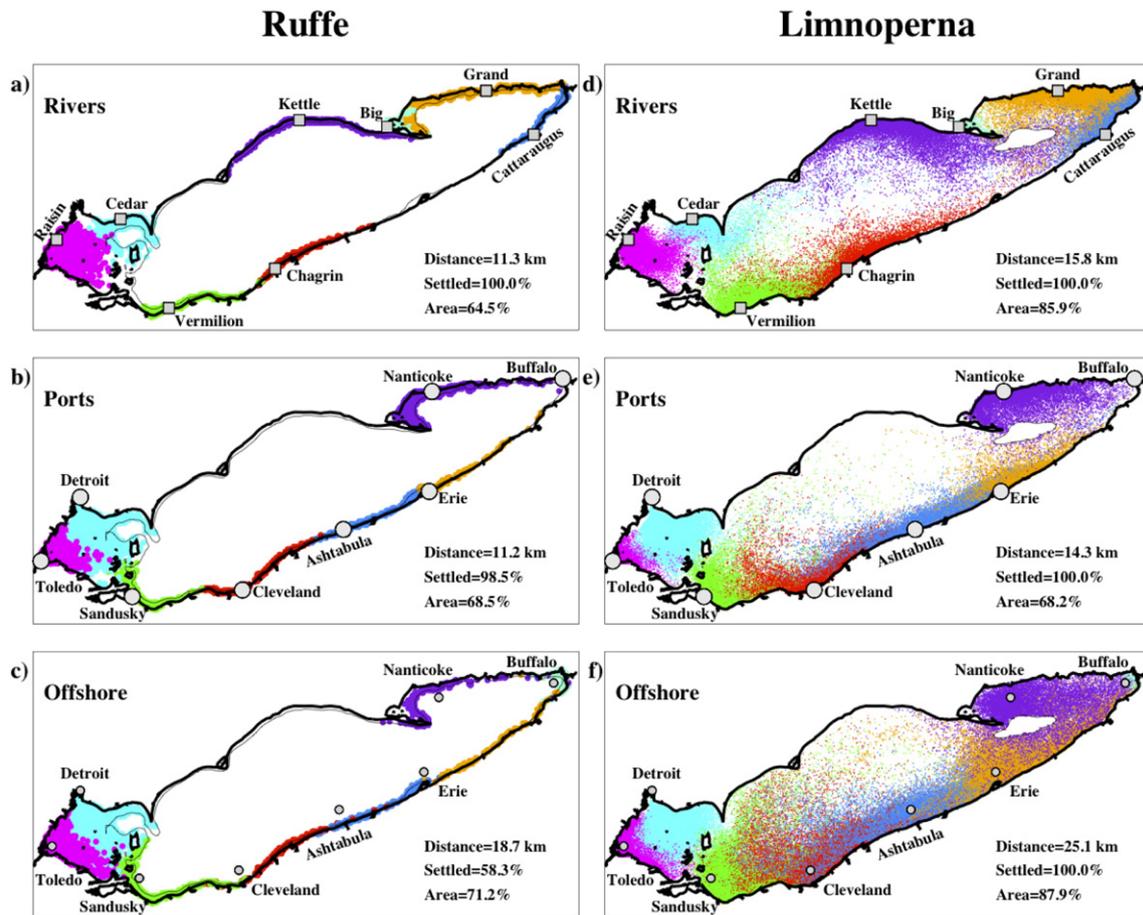


Fig. 5. Modeled larva dispersal in Lake Erie (daily positions within settlement zone, first 36 h are added for Detroit) from individual sites (color coded) during six release years. Left column – ruffe dispersals assuming larva release locations at a) rivers, b) ports, and c) offshore. The 10 m isobath is shown. Right column – *Limnoperna* dispersals assuming larva release locations at d) rivers, e) ports, and f) offshore. The 50 m isobath is shown. Particle size is increased in case of ruffe to enhance visibility.

in Lake Erie (Fig. 2). Regional differences in settlement patterns were quite pronounced in each lake. In Lake Michigan (Fig. 10), most suitable areas for ruffe settlement (depth-wise) are in the northern basin (42%), followed by Green Bay (35%) and the southern basin (24%). This distribution pattern was only seen in ruffe releases offshore, but not in other release types. While results for ports also showed the largest settlement area in the north basin, settlement area in the southern basin was larger than in Green Bay. For rivers, the northern basin had the smallest settlement area while settlement areas in Green Bay and southern basin were about the same. For *Limnoperna*, the northern basin also has the largest available settlement area (45%), followed by the southern basin (34%) and Green Bay (21%). This distribution was repeated in both port and offshore cases. For *Limnoperna* released in rivers, there was a gradual increase in settlement area from Green Bay to the northern basin and a peak in the southern basin.

Differences among basins in available settlement areas were more pronounced in Lake Erie (Fig. 11) than in Lake Michigan (Fig. 10). For *Limnoperna* (Fig. 11), the largest available settlement area was many times larger than the smallest available area. Lake Erie's central basin has the largest area of depths suitable for *Limnoperna* settlement (65%), followed by the eastern and western basins (23 and 12%, respectively). This distribution was clearly reflected in dispersal results from both nearshore and offshore sites. For ruffe, 56% of suitable habitat (depth-wise) was found in Lake Erie's western basin, followed by only 24 and 20% of suitable habitat in the central and eastern basins, respectively. This larger proportion of suitable habitat in the western basin was clearly reflected in the predicted settlement areas across all releases types. Although available settlement area is smaller in the eastern basin

than in the central basin, the model predicted either equal or even larger (e.g., in case of ports) settlement area there.

Comparison with observations

The existing comparable observations of larval spread of either ruffe or *Limnoperna* in our lakes of interest are collections of ruffe in Green Bay, Lake Michigan, first sighted in Escanaba, MI (Fig. 1) in 2002, and of quagga mussel (as a proxy for *Limnoperna*) in Lake Michigan from 1997 to 2005, reported by Nalepa et al. (2010, 2014). We compared model predictions of ruffe larvae drift from the port of Escanaba (and offshore) in 2002 and 2003 with subsequent observations of ruffe in Big Bay de Noc, east of Escanaba in 2004, and near Marinette, WI, south of Escanaba in 2007 (Fig. 12). Model results show that ruffe larvae drifted south and east from Escanaba in both years and reached the vicinity of Big Bay de Noc in both years (especially in offshore releases) and Marinette in 2003 when dispersal was stronger, matching observations in 2004 and 2007. Moreover, lack of ruffe sightings between Escanaba and Marinette can be explained by the possible transport of ruffe larvae by lake currents from source to infested area in a single year.

Similar comparisons between modeled transport of *Limnoperna* larvae from ports, offshore locations and rivers in northeast Lake Michigan to the southern basin and observed spread of quagga mussels from 1997 to 2005 (Nalepa et al., 2014; Nalepa et al., 2001) suggest that larvae could spread quickly from north to south down either coastline. We ran annual simulations of quagga mussel dispersal (with appropriately adjusted spawning period, drift time and settlement depth) starting from their 1997 introduction in northeast Lake Michigan (Nalepa

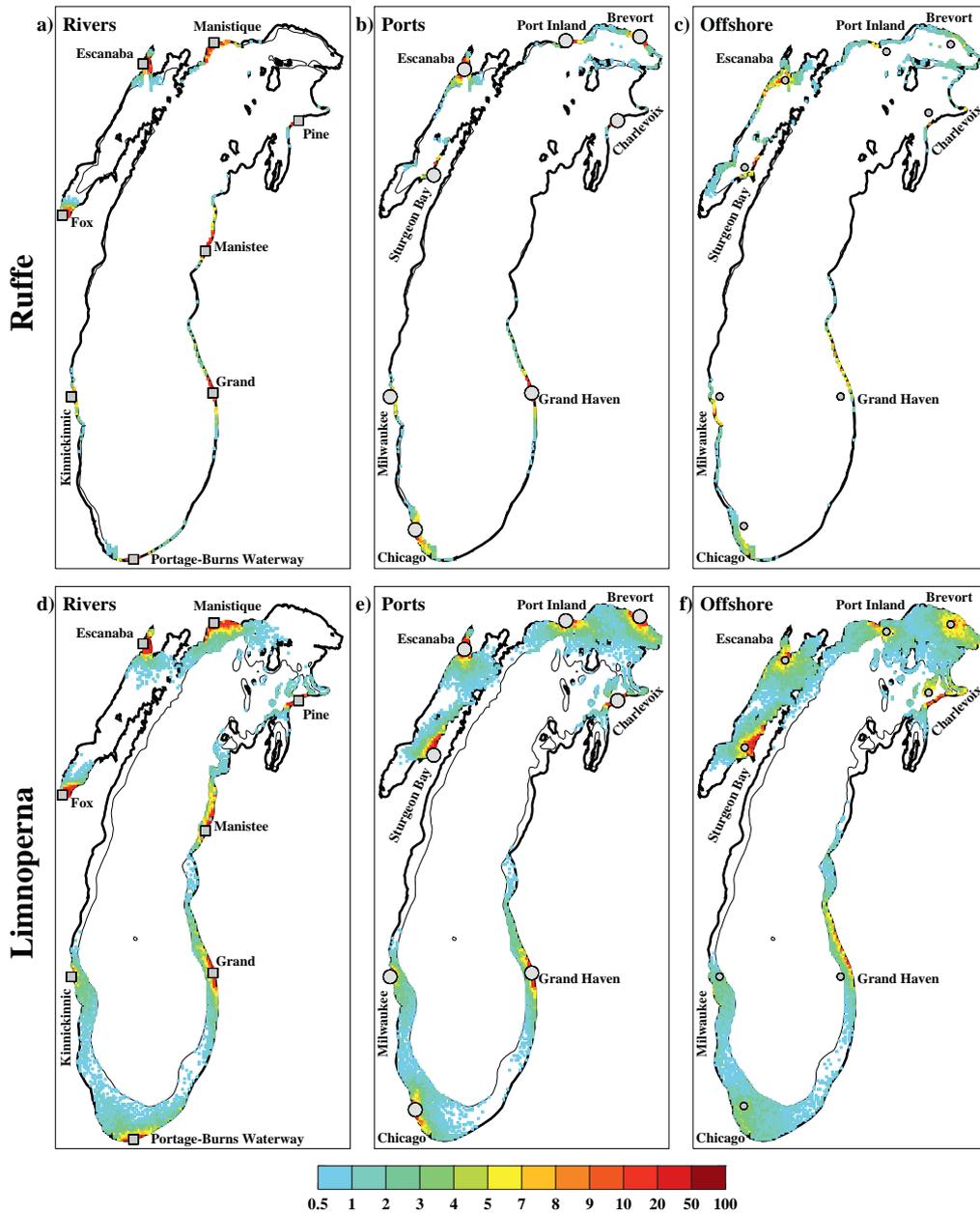


Fig. 6. Probability of settlement in Lake Michigan during six release years (juxtaposition of probability maps calculated for each release site). Top row – ruffe dispersals assuming larvae release locations at a) rivers, b) ports, and c) offshore. The 10 m isobath is shown. Bottom row – *Limnoperna* dispersals assuming larvae release locations at d) rivers, e) ports, and f) offshore. The 50 m isobath is shown.

et al., 2001). For each annual simulation, starting from 1998 (the earliest year for which hydrodynamic model results were available from Beletsky and Schwab (2008)), we predicted spread during the April–November spawning period (Nalepa et al., 2010) using 30 day drift time. No restriction on settlement depth was made as live quaggas were found in Lake Michigan at 207 m depth (Nalepa et al., 2014). To increase spatial coverage, we used in simulation most of the original 64 rivers along with ports and offshore locations since their depth was below the maximum depth (93 m) where quaggas were reported spawning in Lake Michigan (Glyshaw et al., 2015). The number of release points increased from year to year as we sequentially added points on the west and east coasts based on the spread of the previous year’s simulation results (ESM Fig. S3). After the first two years of simulation (by 2000) the model somewhat overestimated observed spread to the west (Fig. 13, upper panel), and the list of release points was reduced. Propagation along the east coast was slow due to an opposing

northward current and much faster along the west coast where southward flowing current assisted the spread (Fig. 13). By 2002, quagga mussel veligers spread down Lake Michigan’s western shore to Chicago, and mussels subsequently began to colonize southeastern Lake Michigan. Overall, model results show that mussel veligers could easily have spread south after initial introduction in the north in 1997, and by 2005, quagga mussel was predicted to cover all of Lake Michigan, matching observations (Nalepa et al., 2014).

Effects of substrate on Limnoperna settlement

Limnoperna’s preference for settling on hard substrate greatly reduced its potential settlement area and success. In Lake Michigan, the hard substrate preferred by *Limnoperna* is available in about 39% of depth-suitable grid cells (Fig. 1), resulting in a 61% reduction in potential settlement area (Table 2). In Lake Erie, hard substrate is available

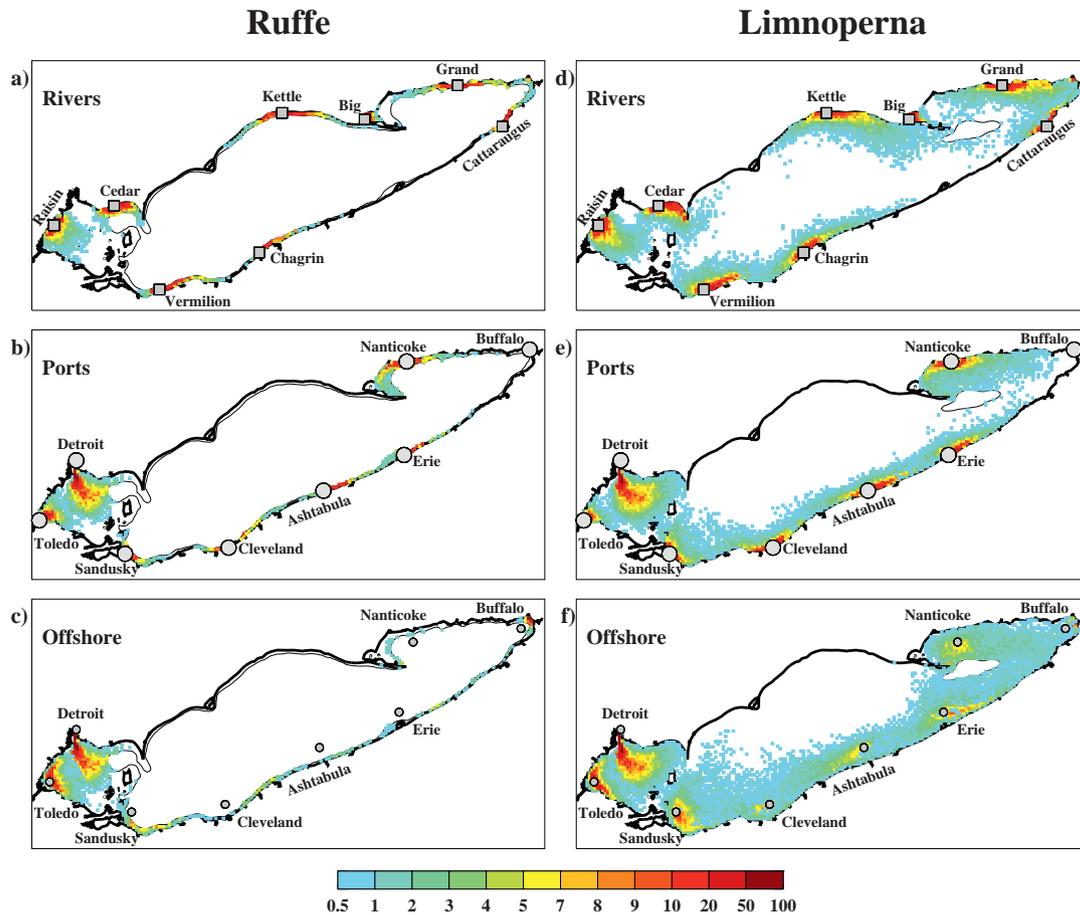


Fig. 7. Probability of settlement in Lake Erie during six release years (juxtaposition of probability maps calculated for each release site). Left column – ruffe dispersals assuming larvae release locations at a) rivers, b) ports, and c) offshore. The 10 m isobath is shown. Right column – *Limnoperna* dispersals assuming larvae release locations at d) rivers, e) ports, and f) offshore. The 50 m isobath is shown.

in only about 4% of depth-suitable grid cells (Fig. 2), resulting in a 96% settlement area reduction (Table 2). Compared to simulations that assumed *Limnoperna* settled with no substrate preference, simulations that assumed *Limnoperna* prefer settling on hard substrate in Lake Michigan resulted in *Limnoperna* being virtually eliminated from Green Bay and a coastal section north of Milwaukee, and between Chicago and Grand Haven (ESM Fig. S4). The reduction in modeled settlement area of 61–64% across various release types (Table 3) practically mirrored the reduction in total available settlement area. Settlement success also was reduced, from nearly 100% to 55% for rivers, 78% for ports and 87% for offshore releases (Table 3).

In Lake Erie, incorporation of hard substrate into the analysis reduced *Limnoperna* settlement to the area around the band of islands in the western basin, and to narrow coastal strips east of Cleveland and between Nanticoke and Buffalo (ESM Fig. S5). Settlement area was reduced by 95–96% across various release types (Table 4) as a result of substrate clipping, that (similar to Lake Michigan) mirrored reduction in available settlement area. Settlement success was reduced from 100% to 43% for rivers, 58% for ports and 36% for offshore releases (Table 4).

Discussion and conclusions

Our model results show that lake currents may be a very effective mechanism for dispersal for AIS larvae with extended pelagic drift phases. In particular, *Limnoperna* larvae continuously released at a limited number of locations (e.g. eight ports and corresponding offshore deballasting points) were predicted to spread in a single year up to 72

and 67% of the available (depth-wise) settlement area in Lake Michigan (Fig. 8) and Erie (Fig. 9) respectively, while ruffe larvae were predicted to spread up to 50% of the available settlement area in Lake Michigan and 52% in Lake Erie. Rapid spread of dreissenid mussels in Lake Michigan (Vanderploeg et al., 2002) can serve as indirect confirmation of our *Limnoperna* dispersal model. Our model results for *Limnoperna* and quagga mussel indicate that advection by lake currents could likely play an important role in the extent and speed of *Limnoperna* dispersal if introduced to the Great Lakes. Ship ballast uptake and release of veligers also may have played a role in dispersing *Dreissena* species larvae in the Great Lakes. Offshore releases, where currents are stronger, resulted in larger dispersal distances and larger settlement areas in most cases. Therefore, offshore releases may maximize spread of AIS larvae and thus be especially detrimental.

Our particle model of AIS larvae dispersal enables exploration of the implications of releasing ruffe and *Limnoperna* from specific locations throughout Lakes Michigan and Erie. The model results suggest there are a limited number of port and river mouth locations where larval drift distances are predicted to be small and where there is likely an increased opportunity to contain and potentially control an incipient population of ruffe or *Limnoperna*. For example, the estimated slow rates of ruffe larval dispersal in Green Bay suggest that the optimal location to focus control efforts may be within Green Bay, especially if spawning activity is largely restricted to large rivers and warmer coastal habitats (Horns et al., 2000; Ogle, 1998). But, our models also illustrate that any containment window is likely narrow and as both species spread into offshore habitats, larval dispersal will accelerate and management options would rapidly diminish. These results emphasize both the

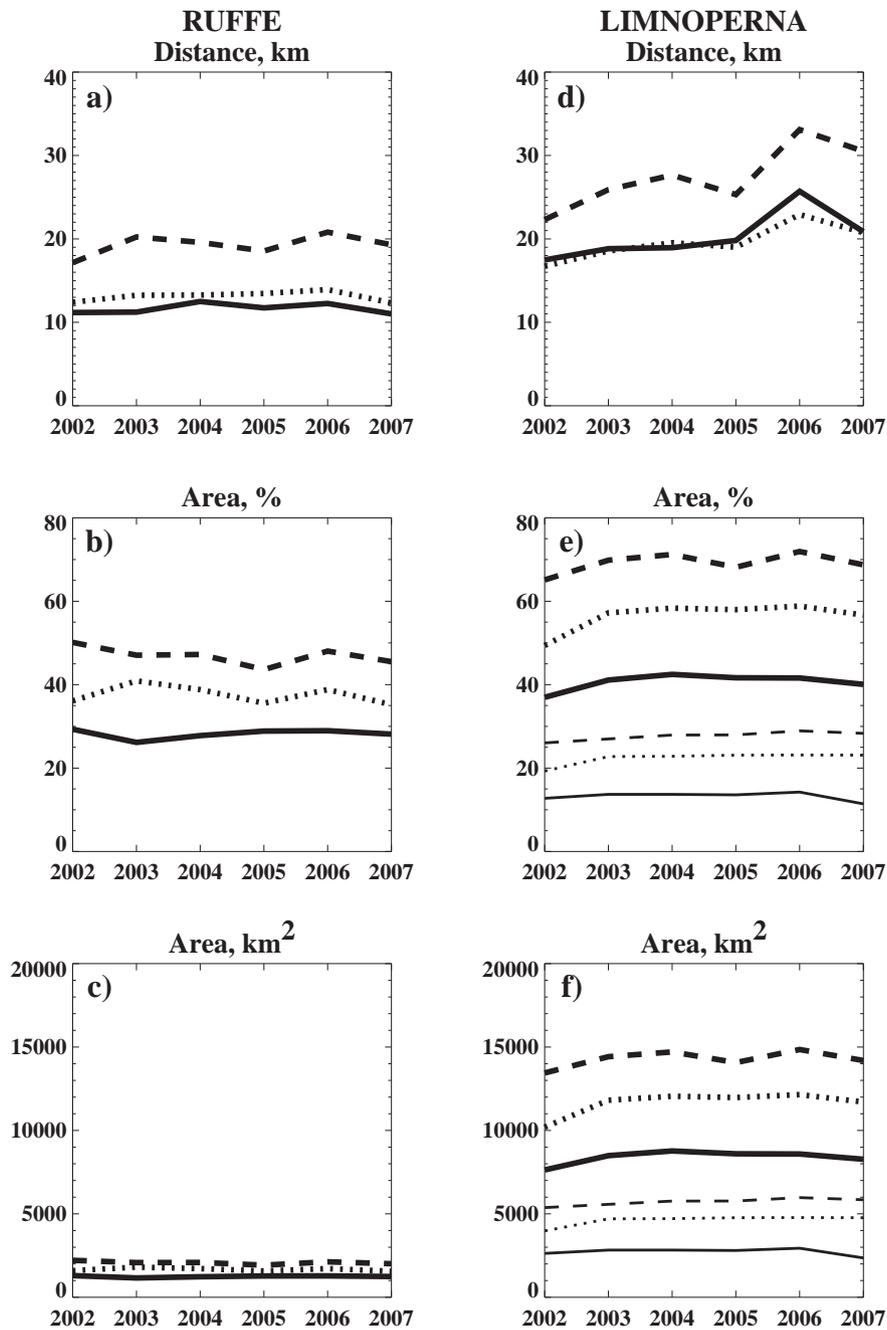


Fig. 8. Modeled dispersal distance, total settlement area (%), and total settlement area (km^2) in Lake Michigan for ruffe (a, b, c) and *Limnoperna* (d, e, f) larvae. Rivers - solid lines, ports - dotted lines, offshore - dashed lines. Thin lines in panels “e” and “f” are substrate clipped cases.

importance of frequent sampling at high risk points of introduction for species with pelagic larvae to maximize the probability of detection while the population is still localized, and that when detected, response action will need to be swift if they are to be contained, and spread prevented in the Great Lakes. The successful incursion response to the detection of *Mytilopsis* sp. in marinas in Darwin Australia provides an example of prompt action that resulted in the successful containment and eradication within 30 days of detection (Bax et al., 2002).

Spread of *Limnoperna* larvae is expected to be greater than for ruffe larvae due to stronger seasonal currents, longer drift time, larger settlement areas and, in Lake Erie, a protracted (practically doubled) spawning period. The difference in settlement area in absolute numbers due to a much wider depth range for *Limnoperna* habitat should also be noted (see Fig. 8c and f and Fig. 9c and f). Our results imply that AIS with

a relatively long pelagic larval phase can be spread rapidly by currents around a Great Lake. If dispersal by lake currents is coupled with dispersal by ballast water exchange, as seen with dreissenid mussels, AIS spread may be accelerated throughout the Great Lakes basin in a matter of years from a single point of introduction. Such accelerated spread could be evident with ruffe where e-DNA sampling indicated its potential presence near Chicago, IL (Tucker et al., 2016), several hundred kilometers from Green Bay, which is beyond the maximum drift in a single year for ruffe and would likely indicate shipping as a vector of spread due to lack of sightings between Green Bay and Chicago.

Our results suggest that managers concerned with controlling AIS spread should pay particular attention to species-specific life history traits of AIS, such as timing, duration and potential location of reproduction. For ruffe, dispersal of larvae via ships originating in Lake Superior

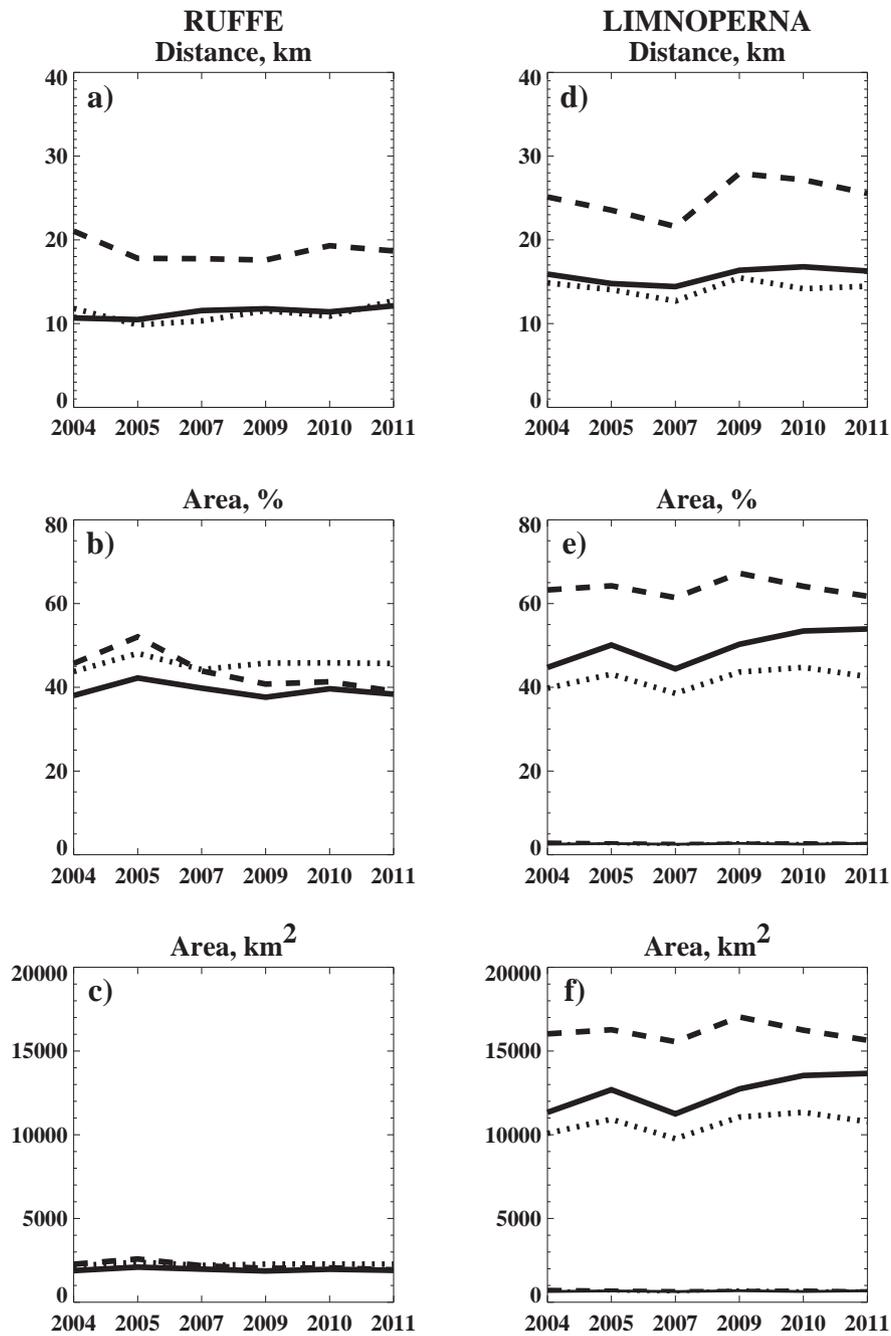


Fig. 9. Modeled dispersal distance, total settlement area (%), and total settlement area (km²) in Lake Erie for ruffe (a, b, c) and *Limnoperna* (d, e, f) larvae. Rivers - solid lines, ports - dotted lines, offshore - dashed lines. Thin lines in panels “e” and “f” are substrate clipped cases.

Table 5
Settlement success for individual year model runs in Lake Michigan and Lake Erie. Offshore releases. S_R – ruffe, S_L – *Limnoperna*, S_{LC} – *Limnoperna* clipped by substrate.

Year	Lake Michigan			Lake Erie		
	S _R (%)	S _L (%)	S _{LC} (%)	S _R (%)	S _L (%)	S _{LC} (%)
2002	64.4	99.7	87.5			
2003	65.8	98.6	84.8			
2004	61.7	99.4	88.4	62.5	100.0	37.1
2005	64.8	99.6	90.5	66.0	100.0	36.1
2006	66.9	98.7	86.7			
2007	62.3	99.7	85.8	58.5	100.0	32.0
2009				53.3	100.0	33.3
2010				56.0	100.0	40.3
2011				53.3	100.0	37.6

Table 6
Minimum, maximum and average values of annual dispersal distance and settlement area for ruffe and *Limnoperna* from model runs in Lake Michigan (2002–2007) and Lake Erie (2004–2005, 2007, 2009–2011).

	Ruffe		<i>Limnoperna</i>	
	Distance (km)	Area (%)	Distance (km)	Area (%)
Michigan				
Rivers	11.0/12.5/11.6	26.2/29.3/28.2	17.5/25.7/20.3	37.0/42.5/40.6
Ports	12.3/13.9/13.1	35.2/40.9/37.6	16.7/22.9/19.6	49.4/58.8/56.4
Offshore	17.1/20.8/19.3	43.6/50.1/46.9	22.3/33.1/27.5	65.1/71.9/69.2
Erie				
Rivers	10.5/12.1/11.3	37.6/42.2/39.3	14.4/16.8/15.8	44.4/54.0/49.5
Ports	9.8/12.7/11.2	43.8/48.1/45.6	12.7/15.5/14.3	38.5/44.8/42.1
Offshore	17.6/21.0/18.7	39.1/52.1/43.8	21.6/27.9/25.1	61.4/67.3/63.7

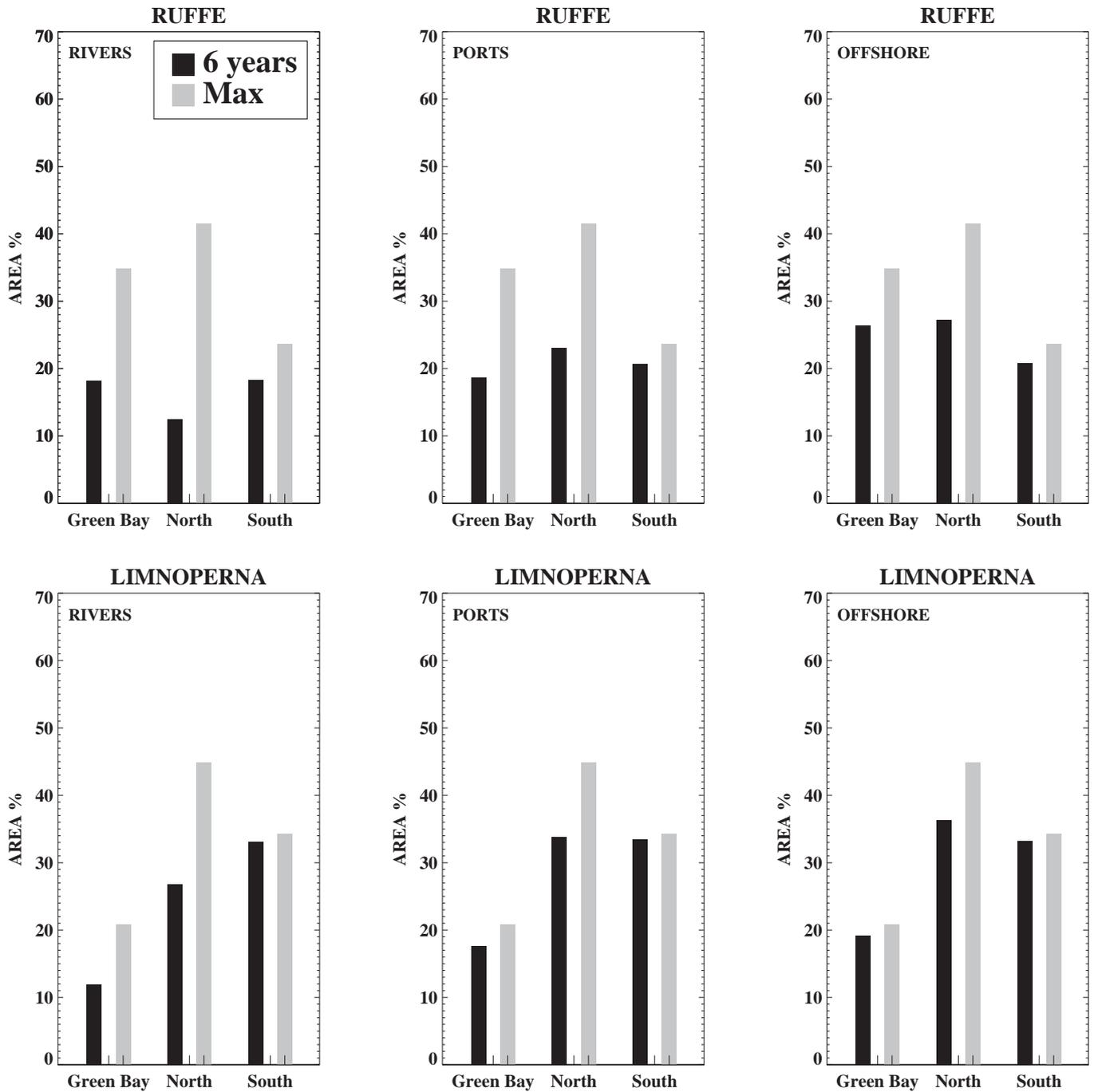


Fig. 10. Settlement area by basin in Lake Michigan for (left to right) rivers, ports and offshore releases for ruffe (upper row) and *Limnoperna* (bottom row). Black – model results, gray – maximum available settlement area in each basin.

also has the potential to increase the length of the release window because ruffe reproduction in Lake Superior may occur later in the season. These results also help illustrate the benefits of proactive management of the secondary spread of invasive species via ballast water exchange within the Great Lakes basin if the spread of current and future invaders is to be slowed or contained (Sieracki et al., 2014).

We found differences between lakes in size of potential settlement areas for ruffe and *Limnoperna*. Although Lake Erie is smaller than Lake Michigan by surface area (only about 44%) (Table 2), it has a higher proportion of suitable habitat. Suitable habitat for ruffe in Lake Erie is 15% larger than in Lake Michigan, and for *Limnoperna* is 23% larger than in Lake Michigan. Therefore, the potential for current-mediated spread of either species is higher in Lake Erie than in Lake Michigan.

At the same time, if substrate composition is allowed to influence settlement of *Limnoperna* larvae, the situation reverses because there is only a very small area of preferred hard substrate in Lake Erie compared with Lake Michigan (Table 2). However, we did not consider potential for *Limnoperna* larvae to settle on existing dreissenid mussels, which would have greatly increased the area potentially available for settlement of *Limnoperna*.

Although model results reveal general tendencies in direction and magnitude of dispersion for the two species we studied, they should be used with caution when predicting dispersal of a new introduction outside of the range of years we studied. The reason is that substantial interannual variability in lake currents results in differences in larval drift and resulting geographic areas of settlement between years.

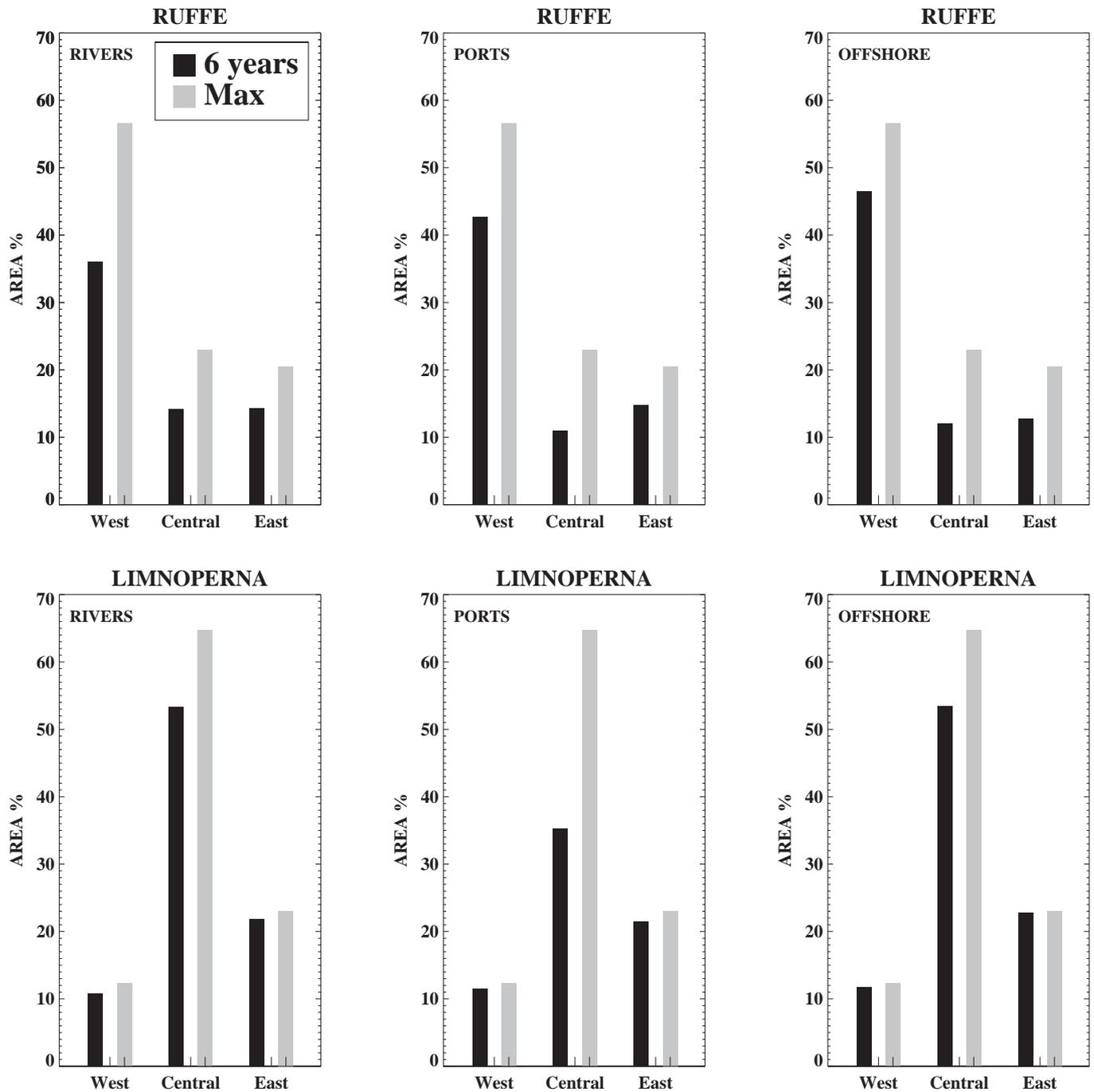


Fig. 11. Settlement area by basin in Lake Erie for (left to right) rivers, ports and offshore releases for ruffe (upper row) and *Limnoperna* (bottom row). Black – model results, gray – maximum available settlement area in each basin.

In addition, because temperature varies between years (and locations), spawning period is variable as well, potentially adding to inter-annual variability in dispersal caused by currents alone (although for the season-long spawning periods we studied, increase in duration by a month did not significantly change the results, likely because settlement area was already close to its upper limit in a situation with a fixed drift time).

Taking all these factors into consideration is especially important for any site-specific short-term predictions of larval transport, when dispersal distance and direction of spread becomes highly dependent on daily or even hourly meteorological conditions (i.e. wind speed and direction) driving lake circulation. For any future invasion it would be

prudent to run the larval transport model with current year conditions (e.g. using output of the Great Lakes Coastal Forecasting System (<http://www.glerl.noaa.gov/res/glcfs/>), especially if results are going to be used to inform delimitation surveys and containment or control measures.

The larval transport model employed in this study is relatively simple and can be improved in future by addressing some of its limitations. For instance, assumptions of neutral buoyancy and passive behavior of AIS larvae may have biased the model outcomes. We assumed that ruffe and *Limnoperna* larvae would drift for a period of 14 and 20 days regardless of larval behavior, lake temperature, light, or prey conditions. Relatively little is known about the behavior of *Limnoperna* or ruffe larvae in lakes, but ruffe larvae are known to exhibit vertical diurnal

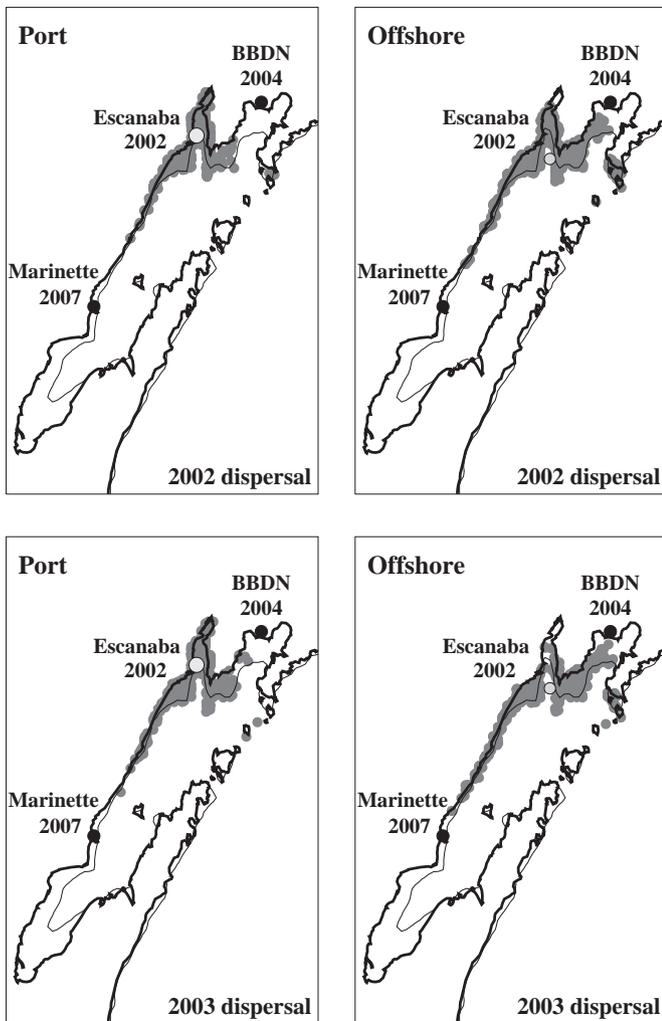


Fig. 12. Dispersal of ruffe larvae from Escanaba area in 2002 (upper panels) and 2003 (lower panels). Large open circles – ports, small open circles – offshore sites. Black filled circles: ruffe sightings in 2004 (Big Bay de Noc (BBDN)) and 2007 (Marinette, WI) after first sighting in Escanaba, MI in 2002 (Bowen and Keppner, 2013).

migrations under some conditions (Brown et al., 1998). In reality, the larval drift period will also be affected by lake temperatures and plankton prey biomass which would affect the growth rate and swimming speed of ruffe and *Limnoperna* larvae and their ability to escape the passive drift phase in the plankton and settle near or on the bottom.

In addition, since accuracy of larval transport model prediction depends on the accuracy of advection fields it uses, there is a need for improving the quality of nearshore circulation in the hydrodynamic model by addressing some limitations of its physics. One important feature of lake hydrodynamics that affects the transport of substances released near shore is the so-called coastal boundary layer (CBL), i.e. the transition zone located within the first 10 km from coast that is characterized by strong lateral shear in currents (Rao and Schwab, 2007). Where the CBL is closest to shore, currents decrease dramatically (in the absence of waves) due to frictional effects that increase as lake depth ultimately decreases to zero towards the shore, leading to a decrease in alongshore larval transport (Largier, 2003; Nickols et al., 2012). In our hydrodynamic model, which uses “free-slip” conditions on lateral boundaries (similar to some other popular models), the long-shore current component is only moderately reduced towards the coast as bottom friction

becomes more and more important in shallow waters (Raudsepp et al., 2003). Consequently, simulated currents that are close to shore are stronger than observed. On the other hand, there is an additional energy source absent in the current hydrodynamic model coming from the high frequency gravity waves and wind wave driven currents. In the surf zone of the Great Lakes these processes can cause velocities to reach up to 50 cm/s in extreme cases (Schwab et al., 1989) and need to be included in future versions of the model.

In addition to limitations of hydrodynamic model physics, the model we used had relatively low horizontal resolution nearshore so did not permit an adequate description of ballast retention in ports (harbors) which can slow the release of AIS into the lake and reduce dispersal distance and settlement area. There are few observations in the Great Lakes that address this issue (Wells et al., 2011) although flushing characteristics of each harbor are certainly unique. Therefore we must caution that predictions of dispersal from ports are likely to overestimate both distance and settlement areas. Increased grid resolution and addition of wave-current coupling in hydrodynamic models should help to alleviate issues with simulating effects of CBL and flushing from harbors on larval transport modeling in the future, but at this stage of knowledge our predictions of larval transport from offshore locations should be considered more accurate than ones that originate very close to or on the coast.

In this study, we considered two potentially invasive species with different life histories, but some dispersal tendencies were relatively similar (e.g. stronger dispersal from offshore locations). Our model also could be used to predict spread of other AIS with pelagic life stages. Model results demonstrate that should an incipient population of a potential aquatic invasive species be detected as part of basin wide surveillance program, response options will be highly dependent on the introduction location due to differences in current regime. Although a full evaluation of management efforts to contain and treat releases of invasive species larvae goes beyond the scope of this work, releases at sites with high rates of natural dispersal generated by strong currents near coasts (e.g. Grand Haven), or by powerful hydraulic flows near connecting channels (e.g. Port of Detroit or Buffalo), will obviate containment options. In contrast, low rates of larvae dispersal observed at the port of Big Creek suggest that containment and biocide treatment may be more feasible. Furthermore, it is also clear that, as efforts are made to improve surveillance, response and control capacity across the Great Lakes region, natural dispersal models that account for high resolution bathymetries, accurate tributary inputs and spatio-temporally variable circulation patterns will be useful tools to inform management decisions for a broad range of representative taxa.

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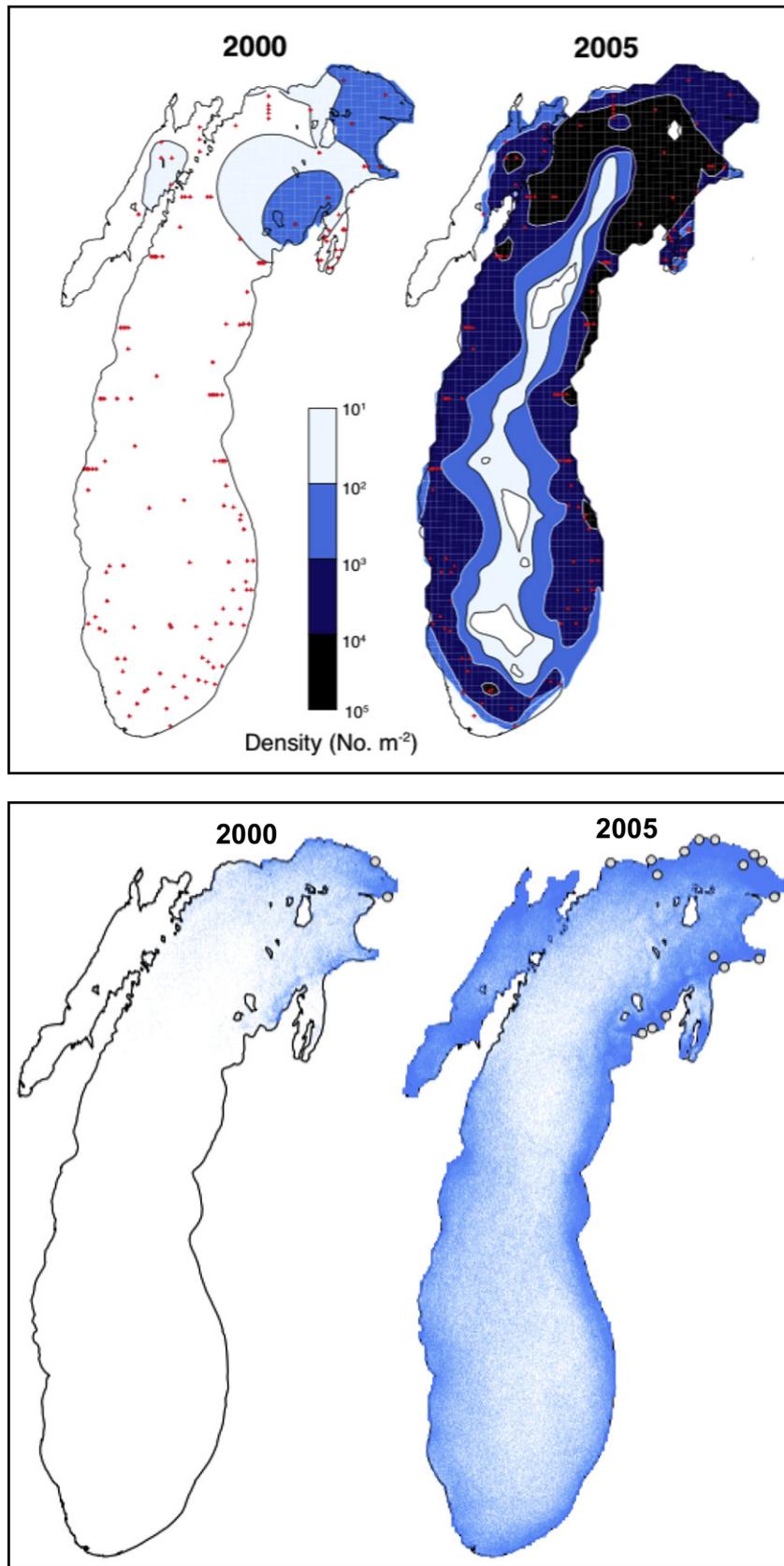


Fig. 13. Dispersal of quagga mussel in Lake Michigan. Upper panel - observations from Nalepa et al. (2014) (mean mussel density in 2000 and 2005). Lower panel - model results (locations of settled larvae) in 2000 (after 1998 and 1999 dispersal) and in 2005 (after 2000–2004 dispersal). Red crosses in observations denote sampling sites. Open circles in model results denote initial sources of larvae in 1998 and 2000.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2017.02.001>.

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