

Secondary spread of zebra mussels (*Dreissena polymorpha*) in coupled lake-stream systems¹

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Abstract: We postulated that dispersal through streams is an important factor in the spread of nonindigenous aquatic species to uninvaded lakes. We tested this hypothesis with zebra mussels (*Dreissena polymorpha*), whose planktonic larvae are particularly prone to transport through streams. To examine this potential mechanism of spread, we (1) assessed populations of zebra mussels in 2000 and 2003 in coupled lake-stream systems of the St. Joseph River basin (Indiana and Michigan, USA) and (2) examined the interconnectedness of lake-stream systems by evaluating all invaded inland lakes and reservoirs in the United States. We compared observed patterns in zebra mussel populations in 2000 and 2003 to patterns predicted by two proposed models of spread: the static source-sink model and the progressive downstream-march model. Adult zebra mussel densities in lake outflows declined with distance downstream of invaded lakes. Maximum downstream occurrences of adults were variable over the years surveyed, but did not increase through time, suggesting that the source-sink model best fit zebra mussel distributions in these lake-stream couplets. For the conterminous US, we examined the connectedness of inland lakes in close proximity to invaded lakes to determine if stream connections were related to invasions. We also measured the distances between invaded lakes and downstream lakes that were potential recipients of colonists to examine the importance of stream distance in relation to zebra mussel invasions. Lakes connected to invaded lakes were more likely to be invaded than non-connected lakes, and the probability of becoming invaded increased with the proximity between lakes. Our results suggest that a better understanding of the role that streams play as pathways for new biological invasions is crucial for directing management and prevention efforts.

Keywords: biological invasions, native mussels, nonindigenous species, source-sink dynamics, stream-lake connections, zebra mussels.

Résumé : Nous avons émis l'hypothèse que les espèces aquatiques non indigènes se dispersent de lacs en lacs par le biais des cours d'eau. Nous avons testé cette hypothèse en étudiant la moule zébrée (*Dreissena polymorpha*) dont les larves planctoniques sont facilement transportées par les cours d'eau. Ce mécanisme de dispersion a été analysé en évaluant les populations de moules zébrées en 2000 et 2003 dans des systèmes de lacs et de cours d'eau du bassin de la rivière Saint-Joseph, en Indiana et au Michigan (États-Unis). Nous avons également examiné l'interconnexion des lacs et des cours d'eau en étudiant tous les lacs et réservoirs de l'intérieur des États-Unis envahis par la moule zébrée. À cet égard, nous avons mesuré les distances séparant les lacs envahis des lacs situés en aval qui pourraient être colonisés par la moule. De plus, nous avons comparé les patrons des populations de moules en 2000 et 2003 aux patrons proposés par deux modèles de dispersion : le modèle statique source-puit et le modèle progressif du déplacement vers l'aval. Les densités de moules zébrées adultes des décharges des lacs envahis diminuent vers l'aval. Le nombre maximal d'adultes dans la partie située en aval des systèmes varie selon les années, mais ce nombre n'augmente pas, ce qui suggère que le modèle source-puit prédit mieux la répartition des moules zébrées que l'autre modèle. Enfin, les lacs reliés à des lacs envahis par le mollusque sont plus susceptibles de l'être à leur tour. En fait, la probabilité d'envahissement augmente avec la proximité des lacs. Il semble donc qu'une meilleure connaissance du rôle joué par les cours d'eau lors de nouvelles invasions biologiques soit essentielle pour prévenir ces invasions et mieux orienter les efforts de contrôle.

Mots-clés : connexions entre cours d'eau et lacs, dynamiques source-puit, espèces exotiques, invasions biologiques, moules indigènes, moule zébrée.

Nomenclature: Pallas, 1771.

Introduction

The primary mode of zebra mussel (*Dreissena polymorpha*) dispersal to North American lakes is believed to be recreational boaters (Johnson, Ricciardi & Carlton, 2001). Although trailered boating is implicated as the most common transport highway for hitchhiking zebra mussels (Buchan & Padilla, 1999; Johnson, Ricciardi & Carlton, 2001), streams may be important alleys for sec-

ondary spread to uninvaded systems (Horvath *et al.*, 1996; Kraft *et al.*, 2002). However, the potential for zebra mussels to spread secondarily from invaded lakes through streams, establish instream populations, and colonize downstream lakes has been far less studied. Since the discovery of zebra mussels in the Great Lakes in 1988 (Hebert, Muncaster & Mackie, 1989), almost 300 inland lakes and drainage networks of the Midwestern US, primarily in Indiana, Michigan, and Wisconsin, have been invaded. The effort to conserve native mussels, reduce economic damage, and control the spread of zebra mus-

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sels may hinge on understanding and managing secondary spread via streams (Horvath *et al.*, 1996).

The spread and population growth of zebra mussels in North America have been aided by their copious propagule production: a single female mussel can release > 1,000,000 eggs during her life span (Sprung, 1993). Fertilized eggs hatch into planktonic larvae (termed veligers), which remain in the water column for 2 to 4 weeks (Smith, 2001). Water flow can carry veligers out of lakes and substantial distances downstream (Horvath & Lamberti, 1999) until they are “competent” to settle on hard substrates (rocks, wood, other molluscs, etc.) using their byssal threads (Smith, 2001). Both outflowing streams and downstream lakes can be colonized by drifting veligers (Horvath & Lamberti, 1999) or adults floating on debris (Horvath & Lamberti, 1997).

The economic and environmental impacts of zebra mussel invasions have been extensive. Economic costs of zebra mussel removal and control have been estimated at \$100 million per year (Pimentel *et al.*, 2000). Zebra mussels are especially problematic in water intake facilities such as power plants and municipal water supplies. A quantitative risk analysis by Leung *et al.* (2002) suggested it would be cost-effective to spend up to \$300,000 annually to prevent a single lake with a power plant from being invaded. However, the US Fish and Wildlife service budget for fiscal year 2005 is only \$5.4 million to deal with all aquatic invasive species in all bodies of water. Environmental costs of zebra mussel invasions, such as in water quality and biological integrity, have also been substantial. For example, zebra mussels can kill native mussels (Unionidae) within a few years of invasion by colonizing their shells and inhibiting filter feeding (Schloesser, Nalepa & Mackie, 1996; Ricciardi, Neves & Rasmussen, 1998). In streams with high densities of zebra mussels, it is difficult to find any live native mussels (A. Bobeldyk, pers. observ.). Unionids are among the most highly endangered organisms in North America, and zebra mussels are a serious threat to their biodiversity (Page *et al.*, 1992; Strayer & Smith, 1996).

Despite the impacts of zebra mussels and their propensity to spread through streams, secondary spread in North America has been studied almost exclusively in large rivers, such as the Illinois River (Stoeckel *et al.*, 1997; Schneider *et al.*, 2003), the Mississippi River (Stoeckel *et al.*, 2004), and the Hudson River (Strayer & Smith, 1996). The lack of emphasis on stream connections is surprising considering the importance of stream connections shown in the distribution of zebra-mussel-invaded lakes in Belarus (Kraft *et al.*, 2002). Kraft *et al.* (2002) demonstrate, in Belarusian lakes, that stream connections “greatly enhance the likelihood of invasion”. In North America, the role of small streams in secondary spread has rarely been addressed (but see Horvath *et al.*, 1996; Miller & Haynes, 1997; Horvath & Lamberti, 1999). Furthermore, forecasts of zebra mussel distributions in North America have focused on habitat suitability (Strayer, 1991; Drake & Bossenbroek, 2004) and patterns of recreational boating activity (Schneider, Ellis & Cummings, 1998; Buchan & Padilla, 1999; Bossenbroek, Kraft & Nekola, 2001). Although Schneider, Ellis, and Cummings (1998) considered stream connections in their model, which predicted

the distribution of zebra mussels in Illinois lakes, these predictions have not been tested empirically.

Horvath *et al.* (1996) proposed three models to describe how zebra mussels spread in drainage networks that contain lakes. The “large-river model”, originally proposed by Strayer (1991), predicts that adult mussels cannot colonize rivers < 30 m wide even when upstream lakes are invaded. This model was not assessed further because zebra mussels have already been found in many smaller rivers and streams. The “source-sink model” predicts that zebra mussels from lakes (source) will colonize streams (sink) a limited distance downstream of the invaded lake outflow. This model suggests that zebra mussel populations in streams are not self-sustaining, but require continuous recruitment from upstream lakes. Streams can, however, act as conduits for the passage of propagules (*i.e.*, veligers and/or adults attached to floating objects). Therefore, the probability of spread to a downstream lake will depend on the number of propagules released from an upstream source and their survival during transit, which is most likely a decreasing function of the distance between the lakes. In contrast, the “downstream-march model” predicts that mussels will be able to colonize streams, such that all lakes, rivers, and streams downstream of an invaded lake eventually will be colonized. In an Indiana-Michigan drainage network, Horvath *et al.* (1996) found preliminary support for the source-sink model from two invaded lake-stream systems (Christiana Lake-Christiana Creek and Syracuse Lake-Turkey Creek). Densities of zebra mussels declined exponentially with increasing distance downstream from colonized lakes, ranging from over 1,000 individuals·m⁻² at the lake outflow to only isolated adults found up to 12 km downstream.

Indiana and Michigan are ideal places to study the potential spread of zebra mussels through drainage networks. The numerous interconnected lake-stream systems in this region, coupled with the ongoing zebra mussel invasion, allow secondary dispersal to be evaluated empirically. An estimated 208 lakes have been invaded by zebra mussels in these two states (32 in Indiana and 176 in Michigan) and about one-third of these lakes are connected via streams to upstream invaded lakes (Johnson, Bossenbroek & Kraft, in press). The first discoveries of zebra mussels in hydrographically isolated inland lakes in the US occurred in 1991 in two Midwestern lakes, Eagle Lake (Michigan) and Lake Wawasee (Indiana), both in the St. Joseph River basin, which straddles the Michigan-Indiana border (USGS, 2003). Since then, zebra mussels have been found in 32 more lakes in this basin (Figure 1), 24 of which have outflowing streams that could potentially result in secondary spread.

In this study our objective was to test two models of zebra mussel spread proposed by Horvath *et al.* (1996) by using two approaches. First, we evaluated current zebra mussel populations in streams in the St. Joseph River basin by determining (1) adult zebra mussel density down the stream course and (2) the farthest downstream distance adult zebra mussels occurred in the outflowing streams of invaded lakes. We then retrospectively compared zebra mussel distribution to that proposed by each of the two models of spread. Second, we assessed the interconnectedness of lake-stream systems at a larger

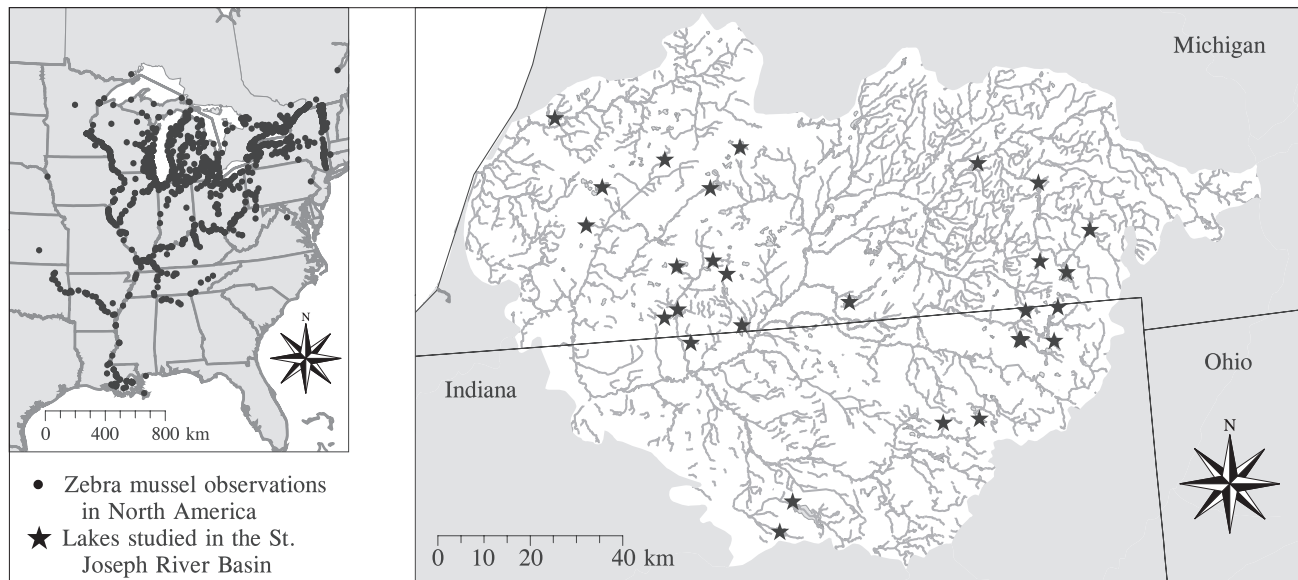


FIGURE 1. Maps illustrating the two components of this study. The left map shows the known distribution of zebra mussels in North America in 2003. The right map shows the St. Joseph River basin with surveyed lakes identified with stars.

scale by examining all invaded inland lakes and reservoirs throughout the United States and their stream connections. We determined the likelihood that new colonization events were a result of downstream transport and the probability that a new lake would be invaded based on its downstream distance from an invaded lake.

If the source–sink model correctly predicts zebra mussel distributions, we expected to find that zebra mussel population densities would be highest at the lake outflow, decline downstream, and not increase over time. In addition, the maximum distance that adult zebra mussels are found from lake outflows should be similar over time. Under the downstream-march model, we predicted that zebra mussel densities would increase over time, and that mussels should progressively colonize further distances downstream. Finally, for the US, we hypothesized that connectedness and downstream distance are both important factors in predicting whether a lake will be invaded. Analyses using gravity models (Bossenbroek, Kraft & Nekola, 2001; Leung, Bossenbroek & Lodge, in press) have shown that simple geographic distance is important for determining the spread of invasive species, but these models do not address connectedness even though it has been shown to be important (Kraft *et al.*, 2002). We predicted that lakes that are not connected to an invaded lake, despite being geographically close, are less likely to be invaded than lakes with stream connections to an invaded lake. Also, for lakes that are connected we predicted that the probability of a downstream lake being invaded by zebra mussels would increase with its proximity (measured as stream length) to an upstream invaded lake.

Methods

ASSESSMENT OF ZEBRA MUSSELS IN THE ST. JOSEPH RIVER BASIN

In the summers of 2000 and 2003, we surveyed streams in the St. Joseph River basin that were directly connected to invaded upstream lakes (17 streams in 2000 and 20 streams in 2003). The St. Joseph River basin

(Figure 1) is an extensive network of nearly 1,000 kettle lakes, streams, and rivers that drain a land area of approximately 12,000 km² into southern Lake Michigan. The geology of the basin is composed primarily of glacial till, and stream substrates are dominated by silt, sand, gravel, and cobble.

In each stream, we determined zebra mussel presence and approximate densities at several longitudinally distributed sites. Physical parameters (stream width, mid-channel depth, velocity), percent substrate composition, and water chemistry (temperature, conductivity, dissolved oxygen) were also measured at each site. The initial sampling site for each stream was at the invaded lake outflow (0 m), with subsequent downstream sampling sites at 10 m and 100 m from the lake outflow. If zebra mussels were found at any of these sites, additional downstream sampling was conducted at accessible locations (*e.g.*, road crossings) until zebra mussels were no longer found. At each sampling site, a 1-m-wide belt transect across the width of the stream was established along which zebra mussel densities were visually estimated on three haphazardly selected samples per substrate type: (1) cobble, (2) large woody debris, and (3) sand/gravel. Cobble and wood pieces were removed from the stream and inspected. A kick net (0.3 × 0.3 m) was used to collect sand/gravel samples from the stream bottom that were inspected for live mussels, druses (a conglomeration of loosely bound zebra mussels), and shells. Because large woody debris was not found at all sites, we did not use these data in our comparisons of zebra mussel densities across sites, but only as an indicator of the presence of zebra mussels. Zebra mussel densities were estimated qualitatively by assigning logarithmic categorical values for each substrate sample: 1 (1-10 mussels), 2 (10-100 mussels), and 3 (100-1,000 mussels). Average cobble substrate size was 0.06 m², and kick net area was approximately 0.15 m². If no zebra mussels were found on substrates, a more thorough search of the site was conducted to determine whether a low density of mussels was present at the site.

ASSESSMENT OF THE UNITED STATES ZEBRA MUSSEL DISTRIBUTION

At a national scale, we analyzed the patterns of zebra-mussel-invaded lakes to determine if connectedness and stream distance influence the likelihood that another lake is invaded. We used stream and lake data acquired from the National Hydrography Dataset, generated by the US Geological Survey and US Environmental Protection Agency, to build a geographic information system for the US that contained all inland lakes (> 25 ha) and stream connections. Using the Nonindigenous Aquatic Species database of the US Geological Survey (USGS, 2003), we identified the US lakes and reservoirs that have been reported as containing zebra mussels.

To assess if connectedness, as opposed to mere proximity, is related to the pattern of zebra-mussel-invaded lakes we identified all lakes within 1 km of a zebra-mussel-invaded lake. Each lake was classified as either “not connected” (*i.e.*, the lake was less than 1 km from an invaded lake but did not have a stream connection to that particular lake), “downstream” of an invaded lake, or “upstream” of an invaded lake. For each lake, we also determined if it was also invaded with zebra mussels.

To test if stream distance is related to whether or not a downstream lake is invaded with zebra mussels, we examined each invaded lake with an outflowing stream. For each lake, we measured the stream distance to the next lake and determined the frequency that the downstream lake contained zebra mussels to examine the relationship between stream distance and the probability of invasion. We also used topographic maps to verify that all lake-to-lake stream connections less than 5 km in length were indeed streams and not wetlands. Lakes that were connected by wetlands were not used in our analyses because zebra mussels rarely disperse through wetlands (Miller & Haynes, 1997).

Results

SPREAD OF ZEBRA MUSSELS IN THE ST. JOSEPH RIVER BASIN FROM 1993-2003

Comparison of zebra mussel dynamics over a 10-y period (1993-2003) in the St. Joseph River basin revealed interesting internal patterns. In Christiana Creek, adults were found 8 km downstream of Christiana Lake in 1993 and 3 km downstream in 2000. In 2003, however, no zebra mussels were found farther than 0.3 km downstream of Christiana Lake, suggesting a contraction of the stream population (Figure 2). In Turkey Creek, adult zebra mussels were found 10 km downstream of Syracuse Lake in 1993, only 0.1 km downstream in 2000, and 4 km downstream in 2003, despite similar collection efforts and methods. Even though we observed variation in the maximum distance downstream, the physical and chemical properties of all streams surveyed with zebra mussels were within the range of known zebra mussel requirements in the literature (Table I) (Horvath *et al.*, 1996).

Our first prediction from the source-sink model was that mussel densities in lake-stream couplets would decline with distance downstream and would not increase over time. In all sampling years, the highest densities of zebra mussels ($2,200\text{--}22,000\cdot\text{m}^{-2}$, estimated from cobble

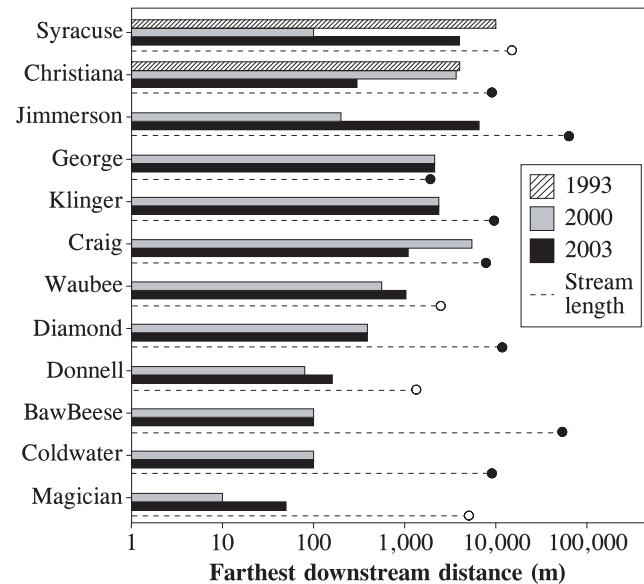


FIGURE 2. Maximum downstream distance that zebra mussels were found in lake outflows in the St. Joseph River basin in 1993, 2000, and 2003. Names are those of source lakes. The broken line indicates total stream length until confluence with a lake or large river. Closed circles at the end of the broken lines indicate that the downstream system also contains zebra mussels. Open circles indicate no known report of zebra mussels in the downstream system.

TABLE I. Physical and chemical properties of surveyed streams with zebra mussels in the St. Joseph River basin.

Parameter	Mean	Range
Stream width (m)	9.22	2.5-20.7
Mid-channel depth (m)	0.55	0.14-1.25
Mid-channel velocity ($\text{m}\cdot\text{s}^{-1}$)	0.43	0.15-0.88
Dissolved oxygen ($\text{mg}\cdot\text{L}^{-1}$)	7.55	5.4-9.6
Conductivity ($\text{e-S}\cdot\text{cm}^{-1}$)	443.54	267-629
Water temperature ($^{\circ}\text{C}$)	22.02	18.1-26
pH	8.30	7.5-9.25
% Boulder	11.53	0-80
% Cobble	19.02	0-70
% Gravel	19.49	0-80
% Sand	33.00	0-90
% Silt	16.77	0-90

samples) occurred at the lake outflow. In all streams, densities decreased with distance from the lake outflow. Four systems are used to demonstrate this decrease in density with distance (Figure 3): the two systems invaded in 1993 and two systems with zebra mussels found beyond 2 km in 2003. In all lakes surveyed in both 2000 and 2003, densities either remained the same or declined except in Jimmerson Lake, where densities appeared to increase slightly at downstream sites.

Our second prediction from the source-sink model was that the maximum distance that adult zebra mussels could be found downstream of an invaded lake would vary, but not increase, over time. Some streams in our survey entered another lake within 1 km, and therefore the maximum distance downstream for zebra mussels could not exceed this distance. Between 2000 and 2003, zebra mussel dynamics downstream of invaded lakes revealed colonization extensions, retractions, or no change (Figure 2). On average, for the 12 streams sur-

veyed both in 2000 and 2003 where zebra mussels were found beyond 10 m downstream, adults were found 0.2 km farther downstream in 2003, suggesting very little longitudinal change. In 2000, the farthest stream distance colonized by zebra mussels was 5.4 km in the outflow of Craig Lake, Michigan. Hard substrate availability was high in this system, with 35% boulder and cobble. In addition, the native mussels found in the stream averaged > 1,000 zebra mussels per shell (*M. Evans-White, pers. observ.*). In 2003, the farthest downstream distance colonized was 6.5 km from Jimmerson Lake, Indiana. Although the entire length of these streams was not colonized, veligers could have leapt over uncolonized stretches of these streams, thereby invading downstream lakes and the St. Joseph River (Figure 2). Across all systems, very few adult zebra mussels were found beyond 4 km downstream of invaded lakes.

SPREAD OF ZEBRA MUSSELS IN US INLAND LAKES SINCE 1988

As of 2003, 295 lakes and reservoirs were reported to contain zebra mussels. There are 194 lakes (> 25 ha) within 1 km of these lakes and 62 of these lakes have been invaded by zebra mussels. Of these 62 lakes, 90% are either upstream or downstream from an invaded lake. We found that downstream lakes connected by streams to an upstream invaded lake were more likely to be invaded with zebra mussels (79%) than lakes upstream from an invaded lake (32%) or not connected (7%) (Table II). It should be noted that within this analysis, invaded lakes often came in pairs (*i.e.*, two connected lakes within 1 km of each other), which thus contributed to both the “upstream” and “downstream” categories.

Of the 295 zebra-mussel-invaded lakes, 154 were drained by streams for which the next large body of water downstream was a Great Lake or a large river (*e.g.*, Ohio River or Mississippi River) and seven entered wetlands, which limit downstream dispersal of zebra mussels

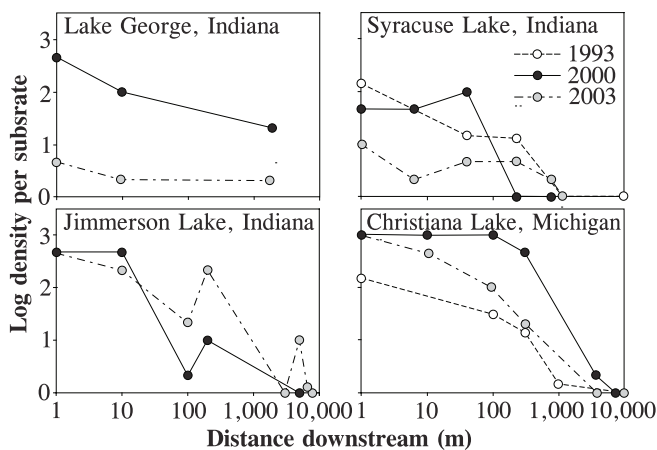


FIGURE 3. Zebra mussel density for selected lake-stream complexes in the St. Joseph River basin, estimated from the lake outflow to farthest downstream distance on log-ranked scale in 2000 and 2003. Density values: 1 (1-10 mussels), 2 (10-100 mussels), 3 (100-1,000 + mussels). Density was estimated on cobble in stream outflows of Lake George, Syracuse Lake, and Jimmerson Lake and from kick net samples in Christiana Lake. Densities in 1993 were estimated from Horvath *et al.* (1996).

(Miller & Haynes, 1997). We thus examined the remaining 134 invaded lakes with stream connections to other lakes and found that 79 lakes were directly connected by streams to other invaded lakes, whereas 55 lakes had stream connections to downstream lakes that were not reported as invaded. The average stream length between all pairs of lakes analyzed was 10.8 km. The average stream distance between invaded lakes (7.2 km) was significantly less ($P = 0.0003$, Welch modified two-sample *t*-test) than the average stream distance between invaded and non-invaded lakes (15.9 km) (Figure 4). There were 25 lakes that were less than 1 km downstream from an invaded lake, and 23 of these have been reported as invaded by zebra mussels. By contrast, there were 26 lakes that were more than 20 km downstream of an invaded lake and only seven have been reported as invaded.

Discussion

Our results suggest that when a lake contains zebra mussels, its outflowing stream and nearby downstream lakes are likely to be invaded by mussels. The source-sink model of zebra mussel spread (Horvath *et al.*, 1996) was most consistent with observed zebra mussel distributions in lake-outlet streams of the St. Joseph River basin. Zebra mussel distributions and densities in most streams did not increase over time, while additional downstream lakes have been invaded. In two streams, we

TABLE II. All lakes (> 25 ha) that are within 1 km of zebra-mussel-invaded lakes in the US. Each lake was classified as either “not connected” (*i.e.*, the lake was less than 1 km from an invaded lake but did not have a stream connection to that particular lake), “downstream” of an invaded lake, or “upstream” of an invaded lake. The proportion of lakes in each category known to be invaded with zebra mussels was also calculated.

Lake category	Total	Proportion with zebra mussels (%)
All	194	32.0
Not connected	84	7.1
Upstream	70	32.8
Downstream	43	79.1

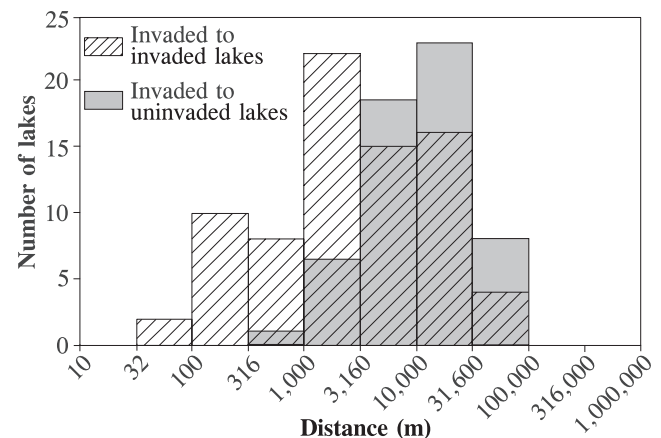


FIGURE 4. Two overlapping-frequency histograms of zebra-mussel-invaded lakes showing stream distances to downstream lakes (invaded or uninvaded). For each invaded lake in the US, the distance to the next lake was measured as well as the invasion status of each lake.

found evidence of an upstream retreat of adult mussels, possibly related to changes in the upstream invaded lake (*e.g.*, veliger output or adult food resources). Our results in aggregate suggest that stream populations and the invasion of downstream lakes are dependent on the upstream lake for recruitment.

The source-sink model predictions also fit with the observed zebra mussel distribution across the US since the probability of a lake being invaded by zebra mussels was related to both the lake being connected to and its proximity to another invaded lake. Almost all lakes (23 of 25) less than 1 km downstream from another invaded lake were invaded. Only 7% (6 of 84) of the lakes that were within 1 km of an invaded lake but not connected were invaded. In addition, lakes with upstream connections greater than 20 km to invaded lakes had a lower chance of being invaded (7 of 26). Similarly, Kraft *et al.* (2002) found in Belarus that nearly all lakes less than 15 km from an invaded lake were also invaded. This pattern suggests that increasing stream distance from an upstream invaded lake results in a lower probability that zebra mussels will become established in a downstream lake (*i.e.*, the source-sink model). In addition, it becomes increasingly difficult to distinguish whether overland transport or downstream dispersal is the most likely source of introduction (discussed in detail in Johnson, Bossenbroek & Kraft, in press). Our findings are in concert with analysis of the secondary spread of a different invader, *Daphnia lumholzi*, in river systems, which found that reservoirs downstream of habitats known to contain the invasive cladoceran were more likely to become invaded than those which were not (Shurin & Havel, 2002). Shurin and Havel (2002) showed the importance of connections, but not distance, which would be interesting to assess in order to compare the downstream dispersal abilities of different aquatic invasive species.

Several possible factors beyond distance may explain why some lakes lack zebra mussels even though they are downstream of an invaded lake. First, lakes may contain zebra mussels but have not been reported as invaded. In areas with numerous lakes, such as southern Michigan, it is likely that some invasions have not yet been detected. Second, wetlands situated between lakes may restrict the transport of veligers between lakes (Miller & Haynes, 1997). Transport of veligers in stream flow (Horvath & Lamberti, 1999) or of adults on plant fragments (Horvath & Lamberti, 1997) may be greatly diminished by the filtering capacity of wetlands. Third, a downstream lake may not be suitable for zebra mussels if water chemistry is the major determinant of suitability. A downstream lake will probably be suitable for zebra mussels if most of the inflowing water comes from a lake known to contain zebra mussels. However, changes in land-use or significant contributions from tributaries or groundwater may alter water chemistry such that the downstream lake is then unsuitable for zebra mussels. Fourth, if the spread of zebra mussels via streams to new lakes also requires a large population in the source lake, zebra mussels may have not yet successfully established populations in a downstream lake despite a high probability of invasion based on distance. It may take several years for source

lakes to develop large enough zebra mussel populations to successfully disperse to downstream lakes, particularly for long-distance stream connections.

Secondary spread of zebra mussels via streams has the potential to impact stream and downstream lake ecosystems. Zebra mussels can significantly alter water quality and plankton density in lakes (MacIsaac *et al.*, 1992; James *et al.*, 2000) and large rivers (Caraco *et al.*, 2000; Canale & Chapra, 2002), and thus indirect effects on filter-feeding biota could occur downstream of invaded lakes. Adult zebra mussels may also impact native mussels (Unionidae) by physically inhibiting their filter feeding or by competing for the same suspended particulate food resources (Horvath *et al.*, 1996; Schloesser, Nalepa & Mackie, 1996). Unionids are rapidly declining in the United States, and zebra mussels have been shown to be one of the leading causes in lakes and rivers (Ricciardi, Neves & Rasmussen, 1998; Williams & Neves, 1995). Unfortunately, no systematic study has been conducted of the impact of zebra mussels on native mussels in small streams. The decline in abundance of adult zebra mussels in streams with distance downstream adds complexity to their potential impacts on native mussels. It is possible that in small streams zebra mussels may severely impact native mussels only within short distances from lakes with persistently high zebra mussel densities. However, if lake plankton supports filter-feeder populations in outflowing streams, then plankton reductions in lakes with large zebra mussel populations may negatively affect both native mussels and zebra mussels in outflowing streams. A full assessment of this relationship is needed to predict the potential impacts of zebra mussels on native mussels in invaded and uninvaded regions of North America.

A primary motivation for preventing further spread of zebra mussels in the US is to prevent further impacts on native mussels. Predictions of the potential distribution of zebra mussels in the United States have emphasized the Southeast, because it contains the most diverse unionid fauna in the United States (Strayer, 1991; Drake & Bossenbroek, 2004). Assessing the true risk to these species will require an assessment of the potential habitat of zebra mussels in areas of high unionid diversity. If small streams are the primary habitat for unionids, the risk of extinctions due to zebra mussel invasion should decrease with distance from invaded lakes. However, if most unionid species live in slow-moving rivers or lakes, the impacts of zebra mussels could be severe and may be amplified by the ability of zebra mussels to colonize lakes downstream of an original source in a "stepping stone" fashion, as shown in our study.

Particular efforts should be made to prevent zebra mussel introductions into headwater lakes of river drainages, because of the potential of veligers to disperse to downstream lakes. In a study of veliger mortality during downstream transport, Horvath and Lamberti (1999) found that many veligers leaving a southwestern Michigan lake were still alive 18 km downstream, although turbulence was suspected to have inflicted substantial instream mortality. At peak veliger transport, an estimated 800 million veligers flowed daily into a downstream mainstem river, of which approximately 144 million were at the

final larval stage ready for settling. Therefore, propagule numbers likely did not limit downstream dispersal in that system, and veligers probably can travel long distances in river flow (Schneider, Ellis & Cummings, 1998).

Understanding the factors that limit the downstream dispersal of zebra mussels and their larvae in small streams can aid in management and prevention efforts. If particular lakes or streams have been identified as ecosystems of concern with respect to the introduction of zebra mussels, management and prevention efforts can be focused on specific aspects of the system. Prevention efforts should first be concentrated on upstream lakes to prevent an initial introduction to a drainage basin that can then disperse throughout the entire drainage network. It is especially important to target boat accesses at these lakes of concern since recreational boaters are the most likely source of an initial invasion to a system. Management could also emphasize aquatic enhancement projects that include restoring wetlands, which appear to limit the spread of zebra mussels, or creating more rapid, turbulent stretches of stream to reduce veliger survival. Implementing suggested management strategies, however, requires a prioritization of lake-stream systems, the availability of funding sources, and an active response from communities to work to prevent the further spread of zebra mussels.

Incorporating the importance of stream connections into modeling and management efforts may improve predictions of future zebra mussel spread and impacts. On a regional scale, the primary means to model zebra mussel dispersal into inland lakes has been the use of gravity models, which model the overland movements of recreational boaters (Schneider, Ellis & Cummings, 1998; Bossenbroek, Kraft & Nekola, 2001). Bossenbroek, Kraft, and Nekola (2001), in particular, parameterized their gravity model based on the number of invaded lakes per US county without consideration of stream connections, and likely overestimated the contribution of overland dispersal by recreational boaters in producing the current distribution of zebra mussels. Particularly in regions with numerous interconnected lakes (*e.g.*, the upper Midwest), the influence of stream connections should be considered in projections of spread.

Secondary dispersal of zebra mussels from source lakes can result in new invaded lakes and impacts on streams. Our study suggests that headwater lakes with outflowing streams should be given the highest priority for prevention efforts to limit the spread and impacts of zebra mussels. Zebra mussels do not establish large populations in small streams, but the role of such streams in mussel dispersal has been greatly underestimated. A better understanding of the role that streams play as pathways for new invasions is crucial to improving management and prevention efforts.

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