

# Wetlands as barriers: effects of vegetated waterways on downstream dispersal of zebra mussels

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## SUMMARY

1. Stream flow is a major vector for zebra mussel spread among inland lakes. Veligers have been found tens to hundreds of km from upstream source lakes in unvegetated stream and river systems. It has been suggested, however, that the downstream transport of zebra mussels is restricted by wetland ecosystems. We hypothesized that vegetated waterways, (i.e. wetland streams) would hinder the downstream dispersal of zebra mussels in connected inland lake systems.

2. Veliger abundance, recruitment and adult mussels were surveyed in four lake-wetland systems in southeastern Michigan, U.S.A. from May to August 2006. Sampling was conducted downstream of the lakes invaded by zebra mussels, beginning at the upstream edge of aquatic vegetation and continuing downstream through the wetland streams.

3. Veliger abundance decreased rapidly in vegetated waterways compared to previously reported rates of decrease in non-vegetated streams. Veligers were rarely found more than 1 km downstream from where vegetation began. Newly recruited individuals and adults were extremely rare beyond open water in the wetland systems.

4. Densely vegetated aquatic ecosystems limit the dispersal of zebra mussels downstream from invaded sources. Natural, remediated and constructed wetlands may therefore serve as a protective barrier to help prevent the spread of zebra mussels and other aquatic invasive species to other lakes and ecosystems.

*Keywords:* *Dreissena polymorpha*, invasive species, source-sink dynamics, spread, veligers, wetlands

## Introduction

An understanding of zebra mussel [*Dreissena polymorpha* (Pallas)] dispersal mechanisms is needed to accurately predict future invasions of inland lakes. Since their introduction in the 1980s, zebra mussels have invaded more than 480 inland lakes throughout the United States (US Geological Survey), causing extensive economic costs (O'Neill, 1997; Pimentel, Zuniga & Morrison, 2005) and diminishing native mussel biodiversity (Schloesser & Nalepa, 1994; Ricciardi, Neves & Rasmussen, 1998; Strayer, 1999). Zebra mussels can disperse between inland lakes either by overland transport (Buchan & Padilla, 1999;

Johnson, Ricciardi & Carlton, 2001) or through stream connections (Horvath *et al.*, 1996; Kraft *et al.*, 2002). Research examining downstream dispersal has focused on rivers and streams (Horvath *et al.*, 1996; Horvath & Lamberti, 1999a,b; Bobeldyk *et al.*, 2005), but has generally disregarded connective wetland systems (but see Miller & Haynes, 1997). Hence, the goal of this study is to quantify the effects of wetland habitats on zebra mussel dispersal.

Overland transport by recreational boaters is the primary dispersal mechanism of zebra mussels (Buchan & Padilla, 1999; Bossenbroek, Kraft & Nekola, 2001; Johnson *et al.*, 2001); however, stream connectivity is responsible for an estimated one-third of all inland lake invasions (Johnson, Bossenbroek & Kraft, 2006). Lakes as far as 15 km downstream of an existing population have a high probability of being colonized by zebra mussels (Kraft *et al.*, 2002;

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Bobeldyk *et al.*, 2005). Veliger (zebra mussel larvae) abundance has been shown to decrease with distance in streams; however, veligers have been found 18 km downstream of an invaded lake in stream systems (Horvath & Lamberti, 1999b). Although recruitment (the settlement and survival of juvenile mussels) is low in streams, the presence of adult mussels varies considerably among locations, with few adults found more than 10 km downstream from a zebra mussel invaded lake (Horvath & Lamberti, 1999b; Bobeldyk *et al.*, 2005). In-stream zebra mussel populations are unlikely to be self-sustaining and are usually dependent on continuous recruitment from source populations of the upstream lake. Hence, coupled lake-stream systems sustain a source-sink model for zebra mussel dispersal (Horvath *et al.*, 1996; Bobeldyk *et al.*, 2005).

Lake-stream systems containing wetlands have been generally overlooked despite evidence that wetlands restrict the downstream transport of veligers (Miller & Haynes, 1997). Miller & Haynes (1997) suggest several potential reasons for the restriction of veligers. Veligers may be physically hampered because aquatic macrophytes can restrict veliger dispersal through reduced water velocity and particle retention (Miller & Haynes, 1997; Horvath, 2004). While filter feeding phytoplankton, adult zebra mussels may also reduce the number of veligers (Miller & Haynes, 1997). Furthermore, zebra mussel transport and colonization in wetlands may be restricted by large fluctuations in abiotic factors resulting in unsuitable conditions for zebra mussel survival. For example, wetlands generally have oxygen regimes that are different from those of open water systems, often experiencing marked diel cycles (Scott, 1924). Anoxic conditions are often a consequence of nocturnal respiration by photosynthesizing organisms (macrophytes, phytoplankton and periphyton) and of high decomposition rates amplified by warm water temperatures (Lingeman, Flik & Ringelberg, 1975; Pokorny, Hammer & Ondok, 1987). Since zebra mussel veligers require a minimum oxygen concentration of  $1.8 \text{ mg L}^{-1}$  (Sprung, 1993), anoxic events may limit colonization. Additionally, submersed aquatic vegetation can influence water temperatures, often increasing the mean annual temperature and the amplitude of daily fluctuations (Crisp, Matthews & Westlake, 1982). Water temperatures and pH beyond the ranges  $0\text{--}30 \text{ }^\circ\text{C}$  and  $7.4\text{--}9.4$ ,

respectively, are likely to render a site unsuitable for zebra mussel survival (Sprung, 1993).

To date, only one study of a single lake-wetland system has examined the possibilities of wetlands hindering the downstream transport of zebra mussel veligers (Miller & Haynes, 1997). Consequently, in the present study, we address the generality of wetland streams limiting downstream dispersal of zebra mussels in connected lake-stream systems. For the purpose of our study, wetlands were defined as connective waterways vegetated by aquatic macrophytes. We quantified zebra mussel presence throughout lake-wetland systems in southeastern Michigan, U.S.A. It was hypothesized that veliger densities would decline with geographic distance downstream throughout the wetland, causing a parallel decline in juvenile settlement and recruitment. The hypothesized reasons for these declines are (i) abiotic factors within wetlands render these ecosystems unsuitable for zebra mussel colonization, and/or (ii) zebra mussel dispersal is prevented by macrophyte particle retention.

## Methods

During May–September 2006, we surveyed four wetland systems in southeastern Michigan that are directly connected to upstream lakes invaded with zebra mussels. In each system, we examined veliger abundances, recruitment and adult mussel presence, as well as water chemistry (temperature, dissolved oxygen, conductivity and pH) and physical characteristics (depth, vegetation density). For each studied waterway, the initial sample site was located near the lake outlet at the upstream edge of vegetation, followed by several downstream sites distributed throughout the vegetated area.

### *Study locations*

Study sites were selected to provide wetlands that were (i) directly connected to an upstream zebra mussel invaded lake, (ii) vegetated by aquatic vegetation and (iii) accessible by waders, canoe, and/or boat. The four lake-wetland systems were located at Vineyard, Evans, Rush and Lower Pettibone Lakes (Table 1).

The outlet of Vineyard Lake flows through dense emergent wetland vegetation, with a conspicuous

**Table 1** Information on the lake-wetland study systems, including county, GPS coordinates, year of first zebra mussel (ZM) discovery, surface area, maximum depth, water velocity (flow) at the upstream edge of vegetation ( $d = 0$ ), and mean depth of the wetland

Lake-wetland system	County	GPS co-ordinates	Year of ZM discovery	Lake		Wetland	
				Surface area (Ha)	Max depth (m)	Flow @ $d = 0$ ( $\text{m s}^{-1}$ )	Mean depth (cm)
Vineyard	Jackson	42.10°N, 84.22°W	2000	204.5	12.8	0.038	66
Evans	Lenawee	42.05°N, 84.11°W	1998	81.0	12.8	0.114	52
Rush	Livingston	42.47°N, 83.88°W	1992	NA	NA	0.131	11
Lower Pettibone	Oakland	42.62°N, 83.61°W	2002	36.0	10.0	0.131	48

channel (average depth = 66 cm) remaining for the duration of the summer. Weedy, submergent and floating-leaved macrophytes grow in a sparse distribution within the channel, and the remainder of the wetland is dominated by emergent macrophytes including *Typha* spp. (cattails), *Nuphar* spp. (spatterdock), *Pontederia cordata* L. (pickerelweed), *Peltandra virginica* (L.) Schott (arrow arum) and *Juncus* spp. (rush).

The Evans Lake outlet is densely vegetated by *Nymphaea* spp. (white pond lily), *Nuphar* spp. and *Pontederia cordata*. A small dam (c. 1.0 m) separates the lake from the outlet. Once over the dam, the outlet enters a woody wetland with dense shrubs after about 10 m.

The Rush Lake outlet is a narrow (c. 0.5 m), meandering channel that passes through a wetland meadow densely vegetated with *Typha* spp. and wetland grasses. The average depth of this channel is 20 cm, and is subject to extremely low water levels during dry periods (<10 cm). After about 85 m, this channel merges with another surface water-fed stream.

Lower Pettibone Lake is located in the Highland State Recreation Area. The outlet is a small stream for about 128 m before entering a wetland densely vegetated with emergent macrophytes, particularly *Peltandra virginica*, *Nuphar* spp. and *Typha* spp. By late June, there was no indication of a visible channel.

### Veliger survey

To determine the dispersal distance of veligers through wetland streams, veliger densities were surveyed at five to seven sampling sites biweekly from May to August 2006 ( $n = 7$  dates). Sampling sites were distributed longitudinally throughout each sampling system beginning at the upstream edge of

vegetation (Table 2). To avoid sediment resuspension, all sampling took place from a canoe or boat, excluding the Rush Lake system where sampling was performed from downstream to upstream. At each sampling site, one sample was collected by passing 100 L of water through a 63- $\mu\text{m}$  mesh plankton net. Plankton samples were preserved in 70% ethanol.

Veligers were identified and enumerated under cross-polarized microscopy as described by Johnson (1995). Samples with high veliger, algae or sediment densities were subsampled using a Folsom Plankton Splitter. Veliger densities were recorded as veligers  $\text{m}^{-3}$ . Wilcoxon paired sample tests were used to test for significant differences between initial (upstream edge of vegetation, distance ( $d$ ) = 0) and final (furthest downstream,  $d$  = max) veliger densities across all sampling dates and systems. Initial samples from Vineyard and Pettibone Lakes were lost due to sample processing errors. Therefore, for the purpose

**Table 2** Distances (m) from the upstream edge of vegetation of sampling sites for veligers and adult recruitment in the wetland systems

Vineyard	Evans	Rush	Pettibone
0 <sup>†,¶</sup>	0	0	0 <sup>†,¶</sup>
73*	57	35 <sup>§</sup>	37
129	71 <sup>‡</sup>	63 <sup>§</sup>	62 <sup>‡</sup>
205*	474 <sup>§</sup>	79 <sup>§</sup>	89*
285		89 <sup>§</sup>	119
394*			166*
508			191

Substrate sampling for adult recruitment was conducted at the locations identified with an asterisk.

<sup>†</sup>Substrates had to be repositioned due to public interference.

<sup>‡</sup>Substrates were lost during the final week of the study.

<sup>§</sup>Substrates experienced low water and were periodically exposed to the air throughout the study period.

<sup>¶</sup>Veliger samples were discarded from analysis due to sample processing error.

of analysis, the next most up-stream samples were used as the initial veliger samples.

To determine the expected dispersal distance of veligers in wetland streams, veliger density data were used to estimate the drop-off distances (the distance at which veliger density = 0) for each wetland stream. Linear regression was used to predict veliger density at a given distance, specifically, the drop-off distances, such that:

$$\log(\text{veliger density}) = \text{distance} + \text{week}.$$

The log of veliger density was used to normalize the distribution of veliger densities. Due to large variation in veliger densities throughout the sampling season, date (Week) was included as a factor. Lower and upper 95% confidence limits of all mean responses were computed as the prediction  $\pm t$ -value  $\times$  standard error. Drop-off distances (i.e. where veliger density = 0) were predicted for each week and then averaged to produce a mean drop-off distance for each wetland stream. Minimum lower and maximum upper confidence limits were used as the overall interval range for each study system.

Dates of peak veliger density for each study system were used to estimate rates of veliger density decline in order to qualitatively compare rates of decline of each system to vegetation density. For these dates, veliger density of each sampling site was regressed against longitudinal distance. The negative slope ( $-m$ , where  $m$  = slope) of the best fit linear regression lines were defined as the rates of veliger density decline for that study system.

All models and statistical analyses were conducted using S-Plus 8.0 (Insightful Corp, 2007 Seattle, Washington, U.S.A.). For all statistical tests,  $\alpha$  was set at 0.05.

#### *Vegetation density*

In mid-July, vegetation density was measured in the wetlands downstream of Evans, Pettibone, Rush and Vineyard Lakes. Three to five belt transects ( $0.5 \times 3.0$  or  $0.5 \times 5.0$  m) were surveyed at randomly selected locations within each wetland. In channelized areas, transects began at the centre of the channel and extended towards one shore. The number of stems within each transect was counted and recorded as stems  $\text{m}^{-2}$ . To examine the relationship between

vegetation density and veliger dispersal, rates of veliger density decline were compared to the mean vegetation density and mean water velocity for each study system.

#### *Recruitment*

Artificial substrates were deployed throughout each wetland to measure zebra mussel recruitment (Table 2). Substrates were in place by late May and collected in October 2006. Substrates were composed of half-block ( $20 \times 20 \times 20$  cm) cement blocks, 0.75 cm (diameter) nylon rope, and 30 cm sections of 5 cm (diameter) PVC pipe (Adapted from Kraft, 1993). At Lower Pettibone Lake, paired substrates were placed at each sampling site, one substrate in the main channel and one in the dense macrophyte bed adjacent to the channel, to determine if there was a difference between these two habitat types. All parts of the substrate (anchor, rope, outer and inner PVC surface) were examined for newly recruited juvenile mussels (2006 cohort), as well as any adult mussels (2005 cohort and older) that had migrated to the substrate. Attached mussels were collected, preserved in 70% ethanol and counted. Due to public interference, some substrates were lost or had to be repositioned on several occasions. Additionally, some substrates were periodically exposed to the air during the study period (See Table 2 for details).

#### *Adult mussel survey*

Surveys were conducted to determine the presence of adult mussels within a 1 m radius of each sampling site. All available substrate (rocks, gravel, logs, macrophytes, etc.) were examined for attached mussels. Low visibility due to sediment resuspension limited surveying methods to either detection by hand, or by using a glass-bottom bucket from a canoe. Any adult mussels incidentally observed at non-sampling sites were also noted. Substrate selection did not differ greatly between study systems, and was primarily limited to macrophytes and occasional woody debris.

#### *Water parameters*

On each sampling occasion, dissolved oxygen, pH, specific conductivity and temperature were measured at mid-depth using an YSI® Model 556 Multi-Probe

System (YSI, Inc., Yellow Springs, OH, U.S.A.). Water parameters were compared to known zebra mussel tolerance ranges as described by Sprung (1993).

Stepwise multiple regression was used to determine what water parameters and abiotic factors were significant predictor variables of veliger density declines in wetland ecosystems. The temporal variation in veliger densities was normalized by using the proportion of initial veliger density ( $V_x/V_0$ ) as the dependent variable instead of raw density.  $V_x/V_0$  is defined as the density of veligers at distance  $x$  divided by veliger density at distance 0, or the percent of veligers dispersing downstream to distance  $x$ . Stepwise backward multiple regression analyses were used to create models to explain variance in  $V_x/V_0$  based on water parameters and abiotic factors (date, distance, temperature, dissolved oxygen, pH and distance interaction factors).

## Results

### Veliger survey

Veliger abundances were significantly higher at the initial sampling sites compared to the final sites (Wilcoxon paired sample test,  $P < 0.0005$ ). Distance and sampling date were significant factors for predicting veliger drop-off distances (distance at which veliger density = 0) for all sampling locations (Table 3). The Vineyard Lake system had the greatest predicted drop-off distance of 4229 m. Pettibone, Evans and Rush Lakes had estimated drop-off distances at 990 m, 473 m and 251 m, respectively (Table 4). Evans Lake and Pettibone Lake generally had higher initial veliger densities than Vineyard

**Table 4** Mean predicted veliger drop-off distance (where veliger density = 0) for each wetland system. Range consists of minimum lower 95% confidence limit and maximum upper 95% confidence limit

Study system	Predicted drop-off distance (m)	Range
Vineyard	4229	2200–10000
Evans	473	120–1180
Rush	251	120–1040
Lower Pettibone	990	440–1960

and Rush Lakes. Rush Lake had the slowest rate of veliger density decline ( $-m = -0.21$ ), while the highest rate of veliger density decline occurred at Pettibone Lake ( $-m = 14.36$ , Fig. 1).

### Recruitment

Recruitment in the wetland streams was limited. A total of 106 settled zebra mussels were found on the substrate samplers at Vineyard, Rush, Pettibone and Evans Lakes, all of which were located within 150 m of the upstream edge of vegetation (Fig. 2). No adult mussels were found at the final sampling sites in any system. Vineyard Lake had the highest recruitment, totalling 60 mussels, all of which were found on the two most upstream substrates. At Vineyard Lake, additional zebra mussel individuals were located near the first sampling site, both on rocks and attached to the upstream side of a dam wall 2 m upstream of the sampling site. Evans Lake had relatively high recruitment with a total of 31 mussels attached to the first sampling substrate together with additional mussels found on submerged tree branches in this system. No

**Table 3** Coefficients and  $P$ -values for the linear regression models for each lake. The regression models were in the form:  $\log(\text{Veliger number}) = \text{distance} + \text{week}$ . These values were used to predict veliger drop-off distances shown in Table 4

Factor	Vineyard Lake		Evans Lake		Rush Lake		Lower Pettibone	
	Coefficient	$P$ -value	Coefficient	$P$ -value	Coefficient	$P$ -value	Coefficient	$P$ -value
Intercept	6.0995	0.0000	7.7141	0.0003	5.1198	0.0000	8.6598	0.0000
Distance	-0.0015	0.0101	-0.0126	0.0031	-0.0253	0.0092	-0.0063	0.0000
Week 2	0.6384	0.0000	NA	NA	-0.517	0.5983	NA	NA
Week 3	1.7037	0.0059	-1.3672	0.3537	1.3145	0.2158	-1.0312	0.0001
Week 4	0.6892	0.0057	NA	NA	0.6695	0.4959	-1.1149	0.0002
Week 5	-0.6919	0.0000	-4.2983	0.0168	3.1662	0.0053	-3.1849	0.0000
Week 6	-1.1732	0.0000	NA	NA	1.1445	0.2488	-5.1439	0.0000
Week 7	-1.2412	0.0011	NA	NA	0.651	0.5323	-4.3171	0.0000

mussels were found downstream of the first sampling site. The Lower Pettibone Lake substrates had a total of 11 attached mussels, and there was no significant difference ( $t$ -test,  $P = 0.68$ ) between in-channel and macrophyte placed substrates. Zebra mussel colonies were present in a culvert and nearby rocks just upstream of where sampling began in the Lower Pettibone outlet stream. Additionally, a few individuals were found near the second sampling site of Pettibone Lake (c. 73m downstream of the initial in-stream vegetation). However, no recruitment was observed beyond 130 m. Recruitment at Rush Lake was low, totalling only six mussels attached to the first substrate. No additional adult mussels were found during the surveys.

#### Water parameters

Although mean values of the observed water parameters were within the known tolerance ranges of zebra mussel veligers, one site experienced abiotic conditions that were outside the tolerable range (Table 5). Evans Lake had a pH range of 7.21–11.15, exceeding the published pH tolerance range of 7.4–9.4. The minimum value of dissolved oxygen concentrations dipped to  $0.63 \text{ mg L}^{-1}$  at Evans Lake, which is below the critical limit of  $1.8 \text{ mg L}^{-1}$ .

Stepwise regression analyses showed that distance and water parameters explained 18.8% of the variation in  $V_x/V_0$  (backward stepwise regression,  $R^2 = 0.19$ ,  $P = 0.07$ ) based on the following model:

$$\frac{V_x}{V_0} = 3.10144 - 0.0028\text{distance}_x - 0.63\text{DO}_x - 0.22\text{pH}_x + 0.00023\text{distance}_x * \text{DO}_x.$$

#### Vegetation density

Vegetation densities ranged from 0 to  $203 \text{ stems m}^{-2}$  across all sampled waterways. The Rush Lake system had no in-stream vegetation and a mean vegetation density of  $0 \text{ stems m}^{-2}$ . Pettibone Lake had the most vegetation, reaching densities of  $203 \text{ stems m}^{-2}$  and a mean vegetation density of  $123 \text{ stems m}^{-2}$ . Vineyard and Evans Lakes had mean vegetation densities of 52 and  $91 \text{ stems m}^{-2}$ , respectively. Vegetation densities were positively related to the rate of veliger density decline for each site ( $R^2 = 0.77$ ,  $P = 0.12$ , Fig. 1), but there was no

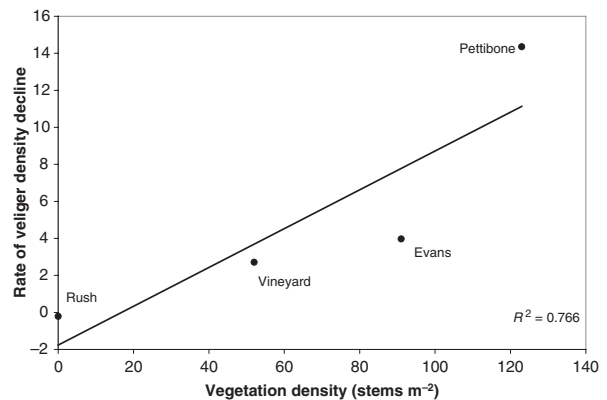


Fig. 1 Rate of veliger decline regressed against vegetation density of each study system. The rate of veliger density decline was defined as  $-m$ , where  $m$  = slope of the regression line of veliger density against distance for the date of peak veliger density.

relationship between water velocity and the rate of veliger density decline ( $R^2 = 0.02$ ,  $P = 0.88$ ).

#### Discussion

Our study revealed that wetland streams limited the dispersal of zebra mussels in lake-stream systems. To our knowledge, this is the first study to quantify the importance of wetlands in slowing the dispersal of an invasive species. Veliger density, recruitment and the presence of adult mussels declined within the areas studied. In three of the four wetland streams examined, veligers declined to zero within about 1 km from the upstream edge of vegetation. Indeed, Evans and Rush Lakes had predicted drop-off distances within

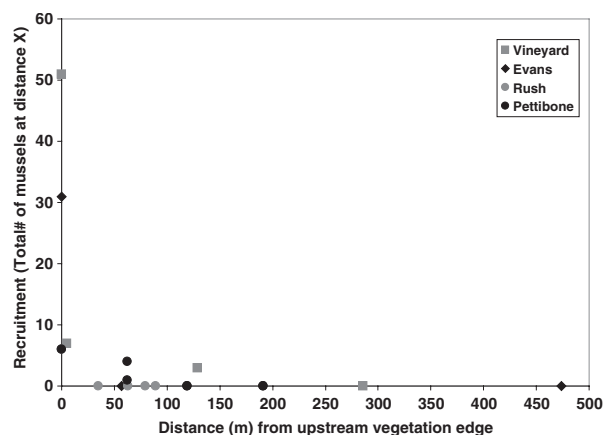


Fig. 2 Zebra mussel recruitment for wetlands at distances from the upstream edge of vegetation ( $d = 0$ ).

**Table 5** Values for selected water quality parameters of each studied wetland

Water parameter	Vineyard mean (range)	Evans mean (range)	Rush mean (range)	Pettibone mean (range)
Temperature (°C)	24.61 (21.97–26.52)	25.02 (22.23–28.84)	23.40 (17.96–26.47)	25.09 (22.23–28.84)
SpCond (mS cm <sup>-1</sup> )	0.47 (0.41–0.55)	0.33 (0.30–0.41)	0.57 (0.48–0.66)	0.71 (0.662–0.779)
DO (mg L <sup>-1</sup> )	6.78 (3.75–10.64)	5.73 (0.63–12.03)*	6.47 (2.66–11.54)	9.27 (6.89–11.74)
pH	7.93 (7.61–8.86)	7.98 (7.21–11.15)*	7.88 (7.51–8.68)	8.31 (8.01–8.82)

\*Values exceeding published zebra mussel veliger tolerance range (Sprung, 1993).

500 m (Table 4). These distances are considerably shorter than the 18 km found in unvegetated stream systems (Horvath & Lamberti, 1999a). The dispersal distance of 18 km in unvegetated streams is likely to be an underestimate of potential distribution since further inference could not be made in Horvath & Lamberti's (1999a) study due to the stream merging with another invaded river. Furthermore, dispersal distances in larger river systems have been recorded as far downstream as 304.6 km (Stoeckel *et al.*, 1997). In comparison, our estimate of veliger dispersal distance through wetlands of about 1 km is remarkably small. Zebra mussel recruitment was also lower than expected, given low veliger densities. Studies examining connective non-vegetated stream systems found adult zebra mussels as far as 10 km downstream of an invaded source lake (Horvath & Lamberti, 1999b; Bobeldyk *et al.*, 2005). In contrast, in our study recruitment numbers declined to zero within 200 m. Adult mussels were even less abundant than recruited juveniles, suggesting that post-settlement juveniles are subject to elevated mortality rates. In addition, no lakes or ponds immediately downstream of the studied lake-wetland systems have yet been reported as zebra mussel invasions, adding further support to our hypothesis of dispersal restriction by wetlands. A number of factors may explain the declines in zebra mussel densities in wetlands systems, including aquatic vegetation, decreased water velocity, unsuitable water characteristics, limited substrate availability, and/or increased predation pressure.

Macrophytes may cause the decline in veliger density because they retain coarse particulate matter and decrease water velocity, which may cause particles to settle out of suspension (Horvath, 2004). It is possible that macrophytes have these same effects on zebra mussel veligers, increasing veliger residence time in a wetland environment. There was no

relationship between water velocity and the rate of veliger density decline for each site ( $R^2 = 0.02$ ,  $P = 0.88$ ). However, densely vegetated wetlands (Pettibone Lake, 123 stems m<sup>-2</sup>; Evans Lake, 91 stems m<sup>-2</sup>) had the highest rates of veliger density decline, indicating that zebra mussel veligers experienced greater resistance during downstream dispersal when dense aquatic vegetation was present. In the channelized wetland system (Vineyard Lake), vegetation was sparse in the main channel and vegetation densities averaged 52 stems m<sup>-2</sup>. Vineyard Lake did, however, have the second slowest rate of veliger density decline and the longest drop-off distance. A comparison of the rates of veliger density decline to vegetation densities suggests that vegetation density influences veliger downstream dispersal. Indeed, the wetland with the densest vegetation had the slowest rate of veliger dispersal.

Since recruitment in dense macrophyte beds did not differ significantly from in-channel recruitment at Lower Pettibone Lake (*t*-test,  $P = 0.68$ ), it is likely that other factors also influence zebra mussel recruitment in wetland systems. Distance, dissolved oxygen, and pH, accounted for about 19% of the variation in longitudinal changes in veliger densities based on the step-wise regression model. Measured water parameters showed only minimal deviation from the known tolerance ranges; however, diel fluctuations were not measured in this study. The unexpected negative effect of dissolved oxygen on veliger abundance is a likely result of diel fluctuations. A large population of photosynthesizing organisms can produce high concentrations of oxygen during the day, but can also consume more oxygen for respiration during hours of darkness, resulting in anoxic events (Lingeman *et al.*, 1975; Pokorny *et al.*, 1987). Furthermore, low concentrations of dissolved oxygen and high concentrations of dissolved carbon dioxide often lower pH levels. If pH levels fell below 7.4, conditions would no longer

be favourable for zebra mussels. Diel fluctuations in dissolved oxygen, and consequently fluctuations in pH, should be further examined as causes of zebra mussel mortality in wetland systems.

Lack of suitable substrate in wetland streams may result in veliger mortality and low recruitment. The artificial substrates used in this study sometimes sank into the sediment and were often subject to sedimentation and growth of algae, both of which inhibit zebra mussel colonization (Sprung, 1993). Additionally, sedimentation on substrate surfaces may obstruct filtering by zebra mussels, thus reducing food intake (Yankovich & Haffner, 1993). Although veligers have been shown to settle on macrophytes, the senescence of plant material with the onset of cooler weather and shorter day lengths can cause zebra mussels to seek other substrates (B.L. Bodamer, unpubl. data). It is thus unlikely that substrates in wetland systems, including aquatic vascular plants, remain suitable for zebra mussel colonization for extended periods of time.

Higher zebra mussel predation in wetlands compared to in-stream environments may also reduce zebra mussel recruitment success. In our wetland systems, we frequently observed crayfish and turtles inhabiting the artificial substrates (B.L. Bodamer, pers. obs.), and both are known to prey on zebra mussels (Love & Savino, 1993; Serrouya, Ricciardi & Whoriskey, 1995; Perry, Lodge & Lamberti, 1997; Bulté & Blouin-Demers, 2008). Wetlands also provide key habitat for muskrats (*Ondatra zibethicus* L.), common carp (*Cyprinus carpio* L.), sunfish (*Centrarchidae*), and waterfowl, all of which consume zebra mussels (Tucker, Cronin & Soergel, 1996; Petrie & Knapton, 1999; Sietman *et al.*, 2003). High densities of zebra mussel predators in wetlands may affect recruitment rates, reducing adults and settled juveniles, thus limiting the ability of zebra mussels to invade downstream lakes.

Identifying lakes at a high risk of zebra mussel invasion will improve effective ecological management and prevention efforts. The results from this study can augment modelling efforts to increase accuracy when predicting future invasions (e.g. Bossenbroek *et al.*, 2007). This study suggests that densely vegetated waterways hinder the downstream spread of zebra mussels (both adults and veligers). Therefore, currently existing wetlands, wetland construction and remediation, and the discontinuation of wetland

dredging and channelization, may function to prevent the spread of zebra mussels to uninvaded lakes, reservoirs, and other aquatic ecosystems from upstream sources. Vegetated waterways with high vegetation density and a longitudinal distance of 1 km or greater would probably be effective in preventing the spread of zebra mussels between connected inland lakes. The ability to predict wetland effectiveness could be improved by research defining the relationship between zebra mussel abundances (at all stages of the life cycle) and vegetation type, density, water velocity, depth, and so on, across a broad range of system types.

Wetlands provide an important limitation to the spread of zebra mussels among inland lakes, adding to the multitude of known environmental benefits of wetlands (including flood and erosion control, ground water recharge and discharge, important fisheries and wildlife habitat, and natural filter of nutrients and pollutants). Preventing zebra mussel spread to uninvaded ecosystems will help preserve native biotic communities (including protecting dwindling unionid mussel populations) and limit the economic costs due to the fouling of industrial and recreational structures. Additionally, if wetland streams are capable of hindering zebra mussel spread, they may also prevent the spread of other aquatic invaders, particularly those with a planktonic larval stage. For example, it is likely that wetlands would also impede the dispersal of the zebra mussel's sister species, the quagga mussel (*Dreissena bugensis* Andrusov). Other invasive species, such as crayfish, may be affected by the frequent periods of low oxygen common in wetland systems, and hence prevent them from passing through and invading new areas. By preventing the spread of invasive species, wetlands protect the native species and biodiversity of wetlands and other aquatic ecosystems further downstream.

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