The effects of wetland streams on the secondary dispersal of zebra mussels (Dreissena polymorpha) in connected lake-stream systems

Betsy L. Bodamer
The University of Toledo

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A Thesis

Entitled

The effects of wetland streams on the secondary dispersal of zebra mussels

(Dreissena polymorpha) in connected lake-stream systems

By

Betsy L. Bodamer

Submitted as partial fulfillment of the requirements for

The Master of Science Degree in Biology (Ecology-track)

Advisor: Dr. Jonathan M. Bossenbroek

Committee Member: Dr. Christine M. Mayer

Committee Member: Dr. Johan F. Gottgens

College of Graduate Studies

The University of Toledo

December 2007
An Abstract of

The effects of wetland streams on the secondary dispersal of zebra mussels
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Stream flow is a major vector for zebra mussel spread among inland lakes. I hypothesized that vegetated waterways, i.e. wetland streams, would hinder downstream dispersal of zebra mussels in connected inland lake systems. To test this hypothesis, veliger (larva) abundance, recruitment, and adult mussels were surveyed in four lake-wetland systems in southeastern Michigan, USA from May through August 2006. Sampling was conducted downstream of the zebra mussel invaded lakes, beginning at the upstream edge of aquatic vegetation and continuing downstream through the wetland streams. Results showed that veliger abundance decreased rapidly in vegetated waterways compared to their 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 study systems. These results suggest that 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.
Acknowledgements

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Chapter One

Introduction

An understanding of zebra mussel (*Dreissena polymorpha*) dispersal mechanisms is needed to accurately predict future invasions of inland lakes. Since their introduction in the 1980s, zebra mussels have invaded more than 390 inland lakes throughout North America (Johnson et al. 2006), causing extensive economic costs (O’Neill 1997; Pimentel et al. 2005) and diminishing native mussel biodiversity (Schloesser and Nalepa 1994; Ricciardi et al. 1998; Strayer 1999). Zebra mussels can disperse between inland lakes either by overland transport (Buchan and Padilla 1999; Johnson et al. 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 and Lamberti 1999; Bobeldyk et al. 2005), but has generally disregarded connective wetland systems (but see Miller and Haynes 1997). Hence, the goal of this study is to quantify the effects of wetland stream habitats on zebra mussel dispersal.

Overland transport by recreational boaters is the primary dispersal mechanism of zebra mussels (Buchan and Padilla 1999; Bossenbroek et al. 2001; Johnson et al. 2001); however, stream connectivity is responsible for an estimated one third of all inland lake
invasions (Johnson et al. 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; Bobeldyk et al. 2005). Veliger (larvae) abundance has been shown to decrease with distance in streams; however, veligers can still be found as far as 18 km downstream of an invaded lake in stream systems (Horvath and Lamberti 1999) and 304.6 km downstream in larger river systems (Stoeckel et al. 1997). 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 infested lake (Horvath and 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 widely overlooked despite evidence that suggests wetlands restrict the downstream transport of veligers (Miller and Haynes 1997). Miller and Haynes (1997) suggest several potential reasons for the restriction of veligers. Veligers may be physically hampered by the biota because aquatic macrophytes can restrict veliger dispersal through reduced water velocity and particle retention (Miller and Haynes 1997; Horvath 2004). Adult zebra mussels may also reduce the number of veligers continuing downstream by filtering out veligers along with phytoplankton while filter feeding (Miller and Haynes 1997). Furthermore, zebra mussel transport and colonization may be restricted by large fluctuations in abiotic factors that may result 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 (i.e. macrophytes, phytoplankton, and periphyton) and high decomposition rates amplified by warm water temperatures (Pokorný et al. 1987, Lingeman et al. 1975). Since zebra mussel veligers require a minimum oxygen concentration of 1.8 mg/L (Sprung 1993), anoxic events may limit colonization. Additionally, submerged aquatic vegetation can influence water temperatures, often increasing the mean annual temperature and the amplitude of daily fluctuations (Crisp et al. 1982). Water temperatures and pH outside of 0-30°C and 7.4-9.4 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 and Haynes 1997). Consequently, in the present study, I address the generality of wetland streams limiting downstream dispersal of zebra mussels in connected lake-stream systems. For the purpose of my study, wetland streams were defined as connective waterways vegetated by aquatic macrophytes. Veliger abundance, recruitment, and adult presence of zebra mussels were quantified throughout four lake-wetland stream systems in southeastern Michigan. I hypothesized that veliger densities would decline with geographic distance downstream throughout the wetland stream, causing a parallel decline in juvenile settlement and recruitment. The hypothesized reasons for these declines are 1) abiotic factors within wetlands that render these ecosystems unsuitable for
zebra mussel colonization, and/or 2) the prevention of zebra mussel dispersal due to macrophyte particle retention.
Chapter Two

Methods

During the summer (May – September) of 2006, I surveyed four vegetated waterway (wetland) systems in southeastern Michigan that are directly connected to upstream lakes invaded with zebra mussels. In each system, I 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

Each system in this study had to be a vegetated waterway directly connected to an upstream zebra mussel infested lake and accessible by waders, canoe, and/or boat. Four wetland systems, located downstream of Vineyard, Evans, Rush, and Lower Pettibone Lakes were chosen as study locations (Table 1).

The outlet of Vineyard Lake passes through dense emergent wetland vegetation, with a conspicuous 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* (cattails), *Nuphar* (spatterdock), *Pontederia* (blue pickerel rush), *Peltandra* (arrow arum) and *Juncus* (common rush).

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

The Rush Lake outlet is a narrow (~0.5 m), meandering channel that passes through a wetland meadow that is densely vegetated by *Typha* 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 ~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 ~128 m before entering a wetland, which is densely vegetated with emergent macrophytes, particularly *Peltandra*, *Nuphar*, and *Typha*. By late June, there was no indication of a visible channel. Depth throughout the wetland averaged 48 cm.

A fifth study system was sampled, Big Portage Lake, located in the Waterloo State Recreation Area. However, sampling sites within this system were located within the lake and not from the small unvegetated outlet. Due to the lack of vegetation in the outlet and location of the sampling sites, Portage Lake was considered a different type of system, differing from the other four “similar” sampling locations in vegetation patterns.
and veliger abundance trends. Hence, Big Portage Lake was excluded from further analyses.

**Veliger Survey**

To determine the dispersal distance of veligers through wetland streams, I surveyed veliger densities biweekly from May through August 2006 (n = 7 dates). Five to seven sampling sites were distributed longitudinally throughout each sampling system (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, 100 L of water was passed through a 63-μm mesh plankton net. Plankton samples were preserved in 70% EtOH. Initial samples from Vineyard and Pettibone Lakes were lost due to sample processing errors. For the purpose of analysis, the next most up-stream samples were used as the initial veliger samples.

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 for each sample as veligers/m$^3$. A Wilcoxon paired sample test was used to test for a significant difference between initial (upstream edge of vegetation, distance (d) = 0) and final (furthest downstream, d = max) veliger densities across all sampling dates and systems.

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 (log(Vel) = Distance + Week) was used to predict veliger density at a given distance, specifically, the drop-off
Due to large variation in veliger densities among sampling events, the linear regression models included week (sampling event) as a factor. Lower and upper 95% confidence limits of all mean responses were computed as the prediction ± t-value*standard error. Drop-off distances (i.e. where log(Vel) = 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 (-1m, where m = slope) of the best fit linear regression lines were defined as the rates of veliger density decline for that study system.

Linear models used for distance predictions were analyzed using S-Plus 8.0 (Insightful Corp., Seattle, Washington, USA). Regression slopes and rates of veliger density decline were formulated by SAS 9.1 (SAS Institute Inc., Cary, North Carolina, USA). For all statistical tests, α was set at 0.05.

**Vegetation Density**

In mid-July, vegetation density was measured at Evans, Pettibone, Rush, and Vineyard Lakes. Three to five belt transects (0.5 x 3.0 or 0.5 x 5.0 m) were surveyed at randomly selected locations within each wetland stream. In channelized areas, transects began at the center of the channel and extended towards one shore. The number of stems within each transect were counted and recorded as stems/m². To examine the relationship
between vegetation density and veliger dispersal, rates of veliger density decline (\( -1m, m = \) slope of the density regression line) were compared to the mean vegetation density and mean water velocity for each study system.

**Recruitment**

Artificial substrates were deployed throughout each wetland stream to measure zebra mussel recruitment. Substrates were composed of half-block (20x20x20 cm) cement blocks, 0.75 cm (diameter) nylon rope, and 30 cm sections of 5 cm (diameter) PVC pipe (Adapted from Kraft 1993). These substrates were deployed throughout each sampling system at most veliger sampling sites (Table 2). 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. Substrates were deployed for the duration of the study period and collected in October 2006. I examined all parts of the substrate (anchor, rope, outer, and inner PVC surface) 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% EtOH, 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 air throughout 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. I examined all available substrate (rocks, gravel, logs, macrophytes, etc.) 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 sporadic woody debris.

**Water Parameters**

For every sampling event, dissolved oxygen, pH, specific conductivity, and temperature were measured at mid-depth using an YSI® Model 556 Multi-Probe System (YSI, Inc., Yellow Springs, Ohio, USA). 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 was used to create a model 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).
Chapter Three

Results

Veliger Survey

Veliger abundances were significantly higher at the initial sampling sites compared to the final sites (Wilcoxon paired sample test, \( p < 0.0005 \)). Veliger drop-off distances (distance at which veliger density = 0) were estimated by regressing averaging veliger densities against distance and sampling date, which were significant 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 and Rush Lakes. Rush Lake had the slowest rate of veliger density decline (-1m = -0.21), and the highest rate of veliger density decline occurred at Pettibone Lake (-1m = 14.36, Figure 1).

Recruitment

Recruitment in the wetland streams was limited. A total of 106 zebra mussels were found on the substrate samplers at Vineyard, Rush, Pettibone and Evans Lakes, all of which were located within 150 m from the upstream edge of vegetation (Figure 2). No
adult mussels were found at the final sampling sites in any system. Vineyard Lake had the highest recruitment, totaling 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 along with additional mussels found on submerged tree branches in this system. No 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 (~73 m downstream of the initial in-stream vegetation), however no recruitment was observed beyond 130 m. Recruitment at Rush Lake was low, totaling only 6 mussels attached to the first substrate. No additional adult mussels were found during the surveys.

**Water Parameters**

The mean values of the observed water parameters were inside the known tolerance ranges of zebra mussel veligers (Table 5). Evans Lake experienced abiotic conditions that were outside of the tolerable range. 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 mg/L at Evans Lake, which is below the critical limit of 1.8 mg/L.
Stepwise regression analyses were conducted to determine the amount of variance in the proportion of initial veliger density ($V_x / V_0$) explained by abiotic factors. Distance and water parameters explained 18.77% of the variation in $V_x / V_0$ (backward stepwise regression, $R^2 = 0.19$, $p = 0.07$) based on the following model:

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

**Vegetation Density**

Vegetation densities ranged from 0 to 203 stems/m$^2$ across all sampled waterways. The Rush Lake system had no in-stream vegetation and a mean vegetation density of 0 stems/m$^2$. Pettibone Lake had the most vegetation, reaching densities of 203 stems/m$^2$ and a mean vegetation density of 123 stems/m$^2$. Vineyard and Evans Lakes had mean vegetation densities of 52 and 91 stems/m$^2$, respectively. Vegetation densities were positively regressed with the rate of veliger density decline for each site ($R^2 = 0.77$, $p = 0.12$, Figure 1), however there was no relationship between water velocity and the rate of veliger density decline ($R^2 = 0.02$, $p = 0.88$).
Chapter Four

Discussion

Wetland streams limited the dispersal of zebra mussels in lake-stream systems. Veliger density, recruitment, and the presence of adult mussels declined within the areas studied (Figures 1 & 2). In three of the four wetland streams examined, veligers were found to drop off within ~1 km from the upstream edge of vegetation. Evans and Rush Lakes had predicted drop-off distances within 500 m (Table 4). These distances are considerably shorter than the 18 km found in unvegetated stream systems (Horvath and Lamberti 1999a). Additionally, zebra mussel recruitment was even lower than expected, given low veliger densities. Studies examining connective non-vegetated stream systems found zebra mussels as far as 10 km downstream from an invaded source (Horvath and Lamberti 1999b, Bobeldyk et al. 2005). In wetland streams, however, recruitment numbers declined to zero within 200 m (Figure 2). Adult mussels were even less abundant than recruited juveniles, suggesting that post-settlement juveniles are subject to high mortality rates. These declines in zebra mussel densities may be due to decreased water velocity, aquatic vegetation, unsuitable water characteristics, and/or increased predation pressure.
Macrophytes may cause the decline in veliger density because macrophytes retain coarse particulate matter (Horvath 2004). Additionally, macrophytes decrease water velocity that may further cause particles to settle out of suspension (Horvath 2004). It is possible that macrophytes have these same effects on zebra mussel veligers, increasing the time in which veligers are subjected to 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$^2$; Evans Lake, 91 stems/m$^2$) had the highest rates of veliger density decline (Figure 1), 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 within the main channel and vegetation densities averaged 52 stems/m$^2$. Vineyard Lake did, however, have the second slowest rate of veliger density decline and the longest drop-off distance (Figure 1, Table 4). A comparison of the rates of veliger density decline to vegetation densities (Figure 1) supports the hypothesis that vegetation density influences veliger travel during downstream dispersal. Specifically, with increasing vegetation density, the distance in which veligers disperse downstream decreases (Figure 1, $R^2 = 0.77$, $p =0.12$).

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. Measured abiotic factors accounted for ~19% of the variation in longitudinal changes in veliger densities based on the step-wise regression model. Distance, dissolved oxygen, and pH were the most influential factors in veliger abundances, all having negative effects on veliger
density. Evans Lake experienced oxygen and pH measurements outside of known zebra mussel tolerance ranges (Table 5); however, these values did not result in low recruitment relative to the other study sites (Figure 2). Although the measured water parameters showed only minimal deviation from the known tolerance ranges, diel fluctuations were not measured in this study.

Dissolved oxygen has a negative effect on veliger abundance based on the regression model, however, it is possible that resulting anoxic events are causing the negative aspect to this parameter. Diel fluctuations in dissolved oxygen often result in low concentrations of dissolved oxygen or anoxia in the absence of photosynthesis during hours of darkness (Lingeman et al. 1975; Pokorný et al. 1987). A large population of photosynthesizing organisms produces high concentrations of oxygen during the day, but also consumes more oxygen for respiration during hours of darkness. Therefore, high daytime concentrations of dissolved oxygen can reflect the consequences of low nighttime dissolved oxygen concentrations. Additionally, low concentrations of dissolved oxygen and high concentrations of dissolved carbon dioxide often lower pH levels. If pH levels were drawn below 7.4, conditions would no longer be favorable 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 extensive sedimentation and algae growth, which inhibit zebra mussel colonization (Sprung 1993). Additionally, sedimentation on substrate surfaces may obstruct filtering by zebra mussel, thus reducing food intake
(Yankovich and 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 (Bodamer, unpublished 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.

Wetlands may have a higher concentration of zebra mussel predators compared to lakes. Crayfish and turtles were often found inhabiting the artificial substrates (Bodamer, pers. obs.), and both are known to prey on zebra mussels (Love and Savino 1993; Serrouya et al. 1995; Perry et al. 1997). Wetlands also provide key habitat for muskrats, waterfowl, carp, and sunfish, all of which eat zebra mussels (Petrie and Knapton 1999; Sietman et al. 2003). High concentrations of zebra mussel predators in wetlands may impact recruitment rates, reducing adults and settled juveniles, thus limiting the ability of zebra mussels to invade downstream lakes.

Knowing which lakes are at greatest risk of becoming invaded by zebra mussels will improve effective ecological management and prevention efforts. The results from this study can augment modeling efforts to increase accuracy for predicting future invasions (i.e. Bossenbroek et al. 2001). This study suggests that densely vegetated waterways hinder the downstream spread of zebra mussels. 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 $\geq 1$ km
would likely 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 life cycles) and vegetation type, density, water velocity, depth, etc. 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 their known environmental benefits (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.
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VI. Tables

Table 1: Information on the upstream lakes of the study systems, including county, GPS coordinates, year of first zebra mussel discovery, surface area, and maximum depth.

<table>
<thead>
<tr>
<th>Lake</th>
<th>County</th>
<th>GPS Coordinates</th>
<th>Year of ZM discovery</th>
<th>Surface Area (Ha)</th>
<th>Max Depth (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vineyard</td>
<td>Jackson</td>
<td>42.10°N, 84.22°W</td>
<td>2000</td>
<td>204.5</td>
<td>12.8</td>
</tr>
<tr>
<td>Evans</td>
<td>Lenawee</td>
<td>42.05°N, 84.11°W</td>
<td>1998</td>
<td>81.0</td>
<td>12.8</td>
</tr>
<tr>
<td>Rush</td>
<td>Livingston</td>
<td>42.28°N, 83.52°W</td>
<td>1992</td>
<td>53.3</td>
<td>20.0</td>
</tr>
<tr>
<td>Lower Pettibone</td>
<td>Oakland</td>
<td>42.62°N, 83.61°W</td>
<td>2002</td>
<td>36.0</td>
<td>10.0</td>
</tr>
</tbody>
</table>
Table 2: Distances (m) from the upstream edge of vegetation of sampling sites for veligers and adult recruitment in the wetland systems. Substrate sampling for adult recruitment was conducted at the locations identified with an *.

<table>
<thead>
<tr>
<th>Vineyard</th>
<th>Evans</th>
<th>Rush</th>
<th>Pettibone</th>
</tr>
</thead>
<tbody>
<tr>
<td>0(^{1,2,4})</td>
<td>0</td>
<td>0</td>
<td>0(^{1,2})</td>
</tr>
<tr>
<td>73*</td>
<td>57</td>
<td>35(^3)</td>
<td>37</td>
</tr>
<tr>
<td>129</td>
<td>71(^2)</td>
<td>63(^3)</td>
<td>62(^2)</td>
</tr>
<tr>
<td>205*</td>
<td>474(^3)</td>
<td>79(^3)</td>
<td>89*</td>
</tr>
<tr>
<td>285</td>
<td>89(^3)</td>
<td></td>
<td>119</td>
</tr>
<tr>
<td>394*</td>
<td></td>
<td>166*</td>
<td></td>
</tr>
<tr>
<td>508</td>
<td></td>
<td></td>
<td>191</td>
</tr>
</tbody>
</table>

Note:  
1. Substrates had to be repositioned due to public interference.  
2. Substrates were lost during the final week of the study.  
3. Substrates experienced low water and were periodically exposed to air throughout the study period.  
4. Veliger samples were discarded from analysis due to sample processing error.
Table 3: Coefficients and $p$-values for the linear regression models for each lake. The regression models were in the form: log(Veliger number) = Distance + Week. These values were used to predict veliger drop-off distances shown in Table 4.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Vineyard Lake</th>
<th>Evans Lake</th>
<th>Rush Lake</th>
<th>Lower Pettibone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coefficient</td>
<td>$p$-value</td>
<td>Coefficient</td>
<td>$p$-value</td>
</tr>
<tr>
<td>Intercept</td>
<td>6.0995</td>
<td>0.0000</td>
<td>7.7141</td>
<td>0.0003</td>
</tr>
<tr>
<td>Distance</td>
<td>-0.0015</td>
<td>0.0101</td>
<td>-0.0126</td>
<td>0.0031</td>
</tr>
<tr>
<td>Week2</td>
<td>0.6384</td>
<td>0.0000</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Week3</td>
<td>1.7037</td>
<td>0.0059</td>
<td>-1.3672</td>
<td>0.3537</td>
</tr>
<tr>
<td>Week4</td>
<td>0.6892</td>
<td>0.0057</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Week5</td>
<td>-0.6919</td>
<td>0.0000</td>
<td>-4.2983</td>
<td>0.0168</td>
</tr>
<tr>
<td>Week6</td>
<td>-1.1732</td>
<td>0.0000</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Week7</td>
<td>-1.2412</td>
<td>0.0011</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>
Table 4: Mean predicted veliger drop-off distance (veliger density = 0) for each study system. Range consists of minimum lower 95% confidence limit and maximum upper 95% confidence limit.

<table>
<thead>
<tr>
<th>Study System</th>
<th>Predicted Drop-off Distance (m)</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vineyard</td>
<td>4229</td>
<td>2200 - 10000</td>
</tr>
<tr>
<td>Evans</td>
<td>473</td>
<td>120 - 1180</td>
</tr>
<tr>
<td>Rush</td>
<td>251</td>
<td>120 - 1040</td>
</tr>
<tr>
<td>Lower Pettibone</td>
<td>990</td>
<td>440 - 1960</td>
</tr>
</tbody>
</table>
Table 5: Values for select water quality parameters of each studied wetland. *Denotes values exceeding published zebra mussel veliger tolerance range (Sprung 1993).

<table>
<thead>
<tr>
<th>Water Parameter</th>
<th>Vineyard mean (range)</th>
<th>Evans mean (range)</th>
<th>Rush mean (range)</th>
<th>Pettibone mean (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp (°C)</td>
<td>24.61 (21.97-26.52)</td>
<td>25.02 (22.23-28.84)</td>
<td>23.40 (17.96-26.47)</td>
<td>25.09 (22.23-28.84)</td>
</tr>
<tr>
<td>SpCond (mS/cm)</td>
<td>0.47 (0.41-0.55)</td>
<td>0.33 (0.30-0.41)</td>
<td>0.57 (0.48-0.66)</td>
<td>0.71 (0.662-0.779)</td>
</tr>
<tr>
<td>DO (mg/L)</td>
<td>6.78 (3.75-10.64)</td>
<td>5.73 (0.63-12.03)*</td>
<td>6.47 (2.66-11.54)</td>
<td>9.27 (6.89-11.74)</td>
</tr>
<tr>
<td>pH</td>
<td>7.93 (7.61-8.86)</td>
<td>7.98 (7.21-11.15)*</td>
<td>7.88 (7.51-8.68)</td>
<td>8.31 (8.01-8.82)</td>
</tr>
</tbody>
</table>
Figure 1: Rate of veliger decline regressed against vegetation density of each study system. The rate of veliger density decline was defined as $-1m$, where $m =$ slope of the veliger density – distance regression line for the date of peak veliger density.
Figure 2: Zebra mussel recruitment for wetlands at different distances from the upstream edge of vegetation.