

Retention and supply of zebra mussel larvae in a large river system: importance of an upstream lake

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SUMMARY

1. Persistence of zebra mussel populations in river systems probably depends upon the presence of upriver sites capable of hosting self-recruiting adult populations that act as sources of larvae. In this paper we examine the importance of Lake Pepin, a natural riverine lake in the Upper Mississippi River, as an upriver source of larvae to the downstream populations of zebra mussels.

2. Field studies and modelling suggest that Lake Pepin plays a major role in maintaining zebra mussel populations in the Upper Mississippi River. Long water residence times in Lake Pepin allow for self-recruitment under the right hydraulic conditions. Larval abundance was low to absent upstream of the lake but increased dramatically downriver in all 3 years of the study. Travel time estimates in the Upper Mississippi River show that newly fertilised larvae drifting out of Lake Pepin can contribute substantially to the major downstream peak in larval abundance. In contrast, backwater and other off-channel sites are unlikely to drive main-channel abundance patterns. Larval abundances in off-channel sites were less than or equal to those in the main channel.

3. A key factor in assessing the importance of Lake Pepin as a source population was the abundance of early stage, unshelled larvae. Studies that consider only abundances of older shelled stages (visible by cross polarised lighting) may yield misleading results. Results of this study suggest that efforts to control zebra mussels in the Upper Mississippi River should focus on controlling adult populations within Lake Pepin and reducing or eliminating larvae exiting the lake.

Keywords: *Dreissena*, larvae, population dynamics, retention, river, zebra mussel

Introduction

Biologists studying introduced species focus on identifying potential invasive species (Kolar & Lodge, 2001), documenting impacts (Vitousek *et al.*, 1996), and preventing spread (Sharov & Liebhold, 1998). Less emphasis has been placed on the ecological

processes maintaining introduced populations once they have become established. For species with a dispersing life stage, the pattern of connectedness among populations can drive local persistence and dynamics (Epifanio, 1995; Bertness, Gaines & Wahle, 1996); however, few studies have quantitatively related propagule supply to invasion success (Sakai *et al.*, 2001).

Because zebra mussel (*Dreissena polymorpha*, Pallas, 1771) larvae are planktonic and net flow in rivers is unidirectional, most larvae produced by riverine populations will be carried downriver and

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will not contribute to recruitment within the population that produced them (Schneider *et al.*, 2003). Recruitment primarily depends upon settlement of larvae produced by upriver source populations (Kern, Borchering & Neumann, 1994; Stoeckel *et al.*, 1997), although upriver transport of adults by barges has the potential to augment recruitment (Keevin, Yarbrough & Miller, 1992). Upstream lakes may allow for the persistence of downstream populations. Studies in the Rhine River, Germany, suggest that adult populations depend on larvae produced in upstream lakes or dammed tributaries for recruitment (Borchering & De Ruyter Van Steveninck, 1992). Models developed from infested and non-infested commercial waterways in the U.S.A. suggest that the presence of upriver impoundment areas is a more important predictor of long-term zebra mussel persistence than is level of commercial traffic (Allen & Ramcharan, 2001). Zebra mussel populations in areas of high retention may self-recruit, thereby eliminating or greatly decreasing their dependence on upriver source populations. These self-recruiting populations in turn can provide a reliable source of recruits to dependent downriver populations. In the Illinois River, for example, zebra mussel populations are likely to function as a metapopulation, with Lake Michigan serving as the uppermost source of new recruits. Larvae drift out of Lake Michigan and enter the Illinois River via a system of locks and dams and canals. These larvae settle and found new populations that in turn provide larval recruits to populations farther downstream (Stoeckel *et al.*, 1997). In contrast, the Mississippi does not have a large, infested lake at its headwaters to serve as a constant source of new recruits (Lake Itasca is uninfested by zebra mussels), yet populations in portions of the Upper Mississippi River have persisted for many years (Cope, Bartsch & Hayden, 1997; Elderkin & Klerks, 2001).

Lake Pepin, a natural riverine lake, is infested with zebra mussels and may be acting as a source for downstream populations. If Lake Pepin functions as the primary upstream source site for larvae in the Upper Mississippi River, then the following conditions need to be satisfied:

1 Water residence times within the lake must be long enough to allow substantial self-recruitment.

2 Zebra mussel larvae must be rare upstream of the lake and abundant downstream with minimal input from downriver floodplain lakes and tributaries.

3 Patterns of abundance downstream of the lake should be consistent with the spatial population dynamics created by an upstream source population.

To assess the potential for Lake Pepin to serve as the primary larval source site in the Upper Mississippi River, we examined larval abundance and size distribution patterns in pools 2–12 of the Mississippi River and calculated travel distances for newly shelled larvae. We also addressed possible alternative explanations for patterns of abundance within the Upper Mississippi River.

Methods

Residence time and self-recruitment in Lake Pepin

To estimate larval retention, we used flushing time V/Q , where V is the lake volume and Q is the river discharge, as a surrogate for residence time. The two are directly related – the smaller the flushing time, the less time a particle will stay in the system. However, because flushing time is a global parameter and residence time is a local parameter (Monsen *et al.* 2002) the two are not always equivalent. Oliveira & Baptista (1997) showed flushing time agreed to within a factor of two with the median residence time in a studied estuary. We regressed our estimates of Lake Pepin flushing time against residence time estimates presented in Heiskary & Walker (1995) for nine river discharge values and found good agreement between the two ($r^2 = 1.000$, $P = 0.000$, slope = 1.022, $n = 9$).

We used daily discharge values obtained from the US Geological Survey (USGS) gauging station at Prescott, Wisconsin to estimate the amount of time larvae were likely to remain in Lake Pepin in 1998, 1999, and 2000. Because the discharge varies with time, t , the residence time of larvae entering the lake T_r at time t_0 was computed from

$$V = \int_{t_0}^{t_0+T_r} Q(t)dt. \quad (1)$$

Larval abundance patterns in the Upper Mississippi River

Study Site. In 1998, the Wisconsin Department of Natural Resources initiated a cooperative zebra mussel larvae monitoring program in the Upper Missis-

ssippi River. As part of this program, the Wisconsin DNR and Iowa DNR collected zooplankton samples at various sites from Lock and Dam 2 (LD 2) to LD 12 from June through September in 1998 and 1999 and from July through September in 2000. LD 2 is located near river mile (RM) 815 (by convention, navigable waterways in the U.S.A. are demarcated in terms of river miles rather than kilometres; here we use RM for specific locations along the river), just upstream of the mouth of the St Croix River. LD12 is located near RM 557, at Bellevue, Iowa, 254 km downriver of LD 2 (Fig. 1). We refer to river stretches between lock and dams as pools, following accepted convention by the US Army Corps of Engineers (USACOE). Each pool is named after the LD at the downstream end (e.g. Pool 12 lies between LD 11 and 12). However, the term 'pool' is misleading. Each pool is not a homogeneous reservoir or pool-like. Rather, riverine habitat is actually varied within and between pools, ranging from high flow regions of braided river channel to reservoir-like impoundment areas.

Monthly LD samples. Zebra mussel larvae were collected once a month from the tailwater area, approxi-

mately 100 m below LD 2–9 from June through September in 1998 and 1999 and from July through September in 2000. Larvae were also collected from tailwater areas below LD 10–12 when possible. At each sampling site, 10 L subsamples were collected at approximately 3 m depth near the left descending bank, mid channel, and right descending bank. We assumed that the water column within the tailwater area was vertically well mixed. Semi-rigid hose attached to a diaphragm pump was lowered to the desired sampling depth. Water was pumped through 55 μm mesh plankton netting to retain zooplankton and collected in a graduated carboy to measure the volume of water sampled. Zooplankton were rinsed from the net into a sample vial and preserved with 10% buffered sugar-formalin (Haney & Hall, 1973). All three subsamples were then combined to form a single, composite sample from each site. Because of resource limitations, replicate composite samples were not collected during most sampling events. However, to estimate sample variability at each site, duplicate composite samples were randomly collected each year for a total of 15 duplicate sampling events during the 3-year study.

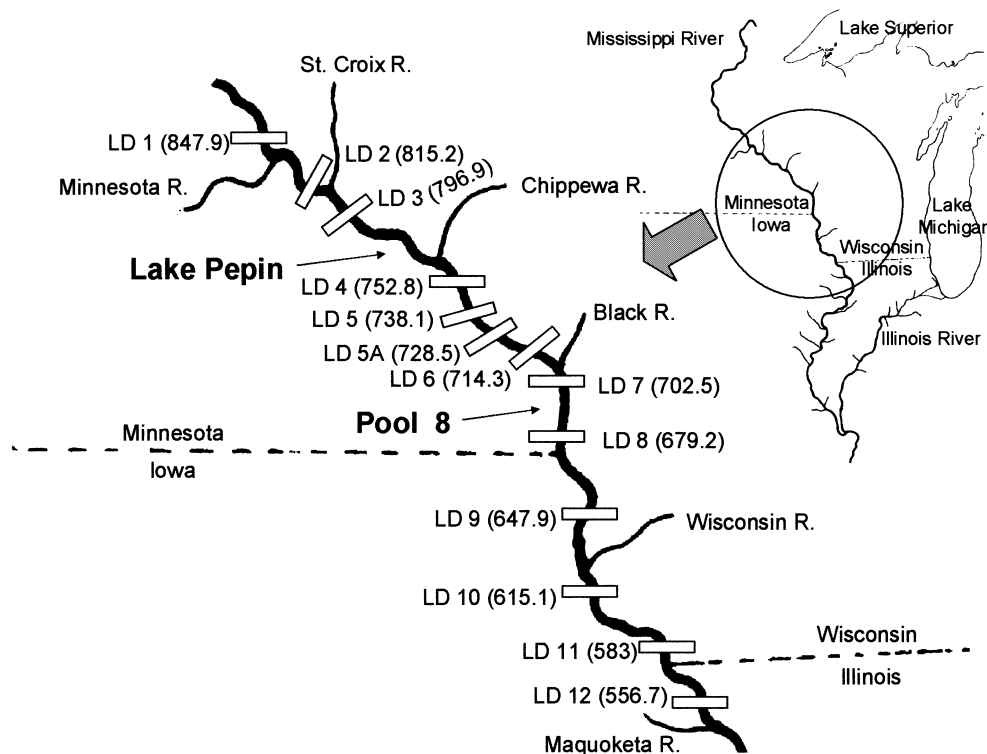


Fig. 1 Map of study area in the Upper Mississippi River extending from LD 2 to LD 12 (numbers in parentheses = river mile).

Habitat samples (Pool 8). To compare main-channel, side-channel, impoundment, and backwater habitats, 20 samples (five samples per habitat) were collected from Pool 8 over a 2-day period in August, 1998 with a stratified random sampling design. Twenty-eight samples (seven samples per habitat) were collected over a 24 h period in August, 1999 with the same sampling design. A total of 30 L was sampled at mid depth at each site, and organisms collected and preserved as described above. A one-way analysis of variance (ANOVA) and multiple comparisons Tukey test were used to test for differences in total abundance among sites and abundance of larvae competent to settle ($>200\ \mu\text{m}$) among habitats in 1998 and 1999. Analyses were conducted using SYSTAT[®] 7.0 (SPSS Inc., Chicago, IL, U.S.A.).

Tributary samples. Four major Upper Mississippi River tributaries between LD 2 and LD 12 were also sampled during this study. The St Croix River was sampled at multiple sites 3 months each year from 1998–2000, and the Chippewa, Wisconsin, and Black Rivers were all sampled at a single site/river in August 2000. Samples from the Chippewa, Wisconsin, and Black rivers were collected within the main channel of each tributary near its confluence with the Mississippi River. Sample collection was similar to that of previously described sample sets with horizontally and vertically integrated subsamples combined to form a single composite sample on each sampling date.

Sample treatment. All samples were shipped to the Illinois River Biological Station of the Illinois Natural History Survey for analysis. Zebra mussel larvae were detected, enumerated with cross-polarised light microscopy (Johnson, 1995), and measured with a computer-assisted video digitising system (Optimus, Bioscan). Zebra mussel larvae were distinguished from *Corbicula fluminea* larvae by characteristics described in Nichols & Black (1994). Cross-polarised lighting was the most efficient means to highlight larvae against the abundant sediment and debris in many of the samples. However, we occasionally received samples in which larvae were present but did not glow under cross-polarised lighting. These samples were stained with Rose-Bengal to facilitate detection of larvae under normal lighting. Some samples that were visible with cross-polarised lighting were also stained with Rose-Bengal and enumer-

ated under both normal and cross-polarised lighting (stained larvae still glowed when subjected to cross-polarised lighting). Staining with Rose-Bengal allowed us to accurately enumerate shelled larvae under normal lighting, although detection of larvae was more difficult and required longer sample processing as compared with using cross-polarised lighting. Unshelled developmental stages ranging from a single-cell fertilised egg through various stages of early development are extremely difficult to accurately identify and enumerate in field samples, even with Rose-Bengal stain. Because cross-polarised lighting is effective only after larvae have produced a shell, embryos and larvae that had not yet entered the D-stage (first shelled stage) were not detected, and thus not enumerated in this study. Empty shells were often found in samples; however, only those larval shells containing soft tissues were considered to be live and reported in this study.

Size of D-stage larvae was defined as the largest shell dimension parallel to the straight hinge. Size of umbonal larvae was defined as the largest shell dimension (Sprung, 1989) and was perpendicular to the anterior-posterior axis. The first 100 larvae detected in each sample were measured and staged according to the criteria described above. Zebra mussel larvae generally enter the D-stage within 1–2 days following fertilisation (Sprung, 1987) when they switch from lecithotrophy to planktotrophy (Sprung, 1993). Shell size of newly formed D-stage larvae generally ranges from 70–100 μm (Sprung, 1993; Martel, Hynes & Buckland-Nicks, 1995). Of the thousands of larvae measured in this study, fewer than 10 had a shell size $<70\ \mu\text{m}$. Therefore, we considered larvae between 70 and 100 μm to be newly shelled. Zebra mussel larvae are planktonic for 1–9 weeks (Martel *et al.*, 1995) and develop from the D-stage to the umbonal stage before settling as pediveligers and crawling on substrate. The size at which larvae are competent to settle varies but it is generally considered to be $>200\ \mu\text{m}$ (Sprung, 1993; Martel *et al.*, 1995; Schneider *et al.*, 2003). In this study, larvae were considered competent to settle when they were $>200\ \mu\text{m}$.

To estimate larval abundance in each sample, samples were concentrated to 50 or 100 mL (depending on debris) and mixed with a plunger. Larvae within consecutive 5 mL subsamples were enumerated until either 60% of the sample had been examined or >100 larvae had been counted. The only exception to this procedure was the tributary samples, which were

examined in their entirety for zebra mussel larvae. To account for potential dilution and flow effects of varying discharge levels on both temporal and spatial scales, larval flux (larvae s^{-1}) was also calculated for all LD sample sites. Daily discharge data from gage stations at each LD were obtained from the USACOE and USGS. Multiplying density (larvae L^{-1}) and discharge ($L s^{-1}$) allowed us to calculate larval flux in terms of larvae s^{-1} drifting past each sampling site.

Transport of Lake Pepin larvae

Because our methods detect larvae only once they have developed a shell, there is a lag between larval production and detection; larvae were first observed downstream of where they were produced. Determining the likely source of larvae requires accounting for advection by the river currents, longitudinal dispersion, and larval growth. The relative importance of advection and longitudinal dispersion is measured by the Péclet number $Pe = UL/K$, where U is the mean velocity, L is the distance between LD 4 and LD 7, and K is the dispersion coefficient. Large values indicate that advective transport dominates dispersive transport. Using $U = 0.4 m s^{-1}$ (see below) and $K = 100 m^2 s^{-1}$ (Falch, Bielke & Stefan, 1979) for the stretch of river between LD 4 and 7 gives Pe approximately 350, which indicates that dispersion is relatively unimportant. Thus, ignoring dispersion and equating the time to travel from the spawning location x_s to a downstream location x to the time for development to a size d gives

$$\int_{x_s}^x \frac{dx'}{U(x')} = T_D + \frac{d - d_1}{\gamma}, \quad (2)$$

where T_D is the time to develop from fertilisation to the D-stage, γ is the growth rate for larvae in the D-stage and larger ($d > d_1 = 70 \mu m$), and x' is a dummy variable of integration. The streamwise variation in mean velocity was computed with the Riverine Emergency Management Model (R. Pomerleau, USACE, personal communication). Discharges averaged from 1 June to 15 September for each year were specified at several gages operated by the USGS and the USACE. Conditions in 1998 and 1999 represented the low and high flow conditions, respectively, for the study years. For the water temperatures during our study, the time from fertilisation to development of a shell (i.e. T_D) was between 1 and 2 days (Sprung,

1987). The growth rate γ was taken to be $17 \mu m day^{-1}$ (Schneider *et al.*, 2003). Equation (2) was used to determine whether Lake Pepin larvae can contribute to abundance peaks at a given downstream location.

Results

Residence time in Lake Pepin

Residence time estimates in Lake Pepin ranged from 5 to 32 days in 1998, 3–16 days in 1999, and 7–37 days in 2000. The longest residence times were typically late in the season, following the period of maximum temperature (Fig. 2).

Larval abundance patterns in the Upper Mississippi River

Error estimate. For the fifteen sampling events when replicate samples were collected, the standard error

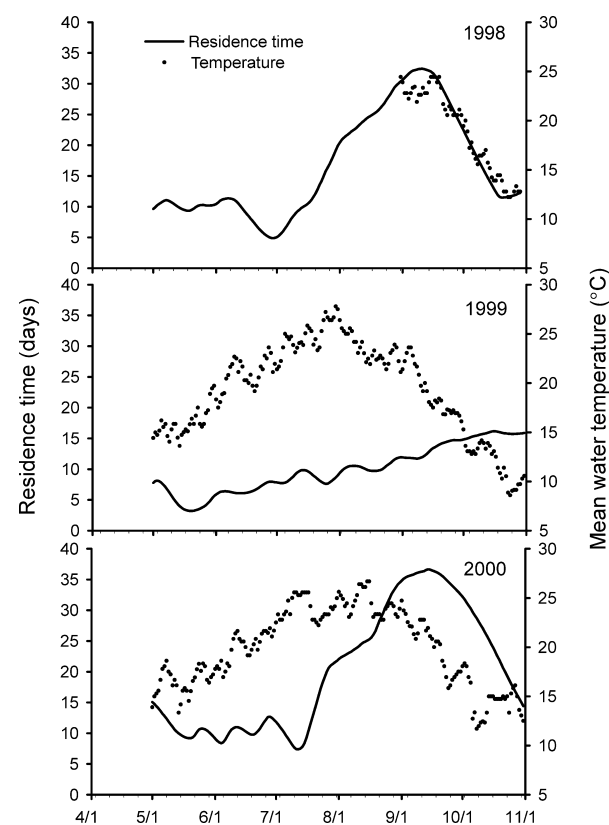


Fig. 2 Mean residence times for larvae entering Lake Pepin in 1998, 1999 and 2000. Daily temperature data were not available for Lake Pepin. Therefore, we averaged daily temperatures for LD 3 (above Lake Pepin) and LD 4 (below Lake Pepin) to estimate Lake Pepin temperature.

averaged 12% of the estimated abundances. These sampling events encompassed a wide range of larval abundances: 0.2–339.5 larvae L⁻¹ over the 3-year study. Although it would have been preferable to have replicate samples for all sampling events, these results indicate that the single composite samples collected in this study provided an accurate assessment of larval abundance.

Monthly LD samples. Larval abundances in the tailwaters below LD 2–12 varied considerably on both a spatial and temporal scale, ranging from <1 to >500 L⁻¹. Peak abundances exceeded 300 larvae L⁻¹ during each of the 3 years of the study. Highest abundances occurred in July and August, and lowest abundances (<100 L⁻¹) occurred in June (Fig. 3). Larval abundance followed a strong spatial pattern in all 3 years of the study (Fig. 4). Larval flux exhibited the same pattern. Abundances never exceeded 5 L⁻¹ upstream of Lake Pepin (LD 2 and 3: RM 815.2 and 796.9), but quickly rose downriver of Lake Pepin (LD 4; RM 752.8), generally peaked near RM 702.5 (LD7), decreased at RM 647.9–615.1 (LD 9, 10) and increased again at RM 615.1–556.7 (LD 10–12) (Figs 3 & 4). Newly shelled larvae accounted for a large proportion of total abundance (Fig. 3), and therefore flux, at all sites throughout the study. Larvae competent to settle (>200 µm) were absent or rare (<3 L⁻¹) and never made up a large proportion of larval abundance at any LD site in this study.

Habitat samples. (Pool 8) Larval abundances varied considerably across all Pool 8 samples in 1998 ranging from 1 to 723 L⁻¹. Greatest variation occurred in impounded habitats. Mean shelled larval abundance was highest in impounded habitat and lowest in backwater habitat (Fig. 5a). However, there was no significant difference in mean abundance across habitat type (ANOVA, $P = 0.152$). Mean abundance of larvae competent to settle was consistently low across habitat types, ranging from 1.0 to 2.5 L⁻¹, and there was no significant difference in abundance among habitat types (ANOVA, $P = 0.357$).

In 1999, larval abundance across all Pool 8 stratified samples ranged from 1 to 429 L⁻¹. Greatest variation, as well as highest mean abundance, occurred in main-channel habitat. Lowest mean abundance occurred in backwater habitat (Fig. 5b). Significant differences in mean abundance were found among habitat types

(ANOVA, $P = 0.006$). Abundance in the main channel was significantly higher than backwater or impounded areas but larval abundance in side-channels was not significantly different from either main channel or backwater and impounded areas (Tukey test, $\alpha = 0.05$). No larvae competent to settle were observed in 1999 Pool 8 samples from any habitat.

Tributary samples. No larvae were found in the Chippewa, Wisconsin, or Black Rivers, sampled in August, 2000. No larvae were found in the St Croix River in July, August, or September 1998. Low abundances (0.02–0.19 larvae L⁻¹) were found in the St Croix River in 1999 and 2000.

Transport of Lake Pepin larvae

Calculations with eqn (2) show that larvae leaving Lake Pepin just after fertilisation reach sizes of 70–100 µm between RM 658 and RM 743 (Fig. 6). Larvae are predicted to be farther downstream if either the duration of the unshelled stage or the river discharge increases. The increase in discharge between 1998 and 1999 did not result in the peak moving downstream (Fig. 3), possibly because of variations in the duration of the unshelled stage. For growth rates of $17 \pm 1.9 \mu\text{m day}^{-1}$ (Schneider *et al.*, 2003), growth rate has little effect. Larval locations computed with discharges from 2000 would be between those using conditions from 1998 and 1999.

Discussion

Self-recruitment in Lake Pepin

Self-recruitment in a waterbody depends on two physical constraints: (1) Larvae must be retained long enough to develop to settlement and (2) the currents must allow larvae to settle where they were produced. Estimates of time required for larvae to develop and settle out range from 7–18 days in Midwestern rivers such as the Illinois (Stoeckel *et al.*, 1997; Schneider *et al.*, 2003), to 7–63 days in lakes (Martel *et al.*, 1995). Estimated residence times of larvae within Lake Pepin ranged from 3 to 37 days during the spawning season (water temperature >12 °C). Although it was beyond the scope of this study to estimate actual growth rates of zebra mussel larvae within Lake Pepin, previous lab studies indicate that growth increases with

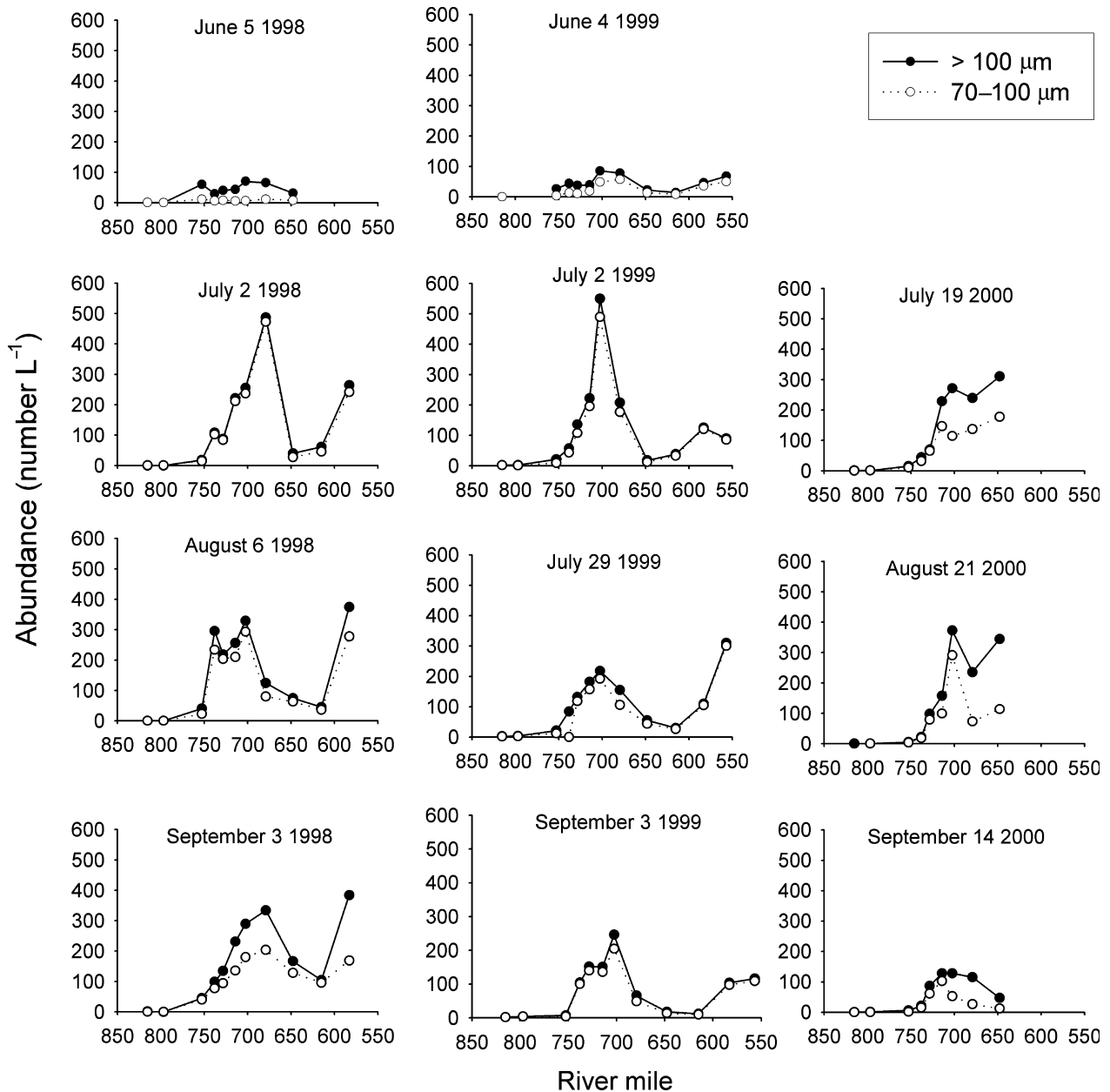


Fig. 3 Shelled veliger abundance patterns on each sampling date in 1998, 1999, and 2000. Size-class abundances are stacked, with total height representing abundance of all shelled size-classes combined. Veligers in the 70–100 µm size-class represent newly formed D-stage larvae (first stage detectable by cross-polarised lighting). Veligers >200 µm (competent to settle) were rarely observed in these samples (maximum abundance = 2.7 L⁻¹).

temperature to approximately 25 °C (Vanderploeg, Liebig & Gluck, 1996) with little or no increase in mortality associated with rising temperatures up to 30 °C (Stoekel, Padilla, Schneider and Rehmann, unpublished data). The ability of larvae to maintain maximum growth rates with little to no increase in mortality as temperatures increase is likely to affect

the potential for self-recruitment in riverine retention zones. In the case of Lake Pepin, larvae can 'take advantage' of maximum growth rates during maximum temperatures (approximately 25 °C) in mid- to late summer, and increased residence times when temperature (and therefore growth rate) decreases in late summer and fall. This increases the chance that

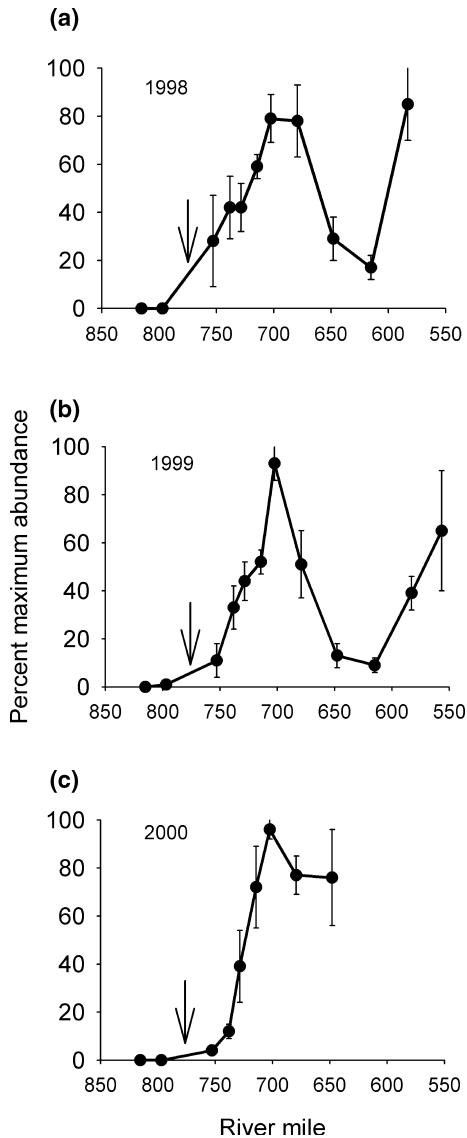


Fig. 4 Combined patterns of larval abundance for 1998, 1999, and 2000. Percent of maximum abundance was calculated by dividing abundance at each site by the maximum abundance recorded on that date and multiplying by 100. Error bars represent ± 1 SE. Arrows indicate location of Lake Pepin.

larvae produced within the lake will settle and replenish local populations rather than being flushed out of the lake. Tolerance of high temperatures could be even more important in retention zones at lower latitudes where mid-summer temperatures in the main channel and associated floodplain can easily reach 30 °C.

Despite long residence times, advection could still move larvae downstream from where they were spawned. Hydrodynamic dead zones or rates of horizontal dispersion sufficient to counter advection

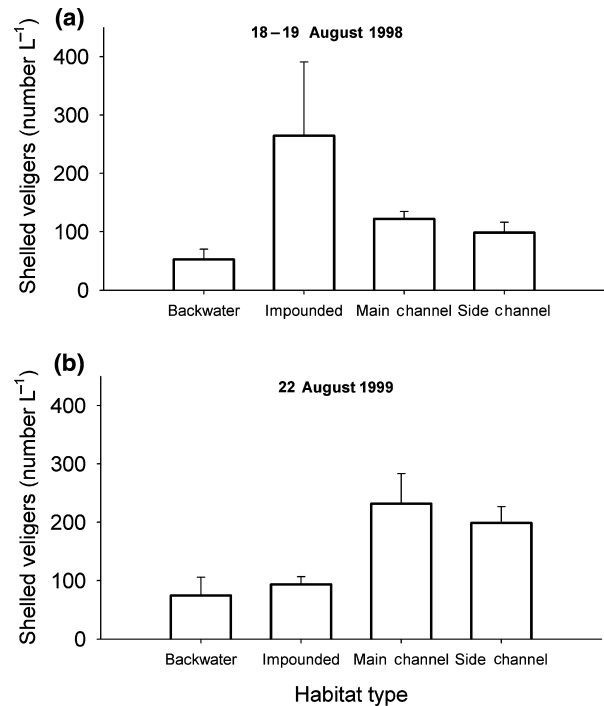


Fig. 5 Shelled veliger abundance in 1998 (a) and 1999 (b) across four habitat types in Pool 8. Error bars represent ± 1 SE.

are required for persistence of source populations (Speirs & Gurney, 2001). Studies of Spring Lake in Pool 2 (Demetracopoulos & Stefan, 1983) and Sturgeon Lake in Pool 3 (Stefan & Anderson, 1980), both upstream of Lake Pepin, show that direction of water current is correlated with wind direction. Based on depth, surface area, and discharge values for the lakes (Stefan & Anderson, 1980; Larson *et al.*, 2002), we estimate flushing times of 3.2 days (Spring Lake) and 1.3 days (Sturgeon Lake) under low flow conditions. Although wind-driven currents might temporarily overcome downstream advection, residence times are too short to allow for self-recruitment in these lakes. However, wind-driven currents in Lake Pepin may provide a mechanism to satisfy constraint number two. Coupled with the findings that very few larvae enter the lake from upstream, and residence times are long, it is likely zebra mussels have established self-sustaining populations in Lake Pepin.

Floodplain lakes and tributaries as larval source sites

Floodplain lakes. Residence times in backwater and impounded areas are almost certainly greater than those in the main channel, suggesting that backwater

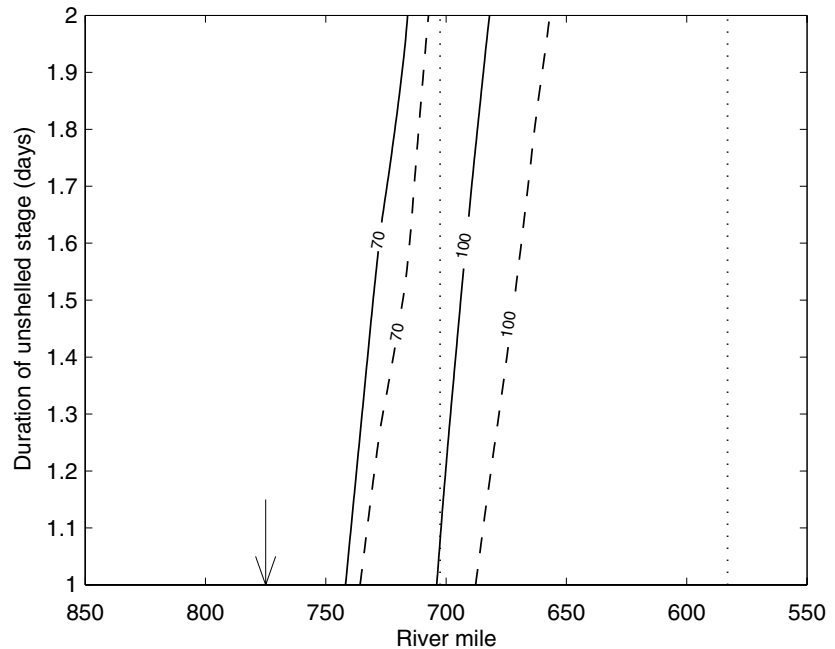


Fig. 6 Predicted locations of larvae leaving Lake Pepin just after fertilisation. Solid lines are computed for the low-flow conditions of 1998, and dashed lines are computed for the high-flow conditions of 1999. For each flow condition the upstream and downstream (i.e. left and right) contours indicate the locations of larvae that have reached sizes of 70 and 100 μm , respectively. Lake Pepin is indicated with an arrow, and LD 7 (RM 702.5) and LD 11 (RM 583) are indicated with dotted lines.

sites may play a similar role as that hypothesised for Lake Pepin. However, there are major differences between an in-line riverine lake such as Lake Pepin and the floodplain lakes that lie to either side of the main channel. Lake Pepin is an in-line retention zone that encompasses the main channel within its length. Continual discharge at the downriver end provides a high percentage of the flow in the main channel on a constant basis. Backwater areas can be better described as lateral retention zones, not always connected to the main channel. Main channel water tends to flow into backwater areas during rising water levels, with backwaters draining back into the main channel during falling water levels, and low exchange occurring during stable water levels. Thus, backwaters provide a lower percentage of discharge to the main channel on a less frequent basis. To examine the effect of impounded and contiguous backwater habitat on larval dynamics in the Upper Mississippi River, we examined the Pool 8 stratified sampling data for evidence of retention or production of larvae at off-channel sites. If larvae had a strong tendency to drift out of the main channel and be retained in off channel sites, or to be produced in higher numbers in off channel sites, we would have expected to see differences in abundances amongst the strata. When significant differences in abundance between habitat types did occur, abundances were highest in main channel

sites with side-channel abundances intermediate between main channel and off channel (backwater, impounded) sites (Fig. 5). These findings argue against higher production of larvae in backwater sites and are supported by previous studies (Tucker & Atwood, 1995) that suggest that environmental conditions in contiguous backwaters of large, floodplain rivers may be inadequate to support large, stable, adult zebra mussel populations.

Tributaries. Four main tributary rivers were located within the sampling area of this study: the St Croix, Chippewa, Wisconsin, and Black Rivers. No evidence was found for any of these rivers serving as an important source of larvae to the Upper Mississippi River, although low numbers of larvae were found in the St Croix River in 1999 and 2000. The presence of zebra mussel larvae in the St Croix River is particularly worrisome as the St Croix also contains a high retention, in-line, waterbody (Lake St Croix). If Lake St Croix becomes heavily infested with zebra mussels, it may also become an important site in the maintenance of zebra mussel populations in the Upper Mississippi River. Similarly, other tributaries of the Upper Mississippi River may also possess retention zones that, once infested, could also contribute to the maintenance of zebra mussel populations in the Upper Mississippi River.

Lake Pepin as a larval source site

Although actual larval abundances varied greatly within and between years, the spatial pattern in relative larval abundance remained remarkably consistent. Larval abundance and flux were always low to absent above Lake Pepin, and increased dramatically below Lake Pepin (Fig. 4). A peak in abundance and flux occurred near LD 7 (RM 702.5) in all three years, and a second peak near LD 11 and 12 (RM 583, 556.7) occurred in the 2 years sites were sampled. This pattern was driven mainly by abundance of newly shelled larvae (Fig. 3); larvae between 70 and 100 μm always accounted for at least half, and usually more, of the larvae observed.

The peak in larval abundance near LD 7 appears to be strongly affected by larvae produced in Lake Pepin. Larvae in Lake Pepin contribute most to the peak in larvae between 70 and 100 μm observed at LD 7 when river discharge and the time T_D to enter the D-stage are high (Fig. 6). As both the time T_D and the mean velocity decrease, larvae that originate in the lake contribute less to those observed at LD 7 but still cause high abundances at the LD sites further upstream (e.g. Fig. 3, 6 August 1998). For Lake Pepin to make no contribution to the peak at LD 7, the growth rate γ must exceed 43 $\mu\text{m day}^{-1}$ when the time to enter the D-stage is taken as 1.5 day. This rate is much higher than the maximum growth rate reported, about 20 $\mu\text{m day}^{-1}$ (Martel *et al.*, 1995). The contribution of Lake Pepin to the peak at LD 7 depends on large numbers of unshelled larvae leaving the lake. Shelled stages also leave the lake, but are likely to have grown beyond the newly shelled stage (70–100 μm) by the time they reach LD 7. Adult zebra mussels are most abundant in the downstream portion of Lake Pepin (James *et al.*, 2000), providing a potential source of young, unshelled larvae near the outflow of Lake Pepin. Development of these larvae from the unshelled (i.e. trochophore) to the shelled stage (D-stage veliger) and thus becoming detectable in our samples could explain the sharp increase in larval abundance consistently observed between LD 4 and 7.

In contrast, the second larval peak observed between LD 11 and LD 12, is caused by larvae produced downstream of Lake Pepin. Travel times computed with both 1998 and 1999 flow conditions show that larvae from Lake Pepin reach 100 μm at

least 119 km upstream of LD 11 (Fig. 6). Therefore, the newly shelled larvae (90–100 μm) constituting the majority of the second abundance peak could not have come from Lake Pepin unless growth rates were small. Lake Pepin has an indirect effect, however, as the newly shelled larvae at LD 11 and 12 could have been produced by adults that were themselves produced in Lake Pepin.

To predict the magnitude of the peak in larval abundance at LD 7, unshelled larvae must be considered. Because the abundance of 70–100 μm larvae upstream of LD 7 was smaller than the value at the peak (Fig. 3), those larvae could not account for the peak even if they were simply advected without experiencing mortality. The increase in abundance is caused by new larvae from Lake Pepin growing and producing a shell as they travelled downstream. These results demonstrate the importance of accounting for unshelled larvae in quantitative predictions of the spatial distribution of zebra mussels.

Implications for conservation and control

The Mississippi River, with its extensive floodplain, braided channel, backwater lakes, riverine lakes such as Lake Pepin, and artificial impoundments created by locks and dams, provides a multitude of potential retention zones that make study of larval dynamics and evaluation of control techniques very difficult. However, results of this study, coupled with previous studies, reveal consistent patterns that provide some insight into zebra mussel metapopulation dynamics in the Upper Mississippi River. Adult (Cope *et al.*, 1997) and larval zebra mussels were absent or rare upriver of Lake Pepin, but become very abundant in downriver pools. Lake Pepin exhibited adequate residence times for larvae produced in the lake to settle out in the lake. Local populations may maintain themselves via self-recruitment if hydraulic conditions are such that larvae can overcome downstream advection within the lake.

We hypothesise that in large river systems, zebra mussel populations require at least one critical habitat area. This habitat must have a high residence time and sufficient connectivity with the river system to allow for downriver dispersal of excess recruits. For the Illinois River, Stoeckel *et al.* (1997) suggested that Lake Michigan provides the critical habitat hosting an

upriver source population that provides a constant source of recruits to downriver populations. In the Upper Mississippi River, Lake Pepin seems to be the critical habitat, playing a disproportionately important role in maintaining zebra mussel populations in the Upper Mississippi River. Manipulation of Lake Pepin residence times to reduce the potential for self-recruitment, or elimination/reduction of larval flux from Lake Pepin, would likely have a significant effect on downriver populations. Elimination of the supply of larvae coming out of Lake Pepin should result in a domino effect. Nearby populations would die out first because of a lack of recruits from Pool 4. As these populations die back and cease to produce larvae, populations further downstream will begin to die back and this effect would cascade downstream. Results of this and previous studies (Stoeckel *et al.*, 1997) suggest that control efforts for zebra mussels in large river systems should be focused on critical habitat areas, with ecosystem-wide control of zebra mussels being at least theoretically possible. Future studies to document the degree of self-recruitment in Lake Pepin and the frequency of barge-mediated transport and recruitment would be of great help in further understanding metapopulation dynamics and implications for maintenance and control of zebra mussels in the Upper Mississippi River.

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