

Research Article

Dispersal of zebra mussels (*Dreissena polymorpha*) downstream of an invaded reservoir

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Abstract

Zebra mussels, *Dreissena polymorpha*, have recently invaded Central Texas. More information is needed to predict their spread in this region and inform management decisions. In this study, we examined riverine zebra mussel dispersal from, and settlement downstream of, a recently invaded reservoir, Lake Belton. Veliger samples and settlement of juveniles on artificial substrata were monitored at sites within Lake Belton and 0.4 to 54.7 river kilometers (rkm) downstream from the lake outlet. Veliger density varied greatly across space and time with peak densities of live veligers found in both early summer (May–June) and fall (October). High juvenile settlement occurred consistently at 2.5 and 6.0 rkm downstream. Juvenile settlement was not observed ≥ 13 rkm downstream until the spring of 2016 after a period of prolonged increased river discharge. Our findings suggest that mussels were dispersal limited in 2015, and prolonged periods of increased river discharge may have facilitated their dispersal further downstream in 2016.

Key words: passive dispersal, invasive species, veligers, dispersal limitation, source-sink dynamics, juvenile settlement

Introduction

The recent invasion of the non-native zebra mussel, *Dreissena polymorpha*, in Texas raises concern because its introduction has had large ecological and economic impacts throughout North America (Strayer 2009). Zebra mussels have life history characteristics such as high fecundity (30,000–40,000 eggs per female), rapid growth rate, and the ability to spawn multiple times a year that allow them to colonize new habitats readily if conditions are favorable (McMahon 1991; Claudi and Mackie 1993). Adults are filter feeders, consuming planktonic algae and zooplankton from the water column and re-directing nutrients and energy from the pelagic to the benthic zone (Molloy et al. 1997; Strayer 2009; Higgins and Vander Zanden 2010; Lindim 2015). Zebra mussels can reach extremely

high densities and are able to filter at up to ten times the rate of native unionid mussels causing drastic declines in both plankton concentration and native species numbers (Higgins and Vander Zanden 2010; Vanderploeg et al. 1995).

Zebra mussels reproduce via broadcast spawning, releasing thousands of gametes into the water column at once (Claudi and Mackie 1993). Zygotes then form and develop in the water column for several weeks until they settle on hard substrate as juveniles (Ackerman et al. 1994). The zebra mussel life cycle is heavily regulated by temperature with the most favorable conditions for spawning and larval development occurring between 18 °C and 24 °C (McMahon 1996). The upper lethal temperature limit for zebra mussels from New York is ~ 31 °C, with mussels tolerating exposure to this limit for varying periods (50–300 hr)

Figure 5. Length frequency distribution of zebra mussels from sites 0–4 (marked as black circles) in October 2015 (n = 100 for sites 0–3 and n = 60 for site 4).

Mussel densities and size distribution across sites

Zebra mussels that were collected in October 2015 from natural river substrata differed in size distributions between sites (Figure 5). While 73% of the mussels in the lake and 58% of the mussels at 0.4 rkm were ≤ 12 mm in shell length, only 3–5% of the mussels at sites 2.5–13.1 rkm were comprised of these smaller size classes. Two individuals at 2.5 rkm had shell lengths of 28 and 34 mm, indicating the presence of mussels greater than a year old (Allen et al. 1999).

Discussion

We found no settled juveniles farther than 13 rkm downstream from the Lake Belton discharge between August 2015 and February 2016, but from April 2016, they were detected up to 54 rkm downstream. This considerable increase in dispersal distance occurred after periods of consistently higher discharge compared to previous years (Figure 2), which may have

facilitated downstream veliger transport. We also found considerable variation in both juvenile settlement and veliger densities across time, likely driven by changes in temperature.

The limitation of substantial settlement of zebra mussels to Leon River sites ≤ 6.0 rkm downstream of Lake Belton was likely influenced by the lowhead dam located at 7 rkm. (Figure 1). The inundation created in the river channel from this impoundment directly effects the habitat in the upper stretch of the Leon River as habitat conditions were notably more lentic due to a deeper channel morphology compared to downstream of the lowhead dam. This idea is supported by another recent study that found zebra mussel recruitment at sites corresponding to impoundments were higher compared to other riverine sites (Smith et al. 2015). In addition, discharge from Belton dam was relatively low (average daily discharge $< 1.0 \text{ m}^3 \text{ s}^{-1}$) from 2013 (estimated time of infestation in Lake Belton) to July 2015 and likely contributed to dispersal of zebra mussels being largely limited to the upper 7 rkm stretch of the Leon River. Only after

periods of drastically increased discharge (after July 2015) were veligers pushed further downstream and individuals settled at distances of 13–54 rkm. The lack of continued settlement or persistence of individuals ≥ 27.3 rkm downstream suggests that they lack consistent recruitment from upstream. In addition, unfavorable habitat conditions (high water velocities, shallow depths, decrease of available substrata etc.) may limit survival of zebra mussels in these areas.

Our data does not exhibit the typical “source-sink” trends observed by Horvath et al. (1996). Although most of our veliger and settlement observations occur in the upper 13 rkm portion of the stream, they do not exhibit an exponential or logarithmic decline as characterized by infested lake-river systems of comparable size (Horvath et al. 1996; Horvath and Lamberti 1999; Bobeldyk et al. 2005). Instead, their densities are greatly variable across seasons, discharge levels, and distances.

Persistent settlement of juveniles at 13.1 rkm (Figure S2) was only observed after April 2016, suggesting new recruitment at this site may be limited. In October 2015, site 4 shows evidence of being newly established compared to upstream sites (2.5 and 6.0 rkm) as both site 2 and 3 had smaller proportions of recently recruited individuals (mussels with shell lengths < 10 mm) compared to site 4 (Figure 5). Moreover, the presence of several individuals > 25 mm at sites 2 and 3 indicates the presence of mussels from multiple generations (Allen et al. 1999). It could be that, in contrast to sites further upstream, site 4 only receives new recruitment during seasonal reproduction peaks when veliger densities are in sufficient quantities. It is unknown whether Lake Belton, or sites upstream of the lowhead dam, or a combination of both, act as a source for sites further downstream. It is also worth noting that while no juvenile settlement was detected on blocks from site 4 until April 2016, mussels ranging in size from 8–20 mm were found on natural substrata in October 2015. This may be due to some a preference for natural substrata over the material of our cinder blocks.

Many previous studies have shown zebra mussel reproduction to be heavily regulated by temperature thresholds (i.e., Sprung 1987; Borcharding 1991) and, like other studies, ours showed a great seasonal variation in veliger densities, most likely due to temperature variations. Like other studies (Stoeckel et al. 1997; Borcharding 1991) our data supports a seasonal trend of higher veliger densities during times of optimal water temperatures. The highest veliger densities were observed in May 2015, whereas no veligers were found at any sites in December when ambient water temperatures fell below the

threshold of 16 °C for reproduction (Sprung 1987; Borcharding 1991). Unlike previous studies, which concentrated on European and northern North American zebra mussel populations (e.g., Mackie and Schloesser 1996), zebra mussel reproduction in Texas seems to exhibit an interruption during peak summer temperatures (Figures 3, 4A), with reproduction continuing in fall when water temperatures drop to suitable levels. Substantial densities of veligers were observed at river sites in September and October 2015 while almost none were seen August of that same year (Figures 3, 4A). Similarly, Churchill (2013) recorded maximum veliger densities in Lake Texoma during late spring and early summer with reduced numbers of veligers re-appearing in the fall. This dominance of late spring-early summer spawning relative to a second fall spawning period seems limited to populations occurring in warmer water bodies (McMahon 1996; Nichols 1996), mostly likely due to elevated temperatures in late summer disrupting reproductive activity.

A large proportion (> 300 veligers m^{-3}) of live veligers were found at river sites in September 2015 directly after several periods when river ambient water temperatures exceeded 30 °C, the upper thermal limit for zebra mussels, from 23rd–25th August and 6th–9th September 2015. Similarly, in late August 2016, veligers were still being collected from Lake Belton and downstream sites even though river temperatures were ≥ 27 °C from July 17 2016, with the Texas Commission on Environmental Quality (TCEQ 2016) reporting lake water temperatures near the Belton dam to be 31 °C on August 11 2016. Therefore, even though temperatures in both the lake and river periodically reach this thermal limit in summer, these limits may not persist long enough to cause much veliger mortality. Zebra mussels may be capable of extending their upper thermal limits through long-term seasonal acclimatization (Hernandez 1995; McMahon 1996). In addition, southwestern US mussel populations appear to have evolved elevated upper thermal limits (Morse 2009). Increased thermal tolerance of Texas mussels may explain our observations of veliger presence at river sites even during periods of elevated water temperatures.

Interestingly, in September 2015, veligers were found at downstream sites but were not detected near the surface in Lake Belton. We recorded low dissolved oxygen (2.3 mg/L) in Lake Belton (but not in the river), which fell just below tolerable levels (i.e., < 2.4 mg/L, see above, McMahon 2015). It is possible that this hypoxia was lethal to the veligers in the upper water column (where we sampled, i.e. ~ 1 m depth), and that veligers stopped swimming, sank in the water column, and accumulated at the thermo-

cline (Churchill 2013), and may then have been transported to the river via the bottom release dam.

This study has yielded valuable information about the downstream dispersal capabilities of zebra mussels within a Texas stream system and of how reproduction varies seasonally and with temperature. Texas has a large number of lowhead dams and our study suggest that a lowhead dam can enhance settlement and recruitment of zebra mussels. However, the role of these and other structures in the river and whether they support the persistence of reproducing populations requires further research.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Veliger density (veligers m⁻³) in Lake Belton and across all downstream sites for all sampling events during the course of this study.

Figure S2. Average cumulative zebra mussel density (individuals per m² ± SE) counted on sampling blocks from each riverine site from August 2015–August 2016.

Table S1. Georeferenced sampling data of average mussel densities on monitoring substrata and veliger density in Lake Belton and downstream.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Olson_etal_SupplementaryFigures.pdf

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Olson_etal_Table_S1.xlsx