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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) depending on acclimation temperature (McMahon 1996). With the exception of Louisiana, zebra mussels in central Texas are currently the most southern population in the United States (Churchill 2013) and their population expansion may be limited by thermal stress. However, southern zebra mussel populations show increased upper thermal tolerance when compared to populations in the northern Great Lakes region (Morse 2009). Surface waters of Texas reservoirs can reach ≥ 31 °C in summer (McMahon 2015) but it is unknown how well populations of zebra mussels within Texas will tolerate higher temperatures or how higher temperature regimes effect reproduction and population dynamics.

Zebra mussels can spread rapidly over long distances by attaching to boats or by veliger larvae being transported in ballast-water of ships (Ruiz and Carlton 2003; Strayer 2009). Even without human-aided transport, zebra mussels have high dispersal potential via downstream transport of their microscopic veliger larvae in the water column. Infested lakes can act as a source for riverine dispersal leading to establishment of new populations in their outflowing rivers and nearby downstream lakes (Horvath et al. 1996; Stoeckel et al. 1997; Bobeldyk et al. 2005). In smaller stream systems (< 30 m width) veliger density and settlement seems to rapidly decline with increased distance downstream and to be generally restricted to ≤ 12 rkm downstream of the invaded source lake, (Horvath et al. 1996; Horvath and Lamberti 1999; Bobeldyk et al. 2005; Lucy et al. 2008). The relatively rapid decline of mussel densities with distance supports a "source-sink" model of dispersal (Horvath et al. 1996). Similarly, studies on large river systems (Stoeckel et al. 1997; Stoeckel et al. 2004) suggest that riverine populations rely on the presence of upstream populations for recruitment but are able to disperse hundreds of river kilometers downstream if aided by the positioning of lakes, dams, and impoundments on such navigable waterways (Horvath et al. 1996; Allen and Ramcharan 2001; Smith et al. 2015). Such impoundments not only facilitate spread with increased boat traffic, but act as "stepping stones" for dispersal as reproducing populations may persist upstream of these dams and provide recruitment to further downstream locations (Smith et al. 2015).

Zebra mussels were first detected in Lake Belton (31.104881ºN; −97.485208ºW), Texas in 2013 (TPWD 2013) and greatest densities were observed in 2014 and early 2015. However, the population began to show signs of decline in the summer of 2015 (McMahon pers. comm.). Lake Belton has a bottom release dam from which water is variably released year-round. Zebra mussel larvae can potentially travel from Lake Belton, through the dam outflow, into the Leon River in the Brazos River Basin. The Leon River is a small to medium sized river (~ 30 m wide) which joins with another small river, the Lampasas River, approximately 28 rkm downstream from Lake Belton, to form the Little River (30–40 m stream width) (Figure 1). One lowhead dam exists along the Leon River approximately 7.0 rkm downstream from the Lake Belton outlet (Figure 1).

Based on the limited dispersal of zebra mussels in smaller streams, it follows that there may be limited dispersal distances (i.e., limited to ≤ 12 rkm downstream) in the Leon River downstream from Lake Belton. Although the presence of a lowhead dam could potentially extend dispersal distances of zebra mussels, the role of lowhead dams as stepping stones has only been suggested for a series of low-head dams, not a single smaller impoundment as in our case. The objectives of this study were to 1) quantify and examine veliger dispersal and zebra mussel settlement downstream of an infested reservoir and 2) examine how warmer water conditions affect the production of veligers and settlement of juveniles in the Leon River. We predicted that dispersal of veligers and juvenile settlement would be limited to distances ≤ 12 rkm as seen in similar river systems. Further, we expected to find a decrease in reproductive activity when water temperatures exceeded 30 °C, and thus a decline in veliger densities.

Material and methods

Study location

The Leon River has a drainage area of 9,277 km^2 (USGS 2016a) and connects with the Lampasas River at 28 rkm to form the Little River (Figure 1). Seven sites were chosen as monitoring sites. Five riverine sites were located along the Leon River at approximately 0.4, 2.5, 6.0, 13.0, and 27.5 rkm with one further site along the Little River approximately 57.0 rkm downstream from the Lake Belton dam outflow. One site was located within Lake Belton at a marina approximately 1.0 km from the dam and about 32 meters above the bottom release of the dam. Downstream sites were arranged on an approximate logarithmic scale to better analyze dispersal distances and based on ease of accessibility. At each site water quality, veliger presence, and juvenile settlement data were gathered. Sampling was performed monthly during zebra mussels' reproductively active season (May–October 2015; and April–August 2016) and bimonthly during their reproductively inactive months (November 2015–March 2016). The Leon River had a mean annual water discharge of 2.1 m^3 s^{-1} in 2013, 0.7 m^3 s^{-1} in 2014, and 16.6 m^3 s^{-1} in 2015 (USGS

Results

Hydrology

Over the study period, the median average daily discharge of the Leon River was 18.4 $m^3 s^{-1}$ with 80 percent and 20 percent of all mean daily discharges falling above 0.4 $m^3 s^{-1}$ and 41.9 $m^3 s^{-1}$ respectively (USGS 2016a). Our most downstream site along the Little River experienced similar variations in flow level with the median average daily discharge of the Little River calculated at 42.5 $m^3 s^{-1}$ with 80 percent and 20 percent of all mean daily discharges falling above 3.1 $m^3 s^{-1}$ and 159.7 $m^3 s^{-1}$ respectively (USGS 2016b). During the sampling period, central Texas experienced two major rain events in June 2015 and October 2015, which led to major flooding in both the Leon and Little Rivers. In late June 2015, discharge increased from a daily average of < 2 $m^3 s^{-1}$ to a maximum daily average of 157 $m^3 s^{-1}$ on June 30, 2015. High daily discharge rates (i.e., > 100 $m^3 s^{-1}$) lasted over extended periods until mid-August 2015 (Figure 2). Similarly, during a flood in late October 2015, mean daily discharge rates for the Leon River increased from < 2 $m^3 s^{-1}$ to a maximum daily average of 139 $m^3 s^{-1}$ on October 27, 2015. High mean daily discharge rates continued through mid-November 2015 and occurred periodically until June 6, 2016 when mean daily discharge remained > 100 $m^3 s^{-1}$ until mid-August 2016 (Figure 2). This high discharge rate was in contrast to the much lower rates that occurred before the study period (2013–June 2015) during which the 80th, median, and 20th percentile average daily discharge values of the Leon River were 0.21 $m^3 s^{-1}$, 0.48 $m^3 s^{-1}$, and 1.13 $m^3 s^{-1}$ while Little River values were 1.4 $m^3 s^{-1}$, 2.35 $m^3 s^{-1}$, and 4.47 $m^3 s^{-1}$ respectively.

Stream measurements taken during a period of low flow (i.e. daily average discharge from dam < 1.0 $m^3 s^{-1}$) show that stream habitat upstream of the lowhead dam was more lentic than stream habitat downstream of the dam. From 0.4–7.0 rkm downstream (i.e., above the lowhead dam), the river channel was wider (average 33.5 m width), deeper (average 4.3m mid-channel depth), and contained slower velocities (average 0.05 $m s^{-1}$ mid-channel velocity) compared to downstream (7.5–54 rkm) sites (average of 19 m channel width, 1.1 m channel depth, 0.16 $m s^{-1}$ mid-channel velocity).

Physico-chemical conditions

Water temperature ranged from 13 to 29 °C in the lake and from 5 to 31.8 °C in the river over the study period (Figures 3, 4). Temperature loggers at sites 2 and 5 showed similar seasonal temperature fluctuations. Water temperatures exceeded 30 °C on 12 days during the entire study period: on June 9, 2015; August 23–25, 2015; September 6–9, 2015; and August 8–11, 2016. During most of the study period, river temperature was within successful zebra mussel reproductive limits (16–24 °C) with temperatures falling below the reproductive threshold for 119 days (site 2) and 76 days (site 5) during the winter (December 2015–March 2016, Figure 4). River temperatures exceeded the upper threshold for successful reproduction (24 °C) from mid-June to September 2015 and from June to August 2016 (Figure 4).

All water quality parameters measured, i.e. pH (range: 6.8–9.1), dissolved oxygen (range: 2.3–11.4 mg L^{-1}), and temperature (range: 16–29.8 °C) did not vary significantly across sites (One way repeated measures ANOVAs: pH: $F_{5,29} = 0.64$, $p = 0.67$; dissolved oxygen: $F_{5,29} = 0.56$, $P = 0.73$; and temperature: $F_{5,29} = 1.35$, $P = 0.27$). With the exception of one low dissolved oxygen reading recorded during the September 2015 sampling event at Lake Belton (2.3 mg L^{-1}) all water parameters fell within tolerable limits (Sprung 1987; Claudi and Mackie 1993; McMahon 2015) of zebra mussels at the time of sampling.

Dispersal of veligers

Within Lake Belton and at the downstream sites, veliger densities varied greatly across season (Figures 3 and 4A, Supplementary material Table S1). In the lake, highest densities were found in October 2015 and April 2016 at temperatures of 19 °C and 27 °C, respectively. No veligers were found in September and December 2015 and low veliger densities were found in August of 2015 and 2016 (Figure 3A). Based on six data points, the quadratic regression between temperature and log (veliger density) was not statistically significant, but temperature explained 55% of the variation in veliger density in the lake ($F_{2,3} = 4.1$, $P = 0.14$, adjusted $R^2 = 0.55$).

In the river, highest veliger densities were found in May (3069 veligers m^{-3}) and June (1323 veligers m^{-3}) of 2015 at 0.4 rkm downstream from Lake Belton (site 1, note that the lake was not sampled during these months, when mean monthly temperatures were around 22–24 °C). Lower densities of veligers were found when temperatures were lower (e.g., December, April), but also when temperatures were higher (e.g., August, October, Figure 3B). The polynomial regression analysis showed that temperature accounted for about 69% of the variation in maximum veliger density ($F_{2,5} = 8.64$, $P = 0.02$, adjusted $R^2 = 0.69$, Figure 3B). Highest veliger densities only occurred during lower discharge conditions, but lower densities of veligers were found both at high and low discharge conditions and there was no apparent relationship between discharge and veliger densities.

Figure 4. Average monthly temperature (dashed line) and monthly minimum and maximum temperature bounds (shaded area) from the site 2 HOBO logger over the study period (June 3rd – October 10th and December 4th – August 24th, 2016) as well as A) maximum veliger density (m^{-3}) in the river, dashed horizontal lines represent the upper (24 °C) and lower (16 °C) reproductive thresholds, and B) average cumulative settlement (solid bars) and average juvenile settlement (cross-hatched bars) at site 2. Vertical dashed line represents the change in settlement monitoring (see methods for details). NA = no sample for that month.

Settlement

A high level of juvenile settlement (mussels m^{-2}) was consistently detected 2.5 rkm downstream from Lake Belton (Figure 4B). These settlement densities ranged from 56–73 mussels m^{-2} from February to August 2016. The second highest number of newly settled juveniles (average mussels m^{-2}) was found downstream at 6.0 rkm in February and April 2016 (46 mussels m^{-2} and 82 ± 10 mussels m^{-2}, respectively). Juvenile mussels were found in the highest numbers (96 mussels m^{-2}) at 13 rkm in August 2016. Settlement of juveniles showed little seasonal variation with average settlement values ranging from 4–96 mussels m^{-2} across all sites from February–August 2016.

No settlement was observed at or below the 13 rkm site from August 2015 until April 2016. At this time, 4 juvenile mussels m^{-2} were found on blocks at 13 rkm, 7 ± 2 (mean ± SE) juvenile mussels m^{-2} found at the 27 rkm site and 65 ± 23 juvenile mussels m^{-2} at the 54 rkm site (i.e., sites 4, 5 and 6, respectively) (see Figure S2). During the last sampling event in August 2016, no settlement was detected at either of the furthest downstream sites (≥ 27 rkm) but juvenile settlement (96 mussels m^{-2}) was still observed at 13 rkm downstream (Figure S2).

Our study recorded similar juvenile (shell length < 5 mm) settlement during sampling in February, April, and August 2016 (range 56–96 mussels m^{-2}) across sites, with the highest rate of juvenile settlement being observed in August 2016 at 13.1 rkm downstream. Cumulative settlement (juveniles and adults) did not vary considerably between June 2015 to February 2016 with the highest cumulative settlement density occurring at 2.5 and 6.0 rkm downstream and ranging from 12 to 1884 ± 570 mussels m^{-2} (Figure S2). Immediately downstream of Lake Belton (0.4 rkm) cumulative settlement was much more variable (0–59 mussels m^{-2}) and lower compared to sites at 2.5 and 6 rkm (Figure S2). Variation in cumulative settlement density was considerable between sites (CV = 180%) and sampling dates (CV = 166%) but both seasonal and spatial patterns (i.e., high cumulative settlement in August and at 2.5 and 6 rkm down-stream) were consistent (Figure S2).

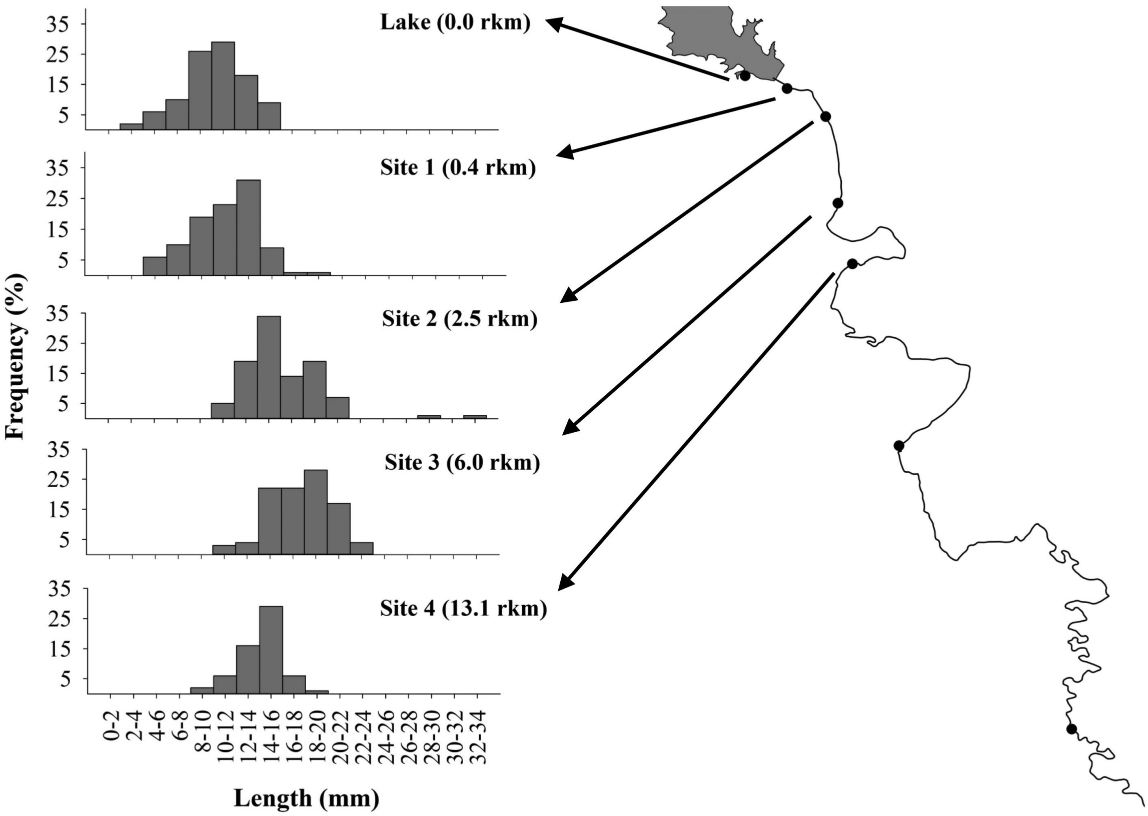

Figure 5. Length frequency distribution of zebra mussels from sites 0–4 (marked as black circles) in October 2015 (n = 100 for sites 0–3 and n = 60 for site 4).

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 ≤ 12mm in shell length, only 3–5% of the mussels at sites 2.5–13.1 rkm were compromised 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 $m^3 s^{-1}$) 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 > 25mm 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; Borcherding 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; Borcherding 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; Borcherding 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 thermocline (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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References

Ackerman JD, Sim B, Nichols SJ, Claudi R (1994) A review of the early life history of zebra mussels (*Dreissena polymorpha*): comparisons with marine bivalves. *Canadian Journal of Zoology* 72: 1169–1179, https://doi.org/10.1139/z94-157

Allen YC, Thompson BA, Ramcharan CW (1999) Growth and mortality rates of the zebra mussel, *Dreissena polymorpha*, in the Lower Mississippi River. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 748–759, https://doi.org/10.1139/f98-212

Allen YC, Ramcharan CW (2001) Dreissena distribution in commercial waterways of the US: using failed invasions to identify limiting factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 898–907, https://doi.org/10.1139/f01-043

Bobeldyk AM, Bossenbroek JM, Evans-White MA, Lodge DM, Lamberti GA (2005) Secondary spread of zebra mussels (*Dreissena polymorpha*) in coupled lake–stream systems. *Ecoscience* 12: 339–346, https://doi.org/10.2980/i1195-6860-12-3-339.1

Borcherding J (1991) The annual reproductive cycle of the freshwater mussel *Dreissena polymorpha* Pallas in lakes. *Oecologia* 87: 208–218, https://doi.org/10.1007/BF00325258

Churchill CJ (2013) Spatio-temporal spawning and larval dynamics of a zebra mussel (*Dreissena polymorpha*) population in a North Texas Reservoir: Implications for invasions in the southern United States. *Aquatic Invasions* 8: 389–406, https://doi.org/10.3391/ai.2013.8.4.03

Claudi R, Mackie GL (1993) Practical Manual for the Monitoring and Control of Macrofouling Mollusks in Fresh Water Systems. CRC Press, Boca, USA, 240 pp

Hernandez MR (1995) Thermal response and tolerance in the introduced freshwater bivalve, *Dreissena polymorpha* (zebra mussel). Master Thesis, University of Texas at Arlington, Arlington, USA, 132 pp

Higgins SN, Vander Zanden MJ (2010) What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecological monographs* 80: 179–196, https://doi.org/10.1890/09-1249.1

Horvath TG, Lamberti GA (1999) Mortality of zebra mussel, *Dreissena polymorpha*, veligers during downstream transport. *Freshwater Biology* 42: 69–76, https://doi.org/10.1046/j.1365-2427.1999.00462.x

Horvath TG, Lamberti GA, Lodge DM, Perry WL (1996) Zebra mussel dispersal in lake-stream systems: source-sink dynamics? *Journal of the North American Benthological Society* 15: 564–575, https://doi.org/10.2307/1467807

Lindim C (2015) Modeling the impact of Zebra mussels (*Dreissena polymorpha*) on phytoplankton and nutrients in a lowland river. *Ecological Modelling* 301: 17–26, https://doi.org/10.1016/j.ecolmodel.2015.01.012

Lucy FE, Minchin D, Boelens R (2008) From lakes to rivers: downstream larval distribution of *Dreissena polymorpha* in Irish river basins. *Aquatic Invasions* 3: 297–304, https://doi.org/10.3391/ai.2008.3.3.4

Mackie GL, Schloesser DW (1996) Comparative Biology of zebra mussels in Europe and North America: an overview. *American Zoologist* 36: 244–258, https://doi.org/10.1093/icb/36.3.244

McMahon RF (1991) Mollusca: Bivalvia. In: Thorp JH, Covich AP (eds), Ecology and Classification of North American Freshwater Invertebrates. Academic Press, San Diego, USA, pp 315–370

McMahon RF (1996) The Physiological Ecology of the Zebra Mussel, *Dreissena polymorpha*, in North America and Europe. *Integrative and Comparative Biology* 36: 339–363, https://doi.org/10.1093/icb/36.3.339

McMahon RF (2015) Implementation of a cost-effective monitoring and early detection program for zebra mussel invasion of Texas water bodies. In: Wong WH, Gerstenberger SL (eds), Biology and Management of Invasive Quagga and Zebra mussels in the Western United States. Boca Raton, FL: CRC Press, Taylor Francis Group, pp 349–374, https://doi.org/10.1201/b18447-31

Molloy DP, Karatayev AY, Burlakova LE, Kurandina DP, Laruelle F (1997) Natural enemies of zebra mussels: Predators, parasites, and ecological competitors. *Reviews in Fisheries Science* 5: 27–97, https://doi.org/10.1080/10641269709388593

Morse JT (2009) Thermal Tolerance, Physiological Condition, and Population Genetics of Dreissenid Mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) Relative to their Invasion of Waters in the Western United States. Ph.D. Dissertation, University of Texas at Arlington, Arlington, USA, 279 pp

Nichols SJ (1996) Variations in the reproductive cycle of *Dreissena polymorpha* in Europe, Russia and North America. *American Zoologist* 36: 311–325, https://doi.org/10.1093/icb/36.3.311

Ruiz GM, Carlton JT (2003) Invasive species: vectors and management strategies. Island Press, Washington, USA, 518 pp

Smith BR, Edds DR, Goeckler JM (2015) Lowhead dams and the downstream dispersal of zebra mussels. *Hydrobiologia* 755: 1–12, https://doi.org/10.1007/s10750-015-2211-7

Sprung M (1987) Ecological requirements for developing *Dreissena polymorpha* eggs. *Archiv für Hydrobiologie*. Supplementband. *Monographische Beiträge* 79(1): 69–86

Stoeckel JA, Schneider DW, Soeken LA, Blodgett KD, Sparks RE (1997) Larval dynamics of a riverine metapopulation: implications for zebra mussel recruitment, dispersal, and control in a large-river system. *Journal of the North American Benthological Society* 16: 586–601, https://doi.org/10.2307/1468146

Stoeckel JA, Rehmann CR, Schneider DW, Padilla DK (2004) Retention and supply of zebra mussel larvae in a large river system: importance of an upstream lake. *Freshwater Biology* 49: 919–930, https://doi.org/10.1111/j.1365-2427.2004.01237.x

Strayer DL (2009) Twenty years of zebra mussels: lessons from the mollusk that made headlines. *Frontiers in Ecology and the Environment* 7: 135–141, https://doi.org/10.1890/080020

TCEQ (2016) Texas Commission on Environmental Quality: Water Quality Data. Lake Belton and Site 11916. https://www.tceq.texas.gov/agency/water_main.html (accessed 6 October 2016)

TPWD (2013) Texas Parks and Wildlife Department: Zebra mussels found in Lake Belton and suspected in Lakes Worth and Joe Pool. http://tpwd.texas.gov/newsmedia/releases/?req=20130926a (accessed 26 September 2016)

USGS (2016a) US Geological Survey: 08102500 Leon River near Belton, TX, National Water Information System: Web Interface http://waterdata.usgs.gov/tx/nwis/dv?referred_module=sw&site_no=08102500 (accessed 12 September 2016)
USGS (2016b) US Geological Survey: 08102400 Little River near Little River Academy, TX, National Water Information System: Web Interface http://waterdata.usgs.gov/tx/nwis/dv?referred_module=sw&site_no=08102500 (accessed 12 September 2016)
Vanderploeg H, Liebig JR, Nalepa TF (1995) From picoplankton to microplankton: Temperature-driven filtration by the unionid bivalve *Lampsilis radiata siliquoidea* in Lake St. Clair. *Canadian Journal of Fisheries and Aquatic Science* 52: 63–74, https://doi.org/10.1139/f95-006

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 cummulative zebra mussel density (individuals per m^{2} ± 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