

DISPERSAL OF ZEBRA MUSSELS, *DREISSENA POLYMORPHA*,
DOWNSTREAM OF AN INVADED RESERVOIR

by

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ABSTRACT

Zebra mussels have recently invaded Central Texas and more information is needed to predict their spread in this region and inform management decisions. Therefore, I examined riverine zebra mussel dispersal, settlement, and growth downstream of Lake Belton, TX, invaded by zebra mussels in 2013. Veliger samples and settlement of juveniles on artificial substrata was monitored at a site in the lake and six sites in the Leon and Little Rivers, 0.4 to 54.7 river kilometers (rkm) downstream of the lake outlet. Veliger density declined with distance downstream with the greatest densities recorded at sites closest to the lake outlet (0.4 and 2.5 rkm). Veligers were found up to 13 rkm downstream. This decline was represented best with a logarithmic decline in May, Aug, Oct 2015 ($R^2 = 0.75$ to 0.94), and with an inverse power relationship in June and September 2015 ($R^2 = 0.53$ to 0.73). No clear pattern was found in April 2016 ($R^2=0.32$, $p = 0.06$). In contrast, maximum juvenile settlement ($437 \pm 75 \text{ m}^{-2}$) occurred 2.5 rkm downstream in August 2016, but not immediately downstream of the lake. Differences in settlement rates between sites could not be explained by differences in physico-chemical parameters such as temperature or turbidity as they did not differ significantly between sites. No mussels were found at 27 and 55 rkm downstream on artificial or natural substrata between May through December of 2015, but juvenile mussels were found there in April 2016. This suggests that zebra mussels were dispersal limited in 2015, and were able to disperse further downstream in 2016 probably facilitated by high discharge from Lake Belton.

I. INTRODUCTION

The invasion of the non-native zebra mussel in Texas, *Dreissena polymorpha*, raises concern because its introduction has had large ecological and economic impacts in North America (Strayer 2009). 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.). This benthification increases water clarity, which can enhance the growth of macrophytes (Ricciardi 2003, Higgins and Vander Zanden 2010). Zebra mussels are effective filter feeders. When scaled by mass, zebra mussels filtered ten times more than *Lamprolaima radiata siliquoidea* (a native unionid mussel) (Vanderploeg *et al.* 1995). Zebra mussel excretion catalyzes nutrient cycling of soluble phosphorus and ammonium, which increases phytoplankton growth (Lindim 2015).

Decreases in pelagic phytoplankton biomass due to filtering activity of zebra mussels can have effects that cascade up to higher trophic level consumers, such as decreases in herbivorous zooplankton and carnivorous fish (Higgins and Vander Zanden 2010). Zebra mussels can also reach extremely high densities and their respiration can cause decreases in dissolved oxygen in the water column (Caraco *et al.* 2000, Effler *et al.* 2004). Finally, introduction of zebra mussels can affect native bivalve populations due to colonization of their valves that impede opening or closing of their shells, and through competition for food resources (Nalepa *et al.* 1996; Karatayev *et al.* 1997, Ricciardi 2003, Strayer and Malcom 2007).

Zebra mussels originated in the Black Sea region (Karatayev *et al.* 2003) and have been in North America since approximately 1986 when they were introduced into the

Great Lakes, where adult colonies were first observed in 1988 (Hebert *et al.* 1989). By December of 1991, there were established colonies in 10 US states (Strayer 2009). They have continued this pattern of quick spread across the US and by 2009, zebra mussels were first detected in Lake Texoma on the Texas-Oklahoma border. By 2013, zebra mussels were found in Lake Belton in central Texas (Texas Parks and Wildlife Department 2009, 2013b, cited in Churchill, 2013) (Fig. 1).

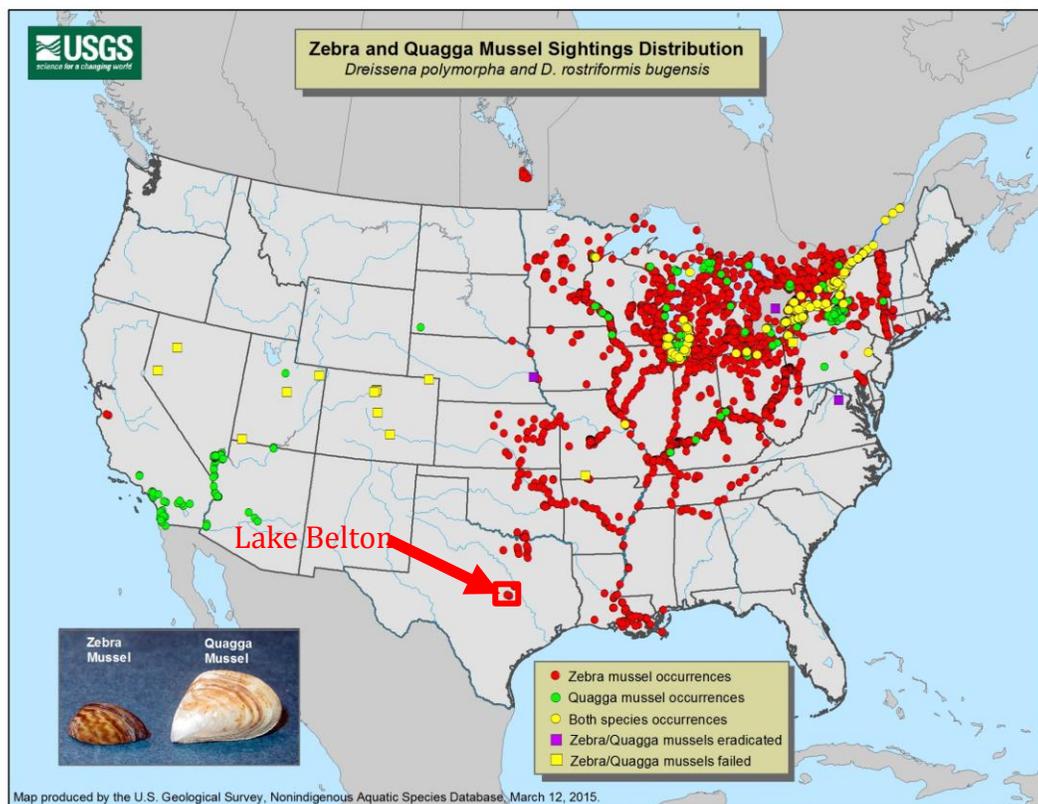


Figure 1- Zebra/Quagga mussel locations throughout the United States, according to the United States Geological Survey (USGS 2016).

Zebra mussels are typically small in size (22-35mm in length) and known for their distinct “D” shaped shells and brown “zebra” striping (Higgins and Vander Zanden 2010,

Hosler 2011). Their planktonic larvae, called veligers, are 70 to 280 μm in length (the longest axis) while still in the free-floating stages (Ackerman *et al.* 1994, Hosler 2011). Once a foot is developed, the larva is considered a pediveliger and can range from 167 to 350 μm in shell length and uses the foot to crawl or swim along the bottom. Once a suitable surface is located, the pediveliger anchors with byssal threads and goes through metamorphosis before reaching the postveliger (plantigrade mussel) stage (158 to 500 μm in shell length) (Ackerman *et al.* 1994). Once settled on hard substratum, they develop into juveniles and then adults that proliferate under favorable conditions (Fig. 2).

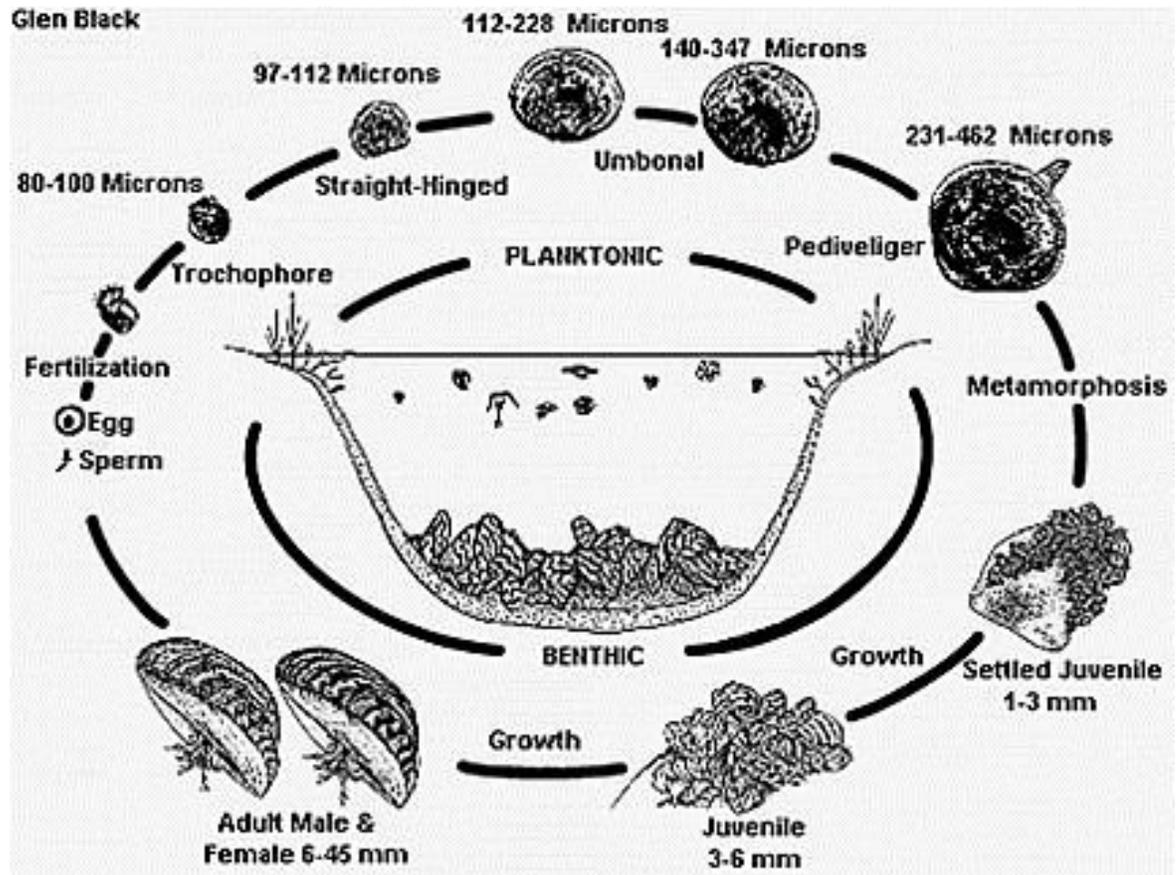


Figure 2- Zebra mussel life cycle (Black, 2003).

Zebra mussels can spread rapidly over long distances by attaching to boats or by veliger larvae being transported in ballast-water of ships (Ruiz 2003, Strayer 2009). Even without human-aided transport, zebra mussels have high dispersal potential via advective transport of microscopic veligers in the water column. Previously colonized lakes can act as a source for larvae being transported downstream by water current (Horvath *et al.* 1996).

Zebra mussels have life history characteristics such as high fecundities (30,000-40,000 eggs per female) and rapid growth rates that allow them to colonize new habitats readily, if conditions are favorable (McMahon 1991, Claudi and Mackie 1993). Favorable habitat conditions include water temperatures that need to be adequate for zebra mussel spawning; larval development needs temperatures between 16°C and 24°C and peaks at 18°C (McMahon 1996). Also, any water temperature below 0°C and above 30-32°C is lethal to zebra mussels (McMahon pers. comm.).

Unfavorable habitat conditions include low calcium levels, low oxygen, low pH, high turbidity, and high turbulence. Zebra mussels tend to colonize waters with >15 mg of Calcium per liter, so they have available calcium to develop their shells (Ramcharan *et al.* 1992, Mellina and Rasmussen 1994, Karatayev *et al.* 1998, Strayer 2008). Even though adult mussels are relatively tolerant of low oxygen levels, juvenile mussels need higher levels of oxygen to survive and mature (Strayer 2008, Sparks and Strayer 1998). Adult zebra mussels can withstand a minimum of 6.5 pH (Sprung 1987, McMahon 1996). Turbidity can negatively affect respiration and filtration of zebra mussels (McMahon 1996, Madon *et al.* 1998, Schneider *et al.* 1998). In addition, turbulence may increase veliger mortality, as shown in lab experiments and suggested by observations of density

declines downstream of lakes (Horvath and Lamberti 1999, Rehmann *et al.* 2003, Horvath and Crane 2010).

Besides Louisiana, mussels in central Texas are currently the most southern zebra mussel population in the United States (Churchill *et al.* 2013) and may be limited by thermal stress. However, Matthews and McMahon (1999) found that zebra mussel populations near the current southernmost extent of the US show increased upper thermal tolerance compared to populations in the northern US.

It is unknown whether flow and habitat conditions in rivers of central Texas located downstream of invaded reservoirs would assist or prevent zebra mussel dispersal and how far downstream zebra mussel may be able to disperse with their veligers and settle as juvenile mussels. An improved knowledge of dispersal abilities and the conditions enhancing or impeding zebra mussel dispersal and settlement in central Texas can aid in understanding the patterns of zebra mussel invasion in the southern US and assist with projecting future invasion patterns. Therefore, the objectives of this study were to examine dispersal of veligers and settlement of juvenile zebra mussels downstream of an infested reservoir and to explore potential limiting factors. Specifically, the aim was to determine (1) how veliger densities decline downstream of Lake Belton, (2) how settlement of juveniles varies in space and time and in comparison with veliger dispersal, (3) how size distribution differs between the lake and different distances downstream and on natural vs. artificial monitoring substrate, and (4) whether dispersal and settlement may be limited by physico-chemical conditions.

II. METHODS

Study area

Zebra mussels were first detected in Lake Belton (31.104881°N, -97.485208°W, 4,977.6 hectares, 218.9 km of shoreline, maximum depth 37.8 m (Tibbs and Baird 2015)) Belton, Texas, Bell County in 2013 (Texas Parks and Wildlife Department 2009, Texas Parks and Wildlife Department 2013b). The lake had a high abundance of zebra mussels, with the greatest densities observed at Frank's Marina in 2014 and early 2015. However, the zebra mussel population began to decline in summer of 2015 (McMahon pers. comm.). Lake Belton has a bottom release dam from which water is released continuously but discharge varies through time.

Water and potentially zebra mussel larvae are released from Lake Belton's dam outflow into the Leon River, in the Brazos River Basin (USGS 2016). Preliminary surveys in April 2015 confirmed the presence of adult zebra mussels in the Leon River as far as 13 river kilometers (rkm) downstream from the dam outflow. The Leon River had an annual water discharge of: 2.07 m³/s in 2013, 0.67 m³/s in 2014, and 16.59 m³/s in 2015. The Leon River has a drainage area of 9,277 km² (USGS 2016) and connects with the Lampasas River to form the Little River (Fig. 3). For this study, six sites downstream from the continuous, bottom release dam were established and repeatedly measured for veligers, juveniles, and water parameters.



Figure 3- Map of Lake Belton, downstream located rivers and 6 study sites downstream from the lake.

Dispersal of veligers

Dispersal of zebra mussel veligers was monitored at 6 sites downstream of Lake Belton, on the Leon River and Little Rivers (Table 1, Fig. 3). In order to sample veligers drifting in the water column ~380L of water was pumped through a 64µm mesh Wisconsin-style zooplankton net with a battery-powered marine bilge pump, at each site. The hose for the pump was taken ~1-2m away from the shore and the water was pumped from the top 1/3 of the water column. Each sample was preserved in the field with 95% ethanol and 0.1g of sodium bicarbonate for each 50ml of ethanol, in order to buffer and

stabilize the pH to keep veliger calcium carbonate shells intact. Samples were transferred to the lab at Texas State University in a cooler and refrigerated until analysis. Veligers were then counted and extracted using a cross polarizing filter on a stereo-microscope at 40x-80x (Nikon SMZ800N, with Nikon DS-Fi2 Camera). Each sample was mixed on a stir plate until equilibrium. Then, 25% of the sample was sub-sampled and analyzed. Samples in 2015 from sites ≥ 27 rkm downstream of the dam were analyzed for presence of zebra mussel DNA using a PCR analysis by Greg Southard at the A.E. Wood Laboratory in San Marcos, TX (Holser 2013).

Table 1- Latitude and longitude for sites in Lake Belton and the sites downstream in the Leon and Little Rivers, and their distances from the lake outlet.

Site Number &Name	Latitude	Longitude	River km from dam
Source: Belton Lake	31.10488°N	-97.485208°W	0.0
Site 1: Miller Springs Park	31.103508°N	-97.103508°W	0.4
Site 2: Hwy 317	31.096414°N	-97.453394°W	2.5
Site 3: Waco Road	31.066439°N	-97.442450°W	6.0
Site 4: East 6 th Ave	31.045878°N	-97.432978°W	13.1
Site 5: Dice Grove	30.984481°N	-97.402267°W	27.3
Site 6: Reed Cemetery Rd	30.896375°N	-97.319136°W	54.7

Sampling was done approximately once a month between May and October 2015, every 2 months between October 2015 and April 2016, and again in August 2016 (Table 2, veliger samples n=7, juveniles observed n=8). High water levels prevented monthly sampling in May and July 2016 (Fig. 4).

Table 2- Maximum discharge and depth on sampling dates (data from USGS site 08102500, Leon River near Belton), and whether plankton net samples were taken or not.

Sample Date	Maximum Daily Discharge (m ³ s ⁻¹)	Maximum Daily Depth (m)	Plankton Net Samples	Cinderblocks Observed
05/14/15	0.4	1.1	Yes	Yes
06/03/15	1.0	1.1	Yes	Yes
07/22/15	98.8	2.1	Yes (not analyzed)	No
08/12/15	37.9	1.7	Yes	Yes
09/07/15	0.8	1.1	Yes	Yes
10/10/15	0.6	1.1	Yes	Yes
12/04/15	41.3	1.7	Yes	No
02/08/16	13.2	1.4	No	Yes
04/08/16	24.3	1.5	Yes	Yes
08/24/16	39.9	1.7	No	Yes

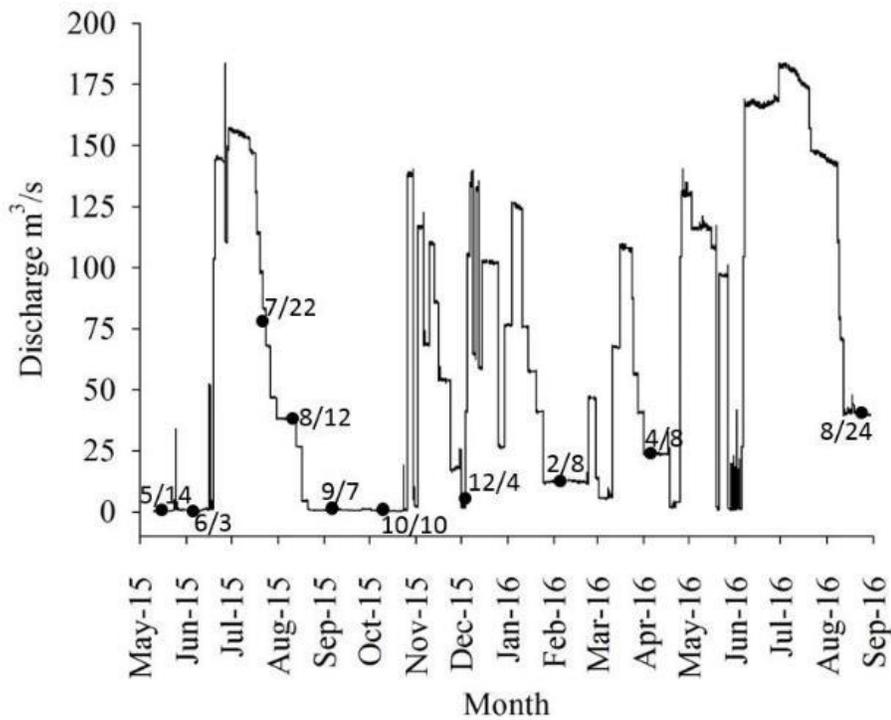


Figure 4- Hydrograph during the study period including sampling dates. Discharge data from USGS site 08102500, Leon River near Belton.

Veliger samples were first taken in the lake in August 2015. Sites were sampled from downstream towards upstream to prevent the risk of contamination or transfer of zebra

mussels or veligers. Also, a vinegar soak was used on equipment such as the plankton tow net between sites in order to break down veliger shells and therefore kill the larvae. A bleach solution wash was used on all field equipment at the end of each sampling day (bilge pump, kayaks, oars, plankton net, and wading boots).

Juvenile Settlement

Settlement of juvenile zebra mussels was monitored at the same six sites as the veliger dispersal and on the same dates except for July 2015, December 2015, and August 2016 (Table 2, Fig. 3). Two cinderblocks (20.3cm x 20.3cm x 40.6cm) were placed in the river at each site on 2 May, 2015, one on each bank, and served as monitoring substrate for juvenile settlement, (Fig. 5). Two additional cinderblocks were placed at each site on 2 August, 2015 and were increased to six cinderblocks on 4 December 2015, to decrease risk of complete data loss from a site in case of vandalism and to get more robust estimates for each site.



Figure 5- A) Cinderblock before placement. B) Cinderblock retrieved after 5 months (Site 3, 10 October 2015).

In 2016, a modified monitoring design was applied by placing eight cinderblocks at each site by 2 February 2016 and in Lake Belton at Frank's Marina on 8 April 2016 (Table A1). Similar to the monitoring in 2015, four of the eight cinderblocks at each site were only observed for total number of attached mussels at each sampling date in order to monitor survivorship and cumulative juvenile settlement. The other four cinderblocks at each site were completely scraped free of zebra mussels (8 February, 8 April, and 24 August 2016), and the mussels taken back to the laboratory at Texas State University in order to determine settlement rates. The scraped off mussels were preserved in a freezer. Shell free dry mass was determined for 30 individuals per site for each sampling date (10 October 2015, 8 April 2016, and 24 August 2016) (or less if < 30 were available) (Fig. A2 & A3). The shell length of each mussel was measured using a caliper to the nearest

0.1mm, and then was separated from the tissue of the mussel after freezing, and placed in a pre-weighed aluminum weigh boat.

The tissue was dried at 55°C for at least 48 hours and each individual's dried tissue was weighed to the nearest 0.001mg to determine dry mass. Mussel tissue from 8 April 2016, were too small and dehydrated to extract via dissection, and shells were decalcified before drying and weighing in a 15% nitric acid solution (Alexander and McMahon 2004), followed by three, 5-minute de-ionized water baths (without removing mussel periostracum).

Settlement rates were calculated using the zebra mussels that were scraped from odd numbered cinderblocks on 8 February 2016, 8 April 2016, and on 24 August 2016 (Table A1). A daily rate of zebra mussel settlement m^{-2} was calculated for each cinderblock, and then extrapolated to get a monthly (30 days) settlement rate of zebra mussels $m^{-2} site^{-1}$. For the purpose of these calculations, it was assumed that no zebra mussels settled and then detached from the artificial substrata. Settlement rates varied over time and site.

Size distribution in Lake Belton vs. the river

Zebra mussels were collected from natural substrata at each site in April 2015. Sixty individuals were collected from the lake, only 15 individuals were found at sites 1-3, and only 1 individual was found at site 4. In October 2015, 100 zebra mussels were collected from natural substrata at the Lake and sites 1-3, but only 60 were found at site 4. The shell length of each mussel was measured using a caliper to the nearest 0.1mm (Fig. 6).



Figure 6- Zebra mussels from natural substrate in October 2015 from the lake and sites 1-4 (0.4-13.1 rkm), separated by site. The lake through site 3 have 100 individual mussels for each, and site 4 has 60 individual mussels.

Physico-chemical conditions

In order to monitor temperature variability, temperature loggers (HOBO Water Temp Pro v2 U22-001, Onset) were installed at all of the six sites downstream from the Lake Belton and recorded water temperature at 1-hour intervals. Temperature loggers were installed between June (site 2), August (site 5), and October 2015 (sites 1, 3, 4, and 6, Table A1), and December 2015 (sites 2, and 5). Only temperature loggers from sites 2 and 5 could be retrieved in August 2016, the others were likely dislodged during a flooding in late October 2015. Unusually high temperature readings around 40°C from site 5 between 4, December 2015 and 27 January, 2016 were removed from the dataset. Loggers may have been exposed to air and heated up in the sun. Daily discharge data were gathered from the USGS station number: 08102500 (USGS 2016) (Fig. 7A). At each site and each sampling date, conductivity, pH, water temperature, and dissolved oxygen were measured with a multi parameter probe (YSI 556).

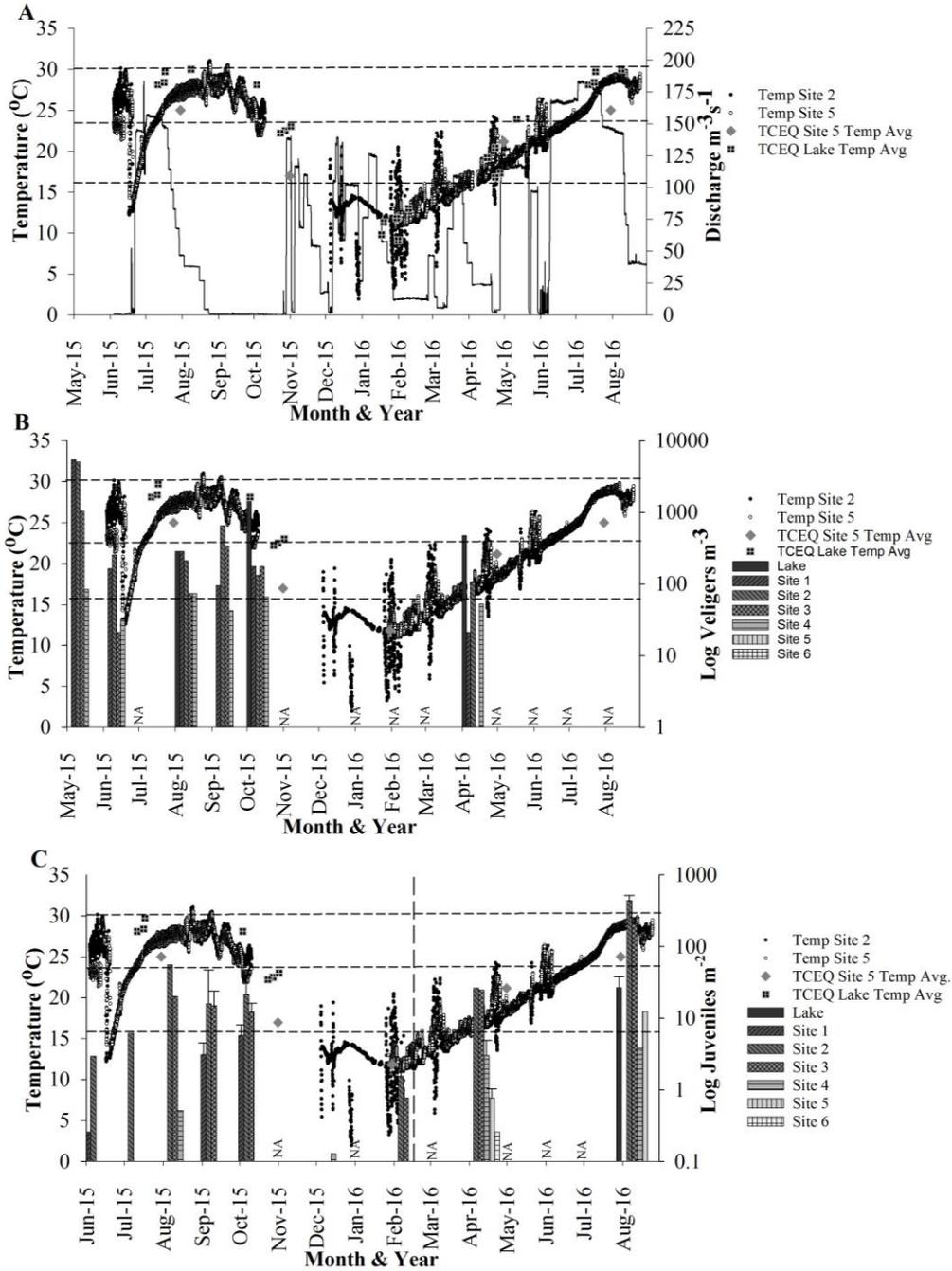


Figure 7- Hourly temperature data ($^{\circ}C$) from HOBO temperature loggers at sites 2 and 5 (June 3rd –October 10th and December 4th- August 24th, 2016), average seasonal river temperatures from TCEQ (from site 11916, years 2012-2016). Dashed horizontal lines represent temperature thresholds. Lethal temperature for zebra mussels is $30^{\circ}C$, upper threshold for reproductive success is $24^{\circ}C$, and lower reproductive threshold is $16^{\circ}C$. Also, seasonal Lake surface temperatures from TCEQ (from site Belton Lake near Dam, years 2012-2016), and A) discharge ($m^{-3} s^{-1}$) (USGS site 08102500, Leon River near Belton), B) veliger densities, C) Number of settled juveniles m^{-2} . NA= data not available.

In addition, temperature data from Belton Lake and a location near site 5 on the Leon River (site 11916), was gathered from the TCEQ surface water quality dataset available online (TCEQ 2016). During my study period, they sampled Lake Belton near the dam 4 times: 14 July, 2015; 1 October, 2015; 28 January, 2016; and 14 April, 2016.

Water samples for analysis of turbidity were taken at each site on 16, 17, and 18 September, 2016 in a well rinsed non-opaque bottle and returned to the lab. Once returned to the lab, turbidity was determined with a turbidimeter (Turner Designs, Trilogy Model). Stream width was also taken at this time using a rangefinder (360R TruPulse) (Table 3).

Table 3- Turbidity and stream width on sampling dates between 16 and 18 September 2016, at the site in Lake Belton and the six river sites. Discharge varied between 1.1 to 2.8 m³/s.

Date	Site	Turbidity (NTU)	Stream Width (m)
18-Sep-16	Lake	8.9	NA
17-Sep-16	Site 1	8.5	32
17-Sep-16	Site 2	7.4	38
17-Sep-16	Site 3	6.5	39
16-Sep-16	Site 4	4.0	20
16-Sep-16	Site 5	6.8	25.5
16-Sep-16	Site 6	19.7	17

Data analysis

The number of veligers counted under the microscope were converted to a density (number of veliger m⁻³). To examine whether veliger density showed a) a logarithmic decline with distance or b) an inverse power relationship, a linear regression was done

with $\log(\text{distance})$ as a predictor variable and (a) veliger density as response variable and (b) the $\log(\text{veliger density}+1)$.

A two-way ANOVA was used to examine (1) Variation in settlement rates of juveniles between sampling dates and sites, (2) variation in presence of veligers between sampling dates and sites, and (3) variation in physico-chemical parameters between sites. Homogeneity of variances was tested with a Bartlett Test. Data from April 2015 shell lengths of zebra mussels on natural substrata were log-transformed followed by an ANOVA. A post-hoc Tukey-test was used to determine differences between sites. To examine the length-weight relationship of juvenile mussels a linear regression was computed with $\log_e(\text{length})$ as a predictor variable and $\log_e(\text{weight})$ as response variable.

III. RESULTS

Dispersal of Veligers

Veliger densities generally declined with distance, but highest densities were found at 2.5 rkm downstream of the lake (site 2) not at the site closest to the dam (0.4 rkm) at 3 out of 6 sampling dates (June, September 2015, and April 2016). Veliger densities at 6 rkm downstream (site 3) were also 3.5 times higher than 0.4 rkm from the dam (site 1) in September and October 2015 (Figs. 8, 9). No veligers were found at sites 5 and 6 (≥ 27 rkm) throughout the study, but zebra mussel DNA was found in the samples from sites 5 and 6 during December 2015 (Data from Greg Southard, Texas Parks and Wildlife Department) (Figs. 8, 9). In the river, larvae showed an approximately logarithmic decline in May, August, and October of 2015 ($R^2 = 0.75-0.94$) (Figs. 9 A, C, E; Table 4), whereas June 2015 and September 2015 were represented better with an inverse power function ($R^2 = 0.53-0.75$). No clear pattern was found in April 2016 (p -value=0.06, $R^2=0.32$), (Figs. 9 B, D, F, Table 4).

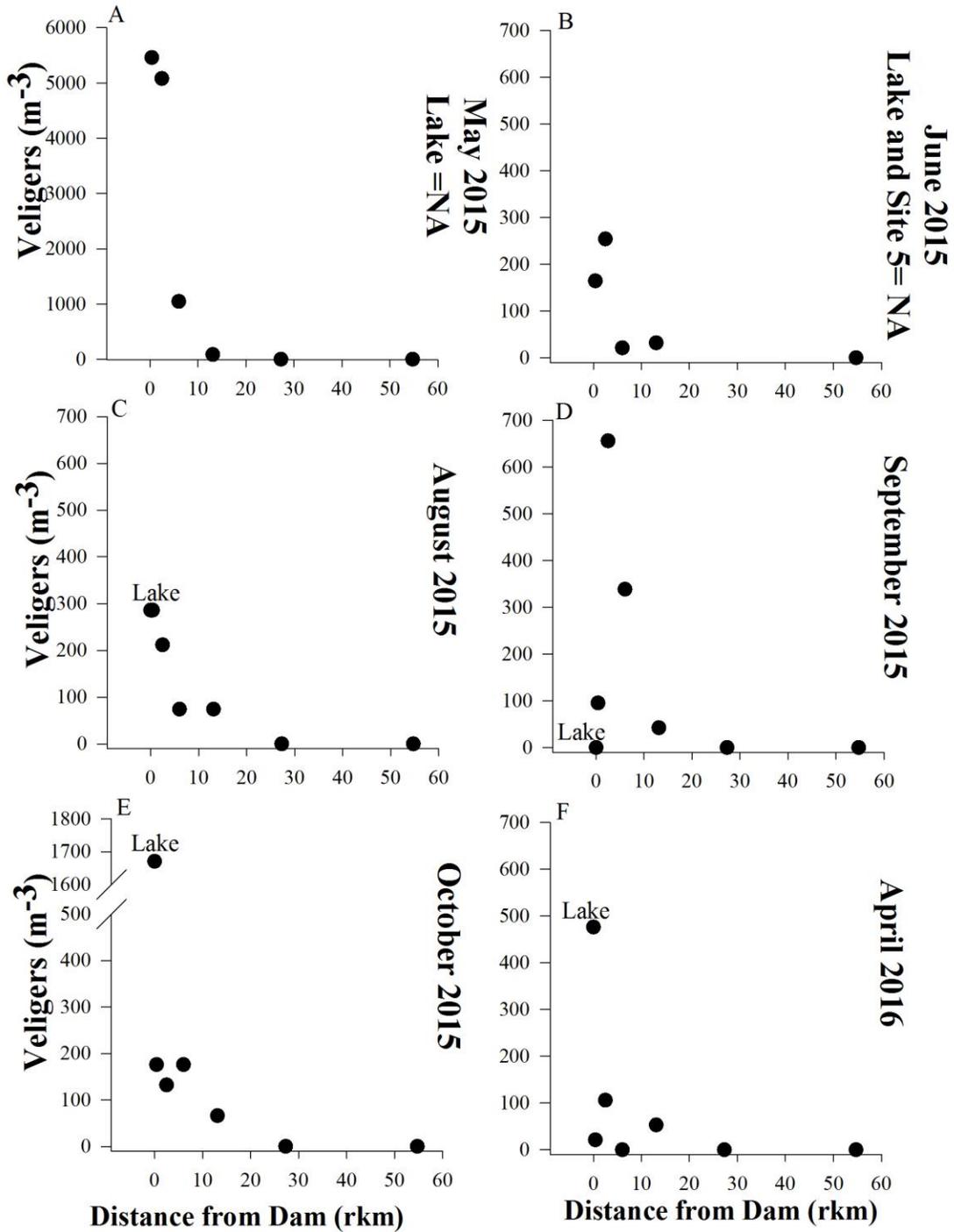


Figure 8– Veliger densities in the lake and 0.4 to 54 rkm downstream for A) May 2015, B) June 2015, C) August 2015, D) September 2015, E) October 2015, and F) April 2016. NA= data not available.

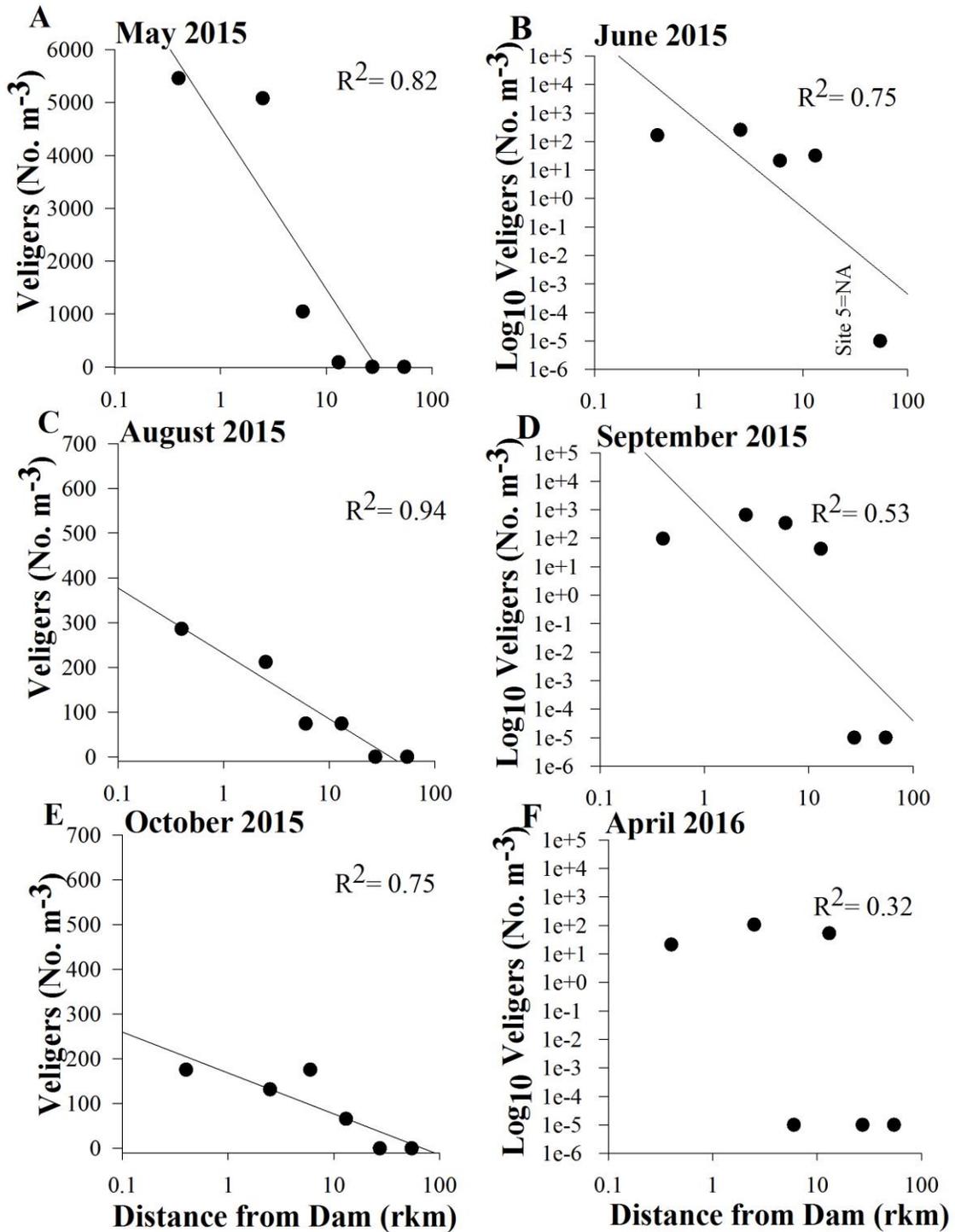


Figure 9- Veliger densities in the river at 6 sites 0.4 to 54 rkm downstream. A, C, E) Veliger density vs. log (distance) for May, August, October 2015. B, D, F) Log (veliger density) vs. log (distance) for June, September, 2015, and April 2016. Lines indicate linear regression.

Table 4- Shell free dry mass equations from 3 different studies.

Study	Equation	R2 value	Size range (mm)	n
French <i>et al.</i> 2007	$9.1 \times 10^{-6} \times \text{Shell length}^{2.84}$	NA	12-24	6-30
Ozerzky 2010	$1.4 \times 10^{-5} \times \text{Shell length}^{2.31}$	0.92	0.5-25	73
This Study	$5.9 \times 10^{-6} \times \text{Shell length}^{2.76}$	0.90	0.2-33	165

Variation between sites (CV= 174) and sampling dates (CV= 141), was large, and a 2-way ANOVA test indicated no significant difference in veliger densities between sites ($F_{6, 39}=0.9$, $p= 0.5$).

Differences in larvae densities between the lake and river were not consistent over time (Figs. 7B, 8). In August 2015, veliger densities in the lake were the same as 0.4 rkm downstream of the dam (285 veligers m^{-3}). No veligers were found in the lake in September 2015, but in the river, predominately 2.5 rkm downstream (site 2, 656 veligers m^{-3}) (Fig. 8B). In October 2015, larval densities in the lake (1670 veligers m^{-3}) were approximately 10 times higher than those in the river (176 veligers m^{-3}) (Fig. 7B, 9).

Veliger density varied with season with the highest density of veligers occurring in May 2015 (5460 veliger m^{-3}) 0.4 rkm from the dam (site 1, Figs. 7B, 9A). The lowest density of veligers was found on 8 April 2016 (0.4 rkm, 21 veligers m^{-3}) and no veligers were found December 2015 (Figs. 7B & 10). The ANOVA and Tukey detected that 14 May, 2015 and 8 April 2016 were different from all other sampling dates ($F_{6, 39}=3.08$, $p= 0.01$, Fig. 7B).

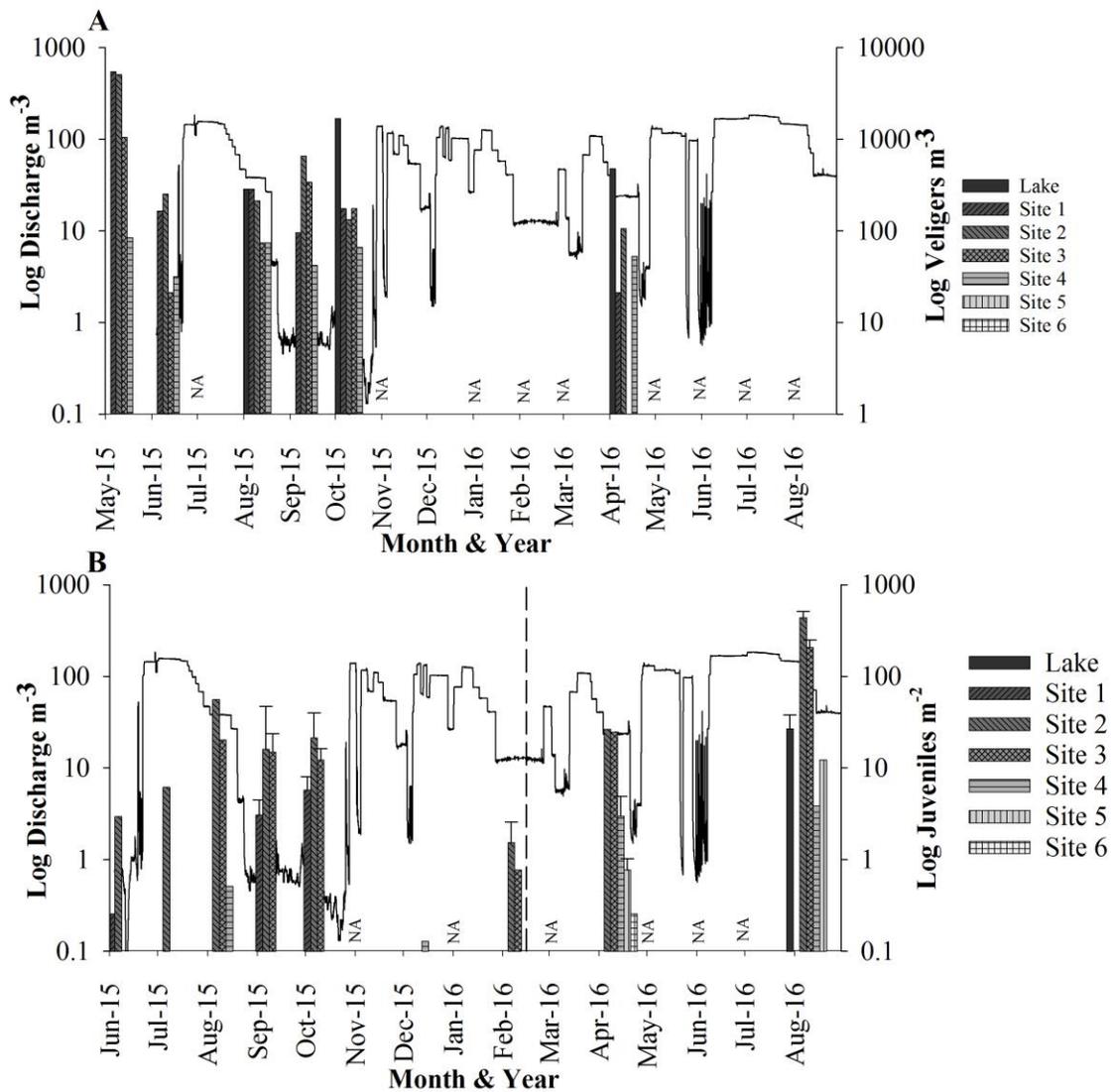


Figure 10- A) Discharge (USGS site 08102500, Leon River near Belton), and log veliger density at each site over the study period. B) Discharge (USGS site 08102500, Leon River near Belton), and log zebra mussel abundance at each site over the study period. NA= data not available.

Juvenile Settlement

The greatest juvenile settlement was detected on artificial substrata at 2.5 and 6 rkm downstream of the dam (Figs. 7C, 11). In August 2015 and 2016 the maximum settled density at 2.5 rkm downstream was 56 and 438 mussels m^{-2} , respectively. The

maximum densities in August 2015 and 2016 at 6 rkm downstream was 20 and 206 mussels m^{-2} , respectively. Lower numbers of settled juveniles were found immediately downstream of the lake outflow (≤ 0.4 rkm, ranging from 6 ± 2 mussels m^{-2} to 3 ± 1 mussels m^{-2}). Settlement was not observed ≥ 27 rkm downstream in summer and fall 2015. In April 2016, 9 individuals were found on 3 cinderblocks at 27 rkm, and 1 individual was found on a single cinderblock at 54 rkm (i.e., 0.3 to 0.8 mussels m^{-2}). In August 2016, no settlement was detected at 54 rkm, and 48 individuals were found on 1 cinderblock at 27 rkm (i.e., 0 to 12.3 mussel m^{-2} , Fig. 11). This was after an extended period of relatively high discharge including discharge pulses that peaked at $184 \text{ m}^{-3} \text{ s}^{-1}$ on 27 June, 2015 and at $138 \text{ m}^{-3} \text{ s}^{-1}$ on 8 December 2015 (Table 2, Fig. 10B).

Settlement of juveniles showed seasonal variation, with peak settlement occurring in late August through October of 2015 and in August 2016 (September and October data not collected in 2016). Lowest settlement occurred in December 2015. Variation was considerable between sites (CV= 180) and sampling dates (CV= 166), and a 2-way ANOVA indicated no significant difference between juvenile density neither between sampling dates nor sites (Sampling Dates: $F_{9,49}=1.8$, $p= 0.10$; Sites: $F_{6,52}=1.2$, $p= 0.34$). It should also be noted that cinderblocks were placed and replaced on different days, making comparisons between sites and dates more difficult (Table A1). However, both seasonal and spatial patterns (i.e., high settlement in August at 2.5 and 6 rkm downstream) were consistent between years.

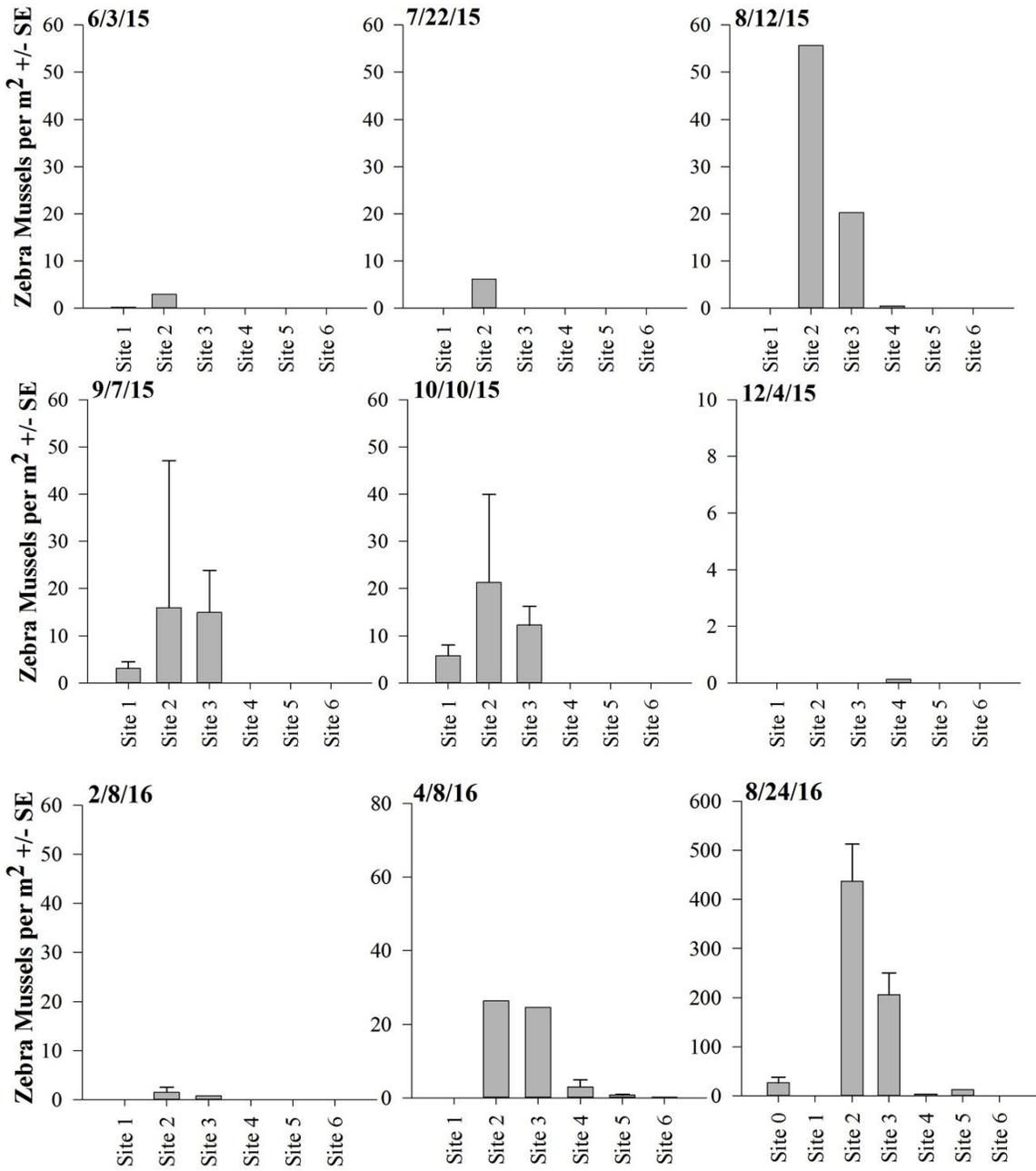


Figure 11- Number of settled juveniles per sampling date and at different sites. Error bars represent \pm standard error.

Additional settlement was expected to increase the number of juveniles with time.

Instead, the number of juveniles on the artificial substrata declined from summer 2016 to

fall 2016. For example, from site 2.5 rkm downstream (site 2): juvenile densities averaged 56 zebra mussels m^{-2} in August 2015 and declined to an average of 16 ± 31 zebra mussels m^{-2} in September 2015 (Fig. 7C & 12). Byssal threads without mussels were found on the cinderblocks on February 8th, 2016 (Fig. 12).



Figure 12- Byssal threads remain on cinderblock after mussels are no longer there (Photo taken on 8 February 2016).

The highest settlement rate occurred in August at 2.5 and 6 rkm downstream with 69 ± 3 mussels $\text{m}^{-2} \text{month}^{-1}$ and 45 ± 8 mussels $\text{m}^{-2} \text{month}^{-1}$ respectively. These rates were 7 to 11 times higher compared to the lake in August. Settlement rates were lower in April with the highest rate per site being (14 ± 10 mussels $\text{m}^{-2} \text{month}^{-1}$) (2.5 rkm) and February settlement rates were even lower, with highest rate per site being 3 ± 2.5 mussels $\text{m}^{-2} \text{month}^{-1}$ (2.5 rkm) (Fig. 13A).

Data from August 2016 showed a power relationship between tissue dry mass and weight for juveniles: $SFDM = 5.9 \times 10^{-6} \times \text{Shell length}^{2.76}$, $R^2=0.90$ (Fig. 14). Settlement rates expressed as dry biomass ($\text{g m}^{-2} \text{month}^{-1}$), showed, not surprisingly, a similar pattern to those described above for juvenile settlement rates (Fig. 13B). But there were also differences. At all dates (February, April, and August 2016), the highest settlement rate was measured at 2.5 rkm, whereas the highest biomass specific settlement rate was measured at 13.1 rkm in February, at 0.04 rkm in April, and at 6 rkm in August 2016. In August 2016, the lake had higher biomass specific settlement rate and settlement rate than the settlement rates at sites 1, 4, 5, and 6 (Fig. 13 A, B).

Size distribution in Lake Belton vs. river

Zebra mussels that were collected in October 2015 from natural substrata in the river showed size differences between sites. Mussels from 0.4-13.1 rkm downstream (sites 1-4) were larger on average than those in the lake. Individuals at sites 1-4 were 6.5%, 59%, 74%, and 39%, larger, respectively, than the individuals from the lake. Highest frequency of mussels for sites 1-4 were in the size categories 12-14 mm, 14-16 mm, 18-20 mm, and 14-16 mm, respectively, but 2 mussels were found between 28-34 mm at site 2, indicating presence of 2-year-old mussels (Fig. 15).

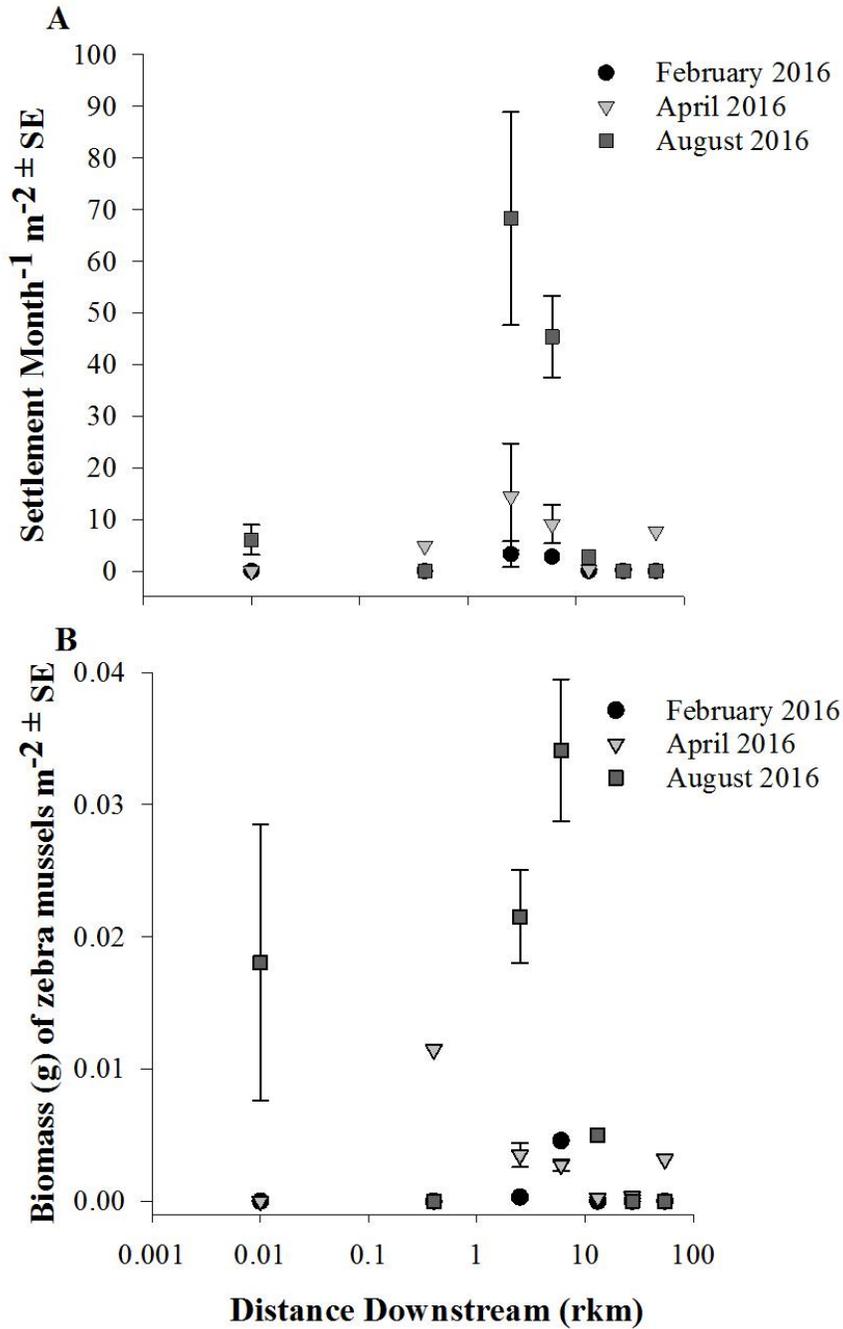


Figure 13- Mean settlement rates at 6 sites 0.4 to 54 rkm downstream for February, April, and August 2016. Settlement rates presented as A) Number of mussels m⁻² month⁻¹ B) Biomass (g m⁻²). Error bars represent standard error for each site: n = 4, except n = 3 for sites 2 & 4 in April and site 2 in February, n = 2 for site 1 & 6 in April, and n = 1 for site 3 in February and site 4 in August.

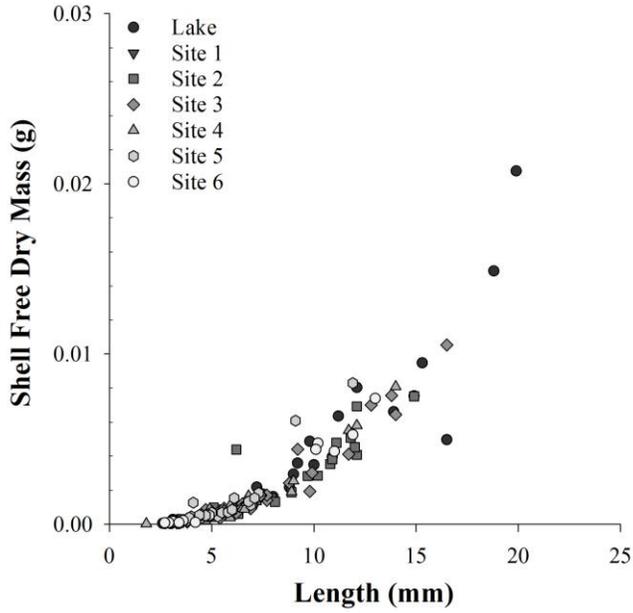


Figure 14- Shell free dry mass (SFDM) of zebra mussels in relation to length for mussels collected on date 24 August 2016 for the lake and sites 1-6.

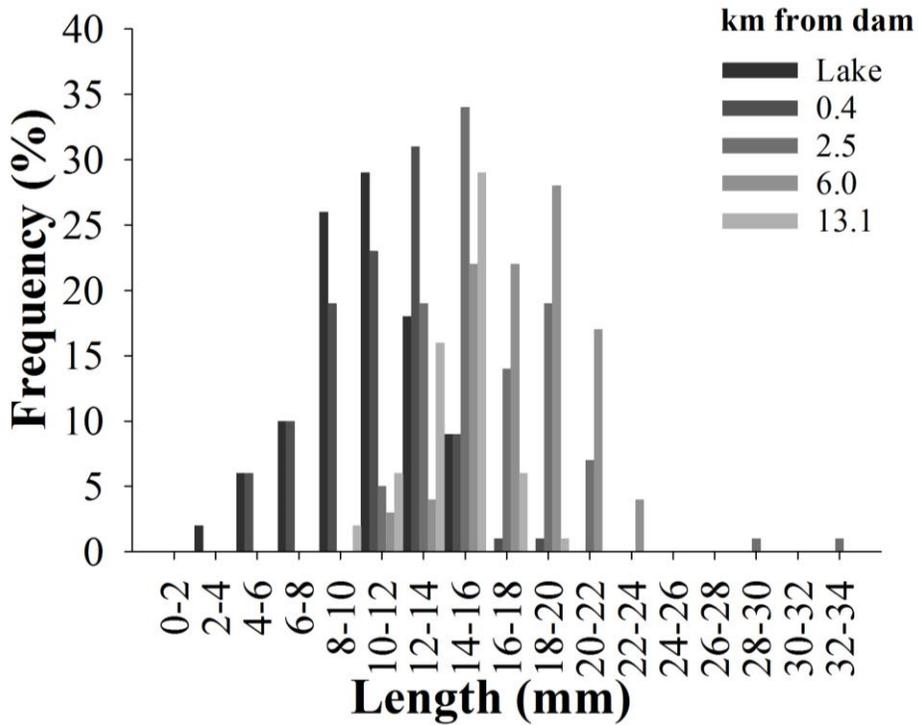


Figure 15- Length frequency distribution for Sites 0-4 on 10 October 2015. Total n is 100 for sites 0-3, and 60 for Site 4.

Physico-chemical conditions

Over all the sampling dates, DO ranged from 2.3 to 11.4 mg L⁻¹, with the lake having the lowest average and site 2 having the highest average. Over all sampling dates, conductivity ranged from 322 to 579 µS/cm, and increased with distance from the dam. Site 6 had the highest average and the lake had the lowest average conductivity. Over all sampling dates, pH ranged from 6.5 to 9.1, with the lake having the highest average pH and site 5 having the lowest average. Over all sampling dates, temperature ranged from 11 to 33.8°C, with the site 6 showing lowest average temperature and the lake showing highest average temperature. Differences between sites were not statistically significant for temperature, pH, or DO, but for Conductivity (Temperature (°C): $F_{1,50} = 2.4$, $p = 0.13$; pH: $F_{1,51} = 2.4$, $p = 0.13$; DO (mg L⁻¹): $F_{1,49} = 0.99$, $p = 0.32$, Conductivity (µS/cm): $F_{1,51} = 13.58$, $p < 0.05$) (Fig. 16).

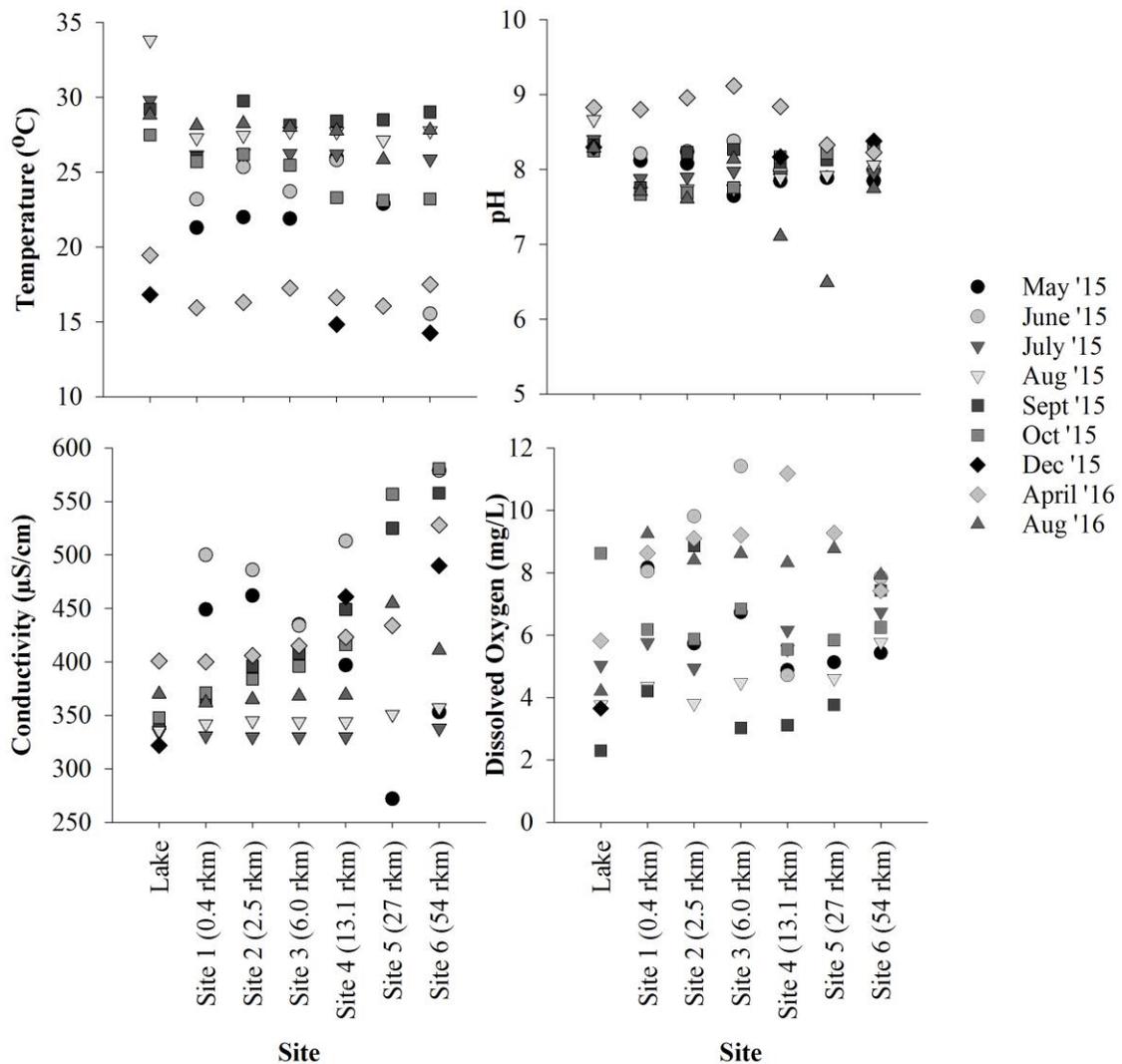


Figure 16- Variation in physico-chemical parameters across sites and sampling dates. Average temperature ($^{\circ}\text{C}$) (A), average conductivity ($\mu\text{S}/\text{cm}$) (B), average DO (mg/L) (C), and average pH (D) from measurements taken each sampling date.

Temperature loggers at site 2 and 5 showed similar temperature fluctuations.

According to temperature logger data, temperature exceeded 30°C (upper threshold for zebra mussel survival) only 6 to 7 days (site 5 and 2 respectively) within the study period during the months of July, August and September, of 2015 and 2016. Temperatures below the reproductive threshold of 16°C occurred during winter of 2015/2016 on 139 days (site 2) and 76 days (site 5) (Fig. 7A).

Temperature data showed that both site 2 and 5 exceeded 24°C (upper threshold for successful reproduction of zebra mussels) nearly all of late June -September 2015. Note that temperature data were missing from 10 October through 4 December 2015 for site 2, and 10 October, 2015 through 27 January, 2016 for site 5. Generally, temperature tended to stay within successful zebra mussel reproductive limits (16-24°C) only during a small time in June of 2015, and mostly during the months between April 2015 and late June 2016 (Fig. 7A). Surface temperature in Lake Belton (according to TCEQ data) was: July= 28.4°C; October= 28.1°C; January= 11.8°C; and April= 19.2°C (Fig. 7) (TCEQ 2016).

During the sampling period of this study, central Texas experienced 2 major rain events, 30 May, 2015 and 30 October, 2015, which led to major flooding in the Leon River. Discharge increased from $\sim 0.0034 \text{ m}^3 \text{ s}^{-1}$ to $\sim 183.21 \text{ m}^3 \text{ s}^{-1}$ for an extended period of time (Fig. 4, Table 2). In June of 2015, when discharge increased to over $141.58 \text{ m}^3 \text{ s}^{-1}$ from a high of $28.32 \text{ m}^3 \text{ s}^{-1}$ in May of 2015, temperature decreased drastically (Fig. 7A). Discharge from 2013, when zebra mussels were first found in Lake Belton, was much lower than that recorded in 2015-2016 (Fig. A1). Turbidity readings ranged from 4 NTU-19.71 NTU. Turbidity readings were highest furthest away from the dam (site 6). The lowest turbidity reading was at 13.1 rkm downstream from the dam (site 3) (Table 3).

IV. DISCUSSION

Our study did not find settled juveniles farther than 13 rkm between May and December 2015, but since April 2016, I detected them up to 54 rkm downstream. This considerable increase in dispersal distance may have been facilitated by a long time period with consistently higher discharge compared to previous years (Fig. A1). Agreeing with the findings of this study, one study on streams in Indiana/Michigan suggested that dispersal in streams (<30m width) is limited to a rather short distance (12 rkm, Horvath *et al.* 1996, 8-10 rkm, Bobeldyk *et al.* 2005, 13 rkm, this study). Other, much larger rivers have had their entire length colonized, such as the Hudson River (507 km) in New York (Jantz and Neumann, 1992, Strayer *et al.* 2011).

It is established that lakes act as source populations for riverine dreissenid mussels (Kern *et al.* 1994, Horvath *et al.* 1996, Stoeckel *et al.* 1997, Stoeckel *et al.* 2004, Bobeldyk *et al.* 2005) from where mussel densities decline exponentially with distance downstream (Horvath *et al.* 1996, Horvath and Lamberti 1999, Bobeldyk *et al.* 2005). In contrast, this study found a better fit with an inverse power relationship in 3 out of the 6 sampling dates.

Veligers were not detected in the Lake Belton in September 2015, after a period of high water temperatures that breached 30°C in the lake 25th-27th August 2015 (Arterburn and McMahon, unpublished data), but veligers were found in the river at this time. Veligers are likely from previous lake production that remained suspended in the water column for an extended period of time. Residence time in pools before a low-head dam (at 6.9 rkm from the lake outlet), may have been sufficient to slow veliger dispersal enough for our collection, before being transported downstream (Smith *et al.* 2015).

Assuming a relatively low mean velocity of 0.1 m s^{-1} , veligers would travel for 36 hours to reach 13 rkm downstream, supporting the idea that larvae produced by stream-dwelling mussels would likely be transported out of the system before maturing (Mackie 1995), and that maintenance of the stream mussel population does rely on the lake population (Horvath *et al.* 1996, Bobeldyk *et al.* 2005). In addition, the largest densities of veligers in this study were found upstream of that dam, suggesting that these veligers were from lake production, as veligers produced in the river would be pushed much further downstream before developing to the pediveligers settlement stage.

Highest veliger density and juvenile settlement was expected at the site closest to the lake as observed in other studies (Horvath *et al.* 1996, Horvath and Lamberti 1999). This pattern was observed for veligers 3 of the 6 months sampled, but the other 3 months (June, September 2015, and April 2016) had highest veliger densities at 2.5 rkm downstream. Juvenile settlement was consistently highest at 2.5 rkm suggesting that settlement was limited ≤ 0.4 rkm by habitat conditions. Potential limiting habitat factors could be turbidity, turbulence, or temperature. Turbidity has been found to have a negative effect on respiration and filtration of mussels (McMahon 1996, Madon *et al.* 1998, Schneider *et al.* 1998) and cause an increase in veliger mortality (Horvath *et al.* 1996, Rehmann *et al.* 2003, Horvath and Crane 2010). High turbidity at the lake outlet could be due to suspended sediment, and the high turbidity 54 rkm downstream was likely due to the confluence of the Leon and the Lampasas River (Table 3). Turbulence was not measured, but it is plausible that it may be higher closer to the dam due to the high outlet of water and channelization of the river. White caps were seen on waves at the lake outlet on every sampling date except when the outlet was under renovation (May

2015- November 2015). Temperature could be potentially lower closer to the lake due to the hypolimnetic releases from the lake, but our measurements did not indicate significant differences to the other sites.

Veliger dispersal varied seasonally with temperature being the most likely driving factor (Burla and Ribi 1998). The highest veliger densities in the river were found in May of 2015, whereas no veligers were found in the lake or the river in December, when temperatures were below the threshold of 16°C for reproduction. Temperature data from the lake indicates that temperatures in Lake Belton did not drop below 16°C until 10 December 2016 (Arterburn and McMahon, pers. comm.). Other studies found veligers year around, and temperature were similar to those found in Lake Belton (Karatayev 1983, Lvova *et al.* 1994, Burlakova 1998, Churchill *et al.* 2013).

Temperatures were above the threshold of 24°C for reproduction in the summer. Nevertheless, veligers were found in the Leon River when temperatures were exceeding successful reproductive upper temperature limits. Another study from Lake Belton also found veligers throughout the summers of 2015 and 2016 (Arterburn and McMahon, pers. comm.). This suggests that zebra mussels in central Texas may actually be able to produce viable offspring at temperatures higher than 24°C, or that temperatures be colder in the deeper depths of the lake.

The seasonal variation of juvenile settlement observed in our study showing a peak in late August differs from previous observations, where highest settlement was found in May 2015 and in January 2016. Mussel mortality is typically caused by thermal stress that occurs during the warmest summer months, and is followed by an increase in density due to settlement of juveniles produced from a fall spawning period that extends

from October to December (Arterburn and McMahon, unpublished data). The unusual seasonal patterns seen in this study, are likely due to mussel mortality caused by temperatures above the lethal threshold for mussels, or higher flows than in previous years (Fig. A1). Byssal threads found on cinderblocks (on 8 February, 2016) suggest that there was mussel mortality or detachment during the winter (McMahon 1996, Burks *et al.* 2002, Toomey *et al.* 2002).

The shell length to dry weight relationship of mussels recorded in this study was similar to that reported from a study from Lake Michigan (French *et al.* 2007) and Lake Simcoe (Ozersky 2010, Table 4).

Clearance rate and size of mussels are directly related (Ackerman 1999). Using the clearance rate equation calculated by Kryger and Riisgård (1988; Clearance Rate = $6.82 * (\text{Dry Weight})^{0.88}$), and the maximum biomass calculated in this study ($0.0341 \text{ g} * \text{m}^{-2}$), zebra mussels in the Leon River may filter up to $34.9 \text{ mL mussel}^{-1} \text{ h}^{-1}$. This value is on the lower end of the range of filtration values found in other studies. Reeders *et al.* (1989) found that zebra mussels of different sizes can filter a range of 2 to $287 \text{ mL mussel}^{-1} \text{ h}^{-1}$. Kryger and Riisgård (1988) found that small zebra mussels (11.2 mm) can filter $68 \text{ mL mussel}^{-1} \text{ h}^{-1}$ and they predicted that large mussels (33.5 mm) can filter $658 \text{ mL mussel}^{-1} \text{ h}^{-1}$. Ackerman (1999) found that dreissenid mussels were able to filter $60\text{-}70 \text{ mL mussel}^{-1} \text{ h}^{-1}$ at low velocities.

Differences in size frequency distribution indicated differences in recruitment between sites. A larger proportion of recent recruitment (mussels < 11mm) decreased with distance from the source population, as also found by French *et al.* (2007). Two generations of zebra mussels occurred at site 3, indicating successful survival in the river.

Mussels in the river could also be potentially larger for their age, because they may be less food limited than in lakes (Horvath and Lamberti 1999, Schwalb *et al.* 2013).

Also, some cinderblocks could have been placed in anoxic water, preventing settlement, specifically at site 1. Water parameters could have been confounded since sites further from the dam were always taken in the morning and sites near the dam were always taken in the evening.

The results of this study illustrate that zebra mussels can spread via riverine dispersal, and can increase dispersal distances within a relatively short time (i.e. 41 rkm within a year). If a lake was located within 50 rkm downstream of Lake Belton it could have been successfully invaded from upstream. This may be especially the case during wet years with consistently higher discharge. In addition, riverine dispersal and temperature as key driving factor for seasonal variation and potential limiting factors should be studied further in Texas.

APPENDIX SECTION

Table A1- Results of linear regression for log (distance) as a predictor variable and (a) veliger density as response variable and (b) the log (veliger density+1).

Date	Type	Slopes	Intercept	R²	P value	Discharge (m³/s)
5/14/2015	Log	-3065.0				
	Linear	±717.2	4535.0 ±788.6	0.82	0.00453	0.4
	Log Log	-2.0 ± 0.5	3.8 ±0.5	0.80	0.0023	
6/3/2015	Log	-99.8				
	Linear	±55.0.	166.8 ±56.0	0.52	0.0587	1.1
	Log Log	-1.2 ±0.3	2.2 ± 0.4	0.76	0.00365	
8/12/2015	Log	-146.3				
	Linear	±19.2	231.2± 21.2	0.94	0.000398	38.2
	Log Log	-1.2 ±0.4	2.5 ±0.4	0.73	0.00405	
9/7/2015	Log	-142.3				
	Linear	±154.1	309.0 ±169.4	0.18	0.142	0.7
	Log Log	-1.2 ±0.5	2.5 ± 0.6	0.53	0.0146	
10/10/2015	Log					
	Linear	-91.3 ±26.7	168.7 ± 29.4	0.75	0.00455	0.6
	Log Log	-1.1±0.4	2.4±0.5	0.64	0.00728	
12/4/2015	Log					
	Linear	0	0	0	-	41.1
	Log Log	0	0	0	-	
4/8/2016	Log					
	Linear	-20.0 ±25.7	46.8 ± 28.3	0.13	0.173	24.1
	Log Log	-0.7 ± 0.	1.5 ± 0.6	0.33	0.0607	

Table A2- Cinderblock and temperature logger placed and encountered at sites over time. H=temperature logger, red H=Temperature logger installed, pink= cinderblocks from which zebra mussels were scraped off at each sampling date, blue= cinderblocks on which cumulative settlement was monitored, black= newly placed cinderblock.

Site	5/2/2015	5/14/2015	6/3/2015	7/22/2015	8/12/2015	9/2/2015	9/7/2015	10/10/2015	12/4/2015	1/27/2016	2/8/2016	4/8/2016	8/24/2016
0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1,2,3,4,5,6,7,8	1,3,5,7,2,4,6,8
1	1,2	1,2	1,2	2	3,2	2,3,4,5	2,4,3,5	H,3,5,2,4	NA	NA	H,6,7,8,9,10,11,12,13	H,7,9,11,13,10,12	H,
2	1,2	1,4	H,1,4	H, 1	H,1,6	H,1,6,3,5	H,6,1,3,5	1,3,5,8	H,7,9,10,11,12,14	NA	H,7,9,11,10,12,14,13,16	H,7,9,11,13,10,12,14,16	7,9,11,13,10,14,16
3	1,2	1,2	1,2	1	1,4	4,1,5,6	1,5,4,6	H, 1,5,4,6	H,3,7,8,9,10,12	NA	H,3,7,9,8,10,12,11,14	H,3,11,8,10,12,14,7,9	H,3,7,9,11,8,10,12,14
4	1,2	1	1,4	1,4	1,6	6,1,3,8	1,3,6,8	H, 1,3,6,8	H,6,8,5,7,9,10	NA	H,5,7,9,6,8,10,11,12	H,5,7,9,11,6,8,10,12	H,5,7,9,6,8
5	1,2	1	NA	NA	H	H,3,4,5,6	H,3,5,4,6	3,4,6	NA	H,3,4,6,7,8,9,10,11	NA	H,3,7,9,11,4,6,8,10	3,7,10
6	1,2	1,2	1,2	1,2	1	1,4,3,6	1,3,4,6	H,1,3,4,8	H,1,3,4,8,9,10	NA	H,1,3,9,4,8,10,11,12	H,1,3,9,11,4,8,10,12	H,1,3,9,4

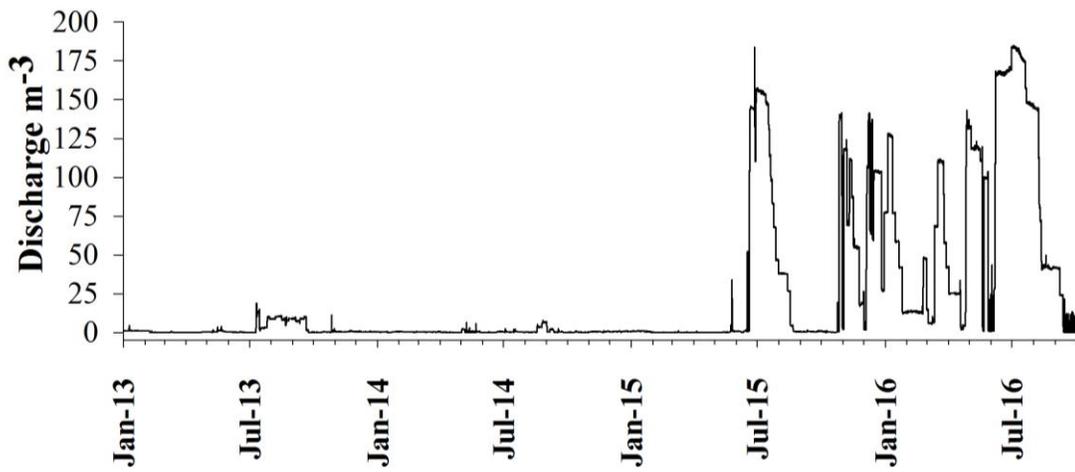


Figure A1- Discharge from January 2013-August 2016 for USGS site 08102500, Leon River near Belton (USGS 2016).

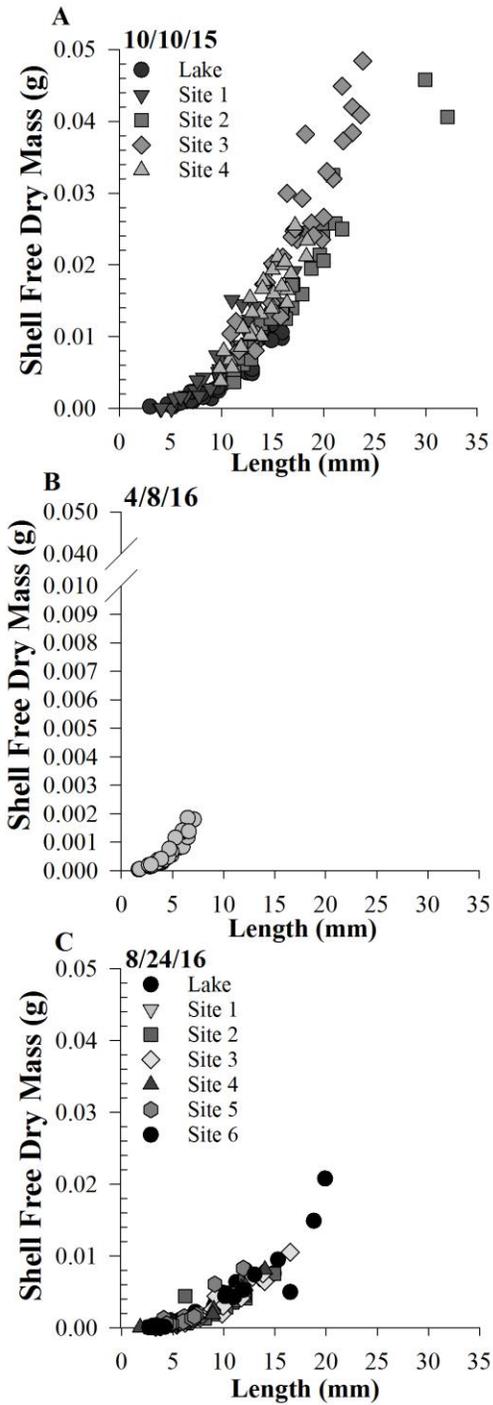


Figure A2- Shell free dry mass (SFDM) of zebra mussels in relation to shell length for mussels collected for each date it was sampled for A) at different sites B) for 8 April 2016 SFDM, C) for 24 August 2016 SFDM at different sites.

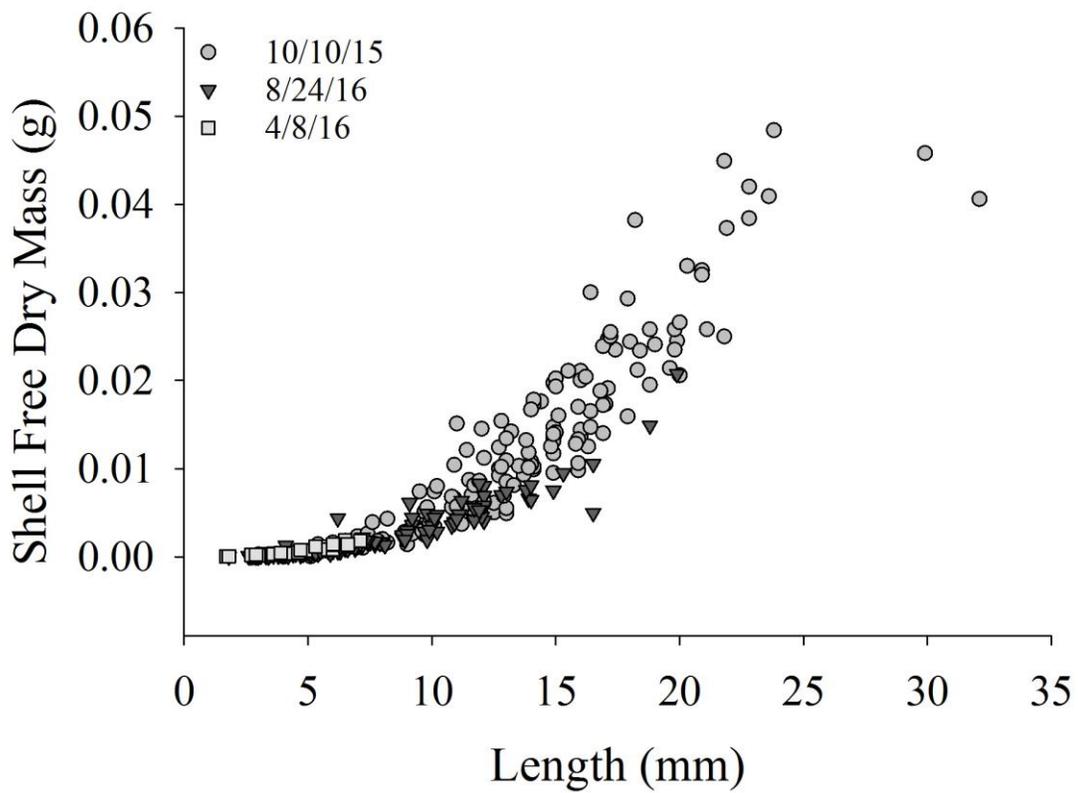


Figure A3- Shell free dry mass (SFDM) of zebra mussels in relation to length for mussels collected on each date it was sampled for, compared to each other.

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