Dispersal of zebra mussels downstream of an invaded reservoir and assessing the risk of dreissenid mussel invasion into lakes of Texas.

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This report consists of two parts written as drafts of two independent manuscript for submission to peer-review journals: Part 1 (Pages 3-30) presents the findings on our project examining the dispersal of zebra mussels downstream of an invaded reservoir, Part 2 (Pages 31-49) reports the results on modeling over-land zebra mussel dispersal in Texas.

1. Downstream dispersal of the invasive zebra mussel (*Dreissena polymorpha*) from two invaded Texas reservoirs

Summary

Zebra mussels have recently invaded Central Texas and more information is needed concerning their downstream dispersal and thermal tolerances to predict their spread and inform management makers. The objective of this study was to quantify and examine dispersal, settlement rates, and growth of zebra mussels in and downstream of the recently invaded Lake Belton (invaded 2013) and Stillhouse Hollow (invaded 2016). Monitoring sites, located in the lakes and 0.4-97.0 river kilometers (rkm) downstream of Lake Belton and 2.5-19.0 rkm downstream of Stillhouse Hollow, were surveyed from August 2016 to August 2017. Veliger density varied greatly across season with peak densities occurring in early summer (May-June) and fall (October). Both, highest veliger densities and juvenile settlement were observed ≤6 rkm downstream of Lake Belton, which was upstream of a low-head dam located at 7rkm. Veligers were occasionally observed as far downstream as 97rkm (September & October 2016, May 2017), and juvenile settlement as far as 55 rkm in October 2016 after a period of prolonged increase in river discharge. In contrast, no juvenile settlement was observed downstream of Stillhouse Hollow and veligers were only observed in June 2017 at 2.5 rkm. Average growth rates of zebra mussels in Lake Belton were higher in early summer (May-June) compared to late summer (July-August). In the Leon River growth rates were lower than in the lake, likely due to lower temperatures and probably food limitation. Our findings suggest that zebra mussels are dispersal limited in rivers, but increased discharge and river impoundments may facilitate and increase dispersal. It is possible that the lack of a low head dam and the more lotic conditions downstream of Stillhouse Hollow has helped to limit recruitment of zebra mussels in the Lampasas River, but further monitoring is necessary. In addition, both growth and reproductive activity continued during high summer temperatures, suggesting that Central Texas zebra mussels may have acclimated to a higher temperature tolerance than their counterparts in more northern regions.

Introduction

Dreissenid mussels are successful aquatic invaders which spread rapidly throughout eastern North America following their arrival from Eurasia more than 20 years ago (Strayer 2009). More recently, zebra mussels (*Dressenia polymorpha*) have started to invade portions of western North America including central Texas. The establishment of dreissenid mussels have drastically altered invaded aquatic ecosystems, because of their ability to act as ecosystem engineers (Karatayev *et al*. 1997). Mussels cause a "benthification" of aquatic ecosystems by re-directing energy from the pelagic to the benthic zone through their high filtering activity and biodeposition of organic material (Higgins and Vander Zanden 2010). Dreissenid mussels also modify benthic habitats through the formation of dense mussel beds. This, in combination with their filtering activity and biodeposition, can lead to various ecosystem changes, ranging from the reduction of zooplankton and fish to increases of macrozoobenthos and macrophytes (Karatayev et al. 2002, Higgins and Vander Zanden 2010). In addition, invasion by dreissenid mussels poses a substantial threat to native unionid mussel fauna. For example, the colonization of the Great Lakes led to considerable declines of native unionid mussels (e.g., Nalepa 1994).

Zebra mussels have spread rapidly over long distances by attaching to boats or by being transported in ballast-water of ships (Ruiz, 2003; Strayer, 2009), but they also have high dispersal potential via advective transport of their planktonic larvae, called veligers (Hosler, 2011). For larger river systems, it has been shown that zebra mussels are able to disperse hundreds of river kilometers downstream if aided by location of lakes, dams, and impoundments found on such navigable waterways (Hovarth *et al*. 1996; Allen & Ramcharan 2001; Smith *et al*. 2015). Such impoundments not only facilitate spread with increased boat traffic, but act as stepping stones as reproducing populations may persist upstream of these dams and provide recruitment to further downstream locations (Smith *et al*. 2015).

In contrast, dispersal abilities in smaller streams (< 35 m width) seems to be more limited and veliger density and settlement was found to rapidly decline in density with increased distance downstream and occurrence of veligers and settled individuals was restricted to ≤ 12 rkm downstream of the invaded lake (Hovarth *et al*. 1996; Hovarth & Lamberti 1999; Bobeldyk *et al.* 2005; Lucy *et al*. 2008). Little is known, however whether and how zebra mussel spread in rivers downstream of infested reservoirs in Texas. Our previous study in the Leon and Little

River downstream of infested Lake Belton, where zebra mussels were first detected in 2013, show that juvenile zebra mussels were not detected > 13 km downstream (rkm) between Spring and Fall 2015, but by Spring 2016 were found 50 km downstream from the reservoir (Olson et al, in review). In summer 2016, zebra mussels were also detected in Stillhouse Hollow, from which water runs into the Lampasas River, which joins with the Leon River (coming from Lake Belton) to from the Little River (Figure 1).

Probably the most important driving factor for zebra mussel reproduction is temperature, with the most favorable conditions for spawning, larval development, and settlement occurring between 18°C and 26°C (McMahon 1996). Some study has been done with regards to the effects of elevated temperature on growth and tissue condition (Allen *et al*. 1999; Garton & Johnson 2000) and results show a seasonal decline during the summer months with increased temperatures and reproduction rates leading to more degraded body condition. However, these studies have focused on populations of mussels found either in northern lakes (Garton & Johnson 2000) or a large river system (Allen *et al*. 1999). No data exsits on the growth rates of mussels in a small southern river system or on comparing growth within a southern coupled lake-river system. The objective of this study was to quantify and examaine dispersal, settlement rates, and growth of zebra mussels in and downstream of the infested Lake Belton and Stillhouse Hollow. The goal was to contribute to a better understanding of how zebra mussels spread downstream of an invaded reservoir and the relative importance of potential limiting or enhancing factors leading to that downstream dispersal, providing crucial information for the management of invasive zebra mussels in Texas reservoirs and rivers.

Methods

Study sites

Both Lake Belton and Stillhouse Hollow have a bottom release dam from which water is variably released year-round into the Leon River (from Lake Belton) and the Lampasas River (Stillhouse Hollow), in the Brazos River Basin. The Leon River is a small to medium sized river (~30-35m wide) and approximately 28 rkm downstream from Lake Belton joins with the Lampasas River to form the Little River (~30-40m stream width) (Figure 1). There exists one low-head dam along the Leon River approximately 7.0 rkm downstream from the Lake Belton outlet (Figure 1). Stream habitat upstream of the lowhead dam is more lentic with a wider and deeper channel compared to stream habitat downstream of the lowhead dam (Olson *et al*. in review).

The Lampasas River is a smaller (~10-20m wide) spring-fed stream that stretches approximately 27.0 rkm downstream from Stillhouse Hollow before joining with the Leon River. Sampling sites were located approximately 0.4, 2.5, 6.0, 13.0, and 27 rkm along the Leon River, approximately 2.5, 5.1, and 13rkm along the Lampasas River, and approximately 57.0 and 94rkm downstream along the Little River (Figure 1). One site was located within each reservoir at marinas approximately 1.0-2.0 km away from their respective dams. Downstream sites were spaced out on an approximate logarithmic scale to facilitate data analysis and based on ease of accessibility.

Field Sampling

Sampling was done monthly during zebra mussels' reproductively active season (March-October) and bimonthly during their reproductively inactive months (November-March). High flow levels prevented monthly sampling at riverine sites in April 2017. Sites were sampled from downstream towards upstream to prevent the risk of contamination or transfer of zebra mussels or veligers.

At each site, data was gathered concerning water quality, veliger presence, mussel density, and juvenile settlement. Temperature was monitored by installing data loggers (HOBO Water Temp Pro v2 U22-001, Onset) at each site to record hourly water temperature from late August 2016-July 2017. During each sampling event, point measurements of pH, dissolved oxygen (mg/L), and water temperature (°C) were measured at each site with a YSI 556 Multi-parameter Instrument. Chlorophyll-a samples were also taken beginning in October 2016. Mean daily discharge data from the Leon River were gathered from USGS station 08102500 located 5.7 rkm downstream from the dam outlet and used for sites located 0.4-27rkm along the Leon River. USGS station 08104500 located at 40 rkm downstream from Lake Belton was used to calculate discharge values for site located at 57 and 94rkm along the Little River. Discharge data for all sites located along the Lampasas River were taken from USGS gage 08104100 located approximately 5rkm downstream from Stillhouse Hollow.

Veliger Dispersal

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. Water was pumped ~1-2 m away from the shore from the top 1/2 of the water column. Samples were rinsed down and preserved in 95% ethanol. Rose Bengal stain was added to aid in veliger detection while approximately 0.1g sodium bicarbonate per 50ml of ethanol was added as a pH buffer to prevent the veligers' calcium carbonate shells from dissolving. Samples were transferred to the lab at Texas State University where a subsample (25%) was then analyzed under a cross-polarizing stereo-microscope at 40x-80x (Nikon SMZ800N, with Nikon DS-Fi2 Camera) in order to enumerate both live veliger numbers.

Mussel Density and Settlement Monitoring

Four cinderblocks ($0.102m^2$) were placed at sampling sites and zebra mussels counted during each sampling event to monitor changes in cumulative mussel density (mussels m^{-2}) at each site. Another four blocks were scraped clean each sampling event to quantify new juvenile (<6mm) settlement. Scraped mussels were taken back to the lab where they were frozen and stored in a freezer (-8°C) before being counted and measured. The number of new juveniles settled on each monitoring devices was converted to a settlement rate (mussels m^{-2} $month^{-1}$) and averaged for each site.

Mussel Growth

In March 2017, mussels were taken from natural substrata in Lake Belton and at sites 0.4 and 6.0rkm along the Leon River. Individuals were measured and sorted into groups based on initial shell length (i.e. 0-5mm, 5-10mm, 10-15mm, etc.). Groups were placed into their own individual mesh bag (1.5-3.0mm), placed into an open cage and attached to a settlement monitor to be kept submerged 1-2m at the site of their collection (Figure A1). Mussel lengths were re-measured during each subsequent sampling event and averaged across each group. Variation in growth rates between size groups and across sites were analyzed by comparing changes in average shell length.

Data Analysis

All estimated veliger densities were log10 transformed. Average monthly temperatures for each site were rounded to the nearest degree, separated based on based on thresholds from the literature (Sprung 1987; McMahon 1996) what category they fell in (cold: <18°C, optimal: 18°-26°C, and warm: ≥27°C) and a one-way ANOVA and subsequent Tukey's poshoc test conducted to determine differences in veliger densities across these thresholds. Linear regression models were used to determine how much variation in veliger density could be explained by distance from the lake vs. temperature category. Temperature data (obtained from data loggers in summer 2015 at 2.5 and 27 rkm in the Leon river) and veliger data from Olson *et al*. (in review) was also used for the analyses.

Results

Discharge and temperature

Discharge rates between September 2016 and August 2017 were considerably lower compared to those encountered in our previous study between May 2015 and August 2016 (Olson et al. in review, Figure 2). Average daily discharge ranged from 0.01 to 111.4 $m^3 s^{-1}$ in the Leon River and 0.23 to 31.9 $m^3 s^{-1}$ in the Lampasas River with level with periods of prolonged elevated discharge primarily corresponding during the fall and spring in both river systems (Figure 2).

All point water quality parameters measured at in lake and river sites, i.e. pH (range: 6.7 to 9.0), dissolved oxygen (range: 3.8 to 13.2 mg L-1), and temperature (13.7-31.2°C) fell within known tolerable limits (Sprung 1987; Claudi & Mackie 1993; McMahon 2015) of zebra mussels at the time of sampling. Water temperature ranged from 11 to 33°C across all sites (Lake Belton, Leon River, Stillhouse Hollow, and the Lampasas River) and sampling events. Temperature loggers showed similar seasonal temperature fluctuations across all sites. During most of the study period, river temperature tended to stay within tolerable zebra mussel limits (≤ 29°C) in the upper stretch of the Leon River with average daily water temperature exceeding 30°C in the lower Leon and Little River starting June 27 (27 rkm) and July 11(at 54 and 97 rkm) until loggers were retrieved on August 11, 2017.

Lake Belton surface water temperature (~2m depth) ranged from 12-32°C with average daily water temperatures occurring ≥30°C for a total of 20 days in summer 2017. Similarly, Stillhouse Hollow water temperatures ranged from 15.5-31.8°C and average daily water temperatures ≥30°C for 25 days from July8-August 1, 2017. Contrastingly, average daily water temperatures in the Lampasas River all measured ≤ 29°C.

Veliger Dispersal

Within Lake Belton, veliger densities varied greatly across season with the largest peak concentrations occurring in early summer and fall (Figure 3). The highest densities of live veligers in Lake Belton were found in June 2017 (3300 veligers m^{-3}), July 2017 (792 veligers m^{-3}), and October 2016 (538 veligers m^{-3}). Downstream of Lake Belton, veliger densities also followed these seasonal patterns and generally declined with distance from the dam outflow with sites upstream of the lowhead dam (0.4-6.0 rkm, see Figure 1) possessing some of the highest veliger densities.

This study found the highest riverine veliger densities at 2.5 and 6.0 rkm downstream of Lake Belton (Figure 4). The largest number of veligers were typically found further downstream at 2.5 and 6.0 rkm (range 11-17,950 veligers m^{-3}). The number of veligers 13.1 rkm downstream from Lake Belton were lower (range 0-665 veligers m^{-3}) compared to 2.5 and 6 rkm except during October 2016 (higher densities) and July 2017 (similar to densities at 6rkm). In October 2016, highest veliger density was found at 13.1 rkm (665 veligers m^{-3}), followed only by those found in Lake Belton during that time (538 veligers m^{-3}). In May 2017, the highest veliger density was found at 27 rkm (528 veligers m^{-3}) with veliger density decreasing as one traveled closer to Lake Belton (Figure 4). Our study found live veligers up to 97rkm downstream from Lake Belton in the fall of 2016 and again in early summer of 2017 (Figure 4). Only one late state pediveliger was found in both Lake Belton and 6.0 rkm downstream in December 2016. No live velgiers were found again until May 2017.

In contrast to our expectations that highest veliger densities should occur in the lake, veliger densities were actually higher in the river compared to the lake in September 2016 (369 (at 2.5rkm) vs 21 veligers m-3), and in July 2017 when veliger densities were orders of magnitude larger at 2.5 and 6.0 rkm compared to the lake (2410-17950 veligers m^{-3} vs. 792 veligers m^{-3}). Relatively similar densities were seen between Lake Belton and river concentrations in May 2017 (300 vs. 528 veligers m^{-3} 54rkm downstream).

Veligers were not detected at our monitoring site in Stillhouse Hollow reservoir (Stillhouse Hollow marina) until May 2017 (Figure 5). Although sites 2.5, 5.0, and 13.0 rkm along the Lampasas River downstream from the Stillhouse Hollow dam were sampled during every sampling event from September 2016- July 2017, veligers were only found once in June 2017 at 2.5 rkm along the Lampasas River (Figure 5). The density of veligers found in the Lampasas River (i.e. 2.5 rkm) were much lower than those found in Stillhouse Hollow (42 vs. 327 veligers m^{-3} in June 2017). Reproduction in Stillhouse Hollow followed a similar trend to those found in Lake Belton. Veligers were first observed in May and June 2017 when average water temperatures fell within optimal reproduction and development ranges (23.5-27°C). However, maximum veliger density (4380 veligers m^{-3}) was no observed until July when average daily surface water temperatures were much higher (≥30°C starting July 8, 2017).

Temperature alone explained 12% of the variation in veliger density ($F_{2,99}$=8.2; $p<0.001$) and veliger densities were significantly lower at colder temperatures (<18°C) compared to the higher temperature categories (18-27°C and ≥27°C). Temperature and distance together explained 26% of the variation in veliger density (adjusted $R^2 = 0.26$, $F_{3,98}$=13.2; $p<0.001$) and sites upstream of the lowhead dam contained significantly higher average veliger densities than sites below the lowhead dam ($F_{1,74}$= 14.57; $p<0.001$).

Cumulative Density and Juvenile Settlement Rate

While variation in cumulative settlement density was considerable between sites and sampling dates both seasonal and spatial patterns (i.e., a considerable increase in cumulative settlement occurring in late summer and higher densities restricted to ≤6rkm downstream) were evident across the entire study period (Figures 6). Cumulative densities for river sites were highest above the location of the lowhead dam (≤6rkm; range 200-1420 mussels m^{-2}, September 2016-July 2017). Zebra mussels were typically not observed past 13 rkm with the exception being that in October 2016, mussels were found in low densities (3-10 mussels m^{-2}) as far downstream as 54.7 rkm and 2 individuals found at 27 rkm in March 2017. Similarly, cumulative mussel densities in Lake Belton were somewhat constant from December 2016-June 2017 (range 313-745 mussels m^{-2}) but increased dramatically in July 2017 to 5988±1280 mussels m^{-2} (Figure 6).

Since December 2016, the highest juvenile settlement rate downstream from Lake Belton was observed at 0.4rkm (Figure 6). Juvenile settlement rate ranged from 65-109 mussels m^{-2} $month^{-1}$ at this site from December 2016 to June 2017 with an increase to 701±560 mussels m^{-2} $month^{-1}$ observed in July 2017. No juvenile settlement was seen ≥13rkm downstream from Lake Belton with the exception of one juvenile being found at 54.7rkm in October 2016 and at 13rkm in May 2017 (Figures 6).

Settlement of zebra mussel individuals was not seen on our monitoring devices in Stillhouse Hollow until March 2017. Since that time, cumulative settlement density has increased from 15-34 mussels m^{-2} from March-May 2017 to 8400-9300 mussels m^{-2} in June-July 2017 (Figure 7). Juvenile settlement rates also follow this trend increasing from 5-9 mussels m^{-2} $month^{-1}$ from March-May 2017 to 784-6000 mussels m^{-2} $month^{-1}$ in June and July 2017 (Figure 7).

Growth Rates

Growth rates of zebra mussels were highest in Lake Belton compared to growth rates at river sites in May and June, but was considerably lower in July and August (Figure 8). Average growth rate were lowest at 0.4rkm in June 2017, but were higher there than either Lake Belton or Site 3 from July-August (Figure 8).

Growth rates across size groups were highly variable (Figure 9). While all size groups in Lake Belton (Figure 9a) followed a singular trend, size groups in the Leon River possessed dissenting trends in growth rates (Figure 9a,b). The largest initial size group (15-20mm) at site 3 showed an overall increase in growth rate from May to August (9.4 to 41.6 µm day^{-1}) while the smallest initial size group (5-10mm) had an overall decrease (37.0 to 5.2 µm day^{-1}) with the middle size group (10-15mm) maintaining a constant growth rate across the entire sampling period (18.1 to 15.9 µm day^{-1}). Growth rates for the 5-10mm group at site 1 sharply increased from June to July (35.2 to 87.5 µm day^{-1}) before sharply decreasing from July to August (87.5 to 9.8 µm day^{-1}) while growth rates for the 10-15mm size class sharply rose during this same time period (4.3 to 75.6 µm day^{-1}).

Discussion

While veligers were found up to 97rkm downstream from Lake Belton, no persisting settlement of zebra mussels was seen further than 13.1rkm downstream (Figures 6), suggesting that input of recruitment from a source population is limited and/or that conditions further downstream are not adequate to support zebra mussel populations. Similar trends were seen in the Lampasas River with veligers not detected >2.5rkm downstream from Stillhouse Hollow dam and zebra mussels (adult or juveniles) only found at the dame outlet (0.2rkm). Variation in veliger densities (from September 2016 to July 2017 and from May 2015-August 2016 from Olson *et al*.) were best explained by differences in temperature, discharge, and location of sites in relation to the lowhead dam (Figure 1).

Many previous studies have shown zebra mussel reproduction to be heavily regulated by temperature thresholds (Sprung 1987; Borcherding 1991) and similar to other studies our data shows seasonal variation in veliger densities correlated with temperature variations. We found highest veliger densities in June 2017, when temperature where optimal (average water temperatures ranged 22-27°C), whereas no veligers were found at any sites in December- March when ambient water temperatures fell below the threshold of 18°C for reproduction (McMahon 1996; Borcherding 1991). Two late stage pediveligers were found in Lake Belton in December 2016 but these individuals were likely from reproduction efforts earlier in the year and "over-wintering" in the water column until temperature rose sufficiently for them to resume development (McMahon 1996). Furthermore, settlement of juveniles was seen in Stillhouse Hollow as early as March 2017 (Figure A3) but veliger presence was not detected until the next sampling event (May 2017). We believe that in March 2017 the new settlement observed on our monitors (Figure A3) was from individuals who had remained in the water column over winter (McMahon 1996). Our sampling method likely limited our ability to detect veligers at higher concentrations (e.g., >10 veligers per m^3).

Zebra mussel reproduction exhibit a bimodal pattern with highest densities of veligers typically found in late spring-early summer and a secondary peak in fall (Nichols1996). This pattern is seen in Texas but unlike in other studies, Texas populations exhibit an extended interruption in reproductive activity during peak summer temperatures (Figure 3) (Churchill 2013). Results from our study also support the hypothesis that southern US zebra mussel populations have increased tolerance for upper thermal limits (Morse 2009). Reproduction and veliger development may occur at higher temperatures due to mussels' ability of extending their upper thermal limits through long-term seasonal acclimatization (Hernandez 1995, McMahon 1996). Evidence of successful reproductive activity (i.e. live veligers) was observed during periods of time when surface water temperature rose above thermal limits stated in previous literature (McMahon 1996, Sprung 1987). Large numbers of veligers (250-350 m^{-3}) were found in Lake Belton and downstream river sites in July 2017 despite average daily water temperatures periodically reaching ≥30°C for significant portions of time including 10 total days for Lake Belton (July15-July25, 2017) and approximately 16 days at site 57rkm and 97rkm downstream (July 12-14 and July 18-31). Similarly, Olson *et al*. (in review) found veligers in Lake Belton and the Leon River in late August 2016, despite river temperatures ≥27°C since July 17, 2016, with the Texas Commission on Environmental Quality (TCEQ 2016) reporting average lake water temperatures near the Belton dam to be 31°C on August 11, 2016. This increased thermal tolerance of Texas mussels may explain our observations of veliger presence at river sites even during periods of elevated water temperatures.

During two sampling events, veliger densities observed at riverine sites were vastly greater than those observed in Lake Belton (i.e. 369 vs 21 veligers m^{-3} in September 2016 and 792 vs. 17950 veligers m^{-3} in July 2017). As these sampling periods occurred during times when average surface water temperature of Lake Belton were higher than optimal for reproduction (Figure 3). It is possible that high surface water temperatures restricted reproduction and veliger development in the upper water column (where we sampled, i.e. ~1m depth), but lower temperatures in deeper layers (i.e., from which water is released into river) may have facilitated veliger survival. Lake Belton was approximately 32 meters deep at the time of this study and seasonal data from TCEQ shows that average water temperature in the upper third of the water column to be consistently warmer by several degrees compared to temperatures found in the lower third. Furthermore, prior to each of these sampling dates (September 2016, and July 2017, and also September 2015 as reported in Olson *et al*.) Lake Belton dam was releasing at a high rate (Figure 1) before the sampling events, probably with larger quantities of live veligers.

Previous studies done on comparable (i.e. < 35m width) river systems (Horvath *et al.* 1996; Horvath and Lamberti 1999; Bobeldyk *et al*. 2005; Lucy *et al*. 2008) haves shown zebra mussel dispersal and settlement to be restricted to approximately ≤12 rkm, which is comparable to the distances observed in our study. However, dissimilar to these studies there were times when we observed veliger and juvenile settlement at greatly increased distances (27-97rkm). These increased distances align with the dispersal distances observed in river systems containing dams and other impoundments along its length (190rkm, Smith *et al*. 2015). Unlike Smith *et al.* (2015) we only observed these large dispersal distances a few times over the course of our entire study period, after periods of elevated and prolonged discharge.

While we did not detect zebra mussels in higher densities (>100 mussels m^{-2}) on our settlement monitors ≥13rkm downstream of Lake Belton it is worth noting that adult mussels were found on natural substrate at site 4 (13rkm) at a density of approximately 600 mussels m^{-2} in July 2017 (Figure A5). These mussels were all of a similar size class (ranged 22-27mm in length) with no smaller or larger sized individuals being found. This evidence suggests that the individuals currently present at 13 rkm settled at relatively the same time during a previous dispersal event. Lack of smaller sized individuals or juveniles suggests a lack of consistent recruitment at ~13 rkm.

Consistently higher numbers of veligers and juveniles upstream of the lowhead dam, suggests that this man-made structure may facilitate recruitment of zebra mussels, probably by creating more lentic conditions facilitating settlement of juveniles. 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). It is possible that the lack of a low head dam and the more lotic conditions (higher flow velocities) downstream of Stillhouse Hollow compared to Lake Belton has helped to limit recruitment of zebra mussels to the Lampasas. However, further monitoring is needed to confirm this.

The considerably lower growth rates observed in Lake Belton during summer is consistent with findings by other studies (Allen *et al*. 1999; Yu & Culver 2000), and may be cause by increased reproductive activity and rising water temperatures (Allen *et al*. 1999). Lower growth rate at Leon River sites might be the result of lower food availability in the Leon River compared to Lake Belton (average chlorophyll-*a* range: 0.5-2.0 vs. 1.7-6.1 µg/L) and/or lower average water temperatures during summer months (average: 22° vs 27°C in June 2017).

Decline in growth rates during late summer months as seen in the literature (Yu & Culver 1999; Allen *et al.* 1999) was not observed in the average growth rates of mussels in the Leon River (Figure 8). This could be due to river mussels already possessing lower average growth rates compared to Lake Belton. The lower rate of growth seen in the Leon River is comparable to growth rates observed in northern lake populations (Garton & Johnson 2000) but more study is needed to determine if mussels in the Leon River experience any elevated rates of growth, as typical for this species (Yu & Culver 1999; Allen *et al*. 1999), or if they remain fairly static year round.

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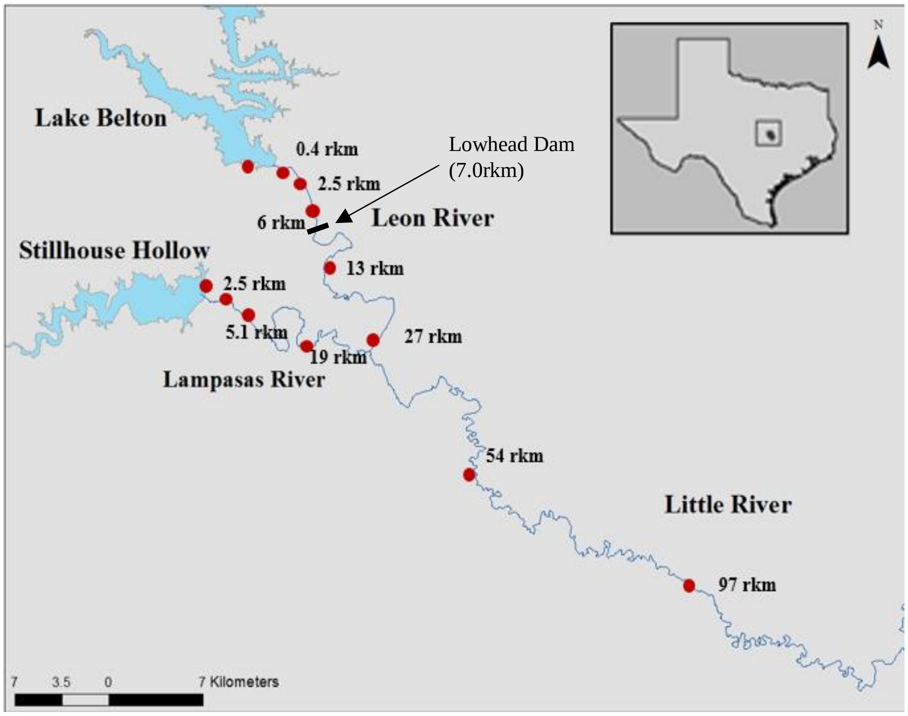

Figure 1. Locations of study area and sampling sites in Lake Belton, Stillhouse Hollow, and along the Leon, Lampasas, and Little River.

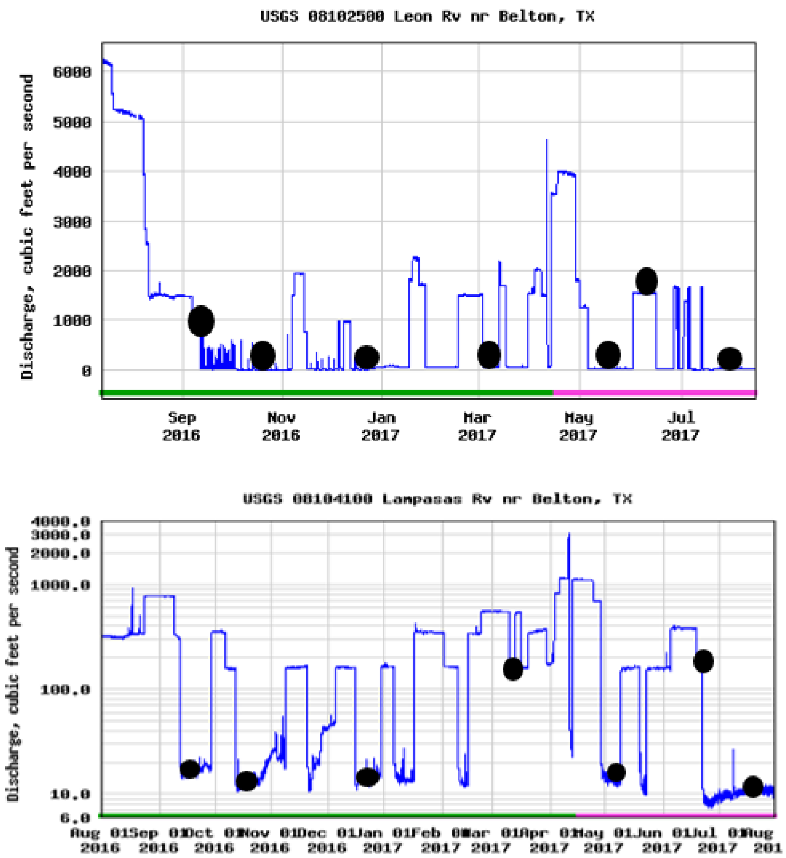

Figure 2. Discharge from USGS gage 08102500 for Leon River (above) and USGS gage 08104100 for the Lampasas River (below) during the course of the study period. Black circles represent sampling events.

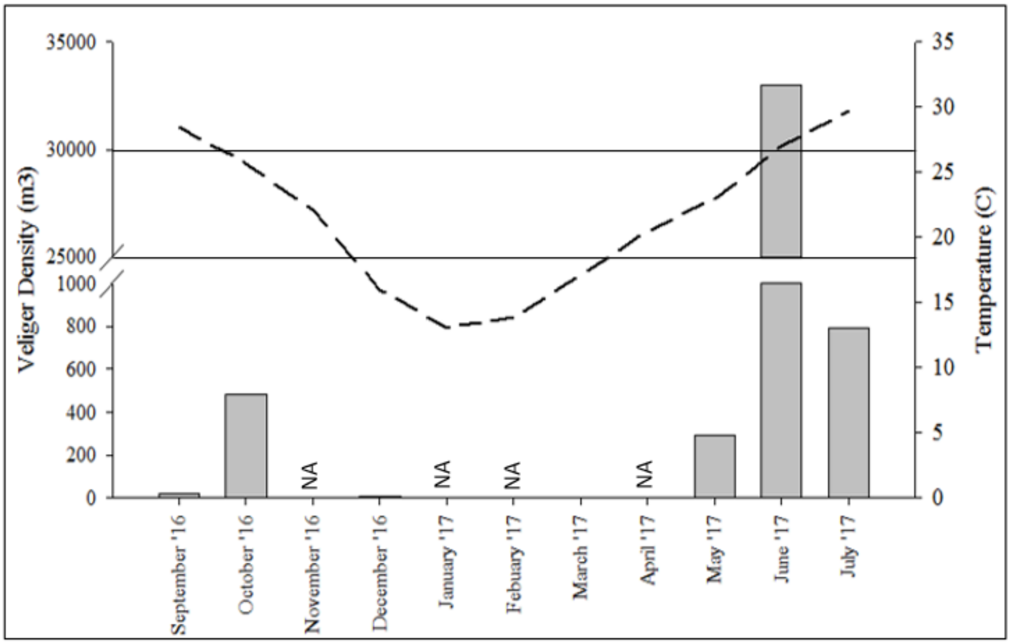

Figure 3. Lake Belton veliger density from September 2016-July 2017. NA represent months veligers samples not taken. Dashed line represents average monthly surface water temperature and horizontal lines represent temperature reproduction thresholds from literature (18-26°C).

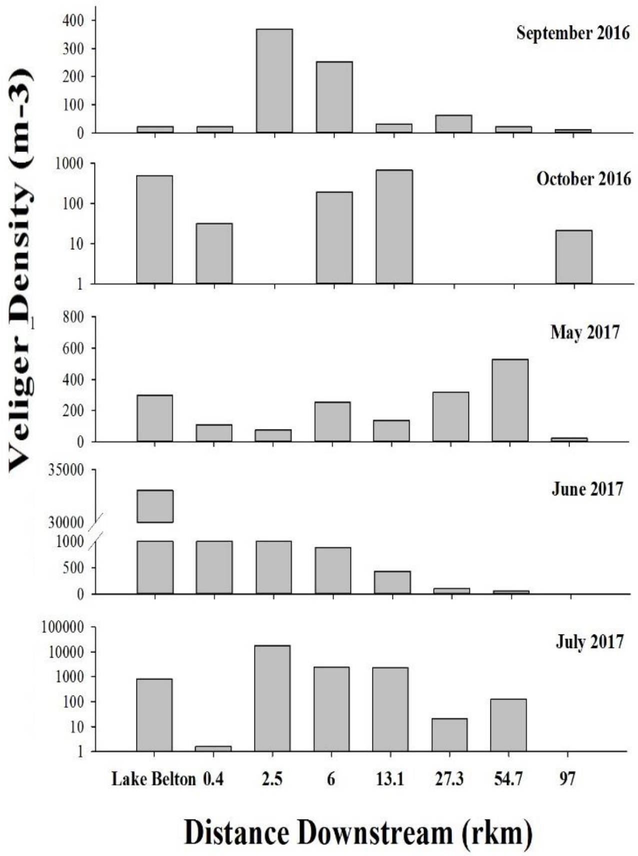

Figure 4. Veliger densities in Lake Belton and downstream sites (0.4-97 rkm) from September 2016-July 2017 (December 2016 and March 2017 omitted due to lack of veligers found)

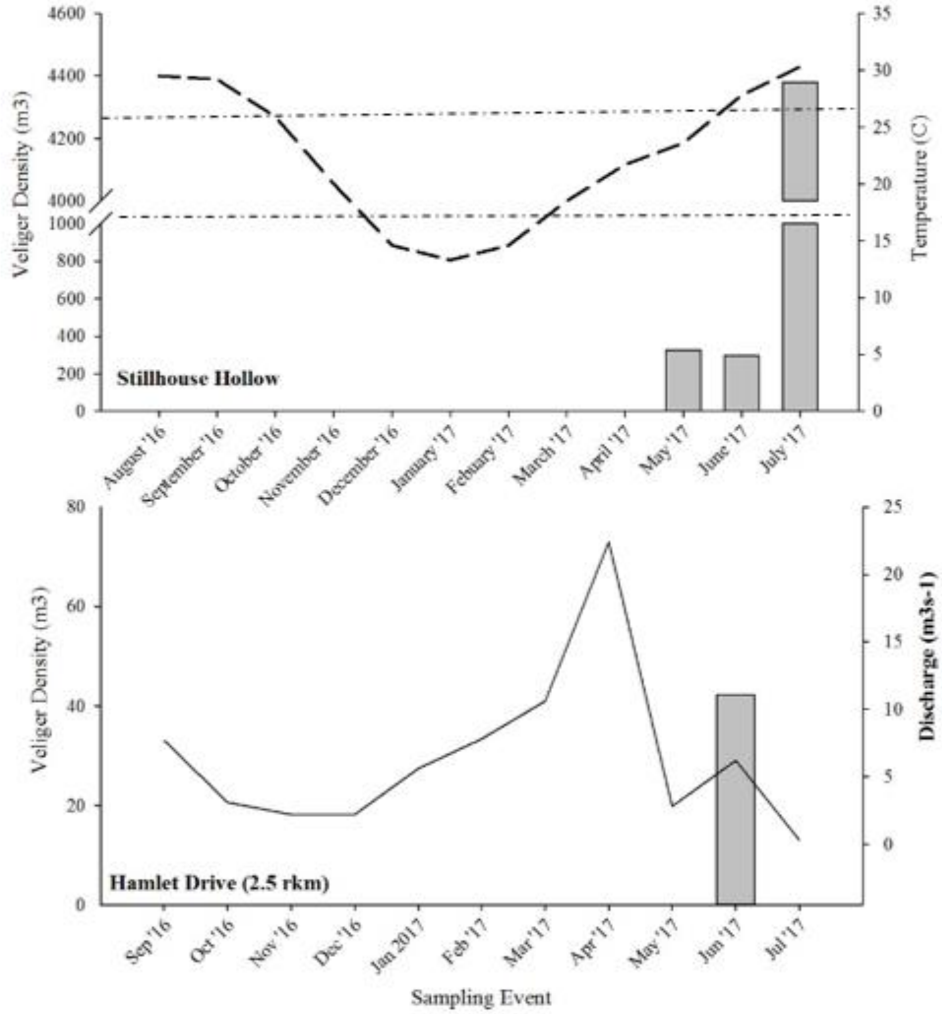

Figure 5. Stillhouse Hollow and Lampasas River veliger density across all sampling dates along with average monthly water temperature. Dashed horizontal lines represent temperature reproduction thresholds from literature (18-26°C) and solid horizontal line represents average monthly discharge.

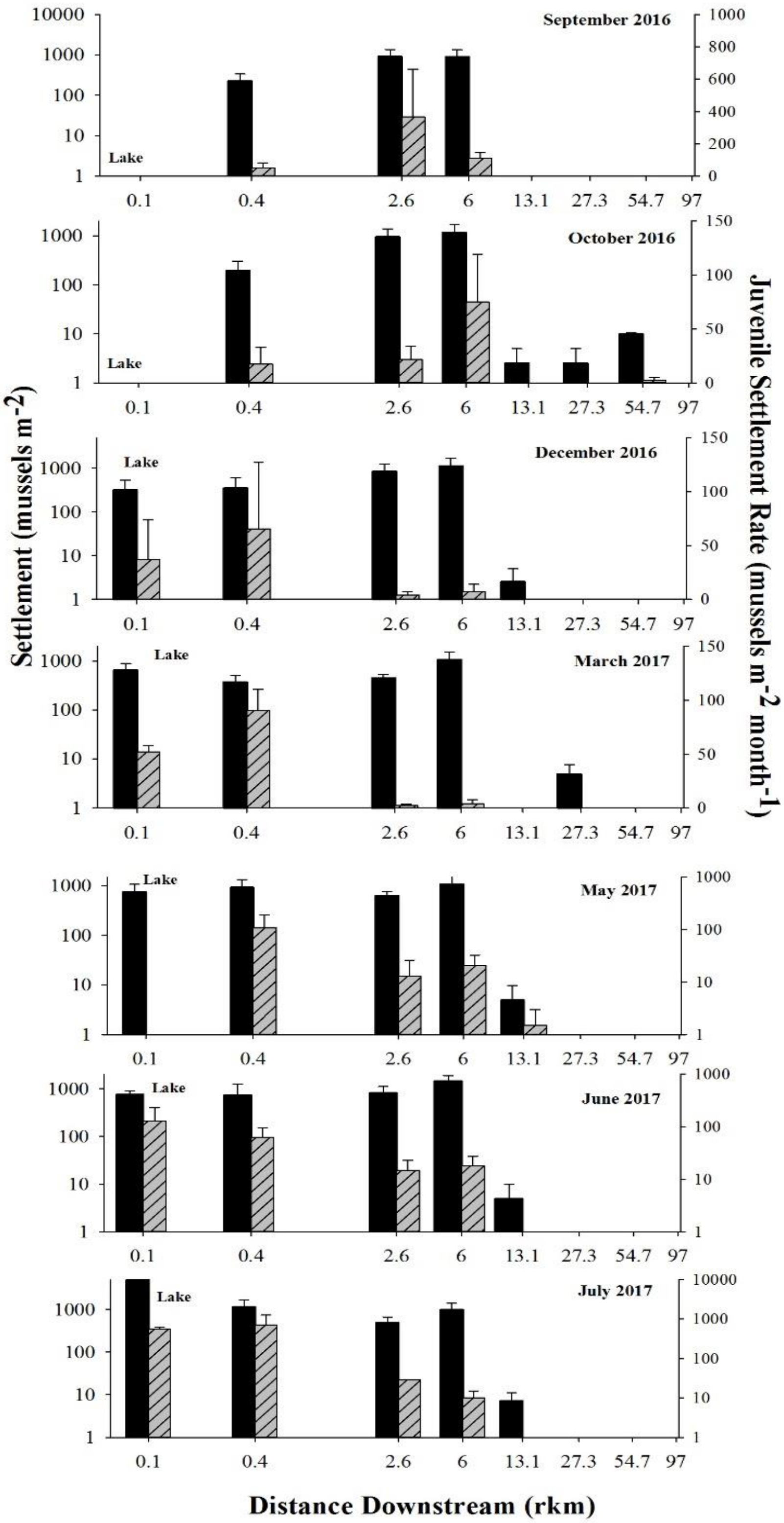

Figure 6. Average ±SE cumulative mussel density and average ±SE juvenile settlement rate (striped bars) at Lake Belton and in the Leon and Little Rivers from September 2016 to July 2017.

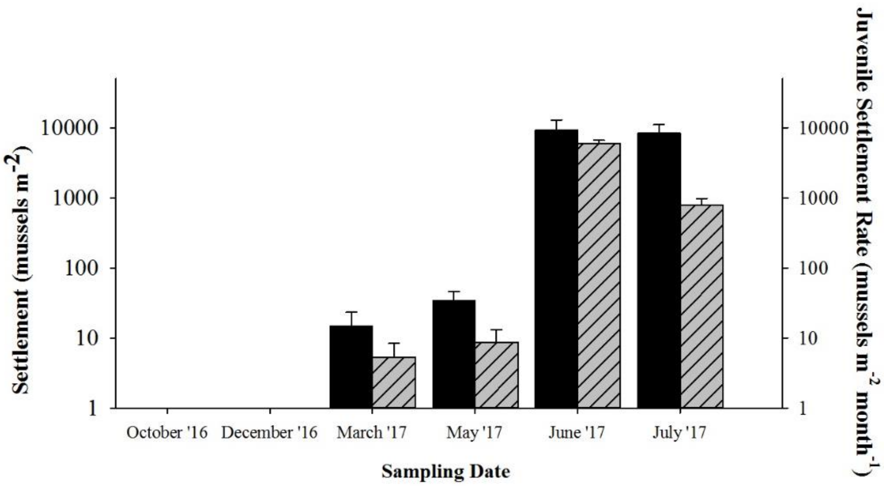

Figure 7. Average ±SE cumulative mussel density (solid bars) and average ±SE juvenile settlement rate (striped bars) at Stillhouse Hollow marina from October 2016 to July 2017.

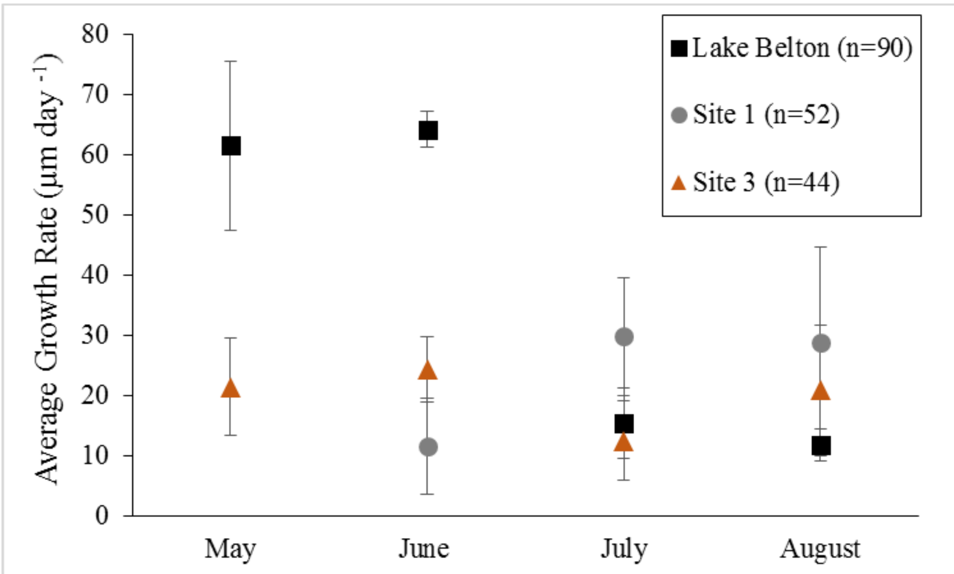

Figure 8. Average growth rates (µm day^{-1}) of all initial size groups for each site from March-August 2017. Error bars represent ±1SE.

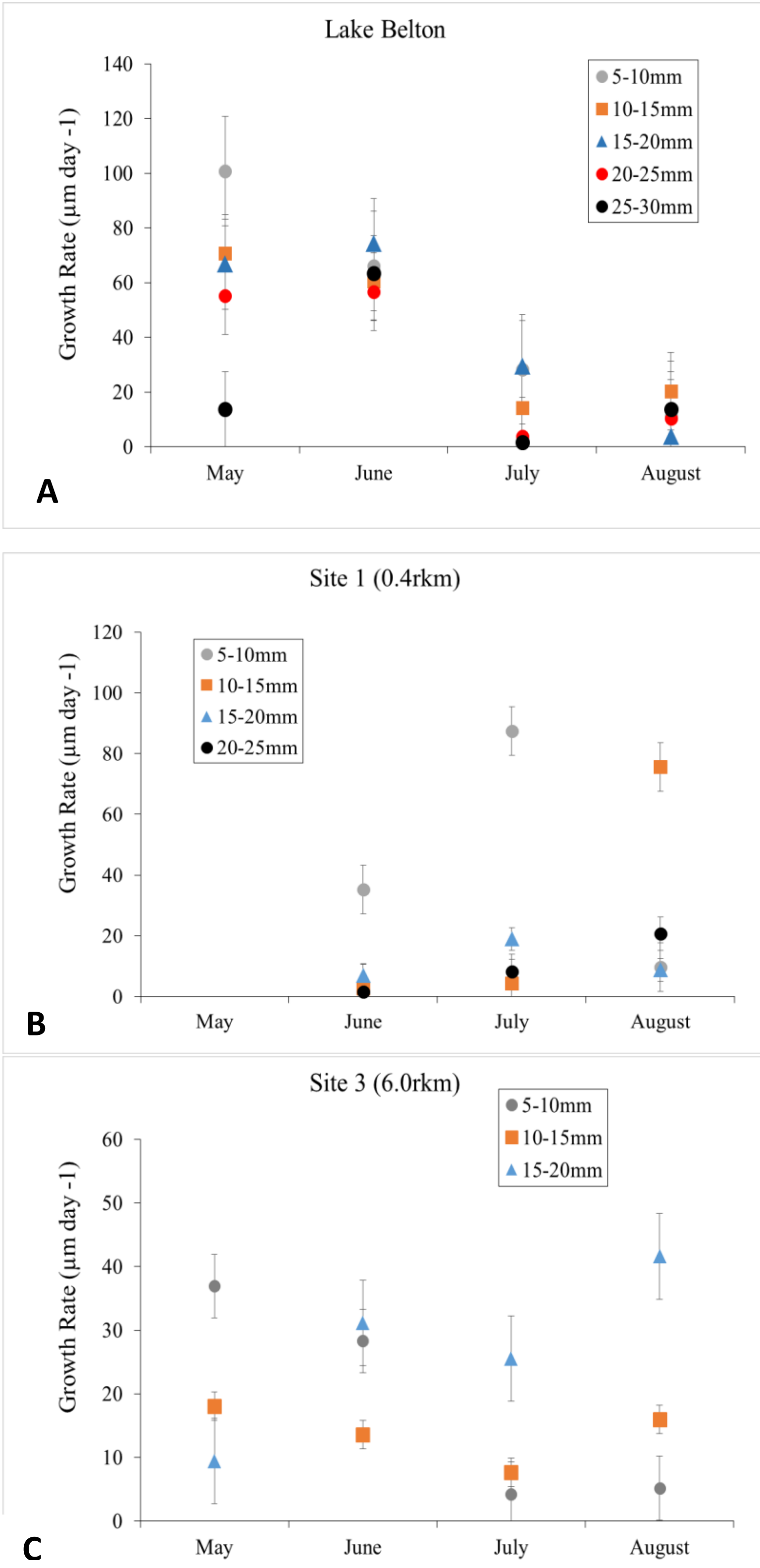

Figure 9. Growth rates (µm day^{-1}) of individual initial size classes for A) Lake Belton, B) Site 1 (0.4rkm), and C) Site 3 (6.0rkm) from May-August 2017.

Appendix – Project Photos

Figure A1. Settlement monitor with cage containing bags used to hold zebra mussels for growth rate analysis, Lake Belton

Figure A2. Condition of settlement monitors in Lake Belton, September 2016 vs. July 2017.

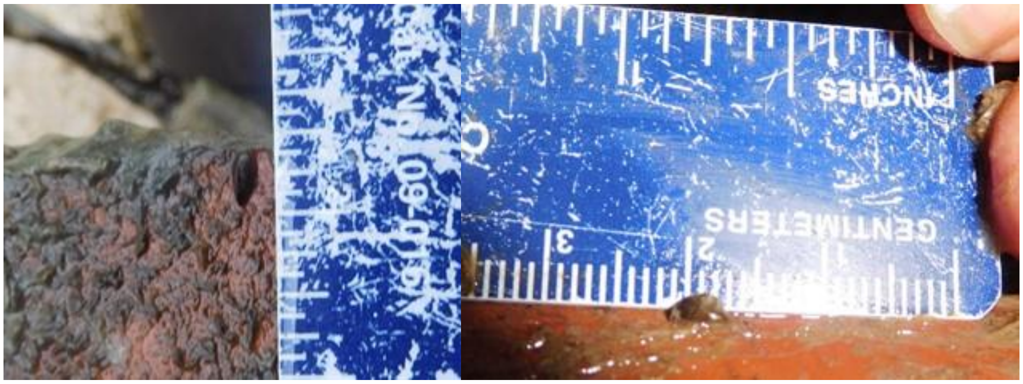

Figure A3. Juvenile zebra mussel growing on settlement monitor in Lake Belton and Stillhouse Hollow in early March 2017.

Figure A4. New juveniles settled on bottom of settlement monitor in Stillhouse Hollow, June 2017.

Figure A5. Zebra mussels observed on natural substrate at 13.1 rkm downstream from Belton dam, July 2017.

Part 2: Predicting Over-land Zebra Mussel (*Dreissena polymorpha*) Dispersal in Texas

Summary

Zebra mussels, *Dreissena polymorpha*, recently invaded Central Texas. More information is needed to predict their spread in this region and inform management decisions. In this study, we examined habitat suitability and boater traffic information using a modified gravity model to predict zebra mussel dispersal in a set of central Texas lakes. All lakes of interest scored a moderate to high risk of invasion based on our habitat suitability criteria. The model was run under three different invasion risk scenarios (low, medium, and high) and found that different subsets of reservoirs became infected under different conditions. Our model only failed to predict the successful introduction of zebra mussels to two of our lakes of interest, Lake Amistad and Lake Livingston, likely due to a combination of their size and increased distance from potential source populations.

Introduction

Since their introduction into the Great Lakes region in the 1980's zebra mussels (*Dreissena polymorpha*) have spread far across the North American continent in a relatively short amount of time. Zebra mussels continue to spread into new territory, most recently into Texas reservoirs in both northern (Lake Texoma in 2009) and central (Lake Belton in 2013) Texas. Estimating dispersal of organisms is difficult and many previous attempts have been made in regards to zebra mussels. Previous habitat suitability models focusing on pH (de Kozlowski et al. 2002) and dissolved calcium (Whittier et al. 2008) have been used to estimate potential zebra mussel distribution but these estimates have been confined to regional scales. The first large scale dispersal model used ambient air temperature to predict probable limits of zebra mussel dispersal and results indicated climate conditions would restrict zebra mussels from colonizing the lowest south and southwest United States (Strayer 1991). Another nation-wide habitat suitability model (Drake & Bossenbroek 2004) used temperature as well as geographic features (bedrock, precipitation, elevation, etc.) in hopes of presenting a more detailed estimation on possible future habitat expansions—results from these models included much of the southern United States as potential suitable habitat, including most of Texas east of the 100th meridian.

However, while predictions of suitable habitat in Texas were present they were highly variable and thus concluded unreliable (Drake and Bossenboek 2004).

Since the inception of such models zebra mussels have colonized and begun dispersing through the network of Texas reservoirs. Such introductions have shown that nation-wide habitat suitability models are not sufficient enough on their own to predict the spread of zebra mussels specifically within Texas. Zebra mussel populations in Texas waters are unique compared to European or even northern latitudinal water bodies. Texas experiences extended periods of elevated temperatures during the summer allowing surface waters to rise >30°C. Such temperatures are at the known tolerance threshold for zebra mussels (McMahon 1996; Sprung 1987), suggesting Texas waters may be close to the maximum temperatures suitable for suitable habitat. It therefore would be beneficial to develop a more fine-scaled habitat suitability model specific to Texas in order to predict and further prevent the spread of zebra mussels within the state.

Previous models have indicated that simple habitat suitability concerning physio-chemical characteristics (e.g., water temperature, pH, calcium level) would not be enough. While zebra mussels are capable of spreading via downstream transport, their introduction and continue spread across river basins is most credited to overland dispersal via boater movement. Consequently, an ideal dispersal model would take into account not only possible habitat suitability but the direction of travel that zebra mussels would most likely take. Bossenbroek et al. (2001) proposed such a dispersal model that relies not on basic habitat suitability characteristics, but on the patterns of boater travel between invaded and uninvaded lakes. Bossenbroek et al. (2001) modeled the likelihood of boats transporting zebra mussel individuals dependent on both the distance an uncolonized lake was from a source as well as lake's size (i.e. attractiveness) to boaters. Such a model has been proven to accurately capture important patterns of boater traffic and thus useful for modeling dispersal across non-contiguous sources (Leung et al. 2006).

The purpose of this study was to construct a modified gravity model based on the one first developed by Bossenbroek et al. (2001) to predict zebra mussel dispersal in central Texas utilizing both habitat suitability criteria and boater traffic data. We tested the dispersal of zebra mussels under 'low', 'medium', and 'high' risk dispersal scenarios. We expected to see a general increase in the total number of invaded reservoirs as dispersal risk increased and the lakes closest to invaded reservoirs to be most at risk for becoming invaded themselves.

Methods

Study Location and Habitat Assessment

A subset of 19 uncolonized central Texas reservoirs as well as 6 reservoirs known to possess zebra mussel populations were included in the gravity model analysis (Figure 1). To develop the risk assessment of the potential spread of zebra mussels across Texas reservoirs we first quantified the physio-chemical characteristics of the uncolonized reservoirs (1-19) of interest. Characteristics such as mean August surface water temperature (°C), dissolved oxygen (mg/L), pH, and calcium concentration (mg/L) were used to determine the potential of each reservoir to support zebra mussel colonization (McMahon 2015). Nineteen major central Texas waterbodies were chosen for the risk assessment model (Figure 1) and their habitat suitability compared to that of Lake Belton (a positive control).

Surface water (< 5m depth) values of temperature, dissolved oxygen, pH, and calcium concentration from multiple sampling sites along each reservoir from the past five years were retrieved from TCEQ's surface water quality database and mean values of each parameter were calculated. Additionally, HOBO temperature loggers were deployed in summer 2016 at each reservoir through September 30, 2016. Loggers were deployed at marinas, boat ramps, and buoys by either local TPWD offices, the researchers, or National Park Services (Lake Amistad). Mean daily water temperature from August 10-September 30, 2016 was determined for all 19 waterbodies. These mean parameter values were compared to threshold values found in the literature (Table 1) and assigned suitability scores. If, for a specific waterbody, a mean parameter values fell outside the known tolerate range the waterbody was given a low risk rating. If one, or more, of the parameters listed in Table 1 fell within the marginal region the water body was given a moderate risk rating. All suitability labels for each four habitat assessments (temperature, dissolved oxygen, pH, and calcium) were combined to give each reservoir an overall rating for likelihood of zebra mussel habitat suitability (Table 5). As lakes already known to support zebra mussel populations (i.e. Lake Belton) received at least a moderate risk invasion score, and as other infested Texas lakes have received this classification in similar past assessments

(McMahon 2015), lakes scoring an overall moderate or high risk invasion score were considered as possessing suitable habitat for our model assessment.

Gravity Model

To quantify the potential spread of zebra mussels within Texas used a modified constrained gravity model developed by Bossenbroek et al. (2001). A total of 25 reservoirs were included to test the model. These lakes included 19 reservoirs of interest were zebra mussels were not previously known to be colonized (Grerorgetown, Granger, Hubbard Creek, Possum Kingdom, Somerville, Stillhouse Hollow, Lake Whitney, Lake Austin, Buchanan, Inks Lake, Lady Bird Lake, Lake LBJ, Marble Falls, Lake Travis, Lake Canyon, Lake Amistad, Cedar Creek, and Richland Chambers). Lake Belton, Lake Texoma, Lake Lewisville, Lake Ray Roberts, Lake Bridgeport and Eagle Mountain were also used in the model as potential zebra mussel sources. Lady Bird Lake and Lake Austin, were combined as one waterbody for the purpose of this model analysis due to their small area connectivity, and identical boater pool. Stillhouse Hollow was added at to the list of potential source populations after zebra mussels were confirmed in late summer 2016. Empirical data incorporated into the gravity model consisted of the number of registered boats in the counties were each lake was located, O_i, the distance of the reservoir to the nearest zebra mussel source, and the surface area of each lake, W_i (Table 2).

The possible colonization of a reservoir was determined by a multi-step process. First, the probability of a boat from a colonized lake picking up juvenile or adult zebra mussels. Second, the likely hood of these transported individuals surviving transport. Third, the proportion of these infested boats traveling to uncolonized reservoirs. Finally, the transported individuals establishing a new colony based on the physio-chemical nature of the reservoir (water temperature, dissolved oxygen, pH, and calcium levels). As a result our model will estimate the potential for colonization based on several factors; 1) the probability of a boat traveling from a zebra mussel source to an uncolonized reservoir, 2) the probability of zebra mussels surviving transport, 3) the probability of zebra mussels released at high enough densities to become established in that uncolonized reservoir.

The first step of the model calculated the number of boats from each reservoir that travel to other reservoirs. The number of boats, T, that travel from lake i to lake *j* was estimated as:

(1) $T_{ij} = A_iO_iW_jC_{ij}^{-\alpha}$

Where, Ai is the scalar, Oi is the number of total boats assigned to lake *i*, W_j is the surface area (km2) of lake *j*, c_{ij} is the distance from lake *i* to lake *j* and α is the distance coefficient (Table 3). Ai is included as a balancing factor to ensure that all boats from lake *i* reach a destination (Bossenbroek et al. 2001). A_i and was estimated using equation,

(2) $A_i = \frac{1}{\sum_{j=1}^{N} WjCij-\alpha}$

where N represents the total number of lakes. The number of infested boats (Z) for lake *i,* was calculated by

(3) $Z_i = O_i P$

where P represents the percentage of boats from lake *i* infested with zebra mussels. Next, the number of infested boats arrive at lake *j* from lake *i* (R_{ij}) was found by multiplying the number of infested boats (Z_i) from lake *i* by the survivability (S) of zebra mussels during transport. The total number of infested boats arriving at a single lake (Q_j) was represented by summing R_{ij} from all lakes. Thus, Qj is the total number of infested boats arriving at lake *i* in one iteration (year) of the model.

The final step of the model consists of determining if these over-land dispersal travel evens led to zebra mussels successfully colonizing a previously uncolonized lake. This in itself is a two-step process: 1) determining if habitat of the uncolonized lake is suitable for zebra mussels and 2) if a sufficient number of introductions are met. Habitat suitability was met if the lake in question scored a moderate or high risk rating on the habitat risk assessment (Table 5). As for the second part, it is unlikely that a single introduction of a few zebra mussel individuals would be enough to guarantee the development of a new population. Multiply introductions are likely needed before as successful colony develops (Johnson et al. 2001). Therefore, a threshold (D) for the relative number of infested boats required to guarantee successful invasion of an uncolonize lake was set. A lake was considered successfully colonized if this threshold (D) was less than the resulting number of arriving infected boats (Q_j) per unit area of lake *j*:

(4) Infected if $D < (Q_j / W_j)$

Our model provides a snapshot of potential movement among the 19 water bodies we modeled. The model quantifies the relative, not absolute, number of boats traveling between each lake in the system. We performed a sensitivity analyses and ran our model through different distance dispersal scenarios (Table 4). These scenarios were changed via manipulating the percentage of infected boats (P), the survivability of zebra mussels during transport (S), and the area threshold (D). A limited number of studies have shown previous estimates of P to be quite variable (<1.0 – 31%; Johnson et al. 2001; Johnson and Carlton 1996) and aerial exposure tolerance (i.e. S) to vary greatly based on temperature and relative humidity (Ricciardi et al. 1994). To simplify the interpretation of our results we chose to test only three distinct scenarios (Table 4), ranging from low to high likelihood of invasion to highlight the behavior of boater movement and invasion risk of our chosen reservoirs.

Results

Habitat Suitability Parameters

According to habitat suitability guidelines (McMahon 2015) all reservoirs fell within either the marginal or suitable region for each of the four habitat parameters (Figure 2). All lakes fell within the suitable region for surface water dissolved oxygen and pH (Table 5). One lake, Cedar Creek, fell in the moderate region of calcium concentration (mg/L) but all other lakes fell in the suitable tolerance limits. Average summer surface water temperature is where most lakes deviated from the suitable habitat limits with Lakes Belton, Cedar Creek, Lake Georgetown, Lake Buchanan, Lake Travis, Lake Whitney, Richland Chambers, and Stillhouse Hollow all falling within the 'marginal' temperature threshold with average surface temperatures falling at ~30°C. Despite this, the no habitat parameter score for any lake was classified as 'low' with all reservoirs receiving a marginal or high risk invasion score (Table 5).

Gravity Model

As expected, our model predicted that the number of uncolonzied lakes infested by zebra mussels increased as dispersal risk increased (Table 6). Three reservoirs, Inks Lake, Marble Falls, and Lake Georgetown, became colonized under the 'low' dispersal scenario. Four more (Granger Lake, Lake LBJ, Possum Kingdom, and Lake Whitney) were colonized under the 'medium' dispersal scenario, and an additional eight reservoirs (Lake Buchanan, Richland Chambers, Cedar Creek, Lake Travis, Canyon Lake, Somerville Lake, Hubbard Creek, and Lake Austin) were colonized under the 'high' risk scenario. Neither Lake Amistad nor Lake Livingston reached 'invaded' status under either of our three model scenarios.

The percentage of infected arriving boats that resulted in an invasion event for an uncolonized lake ranged from 0.1-44.5% across all scenarios and reservoirs. The percentage of infected boats arriving at already infected reservoirs ranged from 2.5-62.5% for all scenarios. Under the low risk scenerio, only small reservoirs (3-5 km^2) relatively close to a source lake were invaded. Next, medium sized lakes (< 100 km^2) that were relatively close to a source were colonized. Finally, larger and further away lakes were colonized under the high risk scenario.

Discussion

Overall, our modified gravity model showed an outward radiation of zebra mussel dispersal from infested reservoir sources. Our model predicted that an increase in dispersal risk would lead to increased colonization of lakes larger and further away from zebra mussel source populations (Table 6). The reservoirs to become invaded under the most restrictive dispersal condition (i.e. low risk) were Inks Lake, Marble Falls, and Georgetown, reservoirs that were both small in size (3-5 km^2) and closest to zebra mussel sources (42-87 km). Meanwhile, Lake Amistad and Lake Livingston both failed to become colonized, even under the most lenient dispersal conditions (i.e. high risk, see Table 4). Likewise, a significant percentage (2.5-62.5%) of boat arriving at already colonized reservoirs were from other invaded reservoir sources (Table 6). This information validates the assumption that our boater traffic is preforming as assumed and accurately mimicking real-world dispersal occurrences. Already within Texas we see invaded reservoirs clustered near together (Lake Belton and Stillhouse Hollow in central Texas; Lake Texoma, Ray Roberts, Bridgeport, Eagle Mountain, and Lake Lewisville in northern Texas) demonstrating that the spread of zebra mussels via overland dispersal occurs most readily between sources in close proximity.

The results of our model show that as the number of infected boats leaving invade reservoirs increased the reservoirs most likely to become invaded were small to medium sized lakes (<100 km^2) within 150km distance while large reservoirs (>250km^2) further away (>200 km) were not colonized. Despite not meeting the “invaded” criteria all lakes received some proportion of infected boats (range 0.04-62.5% of arriving boats across all scenarios). It should be noted that not all lakes required a high proportion of arriving boats to be transporting zebra mussels for them to become invaded as well (ex. Lake Austin became invaded when only 0.6% of arriving boats carried zebra mussels). This is due to the small surface area size of these lakes, meaning that they needed fewer total infected boats arriving for them to overcome the area threshold and become ‘invaded’. This bias could be a potential limiting factor of our model. We assumed an area threshold in order to account for the probable multiple introductions needed for a new colony to successfully establish (Johnson et al. 2001). However, such a bias against larger reservoirs may skew our risk assessment. For example, even though Lake Livingston failed to become “invaded” in any of the three dispersal scenarios TPWD has found evidence of zebra mussels there in the past. Instead of a threshold related to the surface area of a reservoir a threshold related to a more localized factor (i.e. number of marinas or boat ramps) may be more indicative towards the probability of zebra mussel establishment.

Our model was run under the invasion status that our reservoirs of interest held at the end of 2016. Since that time two of the reservoirs in our dataset, Canyon Lake and Lake Travis, were identified as possessing reproducing zebra mussel populations (TPWD 2017). Our model predicted invasion of Lake Canyon and Lake Travis under only medium and high dispersal conditions respectively with both lakes’ arriving boat numbers only containing 0.1-3.0% infected vessels. This could again be due to the limitations of our model and the inherent bias towards closer or smaller lakes. For example, Lake Travis is closer to a source population than either Marble Falls or Inks Lake (Table 2) but it is sufficiently larger than either one (78km^2 vs 3-5 km^2). Contrastingly, Canyon Lake is one of the smaller reservoirs (33km^2) but is situated far from a potential source (142km). Our model also lacks any elements accounting for recreational or human use. Texas is a state rich in fishing culture and various reservoirs around the state hold multiple tournaments throughout the year, attracting large numbers of boaters from all across the state. Our model does not account for such a factor but such a variable could have the potential to divert boater traffic towards lakes otherwise considered “low-risk”.

Concerning the habitat suitability aspect of our model, even though some lakes scored as marginal on one or two parameters, all reservoirs ultimately fell within acceptable habitat conditions and thus, if invaded, are very likely to be able to support zebra mussel populations. Many of the reservoirs had mean surface temperature values fall at ~30°C with maximum temperatures reaching ~32°C (Figure 2). Zebra mussel physiology is highly temperature dependent and these values represent the maximum known adult tolerance for survival (McMahon 1996). Even though most of the study lakes reach temperatures exceeding 30°C this limit may not persist long enough to cause much effect on mortality. It has previously been suggested that zebra mussels are capable of extending their upper thermal limits through long-term seasonal acclimatization (Hernandez 1995, McMahon 1996). In addition, southwestern United States zebra mussel populations may have evolved elevated upper thermal limits (Morse 2009). Increased thermal tolerance of Texas zebra mussels may explain why zebra mussels are dispersing and persisting in waters previously though too warm to support them.

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Table 1. Thresholds of Risk Assessment Parameters for Zebra Mussel habitat suitability (adapted from McMahon 2015).

Habitat Parameter	**Unsuitable**	**Marginal**	**Suitable**	**Reference**
Average water temperature (°C)	>32	30-32	<30	De Kozlowski et al. (2002); Sprung (1987)
pH	<6.8 or >9.5	6.8-7.4	7.4-9.5	De Kozlowski et al. (2002)
Calcium concentration (as mg/L of CaCO3)	<12 mg/L	12-28 mg/L	>28 mg/L	Whittier et al. (2008)
Dissolved Oxygen (mg/L)	< 3.0	3.0-5.0	> 5.0	Johnson & McMahon (1998)

Table 2. List of reservoirs and empirical data incorporated into the gravity model.

	Lake Parameters		
Lake Name	**Surface Area, km² (W_i)**	**Distance to Closest Source Lake (km)**	**Total Boats (O_i)**
International Amistad Reservoir	263	385	1345
Granger Lake	17	41	11703
Lake Buchanan	90	85	5387
Richland Chambers	167	165	3178
Bridgeport Reservoir	49	-	3650
Eagle Mountain	36	-	35731
Inks Lake	5	83	8501
Marble Falls Lake	3	87	5387
Lake Georgetown	5	42	11703
Lake Livingston	336	242	9799
Cedar Creek	132	144	11703
Lake Travis	78	75	29510
Stillhouse Hollow	26	-	7827
Lewisville Lake	117	-	19818
Canyon Lake	33	142	8085
Somerville Lake	47	118	2012
Lake Texoma	360	-	7729
Lake LBJ	26	92	8501
Hubbard Creek	60	115	856
Lake Austin/ Lady Bird Lake	8	83	24123
Ray Roberts Lake	119	-	44047

Possum Kingdom Lake	80	68	4318
Whitney Lake	96	90	2909
Belton Lake	50	-	7827

Table 3 Parameters used in the gravity model to estimate boat movement between selected Texas reservoirs.

Model Parameter	**Description**	**Value Determination**
Tij	Number of boats traveling from lake i to lake j	Equation 1
Ai	Balancing factor	Equation 2
Oi	Number of boats traveling from lake i	Estimated from empirical data
Wj	Attractiveness (surface area) of lake j	Estimated from empirical data
Cij	Distance of lake i from lake j	Estimated from empirical data
α	Distance coefficient	Set parameter
P	Percentage of boats infested with zebra mussels	Set parameter
Zi	Number of boats carrying zebra mussels from lake i	Equation 3
S	Survivability of zebra mussels during transport	Set parameter
D	Number of infested boats (Qj) per unit surface area (Wj)	Set parameter
Rij	Number of boats carrying zebra mussels from lake i arriving at lake j	Z_i x S
Qj	Total number of infested boats arriving at lake j	Σ Rij

Table 4. Set parameter values used to assess low, medium, and high risk dispersal scenarios using the modified gravity model.

Dispersal Risk	Percentage of infected boats in invaded reservoir (P)	Survivability of zebra mussels during transport (S)	Area threshold (infected boats per km^2 of lake j) (D)
Low	20%	20%	6
Medium	50%	50%	4
High	80%	80%	2

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Table 5. Risk Assessment of Zebra Mussel colonization based on habitat parameters.

Reservoir	Temperature	pH	Calcium	Dissolved Oxygen	Risk Level
Lake Belton	Marginal	Suitable	Suitable	Suitable	**Moderate**
Canyon Lake	Suitable	Suitable	Suitable	Suitable	**High**
Cedar Creek	Marginal	Suitable	Marginal	Suitable	**Moderate**
Georgetown Lake	Marginal	Suitable	Suitable	Suitable	**Moderate**
Granger Lake	Suitable	Suitable	Suitable	Suitable	**High**
Hubbard Creek	Suitable	Suitable	Suitable	Suitable	**High**
Inks Lake	Suitable	Suitable	Suitable	Suitable	**High**
Lady Bird Lake	Suitable	Suitable	Suitable	Suitable	**High**
Lake Amistad	Suitable	Suitable	Suitable	Suitable	**High**
Lake Austin	Suitable	Suitable	Suitable	Suitable	**High**
Lake Buchanan	Marginal	Suitable	Suitable	Suitable	**Moderate**
Lake Livingston	Suitable	Suitable	Suitable	Suitable	**High**
Lake Travis	Marginal	Suitable	Suitable	Suitable	**Moderate**
Lake Whitney	Marginal	Suitable	Suitable	Suitable	**High**
LBJ Lake	Suitable	Suitable	Suitable	Suitable	**High**
Marble Falls	Suitable	Suitable	Suitable	Suitable	**High**
Possum Kingdom	Suitable	Suitable	Suitable	Suitable	**High**
Richland Chambers	Marginal	Suitable	Suitable	Suitable	**Moderate**
Somerville Lake	Suitable	Suitable	Suitable	Suitable	**High**
Stillhouse Hollow	Marginal	Suitable	Suitable	Suitable	**Moderate**

Table 6. Percentage of arriving boats carrying zebra mussels under low, medium, and high risk dispersal scenarios and the resulting success of invasion to uncolonized reservoirs based on set area threshold (D).

Lake Name	**Low Risk**		**Medium Risk**		**High Risk**	
	Percent of Arriving Boats Infected	Lake Infected?	Percent of Arriving Boats Infected	Lake Infected?	Percent of Arriving Boats Infected	Lake Infected?
International Amistad Reservoir	0.7	FALSE	4.2	FALSE	10.6	FALSE
Granger Lake	0.9	FALSE	5.6	TRUE	14.0	TRUE
Lake Buchanan	0.1	FALSE	0.6	FALSE	1.6	TRUE
Richland Chambers	0.5	FALSE	3.4	FALSE	8.5	TRUE
Bridgeport Reservoir	15.6	-	39.1	-	62.5	-
Eagle Mountain	10.1	-	25.2	-	40.4	-
Inks Lake	0.1	TRUE	0.6	TRUE	1.6	TRUE
Marble Falls Lake	0.1	TRUE	0.6	TRUE	1.6	TRUE
Lake Georgetown	0.1	TRUE	0.7	TRUE	1.8	TRUE
Lake Livingston	0.9	FALSE	6.0	FALSE	15.0	FALSE
Cedar Creek	1.0	FALSE	6.6	FALSE	16.4	TRUE
Lake Travis	0.1	FALSE	0.7	FALSE	1.8	TRUE
Stillhouse Hollow	9.9	-	24.8	-	39.6	-
Lewisville Lake	11.2	-	28.0	-	44.7	-
Canyon Lake	0.1	FALSE	0.9	FALSE	2.2	TRUE
Somerville Lake	0.4	FALSE	2.2	FALSE	5.7	TRUE
Lake Texoma	6.5	-	16.1	-	25.8	-
Lake LBJ	0.1	FALSE	0.6	TRUE	1.6	TRUE
Hubbard Creek	1.0	FALSE	6.2	FALSE	15.6	TRUE
Lake Austin	0.04	FALSE	0.2	FALSE	0.6	TRUE
Ray Roberts Lake	2.5	-	16.3	-	39.3	-
Possum Kingdom	2.8	FALSE	18.6	TRUE	44.5	TRUE
Whitney Lake	2.3	FALSE	15.1	TRUE	36.7	TRUE
Belton Lake	9.9	-	24.8	-	39.6	-

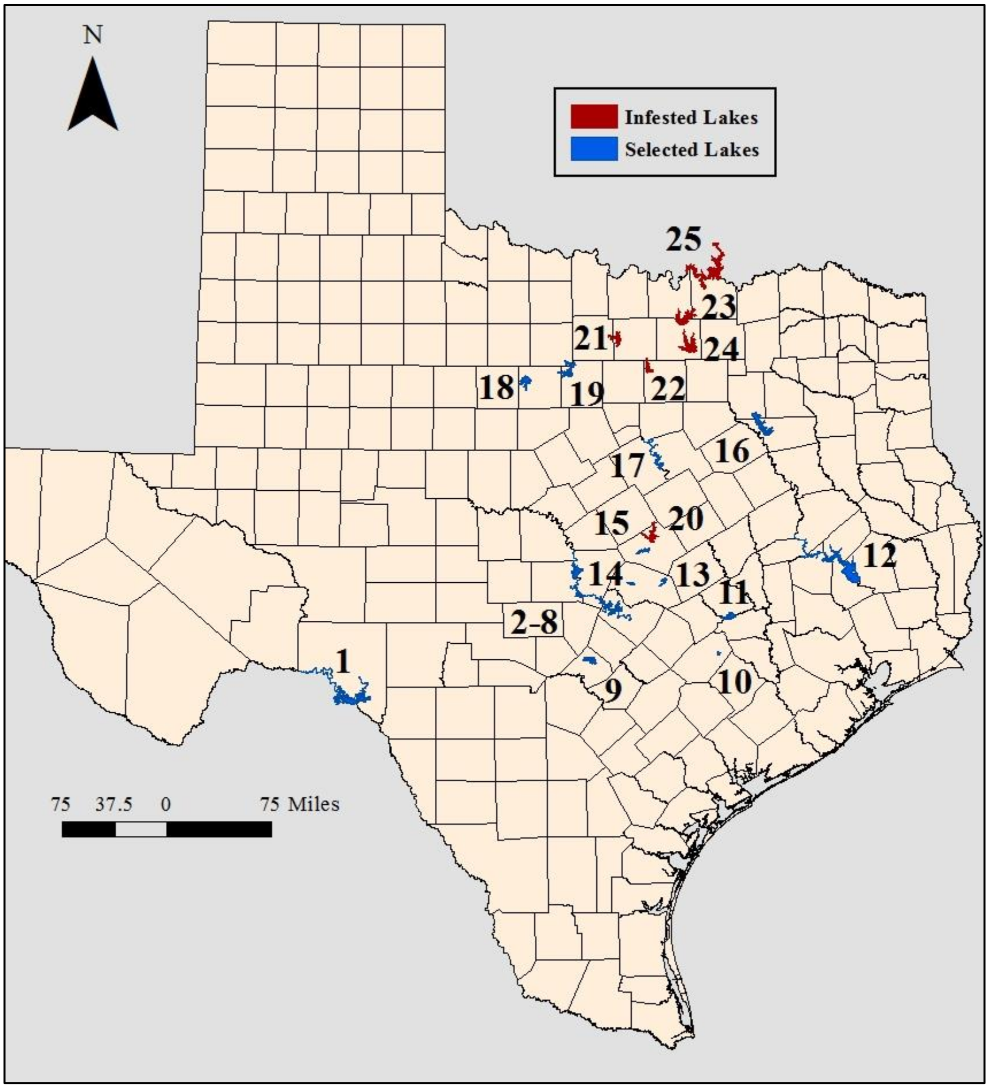

Figure 1. Map of selected central Texas reservoirs (1-19) and already infested reservoirs (20-25) used in the adapted gravity model.

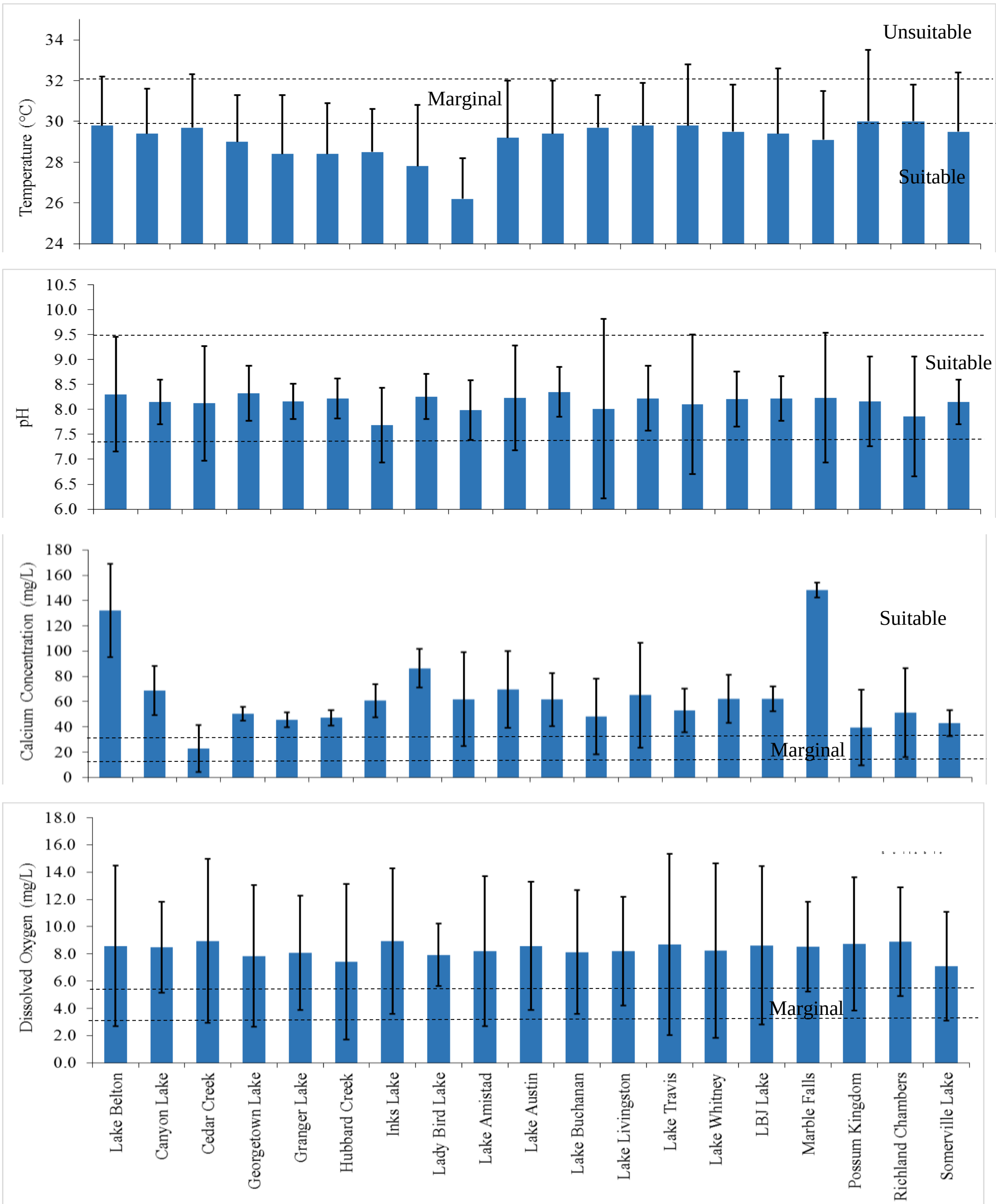

Figure 2. Average A) temperature, B) pH, C) calcium concentration, and D) dissolved oxygen concentrations of surface water (<5m depth) for selected reservoirs. Dashed lines represent thresholds for unsuitable, marginal, or suitable habitat values for zebra mussels (see Table 1). Vertical lines represent range values for pH, DO, and calcium parameter values and maximum values for temperature.