Settlement, density, survival and shell growth of zebra mussels, *Dreissena polymorpha*, in a recently invaded low latitude, warm water Texas reservoir

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Abstract

Zebra mussels, *Dreissena polymorpha*, introduced to US freshwaters in 1986, have expanded into at least 19 Texas reservoir lakes since 2009. In Texas, they occupy the lowest latitudes in their North American and European range where summer surface water temperatures can exceed their upper thermal limit of 30 °C. Little is known of its population dynamics in such warm-water bodies, knowledge of which will be important for development/implementation of effective mussel management strategies. Zebra mussels were first discovered in Belton Lake, central Texas, in 2013 and developed a dense population by 2014. Belton Lake mussel settlement dynamics were studied from March 2016 to May 2017 on steel chains vertically suspended from a floating marina dock. Three chains were deployed at bimonthly intervals with mussel densities recorded monthly thereafter at each meter of depth until experiment termination. Spring cohort settlement occurred from June to September 2016 and fall cohort settlement from November 2016 to May 2017. Peak spring and fall cohort settlement densities were 1,025 mussels m⁻² on July 2016 and 175 mussels m⁻² on February 2017, respectfully. Bottom to surface hypoxia from August (51.58%–71.14% DO) to October 2016 (49.04%–52.13% DO) extirpated the spring cohort by September 2016 and delayed fall cohort settlement until December 2016. Mean mussel settlement density increased with distance downstream from 0 mussels m⁻² in the reservoir’s shallow, inlet end to 21,160 mussels m⁻² at its deeper wider outlet end suggesting that mussel densities tend to be greatest in deeper, wider, low-flow, down-stream ends of impounded water bodies. Mean mussel shell growth rates across six sites were 127.9 μm day⁻¹, one of the fastest recorded for mussels in Europe and North America. Two annual reproductive periods, rapid growth rates and early maturity are likely to lead to zebra mussel population expansion to problematic sizes within 1–2 years after introduction into warm southwestern water bodies, leaving little time for development/implementation of effective mussel macrofouling control/mitigation strategies. Thus, development of effective macrofouling management/mitigation plans should be undertaken prior to establishment of mussels in a water body.

Key words: population dynamics, temperature, hypoxia, flooding, water level, management

Introduction

Zebra mussels, *Dreissena polymorpha* (Pallas, 1771), are among the most successful and destructive aquatic invasive species in North America
(Higgins and Vander Zanden 2010; Karatayev et al. 2015). Once zebra mussels become established, management is difficult and economically costly because they attach via byssal threads to any hard substrate (Coakley et al. 2002; Karatayev et al. 2015) including man-made structures such as scientific equipment, intake and distribution piping in raw-water using facilities, recreation equipment, and navigational buoys, often leading to their deterioration, malfunction or destruction. Zebra mussels have proven to be nearly impossible to contain and fully eradicate once they have become established in a water body (Burlakova et al. 2000; Coakley et al. 2002; Karatayev et al. 2002; Lund et al. 2017; Ricciardi et al. 1998). It has been estimated to cost the United States over one billion dollars annually for mussel management, control, monitoring, damage repair and replacement (Minnesota Sea Grant 2017). Since their initial appearance in the Great Lakes during the mid-1980s (Hebert et al. 1989), zebra mussels have rapidly dispersed down the Mississippi River and up its tributaries, eventually reaching Texas where they were first observed in Lake Texoma on the Red River (Texas/Oklahoma) in 2009 (TPWD 2009). While this species’ original range was in the cooler waters of northern Europe (Hebert et al. 1989), they have now invaded lower latitude, much warmer water bodies in the southwestern United States, particularly in Texas where, as of 2019, they have become established in 19 reservoirs with an additional 10 reservoirs designated as “positive” (i.e., mussels or mussel larvae being detected on more than one occasion) (TPWD 2019).

Belton Lake in Bell County, Texas, was the third Texas water body to be infested with zebra mussels being first reported there in 2013 (TPWD 2013). Despite zebra mussels’ success in temperate regions, their long-term establishment and sustainability at southern latitudes has been somewhat questionable because their presumed upper incipient temperature tolerance limit of 28–30 °C was considered too low to allow them to survive in southern water bodies whose temperatures approach or exceed 30 °C during summer months (McMahon and Tsou 1990; McMahon et al. 1995; McMahon 1996; Karatayev et al. 1998, Beyer et al. 2010; Churchill 2013; Fong et al. 1995; Strayer 1991). However, Morse (2009) has shown that the long-term incipient upper thermal limit of zebra mussels from a warm-water lake in southern Kansas (Winfield City Lake) approached 32 °C. This result suggested that mussels in the southern United States have evolved increased thermal tolerance under the selection pressure of elevated summer water temperatures which has facilitated their establishment in warm Texas water bodies. Because these systems have only recently been invaded, little is known about zebra mussel population dynamics in these warm water bodies (Morse 2009; Churchill 2013, Churchill et al. 2017; Boeckman and Bidwell 2014). In this paper, we describe a one-year study of the impacts of water temperature and hypoxia on zebra mussel settlement, density, and survival patterns at various depths at a site in the
Figure 1. Map of Belton Lake showing the locations of the Leon River Inlet and Outlet, Frank’s Marina where chains were suspended to study mussel settlement, and the nine additional sites where emersed limestone riprap boulders were inspected for the presence of attached, desiccated zebra mussels from the spring 2016 settlement cohort and mussels were collected to determine mussel densities and growth rates. Red areas at reservoir inlets indicate islands when the lake is at conservation pool.

lower portion of Belton Lake, Texas (the lowest latitude at which a study of zebra mussel population dynamics has been published throughout its European and North American range), along with lake-wide variation in mussel density and shell growth rate patterns including the impacts of a major spring flood event.

Materials and methods

Belton Lake

Belton Lake (Figure 1) is a reservoir impoundment of the Leon River in central Texas, USA (31.130394°; −97.508359°), whose construction was completed by the US Corps of Engineers in 1954, attaining conservation pool level of 181 meters above sea level (m.a.s.l.) in 1972 (US Army Corps of Engineers 2019a). At conservation pool, it has a surface area of 5,012 ha and a mean depth of 11 m (maximum depth = 37.7 m) (TWDB 2017). The lake lies within Bell and Coryell Counties, 8 km northwest of the City of Belton, Texas. The shoreline consists of approximately 246 km of natural
Table 1. Geographical locations of the nine sites from which zebra mussel density was estimated on boulders exposed above the waterline and for Frank’s Marina where observations of zebra mussel settlement on submerged chains were conducted along with distances from the major Leon River lake inlet and the outlet of Lake Belton, Texas.

| Geographical Location         | Latitude, Longitude | Km from Leon River Inlet | Km from Lake Outlet |
|------------------------------|---------------------|--------------------------|---------------------|
| White Flint Park             | 31.226305°, −97.474522° | 5.22                     | 27.53               |
| Leona Park                   | 31.22017°, −97.467893° | 5.64                     | 28.54               |
| Owl Creek Park               | 31.217760°, −97.513018° | 10.55                    | 25.59               |
| Cedar Ridge Park            | 31.166679°, −97.453865° | 20.53                    | 17.37               |
| Rogers Park                  | 31.160981°, −97.481172° | 20.97                    | 13.69               |
| Temple Lake Park            | 31.127898°, −97.496130° | 33.51                    | 3.34                |
| Westcliff Park               | 31.121058°, −97.517906 | 31.15                    | 4.49                |
| Arrowhead Park              | 31.123009°, −97.488412° | 34.12                    | 2.30                |
| Belton/Lakeview Park        | 31.104782°, −97.485136  | 33.22                    | 1.23                |
| Frank’s Marina              | 31.105304°, −97.486318 | 33.20                    | 1.24                |

limestone rock (TWDB 2017). It serves as source water for local municipalities, hosts multiple recreational attractions and is a popular site for recreational fishing and boating (TWDB 2017). Seventeen public boat ramps occur throughout the lake.

**Zebra mussel settlement and densities**

Settlement densities were recorded at Belton Lake from March 2016 to May 2017 on sets of steel chains vertically suspended in the water column from a floating dock at Frank’s Marina (31.105615°; −97.486632°). The marina was located in the southernmost cove of the reservoir at Belton/Lakeview Park 1.11 km from the Lake Outlet tower near the dam (Figure 1, Table 1). To estimate temporal mussel recruitment and settlement depth distribution, the steel chains were vertically suspended from above the water’s surface to the sediment bed (approx. depth of 12 m). A 3.6 kg anchor was attached to the end of each chain allowing their vertical suspension throughout the water column. Chain links were 2 cm in circumference and 4 cm long by 1.75 cm in width. One meter of chain length had a surface area of 374 cm².

A set of three chains were deployed side-by-side on 09/03, 16/04, 06/06, 07/08, 16/10, and 11/12 during 2016, and on 02/02/2017. After deployment of each set, all chains remained in place through 21/05/2017 so that a total of 21 chains were deployed at the end of the study. Chains were marked at 1-m intervals with plastic zip ties. Submerged chain lengths were adjusted from their upper end at each sampling visitation such they remained vertically deployed to the sediment bed with changes in lake level. All deployed chains were individually extracted approximately every four weeks over the experimental period (i.e., 16/04, 13/05, 06/06, 10/07, 07/08, 11/09, 16/10, 13/11, and 11/12/2016; and 11/01, 12/02, 12/03, 09/04, and 21/05/2017) to enumerate mussels settled on each submerged meter of chain length. Chains were typically out of the water less than three minutes during mussel enumeration after which they were immediately re-deployed with...
mussels still attached. To minimize mussel mortality and stress during counts, at least two researchers enumerated mussels simultaneously.

Dissolved oxygen, water temperature and lake level

At each site visit, dissolved oxygen determinations were made at 1.5-m intervals from the water’s surface to the bottom substratum using a YSI ProODO Optical Dissolved Oxygen Instrument (YSI Incorporated, Yellow Springs, OH, USA). Dissolved oxygen was computed as a percentage of full air $O_2$ saturation (% DO) which allows $O_2$ concentration levels to be expressed independently of temperature, thus better describing the degree of hyperoxia or hypoxia experienced by the mussels and its impacts. Water temperatures were continuously recorded at 6-hour intervals at three meter depth intervals from the water’s surface to benthic sediments with submersible temperature data loggers (Onset Computer Corporation, Bourne, MA, USA) throughout the study period. Daily variation in Belton Lake surface water levels during 2016–2017 were obtained from the Lakes Online website (2019) (http://belton.lakesonline.com/). Belton Lake is a flood control reservoir (US Army Corps of Engineers 2019a) subject to major increases in surface elevation above conservation pool level during flooding (Figure 2) (US Army Corps of Engineers 2019b). Major surface elevation above conservation pool generally occurs during spring-early summer periods of high rainfall. It is followed by drawdowns to or below conservation pool during late summer, fall and winter when rainfall is reduced.

Figure 2. Surface water level variation in meters above sea level (m.a.s.l) in Belton Lake from 1973 when it attained conservation pool level (181.05 m.a.s.l) through 2019. Dashed line indicates the highest lake level attained during the course of the study (06/03/2016–21/05/2017) at 188.81 m.a.s.l on 07/06/2016.
(Figure 2) by outlet release and water removal for potable use by the Bell County Water Control and Improvement District #1 (US Army Corps of Engineers 2019b).

Shell growth rates and density of the spring 2016 mussel settlement cohort

On 25/09/2016 the distribution, recruitment, and maximum shell growth rates of the 2016 spring mussel cohort were determined at seven of nine examined sites with settled mussels near public boat ramps which had similar abundant riprap limestone boulders extending above and below the water line (Table 1, Figure 1). This date was approximately two months after water levels receded from a period of spring flooding which had allowed juvenile mussels to settle high on the shore to be later emersed by receding water levels. At each site, three limestone boulders were randomly selected on the shore at approximately 184.4 m.a.s.l. (3.3 m above conservation pool on 25/09/2016) as measured by a high precision altimeter (Ziplevel Pro-2000). Analysis of lake levels (Figure 3A) indicated that mussels settled on these rocks when they were submerged above 184.4 m.a.s.l. for 52-days (01/06/2016–22/07/2016) representing the period during which settled mussels could have sustained shell growth.

Sampled rocks with attached mussels were transported to the laboratory in plastic bags. In the laboratory, the firmly attached mussel shells were removed from the rocks, dried at 90 °C for 24 hours, and their dry mass regressed against rock surface area to estimate the density of mussels on each rock. To develop the regression, dried mussel shells (mean = 958, range = 173–3,088) from each of six sites with mussels were equally distributed onto nine 7.62 cm quadrant grids (surface area = 58.1 cm²). The shells were collectively weighed and counted by grid to estimate mussel numbers from dry mass. The surface area of each rock, y, was estimated based on rock weight, x, using an equation specifically developed for riprap limestone: $y = 373.13x^{0.6367}$ where y is surface area in cm² and x is boulder weight in kg (Cooper and Testa 2001). A subsample of mussels from each rock was randomly selected and scanned on a flatbed scanner (600 dpi) allowing their shell lengths (i.e. the greatest linear distance from the umbo to posterior shell margin) to be measured in Photoshop CS6 to the nearest 0.10 mm. The rate of mussel shell growth over the 52-day submergence period was estimated as the mean of the maximum shell lengths of the largest collected mussels across the six sites with extensive mussel settlement (Cedar Ridge Park, Rogers Park, Temple Lake Park, Westcliff Park, Arrowhead Park and Belton Lakeview Park) on the assumption that the largest mussels were the earliest to settle at each site and, therefore, had the longest growing period. While this methodology could potentially lead to a slight overestimate of shell growth rate during the 52-day growth period, it was still assumed to provide a relatively accurate estimate of shell growth rate.
Figure 3. Physical data recorded at the Belton Lake research site over the course of the study (06/03/2016–21/05/2017). A) Surface water level in meters above sea level (m.a.s.l) showing a major increase in water level above conservation pool from April through June 2016 (US Army Corps of Engineers, 2019b). B) Daily water temperatures (°C) at depths of surface, 3 m, 6 m, 9 m and bottom over the course of the study period. C) Water oxygen concentration as percent of full air O$_2$ saturation over the course of the study period. The elongated vertical bar on the x axis separates 2016 from 2017 dates.

Statistical Analyses

Statistical analyses included standard computation of means and standard deviations for lake water level variation, water temperatures, mussel densities at different depths among the sets of three chains deployed bimonthly at Frank's Marina, mussel densities on rocks at different sampling sites throughout Lake Belton and the shell lengths of mussel subsamples taken at those sites. Correlation of mussel densities at sampled sites with distance as the dependent variable from either the lake’s major Leon River inlet or from its outlet were examined by fitting mean density values versus distance as the independent variable to least squares exponential
regressions. One-way Analysis of Variance (ANOVA) was used to analyze significant difference in mussel shell length among sampling sites with subsequent Least Squares Significant Difference testing used to determine significant differences in mean mussel subsample shell length among those sites. Least Squares Linear Regression was utilized to examine the correlation between both mean mussel size and mussel density at each sampling site as dependent variables with distance from the Belton Lake outlet. All statistical analyses were conducted with a Statgraphics Centurion XVI (Warrenton, Virginia) statistical analysis program. A p-value of ≤ 0.05 was considered to represent a significant result in all tests.

Results

Lake physical properties

Water level variation

The historical maximum surface water elevation in Belton Lake occurred on 05/03/1992 at 193.35 m.a.s.l., 12.30 m above conservation pool. The second highest level elevation occurred on 17/07/2007 at 191.91 m.a.s.l., 10.86 m above conservation pool, and the third, during the course of this study on 28/06/2016, at 188.82 m.a.s.l., 7.77 m above conservation pool (Figures 2, 3A). During 2016, water level increased rapidly from a near conservation pool level of 181.24 m.a.s.l. on 17/04/2016 to a peak of 188.82 m.a.s.l. by 28/06/2016, and returned to near conservation pool levels on 11/08/2016 (181.70 m.a.s.l.) after which it remained relatively stable until the end of the study on 21/05/2017 (mean = 181.38 m.a.s.l., sd = ± 0.402, n = 372, range = 181.03–183.47) (Figure 3A) (US Army Corps of Engineers 2019b).

Water temperature

Water temperatures in Belton Lake ranged from 15.27 °C (surface) to 15.1 °C (bottom) at the start of the study on 09/03/2016, rose to peak summer values of 31.45 °C (surface) to 26.81 °C (bottom) on 30/06/2016 followed by a decline to minimal levels of 12.04 °C (surface) to 11.91 °C (bottom) on 09/01/2017 after which they rose to 21.99 °C (surface) and 22.72 °C (bottom) at the time recording ceased on 21/05/2017 (Figure 3B). There was relatively little evidence for development of an extensive thermocline at the study site during the course of the study suggesting that Belton Lake is predominately monomictic. Mean difference in bottom and surface water temperature during the study was 0.936 °C (sd = 0.939, n = 439, range = −0.73–5.39 °C). Maximum difference between surface and bottom temperatures occurred from May through August 2016 as surface waters were warming (mean = 1.49 °C, sd = 1.24, n =123) during the rapid rise in surface water level (Figure 3A, B). A maximum difference of 5.39 °C occurred on 19/06/2016. Thereafter, essentially equivalent surface and bottom temperatures occurred from September 2016 through May 2017 (Figure 3B).
Table 2. Monthly percent of full air oxygen saturation values recorded at three meter intervals from the just below the water’s surface to just above the bottom substratum at Belton Lake, Texas from 16/05/2016 through 17/06/2017.

| Depth (m) | 16/05/2016 | 16/06/2016 | 16/07/2016 | 16/08/2016 | 16/09/2016 | 16/10/2016 | 16/11/2016 |
|----------|------------|------------|------------|------------|------------|------------|------------|
| 0  | 107.00     | 99.68      | 96.64      | 71.14      | 74.24      | 52.13      | 69.30      |
| 3  | 106.42     | 100.99     | 95.45      | 65.79      | 72.39      | 55.70      | 67.13      |
| 6  | 104.24     | 91.67      | 91.23      | 65.70      | 71.67      | 50.20      | 66.32      |
| 9  | 87.43      | 90.47      | 81.05      | 60.99      | 71.08      | 49.7       | 77.4       |
| 12  | 78.81     | 58.77      | 81.03      | 53.95      | 72.48      | 49.04      | 84.83      |
| 15  | 42.07      | 79.83      | 51.58      |            |            |            |            |
| 18  | 36.95      | 74.94      |            |            |            |            |            |
| 21  |            |            |            |            |            |            | 68.05      |

| Date and % of Full Air Oxygen Saturation Values |
|-----------------------------------------------|
| Depth (m) | 16/12/2016 | 17/01/2017 | 17/02/2017 | 17/03/2017 | 17/04/2017 | 17/05/2017 | 17/06/2017 |
|----------|------------|------------|------------|------------|------------|------------|------------|
| 0  | 77.54      | 84.27      | 85.23      | 81.93      | 91.88      | 86.07      | 94.3       |
| 3  | 77.66      | 85.50      | 86.91      | 84.00      | 89.82      | 85.76      | 89.25      |
| 6  | 77.99      | 85.77      | 88.77      | 85.32      | 73.56      | 87.92      | 86.82      |
| 9  | 78.12      | 86.07      | 90.73      | 84.3       | 70.43      | 66.50      | 84.75      |
| 12  | 78.23     | 86.45      |            |            |            |            |            |
| 15  |            |            |            |            |            |            |            |
| 18  |            |            |            |            |            |            |            |
| 21  |            |            |            |            |            |            |            |

Vertical thermal stratification was not as prevalent during May and June of 2017 when lake water levels remained near conservation pool level (Figure 3A, B).

Dissolved oxygen

Percent of full air O₂ saturation decreased with depth over the May to August 2016 period of rapid lake level increase leading to maximal thermal stratification (Table 2, Figure 3A–C). On 16/05/2016, % DO was 104.24% at depths ≤ 6 m below while it declined to 78.81% at a bottom depth of 12 m. Subsequent sampling revealed that % DO stratification further increased. On 16/06/2016, % DO was ≥ 90.47% at depths of ≤ 9 m but declined to 36.95% at a bottom depth of 18 m (Table 2, Figure 3C). By 16/07/2016, % DO with depth increased, ranging from 68.05% at a bottom depth of 21 m to 96.64% at the surface. Thereafter, on 16/08/2016, % DO ranged from 71.14% (surface) to 51.58% (15 m) reflecting a major decline in oxygen concentration at all depths. By 16/10/2016, % DO had further declined to 52.13% to 49.04% across depths of 0–12 m reflecting a major episode of hypoxia (Table 1, Figure 3C). Sampling on 16/11/2016 revealed that % DO had begun to recover, ranging from 84.83%–69.30 over 0–12 m further increasing to 84.30–81.93 over 0–9 m by 17/03/2017 (Table 1, Figure 3C). Oxygen stratification redeveloped by 17/05/2017 with % DO ranging from 91.88% at the surface to 70.43% at a bottom depth of 9 meters, declining further by 17/05/2017 when it ranged from 86.07% (surface) to 66.50% at a bottom depth of 9 m. By 17/06/2017, % DO stratification was greatly reduced ranging from 94.12% at the surface to 84.75% at a bottom depth of 9 m (Table 2, Figure 3C).
Figure 4. Mean density and standard deviations (vertical bars about points) of zebra mussels settled on a set of three steel chains deployed from the water’s surface to the bottom at different times at the Frank’s Marina study site on Belton Lake, TX, from 06/03/2016 through 21/05/2017. Note the major differences in the scale of density on the vertical axes of the graphs. Black arrows indicate dates of chain deployment following which chains remained deployed until the termination of the study. Mussel densities on chains were assessed approximately monthly after deployment. Black points indicate the densities of a spring 2016 settled cohort and red points, densities of a fall 2016 settled cohort separated by a lack of settlement between August and November 2016. The elongated vertical bar on the x axis separates 2016 from 2017 dates. Chains were deployed on A) 06/03/2016, B) 16/04/2016, C) 06/06/2016, D) 07/08/2016, E) 16/10/2016, F) 11/12/2016 and G) 12/02/2017.

Juvenile mussel settlement on chains

Juvenile mussel settlement on chains deployed in March 2016 was minimal through June 2016 with mean densities and standard deviations being 18.9 mussels m\(^{-2}\) ± 5.15, 14.9 m\(^{-2}\) ± 5.51, and 11.9 m\(^{-2}\) ± 20.58 on 16/04/2016, 13/05/2016 and 06/06/2016, respectively (Figure 4A). Major spring mussel cohort settlement was recorded on 10/07/2016 at a mean of 1,025 ± 86.69 mussels m\(^{-2}\). Thereafter, mean spring cohort densities on the March 2016
deployed chains declined, being 198.9 ± 130.0 and 8.8 ± 0.0 on 07/08/2016 and 11/09/2016, respectively, with no mussels of the spring 2016 cohort found on any of the deployed chains from 16/10/2016 through 11/12/2016 (Figure 4A–D). Mussels of the spring cohort disappeared from the March, April, and June 2016 deployed chains by 16/10/2016 (Figure 4A–C). No spring cohort mussels settled on the August 2016 deployed chains indicating that spring mussel settlement had ceased by that time (Figure 4D).

Settlement of a fall mussel cohort was recorded on all deployed sets of chains (Figure 4A–G). Fall cohort densities were much lower than those of the spring cohort (Figure 4A, B). Settlement of the fall 2016 mussel cohort was initiated between 13/11/2016 when no newly settled juveniles were found on chains (Figure 4A–D) and 11/12/2016 when the fall 2016 juvenile cohort first settled on the June 2016 and August 2016 deployed chains at densities of 154.5 ± 215.81 and 11.9 ± 20.85 mussels m⁻², respectively (Figure 4C, D). Settlement of the fall 2016 cohort peaked at 175.3 mussels m⁻² ±158.5 on 12/02/2017 on the August 2016 deployed chains and had declined to 112.9 mussels m⁻² ± 37.11 at the last density observation on 21/05/2017 (Figure 4D). Similar density patterns for the fall 2016 cohort were recorded for the March, April, and June 2016 deployed chains (Figure 4A–C). Mean densities of fall settled mussels on December 2016 and February 2017 chains were low (range = 3 mussels m⁻² ± 5.15–8.90 m⁻² ± 8.81) (Figure 4F, G) indicating that fall mussel settlement had ceased prior to that time. Peak mean fall cohort settlement ranged between 172.3 mussels m⁻² ± 63.23 on 21/05/2017 for the June 2016 deployed chains and 353.5 mussels m⁻² ± 160.76 on 11/01/2017 for the April 2016 deployed chains (Figure 4B, C).

Examination of mean mussel depth density distributions indicated that mussels settled on chains throughout the water column during settlement periods (Figure 5A–D), but there was also a tendency for settlement densities to be reduced at near-surface depths and to increase with increasing depth. This tendency was most apparent in the settlement of the spring 2016 cohort on the March and April 2016 deployed chains in which settlement densities were greatest at depths of 10 to 15 m and extensively declined at lower and higher depths (Figure 5A, B). For this group, decline in settlement density at depths below 15 m may have been a result of the low oxygen concentrations (i.e., 42.07–36.95% DO) occurring on 16/6/2016 when the majority of settlement was occurring (Figure 3C). In contrast, the fall 2016 cohort tended to settle throughout the water column which was 12 m in depth (Figure 5A–D) and well oxygenated at > 70% DO at all depths throughout the settlement period (Figures 3C, 5A–D).

**Growth rates and density of the spring 2016 mussel cohort**

The regression equation developed to estimate mussel count on a rock sample, y, from their dry mass, x, was $y = 67.888x – 43.418$ (n = 6, F = 6.438,
Figure 5. Histograms of mean density of zebra mussels over each meter of depth on a set of three steel chains deployed at Frank’s Marina from the water’s surface to the bottom in Belton Lake, Texas. Black histograms represent settled mussel densities per meter of depth of a spring 2016 settlement cohort and red histograms, that of a fall 2016 settlement cohort. Black arrows indicate dates of chain deployment following which chains remained deployed until the termination of the study on 21/05/2017. The blue lines in each graph indicate bottom depth. Mussel densities with depth on chains were assessed approximately monthly after deployment. The settlement of the spring 2016 and fall 2016 cohorts was separated by a lack of settlement between August and November 2016. Single enlarged black and red points indicate settlement of single individuals. The elongated vertical bar on the x axis separates 2016 from 2017 dates. Chains were deployed on A) 06/03/2016, B) 16/04/2016, C) 06/06/2016, D) 07/08/2016, E) 16/10/2016, F) 11/12/2016 and G) 12/02/2017.

p = 0.0030, r² = 91.20). Mean zebra mussel densities per square meter (± sd, n = 3) sampled from emersed limestone riprap boulders among nine sites on Belton Lake (Figure 1) were White Flint Park (0), Leona Park (0), Owl Creek Park (20 m² ± 30), Cedar Ridge Park (6,430 m² ± 3,430), Rogers Park (5,970 m² ± 3,200), Temple Lake Park (21,160 m² ± 13,630), Westcliff Park (2,630 m² ± 420), Arrowhead Park (16,560 m² ± 7,960) and Belton/Lakeview Park (8,760 m² ± 3,540). Fitting of these mean density values versus distance as the independent variable to exponential regressions indicated that mussel density significantly declined with distance (km) from
the Lake’s outlet tower (n = 8, F = 34.73, p = 0.0006, r² = 81.28, Figure 6A) and increased with distance from the lake’s major Leon River inlet (n = 8, F = 434.83, p < 0.00001, r² = 98.19, Figure 6B). Fitted regression equations were:

\[
\text{Density/m}^2 = e^{(10.454 + (-0.0185 \times (\text{km from outlet}^2))}
\]

\[
\text{Density/m}^2 = e^{(12.836 + (-106.034 \times (\text{km from inlet}^2))}
\]

The shell lengths (SL) of emersed mussels across all sites ranged from 2.2–7.2 mm on 26/09/2016, after approximately 52 days of submergence from initial settlement during 01/06/2016–22/07/2016 (Figures 3A, 7). Mean shell lengths and standard deviations at each site were 4.52 mm ± 0.96 at Belton Lakeview Park, 4.90 mm ± 0.94 at Temple Lake Park, 5.16 mm ± 1.05 at Westcliff Park, 4.61 mm ± 1.12 at Arrowhead Park, 5.27 mm ± 0.86 at Rogers Park and 5.54 mm ± 1.08 at Cedar Ridge Park (Figure 7). One-way Analysis of Variance indicated a significant difference in mean SL among the six sites at which mussels were present (n = 336, F = 9.13, p < 0.00001). Least squares significant difference testing indicated that the mean SL of mussels from Belton Lakeview Park, Westcliff Park, and Arrowhead park (mean SL range = 4.52–4.90) were not significantly (p > 0.05) different from each other. Similarly no significant differences were detected between those from Arrowhead Park, Temple Lake Park and Rogers Park (mean SL range = 4.90–5.27 mm) and those from Rogers Park and Cedar

Figure 6. Mean densities on limestone riprap rocks of the spring settled cohort of zebra mussels on 25/09/2016 at nine different sites in Belton Lake, Texas. Histograms are mean mussel densities with vertical bars above means representing standard deviations. The vertical axes in both figures are mussel density per m². Solid lines in both figures represent exponential regressions relating A) kilometers from the lake outlet and B) from the lake’s major Leon River inlet to mean mussel densities. Exponential regression formulas and statistics relating mussel density to distance from the lake outlet (A) or inlet (B) are provided at the top of each figure.
Figure 7. Mean shell lengths (mm) of zebra mussels (vertical axis) sampled from various sites in Belton Lake, Texas, after approximately 52 days of growth prior to lethal emersion by receding water levels versus distance (km) from the lake outlet (horizontal axis). Black bars around mean shell length points are standard deviations while the red bars indicate the range of sampled shell lengths. Numbers next to mean points indicate sample size. Abbreviations at the top of range bars indicate sampling sites listed in the lower left side of the figure (see Figure 1 for sampling site locations).

Ridge Park (SL range = 5.27–5.54 mm). Least squares linear regression testing indicated that mean SL among the six sites with mussels was significantly correlated with distance from the lake outlet as the independent variable (mean SL (mm) = 4.696 + 0.0475 (density m²), r² = 8.732, F = 35.36, p > 0.00001) but not with mussel density (p = 0.831).

The mean of the maximum shell lengths of the largest collected mussels across the six sites with extensive mussel settlement (Cedar Ridge Park, Rogers Park, Temple Lake Park, Westcliff Park, Arrowhead Park and Belton/Lakeview Park) was determined as 6.65 mm ± 0.0065, range = 6.2–7.2 mm. Based on this mean maximum mussel size, mean shell growth rate over the approximately 52-day submergence period was estimated to be 127.9 μm day⁻¹ ± 0.013. While this approach may have slightly overestimated shell growth rate, it fell within those reported for mussel populations in Texas and Oklahoma as will be discussed below.

Discussion

Juvenile mussel settlement

In Belton Lake, distinct spring and fall periods of zebra mussel settlement were observed during the course of the study. Settlement of the spring cohort was initiated between June and July 2016 when water temperatures ranged from 27.96–28.77 °C (surface) to 24.65–25.80 °C (bottom), respectively,
and ended between August and September 2016 when water temperatures ranged from 29.57–30.77 °C (surface) to 28.57–29.38 °C (bottom), respectively. Subsequently, no juvenile mussel settlement was observed until the appearance of a fall cohort on December 2016 when surface to bottom water temperatures ranged from 16.33–16.25 °C. Individuals of this fall cohort remained on the chains through the end of the study on May 2017. Similarly, Churchill (2013) reported a spring-fall bimodal appearance of zebra mussel veligers in the waters of Lake Texoma (TX/OK) separated by a summer period when surface water temperatures approached or exceeded 30 °C. In contrast, Boeckman and Bidwell (2014) reported only a single spring mussel cohort settlement period in Oologah and Sooner Lakes in northern Oklahoma where summer surface water temperatures also attained 30 °C.

While variation in the temporal density of zebra mussel veligers and juvenile mussel settlement periods throughout a spawning/settlement season has been described for a number of mussel populations in North America and Europe, reports of bimodal spawning with spring and fall juvenile settlement periods outside of Texas water bodies are rare. A search of the literature indicated that only a single period of juvenile settlement generally occurs in North American (Fraleigh et al. 1993; Garton and Haag 1993; MacIsaac 1994; Mackie et al. 1995; Nalepa et al. 1995; Reed et al. 1998; Chase and Baily 1999; Cope et al. 2006; Smith et al. 2016) and European water bodies (Stańczykowska 1964; Morton 1969; Bij de Vaate 1991; Dorgelo 1993; Lewandowski 2001; Wacker and von Elert 2003; Lucy 2006) extending from June–July through October–November in water bodies whose peak summer surface water temperatures do not attain ≥ 30 °C as occurs in Lakes Belton and Texoma (this study; Churchill 2013).

It is possible that even though veligers may be present in the water column throughout the spring, summer, and fall at Lakes Belton (Arteburn and McMahon unpublished) and Texoma (Churchill 2013), elevated temperatures (≥ 30 °C) could prevent mussel larvae survival and development to settlement-competent pediveligers. Sprung (1987) has reported that the sperm of zebra mussels loses its motility and becomes incapable of fertilizing eggs at 26 °C. At ≥ 24 °C, successful development of fertilized eggs to normally behaving veligers was approximately 5% (Sprung 1987). Similarly, Wright et al. (1996) reported that while 48% and 42% of 3–5 day old zebra mussel veligers survived for eight days at 18 °C and 22 °C, respectively, the survival rate for veligers at 26 °C declined precipitously to 6%. Water temperatures at the study site exceeded 26 °C at all depths by the end of June 2016 and did not fall below 26 °C at all depths until mid-October 2016. This may account for the almost complete lack of immediate spring cohort settlement on chains deployed from June 2016 through October 2016 when minimal water temperatures across all depths ranged from 25.33 °C to 25.65 °C or greater near the upper limit for successful
veliger development to settled juveniles. It is this suppression of veliger development at water temperatures ≥ 26 °C that may have accounted for the cessation of juvenile mussel settlement observed in this study at Belton Lake and in Lake Texoma by Churchill (2013). This bimodal spawning/settlement pattern is likely to occur in other warm-water southern lakes as mussels continue to expand southward in North America.

The fall juvenile cohort settled at all depths from the surface to the bottom (≤ 12 m) from November 2016 to February 2017 when percent O₂ levels were ≥ 70% of full saturation. There appeared to be no pattern of initial settlement density with depth in the fall cohort as it was highly variable among chains deployed prior to the fall juvenile settle period. In contrast, the spring cohort displayed a distinct pattern of initial juvenile settlement with depth. On the April 2016 deployed chains, extensive settlement was first noted on July 2016. Maximum juvenile settlement occurred at a depth of 12–13 m at 962.7 juveniles m⁻² with newly settled juveniles occurring between depths of 4 and 16 m and no juveniles settling below 16 m to the bottom depth of 22 m. Wacker and von Elert (2003) noted a similar suppression of juvenile mussel settlement at 15 m depth associated with a distinct thermocline and reduced water temperatures relative to surface water temperatures. In contrast, there was minimal thermal stratification with depth at the time of spring cohort settlement in Belton Lake (Figure 3B) with water temperatures at all depths being greater than the 16–18 °C generally considered the lower limit for initiation of mussel spawning and juvenile settlement (McMahon 1996). Instead, juvenile settlement in Belton Lake may have been suppressed below 16 m depth as a result of the low oxygen concentrations of 42.07% and 36.95% DO) at depths of 15 and 18 m, respectively, recorded on the prior June 2016 sample (Figure 3C).

Interestingly, this surface to bottom hypoxia event recorded during the summer and early fall of 2016 occurred in the latter stages of and after a period of extensive lake flooding. Extensive hypoxia was not recorded during the spring of 2017 when Belton Lake was not subjected to substantial flood-induced water level elevation above conservation pool. This result suggested that the hypoxic conditions recorded in the lake during summer/fall 2016 were associated with the preceding extensive spring flood and resulting rapid water level elevation. Influx of flood waters carrying suspended organic matter can result in extensive hypoxia (Wiebe 1940; Lyman 1944; Huang et al. 2014). In a thermally uniform, monomictic water body like Belton Lake, flood waters laden with organic matter could mix with waters at all depths while high levels of water release would allow its rapid downstream transport creating hypoxic conditions throughout lower portions of the lake (Wiebe 1940; Lyman 1944; Huang et al. 2014). Belton Lake has a maximum depth at conservation pool of 37.8 m (Tibbs and Baird 2019). The lake’s outlet system consists of three gated inlets at a
depth of 33.8 meters (Olson et al. 2018; TWDB 2017), 4.0 meters above its maximum depth at conservation pool level. At this depth water is released from the hypolimnion which is occasionally hypoxic (Olson 2016), potentially allowing organically rich flood waters entering the lake to extend to all depths throughout the lake resulting in the post-flooding hypoxic surface waters throughout the water column as recorded during the summer and fall of 2016.

Sprung (1987) noted in a laboratory study that zebra mussel veliger development was inhibited at oxygen concentrations below 20% DO. De Ventura et al. (2016) reported that adult zebra mussels could tolerate hypoxia at 33% DO, but not at 6% DO. Similarly, Johnson and McMahon (1998), in a laboratory study, determined that the 29-day incipient lower lethal limit for adult zebra mussels was 30% DO. Similar hypoxia tolerance studies have not been conducted for recently settled juvenile zebra mussels. That no settlement of juvenile zebra mussels occurred on chains at depths of 15 m and 18 m where % DO fell to 42.07% and 36.95%, respectively, suggests that pediveliger and/or newly settled juvenile mussels may be less tolerant of hypoxia (i.e., ≤ 42% DO) than adult mussels. On the subsequent August 2016 sampling period, newly settled juveniles extended from the surface to bottom depth of 15 meters at 51.58% DO. This result suggested that the incipient lower O2 limit for pediveliger/newly settled juvenile mussels may lie between 42% and 52% DO.

After an extensive settlement, the spring mussel cohort was completely extirpated from the March and April 2016 deployed chains between August and September 2016. White et al. (2015) reported a major die-off of zebra mussels in Gull Lake, Michigan, during a relatively warm summer even though water temperatures did not approach 30 °C, which is considered the incipient, long-term, upper lethal limit for adult zebra mussels (McMahon 1996). Instead it was postulated that mussel die-off was a result of accumulated degrees above 25 °C equivalent to 70.8 °C degree days (White et al. 2015). In Belton Lake, between August and September 2016, the mean water temperature between the water surface and bottom (> 9 m) was 29.6 °C and 28.9 °C, respectively, during which the respective range of exposure to °C degree days above 25 °C was 165.7 to 139.8 °C degree days, far greater than the 70.8 °C degree days reported by White et al. (2015) to be potentially lethal to zebra mussels. Thus, it is possible that the spring cohort of mussels was extirpated from the chains by a prolonged cumulative thermal stress when water temperatures exceeded 25 °C. However, Morse (2009) found that zebra mussels from Winfield Lake in southern Kansas had a 29-day incipient upper lethal temperature limit of 31.7 °C, 3.7 °C degrees higher than the 28 °C upper limit of concurrently tested mussels from the much cooler Hedges Lake in New York State. This result suggested that zebra mussels inhabiting warm southwestern US water bodies had evolved elevated upper thermal limits relative to mussels in more northern
latitudes. Indeed, the spring mussel cohort in Belton Lake typically has been observed in other years to survive for approximately a year after settlement under approximately the same temperature regime observed in 2016 (Arterburn and McMahon unpublished). Thus, it was unlikely that the summer die-off of the Belton Lake spring cohort of mussels observed in this study was due to thermal stress alone.

Between August and September 2016 when the spring cohort of settled mussels disappeared from spring deployed chains, surface to bottom oxygen concentrations fell from 96.64% DO (surface) to 68.05% DO (bottom) on July 2016 to 52.13% DO (surface) to 49.04% DO (bottom) on October 2016 before rising to ≥ 84.27% DO at all depths on January 2017. All depths remained relatively well oxygenated for the remainder of the study when sampling ceased on May 2017. Johnson and McMahon (1998) found that increasing temperatures from 5–25 °C decreased adult zebra mussel survival times when exposed to hypoxia. Thus, the extended summer-early fall period of relatively extensive hypoxia at all depths combined with elevated temperature stress may have synergistically resulted in the post July 2016 extirpation of the spring cohort.

**Zebra mussel density variation in Belton Lake**

There have been a limited number of studies on variation in zebra mussel densities at different sites within a water body. Marsden et al. (2013) reported that mussel densities at 10 sites in Lake Champlain, NY/VT, generally declined with declining calcium concentrations, mean annual surface water temperatures and primary productivity. In contrast, Nalepa et al. (1995) could find no significant differences in settled mussel densities on hard natural substrata between sampling sites in the outer and inner portions of Saginaw Bay in Lake Huron, MI. At 12 different sites in Lake Trasimeno (Umbria, Italy), zebra mussel densities were impacted by the degree of substrate stability with the greatest densities on concrete, intermediate densities on pebbles, rocks, and emergent vegetation and the lowest densities on sand and silt (Lancioni and Gaino 2006). Similarly, in a newly formed amenity lake in Cardiff Bay, Whales, UK, mussel density recorded at 34 sites was primarily determined by substrate stability being greatest on pebble substrata and vertical, hard-surfaced man-made structures while soft sediments were largely free of mussels (Alix et al. 2016). In Lake Zürich, Switzerland, zebra mussel densities among nine sampling sites were greatest on steep, stony shores and least on more shallowly sloping shores which had a lesser degree of hard-surfaced substrata (Burla and Ribi 1998). Among six sampling sites in Lake Erken, southern Sweden, zebra mussel densities were negatively correlated with the density of roach (*Rutilus rutilus*) a fish predator of zebra mussels, depth, and substratum stability (i.e., rock versus sand) (Naddafi et al. 2010).
In contrast to the above studies, our study involved estimating densities of zebra mussels on the same substratum of limestone riprap boulders at the same depth at nine different sites in Belton Lake. Sampling from the same substratum and depth allowed mussel densities between sites to be directly compared. Results indicated a significant negative correlation between mussel densities and distances from the lake’s outlet (Figure 6A) and, conversely, a positive correlation with distance downstream from its major Leon River inlet (Figure 6B). Since the sites sampled were all made up of similar limestone boulder riprap from the same depth, these correlations with distance from the lake’s inlet and outlet were potentially due to factors other than substratum type with the most likely being flow rate and lake depth. Upstream sites, including White Flint Park, Leona Park, Owl Creek Park, and Cedar Ridge Park, were situated in the Lake’s narrow, shallow inlet arms farthest from the lake outlet (3.1–6.1 m depth at conservation pool level) (TWDB 2017) making them subject to high flow rates during spring rains that could transport veligers downstream preventing mussel settlement as well as lethal emersion of mussels during summer declines in lake surface level. Thus, no mussels were found at the two sampling sites farthest from the lake outlet, White Flint Park (27.5 km from outlet) and Leona Park (28.5 km from outlet) while a low mean mussel density of 20 mussels m⁻² was recorded at Owl Creek Park (25.69 km from outlet) (Figures 1, 6A). At intermediate distances from the lake outlet, mussel densities rose to 6,430 m⁻² and 5,970 m⁻² at Cedar Ridge Park (17.4 km from outlet) and Rogers Park (13.7 km from outlet), respectively (Figures 1, 6A). In contrast, the mean mussel density recorded across the four sites closer to the lake outlet in the much deeper, lower, low-flow portion of Belton Lake [Westcliff Park (4.5 km), Temple Lake Park (3.3 km), Arrowhead Park (2.3 km), and Belton/Lakeview Park (1.2 km)] was 12,277 mussels m⁻² (Figures 1, 6A). The most reasonable hypothesis for this observed tendency for higher mussel densities with decreasing distance from the lake outlet is that, in the deeper, greater water volume of the downstream end of the lake, water currents are reduced allowing veligers enough time to develop into settled mussels than occurs in upper, shallow, high-flow sections of the lake. This result suggests that when monitoring water bodies for mussel invasion, chances for early detection of veligers or newly settled juveniles will be greatest if sampling efforts are focused on the deeper/greater volume locations of those water bodies that are characterized by low flow rates and greater depths, which are generally near outlets in reservoirs.

**Mussel growth rates in Belton Lake**

Among the Belton Lake sites with zebra mussels, there was a significant difference in the mean shell length of newly settled juveniles over a 52-day period before lethal emersion by receding water levels. This difference was
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marked by a weakly significant positive correlation of mean SL with distance from the lake outlet but not with mussel density. Other studies have found that first growing season zebra mussel shell growth rates can vary among different locations within a water body (Chase and Baily 1999; Garton and Johnson 2000; Naddafi et al. 2010; Churchill et al. 2017). A review by Karatayev et al. (2006) identified factors that could negatively impact zebra mussel shell growth rates within a water body including decrease in temperature (Chase and Baily 1999; Churchill et al. 2017), decrease in primary productivity (Chase and Baily 1999; Churchill et al. 2017), increased water velocity, increased depth (Garton and Johnson 2000), increased wave action and increased turbidity/suspended matter (Karatayev et al. 2006). Unlike our results, Naddafi et al. (2010) found that zebra mussel shell growth rate was primarily dependent on population density with lower shell growth rates occurring in dense populations perhaps due to increased competition for food resources. The extensive variation in mussel density among our sites ranging from means of 2,630 mussels m\(^{-2}\) to 21,160 mussels m\(^{-2}\) suggests that either food was so abundant that mussel density did not impact mussel shell growth rate or that there was little competition among mussels for phytoplankton/bacterioplankton food supplies.

In Belton Lake, emersed mussel shells were all sampled at the same level on the shore, thus, mussels had all settled and grown at over the same 52-day time period and depth (184.4 m.a.s.l.) on similar limestone riprap boulders which greatly reduced the number of factors potentially impacting shell growth rates. Thus, comparative studies of environmental impacts on zebra mussel growth rates at different locations within a water body should be conducted with as many other extraneous environmental factors such as depth, settlement/growth periods, flow rate and natural substrate type, etc. standardized as much as possible.

The mean mussel shell growth rate over the 52-day spring cohort settlement period estimated from the mean shell length of the largest mussels found at the six sites with extensive mussel settlement was 127.9 \(\mu\)m day\(^{-1}\). Although, as described in the Methods, this methodology for estimating mean shell growth during the 52-day growth period could have slightly overestimated shell growth as it was based on the largest individuals found at each site, it fell within those recorded for two other southwestern United States reservoirs, Lake Texoma (TX/OK) (mean = 121.4 \(\mu\)m day\(^{-1}\)) (Churchill et al. 2017) and Oologah Lake (OK) (mean = 136.7 \(\mu\)m day\(^{-1}\)) (Boeckman and Bidwell 2014). The shell growth rates of mussels in these three southwestern reservoirs were higher than first season shell growth rates recorded for 12 higher latitude European and North American mussel populations for which shell growth rates could be estimated (see references imbedded in Figure 8). Fitting of first season shell growth rates estimated for these 15 mussel populations to a regression with
the square of shell growth rate as the dependent variable and the reciprocal of latitude as the independent variable indicated a significant negative correlation between first growing season shell growth rate and latitude. Correlation with latitude explained 50.4% of the variation in first growing season shell growth rate with rates declining 3.46 μm day$^{-1}$ per degree increase in latitude, a value similar to that estimated by Churchill et al. (2017) of 3.306 μm day$^{-1}$.

Surface water temperatures at all depths in Belton Lake were greater than 28 °C from July through September 2016 and peaked at 30.39 °C in August. Similar patterns of summer water temperatures approaching or exceeding 30 °C have been reported for Oologah Lake (OK) (Boeckman and Bidwell 2014), and Lake Texoma (TX/OK) (Churchill et al. 2017) where the greatest first growing season shell growth rates have been recorded for zebra mussels. This correlation with latitude suggests that temperature is a major environmental factor affecting mussel shell growth. Thus, zebra mussels invading warm southwestern US water bodies are likely to grow faster, mature earlier and have longer annual reproductive periods than populations at higher latitudes, allowing them to achieve maximum densities in much shorter post-invasion time periods leading to more rapid onset of fouling of raw-water using facilities and negative
environmental impacts than have occurred in water bodies at higher latitudes in North America and Europe. Because of their ability to rapidly reach problematic densities after an invasion of warm, low-latitude water bodies, raw-water using facilities and water managers in the southern US states will have little time to respond after mussels invade their water bodies. Therefore, rapid response, mitigation, and control plans should be developed in advance so that they can be quickly deployed after initial zebra mussel invasion of a low-latitude, warm-water body.

Conclusions

Zebra mussels in Belton Lake displayed two distinct periods of spring and fall juvenile settlement marked by cessation of settlement during summer months when water temperatures were \( \geq 25–26 \) °C. This has been observed in other warm water bodies in Texas (Churchill 2013; Arterburn and McMahon unpublished). Summer cessation of settlement may have been associated with the inability of veligers to fully develop into settlement competent pediveligers at or above these temperatures even though veligers may remain present in the plankton (Sprung 1987). Utilities drawing raw-water from source water bodies that reach or exceed these temperatures in areas such as the southwestern United States could potentially reduce molluscicide usage to prevent zebra mussel fouling by ceasing application of chemical controls during summer months when raw-source water temperatures exceed the 26 °C upper limit for veliger development to a settled juvenile. Juvenile mussel settlement patterns could be monitored by deployment of mussel settlement monitors on a weekly to semimonthly basis and molluscicide application stopped when settlement ceases and resumed when settlement is again detected in the fall. Such an approach could limit use of chemical controls to the May–July and October–January in Texas and other southwestern water bodies.

Spring 2016 flooding increased Belton Lake water levels which resulted in juvenile mussels of the spring cohort densely settling on submerged substrata well above conservation pool. When water levels subsequently returned to conservation pool level during summer, newly settled mussels were lethally emersed preventing them from participating in the fall spawning period even though many had achieved reproductively competent sizes. An apparent result of this massive late summer reduction in numbers of mature spring cohort individuals in Belton Lake was that the densities of the fall cohort were greatly diminished relative to that of the preceding spring cohort. In water bodies where water levels can be controlled, raising water levels prior to spring spawning could cause juveniles to settle high on flooded portions of the shore after which a rapid draw-down would lead to their lethal emersion in high temperatures during summer months, reducing the number of reproductively competent mussels and, thus, the extent of fall juvenile mussel settlement. Thus, such planned control of
water levels could result in a reduction of mussel density relative to that in water bodies with minimal water level variation.

Densities of the spring 2016 mussel cohort in Belton Lake declined significantly with distance downstream from the lake’s major inlet and were maximized in the lower deeper end of the lake. Reductions in density in the upper inlet areas of the lake may have been due to it being relatively shallow exposing mussels to lethal emersion during reductions in lake level and downstream transport of veliger larvae before settlement by relatively high flow rates in narrow, shallow, upstream inflow channels. Thus, water-using facilities located in the deeper, downstream, low-flow areas of source-water bodies are likely to be subjected to more severe mussel macrofouling than those located in shallow, high flow inlet sections of source water reservoirs. This could be a future consideration for location of new water using facilities on source water reservoirs infested with zebra mussels or potentially invaded by them.

Even though Belton Lake mussel first season shell growth rates could have been slightly overestimated because they were based on the mean of the shell lengths of the largest individuals found at each of the six sites with extensive mussel settlement after a 52-day settlement period before emergence by receding water levels, they were similar to and among the highest recorded in the North America and Europe along with those for mussels in Lake Texoma (TX/OK) (Churchill et al. 2017) and Oologah Lake (OK) (Boeckman and Bidwell 2014) which utilized more accurate methods for determining shell growth. When regressed against latitude, the first growing season shell growth rates in zebra mussel populations increased with decreasing latitude suggesting that shell growth rate was at least partially correlated with temperature regime such that mussels grow faster at the higher water temperatures encountered at lower latitudes. During their 52-day settlement period, zebra mussels in Belton Lake attained mean shell lengths ranging from 4.52 mm at Belton/Lakeview Park to 5.54 mm at Cedar Ridge Park for a grand mean shell length of 5.10 mm with maximum recorded shell lengths ranging from 6.2–7.2 mm across all six sites. Delmott and Edds (2014 and references within) studied zebra mussel maturation and seasonal gametogenesis in the warm-water Marion Reservoir (KS) (peak summer surface water temperature = 34.6 °C). They found that zebra mussels reached maturity four weeks after settlement, a shorter period than reported for mussels in Europe and the northern U.S. They also found that 60% of mussels matured at a shell length of 5.0 mm and 100% at 7.0 mm which suggests that at least 50% of mussels in Belton Lake were mature and reproductively active 52 days after their initial spring settlement. Rapid shell growth rates associated with early zebra mussel maturity and spawning and extended periods above spawning temperatures in warm low-latitude water bodies like Belton Lake could result in spring spawned mussels maturing and spawning during fall of the
same year leading to explosive population increase. Thus, zebra mussels reached high densities within a year of their initial discovery in Texas Lakes, Texoma (2009) (McMahon 2015), Ray Roberts (2012) and Belton (2013) (McMahon personal observations). The very rapid zebra mussel population expansions in warm southwestern water bodies leaves little time for raw-water using facilities to implement effective control strategies prior to development of costly mussel macrofouling. Thus, it is imperative that these facilities develop effective plans to prevent/manage zebra mussel macrofouling prior to zebra mussel invasion of their raw source water bodies in areas such as Texas where the number of water bodies infested with zebra mussels has increased exponentially since first being discovered in Lake Texoma in 2009 (USGS 2019).

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