

**Research Report**  
**On work completed for a Texas Parks and Wildlife Department**  
**Funded Research Project Entitled:**

**An Ongoing Study of Zebra Mussel Population Dynamics in Infested Texas Water  
Bodies: Growth Rates, Life Spans, Reproductive Periods, Juvenile Settlement  
Rates, Veliger Size Distributions and Adult Dry Tissue Weights Relative  
to Seasonal Temperature Variation, and Causes of Population  
Collapse in Lakes Texoma, Ray Roberts and Belton**

Report prepared by

**Robert F. McMahon**

Professor Emeritus and Principal Investigator

and

**Heather Arterburn**

Research Assistant

Department of Biology, Box 19498  
The University of Texas at Arlington  
Arlington, Texas 76017  
Phone: 817-272-2412  
Email: r.mcmahon@uta.edu

For submission to

Brian Van Zee

Texas Parks and Wildlife Department  
Inland Fisheries Region 1 (West)  
1601 E. Crest Dr.  
Waco, Texas 76705

Submitted December 18, 2017

## EXECUTIVE SUMMARY

This research on zebra mussels (*Dreissena polymorpha*) in infested Lakes Texoma, Ray Roberts, Belton, Eagle Mountain and Lewisville increased our understanding of the population dynamics of zebra mussels in Texas water bodies where summer surface water temperatures are greater than those experienced by this species anywhere else in its North American or European range. The results demonstrated that Texas zebra mussel populations sustain rapid individual growth (up to 3.0 cm shell length in 1-1.5 years) and have extremely short life spans ( $\approx$ 1-1.9 years) compared to those in northeastern North America and Europe that require life spans of 3-5 years to attain similar sizes. The rapid growth and short life spans of zebra mussels in Texas water bodies allow them to rapidly attain sexual maturity and high densities 1-2 years after invasion, thus, potentially allowing them to foul raw-water using facilities much more rapidly than previously reported for slower growing populations in cooler, more temperate waters. The results also indicated that zebra mussels in Lakes Texoma and Belton, both displayed increases in settlement rates and population densities in spring 2017 after a previous period in 2015 and 2016 of population decline which appeared to be caused by extensive variation in reservoir water levels during a 2015 spring flooding event. On Lake Belton, a notable surface water hypoxia event on 09/25/2016 resulted in a decline in O<sub>2</sub> concentration to 15.1% of full air O<sub>2</sub> saturation, well below 30% of full air O<sub>2</sub> saturation which is considered the lower incipient lethal limit for zebra mussels. This hypoxia event resulted in complete loss of mussels from settlement monitors and an apparent extensive reduction in zebra mussel density at least in our study site if not throughout the reservoir. The Lake Belton zebra mussel population did not recover from this event until 2017 when a massive settlement of the spring 2017 juvenile cohort ensued. In contrast, zebra mussels in Lake Ray Roberts continued to remain at very low population densities following the flood of 2015, likely due to surface water pH being below the 7.4 required for veliger development to settled juveniles since October 2016. Thus, the results of this study suggest that zebra mussel populations in at least some Texas water bodies will undergo boom/bust population dynamics similar to those reported for other populations in North America and Europe.

Furthermore, we found that while reproductive periods marked by the presence of larval mussels (veligers) in the water column may extend for three to four months during spring (May through July) and fall spawning periods (September-December), settlement-competent pediveligers (i.e., those with shell lengths  $\geq$  231  $\mu$ m) occur in the plankton for only limited periods which were correlated with those of juvenile settlement. Thus, assessing the size of veligers through reproductive periods may allow more accurate delineation of settlement periods permitting mussel settlement prevention technologies, including treatment of raw-water systems with molluscicides, to be applied for much shorter durations when mussels are settling in large numbers, both reducing costs and the amounts of molluscicides utilized.

The results also indicated that chlorophyll *a* concentrations tended were significantly ( $p < 0.05$ ) lower in Lakes Texoma and Belton with extensive zebra mussel infestations compared to those of Lake Ray Roberts and newly invaded Lakes Eagle Mountain and Lewisville which had very low mussel densities. This result suggested that mussel filter feeding was reducing phytoplankton densities in these lakes which could negatively impact energy flow to higher trophic levels including sport fish. In contrast, mean total phosphorus (TP) concentrations in Lakes Belton and Ray Roberts were significantly ( $p < 0.05$ ) lower than in Lakes Texoma, Eagle Mountain and Lewisville. Lake Belton which harbored the most dense zebra mussel population also had the lowest TP concentration suggesting that mussels may have been sequestering phosphate from the water column into the substratum with their feces and pseudofeces as reported for water bodies with longer-term mussel infestations in northeastern North America and Europe.

The mean dry tissue weight of large mussels with a standard shell length (SL) of 25 mm from Lake Belton and Winfield City Lake, Southern Kansas (2008) with the most dense mussel populations was significantly ( $p < 0.05$ ) lower than those of mussels from Lakes Texoma and Ray Roberts. This result, correlated with the reduced mean chlorophyll *a* concentrations in Lake Belton relative to Lakes Eagle Mountain and Lewisville with low mussel densities suggested that mussel filter feeding in Lake Belton

was lowering phytoplankton densities leading to a reduction in dry tissue weights. It was interesting that these reductions in dry tissue weights were most apparent in larger individuals of 20 and 25 mm SL. Dry tissue weights in large mussels decreased in Lakes Texoma, Ray Roberts and Belton as well as in Winfield City Lake, KS (2008) during warm summer months suggesting high temperature induced elevation in their metabolic rates resulted in a negative energy balance leading to tissue loss (i.e., starvation). Thus, elevated summer water temperatures coincident with phytoplankton density reductions during summer months in Texas may lead to lethal starvation in larger mussels resulting in attenuated life cycles with loss of spring and fall cohorts during the summer/fall of the year following their initial settlement as was observed in this study. However, such starvation did not appear to be the cause of the post-invasion collapse of zebra mussel populations observed in Lakes Texoma, Ray Roberts and Belton. Instead, their population collapses may have been related to mortality caused by the extensive water level variation in these lakes during the spring floods of 2015. Rising lake levels in spring 2015 caused existing mussel populations to experience lethal hypoxia below the thermocline during spring high water levels followed by lethal emersion of juvenile mussels settled high on the shore during flooding to be subsequently exposed to lethal desiccation as they were exposed to air as water levels receded in late summer and early fall.

Data gathered on zebra mussel growth rates, reproductive periods, periodicity of settlement competent pediveligers in the water column, juvenile settlement rates, and the possible bases for zebra mussel population collapse in the studied water bodies can be used by Texas raw-water using facilities and industries to develop cost-effective strategies for monitoring zebra mussel settlement to guide application of control/mitigation strategies for macrofouling. In addition, they should consider fluctuations in water level along with surface water temperatures to predict years when they are likely to experience extensive mussel macrofouling as opposed to years when mussel settlement may be reduced.

The results of this study indicated that the post-invasion zebra mussel population collapses recorded in Lakes Texoma, Ray Roberts and Belton in 2015-16 are unlikely to be permanent; population recovery is beginning to occur in lakes Texoma and Belton. Rather, zebra mussels appear to be able to recover in 1-2 years from short-term, environmentally induced reductions in densities. Recovery may vary among water bodies as this study demonstrates for the zebra mussel population in Lake Ray Roberts that has remained at very low densities since its collapse in 2015 due to a continued period of low pH preventing veliger development to settled juvenile. For this reason, while raw-water users on newly-infested lakes may need to develop relatively low-cost, short-term plans to control/mitigate mussel fouling of their facilities with molluscicide application, all facilities on at-risk lakes should consider developing plans in advance to make their infrastructure more resistant to mussel fouling, with timelines for rapid implementation after mussels invade their source waters

## **INTRODUCTION**

The freshwater invasive zebra mussel (*Dreissena polymorpha*), was introduced from Europe to the US Great Lakes by transatlantic shipping in 1986 (Benson 2014). It spread rapidly through waters of the US east of the Rocky mountains (Benson 2014) disrupting aquatic ecosystems and fouling industrial raw water facilities resulting in billions of dollars lost in ecological services, human recreation, and mitigation/control of mussel fouling in potable water, power station and industrial raw-water facilities (Claudi and Mackie 1993, Pimentel et al. 2005). Zebra mussels have invaded the major drainages of the Mississippi, St. Lawrence, Hudson and Susquehanna rivers and other isolated water bodies (Figure 1). They now occur in the western drainages of the Mississippi River including the Missouri, Kansas, Osage, White, Arkansas, and Canadian Rivers (Figure 1). Outside these western drainages, major mussel infestations now occur in the Red River of the North (ND) and in Texas. Zebra mussel invasion of Texas water bodies was not expected because their summer surface water temperatures exceeded the mussel's previously recognized upper thermal limit of 28°C (Morse 2019, McMahon 2015). However, since 2009,

zebra mussels have successfully invaded Texas reservoirs in the Red (Lakes Texoma, Dean Gilbert, and Randell), Trinity (Lakes Ray Roberts, Lewisville, Eagle Mountain, Bridgeport, Fishing Hole and Livingston), Brazos (Lakes Belton and Stillhouse Hollow), Colorado (Lakes Travis and Austin) and Guadalupe (Canyon) River drainages (Figure 2). The capacity for zebra mussels to have developed sustainable reproducing populations in Kansas, Oklahoma and Texas strongly suggests their evolution of increased thermal tolerance in the warm water bodies of this region. It appears likely that zebra mussels initially isolated in the warm water bodies of Oklahoma and Kansas (Figure 1) evolved an increased thermal tolerance eventually reaching levels that allowed their invasion of even warmer Texas water bodies. Indeed, Morse (2009) demonstrated that zebra mussels in the warm waters of Winfield City Lake in southern Kansas with summer surface water temperatures approaching 30°C had an incipient upper thermal limit >30°C compared to 28°C for mussels from Hedges Lake, NY, where water temperatures did not exceed 25°C. Thermally induced rapid genetic selection has been reported for Russian zebra mussel populations isolated in power plant thermal effluents (Fetisov et al. 1991). Because elevated temperatures have major impacts on the growth rates, reproductive periods, life spans and energy allocation patterns of aquatic organisms including freshwater bivalves (McMahon and Bogan 2001), it is important to understand the population dynamics and sustainability of zebra mussel populations in thermally stressful Texas water bodies. This information could inform development of appropriate, economically feasible mitigation and control strategies for their macrofouling, especially if zebra mussel populations in Texas water bodies undergo period major density reductions as has been observed to occur in Lakes Texoma, Ray Roberts and Belton (McMahon 2015 and unpublished) and Sooner Lake, OK (Boeckman and Bidwell 2014).

With few exceptions, long-term population dynamics studies of zebra mussels have centered on temporal mussel density variation in cooler, more northern European and North American water bodies. They indicate that mussel density can either vary greatly through time (Strayer and Malcom 2006, Strayer et al. 2011) or decline to very low densities over periods >20 years (Stańczykowska and Lewandowski 1993). In contrast, Boeckman and Bidwell (2014) showed that zebra mussel population density in the warm Sooner Lake, OK, declined from a maximum of 150,000 mussels m<sup>-2</sup> in 2007 to near zero in 2011 suggesting that its warmer thermal environment accelerated mussel population collapse. While these studies demonstrated that mussel population collapses occur, they did not investigate their bases. Laboratory (Walz 1979) and field studies (Morse 2009) have indicated that adult zebra mussels starve during summer months at surface water temperatures above 25°C, loss of body tissue mass being particularly acute in southwestern water bodies with summer surface water temperatures approaching or exceeding 30°C. As mussel filter feeding reduces phytoplankton productivity over successive years, such starvation has been speculated to lead to massive adult population die-offs resulting in severe density reductions or complete population collapse (McMahon 2015). However, the relationship between the impacts of elevated summer surface water temperatures on zebra mussel nutritional condition and population collapse has not been elucidated and other environmental factors may also be involved.

Dr. McMahon's laboratory has been conducting a long-term study of zebra mussel population dynamics in Lakes Texoma, Ray Roberts and Belton since 2011, 2013 and 2014, respectively (Figure 3). This report describes an extension of these studies from 07/01/2016 to 08/31/2017 designed to further understand the unique biology/ecology of zebra mussels in warm Texas water bodies. The study adds to the temporal data already obtained on zebra mussel growth rates (Figures 4 and 5), reproductive periods, veliger size distributions (Figure 6), and seasonal juvenile settlement rates (Figures 7a-c) in addition to recording total phosphorous and chlorophyll *a* concentrations and mussel dry tissue weight variation. It was conducted at three long-term infested water bodies (i.e., Lakes Texoma (2009), Ray Roberts (2012) and Belton (2013) and two newly mussel infested water bodies, Lake Lewisville (2015) and Eagle Mountain Lake (2016) in order to compare differences in the dynamics of well-established and newly invaded populations and increase our understanding of the population dynamics and long-term sustainability of zebra mussels in warm Texas water bodies and the likely causes of their population collapses.

## OBJECTIVES

The main objectives of this research were to extend the P.I.'s ongoing study of the population dynamics of zebra mussels in five infested Texas water bodies including annual growth rates, reproductive periods, veliger size distributions, seasonal juvenile cohort settlement rates, total phosphorous and chlorophyll *a* concentrations and adult mussel dry tissue weight loss at elevated summer water temperatures in order to understand the long-term sustainability of Texas zebra mussel populations, elucidate the bases for observed zebra mussel population collapses and inform development of appropriate, economically feasible, mussel macrofouling mitigation and control measures.

## METHODS

**Sampling sites:** The study was conducted in five Texas water bodies known to be infested with zebra mussels, Lakes Texoma (Red River), Ray Roberts (Elm Fork, Trinity River), Belton (Leon River), Eagle Mountain (West Fork Trinity River) and Lewisville (Elm Fork, Trinity River) (Table 1, Figure 3). The Sampling site on each water body was a marina (Table 1) chosen to have an appropriate water depth (>3.7 m at conservation pool), position in the main body of the lake and ease of access. Information regarding each sample site can be found in Table 1. Sampling at each site took place approximately monthly from July 2016 through August 2017; samples previously taken in January 2016 at Lakes Texoma, Ray Roberts and Belton were also included in the data set (Table 2).

**Physical-chemical parameters:** At each sampling period, air and water temperature, dissolved oxygen, pH, and conductivity were recorded at 1.5-2.0 m depth and just above the substratum using electronic digital meters. Surface water calcium concentrations were measured from surface water samples returned to the laboratory with a Hach® Model ZHAC-DT Total and Calcium Hardness Test Kit using a digital titrator. Surface water temperatures at 1.5-2.0 m depth were continuously recorded at each site at hourly intervals with Onset Hobo® temperature recorders attached to brick-weighted lines over the course of the sampling period from July 2016 to August 2017. In the cases of Lake Texoma, Ray Roberts and Belton, surface water temperatures were monitored from January 2016 to August 2017. Temperature data were downloaded from the data logger at each sampling visit. Mean daily surface water temperatures and standard deviations were subsequently computed from hourly surface water temperature data.

**Population growth rates:** At each sampling site (Table 1, Figure 3), 4-7 artificial mussel settlement substrata (house bricks) were submerged using nylon ropes from the superstructure of floating marina docks (Table 1) at a depth of approximately 1.5-2.0 m. Bricks at Lakes Texoma, Ray Roberts and Belton had been suspended at least one year prior to monthly mussel samples being collected from them on January 2016 through August 2017 while those at Lakes Lewisville and Eagle Mountain were suspended from July 2016 to August 2017 and August 2016 to August 2017, respectively (Table 2). At each site visit, mussel samples ( $n > 100$  if available) were removed from a previously unsampled portion of a brick or bricks using a small, sharp-bladed knife to cut byssal attachments (see Table 2 for sampling dates). Sampled mussels were preserved immediately in the field with 95% ethanol and returned to the laboratory at The University of Texas at Arlington (UT Arlington) where their shell lengths (SL) were measured as the greatest linear distance to the nearest 0.1 mm from the anterior umbo to the posterior shell margin with electronic digital calipers. Size-frequency histograms of mussel SL were visually examined to determine different mussel cohorts in the sample (based on non-overlapping size distributions) resulting from spring or fall spawning events in each sample. Mean cohort shell lengths in each sample were then determined and used across monthly samples to determine cohort growth rates through time and cohort life span.

**Spawning periods and veliger size distributions:** Reproductive periods were determined at all five studied lakes by taking four vertical plankton tows ( $n = 4$ ) at each site visit starting approximately one meter above the substratum and combining them into a single sample. Plankton nets had a 60  $\mu\text{m}$  mesh, a

30.5 cm diameter opening and were 1 m in length. An individual plankton net was dedicated to each sampled water body and only used in that water body. After each use, all components of the plankton nets including tow ropes were thoroughly rinsed with a high pressure water spray and allowed to air dry assuring no survival of veligers before next use. Plankton samples were fixed immediately in approximately 70% ethanol in the field and returned to the laboratory at UT Arlington where they were examined by cross-polarized light microscopy for the presence of zebra mussel veligers using the method of Johnson (1995). If zebra mussel larvae were present, the SL of a random sample of  $\geq 100$  veligers or all available veligers (i.e., only living veligers with observable body tissues, empty shells were not measured) if less than 100 occurred in the sample were measured to the nearest 0.1  $\mu\text{m}$  at 45X under dissecting microscope using a digital scope mounted camera and size analysis computer software (Infinity 1 camera and software, Lumenera Corp.). The resulting veliger sample size distribution was utilized to determine if settlement competent pediveligers (i.e., shell length  $\geq 231 \mu\text{m}$ , Nichols and Black 1994) were present in the sample.

**Juvenile settlement:** Juvenile settlement monitors were constructed from 15.2 x 20.3 cm nylon scrub pads (Figure 8). Scrub pads were re-enforced by using hot glue to attach 1.9 cm wide by 0.64 cm thick Plexiglass bars to both sides of the 15.2 cm ends of the scrub pads (McMahon 2015). Settlement monitors were previously deployed at Lakes Texoma, Ray Roberts and Belton prior to January 2016 and were deployed at Lakes Lewisville and Eagle Mountain in July and August 2016, respectively. The monitors were attached to house brick weighted nylon ropes with plastic electrical ties fed through two holes in the monitor's Plexiglass reinforcement bars. The top of a monitor was attached to a loop tied in the rope and, at the bottom, the electric tie was tightened directly around the rope allowing the monitor to be pulled down the rope such that it was nearly vertical in the water column (Figure 8). Seven monitors were deployed at Lake Texoma, six at Lake Ray Roberts, four at Lake Belton, and four each at Lakes Eagle Mountain and Lewisville. At each sampling visit, monitors are removed and the number of settled mussels counted under a dissecting microscope at 10X power or with 2X power jeweler's glasses depending on mussel size. Monitors were then reattached to the rope and re-submerged. Monitors were out of the water for no more than 30 min during attached mussel counting and were kept in the shade to prevent overheating while not being counted. Counting of mussels on both sides of any one monitor took less than 10 minutes. During counting, mussels were assigned to specific spring or fall cohorts based on shell size ranges which allowed them to be followed through time. These monitors have previously proven successful in monitoring juvenile mussel settlement in Texas water bodies (McMahon 2015).

**Total phosphorous and chlorophyll *a* determinations:** Standard methodologies (Rice et al. 2012) were used to determine total phosphorous and chlorophyll *a* concentrations from water samples taken at each site visit from near the water's surface (1 m depth) and just above the bottom substratum. Triplicate surface and benthic water samples were taken and returned to the laboratory at UT Arlington on the day of collection where they were split into those for chlorophyll *a* and total phosphorous concentration determinations and properly treated, preserved and frozen for later analysis.

**Mussel dry tissue weight determinations:** The SL of  $>50$  mussels with an SL  $> 8$  mm were chosen from each sample (or all sampled individuals if  $<50$  individuals were available in the sample) with a size range similar to that of the entire mussel sample. The shell lengths of selected mussels were then measured to the nearest 0.1 mm using electronic digital calipers. Thereafter, each specimen's dry tissue weight (DTW) was determined by shell dissolution in 15% nitric acid by volume, followed by three rinses in deionized water and removal of the shell periostracum and byssus from the tissues. Tissues were then blotted free of excess water on filter paper. Blotted tissues were then placed in pre-weighed aluminum weighing boats, and dried to a constant weight in a 65°C oven for  $>48$  h (48 h was determined by prior repeated weighings though time of test specimens to be sufficient to attain a constant dry tissue weight). Thereafter, their DTW were determined to the nearest 0.01 mg on an electronic balance. The resulting DTW data were then fitted to a linear regression of individual SL versus the  $\log_{10}$  of DTW as the dependent variable allowing data linearization. The SL vs. DTW regressions were then utilized to

estimate the mean DTW of individuals with standard shell lengths of 10, 15, 20, and 25 mm for each sample. Dry tissue weights were only estimated for standard SLs which fell within the SL size range of the examined mussel sample (example: SL range of all individuals in a DTW sample ranged between 8 and 21 mm, then a standard DTW was computed only for individuals with standard SLs of 10, 15 and 20 mm). Dry tissue weights of standard sized mussels were then compared across monthly samples to determine mussel DTW variation over the course of the sampling period and between sampled water bodies to examine the degree of starvation (i.e., loss of DTW) occurring during summer months when surface water temperatures rose above the critical temperature 25°C where mussels cannot maintain a positive energy balance (Walz 1978) as reported by Morse (2009). The DTW data for standard sized individuals was also used to compare the mean dry tissue weights among established zebra mussel populations in Lakes Texoma, Ray Roberts and Belton and to those previously determined for a zebra mussel population in Winfield City Lake, Kansas, in 2008. Dry tissue weights were not determined for mussels from Lake Eagle Mountain or Lewisville because, at both sites, because very few mussels settled on the submerged house bricks and, those that did, did not attain sizes suitable for DTW analysis. We were able to obtain dry tissue weights for zebra mussels only on our last sample from eagle Mountain Lake on 08/17/2017.

## RESULTS and DISCUSSION

**Physical-chemical parameters:** Surface water (1.5-2.0 m depth) physical parameters of air and water temperature, pH, O<sub>2</sub> concentration as percent of full air O<sub>2</sub> saturation and conductivity (μS) recorded over the course of sampling period at all five water bodies are listed in Table 3. Both pH and % of full air O<sub>2</sub> saturation typically fell above the published lower limits required to sustain high density zebra mussel populations (pH ≥7.4, dissolved O<sub>2</sub> >50% of full air O<sub>2</sub> saturation, McMahon 2015), however, there were some notable exceptions. Surface water pH remained above the 7.4 lower limit for a sustainable reproducing zebra mussel population on all sampling dates in Lake Texoma (Table 3, Figure 9a). While the occasional pH values <7.4 were recorded in Lakes Belton, Eagle Mountain and Lewisville they did not appear to occur long enough to have immediate negative impacts on adult zebra mussel density, however it could have impacted juvenile settlement in these populations because zebra mussel veliger larvae require a pH between 7.4 and 9.4 to fully develop into settlement competent pediveligers (Sprung 1987). In contrast, surface water pH in Lake Ray Roberts was consistently below the 7.4 value required for veliger development to settled juveniles from 10/21/2016 to our last sapling date of 08/17/2017, a period of 301 days (Table 3, Figure 9a). This long period of low pH appeared to have resulted in fall 2016 and spring 2017 mussel spawning and juvenile settlement being suppressed in Lake Ray Roberts as discussed below.

A hypoxic event with surface water oxygen concentration falling to of 15.1% of full air O<sub>2</sub> saturation (1.17 mg O<sub>2</sub>/l) was recorded at Lake Belton on 09/25/2016 (Table 3, Figure 9b). This hypoxic O<sub>2</sub> concentration was well below the lower O<sub>2</sub> concentration limit for zebra mussels of 30% of full air O<sub>2</sub> saturation (Johnson and McMahon 1998). At the subsequent sampling period on 11/01/2016, surface water oxygen concentrations were still reduced at 58.7% of full air O<sub>2</sub> saturation with more normal levels of 85.2% not being attained until 12/12/2016 (Table 3, Figure 9b) indicating a total period of hypoxia of 79 days. Concurrent with the 09/25/2016 Lake Belton hypoxia event, a severe mussel density reduction was noted on the settlement bricks and a near complete loss of mussels on the settlement monitors (Figure 10, panel 3). Members of the spring and fall 2015 cohorts present on the bricks on 08/03/2016 were no longer present on the bricks when subsequently sampled on 09/25/2016. In addition, members of the spring 2016 cohort which were numerous on the bricks and settlement monitors when examined on 08/03/2016, were greatly reduced in density on 09/25/2016 and completely extirpated from the bricks and settlement monitors by the following 11/05/2016 sampling date Figure 10, panel 3). This rapid loss of the spring 2015, fall 2015 and spring 2016 cohorts from the settlement bricks was almost certainly a result of mussels experiencing massive mortality due to exposure to lethal low oxygen concentrations during

September and October of 2016. In contrast, members of spring 2016 cohort were not lost from monitors at Lakes Texoma and Ray Roberts until July and August, 2017, respectively (Figure 10, panels 1 and 2). In addition, settlement by the fall 2016 cohort in Lake Belton appeared to be delayed by the hypoxic event as settlement was first observed on 11/01/2016 whereas it occurred earlier on 09/18/2016 and 09/16/2016 in Lakes Texoma and Ray Roberts, respectively (Figure 10 panels 1, 2, and 3).

Mean surface water calcium concentrations (mg Ca/l) were determined at each lake sampling visit. All five lakes had mean calcium concentrations well above the 24 mg Ca/l lower limit required for zebra mussels to develop dense, sustainable reproducing populations (McMahon 2015) (Table 3, Figure 11). One-way Analysis of Variance followed by a Fishers Least Squares Significant Difference Test for differences among means indicated that calcium concentrations differed significantly among lakes (df =55, F-ratio = 72.92,  $p < 0.00001$ ) with mean calcium concentrations in Lakes Ray Roberts, Lewisville and Eagle Mountain being insignificantly ( $p > 0.05$ ) different from each other, Lake Belton calcium concentration being significantly ( $p < 0.05$ ) higher than that of Ray Roberts and Lewisville, but not different ( $p > 0.05$ ) from that of Eagle Mountain Lake. Lake Texoma had a significantly ( $p < 0.05$ ) higher mean calcium concentration than the other four sampled lakes (Figure 11).

Mean daily surface water temperatures were computed from hourly temperature data recorded at a depth of 1.5-2.0 m over the course of the study period at each lake sampling site (Figure 11). The data indicated that, during the summer of 2016, mean daily surface water temperature exceeded the zebra mussels' 30°C upper limit for normal physiological function for only short periods and did not exceed its incipient upper lethal limit of 32°C (Morse 2009, McMahon 2015) in lakes Texoma, Ray Roberts, Belton, or Eagle Mountain (Figure 12 panels 1, 2, 3 and 5). In contrast, daily mean surface water temperatures were generally equal to or greater than the mussels upper lethal limit of 32°C from 07/22/2016 to 08/17/2016 in Lake Lewisville which was likely to have resulted in a massive mortality of adult mussels. One Way Analysis of Variance (ANOVA) with mean daily surface water temperature during the month of August (the month of highest surface water temperatures) as the dependent variable and lake/year (2016 or 2017) as a factor indicated a significant ( $p < 0.000$ ) difference between lakes and years (Figure 13). While significant ( $p < 0.05$ ) differences in daily mean temperatures during August occurred between lakes, Eagle Mountain (28.68°C sd =  $\pm 0.346$  in 2016) Texoma (29.65°C  $\pm 0.68$  in 2016 and 29.11°C  $\pm 0.576$  in 2017), Belton (29.41°C  $\pm 0.685$  in 2016 and 29.91°C  $\pm 0.337$  in 2017), Ray Roberts (29.96°C  $\pm 1.121$  in 2016 and 30.10°C  $\pm 0.593$  in 2017) and Lewisville (29.65°C  $\pm 0.68$  in 2017) did not have mean daily surface water temperatures during the month of August that rose above the 30°C upper limit for normal physiological function. In contrast, daily surface water temperatures during the month of August in Lake Lewisville at a mean of 31.02°C  $\pm 1.457$  were significantly ( $p < 0.05$ ) greater than that recorded in any of the other lakes in 2016 and 2017 including Lewisville in 2017 (Figure 13).

During August 2016, mean daily surface water temperatures in Lake Lewisville ranged as high as 33.18°C (Figures 12, panel 4 and 13) almost continually exceeding the 30°C upper limit for normal zebra mussel physiological function and periodically exceeding the mussel's upper thermal limit (Figure 12 panel 4). The extremely high surface water temperatures in Lake Lewisville may also have accounted for the fact that only a few veligers occurred in our plankton samples during the fall of 2016 along with very limited juvenile settlement on our monitors (Figure 10 panel 4). Interestingly, zebra mussels settled extensively in some parts of Lake Lewisville during a massive downstream release of veligers into it from upstream mussel-infested Lake Ray Roberts during the spring/summer flooding of 2015 (Texas Parks and Wildlife Department 2015). However, the lake does not appear to have subsequently developed an extensive mussel population, perhaps in part due to conditions that cause it to have elevated summer surface water temperatures to be further discussed below.

**Population shell growth rates:** Non-overlapping shell length (SL) size distributions of mussels sampled monthly from submerged bricks in Lakes Texoma, Ray Roberts and Belton revealed the presence of distinct spring and fall cohorts developed as a result of mid-summer and winter cessations in spawning and juvenile settlement. Mussel sampling in Lake Texoma revealed the presence of spring 2015 and fall



2015 annual cohorts. In Lake Texoma the spring and fall 2015 cohorts had mean SLs of 17.1 mm  $\pm$  2.651 and 5.6 mm  $\pm$  2.47, respectively, on 01/22/2016 (Figure 14). By the next sampling date of 07/10/2016, the spring 2015 cohort had disappeared from the sample with the fall 2015 cohort attaining a mean SL of 19.075 mm  $\pm$  2.03 and the appearance of a newly settled spring 2016 cohort having a mean SL of 5.8 mm  $\pm$  2.08. The Texoma fall 2015 cohort disappeared from the bricks by 09/18/2016 leaving only the spring 2016 cohort. By 01/11/2017, the spring 2016 cohort had attained a mean SL of 10.7 mm  $\pm$  3.12 and a newly settled fall 2016 cohort appeared with a mean SL of 2.6 mm  $\pm$  1.25. By 02/23/2017, the spring 2016 cohort had disappeared from the settlement bricks indicative of mass mortality leaving only members of the fall 2016 cohort at a mean SL of 5.10 mm  $\pm$  1.645. This fall 2016 cohort grew to a mean SL of 19.17 mm  $\pm$  1.781 by the final sampling period of 08/20/2017, similar to that of the fall 2015 cohort on 07/10/2016 at 19.08 mm  $\pm$  2.032 (Figure 14). The spring 2017 cohort first appeared in the 06/06/2017 sample at a mean SL of 1.66 mm  $\pm$  0.996 and grew to a mean SL of 9.15 mm  $\pm$  2.69 by 08/20/2017 (Figure 14). This cohort reached a peak density of 5,136.3 mussels/m<sup>2</sup> on settlement monitors on 07/01/2017 marking a recovery of mussel density relative to that recorded for earlier cohorts for which combined mussel cohort densities did not exceed 388.3 mussels/m<sup>2</sup> on settlement monitors in any one sampling period (Figure 10 panel 1).

The growth rates of the Texoma spring and fall 2015 and spring and fall 2016 cohorts were all somewhat slower than those previously recorded in 2011, 2012, 2013 and 2014 (Figures 4, 5, 14 and 17). The life spans of the 2015 spring and fall cohorts were similar to that previously recorded in Lake Texoma with both cohorts disappearing from samples in the summer of 2016. The spring 2016 cohort in Lake Texoma grew much more slowly than previous spring cohorts (Figures 4, 5, 14 and 17) and disappeared from samples after 01/01/2017 (Figure 14) indicative of an attenuated life span of 7-8 months compared to the 14-15 month life spans previously recorded for fall cohorts (Figures 4, 5, 14 and 17). Also unusual was the apparent suppression of shell growth in this cohort through the late fall and winter of 2016 in which mean cohort SL declined from 11.75 mm  $\pm$  3.18 on 09/18/2016 to 10.69 mm  $\pm$  3.122 on 01/11/2017 after which the cohort disappeared from the samples. The shortened life span and suppressed growth rate of the Texoma spring 2016 cohort suggested that conditions were not favorable for zebra mussel growth and survival in the lake during the fall and winter of 2016, but the specific environmental factors inducing its slowed shell growth and shortened life span were not revealed by this study.

The apparent reduction in the shell growth rates and maximum SL of Texoma spring cohorts across years (Figures 5 and 17) suggests that the food resources (i.e., bacterioplankton and phytoplankton) which support mussel growth and population density may have been reduced through time, however, chlorophyll *a* concentrations did not significantly ( $p > 0.05$ ) differ between Lakes Texoma, Ray Roberts and Belton over the course of this study (see below). That the Ray Roberts and Belton spring 2016 cohorts had more typical shell growth rates and life spans (Figures 15, 16, 17) suggests that food limitation may not have been associated with the suppressed shell growth rate of the Texoma spring 2016 cohort. Interestingly, after the apparent suppression of growth rate and life span in the Texoma spring 2016 cohort, the spring 2017 cohort settled at a relatively high density of 5124.8 mussels/m<sup>2</sup> on 06/29/2017 (Figures 7a and 10 panel 1). The bases for the slow shell growth rates and attenuated life cycle of the Texoma spring 2016 cohort are unknown as water quality parameters remained relatively stable at the sampling site throughout the study period and fell within the limits for a sustainable reproducing population (see Table 3 and Figures 8ab). However, mean surface water chlorophyll *a* concentrations reached minimal levels of 2.17  $\mu$ g/l and 2.87  $\mu$ g/l on 12/04/2016 and 01/11/2017, respectively, just prior to the disappearance of the spring 2016 cohort from the collections on 02/23/2017, but, did not appear to be associated with an extensive loss of dry tissue weight indicative of starvation as discussed below.

Shell length distributions of zebra mussels sampled from submerged bricks in Lake Ray Roberts revealed only the presence of a fall 2015 cohort at low density with a mean SL of 6.43 mm  $\pm$  2.47 on 01/22/2016 (Figure 15). By the next sampling date of 07/10/2016, the fall 2015 cohort had grown to a mean SL of

20.9 mm  $\pm$ 1.46 and a spring 2016 cohort appeared in the sample with a mean SL of 5.8 mm  $\pm$ 2.75. The fall 2015 cohort last appeared on the bricks on 01/09/2017 at a mean SL of 26.1 mm  $\pm$ 0.42. Three individuals of a fall 2016 cohort appeared in the 2/10/2017 sample with a mean SL of 4.1 mm  $\pm$ 1.32 with the much more prevalent spring 2016 cohort having a mean SL of 21.3 mm  $\pm$ 2.93 (Figure 15). The spring 2016 cohort disappeared from the samples after 04/11/2017 when only one individual was found. This cohort attained a maximum mean SL of 21.00 mm  $\pm$ 3.00 on the previous 03/17/2017 collection. The fall 2016 cohort reached a maximum mean SL of 17.7 mm  $\pm$ 1.843 on 05/19/2017, and, thereafter, occurred at very low numbers through the final sample on 08/17/2017 where two individuals had a mean SL of 20.75 mm  $\pm$ 0.21 (Figure 15). The spring 2017 cohort appeared in the samples at low density on 05/19/2017 with a mean SL of 1.3 mm ( $\pm$ 0.141), and reached a mean SL of 6.61 mm  $\pm$ 3.31 by the final sample taken on 08/17/2017 (Figure 15).

Unlike the mussel population in Lake Texoma, the growth rates of the Lake Ray Roberts fall 2015 and spring 2016 cohorts were roughly similar to those recorded for the 2013 and 2014 cohorts as were those of the fall 2016 cohort (Figures 4, 5 and 17). However, the life span of the spring 2016 cohort was reduced compared to those previously recorded in Lake Ray Roberts (Figures 4, 5 and 15). The life span of the fall 2015 cohort was fairly long for zebra mussel populations in Texas being about 18 months on the assumption that it first settled in October 2015 and disappeared from our samples in April 2017. Past research in my laboratory indicated that, typically, the life span of fall cohorts in Lake Texoma, Ray Roberts and Belton was 10-12 months (McMahon unpublished) suggesting that the life span of the Lake Ray Roberts fall 2015 cohort was exceptionally long at 18 months. In contrast, the life span of the Ray Roberts spring 2016 cohort was 12 months (May 2016-April 2017) whereas it was usually 15-16 Months in previous years (Figures 4, 5 and 14). The life span of the fall 2016 cohort was more typical of previous years. Settlement of this cohort was initiated in October 2016 (Figure 10 panel 2) and the last individuals of the cohort were collected from bricks during August 2017 (Figure 15) indicative of a 10-month life span similar to that of 10-12 months recorded for this cohort during previous years. However, the density of the fall 2016 cohort was greatly reduced relative to that recorded for fall cohorts in previous years attaining a maximum of 53.8 mussels/m<sup>2</sup> on 07/03/2017 (Figures 7b and 10 panel 2) compared to densities of 20,116.2/m<sup>2</sup> and 25,576.0/m<sup>2</sup> recorded in 2013 and 2014, respectively (Figure 7b). This reduction in the settlement density of the Ray Roberts fall 2016 cohort may have been associated with surface water pH being consistently below the 7.4 minimum required to support veliger development through juvenile settlement (Sprung 1987) for 301 days from 10/21/2016 to the last collection on 08/17/2017 (Table 3, Figure 9a).

Shell length size distributions of mussels sampled from submerged bricks in Lake Belton on 01/30/2016 revealed the presence of relatively dense spring and fall 2015 cohorts (56.5 and 5,064.6 mussels/m<sup>2</sup> on settlement monitors, respectively) with mean SLs of 15.2 mm  $\pm$ 3.23 and 2.1 mm  $\pm$ 3.23, respectively (Figure 16). By the next sampling date of 08/03/2016 (note that zebra mussels could not be sampled on the previous sampling visit of 07/13/2016 because high lake levels prevented access to the sampling site, Table 2), the spring and fall 2015 cohorts had grown to mean SLs of 27.2 mm  $\pm$ 12.69 and 17.8 mm  $\pm$ 3.11 with a spring 2016 cohort appearing at a mean SL of 7.9 mm  $\pm$ 2.06. By the next sample on 09/25/2016, both the spring and fall 2015 cohorts had disappeared from the sample leaving only individuals of the spring 2016 cohort on the bricks in greatly reduced numbers (4 mussels/m<sup>2</sup> on settlement monitors) with a mean SL of 15.7 mm  $\pm$ 3.51 (Figure 16). This spring 2016 cohort was very short-lived and disappeared by the next sample on 12/12/2016. The sudden disappearance of the spring and fall 2015 and spring 2016 samples from the bricks corresponded with a hypoxia event recorded at the sampling site on 09/25/2016 (See section on Physical-chemical parameters and Table 3 for details). When surface oxygen concentrations returned to more normal levels of 85.2% of full air O<sub>2</sub> saturation on 12/12/2016 (Table 3, Figure 9b) a newly settled fall 2016 cohort appeared on the bricks at a moderate density (1,711.3 mussels/m<sup>2</sup> on settlement monitors) with a mean SL of 1.6 mm  $\pm$ 0.42. Mussels in this fall 2016 cohort continued to grow reaching a maximum mean SL of 20.43 mm  $\pm$ 2.528 on 06/29/2017 after which their mean SL declined to 19.61 mm  $\pm$ 2.06 on the last sample taken on 08/13/2017. A spring 2017 cohort first

appeared in mussel samples on 06/29/2017 at a mean SL of 0.46 mm  $\pm$ 0.273 and grew to a mean SL of 9.30 mm  $\pm$ 2.27 by final sample taken on 08/13/2017 (Figure 16). As also occurred in Lake Texoma, the settlement density of the spring 2017 cohort was extremely high at a peak of 46,349.3 mussels/m<sup>2</sup> on settlement monitors on 06/29/2017 (Figures 7c and 10 panel 3) indicative of a major population recovery after the 09/25/2016 hypoxia induced mussel die-off.

There were not enough mussels settled over a long enough period on submerged bricks at Lakes Eagle Mountain and Lewisville to allow accurate assessment of mussel growth patterns. At Eagle Mountain Lake on 07/03/2017 the sample consisted of a fall 2016 cohort of two mussels, each with an SL of 21.4 mm and a spring 2017 cohort with a mean shell length of 8.4 mm (sd =  $\pm$ 2.55, range = 3.9-15.6 mm, n = 51). In the final Eagle Mountain Lake collection on 08/17/2017 there was a single individual of the fall 2016 cohort with an SL of 18.6 mm and 35 individuals of the spring 2017 cohort with a mean SL of 10.93 mm  $\pm$ 2.11, range = 6.6-14.1 mm, n = 35). At Lake Lewisville a total of seven mussels from the spring 2017 cohort were sampled from the bricks and monitors at the final 08/20/2017 collection. All were members of the spring 2017 cohort and had a mean SL of 9.80 mm  $\pm$ 2.45, range = 5.0-12.3 mm). Thus, mussel cohort grow rates in July and August of 2017 appeared roughly equivalent among all five sampled water bodies.

Zebra mussel cohort settlement patterns in Lakes Texoma, Ray Roberts and Belton over the duration of the sampling period generally followed those recorded in previous years with spring and fall spawning periods leading to settlement of spring 2016, fall 2016 and spring 2017 cohorts. However there were some notable differences in the patterns of settlement and growth in the lakes compared to those observed prior to this study (Figures 4 and 5). In Lake Texoma, the typical pattern of spring and fall mussel cohort settlement occurred in 2015 and 2016, but the growth rate of the spring 2016 cohort was greatly reduced and its life span shortened compared to that for spring cohorts in 2011 through 2014 (Figures 5 and 14). The reasons for this reduction in the shell growth rate of the Texoma spring 2016 cohort were not elucidated in this study but suggested a potential decline in available food resources. However, the Texoma spring 2017 cohort settled in much higher densities suggesting that the Texoma population was potentially recovering from an extended period of decline. In Lake Ray Roberts, no individuals of the spring 2015 cohort were present in the 2016 samples (Figure 15) and the density of the fall 2015 cohort was greatly reduced compared to previous years (Figures 7a and 10 panel 1). In addition, the settlement of a fall 2016 cohort was delayed until February 2017 and was diminished in density compared to previous years, most likely due to an extended period of surface water pH being below the lower 7.4 limit for veliger development to a settled juvenile (Sprung 1987) starting in October 2016 and extending through the end of the sampling period into August 2017, thus encompassing the entire fall 2016 and spring 2017 settlement periods during which juvenile settlement densities remained very low (Figures 7b, 10 panel 2). In Lake Belton, the spring and fall 2015 cohorts and spring 2016 cohort were apparently extirpated from the settlement bricks in September 2016 by exposure to severe hypoxia (15.1% of full air O<sub>2</sub> saturation on 09/25/2016), leaving only the fall 2016 cohort to recolonize the bricks on 12/12/2016 at relatively low settlement densities (Figures 7c and 10 panel 3) after surface water O<sub>2</sub> concentrations returned to more normal levels (Figure 9b). It is highly likely that this hypoxic event resulted in extensive adult mussel mortality accounting for the greatly reduced settlement of the fall 2016 juvenile cohort. After recovery to more normal surface water oxygen concentrations there was a massive settlement of the spring 2017 cohort (Figure 10 panel 3) suggesting that the Lake Belton population was undergoing a major recovery after two years of population decline.

The above results suggest that Texas water bodies may not be as hospitable to zebra mussels as those in the Northeastern United States. It appears that, in the three studied Texas water bodies with extensive mussel populations (i.e., Lakes Texoma, Ray Roberts and Belton), environmental changes such as reduction in bacterio-phytoplankton availability, pH and oxygen concentrations may have been associated with reductions in mussel growth rates and/or densities. However, the apparent rebound of zebra mussel populations in Lakes Texoma and Belton during spring and summer 2017 suggests that zebra mussels in

infested Texas Lakes may be undergoing boom-bust population cycles characteristic of some North American (Strayer and Malcom 2006, Strayer et al. 2011) and European populations (Stańczykowska and Lewandowski 1993). In contrast, the continued 2016 collapse of the Lake Ray Roberts zebra mussel population appears to be closely associated with surface water remaining below the lower pH limit of 7.4 for veliger development to settled juveniles throughout most of the period extending from October 2016 to the end of the study in August 2017. It might be expected that if Lake Ray Roberts surface water pH again rises above this pH 7.4 lower limit for successful juvenile settlement that its zebra mussel population could recover to the relatively high densities that were recorded in 2013-2015 (Figure 7b). Thus, our results suggest that zebra mussel populations in Texas water bodies could vary greatly in density through time such that the recently observed post-invasion collapses of mussel may not be permanent. Instead, these populations may cycle through periods of decline and expansion as a result of changes in environmental conditions including surface water oxygen concentrations and pH identified in this study and, potentially, annual water level variability to be discussed below. The potential revealed in this study for boom/bust zebra mussel population cycles in mussel-infested Texas water bodies may impact mussel management decisions for both water body managers and raw-water using facilities because declines in mussel populations may not be permanent. Certainly, the population densities of zebra mussels in infested Texas reservoirs should continue to be monitored along with environmental conditions to determine if boom/bust cycles are going to be a permanent feature of these populations and to elucidate the environmental conditions that cause them.

**Spawning periods and Veliger Size Distributions:** Presence of veliger larvae in plankton samples at Lakes Texoma, Ray Roberts, Belton, Eagle Mountain and Lewisville revealed the presence of two distinct mussel spawning periods one in spring-mid-summer and a second in fall-early winter. Zebra mussel veligers from a fall 2016 spawning event were present in plankton samples at Lake Texoma from 09/18/2016 through 1/11/2017 (mean daily surface water temperature range recorded from a data logger = 28.6°-8.8°C) and at Ray Roberts from 09/28/2016 through 12/07/2016 (temperature range = 26.7°-14.1°C). At Lake Belton, veligers from the fall 2016 spawning event occurred in the plankton from 09/25/2016 through 12/12/2016 (temperature range = 28.6°-16.5°C). At Eagle Mountain Lake veligers from the fall 2016 spawn were found from 10/03/2016 through 01/16/2017 (temperature range = 26.0°-9.2°C) and at Lake Lewisville they were found in very low numbers only on 10/21/2016 (23.9°C) (Figure 18, panels 1-5). Veligers from a spring 2017 spawning event occurred in plankton samples at Lake Texoma from 04/15/2017 to 08/20/2017 (temperature range = 18.0°-29.1°C), at Lake Ray Roberts from 04/11/2017 to 08/17/2017 (temperature range = 18.8°C-29.1°C), at Lake Belton from 04/13/2017 to 06/29/2017 (temperature range = 20.3°-27.8), at Eagle Mountain Lake from 03/17/2017 to 08/17/2017 (temperature range = 15.8°-29.8°C) and at Lake Lewisville in very low densities from 04/15/2017 to 07/01/2017 (temperature range = 21.1°-28.9°C) (Figure 17 panels 1-5). Note that the spring 2017 spawning period was ongoing in four of the five studied lakes (i.e., Texoma, Ray Roberts, Belton and Eagle Mountain) during our final August 2017 samples (Figure 18).

The mean daily average surface water temperature for initiation and cessation of fall 2016 spawning across the studied lakes was estimated as the mean daily surface water temperature recorded on data loggers on the first and last day of veliger presence in plankton samples in Lakes Texoma, Ray Roberts, Belton and Eagle Mountain (Lake Lewisville was excluded because veligers appeared in only one sample). Thus, veligers from the fall 2016 spawning were first encountered in plankton samples at an average surface water temperature of 27.5°C (n=4, sd ±1.33) and last found in plankton samples at an average temperature of 12.15°C (n = 4, sd ±3.77). Mean daily surface water temperatures similarly computed for first and last encounters of veligers in plankton samples during spring 2017 spawning across all five lakes were 18.8°C (n=5, sd ±2.07) and 28.9°C (n=5, sd ±0.72), respectively. Although a great deal of variation has been reported for the temperature range in which zebra mussels initiate spawning in Europe and North America, general consensus is that spawning occurs above 16-19°C (Nichols 1996) which corresponds to the overall mean of 18.8°C estimated across all studied lakes for the first presence of veligers in plankton samples during the spring 2017 spawning period. This estimate of

the lower ambient temperature for zebra mussel spawning in Texas water bodies also concurs with the 16-18°C lower limit estimated by Churchill (2013) for the initiation of zebra mussel spawning in spring 2010 in Lake Texoma. Sprung (1987 1993) cites 24°C as the upper thermal limit for European zebra mussel veligers to develop to settled juveniles. However, we recorded continued spring 2017 cohort juvenile settlement in all five reservoirs in August 2017 (Figure 10) at an overall mean daily temperature of 28.9°C (range = 27.8°-29.8°C) which exceeded the maximum of 24°C (Walz 1987, 1993) for zebra mussel larval settlement in Europe. Similarly, Garton and Haag (1993) reported continued settlement of zebra mussel juveniles in western Lake Erie when surface water temperatures approached 29°C. These results suggest that zebra mussels in some North American water bodies, including those described herein, may have evolved higher upper temperature limits in the range of 28-30°C for both spawning and veliger development to settled juveniles than have been previously reported for European populations allowing them to invade and thrive in warm Texas and other southwestern water bodies.

In lakes Texoma, Ray Roberts, Belton and Eagle Mountain, where mussel veligers were numerous enough in plankton samples to allow assessment of veliger SL, settlement-competent pediveligers with a  $SL \geq 231 \mu\text{m}$  made up only relatively small proportions of sampled veligers (Figure 18 panels 1-4) suggesting that veliger survival to this stage is very low. In addition, settlement-competent pediveligers during the fall 2016 spawning period tended to be present only in the latter portion of the times that veligers were present in the water column. In contrast, during the spring 2017 spawning period, settlement competent veligers tended to present only during the middle portion of the spawning period suggesting that water temperatures in July and August were too high to allow development to the pediveliger stage (Figure 18 panels 1-5). Thus, periods of veliger development to settlement-competent pediveligers appeared to roughly encompass 30-60 days throughout the much longer periods of veliger presence in the plankton.

Initiation of juvenile settlement was also correlated with the appearance of settlement-competent pediveligers in the water column. In Lake Texoma, major settlement of the fall 2016 cohort was initiated on 12/04/2016 after the first appearance of settlement-competent pediveligers in plankton samples in the preceding 11/05/2016 sample. Similarly, initiation of spring 2017 Texoma juvenile settlement occurred on 5/27/2017 (Figure 10 panel 1) when settlement-competent pediveligers first appeared in plankton samples (Figure 18 panel 1). Initial juvenile settlement of the fall 2016 cohort in Lake Ray Roberts co-occurred with appearance of settlement-competent pediveligers in plankton samples on 10/21/2016 and the spring 2017 cohort settlement was similarly co-incident with appearance of settlement-competent pediveligers in the concurrently taken plankton sample (Figures 10 panel 2 and 18 panel 2). In Lake Belton, the appearance of settlement-competent pediveligers in the plankton on 11/01/2016 was followed by the first settlement of the fall 2016 mussel cohort on 12/12/2016. Similarly, the first appearance of settlement-competent pediveligers in the plankton sample taken on 05/25/2017 occurred concurrently with the initial settlement of juveniles of the spring 2017 cohort (Figures 10 panel 3 and 18 panel 3). In Eagle Mountain Lake, no settlement-competent pediveligers appeared in fall 2016 plankton samples which was correlated with a very limited settlement of the fall 2016 mussel cohort with a maximum density on settlement monitors of 32.3 juveniles/m<sup>2</sup> on 3/17/2017. Subsequently, all members of this cohort were lost from the monitors on 04/11/2017. In contrast, settlement-competent pediveligers appeared in the 05/19/2017 Eagle Mountain plankton sample concurrently with the initial settlement of juvenile mussels of the spring 2017 cohort on settlement monitors (Figures 10 panel 5 and 18 panel 4). There were not enough veligers taken in plankton samples and/or juvenile settlement in Lake Lewisville to draw similar correlations between the presence of settlement-competent pediveligers and juvenile mussel settlement (Figures 10 panel 4 and 18 panel 5).

The extremely low densities of veligers and juvenile settlement rates (Figures 10 panel 4 and 18 panel 5) that occurred in Lake Lewisville throughout this study suggest that its zebra mussel population established by major downstream transport of zebra mussel veligers with high water discharge from the then heavily mussel-infested Lake Ray Roberts during the floods of 2015 may have been extirpated in

2016 perhaps by the 27-day period from 07/22/2016 to 08/17/2016 when mean daily surface water temperatures approached or exceeded the 32°C incipient upper lethal limit for zebra mussels (Figures 12 panel 4 and 13). In addition, recession of high water levels in Lake Lewisville in the fall of 2015 emersed many mussels settled high on the shore during spring and summer high water levels exposing them to lethal desiccation. Therefore, further monitoring of the Lake Lewisville mussel population probably should be undertaken to determine if it will remain thermally resistant to the development of a dense zebra mussel population as it appears to have been in 2016 and 2017.

Our study indicated that periods of juvenile mussel settlement in the studied lakes were strongly correlated with the presence of settlement-competent pediveligers in the water column. In Lakes Texoma, Ray Roberts, Belton and Eagle Mountain, there was a delay of 30-90 days between the appearance of veligers indicative of spawning and the presence of settlement-competent pediveligers in the water column (Figure 18 panels 1-4). Thus, zebra mussel settlement and macrofouling of Texas raw-water using facilities is unlikely to occur throughout any one mussel spawning period. Rather, dense mussel settlement and potential macrofouling will occur only after settlement-competent pediveligers with a SL  $\geq 231 \mu\text{m}$  appear in plankton samples. As such, Texas raw-water using facilities could utilize routine examination of veliger SL ranges in weekly plankton samples to determine when settlement-competent veligers are present in their intake waters leading to major episodes of juvenile mussel settlement. Chemical control measures (molluscicides) would then only need to be applied to prevent mussel macrofouling when settlement-competent pediveligers were present in intake waters as an indicator of juvenile mussel settlement. Applying molluscicides only when settlement competent pediveligers occur in plankton samples could greatly limit both the expense of molluscicide application and the amount of molluscicidal chemicals released by once-through raw-water systems into source waters.

**Juvenile settlement rates:** Zebra mussel settlement densities on the nylon scrub pad settlement monitors deployed at Lakes Texoma, Ray Roberts, Belton, Lewisville and Eagle Mountain over the course of the study are depicted in Figure 10. Settlement of the spring 2016 cohort in Lake Texoma was first detected on 07/10/2016 at a maximum mean density of 2,167.0 mussels/m<sup>2</sup> declining to 2.7 mussels/m<sup>2</sup> by 05/27/2017 with mussels of this cohort disappearing from the monitors by 07/01/2017 (Figure 10 panel 1). The Texoma fall 2016 mussel cohort was first detected on settlement monitors on 11/05/2016 at a mean density of 13.4 mussels/m<sup>2</sup>, reaching a peak settlement of 382.9 mussels/m<sup>2</sup> on 01/01/2017 and declining to 4.6 mussels/m<sup>2</sup> on the final collection of 08/20/2017 (Figure 10, panel 1). In contrast, the spring 2017 cohort displayed a much more extensive settlement, first appearing on the monitors on 05/27/2017 at a mean density of 249.1 mussels/m<sup>2</sup>, reaching a peak density of 5,136.3 mussels/m<sup>2</sup> on 07/01/2017 then declining to a mean density of 5,136.3 mussels/m<sup>2</sup> on the final collection of 08/20/2017 (Figure 10 panel 1). The relatively high settlement density of the spring 2017 cohort suggested that the zebra mussel population in Lake Texoma was recovering after several years of diminished densities extending from mid-2011 to the end of 2016 (Figure 7) (Churchill 2013, McMahon 2015).

The spring 2016 cohort settlement was first detected on monitors in Lake Ray Roberts at a maximum mean of 702.3 mussels/m<sup>2</sup> on 07/10/2016 which declined rapidly to 8.1 mussels/m<sup>2</sup> by 10/21/2016 with a final mean density further declining to 2.7 mussels/m<sup>2</sup> on 07/03/2017, before disappearing from the monitors on the final 08/17/2017 collection (Figure 10 panel 2). The fall 2016 cohort was first noted on settlement monitors on 10/21/2016 at a mean density of 5.4 mussels/m<sup>2</sup>. Subsequently, this cohort attained a peak density of 53.8 mussels/m<sup>2</sup> on 02/10/2017, declining to a mean of 10.8 mussels/m<sup>2</sup> on 07/03/2017 before disappearing from the monitors on 08/17/2017 (Figure 10 panel 2). The spring 2017 cohort at Lake Ray Roberts first appeared on the settlement monitors on 05/19/2017 at a mean density of 2.7 mussels/m<sup>2</sup>, remained at this density on the following 07/03/2017 collection and increased to a peak of 295.5 mussels/m<sup>2</sup> on the final 08/17/2017 collection (Figure 10 panel 2). As has been alluded to above in the section ‘Population shell growth rates’, the reduced settlement rate of the fall 2016 cohort was apparently a result of surface water pH being almost continually below >7.4 required for veliger development to a settled veliger (Sprung 1987) throughout the fall 2016 spawning period (Table 3, Figure

10b). It is also interesting to note that settlement of the spring 2017 cohort was essentially delayed until surface water pH rose above the >7.4 limit for juvenile settlement to 7.79 on 07/03/2017 which was followed by settlement of a mean of 295.2 mussels/m<sup>2</sup> on the settlement monitors on 08/17/2017. This delay in juvenile settlement occurred even though veliger larvae were detected in plankton samples from 04/11/2017 through 07/03/2017 (Figure 18, panel 2). Presence of veligers in Lake Ray Roberts without concurrent settlement of juvenile mussels during the spring 2017 spawning season strongly suggested that surface waters remaining at pH <7.4 may have prevented development of settlement competent pediveligers and juvenile settlement until after surface water pH rose to 7.79 on 07/03/2017 which was followed by limited juvenile settlement on 08/17/2017 (Figures 9a, 10 panel 2, and 18 panel 2). Juvenile settlement has been greatly reduced in Lake Ray Roberts since surface water pH first fell below 7.4 on 10/21/2016. If surface water pH continues to primarily remain below pH 7.4, suppressing veliger development and juvenile settlement in the future, it appears likely that Lake Ray Roberts zebra mussel population will continue to remain at the very low densities recorded in 2016 and 2017.

In Lake Belton on 01/30/2016, members of the fall 2015 cohort were recorded on settlement monitors at a mean density of 5,064.6/m<sup>2</sup> falling to a low of 48.4/m<sup>2</sup> on 08/03/2016 before disappearing from the monitors on 9/25/2016 (Figure 10 panel 3) during a major hypoxia event (Table 3, Figure 9b) as discussed above. Similarly, juveniles of the spring 2016 cohort occurred on settlement monitors at a maximum density of 3,971.6 mussels/m<sup>2</sup> on 07/13/2016, declining to 3,369.2 mussels/m<sup>2</sup> on the subsequent 08/30/2016 observation, further declining to 4.0 mussels/m<sup>2</sup> during the hypoxia event of 09/25/2016 before disappearing from the monitors on the subsequent 11/01/2016 observation. These results along with lack of veligers in the water column (Figure 18 panel 3) strongly suggest that the surface water extreme hypoxic event of 09/25/2016 nearly extirpated the population of zebra mussels at least within the vicinity of our study site but potentially from much of the reservoir. After the hypoxic event of 09/25/2016, members of the Lake Belton fall 2016 cohort were not recorded on settlement monitors until 12/12/2016 at a mean density of 1,711.3 mussels/m<sup>2</sup>. This delay in settlement of the fall 2016 cohort may have been associated with the low surface water oxygen concentrations recorded on 09/25/2016 and 11/01/2016 at 15.1% and 58.7% of full air O<sub>2</sub> saturation, respectively (Table 3, Figure 9b) during which there was a lack of veligers in the water column (Figure 18 panel 3). The initial settlement of the fall 2016 cohort only occurred when surface water O<sub>2</sub> concentrations returned to near-normal levels of 85.2% of full air O<sub>2</sub> saturation on 12/12/2016. Peak settlement of the fall 2016 cohort at 2,332.9 mussels/m<sup>2</sup> occurred on the subsequent 01/13/2017 observation and declined thereafter to a low of 53.8 mussels/m<sup>2</sup> on 6/29/2017 before disappearing from the monitors on 08/13/2017 (Figure 10 panel 3). The peak fall 2016 cohort settlement was much lower than that recorded for previous fall cohorts at the study site (Figure 7c) suggesting that the major decline in settlement density of the fall 2016 cohort was a result of extensive adult mussel mortality due to the 09/25/2016 hypoxic event leaving only a few living adults to participate in the fall 2016 spawning event. Juveniles of the spring 2017 cohort were first recorded on settlement monitors at a mean density of 12.1 mussels/m<sup>2</sup> on 05/25/2017. They attained a very high maximum mean density of 46,349.3 mussels/m<sup>2</sup> on the subsequent 6/29/2017 observation, declining to 9,889.4 mussels/m<sup>2</sup> on the final 08/13/2017 observation. Thus, the Lake Belton zebra mussel population at our sampling site appeared to be undergoing an extensive population recovery after being very depauperated after the 09/25/2016 hypoxic event.

No juvenile mussel settlement was noted on the settlement monitors in Lake Lewisville from their initial deployment on 07/08/2016 until 05/27/2017 when members of the spring 2017 cohort were first recorded on them at a mean density of 5.4 mussels/m<sup>2</sup> reaching a maximum of 53.8 mussels/m<sup>2</sup> by the subsequent 07/01/2017 observation and declining to a mean of 5.4 mussels/m<sup>2</sup> by the final observation on 08/20/2017. As discussed above in the section on “Physical-chemical parameters”, the mean of mean daily surface water temperatures in August 2016 at the Lake Lewisville study site was 31.0°C (sd = ±1.46, range = 29.17°-33.18°C) (Figure 13) indicating that daily mean water temperatures frequently exceeded the 32°C incipient upper thermal limit for zebra mussels in southwestern water bodies (Morse, 2009, McMahon 2015) (Figure 12 panel 4). Indeed, ANOVA analysis of Lake Lewisville the mean of

mean daily surface water temperatures during August 2016 indicated that they were significantly ( $p < 0.05$ ) higher than recorded for any of the five studied lakes in 2016 and 2017 (Figure 13). These lethal August surface water temperatures in Lake Lewisville may have reduced its zebra mussel population previously settled in 2015 by downstream transport from then mussel-infested Lake Ray Roberts during the floods of 2015 (Texas Parks and Wildlife 2015) to the extremely low numbers encountered in our study (Figure 10, panel 4). The overall mean of mean daily surface water temperatures in August 2017 in Lake Lewisville was  $29.8^{\circ}\text{C}$  (sd  $\pm 0.30$ , range  $29.25\text{--}30.3^{\circ}\text{C}$ ) which was similar to that of the four other studied lakes (Figure 13). This decline in August 2017 surface water temperatures appeared to allow veligers to develop in low numbers to settled juveniles (Figures 10 panel 4 and 18 panel 5). However, the very rapid decline in mean settlement density of the spring 2017 cohort from a peak mean of  $53.8$  mussels/ $\text{m}^2$  on 07/01/2017 to  $5.4$  mussels/ $\text{m}^2$  on the final 08/20/2017 collection (Figure 10 panel 4) suggests that Lake Lewisville may be resistant to establishment of a sustainably dense zebra mussel population for environmental reasons other than high summer surface water ambient temperatures alone.

Settlement monitors were initially deployed at Eagle Mountain Lake on 08/17/2016. Thereafter, members of the fall 2016 mussel cohort first settled on the monitors on 03/17/2017 at a density of  $32.3$  mussels/ $\text{m}^2$  (Figure 10 panel 5), but had disappeared from the monitors by the following observation on 04/11/2017. Subsequently, on 05/19/2017, settlement of juveniles of the spring 2017 cohort were first recorded on the monitors at a mean density of  $37.7$  mussels/ $\text{m}^2$  increasing to a peak of  $387$  mussels/ $\text{m}^2$  by the subsequent observation on 07/03/2017. Thereafter, their density declined to  $16.1$  mussels/ $\text{m}^2$  by the final observation on 08/17/2017 (Figure 10 panel 5).

Interestingly, Lakes Lewisville and Eagle Mountain were the shallowest for the five studied reservoirs with maximum depths at conservation level of  $20.4$  m and  $14.3$  m, respectively, as opposed to Lakes Texoma, Ray Roberts and Belton with respective maximum depths of  $30.5$  m,  $32.3$  m and  $37.8$  m (Texas Parks and Wildlife Department (2017a)). These two shallow lakes statistically had the highest August mean of mean daily water temperature, Lake Lewisville in 2016 (mean =  $31.0^{\circ}\text{C}$  sd  $\pm 1.46$ , range  $29.17\text{--}33.18^{\circ}\text{C}$ ) and Eagle Mountain Lake in 2017 (mean =  $30.2^{\circ}\text{C}$  sd  $\pm 0.44$ , range  $29.57\text{--}31.12^{\circ}\text{C}$ ) (Figure 12 panels 4 and 5, Figure 13) suggesting that their reduced depths may result in summer surface water temperatures becoming elevated enough to inhibit mussel larval development and juvenile settlement to levels preventing development of dense mussel populations. This appears to be particularly true of Lake Lewisville which, although it has been receiving veliger larvae hydrologically transported on the outflow from mussel-infested Lake Ray Roberts some  $23$  river km upstream on the Elm Fork of the Trinity River since 2012, has yet to develop a sustainable dense zebra mussel population. This suggestion that deeper Texas water bodies are more susceptible to successful invasion and establishment of zebra mussel populations is supported by the fact that the other Texas reservoirs reported by the Texas Parks and Wildlife Department (2017b) as infested with zebra mussels all have maximum conservation pool depths greater than those of Lakes Lewisville and Eagle Mountain including Lake Livingston ( $23.5$  m), Bridgeport,  $25.9$  m, Stillhouse Hollow ( $32.6$  m), Canyon ( $38.1$  m) and Travis ( $57.9$  m). The exception is Lake Austin with a maximum depth of  $22.7$  m but its summer surface water temperatures are depressed because it receives cool hypolimnetic water from the outflow of Lake Travis just  $24.5$  river km upstream. Thus, the 1982-2009 mean August surface water temperatures of Lake Austin are reported to range from  $24.3^{\circ}\text{C}$  at its headwaters to  $26.7^{\circ}\text{C}$  near its dam, temperatures well below the  $32^{\circ}\text{C}$  incipient upper thermal limit of Texas zebra mussels (Morse 2009, McMahon 2015). Lack of extensive zebra mussel infestations in shallow Texas water bodies suggest that maximum water depth should also be considered to be a zebra mussel risk factor such that lakes with maximum depths  $\geq 23$  m are considered as favorable for successful zebra mussel invasion and establishment of dense populations. Thus, based on average 1982-2009 surface water temperatures (Lower Colorado River Authority 2017), the chain of lakes on the lower Colorado River should all be favorable for establishment of sustainably reproducing zebra mussel populations as follows: Lake Buchanan (maximum depth (MD) =  $40.3$  m, mean August surface water temperature (MASWT) =  $28.9^{\circ}\text{C}$ ; Inks Lake, MD =  $18.3$  m, MASWT =  $25.9^{\circ}\text{C}$ ; Lake Lyndon B. Johnson, MD =  $27.4$  m, MASWT =  $28.9^{\circ}\text{C}$ ; Marble Farms Lake, MD =  $18.3$  m, MASWT =  $29.1^{\circ}\text{C}$ ; and



mussel-infested Lakes Travis, MD 57.9 m, MASWT = 29.8°C and Austin, MD = 22.8 m, MASWT = 24.5°C (Lower Colorado River Authority 2017).

Prior to 2017, peak spring and fall cohort settlement densities on our settlement monitors had been declining in Lakes Texoma, Ray Roberts and Belton since 2011, 2014 and 2015 respectively (Figures 7abc and 10 panels 1-3). In Lake Texoma, peak mean annual juvenile settlement density on settlement monitors was (i.e., sum of all present spring and fall cohort densities) was 64,318 juvenile mussels/m<sup>2</sup> recorded on 06/30/2011 following which peak annual densities declined through time to 6,441.7/m<sup>2</sup> on 8/18/2013, 4,342.9/m<sup>2</sup> on 08/04/2014, 5,682.9/m<sup>2</sup> on 05/16/2015, and 388.2/m<sup>2</sup> on 01/11/2016. After 05/16/2015, Texoma mussel densities began to increase reaching a peak of 5,136.3/m<sup>2</sup> on 07/01/2017 just prior to the last sample taken for this study on 08/20/2017 (5,021/m<sup>2</sup>) (Figures 7a and 10 panel 1). In Lake Belton, a peak settlement of 15,521 mussels/m<sup>2</sup> occurred on 05/25/2015 declining to 5,137.2/m<sup>2</sup> on 01/30/2016 and (Figures 7C and 10 panel 3). In 2017, mussel density recovered to 46,403.0/m<sup>2</sup> on 6/29/2017 just prior to the final sample taken on 08/13/2017 (9889.4/m<sup>2</sup>). Both of these results suggest that the zebra mussel populations in Lakes Texoma and Belton were making density recoveries after four and two years of population declines, respectively. This result suggests that these Texas mussel populations may go through boom and bust periods of annual density increases and declines with a periodicity of 3-4 years as reported in the northeastern United States by Strayer and Malcom (2006) and Strayer et al. (2011) and Europe by Stańczykowska and Lewandowski (1993). In contrast, annual mussel density in Lake Ray Roberts peaked at 29,378.4/m<sup>2</sup> on 12/04/2014, two years after mussel veligers were first discovered in the Lake in the spring of 2012 (McMahon 2015). Thereafter, annual mean peak mussel densities declined to 2,607.4/m<sup>2</sup> on 07/20/2015, 702.3/m<sup>2</sup> on 07/10/2016 and continued to decline to 295.2/m<sup>2</sup> by the final sample taken on 08/17/2017 (Figures 7c and 10 panel 2). The apparent lack of a 2017 recovery of mussel population density in Lake Ray Roberts as occurred in Lakes Texoma and Belton appears to be due to suppression of veliger larval development to settling juveniles induced by surface water pH essentially remaining below the >7.4 required for veliger development to a settled juvenile (Sprung 1987, 1993) from 10/21/2016 through to the last sample taken on 08/17/2017 (Table 3, Figure 9a).

### **Total phosphorous and chlorophyll *a* determinations:**

#### *Chlorophyll *a* Concentrations*

Chlorophyll *a* concentrations were determined for all five studied lakes from initial samples taken in December 2015 in Lake Texoma, Ray Roberts and Belton, July 2016 in Lake Lewisville and August 2016 in Eagle Mountain Lakes through August 2017. Overall, chlorophyll *a* concentration appeared to follow somewhat similar patterns of annual variation in all five studied lakes. Whether sampled in surface waters or just above the substratum, chlorophyll *a* concentrations were minimal in mid-winter and, thereafter, increased to maximal values in spring followed by a decline through summer, again increasing through fall prior to a midwinter decline (Figure 19 panels 1-5). When compared over the sampling period from July 2016 to August 2017 with T-tests there was no significant ( $p > 0.05$ ) difference in mean surface and benthic chlorophyll *a* concentrations in any of the five lakes ( $n = 11$  for each water body,  $p$  range = 0.168-0.940). Thus, both surface and benthic chlorophyll *a* values were combined as the dependent variable with water body as the factor in a one-way ANOVA. The results indicated a significant ( $n = 111$ ,  $df = 109$ ,  $F = 9.98$ ,  $p < 0.00001$ ) difference among water bodies. *Post hoc* least Squares Significant Difference testing indicated that overall mean chlorophyll *a* concentrations for Lakes Belton (6.95  $\mu\text{g/l} \pm 7.71$ ), Texoma (10.02  $\mu\text{g/l} \pm 7.52$ ), and Ray Roberts (12.75  $\mu\text{g/l} \pm 10.00$ ) were insignificantly ( $p > 0.05$ ) different from each other and that the mean chlorophyll *a* concentrations of Lakes Belton and Texoma were significantly ( $p < 0.05$ ) lower than those of Lakes Eagle Mountain (18.70  $\mu\text{g/l} \pm 9.00$ ) and Lewisville (27.70  $\mu\text{g/l} \pm 21.08$ ). Eagle Mountain Lake mean chlorophyll *a* concentration was not significantly ( $P < 0.05$ ) different from that of Ray Roberts while that of Lake Lewisville was significantly ( $p < 0.5$ ) greater than that of the other four water bodies (Figure 20).

Thus, the overall trend in lake chlorophyll *a* concentrations appeared to be that Lakes Texoma, Ray Roberts and Belton harboring established zebra mussel populations tended to have lower mean chlorophyll *a* concentrations compared to newly mussel-invaded Lakes Lewisville and Eagle Mountain which had only very low density zebra mussel populations (Figure 10 panels 1-5). The ability of filter feeding by dense zebra mussel populations to reduce phytoplankton densities and corresponding chlorophyll *a* concentrations has been well documented in North America (MacIsaac 1996, Idrisi et al. 2001, Alderstein et al. 2014) and Europe (Reeders et al. 1993). Similarly, the presence of sustainable reproducing zebra mussel populations in Lake Texoma, Ray Roberts and Belton appear to have reduced phytoplankton densities marked by reductions in chlorophyll *a* concentrations compared to newly-infested Lakes Lewisville and Eagle Mountain harboring low density zebra mussel populations. Reduction in phytoplankton primary productivity can have long-term negative effects on higher food web trophic levels such as zooplankton and fish which depend on energy flow from photosynthetic phytoplankton through food webs to support their growth and reproduction. Thus, zebra mussel invasions can eventually lead to reductions in the population densities and perhaps maximum adult size of higher trophic level species (MacIsaac 1996). Data has not yet been accumulated to prove this to be the case in Texas, but should remain a concern as zebra mussels continue to invade Texas water bodies. It may also be the case that reduction of phytoplankton productivity by zebra mussel filter feeding could cause longer-term reductions in their own productivity leading reductions in mussel growth rates and densities especially during summer months when elevated water temperature can increase zebra mussel metabolic demands to the point that they are in negative energy balance (Walz 1978, McMahon 1996, 2015) leading to lethal levels of starvation (Morse 2009).

#### *Total Phosphorous*

Mean total phosphorous (TP) concentrations in micromoles per liter ( $\mu\text{M/l}$ ) computed from triplicate water samples taken at the water's surface and  $\approx 1$  m above the bottom substratum were taken from July 2016 through August 2017. The resulting data revealed no similar seasonal patterns of TP concentration variation among the five sampled lakes with the exception of minimal phosphorous concentrations tending to occur in February through March and maximal concentrations, in June through October in Lakes Texoma, Belton, Lewisville, and Eagle Mountain. In contrast, this pattern was much less discernable in Lake Ray Roberts (Figure 21 panels 1-5).

Differences between the mean TP concentrations in surface and benthic water samples over the course of the study period in the five studied lakes were examined by paired t-tests. The results indicated that mean surface and benthic water TP concentrations were insignificantly ( $p$  range = 0.231-0.940) different for Lakes Ray Roberts (Surface (S) =  $0.85 \mu\text{M/l} \pm 0.217$ , Benthic (B) =  $1.00 \mu\text{M/l} \pm 0.260$ ), Belton (S =  $1.02 \mu\text{M/l} \pm 0.0418$ , B =  $1.33 \mu\text{M/l} \pm 0.511$ ), Eagle Mountain (S =  $1.85 \mu\text{M/l} \pm 0.307$ , B =  $2.07 \mu\text{M/l} \pm 0.0544$ ) and Lewisville (S =  $1.83 \mu\text{M/l} \pm 0.648$ , B =  $1.91 \mu\text{M/l} \pm 0.443$ ). In contrast, mean benthic TP concentration ( $2.04 \mu\text{M/l} \pm 0.545$ ) was significantly ( $p = 0.0039$ ) higher than mean surface concentration ( $1.41 \mu\text{M/l} \pm 0.351$ ) in Lake Texoma. Multiple Analysis of Variance (MANOVA) with the main effects of sampling site and surface versus benthic samples ( $n = 110$ ) revealed a significant difference between both lakes ( $df = 4$ ,  $F = 22.83$ ,  $p < 0.00001$ ) and surface versus benthic samples ( $df = 1$ ,  $F = 10.49$ ,  $p = 0.0016$ ).

Differences among mean site and depth TP concentrations were then assessed with a *post-hoc* Least Squares Significant Difference testing. This analysis revealed that mean TP concentrations were significantly ( $p > 0.05$ ) greater in benthic samples (mean =  $1.67 \mu\text{M/l}$ ) than in surface samples (mean =  $1.39 \mu\text{M/l}$ ) (Figure 22 lower graph). Among the five water bodies, *post hoc* Least Squares Significant Difference testing indicated that TP concentrations were insignificantly different between Lakes Ray Roberts and Belton and that they were significantly ( $p < 0.05$ ) lower than those of Lakes Texoma, Lewisville and Eagle Mountain which were insignificantly ( $p > 0.05$ ) different from each other (Figure 22 upper graph).

Total phosphorous concentrations are known to decline during spring plankton blooms when phosphate taken up from the water column by rapidly expanding phytoplankton populations is transported to the

hypolimnion as phytoplankton decline. This pattern was apparent in four of the five studied water bodies with the exception of Lake Ray Roberts (Figure 21 panels 1-5). There also appeared to be a slight tendency for TP concentrations in lakes with well-established zebra mussel populations (*e.g.*, Texoma, Ray Roberts and Belton) to have somewhat lower mean TP concentrations compared to lakes in the early stages of mussel infestation (*e.g.*, Lewisville and Eagle Mountain). Zebra mussel filtration of bacterio- and phytoplankton can remove phosphorous from the water column and sequester it in benthic sediments as mussel feces and pseudofeces, leading to a reduction in primary productivity due to reduced dissolved phosphorous availability (for a review see Bootsma and Liao 2014). Thus, zebra mussels may have contributed to the increased concentration of phosphorus in benthic water samples taken just above the substratum in this study. It has been hypothesized that reduced bacterio- and phytoplankton production could increase the likelihood of adult mussel mortality due to starvation especially during warm water summer months when particularly larger, adult mussels cannot ingest enough energy from filter feeding to meet high temperature induced elevations in metabolic demands (Walz 1978). Thus, zebra mussels can experience a negative energy balance leading to starvation and resultant tissue loss when water temperatures rise above 25°C (Walz 1978, Morse 2009, McMahon 2015). The tendency of mussel-infested Lakes Texoma, Ray Roberts and Belton to have reduced TP and chlorophyll *a* concentrations suggests that the associated reduction in phytoplankton densities could be partly responsible for the long-term declines in their mussel population densities (Figure 7a-c). However, the major spring 2017 recoveries of mussel population densities in Lakes Texoma and Belton suggest that mussel reduction of primary productivity leading to starvation during warm summer months may not be the primary cause of these mussel population collapses.

**Mussel dry tissue weights:** Based on available data, the DTW of 15, 20 and 25 mm SL standard individuals in Lake Belton peaked respectively at 20.18 mg on 03/23/2017, and 48.84 mg and 55.41 mg on 05/25/2017 (Figure 23 panel 1). Thereafter, the DTW of 10, 15, 20 and 25 mm SL standard individuals declined in the final 08/13/2017 sample to 3.60 mg, 8.27 mg, 19.01 mg and 43.71 mg, respectively (Figure 23 panel 1). In Lake Texoma, standard mussels of 15, 20 and 25 SL, attained peak respective DTWs of 25.34 mg on 04/15/2017, 49.18 mg on 07/01/2017 and 124.3365 mg on 07/01/2017 (Figure 23 panel 2). In the final sample taken on 08/20/2017, the DTWs of 10 and 15 mm SL standard individuals declined to 3.04 mg and 8.62 mg, respectively (Figure 23 panel 2). In Lake Ray Roberts, 25 mm SL mussels had a minimum DTW of 54.00 mg on 12/06/2017 which increased to 104.35 mg on 04/11/2017 before mussels of this size disappeared from subsequent samples (Figure 23 panel 3). Standard individuals of 20 mm SL had a minimal DTW of 20.08 mg on 09/16/2016 which increased to a maximum of 39.31 mg on 05/19/2017 declining to 19.03 mg on 08/17/2017. Standard 15 mm SL individuals had a minimal DTW of 10.30 mg on 09/16/2016 which then increased to a maximum of 19.62 mg on 05/19/2017 before declining to 8.58 mg in the final 08/17/2017 sample. Similarly 10 mm SL individuals attained a maximum DTW of 5.84 mg on 04/11/2017 which declined to 3.87 mg in the final 08/17/2017 sample (Figure 23 panel 3). At Eagle Mountain Lake, only the final sample on 08/20/2017 had enough mussels ( $n = 33$ ) of a reasonable size range (SL = 7.61-18.51 mm) to determine DTW for standard individuals of 10, 15 and 20 mm SL which were 3.5, 10.21 and 29.77 mg, respectively. The DTW values at of standard 15 and 20 mm SL mussels were slightly greater than those recorded for standard mussels of these sizes in August at Lakes Belton, Texoma and Ray Roberts. Not enough mussels were available at Lake Lewisville for standard DTW analysis.

On examination, these data appear to indicate that zebra mussels in Lakes Belton, Texoma and Ray Roberts generally gained tissue mass through late fall, winter and spring and then began to lose tissue mass in summer and early fall as surface waters attained maximal temperatures suggestive of high temperature induced starvation (Figure 12 panels 1-3 and 23). This pattern was also displayed by a zebra mussel population sampled between 06/16/2008 and 10/15/2008 in Winfield City Lake, southern Kansas (Morse 2009), whose estimated DTWs for 10, 15, 20, and 25 mm standard SL individuals are superimposed as white points and lines over those determined in this study in Figure 23, panels 1-3. Like zebra mussel populations in Lakes Texoma, Ray Roberts and Belton, standard sized Winfield City Lake

individuals attained maximal DTW on 06/29/2008 (i.e., 15 mm SL = 13.39 mg, 20 mm SL = 31.59 mg, 25 mm SL = 61.49 mg) declining to minimal values on 08/08/2008 (i.e., 15 mm SL = 8.55 mg, 20 mm SL = 17.78 mg, 25 mm SL = 31.37 mg) after which DTW again increased through 10/15/2008 (i.e., 15 mm SL = 8.58 mg, 20 mm SL = 20.66 mg, 25 mm SL = 40.89 mg) (Figure 23 panels 1-3, Morse 2009). Thus, apparent summer starvation marked by decline in DTW of standard sized mussels in Winfield City Lake mussels appeared to be even more pronounced than displayed by mussel populations in the three studied Texas lakes (Figure 23 panels 1-3). Interestingly, standard sized 15 and 20 mm SL mussels from the final August 2017 sample in Eagle Mountain Lake had higher DTWs than those collected in the same months from Lakes Texoma, Ray Roberts and Belton. Lakes Texoma and Belton had significantly ( $p < 0.05$ ) lower mean chlorophyll *a* concentrations than Eagle Mountain Lake and while statistically equivalent, a higher mean chlorophyll *a* concentration than Lake Ray Roberts. The higher chlorophyll *a* concentrations at Eagle Mountain Lake may have reflected a greater concentration of phytoplankton allowing mussels to better maintain body mass during the summer starvation period than mussels in Lake Texoma, Ray Roberts and Belton.

Morse (2009) compared the DTWs of standard sized mussels from Winfield City Lake taken from a sample in June 2008 at the height of the population's infestation and its annual DTW cycle to a sample from a zebra mussel population in Lake Oologah, Oklahoma, taken on the same date in June one year earlier just before that population completely collapsed and was essentially extirpated from the lake. He found that standard sized mussels from Lake Oologah just prior to population collapse had estimated DTW's that were significantly much lower than those of the Winfield City Lake population indicative of poor nutritional condition. In Winfield City Lake a standard 25 SL mussel was estimated to lose a maximum of 51% of its peak DTW recorded on 06/29/2008 (61.49 mg) in a sample taken on 08/08/2009 (31.36 mg) (Figure 23) before regaining tissue mass to 40.87 mg DTW (66% of peak DTW on 06/29/2017) on 10/15/2017. This summer DTW loss was considered to be indicative of starvation occurring when ambient surface water temperatures rose above 25°C in early July with positive tissue growth only re-occurring when surface water ambient temperatures once again fell below 25°C in early September (Morse 2009). There are similar reports of natural zebra mussel populations appearing to undergo starvation as ambient water temperatures exceed 20-25°C during the summer (Doregelo and Kraak 1993; Jantz and Neumann 1998; Nalepa et al. 1993, 1995; Stoeckmann and Garton 1997) causing mussels to experience negative energy balance in which metabolic energy demands exceed energy assimilation (Waltz 1978). Morse (2009) and McMahon (2015) have hypothesized that after initial zebra mussel invasion of a water body, rapid mussel population expansion can lead to both reductions in phytoplankton density (Reeders et al. 1993, MacIsaac 1996, Idrisi et al. 2001, Alderstein et al. 2014) and the availability of micronutrients such as phosphorus which phytoplankton productivity is dependent on by sediment deposition with mussel feces and pseudofeces (Lucy et al. 2005, Greg et al. 2009, Bootsma and Liao 2014). Reductions in phytoplankton densities were hypothesized to occur after initial zebra mussel invasion and explosive population growth led to a reduction in micronutrient availability reducing phytoplankton primary productivity. Post-invasion reduction in phytoplankton productivity was hypothesized to reduce the ability of zebra mussels to increase tissue mass over fall, winter and spring when ambient water temperatures were below 25°C such that mussels annually accumulated less tissue mass prior to spring reproduction. Summer tissue loss was hypothesized to eventually reach a point that mussels would not have enough tissue energy stores to survive summer starvation leading to eventual population collapse (Morse 2009, McMahon 2015).

Because starvation at high temperatures becomes much more acute with increasing mussel size (Walz 1978), it is also potentially the reason that spring and fall mussel cohorts in the studied Texas lakes generally do not survive beyond the end of summer in the year following initial settlement leading to shorted life spans of 1.0-1.5 years. Their high shell growth rates (Figures 4, 5, 14, 15, 16 and 17) allow Texas mussels to attain sizes that are susceptible to lethal starvation in Texas lakes that are warmer over much longer periods than lakes in northern North America and Europe where mussel life spans are generally reported to extend over 2-5 years (Mackie 1996, McMahon 1996). Interestingly, similar to the

elevated shell growth rates and 1-1.5 year life spans reported herein for warm Texas lakes, elevated growth rates and one-year mussel life spans have also been reported for mussels living in Polish lakes heated to summer temperatures  $>30^{\circ}\text{C}$  by thermal discharges (Stanczykowska 1976, Kornobis 1977, Sinicyna and Zdanowski 2007). Thus, higher growth rates and abbreviated life spans may be universally characteristic of mussels living in waters approaching their incipient upper thermal limit of  $30\text{-}32^{\circ}\text{C}$  during summer months.

The hypothesis that, in years following initial invasion, Texas zebra mussel populations would be subject to more extensive starvation during warm summer months as mussel filter feeding reduced the availability micronutrients such as phosphorous that support phytoplankton growth by deposition to benthic sediments with their feces and pseudofeces (Morse 2009, McMahon 2015) was not supported by the results of this study. Figure 23 (panels 1-3) shows that the DTW of standard sized mussels sampled after population collapse at all three studied lakes, while having a similar of pattern of summer depression, perhaps due to summer starvation, were essentially similar to the DTW's of standard sized mussels sampled from Winfield City Lake in southern Kansas in 2008 when the population was at maximum density after becoming established in 2006 (Morse 2009). This observation was confirmed when the mean DTW data for mussels at each standard SL estimated for each monthly sample displayed in Figure 23 (panels 1-3) was subjected to Multiple Factor Analysis of Variance (MANOVA) with the mean DTW of standard sized individuals in different samples as the dependent variable, sampled lakes as the main effect and the numerical day of the year (i.e., 1-365) on which samples were collected as a covariate, followed by *post-hoc* Least Squares Significance Difference testing to determine significant ( $p < 0.05$ ) differences between collection date adjusted mean DTWs for standard sized mussels (i.e., SL = 10, 15, 20 or 25 mm) among the three studied Texas lakes and Winfield City Lake (Figure 24). The estimated DTWs of standard SL individuals were only used in this analysis if the SL range individuals in a sample encompassed specific standard SLs. The results of this analysis indicated that the covariate of numerical day of the year was significantly correlated with the estimated DTW of standard sized mussels of 10 mm SL ( $p = 0.0027$ ), 15 mm SL ( $p = 0.0001$ ), 20 mm SL ( $p = 0.0092$ ), and 25 mm SL ( $p = 0.0350$ ). This correlation was due to the fact that standard sized mussel in all four mussel populations showed a similar pattern of seasonal decline in DTW during warm summer months (July-September) followed by tissue mass recovery through fall, winter and early spring prior to spawning in May-June as discussed above and illustrated in Figure 23 (panels 1-3).

The MANOVA results also indicated that the adjusted mean DTWs of 10 and 15 mm standard sized mussels were not significantly different (10 mm SL,  $n = 29$ ,  $F = 0.155$ ,  $p = 0.4395$ ; 15 mm SL,  $n = 28$ ,  $F = 1.96$ ,  $p = 0.14887$ ) among the four sampled lakes (Figures 24ab). In contrast, for a 20 mm SL standard mussel, *post hoc* Least Square Significant difference testing indicated that Lake Belton mussels had a significantly ( $p < 0.05$ ) lower mean DTW than those from Lake Ray Roberts while those from Lakes Winfield City and Texoma had mean DTW's that were not significantly ( $p > 0.05$ ) from each other or from those of Lakes Belton or Winfield City (Figure 24 panel 3). Differences among lakes became even more apparent when examined for standard 25 mm SL mussels. The mean DTW of a standard 25 mm SL mussel from Lakes Belton and Winfield City were insignificantly ( $p > 0.05$ ) from each other but were significantly ( $p < 0.05$ ) lower than those of mussels from Lakes Texoma and Ray Roberts which were also insignificantly ( $p < 0.05$ ) different from each other. Interestingly, this result was not correlated with the mean Chlorophyll *a* concentrations in the lakes where it was lowest in Lake Belton, intermediate in Lake Texoma and highest in Lake Ray Roberts (Figure 20) suggesting that phytoplankton availability was not the main driver of summer tissue loss in the studied mussel populations.

Thus, the data appeared to indicate that the mussel population collapses observed in Lakes Belton, Texoma and Ray Roberts were unlikely to have occurred as a result of increased levels of starvation and tissue loss during warm summer months. Similarly, Sinicyna and Zdanowski (2009) report little difference in DTW among zebra mussel populations inhabiting a chain of lakes in Poland receiving power station thermal effluents on their upstream end resulting in mussel populations being sampled across a

thermal gradient of mean annual temperatures ranging from 20.6°C at the inlet receiving thermal effluents to 13.0°C at the lakes' outlet from 1993-2006. Summer water temperatures in the area receiving thermal effluents exceeded 30°C, presumably greatly increasing mussel metabolic rates which, based on Walz's (1978) laboratory estimate of a maximum temperature of 20-25°C to remain in positive energy balance (i.e., avoid starvation), should have resulted in mussels isolated in areas receiving thermal effluents having a distinctly lower DTW than downstream populations in cooler waters. However, their results showed no differences in the body mass of mussels sampled at six sites across the thermal gradient in the chain of lakes system (Sinicyna and Zdanowski 2009). In our study, standard individuals of 25 mm SL sampled from Winfield City Lake at the height of its zebra mussel population expansion in 2008, had a significantly ( $p < 0.05$ ) lower adjusted overall mean DTW than mussels from Lakes Texoma or Ray Roberts with relatively low population densities while being insignificantly different from that of the Lake Belton mussels which were at a higher population density (Figure 24d). Thus, it appears that competition for limited food resources in high density mussel populations may have a much greater impact on nutritional condition in zebra mussels than elevated summer ambient water temperatures and that zebra mussels may be able to physiologically compensate in yet unknown ways to maintain nutritional condition under high ambient temperatures and low phytoplankton concentrations.

**Major drivers of zebra mussel population dynamics in Texas water bodies:** The results of our study revealed some possible drivers of mussel population dynamics in Texas water bodies including exposure to hypoxic conditions which caused the near extirpation of the zebra mussel population at our sampling site in Lake Belton, pH below the 7.4 minimum for successful veliger development to a settled juvenile as appeared to be suppressing juvenile mussel settlement and population growth in Lake Ray Roberts, and summer surface water temperatures approaching or exceeding the zebra mussel's incipient upper lethal limit of 32°C appearing to suppress successful spawning and juvenile settlement in Lakes Lewisville and Eagle Mountain. In contrast, as described above, for Lakes Texoma, Ray Roberts and Belton while larger mussels (i.e., 20 and 25 mm standard SL) appear to experience starvation at summer water temperatures greater than 25°C, such summer starvation did not appear to be a major factor in the population collapses of zebra mussels recorded in these lakes especially because the mussel populations in Lakes Texoma and Belton experienced density recoveries in the spring and summer of 2017 after an extended period of population decline (Figure 10 panels 1 and 3).

In contrast, water level variation could have major consequences on the population dynamics of zebra mussels which have a limited capacity to survive desiccation during emersion by receding water levels (McMahon et al 1993). Laboratory studies have indicated that zebra mussel desiccation resistance increased with increased relative humidity and decreased with increasing air temperature and decreasing mussel size (McMahon et al. 1993, Ricciardi et al. 1997, Paukstis et al. 1999). Tolerated emergence times across <5% to >95% relative humidity ranged from 10.3-27.9 days at 5°C, 4.5-12.3 days at 15°C and 2.0-5.4 days at 25°C (McMahon et al. 1993). Field studies have indicated that the zebra mussel's low desiccation tolerance causes massive mussel mortalities when populations are emersed by receding water levels. Bowers and Szalay (2004) found that zebra mussel densities were very low in shallow (<35 cm depth) Lake Erie coastal marshes that were intermittently dewatered by seiches and seasonal water level variation. Similarly, near-shore, newly settled zebra mussels at a depth of <1 m experienced nearly 100% mortality when exposed in air for 1-3 days by receding water levels in a Polish reservoir (Wiśniewski 1992). In contrast, Texas water bodies undergo much greater seasonal changes in water level, sometimes receding more than 14-15 m below conservation pool due to drought and/or human water use demands or rising over 9-12 m above conservation pool during periods of high precipitation leading to exceptionally high water inflow rates (US Lakes 2017). Because zebra mussels are highly intolerant of hypoxia with a lower tolerated incipient limit of 30% of full air O<sub>2</sub> saturation (Johnson and McMahon 1998), they can only settle and survive in oxygenated surface waters above the hypolimnion. Thus, massive zebra mussel mortalities can occur when water levels either undergo extensive declines emerging mussels into lethal aerial desiccation or when rising water levels submerge existing mussel populations into hypoxic

conditions below the thermocline. As such, years when water levels are highly variable could result in massive reductions in mussel densities in Texas water bodies leading to major population collapses.

When historical annual water level variations from 2012 through 2017 were examined for the five studied lakes (US Lakes 2017, US Corps of Engineers, Tulsa District 2017), a roughly similar pattern of annual water level variation occurred in all of them (Figures 25a-e). During 2012, 2013, and 2014, water levels were fairly stable at Lakes Texoma, Ray Roberts and Belton (Figures 25a-c and 26a-c) varying by no more than 1.5-3.1 m over the course of the year. During this period, mussel densities on our settlement monitors remained fairly stable or increased (Figure 7). In contrast, water levels greatly varied during the high spring rainfall and flood year of 2015, rising approximately 13.4 m between January and June in Lake Texoma, 5.8 m in Lake Ray Roberts and 9.5 m in Lake Belton (Figures 25a-c). Water levels were also relatively variable in these three lakes from January through September 2016 after which level variation was minimal through the end of this study in August 2017 (Figures 25a-c, and 26a-c respectively). The highly variable water levels in 2015 and the spring and summer of 2016 were associated with declines in the settlement densities of the fall 2015 and spring 2016 cohorts probably as a result of near extirpation of earlier adult cohorts by a cycle of immersion in hypoxic hypolimnetic water with rising water levels followed by emersion of spring 2015 cohorts which settled high on the shore during spring high lake levels and were later emersed by receding water levels in the fall leading to lethal desiccation (Figures 26a-c).

As a result of ensuing low densities of adults, fall 2016 spawning was suppressed leading to the fall 2016 cohort also settling at low densities (Figure 10 panels 1-3). Thereafter, as water levels remained stable, spawning by the fall 2016 cohorts lead to increased settlement densities of the spring 2017 cohorts at Lakes Texoma and Belton (Figures 26ac). A similar increase in the settlement of the spring 2017 cohort did not occur in Lake Ray Roberts because surface water pH essentially remained below 7.4 from October 2016 through August 2017 suppressing veliger development to settled juveniles. Thus, the advent of water level stability from September 2016 through August 2017 (Figures 24ac) appears to have supported a recovery of mussel population densities at Lakes Texoma and Belton (Figure 10 panels 1 and 3) suggesting that the degree of seasonal variation in lake level could account for boom or bust mussel population dynamics in Texas water bodies. As such, Texas water using facilities on mussel-infested reservoirs might expect to experience higher levels of mussel macrofouling after source water levels have been relatively stable for 1-2 years or longer and decreases in mussel macrofouling when source water levels have been relatively unstable for 1-2 years or longer. In addition, it appears that water bodies with relatively stable water levels may be more susceptible to supporting sustainably dense mussel populations after initial invasion than those characterized by highly variable water levels making water level variability a potential component of risk analysis for zebra mussel invasion. Further, manipulations of water levels through planned water drawdowns or retentions could be used to manage zebra mussel populations in infested water bodies where water level control is feasible.

## CONCLUSIONS

Overall, the results of this study indicated that zebra mussel populations in Lakes Texoma, Ray Roberts and Belton were in a state of decline following a poor settlement of the fall 2015 cohort marked by reduced adult densities and juvenile settlement rates along with limited larval development to the pediveliger settlement stage (Figures 7a-c and 10 panels 1-3). Mussel densities made major recoveries with the settlement of spring 2017 cohorts in Lakes Texoma and Belton, but not in Lake Ray Roberts where surface water pH remained below 7.4 required for veliger development to a settled juvenile from October 2016 to the termination of the study in August 2017. In addition, in Lake Belton, a hypoxia event in late September-October 2016 caused a massive die-off of mussels followed by a delayed, much reduced settlement of the fall 2016 cohort in December 2016-January 2017 to replace the previously nearly extirpated mussel population. A major recovery of the Lake Belton population occurred in early

2017 when a massive settlement of the spring 2017 cohort at 46,349.3 juveniles/m<sup>2</sup> was recorded on settlement monitors on 06/29/2017 (Figures 7c and 10 panel 3). Very limited juvenile settlement occurred on settlement monitors in newly mussel-invaded Lakes Lewisville and Eagle Mountain which had maximum spring 2017 cohort settlements of only 53.8 mussels/m<sup>2</sup> on 07/01/2017 and 387.5 mussels/m<sup>2</sup> on 07/03/2017, respectively. The lack of major increases in mussel density in these lakes since their invasions in 2015 and 2016, respectively, appeared to be a result of late summer mean daily surface water temperatures approaching or exceeding the long-term, incipient upper thermal limit for Texas zebra mussels of 32°C which reduced mussel population densities, leading to a suppression of spawning and juvenile settlement. The overall mean of August daily mean surface water temperatures remained below the 30°C limit for maintaining normal function in zebra mussels in Lakes Texoma, Ray Roberts and Belton which appeared to support their rapid post-invasion population expansions. Lakes Texoma, Ray Roberts and Belton were all considerably deeper at conservation pool with maximum depths of 30.5 m (100 ft), 32.3 m (106 ft) and 37.8 m (124 ft), respectively, than either Lakes Lewisville at 20.4 m (67 ft) or Eagle Mountain at 14.3 m (47 ft) (Texas Parks and Wildlife Department 2017a) suggesting that deeper Texas lakes have cooler maximum summer surface water temperatures than shallow lakes making them more hospitable to zebra mussel invasion and population sustainability. Indeed, Lakes Stillhouse Hollow (Texas Parks and Wildlife Department 2016a), Canyon (Texas Parks and Wildlife Department 2017c), and Travis (Texas Parks and Wildlife Department 2017d), newly invaded by zebra mussels in 2016 and 2017 are relatively deep at conservation pool at 32.6 m (107 ft), 38.1 m (125 ft) and 57.9 m (190 ft), respectively (Texas Parks and Wildlife Department 2017a). Thus, it appears that maximum water body depth can also be used along with those of average August surface water temperature, O<sub>2</sub> concentration as percent of full air O<sub>2</sub> saturation, pH and calcium concentration recommended by McMahon (2015) for zebra mussel invasion risk assessment of Texas water bodies as follows:

<b>Physical Parameter</b>	<b>Unsuitable</b>	<b>Marginal</b>	<b>Suitable</b>	<b>Reference</b>
Average August Water Temperature	>32°C	31-32°C	<31°C	de Kozłowski et al. 2002
pH	<6.8 or >9.5	6.8-7.4	7.4-9.5	de Kozłowski et al. 2002
Calcium Ion Concentration.	<12 mg L <sup>-1</sup>	12-28 mg L <sup>-1</sup>	>28 mg L <sup>-1</sup>	Whittier et al. 2008
Dissolved Oxygen as % of Air O <sub>2</sub> Saturation	<30% O <sub>2</sub>	30-50% O <sub>2</sub>	>50% O <sub>2</sub>	Johnson and McMahon 1998
Maximum Lake Level at Conservation Pool	<10 m (33 ft)	10-22 m (33-70 ft)	>22 m (70 ft)	This Study

While lack of mussel settlement in newly infested Lakes Lewisville and Eagle Mountain prevented assessment of mussel growth rates and life spans, zebra mussels in Lakes Texoma, Ray Roberts and Belton had spring and fall spawning and settlement periods with spring cohorts settling at higher densities than fall cohorts (Figures 7 a-c) as previously reported for these populations (McMahon 2015). Both spring and fall cohorts disappeared from the populations in the three lakes by August-September of the



year following settlement suggestive of a 15-16 month life span for spring cohorts and a 10-11 month life span for fall cohorts. At Lakes Ray Roberts and Belton, mussel cohort growth rates were similar to that recorded in previous years with spring and fall cohorts reaching a mean shell length (SL) of 20-25 mm before disappearing from the population during the following summer and early fall (Figures 5, 15 and 16) with the exception that the life spans of the Fall 2015 and Spring 2016 cohorts at Lake Belton were cut short due to near total mussel extirpation by exposure to a severe hypoxic event (15.1% of full air O<sub>2</sub> saturation) on 09/25/2016 (Figures 9b and 16). In contrast, while spring and fall 2016 cohorts settled in Lake Texoma, the growth rates of the spring 2016 cohort appeared to be greatly suppressed attaining mean a SL of only 10.69 mm ±3.12 before disappearing from the samples on 02/23/2017 after an attenuated life span of only 229 days (Figures 14 and 17). Thereafter, the Texoma fall 2016 cohort attained a mean SL of 19.17 mm ±0.81 by the final August 2017 sample which was similar to those of 19.61 mm ± 2.06 and 20.75 mm ± 0.21 attained by the fall 2016 Lake Belton and Ray Roberts cohorts, respectively (Figure 17) indicative of relatively similar fall cohort growth rates in all three populations. The end of life span SL for the Texoma 2016 spring cohort (10.69 mm ±3.12, Figure 14) was greatly reduced compared to that of 24-28 mm SL previously achieved by the spring 2011 and 2012 cohorts (Figure 5). This result suggests that over time growth rates of zebra mussels in infested reservoirs may decline perhaps due to increased competition for declining phytoplankton food resources. However, establishing the bases for declines in zebra mussel growth rates in Texas water bodies will require further long-term concurrent studies of mussel and phytoplankton dynamics.

Mean chlorophyll *a* concentrations in Lake Texoma during the course of the study, although low, were not significantly ( $p > 0.05$ ) different from those at Lakes Belton or Ray Roberts with faster growing cohorts (Figure 20) nor were the DTWs of Lake Texoma standard 10, 15 and 20 mm SL individuals significantly ( $p > 0.5$ ) different than those of mussels in Lakes Belton and Ray Roberts mussels and, for a standard 25 mm SL individual, were equivalent to those from Lake Belton and significantly less than those from Lake Ray Roberts (Figure 24). These results suggested that the suppression of shell growth rate in the spring 2016 Lake Texoma was not due to poor nutritional condition or reduced phytoplankton food availability. Nor did it appear to be due to temperature stress as Lake Texoma had among the lowest overall mean August daily mean surface water temperatures recorded among the five studied lakes, being always below the upper thermal limit of 30°C for normal mussel physiological function (Figures 12 and 13). Thus, the bases for apparent suppression of the Texoma zebra mussel spring 2016 cohort's shell growth rate remains unknown especially because all measured lake physical conditions fell well within that considered suitable for sustainable mussel colonization (Table 3, Figures 9ab, 11 and 13). Zebra mussels were first found in Lake Texoma in 2009 making it the oldest known infestation in Texas. It is possible that the Texoma mussel population has reduced a presently unknown required resource through time so that it is now limiting shell growth rates and perhaps population density.

Analysis of monthly plankton samples for the presence of veliger larvae in the water column clearly indicated that there were two distinct periods of veliger presence in Lakes Texoma, Ray Roberts, Belton and Eagle Mountain over the course of the study. A fall 2016 period of veliger presence extended from September-October 2016 through December 2016 at Texoma, Ray Roberts and Belton and from October 2016 through January 2017 at Eagle Mountain Lake (Figure 18 panels 1-4). During spring and summer 2017, veligers again appeared in the water columns of all four lakes between March and May of 2017 and were still present in the water column in low numbers in August 2017 at Lake Texoma, Ray Roberts and Belton (Figure 18 panels 1-3). Although, only a relatively few veligers were found during the course of the study in plankton samples taken at Lake Lewisville, they exhibited the same bimodal pattern of fall 2016 and spring 2017 occurrence in the water column (Figure 18 panel 5). A spring and fall bimodal annual pattern of veliger presence in the water column has been previously recorded in Lakes Texoma and Ray Roberts by our laboratory from 2011-2015 (Figures 4 and 5). Thus, a bimodal spring and fall spawning period indicated by the presence of veligers in the water column appears to be typical for zebra mussels in Texas water bodies.

General consensus is that zebra mussels initiate spawning in North America and Europe at an ambient water temperature of 17-19°C with a low percentage of living veligers reported to still occur in the lower Mississippi River at temperatures as high as 28-30°C (McMahon 1966, Nichols 1966). Among Lakes Texoma, Ray Roberts, Belton and Eagle Mountain, veligers of the spring 2017 cohort first appeared in the water column in April (Ray Roberts, Belton and Eagle Mountain) and May (Texoma) when mean daily surface water temperatures were 18.28°C  $\pm$ 0.05, 19.62°C  $\pm$ 0.35, 20.51°C  $\pm$ 1.09 and 21.44°C  $\pm$ 0.57, respectively, with veligers still occurring in the water column in August 2017 when at respective mean daily surface water temperatures of 30.10°C  $\pm$ 0.59, 29.91°C  $\pm$ 0.34, 30.16°C  $\pm$ 0.44 and 29.11°C  $\pm$ 0.58. Similarly, veligers first appeared during the fall 2016 spawning period in September at Lakes Texoma, Ray Roberts, and Belton at respective mean daily surface water temperatures of 27.68°C  $\pm$ 0.69, 28.72°C  $\pm$ 0.35 and 29.68°C  $\pm$ 0.52 and in Eagle Mountain Lake in October at 24.25°C  $\pm$ 0.106. Veligers disappeared from plankton samples at Texoma, Ray Roberts, and Belton in December at respective mean daily water temperatures of 13.11°C  $\pm$ 2.28, 11.85°C  $\pm$ 2.05, and 16.05°C  $\pm$ 1.79 and at Eagle Mountain Lake in January 2017 at 9.66°C  $\pm$ 0.77 (Figures 12 and 18). Based on these mean daily water temperatures at first appearance of veligers in plankton samples it appears that zebra mussel spring spawning was initiated in the studied lakes when surface water temperatures rose to 18-21°C and fall spawning, when they dropped below 27-29°C. This zebra mussel spawning range of 18-21°C to 27-29°C is similar to that reported in both North America and Europe (McMahon 1966, Nichols 1966).

The presence of living veligers from the fall mussel spawn in the studied lakes in December and January at monthly temperatures of 9.66-16.05°C may be due to veliger development being slowed by declining water temperatures with the onset of winter, perhaps accounting for previous anomalous reports of veligers being found during winter at temperatures as low as 12-15°C in Europe suggesting that spawning occurred at those temperatures (Nichols 1996). However, based on our study, the presence of living veligers during the winter was not a result of actual spawning at low temperatures. Instead, mussel spawning in the studied Texas lakes appeared to be initiated when water temperatures rose above 17-19°C as reported for zebra mussels in other North American water bodies and ceases in the fall when water temperatures decline below 17-19°C (Nichols 1996). Further, even though veligers were found at relatively high water temperatures during summer months in the studied lakes, there were few (Lake Texoma) or no settlement-competent pediveligers (SL  $\geq$ 231  $\mu$ m) in the plankton samples (Figure 18 panels 1-5). This result suggested that zebra mussel larvae cannot develop to settlement-competent pediveligers as mean daily ambient water temperatures reach 29-30°C, perhaps accounting for the late summer cessation in juvenile settlement that results in the distinct spring and fall juvenile mussel settlement cohorts characteristic of zebra mussel population dynamics in Texas water bodies.

Interestingly, our results indicated that major mussel juvenile settlement was closely associated with the appearance of settlement-competent pediveligers in plankton samples. At all five studied lakes, juvenile settlement occurred either coincidentally or after first appearance of settlement competent pediveligers (SL  $\geq$ 231  $\mu$ m) in plankton samples. Settlement-competent pediveligers did not immediately appear in the first plankton samples containing veligers. Rather, they typically were recorded in plankton samples 1-2 months following the initial appearance of veligers in the water column (Figure 18) when their presence was correlated with the first appearance of a new cohort of juvenile mussels on settlement monitors. Typically, it has been recommended that water using facilities apply molluscicides to their intakes to prevent/control zebra mussel macrofouling when plankton samples first reveal the presence of zebra mussel veliger larvae in the water column (Claudi and Mackie 1994, Mackie and Claudi 2010). However, the results of this study suggest that determination of the shell lengths of veligers ( $n > 100$  individuals) in weekly plankton samples could be used to initiate molluscicide application only at first appearance of settlement-competent pediveligers, marking the start of actual juvenile settlement. Similarly, application of molluscicides could be halted when settlement competent veligers no longer appear in plankton samples for several consecutive weeks. Molluscicide application could be re-initiated if pediveligers appear in later samples. This approach could both reduce the expense of molluscicidal control of zebra

mussel macrofouling and the amount of molluscicide returned to source water bodies by once-through raw-water systems.

The results of this study suggested that the zebra mussel population collapses recorded in Lakes Texoma, Ray Roberts and Belton (Figure 7 panels 1-3) were not likely due to environmental factors such as elevated summer surface water temperatures, low chlorophyll *a* and phosphate concentrations or summer mussel starvation marked by major reductions in DTW to lethal levels at ambient surface water temperatures  $\geq 25^{\circ}\text{C}$ . However, the results did indicate that environmental factors such as a low pH ( $<7.4$ ) inhibiting veliger development and juvenile mussel settlement (*e.g.*, Lake Ray Roberts) and surface water hypoxic events (*e.g.*, Lake Belton) can cause short-term reductions in mussel density from which populations appeared to be able to rapidly recover after conditions again became favorable. The results also suggested that elevated surface water temperatures approaching or exceeding the zebra mussel's incipient upper lethal limit in shallow lakes  $<10$  m in maximum depth at conservation pool could suppress mussel spawning and settlement preventing the development of dense populations. Longer-term suppression of zebra mussel population densities and juvenile settlement recorded in Lakes Texoma, Ray Roberts and Belton all appeared to initially occur in the fall of 2015. They ended with major settlements of the spring 2017 cohorts at Lakes Texoma (maximum mean density of the spring 2017 cohort = 5136.3 mussels/m<sup>2</sup>) and Belton (maximum mean density of the spring 2017 cohort = 46349.3 mussels/m<sup>2</sup>) (Figures 26ac), but continued at Lake Ray Roberts (Figure 26b) due to suppression of veliger development to juvenile settlement by low pH ( $<7.4$ ) (Figure 9a).

It is interesting that these collapses in mussel populations at Lakes Texoma, Ray Roberts and Belton occurred at roughly the same time during the fall of 2015 (Figures 7a-c and 10a-c). In all three lakes, water levels remained relatively stable from 2012-2014 (Figures 25a-c and 26a-c). Then, during extensive spring rains and flooding in 2015, water levels rose precipitously above conservation pool levels in all three lakes from April through June 2015 (Texoma = 10.36 m (34 ft); Ray Roberts = 6.10 m (20 ft); Belton = 9.45 m (31 ft) and returned to normal levels by fall 2015 (Figures 25a-c and 26a-c). Water levels remained variable to a lesser extent in 2016 at Lakes Texoma and Ray Roberts (Figures 25ab, 26ab), but were still highly variable from April through August 2016 at Lake Belton (7.32 m (24 ft) due to construction work on its dam (Figures 25c and 26c). By January through August 2017, water levels in all three lakes returned to being relatively stable (Texoma = 1.83 m, 6ft; Ray Roberts = 0.30 m, 1 ft; Belton = 2.74 m, 9 ft) (Figures 25a-c and 26a-c).

During 2015, when water levels in Lake Texoma, Ray Roberts and Belton rose extensively due to spring flooding, it is likely that existing mussel populations experienced extensive mortality as rising water levels exposed them to lethal hypoxic conditions below the hypolimnion (Johnson and McMahon 1998). Any juveniles of the spring 2015 cohort that would have settled above the hypolimnion high on the shore during elevated spring water levels would then have been emersed in air to suffer lethal desiccation (McMahon et al. 1993, Ussary and McMahon 1995) when lake levels declined to conservation pool in September of 2015. Thus, the high spring and summer 2015 water level variations would have left few spawning adults to produce a fall 2015 cohort as evidenced by highly reduced settlement densities in all three water bodies (Figures 7a-c, 10 panels 1-3, 26a-c). The repeat of extensive water level variation at Lake Belton during the spring and summer of 2016 (Figure 25c) due to dam outlet structure repair was likely appeared to have a similar effect on mussel densities (Figure 7c). These major reductions of zebra mussel population densities at the end of 2015 appeared to result in a depurate spring 2016 spawn marked by relatively poor settlement of a spring 2016 cohort which in turn lead to a reduced settlement of a fall 2016 cohort at all three lakes (Figures 7a-c, 26a-c). As water levels remained relatively stable near conservation pool in 2016 extending into August 2017, the fall 2016 cohorts (Figure 10 panels 1-3) appeared to have settled at densities high enough to support a successful spring 2017 spawn resulting a greatly increased spring 2017 cohort juvenile settlement at Lakes Texoma and Belton, but not Lake Ray Roberts where low pH ( $\leq 7.4$ ) through 2017 continued to suppress veliger development and juvenile settlement (Figures 7a-c, 9 panels 1-3, 25a-c).

In Texas, where annual precipitation and, thus, degree of lake level variation can vary greatly from year to year, it is likely that the resulting annual variations in lake water levels will lead to boom-bust zebra mussel population density cycles similar to those recorded in this study, marked by increases in mussel density during years with relatively stable water levels and decreases during years marked by extensive water level variation. Thus, it is interesting that in 2016 and 2017 when water levels have been relatively stable in many Texas water bodies that new zebra mussel populations have become established in six water bodies including Lakes Stillhouse Hollow, Eagle Mountain, Worth, Canyon, Travis and Austin (Texas Parks and Wildlife Department 2016a, 2016b, 2017c, 2017d, 2017e), a record number of infestations since zebra mussels first arrived in the state at Lake Texoma in 2009 (Texas Parks and Wildlife Department 2009, 2017b). Thus, concerned managers and raw-water using facilities should expect that their source waters are more likely to be infested by mussels during extended periods of water level stability. The potential that extensive water level variation may have caused major reductions in zebra mussel population density and reproductive success in Lakes Texoma, Ray Roberts and Belton in 2015 also suggests that planned water level draw-downs or retentions to raise levels could be a component of zebra mussel control and management in at least those Texas water bodies where such planned water level manipulations are feasible (McMahon et al. 1993, Cohen et al. 2007).

These new results suggest that zebra mussel populations in Texas water bodies may undergo boom-bust population cycles as reported by Strayer and Malcom (2006) and Strayer et al. (2011) in the lower Hudson River, NY. Our study has presented data that suggests that these boom-bust cycles in zebra mussel densities are likely to be associated with the degree to which an infested water body may periodically undergo major annual changes in water level. Based on the results presented here for Lakes Texoma and Belton, it appears to take 1.5-2.0 years for mussel population densities to begin to recover from such crashes and may require 1-2 further years for populations to re-attain the high densities previously developed during periods of relatively stable water levels. The data also suggest that zebra mussels are likely to develop denser populations in water bodies of low annual water level variation as long as surface water temperatures do not exceed the mussel's incipient upper lethal temperature of 32°C during summer months. It also suggests that water bodies routinely undergoing extensive annual water level variation may be more resistant to the establishment of sustainable reproducing zebra mussel populations than those with relatively stable water levels if all other physical-chemical parameters are favorable for mussel invasion.

Because recent zebra mussel population collapses no longer appear to be a permanent feature in Texas water bodies, but, instead, are likely to be cyclic dependent on environmental conditions, raw-water using facilities should not expect that zebra mussel population collapses after initial invasion and subsequent population explosion will be a permanent feature of their source water bodies. Therefore, when developing plans to control mussel macrofouling, they should consider developing long-term, environmentally acceptable control/mitigation solutions including infrastructure modifications that can be implemented relatively rapidly after mussel invasion of their source waters rather than relying only on short-term, stop-gap, less environmentally acceptable solutions such as molluscicide application.

While this research has elucidated the possibility of boom-bust zebra mussel population cycles in Texas water bodies in association with variation in environmental conditions, particularly extensive water level variation, further monitoring of zebra mussel populations in infested Texas water bodies will be required to confirm the existence of such cycles, their durations and causes. Thus, long-term monitoring of zebra mussel populations in both presently-infested and newly-invaded Texas water bodies should continue in order to determine if this preliminary report of collapse-recovery cycles in Lakes Texoma and Belton are unique only to those lakes or are likely to be a general characteristic of the majority of Texas water bodies so as to better inform future zebra mussel management, control and eradication decisions on the part of water body managers, stakeholders and raw-water using facilities.

## **ACKNOWLEDGEMENTS**

The authors wish to express their deep appreciation to Colette O'Byrne McMahon for her assistance with field sampling, field note taking and the compilation of hourly surface water temperatures into daily mean temperatures throughout the course of this study. She did this voluntarily without fee and, without her devoted assistance, this study could not have been completed. We would also like to thank the managers of the marinas where the study was conducted without whose help and cooperation the study could not have been completed. They include, Maria Boren, Office Manager and the staff of the Eisenhower Yacht Club on Lake Texoma, Bill Williams, Manager of the Lake Ray Roberts Marina and Roger who let us use his boat slip to deploy our settlement monitors and collect plankton samples, the entire staff of Franks Marina on Lake Belton who always went out of their way to assist us, Ryan Miller, Manager of the Cottonwood Creek Marina on Lake Lewisville for his courtesy, keen interest and support as well as that of his staff, and Casey Trimble, Harbor Master and Brant Briggs, General Manager, and the staff of the Fort Worth Boat Club on Eagle Mountain Lake for their strong interest in and support of this study. We acknowledge Brian Van Zee and Monica McGarrity of Inland Fisheries, Texas Parks and Wildlife Department, for their extensive review and editing of the initial draft of this report which greatly improved its final version. This research project was supported by a grant from the Texas Parks and Wildlife Department to Robert F. McMahon.

## Literature Cited

- Alderstein S, Nalepa TF, Vanderploeg HA, Fahnenstiel GL. 2014. Trends in phytoplankton, zooplankton, and macroinvertebrates in Saginaw Bay relative to zebra mussel (*Dreissena polymorpha*) colonization: A generalized linear model approach. Pages 525-543 in Quagga and Zebra Mussels: Biology, Impacts, and Control, Second Edition, Nalepa TF, Schoesser DW (Eds.). CRC Press, Boca Raton, FL.
- Benson A. 2014. Chronological history of zebra and quagga mussels (Dreissenidae) in North America, 1988-2010. Pages 9-30 in Quagga and Zebra Mussels: Biology, Impacts, and Control (Nalepa TF, Schoesser DW (Eds.). CRC Press, Boca Raton, FL.
- Boeckman CJ, Bidwell JR. 2014. Density, growth, and reproduction of zebra mussels (*Dreissena polymorpha*) in two Oklahoma reservoirs. Pages 369-382 in Quagga and Zebra mussels: Biology, Impacts, and Control. Nalepa TF, Schloesser DW (Eds.). CRC Press, Boca Raton, FL.
- Bootsma HA, Liao Q. 2014. Nutrient cycling by dreissenid mussels: controlling factors and ecosystem response. Pages 555-574 in Quagga and Zebra Mussels: Biology, Impacts, and Control. Nalepa TF, Schloesser DW (Eds.). CRC Press, Boca Raton.
- Churchill JC. 2013. Spatio-temporal spawning and larval dynamics of a zebra mussel (*Dreissena polymorpha*) population in a north Texas reservoir: implications for invasions in the southern United States. Aquatic Invasions 8: 389-406
- Claudi R, Mackie JL. 1993. Practical Manual for Zebra Mussel Monitoring and Control. Lewis Publishers, Boca Raton, FL. 227 pp.
- Cohen AN, Moll R, Carlton JT, O'Neill RO, Jr., Anderson L, Mole PB. 2007. California's Response to the Zebra/Quagga Mussel Invasion in the West. California Department of Fish and Game, Sacramento, CA. 30 pp. Downloaded from <https://www.usbr.gov/lc/region/programs/quagga/docs/CDFGResponsePlan.pdf> on 09/19/2017.
- Dorgelo J, Kraak MHS. 1993. Seasonal variation in tissue dry biomass and its relative ash and organic carbon and nitrogen content in the freshwater mussel *Dreissena polymorpha* (Pallas). Archiv fur Hydrobiologie 127(4): 409-421.
- Fetisov AN, Rubanovich AV, Slipchenko TS, Shevechenko VA. 1991. Effect of the temperature factor on the genetic structure of populations of *Dreissena polymorpha* (Bivalvia). Soviet Genetics 26: 1159-1162.
- Garton DW, Haag WR. 1993. Seasonal reproductive cycles and settlement patterns of *Dreissena polymorpha* in western Lake Erie. Pages 111-128 in Zebra Mussels: Biology, Impacts, and Control, Nalepa TF, Schloesser DW (Eds.). CRC Press, Inc., Boca Raton, FL.
- Gregs R, Rinke K, Rothhaupt K-O. 2009. Zebra mussels mediate benthic-pelagic coupling by biodeposition and changing detrital stoichiometry. Freshwater Biology 54:1379-1391.
- Idrisi N, Mills EL, Rudstam LG, Stewart DJ. 2001. Impact of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Science 58:1430-1441.
- Jantz B, Neumann D. 1998. Growth and reproductive cycle of the zebra mussel in the River Rhine as studied in a river bypass. Oecologia 114: 213-225.
- Johnson, LE. 1995. Enhanced early detection and enumeration of zebra mussel (*Dreissena* spp.) veligers using cross-polarized microscopy. Hydrobiologia 312: 139-146.
- Johnson PD, McMahon RF. 1998. Effects of temperature and chronic hypoxia on survivorship of the zebra mussel *Dreissena polymorpha* and Asian clam *Corbicula fluminea*. Canadian Journal of Fisheries and Aquatic Science 55: 1564-1572.
- Kornobis S. 1977. Ecology of *Dreissena polymorpha* (Pall.) (Dreissenidae, Bivalvia) in lakes receiving heated water discharges. Polskie Archiwum Hydrobiologii. 24: 531-545.

- de Kozłowski S, Page C, Whetstone J. 2002. Zebra mussels in South Carolina: the potential risk of infestation. South Carolina Department of Natural Resources, Columbia, SC. 14 pp. Downloaded from <http://www.dnr.sc.gov/invasiveweeds/img/zebramusselassessment.pdf> on February 16, 2014.
- Lower Colorado River Authority. 2017. Average surface water temperatures of the Highland Lakes 1982-2009. Downloaded from <https://www.lcra.org/water/quality/Documents/waterLakeTemps.pdf> on 09/11/2017.
- Lucy F, Sullivan M, Minchin D. 2005. Nutrient Levels and the Zebra Mussel Population in Lough Key (2000-MS-M1): Synthesis Report. Environmental Protection Agency. Wexford, Ireland. 25 pp.
- MacIsaac HJ. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *American Zoologist* 36: 287-299.
- Mackie GL, Claudi R. 2010. Monitoring and Control of Macrofouling Mollusks in Freshwater Systems. CRC Press, Boca Raton, FL. 508 pp.
- McMahon RF. 1996. The physiological ecology of the zebra mussel, *Dreissena polymorpha*, in North America and Europe. *American Zoologist* 36: 239-260.
- McMahon RF. 2015. Implementation of a cost-effective monitoring and early detection program for zebra mussel invasion of Texas water bodies. Pages 349-374 in Wong D W-H, Gerstenberger SL (eds.) *Biology and Management of Invasive Quagga/Zebra Mussels in the Western United States*. CRC Press, Boca Raton, FL.
- McMahon RF, Bogan AE. 2001. Bivalves. Pages 331-428 in *Ecology and Classification of North American Freshwater Invertebrates, Second Edition*, Thorp JH, Covich, AP (Eds.). Academic Press, New York, NY.
- McMahon RF, Ussery TA, Clarke M. 1993. Use of Emersion as a Zebra Mussel Control Method. Technical Report EL-93-1. U.S. Army Corps of Engineers, Washington, DC. 27 pp.
- Morse JT. 2009. Thermal tolerance, physiologic condition, and population genetics of dreissenid mussels. PhD. Dissertation, The University of Texas at Arlington. 280 pp.
- Nalepa TF, Cavaletto JF, Ford M, Gordon WM, Wimmer M. 1993. Seasonal and annual variation in weight and biochemical content of the zebra mussel, *Dreissena polymorpha*, in Lake St. Clair. *Journal of Great Lakes Research* 19(3): 541-552.
- Nichols SJ. 1996. Variations in the reproductive cycle of *Dreissena polymorpha* in Europe, Russia, and North America. *American Zoologist* 36: 3311-325.
- Nichols SJ, Black MG. 1994. Identification of larvae: the zebra mussel (*Dreissena polymorpha*), quagga mussel (*Dreissena rostriformis bugensis*) and Asian clam (*Corbicula fluminea*). *Can. J. Zool.* 72:406-417.
- Paukstis GL, Tucker, JK, Bronikowski, AM, Janzen FJ. 1999. Survivorship of aerially exposed zebra mussels (*Dreissena polymorpha*) under laboratory conditions. *Journal of Freshwater Ecology* 14:511-517.
- Pimentel D, Zuniga R, Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273-288.
- Reeders HH, bij de Vaate A, Noordhuis R. 1993. Pages 339-451 in *Zebra Mussels: Biology, Impacts, and Control*, Nalepa TF, Schloesser DW (Eds.). CRC Press, Boca Raton FL.
- Rice EW, Baird RB, Eaton AD, Clesceri LS (Editors). 2012. *Standard Methods for the Examination of Water and Wastewater*, 22<sup>nd</sup> Edition. American Public Health Association, American Water Works Association, Water Environment Federation. 1496 pp.
- Ricciardi AR, Serrouya R, Whoriskey FG. 1995. Aerial exposure tolerance of zebra and quagga mussels (Bivalvia: Dreissenidae): implications for overland dispersal. *Canadian Journal of Fisheries and Aquatic Sciences* 52:470-477.

- Sinicyna OO, Zdanowski B. 2007. Development of the zebra mussel, *Dreissena polymorpha* (Pall.), population in a heated lakes ecosystem. 1. Changes in population structure. Archives of Polish Fisheries 15: 369-385
- Sprung M. 1987. Ecological requirements of developing *Dreissena polymorpha* eggs. Archiv fur Hydrobiologie Supplement 79(1): 69-86.
- Sprung M. 1993. The other life: an account of present knowledge of the larval phase of *Dreissena polymorpha*. Pages 39-53 in Zebra Mussels: Biology, Impacts, and Control, Nalepa TF, Schloesser DW (Eds.). CRC Press, Boca Raton, FL.
- Stańczykowska A. 1976. Occurrence and growth of *Dreissena polymorpha* in lakes included in a cooling system. Roczniki Nauki Ser. H. Rybactwo 97(3): 109-122.
- Stańczykowska A, Lewandowski K. 1993. Thirty years of studies of *Dreissena polymorpha* ecology in Mazurian Lakes of northeastern Poland. Pages 3-37 in Zebra Mussels: Biology, Impacts, and Control, Nalepa TF, Schloesser DW (Eds.). CRC Press, Boca Raton, FL.
- Strayer DL, Malcom HM. 2006. Long-term demography of a zebra mussel (*Dreissena polymorpha*) population. Freshwater Biology 51: 117-130.
- Strayer D L, Cid N, Malcom HM. 2011. Long-term changes in a population of an invasive bivalve and its effects. Oecologia 165: 1063–1072.
- Stoeckmann AM, Garton DW. 1997. A seasonal energy budget for zebra mussels (*Dreissena polymorpha*) in western Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 54: 2743-2751.
- Texas Parks and Wildlife Department. 2009. Lone zebra mussel found in Lake Texoma. Downloaded from <https://tpwd.texas.gov/newsmedia/releases/?req=20090421a> on 09/15/2017.
- Texas Parks and Wildlife Department. 2015. After flood, boaters reminded to help stem spread of invasive zebra mussels. Downloaded from <https://tpwd.texas.gov/newsmedia/releases/?req=20150709b> on 08/30/2017.
- Texas Parks and Wildlife Department. 2016a. Zebra mussels discovered in Stillhouse Hollow reservoir. Downloaded from <https://tpwd.texas.gov/newsmedia/releases/?req=20160812a> on 09/12/2017
- Texas Parks and Wildlife Department. 2016b. Three more Texas lakes affected by zebra mussels. Downloaded from <https://tpwd.texas.gov/newsmedia/releases/?req=20160629b> on 09/15/2017.
- Texas Parks and Wildlife Department. 2017a. Texas freshwater lakes. Downloaded from <https://tpwd.texas.gov/fishboat/fish/recreational/lakes/lakelist.phtml> on 09/04/2017.
- Texas Parks and Wildlife Department. 2017b. News roundup: zebra mussels. Downloaded from [https://tpwd.texas.gov/newsmedia/releases/news\\_roundup/zebra\\_mussels](https://tpwd.texas.gov/newsmedia/releases/news_roundup/zebra_mussels) on 09/04/2017.
- Texas Parks and Wildlife Department. 2017c. Zebra mussels discovered in Canyon Lake. Downloaded from <https://tpwd.texas.gov/newsmedia/releases/?req=20170612a> on 09/12/2017.
- Texas Parks and Wildlife Department. 2017d. Invasive zebra mussels discovered in Lake Travis. Downloaded from <https://tpwd.texas.gov/newsmedia/releases/?req=20170627a> on 09/12/2017.
- Texas Parks and Wildlife Department. 2017e. Lake Austin positive for invasive zebra mussels. Downloaded from <https://tpwd.texas.gov/newsmedia/releases/?req=20170817a> on 09/15/2015.
- US Army Corps of Engineers, Tula District. 2017. DSNT2: Lake Texoma, Denison Dam. Downloaded from <http://www.swt-wc.usace.army.mil/DENI.lakepage.html> on 09/19/2017.
- US Lakes. 2107. Lakes in Texas, United States. Downloaded from <http://www.uslakes.info/USA/Texas/> on 09/18/2017.
- Ussery TA, McMahon RF. 1995. Comparative Study of the Desiccation Resistance of Zebra Mussels (*Dreissena polymorpha*) and Quagga Mussels (*Dreissena bugensis*). Technical Report EL-95-10. U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, MS. 19 pp.
- Walz N. 1978. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance III. Growth under standard conditions. Archiv fur Hydrobiologie Supplement 55(2): 121-141.



- Walz, N. 1979. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. V. Seasonal and nutritional changes in the biochemical composition. Archiv fur Hydrobiologie 55, 235–254.
- Whittier TR, Ringold PL, Herlihy AT, Pierson S. 2008. A calcium-based invasion risk assessment for zebra and quagga mussels (*Dreissena* spp). Frontiers in Ecology and the Environment 6, doi: 10.1890/070073. Accessed from <http://www.esajournals.org/doi/pdf/10.1890/070073> on February 16, 2014.
- Wiśniewski R. 1992. *Dreissena polymorpha* Pallas in the Włocławek Reservoir, its ability to survive during exposure to air. Proceedings of the Ninth International Malacological Congress. 1992:403-406.

Table 1. List of sampling locations for the 2016-2017 study of zebra mussel population dynamics in infested Texas water bodies.

<b>Water Body</b>	<b>Site</b>	<b>Contact</b>	<b>Address</b>	<b>Geographic Coordinates</b>
Lake Belton	Franks Marina	Marina Staff 254-939-76513	3260 Lake Park Road, Belton, Texas 76513	31°6.317' N 97°C 9.169'W
Eagle Mountain Lake	Fort Worth Boat Club	Harbor Master, 817-236-393, ext. 2	10000 Boat Club Road, Fort Worth Texas 76179	32°53.524'N 97°29.146'W
Lake Lewisville	Cottonwood Creek Marina	Marina Manager, 972-292-1100	900 Lobo Lane, Little Elm, Texas 75068	33°8.597'N 96°56.565'W
Lake Ray Roberts	Lake Ray Roberts Marina - Boat House No. 3	Manager, 940-458-7023	1399 Marina Circle, Sanger, Texas 76266	33°22.586'N 97°6.470'W
Lake Texoma	Eisenhower Yacht Club – Boat House No. 6	Office Manager, 903-463-3999 / Superintendent, 817-237-8585	2141 Park Road #20, Denison, Texas 75020	33°49.240'N 96°36.423'W

Table 2. Water body sampling dates for study of zebra mussel population dynamics in five infested Texas water bodies.

<b>Lake Texoma</b>	<b>Lake Ray Roberts</b>	<b>Lake Belton</b>	<b>Eagle Mountain Lake</b>	<b>Lake Lewisville</b>
01/22/2016	01/22/2016	01/30/2016	08/17/2016	07/08/2016
07/10/2016	07/10/2016	07/13/2016*	09/20/2016	09/16/2016
11/05/2016	09/16/2016	08/03/2016	10/30/2016	
12/04/2016	10/21/2016	08/30/2016	12/02/2016	10/21/2016
01/11/2017	12/06/2016	09/25/2016	01/09/2017	12/08/2016
02/23/2017	01/09/2017	11/01/2016	02/10/2017	01/11/2017
03/19/2017	02/10/2017	12/12/2016	03/17/2017	02/23/2017
04/15/2017	03/17/2017	01/13/2017	04/11/2017	03/19/2017
05/27/2017	04/11/2017	02/16/2017	05/19/2017	04/15/2017
07/01/2017	05/19/2017	03/23/2017	07/03/2017	05/27/2017
08/20/2017	07/3/2017	04/13/2017	08/17/2017	07/01/2017
	08/17/2017	05/25/2017		08/20/2017
		06/29/2017		
		08/13/2017		

\*Lake Flooding prevented access to zebra mussel sampling site. Only physical data recorded.

Table 3. Surface water (1.5-2.0 m) physical data (air and water temperature, pH, mg O<sub>2</sub>/l (% O<sub>2</sub>) and conductivity) recorded for each water body sampled for zebra mussels on each sampling date.

Water Body	Drainage	Date	Air Temp (°C)	Water Temp (°C)	pH	mg O <sub>2</sub> /L (% O <sub>2</sub> )	Conductivity (µS)
Belton	Leon-Brazos	01/30/2016	21.1	11.7	7.66	10.33 (95.4%)	388
		07/13/2016*	33.9	29.9	7.53	7.35 (95.9%)	411
		08/03/2016	32.4	29.7	7.67	6.71 (93.5%)	378
		08/30/2016	32.3	29.2	7.86	3.28 (43.6%)	363
		09/25/2016	24.0	28.4	7.25	1.17 (15.1%)	380
		11/01/2016	28.1	24.4	7.45	5.13 (58.7%)	380
		12/12/2016	13.5	16.2	7.73	8.35 (85.2%)	400
		01/13/2017	12.5	12.9	7.65	10.34 (96/1%)	410
		02/16/2017	18.0	14.0	7.54	9.86 (95.1%)	412
		03/23/2017	24.8	17.5	7.60	9.52 (94.5%)	416
		04/13/2017	25.3	20.3	7.83	8.69 (96.7%)	406
		05/25/2017	28.0	23.7	7.65	6.28 (73.5%)	383
		06/29/2017	31.4	27.7	7.51	4.29 (62.5%)	371
08/13/2017	29.9	26.6	7.45	3.68 (48.5%)	379		
Eagle Mountain	Trinity, West Fork	08/17/2016	26.0	29.3	8.08	5.30 (69.7%)	335
		09/20/2016	30.6	29.7	8.39	10.40 (135.9%)	327
		10/30/2016	24.7	22.8	7.65	7.44 (83.55%)	340
		12/02/2016	17.5	16.0	7.28	8.71 (88.0%)	361
		01/9/2017	16.9	8.1	7.64	12.17 (102.2%)	374
		02/10/2017	20.9	12.3	7.58	10.93 (101.9%)	383
		03/17//2017	23.5	16.1	7.82	9.70 (98.8%)	409
		04/11/2017	22.9	19.7	7.68	8.04 (87.6%)	414
		05/19/2017	26.5	23.5	7.63	6.71 (78.9%)	436
07/03/2017	31.6	29.4	8.15	6.64 (86.3%)	402		
08/17/2017	34.3	30.1	7.78	4.52 (60.3%)	452		
Lewisville	Trinity, Elm Fork	07/08/2016	30.9	29.5	8.00	7.51 (98.5%)	268
		09/16/2016	29.6	28.3	8.08	8.12 (114.0%)	268
		10/21/2016	18.6	23.8	NA	7.91 (94.2%)	NA
		12/08/2016	1.9	12.8	7.29	9.71 (91.5%)	326
		01/11/2017	23.5	9.3	7.78	12.46 (107.7%)	332
		02/23/2017	27.6	15.0	7.33	11.08 (109.3%)	337
		03/19/2017	25.6	17.6	7.80	10.91 (113.5%)	348
		04/15/2017	26.1	21.6	8.05	9.10 (102.4%)	361
		05/29/2017	32.0	24.5	7.83	6.68 (85.5%)	351
07/01/2017	27.1	28.8	7.86	5.27 (67.6)	321		
08/20/2017	35.3	30.7	7.87	4.78 (63.2%)	311		

<b>Water Body</b>	<b>Drainage</b>	<b>Date</b>	<b>Air Temp (°C)</b>	<b>Water Temp (°C)</b>	<b>pH</b>	<b>mg O<sub>2</sub>/L (% O<sub>2</sub>)</b>	<b>Conductivity (µS)</b>
Ray Roberts	Trinity, Elm Fork	01/22/2016	3.6	8.2	7.37	11.25 (97.5%)	257
		07/10/2016	25.1	28.3	7.56	6.34 (81.4%)	283
		09/16/2016	26.2	29.1	8.16	7.68 (99.6%)	242
		10/21/2016	15.8	23.0	6.85	7.45 (80.5%)	251
		12/06/2016	11.2	14.2	7.14	9.14 (89.0%)	290
		01/09/2017	9.5	7.2	7.24	12.61 (104.2%)	260
		02/10/2017	14.4	11.1	7.27	11.75 (105.7%)	262
		03/17/2017	20.2	15.0	7.49	9.95 (98.3%)	264
		04/11/2017	16.9	18.6	7.27	9.07 (96.1%)	273
		05/19/2017	25.1	22.3	7.29	7.23 (83.3%)	275
		07/03/2017	27.7	28.5	7.79	5.57 (71.5%)	253
08/17/2017	25.4	28.6	7.24	4.41 (56.8%)	28		
Texoma	Red River	01/22/2016	8.7	8.9	7.74	11.36 (98.5%)	1148
		07/10/2016	30.9	28.8	7.89	6.52 (85.9%)	949
		09/18/2016	23.3	28.5	8.27	7.70 (99.1%)	1175
		11/05/2016	18.2	22.4	7.70	6.29 (72.5%)	1367
		12/04/2016	10.4	16.3	7.49	8.12 (88.7%)	1396
		01/11/2017	19.7	9.2	7.80	11.39 (99.2%)	1603
		02/23/2017	22.0	12.0	7.89	11.39 (105.6%)	1721
		3/19/2017	22.1	13.4	7.77	10.15 (97.5%)	1802
		04/15/2017	22.8	17.8	7.85	7.65 (80.5%)	1876
		05/27/2017	27.0	22.5	7.91	6.17 (70.8%)	1813
		07/1/2017	24.7	26.6	7.82	5.26 (65.8%)	1176
08/20/2017	29.5	28.6	7.84	3.97 (49%)	1590		

## Figures

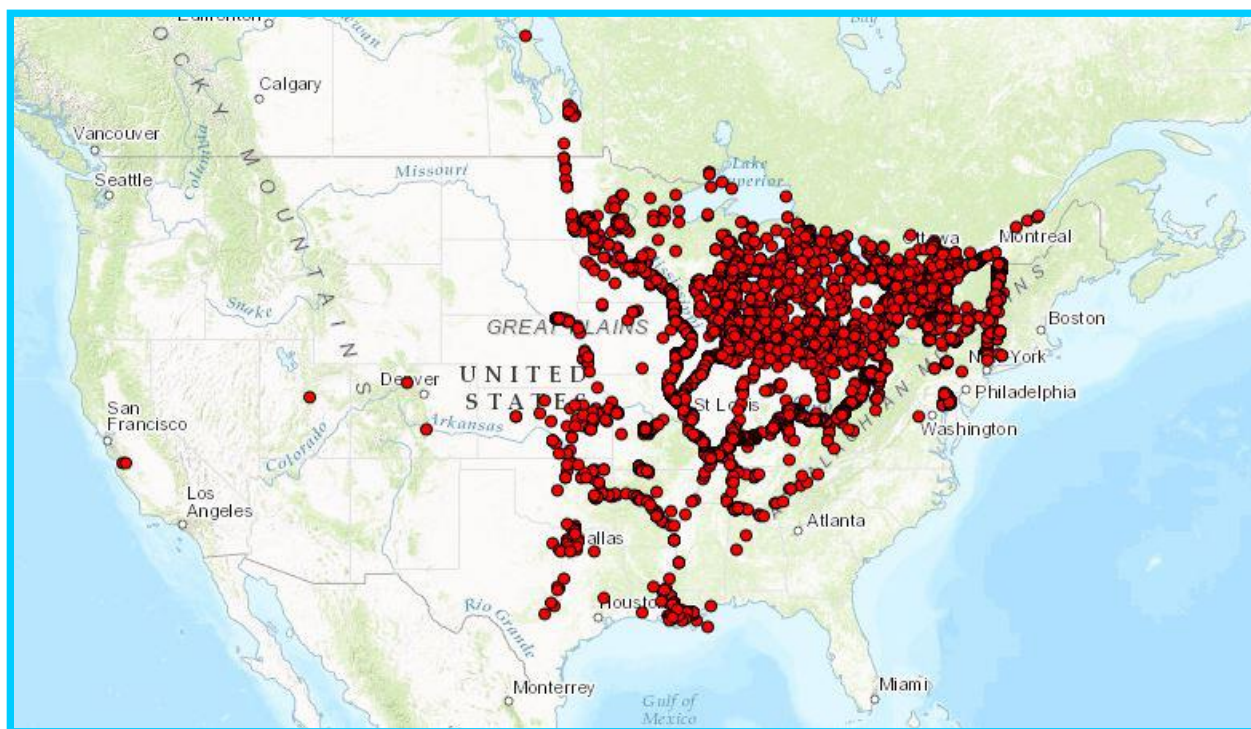


Figure 1. Current distribution of zebra mussel (*Dreissena polymorpha*) sightings in the United States as of 02/03/2017 indicated by red dots. Note the relatively large number of sightings in northeastern and central Texas which have all occurred since 2009 when zebra mussels were first detected in Lake Texoma on the Red River. Source: US Geological Service at <https://nas.er.usgs.gov/queries/SpeciesAnimatedMap.aspx?speciesID=5>.

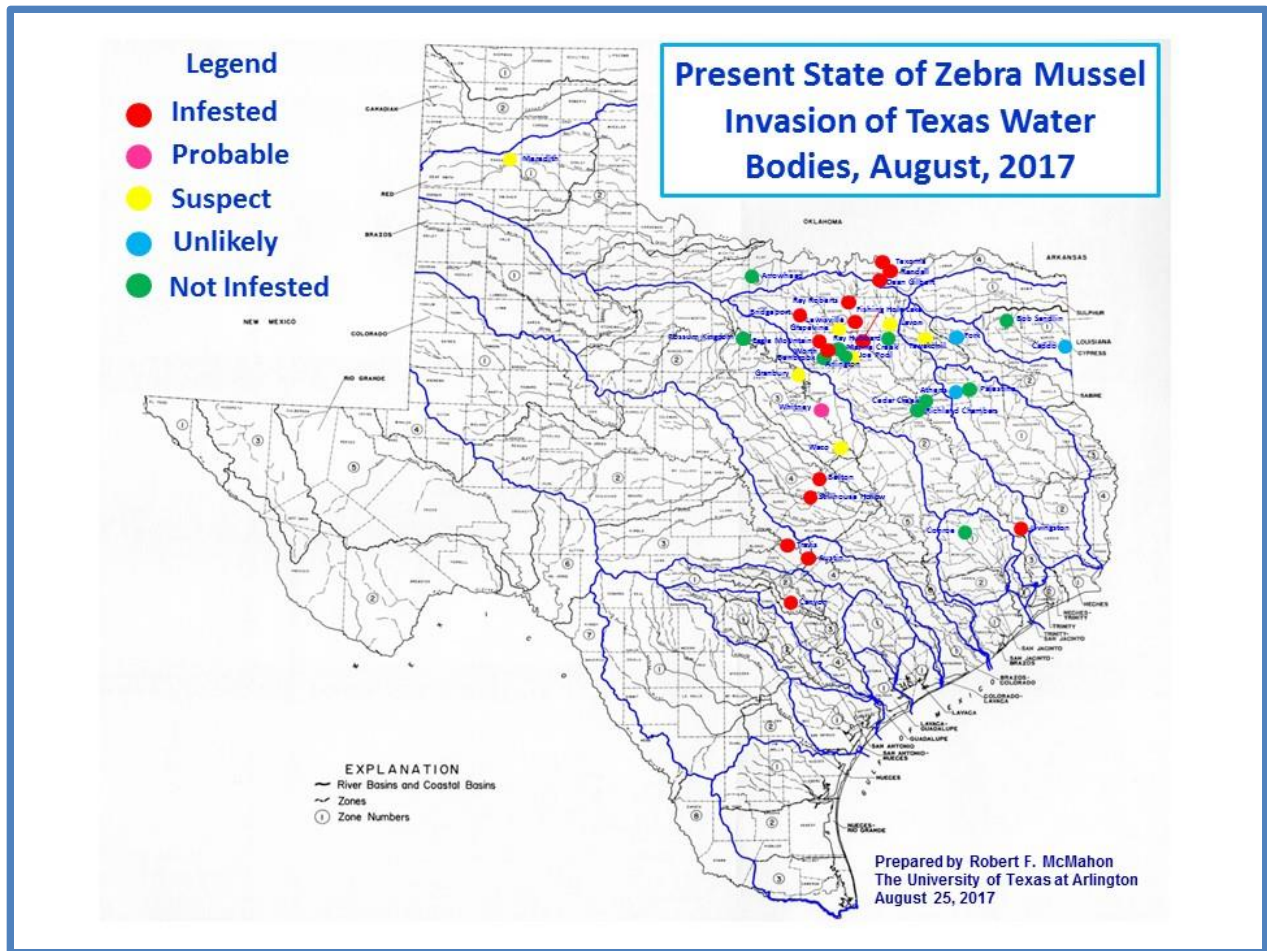


Figure 2. Map of Texas showing the location of water bodies that have been monitored for the presence of zebra mussels. Red dots indicate known zebra mussel infested Texas water bodies (labeled with water body name); magenta dots, probably infested water bodies; yellow dots, suspect water bodies; blue dots, water bodies whose calcium concentrations (<12 mg Ca/l) are too low to support a zebra mussel population; and green dots, monitored lakes able to support a zebra mussel invasion, but not yet reported to harbor zebra mussels as of August 25, 2017.

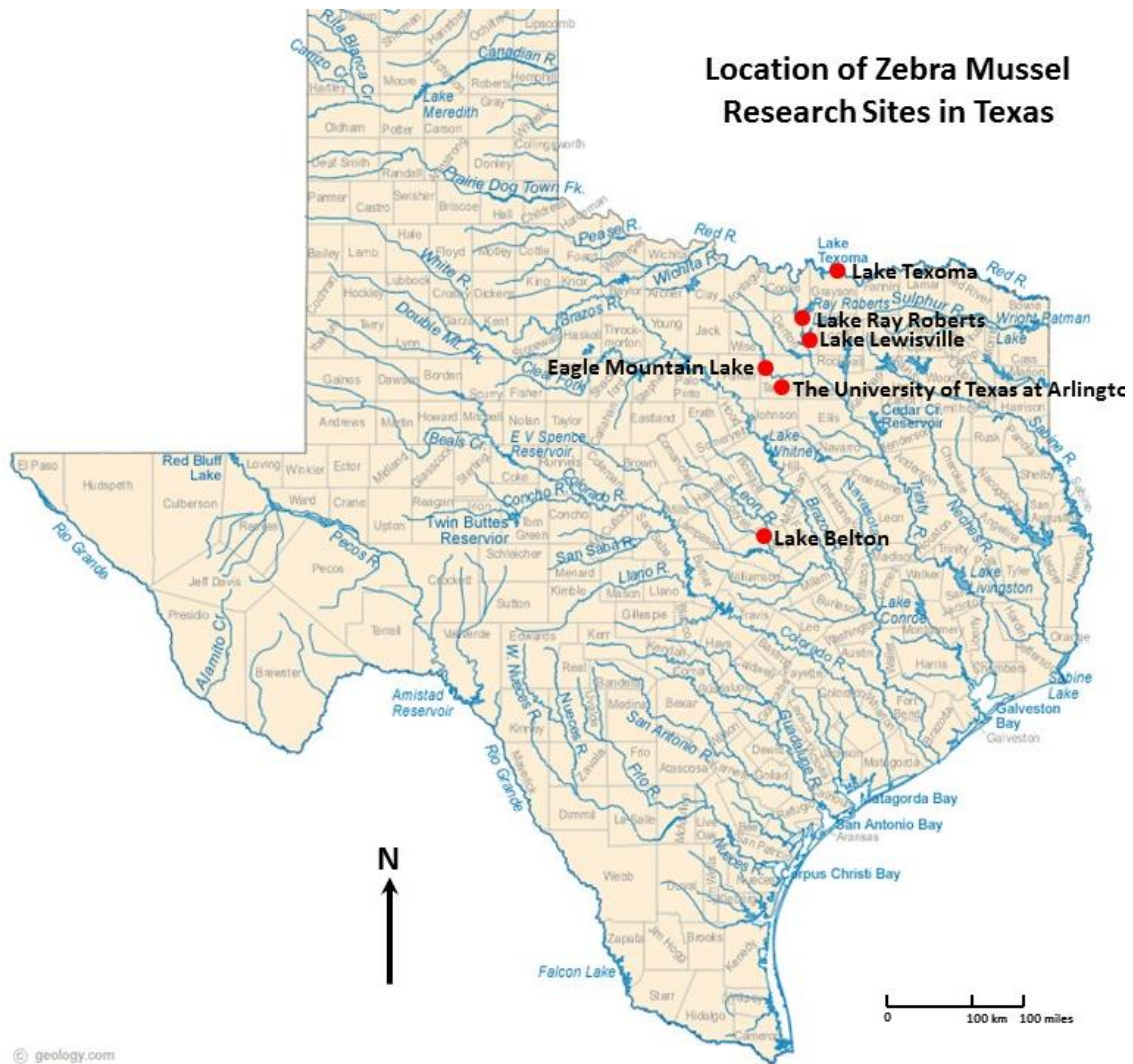


Figure 3. Map of Texas river systems and reservoirs showing the location of the five water bodies, Lakes, Texoma (Red River), Lewisville (Elm Fork, Trinity River), Ray Roberts (Elm Fork, Trinity River), Belton (Leon River) and Eagle Mountain (West Fork, Trinity River) where this study of zebra mussel population dynamics was conducted. These five lakes have sustained zebra mussel infestations since 2009, 2012, 2013, 2015, and 2016 respectively. Laboratory research for this study was conducted and mussel samples maintained in the laboratory of Robert F. McMahon at The University of Texas at Arlington, whose location is also indicated on the map. See Table 1 for specific sampling site location information for the five lakes.

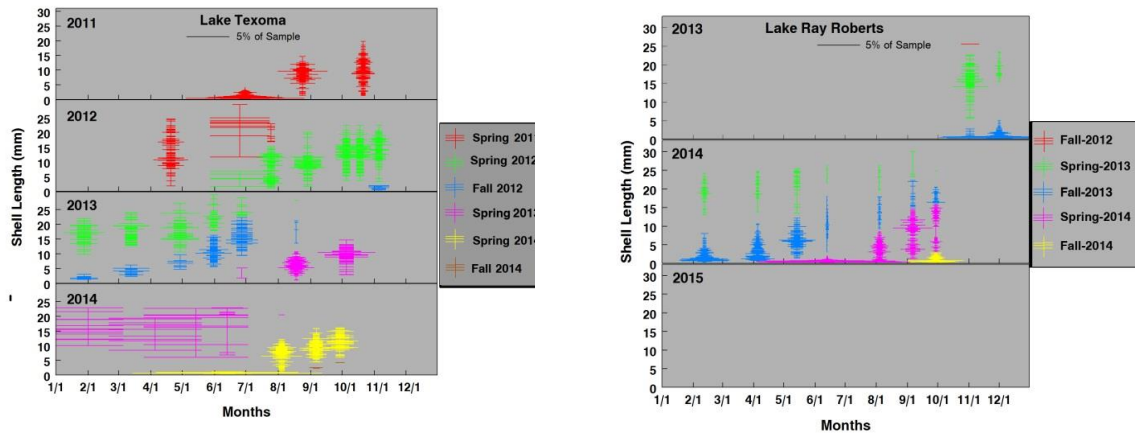


Figure 4. Histograms of shell length distributions of spring and fall cohorts of zebra mussels sampled through time from settlement samplers in Lake Texoma (left panel) and Lake Ray Roberts (right panel). In both panels, different colored histograms represent the size distributions of cohorts settled as a result of spring and fall reproductive events.

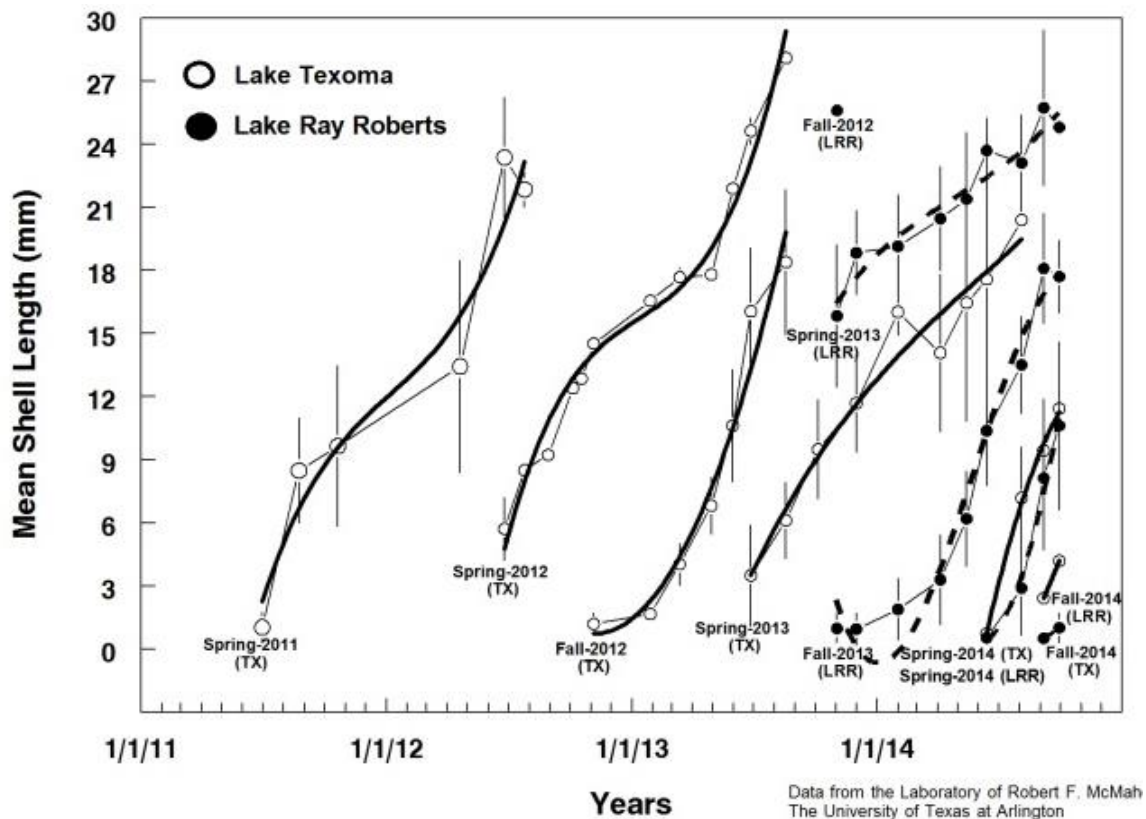


Figure 5. Mean shell lengths of spring and fall juvenile cohorts in monthly-bimonthly samples of zebra mussels taken from settlement samplers in Lake Texoma (open circles, solid lines) and Lake Ray Roberts (closed circles, dashed lines). Lines represent best fits of third order polynomial regressions of cohort mean shell length data to elapsed time in days. Horizontal lines around mean values represent standard errors of the mean.



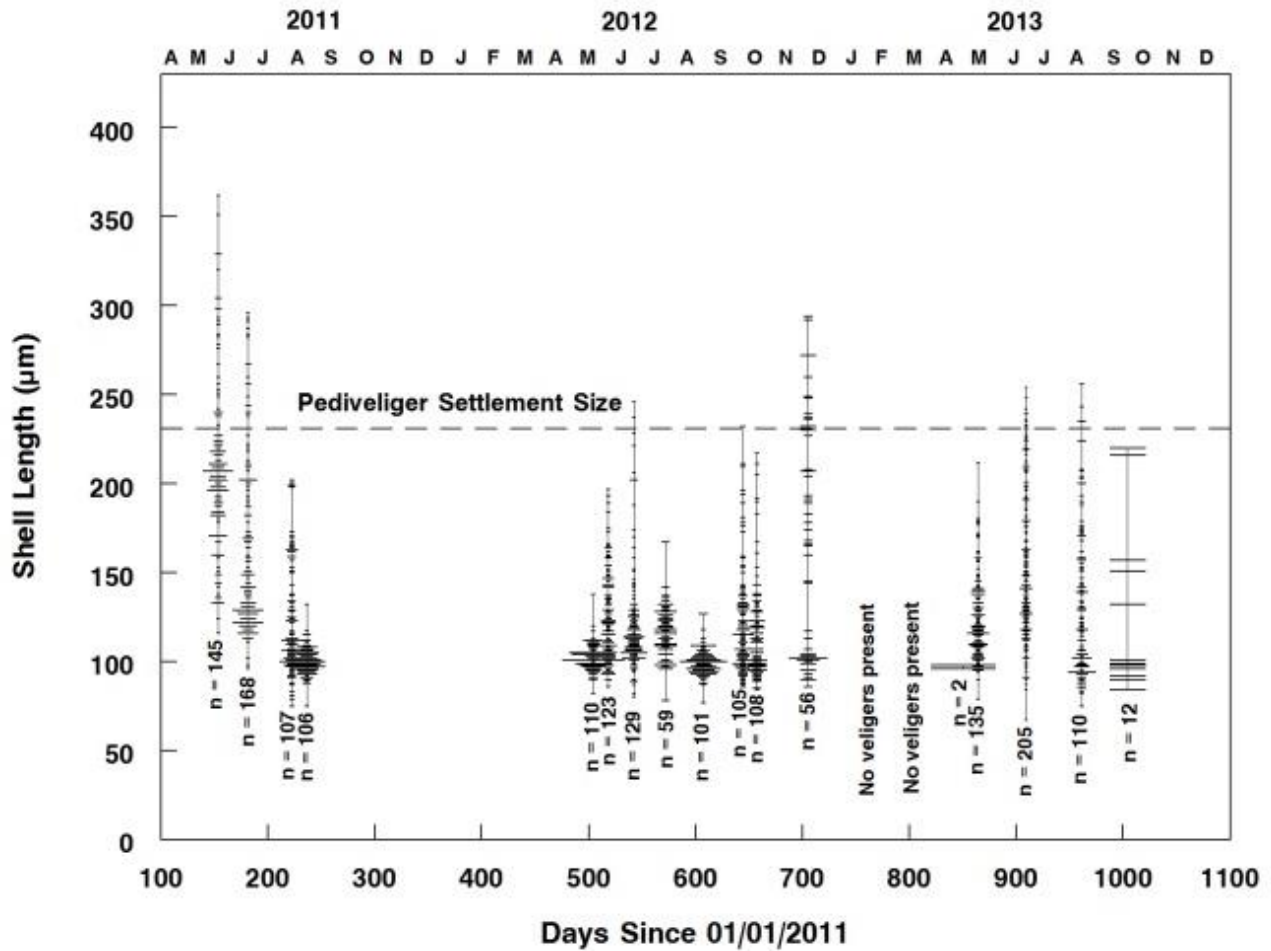


Figure 6. Histograms depicting zebra mussel veliger size distributions in random samples of  $\geq 100$  individuals if available taken during reproductive periods in Lake Texoma from May 2011 through September 2013. Numbers below individual histograms represent sample size. The horizontal dashed line indicates the minimal shell length of 231  $\mu\text{m}$  for veliger larvae to transform into settlement competent pediveligers (Nichols and Black 1994).

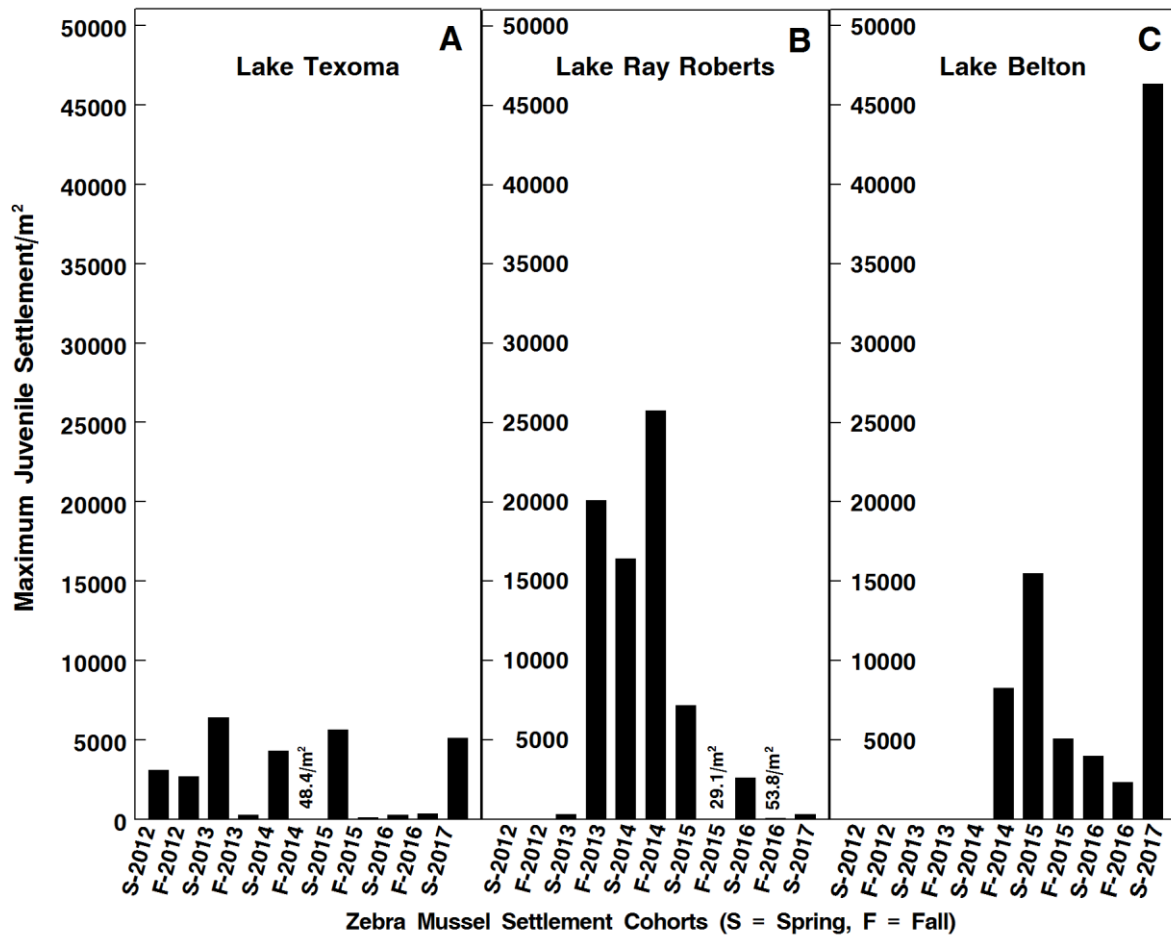


Figure 7. Maximum zebra mussel settlement densities of spring and fall cohorts (vertical axis) recorded on settlement monitors in Texas Lakes Texoma (A), Ray Roberts (B) and Belton (C) during spring (S) and fall (F) settlement periods as indicated by season and year on the horizontal axis.



Figure 8. Nylon scrub pad juvenile mussel settlement monitor fixed to lopes in a house-brick weighted nylon rope with plastic electrical ties. Also note attachment of an Onset™ Hobo temperature data logger fixed to a loop in the rope with a plastic electrical tie.

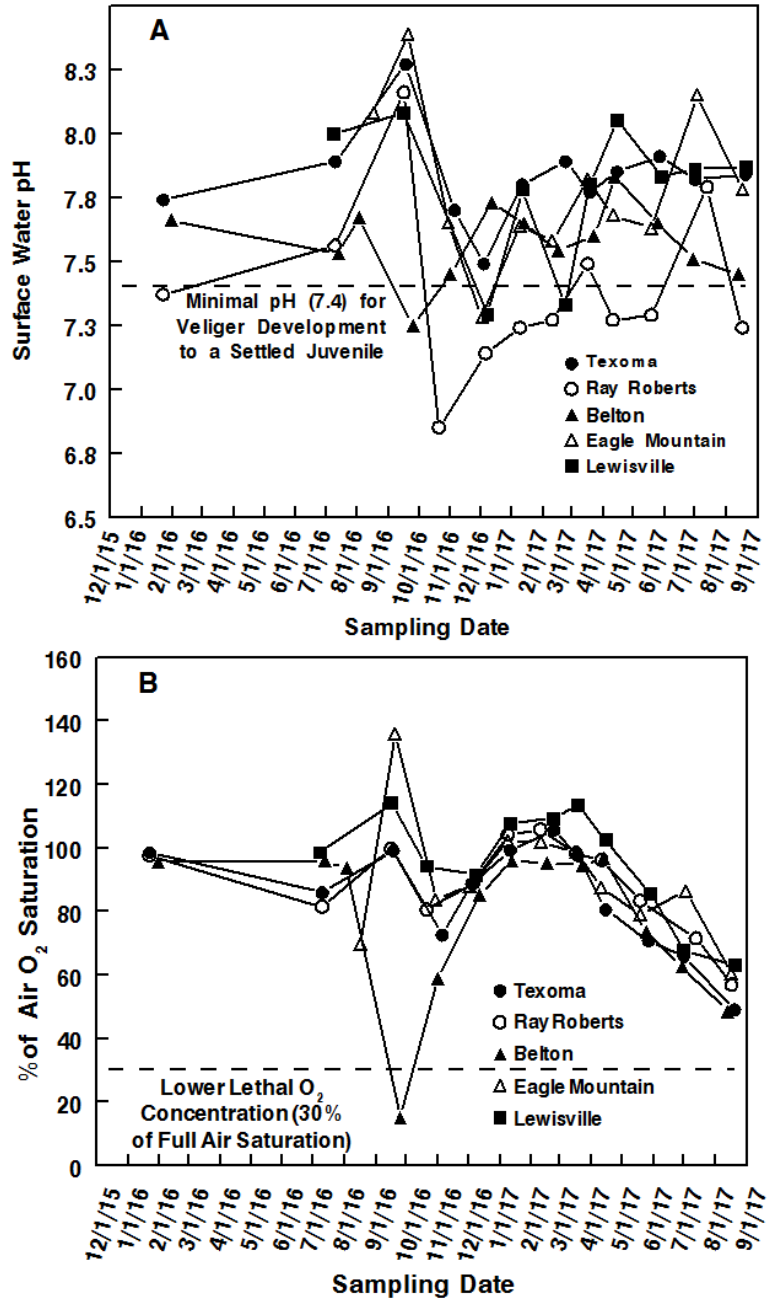


Figure 9. Surface water pH values (Panel A) and oxygen concentrations as percent of full air O<sub>2</sub> saturation (Panel B) from January 2016 through August 2017 taken at sampling sites (Table 1) on Lakes Texoma (solid circles), Ray Roberts (open circles), Belton (solid triangles), Eagle Mountain (open triangles) and Lewisville (solid squares).

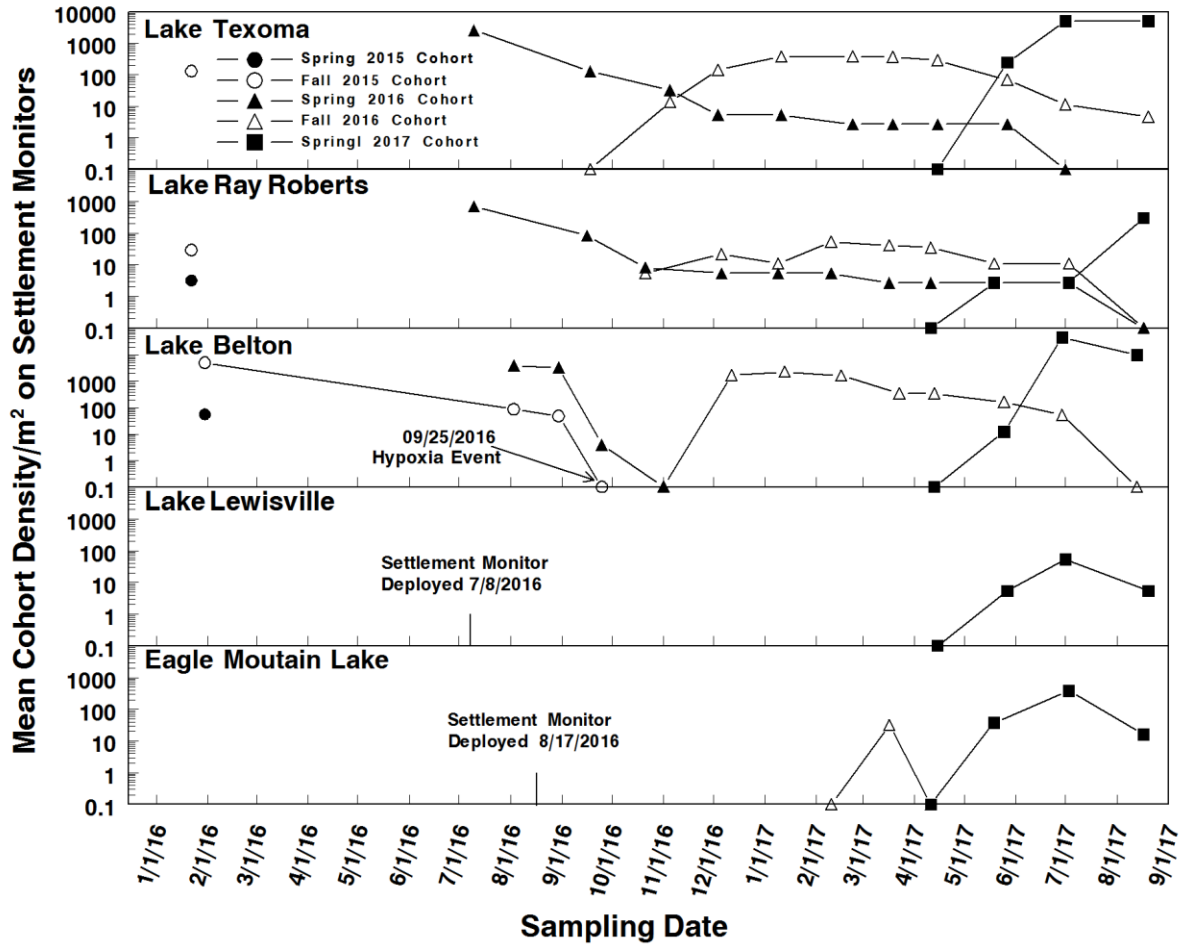


Figure 10. Mean zebra mussel cohort densities (vertical axis) recorded on nylon scouring pad settlement monitors on sampling dates from January 2016 through August 2017 (horizontal axis). Monitors were deployed in Lakes Texoma (first panel), Ray Roberts (second panel), Belton (third panel), Lewisville (fourth panel) and Eagle Mountain (fifth panel) at sites listed in Table 1. Solid circles indicate mean settlement density/m<sup>2</sup> of the spring 2015 mussel cohort; open circles, the fall 2015 cohort; solid triangles, the spring 2016 cohort; open triangles, the fall 2016 cohort; and solid squares, the spring 2017 cohort. Vertical lines from the horizontal axis in the Eagle Mountain Lake and Lake Lewisville panels indicate the dates on which settlement monitors were deployed. Monitors at Lakes Texoma, Ray Roberts and Belton were deployed prior to the start of the study. The arrow in panel 3 indicates a major hypoxia event on 09/25/2016 in Lake Belton where surface water O<sub>2</sub> concentrations fell to 15.1% of full air O<sub>2</sub> saturation lethal to zebra mussels (Table 3, Figure 8b)

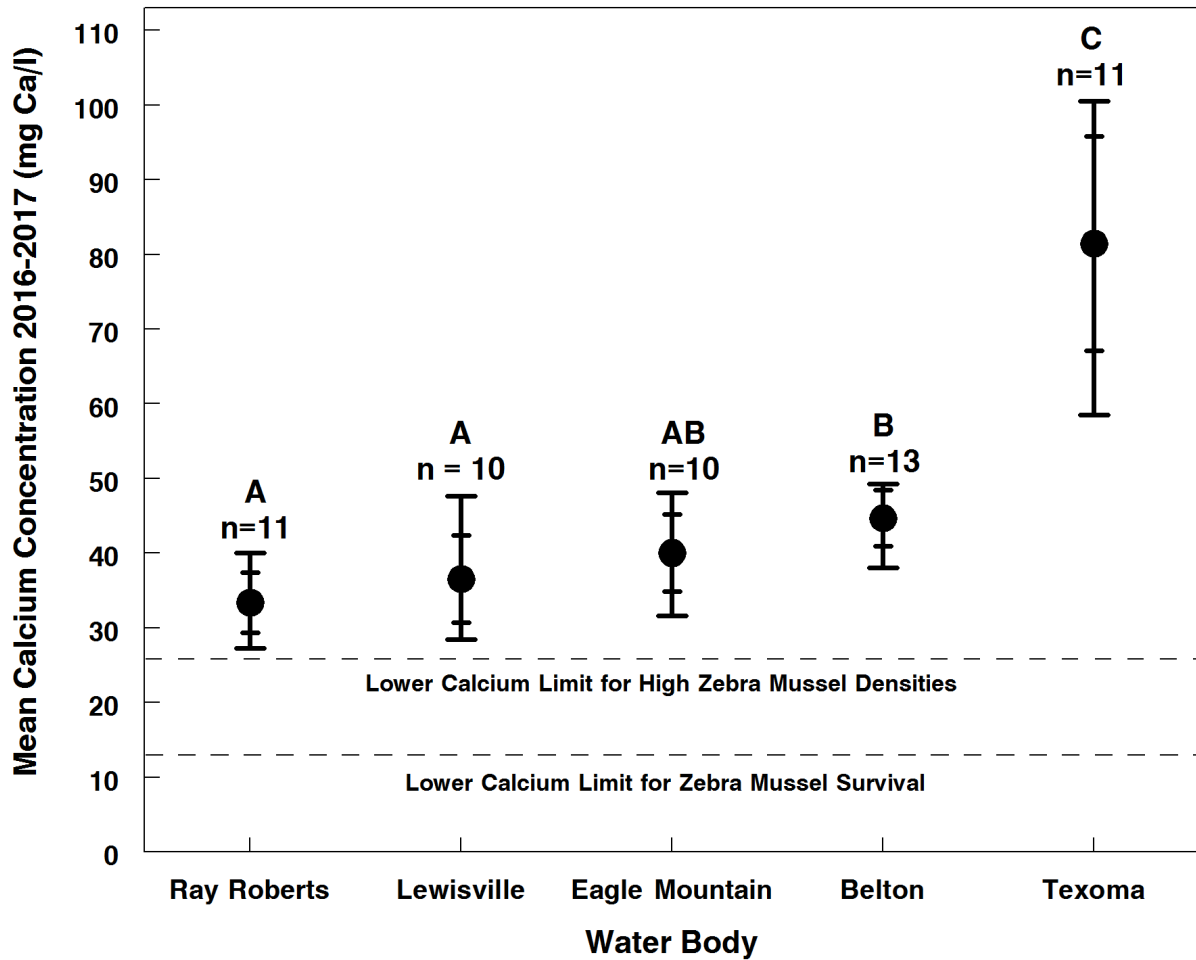


Figure 11. Mean calcium concentrations sampled in Lakes Ray Roberts, Lewisville, Eagle Mountain, Belton, and Texoma between July 2016 and August 2017. Inner vertical error bars around means represent standard deviations of the mean and outer bars the range of recorded concentrations. Different letters above mean points indicate significant ( $p < 0.05$ ) differences in calcium concentration between water bodies as determined by analyzing the data with a one-way Analysis of Variance followed by *post hoc* Fishers Least Squares Significant Difference testing.

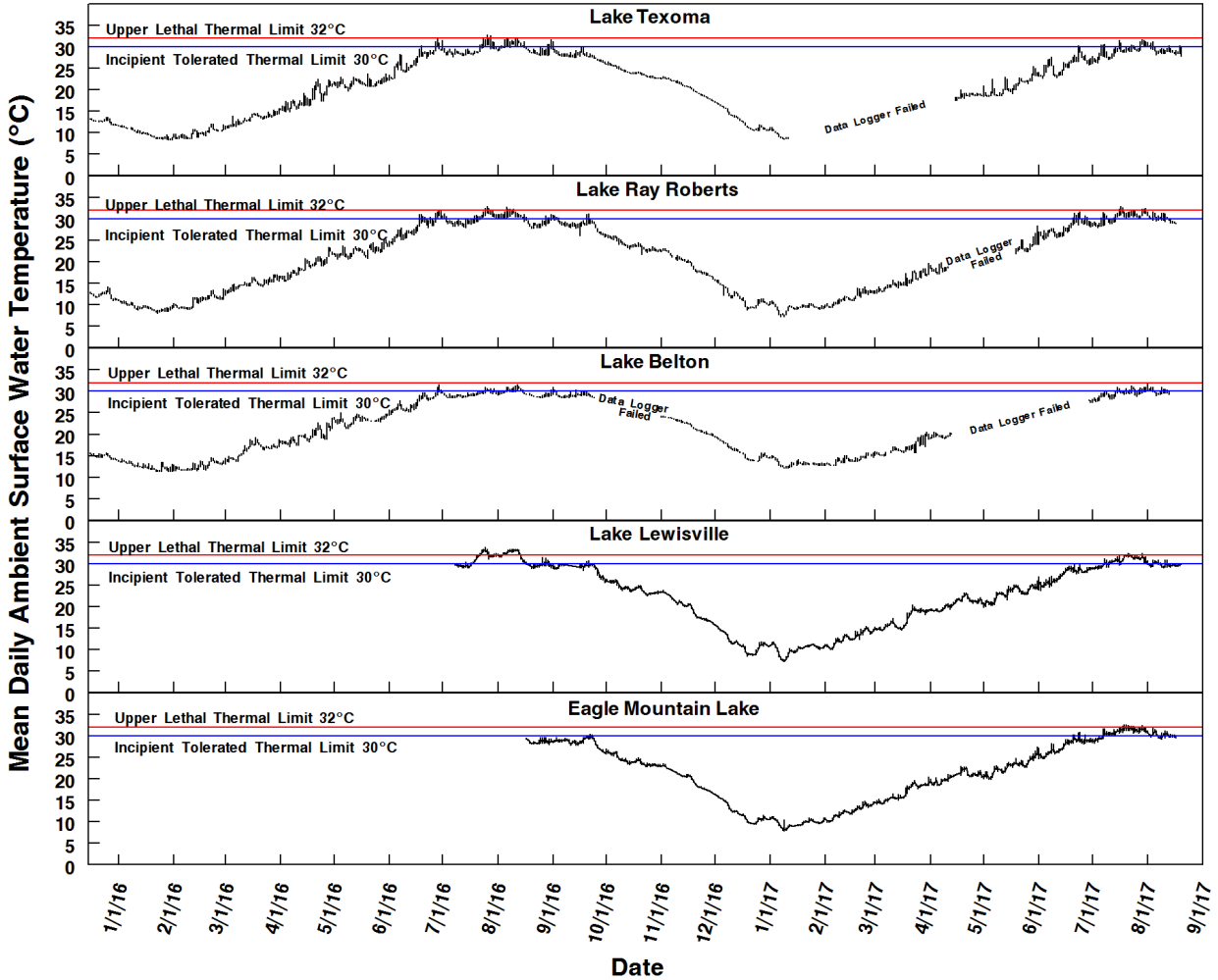


Figure 12. Daily range of ambient water temperatures (vertical bars) recorded from hourly temperature data taken at 1.5-2.0 m depth at each indicated Texas water body sampling site with Onset® Hobo Temperature Data Loggers. The horizontal blue line in each panel represents the long term incipient upper thermal limit of 30°C for maintenance of a zebra mussel population in a Texas water body while the red horizontal line represents the maximum incipient upper lethal limit of 32°C for zebra mussels inhabiting southwestern US water bodies including Texas (Morse 2009, McMahon 2015).

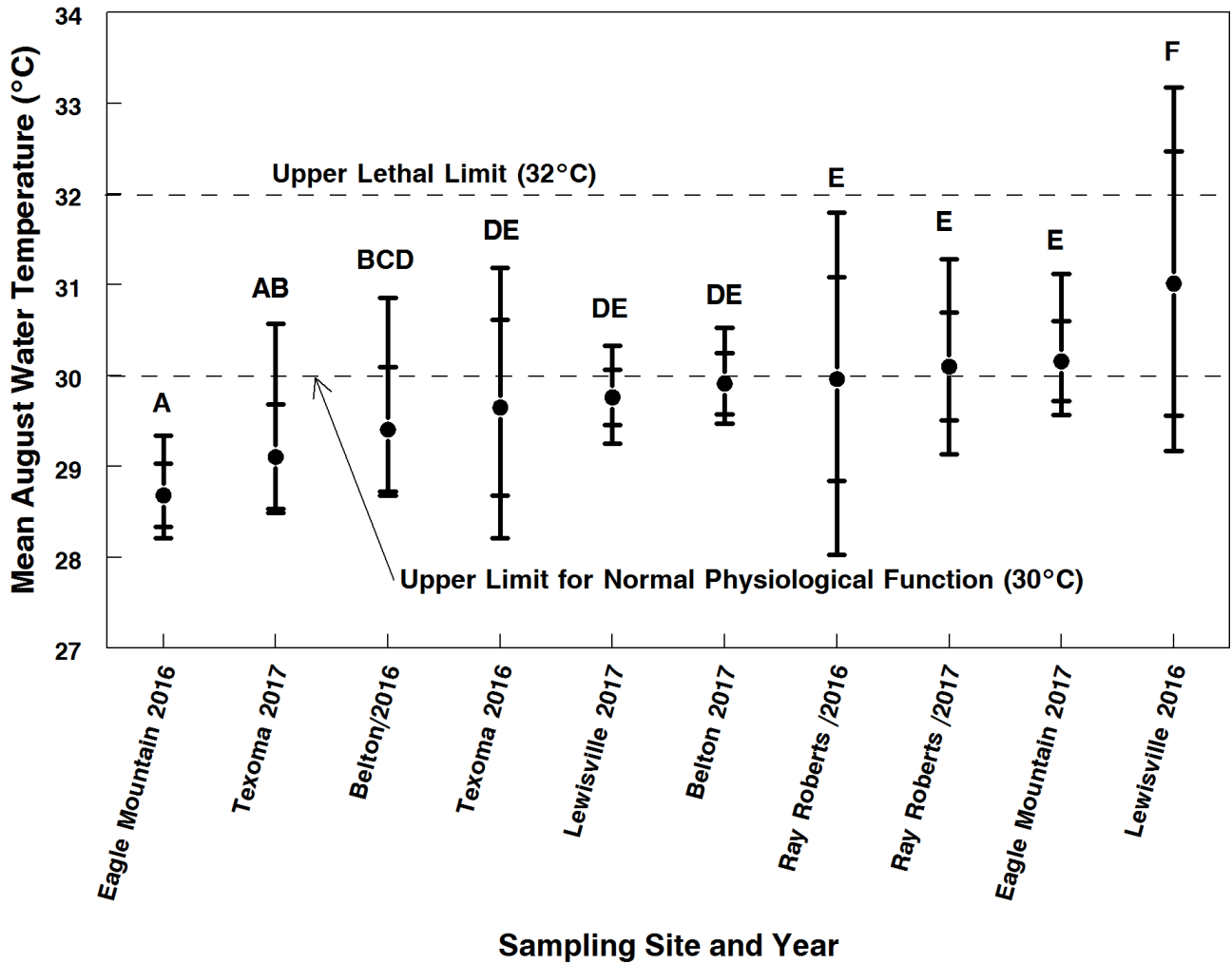


Figure 13. The mean of mean daily surface water temperatures recorded for the month of August in 2016 and 2017 recorded at zebra mussel sampling sites (Table 1) in Lakes Texoma, Ray Roberts, Belton, Lewisville and Eagle Mountain. Inner horizontal bars about means indicate standard deviations while outer bars indicate the minimum and maximum of daily mean temperatures. Similar letters above means indicate that they are not significantly ( $p > 0.05$ ) while dissimilar letters indicate a significant ( $p < 0.05$ ) difference based on Least Squares Significant Difference testing.



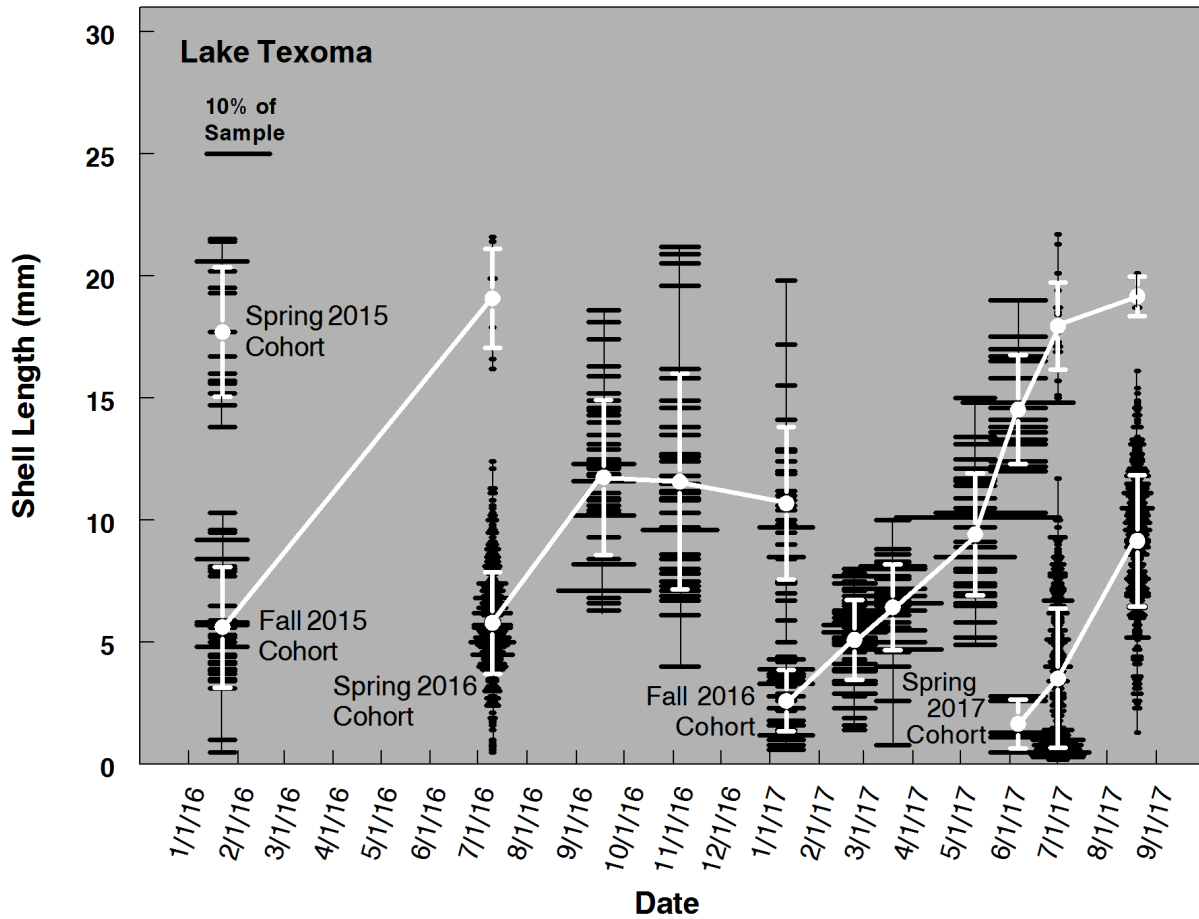


Figure 14. Distribution of zebra mussel shell lengths in samples ( $n > 100$  unless less than 100 specimens were available) taken randomly from settlement bricks at 1.5-2.0 m depth in Lake Texoma from 01/01/16 to 08/20/2017. Horizontal histogram bars for each sample represent percent size-frequency distributions at every 0.1 mm in shell length. Samples are divided into spring and fall reproductive cohorts based on non-overlapping size distributions. Where sample size was  $\leq 10$ , single 5% bars were used to represent individual shell lengths. Solid white circles connected by white lines represent mean cohort shell lengths surrounded by vertical white error bars representing one standard deviation of the mean.

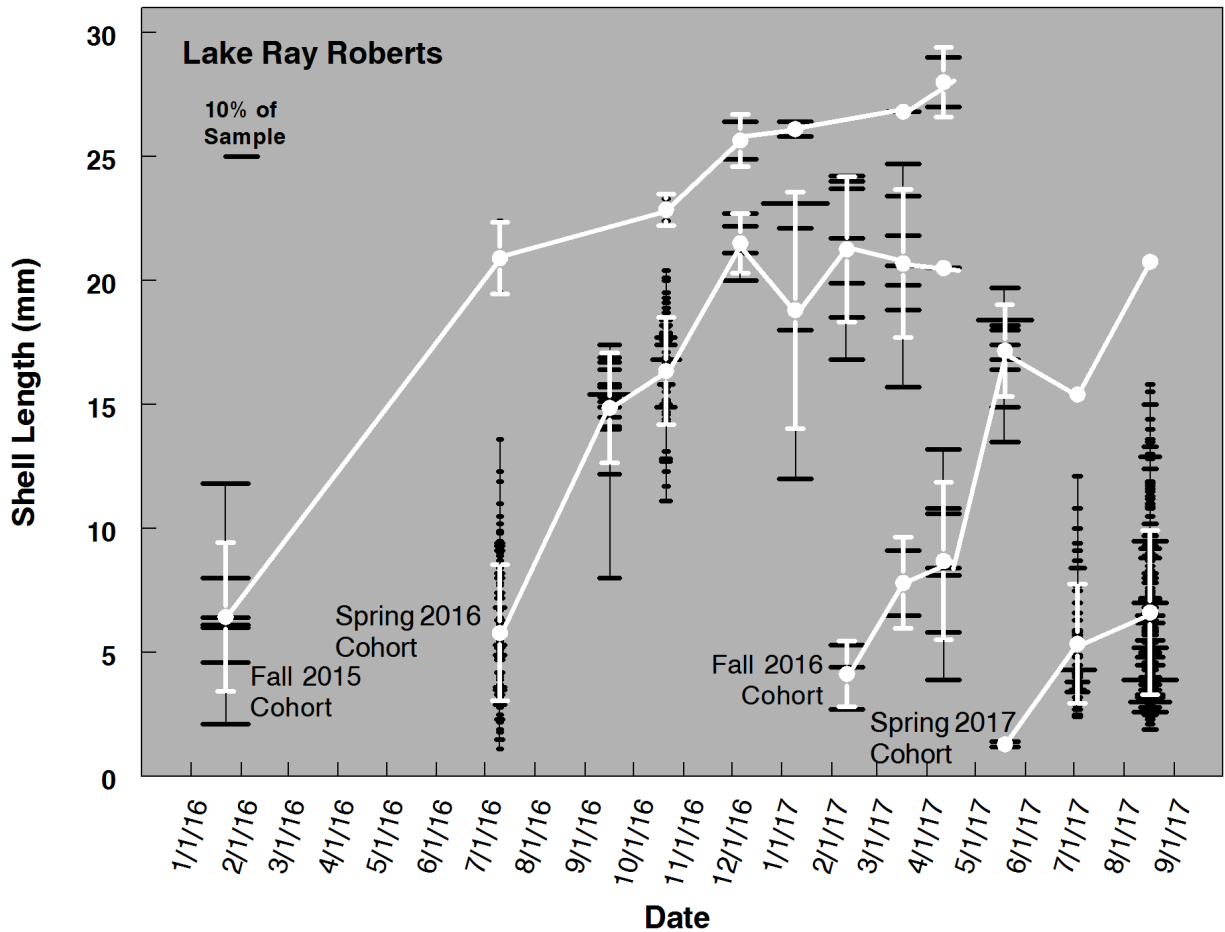


Figure 15. Distribution of zebra mussel shell lengths in samples ( $n > 100$  unless less than 100 specimens were available) taken randomly from settlement bricks at 1.5-2.0 m depth in Lake Ray Roberts from 01/01/16 to 08/17/2017. Horizontal histogram bars for each sample represent percent size-frequency distributions at every 0.1 mm in shell length. Samples are divided into spring and fall reproductive cohorts based on non-overlapping size distributions. Where sample size was  $\leq 10$ , single 5% bars were used to represent individual shell lengths. Solid white circles connected by white lines represent mean cohort shell lengths surrounded by vertical white error bars representing one standard deviation of the mean.

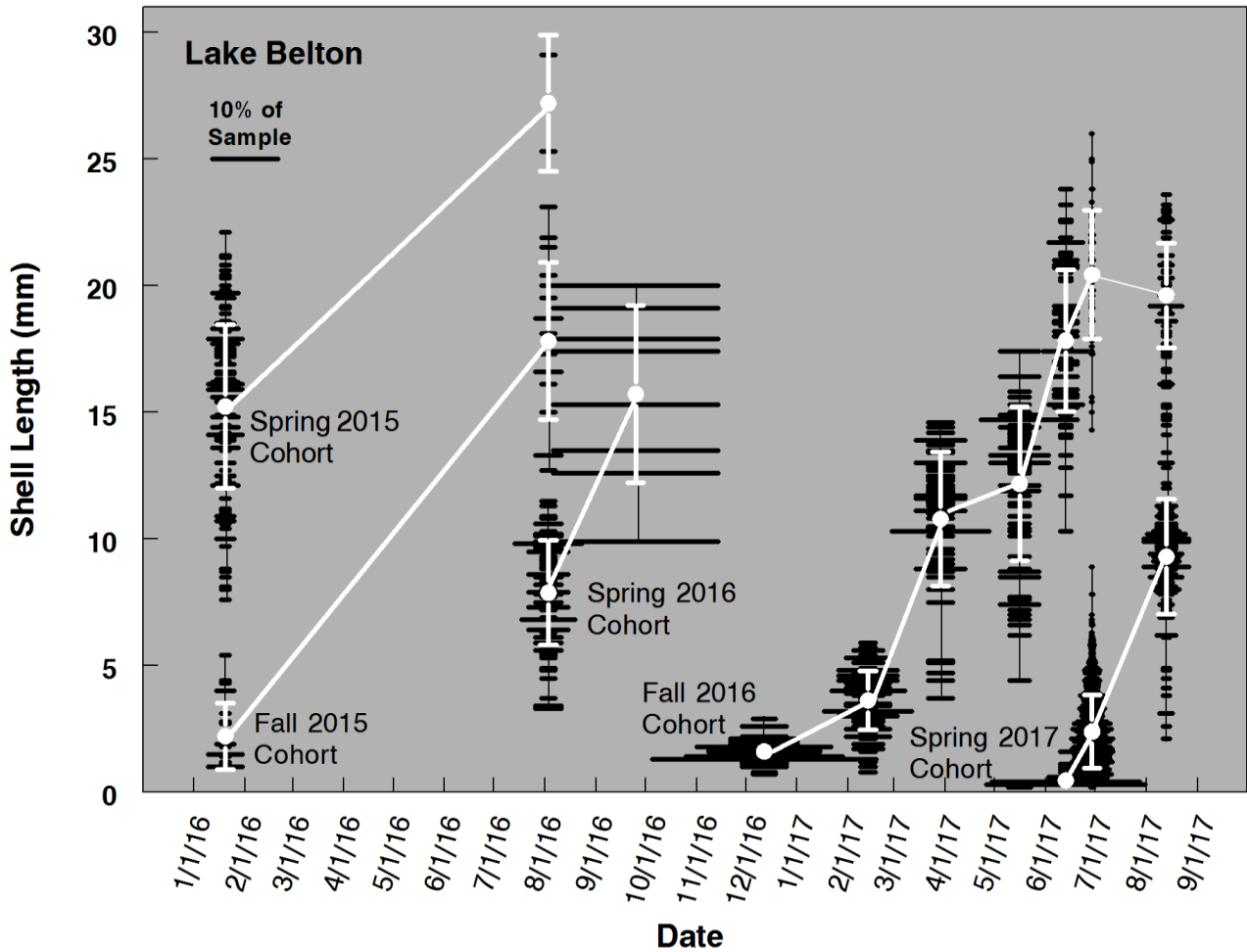


Figure 16. Distribution of zebra mussel shell lengths in samples ( $n > 100$  unless less than 100 specimens were available) taken randomly from settlement bricks at 1.5-2.0 m depth in Lake Belton from 01/01/16 to 08/13/2017. Horizontal histogram bars for each sample represent percent size-frequency distributions at every 0.1 mm in shell length. Samples are divided into spring and fall reproductive cohorts based on non-overlapping size distributions. Where sample size was  $\leq 10$ , single 5% bars were used to represent individual shell lengths. Solid white circles connected by white lines represent mean cohort shell lengths surrounded by vertical white error bars representing one standard deviation of the mean.

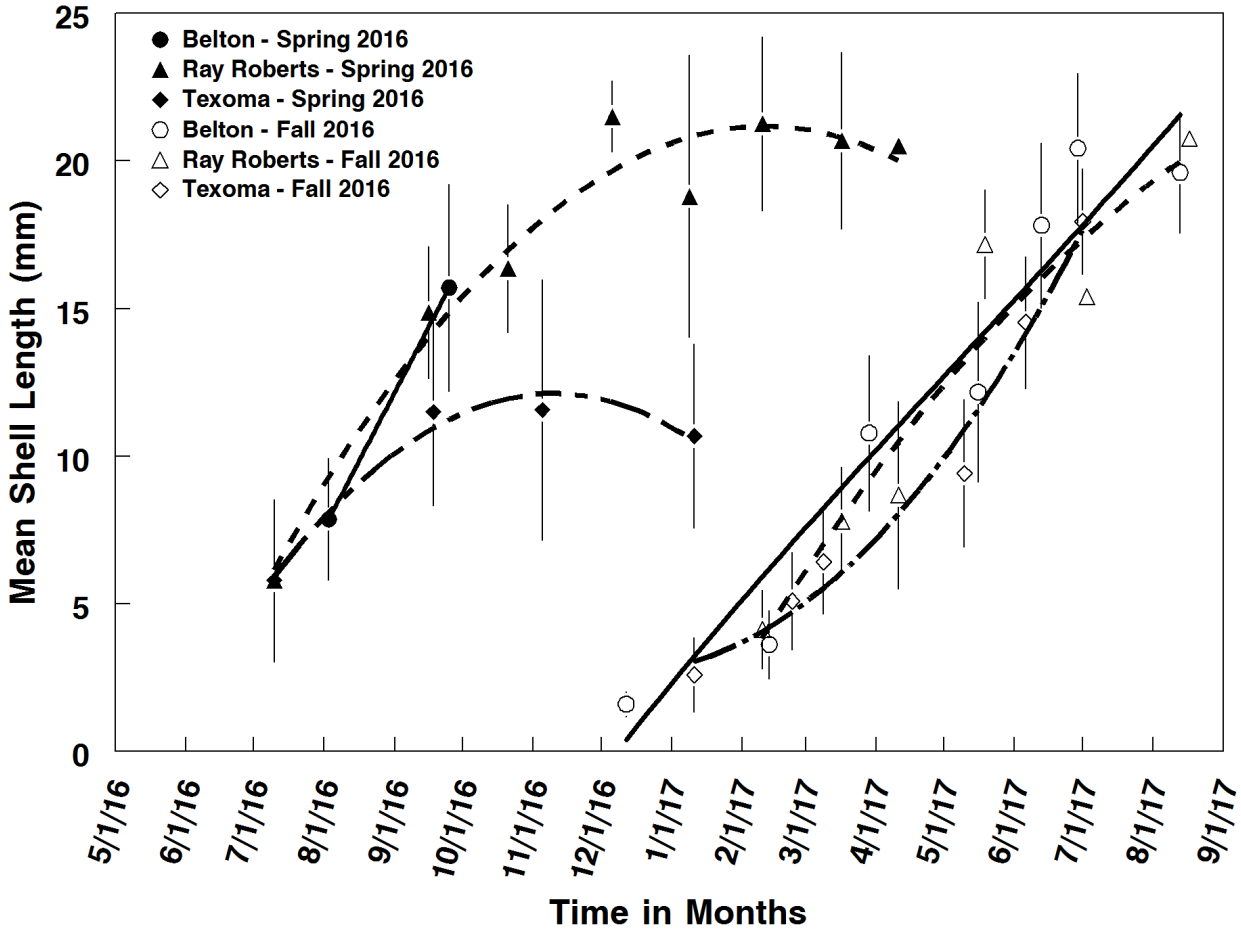


Figure 17. Comparison of the shell length (SL) growth rates over the life span of spring and fall 2016 cohorts of zebra mussels in Lakes Belton, Ray Roberts, and Texoma. Points indicate mean cohort SLs on sampling dates  $\pm$  standard deviations represented as vertical lines about means for spring 2016 cohorts in Lakes Belton (solid circles), Ray Roberts (solid triangles) and Texoma (solid diamonds) and fall 2016 cohorts represented by open circles, open triangles and open diamonds, respectively. Lines represent growth curves computed as fourth order polynomial regressions fitting mean SL as the dependent variable to time of collection with solid lines being growth curves for the spring 2016 and fall 2016 cohorts at Lake Belton, dashed lines for those at Lake Ray Roberts and long-short dashed lines for those at Lake Texoma.

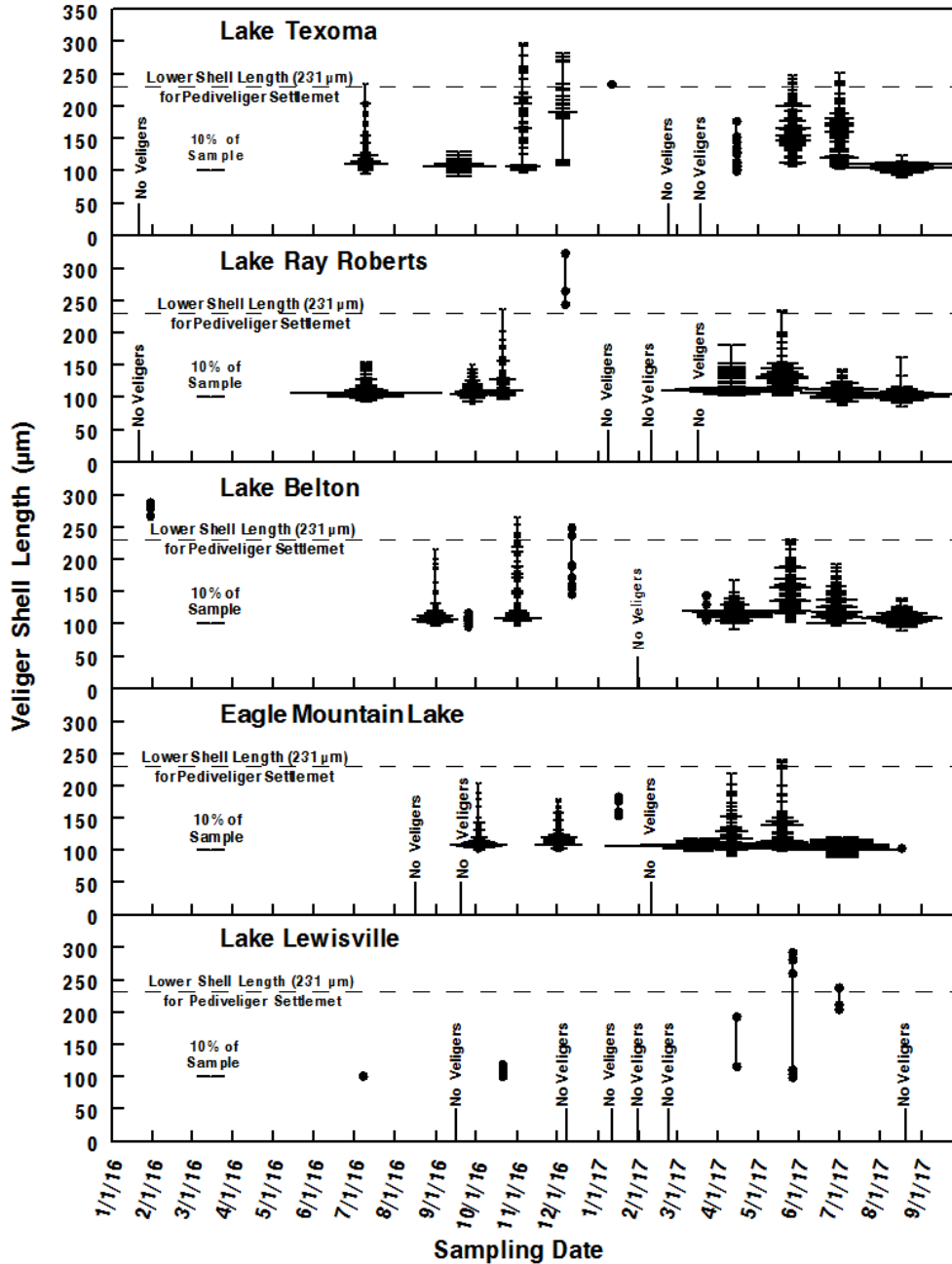


Figure 18. Zebra mussel veliger larvae shell length-frequency distributions of randomly chosen samples of >100 individuals if present in approximately monthly plankton samples at study sites in Texas Lakes Texoma (first panel), Ray Roberts (second panel), Belton (third panel), Eagle Mountain (fourth panel), and Lewisville (fifth panel). Horizontal bars represent the percent of sampled individuals at a given veliger shell length in 1 µm intervals (vertical axis) on each sampling date (horizontal axis). The dashed horizontal line in each graph is the lower veliger shell length limit of 231 µm required for development to a settlement competent pediveliger (Nichols and Black 1994). Vertical lines on the horizontal axis of each figure panel indicate dates when no veligers were taken in plankton samples. For samples containing  $\leq 10$  veligers, veliger SL is indicated by individual black dots above the sampling date.

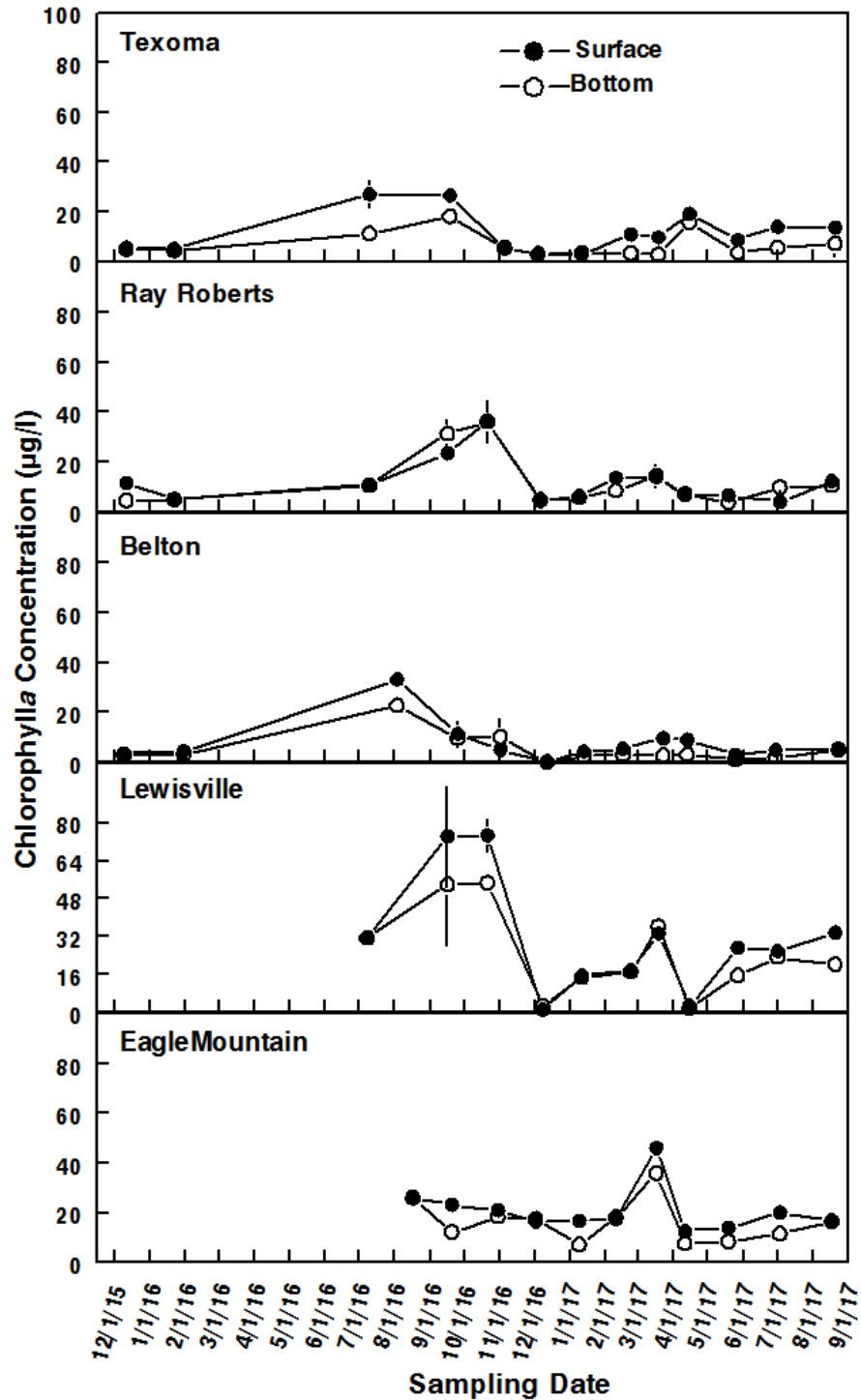


Figure 19. Mean chlorophyll *a* concentrations in µg/l computed from triplicate water samples taken at the water's surface (solid circles) and ≈1 m above the substratum (open circles) in Lakes Texoma (first panel), Ray Roberts (second panel), Belton (third panel), Lewisville (fourth panel) and Eagle Mountain (fifth panel). Vertical bars about means represent standard deviations of the mean. Where bars are not visible, standard deviations were less than the width of the mean point.

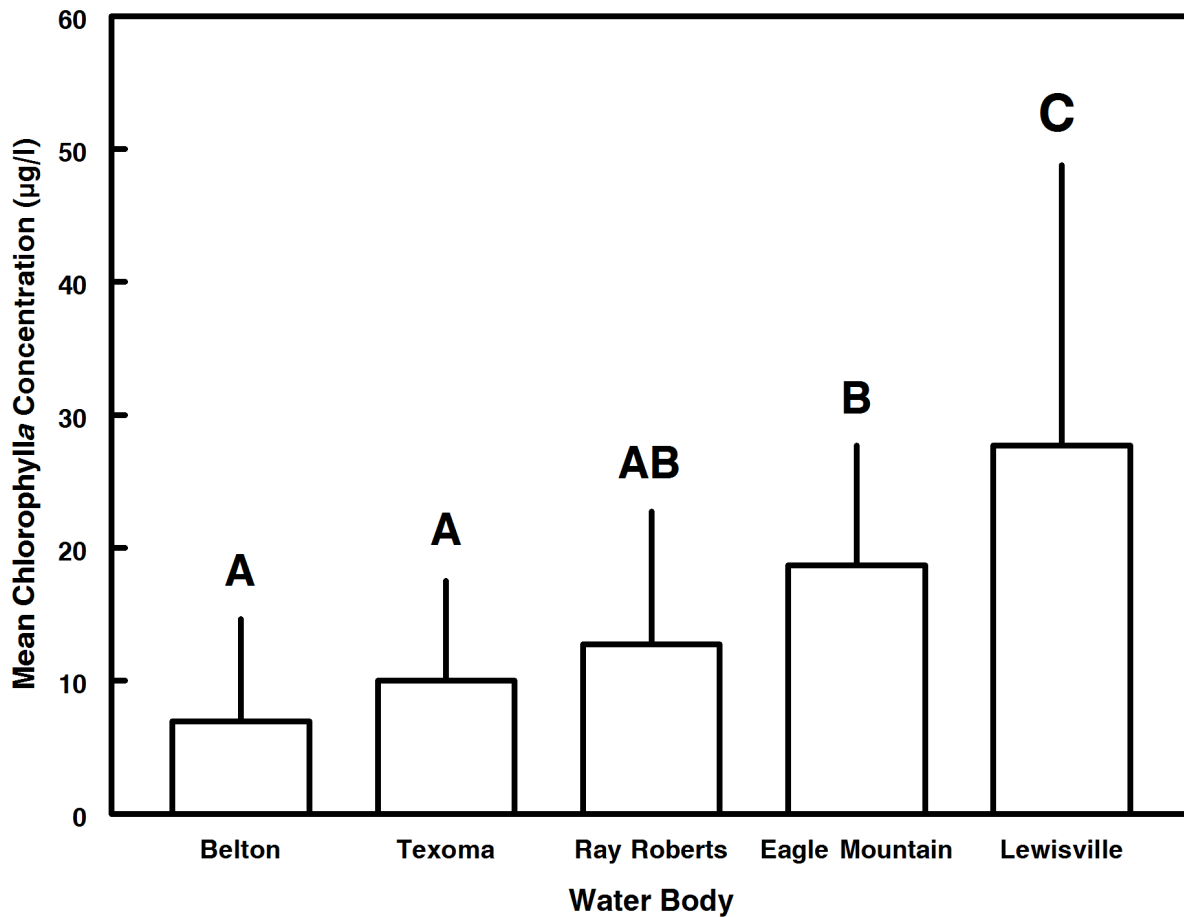


Figure 20. Mean chlorophyll *a* concentrations ( $\mu\text{g/l}$ , vertical axis) computed from combined triplicate sets of surface and benthic (i.e.  $\approx 1$  m above the substratum) water samples taken from July or August 2016 through August 2017 at Texas Lakes Texoma, Ray Roberts, Belton, Lewisville, and Eagle Mountain. Analysis of Variance followed by *post hoc* Least Squares Significant Difference testing revealed significant ( $p < 0.05$ ) differences in chlorophyll *a* concentrations among the five sampled lakes as indicated by dissimilar letters above histograms.

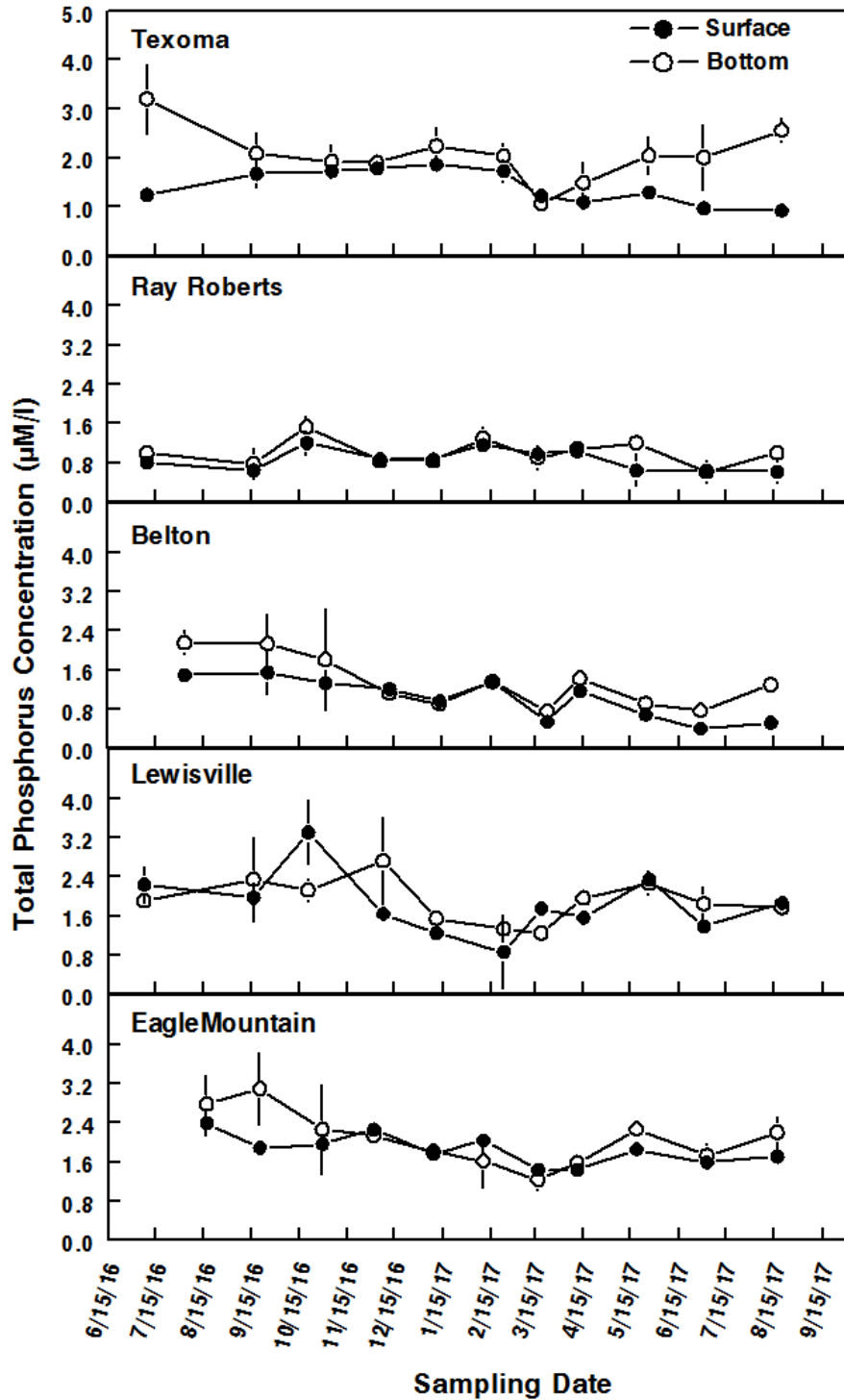


Figure 21. Mean total phosphorus (TP) concentrations in micromoles per liter ( $\mu\text{M/l}$ ) computed from triplicate water samples taken at the water's surface (solid circles) and  $\approx 1$  m above the substratum (open circles) in Lakes Texoma (first panel), Ray Roberts (second panel), Belton (third panel), Lewisville (fourth panel) and Eagle Mountain (fifth panel). Vertical bars about means represent standard deviations of the mean. Where bars are not visible, standard deviations were less than the width of the mean point.



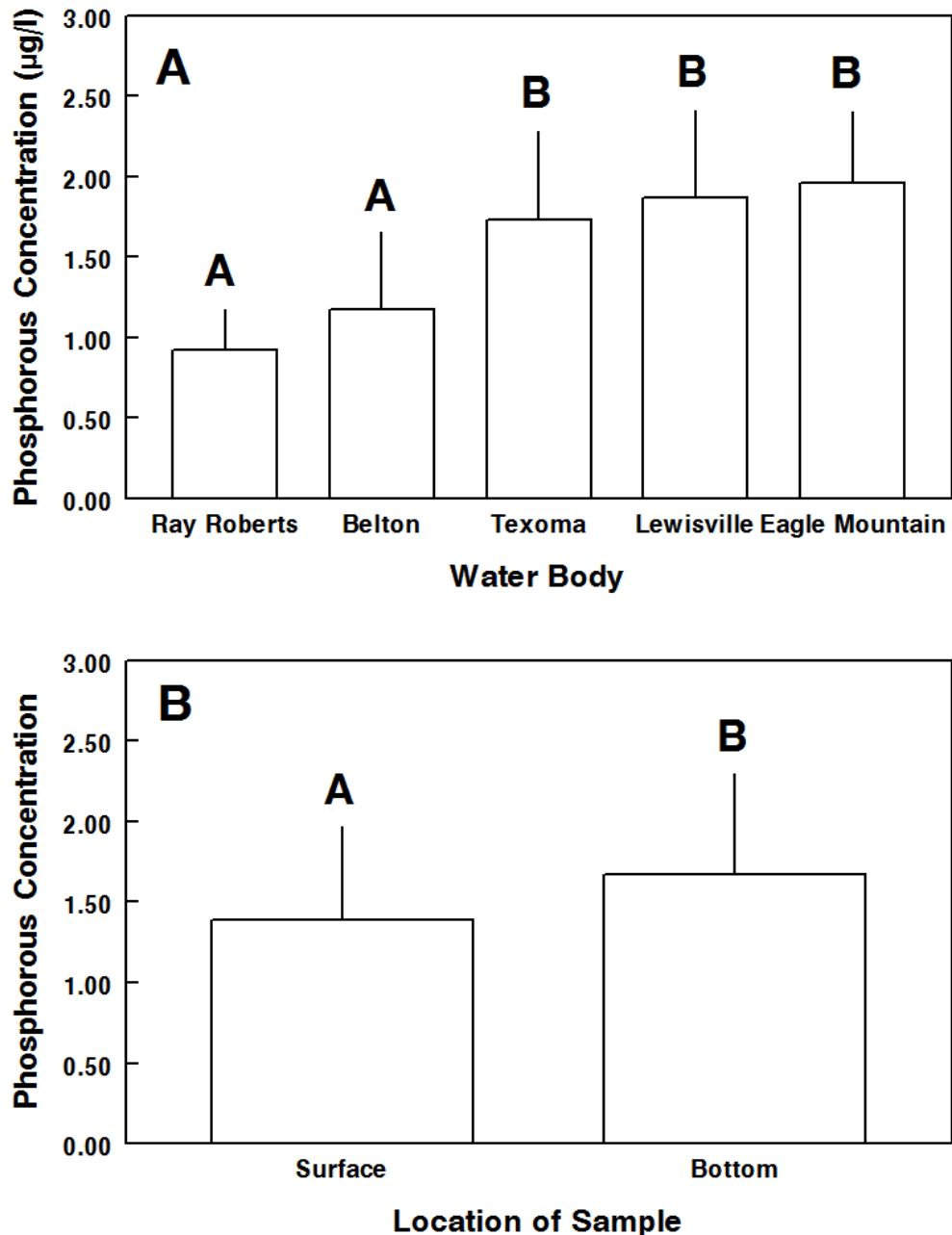


Figure 22. Mean Total Phosphorus (TP) concentrations in micromoles per liter ( $\mu\text{M/l}$ , vertical axis) computed from means of triplicate surface and benthic (i.e.  $\approx 1$  m above the substratum) water samples taken from July or August 2016 through August 2017 at Lakes Texoma, Ray Roberts, Belton, Lewisville and Eagle Mountain. Vertical lines above mean histograms represent standard deviations of the mean. Multiple Analysis of Variance (MANOVA) with main effects of (A) water body sampled and (B) sampling depth (i.e. surface vs bottom) followed by *post hoc* Least Squares Significance Difference testing revealed a significant ( $p < 0.05$ ) difference between water bodies as indicated by dissimilar letters above histograms in figures A and B.

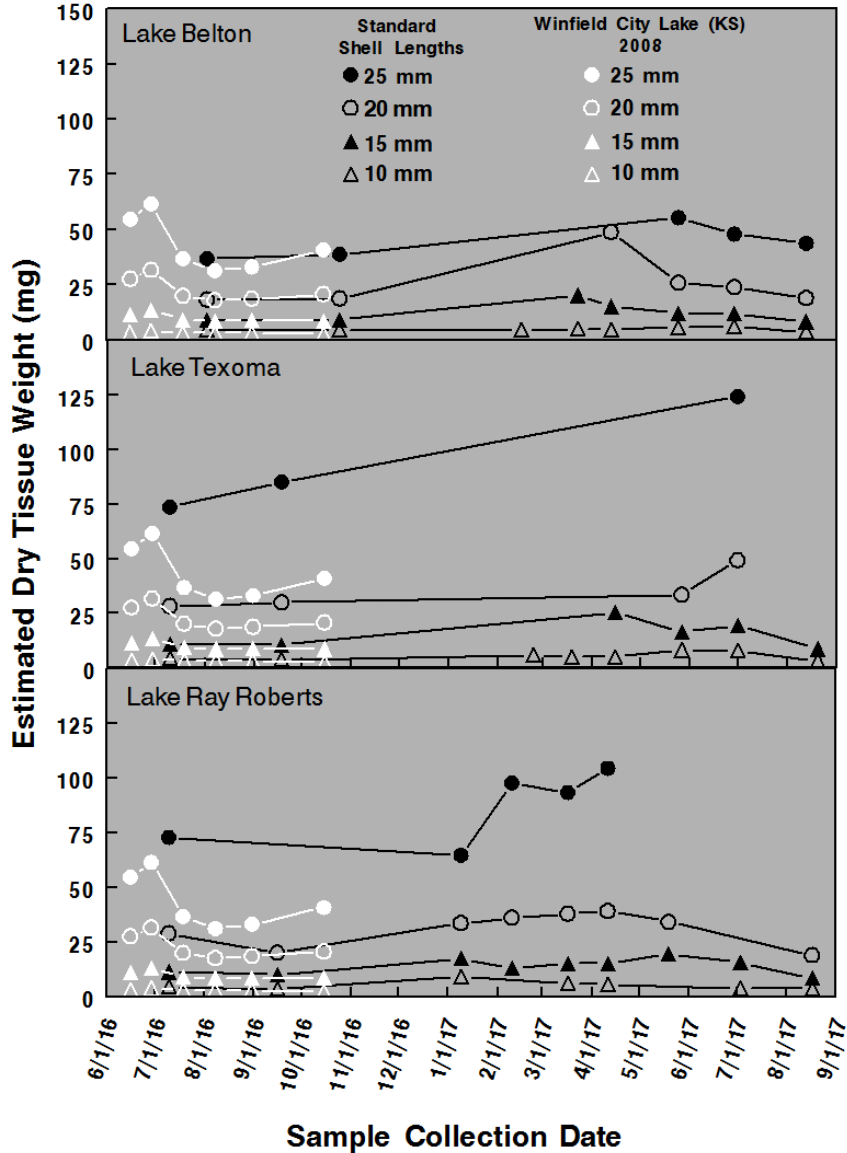


Figure 23. Dry tissue weights (DTW) (mg, vertical axis) for zebra mussels with standard shell lengths (SL) of ● 25 mm, ○ 20 mm, ▲ 15 mm and △ 25 mm estimated from approximately 50 individuals if available from samples settled on house bricks suspended at depths of 1.5-2.0 m at study sites in Texas Lakes Belton (upper panel), Texoma (middle panel) and Ray Roberts (lower panel). Mussels were sampled approximately monthly from July or August 2016 through late August 2017. Mussels were chosen to range in SL from  $\geq 8$  mm to the largest individuals in a sample. Individual  $\log_{10}$  DTW was fitted to a Least Squares Linear Regressions versus SL allowing estimation of DTW at standard SLs. Dry tissue weight estimates were only made for standard SLs encompassed within the SL range of any one sample. Also included in each figure panel were similarly determined DTWs for standard sized mussels sampled in 2008 from a Winfield City Lake, KS, population at the peak of its density (white points and lines).

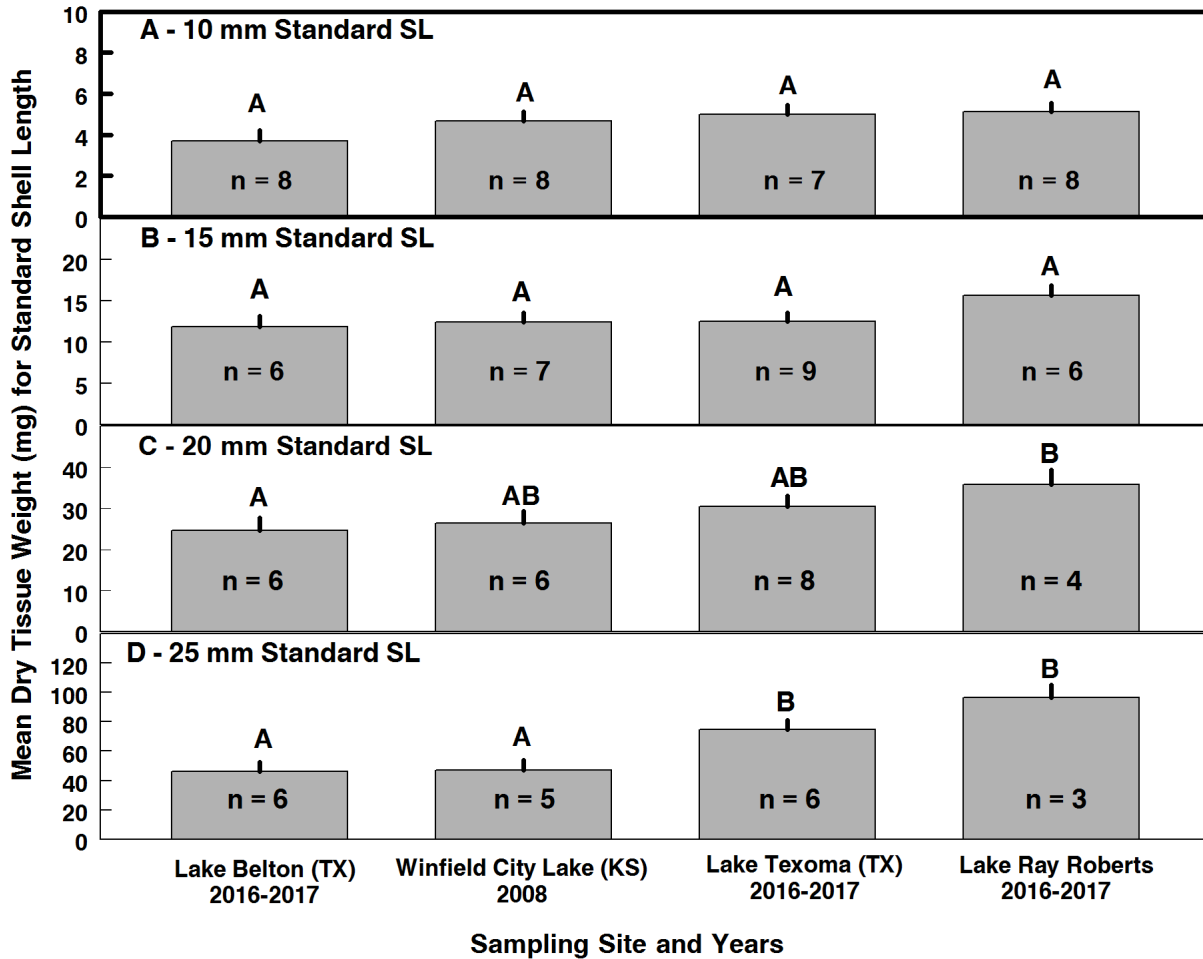


Figure 24. Sampling date adjusted mean dry tissue weights (DTW) (mg, vertical axis) of zebra mussels with standard shell lengths of A) 10 mm, B) 15 mm, C) 20 mm and D) 25 mm, estimated by Multi-factor Analysis of Variance (MANOV) with lake sampled as the main effect (horizontal axis) and numerical day of the year when sampled as a covariate. Mean DTW for standard sized mussels (i.e., histograms with standard errors of the mean represented by vertical lines above means) was estimated from least squares linear regressions of  $\log_{10}$  DTW as the dependent variable fitted to individual mussel SL for each site sampled ( $n > 50$  individuals if available in a sample). The DTWs of standard SL individuals were only estimated if the SL range of individuals in a sample encompassed the standard SL as indicated by n values within each histograms. Multiple Analysis of Variance indicated that the covariate of numerical day of the year was significantly correlated with the estimated DTW of all standard sized mussels ( $p$  range = 0.0001-0.0350). Dissimilar letters above mean DTW histograms indicate significant ( $p < 0.05$ ) differences as determined by *post hoc* Fishers Least Squares Significant Difference Tests.

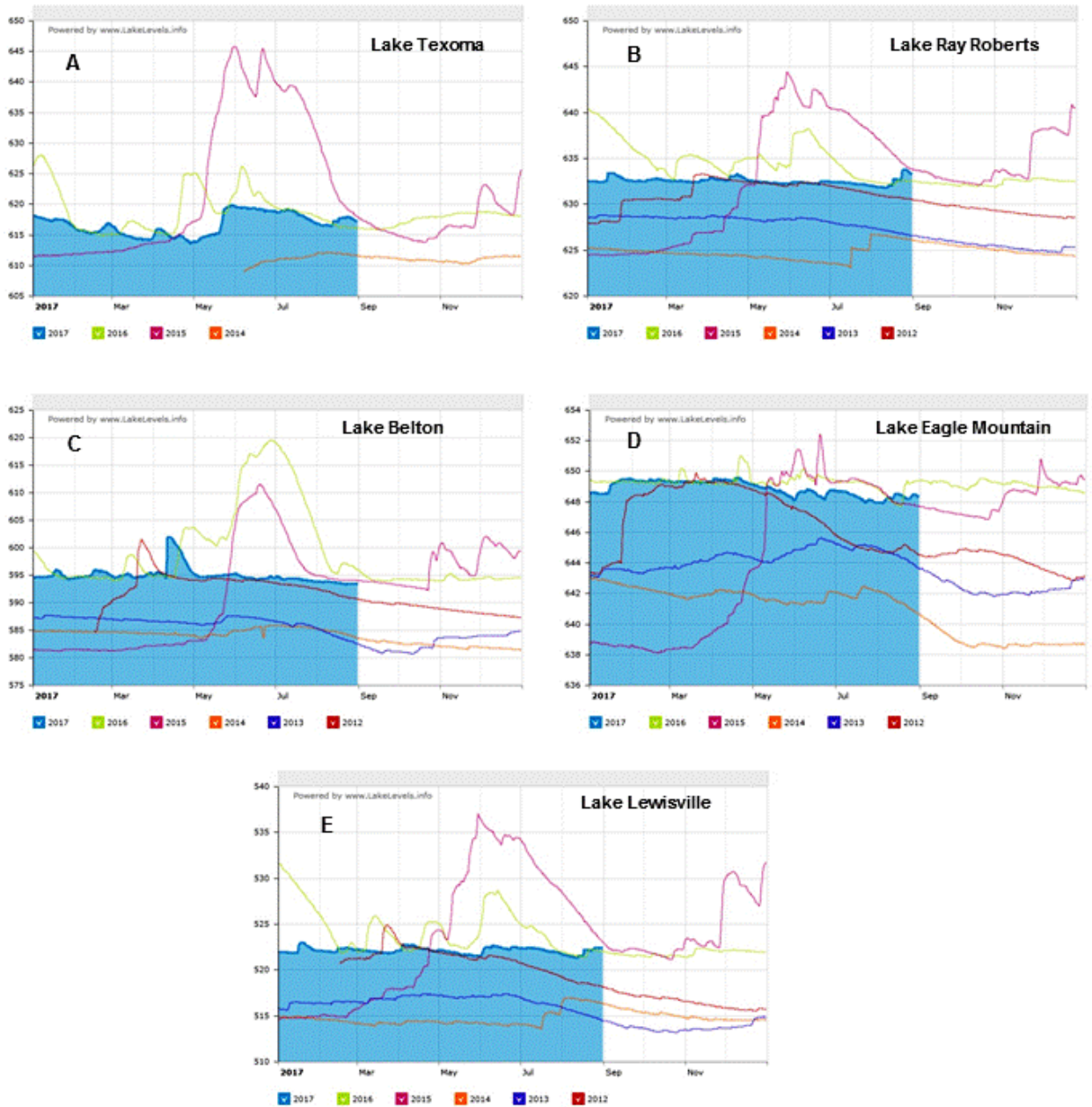


Figure 25. Annual variation in the water levels of Texas Lakes Texoma (A), Ray Roberts (B), Belton (C), Eagle Mountain (D) and Lewisville (E). The vertical axis in all figures is elevation in feet and the horizontal axis, months of the year. Colored lines on graphs represent annual water variation as follows red, 2012; purple, 2013; orange, 2014; magenta, 2015; green, 2016; and blue 2017. Source for maps was US Lakes. 2107, Lakes in Texas, United States. Downloaded from <http://www.uslakes.info/USA/Texas/> on 09/18/2017.

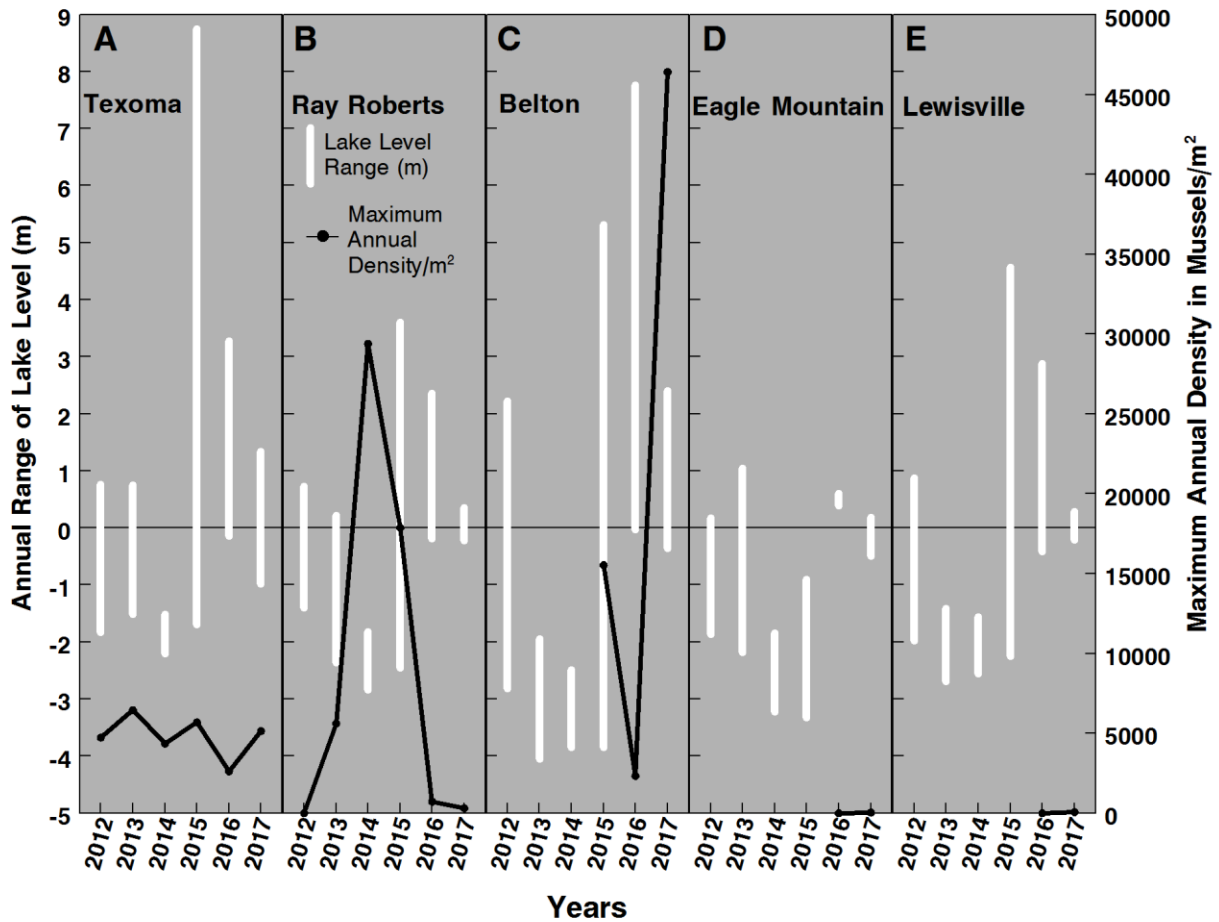


Figure 26. Maximal and minimal annual water level variations in meters (vertical white bars) and maximum annual zebra mussel densities in individuals/m<sup>2</sup> (black lines and solid circles) from 2012-2017 in Texas Lakes Texoma (A), Ray Roberts (B), Belton (C), Eagle Mountain (D), and Lewisville (E). Annual ranges in water levels are represented as deviations from 0 which represents the water level at conservation pool. Data for lake level variation was drawn from U.S. Lakes Information (2017) <http://www.uslakes.info/USA/Texas/> (2017) and US Army Corps of Engineers, Tulsa (2017). <http://www.swt-wc.usace.army.mil/DENI.lakepage.html>.