Aquatic Invasions (2013) Volume 8, Issue 4: 389–406
doi: http://dx.doi.org/10.3391/ai.2013.8.4.03

Research Article

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

Christopher John Churchill
U.S. Geological Survey, Texas Water Science Center, 2775 Altamesa Blvd., Fort Worth, TX 76133, USA
E-mail: cchurchi@usgs.gov

Received: 1 August 2013 / Accepted: 7 October 2013 / Published online: 11 November 2013

Handling editor: David Wong

Abstract

Zebra mussels were first observed in Texas in 2009 in a reservoir (Lake Texoma) on the Texas-Oklahoma border. In 2012, an established population was found in a near-by reservoir, Ray Roberts Lake, and in June 2013, settled mussels were detected in a third north Texas reservoir, Lake Lewisville. An established population was detected in Belton Lake in September 2013. With the exception of Louisiana, these occurrences in Texas mark the current southern extent of the range of this species in the United States. Previous studies indicate that zebra mussel populations could be affected by environmental conditions, especially increased temperatures and extreme droughts, which are characteristic of surface waters of the southern and southwestern United States. Data collected during the first three years (2010–12) of a long-term monitoring program were analyzed to determine if spatio-temporal zebra mussel spawning and larval dynamics were related to physicochemical water properties in Lake Texoma. Reproductive output of the local population was significantly related to water temperature and lake elevation. Estimated mean date of first spawn in Lake Texoma was approximately 1.5 months earlier and peak veliger densities were observed two months earlier than in Lake Erie. Annual maximum veliger density declined significantly during the study period ($p < 0.0001$). A population crash occurred as a result of thermal stress and variability of lake elevation. In summer 2011, water temperatures peaked at 34.3°C and lake elevation declined to the lowest level recorded during the previous 18 years, which resulted in desiccation of substantial numbers of settled mussels in littoral zones. Veliger spatial distributions were associated with physicochemical stratification characteristics. Veligers were observed in the deepest oxygenated water after lake stratification, which occurred in late spring. Results of this study indicate environmental conditions can influence variability of population sizes and spatial distributions of zebra mussels along the current southern frontier of their geographic range. Although the future population size trajectory and geographic range are uncertain, increased temperatures and intermittent, extreme droughts likely will affect spatio-temporal dynamics of established populations if zebra mussels spread farther into the southern and southwestern United States.

Key words: zebra mussel; *Dreissena polymorpha*; geographic spread; veliger; population size trajectories; larval dynamics; population crash; drought; physicochemical stratification

Introduction

Less than two decades after introduction into North America, zebra mussels (*Dreissena polymorpha* [Pallas, 1771]) achieved rapid transcontinental spread (Strayer 2009). By 2009, the southern extent of zebra mussel distribution in the United States included Texas. Incipient detection of zebra mussel adults in Texas was in April 2009 in Lake Texoma, a reservoir in the Red River Basin along the Texas-Oklahoma border (Texas Parks and Wildlife Department 2009). In July 2012, zebra mussels were detected in Ray Roberts Lake, a reservoir in the Trinity River basin near the Dallas-Fort Worth metropolitan area (Texas Parks and Wildlife Department 2012). Both populations are now established. Introduction of zebra mussels into these reservoirs was most likely by overland transport because no upstream source populations have been detected. In June 2013, zebra mussels were detected in a third reservoir in north Texas, Lake Lewisville (Texas Parks and Wildlife Department 2013a). In September 2013, an established population was detected in Belton Lake near Temple, Texas (Texas Parks and Wildlife Department 2013b).

The recent southward spread of zebra mussels into Texas exemplifies the potential for this species to become established in warm waters of the southern United States (Strayer 1991; Allen et al. 1999).

Invasion opportunities for zebra mussels are enhanced in areas containing multiple freshwater impoundments where invaded reservoirs can function as invasion hubs for the secondary spread of propagules (Muirhead and MacIsaac 2005; Johnson et al. 2008). The Dallas-Fort Worth metropolitan region has numerous reservoirs and a network of intra- and interbasin raw water transfers that allow movement of water between reservoirs in the region. In addition to more common transport vectors (overland boat movement and downstream transport from infested source waters), a network of water transfers could further facilitate local and regional spread. Rapid colonization of non-infested waters by dreissenid mussels can be facilitated by life-history characteristics including high larval and juvenile growth rates, high fecundity, and early sexual maturity (Sprung 1992). Although zebra mussels (McMahon 1996) and many other non-native species (Colautti et al. 2006) are generally more likely to establish populations in water bodies that experience perturbations, life history traits of zebra mussels could be less suited to environments that have extreme levels of environmental disturbance. For example, water bodies that experience intermittent, extreme drought could be more resistant to establishment of zebra mussel populations due to decreases in predictability of environmental conditions, resource availability, and mortality factors (Winemiller 2005).

Results from some studies indicate the southern extent of zebra mussel distribution in North America could be limited by environmental conditions, especially temperature (Strayer 1991; McMahon 1996; Drake and Bossenbroek 2004). However, there is no consensus on how zebra mussels will respond to environmental conditions in surface waters of the southern United States (Mackie and Schloesser 1996; Bossenbroek et al. 2007; Whittier et al. 2008). Additionally, zebra mussels have measurable genetic variance (mean heterozygosity 27.0–43.5%) for traits that enhance invasiveness, which confounds predictions of the potential southern distribution of this species (Marsden et al. 1995). Matthews and McMahon (1999) and Morse (2009) found that zebra mussel populations near the current southernmost geographic extent (Oklahoma and Texas) exhibit increased upper thermal tolerances relative to those found at higher latitudes (Minnesota and New York). Increased upper thermal tolerances could facilitate geographic spread of zebra mussels farther into warmer waters of the southern and southwestern United States.

Environmental conditions can influence zebra mussel reproductive phenology, larval (donor propagule) survival (Borcherding 1991), and development time (Sprung 1987, 1989). For example, Sprung (1987) and Ram et al. (1996) found that water temperature can trigger spawning in zebra mussels. Spatial distributions of planktonic larvae (veligers), and subsequently, settled juveniles, are associated with temperature, dissolved oxygen, and wind speed and can affect invasion and population dynamics (Garton and Haag 1993; Martel et al. 1994). Influence of environmental conditions on population-level characteristics of zebra mussels (e.g. population size, reproductive phenology, and veliger spatial distributions) can subsequently affect transport, establishment, rates of local and regional spread, and severity of invasive effects (Dorgelo 1993; Nalepa et al. 1995; Strayer et al. 2011).

Substantial long-term economic and environmental effects of this species have been well-documented during the previous 20 years (see Strayer 2009; Higgins and Vander Zanden 2010, and references therein). A meta-analysis of national economic data estimated costs associated with zebra mussel infestations through direct damages and control measures were $1 billion annually (Pimentel et al. 2005). Effects of zebra mussels on ecosystems are also substantial. Zebra mussels have been associated with alterations of abiotic resources (nutrient cycling and physical habitat), trophic interactions, species abundances, community composition, and ecosystem functioning (Strayer 2009; Higgins and Vander Zanden 2010). Severity of economic and environmental effects associated with zebra mussels can be related to the size and persistence of their populations (Strayer et al. 2006). Effects of established populations of zebra mussels in north Texas include cessation of interbasin water transfer from the North Texas Municipal Water District Lake Texoma Pump Station. During water transfer, water from Lake Texoma is pumped into Sister Grove Creek, which flows into Lavon Lake (both in the Trinity River basin) where, normally, it is utilized as a potable water supply. Water transfer was halted in August 2009 when zebra mussels were discovered in Sister Grove Creek (T. Kilpatrick, pers. commun.). Lake Texoma constitutes 28% of the total water supply for North Texas Municipal Water District, which services 1.6 million residents in the Dallas-Fort Worth metropolitan region.

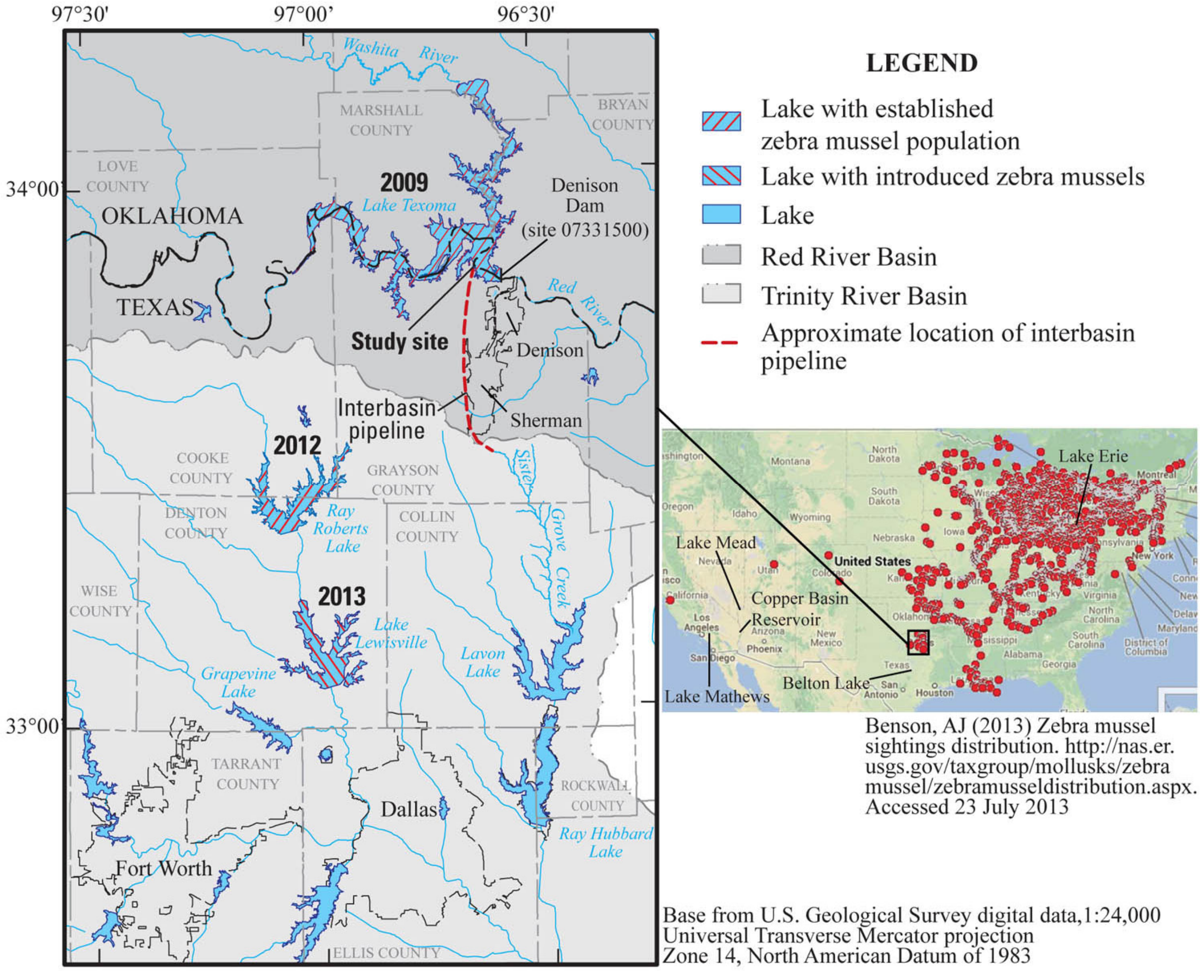
The sizes of zebra mussel populations typically fluctuate over time. Simulation models indicate zebra mussel populations can follow several trajectories including a stable cycle or a boom-bust pattern (Casagrandi et al. 2007). Using long-term empirical studies, Burla and Ribi (1998) and Strayer et al. (2011) found that some populations follow a four- or five-year stable cycle. Nalepa et al. (2006) found that some populations follow irregular or chaotic trajectories. Some populations have been found to follow a boom-bust pattern and they either stabilize at a low population size after an initial boom or are eventually extirpated from the local environment (Stanczykowska and Lewandowski 1993). Water bodies that experience localized extirpation of zebra mussel populations could be susceptible to future invasions if more propagules are introduced. After a population crash, recovery to pre-crash population sizes can occur in one year if conditions are suitable (Ramcharan et al. 1992a). Stanczykowska and Lewandowski (1993), Burla and Ribi (1998), and Strayer et al. (2011) found that interannual fluctuations of population sizes of zebra mussels were related to environ-mental conditions. Cope et al. (1997) found that patterns of zebra mussel abundance could be linked to spatial gradients of physicochemical water properties. Ramcharan et al. (1992a) found that variable zebra mussel populations occurred more frequently in lakes with smaller surface areas, higher calcium concentrations, and lower phosphate concentrations. Ilarri et al. (2011) found that population crashes of invasive bivalves result from chronic exposure to increased temperatures or low dissolved oxygen levels. Additionally, water drawdowns can cause substantial reductions of zebra mussel population sizes in reservoirs (Severson 2010), rivers (Tucker et al. 1997), and wetlands (Bowers and de Szalay 2005). Extreme drought can reduce zebra mussel population sizes by increasing water temperatures, and by reducing flows, dissolved oxygen levels, and water levels (Boeckman 2011). Frequency, intensity, and duration of population size booms could influence invasion-related economic and environmental effects and could influence management and control strategies. For example, temporary relocation of imperiled or sensitive native freshwater mussels during brief zebra mussel population booms could prevent localized extirpation of the native species (Cope and Waller 1995; Strayer 2009).

Long-term datasets are necessary to detect temporal patterns of population dynamics and to determine drivers of population size cycles (Lucy 2006; Strayer et al. 2011). Research conducted on zebra mussel populations that occur in Texas is important, but is currently lacking. This region could serve as a better predictor for spread and population dynamics of zebra mussels in the southern and southwestern United States than could research conducted on populations found at higher latitudes. For this study, biological and environmental data were collected by the United States Geological Survey (USGS) in cooperation with North Texas Municipal Water District, Dallas Water Utilities, Greater Texoma Utility Authority, and City of Sherman Water Utilities as part of the Zebra Mussel Monitoring Program for North Texas (ZMMP) (Churchill and Baldys 2012). ZMMP was designed to assess water quality and zebra mussel occurrence, distribution, and spawning and larval dynamics in north Texas waters. Spawning and larval dynamics were determined by quantification of veliger density, which allows a direct measure of reproductive output of populations and can be used to estimate the size and spatio-temporal dynamics of reproductive populations (Burla and Ribi 1998). Objectives of the current study were to analyze data collected during the first three years of the ZMMP (2010–12) to determine if temporal dynamics and spatial distributions of the local zebra mussel population were related to physicochemical environmental conditions in Lake Texoma. This is the first long-term study to assess zebra mussel spawning and larval dynamics in Texas.

Methods

Study area

Lake Texoma is a monomictic impoundment of the Red and Washita Rivers. At conservation pool elevation, it has a surface area of 302.2 km^2 and a volume of 3.1 (10^6 m^3). It is impounded by Denison Dam and composes part of the Texas–Oklahoma border. Lake Texoma is heavily used by recreational boaters and fishermen, and is nationally recognized for its striped bass fishery (Schorr et al. 1995). Lake Texoma also serves as a drinking water source for residents in the Dallas-Fort Worth metropolitan area. North Texas Municipal Water District and Greater



Benson, AJ (2013) Zebra mussel sightings distribution. http://nas.er.usgs.gov/taxgroup/mollusks/zebra mussel/zebramusseldistribution.aspx. Accessed 23 July 2013

Base from U.S. Geological Survey digital data,1:24,000
Universal Transverse Mercator projection
Zone 14, North American Datum of 1983

Figure 1. Zebra mussel sightings in North America and area of interest including study site at Lake Texoma, raw water interbasin transfer pipeline, and selected reservoirs used for drinking water supply for residents of the Dallas-Fort Worth metropolitan area. Year of first detection of settled zebra mussels is denoted, where applicable.

Texoma Utility Authority withdraw water from Lake Texoma at the Lake Texoma Pump Station (LTPS) near the western shore of the main lake zone (Figure 1). The study site (USGS station 335048096374300) is near the LTPS. This site was added to ZMMP in April 2010 because it is a potential point source interbasin transport vector for zebra mussels.

Site visits

A total of 65 visits were made to the study site during 2010–2012. To determine baseline seasonal reproductive dynamics, eight visits were made between April 2010 and April 2011. To determine spatio-temporal distributions of zebra mussel veligers near LTPS, visits for discrete-depth sampling (n = 5) were conducted on May 4, May 25, June 15, September 20, and October 13, 2011. Veliger densities typically peak during spring and autumn (at the time of the primary and secondary spawns, respectively) in lakes of the central United States (Severson 2010; Boeckman 2011). Therefore, baseline and discrete-depth sampling were concentrated during these reproductive periods. Based on published data (Fraleigh et al. 1993; Garton and Haag 1993) and on baseline data collected during 2010, veliger densities were expected to decrease substantially by mid-summer, so no samples were collected during summer 2011. To quantify overwinter persistence of veligers and annual patterns of reproductive output, weekly water samples (n = 49) were collected between October 2011 and October 2012. Baseline sampling resumed for three visits between October and December 2012.

Environmental data

Discrete measurements of selected water quality properties (temperature, dissolved oxygen [DO], pH, and specific conductance) were made from the surface (0.3-m depth) to a minimum of 15.2 m at 1.5-m intervals using a YSI 6920 V2-2 datasonde (Xylem Analytics, Yellow Springs, OH, USA) during each visit to the study site.

Other discrete data recorded during sample collection included wind speed, water transparency, and lake elevation. The accuracy of the *in situ* wind speed measurements was likely compromised by the proximity of the study site to the LTPS. Therefore, wind speed data were taken from a nearby weather station in Sherman, TX (station KGYI; Weather Underground 2013). Mean wind speed data were reported for the duration of each visit to the study site during discrete-depth sampling in 2011 (n = 5). Water transparency was measured with a Secchi disk. Lake elevation (in feet above the National Geodetic Vertical Datum of 1929; NGVD29) for Lake Texoma were from United States Army Corps of Engineers site 07331500 Lake Texoma near Denison, TX (United States Geological Survey 2013).

Continuous water temperature was recorded at 15-minute intervals by using submersible data loggers (Onset Computer Corporation, Bourne, MA, USA) at 1.5-m depth intervals (from 1.5 to 16.8 m) near the study site beginning April 2011. Water temperatures at the shallowest depth (1.5 m) were considered surface values for the period of continuous data collection. Temperature data were downloaded and were processed and stored, along with other data, in the USGS National Water Information System database (United States Geological Survey 2013).

Biological data

Two types of water samples were collected to estimate veliger density. Composite water samples (n = 60) were collected by lowering a plankton tow net and collection cup with 64-µm mesh (Aquatic Research Instruments, Hope, ID, USA) to a depth of 15.2 m and conducting a vertical tow to the surface. Approximately 1,000 L of water were filtered during each vertical, composite tow. At least three replicate samples were collected during each visit to the study site. Discrete-depth water samples (n = 5, during 2011 only) were collected by using a low-flow centrifugal pump at a constant flow rate of 23 liters per minute. Water was drawn through a 1.9-cm-diameter reinforced polyvinyl chloride (PVC) hose that was lowered to six discrete depths (0.3, 3.0, 6.1, 9.1, 12.2, and 15.2 m). Pump outflow was passed through a plankton tow net and collection cup with 64-µm mesh. Approximately 500 L of water were filtered at each depth. Samples (retained in collection cup) from composite and discrete-depth tows were rinsed into 250-ml polyethylene bottles and preserved in 50% ethanol. Preserved samples were transported to the USGS North Texas Program-Fort Worth laboratory and transferred to 1-L Imhoff settling cones for a minimum of 12 hours. The settled, organic partition of each sample was transferred to a 50-ml centrifuge tube through the bottom of the settling cone. Sample volume in each tube was recorded. Each sample was thoroughly-mixed by pipetting until organic matter was fully suspended. For each sample, five 1-ml replicate aliquots were pulled from the sample tube, placed into a Sedgewick-Rafter counting cell, and analyzed by using cross-polarized light microscopy (Johnson 1995). Following the methodology of Hosler (2011), veliger density (number of veligers per liter, #/L) for each sample was determined by calculating mean veligers in five aliquots, multiplying by sample volume, and dividing by filtered volume (500 or 1,000 L, depending on plankton tow method). Veliger densities were reported as mean of replicates ± standard deviation (SD) unless indicated. Mean veliger densities at all six depths (pooled data) for each of five discrete-depth sample collections were used during comparisons to vertical, composite samples.

An attempt was made to estimate the date of first spawn (DOFS) for the zebra mussel population in Lake Texoma. Data used to estimate DOFS were veliger densities that occurred between the most recent date of non-detect (prior to initial annual detection) and the date of maximum reported veliger density, and all inclusive data. Data were plotted as x = date and y = veliger density. A best-fit curvilinear line, similar in shape to an exponential increase from y = 0, that connected all data points from data collected during spring 2012 was fitted by eye. Because veliger densities were determined weekly during 2012, the best-fit line for data collected during 2012 was used as a baseline for generating best-fit lines for other years. DOFS during each year was the date (x-coordinate) when the best-fit line deviated from the x-axis. These methods were used to estimate DOFS for two comparable studies from Lake Erie (Fraleigh et al. 1993; Garton and Haag 1993).

Settlement rates of zebra mussels are correlated with veliger densities (Martel et al. 1994). Settlement often begins shortly after veliger densities peak during spring (Lucy 2006). Therefore, the duration between DOFS and peak veliger density provides an estimate of the mean length of time individuals of a given cohort remain in their planktonic larval stage (i.e. cohort development time, CDT). Sprung (1987) and Lucy (2006) found that development time of veligers was correlated with temperature. To determine if CDT was related to the rate of daily water temperature increase (RTI) during spring, the mean daily RTI was calculated for a minimum 42-day period that approximates CDT for each year.

Statistical analyses

Statistical analyses were conducted using SAS 9.3 (SAS Institute, Inc., Cary, NC, USA) or SigmaPlot 12 (Systat Software Inc., San Jose, CA, USA). Mean water quality measures of data from all depths were used during analyses of temporal patterns. Data were partitioned three separate ways; all data pooled (65 sampling events), data collected during spring (14 sampling events), and data collected on similar dates during each year of the study (7 sampling events per year). Spring data were from visits to the study site between the first annual sample date (for 2010 and 2011) or the date when water temperature increased to greater than 12°C (for 2012) and the date when peak veliger densities were observed during each year. Data from all three years were combined. Borcherding (1991) found that gametogenesis in lotic systems begins when water temperatures are 10–12°C during spring. Spring data, which incorporate pre- and post-spawn veliger densities, were used to determine which environmental factors were associated with gametogenesis and primary spawning patterns. Data were also partitioned by year because temporal patterns were observed during the study. In 2010, there were seven sampling events. Because sampling frequency changed during each year of the study, dates for analyses of 2011 and 2012 data were selected to approximate those used during 2010 (seven events each year).

Pearson product-moment correlation coefficients were used to screen for collinearity between pairs of environmental variables (Naddafi et al. 2010), then Akaike's information criteria (AIC) were used to determine best-fit models for predicting veliger density from the remaining set of environmental variables (Burnham and Anderson 2002).

Data were analyzed for normality and homoscedasticity. Data were normalized by using natural log transformation when necessary (Smylie 1994). Parametric analyses on ranked data were used when parametric assumptions were violated. Results were considered significant at $p < 0.05$.

Pearson correlation coefficients were calculated for each pair of environmental variables. Collinear variables ($p < 0.05$) were not used during subsequent analyses (Naddafi et al. 2010). DO was significantly negatively correlated with water temperature in all data groupings (pooled, spring, and by year). Water temperature was retained instead of DO because of its importance in zebra mussel reproductive dynamics (Ram et al. 1996; Matthews and McMahon 1999). Veliger density was regressed against environmental variables using all-possible multiple regression model analysis. Candidate models were analyzed using corrected AIC (AICc) scores. Differences in AICc scores between the best-fit model and the given model (ΔAICc) were used to identify models that have substantial support. $\Delta AICc < 2$ indicates a model that has substantial support (Burnham and Anderson 2002). Weighted AICc scores (wAICc) were calculated to determine the best model(s) out of the subset of candidate models with $\Delta AICc < 2$. Evidence ratios (wAICci/wAICcj) were calculated to determine to what extent the best-supported model was better than other candidate models (Burnham and Anderson 2002). Model averaging was done on all variables to determine the importance of variables selected in multiple regression models. The model inference sampling method was unrestricted with replacement and was run 1,000 times (SAS Institute Inc., Cary, NC, USA). Variables selected in at least 20% of the samples ($n \geq 200$) were used during refit analysis. Refit analysis was run 1,000 times. During each run, a best-fit model was generated and selected variables were

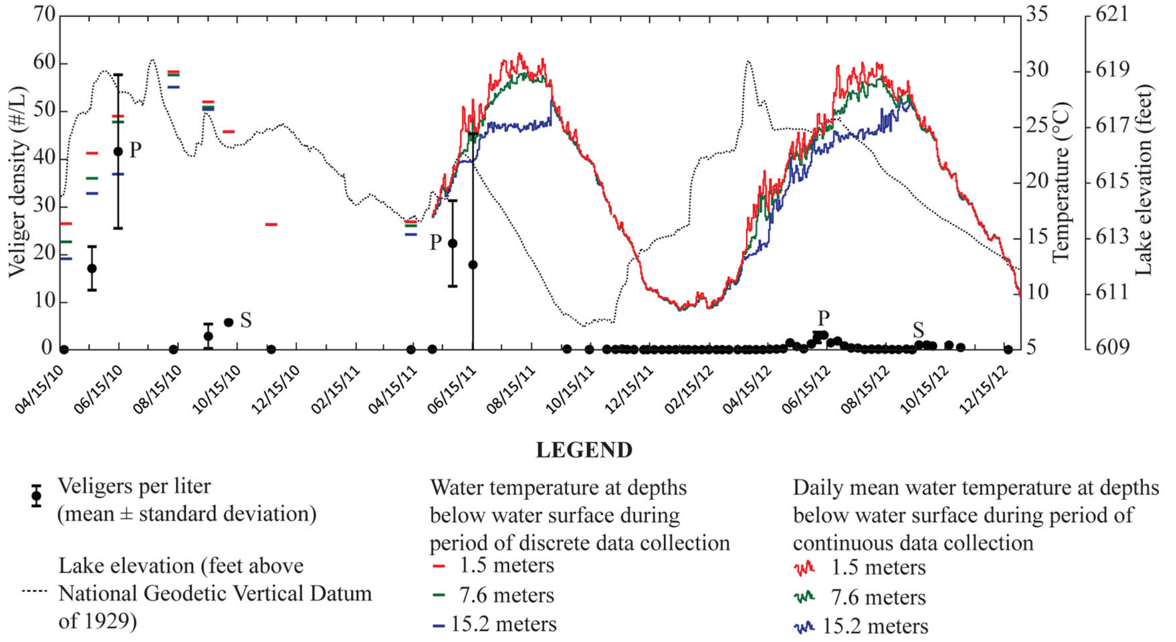


Figure 2. Mean veliger density observed during visits to the study site (n = 65) and continuous lake elevation of Lake Texoma from April 15, 2010 to December 31, 2012. Water temperatures at three depths (1.5, 7.6, and 15.2 m below water surface) observed during periods of discrete (April 15, 2010 to April 14, 2011) and continuous (May 4, 2011 to December 31, 2012) data collection. Primary (P) and secondary (S) spawning events are denoted when observed. Symbols for shallower depths are plotted where temperatures overlap. Error bars for veliger densities are omitted when they were smaller than mean symbol.

recorded. The variable selection percentage describes how often variables were included in best-fit models during 1,000 runs and represents a quantitative measure of variable importance.

To determine if spatial distributions of veligers were influenced by wind-driven mixing, veliger density data from discrete-depth samples (n = 5 dates) were grouped by wind speed (Fraleigh et al. 1993). Veliger density data from the surface to the 6.1-m depth were grouped into two wind speed categories (< 12 kph and > 12 kph). Analyses were repeated after regrouping the data into two alternate wind speed categories (< 21 kph and > 21 kph).

Results

Temporal dynamics

Veliger density maxima declined significantly between each year during the study period (parametric ANOVA on ranked data, $p < 0.0001$; Figure 2). Observed veliger densities peaked during late spring and were lowest during summer and winter each year. In 2010, maximum recorded mean veliger density was 42 ± 16/L (mean ± SD) and was observed on June 14. Maximum mean density measured during 2011 was 22 ± 9.5/L (May 25), which was 52% of the 2010 maximum density. In 2012, observed mean veliger density peaked at 3.3 ± 0.4/L (June 11), which represents a 92% decline from the 2010 maximum.

Secondary spawns were detected in 2010 and 2012 (Figure 2). Maximum mean veliger density during the secondary spawn in 2010 was 5.7 ± 1.5/L (October 6), whereas in 2012 it was 1.2 ± 0.2/L (September 25). Secondary veliger density maxima were 13.6% and 36.4% of the primary maxima in 2010 and 2012, respectively. In both years, maximum veliger densities during secondary spawns were observed after lake turnover when water temperatures were homogenous (24–25°C) throughout the vertical water column. Veligers were detected year-round during 2011/2012; however, densities were very low on most dates in winter/early spring (Figure 2).

Temporal dynamics of zebra mussels in Lake Texoma were most significantly related to water temperature and lake elevation. Multiple regressions

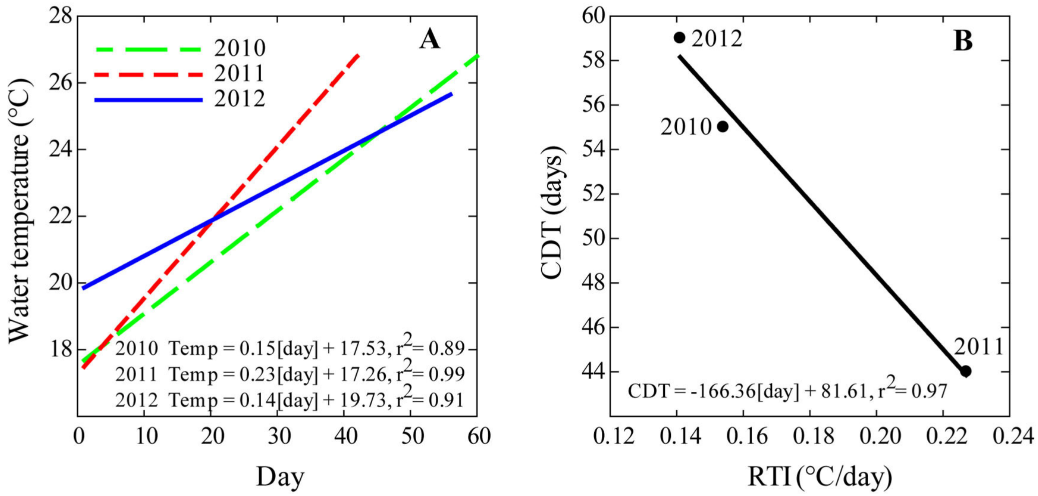


Figure 3. A: Models developed by regressing water temperature on day for data collected during a minimum 42-day period approximating primary cohort development time (CDT, see text) for each year. Slopes represent daily rates of water temperature increase (RTIs) for each year. B: Model developed by regressing CDTs on RTIs for each year. Adjusted coefficients of determination (r2) are shown for both plots.

Table 1. Ranking of candidate regression models predicting zebra mussel veliger density in Lake Texoma. POOLED = pooled data from all 65 dates; Spring = data from 14 dates between the first annual sample date (for 2010 and 2011) or the date when water temperature increased to greater than 12°C (for 2012) and the date when peak veliger densities were observed during each year (data from all three years were combined); 2010, 2011, 2012 = data from seven dates each year. Explanatory variables include water temperature (temp; °C), pH, specific conductance (SC), water transparency (Secchi; m), and lake elevation (elev; feet above NGVD29). Corrected Akaike's information criteria (AICc), difference in AICc values between the best-supported model and the given model (ΔAICc), Akaike weights (wAICc), evidence ratios (best-supported model compared to other candidate models), and adjusted coefficients of determination (R^2) are shown. Models with ΔAICc < 2 are shown.

Model	AICc	ΔAICc	wAICc	Evidence ratio	Adjusted R^2
		POOLED			
Temp, pH, Secchi	91.47	0.00	0.49	n/a	0.51
Temp, pH	92.68	1.21	0.27	1.83	0.49
Temp, pH, Secchi, elev	92.80	1.33	0.25	1.94	0.50
		SPRING			
Temp	33.36	0.00	0.54	n/a	0.72
Temp, Secchi	35.00	1.63	0.24	2.26	0.72
Temp, elev	35.07	1.71	0.23	2.35	0.72
		2010			
Elev	16.33	0.00	1.00	n/a	0.64
		2011			
Elev	17.67	0.00	1.00	n/a	0.32
		2012			
Temp, SC	8.36	0.00	1.00	n/a	0.68

on pooled data yielded three candidate models with ΔAICc < 2 (Table 1). The model with water temperature, pH, and Secchi depth provided the best fit to the data (adjusted R^2 = 0.51, n = 65, F = 22.79, p < 0.0001). This model was 1.8 times more likely than the second model to be the best-fit model. All three models with ΔAICc < 2 included water temperature and pH. Multiple regressions on spring data yielded three models with ΔAICc < 2. The best-supported model included only water temperature (adjusted r^2 = 0.72, n = 14, F = 54.76, p < 0.0001). This model was 2.3 times more likely than the second model to be the best-fit model. All three models with ΔAICc < 2 included water temperature. Models with ΔAICc < 2 included only lake elevation for data collected during 2010 and 2011, and included temperature and specific conductance for data collected during 2012. Water temperature was selected in 95.1, 98.5, and 32.4% of best-fit models

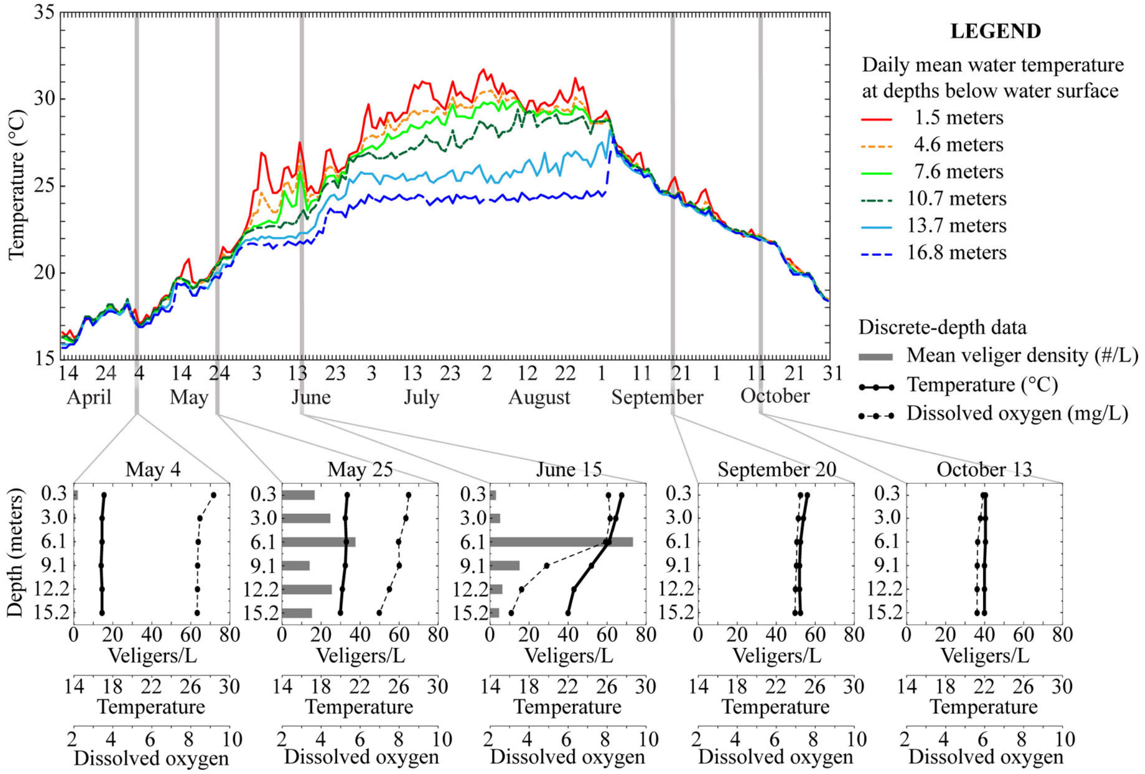


Figure 4. Top: Continuous daily mean water temperature recorded at six depths (1.5, 4.6, 7.6, 10.7, 13.7, and 16.8 m below water surface) using submersible data loggers in Lake Texoma from April 14, 2011 to October 31, 2011. Bottom: Mean veliger density, water temperature, and dissolved oxygen concentration observed at six depths (0.3, 3.0, 6.1, 9.1, 12.2, and 15.2 m below water surface) during visits to the study site on May 4, May 25, June 15, September 20, and October 13, 2011. Veliger densities observed on September 20 and October 13 were too low to visualize at the scale used. Error bars for veliger densities omitted for clarity.

for pooled, spring, and 2012 data, respectively (Table 2). Lake elevation was selected in 64.7 and 36.1% of best-fit models for 2010 and 2011 data, respectively.

These results indicate water temperature and lake elevation were the most important variables for predicting veliger density.

The estimated DOFS in Lake Texoma was in mid-April each year (Table 3). In 2011 and 2012, veligers were first detected during the middle of April when mean water column temperatures were 16–18°C. First collection of veligers during 2010 was observed on the second visit to the study site (May 18), when water temperatures were 20.8°C. It is likely mussels spawned shortly after the first visit to the study site (April 15) when surface water temperatures were approximately 17°C. During each year of the study, spring veliger density maxima were observed when water temperatures were approaching 26°C (Figure 2), the upper thermal limit for veligers reported by Sprung (1987).

RTIs were highest during 2011 and lowest during 2012 (Figure 3A). CDTs were 53 ± 7.8 days (mean ± SD) and were significantly inversely related to RTIs (Figure 3B). CDTs were shortest during 2011 and longest during 2012 indicating more rapid development of veligers during 2011.

Spatial dynamics

Discrete-depth veliger densities observed during 2011 were significantly different over time (repeated measures ANOVA, F = 72.15, $p < 0.0001$). Measurements of physicochemical water properties on May 4 indicated the water column was well mixed (Figure 4, top). On May 25, maximum recorded veliger density (28% of veligers collected at all depths) was observed at the 6.1-m depth (38 ± 9.6/L; mean ± SD). Stratification of physicochemical water properties in the lake was during the beginning of June and by June 15, there was also a strong vertical stratification of veliger densities (Figure 4, bottom). Maximum veliger density (73 ± 12/L; 68% of total) and the metalimnion were observed at the 6.1-m depth. Water temperatures between the surface and the 6.1-m depth differed by 1.3°C (27.5 to 26.2°C), whereas temperatures decreased another 4.2°C between the 6.1- and 15.2-m depths (26.2 to 22.0°C, respectively). A similar pattern was observed with DO concentrations. After lake turnover (September 4), physicochemical water properties and veliger distributions were homogenous throughout the water column. Veliger densities remained very low (0.3/L or less) at all depths during September and October (no secondary spawn was observed).

Mean wind speeds during visits to the study site were 20.6, 28.3, 11.4, 9.0, and 28.3 kph, in chronological order. No significant effect of wind speed on spatial distributions of zebra mussel veligers was found when wind speeds were categorized as < or > 12 kph or < or > 21 kph (parametric ANOVA on ranked data, p = 0.07, 0.99 (12 kph threshold) and p = 0.86, 0.46 (21 kph threshold) for low and high wind speed categories, respectively). This indicates factors other than wind were driving spatial distributions of veligers.

Discussion

Temporal dynamics

Sprung (1989), Borcherding (1991), and Ram et al. (1996) found that reproductive phenology of zebra mussels was associated with environmental factors. Karatayev et al. (1998) found that water temperature was the most important factor controlling gametogenesis and spawning in zebra mussels. Zebra mussel gonads attain maturity at 11°C or greater (Borcherding 1991) and primary spawning occurs when temperatures are 16–18°C (Sprung 1989). Similar associations between gametogenesis/spawning and temperature were observed in zebra mussel populations found in the Great Lakes (Garton and Haag 1993), Kansas (Severson 2010), and Oklahoma (Boeckman 2011) and for invasive quagga mussel (*Dreissena rostriformis bugensis* [Andrusov 1897]) populations in Lake Mead in Arizona and Nevada (Chen et al. 2011; Gerstenberger et al. 2011), and in Copper Basin Reservoir and Lake Mathews in southern California (Reid et al. 2010). Although temperatures associated with primary spawning events of dreissenid mussels are similar throughout North America (16–18°C), earlier annual occurrence of these conditions at lower latitudes is associated with earlier spawning and earlier peaks of veliger densities, which can be important for control and management strategies (Claudi and Evans 1993). In the current study, it was estimated that primary spawning began on April 15 (mean date, n = 3 years), which was 44 days earlier than for three studies in Lake Erie, when the mean DOFS was May 29 (Table 3). Sprung (1989) found that water temperature was inversely related to veliger development time, indicating higher RTIs are associated with reduced CDTs. For example, CDTs were 53 ± 7.8 days (mean ± SD) for the current study and 68 ± 12.9 days for studies conducted in Lake Erie (Fraleigh et al. 1993; Garton and Haag 1993). Also, higher RTIs during

Table 2. Results of multiple regression model averaging for the selection of significant variables for predicting zebra mussel veliger density in Lake Texoma. See Table 1 for data partitioning criteria and variable descriptions. Sampling method was unrestricted with replacement. Samples and refit samples were run 1000 times. Variables included in at least 20% of the samples were used during refit analysis.

Variable	Selection percentage
POOLED	
Temperature	95.1
pH	45.4
Specific conductance	35.5
Secchi	32.9
SPRING	
Temperature	98.5
Lake elevation	30.2
Specific conductance	29.2
2010	
Lake elevation	64.7
Temperature	36.3
Secchi	29.0
Specific conductance	22.0
pH	21.4
2011	
Lake elevation	36.1
Specific conductance	30.7
Secchi	28.1
pH	23.0
2012	
Temperature	32.4
pH	25.0
Secchi	22.5

Table 3. Salient data used to estimate annual date of first spawn (DOFS) for zebra mussel populations in Lake Texoma and Lake Erie.

Lake	State	Estimated DOFS	Date of First Detect	Veliger density (v/L)	Date of Peak Density	Veliger density (v/L)	Reference
Lake Erie	MI	6/5/1989	6/9/1989	1	08/17/1989	451	Garton and Haag 1993
Lake Erie	MI	5/17/1990	5/31/1990	123	08/02/1990	360	Fraleigh et al. 1993
Lake Erie	MI	6/2/1990	6/10/1990	7	07/25/1990	255	Garton and Haag 1993
Lake Texoma	TX	4/20/2010	5/18/2010	17.1	06/14/2010	41.6	Current study
Lake Texoma	TX	4/11/2011	4/12/2011	0.01	05/25/2011	22.4	Current study
Lake Texoma	TX	4/13/2012	4/16/2012	0.1	06/11/2012	3.3	Current study

early spring could influence gametogenesis and DOFS (Lucy 2006). Shorter CDTs and earlier primary spawning resulted in maximum veliger densities occurring approximately two months earlier in Lake Texoma than in Lake Erie (June 6 and August 4, respectively) (Fraleigh et al. 1993; Garton and Haag 1993). As a result of early spawning and shorter CDTs, it was observed that young of the year (YOY) mussels found in Lake Texoma were able to reach maturity prior to the secondary spawn in autumn (C. J. Churchill, pers. observ.). Population generation time would be reduced if YOY mussels were able to reproduce twice during their first year (autumn and the following spring). Establishment of zebra mussels in non-infested waters could be facilitated in regions where YOY individuals are able to grow and reproduce rapidly (Jantz and Neumann 1998). Although temperature and growth of zebra mussels are often positively correlated when temperatures are below upper thermal tolerance levels, chronic exposure to temperatures greater than upper thermal tolerance levels (approximately 30°C) can cause mortality (Smylie 1994; McMahon 1996; Matthews and McMahon, 1999; Morse 2009).

Hincks and Mackie (1997) found that pH was associated with persistence of zebra mussel populations through its effects on survivorship.

Using field observations and laboratory studies, Sprung (1987) and Ramcharan et al. (1992b) found that zebra mussel veliger survival requires a pH of 7.4–9.4 with an optimum of 8.4 and 8.5 for rearing of larvae and minimized production of crippled larvae, respectively. Hincks and Mackie (1997) observed larval growth only when pH was greater than 8.3. Veliger density maxima during the current study were observed when pH was 7.9–8.3. These values are slightly lower than the optimum pH levels reported by other studies, but are within tolerance limits. Hincks and Mackie (1997) found that the probability of mortality of zebra mussels was reduced at low pH levels (6–8) when calcium levels were sufficient for physiological processes (greater than 50 mg/L). Minimum mean calcium concentrations during the current study (78 mg/L; United Stated Geological Survey 2013) were much greater than the minimum required levels (40 mg/L) for veliger development (Sprung 1987).

Spawning and larval dynamics of *D. polymorpha* in Lake Texoma are similar to those of quagga mussels found in Lake Mead. For example, quagga mussel veligers are present year-round in Lake Mead and densities are very low during the coldest months (February to April) (Gerstenberger et al. 2011). In some years, a single annual spawning event occurs between August and October (Beaver et al. 2010; Mueting et al. 2010). Reid et al. (2010), Gerstenberger et al. (2011), and McMahon (2011) observed bivoltine reproduction by the population with primary and secondary spawning occurring between April and June, and August and October, respectively. In contrast to the current study in Lake Texoma, maximum densities of quagga mussel veligers are observed from August to October in most years (secondary spawn) in Lake Mead (Beaver et al. 2010; Mueting et al. 2010; Gerstenberger et al. 2011).

Maximum zebra mussel veliger density in Lake Texoma (42/L in 2010) was similar to reported maximum densities of quagga mussel veligers in Lake Mead. For example, Gerstenberger et al. (2011) reported 29/L, Beaver et al. (2010) reported 33/L, and Wittmann et al. (2010) reported 38/L. Reid et al. (2010) reported 31/L in Copper Basin Reservoir and 52/L in Lake Mathews (both are located along the Colorado River Aqueduct). However, maximum zebra mussel veliger density in Lake Texoma was lower than reported values for conspecific populations in the Great Lakes, Kansas, and Oklahoma. For example, veliger densities in Lake Erie were 250-450/L in the late 1980s to early 1990s (Garton and Haag 1993), 270/L in El Dorado Lake, Kansas in 2007 (Severson 2010), and 480/L in Oologah Lake, Oklahoma in 2006 (Boeckman 2011). Densities observed recently in Oklahoma lakes are similar to those recorded in Lake Erie indicating zebra mussel populations found at lower latitudes can be as productive as those found in the Great Lakes. It is possible that veliger densities in Lake Texoma were greater than 42/L prior to 2010, before the current study began.

Spatial dynamics

Spatial distributions of veligers in Lake Texoma were related to physicochemical stratification dynamics including vertical location of the thermocline. During May 2011, temperatures and DO levels throughout the water column were within reported physiological thresholds (less than 26°C and greater than 4 mg/L, respectively) for veligers (Sprung 1989). Physicochemical stratification resulted in horizontal zones with temperatures and DO concentrations that were outside physiological tolerance ranges for veligers. On June 15, 2011, temperatures exceeded 26°C for depths of 6.1 m or less, while DO concentrations dropped below 4 mg/L for depths greater than 6.1 m. Fraleigh et al. (1993), Smylie (1994), and Barnard et al. (2003) found that temperatures influence spatial distributions of zebra mussel larvae and recruitment dynamics of post-settlement individuals. Lewandowski and Ejsmont-Karabin (1983) and Yu and Culver (1999) found that veligers typically are absent from the hypolimnion because of hypoxic conditions. Unlike zebra mussel adults, which are less mobile, veligers are capable of more rapid active transport and can avoid unsuitable environmental conditions by altering microhabitat selection (Barnard et al. 2003). Actively moving to the coolest, oxygenated water during June 2011 provided protection from high water temperatures (greater than 26°C) observed at shallower depths and provided sufficient DO levels (approximately 8 mg/L). Similar responses of congeneric veligers to temperature and DO levels at depth were observed for quagga mussels in Lake Mead (Chen et al. 2011). Reid et al. (2010) observed maximum quagga mussel veliger densities in the deepest epilimnetic waters during periods of physicochemical stratification in two monomictic water bodies, Copper Basin Reservoir and Lake Mathews.

Annual variation in the vertical location of the thermocline could affect zebra mussel populations by mediating depths at which settlement occurs (Yu and Culver 1999). Therefore, vertical location of the thermocline could influence densities, sizes, and spatial distributions of mussel beds (Naddafi et al. 2010). In the current study, thermoclines were observed near the 6.1-m depth in 2011 (Figure 4, bottom) and near the 3.0-m depth in 2012 (United States Geological Survey 2013). A shallower thermocline observed during 2012 was associated with a vertically larger hypoxic zone at lower depths. Therefore, settlement/recruitment zones available to veligers during 2012 were vertically-compressed towards shallower depths relative to 2011. Shallower distributions of zebra mussels could affect reproductive dynamics, water temperature maxima to which mussels are exposed, and the likelihood of desiccation during the following summer especially if environmental conditions increase variability of lake levels. Boeckman (2011) found that flooding could have similar effects. For example, mussels can settle on substrates at high elevations during flood conditions and later be desiccated when lake levels recede.

Spatial distributions of veligers are also related to the timing of the onset of physicochemical stratification. Prior to the onset of hypoxic conditions at depth during 2011, mussels were observed settled in Lake Texoma on concrete columns below the LTPS to a depth of at least 18.3 m (C. J. Churchill, pers. observ.). Settled mussels at these depths were subsequently exposed to chronic hypoxic conditions that occurred after stratification and were unlikely to survive (Yu and Culver 1999). Strayer et al. (2011) found that adult survival rates were important for population persistence. Hypoxia-induced mortality of individuals below the thermocline, and desiccation of adults in littoral zones, could have contributed to the lack of a secondary spawn during autumn 2011. During 2012, lake stratification was first observed in mid-March (2.5 months earlier than in 2011; Figure 2). Incipient hypoxic conditions at the 15.2-m depth were observed in mid-April, coincidentally, with the DOFS. Mussels were unable to settle below a depth of 15.2 m during 2012 because hypoxic conditions existed below this depth prior to larval development to the settling stage.

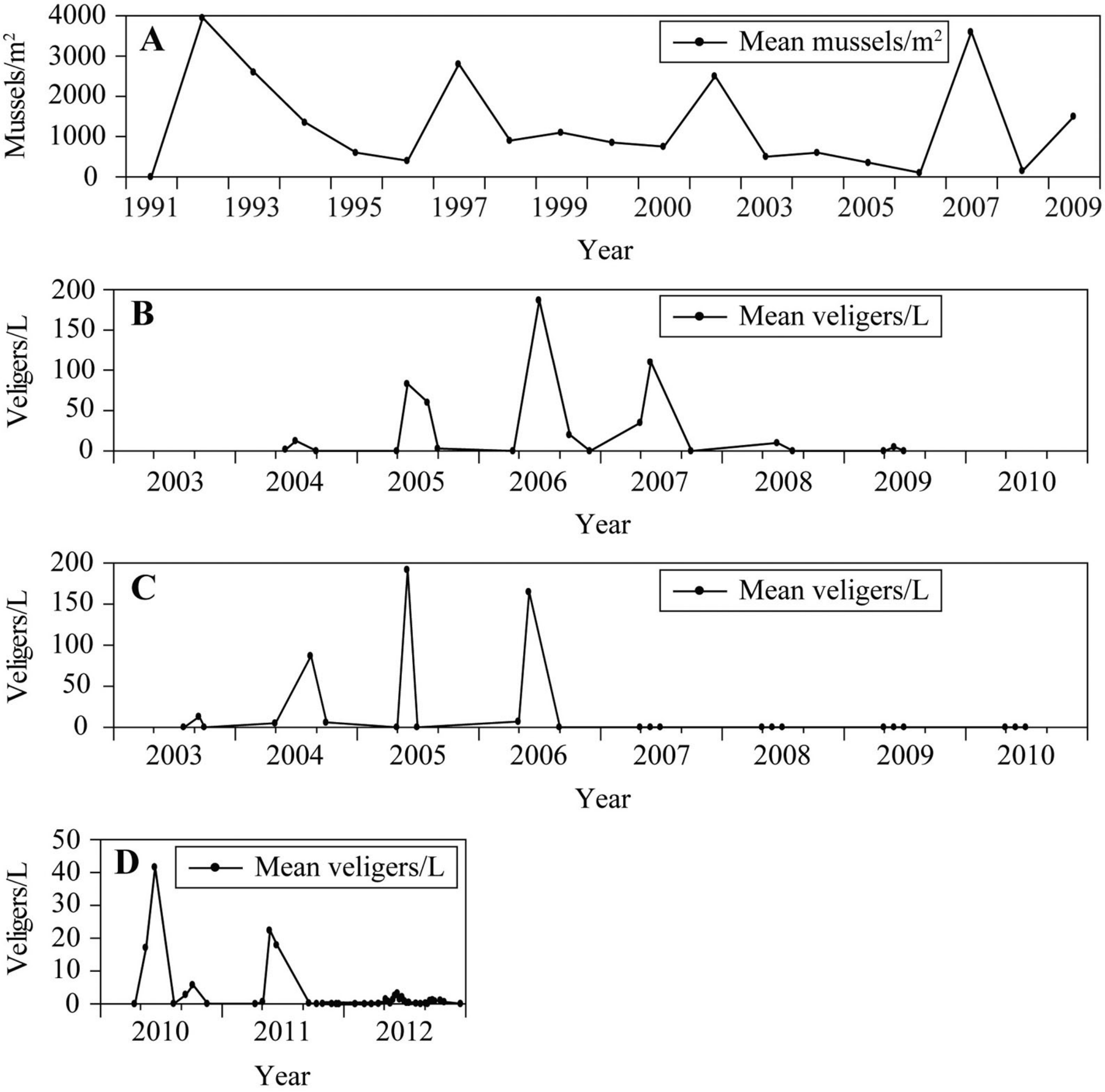


Figure 5. Settled mussel or veliger densities from zebra mussel populations found at different latitudes in North America. A: Hudson River, NY (from Strayer et al. 2011). B: El Dorado Lake, KS (from Severson 2010). C: Oologah Lake, OK (from Boeckman 2011). D: Lake Texoma, TX&OK from current study. A-C are reported as means from multiple sites. A is reported as settled mussel density. B-D are reported as veliger density. Note different axes.

Implications for invasions in the southern United States

Although sizes of reproducing zebra mussel populations could be as large in reservoirs found in the south central United States as they are at higher latitudes, populations in Kansas, Oklahoma, and Texas have each experienced population crashes shortly after establishment and initial peaks in population sizes (Severson 2010; Boeckman 2011; Figure 5B-D). Crashes of zebra mussel populations that occur at higher latitudes are often followed by a recovery to pre-crash levels (Strayer and Malcom 2006; Strayer et al. 2011; Figure 5A). Several causes, including variability of lake levels and high water temperatures, have been linked with zebra mussel population crashes in Kansas (Severson 2010), Oklahoma (Boeckman 2011), and the Lower Mississippi River (Allen et al. 1999). Similar environmental conditions were associated with a population crash observed in Lake Texoma during the current study. Effects of environmental stressors on zebra mussel populations can be exacerbated during periods of drought which concomitantly reduce precipitation, lake inflows, and lake levels and increase temperatures and evaporation, especially during summer. Water bodies found in the southern United States experience more intermittent, extreme droughts than those found at higher latitudes (National Oceanic and Atmospheric Administration 2013). In El Dorado Lake, a substantial drought-induced reduction in lake level likely affected the zebra mussel population. Maximum veliger densities were 270/L during 2007 (Severson 2010). In March 2007, lake levels decreased to 1.8 m below conservation pool level. During this period, substantial numbers of zebra mussels were desiccated. Maximum recorded veliger densities were less than 10/L in 2008 and 2009 when the study ended (Figure 5B). In Oologah Lake, an overall decrease in lake level occurred during a 16-month period of "extreme" drought, from September 2005 to December 2006 (National Oceanic and Atmospheric Administration 2013). Water temperatures reached 30°C at mid-column depths during the period when lake levels decreased. Reported veliger density maximum peaked at 480/L during spring 2006, but remained less than 1/L after the reduction in lake level. Veliger densities stabilized at this lower level from September 2006 to 2010 when the study ended (Boeckman 2011; Figure 5C). Neither the El Dorado nor Oologah Lake zebra mussel population has recovered to pre-crash levels (D. K. Britton, pers. commun.).

During parts of 2011, approximately 88% of Texas was in "exceptional" drought including much of the Red River watershed above Lake Texoma (National Oceanic and Atmospheric Administration 2013). On October 8, 2011, lake elevation in Lake Texoma decreased to the lowest level recorded since before 1995 (609.68 feet above NGVD29; Figure 2, top). During summer and autumn of 2011, the reduced lake levels exposed and desiccated substantial numbers of older, reproductive zebra mussels in Lake Texoma (C. J. Churchill, pers. observ.). Mussels found in littoral zones at depths sufficient to prevent emersion were likely stressed due to high ambient temperatures. In Lake Mead, overall lake levels declined 15 m from 2007 to 2010 (United States Bureau of Reclamation 2013). During this period, however, the quagga mussel population did not experience a crash (Beaver et al. 2010). Because quagga mussels inhabit a greater range of depths and are found in deeper waters than zebra mussels (Nalepa et al. 2010), it is possible drought-induced variability of lake levels could have less effect on quagga mussel populations.

High water temperatures (Lake Texoma reached a maximum temperature of 34.3°C during summer 2011) can reduce survival of veligers, juveniles, and especially post-spawn adults, which are often in poor condition (Allen et al. 1999; Boeckman 2011). Stoeckmann and Garton (2001) found that adult zebra mussels exposed to physiologically-stressful conditions can allocate energy to reproduction at the expense of somatic tissue maintenance, which could increase the probability of post-spawn mortality. A reduction in adult survivorship could have reduced the size of the reproductive population of zebra mussels in Lake Texoma during 2011 and 2012. Secondary spawning was not detected after reduction in lake levels and desiccation of settled adults in littoral zones that occurred during summer and autumn 2011. During the same period, very few zebra mussels settled on artificial substrates (C. J. Churchill, pers. observ.), likely because the veligers were thermally-stressed. Strayer and Malcom (2006) found that substantial reduction in recruitment of one or more cohorts of zebra mussels could affect population size for several generations especially if physiologically-stressful conditions persist. However, recovery of population size could occur if conditions facilitate the development and recruitment of a strong cohort (Strayer and Malcom 2006). Post-crash recovery of populations can occur in one year (Ramcharan et al. 1992a) if a strong spring cohort matures and reproduces by autumn. Morse (2009) suggested post-crash populations could recover if the surviving individuals give rise to a thermally-tolerant population.

It can be difficult to determine patterns and causes of long-term variation in population sizes of invasive species (Simberloff and Gibbons 2004). Other factors that could influence persistence and stability of zebra mussel populations include calcium levels (Whittier et al. 2008), size of the water body (Ramcharan et al. 1992a), and trophic status (Dorgelo 1993; Stanczykowska and Lewandowski 1993). Invasive effects associated with strongly-fluctuating zebra mussel populations are likely to be less severe relative to large, more stable populations that are typical of those found at higher latitudes. For example, Severson (2010) found no significant negative effects of a fluctuating zebra mussel population on the zooplankton community in El Dorado Lake. Strayer and Malcom (2007) found that effects of a cyclic zebra mussel population on native bivalves moderated over time in the Hudson River. It is possible that some water bodies in the southern United States could support large, stable dreissenid mussel populations. Stanczykowska and Lewandowski (1993) suggested stable populations could occur in lakes that are less susceptible to drought-induced environmental variation (e.g. lakes with large volume to surface area ratios or large and far-reaching watersheds). Also, persistent dreissenid populations, especially in lotic environments, could occur in areas that are supported by source propagules (Stoeckel et al. 2004). In many water bodies of the southern and southwestern United States, intermittent reductions in lake levels either by natural (drought) or anthropogenic (water releases) means could facilitate control of dreissenid mussel populations (Tucker et al. 1997). Lake level-related control measures would likely have the greatest effect on invasive populations during summer when mussels are physiologically-stressed.

Conclusions

Results from the current study indicate water temperature, lake level variability, and physicochemical stratification regime influence variability of population sizes and spatial distributions of zebra mussels found near the current southern frontier of their geographic range west of Louisiana. These environmental factors, in part, were associated with a population crash. Continued monitoring in Lake Texoma will determine if the zebra mussel population follows a stable cycle trajectory and recovers to pre-crash levels, stabilizes at reduced densities, follows a chaotic, unpredictable pattern, or if the population crash results in local extirpation. Monitoring established populations in north Texas will provide data that are useful in understanding the influences of environmental conditions on spread and population dynamics of zebra mussels in warm waters of the southern United States. If zebra mussels are introduced into non-infested waters of the southern United States, it is likely environmental conditions (e.g. water temperatures, fluctuations in lake levels, and physicochemical stratification regimes) will affect spatio-temporal population dynamics early in the invasion process. High annual maximum water temperatures and intermittent, extreme drought conditions, which are more common in the southern United States, will likely influence zebra mussel populations that establish in these regions. It is possible that these populations will experience crashes in a few years after establishment and initial peaks in population sizes.

Acknowledgements

The author wishes to thank Ted Kilpatrick (North Texas Municipal Water District), Jerry Chapman (Greater Texoma Utility Authority), and Mike Mocek, John Minahan and Christopher Haeckler (Alan Plummer and Associates, Inc.) for thoughtful discussions during study development, and Brian van Zee (Texas Parks and Wildlife Department) and Denise Hosler (U.S. Bureau of Reclamation) for technical assistance. This manuscript was improved by comments from Dr. David Wong, Dr. Teresa Newton, Amy Beussink, Dr. Thomas La Point, Marc Blouin, Dr. David Britton, and two anonymous reviewers. Comments and figure layouts by Dr. David Hoeinghaus were particularly helpful. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

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

Barnard C, Frenette JJ, Vincent WF (2003) Planktonic invaders of the St. Lawrence estuarine transition zone: environmental factors controlling the distribution of zebra mussel veligers. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1245–1257, http://dx.doi.org/10.1139/f03-103

Beaver JR, Tietjen TE, Blasius-Wert BJ, Kirsch JE, Rosati TC, Holdren GC, Kennedy EM, Hollis RM, Teacher CE, Buccier KM, Evans SK (2010) Persistence of *Daphnia* in the epilimnion of Lake Mead, Arizona-Nevada, during extreme drought and expansion of invasive quagga mussels (2000-2009). *Lake and Reservoir Management* 26: 273–282, http://dx.doi.org/10.1080/07438141.2010.519858

Benson AJ (2013) Zebra mussel sightings distribution. USGS nonindigenous aquatic species site. http://nas.er.usgs.gov/taxgroup/mollusks/zebramussel/zebramusseldistribution.aspx (Accessed 23 July 2013)

Boeckman CJ (2011) Characterizing zebra mussel (*Dreissena polymorpha*) condition, populations, and community effects in Oklahoma habitats. PhD Dissertation, Oklahoma State University, Stillwater, Oklahoma, USA, 185 pp

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

Bossenbroek JM, Johnson LE, Peters B, Lodge DM (2007) Forecasting the expansion of zebra mussels in the United States. *Conservation Biology* 21: 800–810, http://dx.doi.org/10.1111/j.1523-1739.2006.00614.x

Bowers R, de Szalay FA (2005) Effects of water level fluctuations on zebra mussel distribution in a Lake Erie coastal wetland. *Journal of Freshwater Ecology* 20: 85–92, http://dx.doi.org/10.1080/02705060.2005.9664940

Burla H, Ribi G (1998) Density variation of the zebra mussel *Dreissena polymorpha* in Lake Zurich, from 1976 to 1988. *Aquatic Sciences* 60: 145–156, http://dx.doi.org/10.1007/PL00001315

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, USA, 488 pp

Casagrandi R, Mari L, Gatto M (2007) Modeling the local dynamics of the zebra mussel (*Dreissena polymorpha*). *Freshwater Biology* 52: 1223–1238, http://dx.doi.org/10.1111/j.1365-2427.2007.01761.x

Chen D, Gerstenberger SL, Mueting SA, Wong WH (2011) Environmental factors affecting settlement of quagga mussels (*Dreissena rostriformis bugensis*) veligers in Lake Mead, Nevada-Arizona, USA. *Aquatic Invasions* 6: 149–156, http://dx.doi.org/10.3391/ai.2011.6.2.04

Churchill CJ, Baldys S (2012) USGS Zebra Mussel Monitoring Program for North Texas. U.S. Geological Survey Fact Sheet 2012–3077, 6 pp

Claudi R, Evans DW (1993) Chemical addition strategies for zebra mussel (*Dreissena polymorpha*) control in once-through service water systems. In: Nalepa TF, Schloesser DW (eds), Zebra mussels: biology, impacts, and control. CRC Press, Boca Raton, Florida, USA, pp 563–573

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. *Biological Invasions* 8: 1023–1037, http://dx.doi.org/10.1007/s10530-005-3735-y

Cope WG, Waller DL (1995) Evaluation of freshwater mussel relocation as a conservation and management strategy. *Regulated Rivers: Research and Management* 11: 147–155, http://dx.doi.org/10.1002/rrr.3450110204

Cope WG, Bartsch MR, Hayden RR (1997) Longitudinal patterns in abundance of the zebra mussel (*Dreissena polymorpha*) in the Upper Mississippi River. *Journal of Freshwater Ecology* 12: 235–238, http://dx.doi.org/10.1080/02705060.1997.9663531

Dorgelo J (1993) Growth and population structure of the zebra mussel (*Dreissena polymorpha*) in Dutch Lakes of differing trophic state. In: Nalepa TF, Schloesser DW (eds), Zebra mussels: biology, impacts, and control. CRC Press, Boca Raton, Florida, USA, pp 79–94

Drake JM, Bossenbroek JM (2004) The potential distribution of zebra mussels in the United States. *BioScience* 54: 931–941, http://dx.doi.org/10.1641/0006-3568(2004)054[0931:TPDOZM]2.0.CO;2

Fraleigh PC, Klerks PL, Gubanich G, Matisoff G, Stevenson RC (1993) Abundance and settling of zebra mussel (*Dreissena polymorpha*) veligers in western and central Lake Erie. In: Nalepa TF, Schloesser DW (eds), Zebra mussels: biology, impacts, and control. CRC Press, Boca Raton, Florida, USA, pp 129–142

Garton DW, Haag WR (1993) Seasonal reproductive cycles and settlement patterns of *Dreissena polymorpha* in Western Lake Erie. In: Nalepa TF, Schloesser DW (eds), Zebra mussels: biology, impacts, and control. CRC Press, Boca Raton, Florida, USA, pp 111–128

Gerstenberger SL, Mueting SA, Wong WH (2011) Veligers of invasive quagga mussels (*Dreissena rostriformis bugensis*, Andrusov 1897) in Lake Mead, Nevada-Arizona. *Journal of Shellfish Research* 30: 933–938, http://dx.doi.org/10.2983/035.030.0335

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

Hincks SS, Mackie GL (1997) Effects of pH, calcium, alkalinity, hardness, and chlorophyll on the survival, growth, and reproductive success of zebra mussel (*Dreissena polymorpha*) in Ontario lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2049–2057, http://dx.doi.org/10.1139/f97-114

Hosler DM (2011) Early detection of dreissenid species—zebra/quagga mussels in water systems. *Aquatic Invasions* 6: 217–222, http://dx.doi.org/10.3391/ai.2011.6.2.10

Ilarri MI, Antunes C, Guilhermino L, Sousa R (2011) Massive mortality of the Asian clam *Corbicula fluminea* in a highly invaded area. *Biological Invasions* 13: 277–280, http://dx.doi.org/10.1007/s10530-010-9833-5

Jantz B, Neumann D (1998) Growth and reproductive cycle of the zebra mussel in the Rhine River as studied in a river bypass. *Oecologia* 114: 213–225, http://dx.doi.org/10.1007/s004420050439

Johnson LE (1995) Enhanced early detection and enumeration of zebra mussel (*Dreissena* spp.) veligers using cross-polarized light microscopy. *Hydrobiologia* 312: 139–146, http://dx.doi.org/10.1007/BF00020769

Johnson PTJ, Olden JD, Vander Zanden MJ (2008) Dam invaders: impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment* 6: 357–363, http://dx.doi.org/10.1890/070156

Karatayev AY, Burlakova LE, Padilla DK (1998) Physical factors that limit the distribution and abundance of *Dreissena polymorpha* (Pall.). *Journal of Shellfish Research* 17: 1219–1235

Lewandowski K, Ejsmont-Karabin J (1983) Ecology of planktonic larvae of *Dreissena polymorpha* (Pall.) in lakes with different degree of heating. *Polish Archives of Hydrobiology* 30: 89–101

Lucy F (2006) Early life stages of *Dreissena polymorpha* (zebra mussel): the importance of long-term datasets in invasion ecology. *Aquatic Invasions* 1: 171–182, http://dx.doi.org/10.3391/ai.2006.1.3.12

Mackie GL, Schloesser DW (1996) Comparative biology of zebra mussels in Europe and North America: an overview. *American Zoologist* 36: 244–258

Marsden JE, Spidle AP, May B (1995) Genetics of zebra mussel populations throughout the Great Lakes and Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 836–847, http://dx.doi.org/10.1139/f95-083

Martel A, Mathieu AF, Findlay CS, Nepszy SJ, Leach JH (1994) Daily settlement rates of the zebra mussel, *Dreissena polymorpha,* on an artificial substrate correlate with veliger abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 856–861, http://dx.doi.org/10.1139/f94-084

Matthews MA, McMahon RF (1999) Effects of temperature and temperature acclimation on survival of zebra mussel (*Dreissena polymorpha*) and Asian clams (*Corbicula fluminea*) under extreme hypoxia. *Journal of Molluscan Studies* 65: 317–325, http://dx.doi.org/10.1093/mollus/65.3.317

McMahon RF (1996) The physiological ecology of the zebra mussel, *Dreissena polymorpha*, in North America and Europe. *American Zoologist* 36: 339–363

McMahon RF (2011) Quagga mussel (*Dreissena rostriformis bugensis*) population structure during the early invasion of Lakes Mead and Mohave January-March 2007. *Aquatic Invasions* 6: 131–140, http://dx.doi.org/10.3391/ai.2011.6.2.02

Morse JT (2009) Thermal tolerance, physiological condition, and population genetics of Dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) relative to their invasion of waters in the Western United States. PhD

Dissertation, The University of Texas at Arlington, Arlington, Texas, USA, 280 pp

Mueting SA, Gerstenberger SL, Wong WH (2010) An evaluation of artificial substrates for monitoring the quagga mussel (*Dreissena bugensis*) in Lake Mead, Nevada-Arizona. *Lake and Reservoir Management* 26: 283–292, http://dx.doi.org/10.1080/07438141.2010.540700

Muirhead JR, MacIsaac HJ (2005) Development of inland lakes as hubs in an invasion network. *Journal of Applied Ecology* 42: 80–90, http://dx.doi.org/10.1111/j.1365-2664.2004.00988.x

Naddafi R, Pettersson K, Eklov P (2010) Predation and physical environment structure the density and population size structure of zebra mussels. *Journal of the North American Benthological Society* 29: 444–453, http://dx.doi.org/10.1899/09-071.1

Nalepa TF, Wojcik JA, Fanslow DL, Lang GA (1995) Initial colonization of the zebra mussel (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron: population recruitment, density, and size structure. *Journal of Great Lakes Research* 21: 417–434, http://dx.doi.org/10.1016/S0380-1330(95)71056-5

Nalepa TF, Fanslow DL, Foley AJ, Lang GA, Eadie BJ, Quigley MA (2006) Continued disappearance of the benthic amphipod *Diporeia* spp. In Lake Michigan: is there evidence for food limitation? *Canadian Journal of Fisheries and Aquatic Sciences* 63: 872–890, http://dx.doi.org/10.1139/f05-262

Nalepa TF, Fanslow DL, Pothoven SA (2010) Recent changes in density, biomass, recruitment size structure, and nutritional state of *Dreissena* populations in southern Lake Michigan. *Journal of Great Lakes Research* 36: 5–19, http://dx.doi.org/10.1016/j.jglr.2010.03.013

National Oceanic and Atmospheric Administration (2013) U.S. Drought Monitor. http://droughtmonitor.unl.edu/monitor.html (Accessed 2 February 2013)

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, http://dx.doi.org/10.1016/j.ecolecon.2004.10.002

Ram JL, Fong PP, Garton DW (1996) Physiological aspects of zebra mussel reproduction: maturation, spawning, and fertilization. *American Zoologist* 36: 326–338

Ramcharan CW, Padilla DK, Dodson SI (1992a) A multivariate model for predicting population fluctuations of *Dreissena polymorpha* in North American Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 150–158, http://dx.doi.org/10.1139/f92-018

Ramcharan CW, Padilla DK, Dodson SI (1992b) Models to predict potential occurrence and density of the Zebra Mussel, *Dreissena polymorpha*. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2611–2620, http://dx.doi.org/10.1139/f92-289

Reid NJ, Anderson MA, Taylor WD (2010) Distribution of quagga mussel veligers, *Dreissena bugensis*, in the reservoirs of the Colorado River Aqueduct. *Lake and Reservoir Management* 26: 328–335, http://dx.doi.org/10.1080/07438141.2010.542878

Schorr MS, Sah J, Schreiner DF, Meador MR, Hill LG (1995) Regional economic impact of the Lake Texoma (Oklahoma-Texas) striped bass fishery. *Fisheries* 20: 14–18, http://dx.doi.org/10.1577/1548-8446(1995)020<0014:REIOTL>2.0.CO;2

Severson AM (2010) Effects of zebra mussel (*Dreissena polymorpha*) invasion on the aquatic community of a Great Plains reservoir. MS Thesis, Kansas State University, Manhattan, Kansas, USA, 73 pp

Simberloff D, Gibbons L (2004) Now you see them, now you don't! – population crashes of established introduced species. *Biological Invasions* 6: 161–172, http://dx.doi.org/10.1023/B:BINV.0000022133.49752.46

Smylie PHP (1994) Growth and abundance of *Dreissena polymorpha* larvae in relation to temperature and phytoplankton abundance. MS Thesis, The University of Guelph, Guelph, Ontario, Canada, 183 pp

Sprung M (1987) Ecological requirements of developing *Dreissena polymorpha* eggs. *Archiv für Hydrobiologie Supplement* 1: 69–86

Sprung M (1989) Field and laboratory observations of *Dreissena polymorpha* larvae: abundance, growth, mortality, and food demands. *Archiv für Hydrobiologie* 115: 537–561

Sprung M (1992) Observations on shell growth and mortality of *Dreissena polymorpha* in lakes. In: Neumann D, Jenner HA (eds), The zebra mussel *Dreissena polymorpha*: ecology, biological monitoring, and first applications in the water quality management. Gustav Fisher, Stuttgart, Germany, pp 19–28

Stanczykowska A, Lewandowski K (1993) Thirty years of studies of *Dreissena polymorpha* ecology in Mazurian Lakes of Northeastern Poland. In: Nalepa TF, Schloesser DW (eds), Zebra mussels: biology, impacts, and control. CRC Press, Boca Raton, Florida, USA, pp 3–37

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

Stoeckmann AM, Garton DW (2001) Flexible energy allocation in zebra mussels (*Dreissena polymorpha*) in response to different environmental conditions. *Journal of the North American Benthological Society* 20: 486–500, http://dx.doi.org/10.2307/1468043

Strayer DL (1991) The projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1389–1395, http://dx.doi.org/10.1139/f91-166

Strayer DL, Malcom HM (2006) Long-term demography of a zebra mussel (*Dreissena polymorpha*) population. *Freshwater Biology* 51: 117–130, http://dx.doi.org/10.1111/j.1365-2427.2005.01482.x

Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution* 21: 645–651, http://dx.doi.org/10.1016/j.tree.2006.07.007

Strayer DL, Malcom HM (2007) Effects of zebra mussels (*Dreissena polymorpha*) on native bivalves: the beginning of the end or the end of the beginning? *Journal of the North American Benthological Society* 26: 111–122, http://dx.doi.org/10.1899/0887-3593(2007)26[111:EOZMDP]2.0.CO;2

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

Strayer DL, Cid N, Malcom HM (2011) Long-term changes in a population of an invasive bivalve and its effects. *Oecologia* 165: 1063–1072, http://dx.doi.org/10.1007/s00442-010-1792-0

Texas Parks and Wildlife Department (2009) Zebra mussels spreading in Texas. http://www.tpwd.state.tx.us/newsmedia/releases/?req=20090817a (Accessed 19 September 2012)

Texas Parks and Wildlife Department (2012) Zebra mussels found in Lake Ray Roberts. http://www.tpwd.state.tx.us/newsmedia/releases/?req=20120718a (Accessed 8 January 2013)

Texas Parks and Wildlife Department (2013a) Zebra Mussels Documented in Lewisville Lake [Lake Lewisville]. http://www.tpwd.state.tx.us/newsmedia/releases/?req=20130620b (Accessed 22 July 2013)

Texas Parks and Wildlife Department (2013b) Zebra mussels found in Lake Belton and suspected in Lakes Worth and Joe Pool. http://www.tpwd.state.tx.us/newsmedia/releases/?req=20130926a (Accessed 4 November 2013)

Tucker JK, Theiling CH, Janzen FJ, Paukstis GL (1997) Sensitivity to aerial exposure: potential of system-wide drawdowns to manage zebra mussels in the Mississippi River. *Regulated Rivers: Research and Management* 13: 479–487, http://dx.doi.org/10.1002/(SICI)1099-1646(199711/12)13:6<479::AID-RRR469>3.0.CO;2-B

United States Bureau of Reclamation (2013) Lake Mead elevation at Hoover Dam. http://www.usbr.gov/lc/region/g4000/hourly/mead-elv.html (Accessed 24 September 2013)

United States Geological Survey (2013) USGS water data for Texas—National Water Information System. http://waterdata.usgs.gov/tx/nwis/nwis (Accessed 22 February 2013)

Weather Underground (2013) Weather History and Almanac for Sherman – Denison, TX. http://www.wunderground.com/cgi-bin/findweather/hdfForecast?query=kgyi (Accessed 22 February 2013)

Whittier TR, Ringold PL, Herlihy AT, Pierson SM (2008) A calcium-based invasion risk assessment for zebra and quagga mussels (*Dreissena* spp). *Frontiers in Ecology and the Environmen*t 6: 180–184, http://dx.doi.org/10.1890/070073

Winemiller (2005) Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 872–885

Wittmann ME, Chandra S, Caires A, Denton M, Rosen MR, Wong WH, Tietjen T, Turner K, Roefer P, Holdren GC (2010) Early invasion population structure of quagga mussel and associated benthic invertebrate community composition on soft sediment in a large reservoir. *Lake and Reservoir Management* 26: 316–327, http://dx.doi.org/10.1080/07438141.2010.519855

Yu N, Culver DA (1999) *In situ* survival and growth of zebra mussels (*Dreissena polymorpha*) under chronic hypoxia in a stratified lake. *Hydrobiologia* 392: 205–215, http://dx.doi.org/10.1023/A:1003697231917