ZEBRA MUSSEL (*DREISSENA POLYMORPHA*)

POPULATION DYNAMICS AT

SOONER LAKE, OK

By

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Abstract: Zebra mussels (*Dreissena polymorpha*) are native to Europe and were first reported in North America in the late 1980s at Lake St. Clair in Michigan. They negatively impact ecosystems, recreation, and facilities that use surface water such as public water supply plants, power generation facilities, and industrial facilities throughout North America. Understanding the life history characteristics of zebra mussels and the environmental factors that limit their success is critical for managing zebra mussel infestations. Zebra mussel population dynamics are influenced by temperature. Oklahoma was previously considered the southernmost portion of the zebra mussels' invasive range because of increased water temperatures. Zebra mussels are currently distributed as far South as Austin, Texas. This suggests that zebra mussels can and will continue to invade aquatic ecosystems that are characterized by extreme temperatures. Zebra mussels were first reported in Oklahoma in 1993 and in Sooner Lake in 2006. Sooner Lake is used to cool a coal-fired power generation facility that lies directly adjacent to the lake. Heated effluent that continually discharges from the facility has created an artificial thermal gradient with temperatures decreasing away from the discharge channel. This artificial thermal gradient provides a unique opportunity to study how zebra mussels react to a wide range of temperatures within a single reservoir. The purpose of this study was to: 1) document the extent of the thermal gradient at Sooner Lake, and 2) compare zebra mussel veliger densities along the temperature gradient to determine how temperature affects zebra mussel population dynamics and reproductive success. A significant thermal gradient was found at Sooner Lake where temperatures were approximately 10 °C warmer in the discharge channel compared to the main body of the lake during the summer months. Veliger densities differed along this thermal gradient. These differences were not consistent between sites and not always driven by temperature. This indicates that other environmental variables are important for zebra mussels. A maximum density of 120 veligers/L occurred at the intake while on the same date 114 veligers/L were recorded at the discharge buoy where temperatures were much higher. A rapid decrease in temperatures to suboptimal conditions was likely responsible for the lack of a secondary spawn in 2019. This study found that both high and low temperatures can have negative impacts on the reproductive success of zebra mussels. These results suggest that zebra mussels along the southern invasion front have a high tolerance to extreme water temperatures and are capable of persisting long term in such environments.

Keywords: Zebra mussels (*Dreissena polymorpha*), Sooner Lake, temperature, thermal gradient

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CHAPTER I

INTRODUCTION

It is estimated that nearly 50,000 invasive species have been introduced into the United States. Many of these species cause economic losses in agriculture, forestry, and other sectors of the United States (U.S.) economy (Pimentel et al., 2005). Invasive species also negatively impact native species. It is estimated that between 6% (Duenas et al., 2018) and 49% (Wilcove et al., 1998) of native species listed under the United States Endangered Species Act are at risk because of competition or predation from invasive species.

Zebra mussels (*Dreissena polymorpha*) are native to Europe and were first reported in North America in the late 1980s at Lake St. Clair, Michigan (Laney, 2010). Ballast water exchange from transatlantic ships traveling by way of the Great Lakes-St. Lawrence Seaway was most likely responsible for the introduction of zebra mussels into North America (Hebert et al., 1989). They dispersed rapidly down major U.S. river systems eventually leading to the Mississippi River in 1991. They are currently found in at least 31 states (Benson et al., 2019; Figure 1). Zebra mussels were discovered in Oklahoma on the Arkansas River in the McClellan-Kerr Navigation System in 1993 (Laney, 2010). They have since spread to over 20 reservoirs across the state including Sooner Lake located in north-central Oklahoma (Benson et al., 2019; Figure 2).

Sooner Lake was built in 1972 for the primary purpose of cooling a coal-fired power generation facility that is owned and operated by the Oklahoma Gas & Electric Company (OG&E). Zebra mussels were first reported at Sooner Lake in 2006 (Boeckman, 2011). Zebra mussels have biofouled submerged equipment and clogged pipes and screens within the power plant. This resulted in reductions in plant efficiency and economic losses (Matt Grimes, personal communication, Supervisor Environmental/Op. Chem, OG&E, 2019).

Sooner Lake is unique because warm water continuously discharges from the power plant. Heated effluent travels down a channel that is separated from the main body of the lake by an earthen barrier. These circumstances suggest that a thermal gradient exists at Sooner Lake. Sooner Lake is characterized by a wide range of temperatures as a result of these discharges.

Temperature is a limiting factor in the spread and distribution of zebra mussels (Karatayev, 1998; Sprung, 1987; Aldridge et al., 1995; McMahon & Ussery, 1995; Spidle et al., 1995; Lei et al., 1996; Stoeckmann & Garton, 2001; Boeckman, 2011; Churchill, 2013; Churchill et al., 2017; Jost et al., 2015). This study is unique because it provides an opportunity to study how temperature influences zebra mussel population dynamics in a thermally diverse environment.

The objectives of this study were to document the extent of the thermal gradient at Sooner Lake and to compare zebra mussel larval (veliger) densities in the water column along this gradient. Temperature and other water quality parameters that impact zebra mussel reproduction and output of veligers were measured and analyzed. Six sites at Sooner Lake were selected to collect water quality and veliger samples. These six sites were distributed across the lake and were selected to represent differences in temperature and other water quality parameters.

Preliminary sampling of water temperatures at all sites suggest that there is a significant thermal gradient at Sooner Lake. An earthen barrier separates the discharge channel from the main body of the lake further enhancing differences in temperature. It is hypothesized that there is a significant thermal gradient at Sooner Lake resulting from the heated effluent that discharges from the OG&E power plant.

Veliger densities previously peaked during the primary spawn when temperatures were ≤ 28 °C at Oologah Lake in Oklahoma (Boeckman, 2011). Veligers did not re-emerge at Lake Oologah for a secondary spawn until temperatures declined below 26 °C (Boeckman, 2011). Boeckman (2011) reported differences in veliger densities in Sooner Lake and attributed it to the influence of the heated discharge. It is hypothesized that veliger densities will be significantly different along the artificial thermal gradient and that population densities will decline at all sites when temperatures reach or exceed 28 °C. It is further hypothesized that veligers will not re-emerge for a secondary spawn until temperatures decline to ≤ 26 °C.

Adult zebra mussel die offs have previously been documented at Sooner Lake when temperatures exceed 30 °C. Veliger densities remained low at sample sites closer to the heated discharge resulting in seasonal extirpation and reintroduction of adults in a previous study (Boeckman, 2011). This suggests that reproductive output will be greater at sites where mussels are not negatively influenced by temperatures known to cause physiological stress (Aldridge et al, 1995). It is hypothesized that greater veliger densities will be observed at sample sites where water temperatures are not strongly influenced by the heated discharge.

CHAPTER II

REVIEW OF THE LITERATURE

Spread and Distribution in North America

Zebra mussels were found throughout the Great Lakes by 1990. They were later found in the Illinois and Hudson Rivers. They spread to the Mississippi River in 1991(Benson et al., 2019). The rapid spread of zebra mussels throughout the Great Lakes and the major river systems in North America (Figure 1) has been attributed in part to their larval life stage as veligers (Benson et al., 2019).

The larval (veliger) life stage is a free-floating planktonic stage that facilitates zebra mussel dispersal by flowing water. Adult zebra mussels also attach to boats and other overland vectors facilitating dispersal to new water bodies (Mackie, 1991). Colonization of isolated reservoirs by overland transport creates source populations that reproduce. Veligers from these reproducing adults drift downstream to other waterbodies (Horvath et al., 1996). Downstream transport is especially important in states where there are numerous impoundments and high connectivity between rivers and reservoirs. The dispersal of veligers through connected systems moves at a faster rate than overland transport (Johnson & Carlton, 1996).

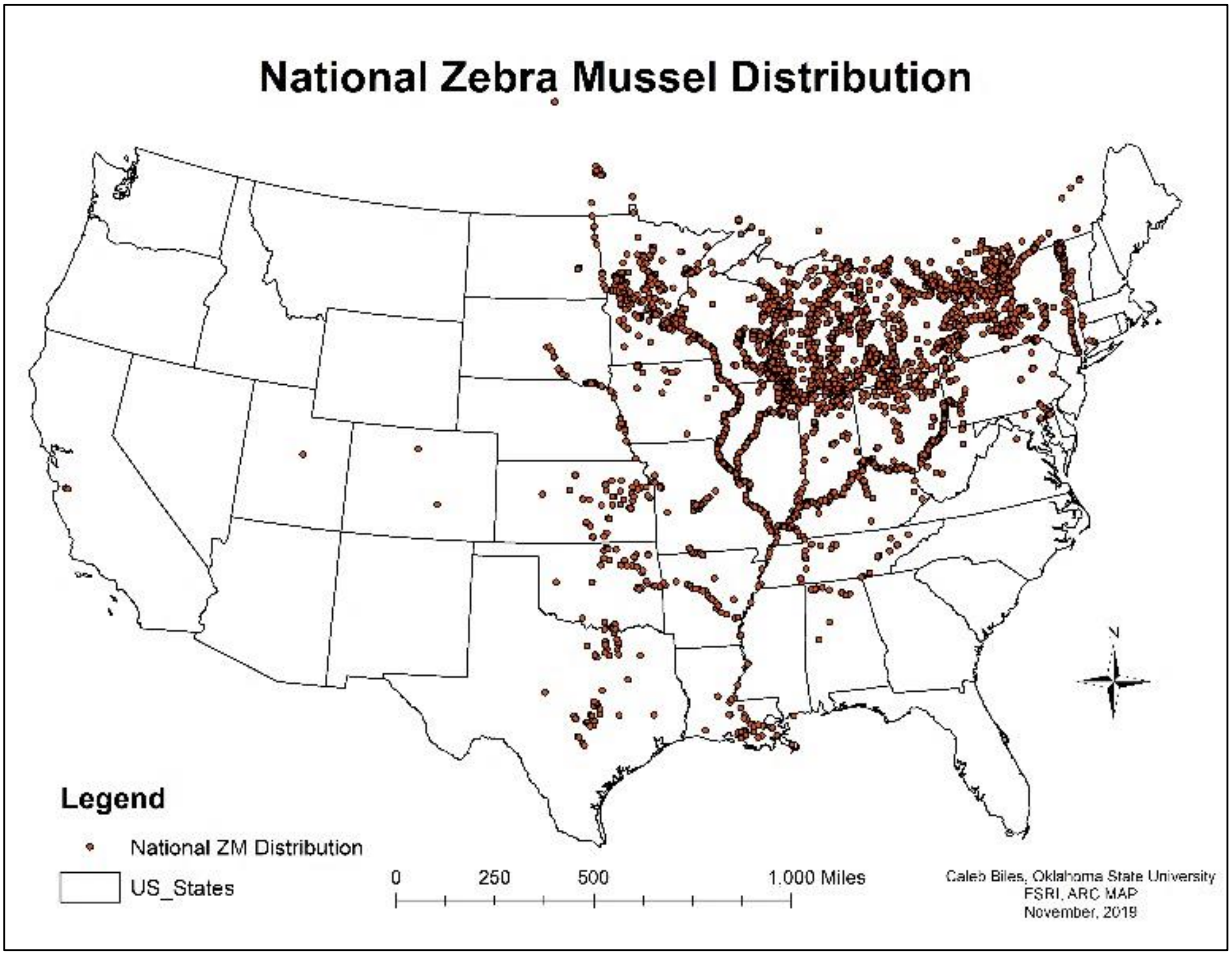

Figure 1. Zebra mussel distribution in the United States as of 2019 (Nonindigenous Aquatic Species Database, USGS, 2019).

Zebra mussels were discovered in Oklahoma in 1993 on the Arkansas River in the McClellan-Kerr Navigation System. The first confirmed reservoir in Oklahoma to be invaded by zebra mussels was Oologah Lake in 2003. Zebra mussels continued to spread down the Arkansas River to more reservoirs and connecting waterbodies (Laney, 2010) including Sooner Lake in 2006 (Boeckman, 2011). They are currently established in over 20 reservoirs in Oklahoma (Benson et al., 2019; Figure 2).

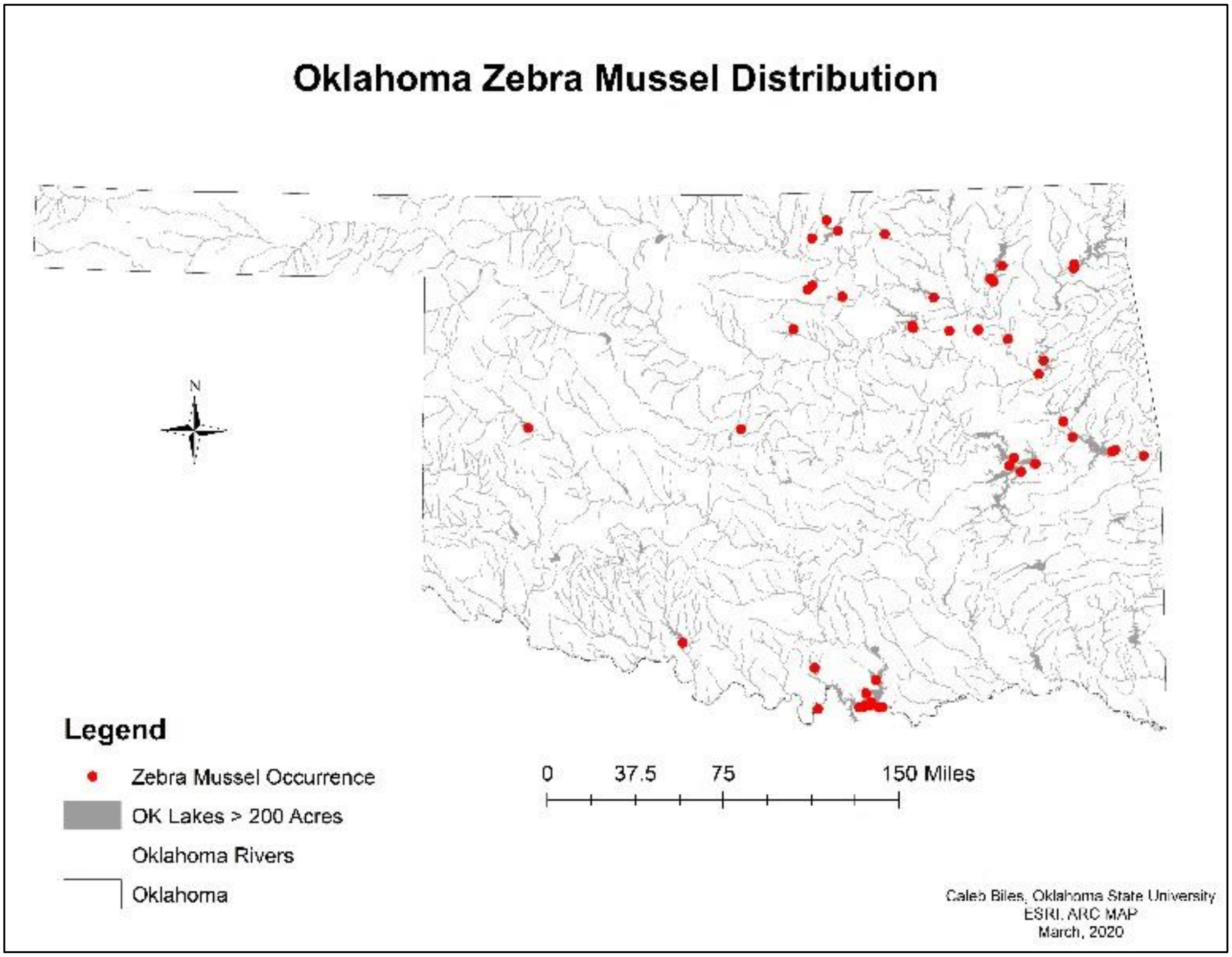

Figure 2. Zebra mussel distribution in the State of Oklahoma as of 2019 (Nonindigenous Aquatic Species Database, USGS, 2019).

Sooner Lake was previously considered a reservoir along the southern portion of the zebra mussel's invasive range in 2011 (Boeckman, 2011). The southern limit of the zebra mussel's range in North America is continually expanding (Benson et al., 2019). Churchill et al. (2017) state that increased invasiveness is possible if zebra mussels portray latitudinal changes in thermal tolerance and become capable of producing thermally tolerant, rapidly growing individuals without excessive mortality. Latitudinal changes in zebra mussel occurrences have been documented since zebra mussels began invading streams and reservoirs in North Texas in

2009. The southernmost reservoir with an established zebra mussel population is Ladybird Lake in Austin, Texas, as of 2018. (Benson et al., 2019).

Life Cycle and Biology

Zebra mussels (*Dreissena polymorpha*) are a small species of shellfish that have a distinct striped pattern on the outer shell (Mackie, 1991). Zebra mussels become reproductively mature when they reach a shell length of approximately 7-9 mm. They generally have two reproductive spawning events each year based on environmental cues such as food supply and temperature (Jantz & Neumann, 1998). The first occurs in the spring between May and June. The second occurs in the Autumn between September and November (Mackie, 1991).

Spawning is largely driven by water temperature and occurs when temperatures reach approximately 12 °C in the spring (Borcherding, 1991; McMahon, 1996; Jantz & Neumann, 1998). Spawning may occur earlier or later depending on geography and environmental conditions including temperature (Borcherding, 1991). Early onset of spawning was initiated at Lake Texoma when temperatures were between 16-18 °C. This occurred 44 days earlier than three cooler lakes in the Great Lakes Region (Churchill, 2013).

Zebra mussels are dioecious. Fertilization occurs outside the body in the water column. Eggs develop within the female and are expelled followed by fertilization by the male (Franzen, 1983; Sprung, 1987). Zebra mussels have high fecundity. Females can expel up to 1.5 million eggs per year (Borcherding, 1991; Neumann et al., 1993). Free-floating veligers emerge within three to five days after fertilization (Benson et al., 2019). They remain in the free-floating planktonic stage for approximately 4 weeks (Mackie, 1991).

Optimal temperatures for veliger development range from 12 to 24 °C (Sprung, 1987). Veligers undergo morphological changes as they develop into pediveligers and then into the plantigrade (post-veliger) and juvenile stage. Juveniles become adults upon further development of the outer shell and onset of sexual maturity. These morphological changes include the development of a siphon, foot, and organ system (Ackerman et al., 1994). Adults grow 1.5 to 2.0 cm in their first year and can develop a shell length of 3.0 cm (Mackie, 1991). The lifespan for adult zebra mussels is between 3 and 9 years (Benson et al., 2019).

Ecological and Environmental Implications

Zebra mussels negatively impact aquatic ecosystems by altering native species composition, species interactions, and ecosystem properties (Karatayev et al., 2002; Karatayev et al., 2015). These alterations in ecosystem functionality include declines in production and biomass of pelagic autotrophs, heterotrophs, herbivorous zooplankton, and planktivores. These declines are due to the shift in nutrients and primary production from the pelagic zone to the benthos (Mackie, 1991).

Zebra mussels are filter feeders that can filter approximately 1-liter of water per day. Filtering is facilitated by an inhalant and exhalant siphon for food uptake and excretion (Benson et al., 2019). Water is almost always circulating through zebra mussel siphons and gills which remove particulates from the water column (Karatayev et al., 2002; Mackie, 1991). Zebra mussels can reduce the abundance of phytoplankton in the water column by as much as 90 % (MacIsaac, 1996). Filtered particles that are not consumed are bound in mucous and excreted as pseudofeces (Karatayev et al., 2002; Mackie, 1991).

Removal of particulates by zebra mussel's increases water clarity and can alter the function of native aquatic ecosystems. Increased water clarity increases light penetration and results in a larger euphotic zone. Attached macrophytes can populate a greater amount of area in this altered environment (Karatayev et al., 2002; Mackie, 1991). Zebra mussels reduced phytoplankton abundance and increased water clarity at Lake Oneida, New York, promoting increased growth of submerged macrophytes (Zhu et al., 2006). There was also a shift from shade-tolerant species to species that tolerate wider ranges of light levels.

Increased macrophyte diversity and occurrence can benefit species of zooplankton, invertebrates, and fish by providing spawning or nursery habitats (Zhu et al., 2006). MacIsaac et al. (1995) contrastingly found that zebra mussels can reduce zooplankton abundance by as much as 71%. This suggests that any benefit to zooplankton communities associated with increased macrophyte diversity may not offset the simultaneous competition between zooplankton and zebra mussels.

Reductions in zooplankton abundance by zebra mussels can be detrimental to some fish species, especially those that are pelagic feeders. Raikow (2004) found that zebra mussels indirectly reduced the growth of larval bluegill. These reductions occurred because zebra mussels directly consumed microzooplankton or depleted the phytoplankton community to such an extent that microzooplankton starved. Reductions in the microzooplankton community resulted in the depletion of a food source for larval Bluegill (Raikow, 2004).

Zebra mussels negatively affect native unionids and crayfish. Zebra mussels settle and grow directly on these native species. Approximately 300 individual zebra mussels were observed on native unionid mussels in Lake St. Claire. Zebra mussel settlement on native unionid shells can be so great that unionids cannot open their valves, or they cannot fully close their shells (Mackie, 1991).

Zebra mussels also compete with native mussels for food resources. Zebra mussels greatly reduced the availability of unicellular *Microcystis* in the Hudson River. *Microcystis* is a preferential food source for native mussels. A lack of an adequate food source will likely result in declines in native mussel populations (Baker and Levinton, 2003).

Economic and Social Implications

Zebra mussels negatively impacted the economy since invading North America. There have been economic repercussions associated with power generation facilities, industrial facilities, and water treatment facilities (Benson et al., 2019). Economic costs at these facilities are associated with plant re-design, fixing or replacing damaged infrastructure, reduced efficiency due to clogged pipe networks, hiring workers to manually scrape mussels off infrastructure, and purchasing molluscicides (Rosaen et al., 2016). It was estimated that Ontario power plants spend approximately $1.2 million/plant/year for monitoring and control purposes (Colautti et al., 2006). The average annual economic cost was estimated at approximately $30 million at power plants, water companies, golf courses, and other industries using surface water in the Great Lakes Region, (Park & Hushak, 1999). A paper company on Lake Michigan spent approximately $1.4 million in 1997 when the company had to remove 400 cubic yards of zebra mussels from its intake (USGS, 1997). Pimental et al. (2005) estimated the total economic loss associated with zebra mussels is approximately $1 billion annually. Reported economic costs associated with zebra mussel infestations are variable. Zebra mussels will continue to incur costly damages to facilities that use surface water.

Zebra mussels negatively impacted navigational and recreational boating in North America (Ludyanskiy et al., 1993). Zebra mussels attach onto the bottom of boats and increase drag. Smaller zebra mussels can get into engine cooling systems of boats and cause overheating and damage. Zebra mussels can colonize a surface to such an extent that buoys have sunk under their weight. Fishing gear in the water is at risk of biofouling from zebra mussel infestations

(Benson et al., 2019). Zebra mussels cost people their time and are an inconvenience. States have required boaters to quarantine their watercraft for up to 30 days if they have come from a state with zebra mussels (Ouellet, 2018).

Zebra mussel infestations have additional impacts. Tourism can be negatively affected by zebra mussels. Large numbers of shells from dead zebra mussels have washed up on beaches at Lake Erie limiting recreational activities and causing foul odors (Ludyanskiy et al., 1993). Dead mussels on beaches are a health hazard because swimmers and animals can cut their feet on shells (Minnesota Department of Natural Resources, 2015). Zebra mussels negatively affect the taste and odor of drinking water. This problem was observed in Chicago on the shores of Lake Michigan (Vogel et al., 1997). Taste and odor problems were also attributed to zebra mussels at Lake Hemlock in New York. Lake Hemlock is the drinking water source for Rochester, New York (Kriewall & Zapa, 2006).

Temperature and Zebra Mussel Distribution

Temperature is a major driver and limiting factor in the spread and distribution of zebra mussels. There is evidence that the thermal tolerance of zebra mussels is variable. North American zebra mussels have a 2 to 3 °C higher upper thermal tolerance compared to Northern European zebra mussel populations (McMahon & Ussery, 1995). Differences in thermal tolerance between these two populations are likely due to the origin of the North American zebra mussel. The origin is thought to be the Black, Arial, and Caspian Seas which are in the southernmost portion of the zebra mussels' range in Europe. This likely resulted in a more thermally tolerant population in the United States compared to populations in the northern reaches of the zebra mussel's European range (McMahon & Ussery, 1995).

The upper thermal limit for adult zebra mussels is approximately 30 °C (Jost et al., 2015) and 28 °C for veligers (Boeckman, 2011). The negative impacts that upper temperatures inflict upon zebra mussel populations varies considerably in the literature despite the thermal limit approximation of 30 °C. Spidle et al. (1995) found that zebra mussels can withstand temperatures of 30 °C for up to 14 days without mortality. Increasing the acclimation temperature in mesocosm studies enhanced mussel survival when exposed to increased temperatures. Zebra and quagga mussels that were acclimated to 15 or 20°C were more likely to survive acute thermal stress than those specimens that were only acclimated to 5°C (Spidle et al., 1995).

Zebra mussels collected from the Niagara River were exceptionally tolerant of higher temperatures. Those that were acclimated at 32°C survived for 35 days without extensive mortality (Aldridge et al.,1995). McMahon and Ussery (1995) also found that zebra mussels can successfully acclimate to warmer temperatures. Zebra mussels were held at temperatures greater than 30°C for extended periods without excessive mortality.

A major zebra mussel die-off was reported at Gull Lake, Michigan, where temperatures were well below 30°C (White et al., 2015). This die-off was associated with accumulated degree hours > 25°C. The die-off at Gull Lake suggested that chronic exposure to sub-lethal temperatures can negatively influence zebra mussel populations. Acute lethal thresholds tend to be higher than chronic lethal thresholds indicating that previous reports may not accurately represent in-situ conditions (White et al., 2015).

Churchill et al. (2017) conducted an in-situ study of zebra mussel mortality at Lake Texoma and reported a strong temperature mortality relationship. Churchill et al. (2017) state that increased invasiveness is possible if zebra mussels portray latitudinal changes in thermal tolerance, and become capable of producing thermally tolerant, rapidly growing individuals without excessive mortality. Zebra mussels were confined to North Texas at the time of the study by Churchill et al. (2017). The 2019 Nonindigenous Aquatic Species Database (Benson et al., 2019) indicates the further spread of zebra mussels into southern portions of Texas.

Sooner Lake Case Study

Sooner Lake is a reservoir in north-central Oklahoma that was built in 1972 for the primary purpose of cooling a coal-fired power generation facility that is owned and operated by the Oklahoma Gas & Electric Company (OG&E). The lake is an impoundment of Greasy Creek, which is a tributary of the Arkansas River. It is classified by the Oklahoma Water Resource Board (2015) as a mesotrophic reservoir based on nutrient and chlorophyll *a* concentrations collected from October of 2014 to July of 2015. The lake covers an area of approximately 5,400 acres and has a holding capacity of 149,000 acre-feet. It has 51.8 miles of shoreline and is at normal pool elevation at 927 feet. The maximum recorded depth at Sooner Lake is 73.5 feet (OWRB, 2015).

OG&E controls reservoir discharge from the dam back into the Arkansas River. The amount discharged varies seasonally depending on reservoir conditions. The power plant discharges approximately 789.12 million gallons per day of cooling water (Matt Grimes, personal communication, Supervisor Environmental/Op. Chem, OG&E, 2019). This results in warmer water temperatures along the discharge channel (Boeckman, 2011).

Costly damages associated with zebra mussels have been observed at Sooner Lake. OG&E spends approximately $100,000 annually at Sooner Lake on the treatment of their 5 intake bays with the mulluscicide Zequanox®. OG&E has reported post-application mortality rates as high as 99% in the intake bays. Zebra mussel colonization on a circulating water pump and a diesel fire pump cost OG&E $310,000. OG&E does not expect regular failures of equipment with continued treatment of the intake bays (Matt Grimes, personal communication, Supervisor Environmental/Op. Chem, OG&E, 2019).

Zebra mussels also cause problems at OG&E by clogging screens on closed cooling water (CCW) heat exchangers. Screens on CCW heat exchangers are cleaned 8-10 times per summer season. This costs cost up to $70,000 to $80,000 annually. Uncleaned screens could lead to reduced efficiency amounting to millions of dollars of lost power generation at the plant (Matt Grimes, personal communication, Supervisor Environmental/Op. Chem, OG&E, 2019).

A monitoring program was initiated in Sooner Lake in 2007. Sampling was conducted from 2007 to 2010 to assess zebra mussel density, reproduction, and growth between sites in the discharge channel and sites in the main body of the lake which represent typical Oklahoma ambient water temperatures (Boeckman, 2011). This previous monitoring program provided an opportunity to evaluate the population dynamics of zebra mussels under different environmental conditions, especially increased water temperatures.

Sooner Lake is unique because it has a relatively large thermal gradient due to the warm water that continuously discharges from the OG&E power plant. The eastern portion of the lake represents typical ambient Oklahoma reservoir temperatures. The western portion has elevated temperatures due to heated effluent.

Peak veliger densities were recorded at 150/L in 2007, 580/L in 2008, 350/L in 2009, and 600/L in 2010. Adults located in the discharge channel never exceeded 10,000 m^2 which resulted in veliger densities of < 100/L. Adult to veliger density ratios were not consistent throughout the study period. Adult densities were recorded at 150,000 m^2 in 2007, 50,000 m^2 in 2008, 60,000 m^2 in 2009, and 30,000 m^2 in 2010. (Boeckman, 2011).

The timing of the first yearly spawns at Sooner Lake between 2007 and 2010 were similar to other Oklahoma reservoirs except at sites within the discharge channel (Figure 3). Veligers were observed in May and peak densities occurred in June in the main body of the lake. Spawning occurred earlier in the discharge channel where water temperatures were consistently warmer. Veligers were first observed at these sites in April followed by peak densities in May. Veliger densities in the thermally altered discharge zone never exceeded 100/L. This was likely because adult mussels were extirpated by July of each year when water temperatures exceeded 30°C for extended periods (Boeckman, 2011).

Winter temperatures at the discharge buoy ranged from 3°C to 10°C. These temperatures supported the growth of young, newly settled veligers throughout the winter months. The swing from temperatures well above 30°C in the summer months to temperatures between 3-10 °C resulted in a cycle of extirpation and reintroduction. This is consistent with Churchill et al. (2017) results. They suggested that after a population crash, young of the year zebra mussels contribute more to the reproductive population size, allowing for the persistence of the species. This cycle consistently resulted in low adult densities in the discharge zone between 2007 and 2010 (Boeckman, 2011).

Isolated die-offs of adult mussels at Sooner Lake were observed in July and August between 2007 and 2010. These die-offs were associated with temperatures greater than 30°C and were restricted to mussels greater than 15 mm in length. Smaller mussels tolerated the higher temperatures. Boeckman (2011) suggested that adult zebra mussels allocated energy towards reproduction, and the remaining amount of energy for somatic growth was insufficient to withstand temperatures above 30°C. This is supported by Aldridge et al. (1995) who stated that energy assimilation rates could not match energetic expenditure for zebra mussels at temperatures above 28°C. Temperatures above 28°C cause increased basal energy expenditure to such an extent that the filter-feeding mechanism cannot compensate (Aldridge et al., 1995). Lei et al. (1996) also found that upper temperatures caused extreme disruption of normal physiological function in zebra mussels.

Zebra mussels do not appear to cease reproduction in order to conserve energy for metabolic maintenance. This makes reproductively mature adults even more susceptible to physical stress (Stoeckmann & Garton, 2001). This reproductive and metabolic energy balance characteristic has also been observed with low food (i.e. chlorophyll *a*) concentrations. The minimum chlorophyll *a* concentration for long term survival is 5 µg/L (Jantz & Neumann, 1998). Low chlorophyll *a* concentrations result in suboptimal conditions for zebra mussel metabolic requirements. These conditions do not necessarily prevent mussels from directing available energy towards reproduction (Palais, et al., 2011). Low chlorophyll *a* concentrations were also reported to have contributed to high mortality rates at Lake Texoma (Churchill et al., 2017).

Boeckman (2011) studied zebra mussel population dynamics at Oologah Lake in Oklahoma. He reported a population crash that resulted in a population decrease from 480/L in 2006 to less than 1/L between 2007 and 2010. Drought conditions and record flood events between 2006 and 2009 were thought to have caused the population crash. Veligers were likely flushed out of the reservoir during flood events or settled in the riparian area. Those veligers settling above the normal pool elevation in riparian areas would have been extirpated when water levels returned to normal (Boeckman, 2011). Churchill et al. (2017) also found that flooding in reservoirs creates a temporarily available substrate in littoral areas. Flooding events during the spawning season cause mussels to settle above the normal pool elevation. They are desiccated when floodwaters recede (Churchill et al., 2017).

Sooner Lake water levels are managed by OG&E to maintain optimal conditions at the power plant (Matt Grimes, personal communication, Supervisor Environmental/Op. Chem, OG&E, 2019). Zebra mussels at Sooner Lake are not exposed to fluctuations in water levels like other reservoirs in the state and may experience more stable population dynamics over time. Minimal fluctuations in lake levels at Sooner Lake suggests that other environmental factors are of more importance in limiting zebra mussel populations.

CHAPTER III

METHODS

Study Area

Zebra mussel veliger population dynamics and water quality were studied at Sooner Lake from August 2018 to November 2018 and from May 2019 to October 2019. Six sample sites (Figure 3) were selected to be consistent with the sites sampled by Boeckman (2011). These sites included the discharge bridge, the discharge buoy, the boat dock at the end of the discharge channel, the dam, the intake buoy, and the intake (Figure 3). The sites located at the discharge bridge, discharge buoy line, and boat dock represent an artificial thermal gradient resulting from warm water discharging from the power plant. The dam, intake buoy, and intake represent sample locations that are not significantly affected by the heated discharge. These sites were sampled approximately every two to three weeks beginning in August 2018 and ending in November of 2018. Sites were sampled approximately every two to three weeks beginning in May 2019 and ending in late October 2019. Samples were not taken from December through April because veliger densities are generally absent or low during this time (McMahon, 1996; Boeckman, 2011)

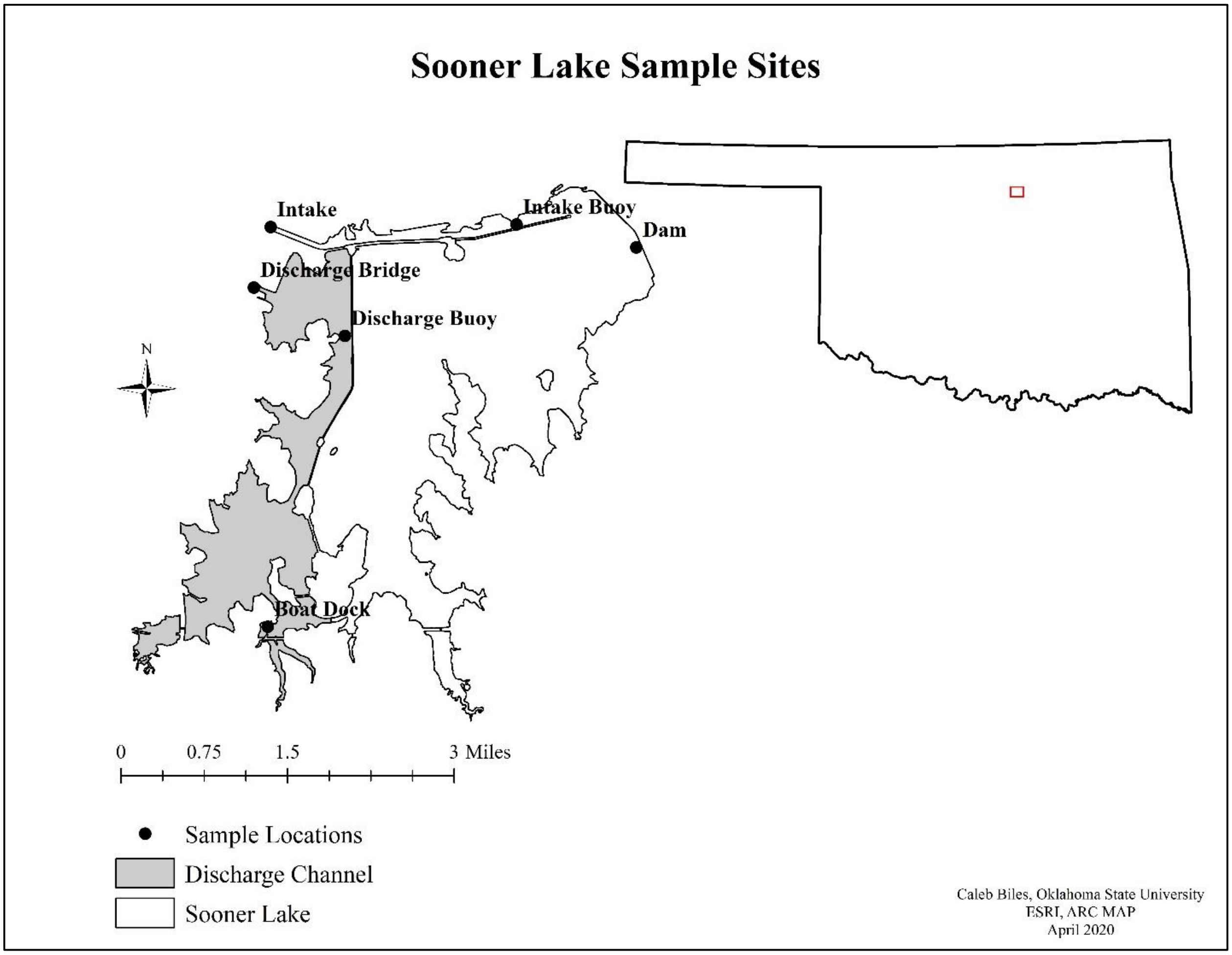

Figure 3. Sample sites at Sooner Lake (discharge bridge, discharge buoys, boat dock, dam, intake buoys, and intake). The discharge channel (gray) represents the heated part of the reservoir. The thermal effluent is released at the Discharge Bridge site.

Water Quality

Water quality data were collected using a YSI multi-parameter probe. Temperature [°C], dissolved oxygen [mg/L], and turbidity [FNU] were collected at the six sample sites on each sample date. Data at each site were collected at 0.5 and 1 m below the surface. Depth profiles were also taken to capture stratification. Data retrieved from the YSI probe were uploaded onto a PC using the YSI KorrDSS desktop software. Datasheets were saved as Microsoft Excel workbook files after they were uploaded. Water clarity was also measured at each site using a standard black and white Secchi Disk [m]. Secchi Disk depths were recorded in a field notebook and organized into Excel spreadsheets.

Water samples were collected for total phosphorus and chlorophyll *a* 1 m below the surface at all sites using a Van Dorn water sampler. Samples were stored in 1 L amber sample bottles and put on ice for transport back to the laboratory. They were then either frozen for total phosphorus measurements or stored at 4 °C for chlorophyll *a* measurements for less than 24 hours and processed.

Algal biomass was measured two ways. Relative fluorescence was measured within 24-hours of collection with a Turner Designs Trilogy Fluorometer. Chlorophyll *a* was measured by vacuum filtering sample water through Whatman 47mm glass microfiber filters (GF/F) within 24 hours of collection. Filters were then quarter folded and individually wrapped in aluminum foil and frozen at -20°C until analysis.

Chlorophyll *a* was extracted using an acidification method (APHA, 2005). Filters were placed in 10 mL of 90% acetone for 2-24 hours in the dark at 4°C before measurement using the Turner Designs Trilogy Fluorometer. The trophic status of Sooner Lake was calculated using chlorophyll *a* concentrations (Carlson, 1977). Total phosphorus was measured colormetrically following potassium persulfate ($K_2S_2O_8$) digestion using a Thermo Scientific Genesys 20 spectrophotometer at 885 nm.

Zebra Mussel Veliger Collection and Enumeration

Veligers were collected at the six sample sites using a 63 µm plankton tow net. Triplicate vertical tows were collected at each site. The depth of vertical tows varied with the sample site and lake elevation. Tows at the discharge buoys, dam, and intake buoys were taken from the surface down to 1 meter above the bottom of the lake. The bottom ranged from approximately 16 m at the dam to approximately 5 m at the discharge and intake buoy sites. Tows at the discharge bridge, boat dock, and intake were only 1 m because of the shallow depths of these sites. The contents of each tow were rinsed into individual 250 ml plastic bottles and preserved in 95% ethanol.

Veligers were enumerated using an Olympus SZX-ILLD100 dissecting microscope with a cross-polarization filter. The cross-polarization filter is useful for identifying veligers. It is especially useful when they are rare or when a sample is cluttered by other organisms, detritus, or debris. Veligers appear white with small black x's when using this type of filter (Johnson, 1995).

Two methods were used to quantify veligers depending on the density within a given sample. The whole sample was counted if there were less than 100 veligers per 20 to 25 ml of sample water. A sub-sample of 15-30 ml was used to quantify veliger densities if there were greater than 100 veligers per 20 to 25 ml of sample water. Veligers were counted in a gridded petri dish. Densities were determined for each sample by dividing the number of veligers counted in a sample by the volume of the plankton net tow.

Adult Zebra Mussel Collection and Enumeration

Sample panels were deployed at the intake buoy site in June 2019 for the collection of adult zebra mussels. Three samplers were attached to a length of PVC pipe and suspended approximately 1 m below the surface. Samplers were composed of 4 stacked masonite tiles that varied in size and were 6", 8", 10", and 12" squares.

The first collection of sample panels was completed on September 9th, 2019 to assess the density of settled adult zebra mussels. These mussels represented the annual primary spawn that typically begins in April (Boeckman, 2011). One sampler from each site was removed from the water and placed into a labeled trash bag for transport back to the laboratory for enumeration. One of the two remaining samplers was thoroughly cleansed of attached zebra mussels. This allowed us to capture the secondary fall cohort counts accurately without the influence of the spring cohort. This collection was completed on October 31st, 2019.

Enumeration of adult zebra mussel densities was conducted by disassembling the samplers. Three tiles were then selected from each sampler and each tile was treated as a grid composed of 4 cm^2 squares. Three squares were randomly selected per tile for counting adult mussels, totaling 9 subsamples. Mussels were removed from subsample squares and preserved with 95% ethanol in glass mason jars until counted at a later date.

Statistical Analysis

A repeated measures statistical approach was used to determine if there were significant differences in temperature and veliger densities between and within the six sample sites throughout the sampling period. The null hypothesis was first applied which assumes no significant differences. The null hypothesis was tested by comparing sites using Two-Way Repeated Measures Analysis of Variance (RM-ANOVA) using Sigma Stat.

Correlations were used to assess relationships between general water quality characteristics and zebra mussel veliger abundance. The correlations were conducted using the Pearson Correlation Coefficient in GraphPad Prism 8.

Box and whisker plots were used to visually represent the distribution of veliger densities within sample sites. These plots showed the minimum, median, mean, and maximum values, the 1st and 3rd quartiles, and the interquartile range.

CHAPTER IV

RESULTS

Documentation of the Thermal Gradient

Results from this study indicated a significant thermal gradient at Sooner Lake (Table 1 & Figure 4). Temperatures were consistently and significantly warmer in the discharge channel compared to sites in the main body of the lake (P = <0.001). Temperatures were also significantly different among sites within the discharge channel (P = <0.001). No significant differences were observed among sites in the main body of the lake (P >0.050).

Table 1. These data represent differences in temperature among the six sample sites at Sooner Lake during the 2018 and 2019 sampling seasons. These data are a result of a Repeated Measures Analysis of Variance.

Comparisons for factor: **Site**					
Comparison	**Diff of Means**	**p**	**q**	**P**	**P<0.050**
Discharge Bridge vs. Intake Buoy	6.12	6	75.173	<0.001	Yes
Discharge Bridge vs. Dam	6.049	6	74.307	<0.001	Yes
Discharge Bridge vs. Intake	5.748	6	70.606	<0.001	Yes
Discharge Bridge vs. Boat Dock	5.453	6	66.984	<0.001	Yes
Discharge Bridge vs. Discharge Buoy	2.432	6	29.87	<0.001	Yes
Discharge Buoy vs. Intake Buoy	3.688	6	45.304	<0.001	Yes
Discharge Buoy vs. Dam	3.618	6	44.437	<0.001	Yes
Discharge Buoy vs. Intake	3.316	6	40.736	<0.001	Yes
Discharge Buoy vs. Boat Dock	3.021	6	37.114	<0.001	Yes
Boat Dock vs. Intake Buoy	0.667	6	8.189	0.009	Yes
Boat Dock vs. Dam	0.596	6	7.323	0.015	Yes
Boat Dock vs. Intake	0.295	6	3.622	0.239	No
Intake vs. Intake Buoy	0.372	6	4.567	0.113	No
Intake vs. Dam	0.301	6	3.701	0.225	Do Not Test
Dam vs. Intake Buoy	0.0705	6	0.866	0.986	Do Not Test

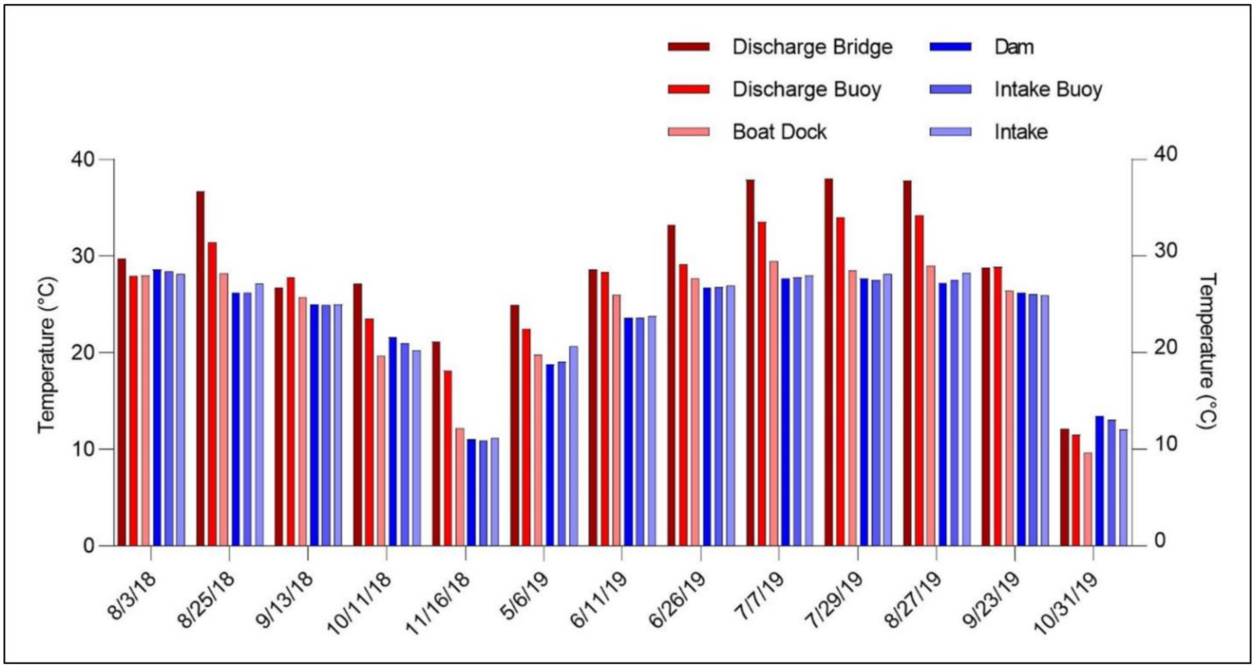

Figure 4. Temperature measurements at Sooner Lake taken from 1 m below the surface. Temperatures were recorded over the course of the 2018 and 2019 sampling periods.

Temperature and Zebra Mussel Veliger Densities in 2018

There were significant differences in veliger densities among the six sample sites for most sample dates in 2018 and 2019 ($P = <0.001$) (Table 2 & Figure 5). The interaction between site and date was also significant for veliger densities ($P = <0.001$) and temperature ($P = <0.001$). These interactions were complex and suggest that differences between sites were not consistent across sample dates. No significant differences in temperatures or veligers were observed between sample sites on some dates. Water temperatures that were significantly warmer did not always correspond to lower veliger densities. Water temperatures that reflected optimal conditions for zebra mussels did not always correspond to high veliger densities.

Table 2. These data represent differences in veliger densities among the six sample sites at Sooner Lake during the 2018 and 2019 sampling seasons. These data are a result of a Repeated Measures Analysis of Variance.

Comparisons for factor: **site**					
Comparison	**Diff of Means**	**p**	**q**	**P**	**P<0.050**
Intake vs. Dam	20.191	6	15.003	<0.001	Yes
Intake vs. Intake Buoy	17.186	6	12.77	<0.001	Yes
Intake vs. Boat Dock	16.324	6	12.129	<0.001	Yes
Intake vs. Discharge Bridge	11.809	6	8.775	<0.001	Yes
Intake vs. Discharge Buoy	6.119	6	4.547	0.064	No
Discharge Buoy vs. Dam	14.071	6	10.456	<0.001	Yes
Discharge Buoy vs. Intake Buoy	11.067	6	8.223	0.001	Yes
Discharge Buoy vs. Boat Dock	10.204	6	7.582	0.002	Yes
Discharge Buoy vs. Discharge Bridge	5.69	6	4.228	0.092	No
Discharge Bridge vs. Dam	8.382	6	6.228	0.009	Yes
Discharge Bridge vs. Intake Buoy	5.377	6	3.995	0.12	No
Discharge Bridge vs. Boat Dock	4.515	6	3.355	0.24	Do Not Test
Boat Dock vs. Dam	3.867	6	2.873	0.38	No
Boat Dock vs. Intake Buoy	0.863	6	0.641	0.997	Do Not Test
Intake Buoy vs. Dam	3.004	6	2.232	0.626	Do Not Test

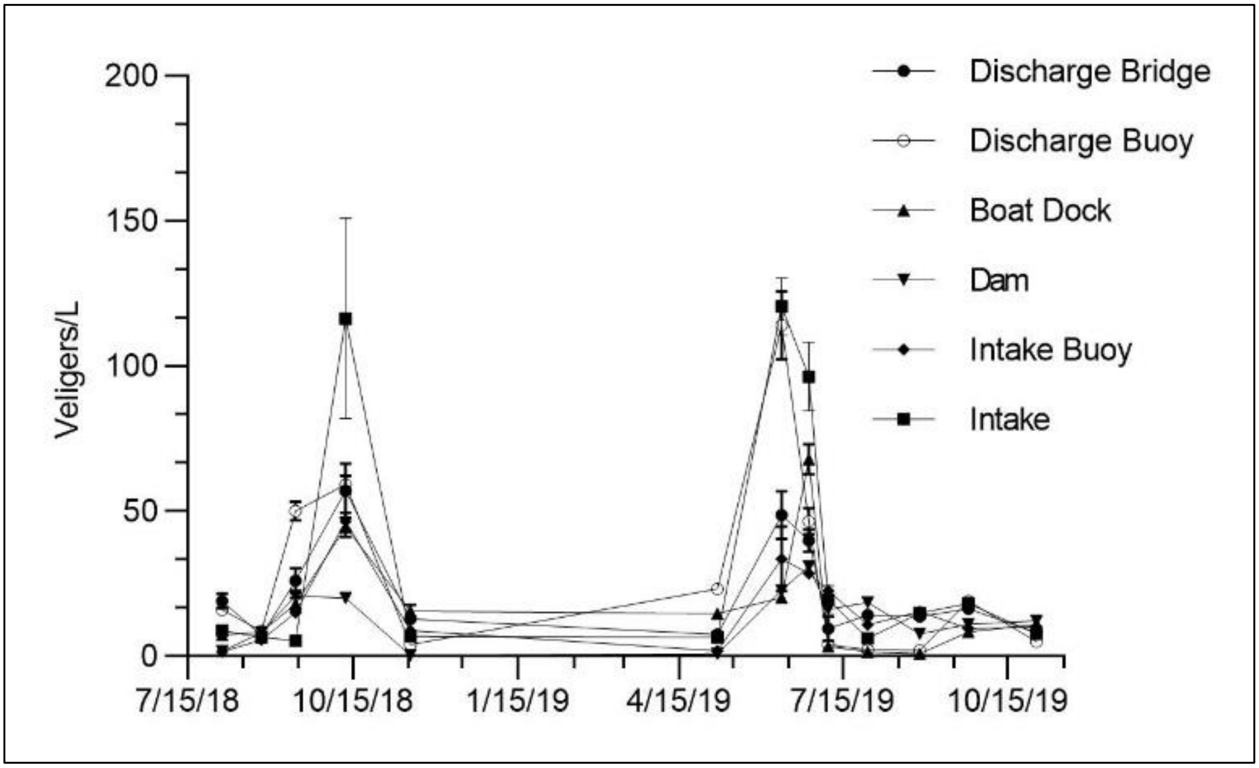

Figure 5. Zebra mussel veliger population densities [Mean ± Standard Error] at Sooner Lake observed over the course of the 2018 and 2019 sampling periods.

A secondary spawn event occurred in the fall of the first year (2018) of monitoring (Figure 5). Veliger densities peaked at all sites in October. A maximum of 116 veligers/L was observed at the intake. The lowest veliger densities recorded in 2018 were in August and November. The primary spawn event was not monitored in 2018 until August.

Veliger densities remained low and no significant differences were observed between sample sites in August ($P > 0.05$). Temperatures at all sites peaked in August and all sites were significantly different from each other ($P < 0.05$) except between the intake buoy and the dam. Temperatures at the discharge bridge and discharge buoy exceeded 30°C by late August (36.6 and 31.3°C). These two sites were the only sites characterized by an increase in temperature between August 3rd and August 25th. Both sites were significantly warmer than the other four sites ($P < 0.001$).

Veliger densities increased at all sites between late August and mid-October indicating the occurrence of a secondary spawn and favorable conditions for reproduction. These increases in veliger densities occurred when temperatures decreased to < 28°C in the discharge channel, and < 26°C at the other sites. Peak densities at all sites occurred in October when temperatures ranged from 21.61°C at the dam to 27.11°C at the discharge bridge ($P < 0.001$).

Densities declined to ≤ 15 veligers/L at all sites in November. Temperatures at the discharge bridge and discharge buoy were 18.1 and 21.1°C. Both of these sites were significantly warmer than the other four sites ($P < 0.001$). A decline in veliger densities was observed in the discharge channel despite optimal temperatures. There were no significant differences in veliger densities between sites in the discharge channel and sites in the main body of the lake ($P > 0.05$).

Zebra mussel veliger densities displayed within-site variability during the 2018 and 2019 sampling seasons (Figure 6). Veliger populations were not evenly distributed within sample sites except at the dam. Populations at all sites were positively skewed. This indicates that population densities were consistently below the mean and more variable at higher population densities. This also indicates that densities approaching maximum values were short lived.

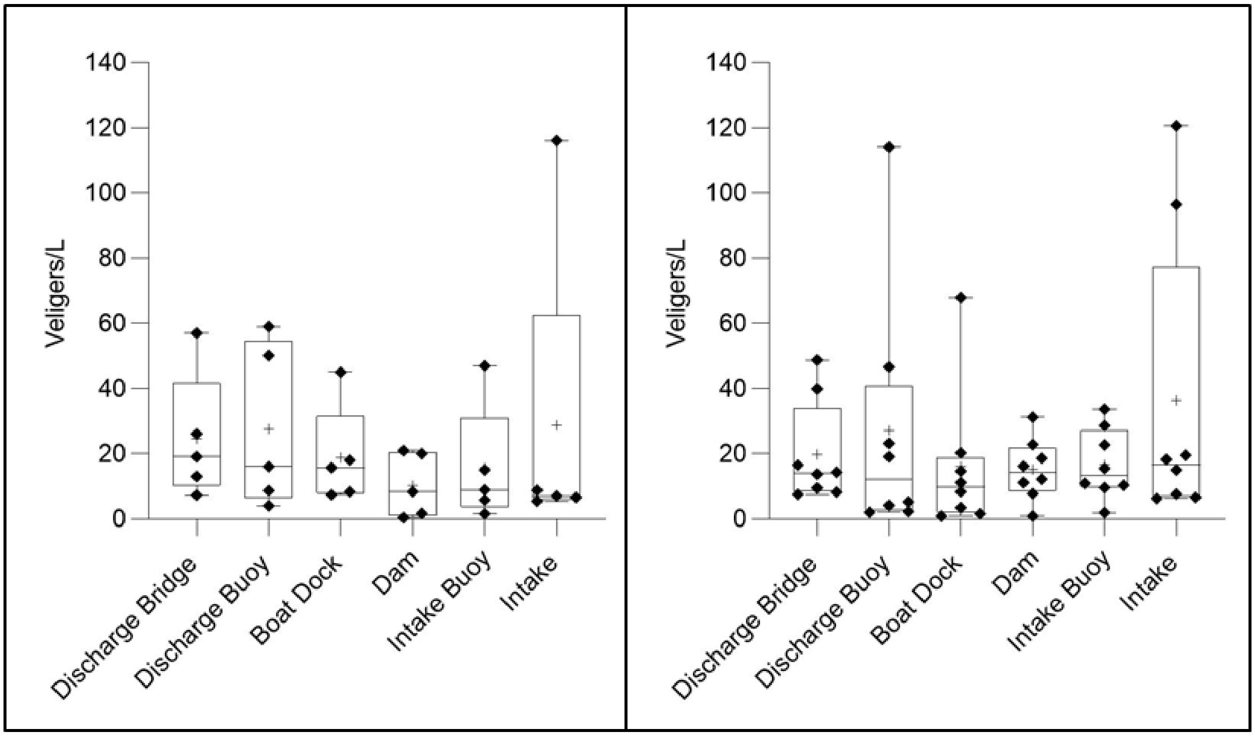

Figure 6. Veliger densities at Sooner Lake showing the minimum and maximum (whiskers), the median (middle line), the mean (+), the 1st and 3rd quartiles (bottom and top of boxes) and the interquartile range (difference between the 1st and 3rd quartiles) for the fall of 2018 (left), and summer and fall of 2019 (right).

Temperature and Zebra Mussel Veliger Densities in 2019

Veligers were observed in early May 2019 at all sites (Figure 5). All sites did not exceed 23 veligers/L. Temperatures were significantly different between all sites in early May ($P < 0.05$), except between the dam and intake buoy line. Temperature ranged from 18.78°C at the dam to 24.94°C at the discharge bridge in May. Temperatures at sites in the discharge channel were significantly greater than in the main body of the lake ($P < 0.05$) throughout the sampling season. Temperatures at the dam, intake buoy, and intake were generally similar throughout the study period in 2019 except in August when temperatures were high, and in October when temperatures rapidly declined ($P > 0.05$).

Peak veliger densities were recorded in mid to late June at all sites. A maximum of 120 veligers/L was recorded at the intake. Temperatures ranged from 23.61°C at the dam to 28.61°C at the discharge bridge in June. Veliger densities declined at all sites between June and July. These declines were only significant in the discharge channel and at the intake site ($P<0.05$). Veliger densities at the dam and the intake buoy sites did not differ significantly between June and July.

Declines in density corresponded to sustained temperatures of $\geq$ 26°C between June and August. Temperatures exceeded above 30°C at the discharge buoy and discharge bridge. Temperatures at the dam site were less variable and generally never exceeded 27°C. Densities never fell below 9 veligers/L during the summer months at the discharge bridge, even though temperatures of 38°C were reported. Temperatures at the discharge bridge remained above 28°C from June to September. Veligers were observed throughout this time at low densities. The lowest veliger densities occurred at the discharge buoy and boat dock, and corresponded with temperatures of 34 and 29°C respectively.

Densities during the secondary spawn in 2019 were lower than that of the previous year's secondary spawn event. Densities peaked at 19/L at the discharge buoy in September. Temperatures decreased to suboptimal temperatures at a much earlier date compared to the previous year. A cold front hit Oklahoma the last week of October 2019 and minimum air temperatures were recorded at -1.6°C (Oklahoma Mesonet, 2020). Water temperatures in mid-October 2018 ranged from approximately 20°C at the intake to 27°C at the discharge bridge. Temperatures ranged from approximately 9 to 12°C at all sites in late October in 2019.

A two-way repeated measures ANOVA confirms that temperatures and veliger densities were significantly different at all sites in October of 2018 compared to October 2019 (P =

<0.001, & P = <0.001). Temperatures in October 2019 rapidly declined at all sites and were significantly different than the previous year (Figure 4). Temperatures dropped ± 15.1°C at all sites between September 23rd and October 31st 2019 (P<0.001). Temperatures dropped ± 3.8°C at all sites between September 13^{rd} and October 11^{th} 2018 (P<0.001).

Adult Zebra Mussel Densities

Adult samples were collected twice from the intake buoy site. Adult populations were approximately 650,000 ± 354,855 adults/m^2 in September 2019. This represented settlement from the primary spawn. Adult populations resulting from the secondary spawn were much lower. This collection took place in late October, and adult densities were approximately 112,000 ± 127,747 adults/m^2. Results from these collections indicated an uneven distribution of adult zebra mussels on sample panels.

Water Quality at Sooner Lake

Chlorophyll a and Relative Fluorescence

Average chlorophyll *a* concentrations in the current study were 6.35 µg/L (range of < 1.0 µg/L to 15 µg/L; Figure 7). This corresponded to a Trophic State Index (TSI) value of 48.73 that classified Sooner Lake as mesotrophic. Chlorophyll *a* concentrations peaked during late summer and early fall of both years of the study, but remained low during the early to mid-summer in 2019.

Samples were also analyzed by determining relative fluorescence which is used as an indicator of algal biomass. There was a significant positive relationship between chlorophyll *a* concentrations and relative fluorescence (r = 0.6831, P = <0.0001). A significant inverse relationship was found between chlorophyll *a* and Secchi Disk depth (r = -0.4910, P = <0.0001). This indicates water clarity decreased with increasing chlorophyll *a* concentrations. No significant correlations were found between chlorophyll *a* and total phosphorus, veliger densities, temperature, turbidity, or dissolved oxygen (Table 3 & 4).

Table 3. Relationships between chlorophyll *a* and veligers and water quality characteristics in Sooner Lake based on Pearson Correlation Coefficients. Significant relationships are bolded.

Chlorophyll *a*	Density (V/L)	Temp. (°C)	DO (mg/L)	Turbidity (FNU)	Relative Fluorescence (RFU)	Secchi Disk (M)
r	-0.1174	-0.0654	-0.0132	0.1206	0.6831	-0.4910
R squared	0.0138	0.0043	0.0002	0.0145	0.4666	0.2410
P value	0.3061	0.5693	0.9088	0.2963	<0.0001	<0.0001
Significant (alpha = 0.05)	No	No	No	No	**Yes**	**Yes**

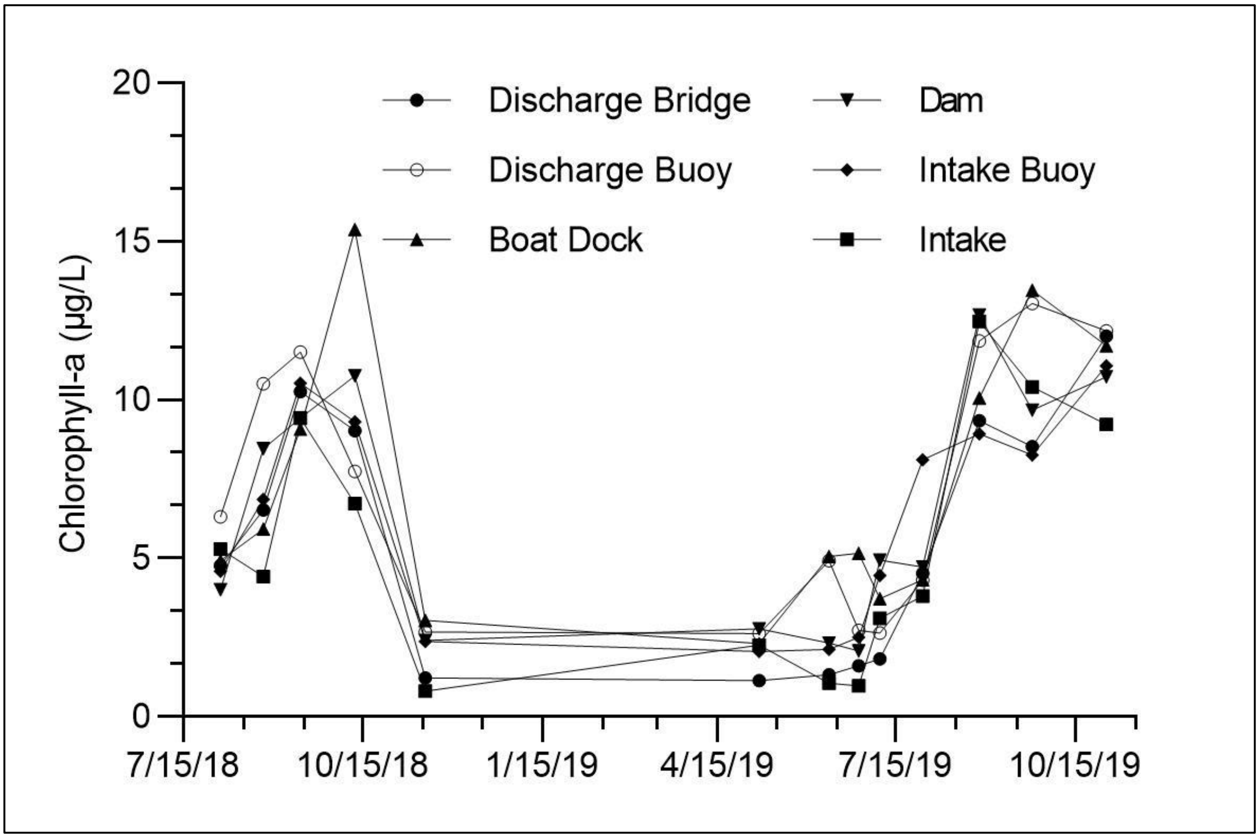

Figure 7. Chlorophyll *a* concentrations at Sooner Lake taken from 1 m below the surface. Concentrations were recorded over the course of the 2018 and 2019 sampling periods.

Total Phosphorus

The average TP concentration at Sooner Lake was 25.08 µg/L, with values ranging from 10.0 to 72.0 µg/L (Figure 8). Peak concentrations of 72.0 µg/L occurred at the boat dock in May 2019. Maximum concentrations at the other sample sites occurred in July. Sites in the discharge channel generally had higher concentrations of TP than those sites located in the main body of the lake.

There was a significant positive relationship between TP and turbidity ($r = 0.6407$, $P = <0.0001$). A significant inverse relationship between TP and Secchi Disk depth ($r = -0.4525$, $P = 0.0012$) was observed. No significant relationships were observed between TP and chlorophyll *a*, relative fluorescence, veliger densities, temperature, or dissolved oxygen (Table 4).

Table 4. Relationships between total phosphorus and veligers and water quality characteristics in Sooner Lake based on Pearson Correlation Coefficients. Significant relationships are bolded.

Total Phosphorus	Density (V/L)	Temp. (°C)	DO (mg/L)	Chl-a (µg/L)	Turb. (FNU)	Rel. Fluoresc. (RFU)	Secchi (M)
r	-0.2258	0.2170	-0.2677	0.0654	0.6407	-0.0231	-0.4525
R squared	0.0510	0.0471	0.0717	0.0043	0.4105	0.0005	0.2047
P value	0.1228	0.1384	0.0658	0.6586	<0.0001	0.8763	0.0012
Significant (alpha = 0.05)	No	No	No	No	**Yes**	No	**Yes**

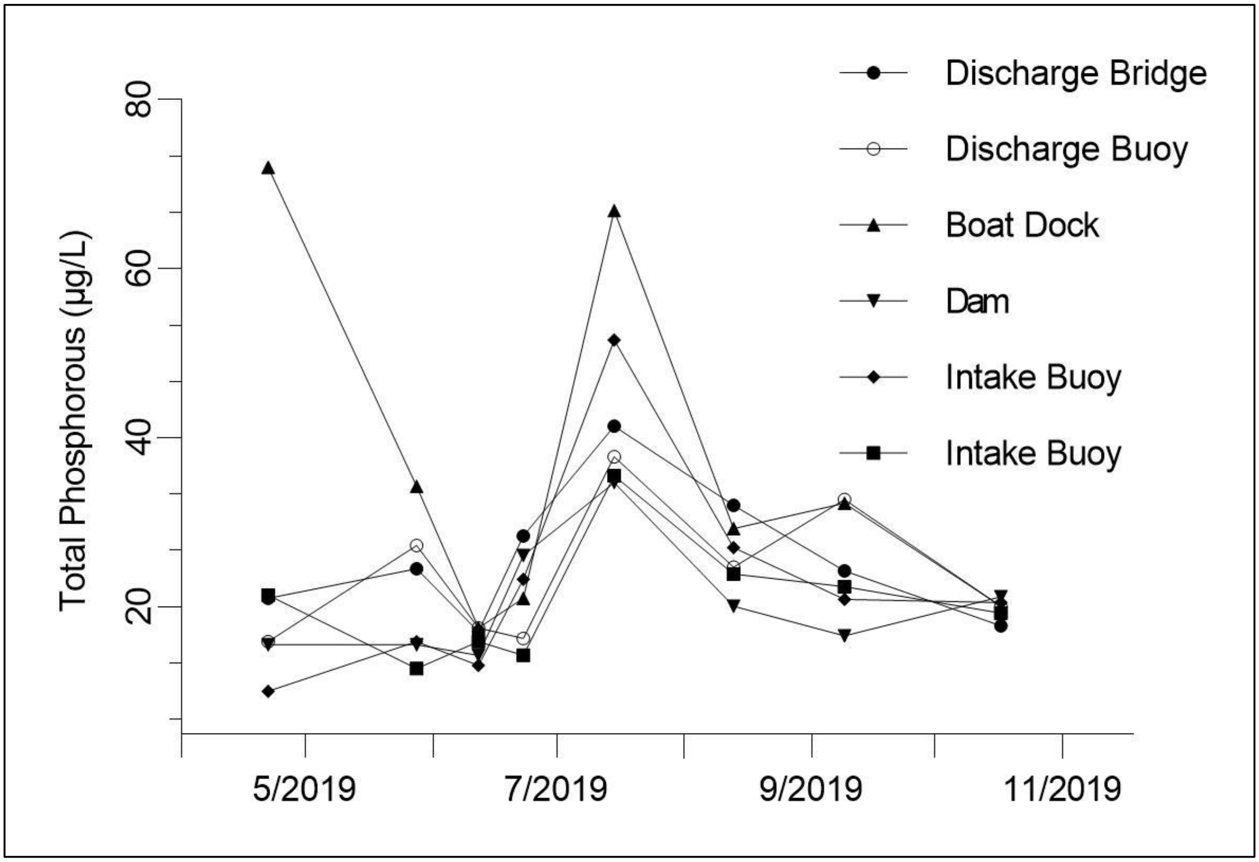

Figure 8. Total phosphorus concentrations at Sooner Lake taken from 1 m below the surface. Concentrations were recorded over the course of the 2019 sampling period.

Dissolved Oxygen

Dissolved oxygen concentrations at the surface (1 m) of Sooner Lake never fell below 6.0 mg/L in this study (Figure 9). Depth profiles taken at the dam (1-17 m) indicated the lake underwent stratification. Depth profiles taken at the five other sites indicated no stratification. Water depths at these sites did not exceed 6 m and were well mixed throughout the sampling periods.

Stratification events at the dam occurred in late summer in 2018 and 2019. The location of the thermocline was noted at depths between 10 and 12 m. DO concentrations were recorded at < 1.0 mg/L at the bottom of the lake during stratification at the dam. Lake turnover occurred both years in September.

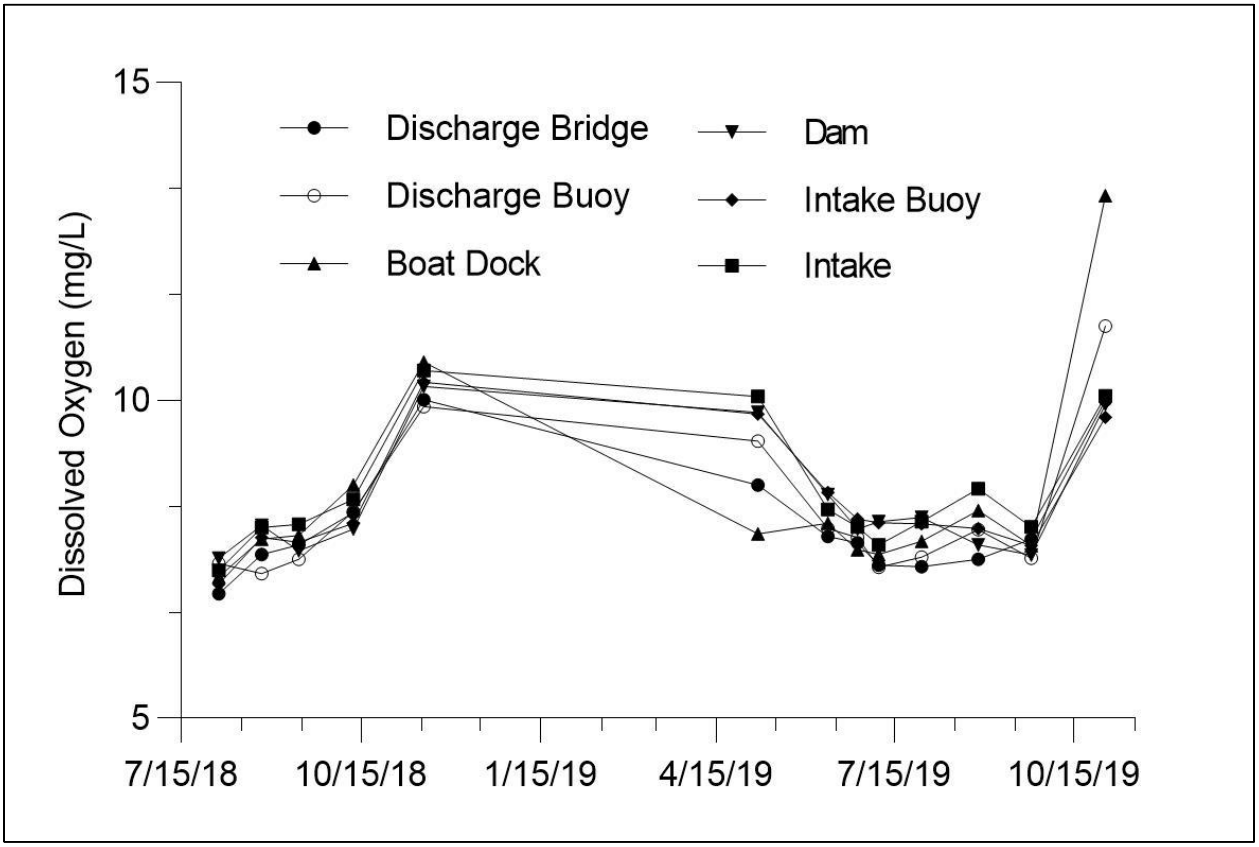

Figure 9. Dissolved oxygen concentrations at Sooner Lake taken from 1 m below the surface. Concentrations were recorded over the course of the 2018 and 2019 sampling periods.

Water Clarity

Water clarity was consistently higher at the dam site compared to the other sites. The dam location had a maximum Secchi Disk value of 3.5 m. Water clarity was lowest at the boat dock with a minimum Secchi Disk value of 0.2 m. Results indicated a significant inverse relationship between water clarity and turbidity ($r = -0.5961$, $P = <0.0001$), an inverse relationship with chlorophyll *a* ($r = -0.4910$, $P = <0.0001$), and an inverse relationship with TP ($r = -0.4525$, $P = 0.0012$). No significant correlations were found between water clarity and veliger densities, temperature, or dissolved oxygen (Table 5).

Table 5. Relationships between Secchi Disk depth and veligers and water quality characteristics in Sooner Lake based on Pearson Correlation Coefficients. Significant relationships are bolded.

Secchi Disk depth	Density (V/L)	Temp. (°C)	DO (mg/L)	Chl-a (µg/L)	Turbidity (FNU)	Relative Fluorescence (RFU)
r	0.0448	-0.0829	0.1144	-0.4910	-0.5961	-0.2344
R squared	0.0020	0.0069	0.0131	0.2410	0.3554	0.0550
P value	0.6973	0.4707	0.3187	<0.0001	<0.0001	0.0475
Significant (alpha = 0.05)	No	No	No	**Yes**	**Yes**	**Yes**

CHAPTER V

DISCUSSION

Zebra Mussel Population Dynamics

Zebra mussel populations generally follow one of three trajectories upon invasion. These include a four to five-year stable population cycle, a chaotic or irregular population cycle, or a boom and bust population cycle (Churchill, 2013). Zebra mussel populations that undertake a boom and bust population dynamic are either extirpated or stabilize at lower densities (Churchill, 2013).

Zebra mussels have maintained a presence in Sooner Lake. This suggests that they will not be completely extirpated from the lake despite extreme water temperatures. Zebra mussels appear to have stabilized at much lower densities in Sooner Lake despite a temporally limited dataset. Boeckman (2011) recorded peak veliger densities at 600 veligers/L in 2010. Veliger densities peaked at 120 veligers/L in 2019.

Zebra mussel populations exhibited crashes in other reservoirs that were associated with extreme drought or flood events. Veligers that settle in the littoral zone die during drought conditions when waters recede. Veligers that settle above the normal pool elevation during flood conditions also die when waters recede (Boeckman, 2011; Churchill et al., 2017). Lake levels at Sooner Lake are manipulated and controlled to maintain water levels for OG&E power plant operations (Matt Grimes, personal communication, Supervisor Environmental/Op. Chem, OG&E, 2019). Zebra mussels at Sooner Lake are not exposed to fluctuations in water levels like other reservoirs in the state and populations should be more stable over time. Additional sampling is needed to continue documenting long term trends in veliger dynamics in the reservoir.

Veligers in the current study reached maximum densities when temperatures were between 19.0 and 28.0 °C. Churchill (2013) and Boeckman (2011) also reported peak densities occurring within this range of temperatures, although veligers began to decline when temperatures exceeded 26.0 °C in those studies. Densities approaching the maximum were few and short lived in the current study. This is consistent with Boeckman (2011) who observed that peak veliger densities lasted one to two weeks at Sooner Lake.

Veliger densities sharply declined and remained low when temperatures exceeded 28.0 °C. Veliger densities did not increase from the secondary spawn in 2018 until temperatures fell below 28.0 °C. Veligers have been reported to re-emerge for secondary spawns when temperatures drop to ≤ 26 °C (Sprung, 1987; Boeckman, 2011). Results from this study suggest that the secondary spawn can occur at higher temperatures. Temperature at all sites reflected this thermal threshold of 26 °C, except for the discharge buoy. Veligers increased from 8 to 50 veligers/L at the discharge buoy from August to September when temperatures were ≥27 °C.

Results indicated that veligers can persist in the water column through extreme temperatures. Low veliger densities were observed at the discharge bridge when temperatures exceeded 36 °C. Peak densities at the discharge bridge (57 veligers/L) occurred when water temperatures were 27 °C in September 2018. Peak densities at the discharge buoy (114 veligers/L) occurred when water temperatures were approximately 28 °C in June 2019. These peaks in veliger densities were short lived, but suggest that adult zebra mussels were plentiful enough to produce high veliger densities in the warm discharge channel. Boeckman (2011) did not observe veliger densities greater than 100 veligers/L in the discharge channel. He attributed low veliger densities to seasonal extirpation and reintroduction which maintained low adult populations.

Adult mussels allocate energy towards reproduction rather than metabolism when they experience physiological stress (Stoeckmann & Garton, 2001; Boeckman, 2011). Physiological stress occurs when temperatures exceed 28 °C (Aldridge et al., 1995). The presence of veligers in the water column suggests that adult zebra mussels at Sooner Lake continued reproducing during the summer months despite temperatures that exceeded 30 °C. This could be why there was not a significant secondary spawn in 2019. Adult zebra mussel populations likely became thermally stressed by the end of summer and either died or were not in a condition to continue reproduction in the fall.

The lack of a secondary spawn in the fall of 2019 was attributed to a rapid decrease in temperatures at all sites. Temperatures declined to suboptimal conditions of ≤ 12 °C at a much earlier date in the fall of 2019 compared to the fall of 2018. Veliger densities never exceeded 20 veligers/L in October 2019. The magnitude of temperature changes from ~30 °C to less than 12 °C in a span of five weeks likely had a negative impact on zebra mussels. Data obtained from the Oklahoma Mesonet (2020) indicate that temperatures changed more rapidly than our limited data set implies. A cold front hit Oklahoma the last week of October and minimum air temperatures were recorded at ≤ -1.6 °C. A rapid change of temperature in either direction and the lack of a sufficient acclimation period could negatively influence the survival of zebra mussels (Spidle et al., 1995).

The maximum change in temperature during a season may be an important factor influencing zebra mussel reproduction in warm reservoirs at the southern extent of its range. Zebra mussel populations have been controlled by rapidly increasing water temperature to kill adult zebra mussels. Condenser discharge was heated to 35 °C within 10 hours and recirculated to submerged equipment colonized by zebra mussels at an Illinois power plant. One hundred percent zebra mussel mortality was observed after 10 hours (Marcus & Wahlert, 1994).

Water Quality

Phytoplankton are an important food source for zebra mussels. Low chlorophyll *a* concentrations can result in suboptimal conditions for zebra mussel metabolic requirements (Palais, et al., 2011) and increased mortality (Churchill, 2017). The minimum chlorophyll a concentration for long term survival of zebra mussels has been reported at 5 µg/L (Jantz & Neumann, 1998).

Low chlorophyll a concentrations observed in Sooner Lake most likely had a negative impact on zebra mussel's reproductive success. Zebra mussels are capable of creating low chlorophyll *a* concentrations as they graze algal particulates from the water column. This could result in the exhaustion of their food source. These trophic interactions may have accounted for the low levels of chlorophyll *a* observed in 2019. Chlorophyll a concentrations of ≤ 5 µg /L were recorded during early to mid-summer. Peak veliger densities occurred at this time suggesting that adult densities were high and utilizing phytoplankton as a food source.

Veliger densities declined during late summer and fall. Chlorophyll *a* concentrations increased to between 8.0 and 13.00 µg /L during this time period. It is not known whether veligers declined because of the exhaustion of their primary food source or because of other environmental factors. Additional research is needed to further understand the relationship between zebra mussels and chlorophyll *a* in the reservoir.

Depth profiles taken at the dam indicated thermal stratification in late summer and early fall. Stratification at the dam site was characterized by temperatures and dissolved oxygen concentrations sharply declining beneath the thermocline. Veliger tows at the dam site extended all the way to the bottom of the lake including beneath the thermocline. Veliger densities were consistently lower at the dam compared to the other sample sites. Low veliger densities may have resulted from a dilution effect of sampling from the oxygen depleted hypolimnion.

Churchill (2013) found that mussels could not survive below depths of 15.2 m at Lake Texoma due to the location of the thermocline and hypoxic conditions. Mussels that settled at the bottom died when lake stratification and hypoxia occurred (Churchill, 2013). Veliger samples should be collected from above the thermocline in future studies at Sooner Lake to avoid a sample dilution affect.

This study did not find any relationship between veliger populations and water clarity. Adult zebra mussels can drastically alter water clarity in reservoirs which can negatively impact aquatic ecosystems (Zhu et al., 2006; Karatayev et al., 2002; Mackie, 1991). Veliger populations at Sooner lake were variable and may not accurately reflect the capacity of adult zebra mussels to increase water clarity. Water clarity and turbidity were likely influenced by record flood events in 2019. This makes it difficult to understand the relationships between zebra mussel population dynamics and water clarity and turbidity. Further research is needed at Sooner Lake to determine the impacts zebra mussels have on water clarity with a focus on adult populations and filtration rates.

CHAPTER VI

CONCLUSIONS

This study was initiated to gain a deeper understanding of zebra mussel population dynamics at Sooner Lake. Sooner Lake provided a unique opportunity to study how zebra mussels react to different thermal regimes within a single reservoir. A similar study was conducted at Sooner Lake between 2007 and 2010 which provided an opportunity to compare current populations with historical ones.

The first hypothesis was that there would be a significant thermal gradient at Sooner Lake resulting from the heated effluent that discharges from the OG&E power generation facility. This first hypothesis was confirmed as Sooner Lake exhibited a significant thermal gradient. Sites located in the discharge channel were consistently and significantly warmer than sites located in the main body of the lake. Sites located within the discharge channel were also significantly different from each other. These differences were not as great as compared to sites in the main body of the lake.

The second hypothesis was that veliger densities would be significantly different along the artificial thermal gradient and that population densities would decline at all sites when temperatures reached or exceeded 28°C. It was further hypothesized that veligers would not re-emerge for a secondary spawn until temperatures declined to ≤ 26°C. Veliger densities were significantly different along the thermal gradient. These differences were not consistent between sites. Interactions between sites and dates were complex. Sample sites that were significantly warmer did not always correspond to low veliger densities. Sample sites that were under a more natural temperature regime did not always exhibit higher or more stable veliger densities. These data suggest that temperature alone cannot be used to estimate veliger densities.

Zebra mussels endured temperatures that exceeded 28°C at Sooner Lake for extended periods of time during the summer months. No massive die-off was observed. Veligers were observed at low densities even when temperatures exceeded 36 °C at the discharge bridge. Densities greater than 100 veligers/L were observed when temperatures exceeded 28 °C. This is counter to our hypothesis. The re- emergence of veligers for a secondary spawn in the fall 2018 generally occurred after temperatures fell below 26°C. The discharge buoy site was an exception to this observation. Veligers re-emerged for a secondary spawn when temperatures were approximately 27 °C.

The current study focused primarily on how absolute temperatures impact zebra mussel populations. Data from this study indicate that the magnitude of temperature change may have a greater impact on veliger populations than absolute temperature values. A secondary spawn in 2019 likely did not occur due to a rapid decrease in temperatures to sub-optimal conditions at all sites. This suggests that a rapid change in either direction could have negative impacts on veliger and adult populations.

The lack of a secondary spawn in 2019 was also attributed to adult zebra mussels likely being physically exhausted after the primary spawn. Zebra mussels likely sacrificed metabolic maintenance in order to continue reproduction throughout the hot summer months. This pattern was not observed in 2018. Adult zebra mussels appeared to have sufficient amounts of energy reserved for a secondary spawn in 2018 as shown by high veliger densities. This indicates that the lack of a secondary spawn in 2019 was primarily the result of rapid decreases in temperatures to sup-optimal conditions.

The third hypothesis was that greater veliger densities would be observed at sample sites where water temperatures were not strongly influenced by the heated discharge. This hypothesis was not consistently supported. Maximum densities were observed at the intake for both years observed. The dam site had some of the lowest densities despite being under an optimal temperature regime for the majority of the study period. The discharge buoy had high densities despite upper temperatures known to cause physiological stress.

Temperature is not the only factor that has the potential to limit zebra mussel populations. Zebra mussels are more reproductively active at certain times of the year and during optimal environmental conditions. Optimal temperatures for veliger development did not always correspond with peak densities, indicating the importance of other environmental variables. Low food supply (Jantz & Neumann, 1998), depletion of oxygen within druses (Boeckman, 2011), and thermal stratification (Churchill, 2013) could also result in lower veliger densities. Further research is needed over a larger temporal scale to more accurately assess these interactions. Zebra mussel populations followed a somewhat chaotic trajectory throughout the study period. This suggests that multiple years of data are needed in order to better understand the population dynamics of zebra mussels.

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